Suggestion of an Environmental Influence on Intercolony Agonism of Formosan Subterranean Termites (Isoptera: Rhinotermitidae)

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Environ. Entomol. 26(3): 632–637 (1997)

ABSTRACT The role of environmental factors in the intercolonial kin recognition of *Coptotermes formosanus* Shiraki was investigated using laboratory colonies under similar environmental conditions. Investigation of the parental field colonies found prediction of agonistic interactions based on geographic distance to be unreliable. Agonism did not occur between non-nestmate groups from laboratory colonies. Pairings of field and laboratory groups demonstrated reduced agonism. These results suggested that an environmental cue is part of a multiple component system for intercolony kin recognition in this species.

KEY WORDS *Coptotermes formosanus,* termite behavior, agonism, kin recognition

A DISCRETE KIN recognition mechanism that correlates with observed intercolonial agonism patterns has not been described for the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Su and Haverty 1991, Shelton and Grace 1996). Markers for specific colonies are necessary to identify the cues that *C. formosanus* uses for kin discrimination. Recent investigations have examined intercolonial variability in mitochondrial DNA (Broughton and Grace 1994), allozymes (Korman and Pashley 1991, Strong and Grace 1993, Wang and Grace 1995), and cuticular hydrocarbons (Su and Haverty 1991, Haverty et al 1996) of *C. formosanus* colonies. Variation was lacking in *C. formosanus* mitochondrial DNA studies (Broughton and Grace 1994). Low variation was found in enzymatic analyses (Korman and Pashley 1991, Strong and Grace 1993), although Wang and Grace (1995) have recently resolved a greater number of variable loci in *C. formosanus.* Su and Haverty (1991) did not find that agonistic behavior of *C. formosanus* colonies was correlated with any patterns of intercolonial variation in cuticular hydrocarbons. Haverty et al. (1996) demonstrated that quantitative intercolonial cuticular hydrocarbon variability exists in *C. formosanus* and can be used to discriminate individual colonies; however, intercolonial agonism among the colonies was not investigated.

Su and Haverty (1991) listed a series of alternative mechanisms for kin recognition in *C. formosanus,* collectively known as the "multiple stimulus hypothesis" (Thorne and Haverty 1991). One of these alternative mechanisms was recognition based upon volatile digestive components (Su and Haverty 1991). Different *C. formosanus* colonies may feed on different food sources (i.e., different wood species) in varying proportions. The colonies might then be qualitatively or quantitatively different in the volatile compounds that are excreted. These compounds should be consistent with the proportions of various materials found in their diets. If *C. formosanus* uses a kin discrimination system based solely upon a digestive volatile emission, then colonies with similar emissions (from having similar diets) should be mutually nonagonistic, and those having different diets (and therefore different emissions) should be mutually agonistic.

Exogenous chemical factors are those factors that are based upon the environment of the termite, such as the volatile digestive components suggested by Su and Haverty (1991). These are in contrast to endogenous chemical components, or factors based upon the phenotype of the termite.

Endogenous factors include cuticular hydrocarbons, polar cuticular substances, and glandular secretions (Su and Haverty 1991). Cuticular hydrocarbons are important in some termite species, including certain *Reticulitermes* spp. (Rhinotermitidae) and at least 1 *Zootermopsis* sp. (Termopsidae), for interspecific recognition (Howard et al. 1982, Haverty and Thorne 1989, Bagnères et al. 1991). A leaf-cutter ant, *Acromyrmex octospinosus* (Reich), may use a system that is a combination of both exogenous and endogenous factors for kin discrimination (Jutsum et al. 1979). Other ants, such as *Odontomachus bauri* Emery, use only endogenous cues for intercolonial recognition (Jaffe and Marcuse 1983). These ants rely on the relative proportions of volatile chemicals produced in the

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Table 1. *Coptotermes formosanus* colonies on Oahu, Hawaii, tested for intercolonial agonism patterns

Colony name	Colony label	Location of in-ground colonies
Andrews amphitheater	A	Amphitheater, UHM campus
Gilmore[a]	B	Gilmore Hall, UHM campus
Hale Halawai[a]	C	Hale Halewai dorms, UHM campus
Miller[a]	D	Miller Hall, UHM campus
North Poamoho	E	Pump station, UH Poamoho field station
Poamoho	F	Field plot, UH Poamoho field station
Pope[a]	G	Pope Hall, UHM campus
Publication[a]	H	Publication building, UHM campus
Waipio	I	Sugar cane field, Waipio peninsula

[a] Denotes colonies used by Su and Haverty (1991), whose letter designations were as follows: Publication, A; Hale Halawai, B; Pope, C; Upper Gilmore, D; Lower Gilmore, E; and Miller, F.

abdominal and cephalic regions for kin recognition. The importance of dietary factors was investigated for *O. bauri,* using paired non-nestmates and nestmates fed with different diets for 30 d. Agonism occurred only among paired non-nestmates no matter which diet was used (Jaffe and Marcuse 1983). *Microcerotermes arboreus* Emerson (Isoptera: Termitidae) uses a genetic component in intercolonial recognition (Adams 1991). Similar work has not been done with *C. formosanus.*

This study examined the potential of 1 exogenous factor, that of digestive emissions, as a cue for kin discrimination in *C. formosanus.* We hypothesized that if digestive emissions are important in kin recognition, then colonies that consume different materials will be mutually agonistic, and colonies that consume the same materials will be mutually nonagonistic. Laboratory colonies of *C. formosanus,* formed from paired alates of known colony origin, were used to explore this. Because these laboratory colonies have identical foraging materials and habitat, they are exogenously similar. Only colonies begun with a male and female alate from the same field colony (i.e., colonies created by sibling mating) were included in this study to avoid variables that might arise from using colonies of mixed parentage.

Materials and Methods

Field Colony Agonism Patterns. The intercolonial agonistic behavior patterns among 9 field colonies of *C. formosanus* were described using a chronic agonism assay. The colonies investigated in these studies were either on the Manoa campus of the University of Hawaii, or at various other locations on the island of Oahu, Hawaii. These colonies included those studied by Su and Haverty (1991) and 4 additional colonies (Table 1). Two of the colonies studied previously, Upper and Lower Gilmore (Hawaiian colonies D and E respectively in Su and Haverty 1991), had at the time of this study been delineated as a single colony by a triple mark–release–recapture technique (Su et al. 1993, Begon 1979). This colony was referred to by the single name "Gilmore." Some comparisons were not made because the Gilmore and North Poamoho colonies became inactive during the test period.

A series of experiments was designed to determine which colony combinations were agonistic. In this study, we used chronic agonism between groups of non-nestmates, as indicated by mortality in each group, to determine agonistic colony combinations.

Coptotermes formosanus foragers were collected from wooden box traps using the methods described by Tamashiro et al. (1973). Box traps (28.5 by 8.5 by 7.5 cm) were made of Douglas-fir, *Pseudotsuga menzeizii* (Mirbel) Franco, with wooden lids, placed over Douglas-fir stakes set into the ground. Traps were housed in 18.9-liter (5 gallon) metal cans with tops and bottoms removed, which were covered with a lid (30.5 by 30.5 cm) of sheet metal. Workers (undifferentiated pseudergates of 3rd instar or older as determined by size) and soldiers were counted and segregated into groups as described below.

A simple arena-type bioassay was designed to allow contact between the non-nestmate groups and between nestmate groups in controls. The assay arena consisted of a single glass petri dish (9.0 by 2.0 cm i.d.,) which contained a disk of filter paper (Whatman #2, 90 mm diameter, Whatman International, Springfield Mill, England) moistened with 1.0 ml of distilled water. Two freshly collected groups of 10 termites (9 workers and 1 soldier) were simultaneously placed in the arena. The arenas were placed in an unlit incubator at 28 ± 1°C and were removed after 24 h to assess overall mortality.

Experimental designs for each comparison included a non-nestmate pairing and 2 nestmate control pairings, 1 from each colony in that particular test. There were 5 replicates of each pairing (or treatment). Proportional 24 h mortality data were transformed by the arcsine of the square root and subjected to analysis of variance (ANOVA) (SAS Institute 1987), and means significantly different at the $\alpha = 0.05$ level were separated using the Ryan–Einot–Gabriel–Welsch multiple F test (SAS Institute 1987). Only those comparisons with significantly greater mortality in the non-nestmate treatment than in both controls were considered agonistic.

Laboratory Colony Rearing Methods. For >10 yr, laboratory colonies of *C. formosanus* have been maintained in a building on the Manoa campus of the University of Hawaii. These colonies were formed by pairing alates taken from field traps according to the methods of Tamashiro et al. (1973). Alates were removed from aggregation traps before flight; males and females were dealat-

ed manually, paired, and placed in vials containing moist vermiculite and sawdust. The vials were kept in an unlit incubator at 28 ± 1°C until 2nd- or 3rd-instar workers were observed. When this occurred, the vials were removed, placed in 3.8-liter (1 gallon) metal cans with moist Douglas-fir lumber, and kept under ambient conditions (≈24°C). After 1 yr of further development, the termites were transferred into 18.9-liter (5 gallon) cans to provide a larger foraging area.

Termites were collected from the laboratory colonies immediately before use in bioassays. Termites were aspirated from the wood surface and placed in marked beakers. Care was taken to avoid the egg chambers and reproductive termites within the colonies.

Laboratory Colony Agonism Patterns. Chronic agonism assays between laboratory colonies were performed to examine whether colonies that were exogenously similar were mutually aggressive. Experiments were designed using the agonism patterns of the field colonies as a guide. Laboratory colonies were paired with laboratory colonies whose parental colonies were mutually aggressive. Non-nestmate foraging groups from laboratory colonies were paired in 24-h assays as described above for field colonies. Colony combinations, and dates of founding by field collected alates, were B-Lab1 (24 April 1989) versus G-Lab2 (5 July 1989), I-Lab1 (29 May 1986) versus G-Lab3 (20 May 1986), and G-Lab1 (5 July 1989) versus I-Lab2 (29 May 1986). Proportional mortality data were transformed by the arcsine of the square root and subjected to ANOVA (SAS Institute 1987).

Means significantly different at the $\alpha = 0.05$ level were separated by 1 of 2 methods. For balanced experiments, the Ryan–Einot–Gabriel–Welsch multiple F test was used to separate means (SAS Institute 1987). Because the populations of the laboratory colonies were not large, and it was often difficult to obtain sufficient termite numbers, the number of control replicates was decreased to not <2 in several instances; means were then separated using the Tukey–Kramer test (Minitab 1994).

Agonism Patterns of Laboratory Colonies Versus Field Colonies. To investigate whether agonism was suppressed by laboratory rearing, laboratory and field colonies were paired in 24-h assays as previously described. Only laboratory colonies of single colony parentage were used in this study, and the agonism patterns of the parental field colonies was used as a guide in deciding which colonies to compare. Field colony D foragers were paired with the following laboratory colonies (and dates of initiation): G-Lab2 (5 July 1989), H-Lab1 (30 May 1990), and H-Lab2 (30 May 1990). Field colony B was paired with the following laboratory colonies: H-Lab3 (30 May 1990) and H-Lab4 (30 May 1990). Field colonies C and H were paired with the following laboratory colonies: H-Lab5 (30 May 1990) and B-Lab2 (18 May 1992), respectively. Mortality data were analyzed as described above.

Results

Field Colony Agonism Patterns. Of the 34 colony combinations examined, 20 (58.8%) were agonistic (Table 2). All colonies examined formed agonistic combinations with at least 2 other colonies. However, no colony was agonistic with every other colony (Table 3). Each of the 9 colonies was agonistic with 2.9 ± 0.9 (mean ± SD; range, 2–4) of the other colonies. Colonies generally fell into 2 groups according to their agonistic patterns—colonies G, E, and H comprised the 1st group, and colonies D, B, and F comprised the 2nd group, with common member A (Fig. 1). Colonies C and I were both nonagonistic with the entire 2nd group but were agonistic with each other. Colonies F and C appeared to overlap both groups partially.

Laboratory Colony Agonism Patterns. There were no significant differences in mortality between the control nestmate pairings and the non-nestmate treatments (Table 4).

Laboratory Colony Versus Field Colony Agonism Patterns. There was a trend toward higher mortality in non-nestmate pairings. However, there also was a great deal of variation in termite responses, and non-nestmate mortality differed significantly from that of the nestmate controls in only 1 instance (Table 5).

Discussion

Geographic separation of termite colonies was not a factor in predicting agonism (Table 1; Fig. 1). For example, colony G was agonistic with some colonies that were very close geographically (A, B, and D) and with a more distant colony (I). If kin recognition in *C. formosanus* has a genetic basis, as with *M. arboreus* (Adams 1991), then one might expect that neighboring colonies would be less agonistic toward one another. However, this was not true for this data set. By the same token, distant colonies were not consistently agonistic. Colony G was not agonistic with distant colonies E and F, but was agonistic with distant colony I.

Table 3 depicts theorized colony markers based upon these results, as well as those developed by Su and Haverty (1991). Colonies with a symbol (marker) in common were a nonaggressive pairing. Those colonies without a symbol in common represent an agonistic pairing. The combinations of Gilmore and Waipio (B and I) and North Poamoho and Waipio (E and I) were not tested because of a drastic decline in activity of both B and E. However, these 2 colonies are included in both Table 3 and Fig. 1 using the results from agonistic pairings with other colonies as a guide where data was not available. As indicated in Table 3, colony C in the current study is not agonistic with colonies B and D, as was the case in Su and Haverty's work

Table 2. Intercolonial agonism patterns of *C. formosanus* colonies on Oahu

Colony	A	B	C	D	E	F	G	H	I
A	—[b]	—[b]	—	—	—	—	—	—	—
B	No		—	—	—	—	—	—	—
	(Pr > F = 0.3349)								
C	No	No	—[b]	—	—	—	—	—	—
	(Pr > F = 0.5347)	(Pr > F = 0.7228)							
D	No	No	No	—[b]	—	—	—	—	—
	(Pr > F = 0.7564)	(Pr > F = 0.7228)	(Pr > F = 0.3222)						
E	No	Yes	Yes	Yes	—[b]	—	—	—	—
	(Pr > F = 0.2976)	(Pr > F = 0.0001)	(Pr > F = 0.0184)	(Pr > F = 0.0001)					
F	No	No	No	No	Yes	—[b]	—	—	—
	(Pr > F = 0.1509)	(Pr > F = 0.0590)	(Pr > F = 0.2087)	(Pr > F = 0.2976)	(Pr > F = 0.0443)				
G	Yes	Yes	No	Yes	No	No	—[b]	—	—
	(Pr > F = 0.0008)	(Pr > F = 0.0050)	(Pr > F = 0.3966)	(Pr > F = 0.0066)	(Pr > F = 0.0404)	(Pr > F = 0.0651)			
H	Yes	Yes	No	Yes	No	Yes	No	—[b]	—
	(Pr > F = 0.0114)	(Pr > F = 0.0346)	(Pr > F = 0.3000)	(Pr > F = 0.0362)	(Pr > F = 0.3966)	(Pr > F = 0.0001)	(Pr > F = 0.4323)		—[b]
I	No	—[a]	Yes	No	—[a]	No	Yes	No	
	(Pr > F = 0.2976)		(Pr > F = 0.0001)	(Pr > F = 0.6186)		(Pr > F = 0.0880)	(Pr > F = 0.0003)	(Pr > F = 0.0519)	

[a] Denotes a comparison that was not performed due to insufficient numbers of foragers available from either colony B or E.
[b] Denotes a nestmate-only combination.

Table 3. Symbolic representation of the agonism patterns of *Coptotermes formosanus* colonies

Colony	Current study, theorized markers[a]	Su and Haverty (1991)	
		Their colony labels	Markers
A	● ■ ▲	Not studied	
B	● ■	D and E	○
C	● ▼	B	□
D	● ■	F	○
E	▲ ◆	Not studied	
F	● ■ ◗	Not studied	
G	▼ ◆ ◗	C	□
H	▼ ◆ ❖	A	□
I	■ ❖	Not studied	

[a] Symbols denote kin recognition markers for the colonies. Colonies with a symbol in common are not agonistic.

(1991). This difference in the agonism patterns may be the result of seasonal variance (Clément 1986) in intercolonial agonism for *C. formosanus*, a factor not examined in this study.

The symbols in Table 3 represent potential kin recognition markers for individual colonies. No inference was made about the nature of these colony markers. The markers may be chemical cues, such as exogenous chemical cues, polar cuticular substances, or mandibular gland exudates, areas listed by Su and Haverty (1991) for investigation into potential intercolonial kin recognition cues in *C. formosanus*; or they may represent behavioral differences between the colonies, such as distinct

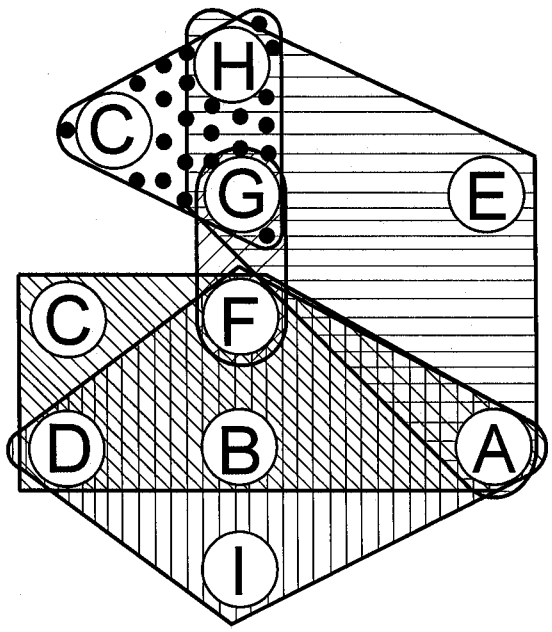

Fig. 1. Graphical representation of the intercolonial agonism patterns among *C. formosanus* colonies. Colonies within the same field are not mutually agonistic, whereas those in separate fields are mutually agonistic.

Table 4. Mean percentage mortality (±SD) for *C. formosanus* laboratory colony agonism assays

Paired colonies[a]	No. replicates	% mortality ± SD	Pr > *F*
B-Lab1 vs. G-Lab2	3	5.00 ± 5.00	0.2561
B-Lab1 vs. B-Lab1 (control)	3	0.00 ± 0.00	—
G-Lab2 vs. G-Lab2 (control)	3	6.67 ± 7.64	—
I-Lab1 vs. G-Lab3	3	16.67 ± 16.07	0.3448
I-Lab1 vs. I-Lab1 (control)	3	5.00 ± 5.00	—
G-Lab3 vs. G-Lab3 (control)	3	10.00 ± 5.00	—
G-Lab1 vs. I-Lab2	3	13.33 ± 5.77	0.0195
G-Lab1 vs. G-Lab1 (control)	2	5.00 ± 7.07	—
I-Lab2 vs. I-Lab2 (control)	2	2.50 ± 3.36	—

[a] Letters refer to field colonies (Table 1) whose alates were paired to form each laboratory colony.

Table 5. Mean percentage mortality (±SD) for *C. formosanus* laboratory colony versus field colony agonism assays

Paired colonies[a]	No. replicates	% Mortality ± SD	Pr > *F*
G-Lab2 vs. D	3	40.00 ± 42.72	0.3268
G-Lab2 vs. G-Lab2 (control)	3	3.33 ± 2.89	—
D vs. D (control)	3	6.67 ± 7.64	—
H-Lab1 vs. D	3	16.67 ± 11.46	0.1133
H-Lab1 vs. H-Lab1 (control)	3	1.67 ± 2.89	—
D vs. D (control)	3	6.67 ± 7.64	—
H-Lab2 vs. D	3	8.33 ± 14.43	0.5108
H-Lab2 vs. H-Lab2 (control)	3	3.33 ± 2.89	—
D vs. D	3	0.00 ± 0.00	—
H-Lab3 vs. B	3	5.00 ± 0.00	0.0001
H-Lab3 vs. H-Lab3 (control)	4	0.00 ± 0.00	—
B vs. B (control)	4	0.00 ± 0.00	—
H-Lab4 vs. B	3	13.33 ± 12.58	0.2100
H-Lab4 vs. H-Lab4 (control)	2	0.00 ± 0.00	—
B vs. B (control)	3	1.67 ± 2.89	—
H-Lab5 vs. C	5	16.00 ± 17.46	0.0745
H-Lab5 vs. H-Lab5 (control)	5	0.00 ± 0.00	—
C vs. C (control)	5	7.00 ± 15.65	—
B-Lab2 vs. H	3	53.33 ± 46.46	0.1588
B-Lab2 vs. B-Lab2 (control)	3	1.67 ± 2.89	—
H vs. H (control)	3	3.33 ± 5.77	—

[a] Letters refer to field colonies (Table 1) whose alates were paired to form each laboratory colony.

greeting behaviors given in a series. In either case, it appears that there may be multiple kin recognition cues for each individual colony of *C. formosanus*. These cues may be all of 1 type or combinations of different types as suggested by the multiple stimulus hypothesis of Su and Haverty (1991; see also Thorne and Haverty 1991). For the colonies studied here, a minimum of 3 markers was needed to distinguish the agonism patterns among the colonies accurately (Table 3). This is in contrast to the 2 markers needed to separate the agonism patterns reported by Su and Haverty (1991) among 5 of the 9 colonies examined here. The increased complexity of these patterns may be caused largely by the increase in the number of colonies examined in the present study.

The results of pairing laboratory colonies suggest that no agonism exists between the exogenously similar, but genetically different, laboratory colonies (Table 4). This would support the hypothesis that exogenous chemical factors, singly or in combination, may be important in *C. formosanus* kin recognition. Similarity in exogenous chemical cues, resulting from similar developmental environments for these colonies, may be the factor limiting agonism between the laboratory colonies examined in this study.

In only 1 of 7 bioassays pairing laboratory with field colonies was a significant difference in mortality found between the non-nestmate treatment and the controls. However, mortality in the non-nestmate treatments was generally higher than in the nestmate controls. This suggests that agonism may have been limited by confusion among the termites. This variation in termite response to non-nestmates could result from a kin recognition system requiring >1 cue for a colony marker. In comparisons of non-nestmate laboratory colonies where exogenous cues should be identical, confusion may still occur from other recognition cues perceived by the termites. Therefore, these data would support inclusion of an exogenous component in the multiple stimulus hypothesis of Su and Haverty 1991, Thorne and Haverty 1991.

An alternative explanation for the reduced agonism between these colonies may be the relative age or size of the colonies, or both. Su and Scheffrahn (1988) suggested that in areas of early *C. formosanus* introduction, colonies merge to reduce intraspecific competition, allowing *C. formosanus* to be more competitive interspecifically to establish a foothold in the new environment. If younger age or small size was the attribute of these newly introduced colonies, allowing them to merge readily, then perhaps the reason for the reduced agonism of the laboratory colonies was a matter of size. The laboratory colonies were small, containing no more than 1,000 individuals, and were completely enclosed in 18.9-liter metal cans, whereas the field colonies contained a minimum of several hundred thousand foragers. Information regarding differences between smaller and larger colony cue composition remains unknown and requires further investigation.

The potential for large field colonies to merge with small laboratory colonies may be more likely than when laboratory colonies of similar size interact. A large colony may find the addition of alien foragers to its work force of more value than losses suffered in an aggressive encounter, even if the large colony won. Thus, large colonies of *C. formosanus* may be more likely to absorb a smaller, and therefore potentially younger, colony than to destroy it in battle.

One argument against this acceptance is the possibility of the smaller colony contributing alates

to the next reproductive swarm, thereby reducing the genetic contribution of the larger colony. Of course, it may be possible for a termite to recognize a non-nestmate and still require another motivational cue to act aggressively on that recognition, as suggested by Su and Haverty (1991), who proposed that recognition cues may differ from aggression stimuli.

It is difficult to see how information on relative colony size could be communicated under our bioassay conditions, where equivalent numbers of workers and soldiers from each colony were paired in a small arena. Preconditioning of these individuals as a result of overall colony age is certainly possible. However, acceptance of an exogenous factor arising from homogenous laboratory rearing conditions as important in reducing agonistic responses is a more parsimonious explanation. An additional complicating factor that remains to be explored in future work with *C. formosanus* is the possibility of seasonal variation in colony agonism, as described by Clément (1986) with temperate *Reticulitermes* spp.

Acknowledgments

We are grateful for the helpful advice and comments of Julian R. Yates III and M. Lee Goff, and the expert technical assistance of Carrie H. M. Tome and Robert J. Oshiro. We also are grateful to Michael I. Haverty and an anonymous reviewer for their helpful comments and suggestions on an early draft of this article. Funding was provided by McIntire Stennis funds for forestry research (Project 906) and USDA–ARS Specific Cooperative Agreements No. 58-6615-9-012 and No. 58-6615-4-037. This is Journal Series No. 4226 of the Hawaii Institute of Tropical Agriculture and Human Resources.

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Received for publication 1 May 1996; accepted 15 November 1996.