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## The Role of Bud Scales in the Dormancy of Apples

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**Abstract.** Removal of bud scales hastened bud burst of several early and late blooming apple cultivars. Descaling was most effective during the onset and end of rest. During deep rest, bud scale removal was effective only when applied 2 weeks before forcing conditions. Extracts of bud scales inhibited apple bud break *in vitro*. Absciscic acid (ABA) may have been responsible for part or all of this bioactivity, since ABA occurred in bud scale diffusates and could replace or reinforce the bud scales *in vitro*. Wound-produced ethylene was not involved in the bud scale removal response.

The passage of temperate zone deciduous trees into and out of dormancy and rest generally is attributed to phytohormones, including both growth promoters and inhibitors (4, 13, 14, 17, 20, 24, 25). Correlations between rest intensity and inhibitor levels, particularly ABA, have been found, but ABA is not always effective in prolonging dormancy; nor are high ABA levels always required for deep rest (7, 9, 14, 17, 20, 22, 25).

Bud scales may be a source of inhibitory compounds which affect bud burst (6, 17, 18, 19, 20). Bud scale removal enhances growth or bud break of *Rhododendron*, *Ribes*, and *Vitis* (12, 18, 19, 26). Bud scales appreciably change the spectrum of light reaching the primordia (16); however, this does not seem to be their primary function (18, 19, 24). Neither do they seem to function by acting as an oxygen barrier (19, 24).

The ABA content of apple bud scales is lower than that found in the primordia (20). The inhibitor level in *Prunus* scales during the dormant period does not seem to vary as much as in the primordia (6, 17). Levels of growth promoters in *Prunus* bud scales are too low to measure (17).

The effect of bud scale removal on the spring growth of several apple (*Malus domestica* Borkh.) phenotypes is reported. Early and late blooming cultivars were used to determine if bud scales play a role in the late blooming characteristic. Previous research had shown that early blooming (EB) cultivars, which bloom with or before most commercial cultivars in the northeastern United States, require less chilling than late blooming (LB) cultivars, which bloom 2–3 weeks later (2, 25). An investigation of apple bud scale biochemistry and role in dormancy also was undertaken.

### Materials and Methods

The effect of bud scale removal on the growth of dormant mixed buds was examined in several apple cultivars throughout the dormant season. Cultivars of different bloom date and chilling requirements were used; thus, at early sampling dates, the EB-low chilling cultivars (C-14, 'Idared', 'Millerspur Deli-

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cious', 'Rosedale', and 'Subtropical' apple) had their chilling requirement more nearly satisfied than the LB-high chilling cultivars ('deLande', 'Shear', and 'Spathbluhender') (3, 25).

*Expt. 1. Effect of chilling and bud scale removal on EB and LB cultivar bud development.* Starting in mid-Oct. 1979, and at monthly intervals thereafter, several 3-year-old branches (containing numerous spur systems) were harvested from C-14, 'Subtropical', 'deLande', and 'Spathbluhender' apple trees grown at the USDA Plant Introduction Station Orchard at Glenn Dale, Md. The outer 5 to 7 bud scales were removed from 20 randomly selected terminal mixed buds. An additional 20 buds were left intact on the same branches as controls. Treated branches were placed in distilled water until they accumulated about 11,000 growing degree hours-base 5°C (3) under forcing conditions in a growth chamber (25° day, 15° night, 16 hr photoperiod). Lighting was provided by a fluorescent light fixture suspended 30 cm above the buds and containing a mixture of cool-white and Gro-Lux (2:1) tubes (200  $\mu\text{mol s}^{-1} \text{m}^{-2}$ ). At the end of forcing, the bud fresh weights were determined. Five to 7 bud scales were removed from intact buds before weighing to allow comparison with buds descaled before forcing.

Because bud scale removal may result in desiccation, data are reported for only the 10 greatest weights per treatment. Main effects (Expt. 1—date, bloom characteristic, scale removal; Expt. 2—date, temperature treatment, scale removal) and interactions of Expt. 1 and 2 were analyzed by ANOVA (23). In Expt. 1, lines-of-best-fit were generated by regression analysis. The reduced number of sampling dates necessitated the use, when appropriate, of Duncan's multiple range test for individual dates in Expt. 2 (23).

*Expt. 2. Effect of chilling and bud scale removal on 'Millerspur Delicious' bud development.* In the winter of 1980–1981, a similar experiment was conducted using 3-year-old (naturally chilled) 'Millerspur Delicious' branches (as in Expt. 1) harvested in mid-December, January, and February from trees grown at the Univ. of Maryland Plant Research Farm, Silver Spring, Md. Three treatments were applied: (a) 20 buds were descaled and then held for 2 weeks at 5°C before transfer to the forcing conditions used in Expt. 1; (b) 20 buds were left intact during the 5° treatment and descaled immediately before forcing; and (c) 20 buds were given 2 weeks of 5° and forced intact. Similar treatments were applied to the LB cultivars 'Spathbluhender' in January and 'deLande' in February.

On 25 Nov. 1979, and in the same orchard as above, two 15-year-old 'Millerspur Delicious' apple trees were covered with a plastic greenhouse. A week later, artificial heat was applied to the greenhouse, and the temperature remained above 15°C but less than 30° throughout the winter. At monthly intervals until April, 3-year-old branches were harvested from these trees and from naturally chilled trees growing in the orchard. Twenty buds were descaled or left intact and forced as in Expt. 1. Bud weights were determined as above.

*Expt. 3. Effect of chilling and bud scale removal on lateral bud break.* The apical dominance effects of the removal of bud scales from the apical bud, and the apical bud decapitation of 'Millerspur Delicious' shoots was determined by comparing the growth of subtending axillary buds to that of nontreated branches. After forcing conditions (as in Expt. 1), lateral bud growth of 25 one-year-old (50 cm) shoots was scored using the following scale: 1 = dormant, 2 = green tip, 3 = 1 cm green, and 4 = 2 cm green growth. The experiments were done monthly (October through February), and analyzed using the Chi-square contingency test ( $P = 0.01$ ) (23).

*Expt. 4. Bioassays of bud scale extracts.* To determine if bud scales contain inhibitors, scales were extracted and the extracts bioassayed for effects on the growth of nonresting axillary buds *in vitro* (8). On 10 Dec. 1980, 27 Jan. 1981, 15 Feb. 1981, 1 Nov. 1982, and 18 Dec. 1982, the 7 outer-most bud scales were removed from 500 mixed apical buds of the orchard-grown 'Millerspur Delicious' trees used in Expt. 2. Each sample was placed immediately in 250 ml of 80% aqueous methanol and held at 0°C for a 24 hr extraction. The methanol was decanted, and the process was repeated for a 2nd extraction. After filtration through prewashed Whatman 2V paper, the combined extract volume was reduced *in vacuo* to less than 10 ml. The extract was adjusted in volume as appropriate with a small quantity of distilled water and taken to pH 6.0 with 0.1 M KOH. Concentrations of this extract, equivalent to 2 or 20 buds per test (10 ml), were added to the culture media of an apple bud explant bioassay identical to that of Dutcher and Powell (8). In this assay, a dormant axillary bud and its adjacent stem section, from a one-year-old 'York' open pollinated apple seedling, were sterilized for 15 min in 0.52% sodium hypochlorite, washed 3 times in sterile water, then placed on the agar (Difco-bacto) media. On basal medium, buds will break and grow, but appropriate concentrations of ABA inhibit growth. The bioactivity of the bud scale extracts was compared with that of 0.5 or 5  $\mu\text{M}$  ABA. Both hormones and bud scale extracts were added before autoclaving or filter sterilization. As no difference in response due to the sterilization method occurred, the data from each were pooled. After 4 weeks in the growth chamber (as described for Expt. 1), the growth of the lateral buds was estimated using the scoring scale described in Expt. 3. Data for each date were combined and analyzed by using Chi-square analysis (23).

*Expt. 5. Effect of ABA and scale removal on *in vitro* apple bud break.* The ability of ABA to inhibit growth of bud primordia of descaled buds was tested on apple bud explants *in vitro*. During the winter-spring of 1979–1980, 2 fifteen bud replicates of 'Idared', an EB cultivar, were harvested from the Cornell Univ. orchard in Ithaca, N.Y. Bud explants, each containing a single apical bud, were cut about 2 cm long and sterilized, as in Expt. 4. Orchard grown material is difficult to sterilize; therefore, to keep the cultures sterile, the bud explants were resterilized and recultured weekly. Three treatments were applied: (a) buds were left intact, (b) buds were descaled, and (c) buds were descaled and multiple levels of ABA (0.01, 0.1, 0.5, 1, 5, or 10  $\mu\text{M}$ ) were added to the culture medium. The percentage of bud break was determined at 21 days. Two collections were made during rest—6 Dec. and 24 Jan.; in addition, 2 collections were made after chilling had been satisfied (3, 25), on 11 Mar. and Apr. 15. Data were analyzed by ANOVA, using treatment and resting state main effects, and linear regression (23).

*Expt. 6. ABA content in bud scale diffusates.* To determine if bud scales from an EB ('Rosedale'), and LB ('Shear') cultivar produced different amounts of diffusible ABA, the 5 to 7 outer bud scales were removed from 25 buds on 9 Mar. 1979, and again after 5 days of greenhouse forcing of 3-year-old branches. At this time, chilling had been satisfied in 'Rosedale' buds while 'Shear' buds were still in rest (25). The scales were placed on their cut end on a prewashed Whatman No. 3 filter paper disk which had been premoistened with distilled water. After 24 hr at room temperature, the filter paper was extracted at 0°C with 80% aqueous methanol for 72 hr. The methanol was changed twice and the combined extract reduced *in vacuo*. Each of the 3 replicates then were purified and assayed by gas chromatog-

raphy (GC) by the method of Swartz and Powell (25). This method included centrifugation, a gravity flow polyvinyl pyrrolidone column and acid-base partitioning with methylene chloride. Other liquid chromatography steps were omitted because the samples were relatively clean. Sample means were compared by ANOVA and Duncan's multiple range test (23).

**Expt. 7. Effect of bud scale removal on ethylene production.** Wounding can stimulate ethylene production in various tissues (1, 15). To determine whether wound ethylene was responsible for the effects of bud scale removal, both growth and ethylene production were measured following: (a) the application of 250 ppm of the ethylene producing chemical, (2-chloroethyl) phosphonic acid (ethephon), to intact buds, and (b) bud scale removal. Buds were harvested and forced in mid-Feb. 1983 under conditions used in Expt. 1. Ethylene production was measured 4 hr after treatment on 4 replicates of intact or descaled 'Millerspur Delicious' explants. Each replicate, containing 2 explants, (the apical bud and 1 cm of wood), was sealed in an air tight 10 ml air syringe at 20°C. Ethylene concentrations in the head space were sampled and assayed by GC (27).

## Results

**Expt. 1 and 2. Effect of chilling and bud scale removal on apple bud development.** Removal of bud scales stimulated the growth of chilled or partially chilled EB or LB apple buds in Expt. 1 (Fig. 1). ANOVA main effects; scale removal  $P = 0.001$ , cultivar-type  $P = 0.01$ , date  $P = 0.05$ , and interactions scale removal  $\times$  cultivar-type  $P = 0.05$ , cultivar-type  $\times$  date  $P = 0.05$  and date  $\times$  scale removal  $P = 0.05$  were statistically different at the indicated levels of significance. The results of Expt. 2 were similar, although only main effects  $P = 0.05$  (scale removal, chilling treatment, date) and a chilling treatment  $\times$  date interaction  $P = 0.005$  were significant (Table 1). Heated resting trees remained in deep rest through April. Bud scale removal did not enhance bud break on forced branches from heated trees except in January  $P = 0.05$ . Buds descaled on the intact heated trees grew, albeit slowly, and set fruit.

Bud scale removal had an insignificant effect on buds in deep rest: viz, the EB cultivars during November and December, the 'Millerspur Delicious' trees kept in nonchilling conditions for 2 months or longer (Table 1), and the LB cultivars during No-

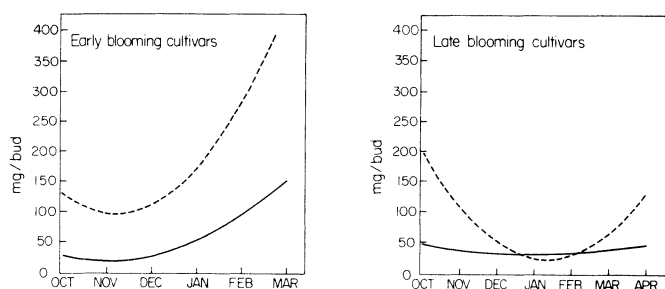


Fig. 1. The effect of bud scale removal on bud growth of early and late blooming apple cultivars; descaled = dashed lines, intact = solid lines. Samples were collected between the 12th and 17th of each month, dates on the abscissa are given in days after 12 Oct. 1979. All quadratic effects were highly significant ( $P = 0.01$ ). (Expt. 1). Lines of best fit for each treatment are: EB-descaled: bud weight (mg/bud) =  $131 - 1.86(\text{day}) + 0.03(\text{day})^2$ ,  $R^2 = 0.3$ ; EB-intact: bud weight (mg/bud) =  $28 - 0.52(\text{day}) + 0.01(\text{day})^2$ ,  $R^2 = 0.4$ ; LB-descaled: bud weight (mg/bud) =  $197 - 3.43(\text{day}) + 0.02(\text{day})^2$ ,  $R^2 = 0.4$ ; LB-intact: bud weight (mg/bud) =  $48 - 0.36(\text{day}) + 0.002(\text{day})^2$ ,  $R^2 = 0.1$ .

Table 1. The effect of bud scale removal on bud growth from naturally chilled (outdoor) or heated (nonchilled) 'Millerspur Delicious' trees in 1979-1980. (Expt. 2).

Month	Bud growth in mg per bud (fresh wt)			
	Outdoor trees		Nonchilled trees	
	Descaled	Buds intact	Descaled	Buds intact
November	275 a <sup>z</sup>	44 b	---	---
December	187 a	120 b	78 bc	42 c
January	218 b	228 b	280 a	119 c
February	720 a	608 a	102 b	39 b
March	---	---	61 a	55 a

<sup>z</sup>Treatment means within a row, separated by Duncan's multiple range test at 5%.

vember through March. In deep rest, an additional 2 weeks of chilling after bud scale removal allowed statistically greater ( $P = 0.05$ ) 'Millerspur Delicious' bud primordia development than intact buds in November and January (Table 2). Buds chilled while intact, but descaled before forcing, did not grow better than intact buds. Similar results also were observed on 'deLande' buds in February; however, there were no significant effects when the same treatments were applied to 'Spatbluhender' buds in January.

**Expt. 3. Effect of chilling and apical bud scale removal on lateral bud break.** When expressed as the percentage of bud break, apical bud or bud scale removal stimulated the growth of subtending buds during various stages of dormancy (Table 3). Removal of scales from the apical bud at any time during rest stimulated the growth of the 1st subtending lateral bud. Once out of rest, this effect was reversed. The removal of the entire apical bud resulted in enhanced growth of the 1st lateral bud from October through December. Apical bud scale removal did not stimulate the growth of buds 2-8. Removal of the entire bud significantly enhanced the growth of the 2nd lateral bud except during deepest rest. Removal of the apical bud had no effect on more proximal buds during rest. Although data were analyzed by comparison of growth stages, the results given in Table 3 are presented as the percentage of bud break, i.e., the percentage of buds in stages 2, 3, or 4. This form allows clear presentation of the data. Apical bud removal, when effective in stimulating lateral bud break, always stimulated increased growth of the resulting shoots, i.e., a greater percentage were scored 3 and 4, when compared to other treatments.

**Expt. 4. Bioassay of bud scale extracts.** Extracts of bud scales were highly effective in inhibiting the growth of buds *in vitro* (Table 4). The biological activity of the extract of the scales from 2 buds was intermediate between control and 0.5  $\mu\text{M}$  (1.3  $\mu\text{g}$  per 10 ml test) ABA treatments. Bud scale extract activity

Table 2. The effect of time of bud scale removal on 'Millerspur Delicious' apple bud growth (Expt. 2).

Month	Bud growth in mg per bud		
	Descaled then chilled	Chilled then descaled	Intact
November	114 a <sup>z</sup>	69 ab	43 b
December	98 a	79 a	40 a
January	350 a	114 ab	32 b

<sup>z</sup>Treatment means within a row, separated by Duncan's multiple range test at 5%.

Table 3. The effect of apical bud or bud scale removal on the percentage of bud break of lateral buds (Expt. 3).

	Percentage of bud break by month				
	Oct.	Nov.	Dec.	Jan.	Feb.
First lateral bud:					
Apical bud removed	81 a'	31 a	50 b	81 b	96 a
Apical bud scales removed	65 b	8 b	76 a	100 a	76 b
Apical bud intact	8 c	0 c	11 c	76 b	92 a
Second lateral bud:					
Apical bud removed	42 a	0 a	0 a	36 a	92 a
Apical bud scales removed	0 b	4 a	0 a	0 b	46 b
Apical bud intact	0 b	0 a	0 a	0 b	36 b
Third to eighth lateral buds:					
Apical bud removed	0 a	0 a	0 a	11 a	64 a
Apical bud scales removed	0 a	0 a	0 a	0 b	11 c
Apical bud intact	4 a	0 a	0 a	0 b	45 b

'Means within the same date and bud with different letters are significantly different ( $P = 0.01$ ) as determined by Chi-square analysis of various bud growth scoring classes.

did not change appreciably during the dormant season (data not shown); therefore, the data were pooled for statistical analysis. On the average, 70 of the 100 replications per treatment were sterile and thus usable.

**Expt. 5. Effect of ABA and scale removal on *in vitro* bud break.** Following scale removal, ABA inhibited *in vitro* bud break to the same degree throughout the experiment. Log-linear regression of  $\mu\text{M}$  ABA applied vs. the percentage of bud break of all sampling dates was statistically significant ( $P = 0.001$ ;  $R^2 = 0.60$ ). The line of regression was: the percentage of bud break =  $20\% - 9.9 (\log_{10} \text{ABA conc. in } \mu\text{M})$ . Thus, when  $0.1 \mu\text{M}$  ABA was applied, bud break was 30%. Removal of scales promoted primordia growth only during rest (0% bud break for intact buds vs. 43% for descaled buds.) During post-rest, 56% of both scaled and intact buds grew.

**Expt. 6. ABA content in bud scale diffusate.** Upon harvest from the field, the amount of ABA diffused from the scales of an EB and LB cultivar was not statistically different (5.7 ng/bud/day). After 5 days of greenhouse forcing, the amount of ABA diffused from the EB cultivar did not change, while ABA in the LB cultivar diffusate was significantly ( $P = 0.05$ ) increased (16.7 ng/bud/day).

Table 4. The effect of apple bud scale extracts on the growth of intact lateral apple buds *in vitro* (Expt. 4).

Treatment	Percentage of buds in the following stages <sup>z</sup>			
	Dormant	Green tip	1 cm green	2 cm green
Basal media	13.5	21.6	31.1	33.8 a
Bud scale extract— 2 buds per test	27.3	45.5	24.2	3.3 b
ABA $0.5 \mu\text{M}$ (1.3 $\mu\text{g}/\text{test}$ )	53.5	20.9	23.3	2.3 c
Bud Scale Extract— 20 buds per test	95.5	1.5	3.0	0 d
ABA $5 \mu\text{M}$ (13.2 $\mu\text{g}/\text{test}$ )	80.7	10.5	8.8	0 d

<sup>z</sup>All treatments differ significantly ( $P = 0.01$ ) in ratio as determined by Chi-square.

**Expt. 7. Effect of bud scale removal on ethylene production.** Bud explants with descaled buds had rates of ethylene evolution equivalent (within 2%) to that in intact bud explants (2.9 nl/g tissue/hr) as has been reported (21). In addition, although ethephon treatment did not affect growth, (337 mg per control bud vs. 334 mg per ethephon-treated bud), it increased ethylene evolution 6 times.

## Discussion

As with certain other species, the scales of apple buds inhibit the growth of the primordia (12, 18, 19, 26). The magnitude of the effect varies through the dormant period, depending upon the intensity of rest. When rest intensity is moderate, (early or late rest), removal of the bud scales permits growth. In deep rest, this removal may not be sufficient (Fig. 1). An additional 2 weeks of chilling after scale removal was beneficial and superior to a similar chilling period with scales intact (Table 2). During this 2 week period, scale-produced inhibitors lose some of their control over bud primordia growth, perhaps through a reduction in concentration or activity relative to growth promoters. Presumably, growth promoting hormones present during late rest cause increased growth once the inhibiting activity of the scales is removed. The role of chilling may be via a hormone system. The fact that gibberellins and cytokinins can replace chilling requirements (4, 11) supports this theory. Endogenous ABA may inhibit the synthesis of the growth-promoting hormonal system. For example, ABA inhibits, while gibberellins promote, alpha-amylase synthesis in barley aleurone layers (5).

ABA diffuses from excised bud scales, and can overcome the effect of bud scale removal *in vitro* (Expt. 5). Thus, ABA may be at least partially responsible for the growth inhibitory effect displayed by bud scales; however, the exact proportion is unknown. Apple bud break was reduced by about 30% *in vitro* by less than  $0.5 \mu\text{M}$  or 1  $\mu\text{g}$  ABA per 10 ml test (Table 4 and Expt. 5). The amount of ABA which would diffuse from the scales of one bud over the course of the forcing treatments would be about 140 ng for the postrest EB cultivar (28 days  $\times$  5 ng/bud/day) and 330 ng for the resting LB cultivar during forcing. Diffusion experiments could underestimate the amount of active transport as the sink is removed. As the amount of ABA diffused was close to the amount of ABA which could be extracted from the scales (20), it is reasonable to assume active ABA synthesis and transport to the cut surface. The fate of transported scale-ABA is unknown; however, the inhibitory effect of the scales is local, since bud scale removal affects only the descaled primordia and its subtending bud (Table 3). If diffused ABA is assumed to represent normally transported and primordia directed ABA, then ABA is responsible for a substantial percentage of the bud scale inhibitory activity.

The biological activity of the scale extract from one bud is roughly equivalent to 300 ng of ABA (Expt. 4). ABA concentrations in bud scale extracts range between 1 and 10 ng/bud (20). This demonstrates the presence of bud scale biological activity due to other biochemicals. The physiologic significance of these inhibitors is unknown since they are found away from their site of action, the primordia. In addition, extraction with methanol releases chemicals which might not normally be transported.

There was no evidence of wound-induced ethylene production. Descaling did not induce wound ethylene and exogenous ethylene was not effective in promoting apple bud break in these experiments or in the related experiments of Paiva and Robitaille (15).

Apple trees placed in heated greenhouses before they received adequate chilling were forced into a deep rest by chill-negating temperatures (Table 1) (3, 10). During this period, bud scale removal was ineffective during the forcing period, as it was in outdoor trees. Thus, the effect of bud scale removal is dependent on the rest intensity of the primordia and not on seasonal effects, such as daylength.

Removal of LB bud scales did not appreciably change the protracted rest-intensity characteristic of LB cultivars (Fig. 1). When compared to EB apples, LB apple bud scales diffuse more ABA upon forcing (Expt. 6) and LB apple buds have more extractable ABA during the initial stages of their bud break (25). If a portion of this diffused ABA was transported to and became active in the bud primordia, LB bud development should be delayed, as observed in Expt. 1. The lack of complete effectiveness of LB bud scale removal, defined as allowing descaled LB cultivars to bloom with EB cultivars, also could be due to the reduced cytokinin activity in LB apple buds (25).

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