Physiological responses of four hazelnut hybrids to water availability in Nebraska

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Summary Ecophysiological and growth responses of four hazelnut hybrids (88BS, BOX1, G17 and GEL502) to water availability (watered and non-watered treatments) were studied during the growing season in the field with the aim to assess their suitability in the semi-arid environment of Nebraska. Soil moisture content declined during the growing season, and significantly differed between watered and non-watered treatment between July and September. The decrease in soil moisture was accompanied with a significant seasonal decline in maximum photosynthesis (A_{max}), daily cumulative photosynthesis (*A*), stomatal conductance (g_s), leaf water potential (Ψ_{pre} and Ψ_{mid}) and specific leaf area (SLA) under both water treatments. Differences among hybrids and water treatments appeared between July and September, and values were lower in non-watered than in watered treatment on several sampling dates depending on the hybrid. Water use efficiency (WUE) significantly increased from June to September but did not differ among hybrids or water treatments. BOX1 exhibited the highest *A*, the least decline in g_s and the most gradient in leaf Ψ_{mid}, whereas *A* and g_s were the lowest, and midday depression in stomatal conductance the highest in GEL502 under both water treatments. Ψ_{mid} differed among hybrids and water treatments, midday water potential gradient ($\Delta\Psi_{mid}$) between water and non-water treatment was lowest in 88BS and highest in BOX1. Carbon isotope discrimination differed among hybrids and was positively but insignificantly correlated with WUE and negatively correlated with leaf nitrogen content. $\delta^{13}C$ differed among hybrids and showed little plasticity in response to water stress except for 88BS. Increase in plant height was the least in GEL502 under both water treatments, and G17 was the only hybrid to display a significant positive response to watering, the remaining hybrids did not differ among each and showed a similar increase in height under both water treatments. Nut production was not affected by water treatment and was highest in 88BS followed by G17, GEL502 and finally BOX1. Overall, hybrids survived the growing season drought stress, and water did not seem to limit hazelnut production in semi-arid Nebraska. However, these hybrids displayed genetic variability and significantly different strategies to deal with weather variability and water stress. While, 88BS and BOX1 showed the most acclimation, they followed different strategies; 88BS was more of a water conserving hybrid; whereas BOX1 was more of a water spender with higher capacity to absorb soil water and reach limited resources. GEL502 and to a lesser extent G17 were more sensitive to water availability than 88BS and BOX1.

Keywords: *Corylus, Great Plains, drought, water potential, photosynthesis, stomatal conductance, water use efficiency, leaf nitrogen, nut production, carbon isotope.*

Introduction

Hazelnut (*Corylus* spp.) is an important nut crop in many countries including Turkey, Spain, Italy and USA (Ercisli and Read 2001). In the USA, the majority of hazelnut production 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). Water shortage in hazelnut can cause reduction in shoot growth and a drop in fruit production and quality (Tasias and Girona 1983). Hazelnut introduced to areas with low (550 - 750 mm), and unevenly distributed rainfall with 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 USA, 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. Americana* Walt. and the European *C. avellana* and *C. colurna* L.) as an alternative crop in agroforestry systems in the Great Plains of the USA (Ercisli and Read 2001). One of the challenges however, is the limited rainfall in this region, with several years of summer drought not uncommon.

In eastern Nebraska, the average annual precipitation is 720 mm, with 75% falling as rain during the growing season. Although this is below the recommended annual average precipitation required for successful European hazelnut plantations (Mingeau et al. 1994), a hazelnut plantation (does not include hybrids selected in this study) that was successfully established in the mid 1990s, currently produces nuts at the Arbor Day Foundation's farm at Nebraska City, NE. This success was attributed to the choice of hybrids, supplemental watering to seedlings during establishment, and because most of the precipitation in Nebraska and the Great Plains falls during the growing season when it is mostly needed.

Interest in hazelnut production as an alternative crop has been rapidly increasing in the Great Plains. However, hybrid selection has been mostly based on commercial values like nut characteristics, production, cold hardiness and disease resistance (Pellett et al. 1998, Rutter 2000) and little research being done on physiological characteristics of hybrids, which has lead to differences in initial establishment success, growth and survival in response to environmental stresses namely, drought. The objectives of this study were to evaluate the ecophysiological and growth responses of four commonly used hazelnut hybrids to weather variability, and to investigate the success and the importance of supplemental watering to the establishment and growth of these hybrids in the semi-arid environment of Nebraska.

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 are crosses between American and European hybrids which were back-crossed with European *C. Avellana* (Farris 2000), and BOX1 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 (*Phytoptus 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 rooted layers were planted in 2001 (initial survival was approximately 80%) in a randomized complete block design on 1 ha of land at the University of Nebraska – Lincoln's East Campus, NE (Latitude 40º 83', Longitude 96º 66' and altitude 371 m). The study design featured 12 replications of 3 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. The annual average temperature on site is 10^{o}C, with minimum average January temperature of -11.3 ^{o}C and maximum average July temperature of 36 ^{o}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 northsouth and east-west directions two weeks later. It was then disked three times, and left to rest over winter. In spring of 2001, a 12.7 cm squirrel-resistant fence composed of heavy duty chicken wire, buried in the ground, with 2 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 mulching with wood chips around each hazelnut seedling. We applied herbicide to remaining weeds within the rows during the growing seasons.

In May of 2003, two treatments were established: watered and non-watered. Twenty individuals per hybrid were selected and marked for the study. Plants averaged 143.2 ± 4.1 cm 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 the afternoons prior to measurements days. Plants in the non-watered treatment remained under ambient conditions. Soil moisture levels in the top 10 cm were monitored throughout the study next to each plant (total of 80 readings) using Time Domain Reflectometry (TDR, TH_2O portable soil moisture meter, Dynamax Inc., Houston, TX). 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 CO_2 concentrations in the system were maintained slightly above ambient. Maximum net photosynthesis (A_{max}, μmol m^{-2} s^{-1}), stomatal conductance (g_s, mol m^{-2} s^{-1}) and instantaneous water use efficiency (WUE = net photosynthesis / transpiration, μmol CO_2 m^{-2} s^{-1} / mmol H_2O m^{-2} s^{-1}) at light saturation (photosynthetically active radiation, PAR 1500 μmol m^{-2} s^{-1}) were taken between 1000 and 1300 h solar time on 7 individuals per hybrid per water treatment. Leaf samples were kept in the chamber for few minutes until readings were stable before recording. Diurnal measurements were followed once a month between 0600 and 1800 h on 3 plants per hybrid per water treatment. We only present the diurnal curves of net photosynthesis (A_n), stomatal conductance (g_s), and the cumulative daily net photosynthetic rate (A) of 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). Water potential was measured on all individuals used for the gas exchange measurements.

Carbon isotope discrimination was determined in September, using mass spectrometry (Kansas State University - Stable Isotope Laboratory). Leaf materials were dried at 75 °C for 72 h and ground to powder. The carbon isotope ratio ($\delta^{13}C$) 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 ($R_{standard}$).

$$\delta^{13}C = [(R_{sample}/R_{standard})-1] \times 1000.$$

Specific leaf area, nitrogen content, height and nut production

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, cm^2 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. Nut production was monitored throughout the study and the total weight of clean nut produced per plant (g $plant^{-1}$) was determined.

Statistical analysis

Repeated measures analyses (two-way analysis of variance, repeated over time) were used to evaluate species seasonal trends in measured parameters and to study the effects of water 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 (10% below the long-term average). Most of the growing season precipitation fell between May and June as expected (total of 260 mm, which is slightly below long-term average, Figure 1), resulting in the lack of significant differences in soil moisture between the two water treatments in June (DOY 152-181, Figure 2). The remaining of the summer was hot and dry with the study site receiving only 35% of long-term average precipitation and the average daily temperatures exceeded 30^{o}C (Figure 1), resulting in significantly drier soils in the non-watered versus the watered treatment (Figure 2).

Gas exchange measurements

Maximum photosynthetic rates (A_{max}) differed among hybrids and within growing season (Table 1). Hybrids in both watered and non-watered treatments had similar and relatively stable A_{max} values between June 10 (DOY 161) and July 18 (DOY 196; Figure 3). Significant differences between water treatments and hybrids appeared between July 29 (DOY 207) and September 25 (DOY 268) as a response to the decline in soil moisture and the increase in PAR and average air temperatures (>30^{o}C). Stomatal conductance (g_s) was generally lower in non-watered treatment and showed a marked decline in both water treatments between July and September except for the watered GEL502, where g_s varied significantly between sampling dates (Figure 3). The largest seasonal decline in g_s was noticed in 88BS (62%) and the least in GEL502 (45%). The decline in g_s was accompanied by a significant increase in instantaneous WUE for all hybrids in September, but WUE did not differ among hybrids or water treatments (Figure 3). We regressed A_{max} as a function of g_s (data not shown) and a significant positive relationship was only noticed for 88BS ($P < 0.05$), under both water treatments.

Diurnal patterns of A_n and g_s were generally sinusoidal in all hybrids except for GEL502 (Figure 4). A_n and A were lower in non-watered treatment and maximum rates of A_n were generally reached at 1200 in June and at 1000 h solar time in August before declining in the afternoon. Slight midday depression in A_n and g_s was noticed in August under non-watered conditions (Figure 4). This depression was however more pronounced 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, Figure 4).

Water status

Predawn leaf water potential (Ψ_{pre}) showed the same seasonal trend and values were similar in both watered and non-watered plants. Ψ_{pre} in both treatments was high early in the growing season (~ -0.3 MPa) and declined to its lowest value in August (~ -0.8 MPa), before recovering in September. Midday leaf water potential (Ψ_{mid}) on the other hand, varied between dates and water treatments (Table 1, Figure 5). Differences between water treatments were pronounced in July and August, where plants experienced water stress. Hybrids responded differently to water stress, Ψ_{mid} gradient ($\Delta\Psi_{mid}$) between watered and non-watered plants (Figure 6) indicated that 88BS displayed the least differences and always maintained a less negative water potential (Figures 5 and 6) than the remaining hybrids, whereas BOX1 exhibited the most differences.

Carbon isotope discrimination ($\delta^{13}C$) was determined in September and is indicative of the WUE in plants over the life of the leaf. Results show that 88BS discriminated the least against carbon isotope under both water treatments (Table 2), and was significantly different from others. Discrimination against carbon isotope decreased in response to drought but the relationship was only significant in 88BS. Discrimination against carbon isotope was positively but insignificantly correlated with instantaneous WUE, and negatively correlated with leaf nitrogen content, the latter also decreased as a response to drought in all hybrids except 88BS (Figure 7).

Specific leaf area and productivity

Specific leaf area (SLA) was measured in June and September (Table 2). SLA 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. SLA was generally lower in non-watered plants than watered, 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 2) 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. Water treatment did not have any significant impact on nut production, differences however appeared between hybrids, with average total nut clean weight being highest in 88BS and G17, followed by GEL502 and finally BOX1 (Table 2).

Discussion

One of the main constraints for hazelnut production is perceived to be water availability (Sarraquine and Mingeau 1986, Tous et al. 1994). Photosynthesis and stomatal conductance in hazelnut were found to be significantly affected when soil moisture dropped below 65% of field capacity (Tombesi 1994). Volumetric soil moisture content (SMC) declined to a less than 60% of field capacity (volumetric SMC at field capacity is ~ 29) in both water treatments, reaching below the wilting points (volumetric SMC at wilting point is 20%) in the non-watered treatment on several sampling dates between July and September, resulting in a significant decline in stomatal conductance, photosynthesis, and an increase in WUE in all hybrids. Hybrids in the watered treatment also experienced similar trends indicating that g_s was not only constrained by water availability but also by high transpirational demands associated with high temperatures (>30 ºC), PAR and vapor pressure deficits (Hampson et al. 1996, Marsal et al. 1997, Awada et al. 2003). The observed depression in g_s under both water treatments is usually achieved 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 (Ψ_{pre}) which is a measure of plant water status and is an indicator of plant water use and adaptation to stresses (Poudyal et al. 2004) did not show the presence of a drought stress before July. Similarly, Girona et al. (1994) reported that differences in Ψ_{pre} in hazelnut appeared in July and peaked in August in Spain. Hazelnut roots are shallow and its requirement for water is low, therefore, limited water supply to the top soil layer is sufficient to help plant Ψ_{pre} recover under drought conditions. Differences, however among water treatments and hybrids appeared at midday with increased evaporative demands, and high vapor pressure deficit, PAR and temperatures (Turner et al. 1984, Tous et al. 1994, Hogg et al. 2000). Hybrids responded differently to drought indicating different strategies to deal with water stress. 88BS displayed the least gradient in $\Delta\Psi_{mid}$ and always maintained less negative water potential in comparison to other hybrids, whereas BOX1 exhibited the steepest gradient. The larger gradient observed in BOX1 confirms the higher driving force in this hybrid to absorb water and explains both the higher stomatal conductance and photosynthesis rates in this hybrid relative to others (Kramer 1983).

The 88BS differed from others in carbon isotope discrimination and was the only hybrid to experience a significant decline in carbon isotope discrimination under non-watered treatment, indicating a relatively low plasticity in this parameter. This 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 does not only indicate differences in stomatal limitations and enzymatic processes, but also differences in metabolites composition and concentrations (Farquhar et al. 1989, Sala et al. 2005). Instantaneous WUE was positively but insignificantly correlated with $\delta^{13}C$, other studies have reported a strong correlation between WUE and $\delta^{13}C$ (e.g. Ehleringer 1990, Zhang and Marshall 1994). The lack of a significant relationship may be related to 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 *N* has been observed in other studies in response to drought (Xu and Baldocchi 2003, Grassi et al. 2005), and may result from the allocation of *N* to roots at the expanse of shoots and leaves in a stressed environment (Brouwer 1983) as 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 *N* concentration and integrated water use efficiency (Grassi et al. 2005).

Specific leaf area, height and productivity are usually negatively affected by drought, our results have shown that these parameters while varied among hybrids, were little affected by watering, clearly indicating that water availability did not constrain growth and productivity in these hybrids in Nebraska. This might be attributed to the crossing of these hybrids with American hazelnuts that are perceived to be better adapted to environmental stresses than the European ones and to the precipitation distribution in the Great Plains. Productivity was least in BOX1 and highest in 88BS; differences between hybrids may be genetic and / or associated with the alternate year productive nature of hazelnut. It is early at this point to draw conclusions solely based on productivity due to the young age of the plants.

Hybrids displayed significant genetic variability in most of measured parameters and exhibited different strategies to cope with water stress. 88BS and BOX1 showed the most acclimation, but followed different strategies. 88BS was more of a water conserving hybrid, with the most decline in g_s, least gradient in $\Delta\Psi_{mid}$ and lower discrimination against carbon isotope, indicating that this species responded to drought by increasing WUE and conserving water (Marsal et al. 1997). BOX1 was more of a water spender, maintaining both higher g_s and A_n, highest gradient in Ψ_{mid} and most negative $\delta^{13}C$, indicating a higher capacity to absorb soil water and reach limited resources. GEL502 and to a lesser extent G17 were more sensitive to water stress than 88BS and BOX1.

The 2003 growing season was dryer than normal (Drought Mitigation Center, NE), nevertheless, all plants in the non-watered treatment survived by following different strategies. Furthermore, growth characteristics did not vary between water treatments, suggesting that the lack of supplemental watering while revealing physiological differences, did not result in differences in growth and nut production.

Acknowledgment

This work was supported by the McEntire Stennis Forest Research Funds-USDA, The Nebraska and Northern Nut Grower Associations, and SARE-USDA. We would like to thank K. Elgersma and E. Schacht for their help with the fieldwork. We also appreciate Drs. D. Wedin, J. Brandle and the reviewers comments on the manuscript. This is a contribution of the University of Nebraska Agricultural Research Division, Lincoln, NE 68583. J.S. No 14985.

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Table 1. Repeated measures analysis of variance for photosynthesis (A_{max}), stomatal conductance (g_s), water use efficiency (WUE) and midday leaf water potential (Ψ_{mid}), in watered and non-watered hazelnut hybrids grown under field conditions. Bold indicates significant differences at P 0.05.

Source		A_{max}		g_s		WUE		Ψ_{mid}	
	DF	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Date	5	2.64	**0.0241**	21.9	**0.0001**	172.86	**0.0001**	7.72	**0.0002**
Water	1	0.35	0.55	0.61	0.43	2.42	0.12	0.60	0.615
Hybrid	3	5.64	**0.0001**	6.26	**0.0004**	0.86	0.46	1.32	0.25
Date x water	5	0.64	0.6686	1.25	0.286	1.44	0.21	0.39	0.93
Date x hybrid	15	1.25	0.2337	1.89	**0.025**	1.62	0.07	0.14	0.93
Water x hybrid	3	2.55	**0.0455**	1.2	0.31	1.93	0.12	4.71	**0.005**
Date x water x hybrid	15	1.35	0.1723	1.26	0.23	1.31	0.199	2.95	**0.005**

Table 2. Mean cumulative daily net photosynthesis (*A*), specific leaf area (SLA), cumulative increase in height, carbon isotope discrimination ($\delta^{13}C$) and total average nut clean weight per plant, in watered (W) and non-watered (NW) hazelnut hybrids grown in the field. Means within month with similar letters are not statistically significant at P 0.05. (*) indicates significant differences between water treatments.

	A (mol m^{-2} d^{-1})		SLA (cm^2 g^{-1})		Height increase (cm)		$\delta^{13}C$ (‰)		Average nut clean weight per plant (g $plant^{-1}$)
	W	NW	W	NW	W	NW	W	NW	W and NW
June									
88BS	0.32 b	0.30 a	97.3 b	95.3 b					
BOX1	0.39 a	0.31 a*	97.9 b	91.4 b					
G17	0.30 b	0.25 b*	114.1 a	102.3 a*					
GEL502	0.31 b	0.24 b*	106.1 ab	102.5 a					
September									
88BS	0.31 b	0.24 b*	88.6 b	83.3 ab	14.3 ab	14.2 a	-27.2 a	-26.8 a*	176.9 a
BOX1	0.35 a	0.27 a*	79.3 b	79.1 b	12.5 ab	12.3 ab	-27.7 b	-27.4 b	30.3 c
G17	0.29 b	0.23 b*	86.7 b	86.9 a	19.0 a	13.5 a*	-27.5 b	-27.2 b	162.3 a
GEL502	0.25 c	0.17 c*	98.7 a	87.4 a*	8.8 b	8.7 b	-27.5 b	-27.3 b	90.7 b

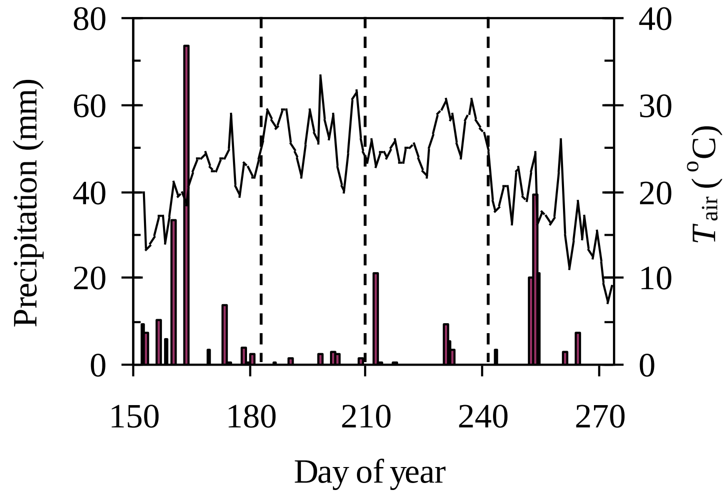

Figure 1. Growing season trends in average daily air temperature (T_{air}, ^oC, solid line) and precipitation (mm, bars) on site. Dashed vertical lines separate the months of June, July, August and September.

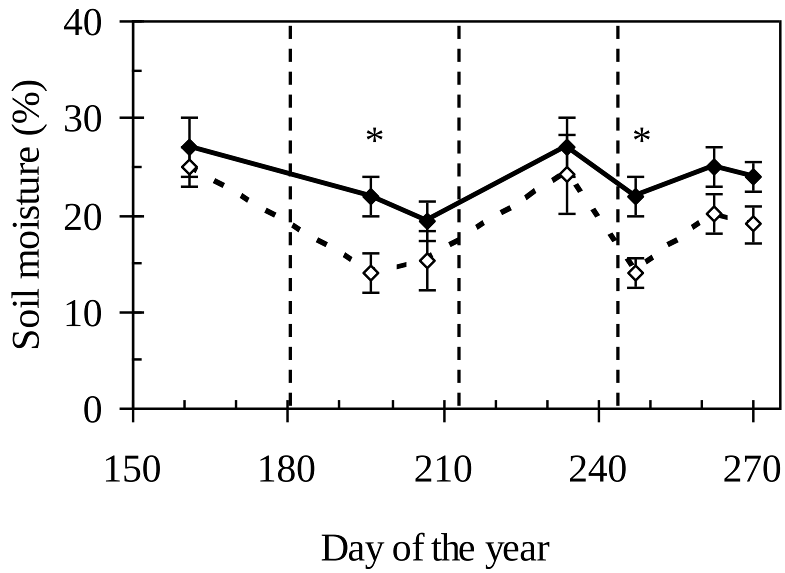

Figure 2. Average volumetric soil moisture contents in the top 10 cm with standard error bars in watered (solid line) and non-watered (dashed line) treatments. (*) indicates significant differences (P<0.05) among treatments within sampling date (n = 40). Dashed vertical lines separate the months of June, July, August and September.

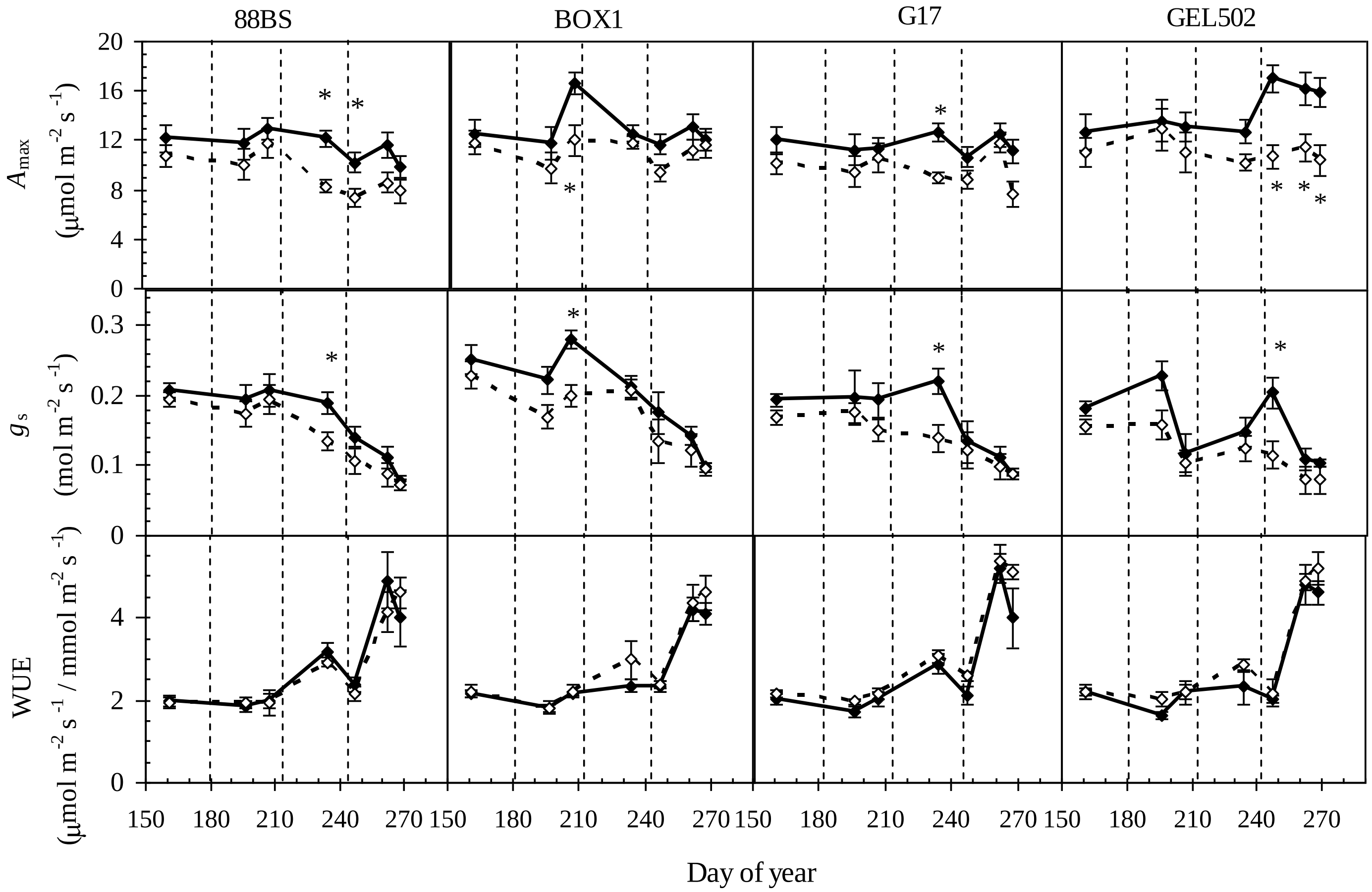

Figure 3. Growing season trends in maximum photosynthesis (A_{max}), stomatal conductance (g_s), water use efficiency (WUE) with standard error bars, in watered (solid line) and non-watered (dashed line) hazelnut hybrids grown under field conditions. (*) indicates significant differences (P<0.05) among water treatments within sampling dates (n = 7). Dashed vertical lines separate the months of June, July, August and September.

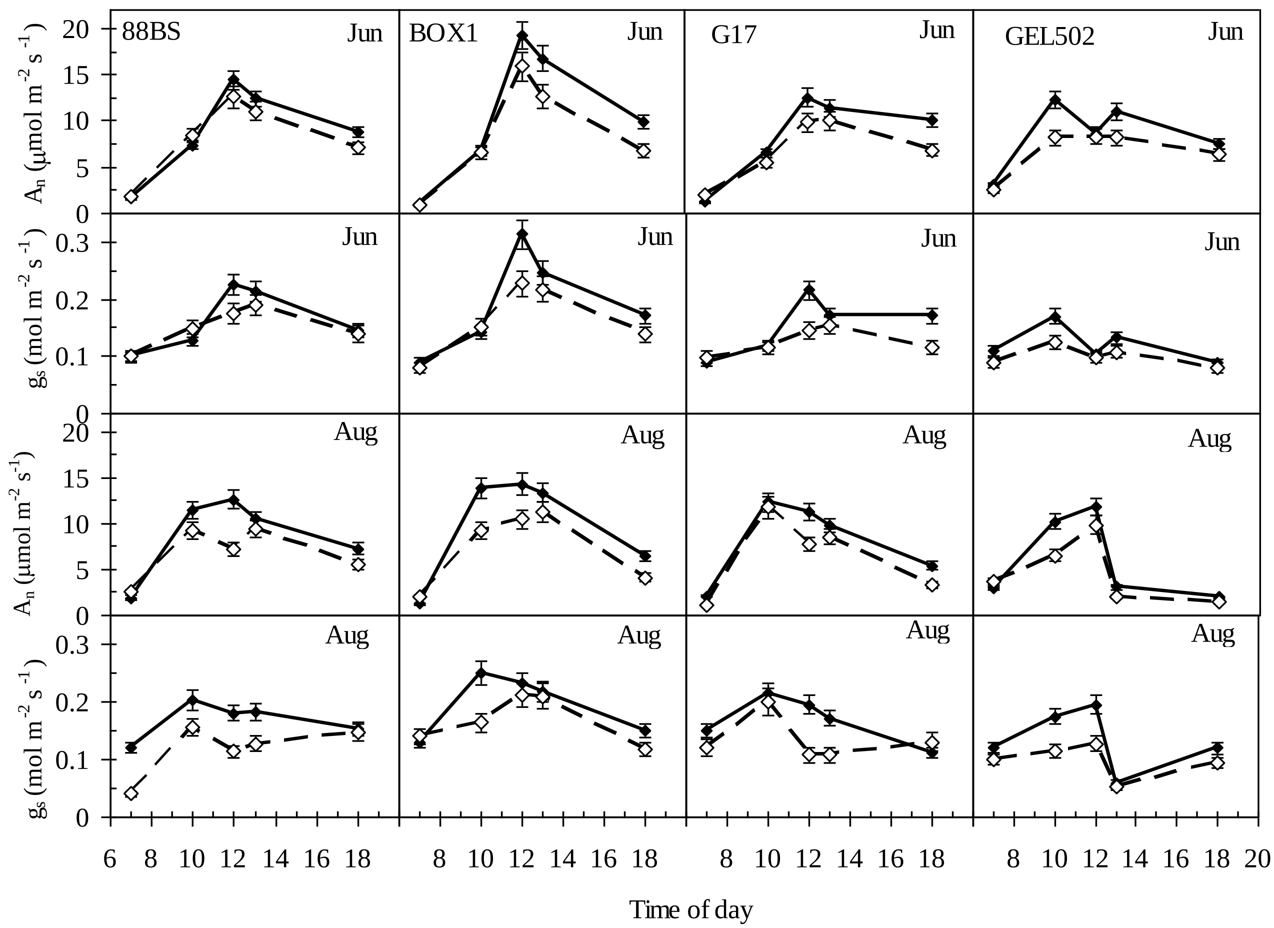

Figure 4. Diurnal curves of net photosynthesis (A_n) and stomatal conductance (g_s) with standard error bars (n = 3), in watered (solid line) and non-watered (dashed line) hazelnut hybrids grown under field conditions. Maximum air temperature was 32.8 and 33.8 ºC, PAR was 1800 and 1450 µmol m^{-2} s^{-1} and vapor pressure deficit was 3.0 and 3.2 kPa, in June 26 and August 22, respectively.

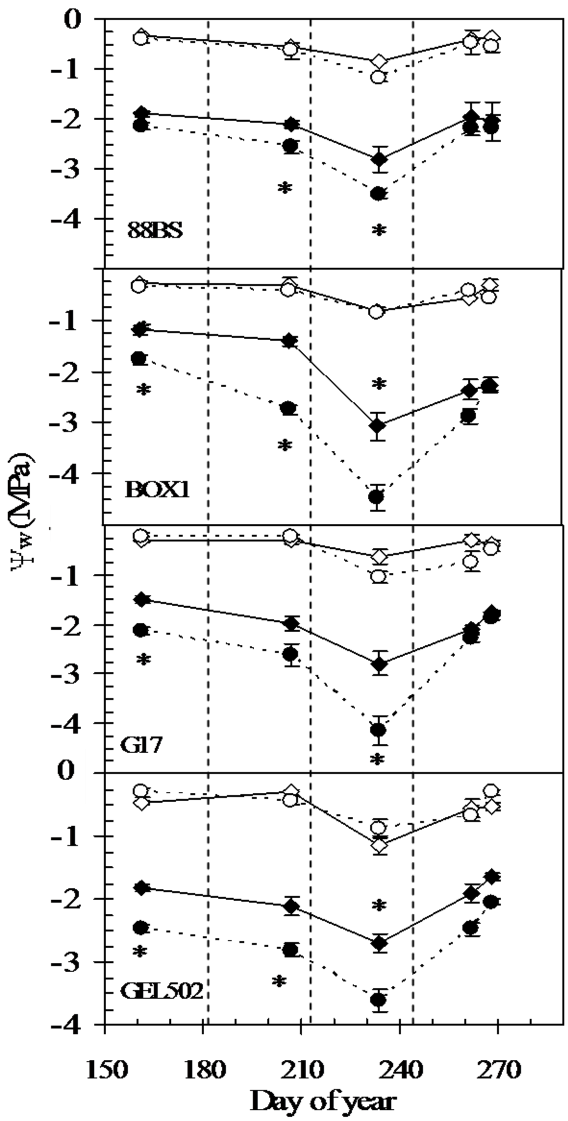

Figure 5. Growing season trends in pre-dawn (Ψ_{pre}, open symbols) and midday (Ψ_{mid}, filled symbols) water potentials with standard error bars, in watered (solid line) and non-watered (dashed line) hazelnut hybrids grown under field conditions. (*) indicates significant differences (P<0.05) among treatments within sampling dates (n = 7). Dashed vertical lines separate the months of June, July, August and September.

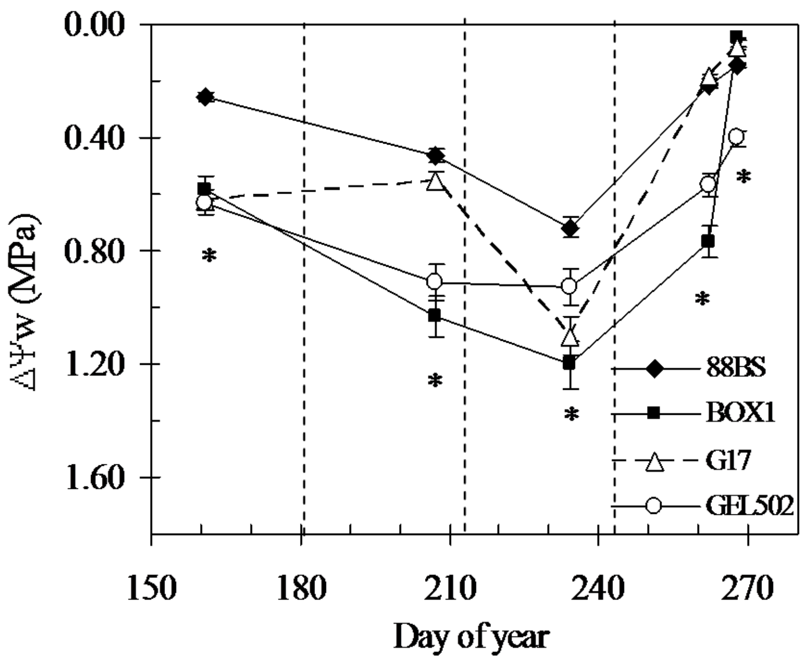

Figure 6. Growing season differences in midday water potential between watered and non-watered hazelnut hybrids ($\Delta\Psi_w = \Psi_{watered}$-$\Psi_{non\text{-}watered}$), with standard error bars under field conditions (n = 7). (*) indicates significant differences (P<0.05) between hybrids within date. Dashed vertical lines separate the months of June, July, August and September.

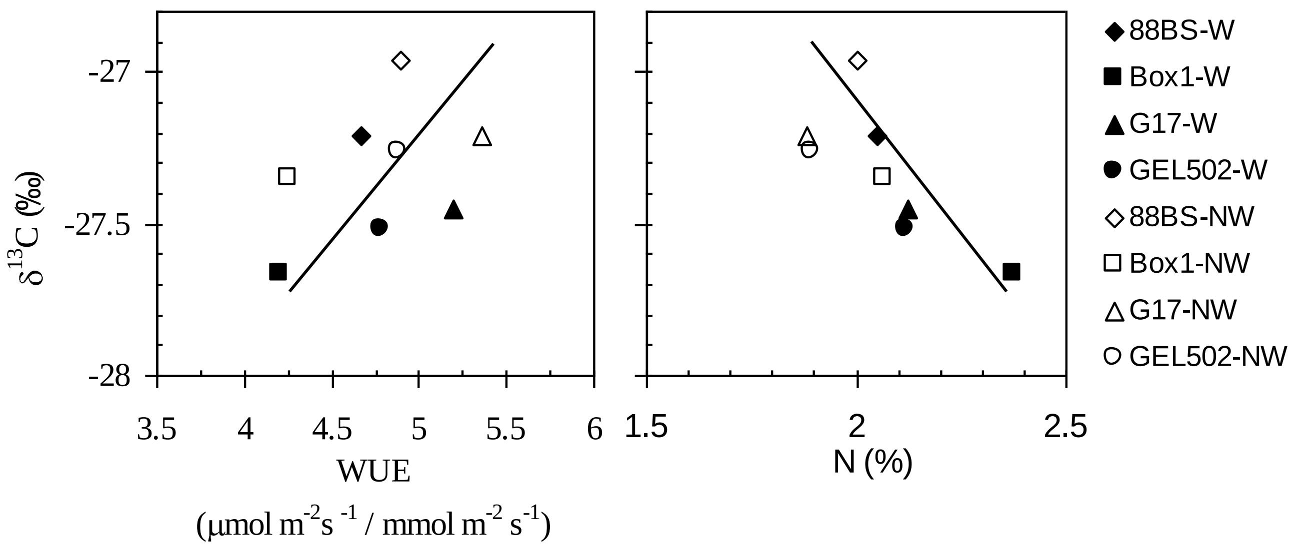

Figure 7. Relationship between carbon isotope discrimination ($\delta^{13}C$) and instantaneous water use efficiency (WUE) or leaf nitrogen concentration (*N*) in watered (W) and non-watered (NW) hazelnut hybrids grown under field conditions. Each data point represents an average of 7 or 10 plants measured in September. $\delta^{13}C = -28.4 + 0.22WUE$, $R^2 = 0.17$, P=0.3; $\delta^{13}C = -25.1 - 1.01N$, $R^2 = 0.57$, P=0.03.