原著論文

Effects of Planting Bed Height and the Use of Plastic Mesh as Ground Cover on the Flowering of Citrus Trees

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Summary

The effects of planting bed height and the use of a plastic mesh as ground cover on the flowering and fruit production of 3-year-old grapefruit trees (*Citrus* × *paradisi* Macfad) were investigated. Trees planted on a raised or flat bed with or without a black polypropylene mesh as ground cover were compared. From August 2014 to January 2015, the expression of one of the flowering-related genes, citrus *FLOWERING LOCUS T* (*CiFT*), was analyzed in stem tissues. The expression level of one of the *CiFT* homologs (i.e., *CiFT2*) started to increase in October, which corresponded to the beginning of the citrus flowering period in southern Texas, USA. *CiFT2* expression levels were higher in trees planted in beds without ground cover than in trees grown in beds with ground cover, regardless of bed height. In the following spring, trees planted in beds without ground cover produced more inflorescences per node than trees grown in beds with ground cover. There was no significant difference in flowering intensity between trees planted in raised and flat beds. Trees planted in covered beds were larger than trees grown in non-covered beds, regardless of bed height. These results suggest that the use of ground cover affects *CiFT2* expression, the balance between generative and vegetative growth, and tree canopy size, all of which may influence fruit yields.

Key words: *CiFT*, *FT*, flat bed, grapefruit, ground cover, raised bed

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Introduction

Flowering is an important event for fruit trees because the number of flowers can determine fruit yield. Flowering behavior may cause some problems during citrus production. For example, citrus trees do not produce flowers during the juvenile phase, resulting in a lack of fruit. Additionally, the number of flowers in mature trees fluctuates annually, potentially leading to inconsistent fruit production. Fully characterizing the mechanism underlying the regulation of flowering in citrus trees is essential for developing effective management practices that stabilize flower numbers. Temperature, water stress, tree age, and fruit-bearing conditions in a previous year influence the number of flowers that are produced in citrus trees (Nishikawa, 2013). In temperate or subtropical climates, citrus flower differentiation is physiologically induced by cool temperatures during the fall and winter. It has been suggested that citrus *FLOWERING LOCUS T* (*CiFT*) is important for the flowering of citrus trees, and that cool temperatures enhance floral induction via up-regulated *CiFT* expression (Nishikawa, 2013; Nishikawa et al., 2007, 2012).

Soil-management practices, including the use of ground covers and raised beds, may improve tree growth. Ground covers can prevent weed growth, limit soil temperature variability, improve root growth, and increase water use efficiency. In some cases, they can also improve soil fertility and health (Tarara, 2000). However, planting trees on raised beds improves water drainage and air infiltration in heavy soils (Morgan et al., 2009), and has been reported to enhance fine root activity (Myburgh and Moolman, 1991). Nevertheless, the effects of ground covers or raised beds on tree growth, in particular on the expression of flowering-related genes, have not been studied in citrus trees.

The objective of this study was to evaluate the effects of orchard soil management (i.e., the use of raised beds and ground covers) on tree canopy growth, number of flowers, expression of flowering-related genes, and number of fruits on citrus trees. Two planting bed conditions (i.e., raised and flat beds) with or without the use of a plastic mesh as ground cover for a total of four treatments were compared for their impacts on floral induction and fruit production in young grapefruit trees.

Materials and Methods

1. Plant materials and soil data collection

Nine-month-old grapefruit *(Citrus* × *paradisi* Macfad) 'Rio Red' trees grafted on sour orange (*Citrus aurantium* L.) trees were planted in the field at the Texas A&M University–Kingsville Citrus Center (Weslaco, Texas, USA) in spring 2012. The effects of a raised or flat bed with or without an UltraWeb 3000 plastic ground cover (DeWitt Company, Inc., Sikeston, MO, USA) were examined. Trees were grown for 2 years before any data were collected. The raised beds were 45–50 cm tall when the trees were planted. Additionally, the plastic ground cover that was installed prior to the planting of trees completely blocked sunlight for total weed control, while remaining permeable to air, water, and nutrients. The beds and ground cover were 3 m wide, and the distance between trees in each row or between rows was also 3 m. All trees were flood irrigated as needed, but at least once a month, from May to September. Soil temperature and volumetric water content at a depth of about 15 cm below one of the trees for each treatment were monitored every 30 min with a 5TE soil moisture, temperature, and electrical conductivity sensor (Decagon Devices, Pullman, WA, USA). Data were collected from July 2014 to January 2015, and monthly averages were calculated.

2. Total RNA extraction and quantitative reverse transcription polymerase chain reaction

For RNA extractions, eight trees that bore few fruits were selected for each treatment in July 2014. Five spring shoots were harvested from each tree once a month from August 2014 to January 2015. The shoots were divided into stems and leaves. The stem tissues (i.e., internodes and nodes from the base to the apex) from individual trees were combined and then frozen in liquid nitrogen. All samples were stored at −80°C until used for RNA extractions. For the quantitative reverse transcription polymerase chain reaction (qRT-PCR) analysis, total RNA was extracted using the RNeasy Plant Mini Kit (Qiagen, Hilden, Germany). After purifying the extracted RNA by on-column DNase digestion, cDNA was synthesized at 37°C for 2 h using 0.4 μg total RNA, a random hexamer, and the High Capacity cDNA Reverse Transcription Kit (Applied Biosystems, Foster City, CA, USA).

The TaqMan MGB probes and primers specific for *CiFT1–3* were designed as described by Shalom et al. (2012), except the reverse primer for *CiFT3*, which was

designed using the qRT-PCR Assay Design Tool (Integrated DNA Technologies, Coralville, IA, USA) (Table 1). The qRT-PCR assay was conducted using the TaqMan Universal PCR Master Mix (Applied Biosystems) and the CFX96 Real Time PCR Detection System (Bio-Rad, Hercules, CA, USA) according to the manufacturers' instructions. Each reaction comprised 900 nM primers, 250 nM TaqMan MGB Probe, and 2.5 μl template cDNA. For an endogenous control, β-actin primers were used (Shalom et al., 2012) (Table 1). A SYBR Green qRT-PCR assay using the Power SYBR Green Universal PCR Master Mix (Applied Biosystems) and the CFX96 Real Time PCR Detection System was completed according to the manufacturers' instructions to quantify the β-actin gene expression level. The *CiFT* and reference genes were analyzed separately. Each reaction comprised 900 nM primers and 2.5 μl template cDNA. The thermal cycling conditions for the TaqMan and SYBR Green PCRs were as follows: 95°C for 10 min; 40 cycles at 95°C for 15 s and 60°C for 60 s. Gene expression levels were analyzed using the CFX Manager software. The *CiFT* expression levels were normalized against those of the β-actin gene.

3. Flowering intensity, tree canopy volume, and fruit production

Flowering intensity was estimated for each treatment in early spring 2015. Fifteen shoots that had flushed in spring 2014, were randomly selected from the trees used for RNA extractions. We recorded the number of vegetative shoots, generative inflorescences containing only flowers, mixed inflorescences containing flowers and leaves, and total nodes. To assess the effects of raised beds and ground covers on tree growth, the canopy volume was estimated for each treatment by measuring the tree diameter and height with a ranging pole (n = 18 for the raised beds; n = 8 for the flat beds) in March 2015. In May 2015, the number of fruits was recorded for each tree.

4. Statistical analysis

The data regarding the effects of the ground cover, bed type, and their interaction on *CiFT* expression, flowering intensity, canopy volume, and fruit production were analyzed by two-way ANOVA.

Results

1.Soil temperature and moisture

Soil temperature and moisture were compared between raised and flat beds and between beds with and without ground cover. The raised beds were approximately 50 cm tall when the trees were planted in 2012, but had decreased to about 20 cm when the experiments ended in 2015. The soil temperature monthly averages for all treatments peaked in August and then decreased in November. The soil temperatures were relativley stable between November and December. However, between December and January, soil temperatures started to decrease again for all treatments. From July to January, soil temperatures were highest in the raised beds with ground cover. The soil temperatures for the other treatments during this period were similar. The soil volumetric water content monthly averages were 0.16–0.29 m^3 m^{-3} for all treatments, with the highest and lowest values recorded for September and October, respectively. From July to October, the soil volumetric water content was lowest under trees planted in naked flat beds. From November to January, the soil water

Table 1. Sequences of the primers and TaqMan MGB probes used for the quantitative reverse transcription polymerase chain reaction analysis of *CiFT1–3* and ß-actin gene expression.

Target	Sequences (5' to 3')	Primer or probe
CiFT1	CTACCAACAAAATTTCATCACTTGAATAG	Forward Primer
	GGTCTCTCTCCCTGCTAGACATATCA	Reveres Primer
	TCTTACTACTTTTGTAGGTTGTTTG	TaqMan MGB probe
CiFT2	CAACAAAATTTCATCACTTGAATAGTC	Forward Primer
	AAACACTCAACAACACTTAGCACAAA	Reveres Primer
	AGGCTGTGTGTGCGTGTA	TaqMan MGB probe
CiFT3	GTGGGGATTCACAGATTCGT	Forward Primer
	CACCGGAGATCCAAGATTGTAA	Reveres Primer
	ACACGTAAAGCAGAATGTTTGTG	TaqMan MGB probe
ß-actin	GTCTGGTCCATCCATTGTCCA	Forward Primer
	CAATGGCCCCAACCTTAGC	Reveres Primer

content in raised beds tended to be higher without ground cover than with ground cover. The soil temperature and volumetric water content data were collected from only one location, and it was unclear if there were significant differences in the measurements.

2.Relationship between *CiFT* expression and bed condition

There were no major differences in the *CiFT1* and *CiFT3* mRNA levels among treatments except for the samples collected in December from trees grown in naked flat beds (Fig. 1A and C). For all treatments, *CiFT2* expression levels started to increase in October and peaked in January (Fig. 1B). The *CiFT2* mRNA levels from September to December were significantly higher ($P < 0.01$) for trees grown in naked beds than for trees grown in covered beds. From August to December, the average *CiFT2* expression levels were higher for trees in flat beds than for trees in raised beds. However, significant differences were detected only in August and September. Additionally, there were no significant interactions between the ground cover and bed type that affected *CiFT2* expression levels.

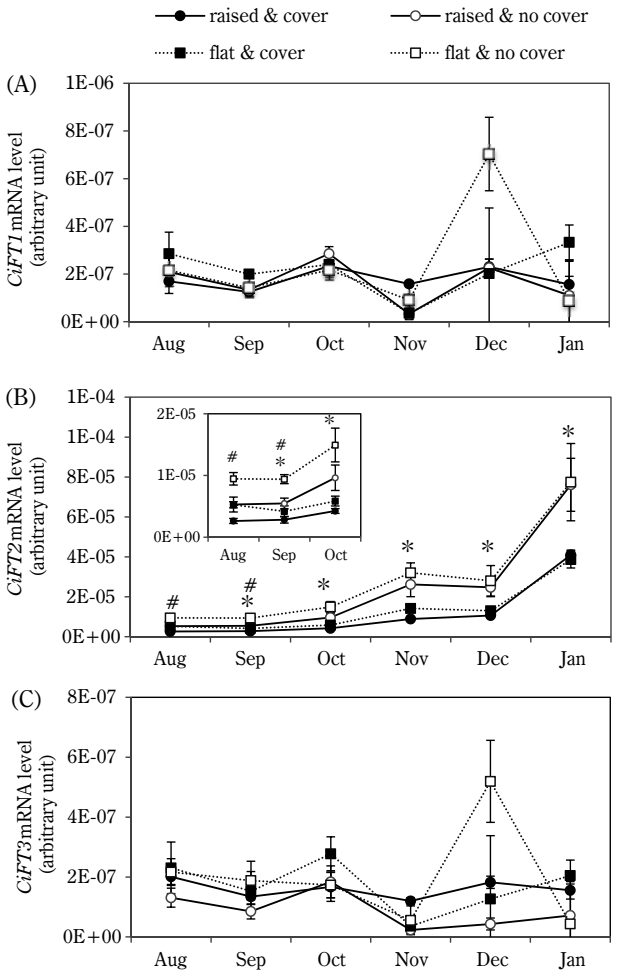

Fig. 1 Changes in *CiFT* expression in the stems of 'Rio Red' grapefruit trees grown in raised or flat beds with or without ground cover. Quantitative reverse transcription polymerase chain reaction analyses were conducted using a gene-specific probe and primers for *CiFT1* (A), *CiFT2* (B), and *CiFT3* (C). The inset of panel (B) focuses specifically on the *CiFT2* expression levels in August, September, and October. Gene expression data are presented as the mean ± standard error (n = 8). *, significant difference ($P < 0.01$) between beds with and without ground cover; #, significant difference ($P < 0.01$) between raised and flat beds.

3.Flowering intensity

There were no signficant interactions between the ground cover and bed type that influenced the number of vegetative shoots, mixed inflorescences, and generative inflorescences per node. In contrast, the abundance of these three bud types was significantly different ($P < 0.01$) between trees grown in beds with and without ground cover (Fig. 2). Additionally, there were more vegetative shoots per node in trees grown with ground cover than in trees lacking ground cover (Fig. 2A). Furthermore, there were fewer mixed and generative inflorescences in trees in covered beds than in trees in naked beds (Fig. 2B and C). Regarding bed height, no significant differences were detected in the number of vegetative shoots or mixed and generative inflorescences. However, the average number of vegetative shoots was higher for trees planted in raised beds than for trees grown in flat beds. In contrast, the average number of generative inflorescences was higher for trees planted in flat beds than for trees in raised beds.

4.Tree canopy volume

Tree canopy volumes were measured in spring 2015 to investigate the effects of raised beds and ground cover on tree size. Two-way ANOVA revealed a significant interaction between ground cover and bed type that affected canopy volume. Additionally, canopy volumes were significantly different depending on the use of ground cover (Fig. 3). Trees planted in covered beds had larger canopy volumes than those grown in naked beds, regardless of bed height. Among trees planted in covered beds, there were no differences in canopy volume between trees in raised and flat beds. However, in the absence of ground cover, canopy volumes were greater for trees in raised beds than for trees in flat beds.

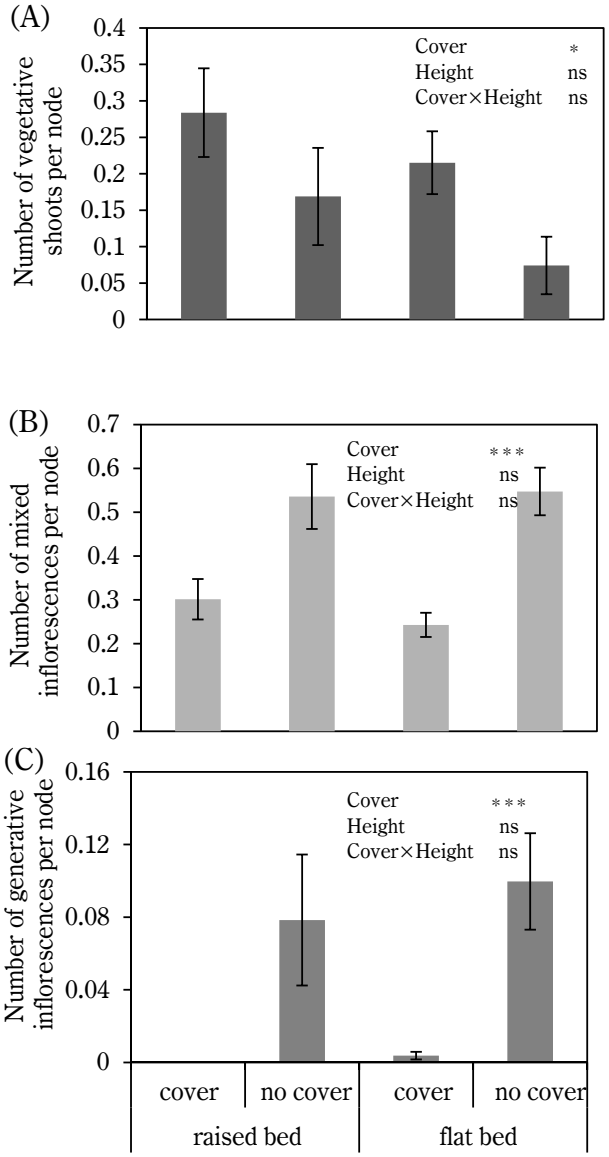

Fig. 2 Number of vegetative shoots (A), mixed inflorescences (B), and generative inflorescences (C) in 'Rio Red' grapefruit trees grown in raised or flat beds with or without ground cover. Columns and bars represent the means and standard errors, respectively (n = 8). * and ***, significant difference at $P < 0.05$ and $P < 0.001$, respectively; ns, not significant.

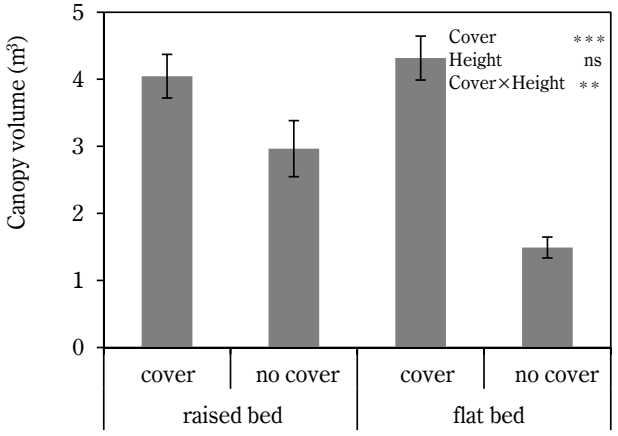

Fig. 3 Canopy volume of 'Rio Red' grapefruit trees grown in raised or flat beds with or without ground cover. Columns and bars represent the means and standard errors, respectively (raised beds: n = 18; flat beds: n = 8). ** and ***, significant difference at $P < 0.01$ and $P < 0.001$, respectively; ns, not significant.

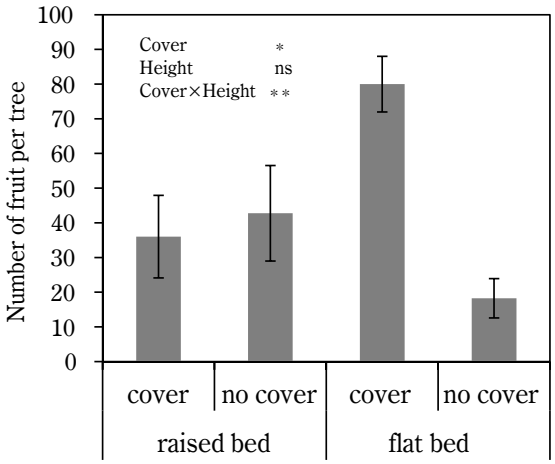

Fig. 4 Number of fruits in 'Rio Red' grapefruit trees grown in raised or flat beds with or without ground cover. Columns and bars represent the means and standard errors, respectively (n = 8). * and **, significant difference at $P < 0.05$ and $P < 0.01$, respectively; ns, not significant.

5.Fruit production

Fruit yields per tree were affected by an interaction between ground cover and bed type. For flat beds, fruit production was 4.4-fold higher for trees grown with ground cover compared with trees lacking ground cover (Fig. 4). In contrast, the use of ground cover did not influence fruit production by trees planted in raised beds. In covered beds, fruit production was 2.2-fold lower for trees planted in raised beds than for trees grown in flat beds. In beds that were left uncovered, fruit yields were 2.3-fold higher for trees planted in raised beds than for trees in flat beds.

Discussion

Temperature, previous fruit-bearing conditions, water stress, and the exogenous application of gibberellin can affect citrus flowering by regulating *CiFT* expression (Chica and Albrigo, 2013; Goldberg-Moeller et al., 2013; Muñoz-Fambuena et al., 2012, 2013; Nishikawa et al., 2007, 2012; Shalom et al., 2012). Three *CiFT* homologs have been identified (Shalom et al., 2012), and expression levels in stems seem to correspond with the induction of flowering in citrus trees (Nishikawa et al., 2007, 2012). Therefore, we used whole stems, including buds, for analyses of *CiFT* expression levels. In Satsuma mandarin

(*Citrus unshiu* Marc.) and Murcott tangor (*Citrus reticulata* Blanco), *CiFT2* (Shalom et al., 2012) and *CiFT3* (Nishikawa et al., 2007) expression levels were observed to be up-regulated during the fall and winter, which coincides with the initiation of the flowering process. Additionally, the accumulation of *CiFT* mRNA is induced by cool conditions (Nishikawa et al., 2007). The *CiFT2* in our study is equivalent to *CiFT3* (Nishikawa et al., 2007) according to Shalom et al. (2012). Therefore, we speculate that the observed induction of *CiFT2* expression after October was due to a decrease in air temperature. The analyzed trees were first exposed to flower-inducing cool temperatures after September. Our data revealed that raising and covering the beds inhibited *CiFT2* expression in August and/or September. These results suggest that a raised bed can regulate *CiFT2* expression at non-flower-inducing temperatures. From October to November, *CiFT2* expression levels were lower in trees planted in covered beds than in trees grown in naked beds. This implies that covering the beds inhibits the accumulation of *CiFT2* transcripts induced by cool temperatures.

The *CiFT2* expression levels were positively correlated with flowering intensity in the following spring. Flowering in citrus trees is generally affected by the fruit-bearing conditions of the previous year (Nishikawa, 2013). However, this study involved 'Rio Red' grapefruit trees, which rarely exhibit an alternate bearing phenotype. Additionally, our analyses involved samples from trees bearing few fruits. Thus, our results were likely unaffected by earlier fruit-bearing conditions. The observed changes in flowering intensity were attributed to the use of raised beds or ground cover. Because *CiFT* promotes flowering (Endo et al., 2005), our results suggest that flowering intensity is affected by ground cover via the regulation of *CiFT2* expression. However, previous studies involving mandarin trees indicated that the expression of *CiFT* homologs other than *CiFT2* was not correlated with floral induction (Nishikawa et al., 2007; Shalom et al., 2012). The results of our study involving grapefruit trees suggest that *CiFT1* and *CiFT3* expression levels are not correlated with flowering intensity, which is consistent with the findings of previous investigations.

Our data also imply that the use of ground cover stimulates vegetative growth and inhibits generative growth. We detected a correlation between flowering intensity and tree canopy volume. Trees with a larger canopy volume produced fewer generative inflorescences and more vegetative shoots compared with trees with a relatively small canopy. Tree canopy volume is generally believed to be dependent on the number and/or growth of specific bud types. Increases in tree size will likely be relatively limited if many flower buds are produced. In contrast, trees are expected to increase in size when many vegetative buds are produced and allowed to grow properly. Therefore, the production of fewer flowers and more vegetative shoots might increase canopy volumes for trees grown in beds with ground cover, which is consistent with our data. We analyzed 3-year-old trees, and trees rarely bloom in the first 2 years after planting. Therefore, most trees usually produce abundant vegetative buds during these initial 2 years. Because data regarding flower production in the first 2 years after planting were unavailable, it is unclear if the canopy volume differences were due to the accumulated effects over 3 years. Regarding bed height, raised beds tended to inhibit generative growth and enhance vegetative growth in young trees. This effect on growth may be correlated with the difference in tree size between raised and flat beds without ground cover. However, the effects of bed height on flowering intensity will need to be confirmed because there was no significant difference in the number of vegetative shoots and generative inflorescences between the raised and flat beds.

In terms of fruit production, trees grown in covered flat beds produced the most fruits even though there were relatively few flowers per node. This may have been because trees in covered flat beds had large canopies and fruit drop was not an important factor. The effects of each treatment on fruit production should be confirmed in future studies.

The use of ground covers or raised beds affects soil conditions, including temperature, moisture, and air infiltration (Tarara, 2000). Floral production, canopy volume, and the expression of a flowering-related gene were influenced by the use of ground cover or raised beds in this experiment. We hypothesize that tree size and the balance between generative and vegetative growth may be affected by the changes to soil conditions induced by the ground cover and raised beds. A previous study concluded that soil and air temperatures of 15°C and 30°C, respectively, can induce flowering in Satsuma mandarin trees (Poerwanto and Inoue, 1990). In contrast, Moss (1976) suggested that root temperatures likely have minimal effects on floral development in sweet orange trees. Drought conditions can induce flowering in citrus trees (Inoue, 1989). Our data did not reveal clear

differences in soil temperature and volumetric water content between raised and flat beds or between beds with and without ground cover. However, because data were collected at only one site, the soil temperature and volumetric water content results may not accurately reflect the treatment effects. Therefore, additional research is required to identify the factor influenced by the use of ground cover or raised beds that inhibits generative growth, while enhancing vegetative growth and increasing tree canopy volume.

Maximizing tree size is important for commercial citrus fruit production, especially just after planting, because tree size generally affects fruit yield. Thus, a method that enables rapid increases in tree size may be useful for shortening the initial period after planting when fruit production is inefficient. Our results suggest that growing trees on covered and raised beds may help increase tree size. However, a larger canopy volume does not guarantee increased fruit yields. Trees planted in covered beds produced relatively large canopies regardless of bed height. However, trees planted in raised beds with ground cover did not produce more fruits than trees planted in flat beds with ground cover. The results of our study suggest that the use of ground cover may enhance fruit production in flat beds, but not in raised beds. A multi-year study will be required to confirm these results.

In conclusion, our results indicate that the use of plastic mesh as ground cover is positively correlated with the number of vegetative shoots, and negatively correlated with the number of generative inflorescences. Trees grown in raised beds tended to produce more vegetative shoots and fewer generative inflorescences than trees planted in flat beds. The *CiFT2* expression levels were relatively high in trees grown in raised beds in August and September and in trees grown using ground cover from September to January. Tree size was positively correlated with the number of vegetative shoots, but negatively correlated with the number of generative inflorescences. Our findings imply that the use of ground covers and raised beds may induce vegetative growth by down-regulating *CiFT2* expression, ultimately contributing to increases in canopy size.

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高畝あるいはマルチはカンキツの花成に影響する

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摘 要

本研究では，高畝の有無及びポリプロピレン製黒色マルチの有無がグレープフルーツ３年生樹の花成に及ぼす影響を調査した。2014年8月から2015年1月まで花成関連遺伝子の一つであるカンキツ *FLOWERING LOCUS T* (*CiFT*) の発現を茎組織で定量した。南テキサスにおいてカンキツの花成は10月に始まるが，*CiFT* ホモログの一つ，*CiFT2* の発現がどの処理区においてもこの月に増大し始めた。実験期間中，*CiFT2* の発現量は高畝・平坦にかかわらず，マルチ無しで植栽された樹で高かった。翌春に観察された花芽数はマルチ有りよりもマルチ無しで多かった。高畝と平坦の間で花芽数に有意差はなかった。樹の大きさは地面の高さに関係なくマルチ有りで大きかった。マルチ無しでは，高畝の方が平坦より樹が大きかった。これらの結果から，マルチ敷設は *CiFT2* の発現，生殖・栄養生長のバランスおよび樹冠容積に影響を与えると思われる。