‘Ben Lear’ and ‘Stevens’ Cranberry Root and Shoot Growth Response to Soil Water Potential

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Abstract. Wisconsin cranberry growers report that fruit production by the cranberry cultivar ‘Ben Lear’ (Vaccinium macrocarpon Ait.) is low in beds with poor drainage, while the cultivar ‘Stevens’ is less sensitive to these conditions. We hypothesized that ‘Ben Lear’ and ‘Stevens’ would differ in their root growth and mortality response to variation in soil water potential. Rooted cuttings of each cultivar were grown in a greenhouse in sand-filled pots with three different soil water potentials which were regulated by a hanging water column below a fritted ceramic plate. A minirhizotron camera was used to record root growth and mortality weekly for five weeks. Root mortality was negligible (2% to 6%). Whole plant relative growth rates were greatest for both cultivars under the wettest conditions. Rooting depth was shallowest under the wettest conditions. Whole-plant relative growth rates of ‘Ben Lear’ were higher than ‘Stevens’ at all soil water potentials. ‘Stevens’ plants had significantly higher root to shoot ratios than ‘Ben Lear’ plants, and produced more total root length than ‘Ben Lear’ plants at all soil water potentials. ‘Stevens’ plants had a significantly higher root to shoot ratio than ‘Ben Lear’. To test these hypotheses, a greenhouse experiment was conducted to determine the optimum soil water potential for root growth of ‘Ben Lear’ and ‘Stevens’ cranberry. ‘Stevens’ is the most commonly grown cultivar in Wisconsin, although ‘Ben Lear’ is also widely planted as an early ripening cultivar with good color. We hypothesized that these two cranberry cultivars would differ in their root growth and mortality response to variation in soil water potential.

Materials And Methods

Experiments were conducted with rooted cuttings of cranberry, cv. ‘Ben Lear’ and cv. ‘Stevens’. Cuttings were collected near Babcock, WI from 4-year-old sand-substrate beds with good runner production. Vegetative cranberry vine cuttings (10 cm) were placed in deionized water to establish roots. After roots appeared (within about 10 d) the water was replaced with a modified Hoagland’s nutrient solution for cranberry and blueberry (Barak et al., 1996), and the culture vessel moved to a greenhouse with supplemental sodium lighting providing a fourteen hour day. Cuttings were allowed to develop for 6 weeks before transplanting into the experimental pots. Experiments were conducted in the same greenhouse used to start cuttings.

Experimental pots (Fig. 1) were built with a top section for plant growth and a bottom water reservoir. Each section was 15.24-cm-high, 25.4-cm-diameter Schedule 40 PCV pipe. The two sections of the pot were separated by a porous ceramic plate (1 bar standard pore size, Soil Moisture, Inc., Santa Barbara, Calif.). The height of the hanging water column in the hose connected to the bottom water reservoir (Fig. 1) regulated water potential at the top surface of the ceramic plate (Hillel, 1982). Water column height for the high water table treatment was 2.5 cm above the ceramic plate. The medium and low water table treatments were 23 and 41 cm below the ceramic plate. The pots were filled with 10 cm of autoclaved, medium textured sand (0.8%
Table 1. Whole-plant growth analysis for ‘Ben Lear’ and ‘Stevens’ cranberry plants grown at high ($\Psi_{soil} = 0$ Mpa, water table 2.5 cm above plate), medium ($\Psi_{soil} = -0.234$ kPa, water table 23 cm below plate), and low ($\Psi_{soil} = -0.418$ kPa, water table 41 cm below plate) water levels. All weight measurements were based on a dry weight basis. Relative growth rate (RGR; g·g$^{-1}$·d$^{-1}$) was based on dry weight gain between planting and harvest. Root length at harvest (m) was determined with WinRHIZO analysis of a scanned subsample. Values are mean ± SE, n = 5 for all data.

| Water table ht (cm) | Whole-plant RGR (g·g$^{-1}$·d$^{-1}$) | Root to shoot ratio (groot/gshoot) | Leaf area ratio (cm$^2$/gplant) | Root length at harvest (m) |
|---------------------|--------------------------------------|----------------------------------|-------------------------------|--------------------------|
| Ben Lear             | Stevens                              | Ben Lear                         | Stevens                       | Ben Lear                 | Stevens                       |
| 2.5                 | 0.023 ± 0.001 0.018 ± 0.001 0.23 ± 0.01 | 0.20 ± 0.03 0.30 ± 0.02 0.16 ± 0.02 | 2.32 ± 0.25 2.45 ± 0.13 | 24.0 ± 0.95 51.9 ± 0.98 |
| 23                  | 0.023 ± 0.001 0.017 ± 0.002 0.20 ± 0.03 | 0.38 ± 0.10 0.21 ± 0.02 0.24 ± 0.04 | 2.39 ± 0.25 1.70 ± 0.15 | 17.6 ± 0.45 37.4 ± 0.80 |
| 41                  | 0.020 ± 0.001 0.18 ± 0.001 0.27 ± 0.03 | 0.27 ± 0.02 0.21 ± 0.02 0.20 ± 0.01 | 2.39 ± 0.25 1.70 ± 0.15 | 17.6 ± 0.45 37.4 ± 0.80 |

Table 2. Results from ANOVA (Proc MIXED, denominator degrees of freedom adjusted with Kenward-Roger procedure). Values are F values, subscripted with numerator and denominator degrees of freedom.

| Parameter            | Cultivar | Water table ht | Cultivar × water table ht |
|----------------------|----------|----------------|--------------------------|
| Whole-plant relative growth rate | Ben Lear | Stevens | Ben Lear | Stevens | Ben Lear | Stevens |
| Root to shoot ratio | 6.07$^{*,**}$ | 6.93$^{*,**}$ | 1.63$^{*,**}$ | 1.03$^{*,**}$ | 1.03$^{*,**}$ | 1.63$^{*,**}$ |
| Root weight ratio   | 4.29$^{*,**}$ | 4.29$^{*,**}$ | 1.01$^{*,**}$ | 1.01$^{*,**}$ | 1.01$^{*,**}$ | 1.01$^{*,**}$ |
| Leaf area ratio     | 30.0$^{*,**}$ | 7.38$^{*,**}$ | 1.15$^{*,**}$ | 1.15$^{*,**}$ | 1.15$^{*,**}$ | 1.15$^{*,**}$ |
| Harvested root length | 19.1$^{*,**}$ | 1.10$^{*,**}$ | 2.55$^{*,**}$ | 2.55$^{*,**}$ | 2.55$^{*,**}$ | 2.55$^{*,**}$ |

*,$**,$***,$****Significant at P < 0.05; 0.01, 0.001, or 0.0001, respectively.

Observations during harvest indicated that root angle and rooting depth varied among the three water potential treatments. Plants growing in the high water table treatment produced shallow, wide spreading roots with extensive development at the soil surface, and no root growth below about 2 cm deep. Roots in the low water table treatment grew straight down, wrapping underneath the minirhizotron tubes. Roots in the intermediate water table treatment were intermediate in root angle, and could be found throughout the soil profile.

‘Ben Lear’ whole-plant RGR (g·g$^{-1}$·d$^{-1}$) was higher than ‘Stevens’ whole-plant RGR at all water potentials (Tables 1 and 2). Whole-plant RGR was greatest for both cultivars at the highest water potential (Tables 1 and 2). ‘Stevens’ cumulative root length production and root length RGR on minirhizotron tubes was significantly greater than that of ‘Ben Lear’ over the course of the experiment (Fig. 2, Table 3). ‘Ben Lear’ root length RGRs were lower than for ‘Stevens’ at all three water levels (Fig. 2A). Root length RGR for both cultivars increased significantly during the experiment (Fig. 2B, Table 3). ‘Stevens’ produced significantly more total root length (measured at harvest) than ‘Ben Lear’ at all water potentials (Tables 1 and 2). Final

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gravel and very coarse sand, 15.9% coarse sand, 77.4% medium sand, 5.6% fine sand, 0.3% very fine and silt particle classifications from U.S. Soil Conservation Service, 1993) collected from the sand pile at a commercial cranberry marsh. Based on the soil moisture release curve for this sand (data not shown), the gravimetric water content at the surface in the high water table treatment was between 10% and 20% soil moisture. Soil water content in the other treatments was <1%.

Four rooted cuttings were planted in each pot, two on each side of the minirhizotron tube. Plants were watered in at planting with 200 mL of the modified Hoagland’s solution, covered with a clear plastic bag, and misted daily to increase humidity and reduce transplant mortality. The plastic bags were removed after 1 week. To mimic conditions in a new cranberry bed, we established minirhizotron tubes for 3 weeks at a medium (23 cm below ceramic plate, −0.23 kPa) water potential before treatments were applied. All weight measurements were based on dry weight gain between planting and harvest. Whole-plant RGR was unable to distinguish individual roots when the entire root mass was scanned. Root length subsamples were stored in 50% ethanol in glass scintillation vials for 1 week before measurements. Before scanning, roots were rinsed in deionized water and immersed in neutral red staining solution (0.5 g L$^{-1}$ for 24 h (Bouma et al., 2000); roots were destained by rinsing in deionized water. Stained roots were cut into pieces about 1 cm long and placed in a Plexiglas tray (20 × 30 cm) with sufficient water to float the roots. Root measurements were collected by scanning and analysis with the program WinRHIZO. We obtained the best imaging of individual cranberry roots by using the maximum scanning resolution (800 dpi) with Lagarde’s method (WinRHIZO). Total length of the harvested roots was estimated based on the proportion of subsample root fresh weight to total root fresh weight at time of harvest.

To obtain an estimate of various plant parameters for calculation of whole-plant relative growth rate (RGR = (ln final dry weight – ln initial dry weight)/time) [Hunt, 1982], we measured the diameter and length of the rooted cuttings at the time of transplanting. A set of twenty cuttings of each cultivar was dried and weighed at this time. There was a strong linear relationship between estimated stem volume (assuming the plant approximated a cylinder) and dry weight (Ben Lear $r^2 = 0.82$, Stevens $r^2 = 0.83$). By using the measurements of plant size at transplanting to estimate initial weight, our RGR estimates include growth for the entire 8 weeks after transplanting, rather than only the 5-week treatment period. They are therefore likely to underestimate treatment effects on RGR.

The experiment was conducted as a randomized complete block design with five replications. Statistical analysis of cranberry variety and water effects on fine root biomass, whole-plant RGR, leaf area ratio, root weight ratio, root to shoot ratio and root length production was conducted with SAS Proc Mixed (SAS Institute, Cary, N.C.). Blocks were random variables and cultivar and water table level were fixed variables. The normality of frequency distribution for each variable was checked with SAS Proc Univariate. Root to shoot ratio data were transformed with the arcsine square root transformation to obtain normality before analysis; all other data were normally distributed. Repeated measures ANOVA in SAS Proc Mixed was used to analyze root length growth and RGR from the minirhizotron measurements.

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cultivars in the different treatments at harvest was similar to that described by Hall (1971), with the deepest rooting in the driest soil. RGRs and total root length accumulation for both cultivars were greatest in the high water potential treatment. This is noteworthy, given grower concerns about the requirements of ‘Ben Lear’ for good soil drainage; both cultivars seem to grow well with a constant high water table. The positive relationship between whole-plant RGR and leaf area ratio, and the negative relationship between whole-plant RGR and root weight ratio is consistent with predictions of functional balance in plant carbon allocation, where increased allocation to root biomass reduces the potential for photosynthetic carbon gain by reducing potential leaf area (Brouwer and DeWit, 1969; Poorter and Lambers, 1991).

Despite our expectations, we found little effect of soil water availability on root mortality. Since the lifespan of cranberry roots was unknown, a sampling period of 1 week was used to minimize overestimation of lifespan due to the appearance and disappearance of roots between sampling periods (Hendrick and Pregitzer, 1996; Tingey et al., 2003). Smaller-diameter roots are expected to be shorter lived than larger diameter roots (Eissenstat, 1992). Although cranberry root diameter was extremely small compared to fine roots of other non-Ericaceous woody plants, it was noteworthy that little mortality occurred within the 5-week study. Longer observations will be needed to determine environmental effects on the lifespan of cranberry roots.

Our study did not address the potential role of root pathogens in reducing plant growth in poorly drained fields. In contrast to Wisconsin grower observations, Massachusetts cranberry growers observe that ‘Stevens’ grows worse than ‘Ben Lear’ under poorly drained conditions (DeMoranville, personal communication). Greater root system damage to ‘Stevens’ than ‘Ben Lear’ by pathogens (e.g., phytophthora root rot) may be responsible for this difference among regions. Phytophthora root rot is common in Massachusetts and New Jersey cranberry beds (Oudemans, 1999), but is rarely detected in Wisconsin (McManus, personal communication).

We observed rapid growth of ‘Ben Lear’ in pots with a stable, extremely high water table. How can this observation be reconciled with grower observations of ‘Ben Lear’ problems with wet feet? A combination of factors is likely to be involved. Based on our observations of shallow root growth in the highest water table treatment, cranberries growing in poorly drained fields are likely to have shallow root systems, as well as low carbon allocation to roots. As most Wisconsin cranberry beds are either on a sand substrate, or were constructed with a sand layer on top of peat, slight changes in water table height are likely to have large effects on root zone water content. Any subsequent lowering of the water table would expose shallow-rooted plants established in poorly drained beds to water stress. Given the greater leaf area ratio and lower root growth potential, for ‘Ben Lear’ than for ‘Stevens’, ‘Ben Lear’ plants are likely to both transpire more and have a lower capacity to acquire water than ‘Stevens’ plants. These growth patterns are likely to make ‘Ben Lear’ more susceptible than ‘Stevens’ plants to water stress under a fluctuating water table.

Field observations of root growth and plant water relations are required to determine if the differences between the two cultivars in root allocation explain grower observations of lower yield of ‘Ben Lear’ in poorly drained beds in Wisconsin.

Table 3. Results from repeated measures ANOVA for the effects of week, cultivar, and water table height on total cumulative root length (cm) and on root length relative growth rate (RGR; cm·cm⁻¹·d⁻¹) over 5 weeks on minirhizotron tube. Initial root length is used as a covariate for analysis of cumulative root length.

| Eff ect | F value | F value |
|---------|---------|---------|
| Observation date | 1.83 | 80.36 |
| Cultivar | 9.92 | 4.35 |
| Cultivar × observation date | 0.89 | 3.72 |
| Water | 0.63 | 2.23 |
| Observation date × water | 0.37 | 0.44 |
| Cultivar × water | 1.74 | 1.23 |
| Cultivar × observation date × water | 0.23 | 0.15 |
| Initial root length | 1.48 | |

Table 3. Significant at P ≤ 0.05; 0.01, 0.001, or 0.0001, respectively.

Fig. 2. (A) Cumulative root length (cm) and (B) root length relative growth rate (cm·cm⁻¹·d⁻¹) measured per pot on minirhizotron tubes for ‘Ben Lear’ and ‘Stevens’ cultivars over 5 weeks, averaged over all water table treatments. Cultivar effects were significant for cumulative root length and relative growth rate; time effects were significant for relative growth rate (Table 3). Error bars are ± standard error.

Fig. 3. Histogram of root diameter (mm) measured on minirhizotron tube at week 5; includes both ‘Ben Lear’ and ‘Stevens’ at all water tables, as neither cultivar or water table treatment had a significant effect on root diameter. Total observations = 7,439 roots. Observation frequencies for roots >0.16 mm diameter are <0.1%.
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