

Blueberry Germplasm Screening at Several Soil pH Regimes. I. Plant Survival and Growth

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Abstract. Thirty-three seedling progenies from crosses among *Vaccinium corymbosum* L., *V. angustifolium* Ait., and *V. corymbosum/V. angustifolium* hybrid-derivative parents, and 'Northblue', 'Northsky', and 'Northcountry' were grown for 2 years at three soil pH levels at Becker, Minn. Iron sulfate and lime were incorporated to amend the soil to pH levels of 4.0 and 6.5, respectively; the native soil, pH 4.5, was the third pH regime. The plants grew well in the low pH regime, poorly in the high pH regime, and intermediately in the native pH regime. Variation among populations was significant for all traits except vitality 18 months after being planted, and pH treatment affected all traits. The pH regime x population interactions were not significant for any of the plant performance characteristics. Nondestructive subjective and objective measurements were positively and highly correlated with total plant dry weight. Therefore, populations could be effectively evaluated for tolerance to higher pH without destroying the plant. *Vaccinium angustifolium* was not a general source of tolerance to higher pH, but some populations derived from *V. angustifolium* were tolerant of high soil pH.

Highbush blueberry (*V. corymbosum*) plants are native to acidic, moist, and well-drained soils that are high in organic matter (Cain, 1952; Coville, 1910; Galletta, 1975; Harmer, 1944; Korcak et al., 1982). Various cultural techniques, such as pH-modifying soil amendments, irrigation, and mulching, allow commercial production on sites that are less than ideal. Acidifying soil amendments can be expensive and may not be long-term solutions for production on high-pH soils. Researchers have spent much effort devising cultural systems to adapt the soil medium to the plant, but less effort has been devoted toward developing cultivars adapted to variable soils.

Upland mineral soils are drier and tend to have a lower organic content and higher pH than ideal blueberry soils (Chandler et al., 1985). The U.S. Dept. Agr. (USDA) Beltsville Agricultural Research Center Fruit Laboratory (blueberry research group) has studied upland mineral soil adaptation in *V. angustifolium* Ait., *V. corymbosum*, *V. ashei* Reade, *V. darrowi* Camp, *V. myrtilloides* Michx., *V. atrococcum* Ait., *V. tenellum* Ait., and *V. myrsinites* Lamarck, largely through hybrid progeny performance (Brown and Draper, 1980; Chandler et al., 1985; Erb et al., 1988; Korcak, 1986a, 1986b; Korcak et al., 1982; and Reich et al., 1982). Most of the research conducted on upland mineral soil adaptation has concentrated on species that have been used to improve southern highbush blueberries. Upland mineral soil adaptation in *V. angustifolium* has been suggested (Chandler et al., 1985; Johnston, 1948; Korcak et al., 1982; Korcak, 1989) and would be valuable to blueberry breeders developing cultivars for more northern regions.

Brown and Draper (1980) described greenhouse solution culture methods for screening for Fe efficiency in blueberry. They suggested that the more Fe-efficient plants would also be more tolerant of higher pH soils. Most greenhouse or field studies using container-grown plants have concentrated on the effects of various

soil characteristics, such as nutrient concentration (Herath and Eaton 1968; Holmes, 1960; Jackson et al., 1976), nutrient form (Cain, 1952; Townsend, 1971), pH levels (Hall et al., 1964; Herath and Eaton, 1968; Korcak et al., 1982; Townsend, 1971), and leachate watering solutions (Korcak et al., 1982; Reich et al., 1982), on plant growth rather than selection for tolerance to higher pH. The heritability of tolerance of higher pH or upland mineral soil adaptability has only recently been examined. Chandler et al. (1985) suggested that variation in adaptability to upland soil is due largely to additive genetic variance. Gupton and Spiers (1992) reported considerable variability and heritabilities of 0.37 and 0.43, respectively, for shoot weight and visual rating for rabbiteye blueberries growing in pots under chlorosis-inducing conditions.

The objectives of this study were to screen blueberries in a field to determine whether variability exists for tolerance of higher soil pH and, if variability exists, to identify tolerant germplasm.

Materials and Methods

To determine tolerance to higher soil pH, blueberry populations were grown in three soil pH regimes and assessed for diverse traits (Table 1). Particular attention in analysis was given to vitality (see Table 1), a trait that could be nondestructively and efficiently evaluated in a breeding program, and aboveground dry weight, which provides an accurate assessment of plant size but is destructive.

The diverse germplasm was divided into the following groups to expose more subtle differences based on population or species ancestry (Tables 2 and 3): 1) Interspecific crosses (*V. angustifolium/V. corymbosum*). Originally 49 populations from a diallel cross among seven parents were to be included for combining ability analysis. However, the seed from these populations germinated poorly, and only 10 of 21 potential populations (ignoring populations from self-pollinations and bulking seed from reciprocal crosses) were available subsequently in adequate numbers. 2) Lowbush crosses. Ten *V. angustifolium* genotypes were crossed in a diallel mating scheme. Sixteen of 45 possible populations (ignoring populations from self pollinations and bulking seed from reciprocal crosses) were included. 3) Fall fruiting lowbush. Four open pollinated populations of largely *V. angustifolium* ancestry initially were selected for high levels of off-season fruiting (Fear

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Table 1. Subjective scores and objective measurements made on field-grown blueberry plants.

Trait	Description
Subjective ²	
Vitality	1–9 scale; 1 = chlorotic, reduced leaf size, or weak; 9 = green, healthy, and vigorous
Root system vitality	1–9 scale; 1 = weak, 9 = vigorous or extensive
Root branching	1–5 scale; 1 = very coarse, 5 = very fine
Objective	
Percent survival, Sept. 1987	
June 1988	
Aug. 1988	The proportion of live plants on three different dates
Ht (cm)	Height of tallest upright stem
Area (cm ²)	Product of two perpendicular plant diameter measurements
Volume (cm ³)	Product of height and area
Dry wt aboveground (g)	Dry weight of the leaves, stems, and the portion of the plant crown above which branching started
Belowground (g)	Dry weight of the roots and the portion of the crown below the soil surface that had no stem branches
Total (g)	Sum of above- and belowground dry weights

²All evaluations were made on plants harvested on 7 Sept. 1988, except as indicated.

Table 2. Ancestry of parents used in crosses and cultivars.

Parent	Ancestry
B-6	<i>Vaccinium corymbosum</i> (G-65) x <i>V. corymbosum</i> ('Ashworth')
B-10	
B-16	
B-22	
GR-1	<i>V. angustifolium</i> x <i>V. corymbosum</i>
GR4-32	<i>V. angustifolium</i> (Cass County, Minn.)
GR11-36	
GR12-28	
GRVa	<i>V. angustifolium</i>
MN-61	<i>V. corymbosum</i> (U.S. Dept. Agr. 11-93) x <i>V. angustifolium</i>
N7084	<i>V. angustifolium</i> (Chippewa N.F., Minn.)
N7068	<i>V. angustifolium</i> (Stead, Manitoba)
N7094	
N70112	
N70100	<i>V. angustifolium</i> (Agassiz Forest Reserve, Manitoba)
N70102	
N70119	
N70146	<i>V. angustifolium</i> (Scooty Lake, Minn.)
N70153	
N70249	<i>V. angustifolium</i> (Beltrami Island State Forest, Minn.)
R2P4	<i>V. corymbosum</i> x <i>V. angustifolium</i>
'Spartan'	<i>V. corymbosum</i>
US-3	<i>V. corymbosum</i> ('Dixi') x <i>V. angustifolium</i> (Mich. Lowbush #1)

et al., 1985). 4) Cultivars. 'Northblue', 'Northcountry', and 'Northsky' were derived from *V. corymbosum* and *V. angustifolium* (Luby et al., 1986).

No pure *V. corymbosum* was included in this germplasm due to its poor adaptation to Minnesota's climate.

Blueberry seeds were sown in Dec. 1986 on sphagnum peat under mist in the greenhouse. Seedlings and rooted microcuttings of the cultivars were transplanted into 5 x 5 x 6 cm peat pots filled with a sphagnum peat/Pro-mix medium and grown until 1 June 1987, in the greenhouse. The seedlings were moved to an outdoor lath house 2 weeks before planting for acclimation to field conditions. The cultivars and seedlings ranged from 10 to 30 cm tall at planting on 23 June 1987.

The planting was located at the Sand Plain Research Farm in Becker, Minn., on a Hubbard loamy sand (sandy, mixed, Udorthentic Haploborolls) with 2% to 3% organic matter and soil pH of 5.5

(1:1, soil : water paste). Selected elemental analyses were as follows (mg·kg⁻¹): P (Bray P1 extraction), 61; K, Ca, and Mg (1N ammonium acetate extraction), 7 1,552, and 88, respectively; Fe, Mn, Zn, and Cu (DTPA extraction) 40, 28, 1.1, and 1.9, respectively. The site was divided into four blocks and, within each block, three pH regimes were randomly assigned to 9 x 15 m sections. Soil pH was monitored from pretreatment through planting, until the plants were harvested from the field. Low pH (≈5.0) and high pH (≈6.5) treatments were established in Oct. 1986, which, along with the native soil (pH ≈5.5), gave three pH regimes. Ground dolomitic limestone equivalent to 10.9 t·ha⁻¹ and FeSO₄·H₂O (20% Fe) equivalent to 5.4 t·ha⁻¹ were incorporated to establish the high and low pH regimes, respectively. An additional 7.1 t·ha⁻¹ of dolomitic limestone was incorporated into the high pH treatment in May 1987.

Black polyethylene (1.2 m wide and 0.4 mm thick) was laid in

strips with 1.8 m between row centers 1 month before planting. The plants, in peat pots, were planted through the black polyethylene mulch on 23 June 1987. The plants were spaced 0.3 m apart within the rows in double rows 0.5 m apart. From two to five plants representing each population were randomly planted as a group within each plot. Fertilizer was not applied during the study because of relatively high initial levels of most nutrients. Weeds were controlled by hand within the rows and by applying 4-(dipropylamino)-3,5-dinitrobenzenesulfonamide (oryzalin) and 2-[1-(ethoxyimino) butyl-5-[2-(ethylthio) propyl]-3-hydroxy-2-cyclohexen-1-one (sethoxydim) between the rows. All blossoms and fruit were removed from the plants. The sandy soil required regular irrigation. Using sprinkler irrigation, 25 mm of water per week were applied during the growing season and up to 50 mm per week during the drought summer of 1988. The irrigation water ranged between pH 7.5 and 8.3. Plants were dug and removed from the field for analysis on 7 Sept. 1988. After being measured for height and diameter, they were dried at 60C for 1 week before measuring dry weight.

Analyses of variance (ANOVA) were calculated as a split plot replicated in four blocks with soil pH regimes as main plots and populations as subplots. Soil pH regimes and populations were considered fixed effects. The effects of pH regime were tested using the pH regime \times block term (error a), and population effects and pH regime \times population interactions were tested using the pH regime \times population \times block term (error b). The ANOVA for all blueberry plant material included all populations, and each group also was analyzed separately for all traits. Because the asexually propagated cultivars were used as controls for performance, they were also included in the overall analysis. The low pH regime had growth measurement variances that differed 10-fold from the high pH regime; therefore, measurements were logarithmically transformed (base 10) for analysis (Steele and Torrie, 1980).

Results and Discussion

When the plants were harvested, the soil pH levels at 0 to 15 cm sample depth were 5.0 ± 0.2 for the low pH treatment, 5.5 ± 0.1 for the native soil, and 6.5 ± 0.3 for the high pH treatment. At 15 to 30 cm, the pH was 5.4 ± 0.2 for all pH regimes.

Visual differences in plant growth indicated clearly that the pH regimes were effective in causing plant growth differences. Since the amendments contained Fe and S or Ca and Mg, the addition of these nutrients also may have affected plant growth in addition to pH-induced changes in nutrient availability. In particular, the Fe supplied by the iron sulfate amendment in the low pH regime might seem to benefit a calcifuge such as blueberry. However, Fe becomes substantially more available in most soils when the pH is lowered by any method (Tisdale et al., 1985). Plants grew very well in the low pH regime, poorly in the high pH regime, and intermediately in the native pH regime, as indicated by vitality and aboveground dry weight (Table 3). The root systems were often extensive in the low pH regime, penetrating up to 30 cm into the soil, whereas in the high pH regime, they often extended only several millimeters beyond the peat pot. Individual plants and populations that appeared to grow better than others could be visually identified.

Individual plant selections were made from the high pH regime for use in the Minnesota breeding program. The selected plants were more vigorous or less chlorotic than other plants, although they were not as vigorous as the plants in the native or low pH regime. Soil samples also were collected from the soil around these

selected plants, to ascertain whether local pH effects differed from the overall pH level of the block. The correlation between the plot pH and the pH measured in the root zone of the selected plants was positive and high ($r = 0.88$, $P \leq 0.01$). This correlation suggests that the plants selected in the high pH treatment were, in fact, exposed to the higher soil pH level and would be candidates for further testing of tolerance to higher pH soils.

Significant variation due to pH regime was observed for root vitality and root branching ($P \leq 0.05$) but not for percent plant survival. Populations varied for root vitality ($P \leq 0.10$), root branching ($P \leq 0.01$), and percent survival ($P \leq 0.05$). The pH regime \times population interactions, indicative of higher pH tolerance, were not significant ($P > 0.10$) for any trait except root branching ($P \leq 0.01$). In the overall populations, survival declined from 96% in Sept. 1987 to 88% in May 1988 to 78% in Aug. 1988.

In general, plants had finer roots in the low pH treatment and coarser roots in the high pH treatment (data not presented). In contrast, Townsend (1971) reported that roots of 'Blueray' grown in solution at pH 3.0 were coarsest and became appreciably finer in plants grown at higher pH levels, up to pH 6.0.

For the aboveground traits, which could be estimated more easily than root traits in a breeding program, the groups were analyzed together and separately to discern the basis for interpopulation variation. In the analysis of all plant material, variation in mean squares among pH regimes and populations was significant, but the pH regime \times population interaction was not significant, for vitality, area, volume, and aboveground dry weight (Table 4). The pH regime mean squares were always much larger than the population or interaction mean squares.

Populations from the interspecific crosses showed little variation, although the effects related to pH regime were significant for all of the traits (Table 4). Lack of variation among populations for this group was surprising because it presumably contained the most genetic diversity.

Since the population \times pH regime interaction was not significant, selecting the most vigorous progenies at low pH should be an effective way to select the most vigorous progenies at high pH. However, the correlations between the dry weight values in Table 3 across the pH regimes were low and not significant ($P > 0.05$) in interspecific crosses ($r = 0.38$, low pH with native pH; $r = 0.19$, low pH with high pH; $r = 0.17$, native pH with high pH; $df = 8$) and the lowbush crosses ($r = 0.19$, low pH \times native pH; $r = 0.29$, low pH by high pH, $r = 0.10$, native pH \times high pH; $df = 14$). These low correlation coefficients may have resulted from high plot-to-plot variation that could be reduced with more replication.

Although the pH regime \times population interactions were not significant, three populations (8602, 8641, and 8645) had larger aboveground dry weight means than all other seedling populations under the high pH treatment (Table 3). These three populations represented interspecific combinations of *V. corymbosum* and *V. angustifolium*. Two of the three populations were derived from GR-1 (8641 and 8645), which was also identified as being more tolerant of high pH in vitro (Finn et al., 1991). GR-1 should be evaluated further as a potential source of higher pH tolerance.

The lowbush crosses and fall fruiting lowbush germplasm groups have largely *V. angustifolium* ancestry. Variation because of pH regime for the objective traits was significant for both groups (Table 4). The lowbush crosses group showed significant variation among populations, while the fall fruiting group did not. This difference between the groups was not surprising, as the lowbush crosses were derived from more diverse sources (Table 2). Although the aboveground dry weight means for this group as a

Table 3. Population means within each treatment for Sept. 1988 vitality scores and the logarithmically transformed aboveground dry weight.

Population (ancestry)	Vitality ^z			Aboveground dry wt.(g, log10) ^y					
	Low pH	Native pH	High pH	Low pH		Native pH		High pH	
Cultivars									
Northsky (B-6 x R2P4)	6.6	6.0	3.8	0.92	(8.3)	0.75	(5.6)	0.05	(1.1)
Northcountry (B-6 x R2P4)	6.6	5.7	4.2	1.08	(12.0)	0.81	(6.5)	0.36	(2.3)
Northblue (B-10 x US-3)	6.8	5.6	5.2	1.20	(8.7)	0.93	(8.5)	0.48	(3.0)
Interspecific crosses									
8602 (MN-61 x GRVa.)	6.4	4.8	4.6	1.30	(20.0)	0.94	(8.7)	0.74	(5.5)
8603 ('Spartan' x GRVa.)	5.9	6.7	2.3	1.16	(14.5)	1.11	(12.9)	0.06	(1.1)
8605 (GR-1 x GRVa.)	5.5	6.2	2.8	1.10	(12.6)	0.86	(7.2)	0.23	(1.7)
8616 (N70249 x 'Spartan')	6.3	6.0	2.4	1.44	(27.5)	1.01	(10.2)	0.23	(1.7)
8617 (N70249 x 'Northblue')	6.2	5.4	3.4	1.16	(14.5)	0.56	(3.6)	0.34	(2.2)
8619 (MN-61 x 'Northblue')	4.9	4.9	3.1	0.92	(8.3)	0.79	(6.2)	0.18	(1.5)
8628 (N70249 x B-16)	5.0	6.0	3.4	1.03	(10.7)	0.84	(6.9)	0.45	(2.8)
8634 (MN-61 x 'Spartan')	7.5	5.1	3.1	1.27	(18.6)	0.81	(6.5)	0.38	(2.4)
8641 (GR-1 x 'Spartan')	5.9	5.6	4.9	1.05	(11.2)	1.01	(10.2)	0.87	(7.4)
8645 ('Northblue' x GR-1)	8.1	6.2	4.1	1.48	(30.2)	1.05	(11.2)	0.66	(4.6)
Fall fruiting lowbush									
85306 ((N70249 x B-22)OP ^x)	6.8	4.4	3.3	0.79	(6.2)	0.63	(4.3)	0.09	(1.2)
85319 (GR4-32 OP ^x)	7.9	5.0	3.0	1.46	(28.8)	0.72	(5.2)	0.03	(1.1)
85335 (GR11-36 OP ^x)	6.5	7.4	3.6	1.05	(11.2)	1.13	(13.5)	0.26	(1.8)
85336 (GR12-28 OP ^x)	5.6	4.9	4.1	1.13	(13.5)	0.28	(1.9)	0.38	(2.4)
Lowbush crosses									
86200 (N7068 x N7084)	5.8	5.3	3.8	0.86	(7.2)	0.68	(4.8)	0.30	(2.0)
86202 (N7068 x N70100)	5.0	4.9	1.5	0.52	(3.3)	0.58	(3.8)	-0.54	(0.3)
86203 (N7068 x N70112)	6.0	4.9	3.1	0.88	(7.6)	0.56	(3.6)	0.47	(2.9)
86204 (N7068 x N70119)	4.9	4.8	3.8	0.60	(4.0)	0.25	(1.8)	0.05	(1.1)
86205 (N7068 x N70146)	4.2	4.9	1.8	0.35	(2.2)	0.51	(3.2)	-0.47	(0.3)
86206 (N7068 x N70153)	5.1	4.5	1.8	0.62	(4.2)	0.62	(4.2)	-0.33	(0.5)
86207 (N7068 x N7094)	8.3	5.3	3.5	1.39	(24.5)	0.59	(3.9)	-0.03	(0.9)
86212 (N7084 x N70102)	4.4	6.0	2.0	0.16	(1.4)	0.63	(4.3)	-0.41	(0.4)
86214 (N7084 x N70146)	4.1	4.5	3.1	0.37	(2.3)	0.66	(4.6)	0.05	(1.1)
86216 (N7094 x N7084)	7.1	2.8	3.4	1.00	(10.0)	-0.01	(1.0)	0.26	(1.8)
86241 (N70102 x N70119)	4.1	5.0	1.3	0.57	(3.7)	0.46	(2.9)	-0.73	(0.2)
86242 (N70102 x N70146)	4.8	5.2	2.8	0.66	(4.6)	0.53	(3.4)	0.00	(1.0)
86261 (N70119 x N7094)	6.4	5.7	2.8	0.79	(6.2)	0.97	(9.3)	0.08	(1.2)
86265 (N70119 x N70146)	6.9	6.4	1.4	1.19	(15.5)	0.95	(8.9)	-0.27	(0.5)
86283 (N70153 x N7098)	8.1	5.7	1.4	1.50	(31.6)	0.70	(5.0)	-0.22	(0.6)
86287 (N70153 x N70146)	7.4	4.8	3.1	1.19	(15.5)	0.79	(6.2)	0.26	(1.8)
LSD 0.05		2.7				0.66			
All plant material	6.1	5.4	3.1	0.98	(9.5)	0.72	(5.2)	0.13	(1.3)

^zVitality scale ranged from 1-9; 1 = weak or chlorotic, 9 = green, healthy, and vigorous.

^yNumbers in parentheses are antilogs of means expressed in grams.

^xOP = open pollinated in a collection of *Vaccinium angustifolium*.

whole were very low, and population differences are probably not horticulturally significant, they suggested that the geographic diversity of *V. angustifolium* germplasm was important.

Variation was detected among the three Minnesota cultivars and among pH regimes, but the pH regime × cultivar interaction was not significant (Table 4). The consistent relative vigor of these cultivars, regardless of pH regime ('Northblue' > 'Northcountry' > 'Northsky'), reflects their performance throughout most other studies [i.e., yield trials, location trials, or commercial plantings (Luby et al., 1986)]. The higher dry weight and greater vitality of 'Northblue' at high pH probably reflects its greater vitality in general.

Analysis of the correlation coefficients suggested several practical implications for blueberry breeding programs (Table 5).

Correlations of plant area, volume, or vitality score with aboveground and total plant dry weights were large and positive. Nondestructive methods effectively evaluated the relative performance of this germplasm as in other studies (Chandler et al., 1985; Gupton and Spiers, 1992). Some loss of precision in selection for dry weight may result when vitality scores are used as a selection criteria, as vitality was not as highly correlated with plant dry weight as area or volume, but scoring vitality is a far less time consuming means of evaluating plant growth. The nearly perfect correlation between aboveground dry weight and total plant dry weight suggested that the aboveground portion of the plant could be harvested for a precise estimation of dry weight production without sacrificing the plant.

Table 4. Mean squares for treatment effects and interactions for all blueberry plant material and the four subgroups for aboveground traits.

Source	df	Mean squares			
		Vitality	Plant area (cm ² , log ₁₀)	Plant volume (cm ³ , log ₁₀)	Aboveground dry wt (g, log ₁₀)
All plant material					
pH regime	2	352.88*	23.11**	40.43**	25.98**
Population (pop.)	32	5.17#	0.69**	1.41**	0.74**
pH regime × pop.	64	3.43	0.18	0.30	0.23
Interspecific crosses					
pH regime	2	87.30#	4.60*	7.97*	6.15*
Pop.	9	2.66	0.12	0.25	0.25
pH regime × pop.	18	2.92	0.07	0.12	0.14
Lowbush crosses					
pH regime	2	185.62*	14.14**	23.98**	13.77**
Pop.	15	4.81	0.61**	1.00**	0.59*
pH regime × pop.	30	4.64	0.28	0.45	0.35
Fall fruiting lowbush					
pH regime	2	41.85*	2.39*	4.30*	3.41*
Pop.	3	2.61	0.18	0.27	0.23
pH regime × pop.	6	4.64	0.18	0.33	0.43
Cultivars					
pH regime	2	15.72#	1.65*	3.10*	1.86*
Cultivar (cult.)	2	0.62	0.30*	0.67*	0.27*
pH regime × cult.	4	0.84	0.01	0.01	0.02

#,*,**Probability that F is >1 ($P \leq 0.10, 0.05$, and 0.01 , respectively)

Table 5. Correlation coefficients over all pH regimes and within each pH regime, among final vitality score, and the logarithmically transformed (base 10) values for height, area, volume, aboveground plant dry weight, and total dry weight.

Trait and pH regime	Plant			Aboveground	Total plant
	Ht (cm, log ₁₀)	Area (cm ² , log ₁₀)	Volume (cm ³ , log ₁₀)	dry wt (g, log ₁₀)	dry wt (g, log ₁₀)
Vitality					
All	0.65 ^z	0.82	0.78	0.82	0.82
Low	0.64	0.81	0.78	0.81	0.81
Native	0.51	0.69	0.65	0.76	0.76
High	0.62	0.73	0.71	0.80	0.80
Plant ht					
All		0.88	0.94	0.89	0.89
Low		0.80	0.90	0.83	0.83
Native		0.79	0.89	0.81	0.82
High		0.87	0.93	0.86	0.86
Plant area					
All			0.99	0.97	0.97
Low			0.98	0.96	0.96
Native			0.98	0.91	0.91
High			0.99	0.92	0.91
Plant volume					
All				0.97	0.97
Low				0.96	0.96
Native				0.92	0.92
High				0.93	0.92
Aboveground dry wt					
All					0.99
Low					0.99
Native					0.99
High					0.99

^zr is not equal to 0 for all values ($P \leq 0.001$, df = 36).

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