

Impact of water stress on reproductive development of sweet peppers (*Capsicum annuum* L.). I. Role of ethylene in water deficit-induced flower abscission

[Kesan sesakan air terhadap perkembangan reproduktif cili sayur (*Capsicum annuum* L.). I. Peranan etilena dalam pengguguran bunga yang teraruh oleh keadaan sesakan air]

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Key words: ethylene evolution, water deficit, sweet pepper, anthesis, flower abscission, dry matter accumulation, water potentials

Abstrak

Kajian ini dijalankan untuk memeriksa peranan etilena dalam mempercepat pengguguran bunga pada cili sayur. Sesakan air meningkatkan pembebasan etilena daripada bunga cili sayur dengan ketara iaitu sebanyak 40 kali ganda sejurus sebelum bunga gugur berbanding dengan sebelum bunga kembang. Pembebasan etilena oleh bunga juga meningkat sebanyak lapan kali ganda berbanding dengan bunga pada pokok kawalan yang tidak mengalami sesakan air. Pada pokok yang tidak mengalami sesakan air, pembebasan etilena daripada bunga dan daun meningkat dengan umur. Walau bagaimanapun, kadar pembebasan etilena oleh bunga sentiasa lebih rendah daripada kadar pembebasan etilena oleh daun. Keadaan ini menandakan daun sebagai tempat etilena disintesis. Pada pokok yang mengalami sesakan air pula, pembebasan etilena oleh bunga melebihi daun sebanyak tiga kali ganda menunjukkan bahawa bunga yang sedang membesar lebih peka terhadap sesakan air. Bunga cili sayur berupaya membentuk lapisan pengguguran di pangkal tangkainya apabila terdedah pada kepekatan etilena dalaman yang tinggi akibat keadaan sesakan air. Bagaimanapun, daun cili sayur yang matang tidak berupaya membuat demikian. Semasa peningkatan pembebasan etilena oleh bunga, bahan kering bahagian pucuk dan pengagihannya ke daun dan batang tidak berkurangan dengan nyata. Oleh itu, kejadian ini tidak boleh dikaitkan dengan corak pembebasan etilena yang berubah-ubah. Susutan pengeluaran asimilat atau pengagihannya ke daun dan batang tidak terbahit secara langsung dengan pengguguran bunga. Semua komponen potensi air menurun semasa pengeluaran etilena meningkat. Akan tetapi perubahan ini tidak boleh dikaitkan dengan peningkatan pembebasan etilena pada bunga dan daun secara konsisten. Susutan yang banyak pada komponen potensi air semasa keadaan sesakan air berlaku secara berperingkat-peringkat, mungkin tidak boleh digunakan untuk meramalkan perubahan pengeluaran etilena yang berkesan untuk

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menggalakkan pengguguran. Keadaan ini mungkin dipengaruhi oleh kehilangan tahap air atau tegahan yang lebih kecil lagi.

Abstract

The study was carried out to examine the role of ethylene in accelerating flower abscission in sweet pepper. Water stress significantly increased ethylene evolution from sweet pepper flowers just before abscission to 40-fold greater than that measured before anthesis. Its evolution from the flowers also increased by up to eightfold compared with unstressed control plants. In unstressed plants, ethylene evolution from the flowers and leaves increased with age but the former always had lower evolution rate than the leaves suggesting that leaves may be the site for ethylene synthesis. In stressed plants, however, ethylene evolution from the flowers was threefold greater than that from the leaves, implying that the developing flowers were more sensitive to water stress. Sweet pepper flowers were capable of forming abscission lines at the base of the pedicels following exposure to elevated endogenous ethylene concentrations caused by water stress. However, mature pepper leaves were incapable of doing so. Shoot dry matter and its partitioning to the leaves and stems did not decline markedly during the period of increased ethylene evolution in the flowers, and therefore could not be correlated with the changing pattern of ethylene evolution. The reductions in assimilate production or partitioning to the leaves and stems were not directly involved in reducing flower abscission. All components of water potentials were decreased during periods of increased ethylene production, but these changes could not be consistently related to increased ethylene evolution from the flowers and leaves. The relatively large decreases in water relations components during progressive water stress may not be useful in predicting the changes in ethylene production which are effective in promoting abscission; instead these may be induced by much smaller losses in water status or turgor.

Introduction

Environmental conditions or treatments that enhance the supply of assimilates to the flower buds or reduce vegetative growth generally reduce abscission and promote flower development (Halevy 1987). Previous work (Jaafar et al. 1994) showed that restriction of early vegetative growth through the gradual imposition of water stress shortly after the appearance of the first visible flower buds favoured their initial development, leading to earlier anthesis of the primary flowers. However, progressive water stress did not enhance the subsequent development of these and later flowers, which were lost by abscission. Jaafar et al. (1994) have shown that the effects of water stress on anthesis and flower abscission were not directly correlated with changes in

water relations in tissues or related to lowering of dry matter accumulation to the flowers *per se*. These, however, may originate from related stress-induced changes in the concentration and distribution of endogenous growth substances involved in promoting flower abscission (Halevy 1975; Abeles et al. 1992).

Ethylene appears to be a major promoter of flower abscission in many plant species under stress conditions (Halevy and Mayak 1981; Sexton et al. 1985). Its production in plants has also been found to increase during water stress (Jordan et al. 1972; Kirkham 1985). Increased ethylene production is associated with lowering of both leaf water (McMichael et al. 1972) and osmotic potentials (Curtis 1981; Miyamoto and Kamisaka 1987; Stumpff and Johnson

1987) and a marked reduction in leaf fresh weight (Apelbaum and Yang 1981). The abscission of flowers and leaves is also known to increase with increasing ethylene production (McMichael et al. 1973; Guinn 1976; Curtis 1981). Although there is much information implicating ethylene in stress-induced abscission, especially of vegetative organs, little attention has been directed to understand its role and mechanisms of action in water stress-induced flower abscission. If ethylene is involved in promoting flower abscission, endogenous ethylene levels may be expected to increase following the imposition of water stress.

This experiment was conducted to measure ethylene production during water stress and examine its role in accelerating flower abscission. Total shoot dry weight, the partitioning of dry matter and changes in plant water status were examined to detect any relationship with changes in ethylene production during water stress period.

Materials and methods

Propagation and seedling management

A glasshouse experiment was carried out at the University of Nottingham between 6 September 1993 and 13 November 1993. Seeds of *Capsicum* hybrid variety Blue Star (Know-You Seed Co., Ltd, Taiwan) were thinly sown in flat trays containing Levington F2 compost (Fisons Horticulture Ltd, Ipswich, UK), then placed on a propagating bed which provided a basal temperature of 24 °C with a glasshouse ambient temperature of 20–22 °C. When the cotyledons had fully expanded, uniform seedlings were pricked out individually into 9-cm diameter pots containing Levington M2 potting compost and placed on benches, under natural lighting conditions. When the third pair of true leaves were about 1 cm long (22 days after germination: DAG), the seedlings were transplanted into 6-L pots containing Levington M2 compost. These pots were arranged in a glasshouse having a mean daily temperature of 26 ± 3 °C with ventilation at 29 °C. The plants received

natural radiation, supplemented with 400 W high-pressure sodium lamps (SON/T) during 0500–2300 h to provide an 18-h daylength and an additional irradiance of 2.5 MJ/m² (PAR; 400–700 nm).

Treatments

Water stress treatments were imposed when the flower buds reached the stage of development most sensitive to stress, i.e. at a bud diameter of 4.0 mm (38 DAG; Jaafar 1995). The experiment comprised two treatments: severe stress (SS), which had previously been shown to exert a consistently detrimental effect by inducing premature flower abscission (Jaafar et al. 1994), and a non-stress (NS) control. The method of imposing water stress treatment relied on measurements of pot weight to indicate the severity of the drought imposed and the levels of water to be supplied (Saito and Ito 1967; Klapwijk and De Lint 1974; Wudiri and Henderson 1985; Menzel et al. 1986; Jaafar et al. 1994). All pots initially received equal volumes of water to maintain them near to the predetermined pot capacity (0.26 L water/L compost), and moisture lost by evapotranspiration (ETP) was replaced on alternate days. Replacement of water at 100% of ETP served as a “no stress” control (NS), whereas watering at 25% of ETP provided a progressive severe stress treatment (SS). The treatment period lasted for 25 days. The treatments were arranged in a randomised complete block design, blocked six times. Each treatment contained 96 plants.

Ethylene evolution and measurement

The rates of ethylene evolution were determined for 16 detached primary flowers and fourth or fifth youngest leaves of each treatment. Care was taken during all sampling and measuring procedures to avoid damage and consequent stress to the plant material. This is because the stress might cause the evolution of additional ethylene which would adversely affect the reliability of the measurements of ethylene evolution

induced by the treatments applied. Ethylene evolution in primary flowers was measured at specific stages of flower growth before anthesis and immediately after first flower abscission. The time to first anthesis and first abscission was predicted using thermal time calculations over a base temperature as suggested by Atherton et al. (1990), Ramin and Atherton (1991), and Jaafar (1995). For sweet pepper variety Blue Star, the base temperature (T_b) is 6.0 °C (Jaafar 1995).

Ethylene evolution from the leaves was measured to determine differences between treatments and to establish how these differences were related to abscission. The organs were excised at the pedicels or petioles using a sharp blade and quickly weighed before inserting their ends into 1 mL of 2% w:v plain agar contained in clean glass vials of known volume: 10 mL vials were used for flowers and 30 mL for the leaf samples. The medium provided mechanical support and helped maintain moisture in the vials thereby minimised additional stress on the excised tissue. The vials were sealed with subaseal rubber caps. Ethylene in the vials was allowed to accumulate for 90 min before being measured using the gas chromatography (GC; PU 4500 Unicam, Phillips, UK) which was fitted with an alumina F1 column (JJ's Chromatography Ltd, Kings Lynn, Norfolk). A 1-mL gas sample was extracted from the vial using a 16-mm hypodermic needle fitted to a 1-mL plastic syringe and injecting it through a rubber septum into the GC column. Before ethylene production from plant tissues was measured, a calibration of 10 $\mu\text{L/L}$ ethylene was injected from a cylinder into the GC, for use as a reference standard (McAfee and Morgan 1971). The rate of ethylene evolution was calculated from the ethylene concentration of the gas sample, the volume of the gas vial and the fresh weight of the sample, and was expressed in units of nanolitres per gram fresh weight per hour ($\eta\text{L/g FW/h}$).

Leaf water status measurement and destructive analyses

Measurement of leaf water status, which coincided closely with the ethylene measurements, was carried out to determine whether plant water relations components were associated with ethylene evolution during flower abscission. Midday water potentials (ψ_1) were measured before first anthesis and first flower abscission in the youngest fully expanded leaf of six plants randomly selected from each treatment using a pressure chamber (PMS Instrument, Corvallis, Oregon). These samples were then used to measure osmotic potential (ψ_s), and turgor potential (ψ_p) was calculated as the difference between the osmotic and water potentials. Each leaf sample was inserted into a clean 1.5-mL plastic Eppendorf vial immediately after measuring ψ_1 , sprayed with a freezing aerosol (dichlorodifluoromethane) and placed in a deep freeze for 24 h at -15 °C. The samples were then thawed and centrifuged at 2 500 rev/min for 15 min and maintained at 4 °C to minimise evaporative losses from the tissue. Osmotic potential was measured using 25-mL samples of the extracted sap with a Roebeling automatic freezing-point osmometer (Ketteweg, Berlin). Care was taken to avoid all sources of measurement error (Squire et al. 1981).

Periodic destructive analyses were conducted to establish effects on dry matter production and distribution. The shoots were severed at the compost surface and subdivided into flowers, leaves and stems before being placed in paper bags and oven-dried at 84 °C for 48 h before weighing.

Results

Flower development

Total accumulated radiation received between the appearance of first visible flower bud and final harvest was 321.8 MJ/m², with a daily mean of 7.85 MJ/m². Values for daily mean and accumulated thermal time were 19.0 and 780.8 degree-days (°C d) respectively. First anthesis and flower abscission in SS occurred at 436 and

537 °C d respectively. First anthesis in NS was observed at 497 °C d.

Ethylene evolution

The rates of ethylene evolution by primary flowers and leaves measured just before first anthesis and flower abscission in the NS and SS treatments are presented in *Table 1*.

There was no significant increase in the rate of ethylene evolution from either the flowers or leaves of stressed plants just before anthesis. Ethylene evolution from the leaves was approximately 10-fold greater than in the flowers in both the NS and SS treatments, implying that the leaves may be a site for ethylene synthesis. Preceding the first abscission in SS, ethylene evolution from the primary flowers was approximately eightfold greater than in the NS treatment ($p < 0.001$) and about 40-fold greater than that measured before anthesis (0.021 vs. 0.851 $\eta\text{L/g FW/h}$). Although ethylene production was lower in NS than in SS, there was still an increase of about sevenfold as compared with the earlier measurements prior to anthesis (0.106 vs. 0.016 $\eta\text{L/g FW/h}$), suggesting that ethylene production in flower increases with age.

During the period before first abscission, higher rates of ethylene evolution were also observed in the leaves of SS plants as compared with NS plants (0.299 vs. 0.140 $\eta\text{L/g FW/h}$; $p < 0.05$) but these levels were approximately threefold lower than in the stressed flowers (*Table 1*). This may imply that developing flowers were more sensitive than the leaves to severe

stress and this was reflected by the higher rates of ethylene evolution. Ethylene evolution from the leaves increased as the duration of the stress period increased, from 0.170 $\eta\text{L/g FW/h}$ before anthesis to 0.299 $\eta\text{L/g FW/h}$ before abscission although the increment was smaller than in the flowers. However, ethylene evolution from NS leaves remained unchanged between anthesis and abscission at 0.140 $\eta\text{L/g FW/h}$, but was consistently higher than in the NS flowers both before anthesis and abscission. These results indicate that under NS growing conditions, the rate of ethylene evolution from the leaves is greater than that from the flowers, although this situation may be reversed in younger plants with less advanced 4-mm flower buds (Jaafar 1995).

Dry matter accumulation and distribution

Dry matter distribution between the shoot components is shown in *Table 2* and *Table 3*. As found in the earlier results by Jaafar et al. (1994), SS significantly reduced total shoot dry weight ($p < 0.01$; about 20%) just before anthesis, and dry matter accumulation in the flowers, leaves and stems were all consistently reduced in the SS treatment (*Table 2*; $p < 0.01$). However, dry matter distribution to these components, expressed as a percentage of the total, remained similar in both the NS and SS treatments (*Figure 1*). Prior to first abscission, no significant reduction was observed in total shoot, leaf or stem dry weights in the SS treatment (*Table 2*) although the dry weight of the flowers ($p < 0.05$) was significantly

Table 1. Effects of water stress on ethylene evolution from primary flowers and leaves just before first anthesis and flower abscission (n = 18)

Water stress	Ethylene evolution before anthesis ($\eta\text{L/g FW/h}$)		Ethylene evolution before abscission ($\eta\text{L/g FW/h}$)	
	Flowers	Leaves	Flowers	Leaves
Non-stress	0.016	0.142	0.106	0.140
Severe stress	0.021	0.170	0.851	0.299
SED	0.005ns	0.023ns	0.110***	0.015*

*significant at $p < 0.05$; *** significant at $p < 0.001$; ns = not significant
SED = standard error of the difference between means

increased, implying that more assimilates may have been directed to the developing flowers after anthesis. During the same period, the percentage of dry matter present in the leaves of NS plants was clearly reduced, while the fraction present in the stems was significantly increased (*Figure 1*; $p < 0.01$). Immediately after first abscission, total shoot dry matter was significantly

decreased in SS (*Table 3*; 11.2 g vs. 13.0 g; $p < 0.001$), as were leaf (7.1 g vs. 8.1 g) and stem dry weights (3.7 g vs. 4.5 g; $p < 0.001$). However, flower dry weight was significantly increased. Neither total shoot dry matter production nor its distribution in SS plants (*Figure 2*) was correlated with the observed increase in the rate of ethylene production (*Figure 1*). The result suggests

Table 2. Effects of water stress on shoot dry matter and its distribution just before first anthesis and flower abscission (n = 18)

Water stress	Dry matter (g) before anthesis				Dry matter (g) before abscission			
	Flower	Leaf	Stem	Total shoot	Flower	Leaf	Stem	Total shoot
Non-stress	0.3	4.5	1.6	6.4	0.3	6.2	2.5	9.0
Severe stress	0.2	3.8	1.2	5.2	0.4	5.9	2.5	8.8
SED	0.10**	0.23**	0.10**	0.33**	0.02*	0.20ns	0.08ns	0.27ns

*significant at $p < 0.05$; ** significant at $p < 0.01$; ns = not significant
 SED = standard error of the difference between means

Table 3. Effects of water stress on shoot dry matter and its distribution after first flower abscission (n = 18)

Water stress	Dry matter (g) after first abscission			
	Flower	Leaf	Stem	Total shoot
Non-stress	0.4	8.1	4.5	13.0
Severe stress	0.6	7.1	3.5	11.2
SED	0.08***	0.22***	0.18***	0.35***

*** significant at $p < 0.001$
 SED = standard error of the difference between means

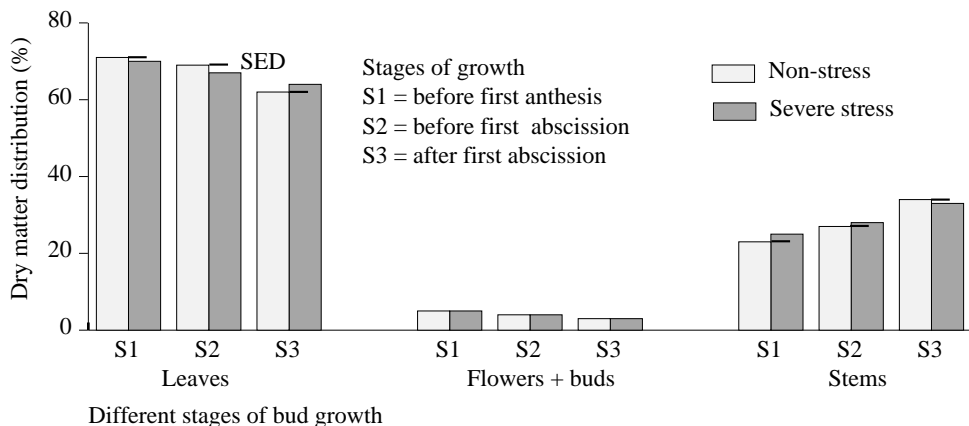


Figure 1. Effects of water stress on dry matter distribution within the shoot before first anthesis and abscission, and after first abscission (n = 18)

that the abscission of primary flowers observed during severe water stress was not directly attributable either to the reduction in total shoot dry weight or to the altered pattern of dry matter distribution.

Plant water relations

Seven days after imposing the SS treatment (i.e. shortly before the first anthesis of primary flowers), ψ_1 and ψ_s were both significantly decreased in SS, while ψ_p was unaffected (Table 4). However, by 12 days before first abscission, SS had caused significant reductions in all water relations components and leaves in the SS treatment lost turgor entirely. The observed decrease in the values for all water relations components coincided with the marked increase in ethylene evolution, which preceded abscission, although the observed changes

were not linearly correlated (data not presented).

Discussion

The previous work by Jaafar et al. (1994) focussed on the growth responses of glasshouse-grown sweet pepper plants to progressive water stress imposed at various stages of flower bud development. Clear relationships were established between growth responses and the severity and duration of stress. Progressive imposition of severe and prolonged water stress on reproductive plants when the first flower bud became macroscopically visible induced early and increased flower abscission. Although reductions in the availability of photoassimilates due to water stress have been suggested by Peltonen-Sainio (1991) as a cause of abscission, no consistent

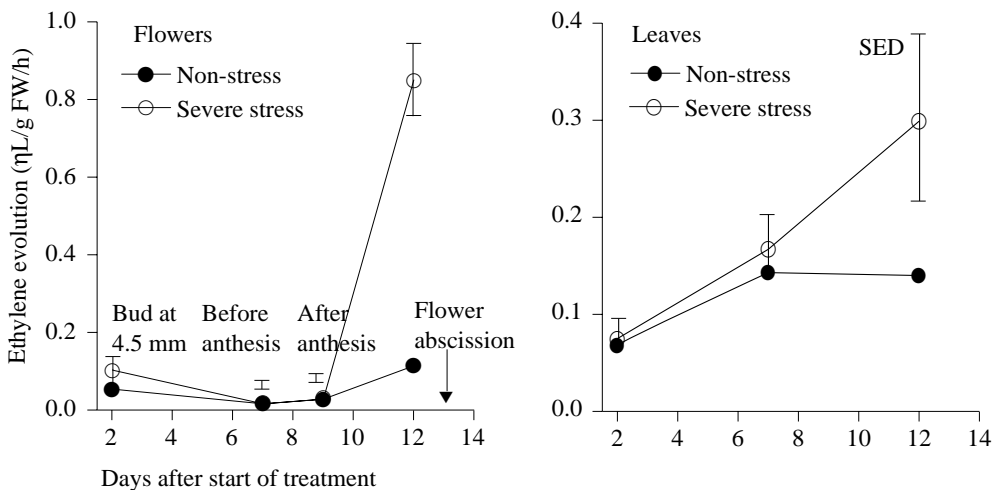


Figure 2. Effects of water stress on the rates of ethylene evolution from flowers and leaves (n = 18)

Table 4. Effects of water stress on the components of plant-water relations just before first anthesis and flower abscission (n = 18)

Water stress	Before first anthesis (MPa)			Before first abscission (MPa)		
	ψ_1	ψ_s	ψ_p	ψ_1	ψ_s	ψ_p
Non-stress	-0.43	-1.02	0.58	-0.83	-1.09	0.27
Severe stress	-0.78	-1.18	0.42	-1.29	-1.27	-0.02
SED	0.07***	0.09*	0.11ns	0.07***	0.04***	0.08***

*significant at $p < 0.05$; ***significant at $p < 0.001$; ns = not significant
 SED = standard error of the difference between means

reduction in total shoot dry matter was observed in the work reported here. The observed decline in turgor shortly before flower abscission could not be related directly to flower abscission or shoot dry matter production, suggesting that other changes occurred much sooner and at lower stress levels than those associated with turgor loss (Hsiao 1973).

The role of ethylene in stress-induced abscission in other species is well documented (Halevy and Mayak 1981; Durieux et al. 1983; Sexton et al. 1985; Ohno 1991; Abeles et al. 1992). While ethylene production has often been found to increase following the imposition of water stress or drought in many species, ultimately resulting in leaf abscission (Jordan et al. 1972; McMichael et al. 1972; El-Beltagy and Hall 1974; Apelbaum and Yang 1981; Kimmerer and Kozlowski 1982; Kirkham 1985), very few studies have examined the role of drought-induced ethylene production in flower abscission in horticultural crops. The work carried out here showed that water stress significantly increased ethylene evolution just before flower abscission to a level 40-fold greater than that measured before anthesis, and by up to eightfold relative to unstressed plants. Ethylene evolution from flowers was also threefold greater than that from leaves in water-stressed plants, whereas the reverse applied in unstressed control plants. A similar involvement of increased ethylene production just before the abscission of water-stressed young cotton bolls has also been reported (Guinn 1976). These observations suggest that the enhancement of ethylene production in flowers by water stress may have increased their susceptibility to abscission.

While water stress induced flower abscission, no simultaneous leaf abscission occurred in the older leaves. The lower rate of ethylene evolution by the leaves just before flower abscission suggests that the developing flowers of sweet pepper may have been more sensitive to water stress.

The differential sensitivity to stress-induced ethylene production between plant organs and species (Sexton et al. 1985) can often be attributed to the presence or absence of a differentiated class of target cells which form the separation layer – the line of abscission (Osborne 1982; Abeles et al. 1992). This line was observed in the present study to develop at the base of the pedicels just before abscission. However, similar abscission lines were not observed at the base of the petioles of mature leaves of sweet pepper, suggesting that the target cells were absent, or that endogenous ethylene levels did not reach the critical level for the induction of leaf abscission. The observed increase in ethylene evolution with time from non-stressed flowers and leaves may indicate that ethylene production increased with the physiological age of individual flowers and the plants themselves (Sexton et al. 1985; Abeles et al. 1992). In non-stressed plants, the leaves also appeared to produce more ethylene than the flowers.

Total shoot dry matter and its partitioning to the leaves and stems did not decline markedly during the period of increased ethylene evolution from flowers, and therefore could not be correlated with the altered pattern of ethylene evolution. This indicates that reductions in assimilate production or dry matter partitioning to the leaves and stems were not directly involved in inducing flower abscission. Decreases in leaf water and osmotic potentials following increases in ethylene production have been reported previously (McMichael et al. 1972; Curtis 1981; Miyamoto and Kamisaka 1987; Stumpff and Johnson 1987), and the results obtained in the present study are consistent with these reports. However, these changes could not be related with ethylene evolution from flowers or leaves. Although decreases in the components of water potentials may indicate the severity of stress in plants, they are not necessarily closely coordinated with hormonal changes, which may be induced at much lower stress levels than those indicated by turgor potential.

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