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Chapter 6

DEFICIT IRRIGATION AS A TOOL FOR MANIPULATING FLOWERING DATE IN LOQUAT (*ERIOBOTRYA JAPONICA* LINDL.)

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ABSTRACT

A frequent response of fruit trees to deficit irrigation (DI) is a promotion of flowering. This response is often explained because of a lesser competition with exuberant vegetative growth. Here, we report the effects of regulated DI on loquat shoot growth and flowering and discuss the possible mechanisms involved in the promotion of flowering in water-stressed trees. Loquat is a subtropical tree crop that bloom in autumn after a period of summer dormancy. Loquat flowers develop in panicles formed at the apex of the new shoots, therefore shoot growth has to cease before flower initiation can take place. In our experiments, the flowering of fully irrigated trees of 'Algerie' loquat was compared with the bloom in trees undergoing three different levels of DI implemented at post-harvest from mid-June to the end of July. DI levels during these six weeks were: light (50% of the water applied to controls), moderate (25% of the water applied to controls) and severe (no watering). Minor effects due to DI were found on flowering intensity. In contrast, water-stressed trees reached bloom before controls (between 10 and 27 days, depending on treatment). The more severe the water stress was, the earlier the blooming resulted. Blooming advancement was produced despite final shoot length and leaf number remained essentially the same. On the contrary, DI profoundly altered the pattern of shoot growth that changed from a single sigmoid to a double sigmoid. This shift was the result of water stress causing an early, but transitory, cease of growth, which was reassumed up to the length of controls when water deficit ended. Observations carried out under scanning electron and conventional microscopy indicate that panicle initiation occurred days before the fully establishment of summer dormancy, when growth rate in the apical meristem slowed down. The advancements of summer dormancy and panicle initiation correlates well with blooming date advancement. Our results question the hypothesis of resource competition between flowering and vegetative growth and suggest that flowering promotion is the result of a diminished growth rate in the apical meristem due to

hormonal changes that favour the process of flower induction. This theory is coherent with the promotion of flowering in response to growth inhibitors and with the negative effects that gibberellins have on tree blooming. The modification of reproductive phenology by the management of the agricultural water may represent a new avenue for improving profitability in tropical and subtropical fruit crops.

INTRODUCTION

A frequent response of fruit trees to deficit irrigation (DI) is the promotion of flowering. This flowering promotion is often explained in terms of a lesser resource competition with vegetative growth effectively restrained by water deficit in evergreen and deciduous fruit trees (Chaikiattiyos et al., 1994; Behboudian and Mills, 1997). This tree response to DI has been successfully exploited to induce out of season blooming and to increase the levels of flowering in many tropical and subtropical fruit crops (Barbera et al., 1985; Crane, 2004; Grierson et al., 1982; Whiley, 1993; Stern et al., 1998; Bally et al., 2000), among them loquat (Cuevas et al., 2007).

Loquat (*Eriobotrya japonica* Lindl.) is a subtropical evergreen fruit tree of the family Rosaceae, subfamily Maloideae that presents an annual cycle reverse to that of the well-known temperate fruit crops. Loquat rests during summer, blooms in autumn, develops its fruit through winter and ripens them in early spring. Its unusual phenology allows growers to obtain high prices for its fruits, especially for early-season harvests. In previous experiences, we have demonstrated that deficit irrigation is a useful strategy to advance harvest date making the crop more profitable (Hueso and Cuevas, 2007).

As occurred in other pomes, loquat blooms apical; in this species forming terminal panicles in current year wood. Apical flowering requires the end of shoot growth before panicle initiation can take place. This occurs in some moment after a period of summer dormancy poorly characterized. New shoot growth become then both support and competitor of flowering. Same flowering habit applies to others tropical and subtropical fruit crops where the management of shoot growth using different techniques has resulted in increasing levels of flowering (Davenport, 2003; Salazar-García and Vázquez-Valdivia, 1997; Stern and Gazit, 1993). Here, we report the effects of different levels of water deficits on shoot growth and flowering and discuss the possible mechanisms involved in the promotion of flowering in response to the imposed water deficit.

MATERIAL AND METHODS

This experience was carried out in season 2005/06 in an experimental orchard of 'Algerie' loquat trees located at the Experimental Station of Cajamar Foundation "Las Palmerillas", in Almería (SE, Spain). The area presents a semi-arid subtropical climate with an average rainfall of 231 mm and evaporation from an "A" pan (Epan) of 1922 mm per year. Mean annual temperature and humidity is 18ºC and 68%, respectively. Orchard soil is a well-aerated sandy-loam (72.4% sand, 14.6% loam, and 13.0% clay), pH 7.8. Field capacity is 13.4%, while wilting point is 5.1%.

Adult 'Algerie' trees grafted on 'Provence' quince were used for the experiments. The trees are vase-trained and 5 x 5 m spaced. Four irrigation treatments were applied to these trees. First treatment was a control in which trees were fully irrigated with about 40% of Epan measured with a Class A pan placed in the orchard. Next three treatments were different DI strategies in which trees received a 50%, a 25% or 0% of the water applied to controls (treatments W50%, W25%, and W0%, respectively) during a period of six weeks, from mid-June (around 8 weeks after the end of previous harvest) to the end of July. Soil water content in response to treatments was monitored using Watermark (Irrometer Co. Inc.) electrical-resistance blocks. The changes in soil moisture were followed using three sets of sensors, one set per block and treatment, placed at 30, 60 and 90 cm depth. Plant water status in response to the treatments was monitored by measuring stem water potential (Ψst) during the period of deficit irrigation using a Scholander pressure chamber. Six mature leaves per treatment were sampled from the outer part of the canopy at 1.75 m height.

Effects of DI treatments on flowering date, length and intensity, and on shoot growth were analyzed following a randomized complete-block design with three replications per treatment. Each replication consisted of one row of trees hydraulically isolated by placing a plastic film 1 m deep, where most quince roots are restricted. The two central trees of the row were chosen for measurements. Tree phenology was followed on these trees from summer rest to bloom using phenological stages described by Cuevas et al. (1997). Flowering date and length and advancement of full bloom with respect to controls were calculated based on observations carried out twice per week. Bloom intensity was estimated on main shoots and secondary late-formed shoots by the percentage of them forming a terminal panicle in ten randomly chosen shoots of each type per tree. The number of flowers per panicle in main and secondary shoots was counted on four panicles per tree.

New growth was followed by counting the new leaves formed from mid-June to the end of September every five days in ten main shoots per tree. Shoot length was also measured with the same periodicity. Plastochron (i.e. days needed between the formation of two consecutive nodes) was calculated along the growing season.

Flower initiation was dated in the most extreme treatments (control versus W0%) by scanning electron and conventional microscopy. To do so, twenty four terminal buds (four per tree) were sampled weekly from mid-July to mid-November. With the aim to process the most representative and uniform samples for each date, the buds once collected at random were taken to the lab and ordered by size. Then, the four intermediate-sized buds were selected for SEM studies and fixed in 3% glutaraldehyde in phosphate buffer, pH 7.2. Before observation, the buds were partially dissected removing most external bracts under binocular, and subsequently dehydrated, critical point dried, sputter-coated with 20 nm gold, and finally observed under a Hitachi S-3000N Scanning Electron Microscopy, mostly operated at 15-20 kV. The remaining twenty buds, also partially dissected, were fixed in a mixture of formalin-glacial acetic acid-alcohol (FAA), dehydrated in tertiary butyl alcohol and ethanol series, and embedded in paraffin wax. The embedded buds were then sectioned at 10 μm using a Leica RM 2125RT microtome. Finally, preferred sections were stained with safranin, crystal violet and light green (Gerlach, 1969).

RESULTS

Deficit Irrigation Effects on Soil and Plant Water Content

Controls trees received circa of 6800 m^3 per ha of water along the season; 990 of them applied during the six-week experimental period. During this time, W50%, W25% trees 450 and 259 m^3 per ha, respectively, while W0% trees were not irrigated at all. Rainfall during the season accounted for a total of 229 mm; there was no rain during the DI period. DI treatments progressively diminished soil water content during this period (Figure 1). The rest of the year water soil content did not differ among treatments (data not shown). At the end of the period of water shortage, soil around W0% trees had Ψm values of -172 kPa, -127 kPa and -123 kPa at 30, 60 and 90 cm depth, respectively while in W25% soil reached Ψm values of -26 kPa at 30 cm, -57 kPa at 60 cm and -83 kPa at 90 cm. Water content of soil around W50% trees was kind of similar to that observed for W25% (-17 kPa, -77 kPa and -97 kPa, for 30, 60 and 90 cm depth, respectively). In contrast, soil around control fully irrigated trees was close of field capacity showing Ψm records between -10 and -20 kPa, along the season. The reduction of soil water moisture in moderate and severe DI treatments translated into the plant, but seemed not to affect to W50% trees. Controls and W50% presented similar Ψst values at the end of July (Ψst=-1.07 MPa for controls versus -1.37 for W50%). More negative records were reached at the end of the water shortage period in W25% and W0% (Ψst=-1.74 and -2.07 MPa, respectively). Differences were significant between these two groups.

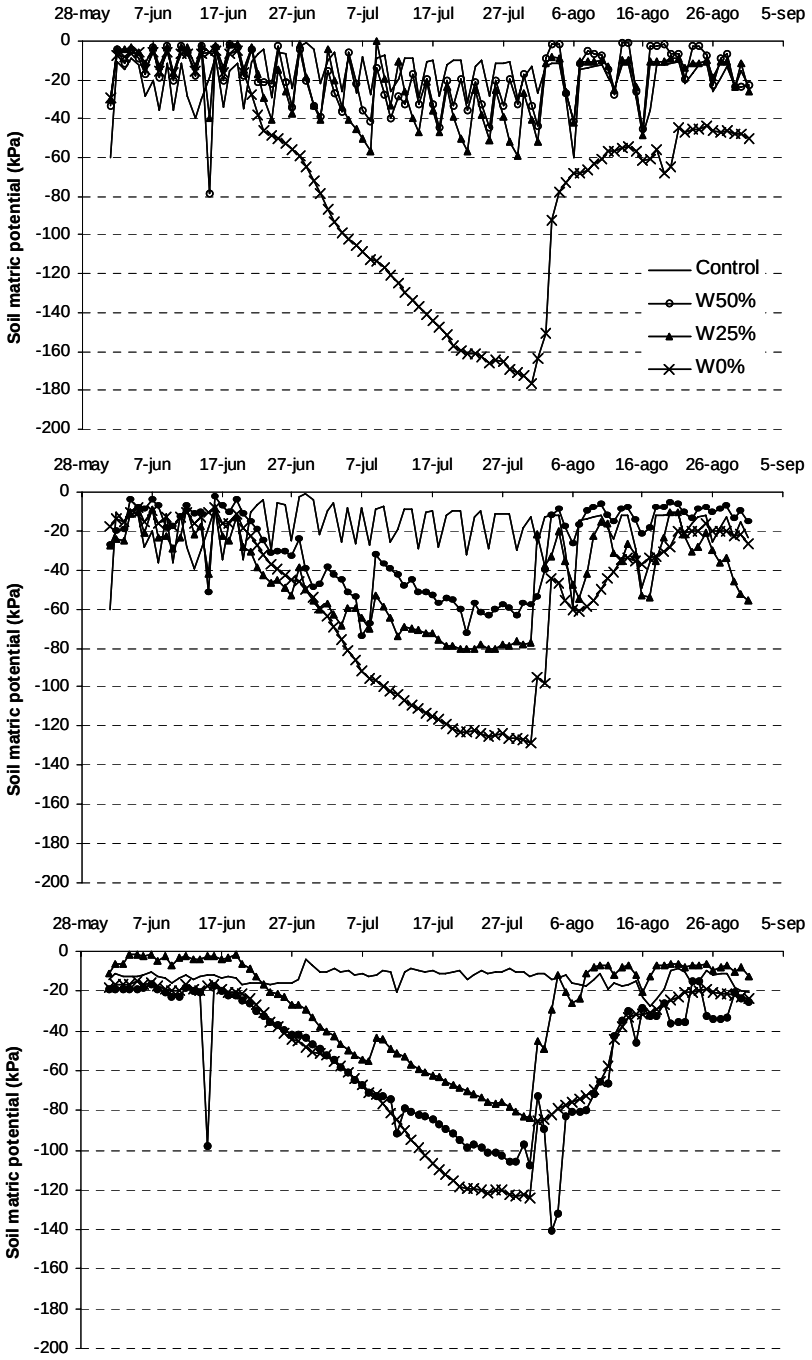

Figure 1: Soil matric potential at 0.3 m (top), 0.6 m (center) and 0.9 m depth (bottom) during the six week experimental period in control full irrigated trees and trees suffering different levels of water deficits.

Deficit Irrigation Effects on Flowering

The alteration of soil and plant water status modified reproductive phenology of 'Algerie' loquat. At this regard, all deficit irrigation treatments promoted earlier flowering. However, the more severe the water stress was, the earlier the blooming resulted. Therefore, the earliest blooming took place in W0% trees (October 22nd, 27 days ahead of control trees). A noticeable advancement in full bloom also occurred in W25% trees, which flowered on October 28th, 21 days before than controls. W50% reached full bloom on November 8th, ten days before control trees (Figure 2). Control trees bloomed on November 18th. The average full bloom date of these trees is November 23rd (9 years controlled). Water-stressed trees not only reach full bloom date earlier than control trees, but they also opened their first flowers before (Figure 2).

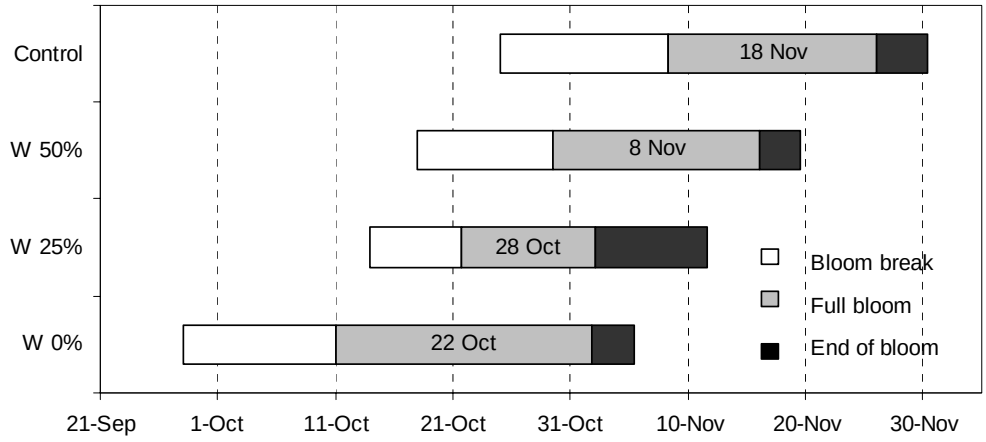

Figure 2: Blooming course of control full irrigated trees and trees suffering different levels of water deficits.

The advancement in full bloom and bloom break dates for water-stressed trees basically coincided with the advancement observed in prior-to-bloom phenophases. In effect, bud dormancy release and panicle differentiation phenophases occurred before in W0% trees followed by W25% and W50% trees (Figure 3). Furthermore, flower initiation date determined by scanning electron and conventional microscopy confirmed that the changes within the bud associated to flower initiation occurred before in samples of water-stressed trees (Figure 4). In these samples, anatomical changes compatible with the initiation of the panicle were recognizable on July 7th in water-stressed trees, while similar stage of development was reached by well-watered trees three weeks later (25th July). The subsequent stages of panicle elongation and individual flower bud initiation were seen in control trees samples during the first weeks of August, and between 12 and 18 days before in water-stressed trees (Figure 4).

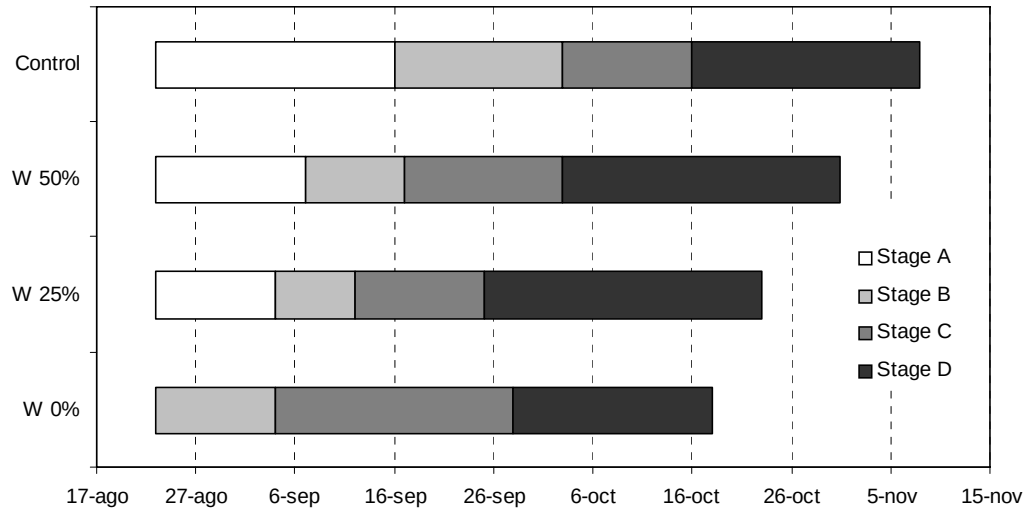

Figure 3: Loquat phenology from dormancy to visible floral buds in control full irrigated trees and trees suffering different levels of water deficits.

On the other hand, no clear pattern in the duration of the phenophases can be inferred from the comparison of treatments. In control trees, 36 days were needed to take a bud from dormancy release to anthesis, while 33 days passed in W50% trees between bud break and bloom, and no less than 39 days in W0% trees (Figure 3). Only W25% trees exhibited a little faster developmental rate during panicle formation phenophases (30 days), also expressed in a more compact blooming period.

Finally, DI only caused minor effects on flowering intensity. The percentage of bearing shoots was slightly enhanced by DI (Table 1). The differences were not significant in main shoots. However, the differences in secondary late-formed shoots, although small, reached statistical significance. No differences were observed in the number of flower per panicle in main shoots, while in secondary shoots the most severe DI treatments (W0%) had a reduced number of flowers per panicle (Table 1).

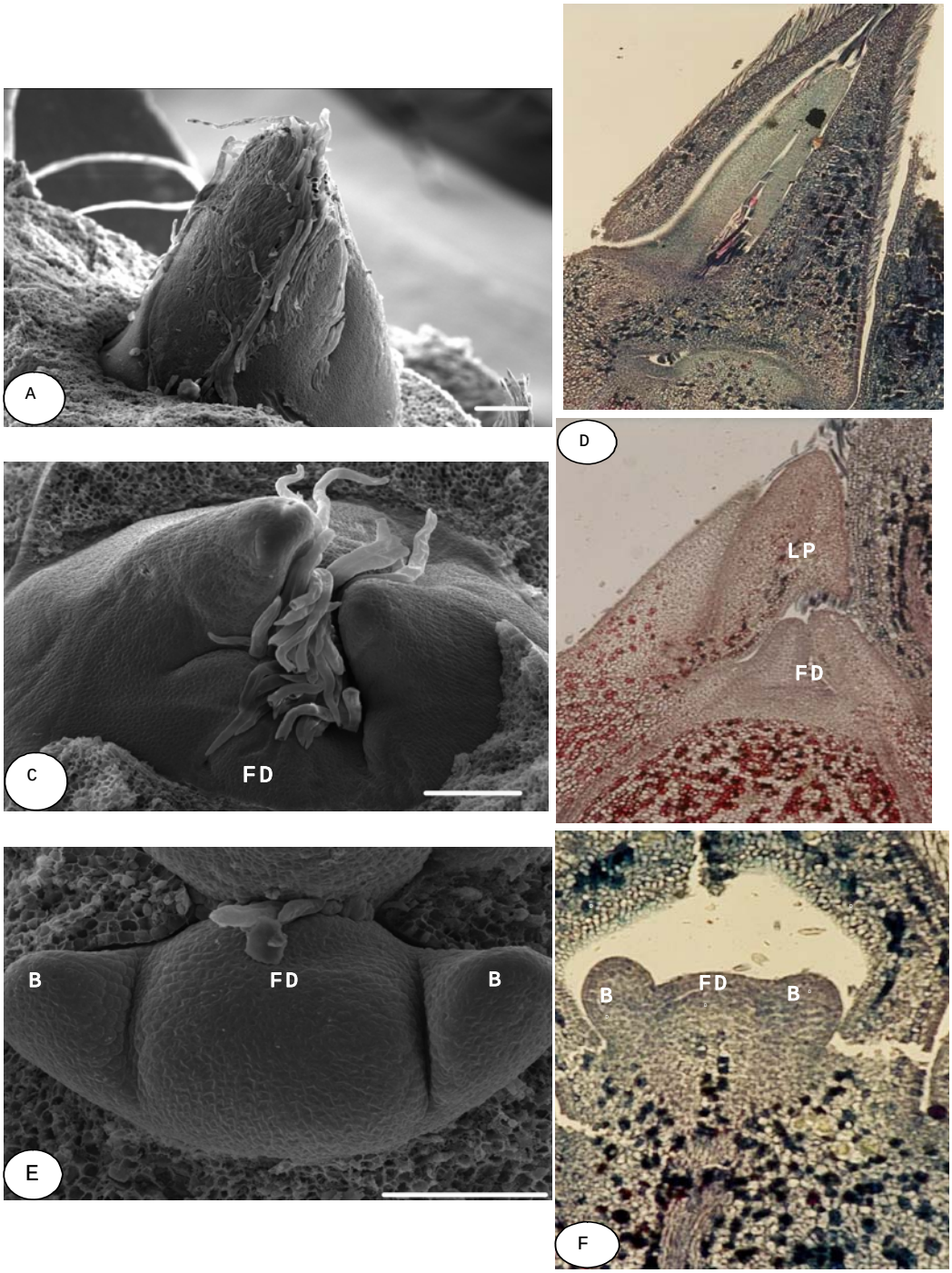

Figure. 4. First stages of panicle initiation and development. A and B. Vegetative meristem. C and D. Panicle raising. E and F. Bracteoles formation. FD: Floral dome. LP: leaf primordia. B: bracteole.

Table 1: Effects of Regulated Deficit Irrigation treatments on bloom intensity and shoot growth

	Bearing shoots (%)		Flowers/panicle		Main shoots	
Treatments	Main shoots	Secondary shoots	Main shoots	Secondary shoots	Leaf Number	Shoot length (cm)
Control	90 a[1]	74 b	265 a	164 ab	17 a	14.3 a
W50%	97 a	89 a	232 a	182 a	16 a	12.2 a
W25%	100 a	98 a	237 a	175 a	17 a	11.1 a
W0%	98 a	93 a	230 a	138 bc	17 a	12.4 a
P	NS	0.05	NS	0.005	NS	NS

[1]Different letters in each column indicate significant differences according to the p-value. NS, not significant (P>0.05). Percentage data were previously arc-sin transformed. Duncan test.

Deficit Irrigation Effects on Shoot Growth

Shoot growth in control well-irrigated trees fitted a sigmoid pattern (Figure 5). New growth started immediately after harvest and kept a regular pace until early August, when summer rest was imposed in apical buds (August 10th). Plastochron length was very regular during the first weeks, but was greatly enlarged as summer rest approached. Control trees abandoned dormancy in early September forming the terminal panicle. Final length of main shoots in control trees reached 14.3 cm. Seventeen new leaves were formed in these main shoots. DI did not diminish the length or the number of leaves per shoot (Table 1). However, DI profoundly altered the pattern of shoot growth that changed from a single sigmoid to a double sigmoid (Figure 5). This shift was the result of water stress causing an early, but transitory, cease of growth, which was reassumed up to the length of controls when water deficit ended. Modification of shoot growth pattern was more acute in trees where irrigation was completely suspended (W0%) and less noticeable in trees where water irrigation was cut by half (W50%). No new nodes were formed in W0% trees since the beginning of July and summer rest was already established two weeks after water withholding. The onset of summer rest occurred last week of July in W25% trees, while it could be dated at the beginning of August in W50% trees. The release of rest in apical buds was almost immediate in all DI treatments after the resumption of full irrigation. On mid-August just a few days after the end of water deficit, the trees responded forming new leaves below the differentiating terminal panicle (Figure 5). The variations in shoot growth rate along the experimental period expressed in large changes in plastochron length of W0% trees from more than 40 days to scarcely 2, when bud dormancy release and rapid growth occurred. Less marked changes took place in W50% and W25% trees.

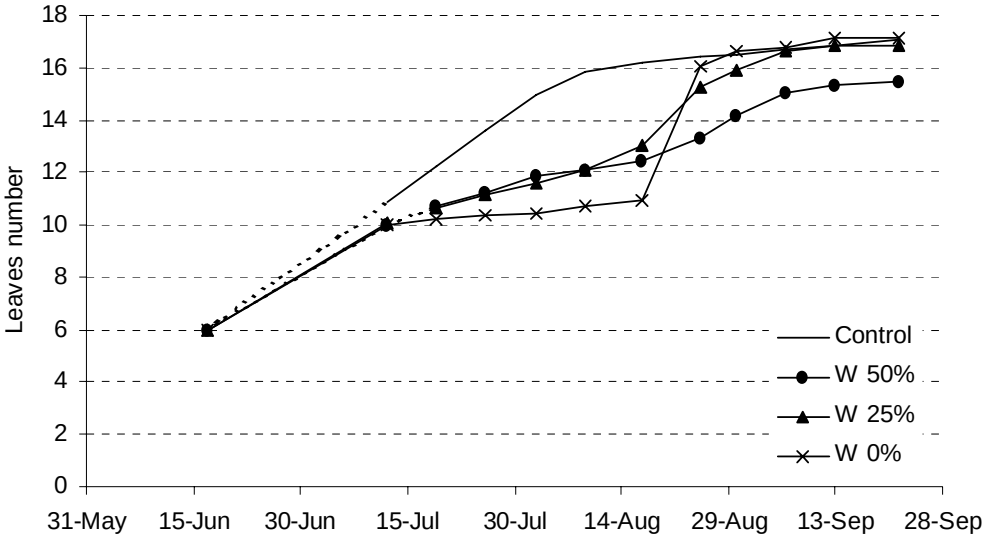

Figure 5: Shoot growth in control full irrigated trees and trees suffering different levels of water deficits.

DISCUSSION

Proximate Causes of Flowering Promotion in Water-Stressed Loquats

Previous experiments have demonstrated that posharvest DI is a useful strategy to advance bloom and harvest dates in loquat, making the crop more profitable (Hueso and Cuevas, 2007). However, the causes determining bloom earliness could not be explored in that experience. Shoot growth involvement in early flowering has been now specifically addressed. The correlation found among the advancements in terminal bud dormancy, panicle development and bloom dates informs that loquat earliness in response to DI is due to a complete displacement of the reproductive cycle, from flower initiation to full bloom and harvest.

This phenological displacement can be explained by DI effects on shoot growth and rest. Our results show that DI treatments progressively reduced soil water content, effect that in turn was translated into the plant. The reduction of water availability determined an earlier suspension of shoot growth in water-stressed trees, allowing terminal buds to differentiate into panicles before. SEM and conventional microscopy images confirm that the first anatomical changes in the apical meristem leading to the formation of the panicle occurred three weeks earlier in W0% trees. This transition to flowering occurred days before the full establishment of dormancy in the apical bud, when the formation of new leaves slowed down (i.e. increasing plastochron length). Panicle initiation preceding bud dormancy has been observed in avocado indicating that rest is not a prerequisite for the transition to flowering

(Salazar-García et al., 1998). Certain growth of buds during the exposure to cool inductive temperatures also appears to be necessary for panicle initiation in mango (Núñez-Elisea and Davenport, 1995). In apple, hand-defoliation soon after harvest makes possible a second annual crop in Indonesia, by preventing dormancy entrance in a time in which flowers are already initiated (Edwards, 1985).

After panicle initiation, flower development will continue if water deficit does not prevent it. At this regard, bud break and panicle development phenophases also proceed first in water-stressed trees, because the timely resumption of full irrigation. On the contrary, a prolongation of DI during August has been proven detrimental for bloom earliness because water stress delays the last steps of panicle elongation (Cuevas et al., 2007). In contrast to the success of moderate and severe DI treatments, pulses of water shortages as those caused by W50% advanced flowering date in a minor extent because they were not able to make buds to enter in dormancy long before controls. Light water-stress caused by a 20% reduction in watering along the season has also failed to substantially modify flowering date in previous experiments (Hueso and Cuevas, 2007). Work in progress is trying to determine the optimum levels of water stress that more rapidly activates the flowering process in loquat. The hypothesis is that a moderate water stress switches on the flowering program without restraining panicle development. A severe stress may serve, however, to extend the positive effect to the whole bud population making blooming season more compact and uniform. The gradual modification of loquat phenology from panicle initiation to bloom in response to increasing water deficits demonstrates that bloom earliness under DI is due to an advancement of the flower induction process and not due to a higher developmental rate in water-stressed trees, as it has been argued in mango (Núñez-Elisea and Davenport, 1994). Bringing first discernible response to DI to summer can be useful to farmers since provides an early indication of success.

Flowering advancement in water-stressed loquats coincides with observations carried out in citrus and mango. Out of season flowering in response to water withholding is a well-known strategy for citrus producers (Barbera et al., 1985). In several species of genus Citrus, a severe water stress imposed in summer provokes, after rewatering, a second bloom that sets a more valuable crop next summer (Maranto and Hake, 1985). In mango, water stress also advance bloom date (Núñez-Elisea and Davenport, 1994; Lu and Chacko, 2000). Because fully irrigated mangoes bloom profusely (as our control trees), Núñez-Elisea and Davenport (1994) conclude that water stress is not essential for induction of floral morphogenesis in mango grown the subtropics, where cool temperatures have been identified as the main flowering stimulus. In the tropics, however, night temperatures remain too high for induction and a dry period is proposed as the environmental cue for flower induction (Lu and Chacko, 2000).

It is worthwhile to mention that although the onset of summer rest took place before in DI treatments, the number of phytomers, structural segments composed of a leaf, bud, node and internode, was not modified by water deficit. From our results is deduced that the last phytomers were initiated and its founder cells recruited at the time water stress was imposed. At this moment, a number of leaves may still expand, but others remain as undifferentiated foliar primordia below the differentiating terminal bud, until the recovery of plant water status. In lychee, a tropical species with terminal panicles, the same levels of DI here applied (50%, 25% and 0%) greatly reduce postharvest shoot growth and increase flowering and yield. This results made to the authors conclude that resource competition among vegetative

and reproductive growth operate in lychee. In loquat, same shoot leaf number and similar length in fully irrigated and water-stressed loquats suggests that the amount of resources allocated to vegetative versus reproductive growth scarcely changed in response to DI.

Ultimate Reasons behind Flowering Promotion in Water-Stressed Fruit Trees

A model for explaining flowering promotion in water-stressed trees is then alternatively proposed. From Arabidopsis studies, we have learned that the transition to flowering in annuals may be regulated by multiple signals and multiple pathways. In Arabidopsis, flowering is controlled by four pathways. All these pathways converge to regulate the meristem identity gene *LEAFY* (Soltis et al., 2002). A *LEAFY-like* gene has been recently isolated in six species of *Maloideae* including loquat, where the highest levels of transcription are expressed at bud break (Esumi et al., 2005; Liu et al., 2007). One of the floral pathways identified in Arabidopsis is GA dependent, but whereas GA is a floral promoter in long-day annuals, it inhibits flowering in fruit trees (Sedgley and Griffin, 1989). This fundamental difference in the role of GA has to be taking into account when proposing a model for flowering in fruit trees. In annuals, an increase in GA activates floral pathways integrators that regulate the formation of flowers (Ausin et al., 2005; Percy, 2005). The situation must be reverse in fruit trees where fast shoot growth as that provided by GA cancel the chance of bud dormancy and flower initiation in fruit trees. For this reason, flower initiation in Angiosperm woody plants is not only compatible but it may require bud dormancy.

In our model, drought promotes abscisic acid (ABA) synthesis and transport to the leaves to induce rapid stomata closure (Beardsell and Cohen, 1975). ABA antagonism with growth promoters hormones, noticeably gibberellins (GA), may eventually lead to a hormonal balance favourable to the onset of terminal bud dormancy (Wareing, 1978; Michalczuk, 2005), allowing flowering program to be expressed. This is not to say that ABA plays a role of floral promoter but that its antagonism with the floral inhibitor (GA) indirectly promotes flowering in water-stressed trees. Goldschmidt and Samach (2004) argue that woody perennials may be constantly induced, but the flowering is repressed by a floral inhibitor (GA in our model) which would act in a similar manner as FLOWERING LOCUS C gene represses flowering transition in Arabidopsis. No need of floral promoter in fruit trees is deduced from this approximation. GA involvement in shoot growth is well documented in annuals and woody plants, where low GA content reduces growth, especially internode elongation. ABA, formerly known as “dormin” (Eagles and Wareing, 1963), specifically inhibits GA biosynthesis and blocks the formation of enzymes as α-amylase that are stimulated by GA to obtain energy for maintenance and growth. Furthermore, GA and ABA are both terpenoids that share the same promoter, the mevalonate, allowing competition for substrate to take place. Common tree flowering promotion in response to triazoles application and ABA may respond to the antagonism of both molecules to GA biosynthesis.

Note that in this model, new leaves as a source of flower inhibitors are not required for explaining lack of flowering in active growing shoots. Rather on the contrary, the presence of new leaves is the negation of the conditions required for flowering transition to occur. Reduced activity in the apical meristem (i.e. increased plastochron) due to water stress is the only switch needed for the activation of the flowering program that includes bud competence

and flower initiation during summer. Some kind of citokinins (CK) involvement in bud dormancy onset and release seems likely since its synthesis in roots and delivery to the leaves is usually decreased in water-stressed plants (Pospíšilová, 2003). Low CK levels during dormancy and an increase during dormancy release suggest to CK may reinforce the role of GA in bud break. This theory is coherent with the promotion of flowering in response to growth inhibitors and with the negative effects that gibberellins have on tree blooming and fits a series of field observations including tree response to pruning, watering and nitrogen overfertilization.

Many others tropical and subtropical fruit crops seem to require reduced vegetative activity for flowering transition. In lychee, a period of vegetative dormancy is needed to initiate floral buds. This dormancy can be induced by low temperatures, water stress, withholding fertilizers, cincturing and auxin sprays (Menzel, 1993). Whiley and Schaffer (1994) have also noted that flower induction in woody subtropical and tropical evergreen species usually follows a period of quiescence in the canopy caused by environmental conditions (temperature and drought). Bower et al. (1990) propose a simple model to explain flowering in avocado in response to low temperatures that also relays on vegetative growth stops and low GA content. In this model lack of shoot growth (low GA) would conduce to a reduction in available carbohydrates and to an increase in CK and ABA synthesis by new roots. In avocado, CK would increase the number of sprouting buds while ABA would regulate the transition to flowering in apical buds. This scenario coincides with Ben-Tal (1986) inhibitory theory, in which vegetative growth end is marked as a necessary step for flowering to take place in fruit trees. Ben-Tal (1986) emphasizes that vegetative growth disturbance is the general rule that explains tree flowering in response to many different inductive factors such as day length, temperature, hormones, plant size and, as in water-stressed loquats, drought.

Although the previous model for flowering promotion in water-stressed loquats seems plausible, an identification of the environmental factors stimulating terminal bud dormancy and flower initiation in well-irrigated loquats is still needed. This floral stimulus must be naturally produced and must be responsive to water-stress. Two different possibilities arise: correlative inhibition (paradormancy) exerted by competing organs and an environmentally induced dormancy (ecodormancy). In temperate-zone trees, paradormancy develops as days shorten in late summer (Faust et al., 1997). During this period, ABA content increases, although dormancy is still relatively shallow. In late fall, dormancy becomes more intense as dehydrins accumulate in the bud triggered by ABA and decreasing air temperatures (Faust et al., 1997). Arora et al. (2003) acknowledge the difficulty delinking the functions of ABA in cold hardiness versus dormancy in the buds of temperate-zone fruit trees. Different results make the authors yet to assign a major role of ABA in cold acclimation. However, this function does not fit into loquat characteristics since its terminal buds are formed in summer and do not exhibit cold resistance (loquats bloom on November). Although the literature commonly infers that the short day length of late summer is responsible of the cessation of shoot growth, many temperate-zone woody plants, as well as loquat, form terminal buds in early summer with long day periods (Powell, 1987). Shoot growth cessation at this time may be due to the competition of numerous metabolic sinks for essential metabolites (Powell, 1987). Whatever the final reason and exact time may be, shot elongation ceases and apical bud dormancy is established. Correlative inhibition of the apex by mature leaves operate in apple as it has been shown in hand-defoliation experiments (Faust et al., 1997). Interestingly,

an ABA decrease, a GA increase and small changes in CK take place in these apple floral buds forced to break paradormancy (Edwards, 1985). Mango apical buds also exhibit foliar paradormancy (Núñez-Elisea and Davenport, 1995). Apical bud paradormancy triggered by an early increase of ABA in mature leaves is compatible with the flowering advancements achieved under DI.

On the other hand, the analysis of loquat phenology has shown that in control trees terminal bud enters in dormancy in August when the evapotranspirative demand and temperatures are high (Cuevas et al., 1997). Water soil content and plant water status in fully irrigated trees negate, however, a situation of water stress, leaving high temperature as the only relevant environmental factor. In this situation the great similarities between seed and bud dormancy (Powell, 1987) may be of help. Seed dormancy induced by high temperature is known as thermodormancy. Thermodormancy inhibits seed germination in late summer in many important crops. ABA and other GA inhibitors cause seed thermodormancy, while chilling and GA release seeds from dormancy. Same situation may apply to loquat buds. This mechanism for inducing ecodormancy is compatible too with the flowering advancement observed under DI. At this regard, it is well known that drought increases leaf temperature which indirectly may advance bud thermodormancy. Rewatering, on the contrary, reduces leaf temperature. Environmental effects on bud dormancy maintenance can be deduced by comparison of loquat behaviour in contrasting climates. In the tropics (San Juan del Obispo, Guatemala), with constant moderate temperatures (25/15ºC) along the year, loquat has modified its annual cycle at high altitudes and forms panicles during a dry period in spring (the usual time for harvest), reaching bloom during the wet summer. This shift suggests a favourable effect of water shortages on flowering transition, but disregards temperatures as main dormancy inducers (B. Sercu, com. pers.). The effects of defoliation and high temperatures on potted loquats are now in study trying to elucidate the factors causing the onset and release of terminal bud dormancy in this species.

CONCLUSION

In conclusion, our results shown that postharvest DI advances loquat bloom dates thru an effect on shoot growth and dormancy onset and release. Apical bud dormancy is briefly preceded by panicle initiation indicating that a large plastochron length (i.e. reduced meristem activity) is the switch that activates the flowering program in loquat. The advancement in harvest date in response to DI and the consumers' appreciation for early season loquats clearly demonstrate that the modification of reproductive phenology by means of the management of the agricultural water is profitable in this species. We also expect from these studies to bring some insight into the endogenous factors controlling flowering in other tree crops. The unusual phenology of loquat makes it a suitable model to explore the role of water stress, bud rest, and hormonal changes in the flowering of fruit crops, more economically important as apple and pear. A major difference with these closely related species is that loquat bud break follows summer rest and no fruits are present at this time. Although water deficit causes an early rest too in these temperate-zone tree crops (and the prolongation of the watering a delay that increases frost risks), the confounding effects of chilling requirements for bud break makes them less amenable for experimentation. Finally, a model for flowering

promotion under DI is proposed and the environmental and endogenous factors leading to flower induction in loquat discussed.

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