Abscission Responses to Moisture Stress, Auxin Transport Inhibitors, and Ethephon

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ABSTRACT

The three abscission-inducing agents—water stress, Ethephon, and auxin transport inhibitors—acted synergistically to promote leaf fall in cotton (Gossypium hirsutum L.). However, the synergism was primarily between stress and Ethephon. Auxin transport inhibitors did not promote the effect of stress alone, only the effect of Ethephon in well watered plants and gave a very small promotion with stress and Ethephon together. Abscission was rapid in stressed plants treated with Ethephon and an auxin transport inhibitor, while leaves fell more slowly from well watered plants treated with Ethephon alone. This suggests that water stress or auxin transport inhibitors influence initial events in abscission; since an auxin transport inhibitor will replace the effect of stress but not Ethephon, an initial event in stress-induced abscission appears to be inhibition of auxin transport. Ethephon promoted lateral bud release, and auxin transport inhibitors did not duplicate that effect alone or promote it in combination with Ethephon.

Several lines of evidence suggest that a relationship may exist between abscission-modifying effects of water stress, auxin transport inhibitors, and ethylene in cotton. First, there is growing evidence that endogenous ethylene regulates leaf abscission (9, 18). The action of ethylene in abscission appears to be due in part to inhibition of auxin transport (4–6). Auxin transport inhibitors increase or hasten leaf abscission induced by exogenous ethylene or Ethephon (15, 16). There is some evidence that ethylene production in cotton petioles increases during water stress (13). Petioles contain levels of ethylene about 10 times higher than leaf blades (12). During water stress or following release from stress by watering, cotton plants defoliate (14). Finally, exogenous ethylene promotes the water stress-induced abscission of cotyledonary leaves (10). The evidence suggests that an increase in the synthesis of ethylene and interruption in the auxin flux serve to trigger the separation process.

The series of interrelations suggested to us that water stress, auxin transport inhibitors, and ethylene might have synergistic effects on leaf abscission. The evidence also suggested a way to investigate the mechanism of stress-induced abscission further.

MATERIALS AND METHODS

Cotton plants (Gossypium hirsutum L., c.v. Stoneville 213) were grown in a greenhouse in sand-peat moss-vermiculite mixture watered with Hoagland solution modified as described previously (17). Plants were in flowering to heavily fruited stage of growth with 12 to 20 expanded true leaves when experiments were initiated by withholding water.

Water stress was initiated by withholding water from the appropriate plants beginning on day zero. Growth regulators were applied when plants reached the desired level of stress; the time of application ranged between 16 and 24 hr before the pots were again watered. Aqueous solutions of the growth regulators were freshly prepared on the day of application to include 0.05% Tween 20 as a surfactant. Compressed air-activated glass atomizers were used to spray plants to a wet but not dripping stage. For dual treatments, plants were allowed to dry before the second growth regulator was applied. The auxin transport-inhibiting compounds applied were N-1-naphthyl phthalamic acid as the sodium salt (Unireal Chemical Co., Alapan) and 3,3a-dihydro-2-(p-methoxyphenyl)-8H-pyrazolo-(5, 1 a) isindol-8-one (E. I. du Pont de Nemours & Co., DPX-1840) (15). They were used interchangeably without apparent difference in our experiments. Ethylene treatment was accomplished by application of Ethephon:2-chloroethanephosphonic acid (Amchem Corp., Ethrel). Concentrations are indicated in the figures and table.

Plant water potentials were determined before dawn on the day of rewatering on the eighth true leaf with a Scholander pressure bomb (10). Abscission of leaves greater than 5 cm in diameter in response to gentle pressure on each main stem leaf was observed daily. In some experiments, plants were maintained for several weeks following the stress-growth regulator treatments and growth of lateral buds was observed.

RESULTS

The combination of the three abscission-inducing agents—water stress, Ethephon, and auxin transport inhibitor (ATI)6—consistently caused the greatest leaf fall, but the extent of abscission was not much greater than that resulting from the combination of water stress and Ethephon without a transport inhibitor (Fig. 1). The combination of agents acted synergistically causing about 32% more total abscission than the sum of the three applied singly. The ATI applied without Ethephon to stressed or well watered plants had no apparent effect, but it gave the marked synergism reported earlier (15) when applied with Ethephon to well watered plants (Fig. 1). These results were confirmed in several other experiments not reported in detail.

1 A preliminary report of this study appeared in Proceedings of the 1974 Beltwide Cotton Production Research Conferences, p. 33 (National Cotton Council, P.O. Box 12285, Memphis, Tenn. 38112).
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5 Abbreviation: ATI: auxin transport inhibitor; Ψ: leaf water potential.
the abscission on stressed plants occurred in the first 24 hr after rewattering; yet, the reverse was true for nonstressed plants treated with Ethephon alone or in combination with ATI (Fig. 2). Another characteristic of the system is that with a fairly severe treatment that maximizes abscission in stressed plants ($10^{-3}$ M Ethephon and $10^{-2}$ M ATI, Figs. 1 and 2), abscission maximizes at the fairly low stress levels of −10 to −12 bars (Fig. 3). Much higher levels of water stress alone are required to maximize abscission (14).

During the course of the study, the experimental treatments were observed to have a significant effect on release of lateral buds from apical dominance. Under the growing conditions employed, the plants characteristically had a single stem. Ethephon and Ethephon plus ATI promoted lateral bud growth significantly above controls (Table I). ATI alone did not promote lateral bud growth; thus, the effect of the ATI plus Ethephon treatment must have been primarily due to the Ethephon. Stressed plants always exhibited greater abscission, but less bud growth, than well watered plants comparing either Ethephon or Ethephon plus ATI treatments. Stress may have irreversibly damaged some buds thereby reducing the potential for lateral bud release. The control abscission value in experiment 1 is unusually high because in this test plants were used which had previously experienced considerable loss of old leaves (Table I).

**DISCUSSION**

The promotion of leaf abscission from water-stressed plants by Ethephon was similar to that described earlier (10). In addition, there appeared to be a slight synergistic promotion of leaf abscis-
sion when auxin transport inhibitor treatments were combined with water stress and Ethephon treatments (Fig. 1). Auxin transport inhibitors alone did not promote abscission of leaves from water-stressed plants, suggesting that water stress and the inhibitors may act similarly. Since the transport inhibitors promoted abscission in well-watered plants treated with Ethephon (Fig. 1), they appear to substitute at least partially for water stress in this system.

The rates of abscission also reflect on the probable roles of the three agents studied here. Following irrigation, abscission of leaves from previously water-stressed plants occurs quickly, usually within the first 24 hr, suggesting that stress prepares the leaf to respond to Ethephon (Fig. 2). Ethephon-induced abscission of leaves from well-watered plants occurs more slowly, suggesting that the final abscission-achieving action of Ethephon is delayed until some preparatory event is satisfied or facilitated by auxin transport inhibitors (Fig. 1). Ethephon and ATI applied at the beginning of the water stress treatment, rather than near the end, failed to promote stress-induced abscission, which suggests a preparatory event which increases sensitivity to ethylene. Thus, both water stress and ATI seem to deal with the preparatory event(s) which is related to auxin supply, inhibition of auxin transport through the petiole and leaf veins being a critical process to that supply (4-6). Ethephon or native ethylene also promotes the final events in abscission: induction of synthesis of hydrolytic enzymes and secretion of some of these enzymes into the cell wall (1, 2, 8, 19). In the stressed or ATI-treated plants, Ethephon was able to initiate these final events more promptly. Ethephon did promote abscission in water-stressed plants, whereas the ATI did not, a result which suggests that stress reduces auxin transport more than it promotes ethylene synthesis. Davenport et al. (7) have recently determined that water stress does inhibit auxin transport in cotton petioles. In this same study, stress did not promote ethylene synthesis in cotyledonary and young leaf petioles, whereas it did promote ethylene production in petioles of old leaves (13) or detached leaves (3). Partial vacuum delayed or reduced water stress-induced chlorosis and abscission in cotton (11), and CO₂ competitively inhibited the effect of exogenous ethylene on leaf abscission from moisture-stressed plants (10). Both of these latter results suggest that ethylene synthesis is involved in stress-induced abscission. Our conclusion is that both processes are involved; however, inhibition of auxin transport is the primary effect and the availability of ethylene limits the degree of stress-induced abscission.

LITERATURE CITED

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