J Plant Growth Regul (1997) 16:129–135

Journal of
Plant
Growth
Regulation

Role of Ethylene Biosynthesis and Auxin Content and Transport in High Temperature-Induced Abscission of Pepper Reproductive Organs

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Received September 27, 1996; accepted March 13, 1997

Abstract. High temperatures induced abscission of pepper (*Capsicum annuum* L. cv. Maor) reproductive organs at various developmental stages. The role of ethylene biosynthesis and auxin economy in high temperature-induced abscission is described. High temperatures somewhat increased ethylene production in the reproductive organs, but the highest temperature treatment, which was the most active in inducing reproductive organ abscission, decreased it. In contrast to ethylene, 1-aminocyclopropane-1-carboxylic acid levels increased significantly in response to high temperatures and correlated positively with the increase in temperature. High temperatures reduced indole-3-acetic acid levels and particularly auxin transport capacity in the reproductive organs. The data suggest that the reduction of auxin transport capacity is the major mechanism by which high temperatures induce reproductive organ abscission in pepper.

Key Words. 1-aminocyclopropane-1-carboxylic acid (ACC)—*Capsicum annuum*—Indole-3-acetic acid (1AA)—1-naphthaleneacetic acid (NAA)—Paprika

When bell peppers (*Capsicum annuum* L.) are subjected to environmental stresses during the flowering and fruiting period, abscission of flower buds, flowers, and fruitlets usually occurs. Although various stresses such as extremes of temperatures, drought, and low light intensity can induce reproductive organ abscission in pepper, high temperature appears to be the most common cause (Wien et al. 1989). The mechanism by which environmental stresses and particularly heat stress induce reproductive organ abscission has not received much attention until recently. A model developed for natural leaf abscission by Morgan (1984) and Osborne (1989) implies that auxin produced by the leaf blade is translocated down to the petiole and retards abscission. When the leaf begins to senesce it produces an elevated level of ethylene which reduces auxin content and transport, resulting in increased sensitivity of the abscission zone to ethylene. Ethylene then acts directly in the abscission zone to induce the activity of hydrolytic enzymes which leads to cell separation. There is some evidence that the above model also applies to reproductive organ abscission. For example, ethylene promoted flower abscission in tomato (Roberts et al. 1984), begonia (Hanisch ten Cate and Bruinsma 1973), and pepper (Beaudry and Kays 1988). Auxin delayed flower abscission in begonia (Hanisch ten Cate and Bruinsma 1973) and prevented it in tomato (Hemphill 1949). In begonia, however, ethylene failed to inhibit auxin transport in flower pedicels (Hanisch ten Cate and Bruinsma 1973). Induction of ethylene production by environmental stresses, including heat stress, is well documented (Abeles et al. 1992, Yang and Hoffman 1984). The rate of ethylene production induced by high temperature stress usually reaches a maximum at 35°C and is inhibited severely by temperatures above 40°C (Abeles et al. 1992, Aloni et al. 1994). In bean, a short exposure to temperatures between 40 and 45°C caused a rise in ethylene production when the tissue was returned to 25°C (Field 1981). Reproductive organs also responded to high temperatures by increased ethylene production, but there was no clear relationship between levels of heat stress-induced ethylene and the abscission response of various pepper (Aloni et al. 1994) and bean (Gross 1992) cultivars. There is evidence for the effect of stress conditions on IAA economy. Water stress reduced both free IAA in cotton bolls and their abscission zones (Guinn and Brummett 1988). High and low temperatures lowered IAA levels and enhanced abscission in tomato flowers (El Abd et al. 1986). Similarly, a short exposure to 38°C reduced auxin-like substances in tomato flower

Abbreviations: IAA, indole-3-acetic acid; ACC, 1-aminocyclopropane-1-carboxylic acid; NAA, 1-naphthaleneacetic acid.

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buds and young fruits (Kuo and Tsai 1984). In contrast, Ofir et al. (1993) did not detect a reduction in extractable IAA in reproductive organs of bean subjected to high temperatures which reduced pod and seed set. However, they observed a significant reduction in exportable IAA in these plants. High night temperatures also stimulated June drop of apple fruitlets and reduced their IAA export (Bangerth 1990).

The aim of the present work was to determine the mechanism by which heat stress induces increased abscission of pepper reproductive organs by examining the various components of the leaf abscission model (Morgan 1984, Osborne 1989). Preliminary results were presented elsewhere (Goren et al. 1993, Wien et al. 1993).

Materials and Methods

Plant Material and Stress Treatments

Bell pepper (*C. annuum* L. cv. Maor) and paprika (*C. annuum* L. cv. Lehava) were grown in a greenhouse in 3-liter pots. Two- to 3-month-old plants were transferred to growth chambers and exposed to the following temperature (°C) day/night regimes: (1) 22/17, (2) 32/27, (3) 40/27. In each 24-h temperature cycle, plants were subjected to the high temperature treatment for the first 8 h of the light period. During the experiments, plants were kept under 70 ± 5% relative humidity and a 16-h photoperiod. Measurements and samplings were done after each 8-h high temperature treatment and/or at the end of each 24-h temperature cycle.

Ethylene Biosynthesis

Ethylene production in excised organs was measured after incubation for 1 h in sealed test tubes. At the end of incubation, 1-mL gas samples were withdrawn with a hypodermic syringe, and ethylene was measured by a gas chromatograph equipped with an alumina column and a flame ionizing detector. ACC was extracted and determined according to Lizada and Yang (1979).

Auxin Transport

The basal side of 10-mm sections of flower and fruitlet peduncles were placed individually on 1.5% agar discs (9 mm in diameter and 3 mm thick). The discs were placed on a Parafilm M layer in Petri dishes, and the dishes were transferred to a humid container. Three μL of H_2O containing 200,000 dpm of [^{3}H]NAA (specific activity 10 mCi/μmol) was applied to the acropetal surface of the explants. The container was then transferred to the desired temperature in a controlled temperature bath. At the end of the experiment, each receiver agar disc was transferred to a vial containing 4 mL of scintillation solution, and [^{3}H]NAA was extracted overnight with constant shaking at room temperature and counted by means of a liquid scintillation counter.

Endogenous IAA Levels

IAA was extracted with 0.01 M phosphate buffer, pH 6.6, containing sodium diethyldithiocarbamate (100 μg/ml) according to Sundberg (1990). The pH of the phosphate buffer extract was raised to 8.5, and phenolics and pigments were removed from the extract by extraction with diisopropyl ether. The remaining water phase was then brought to pH 2.5, and IAA was extracted with diisopropyl ether. The diisopropyl ether fraction was evaporated and dried under nitrogen. The dried extract was redissolved in phosphate buffer, pH 8.0, and passed through a Sep-Pak C_{18} column equilibrated with the same buffer. The eluted solution was then brought to pH 2.5 with acetic acid and passed again through Sep-Pak C_{18} column preconditioned to pH 2.5. Excess acetic acid was washed with distilled water, and IAA was eluted from the column with methanol. The final colorless methanol solution was brought to dryness under nitrogen and diazomethylated (Schlenk and Gellerman 1960). By employing [2-^{14}C]IAA as an internal standard, recovery of IAA was calculated to be about 50%.

IAA was quantified by a radioimmunoassay according to Weiler (1981) with some modifications. Briefly, the immunoassay included 250 μL of phosphate-buffered saline (0.1 M, pH 7.4), 50 μL of 0.6% bovine serum albumin; 50 μL of methylated [^{3}H]IAA (about 20,000 dpm), 50 μL of antiserum, and 100 μL of methylated antigen. The mixtures were shaken and incubated for 30 min at room temperature with occasional shaking. At the end of incubation, 750 μL of saturated $(NH_4)_2SO_4$ was added, and the antibodies were allowed to precipitate for 30 min. The precipitate was collected by centrifugation at 1,700 *g* for 40 min. The supernatant was removed, and 750 μL of 50% $(NH_4)_2SO_4$ was added. The samples were centrifuged as above for 30 min. The supernatant was removed, and the pellet was dissolved in 200 μL of twice-distilled water by shaking. Two mL of scintillation solution was added to each sample; after mixing, the radioactivity in the samples was determined.

For the sake of brevity only results for pepper are described here.

Results

Effect of High Temperatures on Abscission

The effect of high temperatures on the abscission of pepper reproductive organs was recorded during three high temperature cycles. Abscission of flowers and fruitlets in the control (22/17°C) and the two high temperature treatments (32 and 40°C) was already observed during the first temperature cycle (Fig. 1, *A* and *B*). The two high temperature regimes resulted in increased abscission, the highest temperature being the most active in the induction of abscission.

Effect of High Temperatures on Ethylene Production

Ethylene production in flower buds, measured at the end of the 8-h temperature treatment, was increased by the two high temperature regimes by about twofold in all three temperature cycles (Fig. 2*A*). Similar results were also observed in fruitlets (data not presented). Flowers responded similarly to flower buds at the 32/27°C temperature regime (Fig. 3*A*). However, ethylene production in flowers of plants subjected to the highest temperature regime (41/27°C) gradually decreased with the advancement of the temperature cycles, and at the end of the third cycle it was considerably lower than that in the control. Ethylene production usually returned to normal levels after the plants were transferred to the lower temperature period of each cycle (Figs. 2*B* and 3*B*), except for flow-

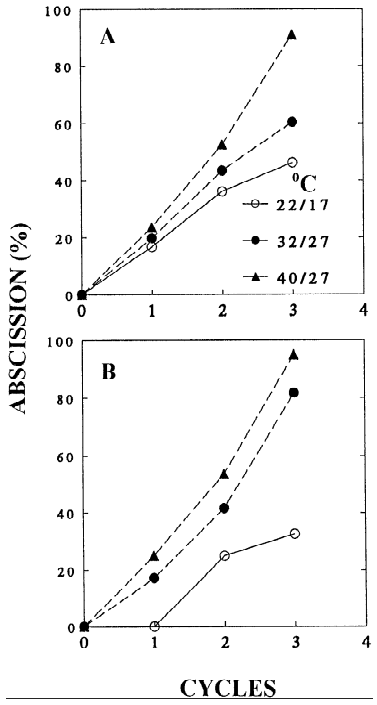

Fig. 1. Effect of high temperature cycles on pepper reproductive organ abscission. Whole plants were subjected to daily cycles of high temperatures for 8 h. Flowers (*A panel*) or fruitlets (*B panel*) which abscised were collected and counted at the end of each temperature cycle. Abscission data are presented as percentage of the total number of reproductive organs.

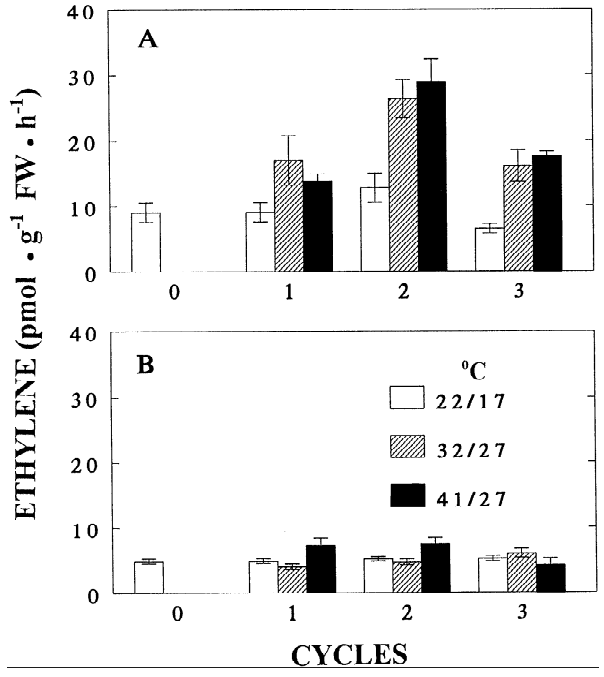

Fig. 2. Effect of high temperature cycles on ethylene production in pepper flower buds. Ethylene was measured daily after the 8 h of the high temperature period (*A panel*) and at the end of the temperature cycle (*B panel*). For ethylene measurement, four flower buds were enclosed in a 9-mL test tube. At the end of a 1-h incubation period, air samples of 1 mL were taken for ethylene measurements. *Vertical bars* indicate ± S.E. ($n = 8$).

ers subjected to the highest temperature regime, in which ethylene production did not recover and remained lower than that in the control (Fig. 3*B*). Ethylene production in flowers was about sixfold higher than that in flower buds.

The above described ethylene measurements were performed in excised organs sampled from high temperature-treated plants. Excision by itself may cause changes in organ physiology. Therefore, we measured the ACC content as an indicator of ethylene biosynthetic potential in the reproductive organs. High temperatures and particularly 40°C increased ACC content in flower buds and petals more consistently and significantly compared with ethylene production (Fig. 4, *A* and *B*). In all treatments, the ACC content in flower buds and petals increased gradually with the advancement of the stress cycles. A similar increase in ACC was observed in fruitlets and fruitlet peduncles (data not shown).

Effect of High Temperatures on Auxin Transport

The effect of high temperatures on auxin transport capacity in peduncle sections of various reproductive organs was examined. Auxin transport capacity was examined first under various incubation temperatures, ranging from 19 to 47°C. A 6-h transport period was selected as the standard since no further increase in [^{3}H]NAA transport was observed in longer incubation periods (data not shown). The highest auxin transport capacity, using fruitlet peduncle sections, was obtained at 34°C, and it decreased gradually at higher temperatures (Fig. 5). At the highest incubation temperature (47°C), auxin transport capacity decreased significantly.

To determine the effect of high temperatures on auxin transport capacity, whole plants were subjected to three temperature regimes, and auxin transport was determined in peduncle sections of flowers and fruitlets at the end of each high temperature treatment. The data obtained clearly show that the two highest temperature regimes caused a significant decrease in auxin transport capacity in all organs tested (Fig. 6, *A* and *B*). In general, the inhibitory effect of high temperatures on auxin transport capacity increased with time, but a significant inhibitory effect was already observed after the first temperature cycle.

Effect of High Temperatures on Endogenous Auxin Level

Similar to the ethylene measurements, the IAA level was determined daily at the end of the 8-h high temperature

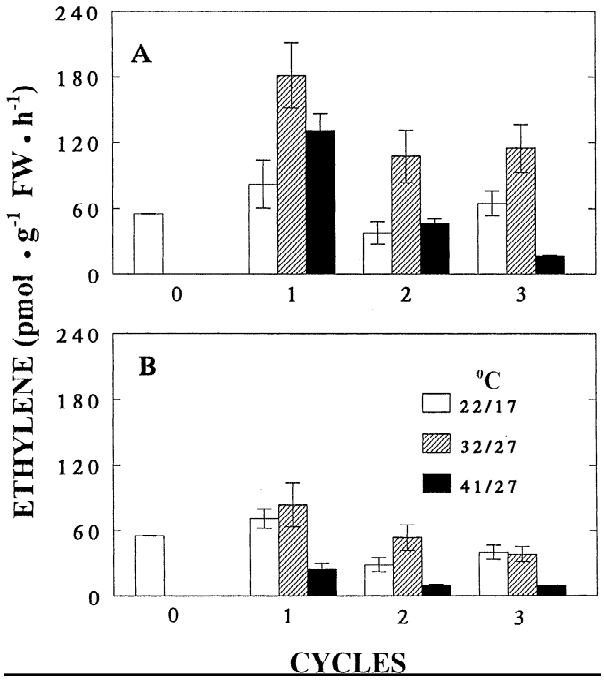

Fig. 3. Effect of high temperature cycles on ethylene production in pepper flowers. Whole plants were subjected to daily cycles of high temperatures for 8 h. For ethylene measurement, two flowers were enclosed in a 14-mL test tube. Other details are as in Fig. 2.

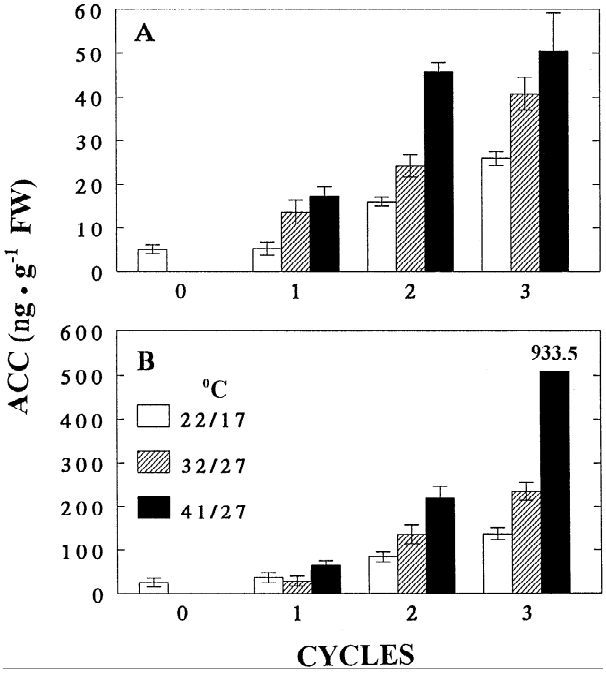

Fig. 4. Effect of high temperature cycles on ACC content in flower buds (*A panel*) and petals (*B panel*). Whole plants were subjected to daily cycles of high temperatures for 8 h. ACC content in flower buds or petals was measured daily at the end of the high temperature period. *Vertical bars* indicate ± S.E. ($n = 8$).

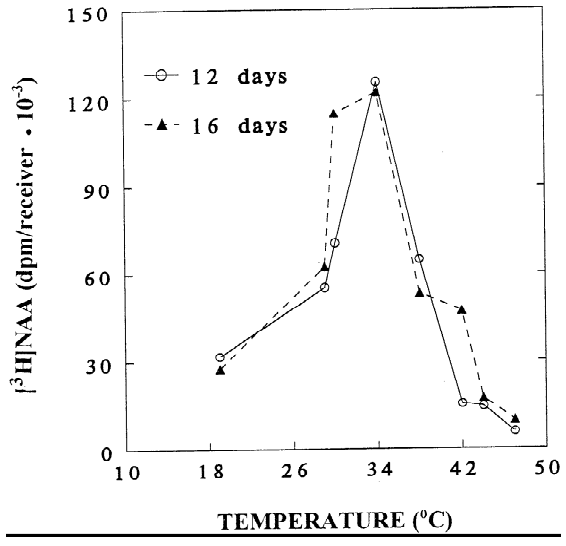

Fig. 5. Effect of temperature during transport on [^{3}H]NAA transport capacity in pepper fruitlet peduncle sections. Fruitlets were sampled 12 and 16 days after petal abscission. [^{3}H]NAA transport duration was 6 h. *Vertical bars* indicate ± S.E. ($n = 8$).

period and also 16 h later (i.e. at the end of the temperature cycle). The IAA level in control plants was usually quite stable throughout the experimental period (Figs. 7*A* and *8A*). In general, temperatures of 32 and 40°C decreased significantly the endogenous titer of IAA in pepper fruitlets and fruitlet peduncles. It seems that at least under the present experimental conditions, the effect of high temperatures on IAA levels was long lasting, since the level of endogenous auxin remained low upon transferring the plants to the lower temperature period of each cycle (Figs. 7*B* and 8*B*).

Experiments with Paprika

Essentially the same results described above for pepper were observed when paprika (*C. annuum* L. cv. Lehava) plants were subjected to the same high temperature regimes.

Discussion

It is well accepted that leaf abscission follows the model proposed by Morgan (1984) and Osborne (1989). In the present work, aimed to determine how high temperatures induce increased abscission of reproductive organs of pepper, we focused on the various components of this model. Accordingly, we examined the role of ethylene biosynthesis and auxin level and transport in high temperature-induced abscission.

It is somewhat surprising that heat stress resulted in only a small increase in ethylene production in the re-

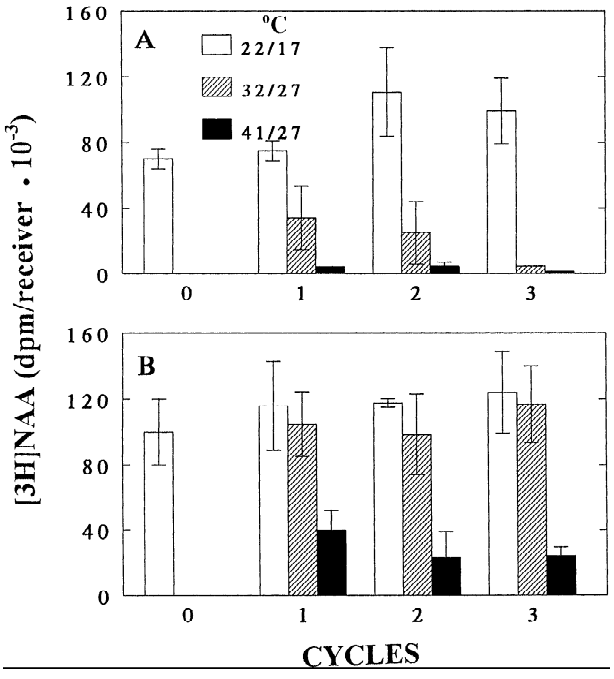

Fig. 6. Effect of high temperature cycles on [^{3}H]NAA transport capacity in pepper flower (*A panel*) and fruitlet (*B panel*) peduncle sections. Whole plants were subjected to daily cycles of high temperature for 8 h. The sections were sampled daily after the 8-h high temperature period. Fruitlets were sampled 12 days after petal abscission. *Vertical bars* indicate ± S.E. ($n = 8$).

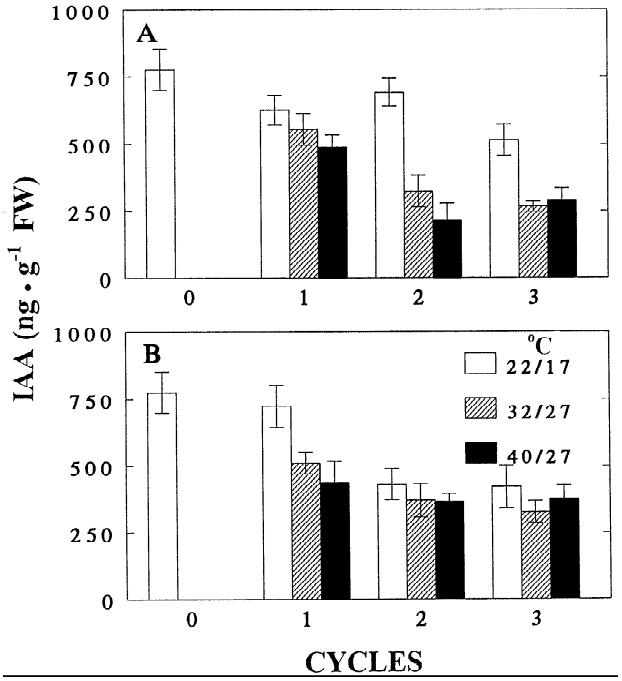

Fig. 7. Effect of high temperature cycles on IAA content in pepper fruitlets. Whole plants were subjected to daily cycles of high temperatures for 8 h. IAA was measured daily after the 8-h high temperature period (*A panel*) and at the end of the temperature cycle (*B panel*). Fruitlets were sampled 12 days after petal abscission. *Vertical bars* indicate ± S.E. ($n = 8$).

productive organs, although the increase was significant (Figs. 2*A* and 3*A*). The highest temperature regime, which was the most active in the induction of reproductive organ abscission (Fig. 1), even reduced ethylene production in flowers (Fig. 3). Similar inhibition of ethylene production by temperature above 35°C has also been reported (Abeles et al. 1992, Aloni et al. 1994). A comparison between ethylene production and abscission responses to high temperature does not show a positive correlation between the two events. Other investigators were also unable to find a close relationship between ethylene production and heat stress-induced abscission (Aloni et al. 1994, Gross 1992). These observations may be interpreted as though ethylene does not play an important role in heat stress-induced abscission. However, this assumption may be incorrect since silver thiosulfate, an ethylene action inhibitor, significantly reduced reproductive organ abscission in heat-stressed pepper (Wien and Zhang 1991). The fact that abscission occurred even at low rates of ethylene production may be explained by increased sensitivity to ethylene, which might be a result of the decreased auxin transport to the abscission zone (Fig. 6, and Morgan 1984, Osborne 1989).

In contrast to ethylene production, ACC levels increased significantly in response to high temperatures and correlated positively with the increase in temperature (Fig. 4). It is possible that the high temperatures applied inhibited ACC oxidase activity as reported previously (Chan 1986, Yu et al. 1980), thus blocking the conversion of ACC to ethylene. This may be the reason why levels of ethylene production increased less compared with ACC and decreased rather than increased at the highest temperature regime. It can also explain why elevated levels of ethylene induced by relatively high temperatures were observed only upon return to room temperature (Field 1981).

Reduction of endogenous IAA level during abscission is well documented (Riov et al. 1982 and literature cited therein). The levels of IAA in plant tissues have been shown to be reduced by stress conditions (Guinn and Brummett 1988). Similarly, high temperatures reduced IAA levels in the reproductive organs of pepper (Figs. 7*A* and *8A*). These observations are in accord with previous reports demonstrating that increased abscission of the reproductive organs of various plants by high temperatures was accompanied by reduction in IAA levels (El Abd et al. 1986, Kuo and Tsai 1984). It should, however, be mentioned that similar to ethylene production, the reduction in IAA levels in heat-stressed pepper was quite low (Figs. 7*A* and 8*A*). Added to this are the observations

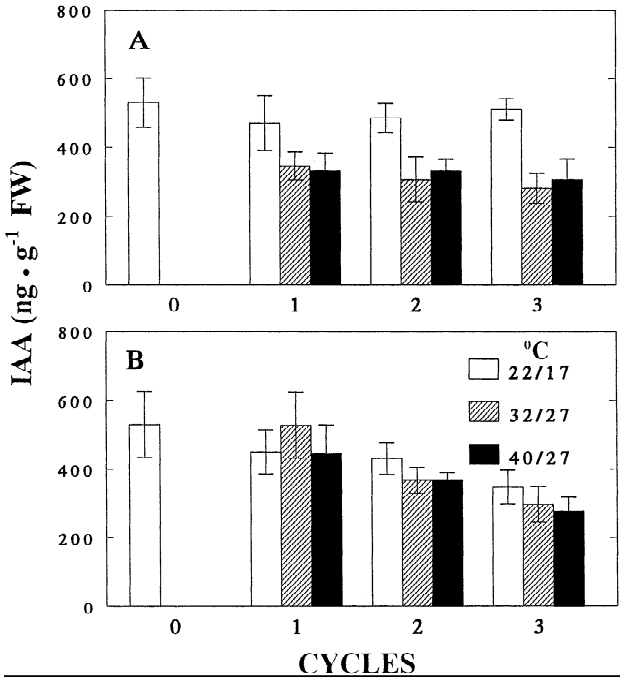

Fig. 8. Effect of high temperature cycles on IAA content in pepper fruitlet peduncles. Whole plants were subjected to daily cycles of high temperature for 8 h. IAA was measured daily after the 8 h of the high temperature period (*A panel*) and at the end of the temperature cycle (*B panel*). Fruitlet peduncles were sampled 12 days after petal abscission. *Vertical bars* indicate ± S.E. ($n = 8$).

by Ofir et al. (1993) that IAA levels in reproductive organs of bean subjected to heat stress were unaffected or even higher than those in the control. This suggests that a direct reduction of auxin level under heat stress conditions is not a generally significant factor in heat stress-induced abscission. It should, however, be mentioned that in the present and the above cited reports the auxin level was not measured specifically in the abscission zone. Therefore, a possible localized auxin reduction, which might have occurred in the abscission zone due to inhibition of auxin transport, was not detected by assaying the whole organ.

Inhibition of auxin transport seems to be the major factor leading to abscission of pepper reproductive organs in response to high temperatures (Fig. 5, *A* and *B*). This was particularly evident in the highest temperature regime, which significantly reduced auxin transport in all organs tested and at the same time significantly stimulated abscission. Since we measured auxin transport in excised sections at one temperature (28°C), it can be concluded that high temperatures affect auxin transport directly and irreversibly. Ofir et al. (1993) also observed that heat stress reduced significantly the diffusion of endogenous IAA from bean reproductive organs into agar, suggesting that it was caused by a direct inhibitory effect of the high temperatures on the transport capacity of the tissues involved. The significance of the inhibition of auxin transport capacity in pepper reproductive organ abscission was also demonstrated by Wien and Zhang (1991) and Wien et al. (1991). They showed that treatment of flower pedicels with 2,3,5-triiodobenzoic acid and ethylene-generating chemicals at concentrations insufficient to cause significant abscission when used alone, induced an almost complete flower abscission.

Reduction of auxin transport capacity during natural abscission is usually believed to be induced by the elevated levels of ethylene during this process (Morgan 1984). Whether ethylene is also involved in the inhibition of auxin transport by heat stress is not yet clear. Since auxin transport was inhibited significantly at the highest temperature regime, which reduced ethylene production, it is possible that high temperature inhibits auxin transport independently of ethylene. Recent observations suggest that increased production of activated oxidative species under stress conditions can reduce auxin transport, which is followed by increased organ abscission (Rina Michaeli, unpublished).

Inhibition of auxin transport is a major component of the natural abscission process of leaves, and this seems to be the case also for stress-induced abscission (Bangerth 1990, Ofir et al. 1993, and present observations). The resulting reduction in the endogenous IAA level in the abscission zone may lead to increased sensitivity of the zone to ethylene in the induction of abscission. Abscission can therefore occur without a significant increase in ethylene production. This can explain why heat stress induced increased abscission without a significant increase or even under decreased ethylene levels.

Acknowledgments. This research was supported by United States-Israel Binational Agricultural Research and Development Fund (BARD) Project US-1706-89R and the Hohenhein University-Faculty of Agriculture Joint Research Program.

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