Tree Physiology 10, 127–139

Effects of water deficit on flower opening in coffee (*Coffea arabica* L.)

CARLOS H. CRISOSTO,[1,2] DAVID A. GRANTZ[1,2,3] and F. C. MEINZER[4]

[1] *USDA, ARS, Hawaiian Sugar Planters' Association, P.O. Box 1057, Aiea, HI 96701, USA*

[2] *Present address: Kearney Agricultural Center, 9240 South Riverbend Avenue, Parlier, CA 93648, USA*

[3] *Author to whom reprint requests should be addressed*

[4] *Crop Science Department, Hawaiian Sugar Planters' Association, P.O. Box 1057, Aiea, HI 96701, USA*

Received May 8, 1991

Summary

The response of coffee (*Coffea arabica* L.) floral buds to different water deficits followed by re-irrigation was investigated. Flower opening was stimulated by irrigation after one period of water deficit if predawn leaf water potential declined below −0.8 MPa. Similar stimulation of flowering was observed when less severe but more prolonged water deficits (ca. −0.3 to −0.5 MPa for two weeks) were imposed, even if water deficit was relieved by re-irrigation several times during this period. Consistent results were obtained in the field and in two greenhouse locations. Stimulation of flower opening by water deficit followed by re-irrigation was restricted to buds at the "open white cluster" stage of development (Stage 4). Only buds at this stage exhibited development of secondary xylem. Split-root experiments indicated that a root signal stimulated flower opening, independently of predawn or midday leaf water status. Frequent irrigation to prevent flowering, followed by a controlled water deficit and re-irrigation to stimulate flowering, may represent a practical method to synchronize flowering and shorten the harvest period in leeward coffee production areas in Hawaii.

Introduction

Coffee growing in many subtropical and tropical production areas is characterized by poorly synchronized floral development and a prolonged harvest period. During the fall–winter period, ripe fruits, large and small green fruits, flowers, and buds at different stages of development may all be found on the same tree. Several of these stages may occur in a single node. In the traditional coffee production area of Kona, island of Hawaii, fruit ripening occurs over a period of about 6 months. Multiple hand-harvests of fully ripe fruits are required to maintain high quality (Beaumont and Fukunaga 1958). Large coffee plantings are currently being established on former pineapple and sugarcane lands in low elevation, leeward environments on the islands of Kauai, Maui and Oahu. The cost of hand-harvesting indicates that efficient mechanical harvesting will be required for successful establishment of this extensive coffee industry in Hawaii. Trials with mechanical harvesters in Hawaii have indicated poor selectivity between ripe fruits and both immature and over-ripe fruits that coexist on bearing trees. Horticultural and genotypic improvements in floral synchronization would facilitate efficient mechanical harvest.

Researchers in different coffee production areas, including India (Gopal and Vasudeva 1972), Kenya (Browning et al. 1975), Zimbabwe (Clowes and Allison 1974), and South America (Alvim 1960, Federico and Maestri 1970, Barros et al. 1978), have concluded that the extended harvest in coffee is associated with a type of floral dormancy. There is little detailed information available on the physiology of dormancy in coffee floral buds. Coffee floral buds in many environments develop for about 2 months after initiation and then become dormant (Wormer and Gituanja 1970, Cannell 1971, Gopal and Vasudeva 1972, Barros et al. 1978). Buds may remain in this dormant condition for weeks or months (Mes 1957, Browning 1973*a*, 1973*b*, Alvim 1986). Anthesis is generally associated with a cycle of drought followed by irrigation or rainfall (Porteres 1946, Alvim 1960, Rees 1964, Clowes and Allison 1974, Oper et al. 1976, Paes de Camargo 1985). It has been suggested (Magalhaes and Angelocci 1976) that release of dormancy by irrigation may be quantitatively related to the intensity of the preceding leaf water deficit.

Research on the relationship between water deficit, re-irrigation and flower opening may lead to cultural practices that consolidate the harvest period in Hawaiian coffee. The present greenhouse experiments and field trial were designed to determine: (1) the specific susceptibility of flower buds at each stage of development to stimulation by water deficit followed by re-irrigation, (2) the level and duration of water deficit required to stimulate flower development, (3) the role of root and edaphic versus leaf and aerial factors in the transduction of the water deficit signal, and (4) the anatomical attributes associated with susceptibility of specific bud stages to water deficit and re-irrigation.

Materials and methods

Greenhouse experiments

Coffee plants (*Coffea arabica* L., cv. Guatemalan) were established from seed in 19-liter pots in a 2/1/1 by volume mix of soil (Molokai Silty Clay Loam, Typic Torrox), potting mix (Jungle Growth, Piedmont Pacific Products, Winder, GA) and volcanic cinders at two low elevation (< 100 m) locations on the island of Oahu, Hawaii (Latitude 21°21′ N, 158°02′ W). The walls of the greenhouses consisted of relatively coarse mesh screen that permitted free exchange of air with the external environment. Maximum values of photosynthetic photon flux density (PPFD) inside the greenhouse were 75% of those in full sunlight. One greenhouse was located near Aiea, HI and the other greenhouse and the field were located 15 miles away at Waipahu. Plants were fertilized at planting (16/7.1/13.3; N/P/K) and at monthly intervals. Pots were irrigated to drainage twice daily at 0700 and 2100 h by an automatic drip system.

At Waipahu, the average daily maximum temperature varied by 3.7 °C, from a high of 30.1 °C in August 1988 to a low of 26.4 °C in January and May 1989. Average daily minimum temperature varied by 4.7 °C, from a high of 23.8 °C in December 1988 to a low of 19.1 °C in January 1989. Precipitation measurements (Class A pan)

at the study site ranged from a high of 252 mm for October 1988 to a low of 41 mm for June 1989. For the 13 months studied, total measured precipitation was 1,796 mm. Measured pan evaporation was highest for July 1989 (213 mm) and lowest for December 1988 (134 mm), totalling 2,311 mm for the 13 months studied. Average total daily solar radiation incident on the site for each month ranged from a high of 486 cal cm^{-2} in August 1988 to a low of 308 cal cm^{-2} in December 1988.

Experiment 1 During December, the normal irrigation regime was withheld from a total of 63 plants (24 months old) in both greenhouse locations until predawn leaf water potentials of individual trees reached values between −0.5 to −2.8 MPa, which required 4–12 days. Immediately after the desired predawn leaf water potentials were reached, twice daily irrigation of the plants was resumed for the following months. Plants subjected to different degrees of water deficit were randomized within each greenhouse.

Experiment 2 Eighteen-month-old coffee plants growing in the greenhouse near Waipahu during November–February (wet season) were subjected to three different irrigation regimes during a 120-day period. Irrigation was applied automatically twice daily, twice weekly, and once weekly by a drip irrigation system. The experiment was a randomized block design with six plants per treatment on each of three benches (blocks). The experiment was replicated on 22-month-old coffee plants during March–June (dry season) with similar results.

Experiment 3 A split-root experiment was carried out during November–February in a completely randomized design. Six months before the experiment began, inarch-grafted coffee plants (18 months old) were prepared according to Hartmann et al. (1990), resulting in plants (24 months old) with two functional root systems in separate pots grafted to a single trunk. Forty grafted plants were assigned to four treatments and randomized in the greenhouse near Waipahu. The four treatments were: (1) both root systems well irrigated, (2) both root systems droughted, (3) original root system well-irrigated with supplementary root system droughted, and (4) original root system droughted with supplementary root system well irrigated. Water was withheld from all droughted pots until those with both root systems droughted reached predawn leaf water potentials lower than −0.8 MPa, when all pots were re-irrigated. The experiment was repeated with an additional 40 plants during the March–June period.

Data from the greenhouse experiments were subjected to analysis of variance (ANOVA).

Field trial

A field trial was conducted in an established coffee orchard (cv. Guatemalan, 18 months of age) near Waipahu, HI. The field, a Molokai Silty Clay Loam (Typic Torrox), was drip-irrigated weekly for 12 h to full replacement through drip emitters placed in the center of each row. The field layout consisted of 12 rows of 36 trees, spaced 0.9 m within and 2.7 m between rows. All rows remained well irrigated until the onset of the trial. Rows 5–7 were then subjected to drought by withholding

irrigation from June 8 to July 12, 1989. Data were collected from 10 trees in rows 6 (droughted) and 10 (control) during a minor bloom occurring in the summer. The principal bloom in this environment is in midwinter.

Water relations

Leaf water potential was determined as leaf xylem pressure potential with a Scholander-type pressure chamber. The terminal portion of a lateral branch from the middle of the canopy, with two to four attached leaves, was enclosed in a plastic bag before excision with a razor blade and insertion into the pressure chamber. Samples were excised before dawn (0530 h) and at midday (1100–1400 h) for determination of leaf water potential.

Phenological measurements

To facilitate phenological measurements coffee buds were classified in seven distinct stages of development (Crisosto and Grantz 1990) as follows: Stage 1 = vegetative bud, 2 = side green, 3 = tight green cluster, 4 = open white cluster, 5 = first white candle, 6 = anthesis, and 7 = small fruits. The stage numbers rather than descriptive names are used throughout this communication. Five branches per tree were premarked for phenological measurements. Number of buds and percent change data are expressed on a per node or per branch basis. A single node represents both axils of a pair of opposite leaves, each of which contains multiple buds (Paes de Camargo 1985).

Histological Observations

A sample of 20 nodes, with many buds at each stage of development, was collected in the field trial on May 12, 1989. For comparison, additional buds were sampled periodically from the greenhouse-grown plants. Samples were fixed in ethanol/glacial acetic acid (3/1), dehydrated and infiltrated with paraplast according to Jensen (1962). Cross sections of pedicels at the base of the flower were made of the uppermost, terminal bud of the three to six buds present in each leaf axil. Sections (10 microns) were cut with a microtome (Spencer 820), mounted on slides, and stained with 1% safranin in 50% ethanol for 3 h, then rinsed in water. Sections were counter-stained with fast green for 5 s, and then dehydrated in ethanol (Jensen 1962). Photomicrographs were taken with a Zeiss microscope using Kodak Professional film (TMAX, ASA 100; Eastman Kodak Company, Rochester, N.Y.).

Results

Experiment 1

Well-watered plants did not flower during this experiment nor over the subsequent 4 months. Flower opening was stimulated only on plants that were subjected to predawn leaf water potentials of less than −0.8 MPa by witholding irrigation, and then re-irrigated (Figure 1). Plants that were droughted but not re-irrigated did not

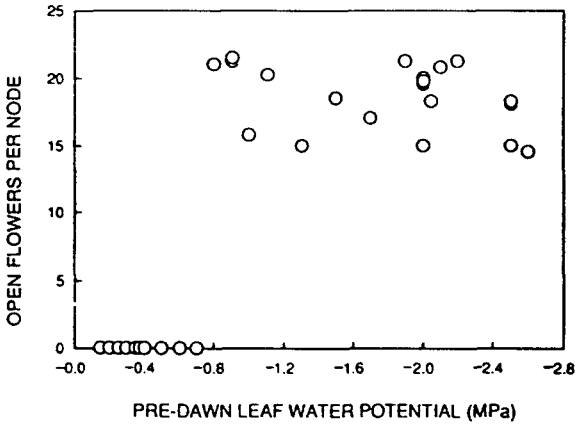

Figure 1. Experiment 1. Effect of a single, rapidly imposed water deficit, followed by re-irrigation, on flower development in greenhouse-grown coffee. Irrigation was withheld from individual trees until predawn leaf water potential reached the value indicated. Each symbol represents the mean of all nodes on five pre-marked branches on one tree (63 trees total).

flower (not shown) even though they remained viable. Imposition of more negative predawn leaf water potentials, over the range −0.8 to −2.8 MPa, followed by re-irrigation, did not promote additional flower opening (Figure 1). A period of 9 to 12 days was required following re-irrigation before floral buds progressed to anthesis.

Experiment 2

Coffee plants that received daily irrigation maintained predawn leaf water potentials above −0.1 MPa (Figure 2). Plants receiving weekly irrigation exhibited predawn leaf water potentials below −1.5 MPa, with recovery to −0.1 MPa every 7 days (Figure 2). This was below the threshold determined in Experiment 1. In plants

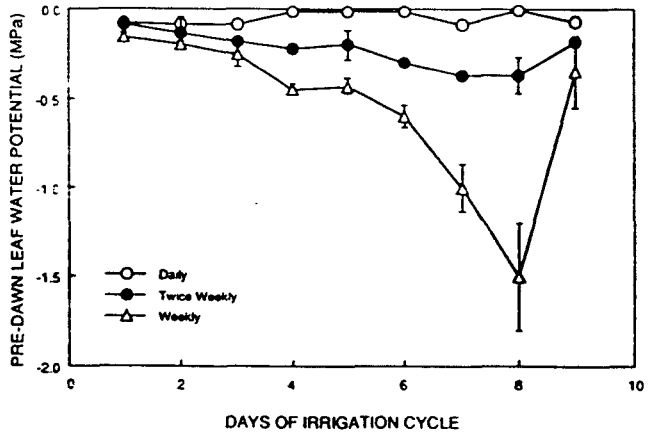

Figure 2. Experiment 2. Time course of predawn leaf water potential in greenhouse-grown coffee plants subjected to three irrigation regimes (mean of nine trees over four weeks, $n = 36$). Bars indicate ± SD.

irrigated twice weekly, leaf water potentials decreased to −0.2 to −0.35 MPa, but returned to about −0.1 MPa every 3 or 4 days (Figure 2). These plants did not reach the threshold identified in Experiment 1.

Flower buds accumulated without progressing to anthesis in the well-irrigated plants. Under these conditions, buds advanced to Stage 4 at which point development was arrested (Figure 3A). Without a water deficit to stimulate flowering, these dormant buds eventually declined in number (Figure 3A: last sample date) because of bud senescence. No buds on well-irrigated plants reached Stage 5.

In plants irrigated weekly, anthesis was observed after two cycles. Given the time required for bud development, this indicated that a single water deficit/re-irrigation cycle was sufficient to stimulate flowering, as expected from the water potential threshold determined in Experiment 1. The twice weekly irrigation treatment, in which predawn leaf water potential never reached the −0.8 MPa threshold, also stimulated flowering, though it required 3–4 cycles for stimulation (Figure 3C). The severe water deficit of the weekly irrigation treatment did not stimulate flowering more than the twice weekly irrigation treatment (Figure 4). The daily irrigation treatment accumulated buds at Stage 4 but the plants did not flower (Figure 4).

Experiment 3

The plants with split-root systems allowed a test of the mechanism by which the stimulation of flowering by water deficit is transduced, because they allowed experimental separation of leaf water status from soil water status. Plants in which both root systems were irrigated were analogous to the well-irrigated controls in Experi-

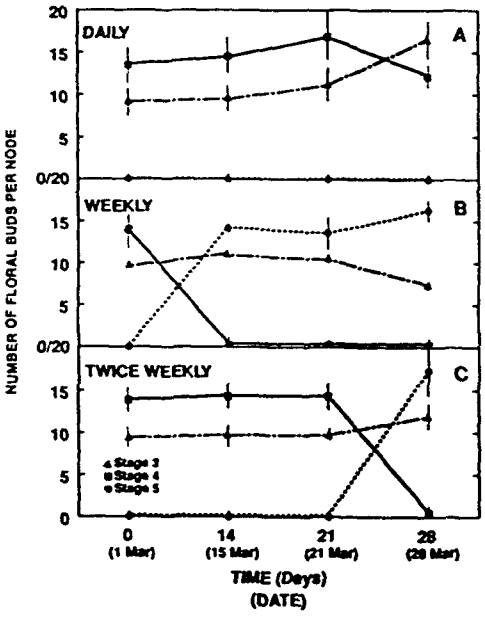

Figure 3. Experiment 2. Effect of irrigation treatment as shown in Figure 2 on the time course of bud development in greenhouse-grown coffee. Day 0 represents the onset of the first cycle of irrigation treatment.

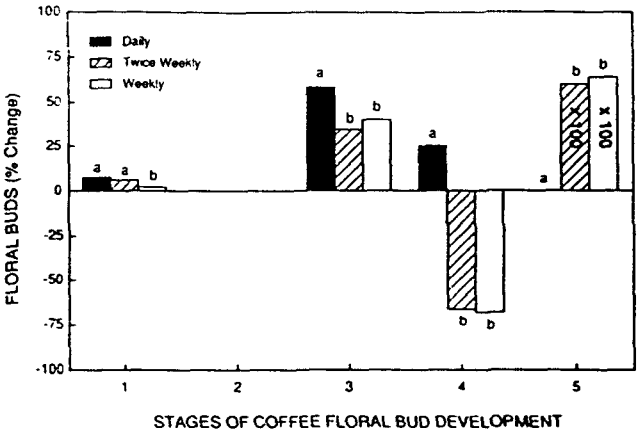

Figure 4. Experiment 2. Effect of irrigation treatment on the relative change in flower buds per branch at each developmental stage, three weeks after onset of irrigation cycles as shown in Figure 2. Within each bud stage, bars with the same letter are not significantly different ($P = 0.05$, $n = 18$).

ments 1 and 2. Leaf water potential did not decline (Table 1) and no flowering was observed. Plants in which both root systems were droughted were analogous to the stressed plants documented in Experiments 2 and 3. These plants exhibited values of both predawn and midday leaf water potentials below the threshold identified in previous experiments, and abundant flowering occurred on re-irrigation. In plants in which only one root system was droughted and the other was well-irrigated (Table 1) neither predawn nor midday leaf water potential declined, yet the same stimulation of flowering was observed as in plants in which both root systems were droughted. The water deficit signal was thus transduced independently of leaf water status and appeared to depend on transport of materials communicating the water status of the driest part of the root system.

Table 1. Effect of a drought and re-irrigation regime on leaf water potential before re-irrigation and on floral bud opening after re-irrigation in coffee plants with split-root systems.

Treatment of original and supplementary root systems	Number of floral buds per node	Leaf water potential (MPa) (before re-irrigation)	
		Predawn	Midday
Both well irrigated	0.00a	−0.15a	−2.20a
Both droughted	21b	−0.90b	−4.50b
Original droughted with supplementary well-irrigated	22b	−0.15a	−2.40a
Original well irrigated with supplementary droughted	18b	−0.15a	−2.50a

Mean separation within column by LSD ($P = 0.05$).

Field trial

In the field, predawn leaf water potentials decreased more slowly than in the greenhouse experiments because of a greater soil volume subject to root exploration and to sporadic light rainfall. Predawn leaf water potentials remained unchanged for about 20 days following suspension of irrigation then declined to −0.47 MPa within 7 days and remained unchanged for the subsequent 10 days until the field was re-irrigated (Figure 5). During this entire period, differences in predawn leaf water potentials between the droughted and weekly-irrigated blocks remained less than ca. 0.3 MPa. These small differences in predawn leaf water status are representative of what may be achieved under Hawaiian field conditions, which are characterized by periodic, year-round rainfall. This drought and re-irrigation treatment, though relatively mild, persisted over a substantial length of time, and stimulated significant differences in flower opening between treated and control plants (Figure 6). When irrigation was suspended (June 8), plants in both treatments exhibited vegetative buds at Stage 1, and reproductive buds at Stages 3 and 4 (Figure 6). Buds passed quickly through Stage 2 without accumulation. There was no progression toward flowering beyond Stage 4 in the well-irrigated plants, nor in the droughted trees during the period without irrigation. Under field conditions, a few buds passed through Stage 4 to anthesis (Stage 6) independently of imposed water deficit (in contrast to the complete arrest at Stage 4 achieved under more controlled greenhouse conditions).

The impact of the water deficit treatment was observed following re-irrigation (Figure 6, July 31 sampling). In the well-irrigated treatment a small increase in number of buds at Stage 4 was observed and a few buds progressed to Stage 6 (Figure 6A). In contrast, in the water deficit treatment (Figure 6B) nearly all buds at Stage 4 progressed to anthesis. This reduced the number of Stage 4 buds to nearly zero and established almost complete synchrony of anthesis at this time. Stimulation of flower opening by water deficit, followed by re-irrigation, was restricted to buds

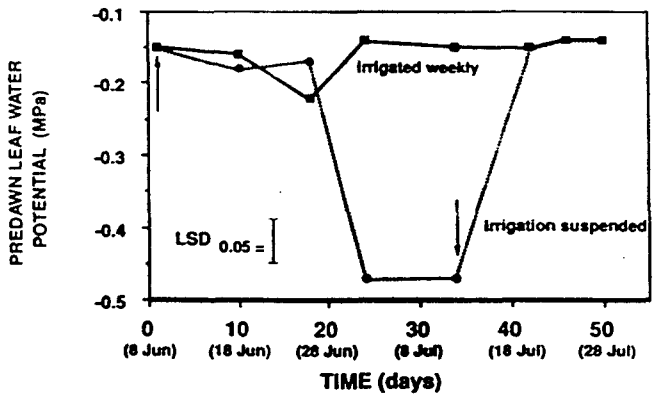

Figure 5. Field Trial. Time course of predawn leaf water potential in field-grown coffee plants with continuous weekly irrigation or with irrigation suspended between June 8 (up arrow) and July 12 (down arrow) 1989. Each symbol represents the mean of two leaves on each of 10 trees.

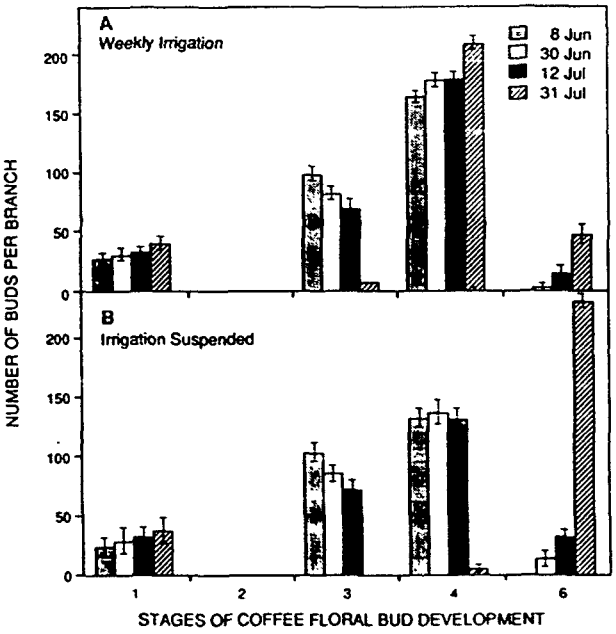

Figure 6. Field Trial. Effect of irrigation treatment on the number of floral buds at each developmental stage on four sample dates. (A) Weekly irrigation. (B) Irrigation suspended as shown in Figure 5. Symbols represent mean × SD of all nodes on five pre-marked branches of 10 trees.

at Stage 4, the open white cluster stage.

Histology

The marked distinction between Stages 3 and 4 in susceptibility to water deficit, even when Stages 3 and 4 appeared within the same node, implicated anatomical features that might be correlated with stages of bud development. This possibility was investigated with particular reference to xylem differentiation in buds collected from the field trial (Figure 7) and from greenhouse experiments (not shown). In Stages 1–3 (e.g., Figure 7A) only primary vascular development was observed. Greater proliferation of metaphloem than metaxylem was apparent in uniform vascular bundles. These were well separated by interfascicular parenchyma cells and distributed in a collateral fashion. In Stage 4 (Figure 7B), Stage 5 (Figure 7C) and Stage 7 (Figure 7D), the formation of secondary vascular tissue was observed within and between the vascular bundles. This resulted in continuous vascular cylinders with files of tracheary elements and rays associated with both xylem and phloem (e.g., Figure 7B). To the exterior of the phloem, multi-seriate rays of collenchyma cells were produced. The remainder of the cortex consisted of parenchymatous tissue, clearly separated from the vascular system. By Stage 5 (Figure 7C) and Stage 7 (Figure 7D), secondary xylem development and pith expansion caused the vascular cylinder to increase in diameter, associated with expansion of the pedicel and continued growth and development of the flower and fruit. Thus, the clear distinction between Stages 1, 2, and 3, in which drought followed by re-irrigation was not

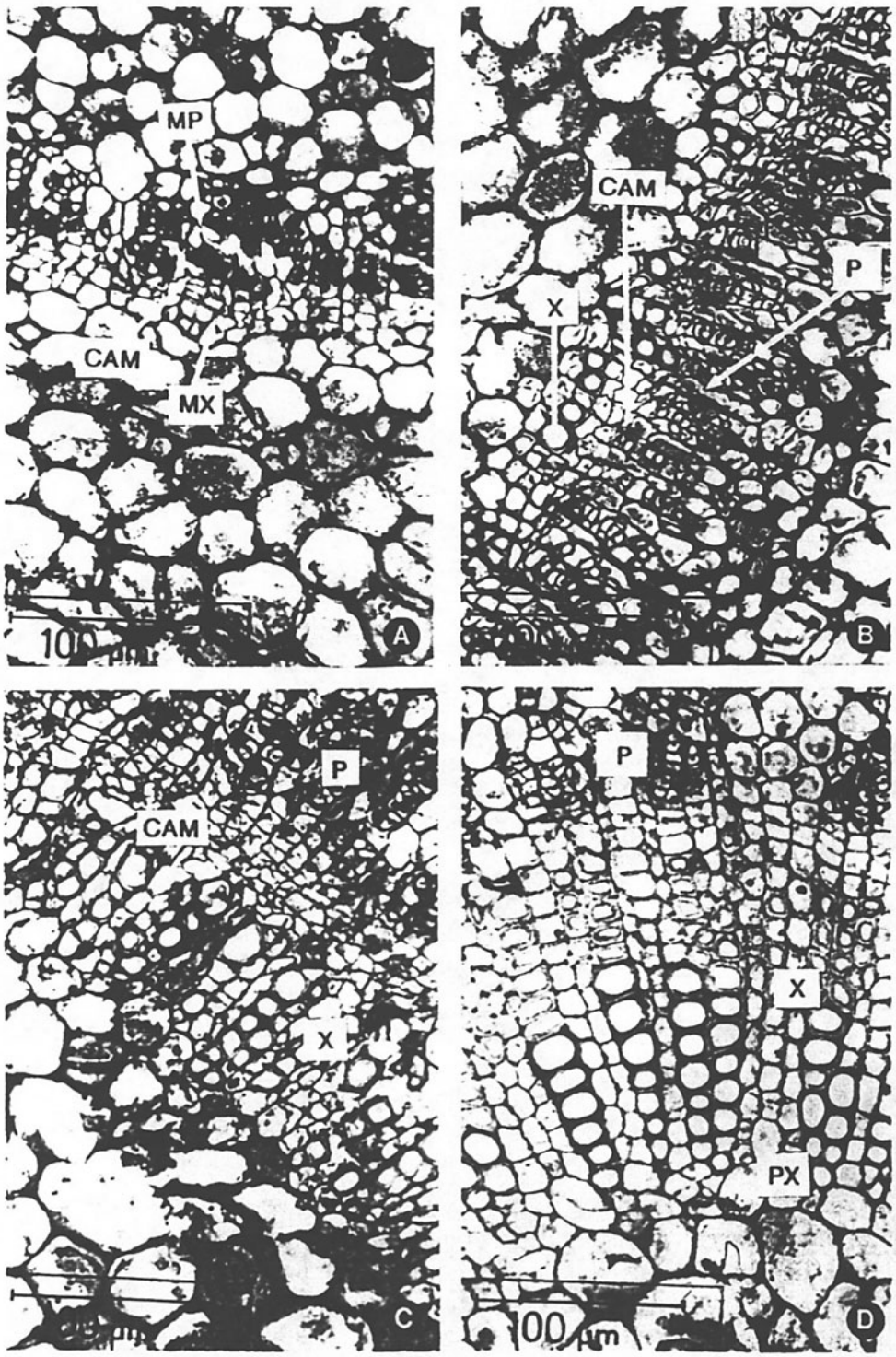

Figure 7. Cross-sections of pedicels showing development of vascular tissue in buds of different developmental stages. (A) Stage 3: Tight green cluster, (B) Stage 4: Open white cluster, (C) Stage 5: First white candle, (D) Stage 7: Small fruits. MX = metaxylem, MP = metaphloem, CAM = cambium, P = phloem, X = xylem.

effective in stimulating flowering, from Stage 4 in which stimulation was observed, is paralleled by differentiation of secondary vasculature in Stage 4 that is not present in Stage 3.

Discussion

Under both greenhouse and field conditions, a period of water deficit followed by re-irrigation stimulated flowering in coffee, by releasing floral buds at Stage 4 from dormancy. Under continuous irrigation or under continuous water deficit, flowering was not observed. Severe water stress was not needed to promote anthesis. A short period of low water potential was equivalent to a longer period of less severe water stress (less negative water potential), suggesting that a stress-day model could be developed to predict flowering in coffee. Reduced leaf water potential was not required. Transduction of the drought treatment required only that part of the root system be subjected to water deficit.

These data help to explain reports of diverse and often contradictory patterns of floral behavior in coffee in different production areas. When an accumulation of buds at Stage 4 coincides with the dry season, anthesis will occur following the first substantial rain. This is the case in some coffee growing regions of Central and South America (e.g., Alvim 1958, Magalhães and Angelocci 1976), India (Gopal and Vasudeva 1972, Browning 1973*a*, 1973*b*), Zimbabwe (Rees 1964, Clowes and Allison 1974), and Hawaii (Kona district, Beaumont and Fukunaga 1958), as well as low elevation production areas of Australia (J. Drinner, personal communication). Flowering in these regions is typically more synchronized than in areas where accumulation of the sensitive stage of floral bud development occurs during the rainy season, as in most of the new, leeward production areas in the Hawaiian islands.

Coffee trees growing under irrigation in Hawaiian areas exhibit a major bloom between December and March, during the rainy season. As the floral buds progress to Stage 4 the plants are exposed to repetitive soil water deficit, which is relieved by sporadic rainfall or by irrigation. Dormancy is broken and development toward anthesis proceeds. This accounts for the nearly total lack of floral synchrony observed in these production areas. Manipulation of irrigation during the main bloom will likely require a protocol of high frequency irrigation to prevent cycling of plant water status, until a substantial number of buds has accumulated at Stage 4, followed by a suspension of irrigation. Flowering would then be induced by the next rain or irrigation. Continued rain would delay imposition of the drought, but would increase the number of buds at Stage 4.

The split-root experiments indicated that a critical level of leaf stem water deficit was not required to stimulate flowering, as long as part of the root system was subjected to soil drying. Detection of soil water content by roots may involve synthesis of chemical messengers in the roots or changes in transport of such substances (Zhang et. al. 1987, Munns and King 1988). Materials arriving at the buds during the stress, or specifically following re-irrigation, may stimulate floral opening. Both cytokinins and gibberellins have been reported in physiologically signifi-

cant concentrations in extracted xylem sap of coffee (Browning 1973*a*, 1973*b*).

The stimulatory effect of water deficit and subsequent irrigation on flowering was restricted to buds at Stage 4, the open white cluster stage (Crisosto and Grantz 1990). This restriction of sensitivity to a single bud stage has been overlooked in previous studies (e.g., Magalhães and Angelocci 1976) due to lack of sufficiently detailed phenological measurements. There were distinct anatomical differences between buds that were capable of stimulation and those that were not. Immature buds that were not susceptible to stimulation by water deficit displayed a low number of small, dispersed primary xylem elements, whereas by Stage 4 a well defined vascular cylinder containing secondary xylem had developed. Anatomical restriction of transport of water, nutrients, or growth substances to buds at Stages 2 and 3 may isolate them from putative root-derived signal metabolites generated during or following root water deficit. This could explain the partial success of exogenously applied growth regulators in promoting flower opening in coffee (Alvim 1958, 1960, 1986, Schuch et al. 1990), though this effect is also largely confined to buds at Stage 4 (Crisosto and Grantz, unpublished observations).

These data suggest that horticultural manipulations of plant water status (or growth regulators) should be timed to coincide with either natural or manipulated accumulation of buds at the receptive Stage 4, in order to maximize effects on floral synchrony. A mild, prolonged soil water deficit was as effective as a short, intense water deficit in promoting floral development in coffee. Thus, periodic interruption of a prolonged soil water deficit by rainfall would not reduce the effectiveness of the water stress. A management protocol involving high frequency irrigation to postpone flowering, subsequent suspension of irrigation to effect a mild but prolonged water deficit, followed by thorough re-irrigation to release dormancy, has promise for horticultural application even in production areas of year-round light rainfall. Differences between available coffee cultivars, in regulation of gas exchange and rates of soil water depletion (Meinzer et al. 1990) suggest some potential for selection of cultivars with enhanced ability to respond to the brief periods of controlled water deficit that can be induced under the conditions that prevail in Hawaiian production areas. It remains to be demonstrated that enhanced synchrony of anthesis will adequately enhance synchrony of harvest some 5 to 7 months later.

Acknowledgments

The authors thank Drs. J.G. Luza and R.V. Osgood for helpful advice.

References

Alvim, P. 1958. Estimulo de la floración y fructificación del cafeto por aspersiones con acido giberelico. Turrialba 8:64–72.

Alvim, P. 1960. Moisture stress as a requirement for flowering of coffee. Science 132:354.

Alvim, P. 1986. Coffee. *In* CRC Handbook of Flowering, Vol 2. Ed. A.H. Havely. CRC Press, Boca Raton, FL. p 23.

Barros, R., S. Maestri and M.P. Coons. 1978. The physiology of flowering in coffee: a review. J. Coffee Res. 8:29–73.

Beaumont, J.H. and E.T. Fukunaga. 1958. Factors affecting the growth and yield of coffee in Kona, Hawaii. Hawaii Expt. Sta. Bull. No. 113.

Browning, G. 1973*a*. Flower bud dormancy in *Coffea arabica* L. I. Studies on gibberellin in flower buds and xylem sap and abscisic acid in flower buds in relation to dormancy release. J. Hort. Sci. 48:29–41.

Browning, G. 1973*b*. Flower bud dormancy in *Coffea arabica* L. II. Relations of cytokinins in xylem sap and flower buds to dormancy release. J. Hort. Sci. 48:297–310.

Cannell, M.G.R. 1971. Photoperiodic response of mature trees of arabica coffee. Turrialba 22:198–205.

Clowes, M.St.J. and J.C.S. Allison. 1974. Physiological factors influencing irrigation management of coffee in Zimbabwe. Zimbabwe J. Agric. Res. 20:1–19.

Crisosto, C.H. and D.A. Grantz. 1990. Response of coffee (*Coffea arabica* L.) bud developmental stage to water stress. XXIII International Horticultural Congress, Firenze. Abstracts. Vol. 1, p 277.

Federico, D. and M. Maestri. 1970. Ciclo de crescimiento dos botões florais de café (*Coffea arabica* L.). Rev. Ceres 27:171–181.

Gopal, N.H. and N. Vasudeva. 1972. Physiological studies in arabica coffee under South Indian conditions. I. Growth of flower buds and flowering. Turrialba 23:146–153.

Hartmann, H.T., D.E. Kester and F.T. Davies. 1990. Plant propagation: principles and practices. Prentice Hall, Englewood Cliffs, NJ, USA. Chap. 12, p 364.

Jensen, W.A. 1962. Botanical histochemistry. Freeman, San Francisco.

Magalhães, A.C. and L.R. Angelocci. 1976. Sudden alteration in water balance associated with flower bud opening in coffee plants. J. Hort. Sci. 51:419–423.

Mes, M.G. 1957. Studies on the flowering of *Coffea arabica* L. II. Breaking the dormancy of coffee buds. Port. Acta Biol. 4:342–354.

Meinzer, F.C., G. Goldstein and D.A. Grantz. 1990. Carbon isotope discrimination in coffee genotypes grown under limited water supply. Plant Physiol. 92:130–135.

Munns, R. and R.W. King. 1988. Abscisic acid is not the only stomatal inhibitor in the transpiration stream of wheat plants. Plant Physiol. 88:703–708.

Oper, P., G. Frankie and H. Baker. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. J. Biogeog. 3:231–236.

Paes de Camargo, A. 1985. Florescimento e frutificação de café arabica nas diferentes regioes (cafeeiras) do Brasil. Pesp. Agropec. Bras. 20:831–839.

Portères, R. 1946. Action de l'eau aprés une periode seche sur le declenchement de la floraison chez. *Coffea arabica* L. Agron. Tropicale. 1:148–158.

Rees, A.R. 1964. Some observations on the flowering behavior of *Coffea rupestris* in Southern Nigeria. J. Ecol. 52:1–7.

Schuch, U.K., L.H. Fuchigami and M.A. Nagao. 1990. Gibberellic acid causes earlier flowering and synchronizes fruit ripening of coffee. Plant Growth Regul. 9:59–64.

Wormer, T.M. and J. Gituanja. 1970. Seasonal patterns of growth and development of arabica coffee in Kenya. II. Flower initiation and differentiation in coffee east of the Rift Valley. Kenya Coffee 35:270–280.

Zhang, J., U. Schurr and W.J. Davies. 1987. Control of stomatal behavior by abscisic acid which apparently originates in the roots. J. Exp. Bot. 38:1174–1181.