Flooding, gas exchange and hydraulic root conductivity of highbush blueberry

Frederick S. Davies and James A. Fiore


Highbush blueberry plants (Vaccinium corymbosum L. cv. Bluecrop) growing in containers were flooded in the laboratory for various durations to determine the effect of flooding on carbon assimilation, photosynthetic response to varying CO₂ and O₂ concentrations and apparent quantum yield as measured in an open flow gas analysis system. Hydraulic conductivity of the root was also measured using a pressure chamber. Root conductivity was lower and the effect of increasing CO₂ levels on carbon assimilation less for flooded than unflooded plants after short-(1-2 days), intermediate-(10-14 days) and long-term (35-40 days) flooding. A reduction in O₂ levels surrounding the leaves from 21 to 2% for unflooded plants increased carbon assimilation by 33% and carboxylation efficiency from 0.012 to 0.021 mol CO₂ fixed (mol CO₂)⁻¹. Carboxylation efficiency of flooded plants, however, was unaffected by a decrease in percentage O₂, averaging 0.005 mol CO₂ fixed (mol CO₂)⁻¹. Apparent quantum yield decreased from 2.2 x 10⁻³ mol of CO₂ fixed (mol light)⁻¹ for unflooded plants to 2.0 x 10⁻³ and 9.0 x 10⁻⁴ for intermediate- and long-term flooding durations, respectively. Short-term flooding reduced carbon assimilation via a decrease in stomatal conductance, while longer flooding durations also decreased the carboxylation efficiency of the leaf.

Additional key words — Carbon assimilation, photosynthesis, stomatal conductance, transpiration, Vaccinium corymbosum.

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Introduction

Highbush blueberries are native to bogs of the northeastern and northern United States. Cultivated highbush plants are generally flooding-sensitive under field conditions (Kender and Brightwell 1966); however, they are flooding-tolerant under controlled conditions unless Phytophthora root rot becomes a problem (Abbott and Gough 1985, Davies and Flore 1986). Korchak (1983) found highbush plants to be more sensitive to low O₂ levels in the soil than other Vaccinium species. Growth of highbush and rabbiteye (V. ashei) species generally ceases after 4-7 days of flooding (Davies and Wilcox 1984, Davies and Flore 1986).

Gas exchange characteristics of many plant species are altered under flooded conditions. Stomatal conductance decreased due to flooding within 6 days for Citrus aurantium (Syvertsen et al. 1983), Prunus sp. (Andersen et al. 1984a), Populus seedlings (Periera and Kozlowski 1977) and Liquidambar styraciflua (Pezeshki and Chambers 1985). Flooding also adversely affects carbon assimilation in a wide range of species including Malus domestica (Childers and White 1942), Lycopersicon esculentum (Brix 1962), Populus deltoides (Regehr et al. 1975), Citrus sinensis (Phung and Knipling 1976), Liquidambar styraciflua (Pezeshki and Chambers 1985) and Vaccinium ashei (Davies and Flore 1985). The decrease in carbon assimilation was attributed to stomatal factors in some species (Regehr et al. 1975, Phung and Knipling 1976) and non-stomatal factors in others (Childers and White 1942, Guy and Wample 1984), including feed-
back inhibition of photosynthesis due to starch accumulation during flooding (Wample and Thornton 1984).

Pereira and KoZlowski (1977) suggested that stomatal closure resulted from an interruption of hormone translocation from root to shoot. In contrast Davies and Wilcox (1984) observed a rapid increase in ψ (values became less negative) of rabbiteye blueberry with root excision and suggested that hydraulic conductivity of the root and cell turgor were regulating g. Similarly, flooding has been shown to decrease root conductivity of tobacco (Kramer and Jackson 1954), citrus (Syvertsen et al. 1983) and Pyrus sp. (Andersen et al. 1984b).

Studies by Davies and Flore (1986) suggested that the stomatal sensitivity of blueberries to flooding varies with duration. Stomatal conductance and transpiration of flooded blueberries were responsive to changes in the environment after 1–2 days, but became less responsive after longer flooding durations. Moreover, carbon assimilation decreased after short-term flooding (1–2 days), becoming zero or negative after longer durations (11–14 days).

Our objectives were to study the effects of short- (1–2 days), intermediate- (10–14 days) and long-term (35–40 days) flooding on gas exchange of highbush blueberries under controlled conditions. Stomatal conductance and carbon assimilation were monitored prior to gas exchange measurements in the laboratory to minimize plant-to-plant variability observed in previous studies (Davies and Wilcox 1984). This ensured that plants would be at similar physiological stages to those suggested by Davies and Flore (1986).

Abbreviations – g'w, residual conductance to CO2; g, stomatal conductance to water vapor; g'c, stomatal conductance to CO2; Ψ, leaf water potential.

Materials and methods

Plant material

One-year old rooted cuttings of cv. Bluecrop highbush blueberry (Vaccinium corymbosum L.) were obtained from a commercial nursery in June 1984 and placed into 3.8 l plastic containers in a sand:peat moss (1:1, v/v) medium. Plants were grown in a polyethylene greenhouse at 50% of full sunlight until October 18, after which 26 uniform plants were transferred to the laboratory (photon flux, 130 μmol m-2 s-1, 20–25°C) for flooding studies. Plants were ca 20–30 cm in height and had formed terminal buds. Additional plants used to determine the effect of O2 on carbon assimilation were maintained in the greenhouse until they were moved to the laboratory on 16 November 1984.

Flooding

Plants were paired visually for size and vigor, and one plant from each pair was flooded by placing the 3.8 l container into a larger container lined with plastic and applying tap water (20–25°C) slowly to the root system. Plants were flooded on various days from October 20–24 in a staggered fashion to insure that there would be plants at various stages of flooding stress as outlined by Davies and Flore (1986):

a) Short-term flooding where g, of flooded plants responded to changes in the environment, but was less than that of unflooded plants (ca 1–2 days).

b) Intermediate-term flooding where g, and carbon assimilation approached zero for flooded plants (ca 10–14 days).

c) Long-term flooding where g, no longer responded to the environment. Stomatal conductance was zero and carbon assimilation was zero or negative (ca 35–40 days).

Leaves of plants were monitored daily beginning 2 days before each stage using a LI 1600 steady state porometer (LI-COR Inc. Lincoln, Nebraska) for g, measurements and an ADC model LCA-2 portable CO2 analyzer (Analytical Development Company, Hertfordshire, England) for carbon assimilation measurements. Plants were selected for further studies based on these preliminary measurements rather than duration of flooding. This system reduced plant-to-plant variability found in previous flooding studies (Davies and Wilcox 1984) and ensured that plants would be at similar physiological stages during subsequent gas exchange studies.

Gas exchange measurements

Four flooded and 4 unflooded plants for short-term flooding and 2 plants each for intermediate and long-term flooding studies were used for gas exchange measurements. One shoot with fully expanded leaves was enclosed in one of 4 environmentally controlled plexiglass chambers (15.3 × 10 × 10 cm, length × width × height) and allowed to equilibrate for 1 h prior to measurements. Gas exchange was monitored using an open flow system consisting of a Beckman 865 infrared gas analyzer and 2 General Eastern 1100 dew point hygrometers as described previously (Sams and Flore 1982). Measurements were made within optimum ranges for highbush blueberries (J. W. Moon, Jr. 1985. Thesis, Michigan State Univ., E. Lansing, MI, USA): photon flux, 1 000 μmol m-2 s-1; leaf temperature 25°C; leaf-to-air vapor pressure deficit 1.0–1.5 kPa. Carbon assimilation, g,', g', and g, were calculated as described by Moon and Flore (1986).

Effect of CO2 concentration on carbon assimilation

The effect of various CO2 concentrations on carbon assimilation was studied for flooded and unflooded plants at each flooding stage. Leaves were equilibrated in chambers at ambient CO2 (330–350 μl l-1), and measurements performed stepwise at ca 350, 250 and 150 μl l-1 of ambient CO2. Non-ambient CO2 concentrations were prepared by mixing ambient air from which the
CO₂ had been scrubbed using soda lime with air from a compressed air tank which contained 4 000–5 000 µl l⁻¹ CO₂. The CO₂ concentration was continuously monitored with a Beckman 865 infrared gas analyzer as previously described by Sams and Flore (1982) or using an ADC Model LCA-2 infrared gas analyzer. This range of CO₂ values corresponds to the RUP, saturated (linear) phase of CO₂ response curves as described by Farquhar and Sharkey (1982) and Moon and Flore (1986) for highbush blueberries.

Effect of O₂ concentration on carbon assimilation

Two unflooded and 2 flooded (1.5 days) plants were used to study the effects of low O₂ concentration on carbon assimilation of flooded and unflooded plants. The CO₂ system was adapted to use varying concentrations of CO₂ and O₂ by connecting O₂ and N₂ tanks to a gas-mixing system using needle valves. The O₂ flowed through a LIDAR oxygen meter and then through the system where it was mixed with CO₂ and N₂. The output of the chambers was monitored continuously with an ADC CO₂ analyzer as described above. In this way CO₂ and O₂ concentrations around the shoot could be controlled and monitored. Plants were allowed to equilibrate at 330-350 µl l⁻¹ CO₂ and 21% O₂ (ambient conditions). Carbon dioxide concentration was then changed stepwise as above, after which O₂ concentration was lowered to 10 and 2% and the procedure repeated. Changes in carbon assimilation occurred within 1 min of changes in gas concentrations.

Apparent quantum yield

The same plants used in the CO₂ response studies were also used to develop light response curves and for calculation of apparent quantum yield. Stomata were allowed to open until stable values were obtained (ca 1 h; photon flux, 1 000 µmol m⁻² s⁻¹; 25°C vapor pressure deficit 1.0-1.5 kPa). Neutral density filters were then placed over each chamber sequentially giving photon fluxes of ca 600, 300, 180, 100 and 50 µmol m⁻² s⁻¹. Plants were allowed to stabilize at each light level for 30 min prior to measurements. Apparent quantum yield was calculated as the slope of the linear portion of light saturation curves (Ehleringer and Björkman 1977).

Hydraulic conductivity of the root

Following light and gas exchange measurements plants were detopped and roots placed into a large pressure chamber. Hydraulic conductivity of the root was measured using a modified pressure chamber as described by Fiscus (1975). The cut stem was pushed through a circular opening in the chamber lid to make a tight seal and the root submerged in 18-20°C water in the chamber which was sealed. A pipet was attached to the stem end via rubber tubing and 0.31 MPa pressure was applied to the chamber. Water movement through the root was monitored for 1 h, after which roots were removed and cross sectional area of the stem measured. The root was divided into structural and fibrous roots and weighed. We found no effect of time in the chamber on root conductivity within the limits of our experiment. Flow through the root was linear for pressures within 0.1–1.0 MPa; however, a pressure of 0.31 MPa was chosen as a realistic value based on similar studies (Wilcox and Davies 1983).

Results and Discussion

Effect of CO₂ concentration on carbon assimilation

Carbon assimilation was linearly correlated with CO₂ concentration for flooded and unflooded plants within the range of 150 to 400 µl l⁻¹; however, carbon assimilation was significantly less for flooded plants at all flooding stages (Figs 1–3). The slopes of the CO₂ response curves differed for unflooded and flooded plants after short-term flooding (Fig. 1) and became substantially less for flooded plants after intermediate- (Fig. 2) and long-term flooding (Fig. 3). During short-term flooding, carbon assimilation of flooded plants was lower than that of unflooded plants and was associated with lower gₛ, although gᵣ was also significantly lower (Fig. 1).

![Fig. 1. Effects of CO₂ concentration on carbon assimilation](image-url)
Stomatal conductance tended to decrease at 400 µl⁻¹ CO₂, possibly due to elevated internal CO₂ levels which approached 260–300 µl⁻¹. Transpiration and gₛ were also significantly less for flooded than unflooded plants at all flooding stages (data not shown). Similar responses to flooding were noted by Davies and Flore (1985) with rabbiteye blueberries. Stomatal conductance to CO₂ continued to decrease during intermediate and long-term flooding and was independent of CO₂ concentration over the ranges studied (Figs 2 and 3).

Changes in carbon assimilation due to ambient CO₂ concentration were associated with gₛ, for unflooded plants at all stages but were independent of gₛ, for flooded plants. It appears that flooding has a rapid (1–2 days) effect on gₛ, but that carboxylation efficiency is also limited, particularly after long-term flooding. Davies and Flore (1985) observed similar responses during short-term flooding of rabbiteye blueberry. They found that flooding for 24 h decreased gₛ, and gₛ, again supporting the idea that carbon assimilation is under stomatal control during early flooding. Regehr et al. (1975) and Phung and Knipling (1976) also suggested that carbon assimilation is controlled primarily by gₛ under flooded conditions.

**Effect of O₂ concentration on carbon assimilation**

Carboxylation efficiency [mol CO₂ fixed (mol ambient CO₂)⁻¹] of flooded plants was less than that of unflooded plants as indicated in Figs 1–3, and influenced differently by low O₂ levels (Fig. 4). Carbon assimilation and response to varying CO₂ concentrations (slope of the line) were greater for unflooded than flooded plants at
all O₂ concentrations. Moreover, a reduction in the concentration of O₂ from 21 to 2% increased carbon assimilation of unflooded plants by 33% at 330 µmol CO₂ l⁻¹. The carboxylation efficiency also increased from 0.012 mol CO₂ fixed (mol of CO₂)⁻¹ at 21% O₂ to 0.021 at 2%. In contrast, although carbon assimilation of flooded plants increased substantially as percentage O₂ decreased, the slopes of the CO₂ response curves were similar and low at all O₂ concentrations.

Carbon dioxide compensation point changed very little for unflooded plants (40-80 µmol l⁻¹), but was significantly reduced for flooded plants under low O₂ conditions from 232 (21% O₂) to 20 (2% O₂). Changes in O₂ concentration affected carbon assimilation through changes in gᵢ, not gᵣ. This situation would be expected since O₂ is a competitive inhibitor of CO₂ for RuBP carboxylase: oxygenase.

The response to low O₂ is similar to that reported for other C₃ plants (Brown 1976). Moreover, the rate of change in carbon assimilation per unit O₂ (0.117) is within the range of values reported by Brown (1976). Carbon dioxide compensation points are typical of other C₃ plants and much greater than those of C₄ plants (Ogren 1976).

### Apparent quantum yield

Apparent quantum yield was significantly less for flooded than unflooded plants at all flooding durations and continued to decrease with flooding duration (Tab. 1). Similarly, Davies and Flore (1985) observed that flooding decreased apparent quantum yield of rabbiteye blueberry plants. The reduction in apparent quantum yield appears to be a function of decreases in gᵢ and gᵣ. Apparent quantum yield of unflooded plants also decreased during the study, possibly because plants had acclimated to lower light levels in the laboratory during the incubation period. Nevertheless, the magnitude of carbon assimilation and slope of CO₂ response curves for flooded plants were consistently less than those of unflooded plants.

Apparent quantum yields for highbush blueberries are similar to those calculated from studies by Teramura et al. (1979) for rabbiteye blueberries and Moon et al. (1984) for highbush blueberries. However, values are considerably lower for highbush blueberry than those of peach (0.30; DeJong, 1983), or citrus (0.29; Sybertsen 1984). Calculated light compensation points are unrealistically low because they are based on best-fit linear regressions. However, observed light compensation points ranged from 25-35 µmol m⁻² s⁻¹ for unflooded plants to 80-102 for plants flooded more than 10 days.

Carbon assimilation is one half to one third of that observed for apple (Avery 1977), sour cherry (Sams and Flore 1982) or peach (Bryers et al. 1984) and is also lower than that reported previously for highbush blueberries (Moon et al. 1984). Light levels during development in the greenhouse and laboratory were lower in our study, which may account for lower carbon assimilation levels.

### Hydraulic conductivity of the root

Root conductivity expressed on a root weight basis was lower for flooded plants within 1-2 days of flooding and continued to decrease to low levels after long-term flooding (Tab. 2). Studies by Syvertsen et al. (1983) for citrus also showed decreases in root hydraulic conductivity for flooded plants within 3 days. Leaf water potential in this study did not differ between unflooded and flooded plants during short- or intermediate-term flooding. Leaf water potential, however, averaged -0.86 and -1.52 MPa for unflooded and flooded leaves, respectively, after long-term (35-40 days) flooding. In contrast, leaf water potential generally remained unchanged during flooding in other plant species (Periera and Kozlowski 1977, Davies and Wilcox 1984, Pezeshki and Chambers 1985).

Highbush blueberry grows poorly under flooded conditions in the field (Kender and Brightwell 1966), however, it is flooding tolerant under controlled conditions.

<table>
<thead>
<tr>
<th>Flooding duration</th>
<th>Light comp. pt (µmol m⁻² s⁻¹)</th>
<th>Apparent quantum yield</th>
<th>mol CO₂ (mol light)⁻¹</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>Days</td>
<td>Exp.</td>
<td>Calc.</td>
<td></td>
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</tr>
<tr>
<td>Unflooded</td>
<td>1-2</td>
<td>25</td>
<td>0.06</td>
<td>0.22</td>
</tr>
<tr>
<td>Flooded</td>
<td>26</td>
<td>-0.52</td>
<td>0.12</td>
<td>0.36</td>
</tr>
<tr>
<td>Unflooded</td>
<td>10-14</td>
<td>25</td>
<td>0.16</td>
<td>0.16</td>
</tr>
<tr>
<td>Flooded</td>
<td>80</td>
<td>-0.26</td>
<td>0.002</td>
<td>0.86</td>
</tr>
<tr>
<td>Unflooded</td>
<td>35-40</td>
<td>35</td>
<td>-1.24</td>
<td>0.13</td>
</tr>
<tr>
<td>Flooded</td>
<td>102</td>
<td>-0.06</td>
<td>0.0009</td>
<td>0.71</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Flooding duration (days)</th>
<th>Root hydraulic conductivity</th>
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<tbody>
<tr>
<td>Unflooded</td>
<td>Flooded</td>
</tr>
<tr>
<td>1-2</td>
<td>0.016±0.003</td>
</tr>
<tr>
<td>10-14</td>
<td>0.006±0.001</td>
</tr>
<tr>
<td>35-40</td>
<td>0.005±0.002</td>
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</table>
if Phytophthora root rot is not a problem (Abbott and Gough 1985, Davies and Flore 1986). Previous studies indicate that g, and transpiration are affected within 4–5 days of flooding (Davies and Wilcox 1984). However, studies with rabbiteye blueberry (Davies and Flore 1986), citrus (Phung and Knippling 1976) and *Liquidi-
dambar* (Pezeshki and Chambers 1984) indicate effects on gas exchange within 24 h. It appears that root hy-
draulic conductivity is significantly reduced within 1–2 days of flooding, which directly or indirectly causes de-
greesed, and transpiration. Such a mechanism would limit transpirational losses (Coutts 1981). This mecha-
nism also leads both to reduced carbon assimilation and starch accumulation (Wample and Thornton 1984).

Other studies indicate that carbon assimilation of high-
bush blueberry becomes negative after 10–14 days of flooding, particularly at temperatures above 28°C (Da-
vies and Flore 1986), suggesting that highbush blue-
berry does not adapt to flooded conditions as observed for *Populus* (Periera and Kozlowski 1977) and *Liqui-
dambar stryaciflua* (Pezeshki and Chambers 1985). Therefore highbush blueberry is physiologically intoler-
ant to flooding and appears to survive prolonged flooding via stomatal closure rather than through mor-
phological or anatomical adaptations, as observed in other plants (Periera and Kozlowski 1977, Wenkert 1981).

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