

Leaf Water Relation Parameters in Almond Compared to Hazelnut Trees during a Deficit Irrigation Period

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ABSTRACT. The influence of deficit irrigation on predawn leaf water potential (ψ_{pd}) and leaf gas-exchange parameters was analyzed in almond [*Prunus dulcis* (Mill.) D.A. Webb] and compared to hazelnut (*Corylus avellana* L.). Both species were planted in adjacent plots in which four irrigation treatments were applied: T-100%, T-130%, and T-70%, which were irrigated at full crop evapotranspiration (ET_c), 1.3 × ET_c, and 0.7 × ET_c, respectively, and a regulated deficit irrigation (RDI) treatment, which consisted of full irrigation for the full season, except from middle June to late August when 0.2 × ET_c was applied. Under nonstressful conditions, hazelnut had a lower net CO₂ assimilation rate (A) (12.2 μmol·m⁻²·s⁻¹) than almond (15.5 μmol·m⁻²·s⁻¹). Reductions in net CO₂ assimilation rate (A) induced by decreases in ψ_{pd} were higher in hazelnut than in almond. Gas-exchange activity from early morning to midday decreased in hazelnut for all irrigation treatments, but in almond increased in the well-watered treatments and decreased slightly or remained constant in the RDI. Hazelnut had a higher A sensitivity to variations in stomatal conductance (g_s) than almond, especially at low g_s values. The ψ_{pd} values in almond and hazelnut of the T-100% and T-130% treatments were affected by decreasing values in midsummer, but in hazelnut ψ_{pd} was probably also affected by sink kernel filling. These facts indicate that hazelnut RDI management could be more problematic than in almond.

Hazelnuts (*Corylus avellana*) are normally grown where rainfall is enough to satisfy crop water requirements fully. However, in some areas, such as the Tarragona province (northeastern Spain, Catalunya) and some areas of France and Italy, irrigation is necessary to produce hazelnuts. Almond (*Prunus dulcis*) trees coexist with hazelnut in Tarragona, but almond is commonly grown on dry lands that make it less productive. The expectations for both crops could be improved if almond was irrigated and hazelnut water requirements could be lowered. The use of regulated deficit irrigation (RDI) strategies (Chalmers et al., 1981; Goldhamer and Shackel, 1990) could help reduce the amounts of water during the less-sensitive periods without substantively affecting yields. One of the physiological processes that is least sensitive to water stress is dry matter translocation (Faust, 1989), and this is the main event in nut trees during the kernel-filling stage. At that time, there is little vegetative growth and the different fruit tissues are near full size (Micke and Kester, 1978). Hazelnut yields have been described to be highly sensitive to water stress from fertilization to kernel filling (Mingeau et al., 1994). Therefore, the proposed RDI deficit irrigation period is located during the kernel-filling period for both species.

Almond trees are considered to be a very drought-tolerant crop (Grasselly and Crossa-Reynaud, 1984). This ability to endure high water deficits is presumably related to adaptive mechanisms, some of which occur at a leaf or root-system level such as osmotic adjustment (Castel and Fereres, 1982; Planes, 1994), stomata

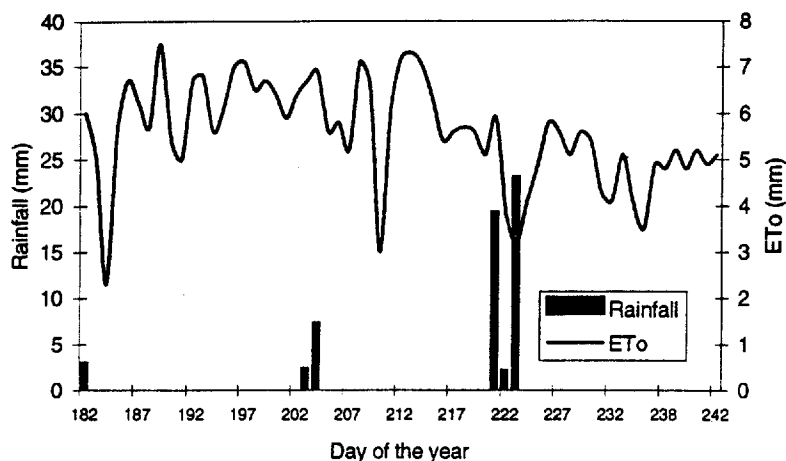


Fig. 1. Daily rainfall and reference evapotranspiration during the time of physiological measurements.

behavior (Torrecillas et al., 1988), leaf shedding (Castel and Fereres, 1982), or increasing the deepness of the root system (Ryugo, 1988). On the other hand, hazelnut's tolerance to water stress is quite low (Girona, 1994; Schulze and Küppers, 1979).

The aim of this paper is to analyze the different ecophysiological responses of the two nut tree species under a progressive 2-month partial water deprivation to improve the understanding of their differential behavior. The data shown is obtained in the context of developing a single RDI strategy that can be applied to almond and hazelnut.

Material and Methods

EXPERIMENTAL ORCHARD. The experiment was carried out in adjacent 0.57-ha almond and 0.30-ha hazelnut plots, with the same soil conditions (Xerochrept calcixerollic) at 2 m, located at the experimental fields of the Centre de Mas Bové-IRTA in Reus, Spain.

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Table 1. Annual applied water 1991 for each irrigation treatment and crop.

Treatment	Almond		Hazelnut	
	Water (mm)	ETc (%)	Water (mm)	ETc (%)
T-70%	400	69	242	68
T-100%	580	100	358	100
T-130%	750	129	464	130
RDI	225	39	150	42

The almond cultivar used was 'Ferragnes', and the pollinizers were 'Ferraduel' and 'Cristomorto'. A total of 192 five-year-old Almond trees on 'GF-677' rootstock was used in this study. Tree spacing was 5 × 6 m. The hazelnut cultivar used was 'Pauetet' with 'Gironell' and 'Negret' as pollinizers. A total of 252 five-year-old hazelnut trees was used from an experimental orchard with a tree spacing of 6 × 1.5 m.

A localized microsprinkler irrigation system was installed in both plots. The wetted area was about 35% of the soil surface. The system was controlled with a time clock and solenoid valves. The plots were managed according to normal commercial practices, including a herbicide strip in the tree rows and cultivation between rows.

EXPERIMENTAL DESIGN. Four treatments were defined for the two

species: T-100%, T-130%, and T-70% of ETc and one RDI schedule. The T-100% treatment was irrigated under full regime (ETc), based on soil water content, predawn leaf water potential (ψ_{pd}), and Penman-determined reference evapotranspiration (ETo) (Doorenbos and Pruitt, 1977). The T-130% and T-70% treatments were irrigated applying 1.3 × ETc and 0.7 × ETc, respectively. RDI was irrigated at full ETc from April to 20 June, 0.2 × ETc from 20 June to harvest (about 15 Sept.), and again full ETc after harvest. This paper presents data from the deficit irrigation period in 1991.

A randomized complete-block design with three replications was used in this experiment (Little and Hills, 1972). For almond, each block consisted of 16 trees (4 × 4), the middle 4 trees being used for experimental measurements and the others as nonexperimental guard trees. For hazelnut, each block consisted of 21 trees (3 rows × 7 trees per row), the 5 middle trees of the middle row being used for experimental measurements and the others as nonexperimental guard trees.

GENERAL MEASUREMENTS. Data from the nearest automated weather station to the study field (1 km) (Xarxa Agrometeorològica de Catalunya; Generalitat de Catalunya, 1994) were used to monitor weather information and estimate crop water use. Average daily values of ETo during July and first week of August was 6.5 mm·d⁻¹ (Fig. 1). Later, from day 212, ETo values averaged 5 mm·d⁻¹.

Soil-water-content (θ_g) was determined using a neutron probe

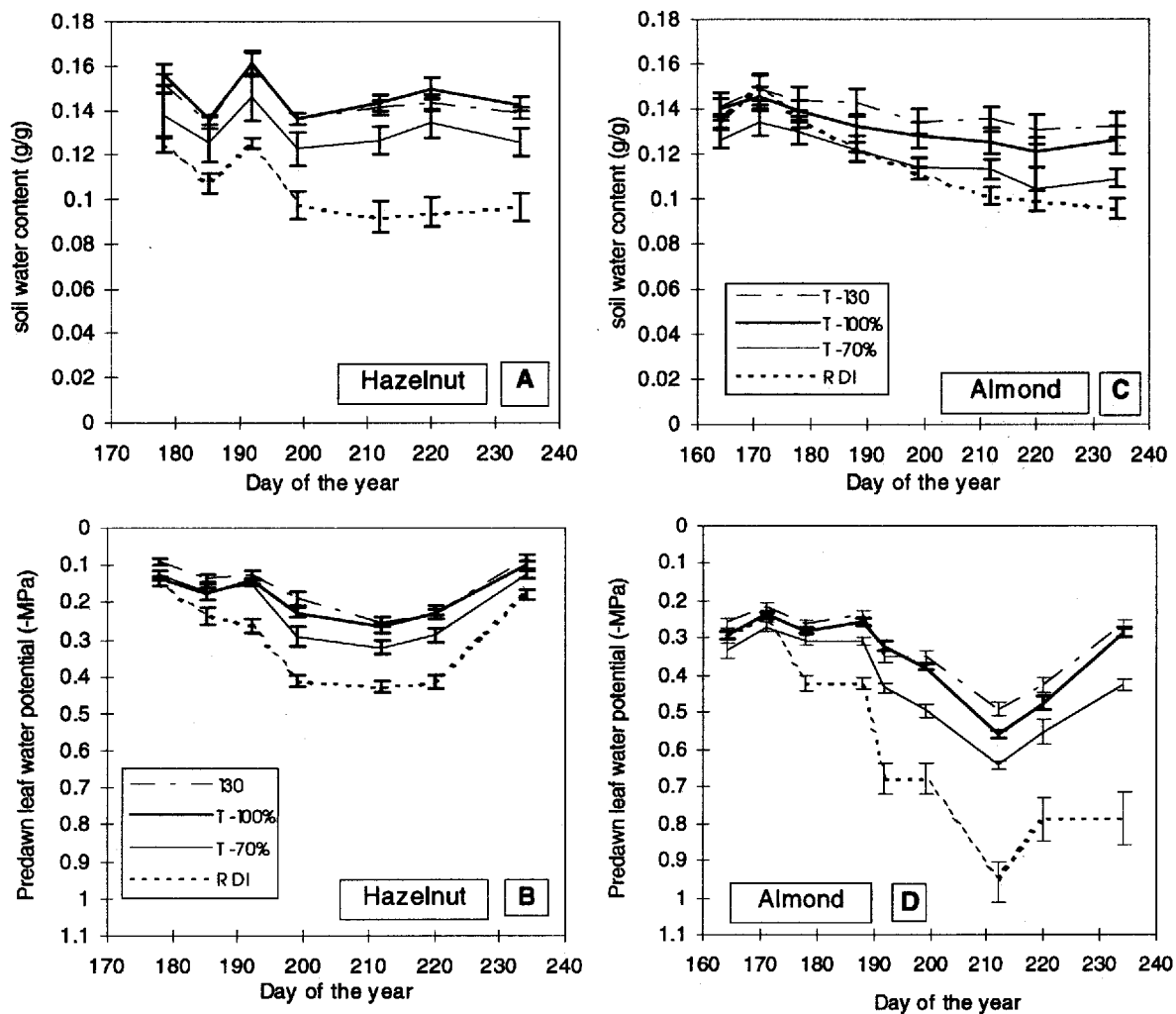


Fig. 2. Seasonal patterns of hazelnut gravimetric soil water content averaged over the 60-cm profile (A), hazelnut predawn leaf water potential (ψ_{pd}) (B), almond gravimetric soil water content averaged over the 160-cm profile (C), and almond ψ_{pd} (D) in response to irrigation treatments. Each point represents mean of six (A and C) and twelve (B and D) measurements \pm SE.

(Hydroprobe model 503; Campbell Scientific, Logan, Utah), which was previously calibrated by gravimetric measurements for the site. Two 2-m access tubes were located in each block-treatment in the wetted area in the tree row. Soil moisture was determined weekly in 20-cm increments from surface to 180 cm deep in the profile. Field capacity and permanent wilting point averaged over 90 cm from soil surface were 0.185 and 0.095 g·g⁻¹, respectively.

Water meters were read weekly for each treatment to evaluate the amount of water applied.

PHYSIOLOGICAL MEASUREMENTS. The ψ_{pd} values were measured weekly before sunrise using the pressure-chamber technique (Scholander et al., 1965) following the recommendations of Turner and Long (1980). Readings were taken with a plant status console (model 3005; Soil Moisture Equipment Corporation, Santa Barbara, Calif.)

Net CO₂ assimilation rate (A), stomatal conductance (g_s), and intercellular CO₂ in the leaf (C_i) were determined using a portable infrared gas analysis (IRGA) system (model ADC LCA-2; Analytical Development Co. Ltd., Hoddesdon, Herts, U.K.), according to the equations given by von Caemmerer and Farquhar (1981). Readings were taken in mature, well-exposed sunlight leaves at weekly intervals at 8 AM, 11 AM, and 2 PM.

Results

APPLIED IRRIGATION WATER. The annual amount of water applied to T-100% treatment was 580 mm for almond and 358 mm for hazelnut. In both crops, the RDI treatment received about 40% less water at the end of the year than the T-100% treatment (Table 1).

SOIL WATER CONTENT. Seasonal patterns of θ_g in both species clearly showed higher water content in the treatments that received more water (Fig. 2 A and C). In trees that received RDI, θ_g declined throughout the season, but at the end of the season the decline was more apparent in almond than in hazelnut, which had constant θ_g values during August (Fig. 2 A and C). The θ_g values for the almond orchard (Fig. 2C) were plotted to a greater depth than for hazelnut because of the differences in root depth; thus, θ_g values between species (Fig. 2 A and C) are not strictly comparable.

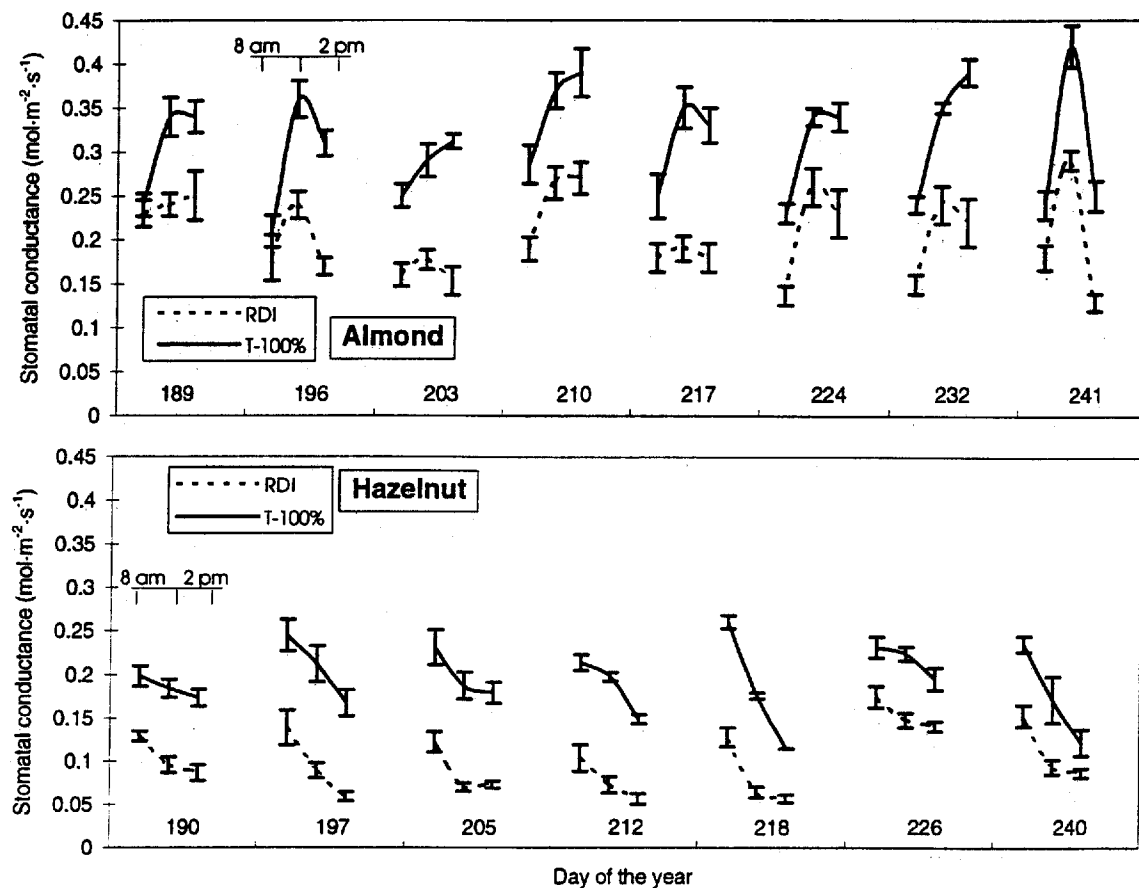
SEASONAL ψ_{pd} PATTERNS. The ψ_{pd} values indicated that the RDI treatment in both species had significant negative effects on plant water status (Fig. 2 B and D). The pattern was quite similar for both species, although there was a noticeable

difference in the lowest values obtained: -1.6 and -0.42 MPa for almond and hazelnut, respectively (Fig. 2 B and D). In hazelnut and almond, there was a period between day of the year 197 and 220 when ψ_{pd} values were more negative in all treatments (Fig. 2 B and D). Subsequently, on day of the year 232, a general recovery of ψ_{pd} values occurred for all treatments in hazelnut, although θ_g remained more or less the same on those days (Fig. 2A).

LEAF GAS-EXCHANGE MEASUREMENTS. Diurnal patterns of g_s during the season showed a very distinct difference in daily pattern between almond and hazelnut (Fig. 3). In almond there was an initial rise in g_s values in the early morning (from 8 AM to 11 AM) followed by a plateau or slight depression at midday, whereas g_s declined in all hazelnut treatments as the day progressed. Hazelnut g_s values in the RDI treatment at 2 PM were quite low, showing that stomata were approaching full closure, at least until day 218 (Fig. 3). On the other hand, g_s in almond RDI at this time showed only a slight decrease relative to morning values. Meanwhile, almond T-100% always maintained higher values at 2 PM than at 8 AM (Fig. 3). Daily and seasonal patterns of A showed similar trends to g_s (data not shown). There was a statistically significant second-order polynomial relationship between A and g_s in both species (Fig. 4). It was also evident that the A vs. g_s relationship was closer in hazelnut than in almond (R² = 0.80 and 0.58, respectively) (Fig. 4 A and B).

A linear relationship between ψ_{pd} and midday A was found (Fig. 5). This relationship was statistically different and steeper for hazelnut than for almond, yielding null A values when hazelnut ψ_{pd}

Fig. 3. Seasonal patterns of stomatal conductance (g_s) at 8 AM, 11 AM, and 2 PM (local time) in almond (up) and hazelnut (down) in response to irrigation treatments. Each point represents mean of nine measurements ± SE.



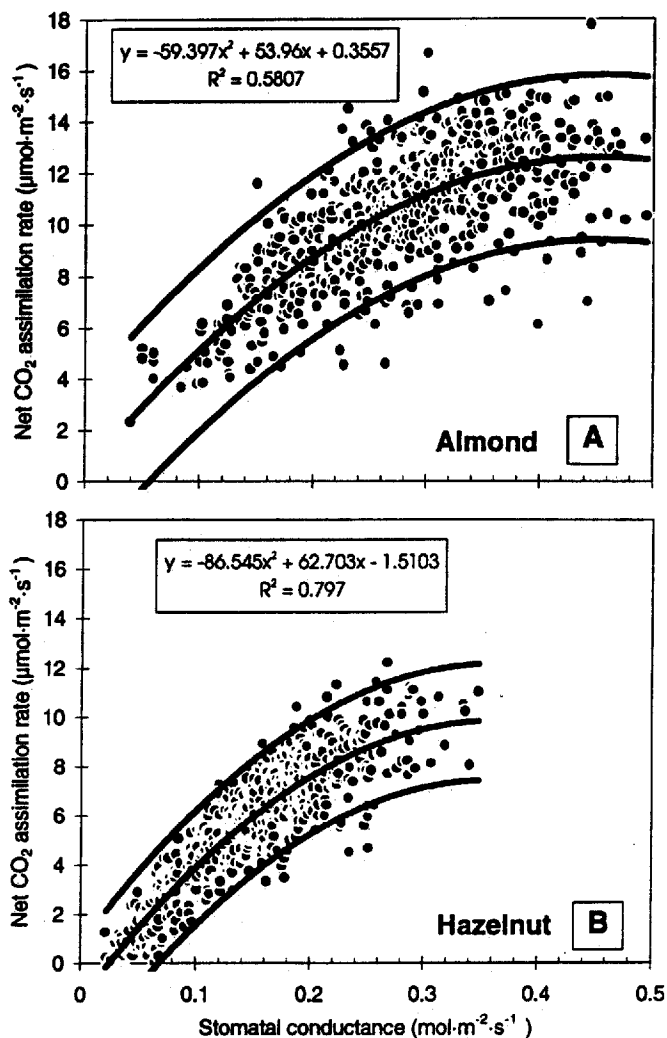


Fig. 4. Relationship between net assimilation rate (A) and stomatal conductance (g.) in almond (A) and hazelnut (B) (readings were taken at midday during the deficit irrigation period). Photosynthetically active radiation (PAR) > 900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and cuvette temperature > 25 °C. Upper and bottom line represents 95% confidence and middle line is the second-order polynomial adjustment. Each point is a single measurement. Fitted lines were statistically significant at $P \leq 0.05$.

reached -0.5 MPa, whereas in almond A positive rates were obtained at ψ_{pd} values as low as -1.6 MPa (Fig. 5).

Discussion

From the time of the initial reduction in applied water to the end of the deficit period, soil water depletion in the RDI almond treatment progressed steadily (Fig. 2C). In hazelnut θ_g (in the 60-cm soil profile) was quite constant for RDI from middle July until the end of August, showing that $0.2 \times \text{ET}_c$ water application was apparently enough to offset drainage and provide a small crop evapotranspiration, as g_s was always very low in RDI treatment during the summer (Fig. 3). Although RDI hazelnut θ_g did not exhibit any late August increase, ψ_{pd} notably increased at the end of August (Fig. 2B). Additionally, hazelnut T-100% showed a midsummer decrease in ψ_{pd} and a further late recovery. The same trend was observed in the overwatered treatment, T-130%, which eliminates the possibility of a suboptimal water-applied effect in the T-100% during midsummer. The same trend was also observed in all almond treatments (Fig. 2D). This generalized midsummer

ψ_{pd} depression could be related to a high evaporative demand during the hottest summer days and a night length that was too short to allow complete plant rehydration. Just before sunrise, the plant might still have been recovering. The low ψ_{pd} values on day 212 could have been the result of predawn transpiration due to a west wind at that time. Anyway, the data obtained would not be useful to assess soil water status since the values are more negative than they would have been if plants were equilibrated with the soil. To overcome these undesirable ψ_{pd} decreases, RDI ψ_{pd} was normalized to T-100% as $\psi_{npd} = (\psi_{pd} \text{ of RDI}) - (\psi_{pd} \text{ of T-100\%})$ (Fig. 6). The results show good agreement of θ_g and ψ_{npd} in almond, with a constant decrease in both variables during the season. However, in hazelnut there was still a late August ψ_{npd} recovery. Kernel dry mass accumulation in 'Pauetet' hazelnut takes place for 1 month between day 197 and 226 (Girona, 1994). This period of high fruit sink activity completely matches the interval of low ψ_{npd} . When nut filling finished (day of the year 226), ψ_{npd} recovered sharply as if fruit sink activity was responsible for an extra decrease in ψ_{npd} . Almond did not show any ψ_{npd} late recovery. This could be explained by the difference in nut filling between these two nut tree species. Almond kernel filling takes place from middle June to the end of August (around 75 d); about 45 d longer than in hazelnut. Also, evaporative demand from day 210 to 240 decreased (Fig. 1). Perhaps, this played a role in the recovery of hazelnut ψ_{npd} and not in almond due to continuing sink demand during this period. Anyway, fruit sink activity effects on ψ in fruit trees have been reported in *Malus domestica* Borkh. (Erf and Proctor, 1987), *Prunus persica* (L.) Batsch (Blanco et al., 1995; DeJong, 1986), and *Citrus unshiu* Marc. (Yahata et al., 1995). In addition, Blanco et al. (1995) reported that when sink activity decreased, after harvest, differences in ψ among fruit load treatments disappeared. On the other hand, none of these authors showed ψ_{pd} data related to fruit load treatments. But DeJong (1986) attributed this extra decrease in ψ to higher stomatal conductance; Buwalda and Lenz (1995), in *Pyrus communis* L., found a 36% increase in water use in fruiting trees compared to nonfruiting trees. Thus, a lower soil water content and, consequently, a lower ψ_{pd} might be expected in higher fruit sinked trees. Nevertheless, inferences of these effects on nut trees are not obvious; unlike fresh fruit, the processes

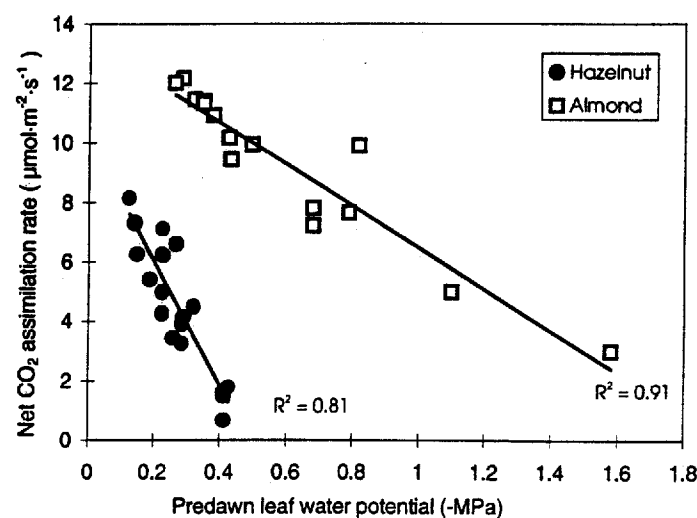


Fig. 5. Relationship between predawn leaf water potential (ψ_{pd}) and net CO_2 assimilation rate (A) in hazelnut (solid circles) and almond (open squares) during the season. Each point represents mean of nine measurements for A and twelve for ψ_{pd} . Fitted lines were statistically different at $P \leq 0.05$, as indicated by Student's t test for comparisons of regression statistics.

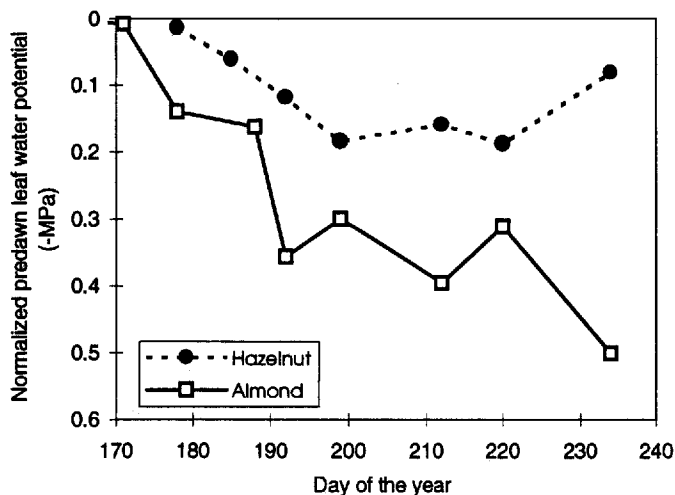


Fig. 6. Seasonal pattern of normalized predawn leaf water potential (ψ_{pd}) [regulated deficit irrigation (RDI) $\psi_{pd} - T-100\% \psi_{pd}$] in almond (open squares) and hazelnut (solid circles).

involved during kernel filling do not include expansive growth. Further studies are needed to confirm the sink effects on ψ in nut trees.

Although from the ψ_{pd} standpoint it seems that almond can extract more water from the soil than hazelnut, this is not easy to confirm simply by comparing θg data. First of all, they have different root development patterns. It is well known that hazelnuts have a shallow root system (Tasias, 1975), while the almond root pattern is considered to be quite deep (Ross and Catlin, 1978). Moreover, the pattern of water extraction can change as soil dries (Johnson et al., 1992; McCutchan, 1990). Thus, it is uncertain which depth of soil water content profile should be correlated with ψ_{pd} . In addition, when comparing species, ψ_{pd} is probably affected by different hydraulic properties such as plant hydraulic resistance (Turner, 1988). The latter factor can be neglected only if it is assumed that at predawn there is no water flow through the vessel tissue, which seems very improbable because at night plant tissues are rehydrating and a certain stem sap flow is commonly reported (Caspari et al., 1993; Schubert, 1939, cited by Zimmerman et al. 1980). Also, there is the possibility of some water loss by the leaf cuticle to the atmosphere on dry nights. Nevertheless, the more negative values of ψ_{pd} displayed in almond were accompanied with higher values of g_s than in hazelnut (Fig. 2 B and C, Fig. 3). This would seem to confirm its higher driving force for absorbing water while maintaining leaf gas exchange. Commonly, the capacity of a specific plant to absorb water is related to its ability to reach higher potential gradients (Kramer, 1983). In this way, almond is much better adapted to use limited water resources than hazelnut.

Midday photosynthetic response was highly dependent on ψ_{pd} in both nut trees (Fig. 5). Améglio et al. (1994) reported a good ψ_{pd} relationship in hazelnut vs. relative transpiration. The A/ψ_{pd} relationship was much steeper in hazelnut than in almond, primarily because hazelnut ψ_{pd} had a narrower range of values. This is a clear symptom of higher photosynthetic sensitivity to water deficits in hazelnut (Fig. 5). Actually, the water status of hazelnut before sunrise could produce an A close to zero, while for almond it would only represent about a 20% decrease over the optimum (Fig. 5).

Daily g_s decreased from early morning (8 AM) in well-watered hazelnut treatments (Fig. 3). Similar patterns have also been found by Tombesi (1994), who attributed this behavior to inadequate water absorption and translocation to the leaves, as if hazelnut had

an insufficient water transport system that could routinely induce plant water deficits (Syversten, 1985). But from the data available, a direct atmospheric humidity effect over stomata cannot be ruled out; it has been described in hazelnut by several authors (Girona, 1994; Schulze and Kupperts, 1979). This feature is not common in well-watered almond treatments, which are able to maintain high g_s values at midday (Fig. 3).

Hazelnut also has less photosynthetic capacity than almond. The maximal hazelnut A values for the upper 95% confidence interval for the polynomial regression of A and g_s were $12.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $0.35 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. Maximal almond values in the upper 95% confidence interval were an A of $15.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a g_s of $0.49 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 4). The T-130% treatments were used to check that the T-100% treatments were really under optimum conditions, so the previous values are maxima at least from the plant water status standpoint.

Analyzing the linear part of the A vs. g_s relationship (linear part was considered to finish at g_s values higher than 0.25 and $0.18 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for almond and hazelnut, respectively), almond had a gentler slope ($A = 2.29 + 31.57 \times g_s$) than hazelnut ($A = -0.64 + 43.7 \times g_s$). These different slopes were statistically different as indicated by Student's t test, which shows that the photosynthetic decrease caused by stomatal closure is more accentuated in hazelnut than almond (Fig. 4). Furthermore, estimates of the relative sensitivity of A to g_s derived directly from the slope at any point of the A/g_s relationship (A and g_s units were expressed in percentages to compare between both variables) (Fig. 7) showed a differential sensitivity. In almond, A decreased at a higher rate than g_s (slope of $A/g_s > 1$) when g_s was below 28%, whereas in hazelnut this occurred sooner, at a g_s level of 43% (Fig. 7). The slope of A/g_s in hazelnut was generally higher than in almond, but this tendency was more apparent at low g_s levels, which suggests that almond is a more efficient water user than hazelnut.

Since hazelnut A was affected more than g_s when stomata were closing, it is possible that, in addition to a stomatal limitation, there might have been a direct negative effect of water stress on mesophyll CO_2 efficiency (Percy, 1983). Negative effects over A were detected in hazelnut using C_i analysis (Long and Hallgren, 1985) as C_i increased while water stress induced g_s to decrease (Fig. 8). Thus, C_i analysis, if accepted, would indicate that hazelnut A was

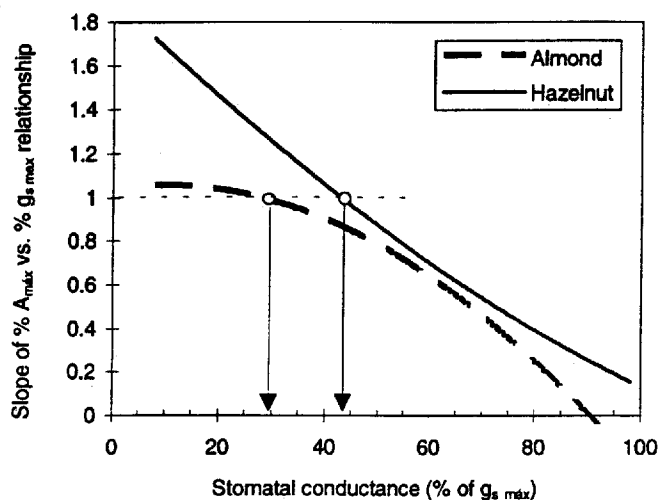


Fig. 7. Relationship between the slope in each point of the net CO_2 assimilation rate (A)/stomatal conductance (g_s) polynomial curve and g_s . The slope was calculated from the A vs. g_s relationship expressed in percentage units calculated over the maximum rates of each variable in each crop. Almond $A_{\text{max}} = 16.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $g_{s\text{max}} = 0.5 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; hazelnut $A_{\text{max}} = 12.2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $g_{s\text{max}} = 0.35 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

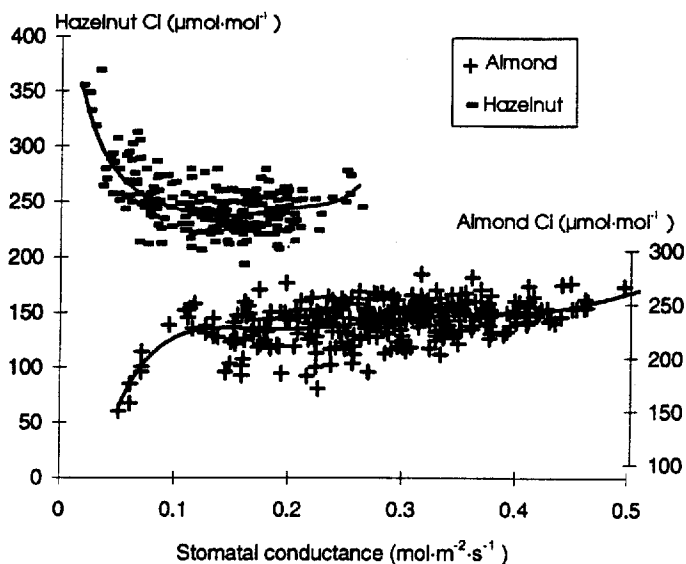


Fig. 8. Relationship between leaf intercellular CO_2 (C_i) and stomatal conductance (g_s) in almond (crosses) and hazelnut (dashes). Each point is a single measurement. Photosynthetically active radiation (PAR) $>900 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and cuvette temperature $>25^\circ\text{C}$.

negatively affected by nonstomatal causes when stomatal conductances were lower than $0.1 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, whereas in almond C_i decreased with g_s , denoting no negative effect over mesophyll activity (Fig. 8). Nevertheless, C_i analysis could be not valid if stomatal patchiness occurred while stomata were closing because it can produce an increase in C_i (Kraalingen, 1990; Ni and Pallardy, 1992; Terashima et al., 1988). If this were the case, C_i would only show that patchy stomatal closure may affect hazelnut more than almond.

From these data on hazelnut leaf photosynthetic activity and its high sensitivity to low g_s , we should expect that hazelnut has a lower capacity to produce assimilates than almond, particularly during the kernel-filling period, because a higher fruit sink activity probably induces an extra decline in water status. Thus, environmental conditions favorable to gas-exchange activity, in addition to an adjusting of applied water to maintain a certain level of photosynthesis during the deficit period, could be the keys to better hazelnut performance using RDI irrigation strategy.

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