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Epinasty of Poinsettias—the Role of Auxin and Ethylene

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ABSTRACT

Upward physical restraint of the normally horizontal bracts of poinsettia (*Euphorbia pulcherrima* Willd.) resulted in increased ethylene production and epinastic curvature of the petioles after 5 days. Downward restraint caused little change in ethylene production or epinasty, indicating that the enhanced ethylene production observed in petioles bent upwards is not due to the bending stress alone. Epinasty, measured upon removal of upward physical restraint, was not affected by spraying plants with aminoxyacetic acid to reduce ethylene production or with silver thiosulfate to prevent ethylene action. Removal of the bract blades prevented the epinastic response of the petiole, and the response was restored by applying indoleacetic acid to the cut petiole end. Redistribution of auxin appears to be responsible for both the epinasty and the increased ethylene production of reoriented poinsettia bracts.

Upward vertical reorientation of the normally horizontal bracts of poinsettia plants causes drooping of the bracts upon removal of the force holding the bract in a vertical position (16). It has recently been concluded by several workers that an endogenous production of C_2H_4 in response to the bending stress during reorientation causes this epinastic reponse (13, 15). This conclusion was based on a correlation between C_2H_4 production by petioles and the epinastic response (14), the partial reduction of the effect by treatment with silver nitrate and the known epinastic response of poinsettia to exogenous C_2H_4 (15).

Although most of the data reported thus far are consistent with the view that the bending stress during reorientation induces production of C_2H_4, which in turn causes epinasty by altering the pattern of auxin distribution (11), this hypothesis has not yet been proved. An alternative hypothesis, namely that the change in orientation itself brings about a redistribution of auxin in the petiole, which not only causes the epinasty but also enhances C_2H_4 production by the petioles can be supported by the following observations:

Poinsettia and other plants become epinastic in the absence of stress if they are rotated on a clinostat; this epinasty is associated with a changed distribution of auxin in the petioles (10).

C_2H_4 production increases in plants rotated on a clinostat (8).

Position-induced epinasty cannot be overcome by hypobaric reduction of O_2 and C_2H_4 concentrations (17).

Ag^+, a potent inhibitor of the epinasty caused by applied C_2H_4 in tomatoes (2, 3), is only partly able to reduce position-induced epinasty in poinsettia (15).

The purpose of the study reported here was to evaluate the relative importance of C_2H_4 and auxin in the epinasty of reoriented poinsettia bracts.

MATERIALS AND METHODS

Poinsettia plants (*Euphorbia pulcherrima* Willd., 'Annette Hegg Diva') were grown in a greenhouse under standard cultural conditions (7) until they reached anthesis. The plants were pinched to give four flowering branches each. The large colored bracts were vertically oriented by bending them upwards or downwards against the stem and holding them in this position with rubber bands. The plants were then held in a dark growth chamber at a constant temperature of 15.5 C for 5 days. After this time, the rubber bands were removed and the large colored bracts were immediately excised and debladed. Epinasty was recorded by placing the excised petioles on a photocopier and making a copy. The angle between tangents to the curve at each end of the petiole was then measured (Fig. 1).

For determination of C_2H_4 production, petioles from each replication were weighed and placed in 55-ml tubes, sealed with serum caps. After 3 h, a 3-ml sample was withdrawn by means of a gas-tight syringe and the C_2H_4 production by the petioles in the tube was determined using a "Carle" gas chromatograph equipped with an "HNU" photoionization detector and a "Keithley" 614C electrometer. Plants were treated with C_2H_4 gas by placing them for 24 h in sealed glass tanks (two plants per tank) ventilated with 40 l/h of air containing 15 μl/l of C_2H_4.

AOA[2] was used as an inhibitor of C_2H_4 production (20) and was dissolved in DI to final concentrations of 2 and 5 mM; plants were sprayed to run-off 2 h before reorientation.

When petioles were to be pretreated with IAA, the bract blades were removed, and IAA was applied at a concentration of 1% in lanolin paste, either to the cut stump or to the adaxial surface of the petiole. The petioles were then reoriented as described before. STS was used to study the effects of an antagonist of C_2H_4 action (18) in normal and debladed petioles, with and without applied IAA. It was prepared by mixing one part of 0.1 M $AgNO_3$ with four parts of 0.1 M $Na_2S_2O_3$ and diluting with DI to a final Ag^+ concentration of 4 mM (12).

RESULTS

Effects of Reorientation and Inhibition of C_2H_4 Production. Upward vertical restraint caused epinasty (Fig. 1) and increased C_2H_4 production in the petioles of poinsettia plants post-restraint (Tables I and II). In contrast, C_2H_4 production post-restraint was unaffected when the petioles were restrained vertically downwards, although this caused a slight, but significant, epinasty (Table I).

C_2H_4 production post-restraint by the upward vertically oriented petioles of plants pretreated with 5 mM AOA was the same as in petioles of control plants oriented horizontally (Table II). The AOA pretreatment did not prevent the epinasty of reoriented petioles.

Effects of the Blades, of IAA and of STS. When the blades of

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[2] Abbreviations: AOA, aminoxyacetic acid; DI, deionized water; STS, silver thiosulfate.

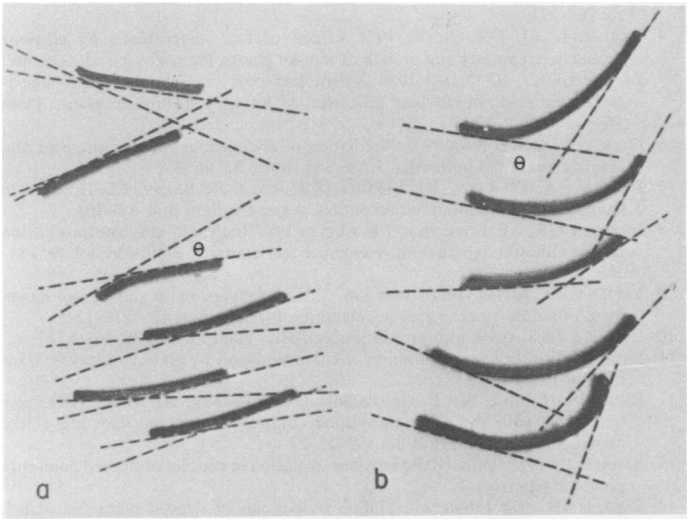

FIG. 1. Method for determining epinastic curvature. Petioles from control (a) and reoriented (b) bracts were excised and copied in a photocopier. The angle between tangents to the curvature of the ends of the petioles (θ) was used as a measure of epinasty.

Table I. *Effect of Reorientation on Post-restraint Epinastic Curvature and C_2H_4 Production by Poinsettia Petioles*

Means of four stems (averaging six petioles each) per treatment. Means in each column with no letter in common are significantly different (P = 0.05, Duncan's Multiple Range Test).

Orientation	Epinastic angle	C_2H_4 production
	degrees	*nl/g·h*
Horizontal	3c	0.62a
Vertical (upwards)	39a	1.67b
Vertical (downwards)	18b	0.65a

Table II. *Post-restraint C_2H_4 Production and Epinastic Angle of Petioles from Poinsettia Plants Sprayed 2 Hours before Reorientation with Various Concentrations of AOA*

Means of five branches, six petioles per branch. Means for each parameter with no subscript letter in common are significantly different (P = 0.05, Duncan's Multiple Range Test).

AOA Concentration	Horizontal		Vertical	
	C_2H_4 production	Epinastic angle	C_2H_4 production	Epinastic angle
mM	*nl/g·h*	*degrees*	*nl/g·h*	*degrees*
0	0.22c	11c	0.86b	46a
2	0.08c	8c	0.62b	44a
5	0.00c	9c	0.27c	40a

poinsettia bracts were removed before reorientation of the petioles, the normal epinastic curvature did not occur, although post-restraint C_2H_4 production by the petioles was similar to that of petioles from intact bracts (Table III). In contrast, debladed petioles whose cut ends were treated with a lanolin paste containing IAA responded to vertical orientation in just the same way as those of intact bracts. C_2H_4 production by IAA-treated petioles post-restraint was many times that of the controls. When IAA in lanolin was applied to the adaxial surface of the petiole, the epinastic angle was greater than 100° (text only).

Spraying plants with 4 mM STS before changing bract orientation had no significant effect on the epinasty caused by the reorientation (Table III). STS pretreatment greatly increased post-restraint C_2H_4 production by all petioles, regardless of other treatments. When poinsettia plants were exposed to 15 μl/l C_2H_4 for 24 h, the strong epinastic response of control plants (epinastic angle 61°) was completely absent in plants which had been sprayed 18 h before the start of the C_2H_4 treatment with 4 mM STS (text only).

Table III. *Effects of Removal of the Blades, Their Replacement with IAA and Spraying with Silver Thiosulfate on Post-restraint Epinastic Curvature and C_2H_4 Production of Reoriented Poinsettia Petioles*

Means of four branches, six petioles per branch. Means in each column with no letter in common are significantly different (P = 0.05, Duncan's Multiple Range Test). C_2H_4 production data were analyzed using a logarithmic transformation.

Treatment	Orientation	Epinastic Angle	C_2H_4 Production
		degrees	*nl/g·h*
Control	Horizontal	3c	0.62g
	Vertical	39a	1.67f
Blades removed	Horizontal	8bc	0.25g
	Vertical	16b	1.03fg
Blades removed + IAA	Horizontal	16b	7.30cd
	Vertical	41a	7.73cd
Silver thiosulfate	Horizontal	3c	3.24ef
	Vertical	32a	27.36a
Blades removed + silver thiosulfate	Horizontal	4c	2.16f
	Vertical	18b	5.25de
Blades removed + silver thiosulfate + IAA	Horizontal	13bc	16.39b
	Vertical	34a	21.04b

DISCUSSION

A marked epinastic response of petioles to changed orientation was attributed by Lyon (10) to a redistribution of auxin in the petiole resulting from the reorientation. This simple hypothesis was challenged by Leather *et al.* (8) who showed that plants rotated on a clinostat produced significant quantities of C_2H_4, and that epinastic responses to changed orientation could be inhibited by 10% CO_2. They contended that position-induced epinasty was analogous to other epinastic responses and was caused by a change in auxin distribution induced by increased endogenous C_2H_4 concentrations.

Recent reports have concluded that the increased C_2H_4 production observed in reoriented poinsettia petioles is caused by the stress of reorientation (13–15). It appears that simple mechanical stress cannot be the cause of increased C_2H_4 production in poinsettia petioles restrained upwards for 5 days. It has already been noted that merely rotating plants on a clinostat results in increased C_2H_4 production (10). Downward bending of the petioles (which imposes, if anything, more mechanical stress than upward bending) did not increase C_2H_4 production rates over those of control petioles (Table I).

Whatever the cause of the enhanced ethylene production in reoriented poinsettia petioles, the data reported here do not support the contention that C_2H_4 is responsible for epinastic curvature. Treatment of poinsettias prior to reorientation with AOA, a specific inhibitor of C_2H_4 synthesis (20), reduced the rate of C_2H_4 production to that of the control petioles (Table II), but the post-restraint epinastic angle of the reoriented petioles was unchanged. Similarly, while treatment with STS, a specific inhibitor of C_2H_4 action (18), completely prevented the epinastic response of poinsettia petioles to exogenous C_2H_4, it had no effect on the development of epinasty in reoriented petioles (Table III). The stimulation of post-restraint C_2H_4 production by STS is similar to the effect of Ag^+ in other vegetative tissues (1).

It appears likely that the epinastic responses observed here result from changed distribution of auxin in the petioles (10, 11). In plants exposed to exogenous C_2H_4 (2) or subject to waterlogging (4, 5), this redistribution is induced by C_2H_4 (11). Redistribution of auxin appears also to be important in the epinastic response of reoriented petioles. When blades were removed from poinsettia bracts, reorientation of the petioles caused no epinasty, although post-restraint C_2H_4 production was enhanced by the reorientation (Table III). Placing 1% IAA in lanolin paste on the cut stump restored the response of the petioles to reorientation. Since the bracts are known to be a source of auxin in poinsettias (6), it is reasonable to assume that the epinastic response results from a changed distribution of auxin in the petiole. Certainly a very striking epinasty was induced by applying IAA to the adaxial surface of the petioles.

Inasmuch as our data fail to support the hypothesis that C_2H_4 is the cause of the redistribution of auxin in reoriented poinsettia petioles, we suggest that in such petioles the redistribution of auxin is the result of the change in orientation itself. This view is supported by the observation that downward reorientation of poinsettia bracts caused only a slight epinastic response (Table I); auxin transport is well known to be inhibited in inverted organs (9). We would suggest that the stimulation of C_2H_4 production in reoriented poinsettia petioles (13–15, 17) is most likely to be a response to changed auxin distribution in the petiole (19).

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