NONINFECTIOUS BUD FAILURE

Noninfectious bud failure (BF) is a disorder caused by a peculiar genetic abnormality characteristic of certain almond varieties. It is a serious economic problem in that many thousands of trees have had to be replaced and at least one variety, Jordanolo, is being eliminated because of its susceptibility to BF. The disorder is expressed by the failure of vegetative buds to grow in the spring. This, along with other roughbark characteristics, results in a distinctive growth pattern sometimes also described as "crazy-top." Trees do not die but production in individual trees is reduced in proportion to the severity of the symptoms. Experimental work on the disorder can be divided into two basic problems discussed here in two separate articles. One concerns the nature of the disorder and the origin of the BF condition, and is studied in the first article. The other (studied in the second article) involves the sporadic appearance of BF in such important varieties as Nonpareil, and deals with practical methods to identify and control it.

Variation in the expression of BF in different seedling almond plants of the same age. These were from a cross of Texas × Jubilee-BF. The differences are shown by different proportions of failing buds on these shoots. Shoot on left is normal.

(1) *The nature and origin*

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THE NAME "noninfectious bud failure" described symptoms in almond trees that are not specific to this disorder. Similar symptoms can result from various other causes. In this study of the nature and origin of the disorder, the term BF is used to designate the particular internal genetic condition associated with this disorder. Almond varieties are *clones* made up of the vegetatively propagated offspring of a single seedling plant (or a bud sport). In breeding programs, any member of a family of seedling plants that are capable of vegetative propagation is a potential clone. The seedling plant originating the clone is said to represent the S-generation, plants propagated vegetatively from it are the S + 1 generation, buds from the S + 1 produce the S + 2 generation, and so on.

Normally, trees of all scion generations of a clone are identical genetically such that the variety can be reproduced more or less indefinitely without change. In varieties that are susceptible to the BF disorder, however, the clone is not constant but has the capability of changing from the normal to the abnormal BF form. Those trees that show obvious symptoms of the disorder are said to show the *BF phenotype*. Other trees of the clone have the BF genetic capacity but may not show symptoms. These are said to have the *BF genotype* with a potential to produce symptoms.

Inheritance studies

Studies of the inheritance of BF in almond were initiated in 1954 after it had become evident that the variety Jordanolo, introduced from the breeding program of the USDA and California Agricultural Experiment Station, had acquired the disorder by inheritance from the parent Nonpareil. Additional cases of BF were then found among other unnamed selections being grown at Davis or Winters, particularly when Jordanolo or Nonpareil was one of the parents.

The first series of studies involved crosses between Nonpareil and Peerless, both normal and BF-affected, in all combinations. In a second series, started several years later, a Nonpareil-BF seed parent was crossed with other varieties of differing BF potential. The object was to identify a possible recessive BF gene among these varieties. Progeny families were planted out and the incidence and severity of BF-affected individuals were recorded annually. In some cases, individuals were propagated into the S + 1 generation. All of these studies have been at Davis where evidence now suggests conditions for producing BF are less favorable than other locations in the state.

The same basic pattern of BF inheritance has been found in all of the cases studied so far (see graph). The principal feature of these families was the variability in BF potential. The offspring *within families* varied in BF potential; the per-

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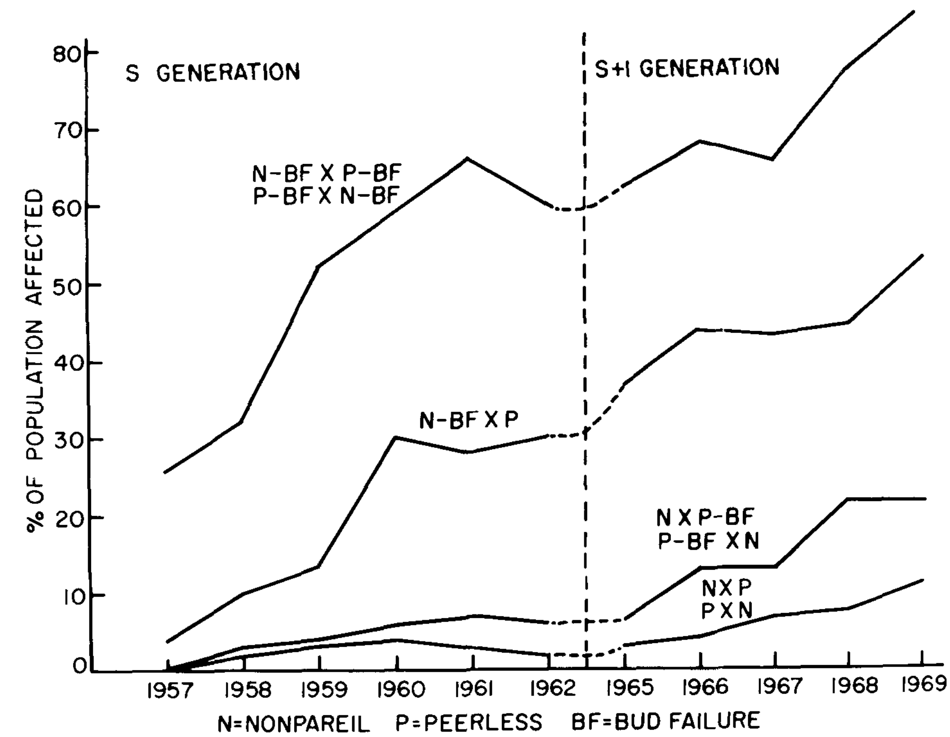
centage of individuals in which BF could be identified increased year by year in all families, indicating a continuous range in BF potential. Differences in the level of BF potential also occurred *between families*. Individuals with the BF potential (some developing BF symptoms as soon as two years from seed) resulted if both parents had BF; individuals with somewhat lower potential resulted if only one parent had BF; and individuals with much lower potential resulted if neither the Nonpareil or Peerless parents had BF symptoms. The percentage of BF-affected offspring is continuing to increase annually. Evidently, the final values for numbers of BF individuals within these families have not yet been achieved.

Variation

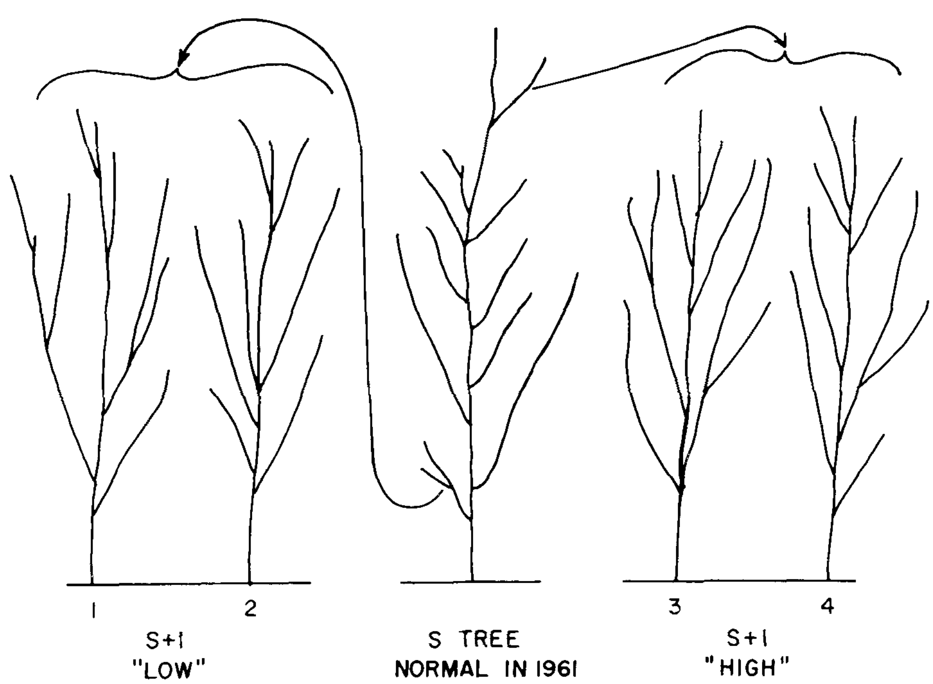
Variation in BF potential was found to exist *within normal trees* of these families. Buds were taken from the upper and lower parts of the tree to reproduce the S + 1 generation. After seven years, trees from buds of the same budstick showed the same BF severity; trees from buds of upper and lower parts of the tree differed markedly. There was no consistent trend in BF potential within the tree, but the lower part of the tree was just as likely to have the higher BF potential as the upper part.

Second series

The second series of experiments indicated that differences in severity of BF within and between trees of the same clone were inherited. Those parts of trees with the most severe BF symptoms produced the highest percentage of seedling offspring trees with BF. Parts of the trees with few or no symptoms produced fewer offspring with BF. Likewise, individual seedling plants with severe symptoms (high BF potential) produced more BF offspring than individuals of the same family with less severe or no symptoms. Whenever Nonpareil-BF was one of the parents, some of the offspring inherited BF. This suggests that BF is more likely to be a dominant factor than a recessive one. In the graph, when normal Nonpareil (rather than Nonpareil-BF) is one of the parents, BF offspring are also produced. In this latter situation, however, the BF potential in the seedling offspring appears to be much lower and a much longer time elapses between the



The graph shows changes that have occurred in the numbers of BF individuals appearing in families produced by crossing Nonpareil and Peerless in all combinations, using trees with and without BF. BF offspring has occurred in all families. The number has increased steadily with time. The results are interpreted to mean that these parental varieties produce offspring with differing BF potential. Differences are expressed here by the age at which one might expect that BF symptoms could appear on some part of the clone.



The diagram illustrates results of an experiment showing that variation in BF potential exists in different parts of the same plant. Trees produced from the same budstick have essentially the same BF potential. Trees produced from budsticks on two parts of the plant may have different BF potential. There was an equal chance for the upper part to have greater BF potential than for the lower part.

time the seedling plant is grown and when BF appears within the clone.

Concept of BF

The picture emerging from these studies is of a cellularly based, unstable condition, probably chromosomal in nature. Changes occur as cells divide and as the plant grows; consequently, variation in BF potential can develop in various parts of the plant and the clone. Some part of the cells' basic metabolic machinery appears to be altered and when the alteration becomes sufficient, symptoms of the disorder appear. Buds used to propagate a new plant carry the BF potential of the cells of the growing point of that bud. Buds from one part of the plant can have a BF potential different from other parts. If the bud carries low BF potential, then the new plant may never produce the BF phenotype. If it carries a high potential, or if change in BF potential is rapid, then the new tree may produce the BF phenotype at an early age. If enough buds of a BF potential clone are propagated, and if trees are grown long enough, it is likely that some trees with BF will eventually appear.

Many unanswered questions, both theoretical and practical, remain. Perhaps the most pressing is how to identify BF potential prior to the time actual symptoms appear. Such information would be applicable both to almond breeding programs and to the development of propagating sources in the case of such varieties as Nonpareil.

Another question to be investigated is what controls levels of BF potential? Can it be altered or reduced? Conditions producing BF symptoms actually appear to develop in summer rather than late winter or spring when symptoms develop. Some evidence now at hand suggests that the BF level is associated with extensive shoot elongation and high temperature during summer. Work directed toward clarifying these and other questions is underway.

One line of investigation concerns interspecific hybridization between BF varieties and peaches in which a different pattern of inheritance than that shown in the graph exists. This breeding procedure is being investigated as a progeny test for BF potential. A second line involves the study of normal and BF tissue as masses of callus in sterile culture. A third series of investigations involves the relationship among growth, temperature, and BF development.

Significance to industry

The BF phenomenon can continue to produce serious problems to the commercial almond industry, and particularly to individual growers. We are unable at present to identify BF potential before it occurs. Consequently, it is not possible to predict how extensive BF will eventually become. Two dangers present themselves. One is that BF may develop in the many new almond varieties that have been introduced from various sources since 1956. Essentially all are, either directly or indirectly, offspring of Nonpareil and there is a probability that at least some have inherited a BF potential. In the varieties already affected, about 10 years have elapsed between the time of their introduction and the time when enough trees had been grown long enough to produce BF.

New acres

Many new acres of almond have recently been planted. Much of this has taken place in southern San Joaquin Valley, predominantly with varieties known to have BF potential. If the pattern of greater incidence of BF in this area continues, the problem may become more acute.

(2) *Identification and control of bud failure in almond varieties*

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THIS ARTICLE describes the current status, identification, and control, of noninfectious bud failure (BF) as it affects particular almond varieties in California. Characteristics of the disorder were described in the accompanying article. A recent survey taken to estimate the prevalence of BF in affected varieties in the almond districts of California is summarized in tables 1, 2, and 3, and is discussed here.

Varieties affected

JORDANOLO. This variety resulted from a cross, Nonpareil × Harriott made in 1923 and introduced in 1937 by the USDA and University of California. It was planted extensively and reached a maximum of 6,000 acres. About ten years after introduction, BF was discovered in the variety and the percentage of affected trees rapidly increased. It has been the most seriously affected variety. In the state as a whole practically all orchards with Jordanolo have affected trees. The percentage of seriously affected trees per orchard ranges from less than 25 to 100 per cent. The incidence of affected trees is somewhat less in the central part of the state as compared with the northern Sacramento and southern San Joaquin valleys. Few orchards with Jordanolo have been planted within the past 10 years and the current (1968) acreage is down to 2,800. The variety is gradually being eliminated.

PEERLESS. This was one of the six major varieties which originated in California prior to 1900 and became the basis of the commercial industry. It comprises 7,000 acres most of which are in the Sacramento Valley. Although BF-affected Peerless trees can be found in most districts, the incidence is relatively low. However, in the Arbuckle district of Colusa County, about 50 per cent of the orchards were reported to have some affected Peerless trees although the percentage per orchard was small.

NONPAREIL. This variety also is one of the six major varieties which originated in California prior to 1900 and is the most important variety in the industry. Currently (1968), it makes up 111,000 acres, somewhat more than one half of the total almond acreage. Nonpareil has been used