Effect of Provenance on Substrate pH Tolerance of *Vaccinium arboreum*

by

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Abstract

Around 400 species of blueberry, huckleberry, and cranberry make up the *Vaccinium* genus found throughout the world. Commercial production of blueberries in North America has developed from using different *Vaccinium* species native to regions where they are produced; wild lowbush blueberries (*V. angustifolium*) are grown in the northeastern U.S. and Canada, highbush blueberries (*V.corymbosum* L. and *V. australe* Small) are grown in the northern U.S. and in coastal regions, and rabbiteye (*V. ashei* Reade) and southern highbush (*V. corymbosum* x *V. darrowii* hybrids) are grown in the southern U.S. Like other members of the Ericaceae family, a major limiting factor for growing blueberries is the need for acidic soils with a pH around 4.5. Consumer demand for *Vaccinium* fruit crops has increased due to recent awareness of the health benefits they possess. As demand for blueberries grows, so does the necessity for innovative cultivation techniques to aid blueberry farmers in maintaining costs. Using a rootstock that is more tolerant of alkaline soil types and that could be mechanically harvested profitably would aid commercial cultivation of blueberries. To identify more tolerant rootstocks, two trials were set up using sparkleberry plants from FL, AL, MS, and TN that were arranged in 30L tubs containing a nutrient solution that had been buffered to one of four pH levels: 5.5, 6.0, 6.5, and 7.0. We observed that the provenances varied significantly in growth (percent change, final fresh weight, final dry weight). In the first study, plants from Green County Mississippi (GCMS) had ~3x higher fresh weight percent change than the other four provenances. On average, sparkleberry plants from the 5 provenances in the first study grown in a nutrient solution of

pH=7.0 exhibited a 40-100% higher fresh weight percent change than those grown in more acidic solutions. In the second experiment, provenance and pH treatment significantly affected growth (percent change). Plants from Polk County Tennessee (PCTN) had ~2x higher fresh weight percent change than plants from Marion County Tennessee (MCTN) and ~200x greater than GCMS and Taylor County Florida (TCFL). In this 2nd experiment, plants grown in a pH=5.5 solution showed ~15x higher fresh weight percent change than plants grown in more basic nutrient solutions. Provenance showed an effect on sparkleberry performance, when substrate pH is varied. However, this was a small study with a limited number of provenance tested. More research should be conducted to find provenances that produce plants that excel in higher pH soils.

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LCAL	Lee County, AL [32° 32’ 59” N, 85° 28’ 12” W]; (Soil pH = 5.13)
ECAL	Elmore County, AL [32° 35’ 24” N, 86° 23’ 24” W]; (Soil pH = 4.96)
PCMS	Pearl County, MS [30° 51’ 00” N, 89° 33’ 36” W]; (Soil pH unknown)
GCMS	Green County, MS [31° 18’ 00” N, 88° 38’ 24” W]; (Soil pH unknown)
NCMS	Noxubee County, MS [33° 18’ 36” N, 88° 59’ 23” W]; (Soil pH unknown)
TCFL	Taylor County, FL [30° 04’ 12” N, 83° 39’ 36” W]; (Soil pH unknown)
MCTN	Marion County, TN [35° 06’ 36” N, 84° 35’ 24” W]; (Soil pH unknown)
PCTN	Polk County, TN [35° 09’ 00” N, 85° 25’ 13” W]; (Soil pH unknown)

CHAPTER I

Literature Review

Genus *Vaccinium*

Around 400 species in the genus *Vaccinium* are located throughout the world; every continent has at least one native blueberry species except Antarctica and Australia (Ballington, 2001). Commercial production of blueberries in North America has developed from using different *Vaccinium* species that are grown in regions to which they are native; wild lowbush blueberries (*V. angustifolium*) are grown in the northeastern U.S. and Canada, highbush blueberries (*V. corymbosum* L. and *V. austral*e Small) are grown in the northern U.S. and in coastal regions, and rabbiteye (*V. ashei* Reade) and southern highbush (*V. corymbosum* × *V. darrowii* hybrids) are grown in the southern U.S. with most of the southern highbush being grown in FL (Williamson et al., 2002).

Like other members of the *Ericaceae* family, a major limiting factor for growing blueberries is the need for acidic soils with a pH of 4.0 – 5.2 (Reese, 1992). In order to compensate for a less than ideal substrate pH many growers incorporate peat moss into the planting holes and pine bark mulch into the rows. Peat moss and pine bark are major costs associated with commercial blueberry production and estimated initiation and maintenance costs associated with first year blueberry plantings can be upwards of $10,000 per acre (Fonsah et al., 2007).

Another factor blueberry growers must consider is the quality of the irrigation water; water with high alkalinity requires acidification before use in order to maintain the proper pH level in the planting area. Commercially cultivated blueberries also require soils with high organic matter and readily available Fe and N, primarily in the NH_4 form (Darnell and Hiss, 2006). The need for ample soil moisture is critical to the growth and production of these shallow fibrously rooted plants, especially in the southern U.S. where summer drought is common. While the need for abundant water is high, blueberries are susceptible to root rot fungus, in particular *Phytophthora cinnamomi*, and are intolerant of areas with poor soil drainage (Erb et al., 1986).

In addition to production and operating costs, profitability in blueberry production is also limited by harvest costs. The United States Department of Agriculture Economic Resource service reported that 55% of the total blueberry production in the U.S. is fresh market blueberries; fresh market blueberries are primarily hand harvested (USDA-ERS, 2013—Table 01, 2013, http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1765). Hand harvesting can cost four to seven times as much as mechanical harvesting and will likely rise (Takeda et al., 2008). Mechanical harvesting techniques have been developed, however there have not been any developments that account for the multi-caned structure of cultivated blueberry plants, such that fruit losses can reach 20 – 30% due to fruit falling through the catcher plates of the harvesters (Mainland, 1993). According to Food and Agriculture Organization of the United Nations, in 2013 the United States and Canada were responsible for growing the most blueberries in the world with 246,573 tonnes, more than doubling the next largest producer, Canada with 120,160. This is a trend that has consistently been seen for well over a decade (Food and Agriculture Organization of the United Nations, FAO, 2013, http://www.fao.org/

faostat/en/#rankings/countries_by_commodity). The USDA reported that in 2012 southeastern blueberry production accounted for 17.5% of the total amount of blueberries produced in the U.S. with 9,720,000 lbs. Alabama's contribution to the overall total in 2012 was 700,000 lbs (USDA-ERS, 2013—Table 02). With suitable soil types in limited supply, the expansion of commercial blueberry production onto old row crop land is becoming more commonplace for growers. This causes more pH issues for blueberry growers to deal with due to the routine liming of these lands in the past by row crop farmers to maintain proper soil pH for their crops.

Consumer demand for *Vaccinium* fruit crops such as cranberries and blueberries has increased due in part to increased knowledge about the health benefits they possess: very high levels of vitamin C, cellulose, pectin and; antitumor, antiulcer, antioxidant, and anti-inflammatory properties (Wang et al., 1999). As demand for blueberries grows, so does the necessity for innovative cultivation techniques to aid blueberry farmers in lowering costs associated with fertilizers, soil amendments, and labor. One species beginning to draw attention from blueberry researchers across the southeastern United States is *Vaccinium arboreum*, also known as the sparkleberry, farkleberry, winter huckleberry, or tree huckleberry.

Vaccinium arboreum

Vaccinium arboreum is a species in the *Vaccinium* section *Batodendron*. Sparkleberry is a wild blueberry species native to the southeastern U.S. with many characteristics considered desirable in commercial blueberry production. Sparkleberry grows well in soils with pH 4.5 – 6.5 (Stockton, 1976), low organic matter (Lyrene and Brooks, 1995), low iron availability, and nitrogen in the nitrate form; i.e. soils that cultivated highbush blueberries poorly tolerate (Lyrene

and Brooks, 1995). Sparkleberry is an evergreen to semi-evergreen, southeastern native plant with leathery, glossy, dark green, entire to elliptical leaves that alternate up the stem (Dirr, 2009). Sparkleberry is most commonly seen as a small monopodial tree standing up to 10m tall with exfoliating bark composed of reddish-browns, oranges, and grays (Brooks and Lyrene, 1998b), but can also be a spreading shrub form that can grow to a fairly large size. The co-national champion sparkleberries stand 7.3 × 10 (24' × 33') in Aiken, SC and 8.8 × 17.3 (29' × 45') in Evergreen, AL (Dirr, 2009).

After the leaves emerge, racemes of small white, sometime pink, bell-shaped, perfect flowers adorn sparkleberries in the late spring. Flowering begins in May and continues through June (Dirr, 2009). The flowers of *Vaccinium* spp. are not arranged structurally to maximize self-fertilization (Ballington et al., 1976; Brooks and Lyrene, 1998a). The stigma of the flower extends beyond the contiguous stamens and the sides of the stamen are angled such that pollen is deflected away as it falls from the anthers (Brooks and Lyrene, 1998a). Unlike the flowers of commercially produced blueberries, the flowers of the sparkleberry are shorter and wider providing bees easier access to the inner flower parts thus increasing pollination (Lyrene and Brooks, 1995). As fall arrives the leaves begin to darken into hues of crimson to reddish- purple and the fruit begin to set (Dirr, 2009). The fruit set on sparkleberries are a shiny, black, persistent fruit between five to eight mm in diameter (Reese, 1992), and are considered inedible due to the berries being dry and gritty (Brooks and Lyrene, 1998b; Dirr, 2009). The fruit will remain on the tree well into winter while the leaves will often endure through the winter as well (Reese, 1992).

Sparkleberry Hardiness

Sparkleberries can be found in the native understory from climatic zone seven to nine (Dirr, 2009) with a native range from FL north to VA, west to NE and south to TX (Dirr, 2009; Huxley, 1992). The vast range sparkleberries cover can be attributed to several factors including: 1) The dissemination of sparkleberry seed by animals (Haywood, 1994); 2) Tolerance to a wide range of heat and drought conditions (Dirr, 2009; Lyrene and Brooks, 1995), 3) Disease resistance to several fungi that are detrimental to highbush cultivars (Lyrene and Brooks, 1995); and 4) The ability to thrive in a wide array of climates, soil types, and land classifications. Most *Vaccinium* species, especially commercially produced cultivars, are limited to soils that have low pH, 3.5-5.5, are low in bicarbonates, high organic matter, and have both high available iron and ammonium (Brooks and Lyrene, 1998b; Darnell and Hiss, 2006; Erb et al., 1993).

Experiments showed that sparkleberry's ability to thrive in a wider range of soils is linked to its ability to acquire iron (Fe) and nitrate (NO_3-) more efficiently than other cultivars of *Vaccinium* species (Darnell and Hiss, 2006). Other *Vaccinium* species supplied with nitrate as their sole source of nitrogen showed decreased growth and yield compared to plants that were supplied with ammonium (Finn et al., 1991; Darnell and Hiss, 2006; Korcak, 1989). Sparkleberries are commonly found growing in dry, sandy, rocky, calcareous soils containing very low amounts of organic matter and maintaining a pH level near or above 6.0 (Brooks and Lyrene, 1998b). In Texas, sparkleberries have been found growing in soils with pH as high as 6.4 and exhibiting no signs of any chlorosis (Lyrene and Brooks, 1995; Stockton, 1976).

Seed Germination and Asexual Propagation

Both Stockton (1976) and Lyrene (1998) report difficulty in propagating sparkleberries either by germinating seed or via softwood cuttings. The highest percent germination recorded was 20% achieved under a white light over a seven-week period; the softwood cuttings that were alive after 60 days resulted in 60% of them living with no roots or callus and the other 40% alive with basal callus formation, but no roots (Lyrene, 1998; Stockton, 1976). Seed stratification along with summer planting has proven to increase percent germination in some instances, but a consistent 30 to 50% germination rate has yet to be achieved (Lyrene, 1998). Compared to the seeds of other sections of *Vaccinium*, sparkleberry seeds have very low germination percentages (Lyrene and Brooks, 1995).

Reproduction by taking cuttings is an inexpensive way to obtain new plant material and allows the reproduction of plants possessing desired traits (Hartman and Kester, 2010). Dirr (1990) states that sparkleberry is difficult and "perhaps" impossible to root. In his first experiment with propagation by cuttings, Stockton (1976) had essentially no rooting and 60% of his attempts didn't form a callus or any roots. Lyrene and Brooks (1995) did report successful rooting using juvenile softwood cuttings taken from seedlings less than six months old when rooted under mist. Successful rooting is dependent on several factors including the type of cutting (hard, soft, or semi-hard), the time of year the cutting was taken, and the juvenility of the source material (Dirr, 2009; Reese, 1992). Cuttings must be kept in a container and they should remain moist and cool and out of direct light (Hartman and Kester, 2010). The great variation in the leaf character of sparkleberry may suggest that rooting success is clonally specific, as is the case in various other difficult-to-root species (Reese, 1992).

Potential Uses for Sparkleberry

Due to its adaptability, hardiness, and ornamental qualities, sparkleberry has the potential to be used in a couple of different settings. Sparkleberry offers an appealing addition to a native landscape (Stockton, 1976), and with remarkable drought resistance, it is an ideal addition to a xeriscape landscape as well. Sparkleberry has been crossed with other *Vaccinium* species with some success in passing on sparkleberry traits creating vigorous and persistent hybrids (Lyrene, 1991; Lyrene and Brooks, 1995). Several sparkleberry specific traits have been passed on and are being expressed in hybrid generations (Brooks and Lyrene, 1998b). The original reason for attempting the cross was to try to breed heat and drought tolerance, increased vigor, and the ability to grow on soils low in organic matter into the progeny of the cross (Brooks and Lyrene, 1995; Brooks and Lyrene, 1998a). Sparkleberry use in breeding highbush varieties results in blueberries that meet commercial standards, and further breeding may produce new commercial highbush cultivars that are more widely adapted and easier to grow (Lyrene and Brooks, 1995).

Grafting onto rootstocks in order to utilize less than ideal soil is a very common practice and has been used on blueberries in the past (Hartman and Kester, 2010). Another possible commercial use for sparkleberry is as a rootstock. Previous studies have found *V. arboreum* successful as rootstock for commercial species *V. ashei* and *V. corymbosum* (Galleta and Fish, 1971; Ballington 1996; Casamali et al., 2016). The treelike form sparkleberry possess is another desirable characteristic in cultivated highbush blueberries which would allow for more economical mechanical harvesting of the fruit. Suitable rootstock should possess the following traits: highbush habit, limited suckering, stout upright growth, ability to grow in a spectrum of soils (Stockton, 1976). Some grafting methods that work effectively with sparkleberry include

whip, bench grafting, chip, and T-budding however, a good union can be technically difficult due to the hardness of the wood and the small diameter of the stems (Reese, 1992).

The incorporation of *Vaccinium arboreum* into commercial blueberry production has several appealing qualities that are furthering the exploration of its potential. Testing to determine if plants from different provenances have different pH tolerances is a necessary step in order to select suitable rootstock. Zobel and Talbert (1984) define a provenance as "the original geographic area from which seed or other propagules were obtained" and go on to state that a more useful definition of the concept would be, "plants from a subdivision of a species consisting of genetically similar individuals, related by common descent, and occupying a particular territory to which it has become adapted through natural selection." Growing sparkleberry in a hydroponic system with a nutrient solution buffered to desired pH levels is an effective way to rapidly test the pH tolerance of plants from different provenances; however, further tests need to be performed in order to determine if the results found in a hydroponic system would translate into similar results in a field setting.

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CHAPTER II

Effect of provenance on substrate pH tolerance in *Vaccinium arboreum*

Abstract

Consumer demand for *Vaccinium* fruit crops such as cranberries and blueberries has increased, in part due to increased knowledge about the health benefits they possess. As demand for blueberries grows, so rises the necessity for cultivation techniques. Novel agriculture techniques to aid blueberry farmers in lowering costs associated with fertilizers, soil amendments, and labor would be beneficial. Tolerance to more alkaline soil types would aid commercial cultivation of blueberries in areas with higher pH soils where *Vaccinium* crop normally would struggle. One species, *Vaccinium arboreum*, or the sparkleberry, has been found growing in areas with soil pH levels as high as 7. The tolerance of a broad range of pH levels, along with a monopodial trunk and excellent drought resistance make *V. arboreum* an ideal candidate for use as a rootstock for a *Vaccinium* species. The objective of these experiments was to determine the effect provenance has on the substrate pH tolerance of sparkleberry. Two hydroponic experiments were set up in 30L tubs containing nutrient solution that had been buffered to one of four pH levels: 5.5, 6.0, 6.5, and 7.0. Plants were obtained from provenances in Florida, Mississippi, Tennessee, and Alabama. We found that the provenances varied significantly in growth (percent change, final fresh weight, final dry weight), as well as other measurements (shoot dry weight, root dry weight, root:shoot ratio, leaf greenness values). In the first study, plants from Greene County, Mississippi (GCMS) had ~3x higher fresh weight percent

change, were 50% higher in final fresh weight, and 30% higher in final dry weight compared to the other four provenances. On average, sparkleberry plants from the 5 provenances in experiment 1 grown in a nutrient solution of pH=7.0 exhibited a 40-100% higher fresh weight percent change than those grown in more acidic solutions. This could be due to a chelated iron source in the nutrient solution that was replaced for a non-chelated source in the second experiment. In the second experiment, provenance and pH treatment significantly affected growth (percent change). Plants from Polk County, Tennessee (PCTN) had ~2x higher fresh weight percent change compared to plants from Marion County, Tennessee (MCTN) and ~200x greater than GCMS and Taylor County, Florida (TCFL). In this 2nd experiment, plants grown in a pH=5.5 solution showed ~15x higher fresh weight percent change than plants grown in more basic nutrient solutions. Provenance had an effect on sparkleberry performance, however this was a small study with a limited number of provenance tested. More research should be conducted to find provenances that produce plants that excel in higher pH soils.

Introduction

Around 400 species in the genus *Vaccinium* are located throughout the world. They are indigenous to 5 of the 7 continents. Commercial production of blueberries in North America has developed from using different *Vaccinium* species based on those native to the region; wild lowbush blueberries (*V. angustifolium*) are grown in the northeastern U.S. and Canada, highbush blueberries (*V. corymbosum* L. and *V. australe* Small) are grown in the northern U.S. and in coastal regions, and rabbiteye (*V. ashei* Reade) and southern highbush (*V. corymbosum* × *V.*

darrowii hybrids) are grown in the southern U.S. with most of the southern highbush being grown in FL (Williamson et al., 2002).

Consumer demand for fresh blueberries had increased over the last several years. This increase can be attributed in part to increased knowledge about the health benefits they possess: very high levels of vitamin C, cellulose, pectin and; antitumor, antiulcer, antioxidant, and anti-inflammatory properties (Wang et al., 1999). With increased demand comes the necessity of innovative cultivation techniques. Currently, commercial blueberry production is limited by several factors including the need for soils that are high in organic matter, well drained, and have a pH level between 4.0 and 5.2 (Reese, 1992). Commercial blueberries are also typically hand harvested due to the losses incurred from berries falling through the catch plates of mechanical harvesters (Mainland, 1993). A cultivation technique utilized in other fruit crop production beneficial to commercial blueberry production is grafting. Utilizing a rootstock that provides a more viable method to mechanically harvest profitably and will perform in higher pH substrates that are low in organic matter and could lower both start up and operating costs for growers.

V. arboreum, also known as sparkleberry, is a blueberry species that is native to the southeastern United States; it has been found growing from VA to FL and as far west as TX (Stockton 1976). Sparkleberry grows well in soils with a pH range of 4.5 – 6.5 (Stockton, 1976), low in organic matter (Lyrene and Brooks, 1995), low in iron availability, and nitrogen in the nitrate form; i.e. soils that cultivated highbush blueberries poorly tolerate (Lyrene and Brooks, 1995). Sparkleberries are dry and gritty and not a viable alternative to blueberries currently found on the market, however, both *V. corymbosum* and *V. ashei* have successfully been grafted onto *V. arboreum* (Galleta and Fish, 1971; Ballington, 1996; Casamali et al., 2016). Because it meets the substrate tolerance requirements being sought and may provide a more cost effective

way to harvest, *V. arboreum* is being looked at by researchers to determine its viability as a rootstock for commercially produced blueberries.

If a particular provenance of plants is discovered to grow better at a higher pH then it could provide a potential rootstock for commercial blueberry production allowing farmers to utilize undesirable land with less input at crop implementation. This study focuses on determining the effect of provenance on sparkleberry substrate pH tolerance. We studied plants from 8 different provenances around AL, FL, MS, and TN.

Materials and Methods

Plant Material and growth conditions

This research was conducted via two different experiments. The first study utilized *Vaccinium arboreum* seeds from the following provenances (coordinates found on list of abbreviations, vi): Green Co. MS (GCMS), Chewacla State Park in Auburn, AL (LCAL), Noxubee Co. MS (NCMS), Deetsville, AL (ECAL), Pearl Co. MS (PCMS). Forty, 15 month old plants from each of 5 provenances were selected for use in the first study. The plants had been grown from seed by staff in the Auburn Horticulture department (see Appendix). In July 2011, the plants were removed from the pots and the roots were washed clean of the potting mix. Plants were weighed and transferred into a deep water culture hydroponic system with constant aeration using Rubbermaid® containers, Coralife SL-38 Super Luft air pumps (Franklin, WI), and Penn Plax Add-a-Stone® air stones (Hauppaug, NY). Two plants from each provenance were placed into each of the 20 containers filled with a nutrient solution initially buffered to a pH of 5.5 to

alleviate transplant shock. After 7 d, the 5.5 pH nutrient solutions were changed to solutions buffered to a pH of either 5.5, 6.0, 6.5, or 7.0 (n=4).

The second study utilized plants from 4 different provenances (coordinates found on list of abbreviations, vi): Green Co. Mississippi (GCMS) that were the same plants from the first study, but now potted in 1 gallon containers, Taylor Co. Florida (TCFL) that were purchased as 4" pots, Marion County, TN (MCTN) (purchased as seedlings) and Polk County (PCTN) in Tennessee (purchased as seedlings). In June 2012, all plants were removed from the pots and the roots were washed clean of the potting mix. The root washing procedure consisted of spraying the roots with clear tap water while massaging them by hand to remove the soil. Plants were then weighed and transferred into a deep-water culture hydroponic system using containers filled with a nutrient solution that was buffered to 5.5 pH for 7 d before being replaced with a nutrient solution that was buffered to a pH of either 5.5, 6.0, 6.5, or 7.0 (n=4).

Experimental Design

The first study took place from July 2011 to September 2011 (74 d). Treatments were arranged in a 5 × 4 factorial (provenance × pH level) in a completely randomized block design with 5 replications that were blocked by plant size and used a single tub per replicate (N=20). The second study took place over the course of 12.5 weeks from June 2012 to September 2012. The second study treatments were arranged in a 4 × 4 factorial (provenance × pH level) in a completely randomized design with 5 replicates per treatment, each individual tub as a replicate (N = 20). Both experiments were set up in a deep-water culture hydroponic system using 38.75 L Rubbermaid® containers. Thirty L of water were added to each tub and the water level was marked. Ten 5.08 cm diameter holes were cut in the lid of each container for the first study; the holes were expanded to 6.35 cm diameter holes for the second study, due to the larger starting

size of some of the plants. Neoprene disks 7 cm in diameter were fitted to individual holes in the lids, to hold the plants in place. The containers were painted white to help reflect solar rays and prevent excessively high nutrient solution temperatures. Each container in the first study was fitted with an air stone attached to polyethylene tubing that was connected to an air pump. The air pump was fitted with a four-way splitter so that each pump supplied air to four containers. The second study had a similar air setup, but the air stones were 5.08 × 3.81 cm (L × W). Each tub was filled with 30 L of nutrient solution that was buffered to the proper pH level and was maintained throughout the experiment (see Appendix).

Nutrient Solutions

During the first study, nutrient stock solutions were mixed ahead of time and stored in 15 L Rubbermaid® containers and was changed every 14 d. The nutrient solution contained (mM): 0.5 K_2HPO_4, 1.0 $MgSO_4$, 0.5 $CaCl_2$+, 0.09 Fe – diethylenetrinopentaacetic acid (Fe – DTPA), 0.045 H_2BO_3, 0.01 $MnSO_4$, 0.01 $ZnSO_4$, and 0.2 µM Na_2MoO_4. The nitrogen source was 0.5M KNO_3 and the nutrient solutions lowered with HCL and buffered at pH 5.5, 6.0, 6.5, or 7.0 with 0.5M 2-(4-morpholino)-ethane sulfonic acid (MES).

The nutrient solutions in the first study had little difference over the course of 14 d, therefore nutrient solutions were changed every 28 d for the second study. The nutrient solution for the second study was adjusted to account for iron availability to the plants; a chelated iron source was used in the first study and affected the iron uptake of individuals based on the pH treatment, the solution for the second study used non-chelated Fe. The nutrient solution for the second study contained 0.5mM NH_4NO_3, 0.86mM H_3PO_4, 0.09mMg $C_6H_5FeO_7$, 2.1mM $MgSO_4$, 0.1mM KOH, and 0.07 CaOH. The nitrogen source was 0.5M NH_4NO_3 and the nutrient

solutions lowered with HCL and buffered at pH 5.5, 6.0, 6.5, or 7.0 with 0.5M 2-(4-morpholino)-ethane sulfonic acid (MES).

Nuturient Solution Management

The pH levels used in both studies were 5.5, 6.0, 6.5, and 7.0. In the first study all 20 tubs were initially set to pH 5.5 and after a 7d acclimatization period KOH was added to raise the pH of the tubs to 6.0, 6.5, and 7.0. The adjustment of pH levels was performed differently in the second study due to concern that the increased levels of K in the tubs with higher pH would differentially affect plant growth and possibly interfere with the uptake of other nutrients. For the second study all 20 tubs were set up at a pH level of 5.5 for as an acclimatization period and then the pH was raised to 7.0 using KOH. Then HCl was added to lower the pH of the tubs that were to be set at 5.5, 6.0, and 6.5. The pH levels were measured and adjusted every Monday, Wednesday, and Friday throughout the duration of both experiments. Before testing the pH level of the nutrient solution, solution volume was adjusted using water so that plant usage and evaporative losses were replenished and the solution volume returned to 30 L per container. If pH needed to be adjusted, 10% HCl was added to lower it and 30% KOH was added to raise it.

Measurements

At the end of each experiment plants were removed from the hydroponic tubs, the roots were dried using paper towels, and the whole plants were weighed. After the plants were weighed the root mass was removed 1" above the topmost root and the root mass was weighed. Next the remaining shoots and leaves were weighed. The root masses, shoots, and leaves were separated and then placed into paper bags and placed in a drying oven at 60°C for 72 hours. After dried, the roots and shoots and leaves were reweighed. During the experiment both SPAD

and photosynthesis measurements were gathered using three, middle aged leaves per plant. SPAD was determined using a leaf chlorophyll concentration measured using a Konica Minolta chlorophyll meter (model SPAD-502, Konica Minolta Sensing Americas, Inc., Ramsey, New Jersey, USA) and photosynthesis was measured using a LI-COR 6400 (Model 1000, LI-COR Biosciences Inc., Lincoln, Nebraska, USA) with the ambient light set at 100%. At the conclusion of each study, 5 leaves were taken from each plant and combined by treatments for a composite leaf nutrient analysis.

Data analysis

Data were analyzed using generalized linear models with the GLIMMIX procedure of SAS (version 9.2; SAS Institute Inc., Cary, NC). Provenances and pH treatments were compared using a one-way analysis of variance (ANOVA) and, if necessary, Tukey HSD post-hoc analysis, also in SAS. Correlations between pH and variables (percent change, fresh weight, shoot dry weight, etc) were run using the Pearson Correlation test. All estimates are described ± 1 S.E. unless stated otherwise.

Results

Experiment 1

Fresh Weight Percent Change

At the end of the study, individuals of *Vaccinium arboreum* ranged in fresh weight percent change from -59 to 376%. The five provenances differed significantly in percent change of fresh weight ($F_{4,185} = 6.09$, $p<0.0001$, Table 1). Noxubee County, Mississippi (NCMS) showed a mean 32.59±8.8% increase in fresh weight over the course of the study. Lee County,

Alabama (LCAL) showed, on average, a 27.97±7.1% increase overall. Greene County, Mississippi (GCMS) had the highest percent change with a mean fresh weight increase of 78.53±17.1%. Pearl River County, Mississippi (PCMS) showed a mean 26.21±8.2% increase. Lastly, Elmore County, Alabama (ECAL) showed a mean 7.79±5.3% increase in size. GCMS had a significantly higher fresh weight percent change than the other four provenances ($p<0.05$ vs. NCMS and LCAL, $p<0.01$ vs. PCMS and ECAL).

The percent change in fresh weight amongst *V. arboreum* individuals in the first study did not differ between pH treatments ($F_{3,186} = 0.95$, $p = 0.42$, Table 2). Individuals grown in a solution of pH=5.5 showed a mean fresh weight increase of 24.88±9.4%. Individuals grown in a solution of pH=6.0 showed a mean 30.22±7.5% increase in fresh weight. *V. arboreum* plants grown in a pH=6.5 solution exhibited a mean 36.82±8.8% increase in fresh weight while plants grown in pH=7.0 solution exhibited the highest fresh weight percent change with a mean of 47.37±12.6% increase in percent change.

Final Fresh Weight

After 10.5 weeks of growth in hydroponic culture, only the provenance offered significant effect in final fresh weight of individuals of *V. arboreum* ($F_{4, 185}=8.037$, $p<0.001$, Table 1). NCMS showed a mean final fresh weight of 17.86±2.1 g. LCAL had a mean fresh weight of 13.55±1.5 g. GCMS showed the largest final fresh weight with a mean of 26.94±3.7 g. PCMS had a mean of 16.95±1.8 g and ECAL had the smallest final fresh weight with 10.49±1.1 g (Table 1). GCMS was significantly larger than the other 4 provenances; 9.08±3.5 g larger than NCMS ($p<0.05$), 13.39±3.3 g larger than LCAL ($p<0.001$), 9.99±3.4 g larger than PCMS ($p<0.01$), and 16.95±3.2 g larger than ECAL ($p<0.001$). ECAL was significantly smaller than all

other provenances (p<0.01 for all comparisons). NCMS, LCAL, and PCMS were all comparable in final fresh weights.

There were no significant effects for pH treatment with final fresh weight ($F_{3,186}$=1.64, p=0.18, Table 2).

Final Dry Weight

As with the final fresh weight, provenance showed a significant effect ($F_{4, 185}$=7.52 p<0.001). As expected, dry weights showed a similar trend as the fresh weight; NCMS showed mean final dry weight of 6.29±1.4 g, LCAL had a mean dry weight of 4.74±1.4 g, GCMS showed the largest dry weight with a mean of 8.46±1.5 g, PCMS had a mean of 6.26±1.4 g and ECAL was again the smallest weight with 3.65±1.4 g (Table 1). GCMS again was significantly larger than the other 4 provenances while ECAL was significantly smaller than all other provenances in final dry weight (p<0.01 for all comparisons). NCMS and PCMS were comparable in final dry weights (p=0.95) and both had significantly higher dry weights than LCAL (p<0.01 for both comparisons). LCAL, while smaller than NCMS, GCMS, and PCMS, showed 1.09±0.3 g greater dry weight than ECAL (p<0.01).

Root:Shoot

Both provenance and pH solution showed a significant effect in the root to shoot ratio of individuals of *V. arboreum* ($F_{4, 185}$=5.27, p<0.001, $F_{3, 186}$=5.34, p<0.01 respectively). NCMS showed a mean root to shoot ratio of 0.43±0.1. LCAL had a mean root to shoot ratio of 0.69±0.1. GCMS and PCMS showed similar mean ratios of 0.50±0.0 and 0.47±0.0 respectively. ECAL had a mean root to shoot ratio of 0.65±0.1. LCAL showed a significantly higher root to shoot ratio than NCMS and PCMS (p<0.01 and p<0.05 respectively). ECAL also showed significantly

higher root to shoot ratio than NCMS (p<0.05, Table 1). When grown in a pH solution of 5.5, individuals of *V. arboreum* had a mean root to shoot ratio of 0.48±0.0. Grown in a solution of pH=6.0 shows a mean root to shoot ratio of 0.49±0.0, and in a solution of pH=6.5 a mean ratio of 0.52±0.0 was exhibited. There was a mean root to shoot ratio of 0.71±0.1 for the plants grown in a solution where the pH=7.0 The mean root to shoot ratio of plants grown in a solution with a pH of 7.0 was significantly higher than the other 3 solution treatments (p<0.01 vs. pH=5.5, 6.0, p<0.05 vs. pH=6.5, Table 2).

There was a significant positive correlation between root to shoot ratio and pH of the solution, where for every unit increase in pH of the solution, root to shoot ratio increased 0.15 (N=190, r=0.25, p<0.001, Table 3).

Shoot dry weight

The shoot dry weights varied significantly amongst the 5 provenances ($F_{4, 185}$=8.44, p<0.001, Table 1). NCMS showed a mean dry shoot weight of 4.51±1.0g. LCAL showed a mean dry shoot weight of 3.11±1.0 g. GCMS show significantly larger mean dry shoot weight than LCAL and ECAL (on average 2.52±0.5 g heavier than LCAL, p<0.001; 3.31±0.5 g heavier than ECAL, p<0.0001). PCMS exhibited a mean dry shoot weight of 4.35±1.0 g. ECAL showed significantly lower dry shoot weight than 3 of the other 4 provenances with a mean weight of 2.32±1.0 g (p<0.01 vs. NCMS; p<0.0001 vs. GCMS; and p<0.05 vs. PCMS).

Root dry weight

Root dry weights also varied significantly by provenance ($F_{4, 185}$=5.17, p<0.001, Table 1). NCMS had a mean root dry weight of 1.77±0.5 g. LCAL showed mean root dry weight of 1.62±0.4 g. GCMS showed significantly higher root dry weight than NCMS, LCAL, and ECAL

with a mean of 2.82±0.5 (1.05±0.2 g higher than NCMS, $p<0.05$, 1.20±0.3 g higher than LCAL, $p<0.01$, and 1.49±0.3 g higher than HT, $p<0.001$). PCMS showed a mean dry root weight of 1.91±0.5 g. ECAL had a mean of 1.33±0.4.

Individuals of *V. arboreum* showed a positive correlation between root dry weight and pH of the solution. Individuals grown in a solution with a pH=5.5 exhibited a mean root dry weight of 1.63±0.5 g. This increased to 1.67±0.5 g for those grown in a solution with a pH=6.0, 1.89±0.5g in a solution with a pH=6.5, and 2.38±0.5 g for plants grown in a solution of pH=7.0 (N=190, r=0.18, $p<0.01$ Table 2, 3). This positive correlation is strengthened in NCMS, PCMS, ECAL (Table 3).

Photosynthesis

Photosynthesis was not significantly affected by either provenance or pH treatment ($F_{4, 185}=0.96$, $p=0.43$, $F_{3, 186}=0.54$, $p=0.66$, respectively, Table 1, 2). There was however a negative correlation found between solution pH and photosynthesis for plants from the ECAL provenance, where for every unit increase in pH solution, photosynthesis decreased by 4.72 (N=38, r=0.32, $p<0.05$, Table 3).

Leaf Greenness (SPAD)

SPAD readings varied significantly by provenance ($F_{4, 185}=13.16$, $p<0.001$, Table 1). NCMS showed mean SPAD readings of 58.14±2.3 and was significantly higher than all other provenances ($p<0.05$ vs. GCMS, $p<0.001$ for all other comparisons). LCAL had mean SPAD readings of 55.88±2.4. GCMS and PCMS had similar SPAD readings of 58.19±2.1 and 52.17±2.2 respectively. ECAL had a mean SPAD reading of 47.01±2.3.

There was a positive correlation between pH and SPAD readings for GCMS and ECAL (p<0.001 for both, Table 3). GCMS plants exhibited a correlation where for each unit increase in pH solution, SPAD readings increased 9.79 units (N=38, r=0.50). ECAL plants exhibited a 6.04 unit increase in SPAD readings for every unit increase in pH solution (N=38, r=0.41).

SPAD readings varied significantly by provenance ($F_{4, 185}$=15.07, p<0.001, Table 1). NCMS showed mean SPAD readings of 61.24±1.5 and was significantly higher than all other provenances (p<0.05 vs. GCMS, p<0.001 for all other comparisons). LCAL had mean SPAD readings of 46.49±2.4. GCMS and PCMS had similar SPAD readings of 54.63±1.9 and 52.27±1.6 respectively. ECAL had a mean SPAD reading of 48.12±1.8.

Experiment 2

Fresh Weight Percent change

The four provenances differed significantly in percent change, when comparing initial weight and final fresh weight ($F_{3, 130}$ = 4.65, p<0.01, Table 4). Because the individual plants for experiment 2 varied in initial size (i.e. some were seedlings and some were potted plants, see methods) provenance can only be compared by percent change as opposed to weights, as done for the first study. TCFL showed a mean 7.03±4.3% increase in fresh weight over the course of the study. GCMS showed a decrease in fresh weight with a mean of -1.11±4.8% change overall. PCTN had the highest fresh weight percent change showing an increase of 221.01±79.3%. This was significantly higher than the TCFL and GCMS (p<0.01 vs. TCFL and p<0.05 vs. GCMS, Fig. 2). MCTN showed a mean 101.36±37.1% increase in size.

The four pH treatments also differed significantly by overall fresh weight percent change in *V. arboretum* individuals ($F_{3, 130} = 11.32$, $p<0.001$). *V. arboreum* grown in a treatment solution with a pH of 5.5 showed significantly higher percent change than the other 3 treatments with an mean of 319.06±91.4% increase in size ($p<0.01$ for all comparisons, Table 5, Fig. 3). The remaining 3 treatments of pH 6.0, 6.5, and 7.0 were similar in percent change with 21.97±9.0, 25.69±6.9, and 6.02±7.4%, respectively.

While the responses to pH treatments differed significantly as a whole, with *V. arboreum* grown in pH=5.5 solutions surpassing the other treatments, individuals provenances differed from this pattern. Plants from TCFL and GCMS grew similarly in response to various pH treatments ($F_{3, 36} = 0.45$, $p = 0.72$, $F_{3, 36} = 0.549$, $p = 0.65$, Table 6). There was a negative correlation between solution pH and fresh weight percent change in PCTN and MCTN plants ($p<0.001$ for both, Table 7, Fig. 4).

Final fresh weight

TCFL, PCTN, and MCTN all showed significant final fresh weight differences between pH treatments ($F_{3, 36} = 3.75$, $p<0.05$, $F_{3, 31} = 13.05$, $p<0.001$, $F_{3, 36} = 7.39$, $p<0.001$ respectively, Table 6). TCFL plants grown in pH=5.0 solutions had a mean final fresh weight of 49.37±8.5 g. Those grown in pH=6.0 and pH=6.5 had similar final fresh weights with means of 36.35±5.0 g and 31.50±5.4 g respectively. TCFL individuals grown in a solution of pH=7.0 had the lowest final fresh weight, significantly lower than pH=5.5 ($p<0.05$). PCTN plants grown in solutions of pH=5.5 ($\bar{x} = 4.67±1.1$ g) had significantly higher final fresh weights than those grown in pH=6.0 ($\bar{x} = 0.57±0.1$ g, $p<0.01$), pH=6.5 ($\bar{x} = 0.49±0.1$ g, $p<0.01$), and pH=7.0 ($\bar{x} = 0.66±0.3$ g, $p<0.01$). The same trend was evident for MCTN plants, where those grown in a pH=5.5 solution

($\bar{x}$ = 2.39±0.6 g) were significantly higher than the other 3 treatments (pH=6.0; $\bar{x}$ = 0.79±0.2 g, p<0.01, pH=6.5; $\bar{x}$ = 0.80±0.2 g, p<0.01, pH=7.0; $\bar{x}$ = 0.40±0.1 g, p<0.01).

Final Dry Weight

All four provenances showed final dry weight variation between pH treatments with plants grown in a solution of pH=5.5 having the highest dry weight in most cases (Table 6). TCFL plants grown in pH=5.5 solution ($\bar{x}$ = 15.52±2.8 g) had significantly higher final dry weight than TCFL plants from in pH=7.0 solution ($\bar{x}$ = 7.63±1.0 g, p<0.05). GCMS plants grown in a solution of pH=6.5 ($\bar{x}$ = 28.61±5.5 g) had a significantly higher final dry weight than those grown in a solution of pH=5.5 ($\bar{x}$ = 13.83±2.3 g, p<0.05). Plants from the PCTN provenance grown in a solution of pH=5.5 ($\bar{x}$ = 1.66±0.4 g) had significantly higher final dry weight than the other three treatments (p<0.01 for all comparisons). The same trend was evident with plants from MCTN, with those grown in a pH=5.5 solution ($\bar{x}$ = 0.75±0.2 g) having significantly higher final dry weights than the other three pH treatments (p<0.05 vs. pH=6.0, 6.5, p<0.01 vs. pH=7.0).

Root:Shoot

There was significant difference in the root to shoot ratio by provenance ($F_{3,130}$ = 6.02, p<0.001, Table 4) as well as by pH treatment ($F_{3,130}$ = 3.03, p<0.05, Table 5). However, none of the individual provenances had root to shoot ratios that differed significantly by pH treatment (p = 0.08, p = 0.49, p = 0.33, p = 0.29, TCFL-MCTN respectively, Table 6). Overall, GCMS had a significantly higher root to shoot ratio with a mean of 2.54±0.4 than TCFL ($\bar{x}$ = 1.70±0.1, p<0.05), PCTN ($\bar{x}$ = 1.12±0.1, p<0.01), and MCTN ($\bar{x}$ = 1.46±0.3, p<0.01). *V. arboreum* plants grown in a solution of pH=6.0, 6.5, and 7.0 were all similar, however plants grown in a solution of pH=5.5 were significantly lower than those grown in a solution of pH=6.0 (Table 5).

There was a positive correlation between root to shoot ratio and pH of the nutrient solution for *V. arboreum* plants from the PCTN. PCTN showed a 0.37 increase in root to shoot ratio for every unit increase in nutrient solution pH (N=35, r=0.30, $p<0.05$, Table 7).

Shoot Dry Weight

Three of the four provenances showed significant differences in shoot dry weight between pH treatments (Table 6). TCFL showed significant differences between the 4 pH solutions ($F_{3,36} = 3.31$, $p<0.05$), with *V. arboreum* grown in solutions of pH=5.5 ($\bar{x}$ = 6.45±1.3 g) being significantly greater than *V. arboreum* grown in a solution of pH=7.0 ($\bar{x}$ = 2.71±0.4 g, $p<0.05$). GCMS showed similar shoot dry weights across treatments with mean of 7.29±1.0 g ($F_{3,15} = 0.52$, $p = 0.67$). PCTN and MCTN plants showed significant shoot dry weight differences between pH treatments ($F_{3,31} = 15.49$, $p<0.001$ and $F_{3,130} = 3.03$, $p<0.05$, respectively). PCTN plants grown in a solution of pH= 5.5 had an average weight of 0.94±0.2 g and was significantly heavier than the other 3 pH treatments ($p<0.01$ for all comparisons). MCTN exhibited a similar trend in which plants grown in a solution of pH=5.5 ($\bar{x}$ = 0.49±0.2 g) showed significantly greater shoot dry weight than the more basic 3 treatments ($p<0.01$ for all comparisons).

Root Dry Weight

Unlike the shoot dry weight, only one provenance showed significant differences in root dry weight between pH treatments. TCFL, GCMS, and MCTN showed all treatments to be similar in root dry weight ($F_{3,36} = 2.17$, $p = 0.11$; $F_{3,15} = 1.55$, $p = 0.24$; $F_{3,36} = 2.62$, $p = 0.07$, respectively, Table 6). PCTN showed difference between the 4 pH treatments when looking at root dry weight, with plants grown in solution of pH=5.5 ($\bar{x}$ = 0.72±0.3 g) having significantly higher root dry weights than those grown in solutions of pH=6.0 and 6.5 ($\bar{x}$ = 0.08±0.0 g for

both, $p<0.05$ for both comparisons). Average root dry weight for TCFL, GCMS, and MCTN were 6.90±0.6 g, 16.33±2.0 g, and 0.16±0.0 g respectively.

Photosynthesis

Photosynthetic activity varied by provenance ($F_{3,130}= 4.71$, $p<0.01$, Table 4). TCFL and PCTN were similar with mean photosynthetic readings of 6.98±0.2 and 6.51±0.2 respectively. GCMS showed a mean of 7.35±0.2 and was significantly higher than the mean photosynthetic reading for MCTN ($\bar{x}$ = 6.29±0.1, $p<0.01$).

TCFL had a mean photosynthetic efficiency of 6.98±0.2. GCMS showed a mean efficiency of 7.23±0.2, and PCTN showed a mean of 6.51±0.2. MCTN showed an average of 6.29±0.1, but showed significant differences amongst the pH treatments of MCTN plants ($F_{3,36}$ = 6.74, $p<0.001$ Table 6). Post-hoc analysis showed MCTN plants grown in a solution of pH=5.5 to be significantly higher than the other treatments ($p<0.05$ vs. pH=6.0, and $p<0.01$ vs. pH=6.5, 7.0). Photosynthesis ranged from a low of 5.87±0.1 for MCTN at pH=7.0 to a high of 8.34±0.5 for GCMS at pH=5.5. The second study showed a negative correlation between solution pH and photosynthesis where for every unit increase in solution pH, there was a 0.68 unit decrease in photosynthesis (r = 0.35, $p<0.001$).

Photosynthesis also varied by substrate pH ($F_{3,113}= 7.00$, $p<0.001$, Table 5). *V. arboreum* individuals grown in a solution of pH=5.5 had significantly higher photosynthesis readings than the other 3 treatments ($p<0.01$ vs. pH=6.0, $p<0.05$ vs. pH=6.5, $p<0.001$ vs. pH=7.0).

Leaf Greenness (SPAD)

SPAD readings from September 2012 varied significantly by provenance as well as growth solution pH ($F_{3, 130}$=4.36, $p<0.01$, $F_{3, 112}$=4.62, $p<0.01$, respectively, Table 4, 5). TCFL

showed mean SPAD readings of 31.27±1.0. GCMS had mean SPAD readings of 36.28±1.5 and was significantly higher mean SPAD readings from PCTN ($\bar{x}$ = 26.85±1.81, p<0.01). MCTN had mean SPAD readings of 30.22±1.8. Similar to the photosynthesis trends, *V. arboreum* plants grown in a solution of pH=5.5 had significantly higher SPAD readings than the other 3 treatments (p<0.01 vs. pH=6.0, p<0.05 vs. pH=6.5, 7.0).

PCTN was the only provenance with SPAD differences between pH treatments ($F_{3, 31}$=7.21, p<0.001). Post-hoc testing showed PCTN plants grown in pH=5.5 solution had significantly higher SPAD readings than those grown in solutions of pH=6.0 or 6.5 (p<0.01 for both comparisons, Table 6). PCTN and MCTN provenances showed significant negative correlations between pH treatments and SPAD readings (p<0.05 for both, Table 7).

SPAD reading varied significantly by pH nutrient solution. Plants grown in a solution of pH = 5.5 showed significantly lower SPAD readings than plants grown in the other 3 pH solutions. Plants grown in a solution of pH=5.5 had a mean SPAD reading of 10.42±1.9, about half as much as plants grown in more basic solutions. Plants grown in solutions of pH=6.0, 6.5, and 7.0 were similar with means of 28.05±1.6, 29.29±1.7, and 29.15±1.4, respectively.

Discussion

In the first study, there was no significant difference in fresh weight percent change between the different pH levels. The plants grown in pH 7.0 did show the most overall growth, but this could be due in part to greater iron availability from the chelated iron source used in the nutrient solution and the increase in K as substrate pH level was increased. Only the provenance affected the final fresh and dry weights. GCMS exceeded the other provenances in regards to

percent change in growth, finished with the largest final fresh weight, and had significantly larger plants from the other provenances. In regards to *V. arboreum,* plant provenance affected growth more than nutrient solution pH in a hydroponic set up with a chelated iron source. We were not able to compare final fresh weights in the second study due to plants being at differing ages at study initiation.

In the second study both provenance and pH affected the root to shoot ratio of individuals *V. arboreum.* The plants grown in pH 7.0 had significantly higher root to shoot ratios than the plants grown in the other pH levels. There was a positive correlation between root to shoot ratio and pH of the solution; for every unit increase in pH of the solution the root to shoot ratio increased 0.15. Lloret et al. (1999) found a positive correlation between root:shoot ratio and survival during times of drought in Mediterranean shrubs. Low resource environments commonly produce plants with high root:shoot ratios, allowing them to exploit any limited resources available (Chapin et al., 1993). Martinsson (1986) found root:shoot ratio has some determination based on provenance and genotype. It is possible that the provenances with higher root:shoot ratios (LCAL and ECAL in experiment 1, GCMS and TCFL in experiment 2) are regions more likely to experience drought or are deficient in some other resource.

Only provenance affected shoot dry weight in the first study. Plants from GCMS had a higher shoot dry weight than all the plants from AL, and plants from ECAL had the lowest shoot dry weight. While not significant, the three provenances from MS (GCMS, NCMS, PCMS) had higher shoot dry weights than plants from AL (ECAL, LCAL).

In a study on maize, Canadell and Zedler (1995) suggested larger root systems may allow plants to utilize water that is deeper in the soil during drier months. Seeking out a provenance that produces larger root systems would be beneficial for drought resistance. In the first study,

root dry weight varied by provenance and there was a positive correlation between root dry weight and pH of the solution suggesting that individuals grown with a chelated iron source in a higher pH would be more drought tolerant. In the second study, only PCTN had significant differences in root dry weights between treatments. The plants from PCTN that were grown in pH 5.5 exhibited higher root dry weights than those grown on pH 6.0 or 6.5.

In the first study, Pn was not affected by provenance or pH, while in the second study Pn varied by provenance and pH. This difference could be due to the use of the chelated iron source in the first study. However, there was a negative correlation between Pn and pH in both studies; in both studies the Pn decreased as the pH increased.

The results of these studies did not lead to the discovery of *V. arboreum* from a provenance that consistently performs well in substrates with a pH higher than 5.5. There were several experimental errors made by the researcher that may have influenced the results of these studies. First, the formula for the nutrient solution had to be changed after the first study due to the use of a chelated iron source and increasing K levels in the tubs at pH levels 6, 6.5, and 7 (Figures 5,6). The higher K was a result of using KOH to buffer the nutrient solution. The second study incorporated a non-chelated iron source to more accurately represent a field setting and used HCl to buffer nutrient solution pH. These added variables could mask or add to effects seen between provenances. Second, the plant provenances had to be changed between experiments due to lack of plant material from several provenances; the second study used two provenances from the first study and incorporated three new provenances. GCMS and NCMS were the two provenances that were studied in both experiments; NCMS all died in the second study and their growth was not analyzed. The researcher attributes their death to excessive root removal at study initiation. Root removal in the second study was required to fit plants into

hydroponic tubs. The first study used plants that were all similarly sized and the second study used a variety of plant sizes: 1 gallon, 4" pot, and seedling. The 1 gallon potted *V. arboreum* had much denser root systems than the 4" pot and the seedling plants; this resulted in the post-wash retention of varying amounts of potting mix in the root systems of these plants. Much of the retained potting mix was observed in the bottom of the tubs during nutrient solution monitoring.

A repeat of this study could benefit from several changes to the way this project was executed. First, as the plants grew they became more unstable and leaned or fell over completely when secured with the neoprene disk alone. For future studies the researcher would forego the deep-water culture system and instead use 1-gallon pots filled with an inert substrate and fertigate via drip irrigation. The desire to use fertigation leads to the second change the researcher would make for future studies, using large stock nutrient solutions versus weighing and measuring nutrients on a per tub basis. The first study utilized stock nutrient solutions and it was observed that this limited human error thus saving labor and ensuring the accurateness of the nutrient solution. This would also allow for a recirculating nutrient delivery system; this would guarantee that every tub within a pH range was receiving exactly the same nutrient solution. Despite these errors, there were findings that were encouraging and demonstrated the need for further research of *V. arboreum* substrate pH tolerance with several of the changes listed above.

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Table 1. Influence of provenance on percent change, final fresh weight (FW), final dry weight (DW), root to shoot ratios, shoot dry weight (DW), root dry weight (DW), photosynthesis (Photo), and soil plant analysis development (SPAD) of *Vaccinium arboreum* individuals from 5 provenances during the 2011; Noxubee County, MS (NCMS), Lee County, AL (LCAL), Greene County, MS (GCMS), Pearl County, MS (PCMS) and Elmore County, AL (ECAL). Values are means from each provenance (± standard error). Rows with different letters after the means are significantly different.

Provenance	% Change	Final FW (g)	Final DW (g)	Root:Shoot	Shoot DW	Root DW	Photo	SPAD 9/8/2011	SPAD 12/9/2011
NCMS	32.59±8.8 *b*	17.86±2.1 *b*	6.29±1.4 *a*	0.43±0.1 *b*	4.51±1.0 *a*	1.77±0.5 *bc*	11.98±1.4	58.14±2.3 *a*	61.24±1.5 *a*
LCAL	27.97±7.1 *b*	13.55±1.5 *c*	4.74±1.4 *b*	0.69±0.1 *a*	3.11±1.0 *b*	1.62±0.4 *bc*	14.95±1.4	55.88±2.4 a*b*	46.49±2.4 c*b*
GCMS	78.53±17.4 *a*	26.94±3.7 *a*	8.46±1.5 *a*	0.50±0.0 *ab*	5.63±1.1 *a*	2.82±0.5 *a*	15.00±1.4	58.19±2.1 *ab*	54.63±1.9 *b*
PCMS	26.21±8.3 *b*	16.95±1.8 *c*	6.26±1.4 *a*	0.47±0.0 *ab*	4.35±1.0 *a*	1.91±0.5 *ab*	13.58±1.2	52.17±2.2 *bc*	52.27±1.6 *bc*
ECAL	7.79±5.3 *b*	10.49±1.1 *d*	3.65±1.4 *c*	0.65±0.1 *a*	2.32±1.0 *c*	1.33±0.4 *c*	12.66±1.4	47.01±2.3 *c*	48.12±1.8 *c*
Significance	***	***	***	**	***	***	$p = 0.24$	***	***

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Table 2. Influence of growth solution pH on percent change, final fresh weight (FW), final dry weight (DW), root to shoot ratios, shoot dry weight (DW), root dry weight (DW), photosynthesis (Photo), and soil plant analysis development (SPAD) of *Vaccinium arboreum* individuals during 2011. Values are means from each pH treatment (± standard error). Rows with different letters after the means are significantly different.

pH	% Change	Final FW	Final DW	Root:Shoot	Shoot DW	Root DW	Photo	SPAD 9/8/2011	SPAD 12/9/2011
5.5	24.88±9.4	15.37±1.7	5.31±0.6	0.48±0.0 *b*	3.70±0.4	1.63±0.5 *c*	14.83±1.3	53.52±1.4	48.63±1.6
6.0	30.22±7.6	15.13±1.5	5.66±0.6	0.49±0.0 *b*	4.00±0.4	1.67±0.5 *c*	13.59±1.0	56.23±1.4	54.29±1.7
6.5	36.82±8.9	17.38±2.1	5.93±0.6	0.52±0.0 *b*	4.01±0.4	1.89±0.5 *b*	12.66±1.1	52.81±1.6	55.28±1.3
7.0	47.37±12.6	20.71±3.1	6.75±0.9	0.71±0.1 *a*	4.32±0.6	2.38±0.5 *a*	13.57±1.4	53.26±1.9	52.88±1.8
Significance	$p = 0.42$	$p = 0.21$	$p = 0.30$	*	$p = 0.68$	**	$p = 0.33$	$p = 0.17$	$p = 0.57$

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Table 3. Correlations between pH of growth solution and various other factors in *Vaccinium arboreum* individuals during 2011. Correlations involve the entire population or a specific provenance in parentheses. Asterisks after the second factor denote level of significance.

First factor	Second factor	r	Equation
pH	Root:shoot ***	0.25	y = 0.15x-0.36
pH	Root DW *	0.18	y = 0.53x-1.43
pH	Root DW (G1)	0.24	y = 0.56x-1.61
pH	Root DW (G4) *	0.27	y = 0.70x-2.49
pH	Root DW (G5) *	0.28	y = 0.46x-1.58
pH	Photo (G5) *	0.32	y = -4.72x+42.19
pH	SPAD (G3) ***	0.50	y = 9.79x-6.75
pH	SPAD (G5) *	0.41	y = 6.04x+10.47

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Table 4. Influence of provenance on fresh weight percent change, root to shoot ratios, photosynthesis, and soil plant analysis development (SPAD) of *Vaccinium arboreum* individuals from 4 provenances during the 2012; Taylor County, FL (TCFL), Greene County, MS (GCMS), Polk County, TN (PCTN) and Marion County, TN (MCTN). Values are means from each provenance (± standard error). Rows with different letters after the means are significantly different.

Provenance	Fresh Weight % Change	Root:shoot	Photo	SPAD
TCFL	7.03±4.3 *b*	1.70±0.1 *a*	6.98±0.2 *ab*	31.27±1.0 *ab*
GCMS	-1.11±4.8 *b*	2.54±0.4 *a*	7.35±0.2 *a*	36.28±1.5 *a*
PCTN	221.01±79.3 *a*	1.12±0.1 *b*	6.51±0.2 *bc*	26.85±1.8 *b*
MCTN	101.36±37.1 *ab*	1.46±0.3 *ab*	6.29±0.1 *c*	30.22±1.8 *ab*
Significance	**	***	**	**

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Table 5. Influence of pH of growth solution on fresh weight percent change, root to shoot ratios, photosynthesis (Photo), and soil plant analysis development (SPAD) of *Vaccinium arboreum* individuals during 2012. Values are means from each pH treatment (± standard error). Rows with different letters after the means are significantly different.

pH	Fresh Weight % Change	Root:shoot	Photo	SPAD
5.5	319.06±91.4 *a*	1.09±0.1 *b*	7.61±0.2 *a*	10.42±1.9 *a*
6	21.97±9.0 *b*	1.99±0.4 *a*	6.55±0.2 *b*	28.05±1.6 *b*
6.5	25.69±6.9 *b*	1.75±0.2 *ab*	6.69±0.2 *b*	29.29±1.7 *b*
7	6.02±7.4 *b*	1.88±0.2 *ab*	6.26±0.1 *b*	29.15±1.4 *b*
Significance	***	*	***	**

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Table 6. Influence of substrate pH on fresh weight percent change, final fresh weight (FW), final dry weight (DW), root to shoot ratios, shoot dry weight (DW), root dry weight (DW), photosynthesis (Photo), and soil plant analysis development (SPAD) of specific provenances of *V. arboreum* individuals during 2012. Values are means from each provenance (± standard error). Asterisks denote significance.

Provenance	pH	Fresh Weight % Change	Final FW (g)	Final DW (g)	Root:Shoot	Shoot DW (g)	Root DW (g)	Photo	SPAD
TCFL									
N=40	5.5	6.78±5.9	49.37±8.5	15.52±2.8	1.40±0.2	6.45±1.3	9.08±1.7	7.16±0.3	34.32±1.8
	6.0	12.19±4.7	36.53±5.0	10.89±1.3	2.03±0.3	3.80±0.5	7.09±1.0	6.84±0.3	29.35±2.3
	6.5	-1.23±5.3	31.50±5.4	11.47±1.9	1.38±0.1	4.93±0.9	6.54±1.1	7.48±0.4	33.01±1.0
	7.0	10.00±14.7	22.23±3.1	7.63±1.0	1.98±0.3	2.71±0.4	4.92±0.7	6.49±0.2	28.56±2.0
Significance		NS	*	*	NS	*	NS	NS	NS
GCMS									
N=19	5.5	6.68±11.4	46.23±7.9	13.83±2.3	1.46±0.2	5.73±1.2	8.10±1.5	8.34±0.5	36.97±1.7
	6.0	-6.22±14.9	74.20±7.9	23.85±3.3	2.39±0.7	8.10±2.5	15.75±2.1	7.30±0.9	29.89±5.8
	6.5	3.14±7.3	97.48±18.4	28.61±5.5	3.17±0.8	8.53±2.0	20.08±3.7	7.20±0.3	36.16±2.5
	7.0	-9.54±9.8	71.86±13.5	21.34±4.7	3.02±0.3	5.75±1.5	15.59±3.3	6.65±0.2	39.85±1.3
Significance		NS	NS	*	NS	NS	NS	NS	NS
PCTN									
N=35	5.5	763.00±230.9	4.67±1.1	1.66±0.4	0.75±0.3	0.94±0.2	0.72±0.3	7.80±0.6	35.63±3.7
	6.0	12.89±21.3	0.57±0.1	0.15±0.0	1.17±0.2	0.07±0.0	0.08±0.0	6.12±0.2	21.19±1.4
	6.5	62.41±18.0	0.49±0.1	0.15±0.0	1.23±0.3	0.07±0.0	0.08±0.0	5.94±0.1	18.55±3.2
	7.0	17.59±21.4	0.66±0.3	0.23±0.1	1.33±0.2	0.10±0.1	0.13±0.1	6.03±0.1	26.61±1.9
Significance		**	***	**	NS	***	*	NS	***
MCTN									
N=40	5.5	325.93±125.3	2.39±0.6	0.75±0.2	0.67±0.1	0.49±0.2	0.27±0.1	7.01±0.3	37.26±4.9
	6.0	46.55±20.6	0.79±0.2	0.27±0.1	2.40±1.2	0.10±0.0	0.17±0.1	6.18±0.2	30.02±2.9
	6.5	33.94±8.6	0.80±0.2	0.26±0.1	1.42±0.2	0.11±0.0	0.15±0.0	6.01±0.1	27.40±2.7
	7.0	-0.97±6.3	0.40±0.1	0.12±0.0	1.37±0.2	0.05±0.0	0.07±0.0	5.87±0.1	24.18±2.1
Significance		***	***	**	NS	*	NS	***	NS

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

Table 7. Correlations between substrate pH fresh weight percent change (% change), root to shoot ratios, photosynthetic activity (Photo), and leaf greenness (SPAD) in *Vaccinium arboreum* individuals during 2012. Correlations involve the entire population or a specific provenance in parentheses. Asterisks after the second factor denote level of significance.

Explanatory Variable	Response Variable	r	Equation
pH	% change (G4) ***	0.55	y = -4.53x+30.62
pH	% change (G5) ***	0.48	y = -1.99x+13.43
pH	Root:shoot (G4) *	0.3	y = 0.37x-1.18
pH	Photo ***	0.35	y = -0.68x+10.99
pH	SPAD (G4) **	0.39	y = -6.85x+6930
pH	SPAD (G5) **	0.41	y = -8.60x+83.46

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Figure 1. Influence of provenance on fresh weight percent change of *Vaccinium arboreum* individuals from 5 provenances during the first study in 2011; Noxubee County, MS (NCMS), Lee County, AL (LCAL), Greene County, MS (GCMS), Pearl County, MS (PCMS) and Elmore County, AL (ECAL). Values are means from each provenance (± standard error). Bars with different letters above are significantly different.

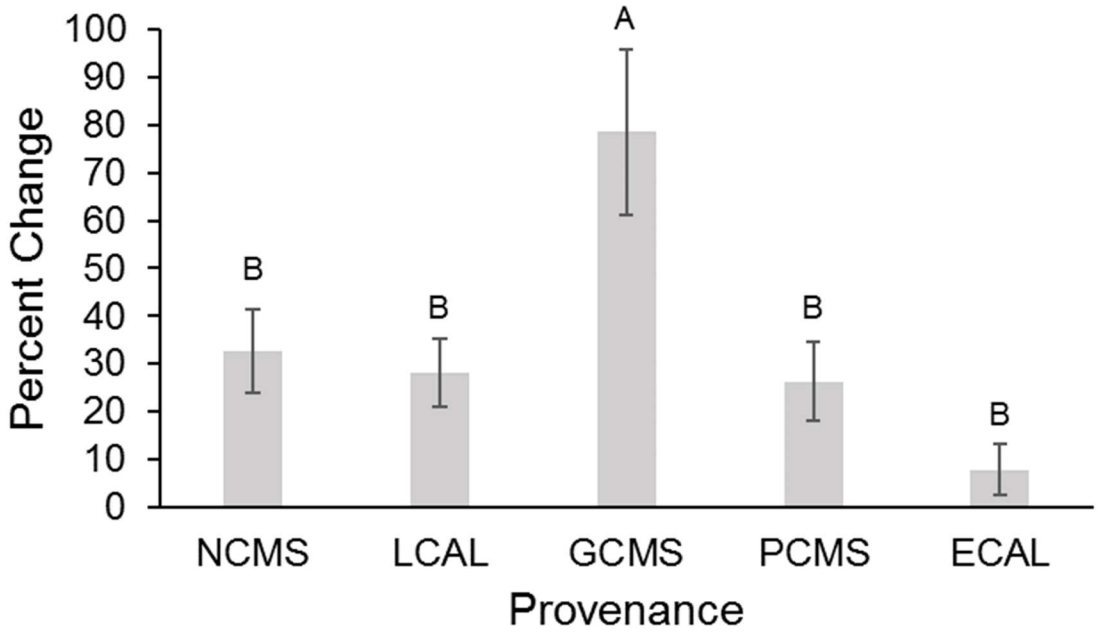


Figure 2. Influence of provenance on fresh weight percent change of Vaccinium arboreum individuals from 4 provenances during the second study in 2012; Taylor County, FL (TCFL), Greene County, MS (GCMS), Polk County, TN (PCTN) and Marion County, TN (MCTN). Values are means from each provenance (± standard error). Bars with different letters above are significantly different.

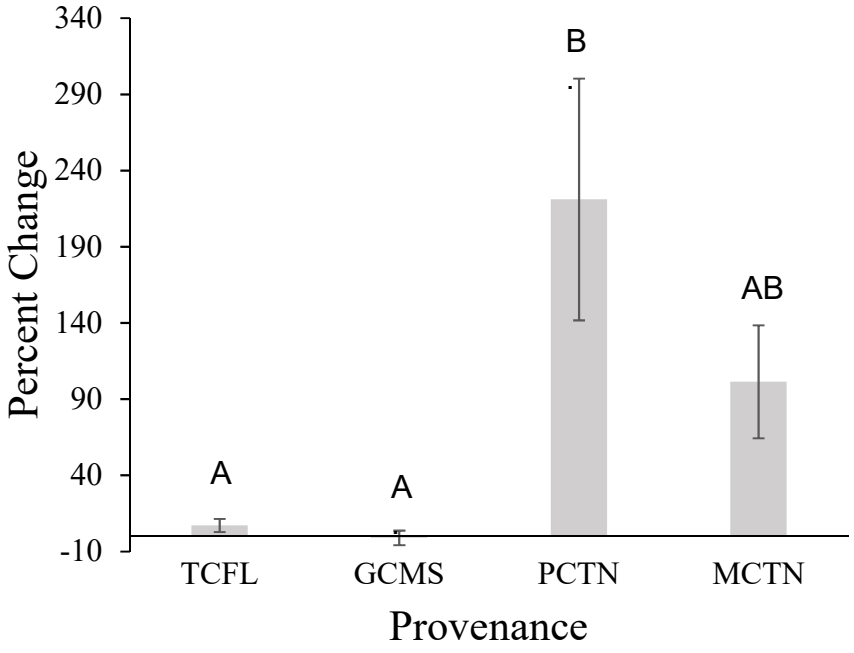


Figure 3. Influence of pH on fresh weight percent change of specific provenances of *Vaccinium arboreum* individuals during the second study in 2012. Values are means from each provenance (± standard error). Bars with different letters above are significantly different.

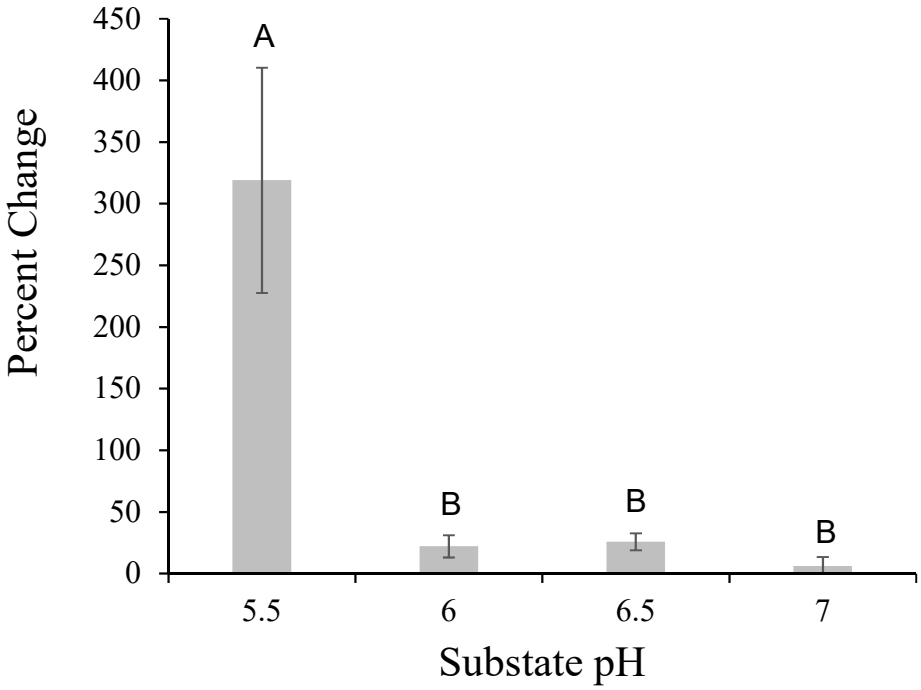


Figure 4. Influence of provenance and substrate pH on fresh weight percent change of *Vaccinium arboreum* during the second study in 2012. Provenances with asterisks above exhibit significantly different growth between pH treatments. * $p<0.05$, ** $p<0.01$, $p<0.001$

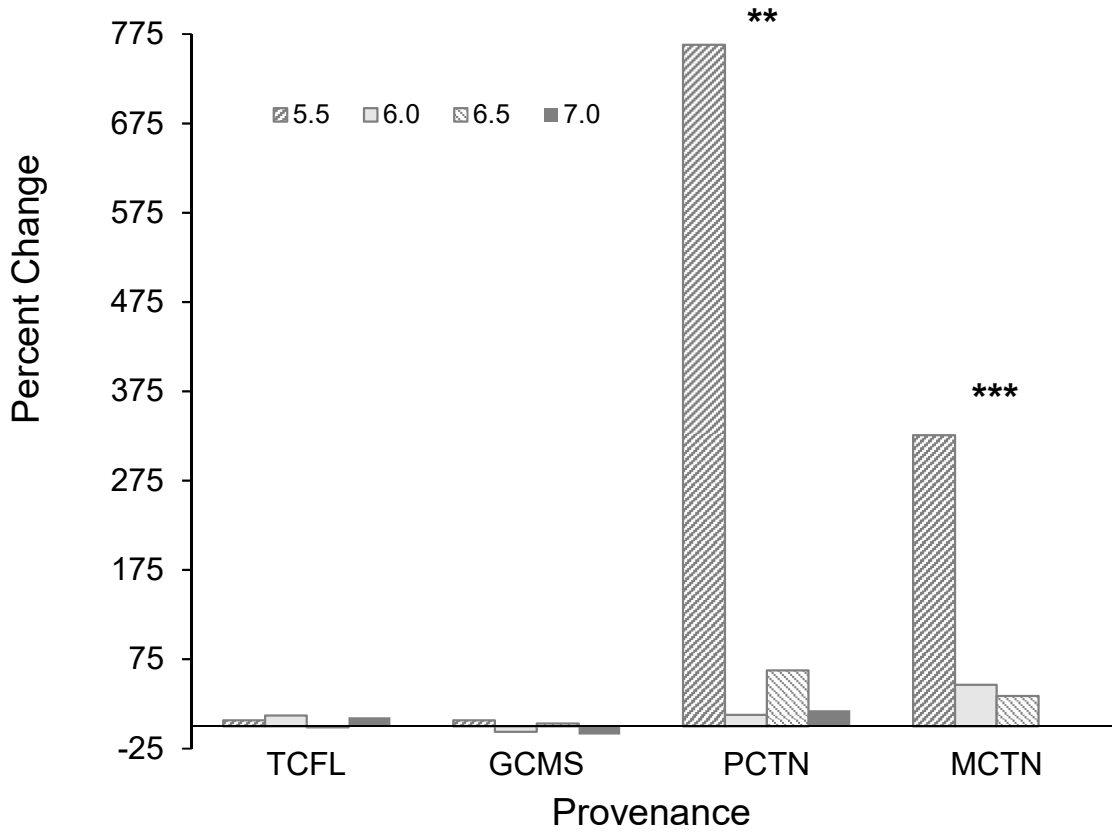


Figure 5. Potassium (K) concentration over time in first study (2011)

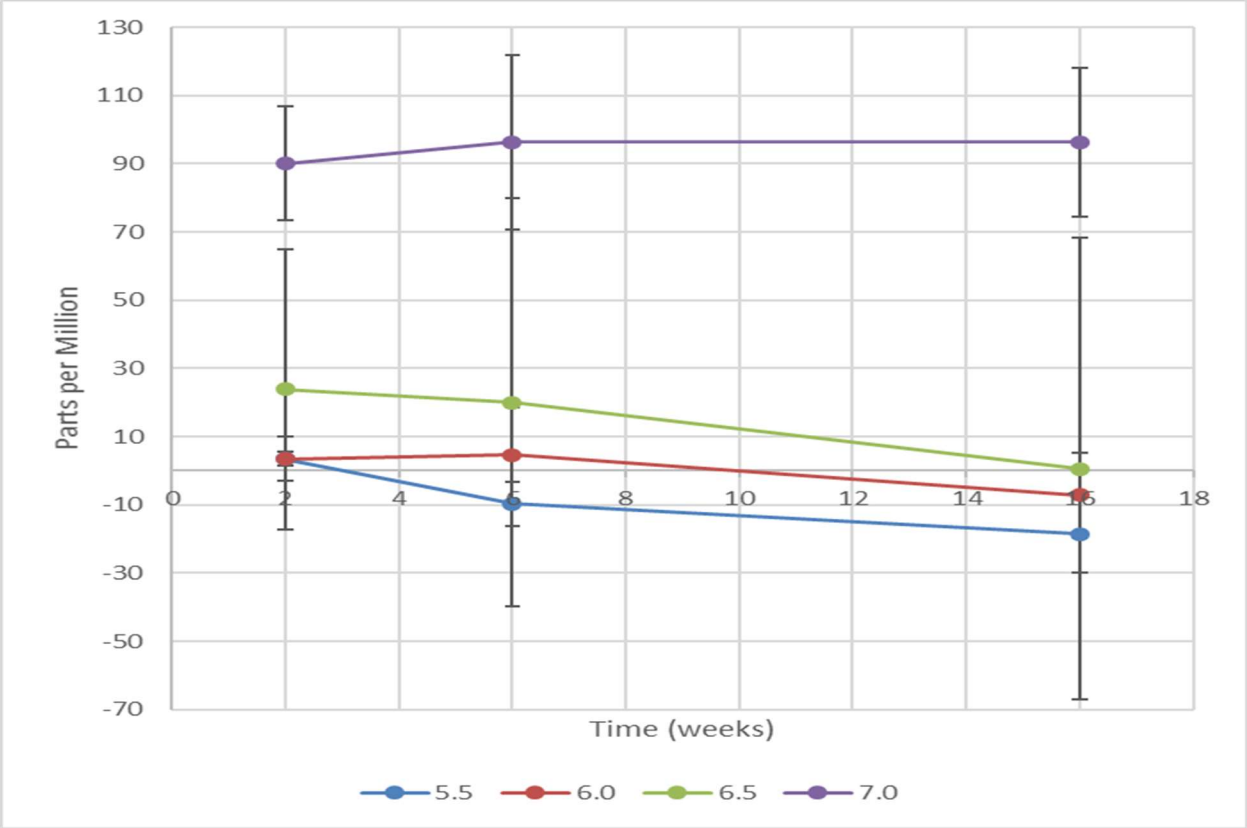
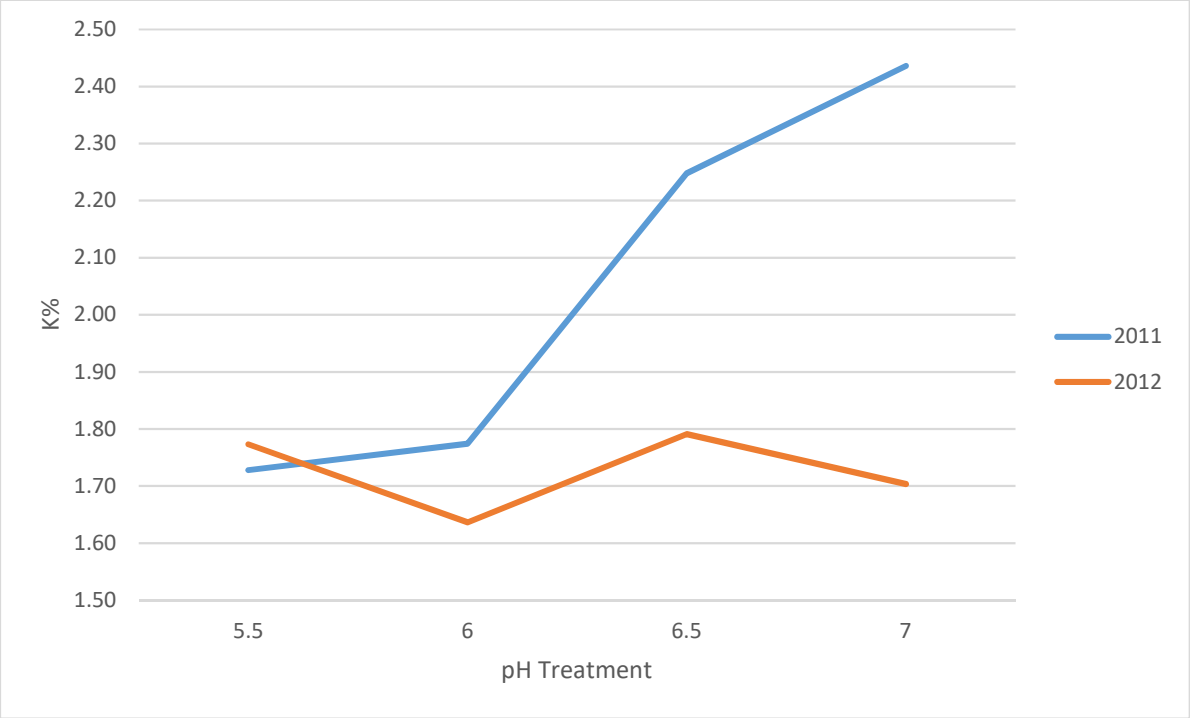
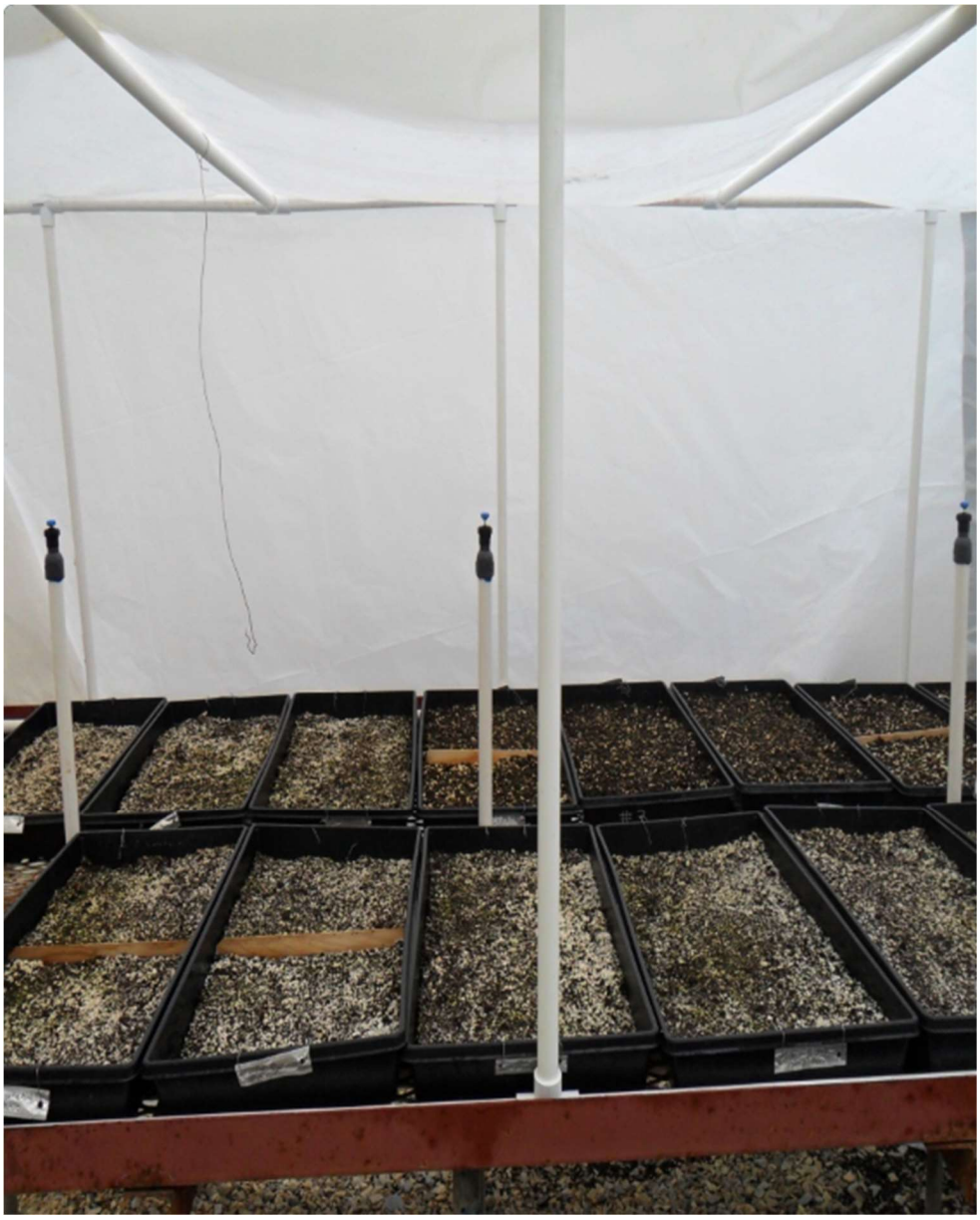


Figure 6. Potassium (K) concentration in leaves



Appendix



Open flats of seedlings grouped by provenance

Seedlings in 4” pots grouped by provenance

Fertigation system

Hydroponic tub setup