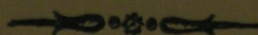


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WATER STRESS MEASUREMENTS IN FRUIT
TREES UNDER DIFFERENT REGULATED
DEFICIT IRRIGATION REGIMES

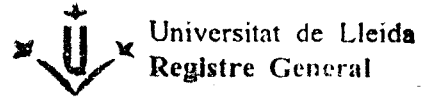
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Tesi Doctoral



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DIFFERENT REGULATED DEFICIT IRRIGATION REGIMES

JORDI MARSAL I VILÀ

Lleida, Desembre 1996

0110-44660

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ESCOLA TECNICA SUPERIOR D'ENGINYERIA AGRÀRIA

WATER STRESS MEASUREMENTS IN FRUIT TREES UNDER
DIFFERENT REGULATED DEFICIT IRRIGATION REGIMES

Tesi presentada per optar al grau de Dr. Enginyer Agrònom . Dirigida per el Dr. Joan Girona i Gomis, Investigador de l'IRTA. Tutorada pel Dr. Xavier Pons i Domènech, Professor del Departament de Producció Vegetal de la Universitat de Lleida.

El Doctorand



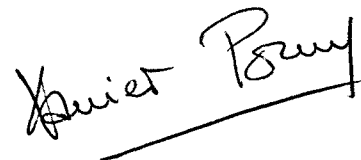
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Lleida, Desembre 1996

RESUM

L'aplicació de Reg Deficitari Controlat (RDC) en parcel·les comercials d'arbres fruiters s'enfronta a una problemàtica variada. En primer lloc cal buscar una metodologia fiable que permeti caracteritzar l'estrès en la planta i en segon lloc, cal valorar quin nivell de dèficit és permisible assolir en un cultiu, de manera que els efectes d'aquest estrès no esdevinguin indesitjables. El treball que es presenta pretèn aprofundir en el coneixement de les relacions hídriques en arbres fruiters amb la intenció de millorar la gestió del RDC.

Un dels factors que ajuda a l'èxit en l'aplicació d'una determinada estratègia de RDC és que el cultiu en qüestió presenti certa tolerància al dèficit hídic. Comparant la resposta fisiològica de l'avellaner respecte la de l'ametller quan han estat sotmesos a un període de 2.5 mesos (15 juny a 31 agost) de limitació progressiva en les aportacions de reg, s'ha demostrat, en l'avellaner, l'alta dependència de la seva capacitat fotosintètica sobre el potencial hídic de la fulla mediat abans del alba. L'avellaner ha mostrat, a més, una limitada capacitat d'experimentar potencials hídrics de fulla baixos, la qual cosa el converteix en un cultiu amb molt poca habilitat d'aprofitament del recurs hídic en condicions limitants, tot al contrari que en l'ametller. Tot això condueix a que les possibles estratègies de RDC a aplicar en avellaner s'hagin de dissenyar amb la màxima precaució.

La posada a la pràctica de RDC necessita d'un seguiment de l'estat hídic de la planta durant el període de reg deficitari. En perseguir els treballs realitzats s'han enfocat sota aquesta perspectiva, en l'àmbit d'una sèrie de tractaments de reg, basats en l'aplicació de reg deficitari en dos estadis diferents del cicle anual del cultiu. Un període de reg deficitari es va aplicar durant la fase II de desenvolupament del fruit (fase d'alentiment del creixement), i l'altre període a postcollita. En aquests treballs s'ha fet avinent que el potencial de fulla al migdia en condicions de mesura estandaritzades (dies complets sense núvols, en fulles que reben radiació directa) pot ser un indicador aconsellable per ajudar a la programació de RDC en perseguir, sobretot en RDC de fase II, degut al alt nivell explicatiu d'aquest paràmetre sobre el comportament estomàtic. En postcollita, el cultiu esdevé més tolerant al dèficit hídic (el potencial hídic de fulla de pèrdua de turgència és més negatiu que durant la fase II) i per sobre d'un determinat nivell d'estat hídic de la fulla, el potencial de fulla al migdia sembla menys determinant sobre l'activitat d'intercanvi de gasos de la fulla. Durant la fase III de desenvolupament del fruit (fase de creixement ràpid del fruit) el potencial hídic de fulla al migdia va estar poc lligat amb la seva activitat estomàtica, el que fa més aconsellable l'ús del potencial hídic de fulla mesurat abans de la sortida del sol.

En perera, una part dels treballs s'han encaminat a avaluar la resposta de la planta al dèficit hídic a nivell de relacions hídriques en la fulla. L'objectiu és el de fonamentar la possible adequació de estratègies de RDC a la perera. Per tal cosa es van aplicar dos cicles de dessecament progressiu mitjançant maneig de l'aigua de reg. Un cicle es va aplicar durant el mes de maig (durant 27 dies) i

l'altre cicle durant el juliol (durant 23 dies). En el cicle de primavera no es va evidenciar amb prou claredat cap mecanisme d'aclimatació al dèficit hídric, però durant el cicle d'estiu es va fer palesa l'existència d'un augment en la fracció d'aigua a l'apoplasma del teixit foliar, que es va traduir en una major baixada del potencial hídric de la fulla dels arbres en dèficit, respecte els de no dèficit, per igual valor de contingut d'aigua relatiu. Aquest major gradient però, solament es produiria a partir de la pèrdua de turgència de la fulla, la qual cosa condueix més a la supervivència de la planta que al manteniment dels processos productius.

En l'altra part dels estudis en perera, s'ha volgut comprobar la resposta del fruit a l'aplicació d'un RDC aplicat en la fase I de creixement del fruit (fase de creixement linial) en unes condicions concretes de cultiu en contenidors de gran capacitat (120 litres). Durant la fase I, els fruits del tractament RDC van augmentar la seva mida a un ritme inferior que els dels arbres Control (tractament de no estrès). En restituir la dosi òptima amb l'inici de la fase II (fase de creixement exponencial del fruit) i durant 2-3 setmanes, els fruits del tractament RDC van experimentar un ritme superior en l'augment del volum de la pera en comparació amb el Control. Aquest ritme però, no es va mantenir durant la resta de la fase II, durant la qual els fruits del tractament Control van tornar a mostrar un creixement superior. S'especula amb el fet que durant la fase I s'afectès negativament el procés de divisió cel.lular del fruit; això explicaria la limitació en la potencialitat del creixement del fruit al final de fase II. Les condicions específiques de l'assaig, amb restricció radicular produïda pels contenidors, ús de portempelts poc vigorosos o el nivell d'estrès hídric assolit durant la fase I del creixement del fruit, podrien també tenir el seu paper en aquesta resposta del fruit al RDC aplicat.

Agraïments

Voldria donar les gràcies a totes aquelles persones de les quals he rebut molt més del que probablement mai els hi podre tornar, molt especialment, al meu mentor i director de tesis Dr. Joan Girona i Gomis. També m'agradaria donar les gràcies als Drs. Ted DeJong, Dave Goldhamer, Ken Shackel i A.M. Boland per la seva inestimable empenta final a aquest treball.

Voldria fer extensiu aquest agraïment a d'altres persones que han contribuït a millorar aquest manuscrit com: Dr. Robert Savé i al Prof. Joan Cecília.

Encara que aquest document tingui una pretesa autoria individual, vull fer avinent que la seva elaboració és fruit d'un treball en equip, amb moltes hores de suor i vetlla compartides. A tots ells, els que encara hi són i als que ja han marxat, el meu més sincer agraïment: Mercè Mata, Simón Alegre, Amadeu Arbonès, Jaime García, Elizabeth Ibarz i Josep Rufat.

Vull agrair també al Dr. Xavier Pons i Domènech per haver acceptat la tutoria d'aquesta tesi.

Cal fer extensiu aquest agraïment a l'Estació Experimental de Lleida ja que els dos darrers capítols de la Tesi, han estat realitzats en el camp experimental de la seva subseu a Corbins.

No voldria acabar sense donar les gràcies a l'IRTA i a la seva Direcció general per la oportunitat i confiança depositada en mi per realitzar aquesta activitat. Estic també agraït al Comissionat de Universitats i Recerca pel seu suport financer del qual he gaudit durant tres anys.

Bé, i parlant de sponsors, no puc evitar l'esmentar a qui m'ha finançat els 31 anys de la meua vida, tampoc a ells els hi podré tornar mai tot el que m'han donat.

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List of the symbols and abbreviations used.

Symbol	Description	Units
θ_g	Gravimetric soil water content	$g \cdot g^{-1}$
θ_v	Volumetric soil water content	$m^3 \cdot m^{-3}$
Ψ_t	Leaf water potential	MPa
Ψ_{pd}	Predawn leaf water potential	MPa
Ψ_{npd}	Normalized predawn leaf water potential	MPa
Ψ_{md}	Midday leaf water potential	MPa
Ψ_{stem}	Stem water potential	MPa
Ψ_p	Turgor leaf potential	MPa
Ψ_π	Osmotic leaf potential	MPa
Ψ_π^{100}	Osmotic leaf potential at full turgor	MPa
Ψ_π^0	Osmotic leaf potential at the turgor loss point	MPa
R	Relative water content	%
$\epsilon_m, \epsilon_{avg}$	Average cell wall elasticity	MPa
Ro	Relative water content at the turgor loss point	%
Rs	Symplast water fraction	dimensionless
S	Slope of relationship Ψ_π vs. R	MPa/%
g_s	Stomatal conductance (H ₂ O)	$mol \cdot m^{-2} \cdot s^{-1}$
A	Net CO ₂ assimilation rate	$\mu mol \cdot m^{-2} \cdot s^{-1}$
Ci	Leaf intercellular CO ₂	$\mu mol \cdot mol^{-1}$
SLW	Specific leaf weight	$mg \cdot cm^{-2}$
T/D	Turgid mass/Dry mass	$g \cdot g^{-1}$
VPD	Vapor Pressure Deficit	kPa
PAR	Photosynthetically Active Radiation	$\mu mol \cdot m^{-2} \cdot s^{-1}$
ETo	Penman reference evapotranspiration	mm
ETc	Crop evapotranspiration	mm
Wi	Pear fruit width	mm
Le	Pear fruit length	mm

1. *General Introduction.*



1.1 Overview

Significant irrigation development has occurred recently in areas of Lleida and most of the new irrigated land are newly planted orchards. Irrigation, in these orchards, can be scheduled on demand and the most widely used irrigation system is drip irrigation. The typical irrigation schedule for a drip system is to replace crop evapotranspiration as it is used. In Catalunya, the local government (Generalitat de Catalunya) has provided a network of automated weather stations (PAC-COM) with the same philosophy as CIMIS in California (Craddock, 1990) which can be implemented with the water budget approach (Goldhamer and Snyder, 1989). Reference evapotranspiration (ET_o) can be calculated from weather data obtained from PAC-COM and multiplied by a crop coefficient value (K_c) to obtain crop evapotranspiration (ET_c). Nevertheless, water resources in this region are scarce and water supply is not always sufficient to maintain maximum yields. Consequently, there is an increasing need for knowledge in irrigation management techniques under non-full ET_c replacement conditions.

In deficit irrigation, crops can be deliberately allowed to sustain some degree of water deficit during a certain stage of crop development. The fundamental goal is to increase water use efficiency, either by reducing irrigation adequacy or by eliminating the least productive irrigations (English et al., 1990). In these conditions, some yield losses can be expected. However, it is widely recognized that when water supplies are limited or water costs are high, the economic optimum level of irrigation will be somewhat less than would be required for maximum yield. Therefore, when the objective is saving water or maximizing profits, deficit irrigation can be a valid and useful strategy. Additional considerations could be that water deficits may also improve fruit quality and increase the sugar percentage in fruits (Lotter et al., 1985; Li et al., 1989). Furthermore, deficit irrigation during postharvest can help in controlling root diseases such as *Phytophthora* ssp. (e.g. postharvest drought is common practice in cherry orchards of Lleida).

One of the terms given to deficit irrigation is Regulated Deficit Irrigation (RDI) (Chalmers et al., 1981). Since the late seventies, RDI has been tested in peach (*Prunus persica* L. Bastch) and pear (*Pyrus communis* L.) with the objective of controlling excessive vegetative growth in high vigor species or in

close tree spacing orchards. To accomplish this, the deficit irrigation period has usually been applied during the period of maximum shoot growth. These experiments led to contrasting results (Chalmers et al., 1981; Girona et al., 1993 b) so, the feasibility of RDI to control excessive vegetative growth whilst still inducing a good performance on fruit growth is not without controversy (DeJong, 1995). However, significant reductions in applied water can be obtained without affecting yields as much as when irrigation has to be reduced proportionally throughout the period (Uriu et al., 1964; Li et al., 1989). Subsequent studies carried out on other species such as French prune (*Prunus domestica* L.) (Lampinen et al., 1995), Asian pear (*Pyrus serotina* Rehd.) (Caspari et al., 1993), and grapefruit (*Citrus paradisi*, Macf.) (Cohen and Goell, 1988) have shown the interest of RDI in fruit trees. On the other hand, the deficit period can also be applied during the postharvest period. Studies carried out on an early peach cultivar (Larson et al., 1988; Johnson et al., 1992) have shown yield maintenance in the year following the postharvest drought, providing that water stress is not too severe.

Regulated deficit irrigation has also been tested in nut trees, mainly in almond (*Prunus amygdalus* L.) (Goldhamer and Shackel, 1990; Girona et al., 1996) and pistachio (*Pistacia vera* L.) (Goldhamer et al., 1987). The primary interest in these drought tolerant species has always been exclusively in saving water, not in controlling vegetative growth. The deficit period, in almond, is applied during the kernel filling period which is acknowledged as a low sensitive process to water stress (Hsiao, 1976). Drought stress is not recommended to occur during vegetative growth period or during bud formation because it will influence the crop load of the following year (Goldhamer and Smith, 1995). Unlike fruit trees, where thinning is often applied to regulate fruit size, in almond trees, kernel size does not influence marketable yield, therefore fruit number is the major factor for maximum economic yield.

To schedule irrigation in an RDI strategy a simple method would be based on adapting the water budget method for the non-deficit part of the annual cycle and establishing, during the deficit period, a certain percentage of reduction over the considered optimal applied water. This percentage would depend on the maximal water stress allowable for that period. Nevertheless, soil and climatic conditions as well as crop factors such as fruit load interact with the irrigation reduction for determining plant water stress. Thus, the manager besides deciding what level of deficit to allow, must also recognize when that level has been

reached. In this way, a reliable plant water stress assessment is essential to help in scheduling irrigation during the deficit period.

Pressure chambers have been used to estimate direct plant water status (leaf water potential) (Scholander et al., 1966), particularly by researchers. On the other hand, although, the pressure chamber is a rugged method and it has a low cost, it has less acceptance for irrigation managers than other methods such as neutron probe or tensiometers. Nevertheless, when stress is manifest, plant based methods are better than soil water status measurements for assessing plant water stress. Additionally, under drip irrigation, the number of soil water measurements needed is particularly large because three dimensional gradients of water exist in the soil around the emitter (Warrick and Nielsen, 1980).

The time of day of leaf water potential measurements becomes particularly important, pressure chamber readings change during the day, with the lowest water potentials occurring when evapotranspiration is highest. If the measurement is taken just before sunrise, it would be an expression of water potential at root surface as it is assumed that there is no potential gradient through the plant by that time (Meyer and Green, 1980). If the measurement is taken at midday it will reflect, in addition, the environmental stress of the moment and also the stomata regulation (Garnier and Berger, 1985; McCutchan and Shackel, 1992). The later time of day is particularly interesting as it shows conditions of typically maximum photosynthetic values at canopy level and environmental demand (Lakso, 1980; Goldhamer and Snyder, 1989). Other parameters obtained with pressure chambers include stem water potential which is often measured at midday in leaves situated near the stem that had been previously bagged with plastic film for long enough to equilibrate water potential of the stem with the leaf (Begg and Turner, 1970). Recent reports have shown the advantages of stem water potential, as it has lower variability than leaf water potential, show a closer relationship with evaporative demand (McCutchan and Shackel, 1992) and has a major representation of plant water stress through its influences on fruit growth (Naor et al., 1995).

Critical values of pressure chamber readings should be established for fruit and nut trees during the deficit period to evaluate whether the water stress applied is too severe. In peach trees it is recognized that water potential values in shaded leaves ranging from -2.5 to -2.7 MPa, induce leaf wilting and

shedding (Proebsting and Middleton, 1980). More research is needed in this field on the way to express a relationship between the level of water stress experienced in a specific period and the corresponding yield variation. In this context, the evaluation of changes in fruit growth during and after the deficit period could also be of valuable help, and some authors have worked towards this objective (Ebel et al., 1995). Nevertheless, under drought conditions, fruit dry matter is a better predictor of final fruit size (Cohen and Goell, 1988). However, differences in fruit dry matter are hardly measurable for a period shorter than 1 week, that is, when water stress could already be too detrimental for long-term fruit growth (Cohen and Goell, 1988).

In general, RDI in fruit trees has been studied with two different aims, perhaps corresponding with two different environmental constraints. In arid climates, where water is scarce, the main interest is saving water, and some yield reductions would be acceptable depending on water price and availability. In humid environments, the objective would be to reduce vigor by restricting root volume with the deficit period. In the later case, other techniques apart from RDI can be applied, such as dwarfing rootstocks or sod competition (Glenn et al., 1996).

1.2 The uncertainties of RDI.

One of the main difficulties in designing an RDI strategy is to establish the relationship between a specific water stress level during a certain period with a concrete change in final yield. However, in order for this problem to be effectively solved, several questions have to be answered: Which parameter has to be used to measure plant stress during the deficit period ? And if we were speaking about leaf water potential, at which moment of the day should it be measured ? And with which criteria ? For instance, should this stress be integrated over the whole period (Myers, 1988) or would it be just a maximum stress level that should be avoided ? Does fruit growth respond better to the integral of stress, or to the maximum stress level reached during the deficit period, or more importantly, to both ? In dealing with this matter, it should be considered that despite the fact that available water in the soil depletes progressively during the deficit period in moderate deep soils, and higher stress integrals could be thought to be correlated with higher maximum stress values, shallow soils do not have to behave

similarly. Furthermore, sudden environmental changes during the deficit period can alter the rhythm of stress development, thus integral stress and maximal levels do not have to give the same information.

On the other hand, the significance of stress parameters can change with crop development (See Chapter III). This implies that a kind of adjustment should be made to interpret plant water stress. Furthermore, the different events of the plant annual cycle are not equally sensitive to water stress, thus the recommendable water stress level should change with phenology. More specific research should be carried out in this area.

In associating a concrete level of stress with current year tree behaviour, an additional consideration arises. How this stress can be reflected in the subsequent campaign. The problem becomes harder to evaluate when the deficit period is applied in fruitless stages and the effect has to be assessed in the long-term. An example is postharvest; a deficit during this time can affect the total tree carbohydrate storage, which can play a major role in the maximum yields of the following years (Feres and Goldhamer, 1990). Consequently, RDI experiments have to be carried out during several years, and evaluated as a whole (Goldhamer and Smith, 1995). A similar problem occurs in alternate bearing species such as olive trees (*Olea europea* L.) where the need to analyze yield during cycles of several years is basic.

A further complication occurs when experimenting together with different lengths of deficit time and levels of stress intensity (Goldhamer and Smith, 1995). This happens, for instance, when working with suboptimal fixed amounts of irrigation, where there is a compromise between distributing water supply with time and the increase of plant water stress during the variable deficit period. The carry over effect under such conditions would be even more difficult to predict and extrapolate to other environments.

Nowadays, there are many questions still unanswered, but with the progress in tree functioning and water stress physiology, answers will be provided and other new RDI strategies could be developed in the future.

1.3 Objectives of the Thesis.

The main aim of this research is to increase knowledge of the physiological response of some temperate fruit and nut trees to Regulated Deficit Irrigation.

In the case of nut trees, the interest is focused on understanding a different productive response to RDI strategy in two species (Almond and Hazelnut) as regards to photosynthetic behaviour and tree water relations.

In peach, the objective is evaluating the possibility of different photosynthetic sensitivity to water stress under different phenological stages such as Stage II of fruit development or postharvest, and if fruit load effects should be taken into account. Additionally, the role of plant water stress indicators under these changing conditions are evaluated.

With pear, the aim is to study the existence of turgor maintenance mechanisms that could justify better fruit performance after the deficit period and to corroborate if pear fruit growth "*per se*" can recover fully after a deficit irrigated period comprising the last four weeks of Stage I of fruit development.

1.4 Approaches followed in the Thesis.

Water stress in a plant varies with the time of day, reacting quickly to atmospheric factors such as temperature, humidity, wind and solar radiation, (Kramer, 1983). Responses to these factors may change as the crop develops (Mooney, 1981). As a result, the task of monitoring plant stress is a complex matter. Measurements of crop water stress must be carried out under consistent conditions and then measurements may need to be corrected for factors which cannot be controlled (e.g. solar radiation, humidity or phenological changes).

For a successful RDI application, two prerequisites need to be accomplished from an orchard standpoint: The presence of plant drought resistance, and the occurrence of periods at any moment of the annual

cycle, in which physiological processes are not very sensitive to water stress. In Chapter 2, the case of two species with different adaptation to water stress is exposed: Almond, which is considered drought resistant, with a reported good productive response to RDI (Goldhamer and Shackel, 1990; Girona et al., 1993a), and hazelnut having less encouraging results under RDI (Girona et al., 1994). A leaf physiological approach is adopted in this chapter to increase the understanding of the differential behaviour between species.

In scheduling deficit irrigation, appropriate indicators of crop water status must be used to determine when irrigation is needed and how much water to apply. In Chapter 3, leaf water potential is evaluated as a useful indicator for decision-making when applying RDI in peach. Additionally, the effects of different crop development stages on evaluating this indicator are considered. The emphasis of this chapter is on the influences of phenology on the relationship between plant water status and leaf photosynthetic activity and also the seasonal evolution of leaf water potential at turgor loss. From a leaf physiological standpoint, leaf turgor loss should be avoided for long periods because it is considered that this is brought about when non-stomatal inhibition of photosynthesis occurs due to a protoplast volume shrinkage plus stromal acidification by osmotic stress (Scarascia-Mugnozza et al., 1986). Subsequently, unrecoverable leaf damage such as leaf burning and shedding start.

Plants adapt to water stress through changes in root:shoot ratio, growth rate and water use efficiency. These are often accompanied by changes in the fundamental properties of their water relations such as the critical water potential or relative water content which prompts stomatal closure, diurnal patterns of stomatal conductance, and predawn water potential. The pressure-volume curve technique can be used to further understand how changes in the parameters which describe this relationship are related to the capacity of the plant to respond to water stress (Hinckley et al., 1980; Robichaux, 1984; Parker and Pallardy, 1987). In Chapter 4, an attempt to evaluate pear tree response to water stress during spring and summer has been carried out using the pressure-volume technique.

In peach RDI strategies are often applied during the apparent latent phase of fruit growth (Stage II; Connors, 1919). On the contrary, in pear, a comparable period during fruit growth does not exist and the

deficit period is often applied during the phase of slow fruit growth (Stage I of fruit growth) (Mitchell et al., 1989). During this phase the main process involved is fruit cell division, which is considered to be sensitive to water stress (Hsiao, 1973). In Chapter 5 the focus is on fruit growth responses to drought during Stage I of pear fruit development. Interaction between RDI and factors associated with canopy are avoided by planting pear trees in containers with a large spacing.

1.5 General Remarks

In this study plant water stress indicators measured with pressure-chamber, leaf water potential at predawn (Ψ_{pd}) and leaf water potential at midday (Ψ_{md}) under different crop conditions and different species have revealed some of the advantages and drawbacks of these measurements. Stem water potential (Ψ_{stem}) measurements were subsequently adopted in Chapters 4 and 5, thus Ψ_{stem} comparison to Ψ_{pd} and Ψ_{md} is restricted to pear trees.

On the whole, Ψ_{pd} was the parameter that best reflected the different treatment irrigations applied (See Fig 1, Fig 2 and Table 2 of Chapter 3). Nevertheless, in Chapter 2, a decline in Ψ_{pd} was shown in midsummer without a corresponding decrease in soil water content, and this occurred in both crops (almond and hazelnut) for T-100% and even in the over watered treatment (T-130%) (Fig 2 of Chapter 2). Lack of equilibrium between leaves and soil during the night could be involved in this unexplained decrease. Meinzer et al. (1988) reported in *Larrea tridentata* that high night-time air *VPD* (Vapor Pressure Deficit) induced significant high night transpiration. In these conditions Ψ_{pd} is not a reliable indicator of soil water status (Reich and Hinckley, 1989). This could have happened also in the conditions described in Chapter 2 as Ψ_{pd} was negatively correlated with wind speed at the time of Ψ_{pd} measurement and with *VPD* at the same time (Table 1). Despite the high Ψ_{pd} treatment differentiation, under certain conditions such as postharvest as described in Chapter 3, comparisons of Ψ_{pd} values between non-stress irrigated (Control) treatment and the stressed treatment led to statistical differences between treatments (Fig 1 of Chapter 3) whereas differences in gas exchange parameters were not detected (Fig 3 of Chapter 3). As a result, this leads to an overestimation of plant water stress evaluated

as stomatal conductance at midday (g_s). Perhaps, the lower sensitivity of gas exchange parameters to leaf water status during postharvest (Fig 4 of Chapter 3) was involved in this overestimation, thus plant performance would not necessarily be affected under certain range of high Ψ_{pd} values.

Table 1.1. Correlation between leaf water potential at predawn (Ψ_{pd}) and environmental variables (VPD and wind speed) for the same time of day in the over-watered irrigation treatments (T-130%) applied to almond and hazelnut during July and August 1991. Other conditions described in Chapter 2.

Crop	Environmental variable	Correlation Coefficient	Probability	Range of Measurement
Almond	VPD	0.841	0.032	0-1.21 kPa
	Wind speed	0.911	0.011	1.5-4.1 m·s ⁻¹
Hazelnut	VPD	0.814	0.048	0-1.21 kPa
	Wind speed	0.828	0.041	1.5-4.1 m·s ⁻¹

On the other hand, Ψ_{md} has been reported to be less efficient in the way to distinguishing between irrigation treatments (Garnier and Berger, 1985). Better approaches to interpret Ψ_{md} and the occurrence of water stress have been proposed by taking into account the environmental stress during the day (Peretz et al., 1984). Nonetheless, during the RDI periods of this study, Ψ_{md} showed a remarkable significant relationship with leaf gas exchange parameters in peach (Fig 4 of Chapter 3). This suggests the interest of Ψ_{md} when assessing plant water status in deficit conditions. Moreover, a good fit in the mentioned relationship was also found in pear during spring and summer time (Fig 1.1A).

Comparing Ψ_{stem} and Ψ_{md} with g_s at midday in pear, Ψ_{stem} showed a relationship more linear than Ψ_{md} , and the determination coefficient (R^2) corresponding to the negative exponential functions, were also better with Ψ_{stem} (Fig. 1.1A, B). Moreover, maximum values of g_s that corresponded with maximal leaf water status parameters were found to be less variable in Ψ_{stem} than in Ψ_{md} (Fig. 1A, B), which would show a higher feasibility to be used under different environmental conditions than Ψ_{md} .

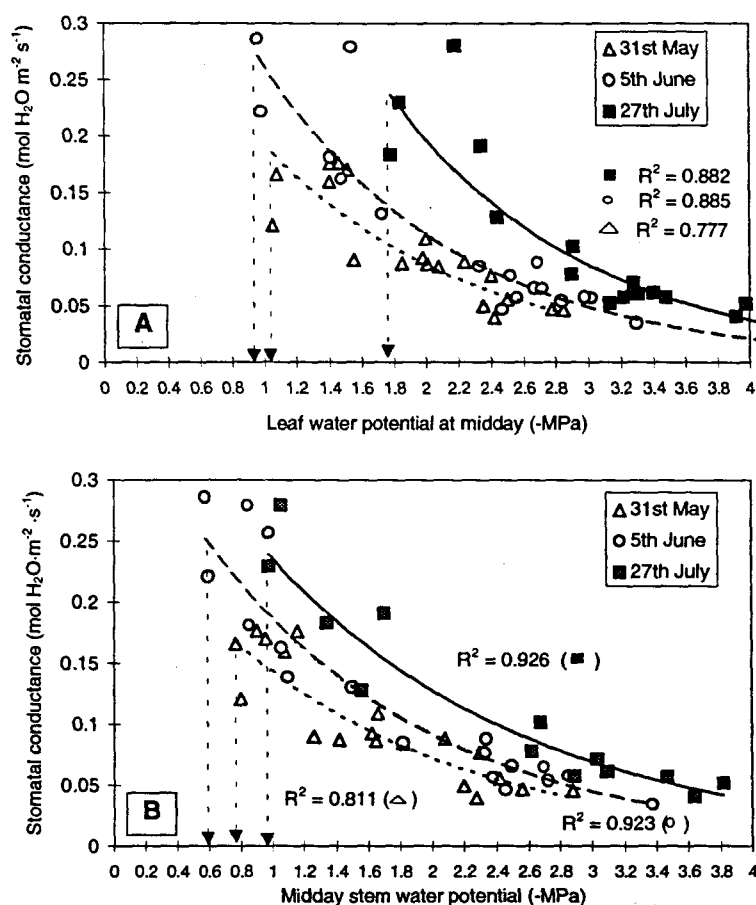


Figure 1.1. Relationship between midday stomatal conductance vs. midday leaf water potential (A) and midday stomatal conductance vs midday stem water potential (B) in response to different irrigation regimes in 3 year-old pear trees planted in containers of high capacity. Deficit irrigated trees were exposed to progressive water deprivation in two cycles of 28 days. One cycle was applied in spring and the other in summer. Each fitted line corresponds to a single day with tree-to-tree differences giving the range of water potential values on that day. The adjusted lines are negative exponential functions. Average temperature and vapor pressure deficit at midday for those days were respectively: 31st May (23.4 °C, 1.86 kPa), 5th June (27.8 °C, 2.31 kPa) and 27th July (32.7 °C, 2.81 kPa). (Data from Marsal et al., 1996).

Ramos et al., (1993) categorized pear tree water status into three classes on Ψ_{stem} basis, wet conditions (>-0.95 MPa), medium (-0.95 to -1.4 MPa) and dry (<-1.4 MPa). These boundaries match perfectly well with our data (See Chapter 5). Moreover, maximum values corresponding to maximum g_s agree with the conditions described as wet (Fig. 1.1). This suggests that Ψ_{stem} data could be more interesting than Ψ_{md} in irrigation scheduling.

From the results obtained in Chapter 4 and comparing Ψ_{pd} with Ψ_{stem} data with the help of soil water content (θ_v) values, there seems to be a range of soil water content, (0.35 to 0.21 $m^3 \cdot m^{-3}$) wherein changes of water content does not greatly induce a variation in Ψ_{pd} values (Fig 1.2A). In contrast, for this same range of θ_v , small but consistent decreases in Ψ_{stem} and Ψ_{md} were measured with reductions in θ_v (Fig 1.2B, C). One of the criticisms of Ψ_{pd} is that plant equilibrates with the wetter parts of the soil during the night, thus producing a bias of Ψ_{pd} towards these wetter parts (Garnier and Berger, 1987; Jones, 1990). The reason why Ψ_{pd} remains insensitive at high θ_v values has been attributed to this fact. On the contrary, pressure chamber measurements carried out while plants are actively transpiring (Ψ_{stem} and Ψ_{md}) seemed to overcome this problem. Nevertheless, and despite this drawback, Ψ_{pd} has been reported to be a reliable stress indicator (Olien et al., 1990; Girona et al., 1993 b). This is because at low θ_v contents, Ψ_{pd} is very sensitive to small changes in θ_v (Fig 1.2A) whereas, the Ψ_{pd} low sensitivity at high θ_v values can be compensated by its much higher consistency than measurements done at midday (e.g. in our experiments, the average coefficient of variation of Ψ_{md} is twice higher than Ψ_{pd} (6.3 and 12.8 %, respectively).

Phenological changes, however, could modify the interpretation of these parameters on absolute values basis. It is well known that leaf or shoot age have a significant effect on tissue osmotic potential and that solute accumulation occurs during leaf development without apparent drought (Abrams, 1988). For instance, the Ψ_{md} levels that induced minimal values of g_s in pear ($0.05 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) was -3.3 MPa in late spring (5th June) but -4.0 MPa in summer (27th July) (Fig 1.1A). A changing sensitivity of Ψ_{md} to g_s relationship due to different environmental conditions (*VPD*) is possible (Tardieu et al., 1996), and could be related to the different boundary of Ψ_{md} that corresponded to minimal g_s . However, when plotting g_s vs. leaf turgor pressure, these different boundaries disappeared near stomatal closure (Fig 1.3), indicating a possible role of leaf turgor loss effect on minimal g_s . Furthermore, zero turgor pressure coincided with values of g_s proximal to stomatal closure (Fig 1.3). This indicates that, in pear, the leaf water potential at turgor loss calculated from pressure-volume technique, is at least a possible way to take into account the effect of phenological changes on the significance of pressure chamber measurements. In addition, this parameter has a biological significance in determining leaf survival in

pear, as leaf damage was detected, in summer, at Ψ_{md} values near to the corresponding values for turgor loss (See Chapter 4, turgor loss values in summer were -3.3 MPa). Similar results have been found in peach where leaf shedding was observed near leaf turgor loss (See Chapter 3).

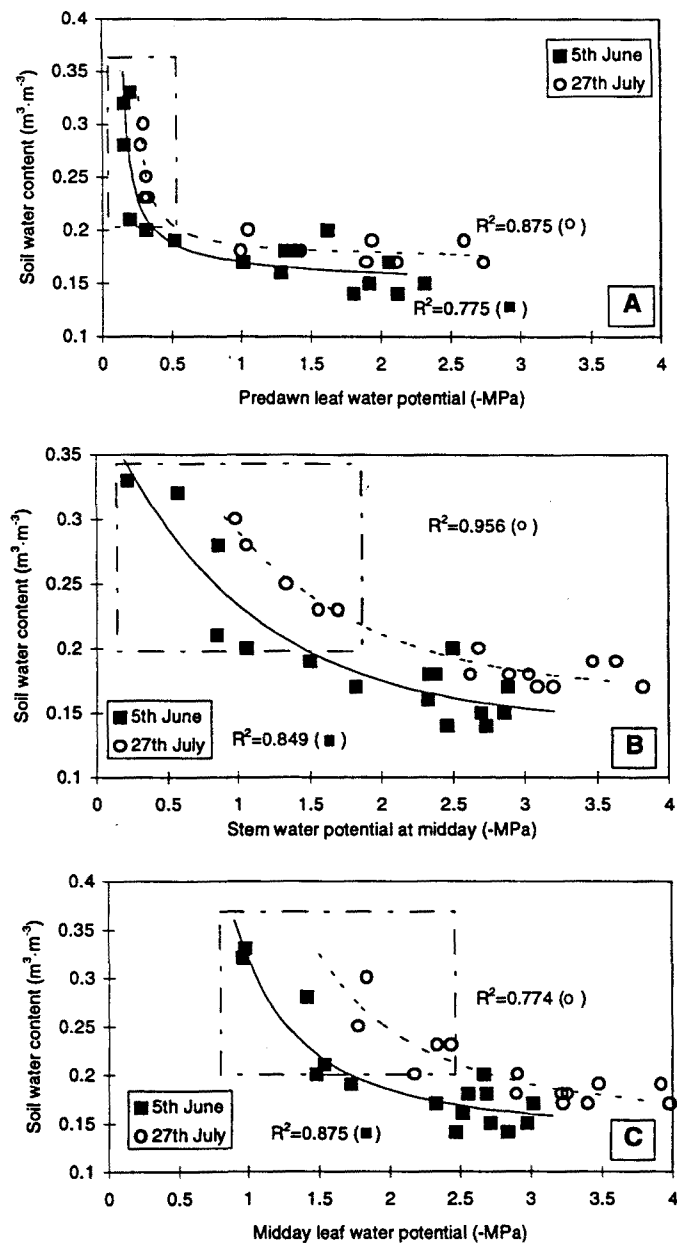


Figure 1.2. Relationships of soil water content vs. predawn leaf water potential (A), soil water content vs. midday stem water potential (B) and soil water content vs. midday leaf water potential (C) in response to different irrigation regimes in 3-year-old pear trees planted in high capacity containers. The square inside each panel defines the area of low Ψ_{pd} sensitivity to θ_v . Each fitted line corresponds to a single day with tree-to-tree differences giving the range of water potential values on that day. The adjusted functions are of the type $Y=(a+c\ln X)/(1+b\ln X)$ (A), $Y=a+be^{-X}$ (B), and $Y=a+bX^2$ (C). Other conditions are described in Fig. 1.2.

To summarize, these results confirm the major interest of Ψ_{stem} to detect incipient conditions of drought as well as to assess plant water stress. For a better interpretation of Ψ_{stem} , slight corrections for environmental and phenological conditions should be made. Additional information provided by Ψ_{pd} and Ψ_{md} would be advisable for a complete diagnosis.

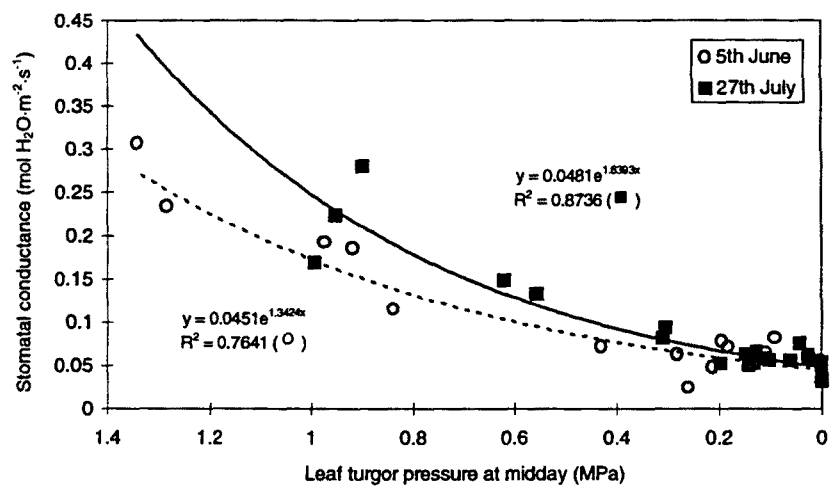


Figure 1.3. Relationship between stomatal conductance at midday and leaf turgor pressure in response to different irrigation regimes in 3-year-old pear trees planted in high capacity containers. Each fitted line corresponds to a single day with tree-to-tree differences giving the range of water potential values on that day. Leaf turgor pressure is calculated from pressure-volume curves, all data belong to chapter 4. Other conditions are described in Fig. 1.2.

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*2. Leaf Water Relation Parameters in Almond compared to Hazelnut Trees during a
Deficit Irrigation Period*

**LEAF WATER RELATION PARAMETERS IN ALMOND COMPARED TO HAZELNUT
TREES DURING A DEFICIT IRRIGATION PERIOD**

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Additional index words: *Prunus amygdalus*, *Corylus avellana*, regulated deficit irrigation, leaf water potential, photosynthesis.

Abstract. The influence of deficit irrigation on predawn leaf water potential and leaf gas exchange parameters was analyzed in almond (*Prunus amygdalus* L.) 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 treatment (RDI) which consisted of full irrigation for the full season, except from mid June to late August when 0.2*ET_c was applied. Under non-stressful 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). A reductions induced by decreases in predawn leaf water potential (Ψ_{pd}) were higher in hazelnut than in almond. Gas exchange activity from early morning to midday decreased in hazelnut for all irrigation treatments, whereas 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 g_s than almond, specially at low g_s values. Ψ_{pd} in almond and hazelnut of T-100% and T-130% 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.

Introduction.

Hazelnuts are normally grown where rainfall is enough to fully satisfy crop water requirements. However, in some areas such as the Tarragona province (north-east Spain, Catalunya) and some areas of France and Italy irrigation is necessary for hazelnut production. Almond 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 enable to 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, 1975). 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 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 (Schulze and Küppers, 1979; Girona et al., 1986).

The aim of this paper is to analyze the different ecophysiological responses of the two nut tree species under a progressive two-month partial water deprivation in order 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 both 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 (Calcixerollic Xerochrept) 2 m deep, located at the experimental fields of the "Centre de Mas Bové-IRTA" in Reus, Spain.

The almond (*Prunus amygdalus* L.) cultivar used was "Ferragnes", and the pollinizers were "Ferraduel" and "Cristomorto". A total of 192 five-year-old Almond trees on "GF-677" rootstock were used in this study. Tree spacing was 5 x 6 m. The hazelnut cultivar (*Corylus avellana* L.) used was "Pauetet" with "Gironell" and "Negret" as pollinizers. A total of 252 five-year-old hazelnut trees were used from an experimental orchard with 6 x 1.5 m tree spacing.

A localized micro-sprinkler 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.

Design of experiment. Four treatments were defined for the two species: T-100%, T-130% and T-70% of ET_c and one RDI (Regulated Deficit Irrigation) schedule. T-100% was irrigated under full regime (ET_c), based on soil water content, predawn leaf water potential and Penman-determined reference evapotranspiration (ET_o) (Doorenbos and Pruitt, 1977). T-130% and T-70% treatments were irrigated applying 1.3*ET_c and 0.7*ET_c respectively. RDI was irrigated at full ET_c from April to 20 June, 0.2*ET_c from 20 June to harvest (about 15 September) and again full ET_c 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). In almond each block consisted of 16 trees (4 x 4), the middle 4 trees being used for experimental measurements and the others as non-experimental guard trees. In hazelnut each block

consisted of 21 trees (3 rows x 7 trees per row), the 5 middle trees of the middle row being used for experimental measurements, and the others as non-experimental guard trees.

General measurements. Data from the nearest automated weather station to the study field (1km) (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-day^{-1} (Fig 1). Lately, from day 212, ETo values averaged 5 mm-day^{-1} .

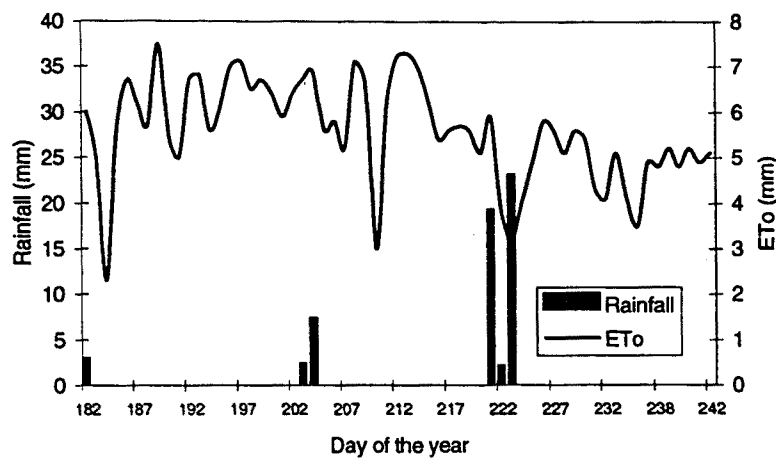


Figure 1. Daily rainfall and reference evapotranspiration during the time of physiological measurements.

Soil-water-content (θ_g) was determined using a neutron probe (Campbell Hydroprobe Model 503) 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 depth in the profile. Field capacity and permanent wilting point averaged over 90 cm from soil surface were, 0.185 and $0.095 \text{ g}\cdot\text{g}^{-1}$, respectively.

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

Physiological measurements. Predawn leaf water potential (Ψ_{pd}) was measured weekly before sunrise using the pressure bomb 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 IRGA system (Model ADC LCA-2, The 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 around 40% less water at the end of the year than the T-100% (Table 1).

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

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

Soil water content. Seasonal patterns of θ_g in both species clearly showed the higher water content in the treatments that received more water (Fig 2A, C). In trees which 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 throughout August (Fig. 2A, C). θ_g in the almond orchard (Fig

2C) was plotted to a greater depth than in hazelnut because of the differences in root depth, thus θ_g values between species (Fig 2A, C) are not strictly comparable.

Seasonal patterns of leaf water potential. Ψ_{pd} indicated that the RDI treatment in both species had significant negative effects on plant water status, (Fig 2B, D). The pattern was quite similar for both species, though there was a noticeable difference in the lowest values obtained; -1.6 and -0.42 MPa for almond and hazelnut, respectively (Fig. 2B, 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. 2B, D).

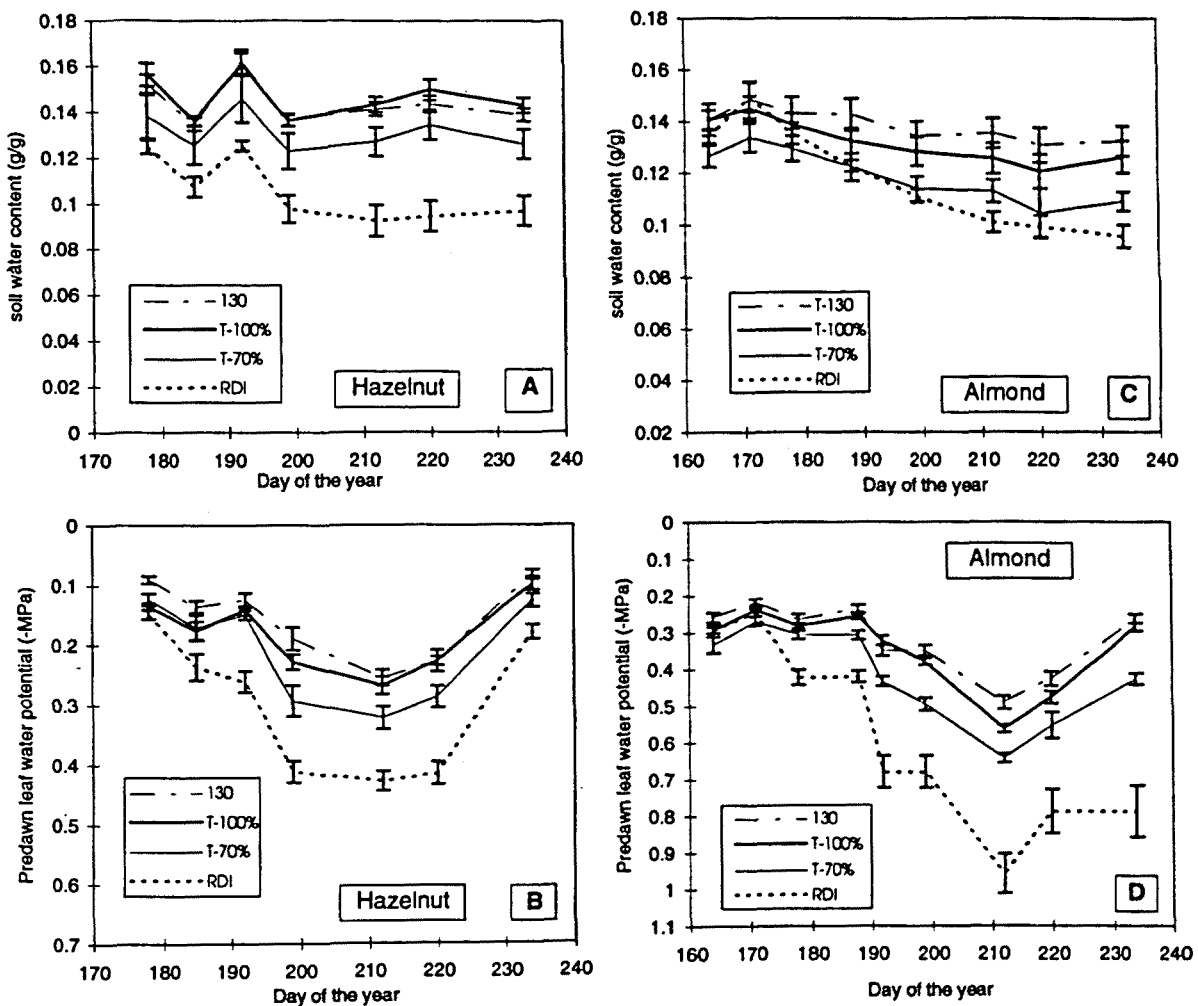


Figure 2. Seasonal patterns of hazelnut gravimetric soil water content averaged over 60 cm profile (A), hazelnut predawn leaf water potential (B), almond gravimetric soil water content averaged over 160 cm profile (C), and almond predawn leaf water potential (D) in response to irrigation treatments.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

Leaf gas exchange measurements. Diurnal patterns of g_s throughout 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 Julian 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 A vs. g_s relationship was closer in hazelnut than in almond ($R^2 = 0.80$, and 0.58, respectively) (Fig 4A, B).

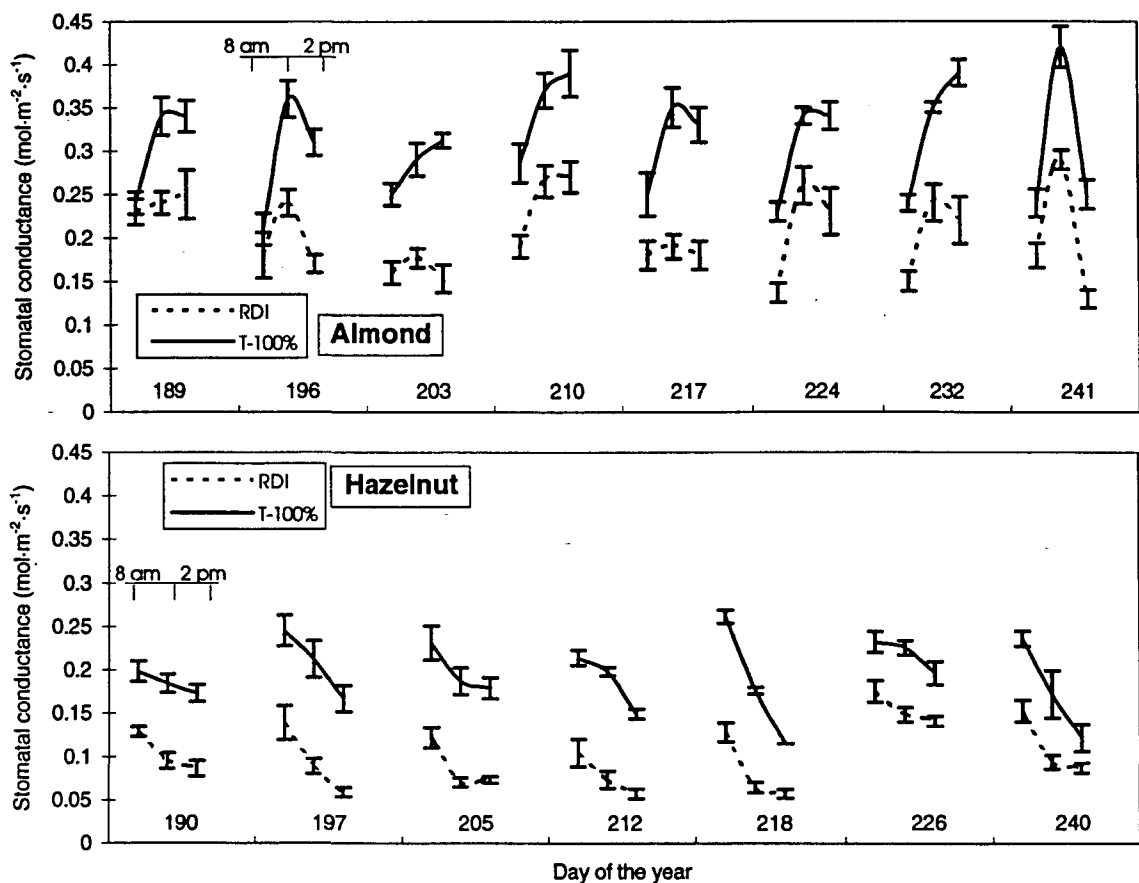


Figure 3. Seasonal patterns of stomatal conductance (g_s) at 8 am, 11 am and 2 pm in almond (up) and hazelnut (down) in response to irrigation treatments. Each point represents mean of 9 measurements \pm SE.

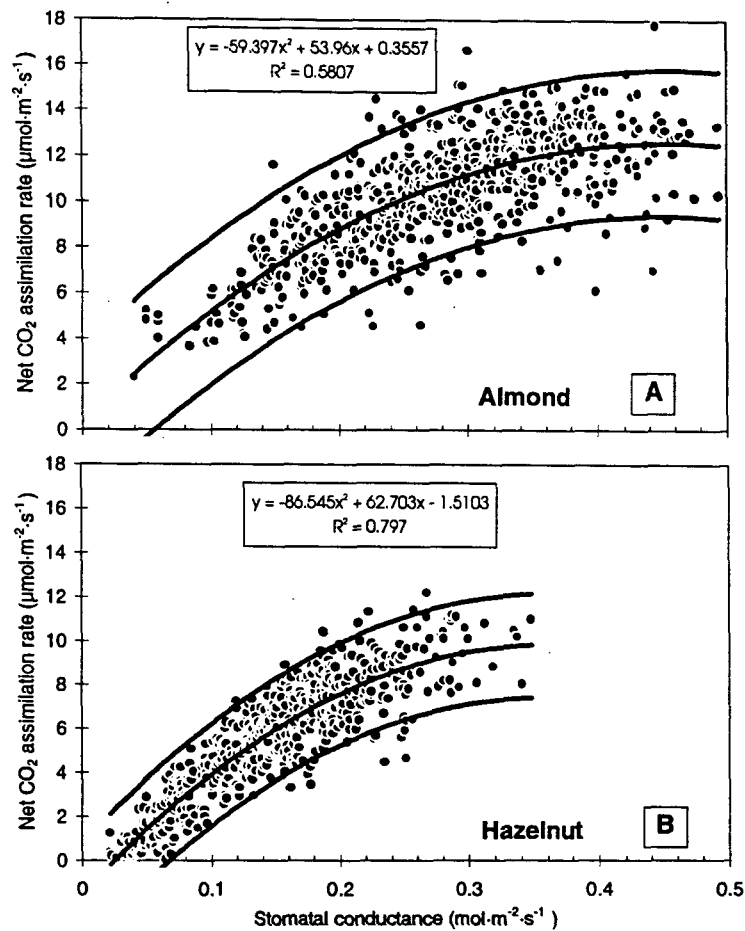


Figure 4. Relationship between net assimilation rate (A) and stomatal conductance (g_s) in almond (A) and hazelnut (B) (readings were taken at midday throughout the deficit irrigation period; $PAR > 900 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and cuvette temperature $> 25^\circ\text{C}$). 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 $P \leq 0.05$.

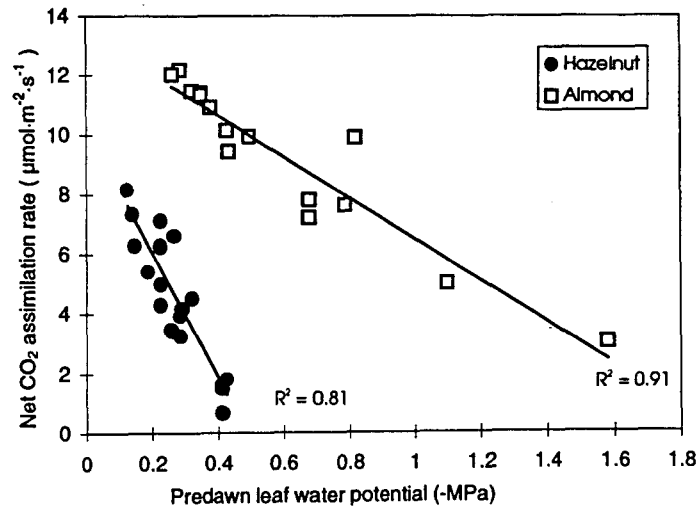


Figure 5. Relationship between predawn leaf water potential (Ψ_{pd}) and net assimilation rate (A) in hazelnut (solid circles) and almond (open squares) through the season. Each point represents mean of nine measurements for A and twelve for Ψ_{pd} . Fitted lines were statistically different at $P \leq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

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} 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 60 cm soil profile) was quite constant for RDI from mid July until the end of August, showing that $0.2 \cdot ET_c$ water application was apparently enough to offset drainage and provide a small crop evapotranspiration, as g_c was always very low in RDI treatment throughout 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 mid-summer decrease in Ψ_{pd} and a further late recovery. The same trend was observed in the over-watered 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. 3B). This generalized midsummer Ψ_{pd} depression could be related to a high evaporative demand during the hottest summer days and a nightlength that was too short to allow complete plant rehydration. Just before sunrise, the plant might still have been in process of recovery. In this case, the data obtained would not be useful to assess soil water status since the values are more negative than they would have been if the plants had had more time to equilibrate with the soil. Thus, the decrease in Ψ_{pd} in early July reflects soil water shortage and also a hot season effect, while the late August recovery should reflect a release of this effect. To overcome this seasonal noise, 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 through the season. However, in hazelnut there was still a late August Ψ_{npd} recovery. Kernel dry weight accumulation in hazelnut cv. "Pauetet" 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. Kernel almond filling takes place from mid June to the end of August (around 75 days); about 45 days 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 leaf water potential in fruit trees have been reported in apple (Erf and Proctor, 1987), peach (DeJong, 1986; Blanco et al., 1995) and mandarin (Yahata et al., 1995). In addition, Blanco et al. (1995) reported that when sink activity decreased, after harvest, differences in leaf water potential among fruit load treatments disappeared. On the other hand, anyone of these authors showed Ψ_{pd} data related to fruit load treatments. But DeJong (1986) attributed this extra decrease in LWP to higher stomatal conductance; Buwalda and Lenz (1995) in pear, found a 36% increase in water use in fruiting trees compared to non-fruiting trees. Thus a lower soil water content and in consequence, 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 fruits, the processes involved during kernel filling do not include expansive growth. Further studies are needed to confirm the sink effects on leaf water potential in nut trees.

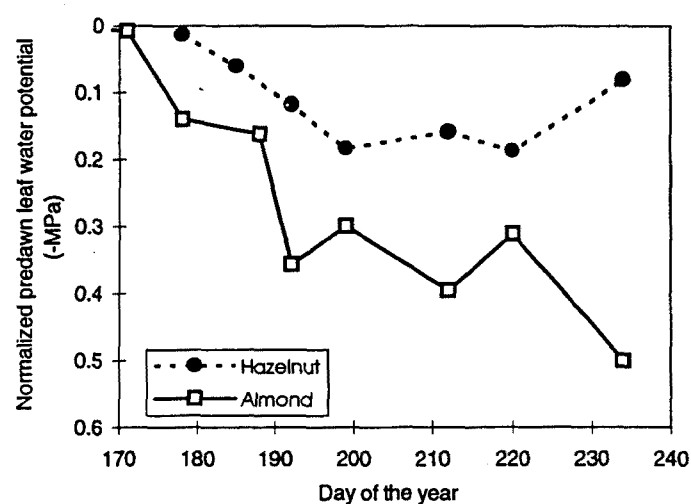


Figure 6. Seasonal pattern of normalized predawn leaf water potential ($RDI\Psi_{pd} - T-100\%\Psi_{pd}$) in almond (open squares) and hazelnut (solid circles).

Although from the Ψ_{pd} standpoint it seems that almond is capable of extracting more water from the soil than hazelnut, this is not easy to confirm simply by comparing θg data. First of all, they have a different root development pattern. 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 (McCutchan, 1990; Johnson et al., 1992). 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 to be very improbable because at night plant tissues are rehydrating, and a certain stem sap flow is commonly reported (Schubert, 1939, cited by Zimmerman et al. 1980; Caspari et al., 1993). 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 2B, C and 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 making use of 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 versus 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 around 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 behaviour 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 (Schulze et al., 1979; Girona, 1994). 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 $15.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and g_s of $0.49 \text{ mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig 4). Treatments T-130% were used to check that T-100% 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 ($A=2.29+31.57\cdot g_s$) than hazelnut ($A=-0.64+43.7\cdot g_s$). 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 sensitive in hazelnut than in 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 in order 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 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 more affected than g_s when stomata were closing, it could be possible that in addition to a stomatal limitation, there might have been a direct negative effect of water stress on the mesophyll CO₂ efficiency (Percy, 1983). Negative effects over A were detected in hazelnut using Ci

analysis (Long and Hallgren, 1985) as C_i increased while water stress induced g_s to decrease (Fig. 8). C_i analysis, if accepted, would indicate that hazelnut A was negatively affected by non stomatal 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 (Terashima et al., 1988; Kraalingen, 1990; Ni and Pallardy, 1992). If this were the case, C_i would only show that patchy stomatal closure may affect hazelnut more than almond.

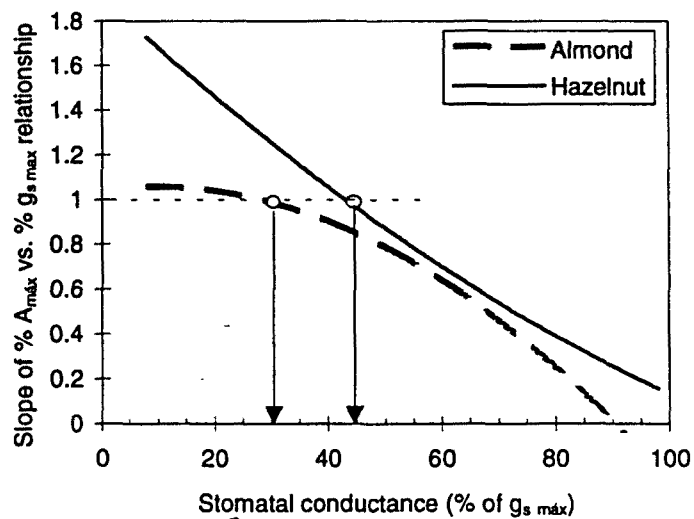


Figure 7. Relationship between the slope in each point of the A/g_s polynomial curve and g_s . The slope was calculated from the A vs. g_s relationship expressed in % units calculated over the maximum rates of each variable in each crop. (Almond $A_{\max}=16.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$,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

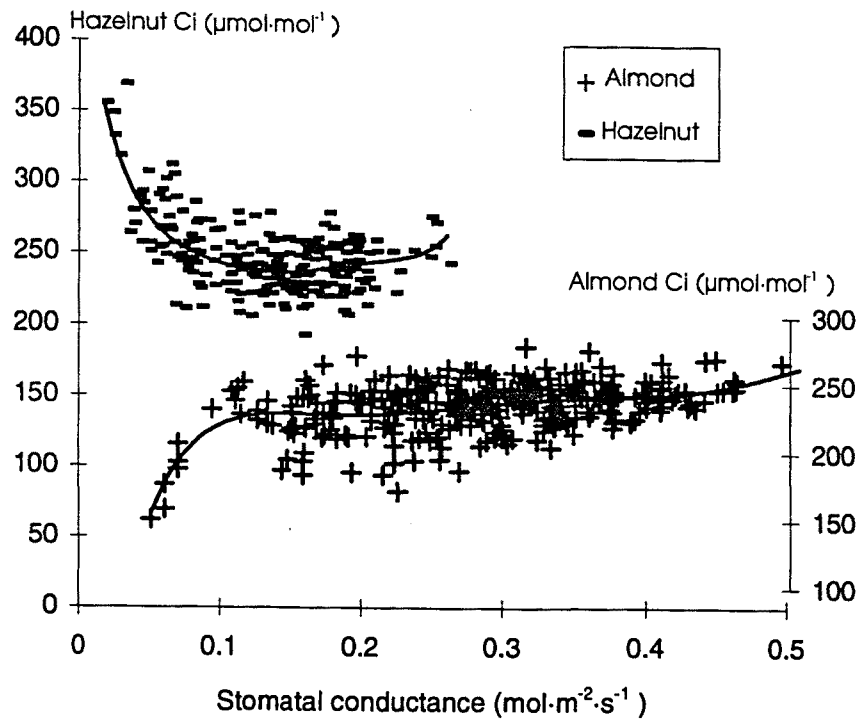


Figure 8. Relationship between leaf intercellular CO₂ (C_i) and stomatal conductance (g_s) in almond (crosses) and hazelnut (dashes). Each point is a single measurement. (*PAR*>900 μmol·m⁻²·s⁻¹ and cuvette temperature>25 °C).

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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October 9, 1996

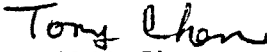
Dr. Joan Girona
Head of Fruit Trees Technology Area
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LLEIDA, SPAIN

Dear Dr. Girona:

I am pleased to inform you that your manuscript JMS #7705 "Leaf Water Relations in Almond Compared to Hazelnut Trees During a Deficit Irrigation Period" is now acceptable for publication in the Journal of the American Society for Horticultural Science. I am forwarding the revised manuscript to Science Editor Dr. Edward L. Proebsting and recommending the acceptance of this paper.

Thank you very much for submitting your paper to the Journal of the American Society for Horticultural Science.

Sincerely


Tony H.H. Chen
Associate Editor

CC. Dr. Edward L. Proebsting
Science Editor



***3. Relationship between Leaf Water Potential and Gas Exchange Activity at different
Phenological Stages and Fruit Load in Peach Trees.***

**RELATIONSHIP BETWEEN LEAF WATER POTENTIAL AND GAS EXCHANGE ACTIVITY
AT DIFFERENT PHENOLOGICAL STAGES AND FRUIT LOAD IN PEACH TREES**

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Additional index words: *Prunus persica*, regulated deficit irrigation, stomatal conductance, photosynthesis.

Abstract. Relationships between midday (Ψ_{md}) and predawn (Ψ_{pd}) leaf water potential, stomatal conductance (g_s) and net CO₂ assimilation rate (A) were determined at different fruit growth stages and two years with different fruit loads in a peach [*Prunus persica* (L) Batsch cv. Sudanel] plot subjected to two regulated deficit irrigation strategies (RDI) plus a control irrigation treatment. A postharvest RDI treatment (PRDI) was irrigated at 0.35 of control after harvest. The second treatment (SPRDI) applied RDI during Stage II, the lag phase of the fruit growth curve, at 0.5 of control and postharvest at 0.35 of control. The control treatment, as well as PRDI and SPRDI when not receiving RDI, was irrigated at 100% of a modified Penman crop water use calculation (ET_o) in 1994, a full crop year, and 80% in 1995, a year of nearly zero crop. In 1995, with 80% of the 1994 irrigation rate and no crop, the Ψ_{md} was higher, probably because of the lower crop load, while Ψ_{pd} was lower, probably because less water applied to the soil. The relation of g_s and A with Ψ_{md} during Stage II was steeper than during postharvest. Low Ψ_{md} was not indicative of a depression in g_s and A in Stage III. Osmotic leaf water potential at turgor loss (Ψ_x^0) as derived from pressure-volume curves was more negative during Stage III and postharvest (about -2.9 MPa) than in Stage II (about -2.7 MPa). Ψ_{md} measurements together with Ψ_x^0 determinations seemed to be more useful to characterize peach tree water status than Ψ_{pd} under soil water deficits because of their better relationship to midday stomatal closure.

Introduction.

Regulated deficit irrigation (RDI) was originally applied to control excessive vegetative growth, by reducing irrigation during Stage II of fruit growth (Chalmers et al., 1981). Subsequently, RDI experiments have been focused on saving water during both pre- and postharvest periods (Johnson *et al.*, 1992; Boland et al., 1993; Girona et al., 1993). If RDI is to be successful, a reliable monitoring of plant water status during the deficit irrigation period is needed. The measurement technique should be an inexpensive and simple indicator of plant water status.

Environmental changes are sensed primarily by leaves (Dickson and Isebrands, 1991) and leaf water potential has been the most commonly used plant water status indicator (Jones, 1990). Particular potentials are usually associated with specific degrees of water stress (Bradford and Hsiao, 1982). Nevertheless use of leaf water potential has been questioned during the last decade because stomatal closure can moderate leaf water potential decreases as water stress develops, diminishing the differences between watered and unwatered plants (Garnier and Berger, 1985). Parameters such as leaf conductance (Davies and Zhang, 1991) and stem water potential (Garnier and Berger, 1985; McCutchan and Shackel, 1992) have been proposed as more useful indicators of plant water stress. Despite the above limitations, leaf water potential is probably the most commonly used plant-based technique for assessing the influence of irrigation treatments on tree water status. With respect to irrigation monitoring, the use of stomatal conductance is limited due to diurnal atmospheric influences (Schulze and Hall, 1982; Tan and Buttery, 1986), feedback photosynthetic responses (Schulze, 1986) and large sampling errors (Jones and Cumming, 1974; cited by Jones 1990). Although plant water stress and its subsequent influence on vegetative growth and gas exchange activity is the cumulative result of plant, atmospheric and soil water factors, only the latter are usually contemplated for practical irrigation management. Plant water stress, as it affects photosynthetic and growth processes, varies widely at a constant soil moisture level as is evident from its diurnal cycle. Therefore a measure of plant water status during the day, when stress develops, is needed to manage water applications during RDI.

The aim of this work is to study the implications of specific values of leaf water potential in peach trees, in relation to leaf gas exchange data. This objective is outlined in the following points: What are the influences of water stress on the relationship between leaf water status at midday and gas exchange activity and how can this relationship change with different developmental conditions ? How is this relationship modified by the presence or absence of fruit and finally, under which conditions can leaf water potential measured at midday be a sensitive indicator of plant water stress ?

Material and Methods.

Experimental orchard. The experiment was conducted during 1994 and 1995 in a 0.7-ha peach plot located in a commercial orchard in Lleida, Spain (41.38 °N, 0.35 °E). The soil is Typic Xerothent, 50 cm loam soil profile. The average annual rainfall was 277 mm with no precipitation during the growth period. In 1994 there was almost no precipitation during the entire spring and summer. Maximum summer temperatures are about 35 °C and midday relative humidities are about 30 %. The trees were heavily cropped in 1994 with a fresh fruit mass yield efficiency (FFMYE) on trunk cross section area basis of 0.9 kg·cm⁻². In 1995, an April freeze eliminated most of the crop (FFMYE = 0.036 kg·cm⁻²).

Experimental design. A total of 352 five-year old trees on peach seedling rootstock and 'Sudanell' scion (medium-late maturing peach) were used. Tree spacing was 5x3 m. and the trees were pruned to a vase system. The plot was oriented North-South. A randomized complete-block design with 4 blocks was originally established, but due to a different soil characteristics in one of the blocks, all the sampling effort was concentrated in the remaining 3 complete blocks. Each block consisted of 3 adjacent tree rows with 10 trees in each row. The center 2 trees of the middle row were used for physiological measurements whereas the center 8 of the middle row were used to measure vegetative and production parameters. A total of 4 leaves (2 per tree) were measured in each replication/block for gas exchange and leaf water potential.

An automated drip irrigation system with 4 compensating emitters (4 L/h) per tree was used with water meters in each replication to monitor applied irrigation water. Surface soil wetted was about 35 % of the shaded area. The plot was managed using commercial practices with a mowed cover crop strip between

rows. The trees were thinned in late May to a commercially acceptable level (430 fruits/tree). Fruit was harvested 3 times between August 3-15.

Treatments. Three irrigation treatments discussed in this manuscript include: Control (C), and 2 RDI regimes: postharvest RDI treatment (PRDI) and a spring plus postharvest RDI treatment (SPRDI). The Control treatment was fully irrigated using crop evapotranspiration (ET_c) calculated from a modified Penman-determined reference crop water use (ET_o) (Doorenbos and Pruitt, 1977) with estimated crop coefficients (K_c) adapted from Goldhamer and Snyder (1989) and modified *in situ* based on plant water status (ET_c = ET_o·K_c). Initial K_{c1} (rapid growth) was 0.25, K_{c2} (mid season)=1 (with a maximum K_{c2} =1.05 during rapid fruit growth) and K_{c3} (late season)=0.55. Trees leafed out on 20th of March, full leaf growth was completed by 15th of June, harvest was finished by 15th of August, and the end of season was on 5th of November. Irrigation began at flowering (first week of March). During 1994, SPRDI trees were irrigated at 50% ET_c during fruit growth Stage II, PRDI and SPRDI were irrigated at 35% ET_c during postharvest (Table 1). Due to lower fruit load in 1995, C was irrigated at 80% ET_c throughout the season. In 1995, trees of the RDI regime during Stage II of fruit growth and postharvest were irrigated at 50% and 35% of C, respectively (Table 1).

Table 1. Applied irrigation as percentage of ET_c during 1994 and 1995 for each stage of fruit development and irrigation treatment.

Year	Treatment	Stage I	Stage II	Stage III	Postharvest
	Control	100%	100%	100%	100%
1994	SPRDI ²	100%	50%	100%	35%
	PRDI ¹	100%	100%	100%	35%
	Control	80%	80%	80%	80%
1995	SPRDI	80%	40%	80%	28%
	PRDI	80%	80%	80%	28%

² SPRDI= Stage II and Postharvest RDI irrigation treatment.

¹ PRDI= Postharvest RDI irrigation treatment.

Measurements. Meteorological data for the Penman equation were collected at the nearest automated weather station (19 km from the study plot). This station is part of the Catalanian network of weather stations (Generalitat de Catalunya, 1994).

Leaf water potential at predawn (Ψ_{pd}) and at midday (Ψ_{md}) (1200 HR local time) was measured weekly on 4 leaves per replication using the pressure chamber (Soil Moisture Equipment Corp., Model 3005, Santa Barbara, Calif.) technique (Scholander et al., 1965) as modified by Turner and Long (1980). Sampled leaves were fully mature, well exposed and dew-free. Stomatal conductance to H₂O (g_s) and net CO₂ assimilation rate (A) were determined using a portable IRGA system (Model ADC LCA-2, The Analytical Development Co. Ltd., Hoddesdon, Herts, U.K.). Gas exchange calculations were made according to the equations given by von Caemmerer and Farquhar (1981). Measurements were taken weekly at midday (4 leaves/replication per treatment) using different leaves for gas exchange and leaf water potential. During 1995, the same leaf was used to measure gas exchange and Ψ_{md} . Sample frequency was lower in 1995 with 2 sampled days during Stage II and 4 during Stage III. All readings were taken on sunny days.

Pressure-Volume curves. Leaves were sampled at 0800 HR local time with the same criteria as described for gas exchange measurements. The cut end of the petioles were immediately placed under water (4 °C) and allowed to rehydrate for 24 hours in darkness. Pressure release curves were generated using the free transpiration dehydration method (Hinckley et al., 1980) and by means of a pressure chamber using a transformation type II (Tyree and Richter, 1981). Each curve was developed using data from 6 to 12 leaves as per Augé (1991). Pressure in the chamber was increased at a rate not higher than 0.02 MPa·s⁻¹ (Kikuta et al., 1985). Pressure-volume curves were corrected for oversaturation by calculating the turgid fresh mass from the linear regression between sample fresh mass and leaf water potential at points clearly above that of turgor loss (Kubiske and Abrams, 1990). Points with Ψ_t higher than -0.08 MPa were excluded from this regression. The turgor loss point was determined by graphical analysis with the aid of a sequentially fitted regression that maximized the linear correlation coefficient. The parameters obtained from each curve were: Osmotic water potential at full turgor (Ψ_x^{100}), osmotic water potential at

the turgor loss point (Ψ_x^0) and average cell wall elasticity (ϵ_m) estimated as the slope of the regression line for turgor potential vs. relative water content (Warren Wilson, 1967).

Results

In 1994, Ψ_{pd} and Ψ_{md} in SPRDI declined progressively during Stage II and Postharvest. In PRDI Ψ_{pd} diminished only during Postharvest (Fig 1A, B). The lowest values occurred at the end of both periods. During Stage III, Ψ_{pd} was generally invariant with time but Ψ_{md} mostly declined (Fig 1A, B).

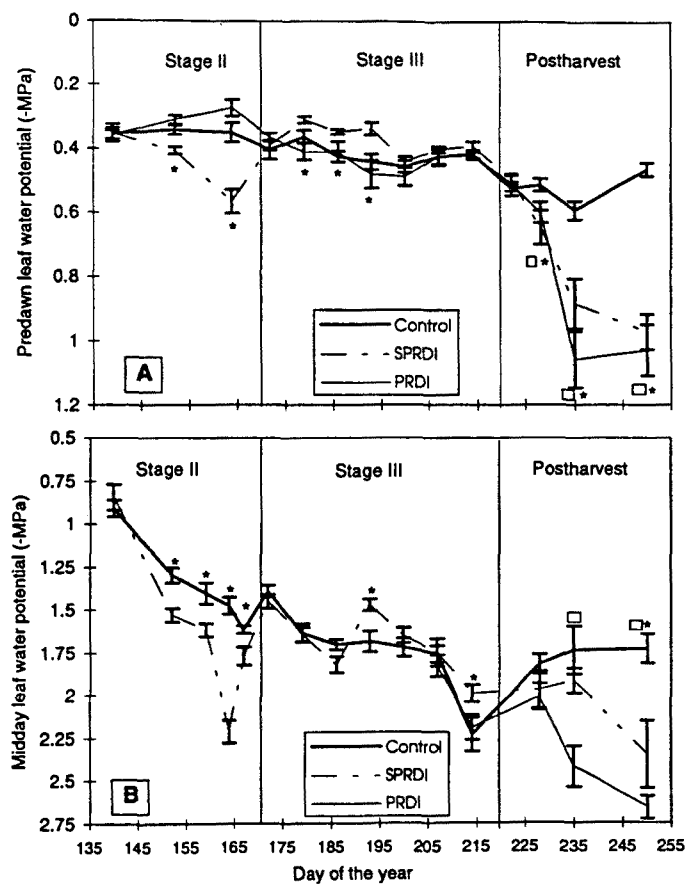


Figure 1. Seasonal patterns of 1994 (A) predawn leaf water potential (Ψ_{pd}); (B) midday leaf water potential (Ψ_{md}), in peach in response to irrigation treatments. Each point represents the mean \pm SE ($n=12$). Points with * indicate significant treatment differences when comparing Control to SPRDI, \square indicate significant treatment differences when comparing Control to PRDI ($P<0.05$, LSD).

In 1995, Ψ_{pd} for the Control treatment was significantly lower than in 1994 during Stage III, probably due to less applied water in 1995 (Table 2). Average atmospheric conditions for the sampled days did

not differ substantially between years, air temperature in 1994 and 1995 was 33.37 ± 0.48 and 32.90 ± 1.45 ($^{\circ}\text{C} \pm \text{SE}$), respectively, and air vapor pressure deficit in 1994 and 1995 was 3.14 ± 0.10 and 3.04 ± 0.11 ($\text{kPa} \pm \text{SE}$), respectively. For SPRDI, differences in Ψ_{pd} relative to C, were greater at the end of Stage II than during Stage III (Table 2). Ψ_{md} values were significantly more negative in 1994 than in 1995 during Stage III and Stage II for all treatments (Table 2). The relationship between Ψ_{pd} and Ψ_{md} for each RDI regime was curvilinear (Fig 2). However, their shape changed in the different periods of time. Nonetheless, the relation between Ψ_{pd} and Ψ_{md} was clear and significant.

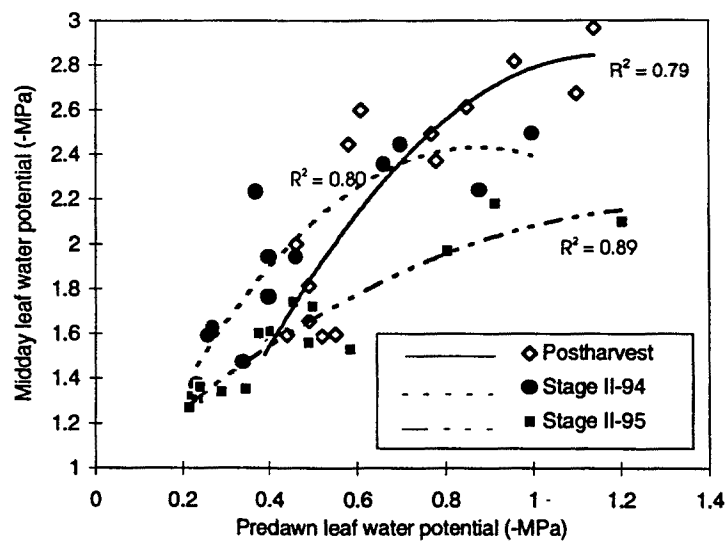


Figure 2. Relationship between predawn leaf water potential (Ψ_{pd}) and midday leaf water potential (Ψ_{md}) for a single controlled day in different stages (Stage II-94= day 164; Stage II-95= day 170; Postharvest-94= day 250). Each point is the mean of four leaves replication/ treatment.

Seasonal patterns of midday A and g_s were similar to Ψ_{md} , with decreases in A and g_s during the deficit irrigation periods. These decreases were greater during postharvest than in Stage II (Fig 3A, B). However, A and g_s were unchanged at the end of Stage III even though Ψ_{md} was significantly lower at this time than in the rest of Stage III (Fig 3A, B).

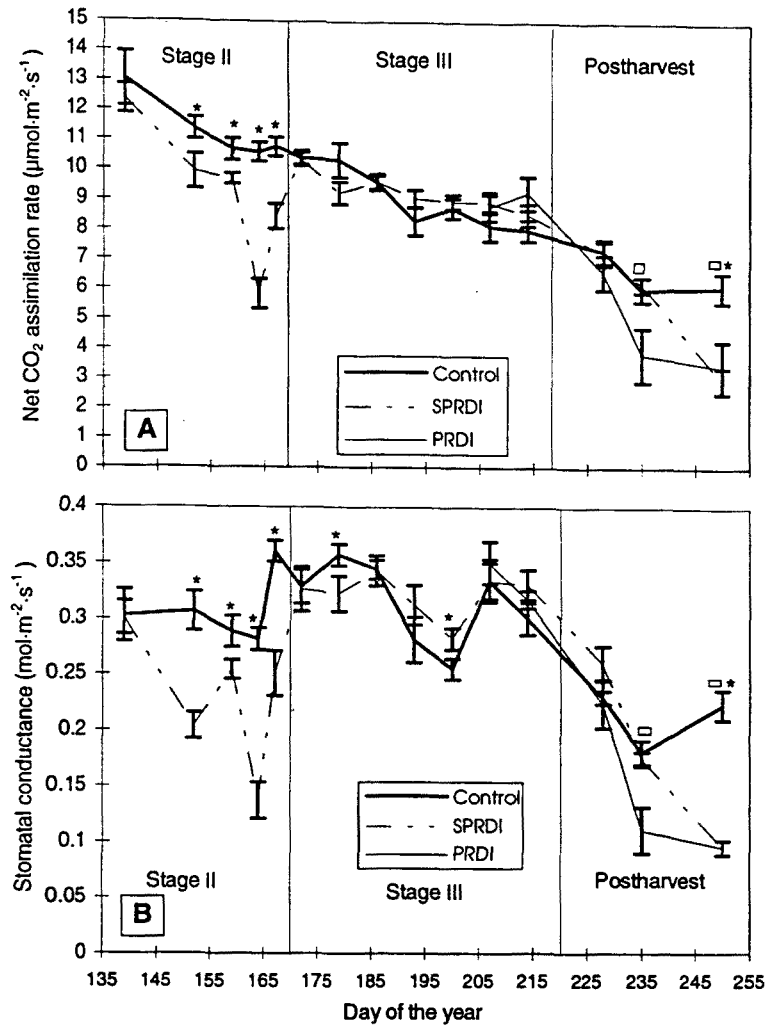


Figure 3. Seasonal patterns of 1994 (A) midday net CO₂ assimilation rate; (B) midday stomatal conductance, in peach in response to irrigation treatments. Each point represents the mean \pm SE (n=12). Points with * indicate significant treatment differences when comparing Control to SPRDI, \square indicate significant treatment differences when comparing Control to PRDI (P<0.05, LSD).

There was a clear distinction between Ψ_{md} influence on A and g_s in the different phenological Stages during 1994 (Fig 4). A decreased with Ψ_{md} during Stage II and postharvest, whereas there was no clear relationship during Stage III (Fig 4A, B). The postharvest A vs. Ψ_{md} relationship showed a clear plateau, but below Ψ_{md} of -2.2 to -2.4 MPa, A declined until it approached zero (Fig 4C). The g_s vs. Ψ_{md} relationships were similar to those of A vs. Ψ_{md} except during Stage II deficit irrigation where g_s declined more rapidly with Ψ_{md} than A (Fig 4D, E, F). During Stages II and III of 1995, the A vs. Ψ_{md} and g_s vs. Ψ_{md} relationships were similar to 1994 but A showed lower rates throughout the Ψ_{md} range of values. In 1995, g_s response was similar during Stage II and had lower values during Stage III (Fig 4A, B, D, E).

Table 2. Average Ψ_{pd} and Ψ_{md} in different stages of fruit growth development and irrigation treatments. Comparison between year 1994 and 1995.

Parameter	Stage	Treatment	Year		LSD
			1994	1995	
Ψ_{pd} (MPa)	Stage II	Control	-0.36	-0.29	ns
		SPRDI ^z	-0.56	-0.87	0.095
	Stage III	Control	-0.42	-0.51	0.002
		SPRDI	-0.36	-0.58	0.001
Ψ_{md} (MPa)	Stage II	Control	-1.48	-1.35	0.035
		SPRDI	-2.18	-1.75	0.007
	Stage III	Control	-1.80	-1.61	0.001
		SPRDI	-1.72	-1.62	0.025

^z SPRDI= Stage II and Postharvest RDI irrigation treatment.

From Stage II to Stage III, ψ_x^{100} and ψ_x^0 decreased and followed constant values during postharvest (Fig 5A, B). There were no consistent differences in ψ_x^{100} between irrigation treatments. In contrast, ψ_x^0 averaged -2.7 MPa at the end of Stage II, Stage III and postharvest values were 0.2 MPa lower (Fig 5A). \mathcal{E}_m tended to be lower from spring to postharvest, and was not influenced by the irrigation regime (Fig 5C).

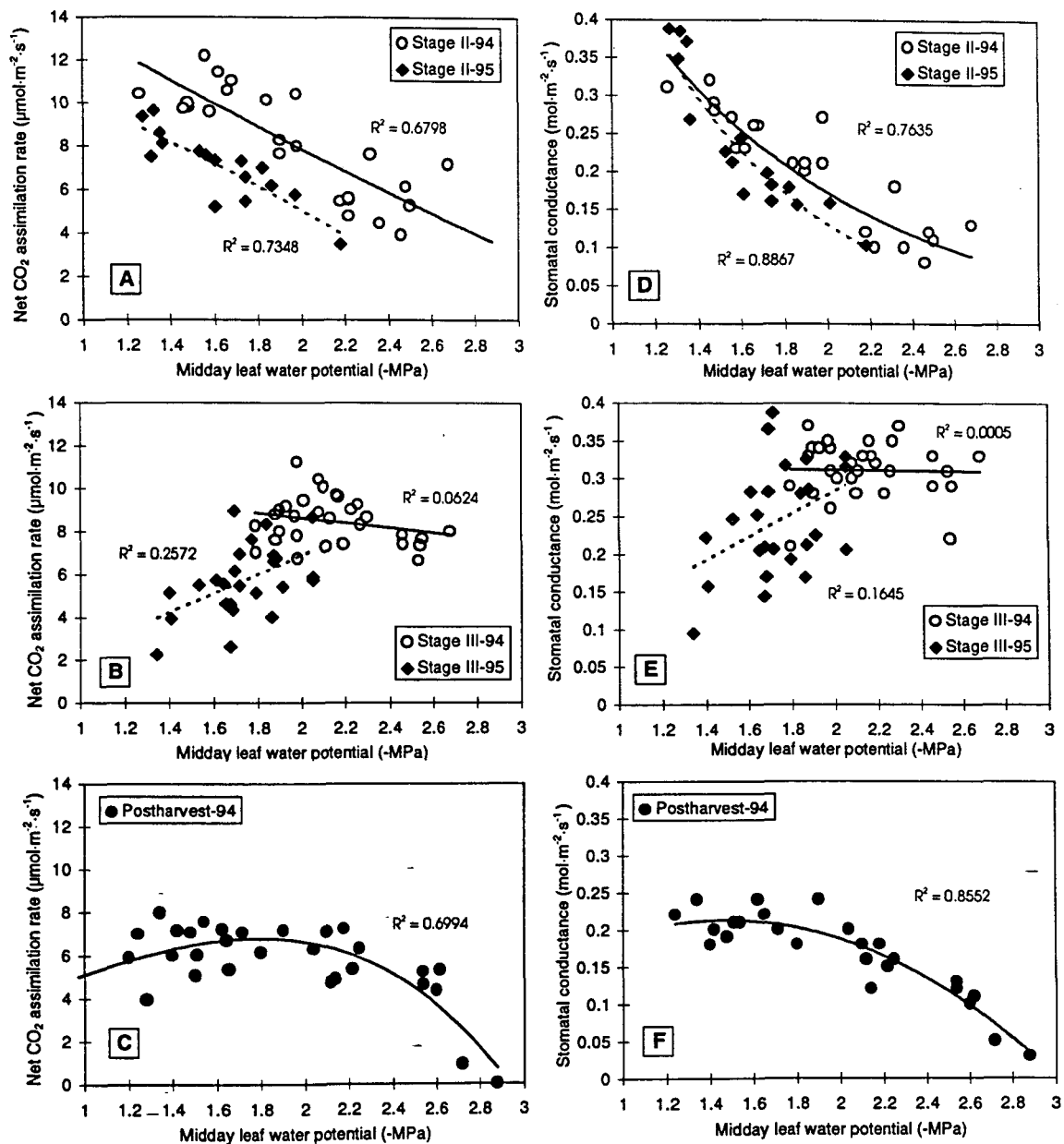


Figure 4. Relationships between midday net CO₂ assimilation rate vs. midday leaf water potential (A/Ψ_{md}) in stage II (A), stage III (B), postharvest (C), and stomatal conductance vs. midday leaf water potential (g_s/Ψ_{md}) in stage II (D), stage III (E), Postharvest (F) in two years. (◆= 1995; ○= 1994). All points in each stage and year were collected on one day (last day of each stage) with tree-to-tree differences giving the range of values on that day. (Stage II-1994= day of the year 164; Stage II-1995= day 170; Stage III-94= day 215; Stage III-1995= day 214; Postharvest-1994= day 235).

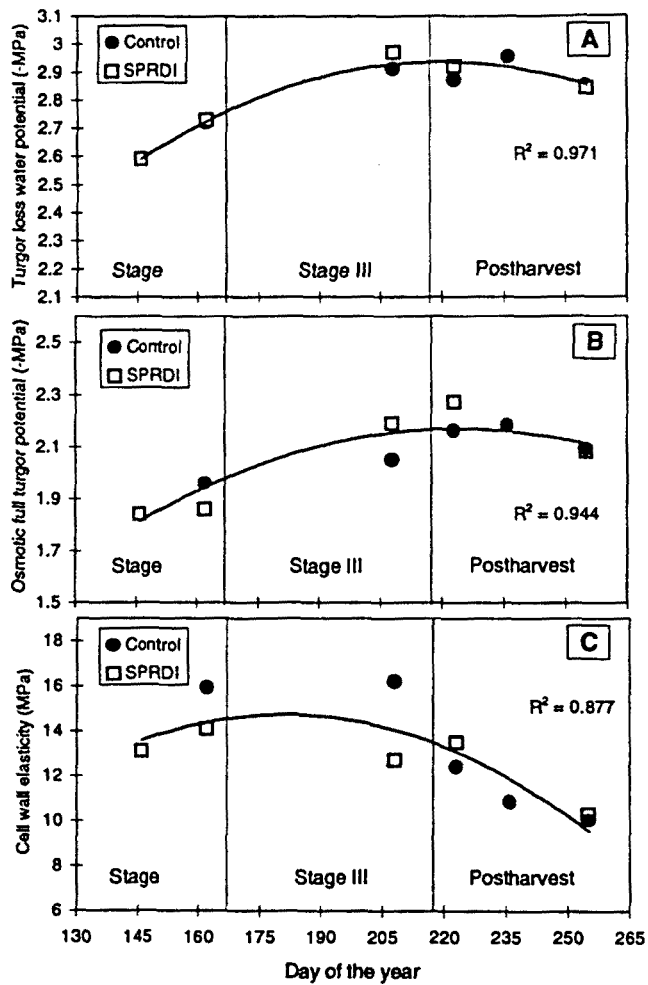


Figure 5. Seasonal patterns of (A) osmotic leaf water potential at turgor loss point (Ψ_x^0); (B) osmotic potential at full turgor (Ψ_x^{100}); (C) average cell wall elasticity (ϵ_m) in peach in response to irrigation treatments (● = Control; □ = spring and postharvest regulated deficit irrigation treatment). Each point is obtained by the contribution of six to twelve leaves. The solid line represents the best fit second degree polynomial for all points.

Discussion

These data support the observation that Ψ_{pd} is a sensitive indicator of soil water stress in peach orchards (Olien and Flore, 1990; Girona et al, 1993). Comparisons of Ψ_{pd} to Ψ_{md} during Stage II for irrigation treatment effects indicated both became significant at the same time after the initial water deprivation (Fig 1A, B) but in the postharvest period, Ψ_{pd} became significant sooner, whereas Ψ_{md} did not reflect differences between irrigation treatments after two weeks for SPRDI and one week for PRDI (Fig 1A, B). Therefore, Ψ_{pd} was more sensitive to irrigation treatments during postharvest. Perhaps the stress preconditioning in the SPRDI treatment during Stage II was the cause of this two weeks delay in water

stress development during postharvest. A similar delay in SPRDI compared to PRDI can be observed for g_s and A (Fig 3A, B). Comparing experimental years, Ψ_{pd} responded to the 20 % reduction in applied water for C and SPRDI treatments during 1995 Stage III (Table 2).

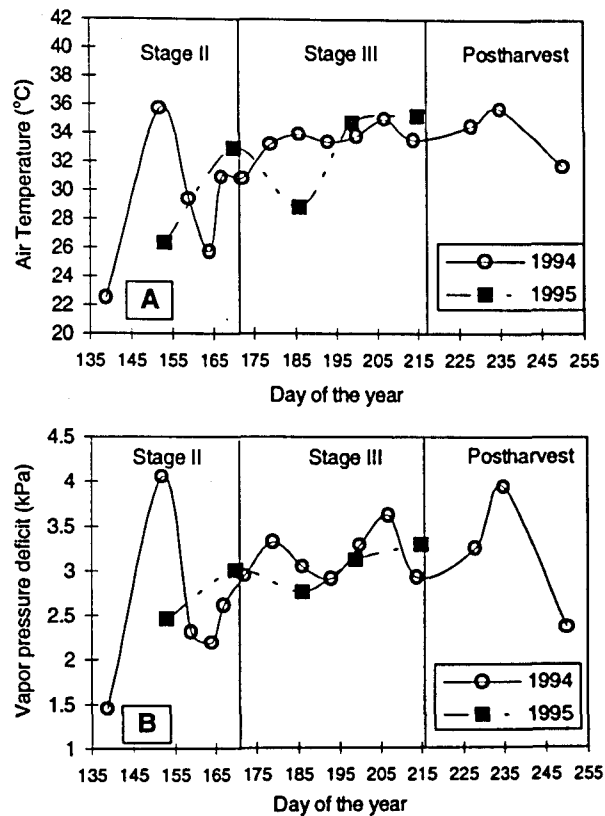


Figure 6. Mean air temperature (A) and vapor pressure deficit (B) measured for the dates and times that correspond to seasonal measurements of gas exchange and Ψ_{md} in 1994 (solid lines) and 1995 (dashed lines).

During Stage II, Ψ_{md} was well correlated with Ψ_{pd} (Fig. 2). Nevertheless, the last day of stage III (day 214) coincided with a general drop in Ψ_{md} while Ψ_{pd} values for the same day remained constant (Fig 1A, B). This occurred even though evaporative demand for day 214 was similar to conditions exhibited on other days of measurement during Stage III (Fig 6). Peaches of cv. 'Sudanell' have an extraordinarily high fruit growth rate at the final end of Stage III, doubling in fruit fresh weight in the last two weeks of expansive growth. This contrasts with other late maturing cvs. such as 'Cal Red' in which fresh weight increased by only 40 % in the last two weeks of Stage III (Girona, 1994). Since fruit sink strength can be related to relative fruit growth rate (Grossman and DeJong, 1994), this suggests that the late Stage III drop in Ψ_{md} could be due to a high fruit sink demand. Chalmers et al., (1983) reported substantial

effects of rapid fruit growth on leaf water potential and g_s , and Ziska et al. (1989) found important increases in g_s during Stage III of fruit growth in *Prunus salicina* L. In peach, DeJong (1986b), found that the presence of fruit in the last Stage of fruit growth induced a 15% higher A rate and that this increase was related to an increase in g_s . Thus, during the short period of high reproductive sink strength, A in our study, could be maintained by decreased sensitivity of g_s to leaf water status. In fact, g_s values in the Ψ_{md} range of -2.2 to -2.5 MPa, were 63% higher during Stage III than in Stage II (Table 3). For the same Ψ_{md} range, A was 32% greater during Stage III than Stage II (Table 3).

Table 3. Average g_s and A at 2.2-2.5 (-MPa) Ψ_{md} range at different stages in 1994. Stage III and postharvest compared with Stage II.

Parameter	Stage II	Stage III	Prob.	Postharvest	Prob.
g_s (2.2-2.5) ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	0.114	0.307	0.0001 ^a	0.170	0.0147 ^b
A (2.2-2.5) ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	5.58	8.00	0.0059	5.34	0.6931

^a Probability level of the LSD contrast between stage II and stage III.

^b Probability level of the LSD contrast between stage II and postharvest.

Moreover, Ψ_{md} failed to indicate the higher irrigation applied in 1994 for C (Table 2). In contrast, more negative values were found during this high fruit load year, suggesting that fruit reduces Ψ_{md} values (Chalmers et al., 1983; DeJong, 1986a; Blanco et al., 1995) (Table 2). Atmospheric related effects on Ψ_{md} differences between both years are unlikely since average temperature and atmospheric vapor pressure deficit (VPD) during Stage III were similar between years (Fig 6).

The lack of A limitation related to Ψ_{md} decrease in Stage III, was presumably due to decreases in Ψ_{md} being related to the fruit sink effect rather than soil water deprivation. At postharvest when there were no fruit and reductions in water were again imposed, A was affected by decreases in Ψ_{md} (Fig 4C). The Ψ_{md} influences exhibited in 1994 during Stage III were surprisingly repeated again in 1995 with minimal fruit load (Fig 4B). This suggests that lack of a relationship between A and Ψ_{md} in Stage III, is perhaps not entirely due to a fruit sink effect, but to the absence of root signals when the source of water stress is related to soil drying. There is increasing evidence of direct stomatal responses to xylem

concentrations of abscisic acid (ABA) which is independent of Ψ_t until a specific Ψ_t level is achieved (Davies and Zhang, 1991; Tardieu *et al.*, 1996), even though there are no reports that show this for peach. The relationship between g_s and Ψ_{md} followed similar patterns to A vs. Ψ_{md} ; high sensitivity of g_s to Ψ_{md} during Stage II, lower sensitivity during postharvest and insensitivity during Stage III (Fig 4D, E, F). Thus, Ψ_{md} would influence g_s only water stress was due to soil water deprivation. Lack of root signals in experiments with detached leaves, could also explain stomatal responses to Ψ_t only when near the turgor loss point (Andersen and Brodbeck, 1988; Yoon and Richter, 1990). Decreases in g_s during Stage II, were already evident at Ψ_{md} values of -1.5 MPa, which is clearly above the turgor loss point during this Stage ($\psi_x^0 = -2.7$ MPa) (Fig 4D and Fig 5A).

In contrast to Stage II, postharvest g_s and A decreases related to Ψ_{md} were only apparent at values of Ψ_{md} lower than -2.2 MPa. This indicates a lower g_s and A sensitivity to Ψ_t in postharvest than in Stage II. A maximum (A_{max}) values during postharvest were clearly lower than in Stage II (Fig 4A, C). This could be related to a leaf age effect (Andersen and Brodbeck, 1988) but perhaps more likely is a photosynthetic limitation resulting from high air temperatures during that period. Tan and Buttery (1986) reported 26 °C as an optimum temperature at PAR (Photosynthetically Active Radiation) levels of 444 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Girona *et al.* (1993), reported a sharp decrease in A between leaf temperatures of 32 °C and 36 °C. Average midday air temperatures during July and August were 34.8 °C and 35.1 °C respectively, compared to 25.5 °C in May.

Stomatal action could also be evaluated by analyzing the Ψ_{pd}/Ψ_{md} relationship. Under high Ψ_{pd} values the relationship between both parameters is somewhat linear but a curved part appears below certain more negative values in Ψ_{pd} (Fig. 2). The reason for the curvature initiation is due in part to progressive stomatal closure, limiting thereby the rhythm of Ψ_{md} decreases with Ψ_{pd} decline. Interestingly, this curvature began at more negative values in Ψ_{md} during postharvest than Stage II, and even at higher levels during Stage II in 1995 with minimal fruit load (Fig. 2). This indicates higher control of water loss during Stage II than postharvest, which seems consistent with the different phenological sensitivity of g_s to Ψ_{md} , (higher during Stage II and lower during postharvest) as mentioned before.

Differential leaf gas exchange sensitivity to Ψ_{md} between stages may be due in part to the influence of the different environmental factors (*VPD*, Temperature, *PAR*) between Stage II and postharvest. Leaf ontogeny between Stage II and postharvest may also have been different. In fact, ψ_x^0 , ψ_x^{100} and ϵ_m were lower during postharvest and Stage III than in Stage II (Fig 5A, B, C). This resulted in a decreased sensitivity of leaf turgor pressure (ψ_p) to Ψ_{md} (ψ_p was derived from pressure-volume curves) (Fig 7). When a linear model was applied to the ψ_p vs. Ψ_{md} relationship, the slope in Stage II ($\psi_p = 1.86 - 0.716 \cdot \Psi_t$) was significantly steeper than the slope during postharvest ($\psi_p = 1.74 - 0.596 \cdot \Psi_t$). This decrease in turgor sensitivity corresponded to lower stomatal response to Ψ_t at near turgor loss levels during postharvest. Turgor loss from water release curves during postharvest occurred at about -3.0 MPa which approached the field Ψ_{md} levels -2.9 MPa (Fig 4F) associated with proximal stomatal closure (g_s approaches 0). Stressed treatments at this time exhibited a general leaf wilting and for the more interior leaves of the tree, leaf yellowing and shedding. During Stage II there was no leaf shedding and only incipient leaf wilting was evident on the most stressed day of this stage (day 164).

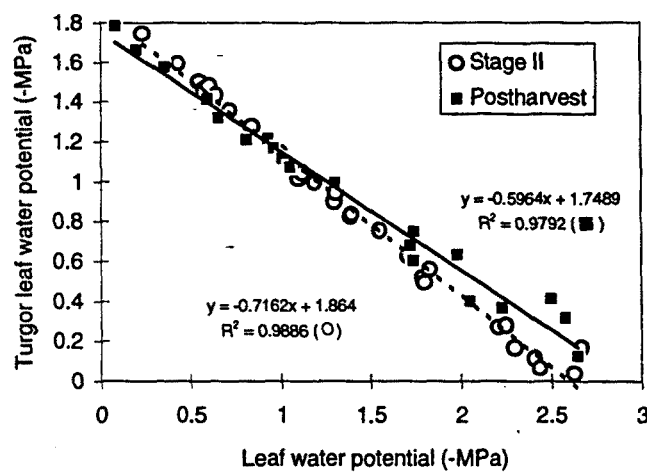


Figure 7. Relationship between turgor leaf water potential and leaf water potential in two different stages of 1994 in peach (■= Postharvest; ○= stage II). Each fitted line is obtained by the contribution of two pressure-volume curves belonging to two different days of each corresponding stage.

Mature peach leaves exhibited no consistent effect of water stress on Ψ_x^{100} which seems to confirm the lack of osmotic adjustment reported by others (Young et al., 1982; Steinberg et al. 1989).

In summary, soil water deprivation in Stage II and postharvest consistently induced decreases in Ψ_{md} during cloudless days and low Ψ_{md} values were related to low g_s and A rates. However in Stage III under full irrigation, decreases in Ψ_{md} may be more indicative of fruit sink strength. Ψ_{md} values lower than Ψ_x^0 give a threshold level that should not be exceeded for a long period if depression in A rates and loss of photosynthetic surface area are to be avoided. From this, under a deficit irrigation period of an RDI strategy in peach, Ψ_{md} together with Ψ_x^0 determinations seem to be more useful than Ψ_{pd} to regulate plant water stress and this could be useful in effectively correcting excessive stress when scheduling deficit irrigation. During postharvest, differences between treatments were detected in Ψ_{pd} while gas exchange differences were not apparent. During postharvest, a wider range of non-stressful conditions was exhibited based on soil water stress, leading to Ψ_{pd} overestimating drought stress. This study shows that if moderate water stress is used to partially inhibit vegetative growth of peach trees during Stage II, reductions in leaf carbon assimilation can be expected depending on the Ψ_{md} level reached.

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Journal of the American Society for Horticultural Science

American Society for Horticultural Science, 600 Cameron Street, Alexandria, VA 22314-2562; Phone 703/836-4606; Fax 703/836-2024; e-mail pubs@ashs.org

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December 19, 1996

Dr. Joan Girona
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Dear Dr. Girona,

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I am pleased to inform you that the contribution noted above, "Relationship between leaf water potential and gas exchange activity at different phenological stages and fruit load in peach trees", has been accepted for publication and will be forwarded shortly to the ASHS Publications Department in Alexandria. Please, **now send a disk** that **only** contains the **final** version of your MS to **Alexandria** so copy editing can proceed. Note that a 3.5-inch diskette is preferred.

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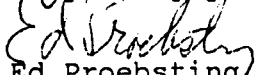
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4. Effects of Water Stress Cycles on Turgor Maintenance Processes in Pear Leaves

(Pyrus communis L.)

EFFECTS OF WATER STRESS CYCLES ON TURGOR MAINTENANCE PROCESSES IN

PEAR LEAVES (*Pyrus communis* L.)

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Keywords. *Pyrus communis*, leaf water potential, leaf osmotic water potential, tissue elasticity, turgor loss, stomatal conductance, deficit irrigation.

Abstract. The effect of water deficits on leaf turgor maintenance processes were analyzed for pear trees (*Pyrus communis* L. 'Barlett') grown in 120 l. containers. Four irrigation treatments were applied. The **Control** treatment was well watered using predawn leaf water potential and Penman ETo as a guide. The **Su** treatment received a summer water stress cycle and the **Sp** treatment a spring water stress cycle by progressively reducing the water applied (from 100% to 20% of **Control** dose) for 27 days in spring and 23 days in summer. The **Sp&Su** treatment received two drought stress cycles, one in spring and the other in summer as in **Su** and **Sp**. Pressure-volume (PV) determinations and stomatal conductance was obtained for pear leaves from each treatment during the spring and summer stress cycle. Leaf water potential (Ψ_x^0) and relative water content (**Ro**) at the turgor loss point of **Control** leaves showed a tendency to decrease from spring to summer. Changes in leaf osmotic water potential at full turgor (Ψ_x^{100}) and in symplast water fraction (**Rs**) did not explain this seasonal decrease in Ψ_x^0 . Changes in Ψ_x^{100} as a consequence of water stress treatments were not detected, while **Rs** was reduced with water stress, particularly in the summer cycle for both **Sp&Su** and **Su**. This change in **Rs** was correlated with an increase in the slope of the linear region of the PV curve. Such a coupled adjustment could have led to a higher water uptake capacity only under non turgor conditions for the water stressed trees. Pear leaves seem to be incapable to actively accumulate solutes. The changes in leaf tissue water relations measured in this study, as a result of leaf acclimation to water stress, seem unlikely to be involved in a supposed fruit productivity maintenance.

Introduction.

Regulated deficit irrigation (RDI) is a technique based on irrigating below full regime during certain stages of tree-fruit growth, while minimizing losses in fruit production. In some situations this technique is only useful for saving water (Girona et al. 1993, Ebel et al. 1995), while in other contexts it seems a good way to improve production and revenues besides saving water (Chalmers et al. 1981, Mitchell et al. 1984). Sometimes the reasons for these discrepancies are related to the impossibility of avoiding the effect of negative water stress on fruit growth. Nevertheless, this negative effect might be offset by any resulting acclimation to water stress that could improve productive leaf physiological behaviour after the deficit period of a specific RDI strategy. Apple (*Malus domestica* Borkh.) leaves subjected to drying cycles become hardened to drought stress and enhance their tolerance to subsequent drought (Lakso et al. 1984). Other authors have found better photosynthetic performance during a drought period in sunflower (*Helianthus annuus* L.) with a prestressed history (Matthews and Boyer 1984). Higher photosynthetic water use efficiencies after a deficit irrigation period have been found in peach trees (*Prunus persica* (L.) Batsch) (Reyes-Lopez 1985, Girona et al. 1993).

There is some evidence in peach of enhanced fruit growth rate above that of normally irrigated trees when full irrigation is restored following RDI (Mitchell and Chalmers 1982). In pear trees Chalmers et al. (1986) found that fruits after the RDI period grew faster than optimum irrigated fruits. They mentioned the possible existence of an osmotic adjustment at fruit or leaf level that could explain these positive responses. Osmotic adjustment, tissue elastic adjustment and decreases osmotic water fraction are processes involved in turgor maintenance and they are of agronomic interest because most growth processes are dependent on positive turgor (Bradford and Hsiao 1982). There are few osmotic adjustment studies on fruit trees species, and these deal primarily with apple (Goode and Higgs 1973, Fanjul and Rosher 1984, Lakso et al. 1984, Yoon 1995) and peach (Young et al. 1981, Young et al. 1982), though information on pear trees is lacking. Knowing whether turgor maintenance responses are present can help in designing a successful RDI strategy for pear orchards.

Pressure-volume analysis was done in this study in order to determine: (a) the ability of cv. 'Barlett' pear trees to develop turgor maintenance processes (Osmotic adjustment, elastic adjustment and changes in osmotic water fraction) in response to spring and summer stress periods; and (b) to compare between spring and summer periods to evaluate a time-of-year effect on these processes.

Material and Methods.

Experimental orchard. The experimental site was located in a semiarid zone with almost no rain in summer 41.38 °N, 0.35 °E, 250 m above sea level belonging to the fields of the Lleida Experimental Station in Corbins, Lleida (Catalunya , Spain).

Thirty 120-liter containers were placed half-buried in 1995 with a spacing of 5x4 m. Containers were arranged in a completely randomized pattern. Pots contain a medium of 3:1 soil and peat (v:v) and 10 cm of gravel in the bottom to avoid a water-holding reservoir. The height of the soil in the container was 35 cm. Two-year-old pear trees (cv. 'Barlett/Mantecosa Hardy/Quince BA-29') were planted at the end of February in containers and 6 field-grown pollenizers (cv. 'Harrow sweet') were evenly placed in the plot. The experiment began two months later in May.

A localized drip irrigation system was installed using 2 pressure-compensating 4 l/h drippers per container in spring, increasing to eight drippers in summer to avoid non-uniformly wetted areas in the container. The system was controlled with a time-clock and solenoid valves. The trees were managed according to common commercial practices, weeds being eliminated manually.

Irrigation Treatments. Four watering treatments were defined: **Control**, **Sp**, **Su** and **Sp&Su**. The **Control** was optimally irrigated taking predawn leaf water potential plus Penman reference evapotranspiration (ET_o) (Doorenbos and Pruitt 1977) as a basis for irrigation scheduling so that the average of -2.8 MPa in **Control** predawn leaf water potential was not allowed to be reached, whereas Penman ET_o was used to estimate seasonal changes in tree water needs. ET_o was obtained from the

nearest automated weather station (Xarxa Agrometeorològica de Catalunya; Generalitat de Catalunya 1994) located at 13 km from the study field. The **Su** treatment received a summer water stress cycle and **Sp** a spring water stress cycle by progressively reducing the water applied (from 100% to 20% of **Control** dose in decremental steps of 20 %) for 27 days in spring and 23 days in summer. During the rest of the year, the **Su** and the **Sp** were irrigated as the **Control**. The **Sp&Su** treatment received two drought stress cycles, one in spring and the other in summer as in **Su** and **Sp**. The Spring cycle ran from Calendar day 129 to 156 inclusive and the summer cycle from 187 to 211. The time elapsed between the end of the spring cycle and the start of the summer cycle was 31 days. The spring cycle was within the Stage I of fruit growth which finished around Calendar day 160 (second week of June) and the summer cycle was within the stage II of fruit development.

General measurements. Data were collected during the whole spring and summer cycle of 1995. Data from treatment **Su** during spring cycle and **Sp** during summer cycle is not reported. During the spring cycle average air temperature and relative humidity was 17.5 °C and 59 % respectively and there was only one day of rainfall (16 mm) at the beginning of spring cycle (Calendar day 129). During the summer cycle there was no rainfall and average temperature and relative humidity was 25.8 °C and 52 % respectively. Volumetric soil water content (θ_v) was determined using a Time Domain Reflectometry system (TDR) (Dalton et al. 1984), according to the equations proposed by Topp et al. (1980). TDR probes consisted of three 0.5 m deep parallel stainless steel rods. Two sets of TDR probes were placed opposite each other in each container. The average of both sets was used to calculate once each week the θ_v . Predawn leaf water potential (Ψ_{pd}) was measured every 4-7 days during the deficit irrigation period using the pressure chamber technique (Scholander et al. 1965) following the recommendations of Turner and Long (1980). Readings were taken with a plant water status console (Model 3005, Soil Moisture Equipment Corporation, Santa Barbara, Calif.). In addition, stomatal conductance (g_s) was determined under light saturating conditions at midday for the same days as Ψ_{pd} using a portable IRGA system (Model ADC LCA-2, The Analytical Development Co. Ltd., Hoddesdon, Herts, U.K.). Stomatal conductance calculations were made according to the equations given by von Caemmerer and Farquhar (1981). After the gas exchange reading, midday leaf water potential (Ψ_{md}) was determined for the same

leaf with the pressure chamber. The oldest fully expanded sunlit mature leaves, were used for all water relations and gas exchange data as well as pressure volume curves as in Meinzer et al. (1990).

Pressure-Volume curves. Pear leaves (six per treatment) were gathered at 0800 HR (local time) and immediately wrapped in plastic bags. The leaves were rehydrated by placing the cut end of the petiole under water, and taken to the laboratory to rehydrate for 2 hours. Care was taken not to overhydrate leaves so as to avoid artefacts in PV analysis associated with plateaus near full turgor (Parker and Pallardy 1987). Pressure-volume curves were generated using the free transpiration method (Hincley et al. 1980) and by means of a pressure chamber as described before using a type II transformation [$1/\Psi_t$ plotted vs. Relative water content (R), where $R = (\text{fresh mass} - \text{dry mass}) / (\text{saturated fresh mass} - \text{dry mass})$] (Tyree and Richter 1981). Periodic measurements of fresh weight and leaf water potential (Ψ_t) were taken until values of -4.0 MPa were reached. The leaf was wrapped in a plastic bag and moist cheesecloth before being placed in the chamber (Hsiao 1990). The actual fresh weight for each pressure determination was assumed to be the weight immediately prior the insertion into the chamber. The difference between leaf weight after and before insertion was never more than 2 mg. Air pressure in the chamber was increased at a rate not higher than 0.02 MPa s^{-1} . Gas was released from the chamber at the same rate to avoid damage to the leaf cells which may occur at higher rates (Kikuta et al. 1985). The initial Ψ_t was always between -0.6 and -0.15 MPa. Turgid fresh weight (TW) was calculated as in Kubiske and Abrams (1990) by linear regression of the data clearly above turgor loss point between balance pressure and sample fresh weight, and extrapolating the line until $\Psi_t = 0$. One single leaf was used to depict each curve and two leaves were managed at the same time, 4 hours being required to determine a whole curve. Four to six points along the linear region were obtained for each sample.

The turgor loss point was determined with a graphical analysis and with the aid of a sequentially fitting regression line beginning with the last 3 data points and adding more points until the goodness of the fit evaluated as of the R^2 lineal regression coefficient was maximal. After the Pressure-volume curve generation was complete, leaf surface was determined by using an area meter (Delta-T device, England). Specific leaf weight (SLW) and Turgid weight / Dry weight ratio (T/D) were obtained after drying

samples for 48 hours in the oven at 70°C. The parameters derived from each curve were: osmotic water potential at full turgor (Ψ_{π}^{100}), osmotic water potential at turgor loss point (Ψ_{π}^0), relative water content at turgor loss point (R_0), slope of Ψ_{π} vs. R (S) and symplasm water fraction at full turgor (R_s) (Turner, 1988). The average tissue elasticity (\mathcal{E}_{avg}) integrated over the full range of positive turgor, was estimated assuming a linear relationship between turgor potential (Ψ_p) and R (Wilson et al. 1979).

$$\mathcal{E}_{avg} = \Psi_{\pi}^{100} / (100 - R_0).$$

Pressure-volume curves for the **Control** treatment were done at the beginning and end of each cycle, and at the time between cycles. Determinations for all treatments were carried out at the end of both stress cycles. Additionally, a test was performed on 25th July comparing mature summer leaves that were fully expanded in April with leaves that were fully mature but still expanding in early June in order to check for a leaf age effect.

Statistical analysis. There were four replicate pressure-volume curves per treatment and five containers per treatment. Statistical analyses of variance including Duncan's multiple range test (SAS Institute Inc. 1988), were performed for treatment comparisons. Treatment differences were considered statistically significant at $P < 0.05$.

Results.

The development of plant water stress due to irrigation treatments is evident from the changes in θ_v , Ψ_{pd} and g_s over time. All the parameters in the stressed treatments decreased as the water applied was being limited (Fig 1A, B, C). Water stress was intended to be imposed gradually, although in **Sp** and **Sp&Su** leaves Ψ_{pd} decreased in an exponential fashion during the spring cycle. This was mainly due to cloudy weather during the first part of the spring cycle which delayed the development of water stress for the first few days. During summer, the imposition of water stress was somewhat more linear. The minimal Ψ_{pd} values reached in both cycles were similar, about -1.8 MPa in the spring cycle and -2.0 MPa in the summer cycle, except for treatment **Sp&Su** which only reached -1.5 MPa in summer. Vegetative growth suppression produced in spring for **Sp&Su** (data not shown) probably limited tree water consumption

and soil water depletion in **Sp&Su** (Fig 1B). Stomatal conductance showed a tendency to decrease as water stress developed until minimal values were reached. These values corresponded to an apparent leaf wilting at the end of both drought cycles (Fig 1C). The low g_s values experienced by the **Control** in Calendar day 150 were probably associated with the relatively low temperatures that day (23.5 °C at time of measurement).

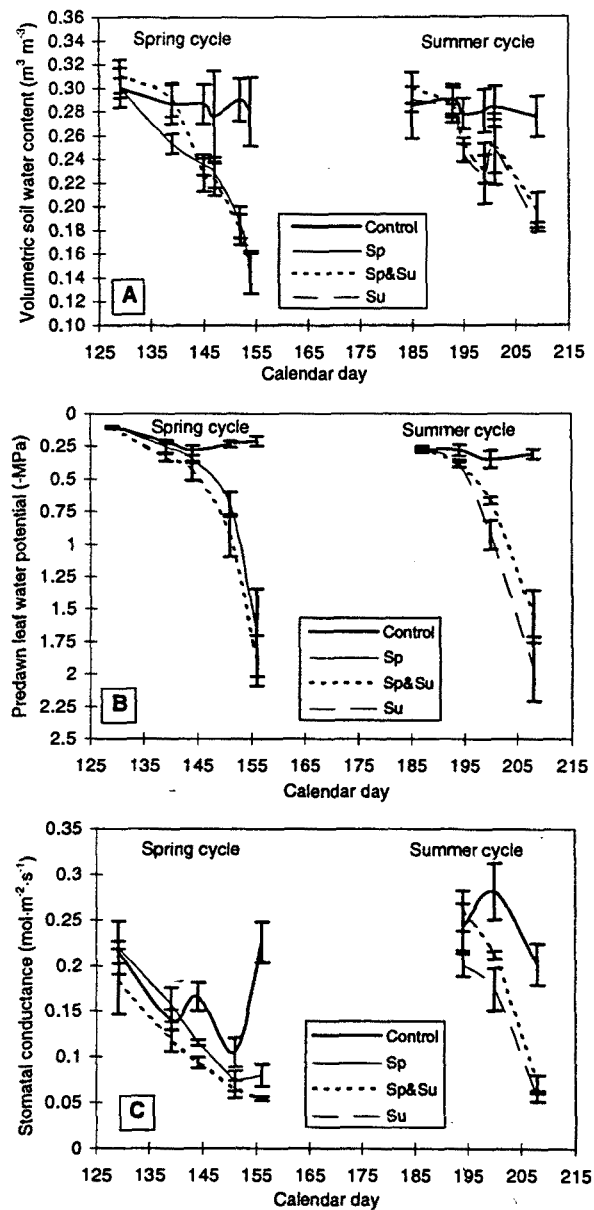


Figure 1. Seasonal patterns of soil water content (θ_v) (A), predawn leaf water potential (Ψ_{pd}) (B) and stomatal conductance (g_s) (C), in response to different irrigation treatments: Control (coarse solid line), Sp (thin solid line), Sp&Su (dotted line) and Su (thin dashed line). Bars denote standard error of 10, 5, 10 measurements for θ_v , Ψ_{pd} and g_s , respectively.

Irrigation treatment effects. In the spring cycle no significant differences were detected in any pressure-volume parameters (Table 1). Symplast water fraction rates were as high as 0.56 for the Control (Table 1). On the other hand, during the summer cycle, statistical differences were found for **Rs** and **S** in response to water stress treatments (Table 2). In the summer cycle, **Rs** values tended to be lower for the water stressed treatments with values of 0.42 and 0.36 for **Sp&Su** and **Su** respectively. In addition, estimates of **S** had a propensity to increase for the water stressed treatments (Table 2). Treatment differences in Ψ_x^0 and Ψ_x^{100} were not detected during either cycle (Table 2).

Table 1. Comparison of mean values for pressure-volume parameters and specific leaf weight during spring drought cycle in response to irrigation treatments. Time₀, before deficit irrigation. Time_t, 5 days before end of spring cycle.

Param.	Treat.	Time ₀	Time _t	Pr>F ^z
		mean	mean	
Ψ_x^0 (MPa)	Control	-2.82	-2.85	0.058
	Sp&Su		-3.09	
Ψ_x^{100} (MPa)	Control	-1.96	-2.19	0.897
	Sp&Su		-2.18	
Ro (%)	Control	89.0	87.9	0.633
	Sp&Su		87.5	
$\bar{\epsilon}_{avg}$ (MPa)	Control	18.0	18.0	0.181
	Sp&Su		17.1	
S (MPa/%)	Control	0.0136	0.0085	0.213
	Sp&Su		0.0099	
Rs	Control	0.41	0.56	0.079
	Sp&Su		0.46	

^z ANOVA probability level.

Phenological changes. Seasonal trends were analyzed using data from the Control treatment only (Fig 2). Osmotic water potential at turgor loss point showed the tendency to decrease its values through the year, from -2.8 MPa in spring to -3.3 MPa in summer (Fig 2A). However, Ψ_x^{100} did not show a similar trend, with values being quite steady throughout the season. Estimates of Ψ_x^{100} were about -2.1 MPa with the exception of the first sampling day (Fig 2A).

Table 2. Comparison of mean values for pressure-volume parameters and specific leaf weight during summer drought cycle in response to irrigation treatments. Time₀, before deficit irrigation. Time_t, 4 days before the end of summer cycle.

Param.	Treat.	Time ₀	Time _t	Pr>F ^z
		mean	mean	
Ψ_{π}^0 (MPa)	Control	-3.01	-3.24	0.707
	Sp&Su		-3.32	
	Su		-3.31	
Ψ_{π}^{100} (MPa)	Control	-2.14	-2.33	0.098
	Sp&Su		-2.06	
	Su		-2.08	
Ro (%)	Control	86.1	85.8	0.283
	Sp&Su		86.9	
	Su		86.1	
\bar{C}_{avg} (MPa)	Control	15.4	16.5	0.245
	Sp&Su		16.0	
	Su		14.4	
S (MPa/%)	Control	0.0092	0.0082 b ^y	0.009
	Sp&Su		0.0135 a	
	Su		0.0117 a	
Rs	Control	0.54	0.53 a	0.002
	Sp&Su		0.36 b	
	Su		0.42 b	

^z ANOVA probability level.

^y Means followed by same letter are not significantly different (Duncan, P=0.05).

Relative water content at turgor loss also decreased throughout the season from 89.3 % on the first sampling day to 85.5 % on the last summer sampling day (Fig 2B). Average leaf elasticity showed a clear decrease after day 153, but then seemed to remain constant for the rest of the summer (Fig 2B, C). Parameters such as, S and Rs did not change significantly during the growing season, with the exception of the first sampling day which had higher S and lower Rs (Fig 2 D, E). Specific leaf weight seemed to increase its values from around 11.5 mg cm⁻² in spring to near 13 mg cm⁻² in summer.

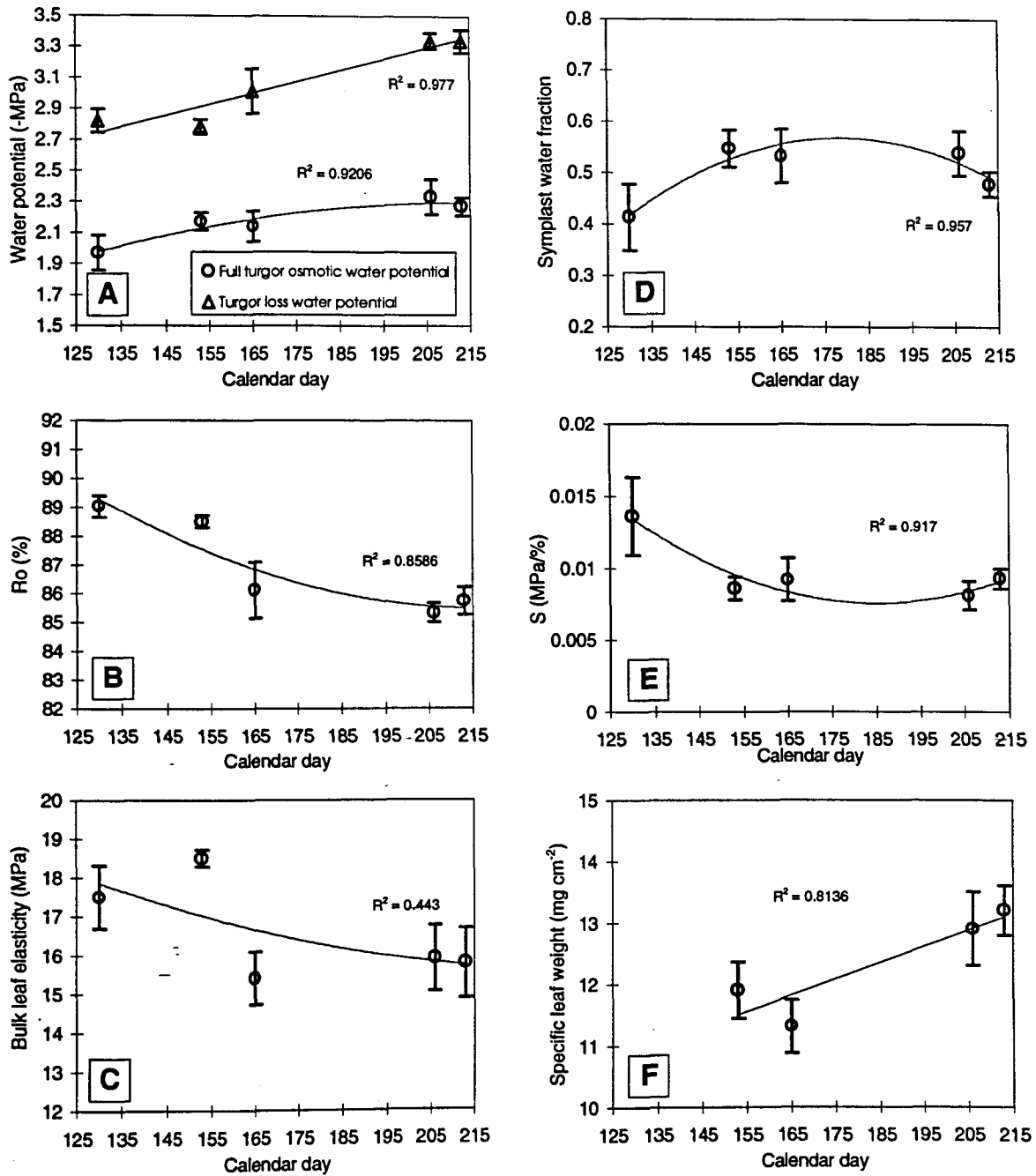


Figure 2. Seasonal evolution of pressure-volume parameters: Full turgor osmotic water potential (circles) (Ψ_x^{100}) and Turgor loss water potential (triangles) (Ψ_x^0) (A), Relative water content at turgor loss point (R_o) (B), Leaf elasticity (ϵ_{avg}) (C), Symplast water fraction (R_s) (D), Slope of the linear region (S) (E) and Specific leaf weight (SLW) (F), under well watered conditions (Control). Bars denote standard error of 4 determinations.

Discussion.

The R_s values shown for the Control were around 0.5. It seems quite odd that half the water in the leaf is located in the apoplasm. Nevertheless, similar values have been reported in *Rosa hybrida* L. (rose) (Augé et al. 1986) and *Ceratonia siliqua* L. (carob) (Nunes et al. 1989). Urban et al. (1993) also obtained similar values in rose and pointed out the hypothesis of Santakumari and Berkowitz (1989) which stated that macromolecules other than cellulose could be associated with these high water percentages.

The Sp&Su treatment during the spring cycle seemed to have little effect on the turgor maintenance process and only a slight decrease in symplast water fraction was detected in comparison to the Control, though it was not statistically significant (Table 1). On the other hand, changes in R_s in the summer cycle were more apparent than in the spring cycle (Table 2). The Sp&Su showed a reduction of 32% in R_s and a 40% increase in S in summer; the Su treatment showed similar trends. A decrease in R_s coupled with an increase in S is regarded as a tolerance mechanism to water stress, since osmotic water potential falls at higher rate as R decreases because of higher S (Radin 1983). As a consequence of this coupled mechanism, osmotic water potential of the water stressed treatment resulted more negative than the Control for R values lower than the point where the Control and water stressed treatment linear region cross (Fig 3). This could have led to an increase in water uptake for water stressed treatments in the summer cycle as a result of a higher potential gradient through the plant. Since this crossover point was found near R_0 (Fig 3), this advantage would only be operative at drought stress levels that induce leaf wilting (Fig 3). However, the physiological impact of this would not be particularly advantageous if turgor is zero. A decrease in R_s seems to be a mechanism which is not uncommon during drought stress episodes and has been reported in species that do not exhibit osmotic adjustment through active solute accumulation, such as carob (Nunes et al. 1989), *Pseudotsuga menziesii* (Mirb.) Franco (Joly and Zaerr 1987) and *Acer rubrum* L. (Nash and Graves 1993).

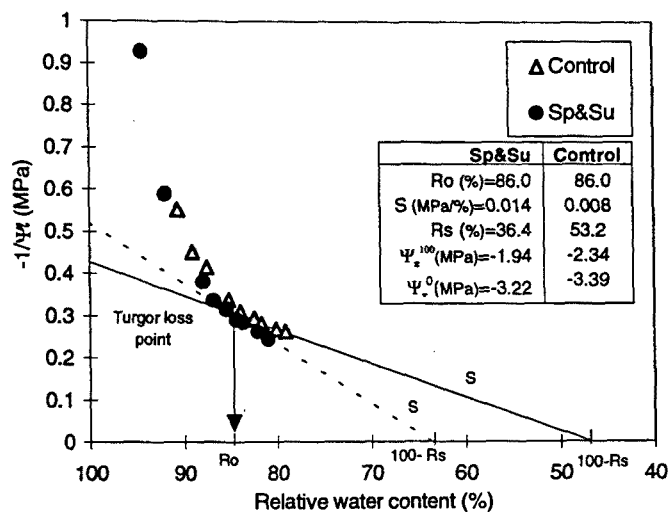


Figure 3. Pressure-volume curves for two leaves belonging to Sp&Su (triangles) and Control (circle) irrigation treatments respectively for the summer cycle, showing different symplast water fraction (Rs) and slope of the linear region (S) characteristics.

The water stress treatments did not show a tendency to decrease Ψ_{π}^{100} either in the spring or the summer cycle, which is indicative of lack of osmotic (Flower and Ludlow 1986). This contrasts with other fruit trees like apple (Lakso et al. 1984, Fanjul and Rosher 1984), *Juglans nigra* L. (black walnut) (Parker and Pallardy 1985) and *Prunus cerasus* L. (cherry) (Ranney et al. 1991) that show decreases of Ψ_{π}^{100} in response to water deficits. Perhaps, pear leaves are genetically incapable of actively accumulating solutes. In addition, osmotic adjustment response seems to be mediated by the capacity for generating new assimilates (Hinckley et al. 1980, Morgan 1984, Augé et al. 1990). Thus a depression in photosynthesis due to water stress could have limited the accumulation of new assimilates since mature leaves are usually incapable of using imported sugars (Dickson and Isebrands 1991). Absence of osmotic adjustment has also been found in *Pyrus serotina* Rehd. (asian pear) (Behboudian et al. 1994), even though the high genotypic variability of this characteristic (Parker and Pallardy 1985, Robichaux et al. 1986) does not enable us to make inferences at the same genus level. On the other hand, young leaves

use imported sugars. In fact, osmotic adjustment has been reported in expanding peach leaves, whereas in mature leaves it has not been detected (Steinberg et al. 1989, Rieger 1995). Therefore, the existence of osmotic adjustment in young expanding pear leaves, is a possibility that cannot be ruled out.

Turner et al. (1987) reported that decreases in turgid weight/dry weight ratio (T/D) were accompanied by osmotic adjustment. In this study, changes in T/D were not detected as a consequence of water stress treatments.

It has been pointed out that water stress has to be imposed slowly in order to allow osmotic adjustment to develop (Turner and Jones 1981). Positive osmotic adjustment responses have been found in other species after 21 days of water stress (Augé et al. 1990). In our research water stress was imposed over a period of twenty days, imitating what could happen in the field. Therefore, it is clear that the lack of osmotic adjustment was not due to a time component.

The levels of Ψ_x^0 decreased steadily from spring to summer (Fig. 2A). The reason for this decrease was apparently not related to Ψ_x^{100} values, which did not change significantly (Fig. 2A). Other parameters such as S and Rs did not seem to be involved in the seasonal variation in Ψ_x^0 , as their values remained relatively constant during the experiment (Fig. 2D, E). Phenological changes in Rs and Ψ_x^{100} were somewhat inversal to S. However, Ro showed a decrease in its values throughout the season (Fig. 2B, C), which would suggest that an ontogenic change in leaf elastic properties was responsible for the decrease in Ψ_x^0 . In fact, $\bar{\epsilon}_{avg}$ and Ro are usually related as they both describe elastic properties of tissues (Parker and Pallardy 1985). Thus, this relationship between decreases in Ψ_x^0 and Ro from spring to summer could be regarded as an acclimation process, because it may help in maintaining the physiological productive process. Lakso et al. (1984) reported a good relationship between Ψ_x^0 and leaf water potential to cause stomatal closure, in apple. When plotting Ψ_p derived from the pressure-volume curves vs. midday leaf water potential (Ψ_{md}), very little in the way of irrigation treatment effect was shown (Fig 4). However, there was a clear shift towards maintenance of slightly higher Ψ_p values at a

given Ψ_{md} from spring to summer, and this could be associated with the lower summer values of Ψ_x^0 and R_o (Fig 4).

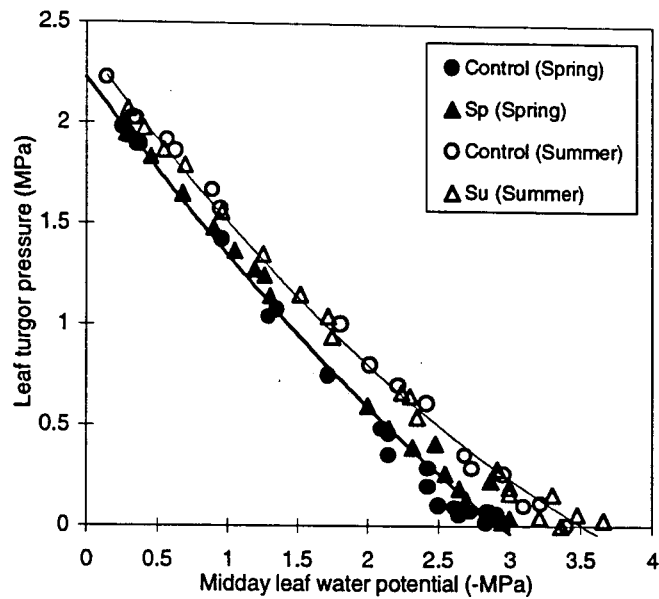


Figure 4. Relationship between leaf turgor pressure and midday leaf water potential in response to irrigation treatments and time of the year. Spring in closed symbols and summer in open symbols. The Control treatment is denoted with a circle and the Sp and Su treatment with a triangle.

It is likely that these seasonal differences in Ψ_x^0 and R_o are due only to a leaf age effect, as leaves sampled during summer and spring were already fully expanded at the end of April. The seasonal increase in SLW seems to confirm the presence of an age effect on leaf characteristics (Andersen and Brodbeck, 1988) (Fig 2F). However, a test performed on 25th July comparing mature leaves that were fully expanded in April with leaves that were still expanding in early June, showed no significant differences in pressure-volume parameters (Table 3). Thus, an environmental effect from spring to summer seemed to be the main cause of this Ψ_x^0 evolution.

Table 3. Comparison of parameters obtained from pressure-volume curves at 25th of July, between Control leaves that were recently expanded in April and June.

Parameter	Pr>F ^z	April leaf	June leaf
Ψ_x^0 (MPa)	0.755	-2.33	-2.27
Ψ_x^{100} (MPa)	0.597	-3.31	-3.34
Ro (%)	0.999	85.75	85.75
ϵ_{avg} (MPa)	0.593	16.47	15.78
S (MPa/%)	0.321	0.0081	0.0093
Rs	0.219	0.53	0.48

^zAnova probability level.

In summary, responses of pressure-volume parameters in pear leaves showed a developmental change, decreasing Ψ_x^0 and **Ro** from spring to summer, whereas a decrease in **Rs** occurred in response to summer water stress. Whilst decreases in **Ro** would be beneficial by delaying turgor loss during summer, **Rs** decrease response to water stress in summer would only be useful when turgor loss was very close, and thus when the effect of water stress on fruit growth would already be severe. Our results showed that the higher fruit growth of RDI trees after a deficit irrigation period reported in 'Barlett' pear (Mitchell et al. 1984) did not appear to be supported merely by turgor maintenance process at leaf level. Therefore, RDI must initiate another physiological process responsible for maintenance of fruit growth. Perhaps, osmotic adjustment at fruit level as has been reported in asian pear (Behboudian et al. 1994), should be analyzed in order to understand the mechanisms that improve fruit growth of RDI pear trees.

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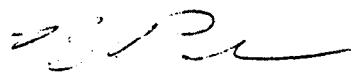
Dr. Jordi Marsal
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Dear Dr. Marsal

I would like to publish a slightly edited version of your revised paper "Effects of water stress cycles on turgor maintenance processes in pear leaves (*Pyrus communis* L.)" in an early spring 1997 issue of *Tree Physiology*. I think some editing is necessary because one or two of the sentences are still a bit awkward. Page proofs of the article and a reprint order form will be mailed to you at the end of the year.

Thank you for the disk.

Yours sincerely



Rozanne Poulson, Ph.D.
Editor

5. Pear Fruit Growth Response to Regulated Deficit Irrigation in Isolated Trees.

PEAR FRUIT GROWTH RESPONSE TO REGULATED DEFICIT IRRIGATION IN ISOLATED TREES.

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Keywords. *Pyrus communis*, stem water potential, fruit volume.

Abstract. The effect of Regulated Deficit Irrigation (RDI) on pear fruit growth was analyzed for pear trees (*Pyrus communis* L. 'Barlett') grown in 120 l. containers. Two irrigation treatments were applied. The **Control** treatment was watered to non-stressful conditions using stem leaf water potential and Penman ETo as a guide. The **I-RDI** treatment (Regulated deficit irrigation treatment in isolated trees) received 0.5 of control dose from calendar day 129 to 152, which is within stage I of pear fruit growth. After day 152 **I-RDI** was irrigated as **Control**. During the deficit period, the increase in fruit volume was lower in **I-RDI** than **Control**. Thereafter, when full irrigation was resumed and during the following three weeks, the increase in fruit volume was higher in **I-RDI** than **Control**. Nevertheless, this compensatory growth did not lead to equal average fresh fruit mass at harvest. The possible factors that could have induced this lower fruit growth in **I-RDI** are discussed.

Introduction.

Regulated deficit irrigation (RDI) (Chalmers et al., 1981) has been reported to be a successful irrigation management in 'Barlett' pear orchards (*Pyrus communis* L.) (Mitchell et al., 1989). With this technique excessive tree growth was controlled without negatively affecting, or even enhancing, fruit growth when deficit irrigation was applied during stage I of fruit development (Mitchell et al., 1989). One of the keys to this success is related to the fact that fruits seem to grow faster after a water stress episode. Published examples are cited for *Prunus persica* (L.) Batsch (peach) (Chalmers et al., 1981), pear (Chalmers et al., 1986), *Pyrus serotina* Rehd. (asian pear) (Behboudian et al., 1994) and *Citrus paradisi* Macf. (grapefruit) (Cohen and Goell, 1988). A reason for these fruit responses has been attributed to fruit osmotic adjustment (Behboudian et al., 1994; Mill et al., 1996). On the other hand, better production has been traditionally related to crop factors derived from the suppression of excessive vegetative growth such as: limitation to fruit growth by excessive canopy shade or low formation of flower buds with loss of productivity during the following year (Guilivo and Xiloyannis, 1988; cited by Faust, 1989). Whereas process related to leaf acclimation to water stress during RDI period in pear seem to be more important for tree survival than for maintaining productive rates (Marsal and Girona, 1997).

Under mediterranean conditions, with recurrent drought cycles and scarcity of water resources, there is an increasing interest in saving water. Stage I of 'Barlett' pear fruit growth takes place during the transition of low (April) to high evaporative demand season (from May to August) and commonly lasts about 65 days, which matches with the 7 to 9 weeks of fruit cell division from full bloom (Westwood, 1976). Under these conditions, the amount of water that can be saved becomes greater and economically more important as the weather becomes drier. It is important, for this, to broaden the knowledge in which RDI actions can be carried out with some guarantees. If the reason of a fruit recovery after RDI has to do mainly with intrinsic physiology of fruit growth, then the apparent success in application of RDI techniques would be reproduced in more generalized conditions than for uniquely vigorous high density orchards. This experiment has been carried out on isolated trees in which crop interactions related to excessive shading are suppressed, therefore eliminating the advantages of high plant density on RDI effect and enhancing the individual action of fruit growth behaviour on final yield.

Material and Methods.

Experimental orchard. The experimental site was located in a semiarid zone 41.38 °N, 0.35 °E, 250 m above sea level, with almost no rain in summer. The study field belong to Estació Experimental de Lleida in Corbins, Lleida (Catalunya, Spain).

Thirty 120-litre containers were placed half-buried in 1995 with a spacing of 5x4 m. Containers were arranged in a completely randomized pattern. Pots contain a medium of 3:1 soil and peat (v:v) and 10 cm of gravel in the bottom to avoid a water-holding reservoir. The height of the soil in the container was 35 cm. Two-year-old pear trees (cv. 'Barlett/Mantecosa Hardy/Quince BA-29') were planted at the end of February 1995 in containers and 6 field-grown pollenizers (cv. 'Harrow sweet') were evenly placed in the plot.

During 1995, trees were used to study leaf physiological response to both a spring and summer drought cycle. This previous experience served to establish the boundaries of plant water stress for the local conditions. Non-stressful conditions were established by relating stomatal conductance with plant water status measured by pressure chamber (leaf water potential and stem water potential at midday) during spring and summer conditions. Stem leaf water potential decreased in a more proportionally linear fashion with the decline in stomatal conductance and also showed less variability than the relationship of leaf water potential vs. stomatal conductance. Maximum stomatal conductance values were obtained at values around -0.8 MPa showing lower dependence on climatic conditions for midday stem water potential (Marsal et al., 1996). According to this, stem water potential at midday was adopted to help in scheduling irrigation. The current study began in May 1996.

A localized drip irrigation system was installed using 2 pressure-compensating 4 l/h drippers per container in spring, increasing to eight drippers in summer to avoid non-uniformly wetted areas in the container. The system was controlled with a timer and solenoid valves. The trees were managed according to common commercial practices, weeds being eliminated manually.

Design of the experiment. Two watering treatments were defined: **Control**, and **I-RDI**. The **Control** was irrigated under non-stressful conditions taking midday stem leaf water potential (Ψ_{stem}) plus Penman reference evapotranspiration (ET_o) (Doorenbos and Pruitt 1977) as a basis for irrigation scheduling. These parameters were used so that the average of -0.8 MPa in Ψ_{stem} (or -0.25 MPa in Ψ_{pd}) of **Control** was not allowed to be reached, whereas Penman ET_o was used to estimate seasonal changes in tree water needs. ET_o was obtained from the nearest automated weather station (Xarxa Agrometeorològica de Catalunya; Generalitat de Catalunya 1994) located 13 km from the study field. The **I-RDI** treatment (Regulated deficit irrigation treatment in isolated trees) was irrigated as **Control** except for the deficit irrigation period when a 50% reduction of the **Control** regime was applied. The deficit irrigation period was elapsed between day of the year 129 (9th of May) and day 152 (1st of June). This was within the Stage I of fruit growth which finished around Calendar day 160 (second week of June). Full bloom occurred in the first week of April (day of the year 95). Harvest was slightly advanced and took place on 3rd of August. **I-RDI** containers were partially covered with plastic only during the deficit period to minimise rain intake.

Twenty-two trees were selected for homogeneity in fruit load and randomly assigned to each irrigation treatment. A completely randomized design was used. Statistical analyses of variance including Duncan's multiple range test (SAS Institute Inc. 1988) were performed for treatment comparisons. Treatment differences were considered statistically significant at $P < 0.05$.

General measurements. Data were collected from 9th of May until harvest date. During the deficit period average air temperature and relative humidity was 17.2 °C and 67 % respectively. Rainfall occurred at the beginning and end of the deficit period with an average of 20 mm (Fig 1). During stage II of fruit development there were several rainfall days (Fig 1). Average temperature and relative humidity were 26.4 °C and 61.3 %, respectively. Volumetric soil water content (θ_v) was determined using a Time Domain Reflectometry system (TDR) (Dalton et al. 1984), according to the equations proposed by Topp et al. (1980). TDR probes consisted of three 0.5 m deep parallel stainless steel rods. Two sets of TDR probes were placed opposite each other in each container. The average of both sets was used to calculate

the θ_v once a week. Midday stem leaf water potential (Ψ_{stem}) and midday leaf water potential (Ψ_{mid}) were measured almost every week. Predawn leaf water potential (Ψ_{pd}) was measured 4 times during the deficit irrigation period and 3 times during stage II. Leaf water potential was determined by using the pressure chamber technique (Scholander et al. 1965) following the recommendations of Turner and Long (1980). Readings were taken with a plant water status console (Model 3005, Soil Moisture Equipment Corporation, Santa Barbara, Calif.). The oldest fully expanded sunlit mature leaves were used for leaf water potential measurements. To determine Ψ_{stem} , 4 hours before the reading, leaves located near the trunk were enclosed inside a plastic bag covered with aluminium foil. Stomatal conductance (g_s) and net CO_2 assimilation rate (A) were determined under light saturating conditions at midday using a portable IRGA system (Model ADC LCA-2, The Analytical Development Co. Ltd., Hoddesdon, Herts, U.K.). Stomatal conductance calculations were made according to the equations given by von Caemmerer and Farquhar (1981).

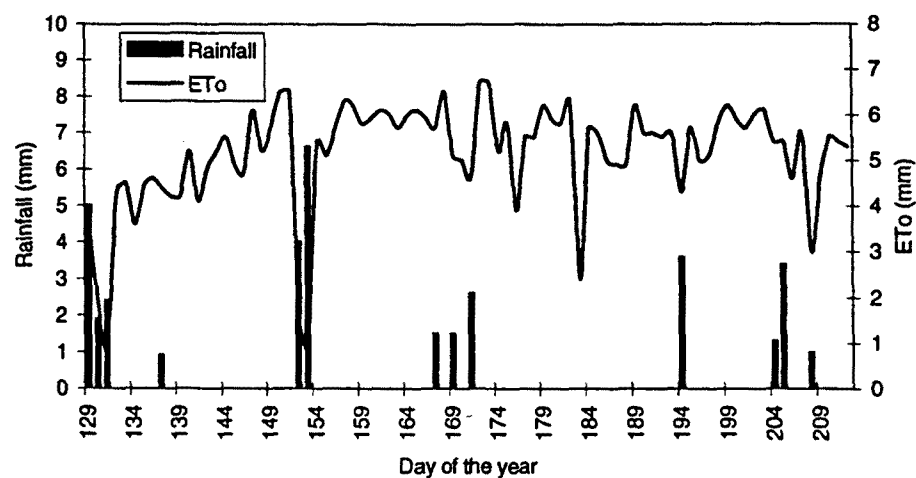


Figure 1. Daily rainfall and reference evapotranspiration during the time of physiological measurements.

Fruit and vegetative growth measurements. Trunk circumference measurements were made on 4th August 20 cm above the graft union. To evaluate if the different water supply on stage I had any effect on shoot growth, six non-terminal shoots per tree were randomly tagged. The length of these shoots was

measured weekly from day 131 until day 156. Shoot growth phase ended around 1 week before the end of stage I of fruit development. A second growth flush occurred in a very weak fashion during the first fortnight of July and only affected watersprouts whereas lateral tagged shoots did not experience further elongative growth.

Fruit growth was evaluated by measuring, every week, the fruit length (Le) and maximal width (Wi) of 8 tagged fruits per tree, using digital calipers. Due to a successive fruit drop produced by strong wind episodes during June and July (90 km/h), only 37 of the total tagged fruits for the Control and 44 for the I-RDI reached harvest. Fruit volume was estimated by the contribution of fruit length and fruit width, assuming the fruit to have a composite shape of a semisphere (bottom region) and a truncate cone (upper region) and using $Volume = [(2/3) \cdot \pi \cdot (Wi/2)^3] + [(1/3) \cdot \pi \cdot (Le - Wi/2) \cdot (b^2 + b \cdot Wi/2 + (Wi/2)^2)]$, where the b parameter represents the smaller base of the truncate cone. The value given to b ($b=11.4026$) was obtained by minimizing the square difference between predicted volume and measured volume from an experimental sample of 114 fruits (least-square procedure). The predictions of real volumes obtained by using this formula were of acceptable accuracy in a broad range of values (Fig. 2). At harvest, total fruit fresh mass was measured and fruit dry mass and flesh firmness was evaluated on all tagged fruits. Firmness was measured using a (Fruit Pressure Tester; FT-327; Italy) penetrometer fitted with an 8 mm plunger. For the dry mass, fruits were oven dried at 70 °C. Fruit soluble solids were measured on day 172 on five fruits per treatment and at harvest on 20 fruits per treatment. Total juice was expressed individually and filtered. A portion of the juice was used for the determinations of % soluble solids with (Atago; ATG-1; Tokyo) refractometer.

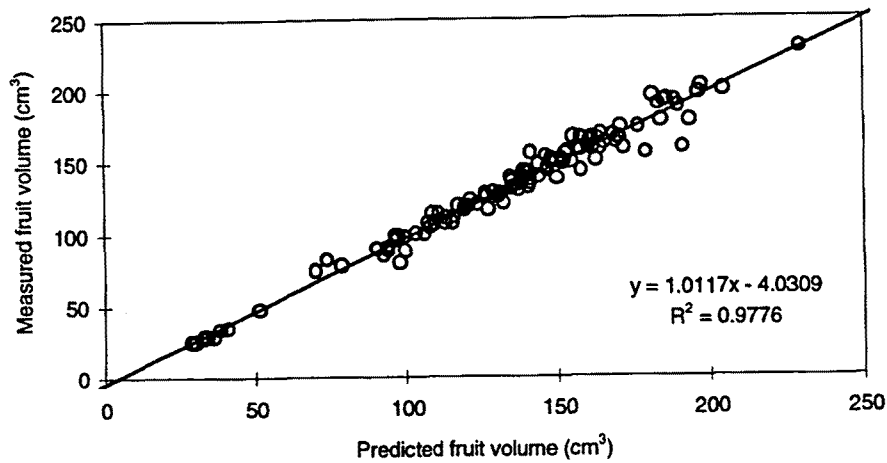


Figure 2. Relationship between predicted and measured pear fruit volume.

Results.

Soil water content was markedly lower in **I-RDI** than in **Control** during the RDI period (Table 1). The use of a plastic cover of **I-RDI** containers allowed the stress to develop during this period. Midday stem leaf water potential indicated that **I-RDI** did have significantly lower plant water status during the deficit period (Fig 3A). Also, Ψ_{pd} and Ψ_{md} showed more negative values in **I-RDI** (Fig 3B, C). Values representative of **I-RDI** during this period (MPa \pm SE) were -0.47 ± 0.094 and -1.41 ± 0.077 for Ψ_{pd} and Ψ_{stem} , respectively. The leaf gas exchange values showed clear differences during the deficit irrigated period; g_s and A were lower for **I-RDI** (Fig 4A, B).

Table 1. Average volumetric soil water content in response to different irrigation treatments at different periods of time ($m^3 \cdot m^{-3} \pm$ standard error).

Period	Control	I-RDI	Probability [*]
Deficit period (May)	0.24 \pm 0.0123	0.145 \pm 0.0082	0.0001
Stage II (June)	0.317 \pm 0.0094	0.344 \pm 0.0071	0.03
Stage II (July)	0.343 \pm 0.0037	0.36 \pm 0.0029	0.0006

^{*} Student's *t* test

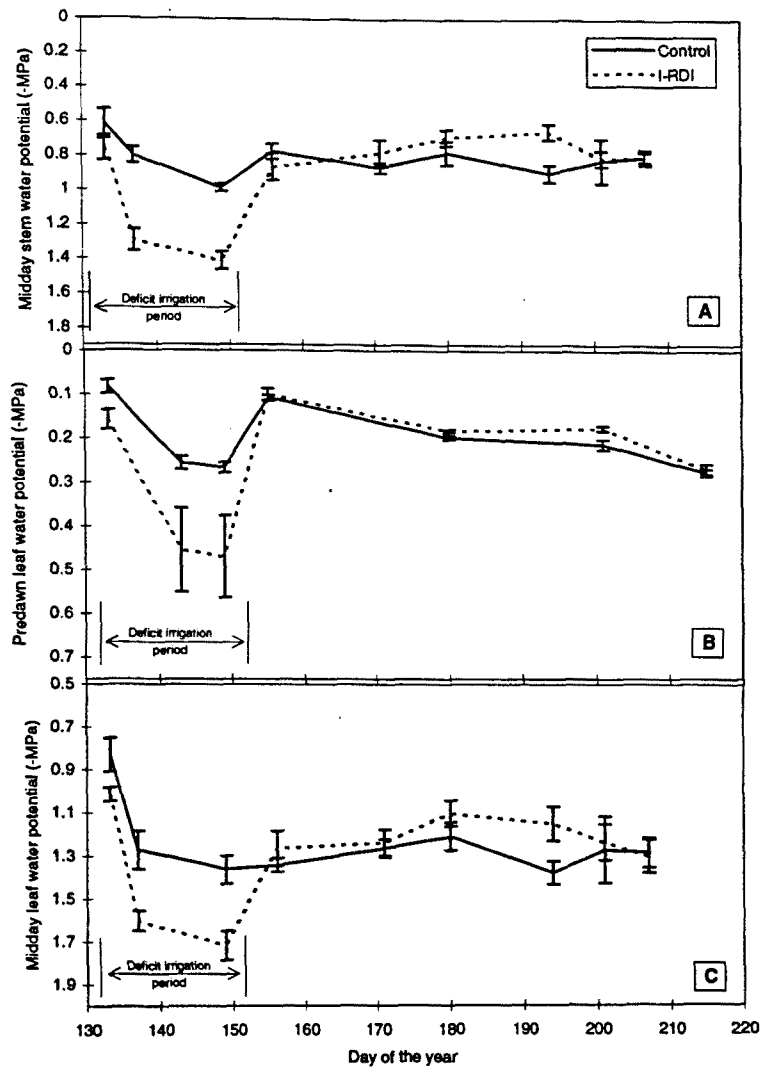


Figure 3. Seasonal patterns of midday stem water potential (A), predawn leaf water potential (B) and midday leaf water potential (C) in response to the irrigation treatments (Solid line represents Control and dotted line I-RDI). Each point is the mean of 11 measurements \pm standard error.

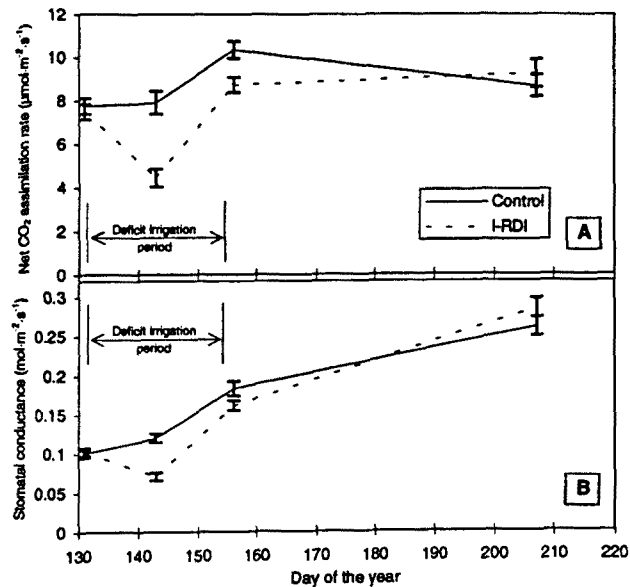


Figure 4. Seasonal patterns of net CO₂ assimilation rate (A) and H₂O stomatal conductance (B) in response to the different irrigation treatments (Solid line represents Control and dotted line I-RDI). Each point is the mean of 11 measurements \pm standard error.

Elongative shoot growth was lower for **I-RDI** (Fig 5). But at harvest time trunk circumference did not show significant differences between both treatments (data not shown). Fruit growth in **I-RDI** was also affected during the deficit period and showed lower increases than **Control**, in fruit volume size, and fruit width, but were not significantly different in fruit length (Fig 6A, B, C).

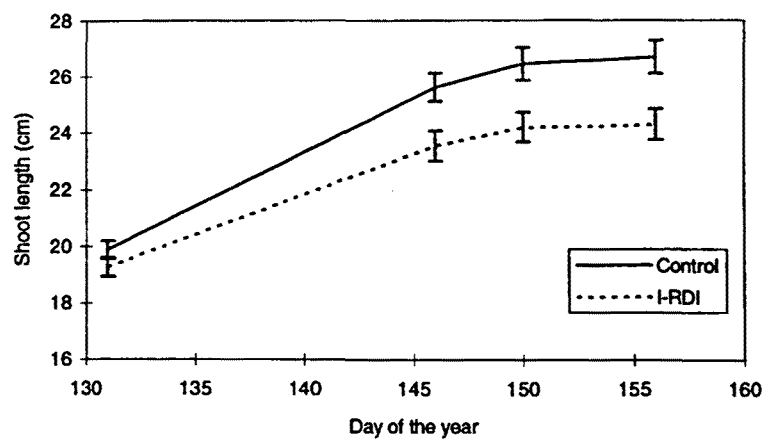


Figure 5. Increase in lateral shoot length during stage I of pear fruit development in response to the different irrigation treatments (Solid line represents **Control** and dotted line **I-RDI**). Each point is the mean of 66 measurements \pm standard error.

After the deficit period, values of θ_v were maintained high for both treatments, though there was a tendency to be slightly higher for **I-RDI** through Stage II. This tendency to present higher values in **I-RDI** was also shown in Ψ_{stem} , Ψ_{pd} , and Ψ_{md} . Fruit volume estimations during stage II, after resumed irrigation, seemed to increase at a slightly higher rate in **I-RDI** than in **Control**; however, in the subsequent weeks, major increases in fruit volume for **I-RDI** were not detected (Fig 6A). Fruit width showed parallel patterns to fruit volume (Fig 6A, B), whereas fruit length patterns during stage II did not seem to be as affected as width by **RDI** treatment and showed more similar values to the **Control** throughout the period (Fig 6C). Fruit firmness was not affected by **RDI** treatment at harvest (Table 2), but **Control** fruits showed significantly higher soluble solids (Table 2).

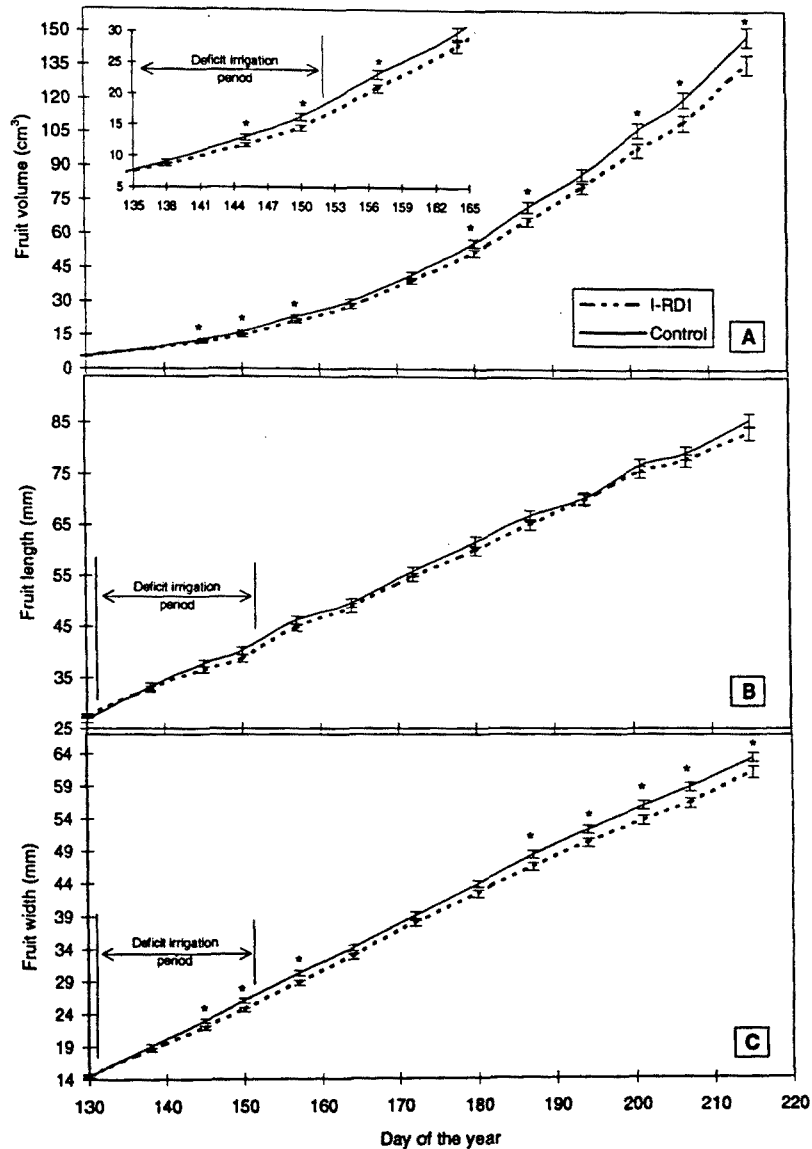


Figure 6. Increase in pear fruit size parameters: estimated fruit volume (A), fruit length (B) and fruit width (C) in response to the different irrigation treatments (Solid line represents Control and dotted line I-RDI). Each point is the mean of 74 and 66 fruit measurements \pm standard error for Control and I-RDI respectively. Points with (*) symbol indicate statistical treatment differences for a Student's *t* test; ($P < 0.05$).

Table 2. Fruit and tree parameters at harvest in response to the irrigation treatments.

Parameter	Control	I-RDI	Probability [*]
Fruit fresh mass (g)	141.1	129.2	0.012
% dry matter	18.03	17.25	n.s. ^y
Firmness (N)	109.7	109.5	n.s.
Soluble solids (%)	12.84	12.46	0.031
Fruit load (# fruits/tree)	7.6	7.2	n.s.
Increase shoot length (cm)	7.56	5.31	0.047
TCSA (cm ²)	12.74	-11.93	n.s.

^{*} Student's *t* test

^y n.s.= not significant at $P < 0.05$

Discussion.

The use of plant water status parameters to schedule irrigation in the way that has been done in this study has been conducted to values of θ_v during the RDI period around $0.24 \text{ m}^3 \cdot \text{m}^{-3}$ for **Control** (Table 1). On the other hand, in summer, θ_v was maintained to values of $0.34 \text{ m}^3 \cdot \text{m}^{-3}$ in order to avoid lower values of Ψ_{stem} and Ψ_{pd} than -0.8 and -0.25 MPa, respectively. This is in agreement with the fact that under high evaporative demand, a more relatively wet soil is required to support plant evapotranspiration (Demmead and Shaw, 1962; cited by McCutchan and Shackel, 1992).

The data show that water stress during the deficit period did develop, plant-based indicators (Ψ_{stem} , Ψ_{pd} , Ψ_{md}) manifested a lower water status though leaf wilting was never reached (Fig 3A, B, C). Photosynthetic values in **I-RDI** descended nearly 40% compared to **Control**, and stomata decreased their conductance in a similar fashion (Fig 4A, B). This information is indicative of the fact that the water stress applied was moderate. As a consequence, shoot growth decreased 30% on **I-RDI** trees (Fig 5). A major reduction occurred during the first ten days of the deficit period when shoot growth was more accentuated (Fig. 5). Afterwards, vegetative activity decreased and a week before the end of stage I, shoot tip buds were apparent in the majority of shoots. Fruit growth was also negatively affected by RDI treatment. Seasonal patterns of fruit size parameters depicted the tendency to show slightly lower values during stage I (Fig 6B, C), but the differences between treatments were clearer in **Wi** and the estimated fruit volume (Fig 6A). Nevertheless, it was not possible to distinguish strictly between real fruit growth and an apparent shrinkage produced by certain level of fruit dehydration as fruit dry mass was not measured during the drought period.

With the application of the full regime after calendar day 156, plant water status of **I-RDI** recovered sharply (Ψ_{stem} , Ψ_{pd} , Ψ_{md}) and maintained its values during stage II (Fig 3A, B, C). The differences between treatments in fruit size during stage I tended to decrease in the following weeks after RDI was discontinued (Fig 6A, B, C). However, **Wi** and fruit volume estimations always had lower averages in **I-RDI** throughout stage II (Fig 6). To a better assesment of these decreases and recoveries, treatment differences in fruit size parameters were normalized for their own size [$100 \times (\text{Control size} - \text{I-RDI}$

size) / (Control size + I-RDI size)]. Seasonal evolution of normalized differences was evaluated (Fig 7A, B and C). The analysis of these parameters showed that the recovery lasted only three weeks after resuming irrigation and did not totally compensate for the differences produced during the drought period (Fig 7A, B and C). This apparent recovery after resumed full irrigation could be partially due to a fruit rehydration. In fact, checking for fruit soluble solids on day 167 (at the end of the recovery period), significant differences were detected between treatments (*t*-Student test, $P < 0.034$); Control and I-RDI soluble solids ($\% \pm SE$) were 9.75 ± 0.088 and 10.06 ± 0.0051 , respectively. Also osmotic adjustment at fruit level as it has been reported in asian pear could be involved in this recovery (Behboudian et al., 1994). After these three weeks (day 172) no further compensatory increases in fruit size were measured in I-RDI (Fig 7A, B and C) and differences in fruit volume were steadily around 8% lower in I-RDI for the rest of stage II (Fig. 7A). As a result, at harvest, I-RDI fruits were significantly lower than Control in fresh mass (Table 2). There is a possibility that water stress during stage I could have affected cell division, thus limiting the potential dimension of pear fruit at harvest. In other studies applying RDI such as in 'barlett' pear (Chalmers et al., 1986) or asian pear (Caspari et al., 1993), no negative effects were detected on fruit growth during the RDI period, and after RDI was discontinued the growth rate of 'barlett' pears in RDI treatment was significantly increased for seven weeks (Chalmers et al., 1986). Fruit maturity evaluated in fruit firmness at harvest (Table 2) was apparently not delayed in I-RDI. Thus superior increases in growth fruit rate for I-RDI should not be expected by delaying the time of harvest.

During stage II, and despite all trees receiving the same amount of applied water, all water status parameters (Ψ_{stem} , Ψ_{pd} , Ψ_{md}) showed the tendency to have less negative values for the I-RDI (Fig 3A, B, C). This phenomenon could be related to soil water content estimates in I-RDI, which also showed a similar tendency to have slightly higher values throughout stage II. Perhaps the reduction exhibited in vegetative growth could have induced a lower tree water use in I-RDI trees (Buwalda and Lenz, 1995). Trees that use more water should exhibit higher depletion in soil water storage, thus lower soil water content should be detected in control trees. In fact, a significant relationship was found between average measured increase in shoot length and the average soil water content during stage II (Fig. 8).

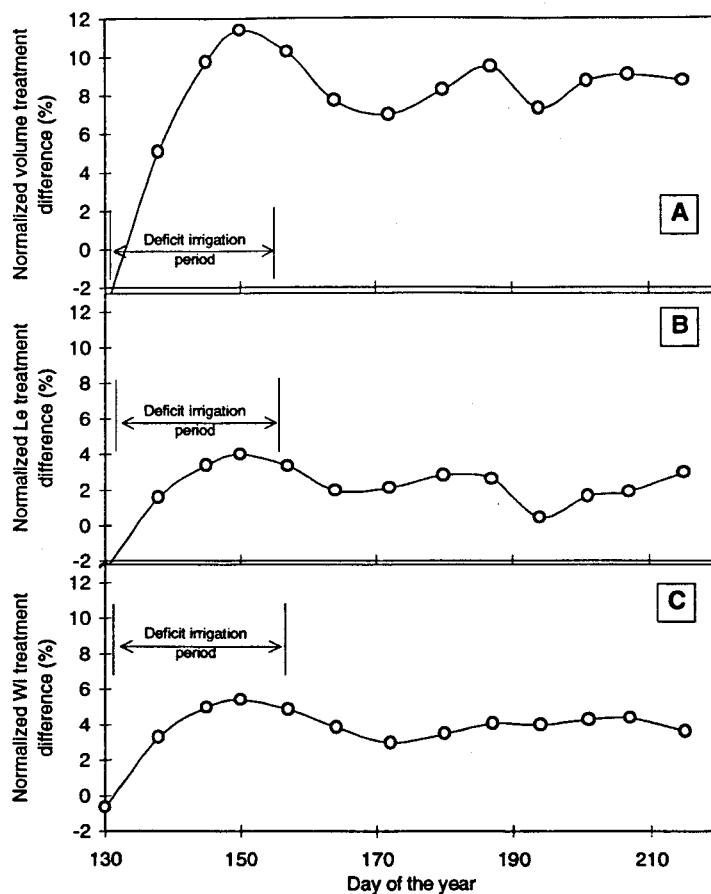


Figure 7. Seasonal patterns of normalized treatment differences in pear fruit size parameters: estimated fruit volume (A), fruit length (B) and fruit width (C) (Solid line represents Control and dotted line I-RDI).

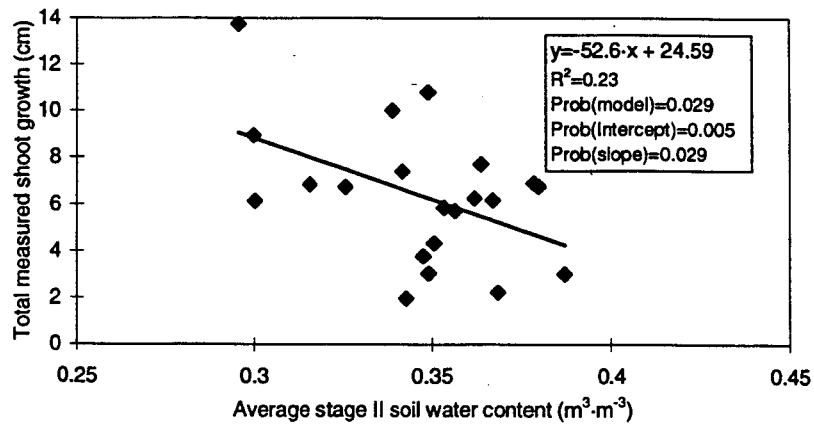


Figure 8. Relationship between the total measured increase in lateral shoot length and the average soil water content during stage II. Each point represents a tree average for each parameter.

Nevertheless, the slightly higher θ_v , Ψ_{stem} , Ψ_{pd} , and Ψ_{md} values in I-RDI were not reflected in higher fruit growth rates, probably because these narrow differences in treatment values were not in the situation of producing limitations to expansive growth. Chalmers et al., (1986) obtained significantly higher values in Ψ_{pd} for the RDI treatment after resuming full irrigation, which seems to reproduce our tendency to show higher leaf water potentials during stage II. However, contrary to our study, they found higher differences between treatments for midday leaf water potential. For instance, the leaf Ψ_{md} values for the Control treatment during stage II were -1.92, -1.79 and -1.56 MPa in chronological order, whereas for the most stressed RDI treatment were much higher -1.69, -1.44 and -1.47 for these same days. This much comparatively better leaf water status of RDI treatment was not found in our study during Stage II (Fig. 3C).

It should be taken into account that in the work of Mitchell et al. (1989), before the RDI treatment commenced, the irrigation was withheld nearly from full bloom in RDI treatments. During the withholding time, in RDI treatments, Ψ_{pd} and Ψ_{md} reached values as low as -0.46 and -1.91 MPa, respectively (Chalmers et al., 1986). The possible advantages and drawbacks of this withholding period cannot be evaluated from the scope of our data.

On the other hand, the negative effects of excessive vegetative growth as regard to canopy competition for light have been avoided, in this study, by using a wide container spacing and grafting a low vigor rootstock. Perhaps under more enhancing RDI conditions (high vigor and tree density) higher water stress levels could have been reached without negatively affecting fruit volume at harvest.

Conclusions.

This study showed that the impact of RDI on isolated trees was negative on fruit size at harvest. The decrease in fruit size during the drought period, though followed by a partial recovery, might have affected the potential for the total fruit growth. Nevertheless, as has been reported in several other studies (Chalmers et al., 1986; Higgs and Jones, 1991), fruit growth was less sensitive to water stress than elongative shoot growth (8% reduction in fruit compared to 30% increase in shoot length in this

study). The negative effects on fruit growth would seem possible to avoid while still reducing shoot growth if the level of water stress applied during the RDI period had been more moderate.

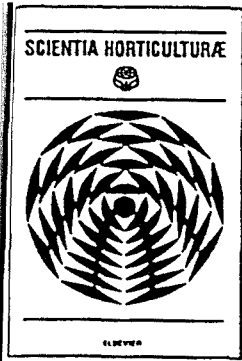


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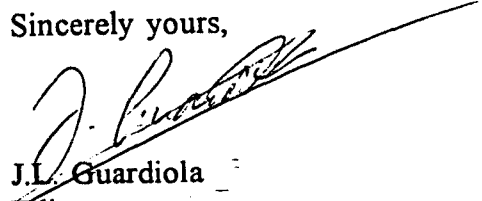
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Dear Dr. Marsal:

Thank you for submitting your article entitled: *Pear fruit growth response to regulated deficit irrigation in isolated trees* by Jordi Marsal and Joan Girona to our Journal.

It will be forwarded to the referees for their comments and you will be informed of their assessment as soon as possible.

Sincerely yours,


J.L. Guardiola
Editor

Ref: 133

Corrigendum

Page 95. Caption of Figure 6: Insted of "...74 and 66 fruit measurements..." should appear "...37 and 44 fruit measurements..."

