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Cool Temperature and Water Deficit Interact during Floral Induction in Citrus

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Cool temperatures (<20 °C) and water deficits have long been known to induce flowering in citrus trees. However, there have been no reports of the combined effects of these two factors in the literature in spite of cool temperatures and water deficit usually occurring naturally together in many citrus-producing regions of the world. We characterized the flowering responses of two citrus species to combined floral-inductive cool temperatures and water deficits under growth chamber and field conditions. Interactions of cool (inductive) and warm (non-inductive) temperatures with water deficit were tested in two separate growth chamber experiments. In both experiments a statistical interaction between the effects of temperature and water deficit was detected. As a result of this interaction, mild water deficit increased the number of inflorescences induced on trees under a thermo-period of 23/18 °C (day/night) compared to trees at 15/10 °C (day night) whereas moderate water deficit increased the number of inflorescences formed at 15 °C (no day/night variation) compared to trees at 23 °C. In the field, water deficit was induced by withholding irrigation or by covering the soil with an impermeable cover during the fall/winter in three different seasons in sweet orange and grapefruit trees. Field trees under water deficit consistently produced more inflorescences than well-irrigated trees. Our results support the hypothesis that low temperature and water deficit interact during floral induction in citrus and that water deficit could be used to manipulate flowering in field trees.

Citrus trees can be induced to flower by prolonged exposure to cool temperatures (<20 °C) or water deficit (Cassin et al., 1969; Moss, 1969). The separate effects of these two factors on citrus floral induction have been extensively characterized (Borroto and Rodríguez, 1979; Cassin et al., 1969; García-Luis et al., 1989; Koshita and Takahara, 2004; Moss, 1969; Southwick and Davenport, 1986; Valiente and Albrigo, 2004) but reports about their combined effect are uncommon (Albrigo et al., 2006b). Cool temperatures are the primary source of floral induction for trees growing in subtropical climates where cool winters occur whereas water deficit is the sole source of induction for trees growing in lowland tropical regions (Cassin et al., 1969). Cool temperatures and low natural precipitation are co-occurring characteristics of the fall and winter season in the humid subtropical climates of southcentral and southeastern China, Florida, and São Paulo, Brazil, which are the largest citrus producers in the world. In these regions, winter can vary significantly from year to year, resulting in warmer- or colder-than-average winters (Hansen, 1999). Year to year temperature variation during the winter and spring period has been related to different levels of floral induction being perceived by the trees and the consequent variation in flowering intensity and yield (Albrigo et al., 2006b; Melgar et al., 2010).

Given that winters in humid subtropical regions are commonly dry, there is potential for complementing floral induction by water deficit when winter temperatures are not optimal for induction. In addition to citrus, other evergreen subtropical species such as mango, avocado or litchi, also can be induced to flower by seasonal cool temperatures and water deficits (Nakata and Watanabe, 1966; Nunez-Elisea and Davenport, 1994; Reece, 1942; Reece et al., 1949; Sukhvibul et al., 1999).

The objective of this study was to determine whether the effects of low temperature and water deficit flower bud induction are additive or interact during the flower bud induction process in two citrus species. Results are discussed in relation to the potential application of our findings to manipulate the level of floral induction in citrus trees grown in humid subtropical climates.

Materials and Methods

Growth chamber experiments

Two factorial growth chamber experiments were conducted between October and November to test for interactions between temperature and tree water status. Prior to both growth chamber experiments, the trees had been kept well-irrigated in a greenhouse with 20 °C minimum temperature for at least 6 months. The most-recent flush on the trees when the experiments started was at least 2 months old.

In the first growth chamber experiment, potted 3-year-old ‘Valencia’ sweet orange (*Citrus sinensis*) trees grafted on ‘Carrizo’ citrange [*C. sinensis* (L.) Osbeck. × *Poncirus trifoliata* (L.) Raf.] were used to test the effects of temperature, water deficit, and length of treatment on flower induction. Two levels of temperature, two levels of water deficit, and four levels of time of induction were tested. The temperatures tested were 15/12 °C and 23/18 °C (day/night), which were assumed to represent optimal inductive and marginally floral-inductive temperatures (respectively) based on reports in the literature (Moss, 1969; Valiente and Albrigo,

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2004). The levels of water deficit were normal irrigation (no water deficit) and a mild water deficit. Water deficit was applied by reducing the irrigation frequency and volume. Midday stem water potential (SWP) was used as a measure of tree water status and was measured using the pressure chamber method with covered leaves (McCutchan and Shackel, 1992; Scholander et al., 1965). Trees under water deficit were maintained at a midday SWP of –1.5 ± 0. 1 MPa whereas well-irrigated control trees had SWP of about –0.75 ± 0.1 MPa. The time periods of induction were 3, 5, 7, and 9 weeks. The illumination in each chamber was 250 μmoles·m^{-2}·s^{-1} at canopy level with a photoperiod of 12 h/12 h (day/night). At the end of the induction treatment, the trees were transferred to a greenhouse kept at 20 °C minimum temperature to promote bud growth, and irrigation was re-established in trees previously under water deficit. Four trees (single tree replicates) per treatment were used. The experiment was conducted using a completely randomized design in factorial arrangement of 2 levels of temperature × 2 levels of water deficit × 4 time periods for the induction treatments.

In the second growth chamber experiment, potted 2-to-3-year-old 'Washington Navel' sweet orange trees propagated as rooted cuttings from mature trees were exposed to cool temperatures and water deficit for 7 weeks as before except that the temperatures were held constant at 15 °C or 23 °C (no day/night temperature variation) and the water deficit was imposed at a more intense level (–2.0 ± 0.1 MPa). This level of water deficit was assumed to represent a moderate water deficit. Well-irrigated trees kept at 23 ° C were assumed to not have been induced to flower and served as the control. Again, four trees (single tree replicates) per treatment were used. The experiment was conducted using a completely randomized design in factorial arrangement of 2 temperatures × 2 levels of water deficit.

Field experiments

Field experiments were conducted during the fall/winter of 2005–06, 2006–07, 2008–09 and 2009–2010 in orchards of mature (>7 year-old) citrus trees at the University of Florida's Citrus Research and Education Center in Lake Alfred (28°5'N, 81°43'W). All the orchards were in sandy soils (Candler sand, hyperthermic, uncoated Typic Quartzipsamments or Apopka fine sand, loamy, siliceous, hyperthermic Grossarenic Paleudults) and irrigated with microsprinklers. The trees had been under standard horticultural care as in neighboring commercial orchards.

In 2005–06, 2006–07, and 2008–09, 'Valencia' sweet orange grafted on 'Carrizo' citrange rootstock trees were maintained without irrigation during the fall/winter for about 80 d beginning in mid-November when ambient night temperatures usually fell below 20 °C at this location. In 2006–07, 2008–09, and 2009–10 trees in the same orchard also were deprived of any source of precipitation during the winter by not only interrupting irrigation in mid-November as before, but also covering the soil underneath the canopies with a sheet of water-proof material (Tyvek®, DuPont) as a rain-out shelter for the duration of the treatments. In another experiment conducted in 2005–06 and 2006–07, 'Marsh' grapefruit trees (*Citrus paradisi* Macfad.) were deprived from irrigation during the fall/winter for 80 d as indicated before for 'Valencia' trees. In all the orchards and for both species tested, another set of similar trees was kept well-irrigated throughout the experiment. For all experiments, the water deficit treatments were interrupted in late-January by removing the soil covers and/or irrigating the orchards for three consecutive days until saturation. SWP was monitored throughout the experiments as above and ranged from –0.8 to –1.1 MPa in well-irrigated trees, from –1.4 to –1.7 MPa in trees that received no irrigation but were exposed to natural precipitation and from –1.9 and –2.5 MPa in trees that received no irrigation and had the soil covered with an impermeable layer as before. Relevant weather parameters for each season are presented in Table 1. Dates of floral differentiation were predicted using phenological models developed for Florida (Albrigo et al., 2002, 2006a; Valiente and Albrigo, 2003). Four trees (single tree replicates) were used in each treatment. Each individual experiment was conducted using a completely randomized design.

Flowering measurements

In all the experiments, the number of inflorescences and vegetative shoots formed following the floral-inductive treatments was counted on 4-month-old to 1-year-old 6–9 nodes-long shoots. In the growth chamber experiments, all shoots with these characteristics were evaluated. In the field experiments, 25 shoots per tree distributed on both sides of the hedgerow were tagged at the beginning of the experiments and evaluated in the following spring. Results were expressed as the average number of new vegetative shoots, flowers or inflorescences per shoot per tree.

Data analyses

Results from both growth chamber experiments were analyzed by ANOVA using a full factorial model for the completely randomized design. The statistical significance of the interactions was determined from the ANOVA. Results from each of the field experiments (each cultivar, each year) were analyzed separately by ANOVA for a completely randomized design. For the field experiments means were separated using Tukey's test at α = 0.05 (each cultivar and year analyzed separately). Numbers of inflorescences and flowers from the growth chamber experiments were square root transformed for analyses due to non-normality of the residuals, however, untransformed values are presented in the figures or tables. Statistically significant differences were declared at $P \leq 0.05$. All statistical analyses were conducted in R (R Development Core Team, 2011).

Table 1. Climatic parameters during fall/winter flower bud induction period in water deficit experiments.

				Accumulated inductive hours[z]					
Season	Start date	End date	Predicted dates of differentiation[z]	at start	at differentiation[z]	Mean temp	Days with precip.	Precip. (mm)	Longest period without precip. (days)
2005–06	14 Nov.	3 Feb.	25 Dec., 4 Jan.	322	1057, 1216	16.7 °C	16	50.5	19
2006–07	15 Nov.	2 Feb.	10 Dec., 27 Dec., 9 Jan.	383	729, 1014, 1156	17.9 °C	19	172.5	20
2008–09	17 Nov.	6 Feb.	6 Dec., 20 Dec., 31Dec.	399	841, 1055, 1214	15.2 °C	13	82.1	14
2009–10	13 Nov.	3 Feb.	14 Jan.	206	1262	15.8 °C	22	178.3	12

[z]As predicted by phenological models developed for Florida (Albrigo et al., 2002, 2006a; Valiente and Albrigo, 2004).

Table 2. Main effects and interactions between temperature (15/10 °C and 23/18 °C, day/night), water deficit [no water deficit and mild (SWP = –1.5 MPa) water deficit] and time of induction (3, 5, 7, and 9 weeks) in the first growth chamber experiment.

		Mean squares		
Source	df	Inflorescences[z]	Flowers[z]	Vegetative[z]
Time of induction	3	0.88**	2.86**	0.52
Temp	1	9.05**	28.91**	0.14
Water deficit	1	0.01	0.01	0.06
Time × Temp	3	0.37	1.13	1.14**
Time × Water deficit	3	0.06	0.29	0.21
Temp × Water deficit	1	1.08*	2.81*	0.01
Time × Temp × Water deficit	3	0.16	0.86	0.33
Residuals	48	0.17	0.62	0.24

[z]Per shoot.
*, **Significant at P <0.05 or <0.01, respectively.

Results and Discussion

In the first growth chamber experiment the main effects of temperature and duration of treatment on the number of inflorescences and flowers induced per shoot were significant whereas no significant main effect was detected for water deficit (Table 2). No significant main effect was detected for the number of new vegetative formed per shoot. In general, more flowers and inflorescences were formed in shoots of trees that had been kept at 15/10 °C than at 23/18 °C, and the maximum number of flowers and inflorescences per shoot were induced after 5 and 7 weeks (Fig. 1), respectively.

Significant interactions were detected between temperature and water deficit (Table 1). Trees that had been kept under water deficit produced more flowers and inflorescences per shoot than well-irrigated trees only at 23/18 °C. An interaction was also detected between temperature and time of induction on the number of new vegetative shoots.

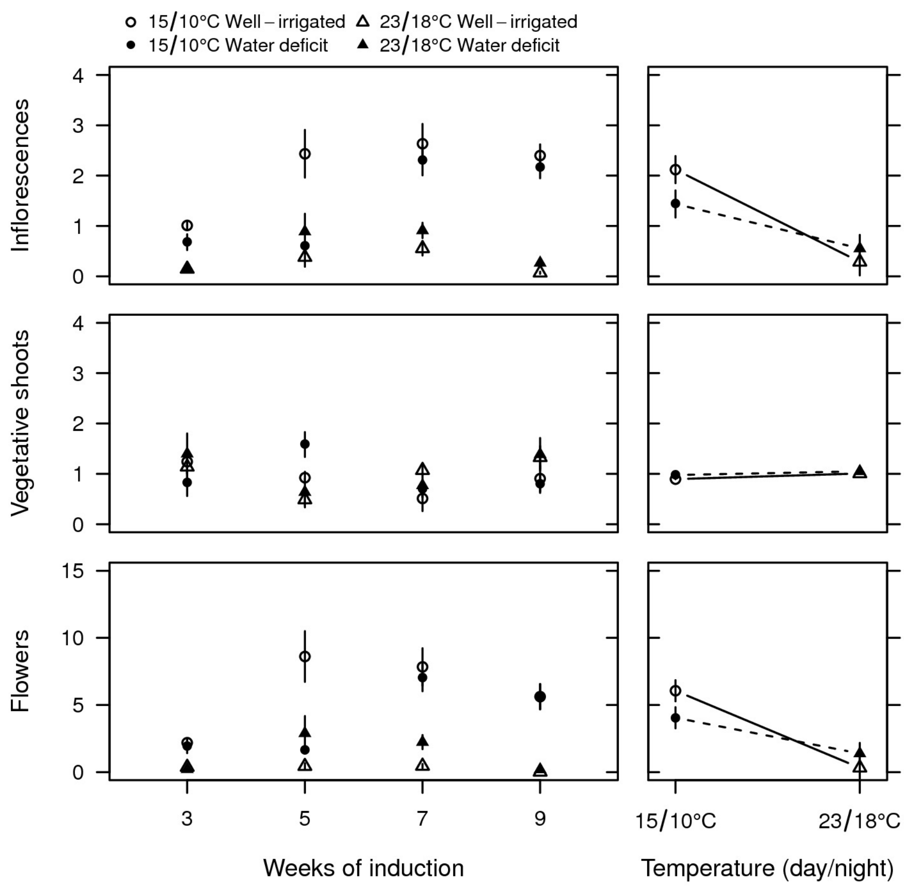

Fig. 1. Number of inflorescences, flowers and new vegetative shoots in shoots of potted 'Valencia' trees exposed to combinations of levels of temperature and tree water status for 3, 5, 7, or 9 weeks (left column graphs, first growth chamber experiment). The effects of the duration of the floral-inductive treatment were additive for the three variables presented. Statistically significant ($P \leq 0.01$) interactions between temperature and tree water status were detected for the number of inflorescences and flowers per shoot (right column graphs). Symbols represent the mean of either four (graphs on left column) or 16 (graphs on right column) tree-replicates ± SE.

Table 3. Main effects and interactions between temperature (15 °C and 23 °C) and water deficit [no water deficit and mild (SWP = –2MPa) water deficit] in the second growth chamber experiment.

		Mean squares		
Source	df	Inflorescences[z]	Flowers[z]	Vegetative[z]
Temp	1	0.78**	1.84**	0.049
Water deficit	1	2.05**	2.15**	2.33**
Temp × Water deficit	1	0.27**	0.89**	0.76**
Residuals	11	0.01	0.04	0.02

[z]Per shoot.
*, **Significant at P <0.05 or <0.01, respectively.

In the second growth chamber experiment, temperature and water deficit had significant main effects on the number of flowers and inflorescences per shoot induced (Table 3). In this experiment, shoots of trees that had been kept under water deficit produced more flowers and inflorescences than irrigated trees regardless of the temperature. More flowers and inflorescences were induced at 15 °C than at 23 °C. A significant interaction between temperature and water deficit was detected for the number of flowers, inflorescences and new vegetative shoots (Fig. 2). More vegetative shoots were formed in trees previously under water deficit than in well irrigated trees with the difference being more marked at 23 °C than at 15 °C.

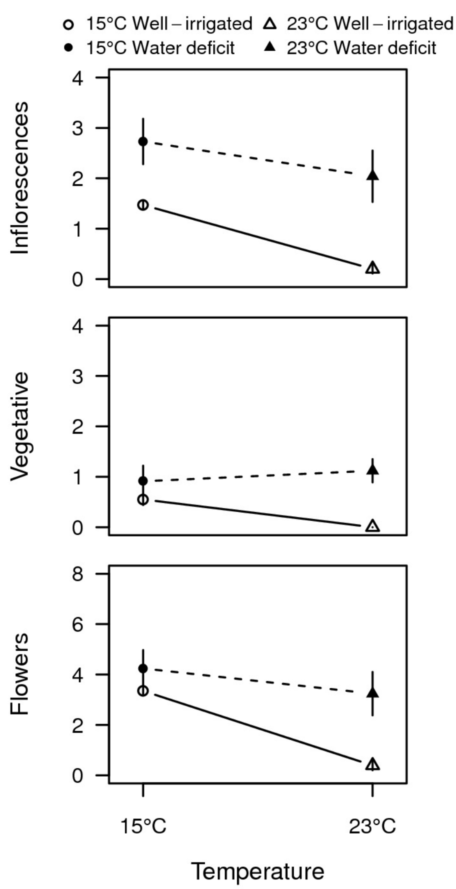

Fig. 2. Number of inflorescences, flowers and new vegetative shoots in shoots of potted 'Washington Navel' trees exposed to combinations of levels of temperature and tree water status for 7 weeks (second growth chamber experiment). Statistically significant ($P \leq 0.05$) interactions between temperature and tree water status were detected for the 3 variables presented. Symbols represent the mean of four tree-replicates ± SE.

Exposing mature citrus trees in the field to different levels of water deficit during the fall/winter in Florida, increased the number of inflorescences and flowers formed in shoots in the following spring (Table 4). In 2005–06, withholding irrigation, allowing only natural precipitation, increased the number of inflorescences and flowers per shoot in the following spring relative to well-irrigated trees. In the following season, however, more natural precipitation occurred and the number of inflorescences and flowers per shoot in well-irrigated and non-irrigated trees was not statistically different. Trees with no irrigation and rain-out shelters, consistently produced more inflorescences and flowers per shoot than well-irrigated trees. Trees that were kept under continuous water deficit produced a single bloom in the spring whereas well-irrigated trees produced multiple or protracted blooms (data not shown). The effect of water deficit during the fall/winter on the number of inflorescences and flowers per shoot was similar in both 'Valencia' sweet orange and 'Marsh' grapefruit trees. In general, the number of new vegetative shoots was higher in well-irrigated trees than in trees under water deficit but this difference was not always statistically significant.

Although the effects of cool temperatures and water deficit on flowering in *Citrus* have been characterized in the literature (Borroto and Rodríguez, 1979; Cassin et al., 1969; García-Luis et al., 1989; Koshita and Takahara, 2004; Moss, 1969; Southwick and Davenport, 1986; Valiente and Albrigo, 2004), there have been no reports directly addressing the combined effects of these two factors. Here, we detected significant interactions between the effects of cool temperatures and water deficit in the number of induced inflorescences formed on shoots of potted citrus trees. The effect of water deficit on inflorescences and flowers was smaller at 12 to 15 °C (considered as optimal inductive temperatures; Moss, 1969; Valiente and Albrigo, 2004) than at 23/18 °C (considered marginally inductive; Moss, 1969). In our experiments, the effect of cool temperature alone was more marked than the effect of water deficit alone. Interestingly, in the first growth chamber experiment, trees under water deficit at 15/10 °C produced fewer inflorescences and flowers per shoot than well-irrigated trees (Fig. 1), whereas in the second growth chamber experiment, trees under water deficit produced more inflorescences and flowers per shoot than well-irrigated trees at 15 °C. This suggests that the effect of the interaction between cool temperatures and water deficit is not always positive. One possible explanation for these differences was that in the first growth chamber experiment, trees were exposed to day/night variation in temperature, night temperatures were 5 °C lower than the day temperature and temperatures were below the optimum. It is possible that the combined effect of cooler temperatures and water deficit may be negative, similar to how temperatures,

Table 4. Influence of water deficit during the fall/winter on the number of inflorescences, new vegetative shoots and flowers induced in shoots of mature field-grown citrus trees.

Season	Treatment	Inflorescences[z]	Flowers[z]	Vegetative[z]
2005–06	'Valencia' well-irrigated[y]	2.0 ± 0.3 b	5.8 ± 0.7 b	0.3 ± 0.1 a
	'Valencia' rain-only[x]	3.5 ± 0.3 a	9.9 ± 1.6 a	0.1 ± 0.0 b
	'Marsh' well-irrigated	1.7 ± 0.2 b	6.0 ± 0.9 b	0.3 ± 0.2 a
	'Marsh' rain-only	2.1 ± 0.3 a	8.7 ± 0.9 a	0.5 ± 0.2 a
2006–07	'Valencia' well-irrigated	4.3 ± 0.3 b	15.7 ± 0.8 a	0.3 ± 0.1 a
	'Valencia' rain-only	4.2 ± 0.3 b	16.5 ± 1.1 a	0.2 ± 0.1 ab
	'Valencia' soil cover[w]	5.2 ± 0.3 a	16.3 ± 2.2 a	0.1 ± 0.0 b
	'Marsh' well-irrigated	4.1 ± 0.1 a	17.4 ± 0.9 a	0.1 ± 0.1 a
	'Marsh' rain-only	4.3 ± 0.3 a	18.6 ± 1.8 a	0.1 ± 0.0 a
2008–09	'Valencia' well-irrigated	2.2 ± 0.4 b	7.1 ± 1.2 b	0.4 ± 0.2 a
	'Valencia' soil cover	3.5 ± 0.3 a	12.4 ± 1.3 a	0.2 ± 0.1 b
2009–10	'Valencia' well-irrigated	2.1 ± 0.4 b	6.5 ± 1.1 b	0.8 ± 0.2 a
	'Valencia' soil cover	3.0 ± 0.2 a	11.0 ± 0.8 a	0.3 ± 0.1 b

[z]Per shoot.
[y]Irrigation as in neighboring commercial groves.
[x]Natural precipitation only, no irrigation.
[w]Natural precipitation excluded by impermeable soil cover, no irrigation.
Values are means of four tree-replicates ± SE. Each cultivar analyzed separately on each season. Different letters next to means for each cultivar on each season indicate statistically significant differences ($P \leq 0.05$) according to Tukey's test in each column.

cooler than 5 °C, induce flowering less intensely than at 10 °C (García-Luis et al., 1992). Another possible explanation is that the mild water deficit applied in the first experiment was not sufficient for maximum induction as compared to the moderate water deficit in the second experiment (about 0.5 MPa lower than in the first experiment), which increased flowering more than in the first growth chamber experiment.

Although we did not test for interactive effects of cool temperatures and water deficit in the field, we measured the flowering response of citrus trees totally or partially deprived of irrigation under natural cool temperature induction in the fall/winter to assess whether withholding irrigation during winter could be used to manipulate the level of floral induction under commercial conditions. Exposing citrus trees in the field to water deficits during the fall/winter under Florida conditions can increase the number of inflorescences and flowers formed in the following spring, particularly in low winter rainfall years. Preventing precipitation during the winter with soil covers, consistently resulted in the induction of almost one extra inflorescence per shoot. Depending on the experiment, one extra inflorescence per shoot represented a 20% to 60% increase in the number of inflorescences induced relative to well-irrigated trees. Depending on the amount of natural winter precipitation conditions during the fall/winter in Florida withholding irrigation during this period could be enough to induce higher levels of flowering in the following spring (Melgar et al., 2010). Similar results could probably be obtained in other regions with humid subtropical climates where moderate winter temperatures are usually accompanied by relatively dry conditions. However, in Mediterranean-like climates, where winters are cool and usually wet, water deficit might negatively affect floral induction similar to trees from our first growth chamber experiment under water deficit at 15/10 °C. Ali and Lovatt (1996) reported positive effects of winter irrigation on citrus yields in a Mediterranean-like climate (California). However, a positive correlation between winter drought and yields was reported for humid subtropical climates (São Paulo, Brazil; Albrigo et al., 2006b). In humid subtropical climates, accumulation of hours at floral-inductive temperatures range widely from year to year, resulting in varying levels of flowering intensity in the following spring (Albrigo et al, 2004; Valiente, 2001). Application of winter water deficit in these climates could be used to increase the number of flowers and inflorescences formed in the following spring and moderate the year-to-year variation in flowering intensity. Furthermore, periods of warm weather in the middle of the winter which commonly occur in humid subtropical climates, usually induce the formation of multiple blooms in the following spring (Valiente and Albrigo, 2003). The intensity of these blooms varies depending on the amount of time buds had been exposed to inductive conditions, with those buds that have started differentiation being unable to respond to additional induction. Such multiple blooms also add to the variability in flowering intensity from year to year because during each warm period, buds have been exposed to different induction intensities. The "Citrus Flower Monitor" (Albrigo et al., 2006a) is a web-based system to track citrus flowering in Florida and recommends short periods of winter drought to inhibit bud growth during intermittent warm periods. In our field experiments, a single bloom was consistently observed in trees kept under water deficit during the winter compared to multiple blooms in well-irrigated trees. Thus, in addition to enhancing flowering, winter water deficit could also be used to avoid the initiation of multiple blooms and reduce year to year variation in flowering duration and intensity. Nonetheless, the manipulation of winter water deficits needs to be balanced against simultaneous moisture needs for the tree especially for late maturing citrus cultivars like 'Valencia' or early maturing cultivars like 'Hamlin' in which fruit drop easily at maturity.

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