Models for Noninfectious Bud Failure in Almond

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The data on Carmel almond were provided by Warren C. Micke, Mario Viveros, and Dale E. Kester. Financial support was provided in part by the Almond Board of California.

Accepted for publication 5 May 1987.

ABSTRACT

Fenton, C. A. L., Kester, D. E., and Kuniyuki, A. H. 1988. Models for noninfectious bud failure in almond. Phytopathology 78:139-143.

Development of bud failure symptoms in populations of Nonpareil and Carmel almond was modeled using the Weibull distribution. The logarithm of the scale parameter was found to be related to degree-days by a linear function. Use of a degree-day temperature threshold of 15–32 C appeared to be optimal in predicting the magnitude of the scale parameter. In addition, a conceptual model was developed to account for the differences between the Nonpareil and Carmel populations.

Additional key words: genetic disorder, *Prunus amygdalus, P. dulcis,* survival data analysis.

Noninfectious bud failure is a disease of almond (*Prunus dulcis* (Miller) D. A. Webb) whose etiology is perceived as genetic (11–13,31) and is grouped in a class with such disorders as cherry crinkle (2) and strawberry yellows (27,28). Noninfectious bud failure was first reported by Milbrath (21) as a bud-shattering condition in the almond cultivars Nonpareil and Peerless. The vegetative buds of susceptible trees develop an internal necrosis at the growing points (9,24). The subsequent failure of these damaged buds and the vigorous growth of the few buds that do grow result in an altered pattern of branch development characteristic of the disorder (31). Within susceptible populations of almond, symptoms increase with both time and vegetative repropagation (31). Although the symptoms superficially resemble those of the viral disease Drake bud failure (22), it has not been possible to transmit the disorder by grafting (31,32). The disorder can be transmitted through seed from either pistillate (29,31) or the pollen (10) parent.

A key aspect in the development of symptoms is the effect of temperature (8,14,16). In an experiment that used populations of identical susceptible-nonsymptomatic Nonpareil trees, symptoms were expressed earlier and with greater severity at warmer locations (14). Greenhouse experiments by Kester et al (17) produced results consistent with the field data.

Survivorship analysis is useful in modeling the time to a given response. In this case, it is the time to the expression of bud failure symptoms in bud failure-susceptible trees. The distribution of survival times (T) is usually characterized by three mathematically related functions: the survivorship function, $S(t)$; the probability density function, $f(t)$; and the hazard function, $h(t)$ (19). The survivorship function, $S(t)$, gives the probability of a tree remaining free of bud failure symptoms until t (time). The probability density function, $f(t)$, gives the rate at which bud failure develops (or the probability per unit time of a tree developing bud failure symptoms during that unit of time). The hazard function, $h(t)$, gives the degree of bud failure risk associated with a nonsymptomatic tree (or the probability of bud failure symptom expression per unit time conditional on assuming freedom from bud failure symptoms before that time).

The Weibull distribution, $S(t) = \exp[-(\lambda t)^{\beta}]$ (25), includes the exponential distribution as a subset (19). It has been used by Weibull (26) to fit a wide variety of data. In addition, it has also been used to study plant disease progression (4,23) and plant disease vector survival (20). It has a scale parameter, λ, and a shape parameter, β (18). (The parameter symbols used by Lawless [18] have been adopted.) The probability density function is $f(t) = \lambda\beta(\lambda t)^{\beta-1}\exp[-(\lambda t)^{\beta}]$, and the hazard function is $h(t) = \lambda\beta(\lambda t)^{\beta-1}$ (18). When the Weibull shape parameter (β) is restricted to a value of 1, this is the exponential case (19). The exponential distribution (or exponential case) is the most important distribution in survival studies (19) and has been found by Davis (5) to be useful in modeling a wide variety of failure data. It has the advantage of being mathematically simple with only one parameter, λ, which equals the hazard rate (19). The Weibull cumulative distribution is referred to in this paper as bud failure model I:

$$F(t) = 1 - \exp[-(\lambda t)^{\beta}].$$

Brannen (3) developed a survivorship model to provide a rationale for nonlogarithmic survival curves. This model was modified to account for heterogenous populations, and is referred to as bud failure model II:

$$F(t) = 1/n \sum_{i=1}^{n} [1 - q(t)]^{(1/b_i)}$$

$F(t)$ = the cumulative probability of bud failure symptom expression, n = the number of subpopulations with different potentials for bud failure, $q(t)$ = an exponential function (exp $[-kt]$) with an environmental constant, k, and b = an arbitrary measure of bud failure potential.

MATERIALS AND METHODS

Disease incidence in populations of Nonpareil trees (source-clone FSPMS 3-8-1-63) growing at eight climatically different locations in California was recorded as a function of time by Kester and Asay (14). Weibull parameters were estimated by maximum likelihood, nonlinear regression, and linear regression. The Statistical Analysis System (SAS) procedure LIFEREG was used for maximum likelihood estimation, tables devised by Billman et al (1) were used to calculate 95% confidence intervals, and approximate 95% confidence intervals were calculated using the parameter standard errors. SAS nonlinear regression was used to regress $\log_e S(t)$ on t. SAS linear regression was used to regress $\log_e[-\log_e S(t)]$ on $\log_e t$ (18). The parameter for the exponential case was estimated by regressing $\log_e S(t)$ on t using SAS linear regression. The slope of the regression line yielded an estimate of the hazard rate. Maximum likelihood estimates for the Weibull model and exponential case ($\beta = 1$) were compared using the likelihood ratio statistic (18). In all cases, time was measured from the date of planting.

Exponential hazard rates for Nonpareil at eight locations were $\log_e$-transformed and regressed on annual degree-days greater than 28 C (Fig. 1A). Values for degree-days greater than 28 C used in Figure 1A were taken from the work of Kester and Asay (14). In an extension of this regression procedure, $\log_e \lambda$ was regressed on annual degree-days calculated using different temperature thresholds. These degree-days were calculated by the single sine method (30) with the University of California Integrated Pest Management computer and data base. Annual degree-days calculated by the single sine method represented averages for the years of the experiment, 1970–1977. The coefficients of determination obtained from this series of regressions were then plotted against the upper and lower threshold values used in the degree-day calculations.

Data on the incidence of bud failure in the cultivar Carmel were collected from the following California commercial orchards: Wasco (Payne), Wasco (Billington), Fresno (Garland), McFarland (Lyda), and McFarland (LaBorde). Weibull parameters were estimated as described above. $\log_e$-transformed scale parameters for Carmel were regressed on annual degree-days greater than 28 C to produce Figure 1B. Values for degree-days greater than 28 C used in Figure 1B were calculated using the single sine method as previously described. The value for each location represented an average for the interval 1980–1985.

Weibull parameter estimates for the Nonpareil and Carmel data were evaluated for fit using Kolmogorov-Smirnov procedures (7) (Table 1). Time was measured from the date of planting.

The cumulative bud failure incidence data for Nonpareil at Lost Hills and Carmel at Wasco (P) were fitted to bud failure model II (Fig. 2). Because the locations are nearly adjacent, the same value was used for the environmental constant in each case. Time was measured from the date of planting. Parameters were estimated by trial and error.

RESULTS

Weibull parameter estimates are given for different estimation methods in Tables 2 (maximum likelihood), 3 (nonlinear

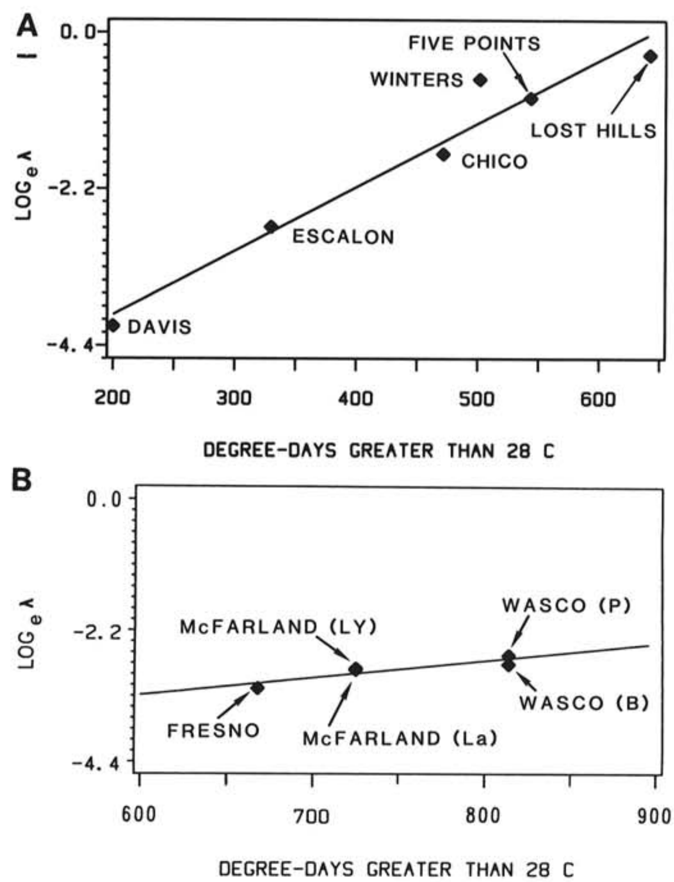

Fig. 1. Relationship between estimated Weibull scale parameter (λ) and annual number of degree-days greater than 28 C for **A,** Nonpareil 3-8-1-63, and **B,** Carmel growing at different California locations.

TABLE 1. Kolmogorov-Smirnov goodness-of-fit D values for different parameter estimates and critical D values for 95% confidence[a]

Cultivar Location	Weibull (MLE)	Weibull (NLR)	Weibull (LR)	Exponential (LR)	Critical D value at $P = 0.05$
Nonpareil					
Lost Hills	0.341	0.120	0.89	0.108	0.093
Five Points	0.221	0.136	0.157	0.137	0.106
Winters	0.263	0.214	0.140	0.180	0.094
Chico	0.140	0.091	0.108	0.124	0.136
Escalon	0.132	0.109	0.114	0.096	0.183
Davis	0.057	0.065	0.059	0.054	0.309
Carmel					
Wasco (P)	0.126	0.048	0.072	...	0.085
Wasco (B)	0.119	0.031	0.029	...	0.078
McFarland (La)	0.082	0.032	0.036	...	0.095
McFarland (Ly)	0.087	0.029	0.031	...	0.095
Fresno (G)	0.039	0.021	0.037	...	0.142

[a] A value of D greater than the critical D value indicates a poor fit (significant difference exists between the actual and predicted cumulative distributions). Parameter estimation methods were maximum likelihood estimation (MLE), nonlinear regression (NLR), and linear regression (LR).

regression), and 4 (linear regression). Exponential parameter estimates are given in Table 4. A comparison of Weibull parameter estimates by Kolmogorov-Smirnov procedures is shown in Table 1.

Nonpareil. Maximum likelihood estimation produced results that suggested the unsuitability of the exponential case for the Nonpareil data. The likelihood ratio statistic showed that the Weibull model with $\beta > 1$ was more appropriate than the exponential case for Nonpareil. In addition, a value of 1 for the shape parameter was found to be outside the 95% confidence interval (Table 2); however, Weibull parameters estimated by maximum likelihood were rejected by Kolmogorov-Smirnov procedures (Table 1). (The apparent poor results with maximum likelihood estimation could possibly be due to poor starting values for the parameter estimates.) Estimation methods that gave more favorable Kolmogorov-Smirnov test results suggested that the exponential case was appropriate for the Nonpareil data. A value of 1 for the Weibull shape parameter was found to be within the 95% confidence interval estimated by nonlinear regression (Table 3). Also, exponential parameter estimates compared favorably with other estimates (Table 1). In addition, the residuals when plotted against time appeared randomly distributed for all linear regressions used to estimate exponential case parameters.

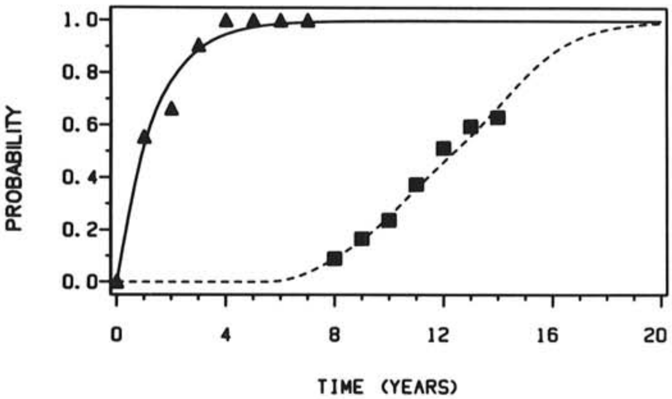

Fig. 2. Application of the alternative bud failure model (model II) to the data of Nonpareil 3-8-1-63 at Lost Hills and Carmel at Wasco (*P*). Solid line shows predicted probability with the following parameters: $k = 0.734$, $n = 1$, and $b = 1$. Dotted line shows predicted probability with the following parameters: $k = 0.734$, $n = 5$, $b_1 = 0.0034$, $b_2 = 0.000666$, $b_3 = 0.000222$, $b_4 = 0.0000417$, and $b_5 = 0.0000154$. Symbols indicate cumulative bud failure incidence with triangles for Nonpareil and squares for Carmel.

A statistically significant (*t* test) linear relationship was found between the natural logarithm of the estimated scale parameter, λ, and annual degree-days (Fig. 1A) ($r^2 = 0.9511$). This was the case with Nonpareil 3-8-1-63 regardless of whether the shape parameter was equal to 1. The number of degree-days between 15 and 32 C was found useful in estimating the rate of bud failure development (Fig. 3).

Carmel. Results from Kolmogorov-Smirnov testing (Table 1) showed that regressing $\log_e[-\log_e S(t)]$ on $\log_e t$ could provide good starting parameter estimates for the subsequent use of nonlinear regression to regress $\log_e S(t)$ on t.

A statistically significant (*t* test) linear relationship was also found between the natural logarithm of the scale parameter, λ, and annual degree-day accumulation for the five Carmel orchards (Fig. 1B) as occurred with Nonpareil (Fig. 1A), $r^2 = 0.8130$.

TABLE 2. Weibull scale and shape parameter estimates determined by maximum likelihood estimation shown with 95% confidence intervals (95% CI)[a]

Cultivar Location	*N*	Scale	95% CI		Shape	95% CI	
Nonpareil							
Lost Hills[a]	227	0.473	0.438	0.512	1.91	1.72	2.16
Five Points[a]	243	0.356	0.322	0.394	1.68	1.46	1.96
Winters[a]	214	0.329	0.296	0.365	1.44	1.29	1.62
Chico[a]	143	0.164	0.142	0.189	1.51	1.27	1.85
Escalon[b]	147	0.0931	0.0761	0.114	1.69	1.36	2.25
Davis[b]	135	0.0502	0.0290	0.0868	1.85	1.27	3.40
Carmel							
Wasco (P)[a]	519	0.0717	0.0697	0.0737	4.75	4.28	5.33
Wasco (B)[b]	639	0.0666	0.0651	0.0682	5.33	4.84	5.93
McFarland (La)[b]	524	0.0611	0.0587	0.0636	4.26	3.78	4.88
McFarland (Ly)	557	0.0623	0.0604	0.0644	5.58	4.95	6.41
Fresno (G)[b]	731	0.0453	0.0408	0.0502	4.41	3.67	5.52

[a] Calculated from the tables of Billman et al (1).
[b] Approximate 95% CI shown for Escalon, Davis, Wasco, Fresno, and McFarland.

TABLE 3. Weibull scale and shape parameter estimates determined by regression log (S)t)) on *t* using nonlinear regression shown with approximate 95% confidence intervals (95% CI)

Cultivar Location	*N*	Scale	95% CI		Shape	95% CI	
Nonpareil							
Lost Hills	227	0.638	0.185	1.09	1.25	0.322	2.82
Five Points	243	0.413	0.308	0.517	0.956	0.385	1.53
Winters	214	0.375	0.286	0.464	1.36	0.956	1.76
Chico	143	0.174	0.145	0.202	1.15	0.526	1.78
Escalon	147	0.0638	0.00628	0.121	1.04	0.197	1.88
Davis	135	0.0251	−0.480	0.0982	1.30	−0.617	3.21
Carmel							
Wasco (P)	519	0.0730	0.0700	0.0756	3.56	2.47	4.64
Wasco (B)	639	0.0626	0.0564	0.0688	2.84	1.69	3.99
McFarland (La)	524	0.0584	0.0529	0.0638	3.16	2.26	4.06
McFarland (Ly)	557	0.0568	0.0480	0.0657	3.27	1.70	4.83
Fresno (G)	731	0.0416	0.0287	0.0546	3.50	1.80	5.21

TABLE 4. Weibull scale and shape parameter estimates[a] determined by regressing $\log_e [-\log_e S(t)]$ on $\log(t)$ using linear regression (18), and exponential parameter (hazard) estimates with approximate 95% confidence intervals (95% CI)

Cultivar Location	Weibull			Exponential		
	N	Scale	Shape	Hazard	95% CI	
Nonpareil						
Lost Hills	227	0.716	0.915	0.734	0.479	0.989
Five Points	243	0.418	0.833	0.397	0.316	0.478
Winters	214	0.466	0.958	0.517	0.419	0.615
Chico	143	0.164	1.04	0.181	0.133	0.229
Escalon	147	0.0595	0.997	0.0647	0.0408	0.0897
Davis	135	0.0138	0.972	0.0161	0.00534	0.0269
Carmel						
Wasco (P)	519	0.0746	4.39	...	...	...
Wasco (B)	639	0.0633	2.98	...	...	...
McFarland (La)	524	0.0577	3.08	...	...	...
McFarland (Ly)	557	0.0561	3.17	...	...	...
Fresno (G)	731	0.0496	4.76	...	...	...

[a] Determined by regressing $\log_e S(t)$ on t using linear regression.

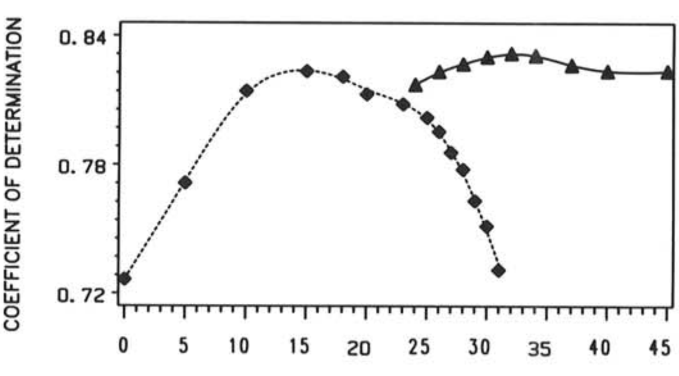

Fig. 3. Relationship between coefficient of determination and temperature threshold when regressing $\log_e \lambda$ on degree-days. Dotted line shows effect of changing the lower threshold temperature (with no upper threshold). Solid line shows effect of holding lower threshold at 15 C and changing upper threshold. Each point represents coefficient of determination derived from a regression as shown in Figure 1 but using a different temperature threshold to calculate degree-days.

Figure 4 A–C shows the results of applying bud failure model I to Nonpareil at Lost Hills and Carmel at Wasco (Payne). The lines in Figure 4A show the predicted cumulative probabilities with the symbols representing actual values. Figure 4B shows the rate of bud failure development (probability density function). Finally, Figure 4C shows the risk to nonsymptomatic almond trees of developing bud failure (hazard function).

The results of fitting bud failure model II to the same Nonpareil and Carmel data are shown in Figure 2. The dotted line in Figure 2 shows the fit to the Carmel data that was achieved by arbitrarily using five subpopulations, each with a different bud failure potential. The solid line in Figure 2 shows the result of using a single population with a uniform bud failure potential. This line closely approximates the data for Nonpareil propagated from a single source tree.

DISCUSSION

This work represents an effort to define more rigorously the pattern of time- and temperature-dependent bud failure symptom expression using the statistical methods of survival analysis. A consequence is the development of two mathematical models that describe bud failure symptom expression in susceptible trees as a function of time and temperature. The proposed models are consistent with previous observations that the number of bud failure symptomatic trees increases with both time and

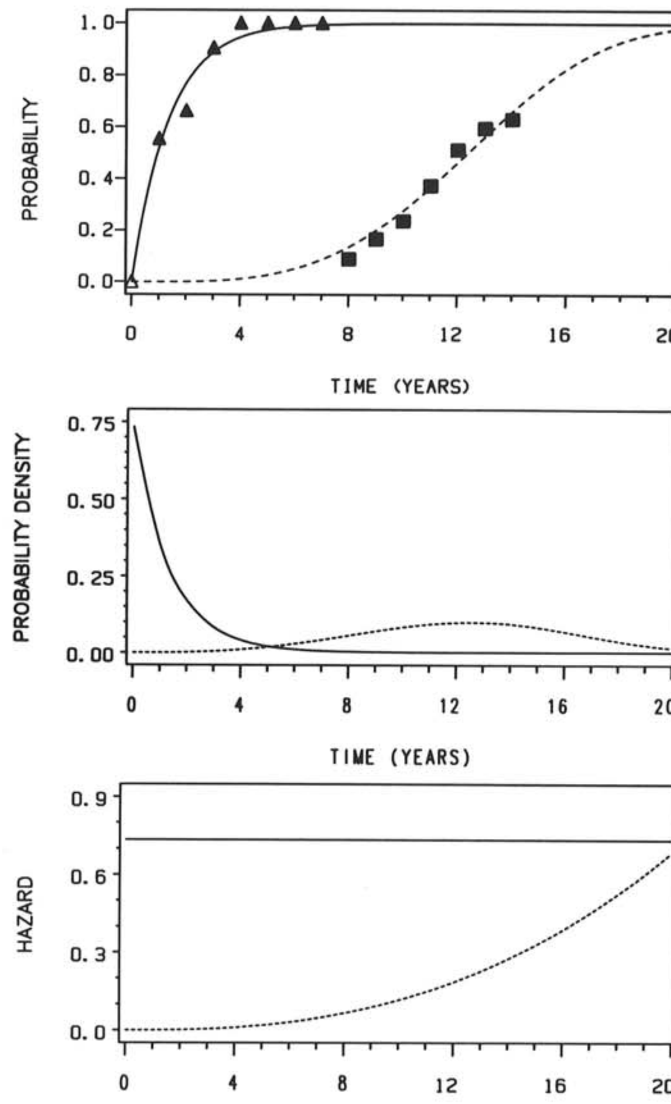

Fig. 4. A, Cumulative probability function, **B,** probability density function, and **C,** hazard function for Nonpareil 3-8-1-63 at Lost Hills (solid lines and triangles) and Carmel at Wasco (*P*) (dotted lines and squares). Symbols show observed values, and lines show values predicted by bud failure model I (Weibull). Time was measured from planting. In biological terms, A shows probability of observing bud failure symptoms, B shows rate of bud failure symptom development, and C shows level of bud failure risk to nonsymptomatic trees (bud failure model I).

temperature. Bud failure model I can be used to characterize the pattern of bud failure symptom development in an orchard of susceptible trees and then predict the future development of bud failure. Probabilities predicted by this model can be converted to numbers of trees by multiplying by the total numbers of susceptible trees.

These models assume a population of bud failure-susceptible trees. Bud failure susceptibility of individual trees cannot be predicted. However, if several trees in a population of trees propagated from a single source develop bud failure symptoms, then it may be inferred that the remaining nonsymptomatic trees are also bud failure-susceptible. In such a case, bud failure model I can be used to predict the rate of bud failure symptom development in the remaining nonsymptomatic-susceptible trees.

An analysis using different thresholds showed that the yearly number of degree-days between 15 and 32 C gave the best correlation with the scale parameter (λ). This analysis was based on the idea that setting the upper and lower temperature thresholds outside of the actual temperature thresholds overestimates the number of biologically significant degree-days, and setting them inside the actual temperature thresholds has the opposite effect. The threshold temperatures that produced the highest coefficient of determination were taken as an estimate of the actual biological threshold temperatures. The estimated optimum threshold of 15–32 C coincides with the temperature range found suitable for almond cell growth (6). This may be an additional indication that bud failure is closely associated with and dependent upon the process of growth. Experiments have shown that pruning trees showing bud failure promotes regrowth with the development of more severe bud failure symptoms (31).

The Nonpareil and Carmel populations appear to represent different stages in a continuum. Given the proper environmental conditions, bud failure potential (or hazard) appears to increase to a maximum. Carmel, described by the Weibull model I with shape greater than 1, had an increasing hazard and appeared to be approaching the higher hazard exhibited by Nonpareil (3-8-1-63). The Nonpareil trees were propagated from a single nonsymptomatic source tree with known bud failure susceptibility (15), and the Carmel trees were in a commercial orchard propagated from a variety of nonsymptomatic source trees. With these differences in mind, bud failure model II was developed. A simple random failure process was assumed. This exponential process was modified by introducing complexity in the form of subpopulations with different bud failure potentials. Increasing the bud failure potential and reducing the number of subpopulations shifted the Carmel pattern of bud failure development to that of Nonpareil (3-8-1-63). This reduction in the number of subpopulations proceeds naturally from an increase in bud failure potential because the members of the subpopulations should eventually reach a uniform maximum bud failure potential. The favorable results shown in Figure 2 are consistent with, but do not prove, the theoretical basis of bud failure model II. More comprehensive and definitive simulations using this alternative model need to be tested in future experiments.

Noninfectious bud failure is not only a serious economic problem in almond production but also represents a unique biological phenomenon that appears to differ fundamentally from other types of variants, including those caused by infectious pathogens and classical mutations. These models are not only fundamental to the biological understanding of the phenomenon but also to the establishment of selection procedures both at the cultivar level and at the propagation source level.

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