Rabbiteye blueberries require a balance of nutrients for maximum production, and most recommendations include the use of a complete fertilizer (9–11, 14, 15). However, rabbiteye blueberries are slow to respond to field fertilization (1, 2) and, in the case of excessive concentrations of soluble salts, the response is often negative (12).

These data agree with previous reports that indicate a number of years are required for rabbiteye blueberries to exhibit positive growth responses to more than minimal fertilization (1, 2). Additionally, these findings are similar to those of Eck (8) with highbush blueberries, in which he found N applications >68 kg·ha⁻¹ possibly detrimental. Townsend (15) also cautioned against the application of nitrogenous fertilizers, since they are major contributors to soil soluble salts. He stated that highbush blueberries have a low fertilizer requirement and are especially sensitive to over-fertilization during the early years of growth.

Negative responses, due to excessive concentrations of soluble salts, occur rapidly and often result in dead plants (12). Salt concentrations are mainly a consequence of natural fertility of the soil, additions of soluble salts (fertilizers), and the soil moisture content. Typically, the lower coastal plains mineral soils of Louisiana, Alabama, and Mississippi are very low in natural fertility and water-holding capacity. A combination of small amounts of fertilizer applied in two or more applications during the growing season in combination with supplemental water should sufficiently dilute the salt concentration and also supply adequate nutrients and moisture for plant growth.

**Literature Cited**


**Growth and Survival of the Highbush Blueberry in Response to Root Zone Flooding**

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Additional index words. Vaccinium corymbosum, oxidation-reduction potential, waterlogging

**Abstract.** Flooded, 2-year-old highbush blueberry plants (Vaccinium corymbosum L. 'Bluecrop') survived 30 months of continuous flooding, but vegetative growth was suppressed after ≈4 months. Plants continuously flooded for 4 months and subsequently placed in the field recovered partially. The greatest number of plants died when flooding began in April and the least number when it was begun in December.

Intermittent flooding of forests and croplands is a problem throughout the world and results in great economic losses (19). The cultivated blueberry is increasing in production, and researchers have begun to evaluate the effects of flooding on the growth of this plant (1, 9, 15). Rabbiteye blueberry (Vaccinium ashei Reade) plants reportedly survived, but were severely damaged, after 49–58 days of continuous flooding (8). This species is considered more tolerant to flooding and reduced soil O₂ levels than highbush blueberry (Vaccinium corymbosum L.) (8, 17). Herath and Eaton (15) flooded 1-year-old 'Bluecrop' (V. corymbosum L.) plants in containers to within 7.5 cm of the soil surface and noted a decrease in nutrient uptake and suppressed plant growth. An important effect of flooding is displacement of O₂ from the soil pores, resulting in O₂ deficiencies and reduced growth (17). Even though wild highbush blueber-
ries are found growing on hummocks in swamps, flooded areas are not recommended for plantations (12). This species has a shallow, fibrous root system (10) adapted to moist, well-aerated soils (7, 12). This type of root system may aid the plant in surviving flooding (10), since high O₂ levels, necessary for root growth, frequently occur close to the soil surface in poorly aerated soils (6).

Vegetative growth, including root growth, has been studied in the highbush blueberry (10, 11). However, little is known of the effects of prolonged flooding on the growth and survival of this species. Because such conditions at times exist in many blueberry plantations in the northeastern United States, this study was undertaken to examine the effects of prolonged seasonal root zone flooding on vegetative growth, development, and survival of cultivated highbush blueberries.

**Materials and Methods**

Two-year-old ‘Bluecrop’ plants and 1-year-old rooted cuttings of ‘Darrow’, ‘Bluecrop’, ‘Coville’, and ‘Bluetta’ were used. The plants were grown in a 1 peat : 1 perlite : 1 sand mixture in 7.6-liter plastic containers (2-year-old plants) and 0.5-liter plastic pots (1-year-old plants).

In a preliminary study, three 95-liter, water-filled tubes were set into the ground. On 1 Dec. 1983, sixteen 2-year-old ‘Bluecrop’ plants and sixteen 1-year-old plants were submerged into the tubs. The water level was maintained 2.5–5.0 cm above the level of the medium in the containers. As controls, twelve 2-year-old ‘Bluecrop’ plants were set into the soil to the depth of their containers. After flooding for 4 months, six plants were removed from the tubs; the root systems of three plants were washed and observed and three plants were set into the field with control plants. The remaining plants were maintained under continuous flooding until dead.

A similar, expanded test was conducted in Apr., Aug., and Dec. 1984 and in Apr. and Aug. 1985. Flooded plants, including seventy-two 2-year-old plants and thirty-six 1-year-old plants were submerged on each date in a black polyethylene-lined, water-filled pit in the field with the water level maintained 2.5–5.0 cm above the level of the medium in the containers. As controls, twelve 2-year-old ‘Bluecrop’ plants were set into the soil to the depth of their containers. After flooding for 4 months, six plants were removed from the tubs; the root systems of three plants were washed and observed and three plants were set into the field with control plants. The remaining plants were maintained under continuous flooding until dead.

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In the Apr. 1984 treatment, of the 21 plants remaining after the initial 4 months of flooding, 13 plants were removed from the pit, five were used for immediate observations, and eight were set into the soil with control plants. In the Apr. 1985 treatment, of the 26 plants remaining after the initial 4 months of flooding, 16 plants were removed from the pit, six were used for immediate observations, and 10 were set into the soil with control plants. Shoot and internode length and number of nodes were measured on 10 shoots per plant, 10 plants per treatment. Length and width of the third fully expanded leaf (numbered basipetally) were measured in June 1985. Percentage of leaf stomata open was determined for plants of the various treatments at 1000, 1200, and 1400 HR EST. Stomata from the third fully expanded leaf (numbered basipetally) from each of the 10 shoots from 10 plants per treatment were examined. The abaxial leaf surface was coated with an acrylic lacquer which formed a negative impression of the stomata. The impressions peeled from the leaf surfaces were mounted in glycerin on a microscope slide and examined by phase-contrast light microscopy.

Root zone temperatures in the submerged containers ("water") and air temperatures within the plant canopy ("air") ≈ 25 cm above the media level in the containers were recorded daily.

Oxidation-reduction potentials of the container media were measured from Apr. through 1 Oct. 1985 using a platinum microelectrode with a saturated calomel reference electrode and a Model Altex Phi 30 pH meter (Beckman). The electrodes were inserted ≈10 cm into the media, allowed to equilibrate for 1 min, and a reading in millivolts was recorded. Three readings were recorded from each container using 10 containers per treatment. The readings were standardized to a pH of 6.0 at 25°C. The adjustment was made by adding to or subtracting from the readings 0.059 mV for each pH unit above or below pH 6.0 (4). Readings also were taken within the drip-line of mature field-grown ‘Bluecrop’ blueberry plants for comparison.

For each of the first 6 weeks following the initiation of the Dec. 1983 flooding, a 2-year-old and a 1-year-old plant were harvested and their roots washed. Visual observations of root
Fig. 2. Color intensity of TTC in roots from flooded 1-year-old containerized blueberry plants in relation to temperature of the media water and air in the plant canopy (Dec. 1983, Apr. 1984, Aug. 1984).

Fig. 3. Oxidation-reduction potential of the media from flooded and control 2-year-old containerized and mature field-grown 'Bluecrop' plants.

Table 1. Shoot growth of two-year-old containerized 'Bluecrop' plants as affected by flooding treatment and date.

<table>
<thead>
<tr>
<th>Treatment date</th>
<th>Control Shoot length (cm)</th>
<th>Control Nodes/shoot</th>
<th>Control Internode length (cm)</th>
<th>Flooded then planted Shoot length (cm)</th>
<th>Flooded then planted Nodes/shoot</th>
<th>Flooded then planted Internode length (cm)</th>
<th>Continuous flooding Shoot length (cm)</th>
<th>Continuous flooding Nodes/shoot</th>
<th>Continuous flooding Internode length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apr. 1984</td>
<td>6.2 bc</td>
<td>8.0 a</td>
<td>0.79 b</td>
<td>2.8 d</td>
<td>4.7 b</td>
<td>0.60 c</td>
<td>1.5 c</td>
<td>2.1 c</td>
<td>0.35 b</td>
</tr>
<tr>
<td>Aug. 1984</td>
<td>5.6 c</td>
<td>7.5 ab</td>
<td>0.76 b</td>
<td>5.0 b</td>
<td>6.7 a</td>
<td>0.75 b</td>
<td>2.3 b</td>
<td>6.4 a</td>
<td>0.36 b</td>
</tr>
<tr>
<td>Dec. 1984</td>
<td>6.4 b</td>
<td>6.4 c</td>
<td>0.93 a</td>
<td>5.7 a</td>
<td>6.3 a</td>
<td>0.91 a</td>
<td>3.8 a</td>
<td>6.6 a</td>
<td>0.57 a</td>
</tr>
<tr>
<td>Apr. 1985</td>
<td>6.1 bc</td>
<td>6.7 bc</td>
<td>0.91 a</td>
<td>4.2 c</td>
<td>5.3 b</td>
<td>0.79 b</td>
<td>1.1 c</td>
<td>5.1 b</td>
<td>0.22 c</td>
</tr>
<tr>
<td>Aug. 1985</td>
<td>7.1 a</td>
<td>7.3 b</td>
<td>0.98 a</td>
<td>4.9 b</td>
<td>6.2 a</td>
<td>0.79 b</td>
<td>3.8 a</td>
<td>6.6 a</td>
<td>0.56 a</td>
</tr>
</tbody>
</table>

*Data are the means of 2 years measured in Nov. 1984 and 1985.
*Data are the means of 1 year measured in Nov. 1985.
*Means within columns separated by Duncan's multiple range test, P = 5%.

growth and health were made before incubating the root system in a reaction mixture consisting of 0.05 M mono- and di-basic phosphate buffers at pH 7.3 and 0.05 M citric acid. The reaction mixture was boiled and allowed to cool before use. One-tenth percent solution of 2,3,5 triphenyl tetrazolium chloride (TTC) then was added to the reaction mixture (3). Washed root systems were incubated for 24 hr at 22°C in this solution. The respiratory indicator (TTC) stained the live cells, providing an indication of the level of root activity. The staining intensity was recorded by visual determination and confirmed by observations of root cell smears with a binocular dissecting scope. The staining intensities subjectively rated included purplish-red (controls), deep-red, bright-red, pink, and colorless (dead) with a lighter color indicating a decrease in root activity.
were similar for both years of the study. For this reason, data
plants were less costly and easier to use. TTC staining intensities
treatment was washed and visual observations were made prior
ing the initial 6 weeks of testing, a 1-year-old plant was harvested
were transformed using arcsin prior to analysis.


regrowth of rabbiteye blueberry shoots after severe pruning and
flooded for only 1 month. Davies and Wilcox (8) measured
regrowth of shoots on plants flooded beyond this length
is primarily a result of a decrease in internode length with only

Results and Discussion

Vegetative growth response. Throughout the duration of the
experiment, vegetative growth, including shoot and internode
were suppressed in response to flooding (Tables 1-3). Growth
responses in the preliminary study in 1983 were similar to those
observed throughout the study. The reduction in shoot growth is
primarily a result of a decrease in internode length with only a slight
decline in the number of nodes (Table 1). After flooding several
tree species for 1 month in the autumn, Andersen et al. (2) noted that reduced leaf size and
number of shoots formed and the growth rate of the shoots
decreased linearly in relation to the number of days the plants
were flooded. Our data suggest that season may affect the degree
to which shoot growth is affected by flooding (Tables 1 and 2). Flooding initiated in April was more damaging than
flooding in August and December. The seasonal effect of flooding
probably is related to the plant’s developmental stage at the
time flooding is initiated. Heinicke flooded apple trees at vari-
ous times of the year and found shoot extension reduced only if flooding occurred when leaves were present (14). Olien found
the effect of flooding in the spring especially severe, reducing
apple shoot extension by 33% (18). In a greenhouse experiment,
Olien showed that dormant apple seedlings grew normally after
8 weeks of flooding, whereas actively growing plants flooded
for 8 weeks were severely stunted (18).

Reduced leaf number, size, and area, and early leaf senes-
cence or abscission in response to flooding have been reported
(2, 5, 15). Andersen et al. (2) noted that reduced leaf size and
number indicated a decline in the absorption and transport of
water by the flooded roots due to xylem dysfunction. Jackson
and Campbell (16) have shown that flooding can reduce the
water flow through roots of tomato. Herath and Eaton (15) ob-
served a decrease in nutrient element concentrations in leaves
of highbush blueberry plants when flooded to within 7.5 cm of
the soil surface. They proposed that inadequate aeration interfered with nutrient uptake of the roots, thus influencing the
growth of the shoots.

Flooding reduced leaf size and percentage of open stomata (Tables 2 and 3). Control plants and plants flooded and then
planted had a much greater percentage of open stomata than
plants continuously flooded (Tables 2 and 3). Stomatal closure
in response to flooding has been considered as a means of
determining a plant’s tolerance to flooding (2, 8). The increase in

<table>
<thead>
<tr>
<th>Treatment date</th>
<th>Control</th>
<th>Flooded then planted</th>
<th>Continuous flooding</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Shoot length (cm)</td>
<td>Nodes/shoot</td>
<td>Internode length (cm)</td>
</tr>
<tr>
<td>Apr. 1984</td>
<td>5.5</td>
<td>7.0</td>
<td>0.79</td>
</tr>
<tr>
<td>Aug. 1984</td>
<td>3.7</td>
<td>6.0</td>
<td>0.62</td>
</tr>
<tr>
<td>Dec. 1984</td>
<td>2.3</td>
<td>5.9</td>
<td>0.38</td>
</tr>
<tr>
<td>Apr. 1985</td>
<td>2.0</td>
<td>5.9</td>
<td>0.38</td>
</tr>
</tbody>
</table>

Means within columns separated by Duncan’s multiple range test, P = 5%.

Means within columns separated by Duncan’s multiple range test, P = 5%.

Table 2. Size of fully expanded leaves and percent open stomata on 2-year-old containerized ‘Bluecrop’ plants as influenced by flooding treatment and date (17 June 1985).

Table 3. Shoot growth, leaf size, and percent open stomata from 2-year-old containerized ‘Bluecrop’ plants as influenced by flooding treatment.
stomatal closure has been linked to a decrease in transpiration, stomatal conductance, and carbon assimilation (2, 8, 9). Davies and Flore found that, in rabbiteye and highbush blueberries, flooding decreased stomatal conductance and transpiration within 4 to 5 days (9). Carbon assimilation through photosynthesis decreased within 9 days, as did stomatal conductance of CO₂, while respiration increased. Stomatal closure may reduce short-term damage to flooded plants, but it can lead to a reduction in photosynthesis, carbon assimilation, and respiration, ultimately affecting plant growth and survival.

The mean reduction in root dry weight as a result of flooding [control (156.6 g) vs. flooded then planted (27.8 g)] vs. continuous flooding (22.1 g) is evidence of suppression of new root growth and decay of existing roots, previously noted for other species (5, 14, 21). The washed root system of the flooded plants appeared black in color, whereas those of the control plants were light-brown. The roots of plants flooded for 4 months and then planted were dark-brown in color. Heinicke (14) noted that there were no apparent effects on root growth when apple trees were flooded in the dormant season. However, root growth was restricted when trees were flooded in the spring and the roots developed a blackened color.

Survival. Some flooded highbush blueberry plants survived continuous flooding for more than 30 months when submerged beginning in December, although growth was minimal (Tables 1 and 2). There is a seasonal effect on survival. Plants flooded beginning in December survive better than those flooded beginning in August. The lowest survival rate occurred in plants flooded beginning in April (Fig. 1), and ≥30–40% of the plants died within 3 months. All of the Apr. 1984 plants were dead within 18 months, and a similar trend was observed in 1985. Previous studies (8, 18) have shown a decrease in the survival rate of fruit plants during spring flooding and a relationship to temperature. Davies and Wilcox (8) found that rabbiteye blueberry plants, which were flooded beginning in the spring, survived as long as 58 days, although the plants were severely damaged. Growth ultimately resumed upon removal of the plants from the flooded conditions. The seasonal effect on flooding may be due in part to differences in temperature. Other researchers have noted increased growth suppression of flooded plants in response to increased temperatures (6, 20, 21). Rowe and Catlin (21) found that several Prunus spp. were less sensitive to flooding at a root zone temperature of 17°C compared to 27°C. The seasonal response of plant survival to flooding corresponded with the staining intensities recorded using TTC. Plants exhibited a purplish-red staining intensity before submergence. However, within 2-weeks, staining intensity decreased to deep-red (Fig. 2). As the duration of flooding increased, the staining intensity decreased. It took ≥1 month more for the plants flooded beginning in December and August to decrease to a pink staining intensity compared to those flooded beginning in April (Fig. 2). This reduction in root activity appears to be related directly to plant growth and survival in flooded conditions. Childers and White (6) observed root growth of flooded apple trees in glass-sided boxes and found that no new roots formed, and all visible roots already formed appeared dead after 18 days of flooding. Harris (13) noted in apples and filberts that a rise in the water table resulted in the cessation of root growth and the eventual death of newly formed roots.

The oxidation-reduction potential of the continuously flooded blueberry plants decreased rapidly within a few hours, and the level was maintained continuously for several months (Fig. 3). There were no statistically significant differences for oxidation-reduction potentials among treatment dates. Boynton (5) grew apple trees under controlled soil O₂ levels and found that when the level dropped below 10% very few rootlets formed and the shoots were injured. He stated that higher O₂ levels are necessary for the production of new roots than for maintaining the existing root system. (5). Furthermore, a reduction in the production of new roots will limit nutrient and water uptake, ultimately affecting the whole plant.

Contrary to earlier beliefs, the cultivated highbush blueberry can survive extended periods of flooding occurring at times other than the spring period of active growth (7, 12), although growth and development of the plant is severely limited. It appears that dormant plants adapt to flooding prior to the initiation of growth, thus improving survival. The mechanism by which the highbush blueberry could survive extended periods under flooded conditions has not yet been determined.

Literature Cited

relationships between leaf : fruit ratio and varying levels of European red mite stress on fruit size and return bloom of apple

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Additional index words.  crop load, Malus domestica, Panonychus ulmi

Abstract.  Fruit size and return bloom of apple (Malus domestica Brokh.) were examined in 1982–84 under varying levels of crop load caused by the European red mite [Panonychus ulmi (Koch)]. Trees of ‘Rome Beauty’/MM.111 and ‘Yorking’ M.26 were subjected to two and three levels of mite stress, respectively, over a range of leaf : fruit ratios (LFRs). Regression models were used to explore the effect of LFR on fruit size and return bloom at the various mite injury levels. There was a curvilinear relationship between mean fruit weight and LFR for most of the check and mite-injured groups. The relationship between bloom density and LFR was linear over the range studied. Both experiments indicated reduced fruit size and return bloom with moderate to high mite damage, regardless of LFR.

The relationship between fruit size or return bloom of apple and crop load has been investigated since the 1920s (see ref. 8 for review). These studies were concerned with optimization of the fruit size and number relationship while maintaining annual bearing, two important components of monetary return to the grower.

Haller and Magnes (12) and Haller (11) were among the first to use leaf : fruit ratio (LFR) (the number of leaves per fruit) in an attempt to optimize crop load. They found a strong correlation between increase in fruit volume and leaf area supplying the fruit. They also noted that there is a LFR at which maximum fruit growth is obtained (30 to 40 for ‘Grimes’ and ‘Ben Davis’, and up to 75 for ‘Delicious’). Similar results were obtained by Murneek (21) and Preston (23). Hansen (13) calculated the saturation leaf area per fruit (i.e., the point at which all available assimilates are fixed in the fruit) as =14–17 leaves per fruit (‘Golden Delicious’), depending on the time of season. Hansen (14) found a positive curvilinear relationship between fruit growth/ m² of leaf area and crop load. Forshey and Elving (8) describe a linear relationship between mean fruit weight and number of fruit/cm² of trunk cross-sectional area (CSA). However, they note that “thinning can quickly reach the point of diminishing returns” and that excessive thinning will lead to a reduction in fruit numbers, hence total yield, that will not be compensated for by an increase in mean fruit size.

Similar results have been obtained with flower bud initiation and return bloom. Harley et al. (15) found that at 10 leaves per fruit, no flower bud initiation occurred, while, at 70 leaves per fruit, all spurs formed flower buds. Aldrich and Fletcher (1) also concluded that the number of leaves per fruit was related positively to percentage bloom and set the following season. Shen (25) found the same positive relationship, and noted that there is a limit of about 700–1400 cm² of leaf area per fruit beyond which flower bud differentiation is not increased.

European red mite (ERM) [Panonychus ulmi (Koch)] injury to leaves also can reduce fruit size and return bloom. ERM damages the tree by removing cell contents, including chlorophyll. Mite feeding may decrease net photosynthesis and transpiration (3, 5, 7, 10). Hoyt et al. (16) found mite injury affected cumulative fruit growth. Asquith (2) and Baker (4) reported that mite injury caused a reduction in fruit size. Klopfenstein (17), Zwick et al. (27), and Ames et al. (10), on the other hand, found no reduction in fruit size. Return bloom has been reported by some (2, 18, 19) to be reduced greatly by mite damage, while others (6, 20, 27) found no effect. Hoyt et al. (16) reported no effect when mite populations occurred mid-season on vigorous trees, but pointed out that the timing of damage may be a crucial factor.

The objective of this investigation was to determine the effects of damage caused by ERM on fruit size and return bloom under varying levels of crop load. If competition among fruits is a primary determinant of fruit size and return bloom, then the effects of ERM damage should increase as LFR decreases.

Materials and Methods

Conceptual model. A conceptual model for the relationship between fruit size and LFR under various levels of mite stress (Fig. 1) illustrates several hypotheses: a) fruit size increases in a curvilinear fashion with increasing LFR, up to a theoretical maximum, which is determined by genetic and environmental factors.