Physiological Responses of Four Hazelnut Hybrids to Water Availability in Nebraska

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PHYSIOLOGICAL RESPONSES OF FOUR HAZELNUT HYBRIDS TO WATER AVAILABILITY IN NEBRASKA

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ABSTRACT—Responses of hazelnut hybrids (88BS, BOX1, G17, and GEL502) to water availability (watered and nonwatered) were examined in the field. The study site received 35% of long-term average precipitation between July and September. Photosynthesis (A), stomatal conductance (gs), water potential (Ψ), and specific leaf area were generally lower in the nonwatered than in the watered treatment and exhibited significant seasonal decline, which was accompanied by an increase in water use efficiency (WUE) under both water treatments. Hybrids exhibited different strategies to cope with water availability. The hybrid 88BS was more water conserving, with the most decline in gs, the least gradient in Ψ, and the lowest discrimination against 13C than in the remaining hybrids, indicating that 88BS responded to drought by increasing WUE and conserving water. BOX1 was more of a water spender, maintaining both higher gs and A, low sensitivity of gs to vapor pressure deficit (VPD) increase, largest gradient in Ψ, and the most negative carbon isotope ratio, indicating a higher capacity to absorb soil water and reach limited resources. GEL502 and G17 were more affected by water stress than were 88BS or BOX1. We conclude that relatively drought-resistant hazelnut hybrids suitable for the Great Plains can be identified for successful plantations.

Key Words: carbon isotope, Corylus, drought, Great Plains, photosynthesis, water potential, water use efficiency

INTRODUCTION

Hazelnut (Corylus spp.) is an important nut tree in many countries including Turkey, Spain, Italy, and the United States (Ercisli and Read 2001). The majority of hazelnut production in the United States (around 30,000 T; FAO 2003) comes from the Willamette Valley in Oregon (Mehlenbacher 2003). Most of these plantations are cultivars of the European hazelnut (Corylus avellana L.; Farris 2000). In its native habitat, hazelnut is usually an understory species, and although its requirement for water is not high, this species is very sensitive to drought stress (Mingeau et al. 1994), high temperatures, and vapor pressure deficits (Girona et al. 1994; Hogg et al. 2000). Hazelnut introduced to areas with low (550-750 mm), unevenly distributed rainfall and dry summers (Mingeau et al. 1994), like southern Europe (e.g., France and Spain), requires supplemental irrigation to avoid late spring and early summer water stress, crucial for vegetative growth, and for providing photosynthates to carry both fruit filling and accumulation of reserves for the following year (Tous et al. 1994). However, in the United States, native drought-tolerant ecotypes of C. cornuta Marsh. have been found in areas receiving less than 150 mm of average annual rainfall (Farris 2000).
In recent years, much interest has been generated for the use of new hybrid hazelnuts (crosses between several species including but not limited to the American *C. american* and the European *C. avellana* and *C. colurna*) as an alternative crop in agroforestry systems in the U.S. Great Plains (Ercisli and Read 2001). One of the challenges, however, is the limited rainfall in this region, in which several years of summer drought is not uncommon.

In eastern Nebraska, the average annual precipitation is 720 mm, and although this is below the recommended water requirement for successful hazelnut plantations (Mingeau et al. 1994), a hazelnut plantation that was successfully established in the mid-1990s currently produces nuts at the Arbor Day Foundation’s farm at Nebraska City, NE (though it does not include hybrids selected in this study). The plantation’s success was attributed to the choice of hybrids, supplemental watering to seedlings during establishment, and precipitation distribution (high in spring and early summer) in the Great Plains, which is important for early vegetative growth.

Interest in hazelnut production as an alternative crop has been rapidly increasing in the Great Plains and elsewhere. However, hybrid selection has been mostly based on commercial values like nut characteristics, productivity, cold hardiness, and disease resistance (Pellett et al. 1998; Rutter 2000), with little research being done on physiological characteristics of hybrids. This approach has led to differences in hazelnut establishment success, growth, and survival in response to environmental stresses, namely drought. The objectives of this study were to evaluate and compare the ecophysiological and growth responses of four commonly used hazelnut hybrids to moisture availability, and to investigate the success and the importance of supplemental watering to hybrids in semiarid regions like the Great Plains.

**MATERIALS AND METHODS**

**Growth Conditions and Site Description**

Four hazelnut hybrids originating from crosses between American and European *Corylus* species were used in the study: 88BS and G17, both crosses between American and European hybrids that were back-crossed with European *C. avellana* (Farris 2000), and BOXI and GELLATLY 502 (GEL502), which are crosses between *C. cornuta* and *C. avellana* (Farris 2000). These hybrids were selected because of their purported resistance to eastern Filbert blight (caused by the fungus *Anisogramma anomola* Karen L.), cold hardiness, resistance to big bud mite (*Phytophthora avellanae* Nal.), good yields, and high-quality moderate-size nuts. American species (*C. americana* and *C. cornuta*) generally offer cold hardiness and resistance to Filbert blight, but unlike the European species, they lack nut size and production characteristics suitable for commercial production (Agriculture and Fisheries Canada 2001).

Hazelnut plants were planted in 2001 in a randomized complete block design on 1 ha of land at the University of Nebraska–Lincoln’s East Campus (latitude 40°83’, longitude 96°66’, and altitude 371 m). Initial survival was approximately 80%; failure to establish could have been related to drying of roots and damage to plants during transporting and planting. The study design featured 12 replications of three plants per hybrid. Plants were spaced 2.7 m apart within rows and 4.2 m apart between rows. A drip irrigation system was installed, with an emitter near each plant. Plants were watered on a regular basis during the 2001 growing season for establishment and when needed during the 2002 growing season. We did not record any mortality after the initial establishment stage or during the experiment. The annual average temperature on site is 10°C, with minimum average January temperature of -11.3°C and maximum average July temperature of 36°C. Soils are classified as silty clay loam.

Prior to hazelnut planting, the site was sprayed with herbicide (Roundup) during the fall of 2000, and then ripped approximately 90 cm deep every 60 cm in both north-south and east-west directions two weeks later. It was then disked three times and left to rest over winter. In the spring of 2001, a 12.7 cm squirrel-resistant fence composed of heavy-duty chicken wire, buried in the ground, with two offset high-voltage wires at the base and top of the fence, was installed. The fence surrounded the site, effectively restricting squirrel entry. Weed control was accomplished by mowing between the rows of hazelnuts and by mulching with wood chips around each hazelnut seedling. We applied herbicide to remaining weeds within the rows during the growing seasons.

In May 2003, two treatments were established: watered and nonwatered. Twenty individuals per hybrid were selected and marked for the study. Plants averaged 1.43 ± 0.04 m in height and were divided at random between the two water treatments (10 plants/hybrid/water treatment). Plants in the watered treatment received drip irrigation (24 L) once or twice a week depending on weather conditions and always during the afternoons prior to measurements. Plants in the nonwatered treatment remained under ambient conditions. Measurements
started in June 2003, after the leaves had completely developed, and ended September 29.

**Gas Exchange Measurements**

Growing season trends in gas exchange were conducted using an open system: infrared gas analyzer, mounted with a LED light source (LICOR-6400-2B, LICOR, Lincoln, NE). Air and leaf temperatures in the chamber were maintained within 1° to 2°C of ambient and CO2 concentrations in the system were maintained slightly above ambient (LICOR Inc.). Maximum net photosynthesis ($A_{max}$, μmol m⁻² s⁻¹), stomatal conductance ($g_s$, μmol m⁻² s⁻¹), and instantaneous water use efficiency (WUE = net photosynthesis/transpiration, μmol CO₂ m⁻² s⁻¹/mmol H₂O m⁻² s⁻¹) at light saturation (photosynthetically active radiation, 1,500 μmol m⁻² s⁻¹) were taken between 1000 and 1300 h solar time on seven individuals per hybrid per water treatment. Leaf samples were kept in the chamber until readings were stable before recording. Diurnal measurements were followed once a month between 0600 and 1800 h on three plants per hybrid per water treatment. We present only the diurnal curves of net photosynthesis ($A_n$), stomatal conductance ($g_s$), and the cumulative daily net photosynthetic rate ($A$) for June and August. These two months represented the general trends observed during the growing season.

**Water Potential and Carbon Isotope**

Seasonal trends in leaf predawn ($Ψ_{pre}$) and midday ($Ψ_{mid}$) water potentials were followed using the 1000 Pressure Chamber Instrument (PMS, OR). Leaf water potential was measured on all individuals used for the gas exchange measurements.

Carbon isotope ratio was determined in September, using mass spectrometry (Stable Isotope Laboratory, Kansas State University). Leaf materials were dried at 75°C for 72 h and ground to powder. The carbon isotope ratio ($δ^{13}C$) of each sample was determined by relating the $^{13}C/^{12}C$ of the sample ($R_{sample}$) to the $^{13}C/^{12}C$ ratio of the VPDB standard ($R_{standard}$):

$$δ^{13}C = [(R_{sample}/R_{standard}) - 1] × 1000.$$  

**Specific Leaf Area, Nitrogen Content, and Height**

Projected leaf area was measured with the LI-3100 (LICOR, Lincoln, NE) using several leaves from each plant in June and September (10 plants/hybrid/water treatment). Materials were dried in an oven for 72 h at 75°C and specific leaf area (SLA = leaf area/dry weight, cm² g⁻¹) was calculated. Leaf nitrogen content was subsequently determined using a FP428 nitrogen determination system 601-700-300 (Leco Corporation, St. Joseph, MO). Plant height (cm) was measured once a month throughout the study.

**Statistical Analysis**

Repeated measures analyses (two-way analysis of variance, repeated over time) were used to evaluate species’ seasonal trends in measured traits and to study the effects of water availability on physiological parameters. Data were analyzed using the Mixed Model Procedure in SAS (SAS 1998). Means were separated using the pairwise mean comparisons in SAS (the probability of difference, Pdiff statement in SAS, $P < 0.05$) (Steel et al. 1997).

**RESULTS**

**Environmental Conditions**

The study site received 650 mm of precipitation in 2003. Most of the growing-season precipitation fell between May and June as expected (total of 260 mm, which is slightly below long-term average; Fig. 1). The remainder of the summer (July-September) was hot and dry, with the study site receiving only 35% of long-term average precipitation and the average daily temperatures exceeding 30°C (Fig. 1).
TABLE 1
ANALYSES OF REPEATED MEASURES OF VARIANCE IN PHYSIOLOGICAL RESPONSES IN WATERED AND NONWATERED HAZELNUT HYBRIDS

<table>
<thead>
<tr>
<th>Source</th>
<th>Maximum photosynthesis ($A_{\text{max}}$)</th>
<th>Stomatal conductance ($g_s$)</th>
<th>Water use efficiency (WUE)</th>
<th>Midday leaf water potential ($\Psi_{\text{mid}}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Source</td>
<td>$F$</td>
<td>$P$</td>
<td>$F$</td>
</tr>
<tr>
<td>Date</td>
<td>DF 5</td>
<td>2.64</td>
<td><strong>0.0241</strong></td>
<td>21.9</td>
</tr>
<tr>
<td>Water</td>
<td>1</td>
<td>0.35</td>
<td>0.55</td>
<td>0.61</td>
</tr>
<tr>
<td>Hybrid</td>
<td>3</td>
<td>5.64</td>
<td><strong>0.0001</strong></td>
<td>6.26</td>
</tr>
<tr>
<td>Date x water</td>
<td>DF 5</td>
<td>0.64</td>
<td>0.6686</td>
<td>1.25</td>
</tr>
<tr>
<td>Date x hybrid</td>
<td>DF 15</td>
<td>1.25</td>
<td>0.2337</td>
<td>1.89</td>
</tr>
<tr>
<td>Water x hybrid</td>
<td>DF 3</td>
<td>2.55</td>
<td><strong>0.0455</strong></td>
<td>1.2</td>
</tr>
<tr>
<td>Date x water x hybrid</td>
<td>DF 15</td>
<td>1.35</td>
<td>0.1723</td>
<td>1.26</td>
</tr>
</tbody>
</table>

Note: Numbers in bold indicate significant differences at “P 0.05.”

Gas Exchange Measurements

Maximum photosynthetic rates ($A_{\text{max}}$) differed among hybrids ($P = 0.0001$) and within growing season ($P = 0.0241$; Table 1). Hybrids in both watered and nonwatered treatments had similar and relatively stable $A_{\text{max}}$ values between June 10 (DOY 161) and July 18 (DOY 196; Fig. 2). Significant differences between water treatments and hybrids appeared between July 29 (DOY 207) and September 25 (DOY 268), depending on the hybrid. Stomatal conductance ($g_s$) did not differ between water treatments ($P = 0.43$, Table 1), although it was generally lower in plants in the nonwatered treatment than in the watered treatment (Fig. 2). Stomatal conductance showed a marked decline in both water treatments between July and September ($P = 0.0001$; Table 1) except for the watered GEL502, where $g_s$ varied significantly between sampling dates (Fig. 2). The seasonal decline in $g_s$ was accompanied by a significant increase in instantaneous WUE for all hybrids. Water use efficiency did not differ among hybrids ($P = 0.46$) or water treatments ($P = 0.12$) (Table 1; Fig. 2). We regressed $A_{\text{max}}$ as a function of $g_s$ (data not shown), and a significant positive relationship was noticed only for 88BS ($P = 0.043$) under both water treatments. Stomatal conductance in GEL502 was sensitive to vapor pressure deficit (VPD), declining when VPD exceeded 2.5 kPa under both water treatments (Fig. 3). In contrast, $g_s$ was less affected by VPD increase in BOX1, G17, and the watered 88BS.

Diurnal patterns of net photosynthesis ($A_n$) and $g_s$ were generally parabolic in all hybrids except GEL502 (Fig. 4). $A_n$ and daily cumulative net photosynthesis ($A$) (Table 2; Fig. 4) were lower in plants in the nonwatered treatment than in the watered treatment, and maximum rates of $A_n$ were generally reached at 1200 h in June and at 1000 h in August before declining in the afternoon. A slight midday depression in $A_n$ and $g_s$ was noticed in August under nonwatered conditions (Fig. 4). This depression was more pronounced, however, in GEL502 under both water treatments, with afternoon recovery reported in June but not in August. Daily cumulative $A$ was highest in BOX1 under both water treatments in June and August. The remaining hybrids did not differ among each other in June; however, GEL502 experienced a significant decrease in $A$ in August relative to others under both water treatments (Table 2; Fig. 4).

Water Status

Predawn leaf water potential ($\Psi_{\text{pre}}$) showed the same seasonal trend in both watered and nonwatered plants. Predawn water potential in both treatments was high early in the growing season and declined to its lowest value in August, before recovering in September. The midday water potential gradient ($\Delta\Psi_{\text{mid}}$) between watered and nonwatered plants (Fig. 5) indicated that 88BS displayed the smallest differences and always maintained a less negative water potential (Fig. 5) than the remaining hybrids, whereas BOX1 exhibited the largest differences.
Figure 2. Growing-season trends in maximum photosynthesis ($A_{\text{max}}$), stomatal conductance ($g_s$), and water use efficiency (WUE), with standard error bars, in watered (solid line) and nonwatered (dashed line) hazelnut hybrids grown under field conditions. Asterisk (*) indicates significant differences ($P < 0.05$) among water treatments within sampling dates ($n = 7$). Dashed vertical lines separate the months of June, July, August, and September.

Figure 3. Relationship between stomatal conductance ($g_s$) and vapor pressure deficit (VPD) in watered (W, filled symbols) and nonwatered (NW, nonfilled) hazelnut hybrids grown under field conditions.
Figure 4. Diurnal curves of net photosynthesis ($A_n$) and stomatal conductance ($g_s$), with standard error bars ($n = 3$), in watered (solid line) and nonwatered (dashed line) hazelnut hybrids grown under field conditions. Maximum air temperature was 32.8°C and 33.8°C, photosynthetically active radiation was 1,800 and 1,450 μmol m$^{-2}$ s$^{-1}$, and vapor pressure deficit was 3.0 and 3.2 kPa, on June 26 and August 22, respectively.

TABLE 2
MEAN CUMULATIVE DAILY NET PHOTOSYNTHESIS IN WATERED AND NONWATERED HAZELNUT HYBRIDS

<table>
<thead>
<tr>
<th>Photosynthesis ($A$) (mol m$^{-2}$ d$^{-1}$)</th>
<th>Watered hybrids</th>
<th>Nonwatered hybrids</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>June</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>88BS</td>
<td>0.32 b</td>
<td>0.30 a</td>
</tr>
<tr>
<td>BOX1</td>
<td>0.39 a</td>
<td>0.31 a*</td>
</tr>
<tr>
<td>G17</td>
<td>0.30 b</td>
<td>0.25 b*</td>
</tr>
<tr>
<td>GEL502</td>
<td>0.31 b</td>
<td>0.24 b*</td>
</tr>
<tr>
<td><strong>August</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>88BS</td>
<td>0.31 b</td>
<td>0.24 b*</td>
</tr>
<tr>
<td>BOX1</td>
<td>0.35 a</td>
<td>0.27 a*</td>
</tr>
<tr>
<td>G17</td>
<td>0.29 b</td>
<td>0.23 b*</td>
</tr>
<tr>
<td>GEL502</td>
<td>0.25 c</td>
<td>0.17 c*</td>
</tr>
</tbody>
</table>

Note: Means with similar letters within a water treatment are not statistically different at “P 0.05.”
*Indicates significant differences between water treatments.

Carbon isotope ratio ($\delta^{13}C$) is indicative of the WUE in plants over the life of the leaf (Table 3). Results showed that 88BS discriminated the least against $^{13}C$ under both treatments, and was significantly different from others. Discrimination against $^{13}C$ decreased in response to drought, but the relationship was only significant in 88BS. Carbon isotope ratio was positively but insignificantly correlated with instantaneous WUE, and negatively correlated with leaf nitrogen content. The latter also decreased in response to drought in all hybrids except 88BS (Fig. 6).

Specific Leaf Area and Plant Height

Specific leaf area (SLA) was measured in June and September (Table 3). Specific leaf area was higher in June at the beginning of the growing season than in September in all hybrids under both water treatments. G17 and GEL502 exhibited the highest SLA under both water treatments. Specific leaf area responded positively
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...to watering; however, significant differences were only detectable for G17 and GEL502 in June and September, respectively. Height was measured on a monthly basis; the overall increase in height between June and September (Table 3) indicated that G17 was the only hybrid to display a significant positive response to watering, and GEL502 showed the least increase under both water treatments. The remaining hybrids did not differ among each other and displayed similar increases in height under both water treatments.

**DISCUSSION**

One of the main constraints to hazelnut production is perceived to be water availability (Sarraquine and Mingeau 1986; Tous et al. 1994). The study site received 35% of long-term average summer precipitation between July and September. This resulted in a significant seasonal decline in stomatal conductance, photosynthesis, and an increase in WUE in all hybrids under both water treatments, indicating that gs was not only constrained by water availability but also by high transpirational demands associated with high temperatures (>30°C), light intensities, and vapor pressure deficits (Tombesi 1994; Hampson et al. 1996; Marsal et al. 1997; Awada et al. 2003; Samartzidis et al. 2005). Similarly, Girona et al. (1994) and Hogg et al. (2000) reported high sensitivity in the gs of hazelnut trees to high temperatures and vapor pressure deficits. Our results have shown that hybrids differed in their responses to VPD increase. The observed

**Figure 5.** Growing season predawn (\(\Psi_{pdr}\)) and differences in midday water potential between watered and nonwatered hazelnut hybrids (\(\Delta\Psi_w = \Psi_{watered} - \Psi_{nonwatered}\)), with standard error bars, under field conditions (n = 7). Asterisk (*) indicates significant differences (P < 0.05) between hybrids within date. Dashed vertical lines separate the months of June, July, August, and September.

**TABLE 3**

<table>
<thead>
<tr>
<th>Specific leaf area (cm² g⁻¹)</th>
<th>Height increase (cm)</th>
<th>Carbon isotope ratio (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>June</strong></td>
<td><strong>September</strong></td>
<td><strong>Watered</strong></td>
</tr>
<tr>
<td>88BS</td>
<td>97.3 b</td>
<td>95.3 b</td>
</tr>
<tr>
<td>BOX1</td>
<td>97.9 b</td>
<td>91.4 b</td>
</tr>
<tr>
<td>G17</td>
<td>114.1 a</td>
<td>102.3 a*</td>
</tr>
<tr>
<td>GEL502</td>
<td>106.1 ab</td>
<td>102.5 a</td>
</tr>
</tbody>
</table>

Note: Means within month and water treatment with similar letters are not statistically different at "P 0.05."

*Indicates significant differences between water treatments within mon
depression in $g_s$ under both water treatments is usually achieved in order to maintain water potential above a minimum threshold value, to avoid cavitation (Hogg et al. 2000), and to help in the recovery of predawn water potential (Aspelmeier and Leuschner 2004).

Predawn leaf water potential ($\Psi_{\text{pre}}$), which is a measure of plant water status and an indicator of plant water use and adaptation to stresses (Poudyal et al. 2004; Eggemeyer et al. 2006), did not show the presence of a drought stress before July. Similarly, Girona et al. (1994) reported that differences in $\Psi_{\text{pre}}$ in hazelnut trees appeared in July and peaked in August in Spain. Hazelnut roots are shallow and the plant’s requirement for water is low; therefore, limited water supply to the topsoil layer is sufficient to help plant $\Psi_{\text{pre}}$ recover under drought conditions (Girona et al. 1994). However, differences among water treatments and hybrids appeared at midday with increased evaporative demands, and with high vapor pressure deficit, photosynthetically active radiation, and temperatures (Turner et al. 1984; Tous et al. 1994; Hogg et al. 2000). Hybrids responded differently to water treatments, indicating the need for different strategies to deal with water availability. Hybrid 88BS displayed the smallest gradient in $\Delta\Psi_{\text{mid}}$ and always maintained less negative water potential in comparison to other hybrids, whereas BOXI exhibited the largest gradient. The larger gradient observed in BOXI in comparison to other hybrids may confirm the higher driving force in this hybrid to absorb water and may explain the limited response of this hybrid to VPD increase, and both the relatively higher diurnal stomatal conductance and daily assimilation rates in this hybrid relative to others (Kramer 1983).

The 88BS differed from others in carbon isotope ratio and was the only hybrid to experience a significant decline in carbon isotope ratio under nonwatered treatment. The other hybrids showed less plasticity in this parameter, which might be attributed to the relative overall stability of internal $C_i$ to external $C_a$ ratio in some species (Aspelmeier and Leuschner 2004; Wallin et al. 2004; Sala et al. 2005). The observed variability among hybrids indicates not only differences in stomatal limitations and enzymatic processes but also possible differences in metabolites composition and concentrations (Farquhar et al. 1989; Sala et al. 2005). The observed variability among hybrids indicates not only differences in stomatal limitations and enzymatic processes but also possible differences in metabolites composition and concentrations (Farquhar et al. 1989; Sala et al. 2005). The observed variability among hybrids indicates not only differences in stomatal limitations and enzymatic processes but also possible differences in metabolites composition and concentrations (Farquhar et al. 1989; Sala et al. 2005). The observed variability among hybrids indicates not only differences in stomatal limitations and enzymatic processes but also possible differences in metabolites composition and concentrations (Farquhar et al. 1989; Sala et al. 2005).

Figure 6. Relationship between carbon isotope ratio ($\delta^{13}C$) and instantaneous water use efficiency (WUE) or leaf nitrogen concentration (N) in watered (W) and nonwatered (NW) hazelnut hybrids grown under field conditions. Each data point represents an average of 7 or 10 plants measured in September. $\delta^{13}C = -28.4 + 0.22 \times \text{WUE}, R^2 = 0.17, P = 0.3; \delta^{13}C = -25.1 - 1.01 \times \text{N}, R^2 = 0.57, P = 0.03$. The observed variability among hybrids indicates not only differences in stomatal limitations and enzymatic processes but also possible differences in metabolites composition and concentrations (Farquhar et al. 1989; Sala et al. 2005). The lack of a significant relationship may be related to the fact that $\delta^{13}C$ value is integrated over the life of the leaf, whereas instantaneous WUE is highly sensitive to external factors such as vapor pressure deficit, temperature, light, and water status at the time of measurement (Guehl et al. 1995).

Leaf nitrogen content decreased in response to water stress and was negatively correlated with $\delta^{13}C$. Similar decline in nitrogen was observed in other studies in response to drought (Xu and Baldocchi 2003; Grassi et al. 2005), and may result from the allocation of nitrogen to roots at the expense of shoots and leaves in a stressed environment (Brouwer 1983). Such allocation is a consequence of plant investment in parts that are acquiring the limited resource, in this case water, rather than parts that have the requirement for that resource (Lambers et al. 1998). This potential allocation may explain the observed
relation between nitrogen concentration and integrated water use efficiency (Grassi et al. 2005). Specific leaf area and height are usually negatively affected by water availability. Our results have shown that these parameters, while varied among hybrids, were little affected by supplemental watering, indicating that water availability did not constrain growth in these hybrids. The higher SLA in GEL205 and G17 may have intensified the drought stress in plants through increasing the total transpirational area under limited water supply.

Hybrids displayed significant genetic variability in most of the measured traits and exhibited different strategies to cope with water availability. The 88BS was the more water-conserving hybrid, as demonstrated by the decline in gs, least gradient in \( \Delta W_{\text{mid}} \), and lower discrimination against carbon isotope than the remaining hybrids, indicating that 88BS responded to water stress by increasing WUE and conserving water (Marsal et al. 1997). BOX1 was more of a water spender, maintaining both higher gs and \( A \), less sensitivity to VPD increase, highest gradient in \( \Delta W_{\text{mid}} \), and most negative \( \delta^{13} \text{C} \), indicating a higher capacity to absorb soil water and reach limited resources (Kramer 1983). GEL502 and to a lesser extent G17 were more affected by water stress than were 88BS and BOX1, indicating that hybrids with acclimation strategies similar to those of GEL502 and G17 may not be suitable for semiarid environments like the Great Plains.

The 2003 growing season was significantly dryer than normal, receiving 35% of the July-to-September long-term average precipitation (Drought Mitigation Center, NE). Nevertheless, the physiology and growth of 88BS and BOX1 hybrids in the nonwatered treatment were mildly affected, and therefore, supplemental watering did not significantly improve their responses, contrary to the responses of GEL502 and G17. This might be attributed to the crossing of these hybrids with American hazelnuts that are perceived to be better adapted to environmental stresses than their European counterparts. However, it will be important to evaluate drought responses in more mature individuals and the potential impacts on nut production and quality. We conclude that functional variability among hybrids in response to local environments could be behind unsuccessful establishment of hazelnut in certain areas and should be considered during management.

ACKNOWLEDGMENTS

This work was supported by the McEntire Stennis Forest Research Funds, USDA; the Nebraska and Northern Nut Growers associations; and Sustainable Research and Education-USDA. We would like to thank K. Elgersma and E. Schacht for their help with the fieldwork, and Drs. D. Wedin and J. Brandle for their comments. We also thank the three anonymous reviewers for their comments, which greatly improved the manuscript.

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