

Flowering, Ethylene Production, and Ion Leakage of Coffee in Response to Water Stress and Gibberellic Acid

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Abstract. The effects of water stress and GA₃ on breaking dormancy of flower buds of coffee (*Coffea arabica* L.) were investigated. In the first experiment, water was withheld until the trees reached leaf water potentials (WP) of -1.20, -1.75, -2.65, or -3.50 MPa. Water potential, ethylene production, and ion leakage of flower buds and leaf disks were examined from release from water stress until anthesis. Trees that had experienced leaf WP of less than -2.65 MPa, and flower bud WP of about -4.0 MPa flowered within 9 days after irrigation. In flower buds where dormancy had been broken with water stress, ethylene production was low compared to dormant buds and flowers at anthesis. In the second experiment, 0, 50, 100, or 200 mg GA₃/liter was painted on branches of nonstressed trees. In experiment three, water was withheld until plants reached leaf WP of -0.6, -1.3, -2.1, or -3.0 MPa, then two branches per tree were painted with 0, 50, and 100 mg GA₃/liter. Gibberellic acid partially compensated for insufficient water stress to initiate flower opening. Ethylene evolution of flower buds was affected by water stress but not by GA₃ treatment. Severe water stress treatments and GA₃ treatment (200 mg-liter⁻¹) increased ethylene evolution of leaf disks. Ion leakage of flower buds and leaf disks was increased by severe water stress. Ion leakage of flower buds was highest at anthesis. After water stress, dormant and nondormant flower buds at the 4-mm stage could be distinguished based on their ethylene evolution. Chemical name used: gibberellic acid (GA₃).

Based on its flowering pattern, coffee is classified as a gregarious species, with individual plants flowering simultaneously over extended areas and within a short time (Cannell, 1985). Coffee flower buds become dormant after reaching 4 to 6 mm in length (Mes, 1957). Water stress breaks dormancy and is considered mandatory for normal flower development (Alvim, 1960; Piringer and Borthwick, 1955). After dormancy is broken, irrigation or exogenous GA₃ is required to stimulate development of the flower buds to anthesis within 8 to 12 days (Alvim, 1958; Browning, 1975; van der Veen, 1968). Once nondormant flower buds respond to the growth stimulus by starting to elongate, they are committed to flower, whereas dormant buds will remain at the 4- to 6-mm stage. Dormant and nondormant buds cannot be distinguished by morphology or anatomy until 3 to 4 days after irrigation when nondormant flower buds begin to elongate (Mes, 1957).

Magalhaes and Angelocci (1976) found that dormancy was broken and flowering induced when coffee plants were subjected to water stress with a threshold leaf WP of -1.2 MPa or less. Water movement into a flower bud occurs with increasing water stress and is enhanced by the presence of a leaf subtending the flower bud, compared to defoliated nodes (Astegiano et al., 1988).

Environmental conditions or chemical agents that produce near lethal stress can break bud dormancy in temperate woody

plants (Fuchigami and Nee, 1987). Increased ion leakage and ethylene production are related to the degree of stress and breaking of dormancy in crabapple (*Malus floribunda* Sieb) and red-osier dogwood (*Cornus stolonifera* Michx.) (Nee, 1986). An increase in ethylene production with increasing water loss was observed in plum leaves (*Prunus insititia* L.) (Kobayashi et al., 1981). Increased ion leakage coincided with peak ethylene production in freeze-damaged *rhododendron* leaf disks, suggesting the onset of membrane disintegration (Harber and Fuchigami, 1986).

In a previous field study we found that buds at the 4-mm stage treated with 100 mg GA₃/liter flowered in the absence of rain (Schuch et al., 1990). Exposure to water stress in the field could not be controlled and was not monitored. Therefore, we were unable to separate effects of water stress and GA₃. The first objective of the current study was to use controlled environments to determine the effects of water stress and GA₃, individually and in combination, on coffee flower bud development. Secondly, we investigated how ethylene evolution and ion leakage of flower buds and leaf tissues were affected by treatments that break dormancy.

Materials and Methods

Coffee (cv. Guatemala) trees were grown from seed in 4-liter plastic pots in a mixture of 2 pumice : 1 peat : 1 soil (by volume) for 2 years in a greenhouse under 25/19C day/night cycles and natural photoperiod (Corvallis, Ore., 44°N latitude). Plants with flower buds ≤ 4 mm long were transferred to a growth chamber with an 8-h photoperiod (600 μmol·m⁻²·s⁻¹), 26/23 (± 2)C day/night, 60% to 80% relative humidity and were acclimated for 3 weeks before the experiments were started. Plants were irrigated every other day.

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Abbreviation: WP, water potential.

Water potential (Expt. I). Water was withheld from 4 Oct. 1989 until the leaf WP of three trees each averaged -1.20 , -1.75 , -2.65 , or $-3.50 (\pm 0.2)$ MPa. When the desired WP were attained (day 0), plants were watered to container capacity, and thereafter, the pots were irrigated daily with 500 ml of water. Each water-stress treatment was applied to three trees in a completely randomized design. Ten nodes per tree, tagged at the beginning of the experiment, were monitored for anthesis. The criteria for anthesis was a minimum of two open flowers per node, at least one in each leaf axil. Leaf and flower bud WP, ethylene evolution, and ion leakage were determined on day 0 before irrigation of the water-stressed plants, and 3, 6, and 9 days after irrigation to release water stress. Leaf WP was determined from two leaves of each tree. Twenty flower buds were randomly collected from the three trees of each leaf WP treatment, 10 buds each were used to determine flower-bud WP and ethylene evolution. Six mature leaves from the upper part of the canopy were randomly collected from the trees of each leaf WP treatment. Five samples with two leaf disks each were used to measure ethylene evolution. Ion leakage was measured from flower buds and leaf disks that were used for ethylene determination.

Gibberellic acid (Expt. II). On 6 Jan. 1990, four lateral branches were selected on each of 10 coffee trees growing in the greenhouse. On each branch, aqueous solutions of 0, 50, 100, or 200 mg GA₃/liter (Sigma, St. Louis; dissolved in ethanol, then diluted with distilled water) plus 0.2% Tween 20 (US Biochemical Corp., Cleveland) were applied with a brush to buds, foliage, and stems. Control branches were painted with solutions containing ethanol, Tween 20, and distilled water. Trees were irrigated daily with 500 ml of water. Ethylene evolution of two flower buds from treated branches on each tree was determined every 5 days until 20 days after GA₃ application (26 Jan. 1990). The number of open flowers per node and percentage of nodes at anthesis on five preselected nodes per treatment on each tree were recorded. The data were analyzed as a randomized complete-block design with one tree representing a block.

WP and gibberellic acid (Expt. III). Water was withheld from 4 Dec. 1989 until the leaf WP of three trees each averaged -0.6 , -1.3 , -2.1 , or -3.0 MPa. At rewatering (day 0), aqueous solutions, prepared as in Expt. II, of 0, 50, and 100 mg GA₃/liter were applied with a brush to buds, foliage, and stems of individual lateral branches. The experiment was a split-plot design with water stress as the main plot applied to three trees each, and each GA₃ concentration applied to two branches per tree as the subplot. On each tree, five preselected nodes per GA₃ treatment were monitored for anthesis and flower bud length. Leaf WP, and ethylene production and ion leakage of flower buds and leaf disks were determined on day 0 before irrigation of water-stressed trees, and 3, 6, and 9 days after rewatering. Sampling procedures and number of samples were the same for each leaf WP/GA₃ treatment combination as for each leaf WP treatment in Expt. I.

WP measurements. On each sampling date, leaf xylem WP of the two most recently fully expanded leaves on a lateral branch in the upper half of the canopy was measured with a pressure chamber (PMS, Corvallis, Ore.) for each tree. Leaf and flower bud samples were taken between 1 and 3 h after the onset of the photoperiod in the growth chambers. Water potential of flower buds was measured with a thermocouple psychrometer (Decagon Devices, Pullman, Wash.) Flower buds were cut at the base of the pedicel, and two buds were equilibrated in thermocouple cups for 2 h before the measurements

were taken. The psychrometer was calibrated with two or three standard KCl solutions at each sampling time.

Ethylene measurements. For each sample, two flower buds or two 10-mm leaf disks were incubated with a drop of water in 5-ml syringes for 2 h in the dark at room temperature (22 to 24°C). A 1.0-ml gas sample was injected in a Gow-Mac Series 580 (Gow-Mac Instrument, Bridgewater, N.J.) gas chromatography with a flame ionization detector and activated alumina column. Column, detector, and injector temperatures were 80, 100, and 90°C, respectively. Flow rates for helium and hydrogen were 25 ml·min⁻¹ and 200 ml·min⁻¹ for air.

Ion leakage. Flower buds and leaf disks used for ethylene determination were incubated in stoppered vials with 3 ml of double-distilled water, placed on a shaker for 24 h, and initial ion leakage was measured with a conductivity meter (Electromark Analyzer, Markson Sci., Phoenix, Ariz.). The final leakage was determined after vials were placed in a 60°C waterbath for 2 h to kill the plant tissue, and incubated for another 24 h on the shaker. Percent leakage was calculated as the ratio of initial : final values $\times 100$.

Results

WP. Plants that attained leaf xylem WP of -2.65 and -3.5 MPa reached anthesis within 9 days after irrigation, whereas those exposed to -1.2 and -1.75 MPa leaf WP did not flower (Fig. 1). Flower buds that developed to anthesis (-2.65 and -3.5 MPa leaf WP treatments) had a WP of about -4.0 MPa before plants were irrigated (Fig. 1). Three days after irrigation, all treatments had equilibrated to flower-bud WP of -2.5 (± 0.2) MPa, and thereafter WP ranged between -1.8 and -2.7 MPa. Leaf WP of all trees ranged between -0.6 and -1.1 MPa 3, 6, and 9 days after irrigation.

Flower buds from plants that were stressed to leaf WP of -2.65 and -3.5 MPa and developed to anthesis produced significantly ($P = 0.01$) less ethylene at 0, 3, and 6 days after irrigation than buds from plants exposed to less severe water stress (Fig. 2). Ethylene evolution of flower buds did not differ between treatments 9 days after irrigation. Leaf disks from plants that were stressed to -2.65 and -3.5 MPa produced more ethylene 3 and 6 days after irrigation than disks from plants stressed to -1.2 and -1.75 MPa (Table 1).

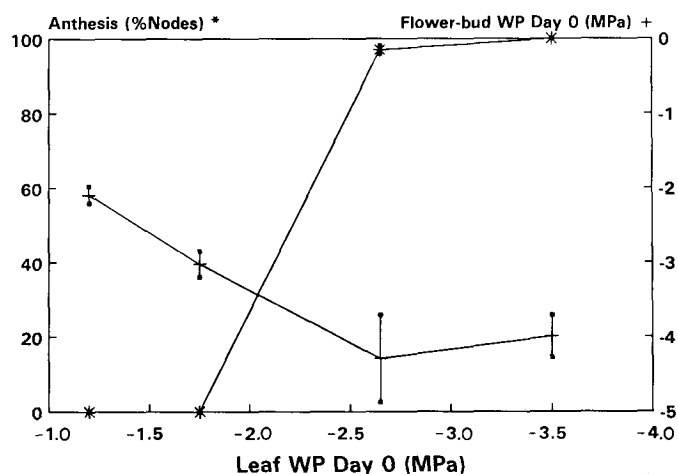


Fig. 1. Relationship between leaf xylem WP at day 0 and anthesis at day 9 and flower-bud WP at day 0 (Expt. I). Leaf and flower-bud WP were measured immediately before irrigation of water-stressed plants. Flowering occurred 9 days after irrigation. Vertical bars represent \pm SE.

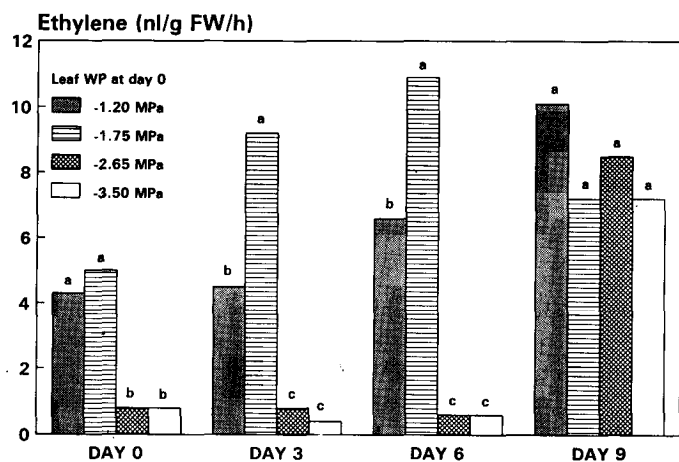


Fig. 2. Effect of water stress on ethylene evolution from flower buds 0, 3, 6, and 9 days after irrigating to release water stress (Expt. I). Each mean represents five replications. Columns with different letters within a sampling date indicate significant differences between treatments at $P = 0.05$, Tukey's studentized range test.

Table 1. Ethylene evolution of leaf disks from trees that were water stressed (Expt. I).

Leaf WP ^a (MPa)	Ethylene evolution (nl/g fresh wt per hour)			
	Days after treatment			
	0	3	6	9
-1.20	0.8 ab ^y	0.6 a	0.8 a	0.8 a
-1.75	0.5 a	0.6 a	0.7 a	1.0 a
-2.65	1.1 ab	1.6 b	1.3 b	0.8 a
-3.50	1.6 b	1.3 b	1.3 b	2.3 b

^aWP is leaf water potential at day 0, immediately before trees were irrigated.

^yMeans within a column followed by different letters indicate significant differences between treatments at $P = 0.05$, Tukey's studentized range test.

Table 2. Ion leakage of flower buds and leaf disks from water-stressed trees (Expt. I).

Leaf WP ^a (MPa)	Ion leakage (%)			
	Days after treatment			
	0	3	6	9
<i>Flower buds</i>				
-1.20	7.0 a ^y	5.4 a	7.0 a	4.9 a
-1.75	5.1 a	3.1 a	5.8 a	5.0 a
-2.65	6.2 a	10.3 b	8.3 a	39.1 b
-3.50	10.5 a	4.7 a	21.9 b	53.6 c
<i>Leaf disks</i>				
-1.20	5.2 a	7.4 b	10.5 b	5.8 a
-1.75	6.3 a	5.7 a	8.8 ab	9.4 b
-2.65	7.1 a	8.3 b	8.4 ab	7.8 ab
-3.50	10.4 b	5.2 a	7.6 a	8.8 b

^aWater potential at day 0, immediately before trees were irrigated.

^yMeans within a column followed by different letters indicate significant differences between treatments at $P = 0.05$, Tukey's studentized range test.

Ion leakage of flower buds and leaf disks was generally higher in plants exposed to greater water stress, but the effect was not consistent (Table 2). Flower buds exhibited the highest amount of ion leakage at anthesis. Ion leakage ranged between 3% and 10% for leaf disks and flower buds at all other sampling times.

Gibberellic acid. Branches treated with 200 mg GA₃/liter had the most flowers per node that had reached anthesis 10 days after treatment (Table 3). The percentage of nodes with flowers at anthesis varied considerably between trees (Table 3). Abnormal flower buds occurred in all treatments, either as safflowers (van der Veen, 1968) that opened when buds were still ≤ 4 mm long, or 4-mm buds remained closed with the style elongating beyond the petals (Cambrony and Snoeck, 1983; Huxley and Ismail, 1969). In either case, flowers aborted within 2 weeks after opening or style elongation. Styles of flowers treated with the highest GA₃ concentration elongated to 8 to 12 mm, whereas styles were shorter using lower GA₃ concentrations.

Gibberellic acid did not influence ethylene production (nanoliters per gram fresh weight per hour) of flower buds, except 15 days after irrigation ($P = 0.01$), when buds treated with 100 or 200 mg GA₃/liter evolved 6.6 and 7.8 nl/g fresh weight per h; those treated with 0 or 50 mg GA₃/liter produced 5.1 and 5.3 nl/g fresh weight per h, respectively. Ethylene evolution of flower buds ranged from 4.4 to 7.8 nl/g fresh weight per h for all samples.

WP and gibberellic acid. Plants stressed to leaf WP of -3.0 MPa flowered within 8 days after irrigation, regardless of the GA₃ treatment (Table 4). Anthesis was delayed on a small percentage of nodes from plants stressed to leaf WP of -2.1 MPa or less (Table 4).

Flower buds of plants that were stressed to -3.0 MPa produced ($P = 0.01$) less ethylene 0, 3, and 6 days after irrigation, and more ethylene 9 days after irrigation than flower buds of plants that were exposed to leaf xylem WP of -2.1 , -1.2 , or -0.6 MPa (Fig. 3). Because GA₃ treatment did not influence

Table 3. Anthesis of coffee flower buds 10 days after treatment with GA₃ (Expt. II).

GA ₃ (mg·liter ⁻¹)	Flowers/node at anthesis	Flowering nodes (%)
0	1.0 ^z	34 (8.4) ^y
50	1.4 ^{NS}	40 (9.6)
100	0.9 ^{NS}	36 (7.5)
200	2.6 [*]	64 (14.8)

^zMeans within a column followed by * or NS indicate significant or no significant difference at $P = 0.05$, respectively, between control and GA₃ treatments (Dunnnett's Test).

^yMean (standard error).

Table 4. Percentage of nodes with flowers at anthesis 8 and 28 days after plants at different leaf xylem water potentials (WP) were treated with GA₃ (Expt. III).

WP (MPa)	GA ₃ (mg·liter ⁻¹)	Flowering nodes (%) ^a after	
		8 days	28 days
-0.6	0	0	10.0 (5.8)
	50	0	26.7 (17.7)
	100	0	30.0 (19.8)
-1.3	0	0	0
	50	0	0
	100	0	10.0 (9.9)
-2.1	0	0	0
	50	10.0 (5.8)	0
	100	23.3 (14.5)	6.0 (5.4)
-3.0	0	93.3 (6.7)	0
	50	96.7 (3.3)	0
	100	100.0	0

^aEach mean (standard error) is calculated from 30 nodes (10 nodes replicated on three trees).

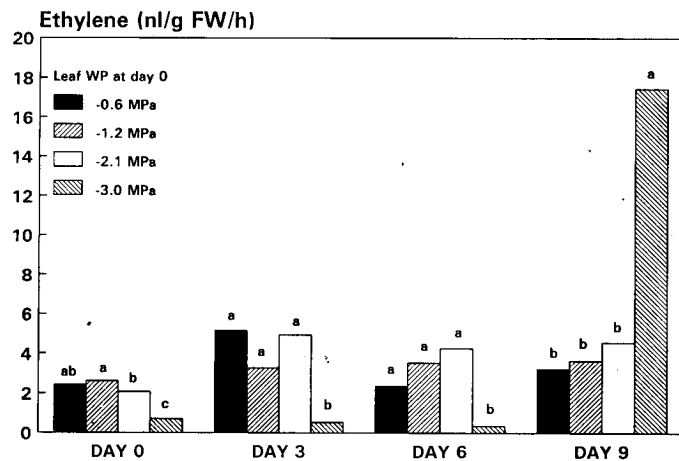


Fig. 3. Effect of water stress and GA₃ on ethylene evolution of flower buds 0, 3, 6, and 9 days after irrigating to release water stress (Expt. III). Means are pooled over GA₃ treatments (0, 50, 100 mg-liter⁻¹), each bar represents 20 replications. Columns with different letters within a sampling date indicate significant differences between treatments at $P = 0.05$, Tukey's studentized range test.

Table 5. Ethylene evolution from leaf disks from coffee trees that were water stressed and received GA₃ treatments (Expt. III).

Leaf WP ^z (MPa)	Ethylene evolution (nl/g fresh wt per hour)			
	Days after treatment			
	0	3	6	9
-0.6	1.0 ^a	0.7 a	1.0 a	0.6 ab
-1.2	0.4 b	1.9 b	0.8 a	0.5 a
-2.1	0.7 ab	1.1 ab	1.1 a	0.7 ab
-3.0	0.9 a	1.5 ab	1.2 a	0.9 b
GA ₃ (mg-liter ⁻¹)				
0	1.0	0.9 ^w	0.6	0.5
50	---	1.2 ^{NS}	1.1 ^{NS}	0.7 ^{NS}
100	---	1.8*	1.3*	0.8*

^zWater potential at day 0, immediately before trees were irrigated and GA₃ was applied.

^wMeans are pooled by main effects and represent 15 and 20 replications for WP and GA₃, respectively.

^aMeans within a column followed by different letters indicate significant differences between treatments at $P = 0.05$, Tukey's studentized range test.

^wMeans within a column followed by * or NS indicate significant or no significant difference at $P = 0.05$, respectively, between control and GA₃ treatments (Dunnnett's test).

ethylene production of flower buds except on the day of anthesis, the data were pooled, and no interaction was observed on day 0, 3, and 6 (Fig. 3). On day 9 there was a significant ($P = 0.05$) interaction between WP and GA₃ treatment affecting ethylene evolution.

Ethylene evolution of leaf disks was significantly ($P = 0.05$) influenced by WP 0, 3, and 9 days after irrigation, and by GA₃ treatment 3, 6, and 9 days after treatment (Table 5). No significant interactions were found at any sampling time. Ethylene evolution of leaf disks treated with 100 mg GA₃/liter was always higher than that of the control, but the difference decreased over time (Table 5).

Ion leakage of flower buds and leaf disks was significantly ($P = 0.05$) affected by water stress treatments at all sampling times (Table 6). Because GA₃ had no effect on ethylene evolution of flower buds, the data were pooled for all GA₃ treat-

Table 6. Ion leakage of flower buds and leaf disks from coffee trees following water stress and GA₃ treatments (Expt. III).

Leaf WP ^z (MPa)	Ion leakage(%)			
	Days after treatment			
	0	3	6	9
<i>Flower buds</i>				
-0.6	6.6 a ^{y,x}	6.9 a	5.8 a	4.9 a
-1.2	4.8 a	7.4 a	8.7 ab	4.6 a
-2.1	9.8 b	6.0 a	8.8 ab	16.8 b
-3.0	11.3 b	10.4 b	10.2 b	57.9 c
<i>Leaf disks</i>				
-0.6	8.8 a ^w	6.3 a	9.8 bc	8.6 ab
-1.2	5.6 a	7.9 ab	11.1 c	7.7 ab
-2.1	8.0 a	7.4 ab	8.6 bc	7.2 a
-3.0	14.3 b	8.6 b	7.5 a	9.0 b
GA ₃ (mg-liter ⁻¹)				
0	9.2	7.6 ^v	8.5	7.4
50	---	7.3 ^{NS}	9.0 ^{NS}	8.3 ^{NS}
100	---	7.8 ^{NS}	10.3*	8.7*

^zWater potential at day 0, immediately before trees were irrigated and GA₃ was applied.

^vMeans are pooled for GA₃ and represent 20 replications.

^wMeans within a column followed by different letters indicate significant differences between treatments at $P = 0.05$, Tukey's studentized range test.

^xMeans represent 20 and 15 replications for GA₃ and leaf WP treatment, respectively.

^yMeans within a column followed by * or NS indicate significant or no significant difference at $P = 0.05$, respectively, between control and GA₃ treatments (Dunnnett's test).

ments. Ion leakage of flower buds at day 0 was about twice as high for the -2.1 and -3.0 MPa treatments as for the lower water stress treatments (Table 6), and buds from these treatments had the highest ion leakage at anthesis, 9 days after irrigation (Table 6).

In leaf disks from -3.0 MPa-stressed plants, almost twice the percentage of ion leakage occurred as in those from other treatments (Table 6) at day 0. The main effects of leaf WP and GA₃ treatment on ion leakage of leaf disks are shown, because of a significant ($P = 0.05$) interaction between leaf WP and GA₃ 6 days after irrigation.

When plants were exposed to water stress, flower buds were between 4 and 6 mm long. Three days after irrigation to release water stress, flower buds that developed subsequently to anthesis had expanded to 9 to 12 mm, and doubled this length within the next 3 days. Flower buds were up to 25 mm long before anthesis. Flower buds treated with GA₃ tended to expand slightly faster than untreated ones, but differences were not statistically significant. Flower buds that remained dormant did not elongate.

Discussion

Studies on coffee flowering have shown that water stress is required for flower buds to break dormancy and develop to anthesis. Flowering observed 8 to 10 days after irrigation of stressed plants indicated that flower bud dormancy had been broken by water stress (Alvim, 1960; Piringer and Borthwick, 1955; van der Veen, 1968). However, unlike Magalhaes and Angelocci (1976), who reported a minimum threshold leaf WP of -1.2 MPa and flower-bud WP of -1.4 MPa to break dormancy, greater water stress was needed in our Expts. I and III (Fig. 1, Table 4). Under a daily watering regime, leaf WP were

between -0.6 and -1.1 MPa in unstressed trees or in trees that were irrigated to release water stress, whereas the -1.2 MPa leaf WP reported by Magalhaes and Angelocci (1976) was sufficient to break dormancy in their coffee flower buds. This difference might be due to the time of sampling, position of sampling, plant cultivar, and plant age.

Some plants stressed to a leaf WP of -2.1 MPa flowered partially 8 days after rewatering, but only when treated with GA_3 (Table 4). It appears that GA_3 , in combination with mild water stress, can stimulate anthesis, possibly by compensating for low endogenous GA. These results agree with Alvim's (1958) observations that GA_3 was more effective in breaking dormancy in water-stressed than in unstressed coffee plants, and that GA_3 application during the rainy season did not affect flowering. Browning (1973) suggested that a rise in endogenous GA content is the stimulus for releasing dormant coffee flower buds. He showed that after bud dormancy was broken with water stress and regrowth stimulated by irrigation or rain, the endogenous GA concentration in flower buds increased significantly before buds gained fresh weight. Since GA biosynthesis inhibitors did not prevent dormancy release, he suggested that GA is converted from a bound form to a free, active form at the time of release from dormancy. We found that a GA biosynthesis inhibitor (paclobutrazol, applied before water stress as a soil drench in 500 ml of water at concentrations of 0, 5, 50, and 100 mg/pot) did not inhibit flowering after plants were released from dormancy (data not shown).

Differences in transpiration and soil moisture content between plants result in different levels of water stress and can lead to varying dormancy status and different responsiveness to GA in flower buds. Factors that favor release from dormancy might accumulate, similar to chilling accumulation observed in dormant plants in temperate zones (Alvim, 1960). Flowering in Expt. II (Table 3) and the uncharacteristic flowering 28 days after release from water stress in Expt. III (Table 4) might be the result of different dormancy status of flower buds at the beginning of the two experiments. Gibberellic acid might provide the required stimulus for continued bud development after water stress or compensate for water stress that is inadequate for breaking dormancy, as indicated by increased blossoming with higher GA concentrations in less stressed trees (Table 4).

Ethylene evolution of dormant flower buds was always higher than in buds in which dormancy had been broken by water stress (Figs. 2 and 3). The severe water stress required to remove dormancy did not increase ethylene production, an unexpected result, since ethylene evolution generally increases in stressed tissues (Abeles, 1973). In contrast to coffee flower buds, tight orchid (*Arachnis hookerana* \times *Vanda* 'Hilo Blue') buds produce relatively high concentrations of ethylene throughout their development (Yip and Hew, 1988). The physiological stage of flower buds determines ethylene evolution, which was found to vary considerably between orchid genera (Gob et al., 1985). We observed increased ethylene production at anthesis, which may be due to pollination, as reported by Reid (1988). The difference in ethylene production by dormant and nondormant coffee flower buds is an important finding that allows separation of physiological stages that cannot be distinguished by morphology or anatomy.

Throughout the experiment, ethylene evolution of leaf disks (Tables 1 and 5) was highest from severely water-stressed plants. Similarly, Kobayashi et al. (1981) showed that ethylene production increased in water-stressed plum leaves as moisture loss increased. The general pattern of increasing ethylene production

by tissues under stress was confirmed in this study for leaf disks from coffee plants, but the opposite was found for flower buds.

The most severely water-stressed plants showed the highest amount of ion leakage from flower buds and leaf disks at the end of the water stress treatment, but before irrigation was applied (Tables 2 and 6). An increase in ion leakage was found in severely dehydrated plum leaves, when $\geq 50\%$ moisture was lost (Kobayashi et al., 1981). Similar observations were made in tissues that were damaged by freezing stress (Harber and Fuchigami, 1986). Fluctuating values for flower-bud and leaf tissue indicate that the increase in ion leakage was temporary, and that the initial high values for severely stressed tissue caused no permanent damage to membrane permeability or cell death. In flower buds that continued to develop to anthesis, ion leakage increased as buds grew rapidly. Increased ion leakage of flower buds and leaf disks was related to severe stress before water-stressed plants were irrigated. Unlike ethylene evolution, ion leakage of flower buds was not related to the dormancy status.

These experiments show that threshold leaf and bud WP were necessary to break dormancy in coffee flower buds. In flower buds, where dormancy was not completely broken by water stress, GA_3 stimulated development to anthesis, possibly by compensating for a lack of endogenous GA. Ethylene evolution was found to be useful in distinguishing between dormant and nondormant flower buds.

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