Noninfectious Bud-Failure from Breeding Programs of Almond (*Prunus amygdalus* Batsch)[1]

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Abstract. Potentiality exists for noninfectious bud-failure (BF) to develop in stocks from almond breeding programs. The manifestation of BF among varieties introduced in California since 1920 is similar to the pattern of development of BF among offspring of controlled crosses. Nonpareil, the leading almond variety, has been a parent of most newer varieties, and is predominantly featured in breeding programs. Nonpareil has BF-potential and can transmit it to offspring.

Noninfectious bud-failure (BF) is a serious genetic disorder of almond (*Prunus amygdalus* Batsch) that occurs in certain California varieties. BF is expressed as a variable phenotype, in which different phases are bud-perpetuated. Evidence indicates that BF is inherited as a dominant factor and that either parent can transmit BF to its seedling offspring (12, 14).

The BF phenotype is identified by characteristic *bud-failure* symptoms in early spring, by *roughbark* areas on branches, or both. A third symptom, *leafblotch,* has sometimes been observed, and, in at least some cases, is associated with BF.

Individual seedling offspring may not show the BF phenotype immediately. Seedlings differ both in the age at which the phenotype appears and in the severity of the malady when it does appear. Although offspring with BF-potential cannot be identified prior to the time that the BF phenotype appears, one can predict that certain populations contain individuals that will eventually become BF plants (13). The age at which BF appears in individual offspring is related to the severity of BF in the parental trees; i.e., the more severe the condition in the parents, the earlier it will appear in the offspring (14).

Materials and Methods Used in Almond Variety Development

California almond varieties have arisen from a number of sources. Imported almond varieties were first grown as early as 1853 (20). These were unadapted, and none became an important commercial variety. From then until 1900, many seedling plants were grown, and promising selections were named and introduced. Since about 1920, 6 varieties—'Nonpareil', 'Texas (Mission)', 'Ne Plus Ultra', 'Peerless', 'Drake', and 'I.X.L.'—originating as chance seedlings before 1900 and, planted in combination for cross-pollination, have accounted for 90 to 95 percent of the acreage planted.

Many new varieties have been introduced to the industry since 1930 (15). Breeding programs have been one source of varieties. The first such program was started by the U. S. Department of Agriculture and the University of California in 1923. Two varieties—'Jordanolo' and 'Harpareil'—were introduced in 1939; but only 'Jordanolo' was planted in significant numbers (21). However, 'Jordanolo' has been so susceptible to BF that it is no longer planted (18). More recently private breeders have become a source of new varieties (15). Chance seedlings originating in and near commercial orchards have also been an important source of new varieties. In addition, a number of budsports of 'Nonpareil' have been introduced.

The procedure for variety development used by the University of California and the U. S. Department of Agriculture has been as follows. Crosses are made between selected parents. Seeds are germinated, and the resulting families of seedlings are grown. Individual plants are examined for commercial potentiality, and those considered promising for further testing or for breeding are retained. The remaining plants are discarded. Entire populations are studied only through the 4th or 5th year, with 5 to 10 percent or less retained for further study. Scions from these selections are grafted to rootstock trees in a selection block or, sometimes, directly to trees in commercial orchards for trial.

Chance seedlings and budsports have been selected by growers from orchard observation. The grower usually is attracted by high productivity, although other characteristics, such as late bloom, might be a basis for selection. Frequently, nut samples from such trees are submitted to public or private horticulturists, almond buyers and processors, and nurserymen for evaluation. Ordinarily, selected trees of this type are propagated commercially in cooperation with a nursery, and trees from this source invariably have been patented. In this paper, the term "seedling" refers to a plant propagated from a seed. A given seedling may be further designated as the *S* tree, or original scion source. Generations of trees originating by consecutive vegetative propagations from an *S* tree are identified as $S+1$, $S+2$, and so forth (19).

Results

I. BF among older major almond varieties of California.

Among the major older varieties, 'Nonpareil' and 'Peerless' have varying degrees of susceptibility to BF (Table 1). Affected trees have been observed in both varieties at least since the 1920's. 'Nonpareil' is the principal commercial variety, and accounts for over 50 percent of the total production and 61 percent of new acreage (data of California State Department of Agriculture, Sacramento). BF occurs sporadically in this variety in all production areas and in trees of all ages. There has been an increasing incidence of BF in 'Nonpareil' orchards coincident with the acreage expansion of this variety. The BF phenotype occurs sporadically in Peerless, but the variety has not been planted extensively in recent years, such that the incidence of BF has not been significant.

No indication of BF has been observed in 'Texas', 'Ne Plus Ultra', 'I.X.L.', or 'Drake' (Table 2). At present, these varieties may be considered as free of the disorder.

II. Distribution of BF within breeding lines in the U. S. Department of Agriculture and University of California programs.

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Table 1. California almond varieties with known susceptibility to BF.

Variety	Origin	Improvement program[b]	1968 Acreage	When BF first observed	Extent of BF in the variety
Nonpareil (20)[a]	Rootstock seedling; selected by A. T. Hatch; 1884	1	111,324	At least by 1920's	Possibly half of orchards have some BF trees (1 to 30%) depending on age and district.
Peerless (20)	Seedling selection of unknown origin before 1900	1	7,126	At least by 1920's	Less than half of orchards with BF trees. No. in orchards less than 10%.
Jordanolo (21)	Nonpareil × Harriott; introduced 1939	5	2,818	1948	Almost all orchards with BF trees. No. in orchards 25–100%.
Harpareil (21)	same as Jordanolo	5	200 trees of less	1967	Single tree in variety collection affected.
Jubilee (5)	Probably Nonpareil × Texas; introduced about 1929	2	unknown; probably less than 200 A	1953	Most orchards have some BF trees. Can go to 100% in some orchards.
Merced (4)	Probably Nonpareil × Texas, introduced 1957	2	9,476	1968	Uncertain; About 10% in some orchards.

[a]See Literature Cited.
[b]Improvement Program: 1. Early California selection; 2. Chance seedlings; 3. Mutation of Nonpareil; 4. Breeding program—private; 5. Breeding program—UC and USDA.

Table 2. California almond varieties with no history of BF to date.

Variety	1968 acreage	Improvement program[b]	When introduced	Origin
Texas (Mission) (20)[a]	35,704	1	before 1900	Unknown
Ne Plus Ultra (20)	17,943	1	1884	Rootstock seedling selected by A. T. Hatch
Drake (20)	5,694	1	1880	Rootstock seedling selected by H. C. Drake
I.X.L. (20)	3,500	1	1884	Rootstock seedling selected by A. T. Hatch
Davey (17)	3,670	5	1962	USDA-UC breeding program; Nonpareil × Sans Faute
Tardy Nonpareil (1)	very few	3	1955	Bud mutation of Nonpareil
Profuse (3)	very few	2	1957	Probably Nonpareil × Jordanolo
Ballico (2)	very few	2	1957	Unknown
Thompson (2)	3,000(?)	2	1957	Probably Nonpareil × Texas
Ruby (3)	very few	2, 4	1958	Unknown
Emerald (6)	very few	4	1962	Texas × (Nonpareil × Texas)
Kapareil (16)	250(?)	5	1962	Nonpareil × Selection 24–6
Ripon (6)	very few	4	1962	Open pollinated seedling of late Nonpareil sport
Butte (7)	very few	4	1962	Texas × Nonpareil
Cressey (7)	very few	3	1963	Supposed sport of Nonpareil
Norman (7)	very few	2, 4	1963	Rootstock sucker
Paxman (7)	very few	2	1963	Unknown
Empire (7)	very few	4	1963	Texas × peach-almond seedling
Price (7)	very few	2	1963	Unknown
Yosemite (8)	very few	4	1965	Texas × probably Nonpareil
Wawona (9)	very few	4	1965	Ruby × Texas
Carmel (10)	very few	3	1966	Supposed to be Nonpareil sport
Tioga (10)	very few	4	1966	Nonpareil sport × probably Texas
Kern Royal (11)	very few	3	1967	Bud mutation of Nonpareil
Reinero (11)	very few	2	1968	Seedling of Nonpareil
Vesta (11)	very few	5	1968	Nonpareil sport × 5A-3 (second generation Nonpareil-Eureka seedling)

[a]See Literature Cited.
[b]Improvement program: 1. Early California selection; 2. Chance seedlings; 3. Mutation of Nonpareil; 4. Breeding program—private; 5. Breeding program—UC and USDA.

One of the major breeding lines of the USDA–UC breeding program has involved 'Nonpareil' and 'Harriott'. The original cross (Fig. 1) was made in 1923. The 3 selections made from this cross were phenotypically normal as seedling trees. Selection A9-18 was discarded without repropagation. The other selections, later named 'Jordanolo' and 'Harpareil', were tested together in commercial orchards as $S+1$ trees. The BF phenotype was discovered in 'Jordanolo' about 1948 (Table 1) in young $S+2$ trees in commercial orchards. Several years later BF developed in the $S+1$ trees, which were then about 15 years old.

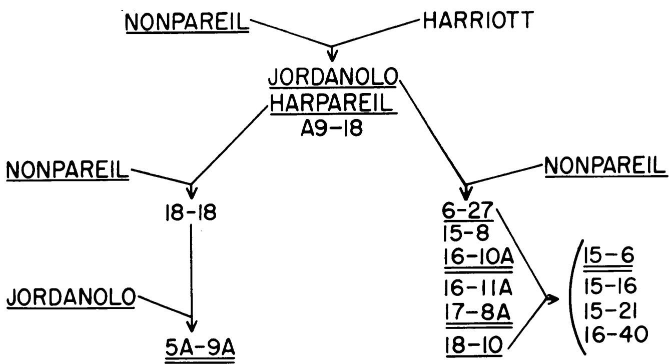

Fig. 1. Breeding line of Nonpareil × Harriott showing BF transmission. See text for explanation. No underscore = phenotypically normal and no evidence of BF in clone; single underscore = phenotypically normal but BF exists in the clone; double underscore = phenotypically BF.

'Harpareil' has not been grown much commercially so a comparable history is not available. In 1967, BF was discovered in a single $S+1$ tree that was then about 30 years old.

The 'Nonpareil' × 'Harriott' cross was repeated in 1949 by E. F. Serr by using parents which were phenotypically normal. As reported in an earlier paper (11), 4 of the 174 offspring seedlings had BF symptoms. Five other selections were propagated into the $S+1$ generation. One of the 5 selections had developed BF-like symptoms and one has developed severe leaf blotch.

'Nonpareil' was crossed with 'Harpareil' in 1937. From this cross 54 seedlings were grown between 1939 and 1950. The only selection, 18–18, was propagated but has not produced BF to date.

'Jordanolo' was crossed to 18–18 in 1946. From it, 45 seedlings were examined through 1950. The only seedling selection saved, 5A–9A, produced BF in the $S+1$ generation within 3 years of propagation.

'Nonpareil' was crossed to 'Jordanolo' in 1935. As reported earlier (12), 15 selections were propagated to selection blocks; 5 produced BF. The 6 numbered selections from cross 4, shown in Fig. 1, were propagated in 1951 in another test; 17–8A produced BF almost immediately in $S+1$, 16–10A very soon; 6–27 and 18–10 produced no BF evidence until 1968. To date, 15–8 and 16–11A are normal.

From the cross 6–27 × 18–10, made in 1950, 80 individuals were studied. No distinctly BF plants were found initially, but 4 had leaf blotch characteristics. Later, 4 numbered selections from this cross were propagated; one (Selection 15–6) produced BF trees at 2 years.

Many additional crosses have been made in the 2 programs since 1920. Since 1948, recordings of data in the University of California program have included notes of obvious off-type or unusual seedlings. Of 228 families examined, 68 contained 1 or more seedling offspring with characteristics resembling those of bud-failure, roughbark or leaf blotch. Table 3 is a tabulation of the parental varieties related to these 68 families. Members of one group of varieties Nonpareil, Jordanolo, Merced, Jubilee, 6–27, and 18–10, appear to carry the BF factor and can transmit it directly to offspring. Members of another group, 'Texas', 'Harriott', possibly 'Thompson' and 'McLish', do not appear to carry the factor and are not likely to produce BF offspring except when crossed to a variety that can. Transmissibility from a third group—'California', 'Reams', 'Kapareil', 'Davey' and 18–18—is uncertain.

III. BF among other variety introductions.

Tables 1 and 2 also list variety introductions that have been made by private breeders and orchardists. These originate from 3 principal sources: chance seedlings in and about growers' orchards; bud mutations of 'Nonpareil'; and private breeding programs.

Chance seedlings are widely disseminated throughout commercial orchard areas. Samples from approximately 50 such plants have been examined since 1951. Although some of these plants may be unbudded rootstock materials or relics of the earlier period of seedling growing, a high percentage appear to be hybrids of 'Nonpareil' and Texas, arising as seedlings from either variety as seed parent. Indicating such origin is the fact that these 2 varieties have been predominant in almost all almond districts since 1920, and the observation that nuts and trees are intermediate in appearance between that of the 2 putative parents. Moreover, they resemble progeny with this parentage which have been studied from controlled crosses.

'Jubilee' was the first variety of this group (Table 1) extensively planted. It had been growing in a limited amount in the Paso Robles district in San Luis Abispo County. In 1950, trees were established at Davis, Winters and in parts of the San Joaquin Valley. BF was discovered in trees of the variety in 1953 and a survey of the Paso Robles area revealed that BF had existed in the variety for several years prior.

'Merced' has been the most extensively planted new variety in recent years (see Table 1). In 1968, BF was discovered within the variety, although some affected trees had evidently existed prior to that. It was present in trees of the $S+1$ generation 10 or more years old and in trees of the $S+2$ generation 6 or more years old. Only a small percentage of trees of any one block was affected at the time of the initial observation. BF has been found in 'Merced' orchards of the southern and central San Joaquin Valley and in the Sacramento Valley. The pattern of distribution is similar to that found in 'Jordanolo' and 'Jubilee'.

Tables 1 and 2 list additional varieties. Of 9 varieties listed as "chance seedlings" and introduced since 1952, 6 (including 'Jubilee' and 'Merced') appear to be hybrids of 'Nonpareil'–'Texas', 1 is a hybrid of 'Nonpareil' and 'Jordanolo' while the percentage of 2 is unknown. Three bud-mutations of 'Nonpareil' exist. Of 7 varieties arising from private breeding programs listed in Table 2, 6 are derived from 'Nonpareil' lines.

Discussion

The pattern of BF inheritance and development described previously (13, 14) can be used to interpret BF occurrence in current variety development programs in California. Variety development in California has taken place in 2 stages. The first was the selection of 6 major

Table 3. Almond varieties and selections used as parents whose progeny has produced some individuals with known or suspected bud-failure. No distinction is made between seed or pollen parent.

Varieties producing families with one or more BF suspected offspring	Families where used as a parent	Families with individuals of suspected BF or other character		The other parent in families producing BF individuals
	No.	No.	%	
Nonpareil*	31	17	55	Harriott, Texas, Thompson, Jordanolo*, McLish, Davey, Kapareil, many numbered selections.
Jordanolo*	6	5	83	All numbered selections.
Tardy Nonpareil	19	7	36	Reams, Texas, Thompson, California, numbered selection.
California	10	3	30	Frostproof, Tardy Nonpareil, numbered selection.
Texas (Mission)	29	4	14	Nonpareil*, Jubilee*, Merced*, numbered selections.
Merced*	2	2	100	Nonpareil,* Texas.
Thompson	4	3	75	Nonpareil*, Tardy Nonpareil, numbered selection.
Jubilee*	4	1	25	Texas.
Kapareil	6	2	33	Nonpareil*, Davey.
Davey	16	5	31	Nonpareil*, 18–18, other numbered selections.
6–27*†	3	2	67	18–10*, other numbered selections.
18–10*†	5	3	60	6–27*, Nonpareil*, other numbered selections.
18–18†	3	3	100	Davey, Nonpareil*, Jordanolo*.
Harriott	2	1	50	Nonpareil*.

*Varieties known to develop bud-failure.
†See Figure 1 for parentage.

varieties from seedling populations grown from 1850 to 1900. The second was the selection of varieties from the offspring generations of this original group. Nonpareil was one of the parents of the 4 varieties that now show BF, in the second group, and BF did not appear until a large number of trees had been propagated vegetatively or a considerable age had been reached, or both.

In each case, the appearance of BF within the clone was not immediately universal; rather it occurred at different times from different propagation lines. This pattern of delayed and sporadic development within individual clones has been one of the confusing aspects of BF development, but it can be understood in terms of the BF inheritance pattern (12, 13). When the individual plant used as a parent has obvious BF symptoms, many of its offspring will also show BF symptoms at an early age. On the other hand, if trees used as parents carry the BF factor but have no symptoms (i.e., they have a low BF-potential), some of their seedling offspring will inherit BF-potential; but development of BF symptoms may not occur for many years. Variation among individuals is further revealed when they are propagated consecutively as clones. Some clones (varieties) will develop BF relatively soon; others with a less BF potential may require much longer time and more extensive propagation.

The significant point is that parental varieties may be phenotypically normal but have low BF-potential which can be transmitted to offspring. BF cannot be identified immediately in such offspring which, like their parents, may be propagated through many scion generations and become named varieties before symptoms appear.

If the chosen parents had had obvious BF characteristics, they would have been avoided as parents. Furthermore, if used, BF would have appeared in some of their offspring at an early stage of propagation. Such seedlings would automatically be eliminated in selection and probably the breeding line would be eliminated.

The analysis reveals that the breeding lines now being utilized in the various variety improvement programs in California carry a high potentiality for BF development. None of the varieties listed in Table 2, with the possible exception of Davey and Thompson, have been propagated sufficiently to reveal the BF potentiality that could be present.

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Influence of Nursery Harvest Date, Cold Storage, and Planting Date on Performance of Winter Planted California Strawberries[1]

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Abstract. Eight non-everbearing California strawberry cultivars were evaluated under the standard winter planting system (October-November) in comparisons involving differentials in plant harvest and transplanting dates and comparing approximately 30, 15 and 0 days of cold storage conditioning at Santa Ana, a relatively warm-winter south coastal California site. The varieties differed greatly in performance and the results were consistent with that which is known of their varying performance under commercial conditions. 'Sequoia' was almost an ideal performer but the fruit lacks firmness. Photoperiod is important in governing the reproductive response under this planting system since the duration of the fruiting period for a given variety was directly associated with how long the plant had grown under short days. However, chilling appeared to be the dominant factor governing *acceptable* performance in all varieties except 'Sequoia'. 'Sequoia' performed satisfactorily over the entire range of treatments and although it responded to chilling, apparently it has a short rest period. Of the other varieties that are of great economic importance in California, 'Fresno' and 'Shasta' evidently have relatively long rest periods and cannot be manipulated satisfactorily under the winter planting system whereas 'Tioga' is intermediate and responds favorably to manipulation.

About 25% of the California strawberry acreage is winter planted. Since early fruit production is the main reason for winter planting, most of it is done in coastal southern California where the winters are mild. Plants are harvested from high elevation nurseries in northern California in October, and either transplanted directly or after receiving from about 10 to 20 days of cold storage. Planting is usually completed for most cultivars by about November 10.

The success of winter planting depends entirely upon how well the plants grow during the short days of December and January. The more active they are, the more flower buds are initiated and the greater the crop. Ambient temperatures control the rate of growth and soil temperatures may be increased significantly by the use of clear polyethylene bed mulch, a standard practice in California (3, 5). The chilling history of the plant also affects the growth rate and performance (1, 2, 4). If the plants fail to receive enough chilling, they lack vigor and will not grow rapidly enough to produce a good early crop although they flower profusely for a long time. If they receive too much chilling, they will be very vigorous producing runners instead of fruit. The optimum planting date and the amount of cold storage that will benefit the plants can be determined for a given cultivar so that the plants can be manipulated accordingly.

The experiments described in this report were designed to increase our understanding of the interaction of the factors that govern the reproductive response of cultivated non-everbearing strawberries; to characterize cultivars that have been or are now used in winter planting in California with regard to optimum nursery harvest and transplanting dates; and to evaluate their chilling requirements.

Materials and Methods

Plants of University cultivars 'Sequoia', 'Tioga', 'Fresno', 'Torrey', 'Aliso', 'Salinas', 'Shasta' and 'Lassen' from commercial high elevation nurseries (near McArthur, Shasta County, Latitude 41°N, elevation circa 1,000 M) were compared in plantings from plant harvests of October 13, October 30 and November 11. 'Tioga' plants were not available for the last harvest. For each lot and each cultivar, plants transplanted immediately after minimum storage were compared with those from the same lot transplanted after about 15 days or about 30 days of cold storage. Fruiting sites were south coastal California (Santa Ana) and central coastal California (Watsonville and Salinas). The cold storage box temperature was 28°F (−2.2°C).

Double row raised beds were used, spaced at 40 inches with 9 inches between plants and 16 plants per plot under the hill system. Clear polyethylene bed mulch was applied within 2 weeks after transplanting, a standard practice for winter plantings.

The soil at a given location was very uniform in composition and texture. The experimental design was a modified randomized complete block with a minimum of 4 replicates. Replications were across the rows so that any

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