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AN ABSTRACT OF THE THESIS OF

Patrick Heilbron Kingston for the degree of Master of Science in Horticulture presented on June 6, 2017.

Title: Substrate Production of Blueberry: Evaluation of Soilless Media and Potassium, Nitrogen Fertility on Growth and Nutrition

Abstract approved: ____

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As blueberry (*Vaccinium* sp.) production has increased in recent decades, a new interest has developed in the cultivation of blueberry in soilless substrate containers. Historically, blueberry has been propagated and grown in soilless substrate at nurseries, but nursery production is short in duration and plants are small relative to a mature blueberry. There is little literature on the subject of substrate blueberry production, and because blueberry is a long-term perennial that prefers soil pH in the range of 4.5-5.5, it is likely requirements are different than most other small fruit crops grown in soilless substrate for fruit production. Three studies were conducted in Corvallis, OR with container grown northern (*V. corymbosum* L.) and southern highbush blueberry (interspecific hybrids of *V. corymbosum* L. and *V. darrowii* Camp.) to investigate how media and fertilizer composition influence growth and nutrient uptake.

In two studies we investigated the effects of various substrate ingredients on blueberry growth and nutrition in a greenhouse for 3-4 months. The first study evaluated cultivar ‘Snowchaser’ in eleven unique treatments, 10 from combining sphagnum peat moss,

coconut coir (*Cocos nucifera* L.), and douglas fir bark [*Pseudostuga menzii* Mirb. (Franco)] with 10% perlite by volume and one commercially available mix. The second study evaluated 16 different mixtures of peat moss, coir, and perlite on one northern highbush cultivar (‘Liberty’) and one southern highbush (‘Jewel’). Treatments in the second study consisted of four levels of perlite (0, 10, 20, and 30% by volume) and four ratios of peat:coir (1:0, 2:1, 1:2, and 0:1). All plants in both studies were fertigated with a complete nutrient solution suitable for blueberry and target leachate drainage was 25%. Every 2 weeks, leachate was collected from treatments and analyzed for pH and electrical conductivity (EC). Plants were destructively harvested and dry weight and nutrient content were measured. In the first study, total dry weight of the plants was similar among the treatments at 72 d after transplanting but was nearly twice as much, on average, in the commercial mix, and media with ≥ 60% peat or coir than in those with ≥ 60% bark at 128 d. Bark had lower porosity and water holding capacity than peat, coir, or the commercial mix. Increasing bark in the medium also reduced nutrient uptake efficiency of N, P, K, S, Ca, Mg, Fe, Mn, B, Cu, and Zn relative to peat or coir. The effects of bark on nutrient uptake efficiency were largely driven by differences in dry weight. In the second study, increasing the amount of perlite in the media decreased dry weight in ‘Jewel’ and had no effect on dry weight in ‘Liberty’. When media contained perlite, the proportion of peat and coir in the media had no effect on dry weight of either cultivar, supporting the results of the first study. When no perlite was in the media, increasing the amount of peat (decreasing coir) in the media increased dry weight in ‘Liberty’. Increasing peat (decreasing coir) in the media improved nutrient uptake efficiency for P, K, Mg and Zn for both cultivars, and N, Ca, S, and B in ‘Liberty’. In addition, increasing the amount of peat in the media increased whole-plant concentration of P and Mg in 'Jewel' and N, P, K, and B in 'Liberty'. The amount of perlite in the media had no effect on leachate pH. In both studies leachate pH was lowest for peat-containing mixes and highest for coir mixes; however, pH was similar in all mixes by the end of the studies. Results from our two media studies indicate that high levels of perlite or bark in the media can negatively impact initial growth of young blueberry plants through their influence on media water holding capacity. Initial growth of young blueberry plants is similar in media containing peat or coir; however nutritional differences between the two media components may necessitate differences in nutrient management.

The third study evaluated the effects of K fertilizer source and rate, in combination with two N sources on shoot growth, fruit yield, fruit size and fruit firmness of 'Liberty' blueberry from 2015 to 2016. Plants were grown in 25 L containers with a substrate mixture of 3 sphagnum peat: 1 coir : 1 perlite. The three K sources used were potassium sulfate (KS), potassium thiosulfate (KTS), and potassium acetate (KA) at rates of 0, 50, and 150 ppm K in ammonium sulfate and urea. Additionally, KTS and KS were applied at 100 and 200 ppm K in ammonium sulfate. Every two weeks leachate from pots was collected and analyzed for pH and EC. During the second growing season fruit yield, quality (size and firmness), and nutrient content, and shoot growth (dry weight) and leaf nutrient concentrations were determined. When the plants were fertilized with ammonium sulfate, shoot dry weight increased with a moderate rate (50 ppm K) of KS or KA (396 and 370 g dry wt. per plant, respectively) versus the 0 ppm K control (269 g dry wt. per plant), but there was no effect of K fertilization on fruit yield or quality. When

plants were fertilized with urea, K fertilizer had no influence on shoot growth, yield, or fruit quality. Increasing concentration of K in fertilizer increased leaf K concentrations and decreased leaf Ca and Mg concentrations in both N fertilizers. Increasing fertilizer K also increased fruit K concentration in urea but not in ammonium sulfate. Leaf and fruit S concentrations were enhanced by the addition of KTS ($\bar{X}$ = 0.3% and 0.10%, respectively) but not KS ($\bar{X}$ = 0.2% and 0.09%, respectively). Both KTS and KS reduced leachate pH ($\bar{X}$ = 4.58 and 5.01, respectively) relative to no K ($\bar{X}$ = 5.44), whereas KA had no effect on leachate pH. Fertilizing substrate grown blueberry with K can have positive benefits on early growth and nutrition provided the appropriate K source and rate and N source are used.

Substrate Production of Blueberry: Evaluation of Soilless Media and Potassium, Nitrogen Fertility on Growth and Nutrition

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TABLE OF CONTENTS

Page

LIST OF FIGURES

Figure | Page

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF APPENDIX TABLES

Chapter 1: General Introduction.

Blueberry (*Vaccinium* sp.) has become a widely grown crop in North America and across the world. Native to North America and cultivated to some degree by Native Americans, its first domestication can be traced to Frederick Coville in 1908 (Coville, 1910; Moerman, 1998; Retamales and Hancock, 2012). Coville was the first to classify growing habits as well as begin a breeding program. Remarkably, some of his seedlings, most notably, cultivar 'Bluecrop', are still cultivated varieties used today (Retamales and Hancock 2012). Today, the predominant types of cultivated blueberry are highbush (*V. corymbosum* L. and complex interspecific hybrids with wild plants such as *V. darrowii* Camp.), rabbiteye (*V. virgatum* Ait.), and lowbush blueberries (*V. angustifolium* Ait.) [Boches et al., 2006; Retamales and Hancock, 2012]. Highbush blueberry is further divided into northern highbush (NHB; predominantly *V. corymbosum* L.) and southern highbush (SHB; complex interspecific hybrids of *V. corymbosum* L. and *V. darrowii* Camp.). They are classified based on their cold hardiness and chilling requirements, with NHB requiring 800-1000 chilling hours below 7 °C and SHB requiring less than 300 chilling hours (Draper, 1997; Retamales and Hancock, 2012; Sharpe and Darrow, 1959).

Members of the family Ericaceae, blueberry plants favor a well-drained soil with a low pH (4.5-5.5) and high in organic matter (Retamales and Hancock, 2012). Classified as a 'calcifuge' (lime hating), blueberry has evolved to thrive in low pH soil with relatively poor availability of most macro nutrients: NO_3-N, P, K, Ca, Mg (Korcak, 1988). One adaptation to these soil conditions is low nutrient tissue content and requirement, as blueberry has much lower tissue concentrations (Korcak, 1988; Hart et al., 2006a) of major macronutrients than other crops like apple (*Malus domestica* Mill.; Righetti et al., 1998), raspberry (*Rubus idaeus* L.; Hart et al., 2006b), and blackberry (*Rubus* sp.; Hart et al., 2006b). Lacking root hairs, blueberry nutrient uptake is at a disadvantage, and symbiosis with mycorrhizal fungi, another adaptation, can aid in uptake (Coville 1910; Jacobs et al., 1982). Highbush blueberry is a woody perennial plant that typically grows as a bush or shrub and can live more than 30 years in the field (Bernadine Strik, personal communication). A deciduous plant, blueberry has simple buds (Gough and Shutak, 1978). Floral buds form on the terminal ends of shoots formed during the previous year's growth. At bud break in the spring, flowers emerge first and pollination has been shown to enhance fruit size in NHB (Hancock, 1989). Shoot growth occurs from lateral buds below floral buds, or from adventitious shoots at the crown, referred to as 'whips'. Fruit ripens within 42 to 90 d in NHB and 55 to 60 d in SHB, depending upon cultivar (Darnell, 2006). After harvest, plants begin allocating nutrient reserves to roots in preparation for dormancy and leaf drop. Plants are pruned during dormancy to promote an open-vase form and remove twiggy, non-productive canes. Root growth is contained within the bed, as blueberry has shallow, fibrous roots (Retamales and Hancock, 2012).

In recent decades, blueberry production has dramatically increased. Driven largely by the designation of its fruit as a super food with nutritional benefits and antioxidants (Kalt and Dufour, 1997; Bomser et al., 1996), global fruit production has increased from over 22,000 tonnes of fruit in 1995 to over 540,000 tonnes in 2014 (Brazelton, 2016). Planted area has increased from over 42,000 hectares in 2005, to over

109,000 hectares in 2014 (Brazelton, 2016). Due to blueberry's unique soil requirements, suitable land for cultivation is limited relative to other crops. This fact coupled with the required dormancy period, necessitates a global production scheme to ensure fresh fruit is available to consumers year round (Brazelton, 2016). Recently, growers have been looking at alternative methods for production in order to reduce the need for a global production model and one such alternative is soilless substrate production.

Soilless substrate production is the practice of growing plants in a container filled with various organic and non-organic materials to provide nutrient and water retention as well as stability for roots (Raviv and Lieth, 2008). Substrate production can be conducted in any location given adequate environmental conditions which is often achieved in a glasshouse. These controlled environments allow for local, off-cycle production, enabling growers to sell fruit when prices are higher, subsidizing the elevated costs of this production method. Another advantage to substrate production, precise irrigation and fertilization, ensures nutrients are in optimal quantity for developing plants and allows for careful management of media pH. There is a plethora of literature about substrate production of plants (Raviv and Lieth, 2008; Bilderback et al., 2013), but because of blueberry's unique soil and nutrient requirements, it is likely that these methods will need to be altered and specifically tailored for optimal growth and yield. Growing blueberry in containers for fruit production is a novel concept and there is limited published research on fruit production of blueberry in substrate (Voogt et al., 2014). Few conclusions have been reached regarding best practices, thus a broad range of basic research is still required to optimize substrate management practices.

Blueberry nurseries have been propagating and growing plants in soilless substrate for years (Fulcher al., 2015), but it is unclear whether the media ingredients used in nurseries will be optimal for long-term production. Typical media substrate ingredients used in the northwestern United States include partially decomposed Sphagnum peat moss, coconut coir, milled tree bark, and inorganic materials such as perlite. Peat moss is sourced from bogs of various mosses in temperate regions. The most commonly used peat in horticulture is from the Sphagnum genus (Hammond, 1975). Processed peat moss provides high water holding capacity and cation exchange capacity to container grown plants, is relatively resistant to decomposition and has a low pH (3.5-4.5) (Hammond, 1975). Coconut coir is the pithy byproduct of the coconut (*Cocos nucifera* L.) husk and has become increasingly common as an alternative to peat moss (Evans et al., 1996). The processing of coir can lead to increased salts (K, Na and Cl) and a higher pH (5.6-6.9) than peat moss (Konduru et al., 1999), but nevertheless has been shown to be successful at growing ericaceous plants (Scagel et al., 2003). Milled bark of douglas fir [*Pseudostsuga menziesii Mirb*. (Franco)] is commonly used in the nursery industry of the northwestern United States, has a low pH (3.7-4.4), and adequate water holding capacity for plant growth (Buamscha et al., 2007). An inert ingredient is often incorporated into substrate mixtures to increase drainage and provide a material that is resistant to decomposition (Raviv and Lieth, 2008). Perlite is a commonly used mineral ingredient that is mined from rhyolitic volcanic sources and heated to 800-1100 °C, evaporating the water inside the material to ‘pop’ it, thus creating air space and water holding capacity (Alkan and Dogan, 1998). Growers typically create mixtures of various ingredients to tailor physical and chemical properties to within a specific range required by their plants. Optimal mixtures for plants are often developed through experience and analysis of the physical and chemical properties of specific mixtures, as these properties are difficult to predict when mixing multiple ingredients (Blythe and Merhaut, 2007). While various guidelines on acceptable media properties exist for container production other plants (Bilderback et al., 2013), no guidelines exist for blueberry. Proper substrate selection is a critical element for successful production, and this study sought to determine optimal media for blueberry in containers.

As a calcifuge, blueberry has unique nutrient requirements relative to other plants. Recent studies on field grown plants have developed fertilization guidelines for plantings of blueberry (Bryla and Strik, 2015; Strik and Vance, 2015; Vargas and Bryla, 2015). Traditionally fertilized with granular applications, Vargas and Bryla (2015) demonstrated blueberry's preference for fertigation through a drip system with ammonium sulfate over urea. Nitrogen is the most abundant element in blueberry, but unlike most plants, plants prefer the ammonium form of N (NH_4-N) to nitrate (NO_3-N) (Merhaut and Darnell, 1996). This is due to limited nitrate reductase activity in blueberry (Merhaut and Darnell, 1996), as well as the inhibition of nitrification at low soil pH resulting in greater concentration of NH_4-N present in the soil (Havlin et al., 2014). While N dynamics of blueberry in field production have been recently studied (Bañados et al., 2012; Bryla et al., 2012), little is known about K nutrition, the second most required element in blueberry.

Potassium in plants is taken up as K^+ and while not utilized in any molecules, it is critical for cellular functions through maintenance of concentration gradients and in plants for proper function of stomata guard cells (Marschner, 2011). Additionally, K is accumulated at high levels in fruit (Havlin et al., 2014). Proper K nutrition has been demonstrated to be important for improving fruit quality in tomato (Chapagain et al, 2003) and pepper (Baghour et al., 2001) grown in substrate. Potassium sulfate is the most commonly applied form of K in blueberry, but growers also use potassium acetate and potassium thiosulfate for their anion's effects on raising and lowering soil pH, respectively (David Bryla, personal communication). Little research exists on the exact mechanisms for the pH effects of these K sources. The ions K^+ and NH_4^+ have similar sized radii and charge, and therefore bind to the same exchange sites and absorbed by roots using the same ion transporters (Bar-Tal, 2011). As a result, there are numerous interactions in soil solution where these ions compete directly, and their mutual presence can affect balanced uptake of cations (Bar-Tal et al., 2001). Because NH_4-N is the predominant form taken up by blueberry, there is likely a greater chance for interactions between N and K in soil solution than most plants where NO_3-N is the predominant available N form.

The objective of this thesis was to perform foundational research on soilless substrate blueberry production that provides growers with the basic information needed to optimize this new form of cultivation. The first goal was to investigate suitable substrate materials and mixtures for container production of blueberry. Two short-duration (3-4 months) greenhouse studies were conducted in Corvallis, OR to evaluate the effect of altering proportions of sphagnum peat moss, coir, douglas fir bark, and perlite on the growth and nutrition of both northern highbush and southern highbush blueberry. The second goal was to investigate the K nutrition in blueberry and how it is influenced by K source, rate and N source. This study was conducted in a high tunnel for approximately 1 year (July 2015-Aug. 2016) to evaluate K fertility on blueberry growth, nutrition, and fruit production.

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Chapter 2: Suitability of sphagnum peat moss, coir, and douglas fir bark as growing substrate for container production of highbush blueberry.

Abstract

Blueberry (*Vaccinium* sp.) production has greatly increased in recent years, and many producers are looking for ways to grow plants in regions with sub-optimal soil conditions, such as container production in soilless substrate. The purpose of the present study was to investigate the suitability of different combinations of sphagnum peat moss, coir, and douglas fir [*Pseudotsuga menziesii* Mirb. (Franco)] bark for container production of highbush blueberry. Young plants of 'Snowchaser' blueberry were grown in 4.4-L pots filled with a commercially available mix of peat, perlite and pumice, or media containing 10% perlite and varying proportions of peat, coir, and bark. Total dry dry weight of the plants was similar among the treatments at 72 d after transplanting but was nearly twice as much, on average, in the commercial mix, and media with ≥ 60% peat or coir than in those with ≥ 60% bark at 128 d. Bark had lower porosity and water holding capacity than peat, coir, or the commercial mix. Increasing bark in the medium reduced nutrient uptake efficiency (NUE) for N, P, K, S, Ca, Mg, Fe, Mn, B, Cu, and Zn relative to peat or coir. Effects of bark on NUE were largely driven by differences in dry weight. Prior to planting, coir had the greatest concentration of P and K, while peat had the greatest concentration of Ca and Mg. The NUE for P, K, Mg, Fe and Mn differed for plants grown in peat or coir and was correlated to initial concentration of nutrients in the media. Leachate pH was lowest for peat-containing mixes and highest for coir mixes; however, pH was similar among media by the end of the study. Electrical conductivity of

leachate never exceeded 0.84 $dS \cdot m^{-1}$ in any treatment. After 128 d, plants grew better with greater amounts of peat or coir in the media than in media with greater amounts of bark. Irrigation frequency likely played a role in the poor performance of bark, which may require more frequent watering than peat or coir when used in media for substrate blueberry production.

Introduction

Worldwide production of highbush blueberry (*Vaccinium* sp.) has increased tremendously in recent years, from ≈42,000 ha in 2005 to over 109,000 ha in 2014. This rapid growth is driven by strong consumer demand and recent development of new cultivars and production systems that have increased availability of fresh blueberries in the market year round (Brazelton, 2016).

Blueberry is a member of the Ericaceae family, which has unique characteristics such as a very fine root system with no root hairs, low soil pH requirements (4.5 to 5.5), and preference for ammonium-N (NH_4-N) over nitrate-N (NO_3-N) (Coville, 1910; Merhaut and Darnell, 1996; Rosen et al., 1990). Many Ericaceaeous plants grow in nutrient poor soils and have developed a symbiotic relationship with mycorrhizal fungi to improve nutrient uptake. Compared to many non-ericaceous crops, blueberry plants contain much lower concentrations of most nutrients and therefore tend to have lower nutrient requirements, with the exception of Fe, Cu, and S (Korcak, 1988) than other crops like apple (*Malus domestica* Mill.; Righetti et al., 1998), raspberry (*Rubus idaeus* L.; Hart et al., 2006b), and blackberry (*Rubus* sp.; Hart et al., 2006b).

Because of the unique soil and nutritional requirements, many producers are looking for novel ways to grow blueberries in regions with sub-optimal soil conditions. One such method involves cultivation in containers with a soilless substrate and highly controlled fertigation management systems (Voogt et al., 2014). While nurseries have been growing blueberry in soilless substrate for many years, the concept of commercial fruit production in containers is a relatively novel idea (Fulcher et al., 2015). Substrate mixes used in nursery production of ericaceous plants frequently contain components including bark, peat moss, perlite, compost, and other soilless components. It is unclear whether the specific components and their ratios used for growing blueberry in nurseries are optimal for fruit production. Peat, coir and douglas fir bark, common ingredients used for fruit production of other crops in soilless culture, were selected for this study to investigate their suitability for blueberry fruit production.

Partially decomposed peat moss, derived from *Sphagnum* moss, has historically been used for production of container-grown plants. The high water holding capacity (WHC), cation exchange capacity (CEC), resistance to decomposition and relative abundance in peat bogs of the northern hemisphere, makes peat an ideal soilless substrate (Hammond, 1975). The naturally low pH (3.5-4.5) of peat makes it an ideal substrate for acid-loving ericaceous plants such as blueberry (Knight et al., 1998; Scagel, 2003).

Coconut coir is the pithy and fibrous material from the husk of (*Cocos nucifera* L.) obtained as a by-product of coconut production. Coir is a common alternative to peat and works well as an organic substrate due to its high WHC and widespread geographic availability (Evans et al., 1996). Despite coir's higher pH (5.6-6.9; Evans et al., 1996) than peat, it has been found suitable for container production of ericaceous plants. Scagel (2003) reported improved growth in a wide range of ericaceous species when the plants were grown in media with coir instead of peat. However, the media never contained more than 20% peat or coir by volume. Berruti and Scariot (2011) substituted a peat-based medium with up to 50% coir and found improved growth of several *Rhododendron* sp. in the mixes with coir.

Growers also often use inexpensive, locally available organic products, such as milled tree bark, as substrate for containers. In the northwestern United States, douglas fir bark is widely available as a waste product from the logging industry, and therefore is a common ingredient in container production (Buamscha et al., 2007). Douglas fir bark varies widely in quality and properties depending on how it is treated (fresh, aged, or composted), but it often has a low pH (3.7-4.4) and is amended with lime for most plant applications (Altland and Buamscha, 2008). However, these authors are not aware of any published research on blueberry performance when grown in containers with douglas fir bark substrate.

The purpose of the present study was to investigate the suitability of different combinations of sphagnum peat moss, coir, and douglas fir bark for container production of highbush blueberry. These ingredients were chosen because of their widespread use in soilless cultivation. We hypothesized that blueberry would grow best in substrates with a high proportion of peat or douglas fir bark because of the lower pH allowing for optimal nutrient uptake for blueberry. To test the hypothesis, southern highbush blueberry (a complex hybrid based largely on *V. corymbosum* L. and *V. darrowii* Camp.) plants were grown in a glasshouse for ~ 5 months in 11 different substrate mixtures.

Materials and Methods

Experimental setup. The study was conducted at the USDA-ARS Horticultural Crops Research Unit in Corvallis, OR (lat. 44°34'3" N, long. 123°17'19" W). Eleven media mixtures were evaluated, including 10 of which contained 10% perlite (Horticulture expanded grade, OBC Northwest Inc., Canby, OR), by volume, for drainage and 0% to 90% sphagnum peat moss (Sun Gro Horticulture, Hubbard, OR), coir (Sun Gro Horticulture), and aged douglas fir bark (The Bark Place, Philomath, OR) (Table 2.1). These 10 treatments were created as a simplex-lattice mixture design such that each media component was treated as a continuous variable, allowing estimation of treatment response for media mixtures not included in the 10 treatments (Cornell, 2011). A commercially available potting mix (Sunshine Professional Growing Mix #4 'LA4 P', Sun Gro Horticulture Distribution Inc., MA) was also included in the study for comparison.

On 18 Mar. 2015, 70-mL containers of 'Snowchaser' blueberry were obtained from a commercial nursery (Fall Creek Farm & Nursery, Lowell, OR) and transplanted into 4.4-L pots (19.7-cm diam. × 16.5-cm tall; #2 Short, Anderson Pots, Portland, OR) filled with one of the 11 media mixtures. One plant was placed in each pot, and each treatment had 10 pots, for a total of 110 plants in the experiment. All pots from the 11 treatments were arranged in a randomized complete block design (RCBD) with two pots per experimental unit in each of five blocks. The pots were located on two adjacent greenhouse benches and spaced 0.1-m apart on each bench.

Each bench was illuminated with two 1000-W high-pressure-sodium lamps from 0700–2100 HR, and a thermostat was set to cool the glasshouse when temperature was > 27 °C and to heat the glasshouse when temperature was < 15 °C. Air temperature, relative humidity, and photosynthetically active radiation (PAR) were measured every 15 min at the top of the canopy using a data logger (model LI-1400; LI-COR Biosciences, Lincoln, NE) connected to a combination temperature and humidity probe (model Humitter 50 YC; Vaisala Inc., Woburn, MA) and a pyranometer (model LI-190, LI-COR Biosciences, Lincoln, NE). The data logger was installed on 22 Apr. but malfunctioned between 29 May and 26 June. Mean daily air temperature in the glasshouse ranged from 14–38 °C and averaged 22 °C from 22 Apr. to 29 May and 26 °C from 26 June to 24 July. Relative humidity and PAR averaged 51% and 20.8 $mol \cdot m^{-2} \cdot d^{-1}$, respectively.

The plants were irrigated with one 2-$L \cdot hr^{-1}$ (LPH) drip emitter per pot (model DPC02-MA-AL-Blue Toro Company, El Cajon, CA) from 18 Mar. to 5 Apr., as needed, and, thereafter, were fertigated daily through the system with a modified Hoagland's nutrient solution (Hoagland and Arnon, 1938). The nutrient solution contained 5.5 mM N from $(NH_4)_2SO_4$ and $(NH_4)_2HPO_4$ + 1.14 mM N as a chelating agent used to deliver calcium; 0.51 mM P from $(NH_4)_2HPO_4$; 3.07 mM K from K_2SO_4; 2 mM Ca from chelated Ca product (ProNatural Calcium, Wilbur Ellis, Aurora, CO); 0.74 mM Mg from $MgSO_4*7H_2O$.; 25 µM Fe from Fe-DTPA; 25 µM B from H_3BO_3; 3 µM Mn from $MnCl_2*4H_2O$; and 4 µM Zn from $ZnSO_4*7H_2O$. Sulfuric acid was also added to reduce the pH of solution to 5.2. Each plant received the same volume of nutrient solution. Drainage as percent of total irrigation was evaluated two to three times per week in one block, by collecting water that drained through the bottom of the pot and calculating the percent drain relevant to the total volume applied. If needed, plants were supplemented with additional irrigation through a separate drip system, using the same emitter set-up described above for fertigation, to produce 25% drainage of the total solution applied to the pots.

Measurements. Physical and chemical properties of the media were analyzed by a commercial laboratory (Soil Control Laboratory, Watsonville, CA). Air-filled (Air CC), water holding capacity (WHC), total porosity, bulk density, and particle density of the media were determined using the method described by Niedziela and Nelson (1992). Particle size distribution was determined by shaking 100 g of dry media through stacked sieves with openings decreasing in size (25, 16, 9.5, 6.3, 4, 2.36, and 0.85 mm) for 5 minutes and obtaining the percent of material (w/w %) in each sieve. Percent C and N were determined by combustion followed by a thermal conductivity detector. NH_4-N, Cl, SO_4, EC and pH were measured in a 1:5 substrate: deionized water extract. Nutrient composition of media samples were determined by ICP spectrophotometry after extraction using Mehlich 1 for P, K, Ca, Mg, and Na, DPTA for Cu, Zn, Fe and Mn, and hot water for B (Gavlak et al., 2003).

Leachate was collected from the pots every 2 weeks from three blocks per treatment using a modified pour-through method (Wright, 1986) and analyzed for pH and EC using a pH/ion/conductivity meter (model SevenGo Duo pro with an InLab Expert

Pro-ISM-IP67 probe for pH and an InLab 738 ISM conductivity probe for EC; Mettler-Toledo, Columbus, OH). The pots were irrigated with 67 mL of water at ≈1 h after a fertigation event, and 50 mL of leachate was collected from saucers placed under the pots. The leachate was then stored at 3 °C until analysis and later measured at 25 °C in a water bath. Leachate was only collected from pots in four specific treatments ($S_{30}C_{30}B_{30}$, S_{90}, C_{90}, and B_{90}; Table 2.1).

Ion-selective membrane probes (WesternAg Innovations, Saskatoon, Saskatchewan, Canada) were installed in the treatments used for leachate measurements (i.e., $S_{30}C_{30}B_{30}$, S_{90}, C_{90}, and B_{90}). Two anion and two cation plant root simulator (PRS) probes were inserted vertically into the medium at 2.5 cm from the edge of each pot. The probes were buried every 2 weeks for a period of 7 d (on the same day as the pour-throughs) and then sent to the manufacturer for analysis of NO_3^-, NH_4^+, P, K, Ca, Mg, S, Fe, Mn, Cu, Zn, B, Al, Pb, and Cd absorbed on the membranes.

Plants were destructively harvested at 0, 72, and 128 d after transplanting. At each harvest, the shoots were cut off at soil level, rinsed with distilled water, separated into stems and leaves, and oven-dried at 60 °C until no change in mass was observed over a 24-h period. The pots were then placed in a cooler set at 3 °C, and roots were later removed from the media by washing and oven-dried at 60 °C. Each component of the plants was then weighed and ground to pass through a 1-mm screen. The ground samples were analyzed for N using a combustion analyzer and for P, K, S, Ca, Mg, Fe, B, Cu, Mn, Zn, and Na using an ICP spectrophotometer after digestion with nitric acid in a microwave (Gavlak et al., 2003).

Whole plant dry weight was obtained by adding the dry mass of all plant tissues for a given experimental unit. For each nutrient, whole plant concentration was calculated by adding the nutrient content in each tissue and dividing by the whole plant dry weight. The (NUE) was calculated by dividing net uptake of each nutrient [i.e., difference in the total content of the nutrient at transplanting (day 0) and at 128 d after transplanting] by the quantity of that nutrient available from the medium (obtained from chemical analysis of the media) and nutrients added during fertigation.

Data analysis. Data were analyzed using RStudio (version 0.99.903, RStudio INC., Boston, MA, USA) running R (version 3.3.1, R Core Team, 2016). For dry weight, NUE, and nutrient concentration data, Scheffé's linear polynomial models (1958) were fit to account for the simplex-lattice design and allow estimates of the effect of each ingredient proportion using the 'lm' function; the commercial mix treatment was excluded from the analysis. One plant died in a pot filled with a 2:1 mix of peat and bark prior to the second harvest date (due to an accidental loss of irrigation) and, therefore, was also removed from the analysis. Pearson's r correlation coefficient was used to estimate correlative relationships of physical and chemical properties of the media mixtures with individual media proportions and plant dry weight at 72 and 128 d after transplanting.

Data from pour-through leachate and ion-selective membrane probes were analyzed using a linear mixed model (package 'nlme'), and all pairwise comparisons were made using Tukey's honestly significant difference test at the 0.05 level in the 'lsmeans' package (Lenth, 2016; Pinheiro et al., 2016).

Comparisons between all treatments and the commercial control were done using the PROC MIXED procedure in SAS (v. 9.4 SAS Institute Inc. Cary, NC) and the Duncan-Hsu adjustment for multiple group comparisons.

Results

At approximately 6 weeks after transplanting, plants in 90% bark had red tinged leaves, a common symptom of N deficiency in blueberry (Hart et al., 2006a). Following this discovery and coupled with data on differences in percent drainage among treatments (data not shown), the fertigation schedule was changed from every other day to every day to reduce large discrepancies in drainage. This change in fertigation frequency kept more fertilizer solution in the root-zone and eliminated any N deficiency symptoms by 78 d after transplanting.

Media composition. The physical and chemical characteristics differed among the 11 media (Table 2.2; Table 2.3; Table 2.4). Increasing bark in the medium was positively correlated with bulk density, C:N ratio, and Fe and Cu concentration and was negatively correlated with total porosity, WHC, fine particles, and C, N, B, and Zn concentration. The proportion of peat in the medium was positively correlated with total porosity, CEC, and N and Ca concentration and was negatively correlated with medium particle size, pH, and C:N ratio. Increasing coir in the medium was positively correlated with WHC, the proportion of medium and fine particles, pH, EC, and P, K, SO_4-S, B, Cl, and Na concentration and was negatively correlated with air-filled porosity, the proportion of course particles, CEC, and Fe concentration.

Plant dry weight. At 72 and 128 d after planting, total dry weight of the plants increased linearly with greater proportions of peat or coir in the medium and decreased linearly with greater proportions of bark in the medium (Table 2.5). In general, media with ≥ 60% bark resulted in less plant dry weight than those with ≥ 60% coir or peat in the mix, and the latter treatments resulted in the same amount of dry weight in each part of the plant as the commercial mix. Fig. 2.1 is a graphical representation of all possible combinations of peat moss, coir and douglas fir bark on total plant dry weight. Within the plant, increasing the proportion of bark in the medium decreased leaf dry weight at 72 d but had no influence on dry weight of other plant parts at 72 d (i.e., stems or roots) and reduced dry weight in all plant parts at 128 d (Table 2.5).

Whole plant nutrient concentration. There was no effect of media mixture on whole plant P, Ca, Mg, S and Zn concentrations (Table 2.6). Increasing the proportion of bark in the medium increased whole plant concentration of B, Fe, and Mn relative to both peat and coir. Increasing peat proportion in the medium increased whole plant N concentration relative to coir, and decreased K concentration relative to coir and bark. Increasing the coir proportion in the medium increased whole plant Cu concentration relative to peat but not bark.

Nutrient uptake efficiency. Increasing the proportion of bark in the medium reduced NUE of N, P, K, S, Ca, Mg, Fe, Mn, B, Cu, and Zn relative to peat and/or coir (Table 2.7). The NUE for P, K, Mg, Fe, and Mn differed between peat or coir treatments. Treatments with a greater proportion of coir had greater NUE of Mg and Fe than peat, while the opposite trend was observed for P, K, and Mn. With few exceptions, plants grown in the commercial mix had lower NUE of N, P, S, Ca, Mg, Mn, and Zn than plants grown in media containing ≥ 60% peat or coir, and greater NUE of K, Ca, Fe, B, Cu, and Zn than plants grown in ≥ 60% bark.

Leachate pH and EC. In general, the effect of media composition on leachate pH diminished during the experiment (Fig. 2.2). Initially, leachate pH was highest in 90% coir media and lowest in 90% peat moss. However, media composition had little influence on leachate pH between 75 and 119 d after transplanting. Leachate pH varied among measurement dates ($P \leq 0.05$), but when individual dates within a treatment were compared, only 90% peat moss media and 90% bark media differed in leachate pH between 35 d and 119 d after transplanting. Leachate pH increased from 4.3 to 5.5 in 90% peat moss and from 5.9 to 6.9 in 90% bark.

Media composition only influenced leachate EC on two of the seven measurement dates (data not shown). Leachate EC was greater in 90% bark (0.84 $dS \cdot m^{-1}$) than in 90% peat moss or coir (0.34 and 0.46 $dS \cdot m^{-1}$, respectively) at 35 d after transplanting, and was greater in 90% coir (0.38 $dS \cdot m^{-1}$) than in 90% peat moss or bark (0.12 and 0.16 $dS \cdot m^{-1}$, respectively) 119 d after transplanting. The EC differences among the four treatments varied between measurement dates ($P \leq 0.05$), but there was no consistent pattern over time. Mean values never exceeded 0.87 $dS \cdot m^{-1}$ in any treatment during the experiment.

Nutrient availability. Nutrient availability (estimated using PRS probes) differed among the four media treatments evaluated (Fig. 2.3). By the end of the study, the mix with 90% coir had two to four times more available NO_3-N, P, and K than the other three treatments. Availability of NO_3-N did not differ between the 90% peat, 90% bark, and

$S_{30}C_{30}B_{30}$ treatments. The mix with 90% peat moss had three times more available P than the 90% bark and the $S_{30}C_{30}B_{30}$ treatments. The $S_{30}C_{30}B_{30}$ had two times more available K than the 90% peat and 90% bark treatment. Differences in available Ca were only detected between media containing 90% peat and 90% coir where 90% peat had more available Ca than 90% coir. The 90% bark and $S_{30}C_{30}B_{30}$ treatments had two to four times more available Fe and Mn than the other media by the end of the study.

Discussion

In the present study, media containing a high proportion of douglas fir bark reduced plant growth of blueberry compared to media containing high proportions of peat or coir. The negative influence of douglas fir bark on growth was likely due to sub-optimal media physical properties, particularly WHC and its effect on substrate water relations (Table 2.2). Peat and coir had higher WHC than bark, which at 47% is at the low end of the range recommended for media used for container production of nursery plants (Bilderback et al., 2013). In soilless substrate, plants will experience drought stress at much higher tensions (less water depletion) than soil-grown plants (-10 kPa and -1500 kPa, in substrate and soil, respectively; Raviv et al., 2001). De Boodt and Verdonck (1971) defined easily available water (EAW, the volume of water released between -1 and -5 kPa) and water buffering capacity (WBC, the volume released between -5 and -10 kPa) as two critical aspects of substrate water relations. Fields et al. (2014) measured EAW and WBC for peat, coir, and pine bark with similar WHC values to the ingredients in this experiment and found the EAW of bark to be 20% of that for peat and coir.

Gabriel et al. (2009) observed a positive linear relationship of EAW with the addition of peat to douglas fir bark media, suggesting peat has a higher EAW than douglas fir bark. Though not measured directly in the current study, results from other studies suggest that EAW and WBC in the mixes containing a high proportion of douglas fir bark were likely lower than for mixes containing high amounts of peat and coir in this experiment.

The effects of media physical properties on water distribution in containers may also have played a role in the growth of the young plants in the current study. Owen and Altland (2008) observed vertical stratification of WHC in containers of douglas fir bark, with WHC as much as 50% lower in the top 2.5 cm of a 15-cm-tall container as compared to the bottom 2.5 cm. With a measured WHC near the low range of sufficiency for the douglas fir bark, and a root ball that was only 7 cm long at transplanting into a 16.5 cm container, it is likely the roots in media containing a high proportion of bark experienced zones of substrate with a WHC below the recommended range.

A small decrease in available water will reduce stomatal conductance (Améglio et al., 2000), cell expansion, and photosynthetic productivity in blueberry (Andersen et al., 1979; Cameron et al., 1988). Because all treatments were irrigated on the same schedule, a result of the experimental design, media with high amounts of douglas fir bark likely reached stressful tension levels and growth limiting conditions sooner than media with more peat or coir. The observation of improved growth and a reversal of N deficiency symptoms in 90% douglas fir treatments after altering fertigation from every other day to everyday, 51 d after transplanting, further supports the theory of differential water relations between treatments and its impact on plant growth in the current study.

The influence of substrate moisture retention on nutrient availability can also effect plant response to media components. Dry substrate with a low WHC at the top of the container can lead to water channeling and quick drainage of solution (Hoskins et al., 2014). Higher cumulative drainage in douglas fir bark compared to peat and coir treatments (Table 2.1) confirmed a reduction in fertigation solution retention, which likely contributed to the reduced nutrient availability of P and K compared to peat and coir treatments. The reduced N uptake efficiency of N in douglas fir bark as compared to peat and coir grown plants (Table 2.7) coupled with observations of N deficiency, higher C:N ratio (Table 2.3), and possibly lower NH_4-N availability (non significant) on PRS probes (Fig. 2.3), suggest that early N deficiency may also have contributed to the reduced plant growth in bark.

While plants grown in peat and coir did not differ in dry weight at 128 d, there were some notable differences in nutrient uptake efficiency between these systems. Increasing peat in the media improved NUE of P, K, and Mn, and decreased NUE of Mg and Fe, relative to increasing coir in the media (Table 2.7). Differences in NUE of P, K, Mg and Fe were likely related to relative content of these nutrients supplied by the media itself. Peat contained an order of magnitude more Mg and Fe than coir, while coir contained an order of magnitude more P and K than peat. Peat- and coir-grown plants did not differ in dry weight or whole plant concentration of P, Mg, and Fe (Table 2.6), leaving the initial nutrient content of the media (the denominator in the NUE calculation) as the driving factor for the observed treatment effects on NUE for these nutrients.

While NUE of K was greater for peat treatments, plant tissue K concentrations were greater with coir (Table 2.6). However, the higher NUE found with peat was likely a result of the very large difference in media K concentration prior to planting (Table 2.3). Uptake of K occurs through diffusion and is dependent upon the concentration of K cations in the soil-solution in contact with the roots. The higher K concentration in coir-grown plants was not enough to offset the negative effect of the very high K concentration in the coir media on its NUE. The NUE of Mn was greater in peat than coir, despite comparable media values (21 vs 29 ppm, respectively), tissue concentration (Table 2.7), and tissue content (data not shown). This suggests peat had enhanced Mn uptake likely due to the lower leachate pH (Fig. 2.2), improving the availability of Mn to the roots (Haynes and Swift, 1985).

The commercial mix used for comparison resulted in a lower NUE for plants of similar size grown in peat and coir for most nutrients, with the exception of K, Fe, B and Cu (Table 2.7). The reason for this is likely the same as mentioned above, high initial nutrient concentrations in the media. The commercial mix came with a starter fertilizer mixed in, resulting in high concentrations of nutrients (Table 2.3; Table 2.4).

The elevated availability of NO_3-N in the 90% coir treatment (Fig. 2.3) as compared with the other treatments was an unexpected result. The greater abundance of NO_3-N may be explained by greater nitrification resulting from the higher leachate pH in the coir treatment as compared to the other treatments soon after planting (Havlin et al., 2014; Fig. 2.2). Because there were no differences in availability of NH_4-N, the constant fertigation appeared to have supplied adequate NH_4-N to overcome any losses to nitrification in the 90% coir treatment. However, blueberry prefers NH_4-N to NO_3-N (Merhaut and Darnell, 1996) and these findings illustrate the importance of pH management of substrate, particularly in long-term production to maintain N in the desired NH_4-N form.

Because most of the differences in NUE in this study were the result of initial media concentrations, a longer duration study is needed to evaluate the impact of these media components on nutrient uptake from fertilization. After 128 d, it did not appear blueberry plants grown in peat or coir required different fertilization, as growth was similar between these ingredients. However, the multi-year duration of fruit production could lead to changes in media properties such as nutrient retention or porosity. Numerous studies have documented the change in substrate physical and chemical properties as a result of long-term plant growth and media decomposition (Altland et al., 2011; Prasad and O'Shea, 1997; Prasad and Maher, 2003). Further research is needed to predict long term changes in the characteristics of peat- and coir-containing substrates and their potential impact on blueberry production.

While douglas fir bark is a common substrate ingredient in the Pacific Northwest, its physical properties require a different watering regime than either coir or peat. The design of this study with 11 different media mixtures, fertigated simultaneously presented a challenge to irrigate every substrate optimally. The change in fertigation frequency from every other day to every day at 51 d after transplanting, reduced the leachate in the bark treatments and helped to reverse N deficiency symptoms observed 44 d after transplanting. This experience coupled with the widespread use of douglas fir bark by northwest nursery producers and pine bark by southeast nurseries suggests that the poor growth of the plants in bark in this study was a result of a sub-optimal irrigation regime, particularly early in the experiment. Future research on media selection for blueberry should focus on maintaining equal or adequate moisture levels in all media.

A second limit of this study's scope of inference is its short duration (i.e., 4 months). For fruit production, blueberry plants are often grown in containers for several years. Widespread changes in media properties occur over that timeframe as well as root dynamics and plant size/demand (Jackson et al., 2009; Raviv, 2016). Therefore, caution should be exercised when extrapolating the results of this study to long-term effects of media composition on blueberry growth.

We did not find any differences in dry weight between peat- and coir-grown plants in this study. In order to better investigate their different potential effects on growth of blueberry, a second study was conducted. The second study, discussed in Chapter 3, included a greater range of peat and coir mixtures to improve granularity of their different effects on blueberry growth.

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Table 2.1. Composition of and irrigation drainage from 11 different media mixes used to grow ‘Snowchaser’ blueberry in pots. The plants were grown in the pots for 72 or 128 d.

Treatment ID[z]	Media composition (% v/v)				Cumulative drainage (%)[y]	
	Sphagnum Peat Moss (S)	Coconut Coir (C)	Aged Douglas Fir Bark (B)	Perlite	72 d	128 d
Comm.	55-65	0	0	25-30	45	24
$S_{30}C_{30}B_{30}$	30	30	30	10	37	26
S_{90}	90	0	0	10	40	30
$S_{60}B_{30}$	60	0	30	10	38	32
$S_{60}C_{30}$	60	30	0	10	44	25
C_{90}	0	90	0	10	37	33
$C_{60}B_{30}$	0	60	30	10	39	26
$C_{60}S_{30}$	30	60	0	10	36	25
B_{90}	0	0	90	10	60	47
$B_{60}C_{30}$	0	30	60	10	48	40
$B_{60}S_{30}$	30	0	60	10	45	38

[z]Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B=Bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Comm. is a commercially available mixture.

[y]Cumulative drainage (mL per pot) divided by cumulative solution added (mL fertilizer per pot + mL water per pot) at 72 d (29 May 2015) and 128 d (24 July 2015) after transplanting. Irrigation values from 13 Apr. to 20 Apr. 2015 were removed due to irrigation malfunction applying 2 L of water per pot over 7 d and the confounding effect on total drainage.

Table 2.2. Physical characteristics of 11 media mixes used to grow ‘Snowchaser’ blueberry plants.[z]

Treatment ID[y]	Bulk density (gg cc^{-3})	Porosity (%)	Air CC	WHC	Particle size (%) Coarse >2.36mm	Medium >0.85mm	Fine <0.85mm	CEC (meq 100 g^{-1})
Comm.	0.14	81.8	27.4	54.4	47.6	26.2	26.3	28
$S_{30}C_{30}B_{30}$	0.16	82.4	21.0	60.8	52.6	22.8	24.6	21
S_{90}	0.08	86.3	30.1	56.2	58.1	20.8	21.1	27
$S_{60}B_{30}$	0.14	83.5	26.8	56.7	62.2	20.0	17.8	28
$S_{60}C_{30}$	0.08	58.8	22.5	63.3	47.1	24.5	28.4	22
C_{90}	0.08	84.7	19.6	65.1	19.9	31.6	48.5	15
$C_{60}B_{30}$	0.18	79.7	22.3	57.4	44.9	25.5	29.6	18
$C_{60}S_{30}$	0.08	85.9	21.2	64.6	34.9	25.8	39.3	19
B_{90}	0.31	76.4	29.7	46.8	59.7	25.9	14.3	24
$B_{60}C_{30}$	0.25	76.9	23.6	53.3	51.3	26.9	21.8	23
$B_{60}S_{30}$	0.24	79.3	25.2	54.2	58.7	24.9	16.4	23
Media Component Correlations[x]								
Peat	*ns*	0.6772	*ns*	*ns*	*ns*	-0.7664	*ns*	0.6369
Coir	*ns*	*ns*	-0.8398	0.7029	-0.9567	0.7374	0.9436	-0.9288
Bark	0.9922	-0.9430	*ns*	-0.8827	*ns*	*ns*	-0.6908	*ns*
Dry weight Correlations[x]								
72 d	-0.6481	0.6396	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
128 d	-0.8868	0.7853	*ns*	0.7597	*ns*	*ns*	*ns*	*ns*

[z]Media bulk density, and total porosity (porosity), percent air filled porosity (Air CC) and water holding capacity (WHC); particle size distribution of coarse (Coarse), medium (Medium), and fine particles (Fine); and media cation exchange capacity (CEC).
[y]Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B=douglas fir bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Comm. is a commercially available mixture used only for dry weight correlations.
[x]Values are Pearson r, significant at $P < 0.05$, for relationships between proportion of sphagnum peat (Peat), coir (Coir), and douglas fir bark (Bark) in substrate and media property. Media ingredient correlations (n=10) and dry weight correlations at 72 d and 128 d (n=11). No significant linear relationships between variables denoted by ‘*ns*’.

Table 2.3. Chemical characteristics and macronutrient concentration of 11 media mixes used to grow 'Snowchaser' blueberry plants.

Treatment ID[z]	pH[y]	EC (dS m^{-1})[y]	C:N ratio[y]	Nutrient composition						
				(%)		(ppm)				
				C	N	NH_4	P	K	Ca	SO4
Comm.	5.7	4.95	31	18.5	0.59	3.4	590	1386	5539	2353
$S_{30}C_{30}B_{30}$	5.6	0.46	73	30.4	0.42	2.4	169	2973	287	65
S_{90}	4.4	0.31	44	36.5	0.83	3.1	7	128	8017	68
$S_{60}B_{30}$	5.1	0.19	54	32.2	0.59	3.0	39	479	4788	48
$S_{60}C_{30}$	5.2	0.66	52	35.8	0.68	3.5	121	2999	5774	98
C_{90}	6.6	1.20	70	34.0	0.50	3.4	493	8689	3124	183
$C_{60}B_{30}$	5.9	0.74	80	31.5	0.39	2.5	89	3290	3471	86
$C_{60}S_{30}$	5.8	0.91	55	33.0	0.60	2.2	280	6185	5380	140
B_{90}	5.8	0.22	103	31.7	0.31	1.8	10	570	3059	24
$B_{60}C_{30}$	5.8	0.45	80	27.8	0.35	1.8	25	1459	3033	55
$B_{60}S_{30}$	5.4	0.22	78	26.6	0.34	2.0	13	602	3701	31
Media Component Correlations[x]										
Peat	-0.9003	*ns*	-0.8261	*ns*	0.8524	*ns*	*ns*	*ns*	0.7087	*ns*
Coir	0.7563	0.9726	*ns*	*ns*	*ns*	*ns*	0.8674	0.9441	*ns*	0.8743
Bark	*ns*	*ns*	0.8499	-0.7190	-0.8030	-0.7890	*ns*	*ns*	*ns*	-0.7527
Dry weight Correlations[x]										
72 d	*ns*	*ns*	-0.6194	*ns*	0.6080	*ns*	*ns*	*ns*	*ns*	*ns*
128 d	*ns*	*ns*	-0.7285	*ns*	0.6501	0.7183	*ns*	*ns*	*ns*	*ns*

[z]Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B= douglas fir bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Comm. is a commercially available mixture used only for dry weight correlations.
[y]Media pH, electrical conductivity (EC), ratio of carbon to nitrogen (C:N Ratio) and nutrient composition of media.
[x]Values are Pearson r, significant at $P < 0.05$, for relationships between proportion of sphagnum peat (Peat), coir (Coir), and douglas fir bark (Bark) in substrate and media property. Media ingredient correlations (n=10) and dry weight correlations at 72 d and 128 d (n=11). No significant linear relationships between variables denoted by '*ns*'.

Table 2.4: Micronutrient concentration of 11 media mixes used to grow 'Snowchaser' blueberry plants.

Treatment ID[z]	Nutrient Composition (ppm)					
	Fe	B	Cu	Zn	Cl	Na
Comm.	134	1.3	1.2	10.3	43	152
$S_{30}C_{30}B_{30}$	1047	1.9	6.1	8.0	160	443
S_{90}	411	1.4	1.0	7.0	25	85
$S_{60}B_{30}$	1260	1.2	5.2	8.1	8	300
$S_{60}C_{30}$	284	2.9	1.2	8.1	323	469
C_{90}	40	4.8	1.5	9.1	861	1260
$C_{60}B_{30}$	436	1.9	3.0	5.0	290	661
$C_{60}S_{30}$	137	4.0	1.5	7.9	580	912
B_{90}	885	1.0	5.1	4.4	5	307
$B_{60}C_{30}$	848	1.4	5.0	5.0	113	437
$B_{60}S_{30}$	1056	1.0	5.9	6.6	7	345
Media Component Correlations[y]						
Peat	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Coir	-0.7262	0.8670	*ns*	*ns*	0.9346	0.9432
Bark	0.6877	-0.6920	0.7951	-0.7633	*ns*	*ns*
Dry weight Correlations[y]						
72 d	*ns*	*ns*	-0.6135	*ns*	*ns*	*ns*
128 d	*ns*	*ns*	-0.6699	0.6136	*ns*	*ns*

[z]Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B= douglas fir bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Comm. is a commercially available mixture used only for dry weight correlations.
[y]Values are Pearson r, significant at $P < 0.05$, for relationships between proportion of sphagnum peat (Peat), coir (Coir), and douglas fir bark (Bark) in substrate and media property. Media ingredient correlations (n=10) and dry weight correlations at 72 d and 128 d (n=11). No significant linear relationships between variables denoted by '*ns*'.

Table 2.5. The effect of 11 different media mixes on plant growth of 'Snowchaser' blueberry grown in pots for 72 or 128 d.

Treatment ID[z]	Dry weight (g/plant)[y]							
	72 d				128 d			
	Total	Roots	Stems	Leaves	Total	Roots	Stems	Leaves
Comm.	7.6	2.1	1.5	4.0	45.7	9.7	11.4	24.6
$S_{30}C_{30}B_{30}$	6.6	2.1	1.4	3.1	42.8	9.4	12.3	21.1
S_{90}	8.0	1.9	1.4	4.6	45.3	10.4	13.4	21.5
$S_{60}B_{30}$	6.5	1.8	1.3	3.3	39.9	9.5	11.4	19.0*
$S_{60}C_{30}$	8.2	2.1	1.8	4.3	48.0	9.4	14.1	24.5
C_{90}	6.2	1.9	1.3	3.0	43.1	10.5	11.5	21.1
$C_{60}B_{30}$	8.1	2.1	1.6	4.5	47.7	11.2	14.1	22.4
$C_{60}S_{30}$	8.4	2.2	1.5	4.6	46.3	13.2	12.7	20.5
B_{90}	5.3	1.8	1.3	2.2	15.3*	3.8	4.7*	6.8*
$B_{60}C_{30}$	5.3	1.6	1.3	2.4	28.3*	8.2	7.7	12.4*
$B_{60}S_{30}$	7.3	2.1	1.4	3.7	24.9*	6.5	7.5*	11.0*
Linear mixed model[x]								
P value	0.0473	0.6425	0.4375	0.0105	<0.0001	0.0005	<0.0001	<0.0001
r^2_{adj}	0.1216	0.0187	0.0573	0.1762	0.6392	0.2800	0.5743	0.6566
Coefficients[x]								
Peat	8.1 a	2.0 a	1.5 a	4.5 a	46.9 a	10.3 a	13.8 a	22.7 a
Coir	7.4 ab	2.0 a	1.5 a	3.8 a	49.2 a	12.2 a	13.5 a	23.4 a
Bark	5.5 b	1.8 a	1.3 a	2.3 b	18.3 b	5.0 b	5.5 b	7.9 b

[z]Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B= douglas fir bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Comm. is a commercially available mixture used for comparison.
[y]Dry weight of roots, stems and leaves 72 d and 128 d after planting. Mean values of 5 replications except $S_{60}C_{30}$ where n=4 at 128 d.
[x]*P*-values are for a linear mixture model (Model); adjusted correlation coefficient for linear mixture model (r^2_{adj}); and coefficients for each model component. Coefficients followed by the same lower case letter within a column are not significantly different based on Tukey's honestly significant difference test ($P \leq 0.05$). *Denotes treatment mean significantly different than Comm. treatment at a 95% level using Dunnett-Hsu adjustment.

Table 2.6: Whole plant concentration of nutrients in 'Snowchaser' blueberry plants grown for 128 d in 11 different mixes.

Treatment ID[z]	Concentration (mg/g)[y]						Concentration (mg/kg)[y]				
	N	P	K	S	Ca	Mg	Fe	Mn	B	Cu	Zn
Comm.	9.7	1.05	5.5	1.1	3.2	1.7	69	87	26	13	14
$S_{30}C_{30}B_{30}$	9.2	1.02	5.7	1.2	3.5	1.5	116	480	28	14	11
S_{90}	10.7	1.06	4.9	1.6	3.9	1.7	74	134	27	11	14
$S_{60}B_{30}$	9.8	1.02	5.3	1.3	4.0	1.7	153	542	28	13	12
$S_{60}C_{30}$	9.4	0.98	5.1	1.2	3.8	1.7	86	130	25	10	14
C_{90}	9.2	1.03	6.5	1.5	4.6	1.8	84	114	28	15	13
$C_{60}B_{30}$	8.9	1.11	6.4	1.1	3.7	1.5	197	385	31	15	14
$C_{60}S_{30}$	8.8	0.99	5.4	1.1	3.3	1.4	69	135	23	13	12
B_{90}	9.5	0.92	6.2	1.2	3.8	1.5	267	589	32	12	13
$B_{60}C_{30}$	9.1	0.97	5.7	1.2	3.2	1.5	341	495	30	17	11
$B_{60}S_{30}$	9.8	1.04	5.6	1.3	3.6	1.5	218	552	28	12	11
Mixture Model Results[x]											
P-values											
Model	0.0214	0.4056	0.0190	0.3609	0.6300	0.1889	<0.0001	<0.0001	0.0037	0.0861	0.7018
r^2_{adj}	0.1539	0.0385	0.1583	0.0433	0.0199	0.0699	0.3337	0.9209	0.2163	0.1011	0.0153
Coefficients[x]											
Peat	10.2 a	1.03 a	4.8 b	1.4 a	3.8 a	1.7 a	75 b	138 b	25 b	10.5 b	13 a
Coir	8.7 b	1.04 a	6.5 a	1.2 a	3.9 a	1.6 a	94 b	118 b	27 b	15.1 a	13 a
Bark	9.4 ab	0.97 a	6.0 a	1.2 a	3.5 a	1.4 a	373 a	518 a	32 a	14.2 ab	11 a

[z]Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B=douglas fir bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Comm. is a commercially available mixture used for comparison.
[y]Whole plant concentration (mg/g and mg/kg on a dry weight basis) of roots, stems and leaves combined. Mean values of 5 replications except $P_{60}C_{30}$ where n=4.
[x]*P*-values are for a linear mixture model (Model); adjusted correlation coefficient for linear mixture model (r^2_{adj}); and coefficients for each model component. Coefficients followed by the same lower case letter are not significantly different based on 95% confidence intervals from Tukey's Honestly Significant Difference test.

Table 2.7: Nutrient uptake efficiency (NUE) of 'Snowchaser' blueberry plants grown for 128 d in 11 different media mixes.

Treatment ID[z]	Nutrient Uptake Efficiency (% of nutrient supplied in fertilizer and in media mix)[y]										
	N	P	K	S	Ca	Mg	Fe	Mn	B	Cu	Zn
Comm.	39	19	17	1.8	4	5	3.9	28	41	75	8
$S_{30}C_{30}B_{30}$	58*	27	10*	3.6*	19*	33*	0.7*	32	35	14*	6
S_{90}	74*	41*	26*	5.2*	6	14*	2.5	79*	47	154*	16*
$S_{60}B_{30}$	61*	33*	20	3.7*	5	10*	0.9	44	40	18	8
$S_{60}C_{30}$	67*	36*	15	4.0*	7*	10*	4.3	64*	39	125	14*
C_{90}	69*	24	10*	4.2*	11*	41*	20.2*	46	32	129	11
$C_{60}B_{30}$	63*	38*	11*	3.7*	6	8*	2.9	53*	42	30*	12
$C_{60}S_{30}$	61*	30*	10*	3.6*	7*	11*	6.5	59*	31	122	13*
B_{90}	21*	12	7*	1.3	1*	2*	0.4*	24	14*	3*	3*
$B_{60}C_{30}$	35	22	8*	2.2	2*	4	1.1	27	22*	8*	4*
$B_{60}S_{30}$	34	22	11*	2.2	2*	4	0.5*	18	22*	5*	3*
Mixture Model Results[x]											
Model	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
r^2_{adj}	0.5916	0.4663	0.6388	0.5712	0.5527	0.5466	0.6286	0.5037	0.4737	0.8838	0.6698
Coefficients[x]											
Peat	76 a	37 a	22 a	5 a	7 a	13 b	1.9 b	69 a	46 a	140 a	13 a
Coir	67 a	21 b	7 b	4 a	11 a	25 a	14 a	52 b	37 a	146 a	14 a
Bark	25 b	15 b	6 b	1 b	2 b	3 c	0.3 c	14 c	17 b	2 b	2 b

[z]Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B=douglas fir bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Comm. is a commercially available mixture used for comparison.

[y]Nutrient uptake efficiency based on cumulative fertilizer application over 128 d and initial nutrient composition of media. Mean values of 5 replications except $S_{60}C_{30}$ where n=4.

[x]*P*-values are for a linear mixture model (Model); adjusted correlation coefficient for linear mixture model (r^2_{adj}); and coefficients for each model component. Coefficients followed by the same lower case letter are not significantly different based on 95% confidence intervals from Tukey's Honestly Significant Difference test. *Denotes treatment mean significantly different than Comm. treatment at a 0.05 significance level using Dunnett-Hsu adjustment.

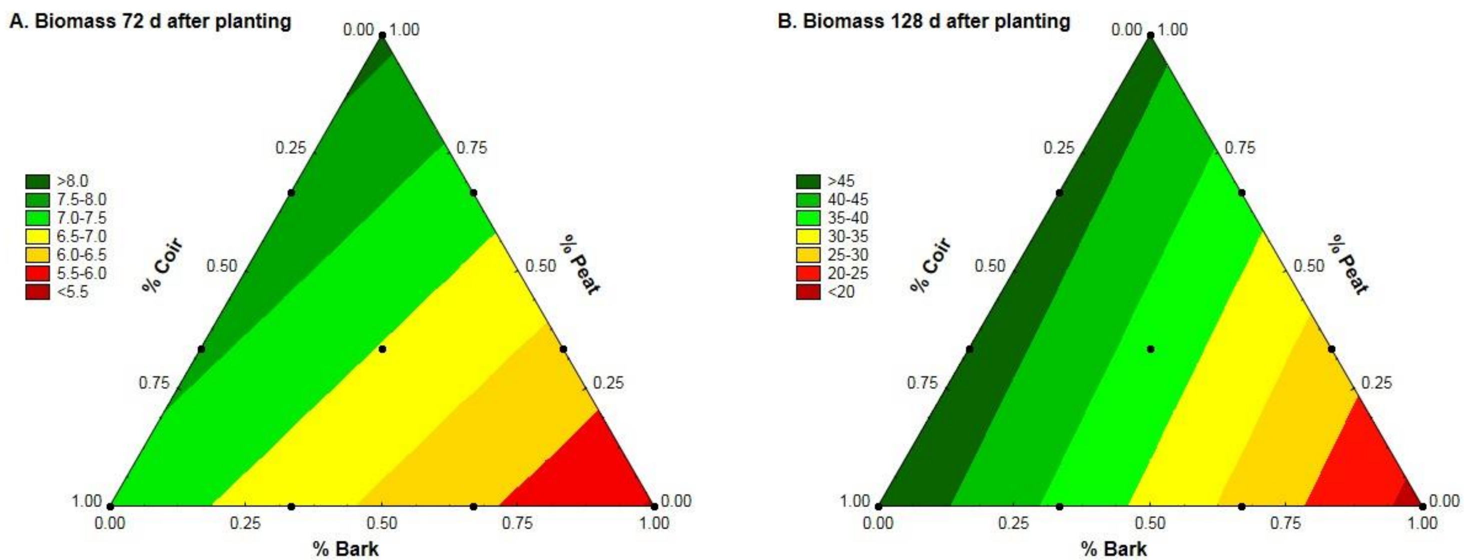


Fig. 2.1: Total biomass response (g dry weight per plant) in 'Snowchaser' blueberry plants to media composition 72 d (A) and 128 d (B) after planting. Each side of the triangle represents the proportion of the ingredient contained in the mixture. Dry weight responded linearly with respect to each ingredient composing the media mixture.

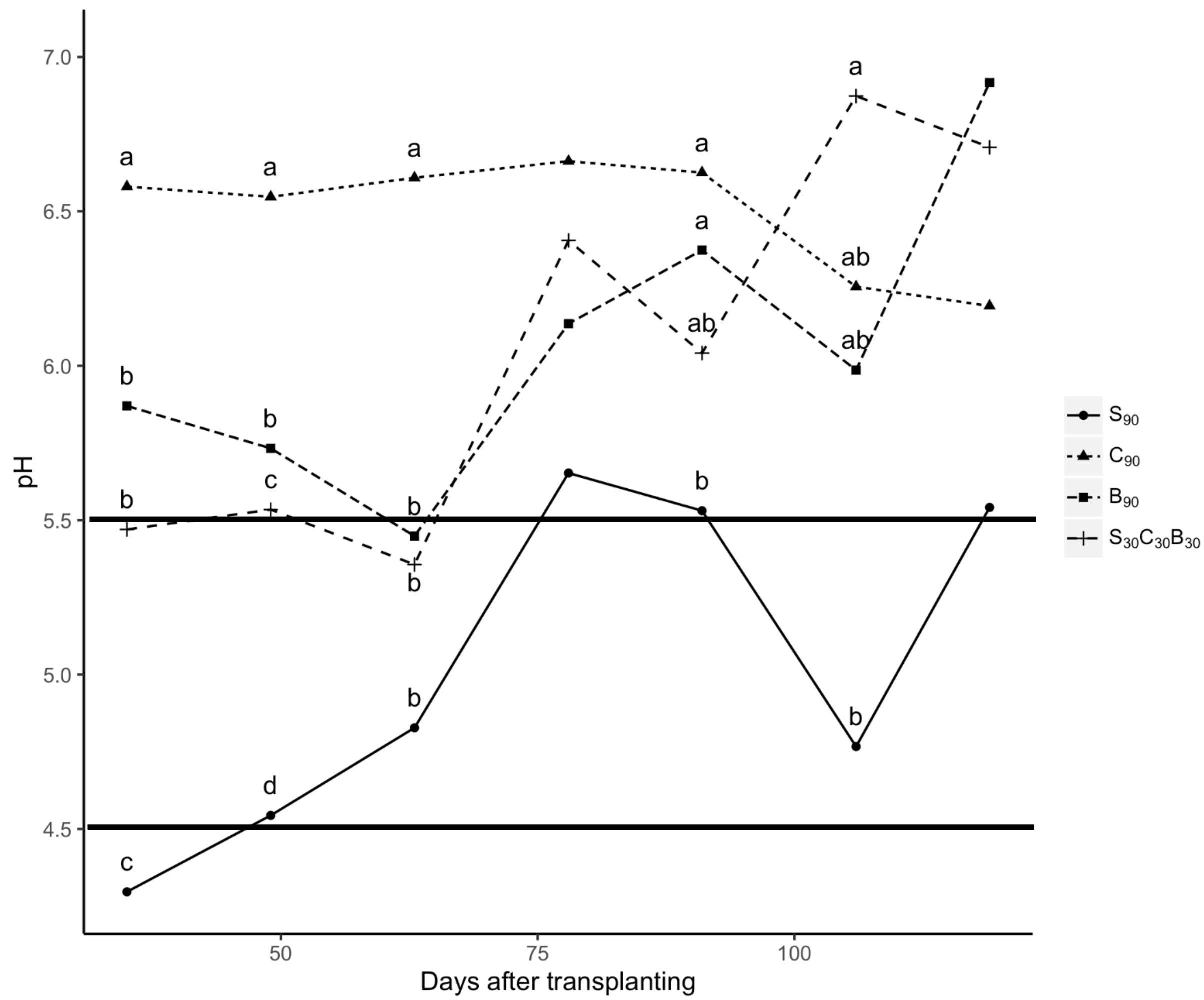
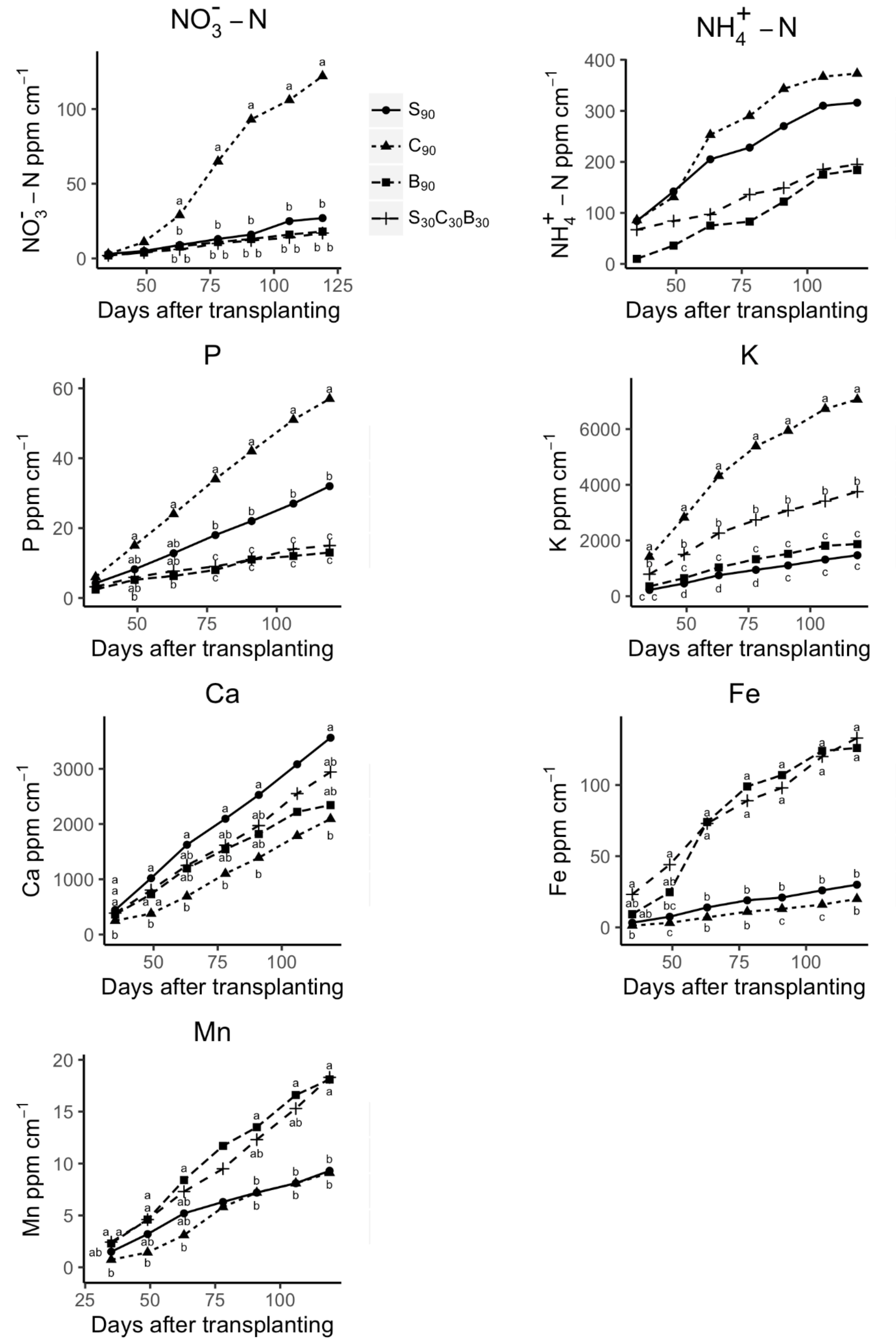


Fig. 2.2: The pH of pour-through leachate from four media mixes used to grow 'Snowchaser' blueberry in pots. Each treatment contained 10% perlite, by volume, and 90% sphagnum peat moss (S_{90}), 90% coir (C_{90}), 90% douglas fir bark (B_{90}), or 30% each of peat, coir, and bark ($S_{30}C_{30}B_{30}$). Mean values denoted by the same lower case letter on a given date are not significantly different at $P \leq 0.05$. Horizontal lines at pH 4.5 and 5.5 represent optimal soil pH for blueberry (Hart et al., 2006).

Fig. 2.3: Cumulative availability of seven nutrients in four treatments from PRS probes. Each graph shows the cumulative nutrient concentration in potting media of four treatments over the duration of the study. PRS probes were buried for one week intervals, every two weeks. Treatment IDs are abbreviated with the component listed (S=Sphagnum peat moss, C=Coir, B= douglas fir bark) and its respective percent of total media in subscript (e.g. $S_{30}C_{30}B_{30}$ is 30% peat, 30% coir, and 30% aged douglas fir bark). Different lower case letters represent significantly

Fig. 2.3 (Continued)



Chapter 3: Growth and nutrient uptake of two highbush blueberry cultivars grown in soilless substrate with different ratios of sphagnum peat moss, coconut coir, and perlite.

Abstract

A greenhouse study was conducted to investigate how media composition alters growth and nutrition of young blueberry plants. Northern (‘Liberty’; *Vaccinium corymbosum* L.), and southern highbush blueberry (‘Jewel’; interspecific hybrid of *V. corymbosum* L. and *V. darrowii* Camp.) were grown for 3 months in 16 different media mixtures containing varying proportions of perlite, sphagnum peat moss, and coconut coir. Perlite accounted for 0% to 30% of the media, by volume, while the remaining volume consisted of four ratios of peat to coir (1:0, 2:1, 1:2, and 0:1). Plants were fertigated daily with a modified Hoagland’s nutrient solution adapted for acidic plants. Drainage was targeted at 25% of total volume of solution applied. Every two weeks, pH and electrical conductivity of leachate from containers was measured. Plant dry weight and nutrient composition were determined after 95 d of growth. The amount of perlite in the media had no effect on leachate pH, but media containing high amounts of peat had lower leachate pH than media containing high amounts of coir until 55 d after transplanting. Increasing the amount of perlite in the media decreased dry weight in ‘Jewel’ but had no effect on dry weight in ‘Liberty’. When media contained perlite, the proportion of peat and coir in the media had no effect on dry weight of either cultivar. When no perlite was in the media, increasing the amount of peat (decreasing coir) increased dry weight in ‘Liberty’. Increasing the proportion of peat (decreasing coir) improved nutrient uptake efficiency [nutrient uptake / (nutrient applied + nutrient in initial media)] for P, K, Mg and Zn for

both cultivars, and N, Ca, S, and B in ‘Liberty’. In addition, increasing the amount of peat increased whole-plant concentration of P and Mg in ‘Jewel’ and N, P, K, and B in ‘Liberty’. Our results indicate that high levels of perlite in the media can negatively impact initial growth of young blueberry plants through its influence on media water holding capacity. Initial growth of young blueberry plants is similar in media containing peat or coir; however, the different effects of media composition on plant nutrition suggest fertilizer management in substrate production for long-term growth should be tailored for whether peat or coir is used.

Introduction

Previously, we investigated how growth and nutrition of ‘Snowchaser’ southern highbush blueberry was influenced by altering the ratios of three common media ingredients (peat, coir and douglas fir bark) in substrates containing 10% perlite by volume (Chapter 2). We found that after 128 d, douglas fir bark negatively affected plant growth and was a poor choice of substrate when grown with a similar water regime to peat and coir. In addition, there were no differences in dry weight between plants grown in peat or coir, suggesting that both of the ingredients are suitable for container production of southern highbush blueberry. In our previous study, the amount of perlite, a media component commonly used by growers, was held constant at 10% by volume. It is unclear whether varying the amount of perlite in the media may alter the response of the plants to peat and coir.

Perlite is a common inorganic and inert substrate ingredient added to media. Mined from rhyolitic volcanic minerals, it is heated to 800-1100 °C to evaporate the water inside and ‘pop’ the particles, creating air-filled pores and a lightweight particle (Alkan and Dogan, 1998). Perlite is commonly added to substrate media to improve drainage, increase air space, and provide a stable component that is resistant to decomposition (Raviv and Lieth, 2008; Nelson, 2011). Perlite commonly used in horticulture has particles ranging in size from 0 to 4 mm. Burés et al. (1997) observed that small particles (0.25-0.5 mm) held onto more water at lower tensions than larger particles (0.5-1 mm). However, when mixed with other ingredients, the influence of perlite on physical properties is less predictable.

A great deal of research has focused on predicting physical properties for mixes of pure ingredients, but none of the models have proven to be fully successful (Blythe and Merhaut, 2007; Gabriel et al., 2009; Rhie and Kim, 2017). Rather, empirical data are required to accurately obtain media properties. With peat and perlite blends, Fields et al. (2014) found no difference in physical properties between peat mixtures with 10% to 40% perlite by volume, which perhaps was an effect of particles settling into pore spaces in the media. This result suggests that a high volume of perlite in the mix may not have an impact on aeration or drainage but could be used potentially to improve stability of the substrate.

Container production of blueberry for fruit requires plants to remain in the same substrate for at least 4 years, economically (B. Strik, personal observations). During this time, it is likely that the physical and chemical properties of the media will change due to decomposition. Peat and coir have different organic origins, but both decompose slowly when used as a growing substrate for plants. Peat’s resistance to decomposition comes from unique lignins, pectin-like substances, and phenolic antimicrobial compounds

(Hájek et al., 2011; Rydin and Jeglum, 2013; Thormann, 2011). Coir has resistant lignocellulosic molecules as well as phenolic substances that help resist decomposition (Ma and Nichols, 2004). Due to its inorganic origins, perlite does not undergo biological decomposition and can add long-term stability to media (Bilderback et al., 2005). Therefore, growers are interested in media with high proportions of perlite or other inert ingredients for production of blueberry. Additionally, successful production of blueberry in a wide range of substrate would give a farmer flexibility to choose media ratios based upon availability and economic concerns.

Highbush blueberry cultivars used for fruit production are grouped by their dormant chilling requirement and genetic origins. Southern highbush blueberry (SHB) requires little winter chill (< 500 chilling hours) due largely to their hybridization with *V. darrowii* Camp. and other native *Vaccinium* species (Draper, 1997; Sharpe and Darrow, 1959). In addition to low chill requirements, *V. darrowii* genetics improve the drought tolerance of the progeny, suggesting different water requirements under cultivation (Erb et al., 1993). Northern highbush blueberry (NHB) requires 800-1000 hours of chill to break dormancy and are predominantly intra species hybrids of *V. corymbosum* L. (Retamales and Hancock, 2012). Bryla and Strik (2007) observed different water requirements among NHB cultivars attributed to timing of fruiting, peak water demand, and environmental conditions during fruiting. Different genetic backgrounds involving drought tolerance between NHB and SHB blueberry as well as timing of fruiting suggest that they may grow differently in the altered root environment of soilless substrate.

The objectives of the current study were to determine whether increasing the perlite content in the media alters blueberry growth and nutrition in NHB and SHB. We hypothesized that increasing perlite content would negatively affect blueberry growth and nutrition through its influence on media water holding capacity, while peat and coir would have similar effects, regardless of the amount of perlite in the media.

Materials and Methods

Experimental setup. The study was conducted in a greenhouse from 8 Apr. to 12 July 2016 at the USDA-ARS-Horticultural Crops Research Laboratory in Corvallis, Oregon, USA (lat. 44°34'3" N, long. 123°17'19" W). Sixteen unique media mixtures were evaluated, including those contained specific proportions of perlite, sphagnum peat, coconut coir (Pro Gro Mixes, Sherwood, OR) (Table 3.1). Four rates of perlite were used (0%, 10%, 20%, 30% by volume), and the remaining volume was divided between peat and coir at one of four ratios (1:0, 2:1, 1:2, 0:1 by volume of peat and coir).

On 24 Feb. 2016, dormant plants of ‘Jewel’ and ‘Liberty’ in 70-mL containers (obtained from Fall Creek Farm and Nursery, Lowell, OR) were removed from a 3 °C cooler and placed outside in partial shade and irrigated as needed. On 8 Apr. 2016, plants were transplanted individually into 4.4-L pots [19.7-cm diameter and 16.5-cm tall (#2 Short); Anderson Pots, Portland, OR] containing one of the 16 treatments and moved to a greenhouse. Each treatment had 5 replications for each cultivar for a total of 160 plants. Pots were arranged in a randomized complete block design (RCBD) across two greenhouse benches as described previously (Chapter 2).

Immediately after planting, plants were fertigated each day with 100 mL of modified Hoagland’s solution (Chapter 2). Beginning on 20 Apr., drainage solution was collected from the pots at least every 2 weeks. Extra water was added, as needed, to increase drainage to 25% of the total volume of solution added. During the remainder of the experiment, plants were fertigated daily, and the volume was adjusted according to plant needs.

Beginning on 15 May, air temperature (T_{air}), relative humidity (RH), and solar radiation (flux density of light, 200-1100 nm) were measured every 15 min using a CR10X datalogger (Campbell Scientific, Logan, UT) connected to Humitter 50 YC RH probe (Vaisala, Wodburn, MA) and a LI200X-L light meter (LI-COR Environmental, Lincoln, NE). The LI200X-L data (KWm^{-2}) was converted to PAR (μmols $m^{-2}s^{-1}$) (Biggs 1986). From 15 May to 25 July, the mean daily maximum T_{air} was 28.5 °C and the minimum was 14.8 °C, and the mean daily average was 22.8 °C. The mean RH was 59%, and mean photosynthetically active radiation (PAR) was 28 $mol{\cdot}m^{-2}{\cdot}d^{-1}$.

Measurements and data collection. Beginning on 22 Apr. 2016, leachate was collected every 2 weeks using a modified pour-through method (PT; Wright, 1986) from all treatments in 3 blocks (32 treatments x 3 blocks x 7 dates = 672 samples) and analyzed for pH and EC (Chapter 2). On 8 Apr. and 12 July (0 and 95 d after planting, respectively), plants were destructively harvested as described in Chapter 2, except shoots were separated into 'non-whip' and 'whip' tissue. 'Non-whip' shoots were defined as growth that originated from a cane present upon planting (from an axial bud), and 'whip' shoots were defined as shoots that arose from latent buds from either the crown of the plant or the first cm of the shoot above the media. Pots were rinsed to remove media from roots. Plant material was placed in an oven at 60 °C and dried until no change in mass was observed over a 24-h period. Dry samples were weighed and analyzed for nutrient concentrations as described previously (Chapter 2).

Whole plant dry weight was obtained by adding the dry mass of all plant tissues for a given experimental unit. Tissue nutrient content was calculated by multiplying nutrient concentration by tissue dry weight. For each nutrient, whole plant concentration was calculated by adding the nutrient content in each tissue and dividing by the whole plant dry weight. Nutrient uptake efficiency was calculated by dividing net uptake of each nutrient [i.e., difference in the total content of the nutrient at transplanting (day 0) and at 95 d after transplanting] by the quantity of that nutrient available from the medium (obtained from chemical analysis of the medium) and nutrients added during fertigation.

Data analysis. Data were analyzed using SAS (v. 9.4, SAS Institute Inc. Cary, NC, USA). Model selection for dry weight, whole plant nutrient concentration and nutrient uptake efficiency data was performed using PROC GLMSELECT using backwards stepwise selection for each variable. Selected models were analyzed using a linear mixed model with the PROC MIXED procedure with percent sphagnum peat (S), percent perlite (P), and cultivar forming the fixed effects. Because percentage of peat and coir were not independent of each other, only one was used in the model (peat). If non-homogenous variance of residuals or a non-normal distribution was observed, data were transformed using a natural logarithm to meet the necessary statistical assumptions. Nutrient uptake efficiency data for Fe and Mn did not meet regression assumptions and therefore Spearman’s R correlation was calculated using PROC CORR in SAS. Data for leachate pH and EC were analyzed as a mixed effect factorial design for perlite and S:C ratio, but separately for each date and cultivar using RStudio (version 0.99.903, RStudio INC., Boston, MA, USA) running R (version 3.3.1, R Core Team, 2016) with package ‘nlme’ (Pinheiro et al. 2016). Pairwise comparisons between treatments were made using

Tukey's Honestly Significant Difference for equal sample size, and Tukey-Kramer test for unequal data, at a 95% confidence level. Spearman's R correlation was used to estimate correlative relationships between physical and chemical properties of the media with the various ingredient proportions, and plant dry weight with RStudio. For each correlation, sample size was n=16, for the 16 unique treatments and cultivars were analyzed separately for mean dry weight correlations.

Results

Media composition. Increasing the proportion of peat (decreasing coir) in the media was correlated with several media physical and chemical characteristics (Table 3.2; Table 3.3). In contrast, greater perlite in the media influenced few of the physical and chemical characteristics measured. The proportion of perlite in the media was positively correlated with bulk density and particle size and negatively correlated with the percentage of N in the media, while the proportion of peat was positively correlated with N, Ca, Mg, Fe, and Mn in the media and negatively correlated with air filled porosity, C:N ratio, pH, EC and P, K, Na, B, and Cu in the media. Peat and coir proportions were inversely related. Therefore, coir had opposite correlations with media characteristics than peat.

Dry weight. Dry weight response to media ingredients varied between cultivars. 'Jewel' dry weight was only influenced by altering the percentage of perlite in the media (Table 3.4). In contrast, the percentage of peat and coir in the media altered dry weight of 'Liberty', and the dry weight response to peat depended on the proportion of perlite (Table 3.5).

Increasing the amount of perlite in the media decreased total dry weight of 'Jewel' (Table 3.4). This negative linear response to perlite in 'Jewel' was driven primarily by the dry weight response of non-whip canes and whip leaves. Perlite had no influence on root, whip cane, or non-whip leaf dry weight in 'Jewel'. Even though perlite had no influence on total dry weight in 'Liberty' across all levels of peat and coir in the media, increasing the proportion of perlite decreased the dry weight of non-whip leaves (β_0=9.03, β_1= -0.08, P = 0.0185).

In 'Liberty', increasing the proportion of peat increased total dry weight when no perlite was present but had no effect on total dry weight when media contained perlite (10%, 20%, or 30%, by volume) (Table 3.5). The effect of peat on total dry weight was driven by the growth response of roots, whip canes, and whip leaves in 'Liberty'. Increasing the amount of peat in the media had no influence on dry weight of non-whip canes and non-whip leaves in 'Liberty' (data not shown).

Plant dry weight accumulation was correlated with only a few of the initial media physical and chemical characteristics. In both cultivars, dry weight accumulation was positively correlated with media N ('Jewel': r = 0.6181, P = 0.0107; 'Liberty': r = 0.5460, P = 0.0288). In addition, dry weight accumulation in 'Jewel' was positively correlated with 0-2mm particles (r = 0.6289, P = 0.0091) and negatively correlated with >4-mm particles (r = -0.5155, P = 0.0409).

Nutrient uptake efficiency. The proportion of peat and coir in the media had a greater influence on nutrient uptake efficiency than perlite. The amount of perlite in the media only altered nutrient uptake efficiency for N in 'Jewel' [i.e., increasing perlite decreased N uptake efficiency in 'Jewel' (β_0 = 51.05, β_1 = -0.27, P = 0.0185)]. In both cultivars, increasing the percentage of peat in the media enhanced NUE for P, K, Mg and Zn (Table 3.6). Increasing peat also improved NUE of N, Ca, S and B in 'Liberty' plants but had no effect on NUE for these nutrients in 'Jewel' plants.

The effect of peat on NUE for most nutrients was similar in all levels of perlite. In 'Liberty', the effect of peat on NUE of N was approximately two times greater in media without perlite compared to media with perlite. For some nutrients, peat and coir only influenced NUE when there was no perlite in the media. Increasing peat improved NUE of Mg in both cultivars and for Ca and Zn in 'Liberty' when no perlite was in the media but had no effect on NUE for these nutrients when media contained perlite.

In both cultivars, NUE for Fe and Mn were highly variable, and linear models between media components and NUE were not appropriate. There were negative relationships between the percentage of peat in the media and Fe uptake efficiency in both cultivars across all perlite levels ('Jewel': $r = -0.62$, $P < 0.0001$; 'Liberty': $r = -0.49$, $P < 0.0001$). The relationship between Mn uptake efficiency and the amount of peat in the media varied between cultivars and depended on how much perlite was in the media. In 'Jewel', there was a negative relationship between the amount of peat in the media and Mn uptake efficiency when media contained 10% ($r = -0.63$, $P = 0.0035$) or 20% perlite ($r = -0.49$, $P = 0.0288$), and no relationship when media contained 0% or 30% perlite. In 'Liberty', there was a positive relationship between the amount of peat in the media and Mn uptake efficiency when no perlite was in the media (0% perlite, $r = 0.77$, $P < 0.0001$), but not when perlite was present in the media (10-30% perlite).

Whole plant nutrient concentration. The effects of media composition on whole plant nutrient concentration differed between cultivars (Table 3.7). With high amounts of perlite in the media (20% or 30%) there was a relationship between peat and plant N and P concentrations. Increasing the amount of peat in the media increased plant N and P concentration in ‘Liberty’ when media contained 30% perlite, and peat increased plant P concentration in ‘Jewel’ when media contained 20 or 30% perlite. The influence of peat on plant K, Mg, and B concentrations was similar across perlite levels. Increasing peat increased plant K and B concentrations in ‘Liberty’ and Mg concentration in ‘Jewel’. In both cultivars, the proportion of peat or perlite in the media had no influence on plant S, Ca, Fe, Mn, or Zn concentrations.

pH and EC of leachate. The leachate pH varied among measurement dates (Figure 1). With the exception of ‘Jewel’ at 14 and 55 d after transplanting, perlite level had no effect on leachate pH in either cultivar (Fig. 3.1A and 3.1B). However, there was a strong effect of peat in the media on leachate pH from 14 to 55 d, with mixes containing the greatest amount of peat having the lowest leachate pH (Fig. 3.1C and 3.1D).

Electrical conductivity (EC) of leachate varied dramatically with no consistent treatment effect and generally decreased over time (data not shown). Leachate EC was highest at 14 d after transplanting ($\bar{X} = 2.30\ dS \cdot m^{-1}$) and decreased to $\bar{X} = 0.53\ dS \cdot m^{-1}$, 95 d after planting.

Discussion

Peat and coir effects on plant growth. The results of this study support and strengthen the findings from our previous study (Chapter 2), which showed that altering the proportion of peat or coir in the media had no effect on growth of ‘Snowchaser’ blueberry after 3-4 months when perlite was present in the media. This suggests that a grower can select a blend of peat and coir of their choice and add between 10% and 30% perlite by volume, and not expect differences in short-term growth.

In our previous study (Chapter 2), differences in dry weight between media containing bark and those containing peat and coir were attributed to suboptimal plant-water relations caused by high amounts of douglas fir bark in media and the inability to alter irrigation frequency by treatment due to the study's design. The water holding capacity (WHC) reported in Chapter 2 were 56% and 65% for mixes with 90% peat and coir, respectively. These WHC values were similar to those in the current study (63% and 53%, respectively, for mixes with 90% peat or coir) and are within the recommended ranges for soilless substrate (Bilderback et al., 2013). Our results from Chapter 2 and the current study indicate that media with WHC within these ranges will not adversely affect dry weight accumulation of blueberry plants for at least 3 months after transplanting. Multiple studies have substituted coir for peat with no effect on plant growth of ericaceous plants (Berruti and Scariot, 2011; Larcher and Scariot , 2009; Scagel, 2003), but none of these experiments have replaced more than 50% of the peat with coir. Our findings suggest that if some perlite is in the medium, peat can be completely substituted with coir without impacting short-term growth.

Peat and coir effects on plant nutrition. Altering the proportions of peat and coir in media impacted plant nutrition without observable effects on plant dry weight accumulation. This result was surprising given the large differences in chemical composition and origins of peat and coir, but supports the findings in Chapter 2. Scagel (2003) observed enhanced uptake of various nutrients in ericaceous plants grown in coir compared with peat, but the media used contained 20% or less of peat and coir. While minimal literature exists on the effects of peat and coir on uptake of nutrients in blueberry plants, considerable literature exists for other plants suggesting coir is a suitable alternative to peat but requires adjustments to the nutrient solution applied (Mak and Yeh, 2001; Meerow, 1994; Stamps and Evans, 1997). However, few of these studies evaluated nutrient uptake through tissue nutrient analysis and instead based fertilizer recommendations on plant dry weight response, limiting their usefulness as comparisons to the current study.

Peat increased the uptake efficiency of N in ‘Liberty’ and this result could be explained by the higher N content in peat than coir prior to planting (Table 3.3). However, despite improved N uptake efficiency, there was minimal impact on whole plant concentration of N in the current study (Table 3.7). In *Petunia* sp. (Juss.), Handreck (1993) observed reduced availability of applied N in coir as compared to peat, attributed to immobilization in coir. In the current study, increasing proportions of coir was correlated with greater C:N ratio of the media (Table 3.7), but the differences between the pure ingredients were minor (C:N ratio of 49 vs. 56, 100% peat vs 100% coir, respectively). One possible explanation for improved nutrient uptake efficiency in peat in the current study was its lower pH and the effect on mineral N form present in solution. Blueberry prefers NH_4-N (Merhaut and Darnell, 1996), which is more prevalent at lower pH, as nitrification is inhibited (Havlin et al., 2014). In Chapter 2, NO_3-N availability (as detected by PRS probes) in coir was greater than in peat, suggesting different mineral N dynamics in the two media, which could be driven by media pH. Differences in N uptake efficiency could have implications for longer term N nutrition, as coir may require more N and careful management of pH to keep N in the NH_4 form.

The effects of media composition on K nutrition have implications for fertilizer management in substrate production of blueberry. Increasing the amount of peat in the media improved K uptake efficiency in both cultivars but reduced whole plant K concentration in ‘Liberty’. These effects on K nutrition are likely due to the very large differences in initial media K concentrations between peat and coir, similar to results reported in Chapter 2 (Handreck, 1993; Meerow, 1994; Stamps and Evans, 1997). Uptake of K is largely driven by soil solution concentration (Silber et al., 2003), and coir in this study had very high levels of K relative to peat (Table 3.3). The negative effect of peat on whole plant K concentration in ‘Liberty’ but not ‘Jewel’ could be a result of differences in K requirements between cultivars, as cultivars often have different nutrient demands and tissue levels (Strik and Vance, 2015). Blueberry requires K fertilization because substantial quantities are removed in fruit and during pruning (Bryla et al., 2012) and K is important for proper functioning of many cellular functions (Marschner, 2011). When growers use coir in the media, it is possible they could reduce initial K fertilizer applications, until the K in the media is consumed, reducing fertilizer applications early during production. Additionally, without the addition of K in media containing high amounts of peat, K deficiency may occur.

The effects of media composition on P nutrition may be related to differences in initial media pH between peat and coir. Increasing the amount of peat improved the nutrient uptake efficiency for P and increased whole plant P concentration in media containing 30% perlite , despite having less P supplied by the media. Low pH in substrates has been shown to favor P uptake (Altland and Buamscha, 2008; Argo and Biernbaum, 1996). Early in our study, increasing peat in the media decreased leachate pH, a possible explanation for the improved uptake. Our results differ from Scagel (2003), who observed improved P uptake in coir, and hypothesized peat had a higher rate of P in a non-available form. In the Scagel study, peat and coir were < 20% of the total media composition, and it is possible the media in the current study with higher peat and coir content had different effects on P dynamics. In Chapter 2, coir treatments had a greater availability of $H_2PO_4^-$ than peat as measured by plant root simulator (PRS) probes, supporting the hypothesis of Scagel (2003). However, there were no differences in tissue P concentrations (Chapter 2), supporting the results of the current study's findings at the 10% perlite level, that peat and coir had no effect on whole plant P.

Despite differences in nutrient uptake between peat- and coir-grown plants, there were no effects on dry weight accumulation in the short duration of the current study. For longer-term production, growers should monitor plant nutrient status closely, as we did observe differences in blueberry nutrition between peat and coir.

Perlite effects on plant growth. Increasing the amount of perlite in the medium can negatively impact growth of young blueberry plants. Perlite had a negative impact on dry weight accumulation of several plant parts in 'Jewel' and non-whip leaves in 'Liberty'. This may have been due to the effects of perlite on media water relations. Blueberry is known to reduce transpiration with moderate water stress (Améglio et al., 2000). Increasing the proportion of larger particle sizes in media by using perlite or douglas fir bark can decrease easily available water (held between -1 kPa and -5 kPa) by increasing total porosity and decreasing water holding capacity (WHC) (Chapter 2; Fields et al., 2014). Decreased water holding capacity and easily available water can in turn reduce blueberry plant dry weight (Chapter 2). In the current study, the amount of perlite was not correlated with air filled porosity, water holding capacity or total porosity (Table 3.2). Due to a laboratory error, there were concerns about incorrect methodology in determining the air filled porosity, WHC, and total porosity of the samples, and therefore the porosity and WHC data from this study may not be reliable. However, the findings of others may help to explain our results. Bunt (1983) observed an increase in air filled porosity and a decrease in easily available water when increasing the proportion of perlite in peat. Evans and Gachukia (2007) observed a decrease in water WHC when perlite proportion was increased in the media. The negative effect of perlite on water holding capacity observed in the aforementioned studies provide evidence that the effect of perlite on growth was likely a result of water relations.

Perlite can also affect plant growth indirectly through its interaction with other media components. When no perlite was present, ‘Liberty’ dry weight and nutrient uptake efficiency for many nutrients increased with increasing peat, but any level of perlite negated this effect. It is possible that the addition of perlite mitigated the negative effect of coir on ‘Liberty’ growth. Chemically, pure coir had a high EC (3.39 dS m^{-1}) , and higher Na concentrations than peat. High initial concentrations of Na may have had a negative effect on plant growth early, as blueberry is very sensitive to the ion (Muralitharan et al., 1992). The addition of perlite reduced the proportion of coir in the medium, reducing EC as a result of dilution. Adding perlite to a medium may help mitigate negative effects of pure ingredients, allowing more flexibility in media selection and sourcing.

Cultivar differences. 'Liberty' and 'Jewel' responded differently to media composition. Perlite reduced growth of 'Jewel' plants but peat had no influence on growth. In contrast, 'Liberty' grew better in peat when no perlite was present but was not affected directly by the proportion of perlite in the medium. Since increasing perlite likely reduced WHC, 'Jewel' may be more sensitive to water limitations than 'Liberty'. This conflicts with the literature, which suggests SHB cultivars are more drought tolerant than NHB cultivars due to differences in their pedigree. 'Jewel' has *V. darrowii* Camp. (Lyrene, 1997) in its lineage, and the addition of these southeastern natives has been shown to improve drought tolerance (Erb et al., 1993). 'Liberty', on the other hand, has *V. corymbosum* parentage and does not contain any genetics from drought-tolerant southeastern native species. If inherent drought tolerance was responsible for a negative response to increasing perlite, we would expect 'Liberty' to have been more affected by high proportions of perlite in the media. Instead, 'Jewel' was more sensitive than 'Liberty'. It is possible that the adaptations of SHB to drought conditions, such as altered biomass partitioning (Erb et al., 1993), were not as effective in the restricted rooting environment of containers. Regardless of the causality of perlite's effect on 'Jewel', it is clear that NHB and SHB cultivars grew and behaved differently in substrate, and irrigation and nutrient management in substrate production may need to be optimized for different cultivars.

In summary, both cultivars grew well in media containing either peat or coir when some perlite was present. This result supports the conclusions from Chapter 2. Peat and coir affected nutrient uptake differently, and therefore, plant nutrition for long-term production should be monitored carefully and adjusted accordingly for the respective media components. Because blueberry production in containers can last for multiple years, long-term research on growth, nutrition, and stability of media components is needed.

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Table 3.1. Composition and estimated drainage of 16 media mixtures used to grow 'Jewel' and 'Liberty' blueberry plants in containers for 95 d.

Treatment Mixture[z]		Media Composition (% by volume)			Estimate of Drainage (%)[y]	
Perlite Level	S : C	Perlite	Sphagnum Peat Moss	Coconut Coir	'Jewel'	'Liberty'
P30	1S:0C	30	70	0	32	31
	2S:1C	30	47	23	32	22
	1S:2C	30	23	47	17	35
	0S:1C	30	0	70	21	34
P20	1S:0C	20	80	0	28	15
	2S:1C	20	53	27	26	26
	1S:2C	20	27	53	39	20
	0S:1C	20	0	80	43	28
P10	1S:0C	10	90	0	19	26
	2S:1C	10	60	30	21	34
	1S:2C	10	30	60	16	31
	0S:1C	10	0	90	44	46
P0	1S:0C	0	100	0	22	13
	2S:1C	0	67	33	23	21
	1S:2C	0	33	67	26	13
	0S:1C	0	0	100	33	46

[z]Four rates of perlite (P) were used (0%, 10%, 20%, 30% by volume), and the remaining volume was divided between sphagnum peat (S) and coir (C) at one of four ratios [S : C] (1:0, 2:1, 1:2, 0:1 by volume of peat and coir).
[y]Mean value of the drainage collection events 14, 26, 39, 54, 67, 82, and 95 d after planting.

Table 3.2. Physical characteristics of 16 media mixes used to grow 'Jewel' and 'Liberty' blueberry in containers for 95 d.

Media Composition (% by volume)			Bulk Density (g cc^{-3})	Air Filled Porosity^z	Water Holding Capacity^z	Total Porosity (%)	Particle Size (%)		
Perlite	Peat	Coir					4mm Sieve	2mm Sieve	0mm Sieve
30	70	0	0.102	8	54	62	14	33	53
30	47	23	0.079	10	66	76	49	20	31
30	23	47	0.103	12	68	80	24	28	48
30	0	70	0.135	32	60	92	24	22	54
20	80	0	0.082	11	62	73	31	23	46
20	53	27	0.080	12	63	76	27	30	43
20	27	53	0.086	35	68	103	15	25	60
20	0	80	0.091	24	63	87	7	17	76
10	90	0	0.112	5	63	68	29	13	58
10	60	30	0.083	13	63	76	9	18	73
10	30	60	0.094	13	67	80	5	20	75
10	0	90	0.070	33	53	86	3	17	81
0	100	0	0.070	4	49	53	6	7	87
0	67	33	0.079	14	66	81	5	7	89
0	33	67	0.092	18	65	83	5	6	89
0	0	100	0.077	22	63	85	7	6	87
Correlations with Media Components^y									
Perlite			*0.4736*	*ns*	*ns*	*ns*	*0.6699*	*0.8453*	*-0.8501*
Peat			*ns*	*-0.8175*	*ns*	*-0.8684*	*ns*	*ns*	*ns*

^{z}Air filled porosity and water holding capacity (% by volume)
^{y}Spearman's *r* for significant correlations between variables. Non-significant ($P > 0.05$) relationships between variables are denoted by '*ns*'.

Table 3.3: Chemical characteristics of 16 media mixes used to grow 'Jewel' and 'Liberty' blueberry plants in containers for 95 d.

Media Composition (% by volume)			C:N		EC[z]	N	P	K	Ca	Mg	Na	Fe	Mn	B	Cu
Perlite	Peat	Coir	Ratio	pH	(dS m^{-1})	(%)	(ppm)								
30	70	0	45	3.98	0.179	0.42	4	80	1046	537	176	88	19	0.28	0.16
30	47	23	47	4.41	0.624	0.44	13	660	878	426	263	74	15	0.42	0.38
30	23	47	51	4.87	1.170	0.38	22	1201	974	401	398	64	12	0.55	0.59
30	0	70	54	5.21	0.871	0.31	25	1425	595	273	424	24	10	0.59	0.53
20	80	0	49	4.00	0.288	0.58	2	139	1398	693	146	104	23	0.28	0.17
20	53	27	49	4.43	1.178	0.47	8	759	757	418	227	72	14	0.38	0.29
20	27	53	48	5.06	1.490	0.50	25	1469	727	367	395	59	13	0.59	0.47
20	0	80	61	5.66	1.972	0.37	31	1880	498	245	440	15	8	0.61	0.46
10	90	0	49	4.09	0.252	0.74	1	94	1117	586	89	114	24	0.26	0.20
10	60	30	52	4.69	0.896	0.69	12	1051	965	510	269	86	18	0.44	0.32
10	30	60	56	5.24	1.702	0.58	23	1564	677	358	358	59	13	0.61	0.44
10	0	90	61	5.75	2.799	0.54	32	1883	428	225	407	16	9	0.65	0.47
0	100	0	49	4.19	0.345	0.87	2	111	764	436	51	101	24	0.27	0.23
0	67	33	52	4.64	1.044	0.82	11	985	1152	480	236	87	18	0.42	0.41
0	33	67	58	5.09	1.596	0.72	21	1643	734	380	337	38	9	0.51	0.33
0	0	100	56	5.58	3.390	0.66	46	2126	619	294	520	21	11	0.93	0.60
Correlations with Media Component[y]															
Perlite			*-0.4408*	*ns*	*ns*	*-0.8798*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
Peat			*-0.6290*	*-0.8963*	*-0.7808*	*0.5767*	*-0.9651*	*-0.8756*	*0.8119*	*0.9185*	*-0.9778*	*0.9533*	*0.9294*	*-0.9346*	*-0.8903*

[z]Electrical conductivity

[y]Spearman's R for significant correlations between variables. No significant (P >0.05) relationships between variables denoted by '*ns*'.

Table 3.4: Effect of perlite (% by volume) in the media on dry weight (g dw) response of 'Jewel' blueberry plants grown in 16 different substrate mixtures for 95 d.

Tissue Type		Regression Coefficients[z]		*P*-value[y]
		β_0	β_1	
Total		43.85	-0.27[x]	*0.0147*
Roots		4.33	-	*ns*
Canes				
	All	10.85	-0.07	*0.0092*
	Non-whip	3.31	-0.03	*0.0446*
	Whip	7.54	-	*ns*
Leaves				
	All	28.68	-0.18	*0.0148*
	Non-whip	9.23	-	*ns*
	Whip	19.44	-0.13	*0.0432*

[z]Regression coefficients [intercept (β_0) and slope (β_1)] for relationships between the percentage of perlite in the media and total plant dry weight (total) and dry weight of specific plant structures. All includes both non-whip and whip portions of canes or leaves. The percentage of peat/coir in the media did not account for a significant ($P >$ 0.05) portion of the variation in response variable. Relationships are across all levels of peat/coir in media. Units are grams oven dry weight per plant.
[y]*P*-values for β_1 coefficients. No significant ($P > 0.05$) linear relationships between variables denoted by '*ns*'.

Table 3.5: Effect of peat (% v/v) in the media on dry weight (g dw) response of 'Liberty' blueberry plants grown in 16 different substrate mixtures for 95 d.

Tissue Type		Perlite Levels in Model[z]	Regression Coefficients[y]		*P*- value[x]
			β_0	β_1	
Total		0	28.28	0.26	*0.0003*
		10, 20, 30	31.92	-	*ns*
Roots		0	3.89	0.02	*0.0408*
		10	4.15	-	*ns*
		20	3.40	-	*ns*
		30	5.18	-0.03	*0.0289*
Canes					
	All	0	8.44	0.10	*<0.0001*
		10, 20, 30	10.35	-	*ns*
	Whip	0	5.38	0.08	*<0.0001*
		10, 20, 30	6.70	-	*ns*
Leaves					
	All	0	15.95	0.14	*0.0008*
		10, 20, 30	17.43	-	*ns*
	Whip	All	9.48	0.06	*0.0006*

[z]When a significant interaction existed between perlite and peat ($P < 0.05$), data was split by perlite level to investigate effect of perlite level on peat's effect.
[y]Regression coefficients [intercept (β_0) and slope (β_1)] for relationships between the percentage of peat in the media and total plant dry weight (total) and dry weight of specific plant structures. All includes both non-whip and whip portions of canes or leaves. Units are grams oven dry weight per plant
[x]*P*-values for β_1 coefficients. No significant (P >0.05) linear relationships between variables denoted by '*ns*.

Table 3.6: Effect of peat (% by volume) in the media on nutrient uptake efficiency of 'Jewel' and 'Liberty' blueberry plants grown in 16 different substrate mixtures for 95 d.

Cultivar	Nutrient	Perlite Levels in Model[z]	Regression Coefficients[y]		*P*- value[x]
			β_0	β_1	
'Jewel'	P	All	21.98	0.10	*<0.0001*
	K	All	7.39	0.12	*<0.0001*
	Mg	0	10.96	0.05	*0.0421*
		10, 20, 30	11.47	-	*ns*
	Zn	All	14.75	0.11	*<0.0001*
'Liberty'	N	0	35.21	0.33	*<0.0001*
		10, 20, 30	38.64	0.16	*0.0108*
	P	All	19.79	0.18	*<0.0001*
	K	All	5.46	0.14	*<0.0001*
	Ca	0	9.65	0.09	*0.0119*
		10, 20, 30	10.42	-	*ns*
	Mg	0	6.96	0.12	*<0.0001*
		10, 20, 30	9.99	-	*ns*
	S	All	4.22	0.02	*0.0016*
	B	All	29.87	0.14	*0.0019*
	Zn	0	8.12	0.25	*<0.0001*
		10, 20, 30	17.74	-	*ns*

[z]When a significant interaction existed between perlite and peat ($P < 0.05$), data was split by perlite level to investigate effect of perlite level on peat's effect.
[z]Regression coefficients [intercept (β_0) and slope (β_1)] for relationships between the percentage of peat in the media and nutrient uptake efficiency of various nutrients. Units are percent nutrient uptake efficiency. [nutrient uptake efficiency= (mg nutrient at harvest – mg nutrient at T0) / (mg nutrient added in fertilizer + mg nutrient available from media)]
[x]*P*-values for β_1 coefficients. No significant (P >0.05) linear relationships between variables denoted by '*ns*'.

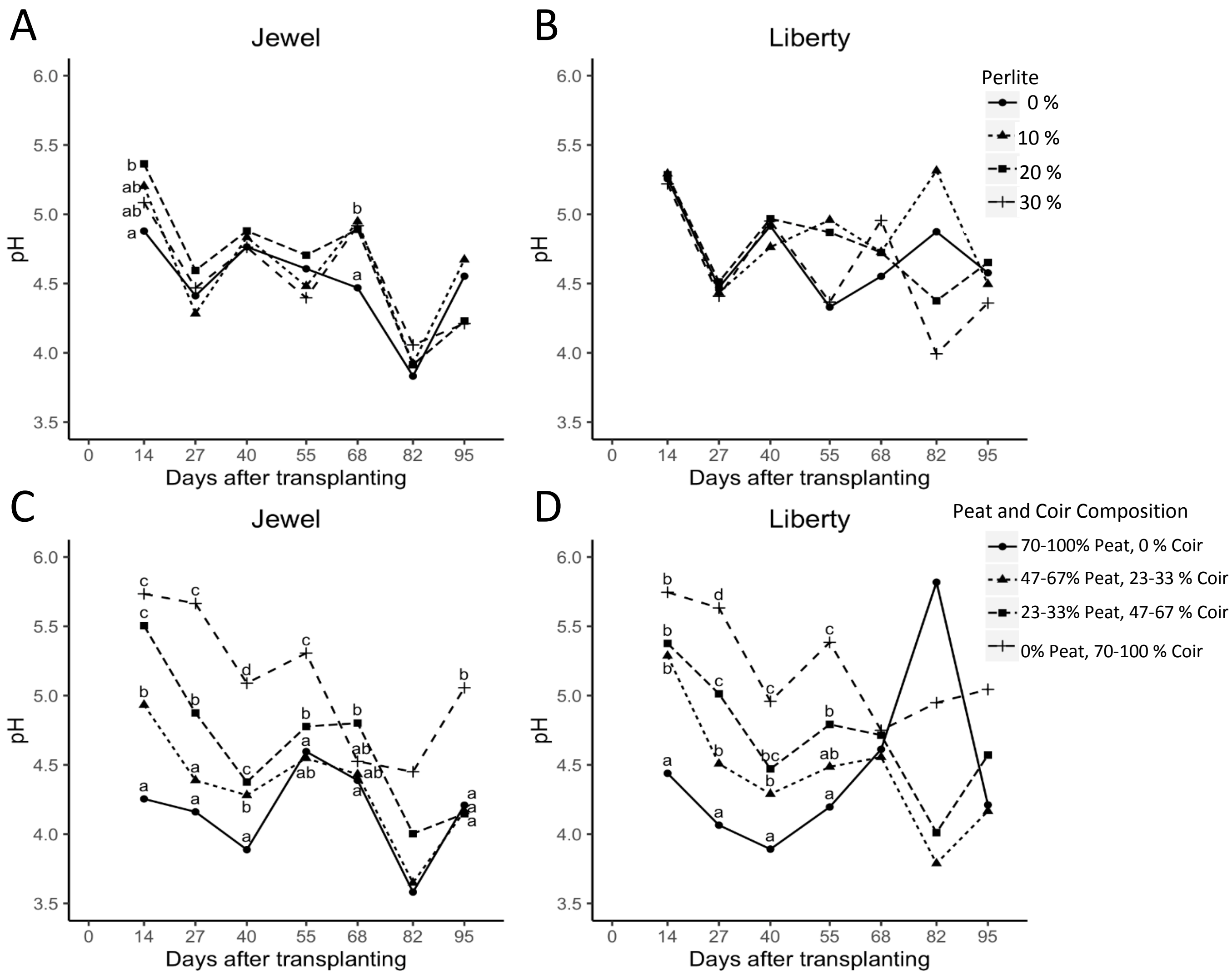
Table 3.7: Effect of peat (% v/v) in the media on whole plant concentration (mg/g dw) of nutrients in 'Jewel' and 'Liberty' blueberry plants grown in 16 different substrate mixtures for 95 d.

Cultivar	Nutrient	Perlite Levels in Model[z]	Regression Coefficients[y]		*P*- value[x]
			β_0	β_1	
'Jewel'	P	0	1.19	-	*ns*
		10	1.18	-	*ns*
		20	1.16	0.27	*0.0085*
		30	1.15	0.37	*0.0029*
	Mg	All	1.42	0.27	*<0.0001*
'Liberty'	N	0	12.36	-	*ns*
		10	11.92	-	*ns*
		20	12.72	-	*ns*
		30	11.46	3.91	*0.0047*
	P	0	1.44	-	*ns*
		10	1.33	-	*ns*
		20	1.47	-	*ns*
		30	1.37	0.28	*0.0488*
	K	All	7.06	-0.82	*0.0012*
	B	All	0.041	-0.007	*0.0111*

[z]When a significant interaction existed between perlite and peat ($P < 0.05$), data was split by perlite level to investigate effect of perlite level on peat's effect.
[z]Regression coefficients [intercept (β_0) and slope (β_1)] for relationships between the percentage of peat in the media and whole plant concentration (mg/g dry weight).
[x]*P*-values for β_1 coefficients. No significant ($P > 0.05$) relationships between variables denoted by '*ns*'.

Fig. 3.1. pH of leachate from different media used to growth Jewel' and 'Liberty' blueberry plants for 95 d. (A, B) Leachate pH media containing 0, 10, 20, and 30 % (by volume)and (C) four peat and coir ratios (listed as % of ingredients). Means (n=5) denoted by the same lower case letter within a date or without a letter listed are not significantly different based on 95 % confidence intervals from Tukey's Honestly Significant Difference test.

Fig. 3.1 (continued)



Chapter 4: Effect of different sources and rates of potassium fertilizer and their interaction with nitrogen source on growth, yield, and mineral nutrition of northern highbush blueberry in soilless substrate.

Abstract

A study was conducted to investigate the effects of varying rates and sources of K fertilizer and their interaction with two N fertilizer sources on the growth, yield, and mineral nutrition of northern highbush blueberry (*Vaccinium corymbosum* L. 'Liberty') grown in a soilless substrate. Plants were grown in 25-L containers filled with a mix of 3 sphagnum peat : 1 coir : 1 perlite (by volume). Plants were fertigated at every irrigation with a solution that contained 75 ppm N from either ammonium sulfate or urea, 0 to 200 ppm K from one of three K sources, and the remaining mineral nutrients required for blueberry production. The K sources included potassium sulfate (KS), potassium thiosulfate (KTS), and potassium acetate (KA). All three K sources were applied at rates of 50 ppm and 150 ppm K in urea, KA was applied at 50 ppm and 150 ppm K in ammonium sulfate while KS and KTS were applied at 50, 100, 150, and 200 ppm K in ammonium sulfate. There was also a no K control for both N sources. When the plants were fertilized with ammonium sulfate, shoot dry weight increased with a moderate rate (50 ppm K) of KS or KA (396 and 370 g dry wt. per plant, respectively) versus the 0 ppm K control (269 g dry wt. per plant), but there was no effect of K fertilization on fruit yield or quality. When plants were fertilized with urea, K fertilizer had no influence on shoot growth, yield, or fruit firmness. Increasing concentration of K in both N sources increased leaf K concentration and decreased leaf Ca and Mg concentrations. Increasing fertilizer K also increased fruit K concentration with urea but not with ammonium sulfate. Leaf and fruit S concentrations were enhanced by the addition of KTS (0.3% and 0.10%, respectively) but not KS (0.2% and 0.09%, respectively). Both KTS and KS reduced leachate pH (4.58 and 5.01, respectively) relative to no K (5.44), whereas KA had no effect on leachate pH. Fertilizing substrate-grown blueberry with K can have positive benefits on growth and nutrition during the first growing season. Benefits of K fertilizer will depend on the source and rate of K used and whether plants are grown using urea or ammonium sulfate as the N source.

Introduction

Blueberry has fairly unique growing requirements relative to most fruit and vegetable crops. The plants are well-adapted to acidic soil conditions (pH 4.2–5.5) and acquire primarily the NH_4 form of N over NO_3-N (Merhaut and Darnell, 1995; Retamales and Hancock, 2012). They also tolerate relatively low levels of P, K, Ca, and Mg in the soil and high concentrations of plant-available metals such as Mn and Al (Korcak, 1988). Blueberry is readily susceptible to drought and salinity (Bryla and Strik, 2007; Machado et al., 2014). Usually, blueberry plants are fertilized with ammonium sulfate or urea under field conditions and are fertigated with other nutrients, as needed, based on leaf tissue analysis (Bryla and Strik, 2015). However, there is little information available on the nutrient requirements of blueberry in soilless culture (Voogt et al., 2014). Soilless substrates are often deficient in many nutrients and, therefore, usually require a constant supply of fertilizers for healthy plant production. Most substrate systems also have restricted rooting volumes and plants are irrigated by drip or flooding and fertigated with liquid fertilizers (Raviv and Lieth, 2008).

Few studies have examined the use of K fertilizers in blueberry (Eck, 1983; Hancock and Nelson, 1988; Percival and Sanderson, 2004). The literature on K fertilization in substrate blueberry is even sparser and the only mention of K fertility requirements comes from Voogt et al. (2014), who observed K deficiency and suggested that application of K at 1.3 $mmol \cdot L^{-1}$ in nutrient solution was too low. Fertilizing with certain K sources can also alter pH. For example, application of potassium thiosulfate (KTS) may be particularly useful in high pH soils and substrates because thiosulfate is readily oxidized by *Thiobacillus* and other soil bacteria to produce sulfuric acid (Havlin et al., 2014). Application of potassium acetate (KA), on the other hand, may increase pH through the decomposition of the acetate anion (Inoue et al., 2001; Yan et al., 1996), while application of potassium sulfate (KS) usually has no effect on pH (Havlin et al., 2014). Use of such fertilizers could be helpful for managing pH during substrate culture of blueberry.

Nitrogen fertilizer source can also impact pH management, as ammonium sulfate is roughly twice as acidifying as urea (Hart et al., 2013). In a field study on northern highbush blueberry (*V. corymbosum* L.), fertigation with ammonium sulfate resulted in more growth and fruit production than fertigation with urea (Vargas and Bryla, 2015). This was attributed to lower pH and higher concentration of NH_4-N in soil solution with ammonium sulfate (Machado et al., 2014). Ammonium and K^+ ions are of a similar ionic radius and charge and, therefore, interact through competition in soil exchange surface adsorption and root uptake (Marschner, 2011). Because of the preference of blueberry for NH_4-N and potential for competition with K^+, development of K fertility guidelines for substrate production should also include different sources of N fertilizer.

The objective of the present study was to determine whether K fertilizer application has any benefits to northern highbush blueberry grown in soilless media, and if so, whether the responses to K are affected by the source of N fertilizer applied. Since nutrients are often limited in soilless media, it was reasonable to expect that K fertilizer would increase plant growth and early fruit production. We also expected that growth and yield would be greater with KS or KTS than with KA, particularly when less acidifying N fertilizers such as urea were used as the primary N source.

Materials and Methods

Plant culture and growing environment. The study was conducted in a high tunnel using potted plants of ‘Liberty’ and ‘Misty’, northern and southern highbush blueberry, respectively. The tunnel was located at the USDA-ARS National Clonal Germplasm Repository in Corvallis, OR (lat. 44°33'29" N, long. 123°13'48" W) and was constructed with a gravel floor and a clear-plastic poly covering. The plants were obtained in 1-L pots from a nursery (Fall Creek Farm and Nursery, Lowell, OR), and were transplanted on 9 July 2015 to round 25-L black polyethylene pots (Plantlogic LLC, Smyrna, GA) filled with a mix of 3 sphagnum peat : 1 coir : 1 perlite (by volume) (Pro-Gro Mixes, Sherwood, OR). Legs molded on the bottom of the pots lifted the bottom drain holes ≈30 mm off the ground to improve drainage and air diffusion into the lower layers of the potting medium. The pots were centered at least a 0.5m apart, with a path down the middle of the tunnel, and irrigation was applied using two to four pressure-compensating drip emitters (Toro, El Cajon, CA) in order to supply $10\text{-L}\cdot\text{h}^{-1}$ to each pot while allowing for different rates of K fertilizer. All emitters were placed at the base of the crown of the plant.

Air temperature and relative humidity were monitored inside the tunnel using a capacitive humidity sensor with an integrated thermocouple (model HUMITTER 50YX; Vaisala, Inc., Woburn, MA). Photosynthetically active radiation (PAR) was also measured using a quantum sensor (model LI-190R; LI-COR, Inc., Lincoln, NE). The measurements were taken near the top of the canopy of the plants and were recorded every 15 min using a data logger (model LI-1400; LI-COR, Inc.). Height of sensors was readjusted for plant growth, as needed. During the growing season (July–Oct. 2015 and Apr.-Aug. 2016), daily temperatures averaged a maximum of 32.0 °C and a minimum of 11.8 °C, relative humidity averaged 60% ± 11% SD over a 24 h period, and daily light integrals averaged 14.9 ± 6.6 SD $mol \cdot m^{-2} \cdot d^{-1}$. The sides of the tunnel were opened to a height of 1.2 m from 9 July- 5 Nov. 2015 and 1 Apr.- 11 Aug. and closed 5 Nov. 2015 to 1 Apr. 2016. When the tunnel sides were down (Nov. 2015- Apr. 2016), the temperature of the tunnel was maintained above 1 °C using a thermostatically controlled heater. During this period, daily temperatures averaged a maximum of 18.4 °C and a minimum of 5.8 °C, relative humidity averaged 81% ± 8.4% SD over a 24 h period, and daily light integrals averaged 5.3 ± 4.4 SD $mol \cdot m^{-2} \cdot d^{-1}$.

Flower buds were removed from the plants by pruning during the first year after transplanting to encourage vegetative growth and root development. The first crop was produced the following summer, without pruning the preceding winter. A honey bee (*Apis mellifera* L.) hive was placed next to the tunnel during flowering in March. No pesticides were applied to the plants at any time during the study.

Fertilizer treatments. The plants were fertigated using 18 different fertilizer treatments (Table 4.1). Treatments consisted of a combination of two powdered sources of N fertilizer dissolved in deionized water, ammonium sulfate (21N–0P–0K–24S; > 99% pure; Fischer Scientific, Pittsburgh, PA) and urea (46N–0P–0K; J.R. Simplot Company, Boise, ID), and varying sources and rates of K fertilizer, including two no K treatments that were fertilized with either urea or NH_4-N. Both N sources were applied to all plants at a rate of 75 ppm NH_4-N. The K fertilizers included potassium sulfate (KS) (0N–0P–52K–18S; dissolved in deionized water at a concentration of 55 $g \cdot L^{-1}$), potassium thiosulfate (KTS) (0N–0P–52K–17S; pH 7.4–8.0; Tessenderlo-Kerley, Inc., Phoenix, AZ), and potassium acetate (KA) (0N–0P–48K; dissolved in deionized water at a concentration of 61 $g \cdot L^{-1}$), each of which was applied with ammonium sulfate or urea at a rate of 50 or 150 ppm K (two N sources, three K sources, and two K rates). Potassium sulfate and KTS were also applied at a rate of 100 or 200 ppm K (with ammonium sulfate only) to develop response curves to the fertilizers (i.e., 50–200 ppm K). The treatments were arranged in a randomized complete block design with five replicates (plants).

The fertilizer treatments were initially applied by hand (27 July and 4 Aug. 2015) with each plant receiving 1 L of complete fertilizer solution blended with the appropriate N source, K source, and K rate on each date. However, due to a calculation error, KTS plants received a concentration 10x greater than intended on 27 July. As a result, plants were leached with daily application of 1 L water from 31 July to 4 Aug. Starting 11 Aug. 2015, fertilizers were injected into the drip system using water-driven proportional injector pumps (model D25RE2; Dosatron International, Inc., Clearwater, FL). Total flow rate to each pot was 10 $L \cdot h^{-1}$ from a range of 2-4 emitters of varying flow rates depending upon the treatment K rate. Prior to injection of fertilizer, all irrigation water was acidified with 2 mM phosphoric acid to reduce pH of the water to 5.8 and provide H_2PO_4-P. One 2 $L \cdot h^{-1}$ emitter in each pot supplied the N treatment mixed with the other nutrients, including 2 mM Ca from chelated Ca product (ProNatural Calcium; Wilbur Ellis, Aurora, CO), 0.74 mM, Mg from $MgSO_4*7H_2O$, 25 μM Fe from Fe-DTPA, 25 μM B from H_3BO_3, 3 μM Mn from $MnCl_2*4H_2O$, and 4 μM Zn from $ZnSO_4*7H_2O$. The remaining 8 $L \cdot h^{-1}$ of fertigation solution delivered to each pot was supplied via 1-3 emitters of varying flow rates to apply the appropriate rate of K fertilizer.

Electrical conductivity (EC) of all solution applied was measured at the drip emitters of each treatment (one replicate per treatment) using a combination pH/ion/conductivity meter (model SevenGo Duo pro with an InLab 738 ISM conductivity probe for EC; Mettler-Toledo, Columbus, OH). Electrical conductivity values of fertilizer solutions ranged from 0.81 to 1.98 $dS \cdot m^{-1}$ (Table 4.1). Plants were fertigated two to seven times per week, depending on plant water demand (determined through drainage collection), until 8 Oct. 2015, after which N was reduced by one-third for 2 weeks to induce dormancy but all other nutrient concentrations remained the same.

Every 1–2 weeks, irrigation drainage was collected from 6-8 plants with the largest canopy (randomly selected at each collection event) to assess drainage, and fertigation volume was adjusted, if necessary, to achieve a target drainage of 25%. During the winter, the plants were only irrigated with water, as needed, to prevent the media from drying out. Fertigation was resumed on 17 Mar. 2016, and the volume was adjusted according to plant needs and to achieve 25% drainage.

Data collection. Leachate was collected from three pots per treatment, each week from 8 Oct. 2015 to 12 Nov. 2015 and every other week from 17 Mar. to 22 July 2016, using a modified pour-through method (Wright, 1986). To collect the samples, the pots were first fully irrigated, allowed to drain freely for an hour, and placed on top of saucers (Premier Tech Home and Garden, Ontario, Canada) designed to collect the drainage. Then, an additional 110 mL of water was applied to each pot, and 50 mL of leachate was collected from the saucers. The leachate was analyzed for pH and EC using a combination pH/ion/conductivity meter as described above.

Ripe fruit were harvested and weighed, every 2 weeks from 6 June and 2 Aug. 2016 and stored in a cooler at 3 °C. Within 24 h of harvest, 25 berries were randomly sampled from each replicate and measured for firmness and diameter using a fruit firmness tester (model FirmTech 2; BioWorks, Inc., Wamego, KS). Each berry was compressed equatorially, with the pedicel end facing towards the center of the turntable on the instrument. Deflection threshold was set at a minimum of 50 g, and compression force was set to a maximum of 300 g. Once firmness was measured, the berries were combined from each replicate and weighed to determine average berry weight. The samples were then oven-dried at 60 °C (until no further change in mass was observed over 24-h period) and weighed again to estimate the total dry weight of the fruit. Finally, the dried samples from each replicate were ground with a mortar and pestle and analyzed for N and S using a combustion analyzer and for P, K, Ca, Mg, B, Cu, Fe, Mn, Zn, and Na using an ICP spectrophotometer (Gavlak et al., 2003)

Leaves were sampled for nutrient analysis on 9 Aug. 2016, following procedures outlined by Hart et al. (2006). Leaf samples were oven-dried at 60 °C, ground with a wiley mill to pass through a 1-mm screen, and analyzed for N and other nutrients as described above. Once the leaves were collected, the remainder of the shoots on each plant were harvested destructively on 9–11 Aug. 2016. Shoots were cut-off at the crown, oven-dried at 60 °C, and weighed.

Statistical analysis. Data collected for ‘Misty’ plants were excluded from analysis. More than half of the plants had < 70 g dry weight of aboveground biomass by the end of the experiment, and more than half of those weighed < 10 g. Above ground biomass of the remaining plants ranged from 142 to 420 g dry weight (data not shown). Differences in biomass were unrelated to the source or rate of fertilizer applied, and there were no obvious pest or disease problems on the plants. Figure 4.1 illustrates the difference in root growth between the cultivars. Because the cause of poor plant growth was unknown, ‘Misty’ was removed from any further analysis in the study.

All data for ‘Liberty’ were analyzed using the Statistica analytical software system (Version 13; Dell, Inc., Tulsa, OK). Leachate pH and EC were averaged over time for each year of the study (2015, 2016). Growth and yield, leaf and fruit nutrient, and leachate pH and EC values were analyzed using two different mixed models. To evaluate whether K fertilizer application altered responses of plants grown with urea or ammonium sulfate, data were analyzed using a 2 × 7 factorial design [2 N sources × 7 K sources and rates (0 ppm control and 50 and 150 ppm K of KS, KTS, and KA)], and means were compared using specific orthogonal contrasts at $P \leq 0.05$. Categorical regression was used to evaluate how rate of KTS and KS application influenced responses of plants grown with ammonium sulfate. Polynomial contrasts were used to evaluate the shape of the response to increasing K from 0 to 200 ppm for KS and KTS.

Results and Discussion

Fertilizing with K improved shoot dry weight of substrate grown ‘Liberty’ blueberry when grown in ammonium sulfate with either KS or KA at 50 ppm (Fig. 4.2). Potassium fertilization had no effect on fruit yield (fresh $\overline{X}$ = 0.51 kg/plant and dried $\overline{X}$ = 74 g/plant), berry number ($\overline{X}$ = 261 berries/plant), berry weight (fresh $\overline{X}$ = 1.97 g and dried $\overline{X}$ = 0.29 g), berry diameter ($\overline{X}$ = 15.2 mm), or berry firmness ($\overline{X}$ = 218 $g \cdot mm^{-1}$). The effect of K fertilizer on shoot dry weight depended upon the N source used (N × K treatment interaction, $P = 0.009$). When plants were fertilized with ammonium sulfate, application of KS or KA at 50 ppm K improved shoot dry weight compared to the no K control, the 50 ppm KTS treatment, and all three K sources at 150 ppm (Fig. 4.2). Additionally, plants fertilized with KS and KA at 50 ppm K had greater shoot dry weight with ammonium sulfate than with urea. When the concentration of KTS or KS was increased from 0 to 200 ppm K with ammonium sulfate, the effect of K concentration on shoot dry weight varied with K source (K source × K rate interaction, $P = 0.0426$). Shoot dry weight had a quadratic relationship with concentration of KS ($P = 0.0078$) but no significant relationship with KTS (Fig. 4.3). These results indicate that fertilizing with K can improve shoot growth of young substrate-grown blueberry using ammonium sulfate if the correct K sources are used at a rate of less than 100 ppm K.

Potassium fertilizer can be beneficial to growth of various crops in soilless media, depending on the sources of K and N fertilizer used. In substrate production, yield and quality of peppers (*Capsicum annum* L.) increased with more K fertilizer applied (Baghour et al., 2001; Johnson and Decoteau, 1996). It is unknown if the effects of K on shoot growth in the current study would have resulted in greater yield the following year. Usually, yield increases with plant size in northern highbush blueberry, at least until full production is reached. However, the effect of K fertilization on blueberry fruit production is unclear in the literature. Eck (1983) reported that K fertilizer increased yield in 3 out of 6 years in mature ‘Bluecrop’ blueberry when ammonium nitrate was the N source. In lowbush blueberry (*V. angustifolium* Ait.), Percival and Sanderson (2004) observed a positive effect of K fertilization on fruit production in 1 of 2 fields when urea was the N source. In contrast, K fertilization had no effect on yield over 3 years while using urea (Hancock and Nelson, 1988), similar to the results of the current study.

In our study, the absence of a yield effect accompanying the influence of K on shoot growth may be explained in part by the short duration of treatment application prior to floral bud initiation. In northern highbush blueberry, flower bud initiation occurs under short-day photoperiods when shoot growth has stopped and begins in early August (Gough et al., 1978). Because fertilization began 27 July, there was little time for adequate shoot growth under the imposed fertilizer treatments prior to onset of the short-day photoperiod. Greater shoot growth was observed during the second growing season (Patrick Kingston, personal observation), and because northern highbush blueberry requires floral bud initiation and dormancy prior to fruiting, the full effects of increased shoot growth on yield potential were not realized in this study. Given the conflicting results in the literature and relatively few studies on K fertilization in blueberry, more research is needed, particularly in substrate, to determine the long-term effects of altering K fertility.

Potassium source had no effect on shoot dry weight with urea (Fig. 4.2), but fresh fruit production (yield and berry number) was reduced with urea compared to ammonium sulfate (Table 4.2). Additionally, the 50 ppm rate of KS and KA led to larger plants with ammonium sulfate than urea. It is unclear why use of urea reduced fruit yield. Urea-N leaches readily compared to ammonium sulfate-N, is less acidifying and has less NH_4-N available in blueberry fields (Machado et al., 2014), and can cause leaves to have lower N concentration (Vargas and Bryla, 2015). However, these factors would likely have affected shoot growth, or have been reflected in leaf tissue N (Table 4.6) but were not. It remains unclear why urea-grown plants produced less fruit than ammonium-sulfate grown plants in substrate, because these fertilizers are both effectively used for field production of NHB blueberry (Hart et al., 2006). Further research on urea's suitability in substrate production is warranted, as urea is an inexpensive source of N and could be useful to reduce potential over-acidification with ammonium sulfate in long-term substrate production.

Potassium source has been shown to influence yield and quality of tomatoes, but differences between K sources were attributed to the effects of the anions accompanying the K^+, as the Cl^- anion was preferable to NO_3^- (Chapagain et al., 2003; Chapagain and Wiesman, 2004). In the current study, K sources were selected for their potential to influence substrate pH, resulting from decomposition of the accompanying anions. Because blueberry grows best in low pH soil (4.5-5.5), it was hypothesized that KTS and KS would improve growth and yield relative to KA, due to their acidifying and neutral effects on soil pH, respectively. However, the results reject this hypothesis, as the effect of K source on leachate pH did not match the effect on shoot growth discussed above.

There are currently no guidelines for leachate pH in substrate production. However, use of published soil guidelines (e.g. 4.5-5.5; Hart et al., 2006) can provide a good starting point. All ammonium sulfate treatments had a mean leachate pH value within this range in 2015 and 2016 ($\overline{X}$ = 5.43 and $\overline{X}$ = 4.67, respectively) while the mean leachate pH of urea treatments was above the range in both 2015 and 2016 ($\overline{X}$ = 5.99 and $\overline{X}$ = 5.52, respectively; Appendix 1). Following the soil guidelines helps to ensure adequate quantities of pH-dependent nutrients, such as Mn, are available for uptake. Because urea treatments had a pH outside of this range, there may have been some negative effects on tissue nutrient concentrations.

Potassium thiosulfate at both 50 ppm and 150 ppm reduced leachate pH relative to the control but was no different than KS (Table 4.3). Increasing the concentration of K from 0 to 200 ppm in ammonium sulfate reduced leachate pH linearly with KTS in 2015 and both KTS and KS in 2016 (Table 4.4), and the overall mean leachate pH of both years was lower in KTS than KS ($\overline{X}$ = 4.58 and $\overline{X}$ = 5.01, respectively; $P \leq 0.01$; Appendix 2). The application of KTS reduced leachate pH as expected, but the reduction in leachate pH of KS relative to the control (Table 4.3) was surprising. It is unclear how KS acidified the leachate. Because SO_4^{-2} is fully oxidized, it does not undergo further biological decomposition to release H^+ ions, as does thiosulfate ($S_2O_3^{-2}$). Therefore, another mechanism was likely responsible for the observed decrease in pH with KS fertilization. The acidifying effects of both KTS and KS suggest they could be useful in media with inherently higher pH or where acid injection is unavailable. However, in the higher pH substrate of urea treatments there were no effects of K source on leachate pH (Table 4.3). It is unclear why urea inhibited any K source effect on leachate pH, as thiosulfate oxidation is a biological process (Germida et al., 1992) and appeared to have progressed in the ammonium sulfate fertilized treatments.

Potassium acetate did not raise leachate pH relative to either the control or KS with ammonium sulfate and had no effect on leachate pH with urea (Table 4.3). There is debate in the literature regarding the efficacy of acetate anions to raise soil pH (Inoue et al., 2001; Yan et al., 1996) and the current study found no effect of acetate on leachate pH.

Leachate EC is used to monitor salt content of substrate containers, and blueberry is considered sensitive to a soil solution EC over 2 $dS \cdot m^{-1}$ (Patten et al., 1988). As expected, ammonium sulfate treatments had higher leachate EC than urea ($\overline{X}$ = 2.15 and 1.76 $dS \cdot m^{-1}$, respectively; $P \leq 0.001$; Appendix 1). Leachate EC was greatest in KTS, and there were positive linear relationships between K concentration and leachate EC in treatments fertilized with KS and KTS and ammonium sulfate. Additionally, mean leachate EC was greater in KTS than in KS (1.80 and 2.22 $dS \cdot m^{-1}$, respectively; $P \leq 0.05$ Appendix 2) across all K rates with ammonium sulfate. Because high rates of K (> 100 ppm) had no positive effect on shoot growth and increased leachate EC, fertilizing with high K rates should be carefully considered in substrate-grown blueberry, especially in combination with ammonium sulfate to prevent potential salt-induced stress/damage.

Fertilizing with K altered leaf K, Ca, Mg, and S concentrations (Table 4.5; Fig. 4.4) relative to the no K control. Leaf N was affected by K source but was not greater than in the control (Table 4.5). Plants grown with urea had greater leaf B and Na concentrations than with ammonium sulfate (Appendix 3). There was no effect of K or N fertilization treatment on leaf P, Fe, Mn, Cu, or Zn (data not shown). Fertilizing with K increased fruit concentration of K, but only with urea (Table 4.3), while fertilizing with KTS with ammonium sulfate increased fruit S concentration (Fig. 4.4). Potassium fertilization also reduced fruit Mn concentration with ammonium sulfate, and reduced fruit Na concentration with both N sources (Table 4.5). Fruit from plants grown with ammonium sulfate had greater concentrations of Mn than urea ($\overline{X}$ = 56 ppm and $\overline{X}$ = 47 ppm, respectively; $P \leq 0.05$) and greater concentrations of Zn than urea ($\overline{X}$ = 2.0 ppm and $\overline{X}$ = 1.7 ppm, respectively; $P \leq 0.05$; Appendix 3). There was no effect of N or K fertilization treatment on fruit concentration of N, P, Ca, Mg, Fe, B, or Cu (data not shown).

Rate of potassium uptake in substrate is largely a result of root zone concentration (Silber et al., 2003). In Chapters 2 and 3, elevated K concentration in coir increased uptake in ‘Liberty’ and two southern highbush blueberry cultivars (interspecific hybrids of *V. corymbosum* L. and *V. darrowii* Camp.) ‘Snowchaser’ and ‘Jewel’. However, fertilization with high rates of K can have negative effects on the uptake of other cations (Ca^{2+}, Mg^{2+}; Marschner, 2011) and, indeed, reduced leaf Ca and Mg when K fertilizer was supplied in conjunction with ammonium sulfate in the present study (Table 4.5). While leaf Ca and Mg never dropped below the recommended sufficiency ranges for soil-grown blueberry (Table 4.5; Hart et al., 2006), the negative linear effects of increasing K fertilizer rate on nutrient accumulation in leaves (Table 4.6) warrant careful management of Ca and Mg nutrition when K fertilizer is used in substrate blueberry to prevent cation deficiencies.

Ammonium has been shown to inhibit K^+ uptake due to their similar ionic charge and size, but K^+ rarely inhibits NH_4-N uptake (Rufty et al., 1982). The leaf N data from the current study are in agreement with the latter statement, as K rate had no effect on leaf N concentration (Table 4.5). Because ammonium sulfate has been shown to have a higher concentration of NH_4^+ in soil solution than urea (Machado et al., 2014), it was hypothesized that N source would influence N form and compete with K^+ to inhibit K uptake in the present study. However, leaf K from plants grown with ammonium sulfate was not different than plants grown with urea ($\bar{X}$ = 0.52% and 0.56%, respectively). There is some evidence to suggest fruit K uptake was limited with ammonium sulfate, as high rates of KA and KS had higher fruit K in urea (Table 4.5). However, because ammonium sulfate had greater fruit yield than urea, the lower fruit K with ammonium sulfate in these treatments could be a result of dilution, rather than inhibition of uptake.

Fertilizing with 150 ppm KTS and ammonium sulfate increased the S concentration in leaves and berries (Fig. 4.4) and increasing concentrations of KTS from (0–200 ppm) had a positive linear effect on leaf and berry S (Fig. 4.5). While SO_4-S is the predominant form of S taken up by roots, uptake of thiosulfate ($S_2O_3^{-2}$) can also occur if provided by fertilizer (Havlin et al., 2014). In fact, thiosulfate requires less energy to reduce the S atom for assimilation into amino acids (Havlin et al., 2014) a potential benefit for plant growth. Surprisingly, KS had no effect on tissue S concentrations, suggesting either the uptake pathway was already saturated, or the SO_4^{-2} ions were readily leached out of the substrate. However, due to the constant fertigation with KS, it is unlikely the extra SO_4-S was all leached out, suggesting that the SO_4-S uptake pathway was saturated. Thiosulfate can act as a slow-release form of S, as its microbial decomposition can tie up some of the sulfur, reducing its immediate availability (Janzen and Bettany, 1986). While blueberry is rarely deficient in S (Hart et al., 2006), the enhanced uptake from thiosulfate could be useful for other crops where S deficiency is more common, such as corn (Camberato et al., 2012).

Conclusions

Fertilization with K increased early shoot growth in substrate-grown ‘Liberty’ blueberry plants when ammonium sulfate was used as the N source. Only KS and KA increased shoot growth, and the optimal K rate for shoot growth was < 100 ppm. Blueberry growth responded differently to the K sources with ammonium sulfate and urea, likely a result of different substrate pH values. Plants grown with ammonium sulfate maintained leachate pH within the recommended range for soil pH (4.5-5.5), while those grown with urea as the N source did not.

Potassium acetate had no effect on leachate pH, while both KS and KTS reduced pH. There appears to be an additional method of acidification, as KS was not expected to lower substrate pH. Additionally, no K source altered leachate pH in urea solutions, and it is unclear why the acidifying fertilizer KTS did not reduce pH.

Increasing the concentration of K fertilizer increased leaf K concentration regardless of the K or N source used. Additionally, leaf Ca and Mg concentrations decreased with increasing K fertilization, suggesting ion competition. Leaf cation concentrations should be carefully monitored to prevent potential deficiencies with high rates of K fertilizer. Leaf and fruit S concentration was enhanced by KTS but not KS, suggesting that tissue S can be further increased through the uptake of thiosulfate. More research to develop nutrient solution standards for substrate blueberry is needed, but the current study provides foundational information regarding K fertilization and rate in blueberry, as well as novel findings regarding S uptake.

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Table 4.1. Electrical conductivity (EC) of fertigation solutions with different combinations of N and K fertilizers.[z]

K source and supply	EC of fertigation solution ($dS \cdot m^{-1}$)[y]	
	Ammonium sulfate[x]	Urea[x]
None	1.41	0.81
Potassium sulfate		
50 ppm K	1.54	0.96
100 ppm K	1.69	–
150 ppm K	1.81	1.24
200 ppm K	1.98	–
Potassium thiosulfate		
50 ppm K	1.54	0.92
100 ppm K	1.64	–
150 ppm K	1.76	1.21
200 ppm K	1.92	–
Potassium acetate		
50 ppm K	1.51	0.94
150 ppm K	1.75	1.16

[z]Other nutrients were also added to each solution, including 62 ppm P from H_3PO_4, 80 ppm Ca from ProNatural Calcium Plus (Wilbur Ellis Aurora, CO), 20 ppm Mg from $MgSO_4*7H_2O$, 0.3 ppm B from H_3BO_3, 0.7 ppm Fe from Fe-DTPA, 0.2 ppm Mn from $MnCl_2*4H_2O$, and 0.25 ppm Zn from $ZnSO_4*7H_2O$.
[y]Collected at the drip emitter.
[x]Supplied at 75 ppm

Table 4.2. Effect of N source on fruit production of 'Liberty' northern highbush blueberry grown in soilless media.[z]

N source	Yield (kg/plant)	No. berries/plant
Ammonium sulfate	0.56	289
Urea	0.46	232
Difference	0.10**	57***

[z]Data are pooled across three K sources (potassium sulfate, potassium thiosulfate, and potassium acetate) and rate (0, 50, and 150 ppm K). **,***Significant at $P \leq 0.01$ or 0.001, respectively.

Table 4.3. Effects of N source and K source and supply on pH and electrical conductivity (EC) of pour-through leachate collected from pots of ‘Liberty’ northern highbush blueberry grown in soilless media.[z]

K source	K supply (ppm)	Leachate pH			Leachate EC ($dS\cdot m^{-1}$)
		Ammonium sulfate	Urea	Difference	
None	0	5.44 a[y]	5.48 a	-0.04[NS]	1.65 c
Potassium sulfate	50	5.06 abc	5.94 a	-0.88*	1.82 c
	150	4.89 bc	5.72 a	-0.83*	2.16 ab
Potassium thiosulfate	50	4.87 bc	5.78 a	-0.91*	1.98 bc
	150	4.54 c	5.53 a	-1.00*	2.47 a
Potassium acetate	50	5.23 ab	5.76 a	-0.54*	1.70 c
	150	5.32 ab	6.06 a	-0.74*	1.92 c

[z]Samples were collected weekly or bi-weekly during the first two growing seasons (2015 and 2016). Data are averaged within a growing season and pooled across years. Leachate EC is also pooled across two N sources (ammonium sulfate and urea).
[y]Means followed by the same letter within a column are not significant different at P = 0.05 (Tukey’s test). [NS,*]Nonsignificant or significant at $P \leq 0.05$, respectively.

Table 4.4. Effect of increasing K supply from potassium sulfate (KS) or potassium thiosulfate (KTS) on pH and electrical conductivity (EC) of pour-through leachate collected from pots of 'Liberty' northern highbush blueberry grown in soilless media.[z]

K supply (ppm)	Leachate pH			Leachate EC ($dS \cdot m^{-1}$)		
	2015			2015		
	KS	KTS	2016	KS	KTS	2016
0	5.52	5.52	5.44	1.74	1.74	1.54
50	5.40	5.15	4.67	2.17	2.11	2.02
100	5.31	5.17	4.99	1.98	2.30	1.69
150	5.00	4.98	4.40	2.46	3.02	2.49
200	5.26	4.26	4.48	2.34	2.90	2.33
Trend	NS	L***	L***	L***	L***	L**

[z]Samples were collected weekly or bi-weekly during the first two growing seasons (2015 and 2016). Data are averaged within a growing season and pooled across two K sources (KS and KTS) in 2016. L – linear; [NS,**,***]Nonsignificant or significant at $P \leq 0.01$ or 0.001, respectively.

Table 4.5. Effects of N source and K source and supply on concentration of nutrients in the leaves and berries of ‘Liberty’ northern highbush blueberry grown in soilless media.

K source	K supply (ppm)	Leaves[z]						Berries						
					Mg (%)			K (%)			Mn (ppm)			
		N (%)[y]	K (%)[y]	Ca (%)[y]	Ammonium sulfate	Urea	Difference	Ammonium sulfate	Urea	Difference	Ammonium sulfate	Urea	Difference	Na (ppm)[y]
None	0	1.70 ab[x]	0.44 c	0.57 a	0.23 a	0.17 a	0.06^{NS}	0.62 a	0.52 c	0.10^{NS}	74 a	41 a	34*	112 a
Potassium sulfate	50	1.69 ab	0.53 abc	0.47 c	0.17 ab	0.17 a	0.01^{NS}	0.60 a	0.62 bc	-0.02^{NS}	49 b	52 a	-3^{NS}	85 ab
	150	1.62 b	0.61 ab	0.48 bc	0.15 b	0.15 a	0.00^{NS}	0.60 a	0.73 ab	-0.13*	47 b	59 a	-13^{NS}	51 b
Potassium thiosulfate	50	1.79 a	0.51 bc	0.49 bc	0.20 ab	0.17 a	0.03^{NS}	0.61 a	0.61 bc	0.01^{NS}	64 ab	51 a	12^{NS}	81 ab
	150	1.81 a	0.57 ab	0.52 ab	0.25 a	0.17 a	0.08*	0.67 a	0.60 c	0.06^{NS}	60 ab	41 a	18^{NS}	61 b
Potassium acetate	50	1.69 ab	0.50 bc	0.52 ab	0.20 ab	0.19 a	0.01^{NS}	0.61 a	0.57 c	0.04^{NS}	48 b	44 a	4^{NS}	70 ab
	150	1.78 a	0.65 a	0.47 c	0.18 ab	0.16 a	0.02^{NS}	0.64 a	0.78 a	-0.14*	51 b	43 a	8^{NS}	74 ab

[z]Concentrations of 1.76% to 2.00% N, 0.41% to 0.70% K, 0.41% to 0.80% Ca, and 0.13% to 0.25% Mg in the leaves are considered sufficient for northern highbush blueberry (Hart et al., 2006).
[y]Data are pooled across two N sources (ammonium sulfate and urea).
[x]Means followed by the same letter within a column are not significant different at $P = 0.05$ (Tukey’s test). ^{NS,*}Nonignificant or significant at $P \leq 0.05$.

Table 4.6. Effect of increasing K supply from potassium sulfate (KS) or potassium thiosulfate (KTS) on leaf and berry nutrients of ‘Liberty’ northern highbush blueberry grown in soilless media.

K supply (ppm)	Leaves						Berries		
	N (%)				Mg (%)				
	KS	KTS	K (%)^z	Ca (%)^z	KS	KTS	B (ppm)^z	Mn (ppm)^z	Na (ppm)^z
0	1.77	1.77	0.45	0.62	0.24	0.24	18	6.3	128
50	1.64	1.82	0.49	0.46	0.18	0.20	15	4.6	67
100	1.74	1.78	0.50	0.58	0.22	0.22	15	5.4	65
150	1.55	1.78	0.56	0.52	0.15	0.24	15	3.8	54
200	1.81	1.81	0.52	0.51	0.15	0.24	15	4.9	77
Trend	Q**	NS	L**	L*	L***	NS	L*	L*,Q*	L*,Q**

^{z}Data are pooled across two K sources (KS and KTS).
L – linear; Q – quadratic; ^{NS,*,**,***}Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Fig. 4.1. Washed roots from both cultivars were photographed after plant harvest (Aug. 2016) to illustrate the poor growth of 'Misty' and its reason for exclusion from data analysis.

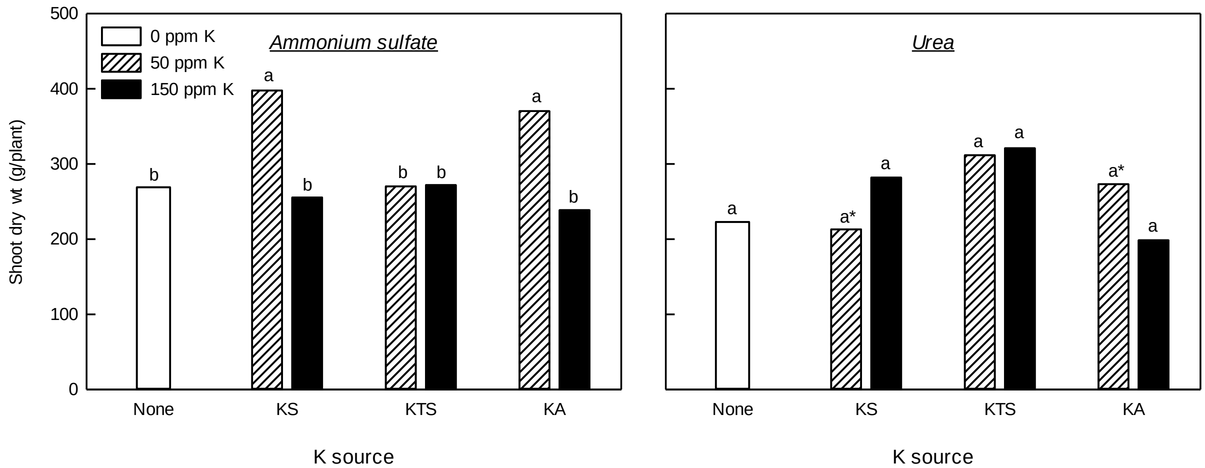

Fig. 4.2. Effects of N source (ammonium sulfate or urea) and K source [potassium sulfate (KS), potassium thiosulfate (KTS), or potassium acetate (KA)] and supply (0, 50, or 150 ppm K) on total shoot dry weight of ‘Liberty’ northern highbush blueberry grown in soilless media. Means with the same letter above the bars are not significant different at $P = 0.05$ (Tukey’s test) within a given N source. An asterisk after a letter indicates the means differ between N sources within a given K treatment ($P \leq 0.05$).

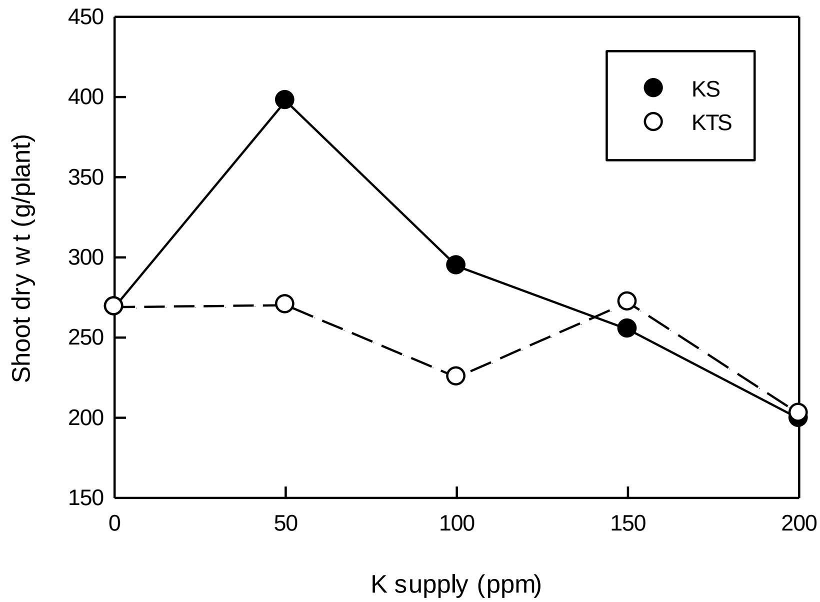

Fig. 4.3. Effect of increasing K supply from potassium sulfate (KS) or potassium thiosulfate (KTS) on total shoot dry weight of 'Liberty' northern highbush blueberry grown in soilless media.

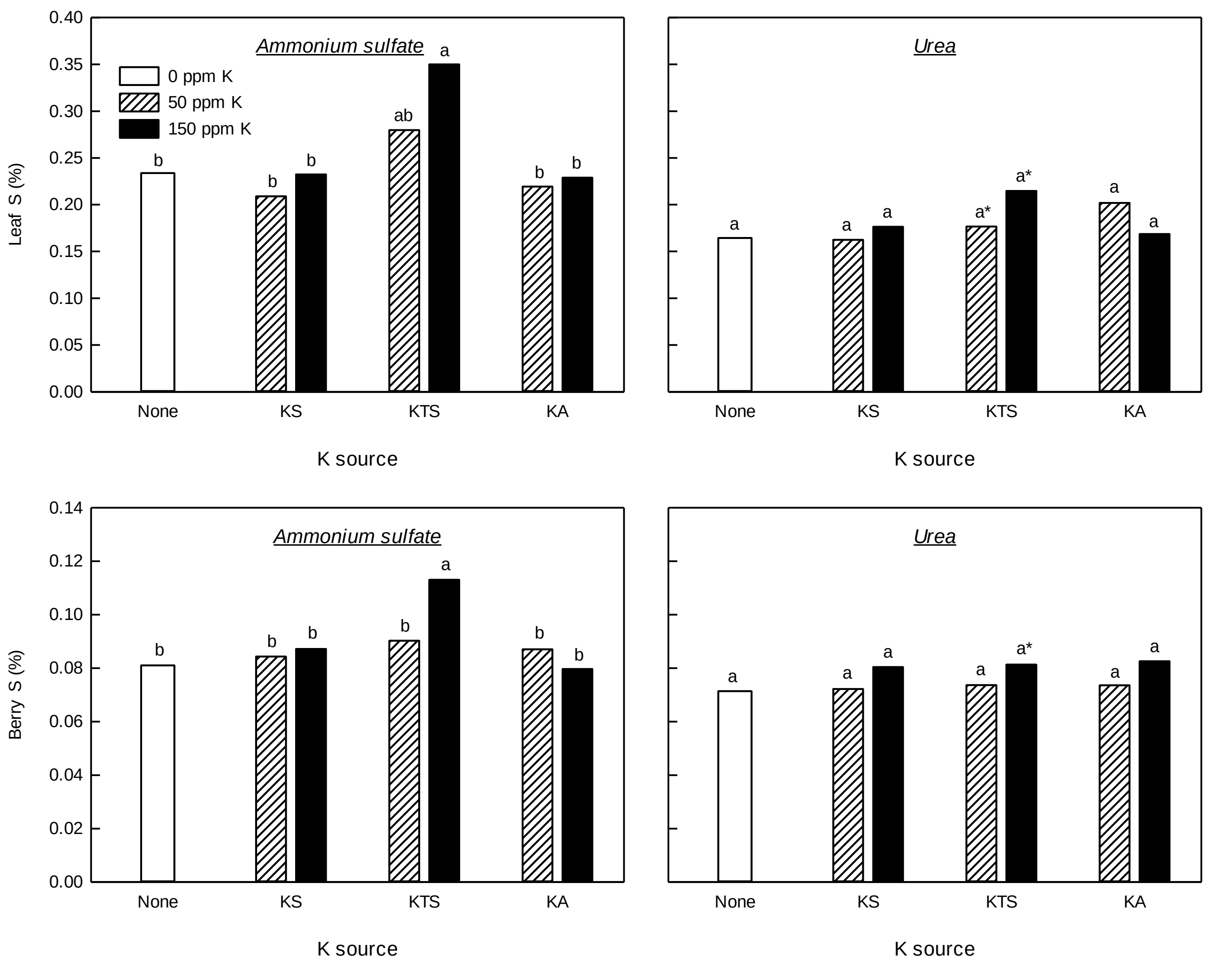

Fig. 4.4. Effects of N source (ammonium sulfate or urea) and K source [potassium sulfate (KS), potassium thiosulfate (KTS), or potassium acetate (KA)] and supply (0, 50, or 150 ppm K) on the concentration of S in the leaves and berries of 'Liberty' northern highbush blueberry grown in soilless media. A concentration of 0.11% to 0.16% S in the leaves is considered sufficient for northern highbush blueberry (Hart et al., 2006). Means with the same letter above the bars are not significant different at $P = 0.05$ (Tukey's test) within a given N source. An asterisk after a letter indicates the means differ between N sources within a given K treatment ($P \leq 0.05$).

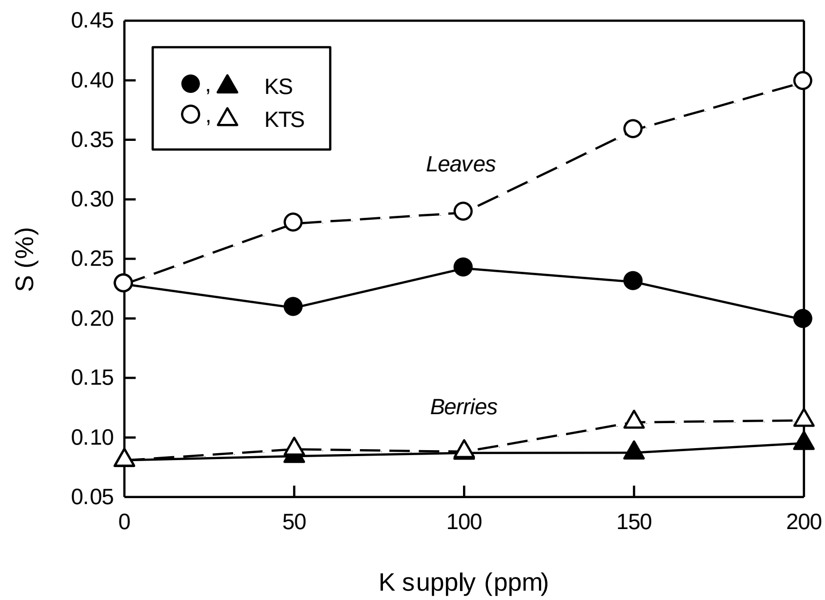

Fig. 4.5. Effect of increasing K supply from potassium sulfate (KS) or potassium thiosulfate (KTS) on the concentration of S in the leaves and berries of 'Liberty' northern highbush blueberry grown in soilless media. A concentration of 0.11% to 0.16% S in the leaves is considered sufficient for northern highbush blueberry (Hart et al., 2006).

Chapter 5: General Conclusions

Based on our results, the performance of northern and southern highbush blueberry can be affected by the soilless substrate mix used. Altering peat and coir proportions in the substrate had no effect on plant dry weight in blueberry when grown for 3-4 months if the media contained at least 10% perlite by volume. Without perlite, ‘Liberty’ blueberry grew better in media containing high proportions of peat than media with coir, while ‘Jewel’ grew equally well. Increasing perlite in the media reduced growth of ‘Jewel’, likely a result of reduced water availability but had no effect on ‘Liberty’, suggesting a difference in media requirements for blueberry types. Douglas fir bark was not a good media choice for blueberry, at least when irrigated with the same regime as peat and coir. While there were minimal differences in plant growth, peat and coir altered the nutrition of blueberry, particularly N, P, K, and Ca. Leachate pH was lower in peat and may have accounted for some of the nutrient uptake differences, while coir had high K concentrations prior to planting, influencing K nutrition. Long-term blueberry production in containers should be carefully monitored for nutrient deficiencies, as the restricted root environment limits nutrient storage, and peat and coir affected plant nutrition in just 3-4 months.

Fertilization with K improved early shoot growth in blueberry and could also improve fruit production, given appropriate sources of K and N are used and K is applied at a rate less than 100 ppm. Plants fertilized with urea were not affected by K source, and urea did not appear to be a good N source for container production, as plants had a lower early yield than with ammonium sulfate. Moderate rates (50 ppm K) of potassium sulfate and potassium acetate improved blueberry shoot growth when using ammonium sulfate as the N source. Potassium thiosulfate and potassium sulfate acidified the leachate when using ammonium sulfate, with the former reducing pH the most, while no K sources affected leachate pH of substrates fertilized with urea. The effect of potassium sulfate on acidification was unexpected and the mechanism is not currently known. Potassium acetate did not raise leachate pH, but proved to be an acceptable K source when using ammonium sulfate.

Our results provide foundational research on substrate production of blueberry. More work is needed to evaluate long-term effects of media composition. Blueberry plants may be grown upwards of 4 years in containers and organic materials such as peat and coir tend to decompose, altering physical properties. Additionally, our results demonstrating the positive effect of K fertilization can be used by the blueberry industry as a whole, which is lacking in detailed knowledge of K nutrition.

Appendix

Appendix 1. Effect of N source on pH and electrical conductivity (EC) of pour-through leachate collected from pots of 'Liberty' northern highbush blueberry grown in soilless media.[z]

N source	Leachate pH			Leachate EC ($dS\cdot m^{-1}$)
	2015	2016	Difference	
Ammonium sulfate	5.43	4.67	0.75*	2.15
Urea	5.99	5.52	0.47^{NS}	1.76
Difference	-0.57^{NS}	-0.84*		0.38***

[z]Samples were collected weekly or bi-weekly during the first two growing seasons (2015 and 2016). Data are averaged within a growing season and pooled across three K sources (potassium sulfate, potassium thiosulfate, and potassium acetate) and supplies (0, 50, and 150 ppm K). Leachate EC is also pooled across years. ^{NS,*,***}Nonsignificant or significant at $P \leq 0.05$ or 0.001, respectively.

Appendix 2. Effect of K source on pH and electrical conductivity (EC) of pour-through leachate collected from pots of 'Liberty' northern highbush blueberry grown in soilless media.[z]

K source	Leachate pH	Leachate EC ($dS\cdot m^{-1}$)
Potassium sulfate	5.01	1.80
Potassium thiosulfate	4.58	2.22
Difference	0.43**	-0.42*

[z]Samples were collected bi-weekly during the second growing season (2016). Data are pooled across five K supply treatments (0, 50, 100, 150, and 200 ppm K).

Appendix 3. Effect of N source on concentration of nutrients in the leaves and berries of 'Liberty' northern highbush blueberry grown in soilless media.[z]

N source	Leaves		Berry
	B (ppm)[y]	Na (ppm)	Zn (ppm)
Ammonium sulfate	66	104	2.0
Urea	75	162	1.7
Difference	-9*	-55**	0.3*

[z]Data are pooled across three K sources (potassium sulfate, potassium thiosulfate, and potassium acetate) and supplies (0, 50, and 150 ppm K).
[y]A concentration of 31 to 80 ppm B in the leaves is considered sufficient for northern highbush blueberry (Hart et al., 2006). *,**Significant at $P \leq 0.05$ or 0.01, respectively.