

Auxin-induced Ethylene Synthesis during Rooting and Inhibition of Budbreak of 'Royalty' Rose Cuttings

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Abstract. Single-node 'Royalty' rose (*Rosa hybrida* L.) cuttings were used to examine the relationship between adventitious root formation, budbreak, and ethylene synthesis following IBA treatment. IBA was applied as a lo-second basal quick dip before rooting, and AIB, GA₃, STS, and ethephon were applied either as basal dips or foliar sprays. IBA application increased rooting and inhibited budbreak of cuttings. IBA 2 600 mg·liter⁻¹ greatly inhibited budbreak during 4 weeks of rooting. IBA treatment stimulated ethylene synthesis, which was inversely correlated with budbreak of cuttings. Ethephon also significantly inhibited budbreak. Budbreak of rose cuttings was completely prevented by repeated ethephon sprays used to maintain high endogenous ethylene levels during the first 10 days. Treatment with STS, an ethylene-action inhibitor, improved budbreak. The inhibition of budbreak by IBA treatment resulted primarily from elevated ethylene levels. Root initiation and root elongation of cuttings initially inhibited budbreak, but later promoted budbreak. Chemical names used: indole-3-butyric acid (IBA); gibberellic acid (GA₃); silver thiosulfate (STS); AIB, aminoisobutyric acid (AIB); (2-chloro-ethyl)-phosphoric acid (ethephon).

Stem cuttings are treated with synthetic auxins, such as indole-3-butyric acid (IBA) and naphthaleneacetic acid (NAA), to promote adventitious root formation. However, application of synthetic auxins inhibits bud development of cuttings in several species (Christensen et al., 1980; DeVries and Dubois, 1988). Auxins applied at high concentrations may even prevent shoot growth or result in the abscission of the young shoot as a whole after budbreak, despite adequate rooting (Hartmann et al., 1990). For example, IBA at 1000 to 2500 mg·liter⁻¹ caused almost complete bud abscission of hazelnut (*Corylus avellana* L.) softwood cuttings (Bassil et al., 1991). Auxins also inhibited epicormic shoot formation (Bachelard, 1969; Bowerson and Ward, 1968) and budbreak of in vitro-propagated plants (Banko and Stefani, 1989). In many species, rooted cuttings undertook a period of dormancy before they were able to resume shoot growth (Goodman and Stimart, 1987; Hartmann et al., 1990; Smalley and Dirr, 1986). Early budbreak and shoot growth were considered important factors correlated with the overwinter survival of newly propagated *Acer*, *Cornus*, *Hamamelis*, *Magnolia*, *Prunus*, *Rhododendron*, and *Viburnum* cuttings (Goodman and Stimart, 1987; Smalley and Dirr, 1986). Smalley and Dirr (1986) proposed that unfavorable environmental conditions during rooting affect the hormone levels in cuttings, which in turn impose or induce bud dormancy. However, little is known about the nature of such dormancy of rooted cuttings.

Some auxin effects are claimed to be mediated by ethylene synthesis (Burg and Burg, 1968a; Riov and Yang, 1989). In previous work with rose, silver thiosulfate (STS, an ethylene action inhibitor) stimulated budbreak and partially reversed IBA-induced bud inhibition (Sun and Bassuk, 1991). Our hypothesis is that basally applied IBA increases ethylene synthesis in the apical part of the cutting and, as a result, budbreak is inhibited. In this study, 'Royalty' rose cuttings were used as a model system to examine this hypothesis. The quantitative relationships were also examined between endogenous ethylene level, root formation, and budbreak of cuttings treated with aminoisobutyric acid (AIB, an

ethylene synthesis inhibitor), gibberellic acid (GA₃, a growth promoter), IBA, and STS.

Materials and Methods

Five- to 6-year-old stock plants of 'Royalty' rose were grown in benches or containers with 1 perlite : 1 peat : 1 soil (by volume). The greenhouse was at 21/16C (±2C) (day/night) in spring and winter, and supplemented with 16-h light by high-intensity discharge lamps hanging 2 m apart and 1.5 m above plants. Fertilizer of 20N-8.8P-16.6K was applied weekly at 200 mg N/liter. Single-node cuttings with four leaflets were taken only from nodes 4 to 8 (distal to proximal) to obtain uniform cutting material.

Chemical treatments before rooting included ethephon, AIB, GA₃, STS, and IBA. Ethephon, AIB, and GA₃ were directly dissolved or diluted in water. STS solution was prepared according to Reid et al. (1980). To apply ethephon, AIB, GA₃, and STS, the bases of cuttings were placed into beakers containing those solutions for 20 min indoors without direct light at room temperature (20 to 28C). The control cuttings were placed into water. Afterwards, the IBA treatment (dissolved in 50% aqueous ethanol) was applied as a 10-s basal dip, and treated cuttings were allowed to dry for 8 to 10 min before placing them into the rooting medium. The 50% ethanol solution did not affect ethylene synthesis (Fig. 1), rooting, and budbreak of cuttings (data not shown). Therefore, the control with water was not used in other experiments. Ethephon was used at concentrations from 200 to 400 mg·liter⁻¹, AIB and GA₃ at 100 mg·liter⁻¹, STS at 170 mg·liter⁻¹ (Ag⁺), and IBA from 100 to 1200 mg·liter⁻¹. Ethephon foliar sprays were applied once daily at 10:00 AM for the first 10 days at 500 mg·liter⁻¹, until runoff.

Cuttings were rooted in a medium of 3 perlite : 1 peatmoss (by volume) under intermittent mist operated for 5 s every 4 min from 6:00 AM to 10:00 PM. The rooting medium was at 20 to 23C in spring and winter. Percent budbreak of cuttings was recorded at 2- to 5-day intervals. A lateral bud ≥0.7 cm in length was counted as broken, and a leaf was counted as senescent if more than half of it was yellow. Cuttings were harvested after 20 to 30 days. Data were collected with respect to percent rooting, roots per rooted cutting, root length, and dry weight. All cuttings with roots 21 mm were considered as rooted.

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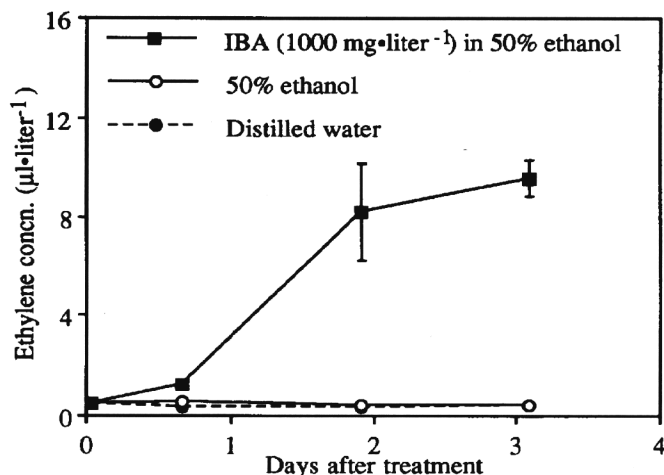


Fig. 1. Effect of ethanol and IBA on ethylene synthesis of 'Royalty' rose cuttings during rooting. Three samples of five cuttings were taken for ethylene determination. Bars are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

For endogenous ethylene determination, three or four samples of four to five cuttings selected at random were taken at each sampling time, except for one experiment in which one sample of eight cuttings was used (see Fig. 5A). Internal ethylene was extracted by placing cuttings in de-gassed water in a vacuum desiccator and reducing air pressure to a range of 91 to 95 kPa (50 to 80 mm Hg height) for 4 min. An inverted funnel sealed with a rubber stopper was placed over the cuttings to collect gas bubbles. With this method, 1 to 1.5 ml of gas could be collected from four cuttings and 0.8 to 1.0 ml was injected for gas chromatographic analysis immediately after vacuum was released. A C_{18} column and flame ionization detector were used, and operating conditions were as follows: column temperature at 80°C, injector and detector temperatures at 150°C, N flow rate at 25 ml·min⁻¹. To avoid the interference of stress-induced ethylene due to sampling disturbances, measurements of all samples taken at the same time were completed within 45 to 50 min.

A completely randomized design was used in this study with four to five replications of 10 to 24 cuttings per replication, except for the IBA concentration response experiment, which had only two replications of 16 to 18 cuttings each. Data were tested by analysis of variance or regression. Percentage data were arcsin-transformed before analysis, except for a few data sets that were normally distributed without data transformation.

Results

Rooting and budbreak of cuttings in response to applied IBA.

The number of roots per cutting in response to applied IBA demonstrated a quadratic pattern at concentrations from 0 to 1200 mg liter⁻¹ ($P = 0.0001$). The root count increased with IBA treatments of increasing concentration up to 600 mg·liter⁻¹, but did not increase with higher concentrations (Fig. 2). IBA ≥ 600 mg·liter⁻¹ inhibited budbreak almost completely during the 4-week rooting period. Even at concentrations as low as 100 mg·liter⁻¹, percent budbreak was halved. Budbreak and the root count were correlated negatively ($r = -0.807$, $P = 0.0002$). However, the inhibition of budbreak in response to IBA treatment (Fig. 3) could not be explained adequately by competition from increased root formation. The number of roots per cutting after 22 days was 7, 34, and 33 for 0, 500, and 1000 mg IBA/liter, respectively. Root dry weight

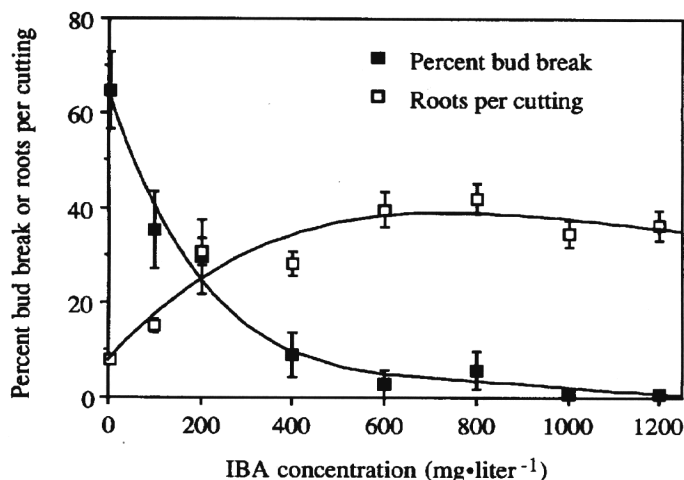


Fig. 2. Rooting and budbreak of 'Royalty' rose single-node cuttings following IBA treatment before rooting. Each treatment used 33 to 35 cuttings, which were harvested after 28 days. Bars are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

per cutting after 43 days was 82, 180, and 168 mg, respectively. No difference in root formation and growth was found between the two IBA concentrations; however, IBA at 1000 mg·liter⁻¹ was significantly more inhibitory to budbreak than IBA at 500 mg·liter⁻¹ (Fig. 3).

Endogenous ethylene concentration and budbreak of cuttings. IBA stimulated ethylene synthesis significantly in rose cuttings (Fig. 4). Endogenous ethylene concentration peaked after 2 or 3 days following IBA treatment. During this period, ethylene concentration of cuttings treated with 500 or 1000 mg IBA/liter was 4 and 10 times that of the control cuttings, respectively. Slight, but significant, differences in ethylene production of cuttings were still observed even after 20 days. High ethylene concentrations were associated closely with the inhibition of budbreak. The control cuttings contained the least ethylene (Fig. 4), but had the highest percent budbreak (Fig. 3). IBA treatment at 1000 mg·liter⁻¹ stimulated more ethylene production and delayed budbreak of cuttings more severely than did 500-mg IBA/liter treatment (Fig. 3). For the control cuttings, the course of budbreak could be divided

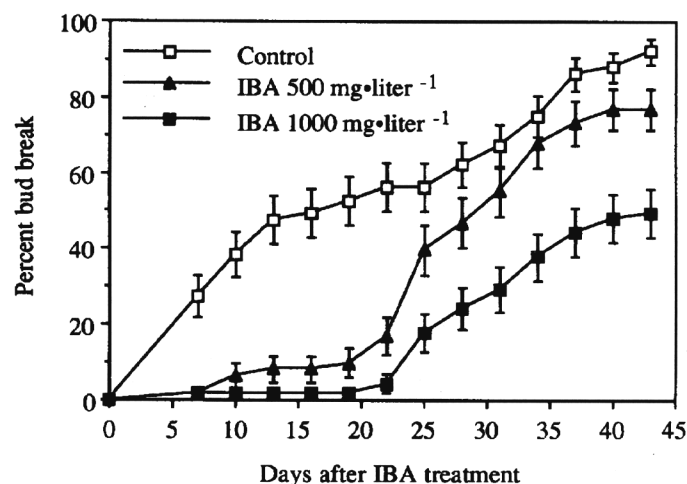


Fig. 3. Budbreak of 'Royalty' rose single-node cuttings following IBA treatment before rooting. Each point is the average value of four replications with 14 to 18 cuttings in one replication. Bars are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

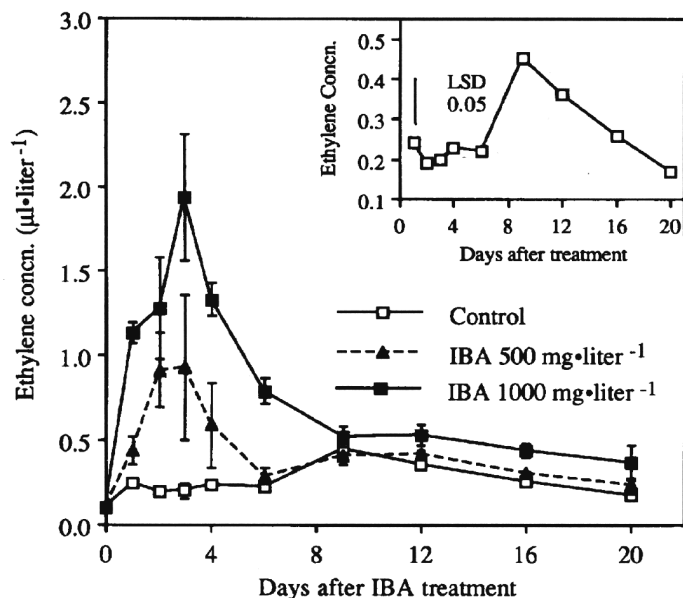


Fig. 4. Endogenous ethylene concentration of 'Royalty' rose single-node cuttings following IBA treatment before rooting. The inset shows the change of ethylene concentration of the control cuttings in another scale. Three samples of four cuttings were taken for ethylene determination. Bars are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

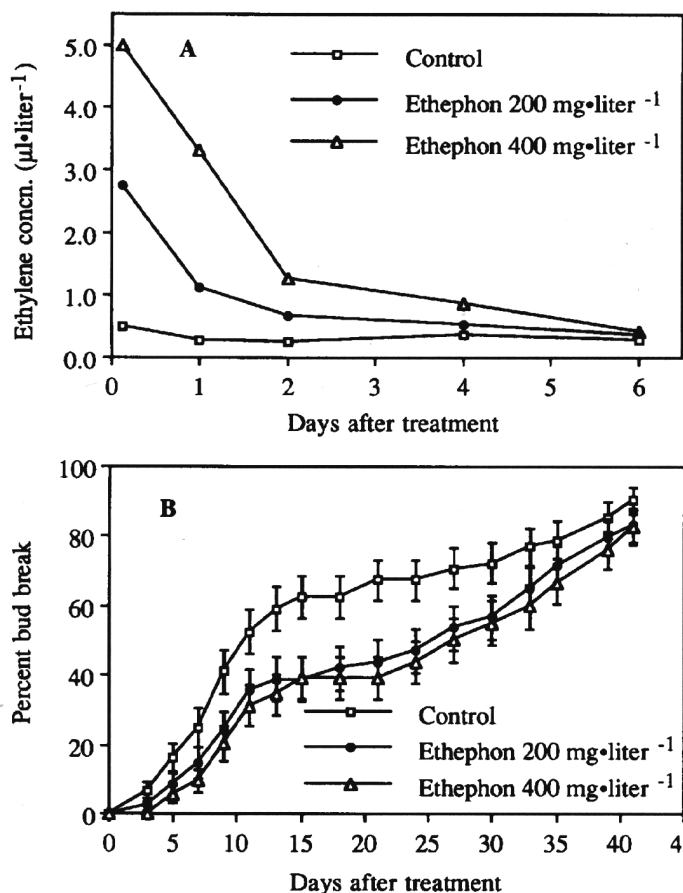


Fig. 5. Ethylene concentration (A) and budbreak (B) in ethephon-treated 'Royalty' rose cuttings. Cuttings were dipped into ethephon solution for 20 min before rooting. In (A), each sample contained eight cuttings for ethylene determination without replication. Data of budbreak were means of four replications with 14 to 20 cuttings each. Bars in (B) are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

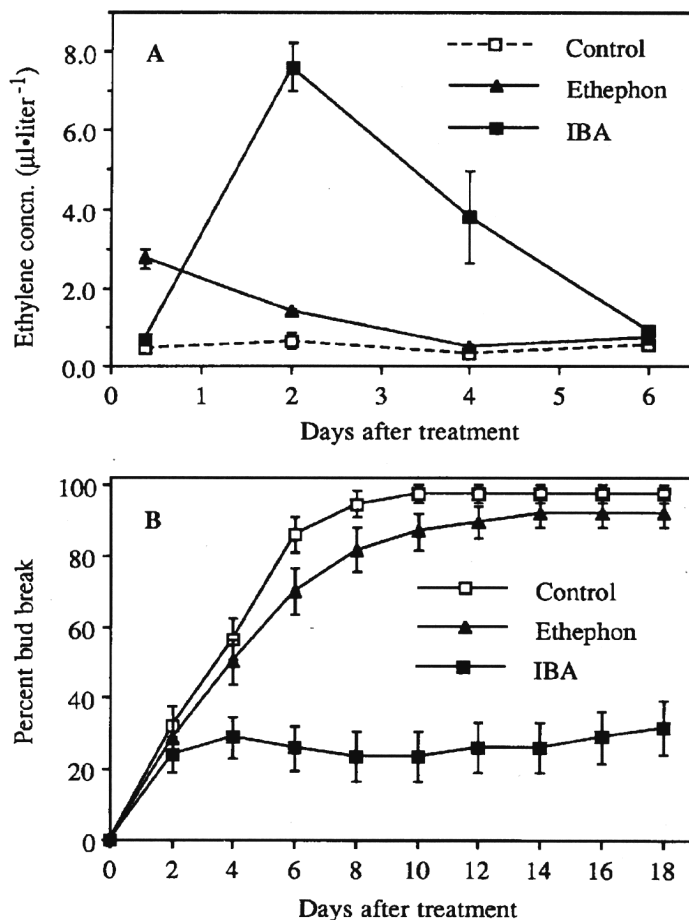


Fig. 6. Ethylene concentration (A) and budbreak (B) in ethephon- and IBA-treated 'Royalty' rose cuttings. Cuttings were dipped into ethephon solution at 200 mg·liter⁻¹ for 20 min or IBA solution at 500 mg·liter⁻¹ for 10 s before rooting. Ethylene concentration is the mean of three samples. Data for budbreak were means of four replications with 21 to 20 cuttings. Bars are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

into three distinct periods, from 0 to 13 days, 13 to 25 days, and 25 to 43 days. The rate of change in budbreak was a constant within each period (Fig. 3). The regression-estimated slopes were 3.6%, 0.8%, and 2.4% per day for three periods, respectively. Budbreak in those control cuttings during the second period was significantly slower than those of the other two periods ($P = 0.0001$). It was interesting to note reduction of the rate of change in budbreak from the first to the second period (Fig. 3) preceded by a high endogenous ethylene level between 8 and 16 days in the control cuttings (Fig. 4).

Effects of ethephon on rooting and budbreak of cuttings. According to our preliminary experiments, the maximum ethylene release occurred about 2 to 3 h after ethephon application through basal uptake (data not presented). By 3 h, the ethylene concentration of cuttings for 200 and 400 mg ethephon/liter was 5 to 10 times that for the control, respectively (Fig. 5A). However, the ethephon-induced ethylene accumulation declined rapidly. No differences in endogenous ethylene concentration were found between treatments after 6 days. Most of the ethephon may have already broken down to ethylene after 2 days (Fig. 5A). Ethephon treatments had no effect on rooting percentage and the number of roots per cutting (data not presented). During the first 21 days, budbreak of cuttings was significantly inhibited by basal ethephon uptake ($P = 0.0001$) (Fig. 5B). However, budbreak was similar for the two ethephon concentrations. After 30 days, the rate of change in budbreak of

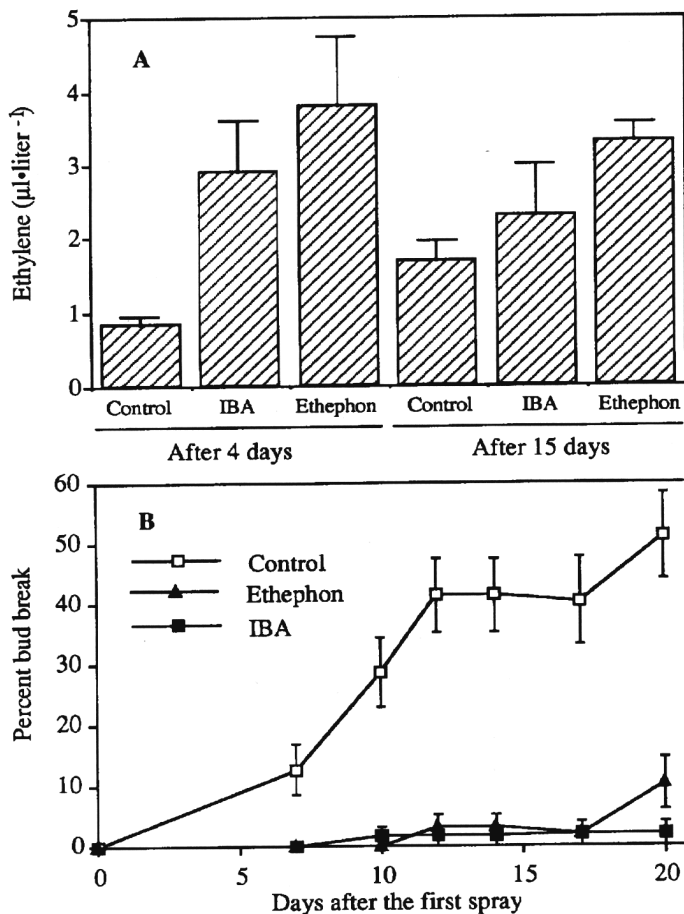


Fig. 7. Ethylene concentration (A) and budbreak (B) of rose cuttings following IBA application and ethephon sprays. IBA at 600 mg·liter⁻¹ was applied through a 1-s dip before rooting, and ethephon at 500 mg·liter⁻¹ was sprayed on leaves of cuttings daily at 10:00 AM at the first 10 days. Data for budbreak are means of four replications of 15 to 16 cuttings. Ethylene concentration is the mean of four samples. Bars are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

ethephon-treated cuttings was significantly greater than that of the control cuttings ($P = 0.0001$) because those cuttings inhibited by ethephon previously started to break bud. The slopes of percent budbreak after 21 days were 1.3 and 2.2 for the control and treated cuttings, respectively. Therefore, ethephon inhibited budbreak only temporarily in these cuttings.

Ethylene production in plant tissues is very sensitive to changes in environmental conditions. Although the same conclusion can be drawn from an experiment repeated at different times, the ethylene level measured may vary greatly (Figs. 1 and 4). The results reported above did not compare directly the effects of IBA and ethephon on ethylene formation and budbreak of cuttings because those experiments were conducted a few weeks apart. Thus, another experiment was conducted to compare directly the effects of ethephon and IBA on budbreak. IBA at 500 mg·liter⁻¹ resulted in much higher endogenous ethylene levels than did ethephon (Fig. 6). Average ethylene concentrations during the first 6 days were 0.5, 1.3, and 3.3 $\mu\text{l}\cdot\text{liter}^{-1}$ for the control, ethephon-, and IBA-treated cuttings, respectively. Percent budbreak was significantly lower in ethephon and IBA-treated cuttings than in the controls, and IBA was more inhibitory to budbreak than ethephon. However, when a foliar ethephon spray at 500 mg·liter⁻¹ was applied once daily for the first 10 days to maintain high endogenous ethylene levels that were similar to those in IBA-treated cuttings

Table 1. Effects of GA₃, AIB, STS, and IBA on endogenous ethylene level, leaf senescence, and rooting of 'Royalty' rose cuttings (see Fig. 8 for application rate and method). Cuttings were harvested after 30 days.

Treatments	Ethylene concn ($\mu\text{l}\cdot\text{liter}^{-1}$)	Percent yellowing leaf	Percent rooting	Roots per cutting	Root length (cm)
Control	0.8 ^z	0 ^y	99	12	3.6
AIB	0.6	0	100	11	4.3
GA ₃	0.8	0	88	5	1.9
STS	1.4	0	92	7	1.3
IBA	5.4	17	92	26	5.4
AIB + IBA	5.0	26	87	26	5.0
GA ₃ + IBA	7.6	31	85	11	4.5
STS + IBA	9.7	0	94	24	3.1

Significance of contrasts

IBA vs. no IBA	***	***	*	***	***
AIB vs. no AIB	NS	NS	NS	NS	ns
GA ₃ vs. no GA ₃	NS	**	*	***	***
STS vs. no STS	**	***	NS	**	***
IBA \times AIB	NS	NS	NS	NS	**
IBA \times GA ₃	NS	**	NS	***	**
IBA \times STS	NS	***	NS	NS	ns

^zEthylene concentrations determined from four samples of 5 cuttings at day 5.

^yLeaves with more than half of their area yellow recorded as senescent at day 15.

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

(Fig. 7A), ethephon inhibited budbreak to a similar degree as did the IBA treatment (Fig. 7B), and again had no effect on either rooting percentage or roots per cutting (data not shown).

Effects of AIB, GA₃, and STS on ethylene level, rooting, and budbreak. STS (170 mg·liter⁻¹ Ag⁺) and IBA (1000 mg·liter⁻¹) treatments increased endogenous ethylene concentrations of cuttings, while GA₃ (100 mg·liter⁻¹) and AIB (100 mg·liter⁻¹) had no significant effect (Table 1). Cuttings treated with STS plus IBA had the highest ethylene concentrations; however, they did not show any leaf yellowing, possibly because STS blocked ethylene action. GA₃- and STS-treated cuttings had significantly fewer and shorter roots than cuttings of other treatments. AIB influenced neither the number of roots nor root length. Ethylene concentration of cuttings was correlated positively with the number of roots

Table 2. Regression coefficients between ethylene concentration, rooting, and budbreak of 'Royalty' rose cuttings treated with GA₃, AIB, STS, and IBA. The analysis was based on the data in Table 1 only and the budbreak was analyzed separately from days 0 to 10, 11 to 20, and 21 to 30. Values in this table are the correspondent slopes of variables from linear regression models.

Dependent variables	Independent variables			r^2 value
	Ethylene concn ($\mu\text{l}\cdot\text{liter}^{-1}$)	Roots per cutting	Root length (cm)	
Roots per cutting	1.17**	---	---	0.295
Root length (cm)	NS	---	---	
Budbreak during days				
the 1st 10 days	-2.26 **	NS	-5.23 *	0.584
the 2nd 10 days	NS	NS	NS	
the 3rd 10 days	-1.65 *	1.29 **	8.76 ***	0.759

^zVariable was not included in the optimal regression model.

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

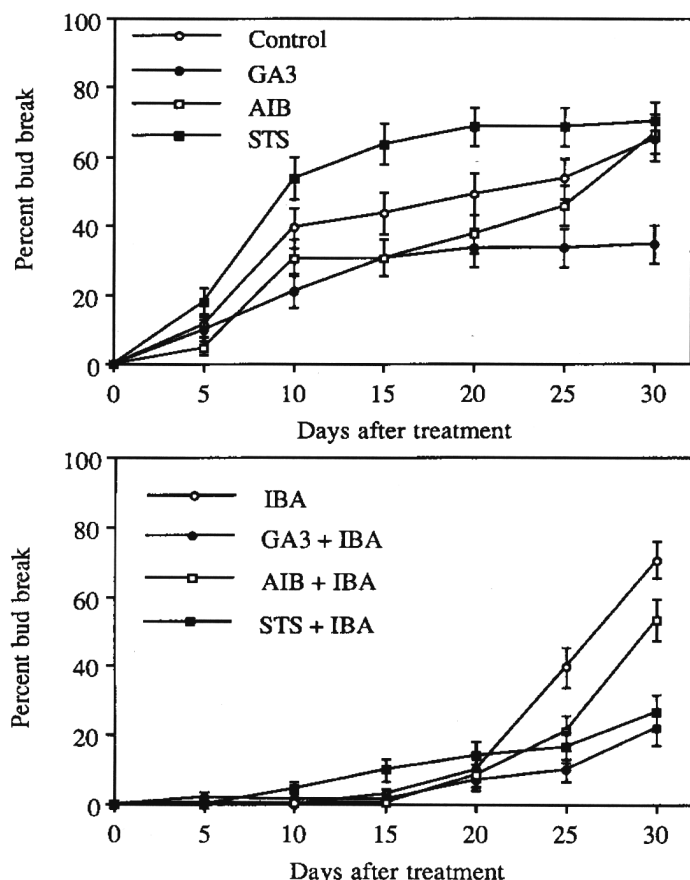


Fig. 8. Budbreak of 'Royalty' rose cuttings following GA₃ (100 mg·liter⁻¹), AIB (100 mg·liter⁻¹), STS (170 mg·liter⁻¹ Ag⁺), and IBA (1000 mg·liter⁻¹) treatment. Cuttings were dipped into GA₃, AIB, or STS solutions for 20 min, and then into IBA solution for 10 s before rooting. Data were means of four replications with 18 to 23 cuttings in each replication. Bars are \pm SE of the mean and the absence of an error bar indicates that it was smaller than the symbol.

formed on cuttings (Table 2). AIB, GA₃, and STS affected budbreak of cuttings with or without IBA treatment. STS alone stimulated, AIB delayed, and GA₃ inhibited budbreak of cuttings (Fig. 8). When combined with IBA treatment, AIB slightly inhibited, and GA₃ and STS significantly inhibited budbreak of cuttings. However, only STS-treated cuttings showed budbreak during the first 15 days of rooting when IBA was applied. The relationships between ethylene concentration, root formation, root growth, and budbreak of cuttings following AIB, GA₃, STS, and IBA treatments were analyzed quantitatively (Table 2). Roots on 'Royalty' rose cuttings usually emerged after 10 days following placement into rooting medium and started to grow extensively after 20 days. The data for budbreak were separated into three periods: from days 0 to 10, 11 to 20, and 21 to 30. Budbreak of cuttings from days 0 to 10 and 20 to 30 had a significant negative relationship with the ethylene concentration in the cuttings. Root length was also correlated negatively with budbreak from days 0 to 10; however, root length and the number of roots per cutting were correlated positively with budbreak from days 21 to 30. No significant relationship was found between ethylene, rooting, and budbreak of cuttings from days 11 to 20.

Discussion

The role of ethylene in adventitious root formation of cuttings is controversial. Studies with ethylene applied exogenously or

ethylene-releasing chemicals produced contradictory results (Mudge, 1988). Using ethylene precursors and inhibitors, recent studies concluded that endogenous ethylene played an important role in root formation of cuttings (Gonzalez et al., 1991; Liu et al., 1990; Riov and Yang, 1989). In our work, IBA-induced root formation in rose cuttings was correlated with increased ethylene concentrations (Table 1; Figs. 4 and 6). In one experiment, the endogenous ethylene concentration was correlated significantly with the number of roots formed on cuttings (Table 2). However, none of our experiments showed any root promotion by ethephon applied exogenously at various concentrations either applied by basal uptake or as a spray.

Although rooting was negatively correlated with budbreak of IBA-treated cuttings (Fig. 2), budbreak inhibition by IBA did not appear to be the result of rooting promotion (Fig. 3). Similar results were also observed in hazelnut softwood cuttings (Bassil et al., 1991). Further analysis revealed that rooting was correlated negatively with budbreak at the early stage of rooting, but the two had a positive correlation at the later stage (Table 2). Thus, substantial rooting tended to be accompanied by the enhancement of budbreak of rooted cuttings at the later stage. In Douglas fir [*Pseudotsuga menziesii* (Mirbel) Franco] and *Citrus* cuttings, treatments yielding the best rooting had more budbreak (Proebsting, 1984; Singh and Sandhu, 1985). Factors other than rooting are probably responsible for the budbreak inhibition.

In this study, endogenous ethylene levels were always correlated inversely with budbreak (Figs. 3-7; Table 2). Ethephon, when applied through a basal dip before rooting and as a foliar spray during rooting, also inhibited budbreak (Figs. 5 and 7). Ethylene applied to pea (*Pisum sativum* L.) nodal sections and decapitated stem cuttings retarded axillary bud development effectively, and buds lost their ability for further development when ethylene treatment lasted more than 3 days (Burg and Burg, 1968b). Ethephon suppressed axillary bud development when it was applied to nodes, axillary buds, or the cuts of decapitated plants (Yeang and Hillman, 1982). Ethylene-inhibited sprouting was also seen in potato (*Solanum tuberosum* L.) tubers (Burton, 1952; Pratt and Goeschl, 1969). In this study, IBA treatment at 1000 mg·liter⁻¹ increased ethylene production dramatically in rose cuttings over the first week (Figs. 4 and 6). Significant, although small, differences in ethylene concentrations between the control and IBA-treated cuttings (1000 mg·liter⁻¹) were still apparent even after 20 days (Fig. 4). We also observed that STS stimulated budbreak in cuttings in the absence of IBA and increased early budbreak of IBA-treated cuttings. STS is an ethylene action inhibitor and it possibly stimulates budbreak by blocking ethylene action. Reduced budbreak at the later stage was probably due to the poor rooting of STS plus IBA-treated cuttings (Fig. 8).

In *Prunus* sp., fall-applied ethephon delayed bloom the following spring (Crisosto et al., 1989; Sun et al., 1991). Such a delay was attributed to the less-developed vascular system connecting the buds and the existing xylem vessels (Sun et al., 1991) and to the late differentiation of floral organs, which had resulted probably from high abscisic acid and ethylene levels (Crisosto et al., 1989). The ethephon sprays did not affect the chilling requirement for breaking bud dormancy (Crisosto et al., 1989). It appeared that the high ethylene concentration most likely suppressed bud development rather than induced bud dormancy. This inference is well-supported by our results that the basal application of ethephon only temporarily delayed budbreak and repeated ethephon sprays are required to inhibit budbreak (Fig. 7).

Contrary to our results, there are several lines of evidence that suggest the involvement of ethylene in breaking bud dormancy and

stimulation of the outgrowth of lateral buds. Ethylene production was correlated with the outgrowth of lateral buds of in vitro bromeliads. The addition of 1-aminocyclopropane-1-carboxylic acid (ACC) into media containing BA promoted ethylene synthesis and budbreak, while AIB, AVG, and STS prevented bud growth or reduced the number of lateral shoots (van Dijck et al., 1988). ACC, *s*-adenosylmethionine (SAM) and ethylene production increased during the period of budbreak in apple (*Malus domestica* Borkh.) (Wang et al., 1986). The inhibition of ethylene biosynthesis inhibited bud growth of decapitated pea plants (Yeang and Hillman, 1982) and budbreak of apple and crabapple (*Malus hupehensis* Rehd.) after dormancy (Zimmerman et al., 1977). These studies, however, do not exclude the possibility that high endogenous levels of ethylene inhibit budbreak. Moreover, ethylene applied exogenously and ethylene-releasing chemicals had no effect on budbreak during the dormant period (Paiva and Robitaille, 1978; Wang et al., 1986). In those studies, ethylene was not involved in breaking bud dormancy, but probably had a role in the initial growth stage (Zimmerman et al., 1977).

Recent work conducted in two laboratories supports our hypothesis regarding to IBA-inhibited budbreak in cuttings. Wiesman et al. (1988, 1989) showed that IBA applied at the cutting base was transported to the upper part of the cutting to a greater extent than IAA, and rapidly metabolized into IBA conjugates, such as indole-3-butyrylaspartic acid (IBAsp); these conjugates were even superior to free IBA in serving as the auxin source during the later stages of rooting. Moreover, Riov and Yang (1989) observed that IBA-treated mung bean (*Vigna radiata* L.) cuttings had higher levels of ACC, 1-(malonylamino)cyclopropane-1-carboxylic acid (MACC), and ethylene in the upper part of the cutting during most of the rooting period. These studies, together with our present results, suggest that applied auxin is transported to the upper part of the cutting, where it causes increased ethylene production. As a result, budbreak of cuttings is inhibited. Auxin-induced ethylene synthesis is primarily responsible for the budbreak inhibition of auxin-treated cuttings.

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