

EFFECTS OF STAGE OF NUT DEVELOPMENT AND SIMULATED RAT DAMAGE ON MACADAMIA YIELDS

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ABSTRACT: Black rats (*Rattus rattus*) cause extensive damage in Hawaiian macadamia (*Macadamia integrifolia*) orchards. In a previous study, extensive and persistent snap trapping significantly reduced rat populations and depredations on developing macadamia nuts, but had little effect on subsequent yields of mature nuts. This suggested that macadamia trees may compensate for rat damage, and that commonly used indices based on rodent activity and proportion of nuts damaged may overestimate the impact of rodent depredations and exaggerate the effectiveness of control measures. To clarify the effects of rat feeding on developing macadamia nuts, two levels of damage at two times during nut development and evaluated yields of mature nuts were simulated. Both number of nuts per raceme ($P = 0.0001$) and total weight of mature kernels per raceme ($P = 0.0001$), but not mean weight per mature kernel ($P = 0.90$), varied among treatments. Both number of nuts and total weight of kernels decreased ($P < 0.05$) with increasing damage. Time during nut development that damage was simulated had no apparent effect ($P > 0.05$) on yields. These results indicate that racemes did not compensate for damage by retaining other nuts on the same raceme that might otherwise have dropped prematurely. A variance component analysis was also conducted to determine how best to sample the orchard in a practical fashion while minimizing potential sources of bias and retaining sensitivity for distinguishing among treatment effects. All of the random variability in the number of nuts per raceme and total weight of nuts per raceme, and $>93\%$ of the variability in mean weight per mature nut were due to variability between racemes on a tree. Thus, blocking was not needed to control for variability among the different areas in the orchard; sampling fewer trees and concentrating available resources on measuring more racemes per tree would have provided a more sensitive comparison of treatments. Focusing on entire branches or trees instead of racemes as experimental units might have provided a more realistic model for investigating compensatory mechanisms in macadamia trees.

KEY WORDS: animal damage control, compensatory growth, integrated pest management, *Macadamia integrifolia*, *Rattus rattus*

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INTRODUCTION

Black rats (*Rattus rattus*) cause widespread damage in Hawaiian macadamia orchards (Tobin 1992). These arboreal rodents feed on macadamia nuts from the time kernels are small, fleshy unprotected fruits to when they are fully developed, high in energy-rich oils, and surrounded by shells and fibrous husks. Most damaged nuts are either pulled from the tree by rats or abscise prematurely and drop to the ground.

Many macadamia growers use toxic baits to control rat depredations in their orchards on the assumption that fewer rats result in less damage and, thus, higher yields. However, low levels of nut damage may have little or no impact on yield of mature nuts. A recent study (Tobin et al. 1993) indicated that although extensive and persistent snap trapping reduced rat populations and depredations on developing macadamia nuts, it had little effect on subsequent yields of mature nuts. Likewise, koa seedworm (*Cryptophlebia* spp.) feeding on developing macadamia nuts had little effect on premature nut drop until nut damage levels exceeded about 25% (Jones and Tome 1993).

These studies indicate that macadamia trees may compensate for low levels of damage. If so, the cost-effectiveness of rodent control programs may be

questionable in some situations. Commonly used indices based on rodent activity and proportion of nuts damaged may overestimate the impact of rodent depredations and exaggerate the effectiveness of control measures.

In 1994 a study was initiated to determine the effects of simulated rat damage on yields of mature nuts. The objective was to determine whether simulated rat damage to developing nuts results in reduced yields of mature macadamia nuts on the same raceme. The authors also investigated how best to sample in a macadamia orchard so that uncontrollable sources of variation were best addressed when conducting field studies.

METHODS

The study was conducted during the 1994 crop season at the Kau Agribusiness, Inc. macadamia orchard in Keaau, Hawaii. The authors divided 310 fifteen-year-old macadamia trees of variety 344 into 62 blocks of 5 trees each and randomly assigned 5 treatments to the trees in each block. The same assigned treatment was applied to two 4-nut racemes on opposite sides of each tree. Half of the branches for each treatment faced the adjacent trees within the row, and half faced the nearest trees in the adjacent rows. Damage was simulated by removing one or two nuts from each raceme at 100 or 150 days after

anthesis (as estimated by G. Ueunten, Kau Agribusiness, Inc., pers. comm.). The authors also evaluated a control group from which no nuts were removed. For each treatment, an approximately equal number of nuts from the proximal, middle, and distal portions of racemes were removed. The racemes were bagged with plastic mesh to prevent injury by rats and to catch abscised nuts.

At 150, 200, and 230 days after peak anthesis, the authors collected, weighed and evaluated the maturity of nuts that had abscised and fallen into the bags. At 230 days after peak anthesis they also collected any remaining nuts attached to the racemes. The nuts were husked and weighed, allowed to air-dry in the laboratory for five to seven days to equalize their moisture content, and placed in a convection oven at 75°C for 72 hours to reduce moisture to 1.0-1.5% (M. Tsang, Univ. Hawaii at Hilo, pers. comm.). The authors then shelled the nuts, extracted and weighed the kernels, and floated each kernel in deionized water to determine whether its specific gravity was >1.0, an indication that the oil content was >72% and the nut was fully mature (Cavaletto 1980).

Randomized blocks ANOVAs were conducted using SAS PROC GLM (SAS Instit. 1988) to compare the effects of level (removed 0, 1, or 2 nuts) and timing (100 or 150 days after anthesis) of damage on the number of nuts, total weight of kernels, and mean weight per kernel harvested per raceme. The authors used Duncan's multiple range test with $P < 0.05$ (Saville 1990) to separate treatment means.

Variance components were analyzed to identify which random effects in the randomized block ANOVA model

contributed most to the variance in the measured variables. SAS PROC VARCOMP (SAS Instit. 1988) were used to iteratively apply a restricted maximum likelihood method because variance components are constrained to be positive and the method separates the likelihood into a part containing fixed effects and a part containing random effects (Patterson and Thompson 1971).

RESULTS

By 230 days post anthesis, all except 15 nuts on ten racemes had abscised. The authors harvested 1.8 to 3.6 mature nuts ($F = 174, 4, 242 \text{ df}, P = 0.0001$) weighing 4.1-8.1 g ($F = 103, 4, 242 \text{ df}, P = 0.0001$) per raceme (Table 1). Both the number of nuts and total weight of nuts were highest ($P < 0.05$) for racemes with no simulated damage, and were higher ($P < 0.05$) for racemes from which only one nut was removed than for racemes from which two nuts were removed. Timing of damage had no apparent effect on number of mature nuts or total weight of mature kernels harvested per raceme ($P > 0.05$). Mean weight per mature kernel (2.2 g) did not vary among the treatments ($F = 0.24, 4, 242 \text{ df}, P = 0.90$).

Nearly all of the random variability in the number of nuts per raceme, total weight of mature kernels per raceme, and mean weight per mature kernel was due to variability among racemes on a tree (Table 2). The other random effects in the design (blocks and block x treatment interaction) resulted in zero or negligible estimates of their variance components.

Table 1. Mean number of nuts per raceme, weight of kernels per raceme, and weight per kernel harvested from racemes with different levels of simulated rat damage in a macadamia orchard near Hilo, Hawaii, August to November 1994. Rat damage was simulated by removing 0, 1, or 2 nuts per raceme at 100 or 150 days after anthesis. Abscised nuts were collected at 150, 200, and 230 days after anthesis.

Days After Anthesis	Number of Nuts Removed	Number of Racemes	Yield ^a					
			Number of Nuts Per Raceme		Weight (g) of Kernels Per Raceme		Weight (g) Per Kernel	
			\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
--	0	122	3.6 ^A	0.07	8.1 ^A	0.21	2.2 ^A	0.04
100	1	119	2.7 ^B	0.05	5.9 ^B	0.15	2.2 ^A	0.04
150	1	119	2.7 ^B	0.06	6.1 ^B	0.19	2.2 ^A	0.04
100	2	120	1.9 ^C	0.04	4.1 ^C	0.11	2.2 ^A	0.04
150	2	112	1.8 ^C	0.05	4.1 ^C	0.12	2.2 ^A	0.04

^aMeans that share a common letter in each column do not differ ($P > 0.05$) based on Duncan's multiple range test.

Table 2. Contribution of each random effect in the randomized block ANOVA model to the variance in the number of nuts, the total weight of nuts, and the weight per nut harvested in a macadamia orchard near Hilo, Hawaii, during August to November 1994. Treatments consisted of removing 0, 1, or 2 nuts from each of 2 racemes on each tree at 100 or 150 days after anthesis. Abscised nuts were collected at 150, 200, and 230 days after anthesis.

Variance Components	Variable		
	Number of Nuts Per Raceme	Weight (g) of Kernels Per Raceme	Weight (g) Per Kernel
Block	0.000	0.000	0.013
Block x treatment	0.000	0.000	0.002
Raceme	0.339	3.067	0.187

DISCUSSION

Macadamia flowers and fruits abscise throughout the entire period of nut development, from anthesis through fruit maturity 28 to 30 weeks later (Sakai and Nagao 1984). A typical macadamia raceme produces 200 to 300 flowers, of which usually <1% develop to full nut maturity (Sakai and Nagao 1984). This high premature abscission is a major constraint on nut production (Nagao and Hirae 1992) and has been the focus of much research aimed at increasing fruit set and yields (Williams 1980; Nagao et al. 1982; Ueunten 1989; Nagao and Sakai 1990).

The bearing capacity of macadamia trees may be limited by the availability of nutrients and stored carbohydrates (Cormack and Bate 1976; Stephenson and Gallagher 1989; Stephenson et al. 1989a,b). Nagao et al. (1988) observed that macadamia trees had similar yields over the course of a four-year study despite differing flowering intensities; trees that initially had more flowers or immature nuts experienced higher premature abscission. Likewise, the authors' earlier work indicated that in some situations rat predation on developing nuts has no measurable effect on yields (Tobin et al. 1993). These studies imply that macadamia trees can compensate for some levels of damage.

Most studies of premature macadamia nut drop have focused on the early stages of nut development (e.g., Williams 1980; Nagao et al. 1988; Ueunten 1989; Nagao and Sakai 1990). However, rats may be most attracted to macadamia nuts during the latter half of the developmental process, when nuts accumulate high-energy fatty acids (Cavaletto 1980). A better understanding of the dynamics of premature nut drop during the latter half of the crop cycle would help determine the effects of rat damage, as well as of drought, insect damage, and disease.

The authors measured the effects on individual racemes of damage simulated at 100 days after anthesis (after the kernel has reached full size but just before the embryo begins to form and accumulate oil) and at 150 days after anthesis (when almost 50% of the dry nut weight is oil) (Cavaletto 1980). Yields (both number of nuts and total weight of kernels) decreased with increasing damage, indicating that racemes did not compensate for

damage by retaining other nuts on the same raceme that might otherwise have dropped prematurely. Timing of damage had no discernable effect on yields. The similar size of mature nuts in all groups indicates that trees did not compensate for damaged nuts by putting more resources into remaining undamaged nuts.

Macadamia trees translocate assimilates and other growth factors not only among nuts on a raceme, but also among racemes and branches (Ueunten 1989). This study investigated interactions only among nuts on individual racemes. Focusing on entire branches or trees as experimental units might have provided a more realistic model for investigating compensatory mechanisms in macadamia trees.

Macadamia fruit growth and abscission are complex, dynamic processes that are influenced by the variety, age, and condition of the tree. Varieties with extended flowering and nut drop may have enhanced opportunities to compensate for damage because resources that might otherwise have gone into damaged nuts can be assimilated by later developing nuts. The authors' previous study, that failed to detect a relationship between rat damage and macadamia yields (Tobin et al. 1993), was conducted mainly with variety 508, which in Hawaii flowers throughout most of the year. The current study utilized variety 344, which has a much more restricted flowering period and thus decreased opportunities for compensatory nut development. Age of tree also affects flowering; young trees flower over more restricted periods and thus may have diminished opportunities for compensatory growth. Further research would help clarify the effects of variety, flowering synchrony, and damage during the latter half of nut development on yields of mature nuts.

Investigations into responses of macadamia trees to nut damage pose logistical dilemmas about how best to sample an orchard in a practical fashion while minimizing potential sources of bias and retaining sensitivity for distinguishing among treatment effects. In this study, which utilized trees of uniform variety and age, almost all of the variability in yield was between racemes on the same tree. Neither the area of the orchard sampled (block) nor the application of the different treatments across the areas (block x treatment interaction) contributed any appreciable variability. This indicates

that blocking was not needed to control for variability among the different areas in the orchard. A completely randomized design for assigning treatments to the same number of trees would have increased the degrees of freedom, and thus the sensitivity, for comparing treatment effects. Likewise, sampling fewer trees and concentrating available resources on measuring more racemes per tree would also have provided a more sensitive comparison of treatments. A different experimental design might be more appropriate for examining yields in orchards with a greater diversity of tree varieties and ages or more varied orchard topography.

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LITERATURE CITED

- CAVALETTO, C. G. 1980. Macadamia nuts. Pages 542-561 in S. Nagy and P. E. Shaws, eds. Tropical and subtropical fruits: composition, nutrition values, properties, and uses. Avi Publications, Westport, CT.
- CORMACK, D. B., and G. C. BATE. 1976. Seasonal fluctuation of total non-structural carbohydrate levels within the *Macadamia integrifolia* cultivar *Kakea* and its relation to shoot extension. *Rhod. J. Agric. Res.* 14:39-45.
- JONES, V. P., and C. H. TOME. 1993. Effect of husk feeding by (*Cryptophlebia* spp.) on macadamia in Hawaii. *Proc. Internl. Macadamia Conf.* 1:41-45.
- NAGAO, M. A., and H. H. HIRAE. 1992. Macadamia: cultivation and physiology. *Critical Reviews in Plant Sciences* 10:441-470.
- NAGAO, M. A., K. D. KOBAYASHI, and W. S. SAKAI. 1988. Flowering, nut set and premature nut drop of macadamia. *Proc. Macadamia Nut Assoc.* 28:54-59.
- NAGAO, M. A., and W. S. SAKAI. 1990. Effects of gibberellic acid, ethephon or girdling on the production of racemes in *Macadamia integrifolia*. *Scientia Horticulturae* 42:47-54.
- NAGAO, M. A., W. S. SAKAI, S. SHIROMA, and J. M. TOBARA. 1982. Growth regulator experiments on nut drop of macadamia. *Proc. Hawaii Macadamia Prod. Assoc.* 22:84-93.
- PATTERSON, H. D., and R. THOMPSON. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* 58:545-554.
- SAKAI, W. S., and M. A. NAGAO. 1984. Fruit growth and abscission in *Macadamia integrifolia*. *Physiol. Plant.* 64:455-460.
- SAS INSTITUTE, INC. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute, Inc., Cary, NC. 1028 pp.
- SAVILLE, D. J. 1990. Multiple comparison procedures: the practical solution. *Am. Stat.* 44:174-180.
- STEPHENSON, R. A., and E. C. GALLAGHER. 1989. Timing of nitrogen application to macadamias 3. reproductive growth, yield and quality. *Aust. J. Exp. Agric.* 29:581-585.
- STEPHENSON, R. A., E. C. GALLAGHER, and T. S. RASMUSSEN. 1989a. Effects of growth manipulation on carbohydrate reserves of macadamia trees. *Scientia Hort.* 40:227-235.
- STEPHENSON, R. A., T. S. RASMUSSEN, and E. C. GALLAGHER. 1989b. Timing of nitrogen application to macadamias 2. storage carbohydrates. *Aust. J. Exp. Agric.* 29:575-579.
- TOBIN, M. E. 1992. Rodent damage to Hawaiian macadamia orchards. *Proc. Vertebr. Pest Conf.* 15:272-276.
- TOBIN, M. E., A. E. KOEHLER, R. T. SUGIHARA, G. R. UEUNTEN, and A. M. YAMAGUCHI. 1993. Effects of trapping on rat populations and subsequent damage and yields of macadamia nuts. *Crop Prot.* 12:243-248.
- UEUNTEN, G. R. 1989. Effects of raceme thinning, fruit thinning and girdling on final fruit set of macadamia. M.S. Thesis, Univ. Hawaii, Honolulu. 62 pp.
- WILLIAMS, R. R. 1980. Control of premature fruit drop in *Macadamia integrifolia*: effects of naphthalene acetic acid application, cincturing, and shoot-tip removal. *Aust. J. Exp. Agric. Anim. Husb.* 20:740-742.