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Seasonal Development of Symptoms of Noninfectious Bud-failure in Almond *(Prunus amygdalus* Batsch)[1]

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Abstract. **Shoots of 'Nonpareil', 'Jordanolo' and their hybrid progenies expressing bud-failure symptoms grew more vigorously and longer than those of normal plants. Viability of lateral buds decreased on abnormal shoots during the summer prior to bud failure, whereas those on normal shoots retained their viability. On abnormal shoots there was an increasing trend of bud-failure from the basal portion to the shoot tip. When propagated in a control nursery, buds collected from trees growing in a warmer area exhibited more bud-failure than those from a cooler zone. When shoots collected over the season from the above trees were treated with potassium salt of gibberellic acid, the inhibition of budbreak was proportional to hormone concentration; the treatment resulted in fewer bud breaks in abnormal shoots than normal ones. Bioassays of extracts from shoot apices from normal and abnormal shoots revealed large variation in hormonal levels.**

Noninfectious bud-failure (BF) is a disorder that affects certain cultivars of almond. BF induction in normal trees is temp-dependent (10) and the potential for BF is seed transmissible (7).

The principal symptom is the lack of viability of vegetative buds which leads to failure of buds to grow in the spring (12, 13). In severe cases the entire shoot dies; sometimes only a delay in bud emergence occurs. Flower buds are usually not affected except for an occasional delay in time of bloom. There may be a reduction in bloom density (13) that can lead to yield reduction (4). For any particular tree, the condition is apt to become worse rather than improve.

Since potential for BF is present in somatic tissue, budwood collected from some trees has produced trees expressing varying degrees of BF. Variability in the proportion of BF trees and severity of symptoms within a single budwood source has been shown to develop with time when trees are grown in different climatic locations in California (9). High temp during growing periods has been identified as a major environmental component contributing to bud-failure but apparently only for certain sensitive cultivars (10).

This study was initiated to 1) ascertain when lateral buds lose their viability, or conversely, develop their potential for bud-failure, 2) determine if the distribution pattern of failing buds on shoots was associated with change in temp during the summer months, and 3) explore the hormonal levels of apices from normal and abnormal shoots.

Materials and Methods

The clones used were: 'Nonpareil', 'Jordanolo', and hybrid selections. The selections 23-1, 23-3, 23-5, and 23-10 are hybrids of 'Nonpareil' (BF) x 'Jordanolo' (BF) (6).

Trees of 'Nonpareil' and 'Jordanolo' were grown on the University farm in Davis and at the West Side Field Station (WSFS), Five Points, California; at the latter site, high summer temp prevail each year; in the former location, summer temp are somewhat milder.

The numbers of nodes and lengths of internodes on thirty shoots chosen at random on 1 or 2 trees were measured periodically throughout the growing season.

During the following spring the location of non-emerging buds distributed along the shoot was determined visually. The time when buds lost their viability during the season was estimated, 1) by propagating individual buds from shoots of normal and BF trees onto almond seedlings and 2) by forcing buds on similar branches with solutions of potassium gibberellate (KGA). In the propagation studies, 3 budsticks each having 15 buds were collected from normal and BF trees at 1 month intervals from May to Sept. Buds were propagated onto upper branches of 2-year-old almond seedling rootstocks at Davis. After 3 weeks, the stock was cut back to the inserted bud to induce shoot growth. Buds which grew immediately and those which emerged the following spring were considered as surviving buds.

In bud-breaking tests, shoots 15 to 25 cm long were collected at 2 week intervals from July through Sept., defoliated, and immersed in KGA solutions of 5, 20, or 50 ppm for 90 min (5). Shoots were then placed in a mist propagation bed for 20 days when the no. of buds which grew were noted.

For hormone determination, shoot apices were collected from BF and normal trees and placed on 1.5% agar for 18 hr. Diffusates in agar and methanolic extracts of apices after the diffusion period were bioassayed for indole-3-acetic acid (IAA), abscisic acid (ABA) and gibberellin (GA) by chromatographing an equivalent of 500 mg of fresh apex wt on 3MM Whatman

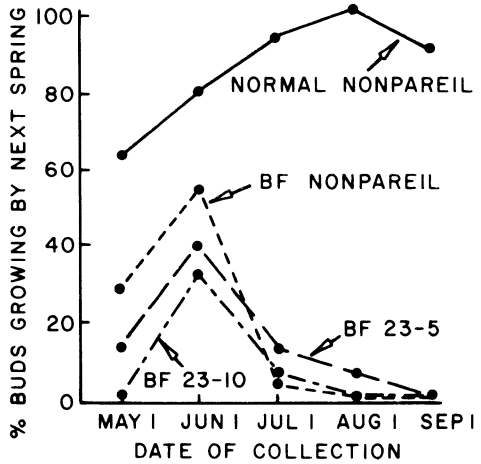

Fig. 1. Survival of buds collected from normal and BF-trees at various times of the season, and propagated onto seedling rootstocks. Data obtained the following spring. BF 23-10 and BF 23-5 are BF segregants of BF 'Nonpareil' x BF 'Peerless'.

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Table 1. Number of buds, distribution of nonemerging buds, and internodal length of normal and BF almond trees at Davis and West Side Field Station (WSFS), Five Points, California.

Location	Cultivar		No. of shoots	No. of buds	Nonemerging buds as % of total buds	Mean internode length (cm)	Distribution of nonemerging buds (%)		
							Basal	Middle	Tip
Davis	Jordanolo	Normal	30	390	10 ± 2	0.67			
		BF	30	833	38 ± 3	1.28	17 ± 2	32 ± 3	67 ± 3
	Nonpareil	Normal	30	510	3 ± 1	0.75			
		BF	30	1980	0	1.28			
	Sel. 23-3	BF	20	522	87 ± 3	1.40	86 ± 3	83 ± 3	93 ± 3
	Sel. 23-1	BF	10	218	62 ± 4	1.23	27 ± 3	65 ± 3	95 ± 1
WSFS	Nonpareil	BF[z]	10	338	74 ± 3	1.82	71 ± 4	80 ± 3	71 ± 3
		BF[y]	20	543	67 ± 4	1.63	60 ± 4	67 ± 4	88 ± 3

[z]Trees 2, 6.
[y]Trees 1, 3, 4, 5.

paper (20 x 20 cm). The chromatograms were developed unidirectionally with isopropanol, ammonium hydroxide and water (10:1:1, v/v/v). After drying the chromatograms were cut into 10 strips of equal width and bioassayed for IAA and ABA, by the wheat coleoptile straight growth test (11), and for GA by determining the amount of sugar induced by the GA-activated α-amylase in the barley aleurone layer (1, 2, 3).

Results

Shoot growth and bud-failure patterns. Shoot growth of normal 'Jordanolo' and 'Nonpareil' was significantly less in total length, no. of nodes, and average internode length than the BF 'Jordanolo', BF 'Nonpareil', and BF selections of the same age in the same orchard (Table 1). Shoot growth on normal plants occurred mostly during March and April, terminating in mid-May. Buds that failed to emerge on normal shoots were 3% on the 'Nonpareil' and about 10% on the 'Jordanolo', the amount being the same on the basal, median, and distal segments. In contrast, 38–87% of the buds on BF trees failed to emerge.

Shoots of BF 'Jordanolo' trees in the adjacent row grew almost 5 times longer than those of normal trees with 3 times the no. of nodes and twice the average internodal length. Shoots grew not only in March and April but both node production and internode length increased in May with some increase in internode length occurring in June.

The two BF seedling hybrids Sel. 23-1 and 23-3 showed similar patterns of growth as the BF 'Jordanolo' and 'Nonpareil' with some differences associated with the severity of BF symptoms. Shoots of Sel. 23-1 grew mostly in March and April, and continued into May with a slight increase in internode length occurring in June. Sel. 23-3 was more severely affected with an overall bud-failure of 87%. There was indication that the start of shoot growth was delayed but growth occurred rapidly through March, April, and May. Total length was longer than Sel. 23-1 and there were more nodes and longer internodes as compared to normal shoots.

Six-year-old 'Nonpareil' trees growing at Five Points with severe BF symptoms grew throughout the entire growing season. Two patterns of growth occurred. The predominant pattern exhibited by 4 trees was characterized by rapid growth during March, April, May and June, followed by slow growth during mid-summer and finally ceasing in Sept. The other growth rate pattern was similar but evidently growth began later, and was more rapid during the entire growing season which extended into Sept.

In all cases BF symptoms, as shown by failed buds on the basal, middle and apical sections of shoots appeared as an increasing trend from base to shoot apex (Table 1).

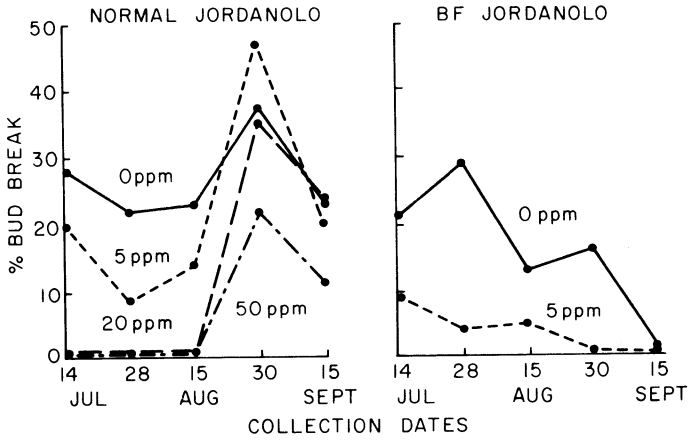

Fig. 2. Bud break in response to immersion in potassium gibberellate (KGA) solutions for almond shoots from normal and BF 'Jordanolo' trees growing at Davis, Calif. Each value is the average of 35 to 60 buds/3 shoots. No buds from BF 'Jordanolo' shoots treated with 20 or 50 ppm KGA grew.

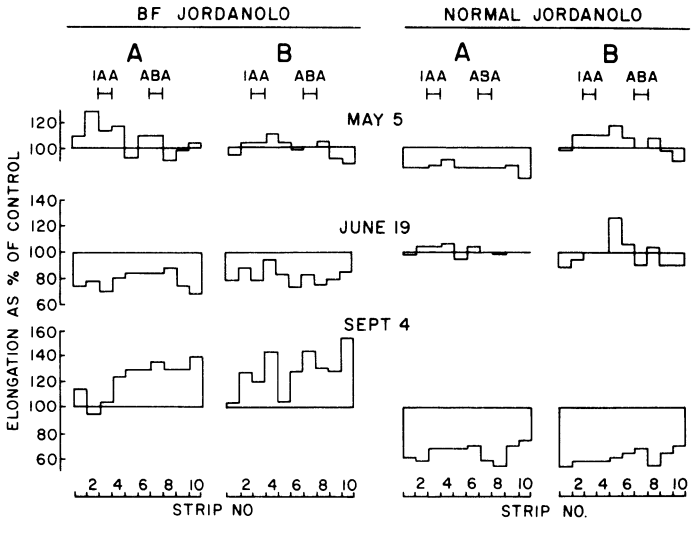

Fig. 3. Histograms of agar-diffusible (A) and extractable (B) substances from BF and normal 'Jordanolo' shoot apices chromatographed and bioassayed with the wheat coleoptile straight growth test for IAA and ABA. Solvent: isopropanol, ammonium hydroxide and water (10:1:1, v/v/v). The migration characteristics of IAA and ABA in the solvent system are indicated by horizontal bars.

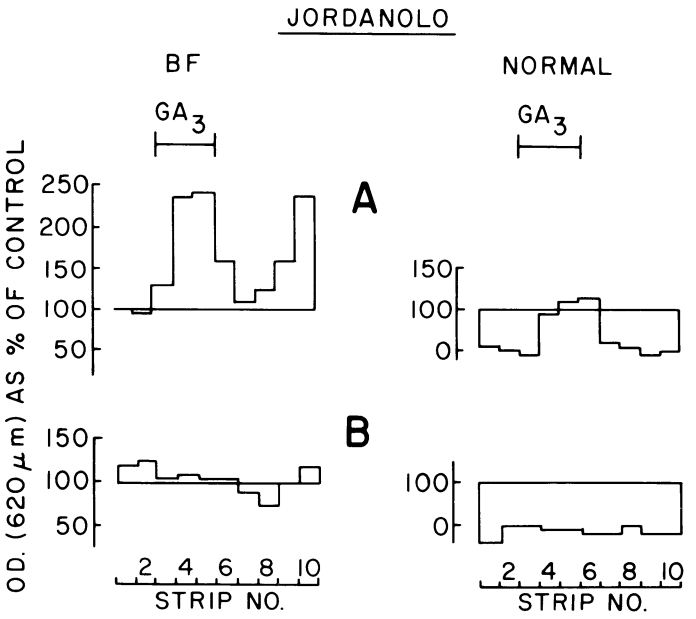

Fig. 4. Histograms of agar-diffusible (A) and extractable (B) substances from BF and normal 'Jordanolo' shoot apices chromatographed and bioassayed with the barley endosperm test for GA. Sample taken September 4. Solvent system: isopropanol, ammonium hydroxide and water (10:1:1, v/v/v).

Bud-failure as influenced by budwood source, bud position on stem, and collection time. Buds collected from a normal 'Nonpareil' tree growing at Davis showed increasing ability to survive the budding operation from May 1 through the rest of the summer (Fig. 1). Survival of buds collected from BF plants in early May was low and could be attributed to either 1) low viability (i.e., bud-failure) or 2) delay in bud maturity from BF shoots. The optimum time for budding this particular BF material was June 1. Following this period bud survival decreased sharply to zero.

When stem pieces from a normal 'Jordanolo' plant were collected at different times during the summer, and placed under mist, the no. of shoots that grew from lateral buds varied between 25 to 35% (Fig. 2). The trend was relatively constant with time except for an increase in the % bud break on stem pieces from the August 30 collection.

Inhibition of bud development by KGA. The ability of buds on normal shoots of 'Jordanolo' to grow into shoots decreased during the season. Buds on BF shoots were sensitive to applications of KGA; at 5 ppm growth inhibition was slight but above 12 ppm, it was complete.

Endogenous hormone levels. Levels of substances in shoot apices which enhanced or inhibited wheat coleoptile elongation fluctuated from one sample to the next, exhibiting no pattern which correlates with the development of BF symptoms nor shoot elongation. These fluctuations were noted whether the apices were collected from normal or BF trees (Fig. 3). Both agar-diffusible substances and extractable ones from BF 'Jordanolo' apices enhanced elongation of wheat coleoptile segments over the controls. However, the activity reduced in strips 1 and 2 by agar diffusible substances and strips 1 and 5 on chromatograms derived from the acidic fraction of extracts were equal to those of the control (Fig. 3).

Tests for GA-like substances in shoot apices showed that diffusate of normal 'Jordanolo' had growth-promoting activity in strips 5 and 6 but inhibition from strips 1 to 4 and from 7 to 10 (Fig. 4). The acidic fraction had a strong inhibitory activity over the entire chromatogram. The agar diffusate from BF 'Jordanolo' contained substances promoting α-amylase activity in strips 5 and 6 and also in 9 and 10. No promotive or inhibitory activity was shown by the acidic fraction of the extract.

Discussion

Seasonal patterns of BF symptom development at different orchard sites indicate that marked changes in the internal physiology occurs. In a BF shoot, basal buds tend to be normal and are capable of emerging to produce new shoots the following spring, whereas those in the middle and distal portion have greater probability of failing. If the apical bud fails, "dieback" results.

As a consequence of the physiological conditions imposed by BF or, alternatively, because few shoots grow as the result of bud-failure, the growth rates of BF shoots were faster and persisted longer than those of normal shoots. BF potential is least detectable in the initial growth in the spring but becomes progressively more evident during the summer in the newer parts of the shoot. The viability of buds laid down in late summer and early fall is diminished.

The induction and appearance of BF symptoms follow a seasonal pattern which is directly related to the mean maximum summer temp to which trees are exposed in different production areas of California (8, 9). If total exposure rather than periods of exposure to extreme heat were a factor, one would expect the basal buds to be most affected. Insofar as the basal buds usually survive and develop into shoots, while those on middle and apical portions of the stem are affected, it appears that extreme midsummer temp has the greatest influence in inducing BF. Symptoms of "rough bark" associated with BF also appear as lesions in mid-sections of long stems. In advanced cases, the disorder can become lethal to young almond trees by inhibiting all vegetative buds as was demonstrated in controlled greenhouse tests (10). Shoot growth patterns observed in these tests were comparable to those seen in field, except that with additional exposure to heat, more bud necrosis occurred.

Excessive shoot growth alone is not responsible for BF although it may be symptomatic. Normal young 'Nonpareil' trees grow vigorously at Davis, but without symptoms. Hence, there must be an interaction between the inherent capacity to produce BF and temp.

Based on bioassays of tissue extracts, GA metabolism may be disturbed by the occurrence of BF. However, it can not be concluded here whether high GA production might be the cause of BF or a result of excessive growth associated with the disorder. Evidence that the disorder may be hormonally related was reported by R. W. Jones (personal communication) in that the growth retardant succinic acid-2,2-dimethyl hydrazide, which acts as a GA antagonist (6, 14) reduced BF potential and branches treated with GA mimicked BF symptoms. Although abnormal hormonal metabolism might occur with BF, it is not known whether this is the cause or an effect. Based on the findings reported in this paper, BF shoots produce considerably more growth promoting auxin-like and GA-like substances than normal almond shoots.

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Inheritance of Time to Flowering and its Relationship to Crop Maturity in Cucumber[1]

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Abstract. **Early and late flowering cultivars of cucumber (*Cucumis sativus* L.) and their progenies were used to determine the inheritance of the time required to reach anthesis and its importance as a component of earliness. Genetic variance was primarily additive; however, partial dominance for early flowering and low nodal position of the first flower was noted. Days to first flower appeared to be controlled by relatively few genes, and heritability estimates for this trait were moderately high (0.46 to 0.62). Number of days to flowering was found to be more important in early crop maturity than was rate of seedling emergence. Lower temperatures delayed flowering, and thus maturity, by slowing plant growth and raising the node number at which the first flower appeared. A significant correlation coefficient of 0.82 was obtained between flowering time and mean maturity date.**

Early maturity of pickling cucumber is an important factor in commercial production. The necessary equipment for mechanization is expensive, and continuous use is required to minimize costs. Efficient equipment utilization can be achieved by staggered plantings and by multiple cropping. Early maturing cultivars can reduce production costs by shortening the growing season.

Early flowering should be an important factor in crop maturity. In previous investigations with cucumber (7, 8), substantial intraspecific variability was observed for time from planting to first flower, suggesting that this trait might be under genetic control. Inheritance patterns for days to flowering in watermelon, *Citrullus vulgaris* Schrad, and muskmelon, *Cucumis melo* L., have been reported (13, 2). Shifriss and George (12) using a parental cultivar which was day neutral with respect to flowering and one which required short days for normal flowering reported that the differential photoperiodic flowering behavior of these cultivars in long days was controlled by a single recessive gene.

This investigation was undertaken to determine the inheritance of days to flowering and node of the first flower and to evaluate the importance of early flowering to early crop maturity in cucumber.

Materials and Methods

Plant material and traits measured. Two early flowering lines, EF-MSU 0612 and EF-TXL 29, and 2 late flowering lines, LF-'Poinsett' and LF-MSU 713-5, were used as parents. EF-TXL 29 was derived from Peto experimental hybrid 36-65, which was early flowering. LF-'Poinsett' was selected from the late flowering 'Poinsett'. No progress was made by selfing and selection for early and late flowering, respectively, in EF-MSU 0612 and LF-MSU 713-5. EF-MSU 0612 and LF-'Poinsett' are monoecious, whereas LF-MSU 713-5 and EF-TXL 29 are gynoecious. LF-MSU 713-5 initiates flowers relatively early, but flower abortion is encountered at the first few nodes, resulting in late flowering.

Selfed progeny of the 4 parental lines were crossed to develop F_1, F_2, BC_1, and BC_2 populations. Three separate families were generated: Family I (EF-TXL 29 x LF-'Poinsett'), Family II (EF-MSU 0612 x LF-'Poinsett'), and Family III (EF-MSU 0612 x LF-MSU 713-5).

Date and sex of each new flower were recorded on each entry through the 10th node. Two criteria were judged to best detect genotypic differences in flowering behavior. These were days from planting to first flower and the node at which the first flower appeared. The cotyledonary node was designated node 0, with the node at which the first true leaf appeared considered node 1.

Genetic analyses. Quantitative genetic procedures were used to analyze the data. Analyses of variance were conducted to evaluate the possibility of maternal effects. Scaling tests (6) tested the conformity of the data to the additive-dominance model. Estimates of additive, dominance, and environmental variances were obtained (6). Heterosis (measured as % deviation from the mid-parental values) and degree of dominance (estimated by dividing the square root of dominance variance by the square root of additive variance) were calculated. Narrow and broad sense heritability estimates were computed as the ratio of additive genetic variance to phenotypic variance and the

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