Response of *Reticulitermes* spp. (Isoptera: Rhinotermitidae) in Northern California to Baiting with Hexaflumuron with Sentricon Termite Colony Elimination System

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ABSTRACT Colonies of *Reticulitermes* spp. were baited with prototype and commercial Sentricon stations (Dow AgroSciences LLC, Indianapolis, IN) to test the efficacy of hexaflumuron in different concentrations and bait matrices and to document reinvasion of the foraging territories vacated by eliminated colonies. Seven colonies of *Reticulitermes* spp. from two sites were characterized with cuticular hydrocarbon analyses and mark-release-recapture and agonistic behavioral studies. Three colonies were observed as controls and four colonies were baited. When a connection between the bait station and the monitoring station could not be confirmed by mark-release-recapture studies, the results of the baiting were equivocal. The monitoring stations of a colony at our wildland site were devoid of termites 406 d after baiting with one Sentricon station, but became reoccupied with the same species of termites ≈6 mo after baiting. A colony at the residential site was baited with 0.5% hexaflumuron in the Recurit II bait matrix; 60 d later termites were absent from all monitoring stations. These monitoring stations remained unoccupied for ≥18 mo. Foraging *Reticulitermes* spp. appeared in three of the seven monitoring stations 18, 24, and 36 mo after baiting, respectively. Using cuticular hydrocarbon analyses and agonistic behavior studies, we determined that the *Reticulitermes* spp. occupying these monitoring stations were from three different colonies; none were members of the original colony destroyed by baiting. Another colony at the residential site was baited using a noncommercial, experimental bait; 52 d later termites were absent from all monitoring stations. The monitoring stations remained unoccupied for ≥9 mo. A different *Reticulitermes* sp. colony invaded one monitoring station 9 mo after baiting.

KEY WORDS subterranean termites, chitin synthesis inhibitor, termite baits, termite colony elimination, termite colony suppression, termite control

THE USE OF baits for the control of subterranean termites has been a goal for decades (Randall and Doody 1934), with a significant amount of research effort during the past 30 yr (Beard 1974, Esenther and Beal 1974, 1978; French and Robinson 1981; French 1991; Su 1991, 1994; Grace et al. 1995; Forschler and Ryder 1996a, 1996b; Potter 1997; Haagsma and Bean 1998; Su and Scheffrahn 1998). The success of termite bait development rests not only in the knowledge of termite responses to the toxicant but also in an understanding of the biology and ecology of these insects (Traniello and Thorne 1994; Lewis et al. 1998; Getty et al. 1999a, 1999b; Haverty et al. 1999a, 1999b, 2000). Many variables, such as seasonal weather patterns, predation, competition between nearby colonies, size or age of a colony, and the number of alternative food sources available can affect the viability of a termite colony and confound the interpretation of the action of the bait (Forschler and Ryder 1996a, 1996b).

Because of the cryptic lifestyle of subterranean termites, it can be difficult to assess the efficacy of a termite bait. From a research perspective, once a bait is deployed it is imperative that there be a system for observing the effects on termites that does not include using the bait itself for monitoring. Because termites may return to a baited area, a distinction between termites of a previously baited colony and those from neighboring colonies or species of *Reticulitermes* reinvading previously occupied sites must be made to determine whether suppression or elimination has been achieved (Su and Scheffrahn 1996). Active subterranean termite monitoring stations that are known to be connected to a bait station or delivery device become important windows into a colony and a tool for observing the effects of baiting (Su and Scheffrahn 1996, Lewis et al. 1998).

After a colony has been suppressed or eliminated as a result of baiting, identification of colonies invading the baited territory (monitoring stations previously

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occupied) is the final factor in understanding the success of this technology (Getty et al. 1999b, 2000). Distinction of colonies of *Reticulitermes* from northern California can be made via a combination of technologies, including cuticular hydrocarbon analysis, mark-release-recapture studies, and assessment of agonistic behavior between workers of newly discovered foraging groups and laboratory cultures of the baited colony (Haverty and Nelson 1997; Haverty et al. 1999a; Getty et al. 1999b, 2000). Herein we report on assessments of the efficacy of hexaflumuron in the prototype and commercial versions of the Sentricon Termite Colony Elimination System, and a noncommercial, experimental bait with the Sentricon System. Also described is the reoccupation of the foraging area vacated by *Reticulitermes* colonies destroyed by baiting.

Materials and Methods

Study Locations. One wildland location was used to study *Reticulitermes* colonies in an undeveloped setting. This portion of the study was conducted in the Eddy Arboretum in the western portion of the USDA Forest Service, Pacific Southwest Research Station's Institute of Forest Genetics near Placerville, CA. We also used a residential site, the St. Francis of Assisi Church, in Novato, Marin County, CA. The colonies at the residential site were in the immediate vicinity (≈0–4 m from the foundation) of a single-family dwelling that serves as the church rectory. No remedial control with soil termiticides was initiated to terminate the attack on the structure at the Novato site during the course of our study nor had soil termiticides been applied at least since 1990. However, a sand barrier was placed inside the foundation to prevent termites from attacking the structure from this venue (Lewis et al. 1996). Both sites were used previously to study the ecology and behavior of *Reticulitermes* (Haverty and Nelson 1997; Lewis et al. 1998; Getty et al. 1999a, 1999b, 2000; Haverty et al. 1999a, 1999b, 2000).

Bait Delivery Devices and Monitoring Stations. Two types of stations were used during the course of this study: (1) prototype and commercial Sentricon stations (Dow AgroSciences, Indianapolis, IN) were used to deliver a hexaflumuron bait and an experimental bait, and (2) monitoring stations of ABS (acrylonitrile butadiene styrene) plastic pipe (Truitt and White Lumber Company, Berkeley, CA) for observing termite foraging activity (Lewis et al. 1998). At the Institute of Forest Genetics, Sentricon stations were placed around infested wooden stakes or monitoring stations actively used by termites. Sentricon stations and ABS monitoring stations were installed around the perimeter of the structure and along fence lines at the Novato site. Before this study on the impact of baiting *Reticulitermes* spp. with hexaflumuron or the experimental bait, the ABS monitoring stations were used to determine the size and dispersion (Haverty et al. 2000) and the seasonal foraging and feeding behavior (Getty et al. 1999a, Haverty et al. 1999b) of *Reticulitermes* spp. colonies. These same monitoring stations also were used to observe the behavior of *Reticulitermes* spp. colonies after baiting.

Characterization of Colonies. Each month, termites were collected from all actively occupied monitoring stations. Separate laboratory cultures were established for each ABS monitoring station for field-collected foraging termites (Getty et al. 2000). Two hundred workers were removed from each monthly collection for characterization of the cuticular hydrocarbons to determine the phenotype of *Reticulitermes* spp. occupying the ABS monitoring station (Haverty and Nelson 1997).

For this study, we considered a colony to be a group of individuals of the same species that constructs a nest of dispersed galleries and chambers, rears offspring in a cooperative manner, and shares the interconnected gallery system (Wilson 1971, Su and Scheffrahn 1998). Association of foraging groups of *Reticulitermes* spp. in the various monitoring stations as members of the same colony was determined by characterization of the cuticular hydrocarbons (Haverty and Nelson 1997) and by mark-release-recapture (Haverty et al. 2000) and agonistic behavior studies (Haverty et al. 1999a). Monitoring stations containing termites determined to be from the same colony were collectively grouped and labeled to coincide with labels used in Haverty et al. (2000). To avoid confusion, colonies from the Institute of Forest Genetics in Placerville, CA, were given the prefix IFG and those from Novato, Marin County, CA, were given the prefix Marin.

To characterize the size of the foraging population and the foraging territory of specific colonies, all termites from one monitoring station were removed, returned to the laboratory, and fed filter paper impregnated with either 0.1% Nile Blue A (Fisher Scientific, Pittsburgh, PA) or 0.5% Sudan Red 7B (Fisher Scientific) for 14 d, and released into the same monitoring station. At the regularly scheduled site visit (≈14 d later), collections were made from all active ABS monitoring stations and Sentricon stations. Those stations containing marked termites were considered foraging sites of one colony.

Affiliation of foraging groups of *Reticulitermes* spp. in the various monitoring stations after baiting was determined by conducting agonistic bouts among termites from different monitoring stations to confirm inter- and intracolonial and inter- and intraphenotype relationships (Haverty et al. 1999a). Because cultures of termites originally collected from each monitoring station were maintained in the laboratory, agonistic behavior among workers from different and the same monitoring station could be assessed to determine whether a new colony of the same phenotype had displaced the original colony (Getty et al. 1999b, 2000).

Baiting Procedures. We used one of three baits: a prototype Baitube device with 0.1% hexaflumuron, Recruit II termite bait with 0.5% hexaflumuron, or a noncommercial, experimental bait (Dow AgroSciences). Until the summer of 1995, the prototype Baitube devices were used and consisted of a plastic cylinder (16.5 cm long by 3.8 cm diameter) with 72 holes (2 mm diameter) drilled in nine rows of eight holes each around the circumference. The first row of

Table 1. Colonies baited with the Sentricon Termite Colony Elimination System at the Institute of Forest Genetics near Placerville, CA, and at a residential setting in Novato, CA

Location/ Colony[a]	Monitoring stations[a]	Phenotype[b]	Foraging population[c]	Bait[d]	Termites[e]	Days[f]
IFG-1	Yk32	A	73,092–128,597	I	400	—
IFG-2	Yq31 Yq30 Yr33 Sentricon-2	A	40,809–67,284	I	25	≈406
IFG-4	Yr19 Ys19 Yt19	A	Unknown			Not baited
IFG-5	Wg46 Wt46	A	Unknown			Not baited
Marin-1	St18 St25	A′	473,420–491,901	I	15	—
Marin-1[g]	St18 St25	A′	473,420–491,901	II	0	—
Marin-1[h]	St18 St25 St12 Sentricon-4	A′	473,420–491,901	Exp. Bait	0	52
Marin-3	St63 St35 St40 St66 St69 St71 St78 Sentricon-5	A′	71,483–132,106	II	50	58

[a] Colony and monitoring station(s). Institute of Forest Genetics (IFG) colonies are from a location near Placerville, CA. Marin colonies are from Novato in Marin County, CA. Colonies IFG-2, Marin-1 (when baited with an experimental bait), and Marin-3 were connected to the Sentricon station by mark-release-recapture.

[b] Hydrocarbon phenotype as described in Haverty and Nelson (1997). The exact species of *Reticulitermes* has not been determined.

[c] Estimated size of the foraging population based on the Lincoln Index or Weighted Mean Model (Haverty et al. 2000).

[d] I is for first prototype Recruit termite bait (0.1% [AI] hexaflumuron), and II is for Recruit II termite bait (0.5% [AI] hexaflumuron).

[e] Number of termites initially used in the Self-Recruitment procedure.

[f] The number of days until all connected monitoring stations were devoid of termites. For colonies IFG-1 and Marin-1 termites remained in the monitoring stations after baiting, and no connection was ever made between any Sentricon station and the monitoring station(s) occupied by these colonies.

[g] Recruit II termite bait (without termites) was placed in the Sentricon station. Approximately 60 d later, 200 termites were observed in the Baitube, and 90 d later no termites were found in the Sentricon station or any of the Marin-1 stations until March 1997.

[h] Noncommercial, experimental bait (without termites) was placed in this Sentricon station.

holes was positioned 2 cm below the top of the tube and each tube was filled to 1 cm of the top with bait, leaving a void where termites removed from the monitoring devices would be placed according to the Self-Recruitment procedure (Su 1994). The prototype Baitube devices contained a bait matrix consisting of shavings of pine (*Pinus* spp.) or spruce (*Picea* spp.) wood flour (similar to sawdust) that was impregnated with 0.1% hexaflumuron.

Recruit II termite bait became commercially available in the summer of 1995 and consisted of a plastic cylinder (22 cm long by 3.8 cm diameter) with 2.5 by 1.5-cm slots in 12 rows of four slots each around the circumference. The first row of slots was positioned 5.5 cm below the top of the tube and each tube was filled to 4.5 cm of the top with bait matrix, leaving a void where termites removed from the monitoring devices would be placed according to the Self-Recruitment procedure. The Recruit II termite bait contained a bait matrix consisting of rolled, cellulose paper impregnated with 0.5% hexaflumuron. In 1998, a bait containing an experimental active ingredient (Dow AgroSciences) was tested on one colony at the Marin site with the same Baitube device design and matrix as Recruit II termite bait.

Prototype Baitube devices were used to bait two colonies at the Institute of Forest Genetics and one colony at the Novato site. Recruit II termite bait was used to bait two colonies at the Novato site and the experimental bait was used to bait one colony at the Novato site (Table 1).

The Self-Recruitment procedure required the removal of all termites from the infested monitoring devices by tapping them onto a small tray. After adding ≈5–8 ml of water to the cellulose matrix in the Baitube device, termites were poured from the collection tray into the chamber inside the Baitube device and the cap was replaced. This procedure forces

the termites to tunnel through the bait matrix to reestablish contact with previously constructed foraging tunnels or to build new foraging tunnels to establish contact with their colony (Su 1994).

Baiting was initiated only after colonies were characterized, through mark-release-recapture studies, agonistic behavior assessments, cuticular hydrocarbon determinations and wood consumption patterns were established (Haverty and Nelson 1997; Getty et al. 1999a; Haverty et al. 1999a, 1999b). Interconnections among Sentricon stations and ABS monitoring stations were confirmed by the presence of marked termites during the mark-release-recapture process.

Assessment of Bait Efficacy. Before and after baiting, termite activity (presence of termites and wood consumption) was recorded in the ABS monitoring stations as well as in the baited Sentricon stations (Getty et al. 1999a; Haverty et al. 1999b, 2000). Each monitoring station was inspected monthly. Wooden bundles from the monitoring stations were removed and replaced with another preweighed, water-soaked bundle (Getty et al. 1999a, Haverty et al. 1999b).

Presence or absence of termites or termite activity was noted (Lewis et al. 1998). All termites contained within the wooden bundle were tapped onto a tray and the number of termites visually estimated (size classes were as follows: 0 = 0, 1 = 1–100, 2 = 101–300, 3 = 301–1,000, and 4 = >1,000). Termites were then placed in a labeled 14 by 10 by 3.5-cm plastic box provisioned with a damp paper towel (22.8 by 26.0-cm, brown, singlefold, ≥80% recycled paper, James River Corp., Norwalk, CT) and returned to the laboratory to be weighed and placed in culture. The total estimated number of termites at each inspection was determined for each monitoring station (and summed for the colony if more than one monitoring station was occupied) with the midpoint of the size class (0 = 0, 1 = 50, 2 = 200, 3 = 650, and 4 = 5,000), an estimating procedure similar to that used by Haverty et al. (1974) and La Fage et al. (1976).

All pieces of wood in a bundle were returned to the laboratory to determine the amount of wood removed (g/d) and an average wood consumption for the colony calculated (Haverty et al. 1999b). Wood lost in monitoring stations with no termite activity was measured to compare with wood consumption in baited colonies. When termites were no longer present in the ABS monitoring stations and wood removal declined to the level in the control monitoring stations, we considered the colony to have been destroyed.

Results and Discussion

In two instances (colonies IFG-1 and Marin-1), tunneling could be seen in the prototype Baitube devices and small amounts of sawdust were found outside of the prototype Baitube devices and inside the Sentricon station. The number of termites in the prototype Baitube device of colony IFG-1, IFG-2, and Marin-1 declined to zero 1 mo after baiting and this trend continued until the end of the baiting cycle. It was difficult to assess whether this decline was a result of the efficacy of the bait or of the palatability of the bait matrix. *Reticulitermes* spp. head capsules with fungal hyphae were noted in addition to a wet and moldy matrix.

The Recruit II termite bait appeared to have more tunneling and matrix removal than the prototype termite bait. Termites were found in the Baitube devices during subsequent inspections. The cellulose matrix in Recruit II termite bait appeared to have less fungal growth than the prototype wood flour. During some inspections, Baitube devices were removed and the termites tapped onto a tray. Most of the termites present in Baitube devices had tunneled into the center of the foldings of the hexaflumuron-impregnated paper. This folding provided areas for tunneling and placement of soil.

IFG-1 was a medium-sized colony estimated to contain a foraging population of 73,092–128,597 and occupied a single monitoring station (Table 1; Haverty et al. 2000). No connection was documented between the ABS monitoring station (Yk32) and the Sentricon station (Sentricon-1) ≈30 cm away (Fig. 1A). On 5 October 1995, a Baitube device (containing 0.1% hexaflumuron in wood flour) was inserted into the Sentricon-1 station with 400 termites in the Self-Recruitment procedure. On 2 November 1995, some bait matrix appeared to have been removed with some of the matrix scattered inside the Sentricon-1 station. No termites were observed in the Baitube device. Tunneling was seen inside the Baitube device; the 400 termites apparently exited. From 30 November 1995 until the end of the study on 16 December 1996, no termite activity was observed in this baited Sentricon-1 station. Although no connection was ever made between the IFG-1 monitoring station and the Sentricon-1 station, the monitoring station displayed a decline in termites occupying the station from 5 October 1995 (estimated at 5,000 termites) until on 27 March 1996 (estimated at 50 termites; Figs. 1B and 2). This decline was likely a result of the seasonal patterns of activity and feeding (Haverty et al. 1999b) and not the adverse result of the bait on the colony. From 22 May 1996 to 11 December 1996, the number of termites in the monitoring station appeared to be equivalent to those found in 1994 and 1995 (Fig. 2). Wood consumption by the termites in IFG-1 declined slightly in 1996, but this was a general trend observed throughout the site (Fig. 2; Haverty et al. 1999b).

IFG-2 had an estimated foraging population of 40,809–67,284 and occupied three monitoring stations that were a maximum distance of 12.8 m apart (Table 1; Fig. 1A; Haverty et al. 2000). All three of the monitoring stations occupied by IFG-2 usually contained ≈200 termites in each monitoring station on a monthly basis before baiting. During the characterization of this colony, we found blue stained termites in a Sentricon-2 station that was ≈30 cm from the IFG-2 monitoring station where stained termites were first introduced (Yq31; Fig. 1A). On 5 October 1995, a prototype Baitube device was introduced into this colony via the Sentricon-2 station with ≈25 termites in the Self-Recruitment procedure (Table 1). At the first inspection date, 2 November 1995, no termites

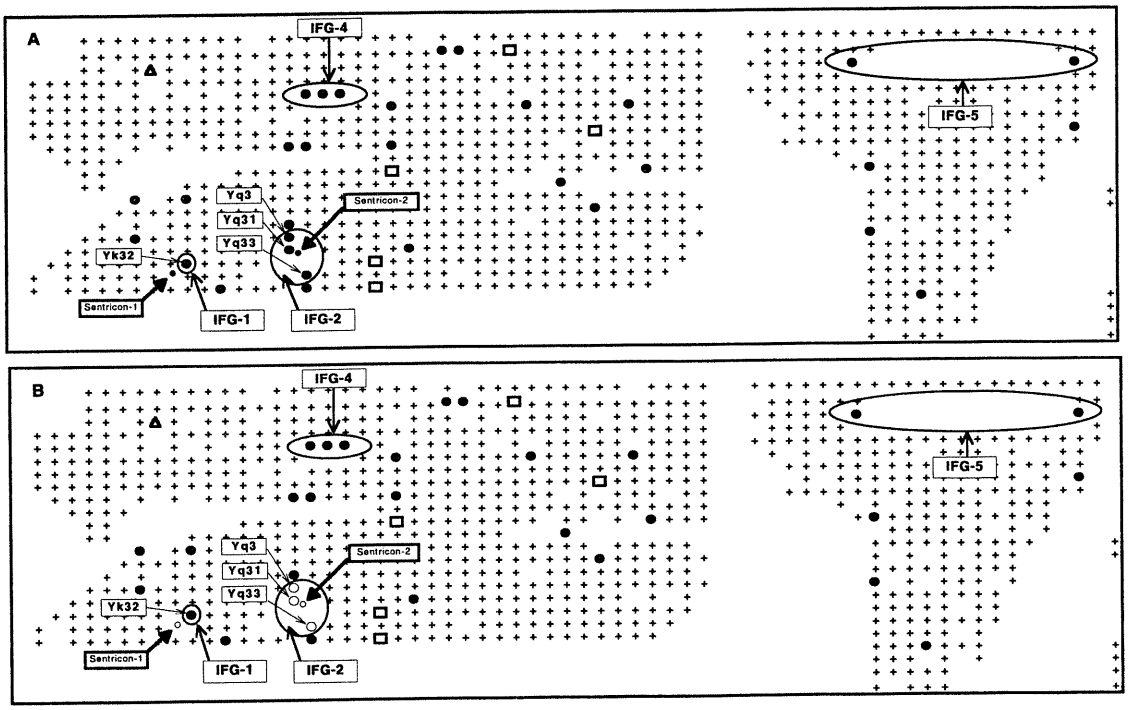


Fig. 1. Western portion of the Institute of Forest Genetics (IFG) site before baiting with hexaflumuron (A) and after baiting with hexaflumuron (B). Solid circles represent ABS monitoring stations occupied by *Reticulitermes* Phenotype A, squares by Phenotype B, and triangles Phenotype C. Wooden stakes are represented by +. Monitoring stations used by a single colony were connected by mark-release-recapture studies, agonistic studies and/or cuticular hydrocarbon analyses and are encircled by large polygons. Empty circles depict monitoring or Sentricon stations devoid of termites. IFG-1 and Sentricon-1 stations were not found to be connected by mark-release-recapture studies.

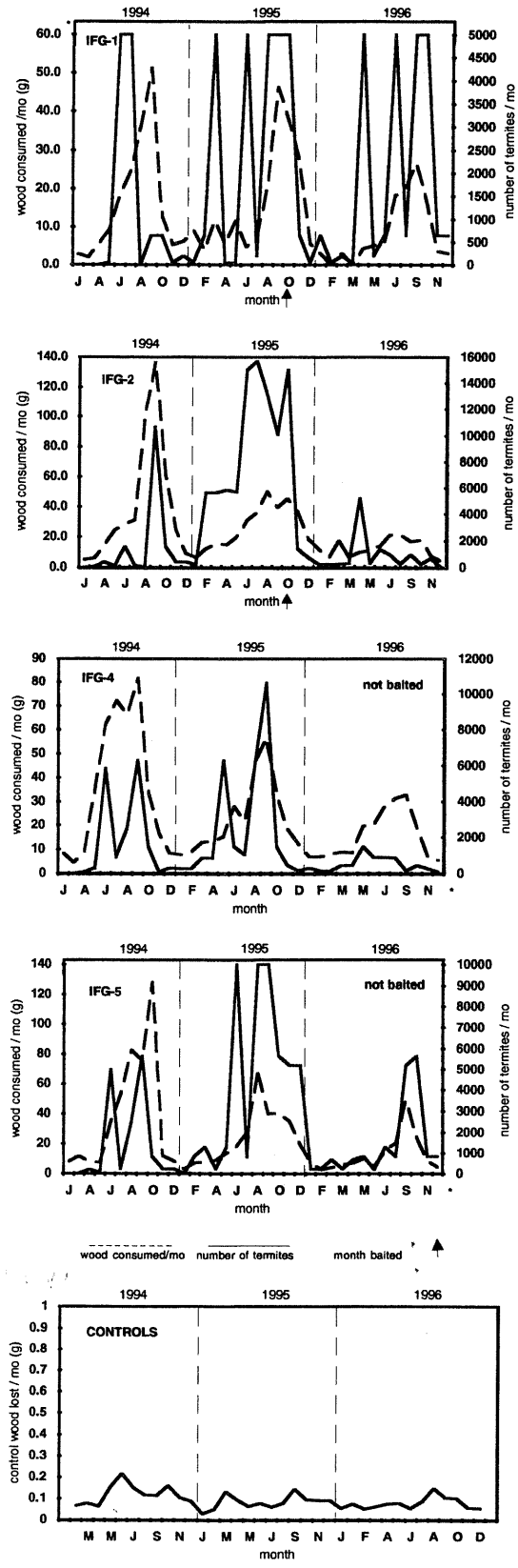
occupied the Sentricon station and all of the IFG-2 monitoring stations showed a decline in numbers of termites. This trend continued until 16 December 1996 (406 d) with no active infestation of any of the IFG-2 monitoring stations or the Sentricon-2 station (Figs. 1B and 2). During the baiting of colony IFG-2, ≈25% of the matrix was removed by termites. Wood consumption by the termites in the IFG-2 colony declined dramatically in 1996 (Fig. 2).

Although not baited, colonies IFG-4 and IFG-5 were monitored for seasonal trends in termite foraging and wood consumption, for purposes of comparison to a baited wildland colony (Figs. 1 and 2). Both colonies had termite numbers following seasonal trends of low numbers in the late fall through early spring and peak numbers from June to October. These trends continued through 1999. Wood consumed by termites in IFG-4 and IFG-5 also followed seasonal trends (Haverty et al. 1999b) and greatly exceeded the weight of wood lost in control monitoring stations (Fig. 2).

From 31 May 1995 to 16 May 1996, Marin-1 comprised two monitoring stations (18 and 25) a maximum distance of 10 m apart and contained a large foraging population estimated to be 473,420–491,901 (Table 1; Fig. 3A; Haverty et al. 2000). During this period, monitoring station 12 was occupied by D phenotype *Reticulitermes* and not part of the Marin-1 A′ phenotype colony (Fig. 3A). Between 22 February 1996 and 16 May 1996, no termites were found occupying monitoring station 12; however, when termites were found in this monitoring station again, on 11 June 1996, they were determined to be A′ phenotype *Reticulitermes* and connected to Marin-1 via mark-release-recapture studies (Table 1; Fig. 3A).

Prototype Baitube devices were tested at the Novato site beginning on 26 September 1995 near Marin-1 (Fig. 3A). After the introduction of dyed termites into a monitoring station (St18) in the Marin-1 colony, no dyed termites were observed in any of the Sentricon stations nearby. On 26 September 1995, we introduced the prototype bait, with 15 worker termites for the Self-Recruitment procedure, into a Sentricon station (Sentricon-3) that was in close proximity to Marin-1 ABS monitoring station 25 (Fig. 3A). Each month thereafter until 4 April 1996, no termites occupied Sentricon-3 and only a small amount of bait matrix was removed. The Marin-1 monitoring stations nearby continued to have an estimated 5,000 plus termites occupying the stations, and wood consumption continued at a normal pace (Fig. 4; Haverty et al. 1999b).

On 4 April 1996, the prototype Baitube device, in Sentricon-3 near the Marin-1 colony, was removed and replaced with a Recruit II termite bait without using any termites for the Self-Recruitment procedure or documenting a connection between any monitor-



ing stations and the Sentricon-3 station (Table 1; Fig. 3A). Termites were not found occupying the Recruit II Baitube device until the 11 June 1996 inspection (67 d later) when ≈100 termites were observed in the Sentricon-3 Baitube device. On the same inspection day, monitoring station 12 was determined to have phenotype A′ *Reticulitermes* and a connection to the Marin-1 colony with mark-release-recapture. An increase in the number of termites between April and June 1996 occupying the Marin-1 monitoring stations was noted as well (Fig. 4). On 9 July 1996, the Baitube device was inspected and ≈50% of the bait matrix had been removed by termites. A new Baitube device was placed in the Sentricon-3 station without termites for the Self-Recruitment procedure. By 10 October 1996, only 12 termites (all soldiers) were seen in the Sentricon-3 station Baitube device and the number of termites (≈100) in the Marin-1 monitoring stations continued to decline (Fig. 4). The termites in the Sentricon-3 station, as well as all three Marin-1 colony monitoring stations, appeared sluggish, had an opaque appearance and many were in a jack-knifed position, the telltale signs of exposure to hexaflumuron (Su 1994). By 16 December 1996, termites were not found in any of the Marin-1 monitoring stations or the Sentricon-3 station (Figs. 3B and 4) and the Baitube device was permanently removed and monitoring devices were replaced in the Sentricon-3 station. Termites were never found again in this Sentricon-3 station subsequent to replacing the Baitube device with monitoring devices.

This Marin-1 colony was the only one that the prototype bait was switched (16 September 1996) midstudy to accommodate the commercially available Recruit II termite bait. It was after this introduction that the Marin-1 population appeared to plummet to zero by 16 December 1996 (Figs. 3B and 4). However, the removal of the Baitube device may have been premature, because >6,200 termites were discovered on 25 March 1997 in all three monitoring stations in Marin-1 (Fig. 4). This trend continued for >15 mo until 13 June 1998 when a bait with an experimental active ingredient was placed in a Sentricon-4 station near monitoring station 12 that was determined to be connected to monitoring station 12 in the Marin-1 colony (Figs. 3A and 4; Getty et al. 2000). Upon inspection 18 d later on 2 July 1998, ≈40% of the experimental bait matrix had been consumed by termites and >400 termites were found occupying the Baitube device (Fig. 4). The Marin-1 monitoring stations and Sentricon-4 station were devoid of termites an additional 34 d later, at the 5 August 1998 inspection, and remained as such until 17 May 1999 (Figs. 3B and 4). On 17 May 1999, monitoring station 12 was found occupied by termites. Using cuticular hydrocarbon analysis, we determined

Fig. 2. Estimates of monthly wood consumption (dashed line) and the number of termites (solid line) in monitoring station(s) for two baited colonies (IFG-1 and IFG-2) and for two unbaited colonies (IFG-4 and IFG-5) at the Institute of Forest Genetics. Controls depict wood lost per month in monitoring stations with no termites present.

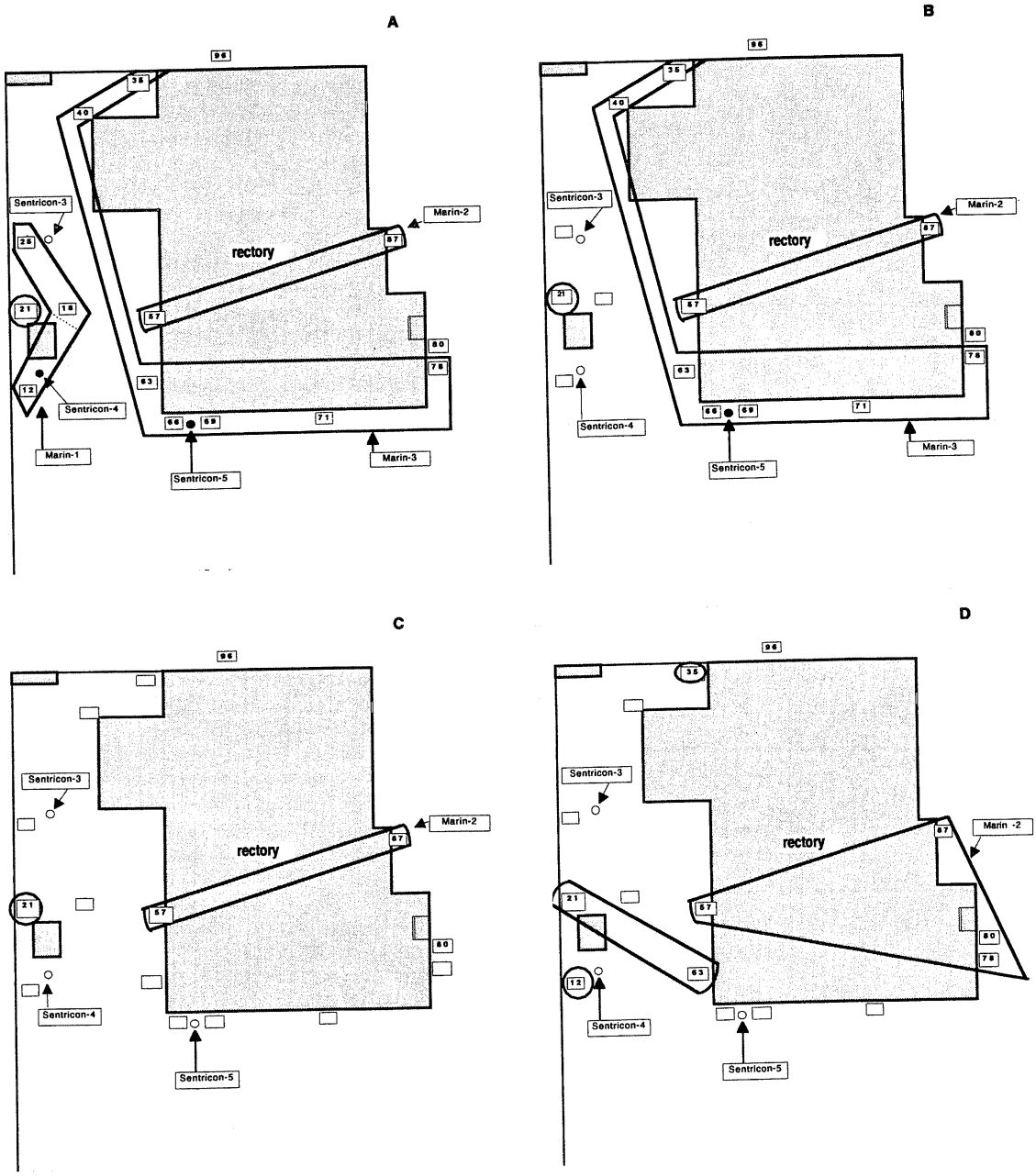


Fig. 3. Novato site. Rectangles with numbers represent ABS monitoring stations with termites present; rectangles without numbers represent monitoring stations devoid of termites. Monitoring stations subtended by a polygon are connected and occupied by termites from the same colony. (A) Monitoring station 12 and Sentricon-4 station were found to be connected to Marin-1 after this colony was baited with prototype 0.1% hexaflumuron bait but before baiting with 0.5% hexaflumuron in Recruit II termite bait. Monitoring stations 21 and 96 were occupied by phenotype D *Reticulitermes*, whereas all others were occupied by phenotype A′; (B) Fifty-two days after baiting Sentricon-4 near Marin-1 with Recruit II termite bait with an experimental AI. Monitoring stations 12, 18, and 25 and Sentricon-3 were devoid of termites. Monitoring stations 21 and 96 were occupied by phenotype D *Reticulitermes*, whereas all others were occupied by phenotype A′ *Reticulitermes*; (C) Fifty-eight days after baiting Sentricon-5 in Marin-3 with Recruit II termite bait with 0.5% hexaflumuron. Monitoring stations 35, 40, 63, 66, 69, 71, and 78 and Sentricon-3 were devoid of termites. Monitoring stations 21 and 96 were occupied by phenotype D *Reticulitermes*, and monitoring stations 57 and 87 were occupied by phenotype A′ *Reticulitermes*; (D) Unbaited colonies invaded the territory of Marin-3 3 yr after it was destroyed by baiting. Monitoring stations and Sentricon-5 circle were devoid of termites. Monitoring stations 12, 21, 35, 63, and 96 were occupied by phenotype D *Reticulitermes*, whereas monitoring stations 57, 78, 80, and 87 were occupied by phenotype A′ *Reticulitermes*.

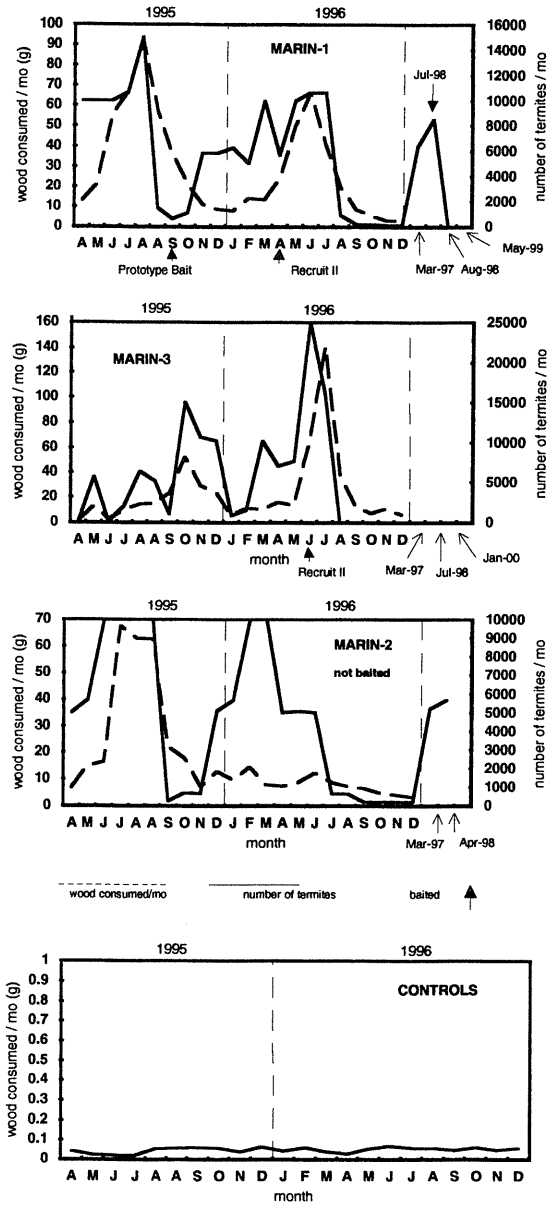


Fig. 4. Estimates of monthly wood consumption (dashed line) and the number of termites (solid line) for two baited colonies (Marin-1 and Marin-3) and for one unbaited phenotype A′ colony (Marin-2) at the Novato site. Controls depict wood lost per month in monitoring stations with no termites.

these termites to be phenotype D *Reticulitermes*, and therefore from a different colony (Fig. 3D).

On 16 March 1996, we initiated another series of mark-release-recapture studies at the Novato site. Blue-stained workers were released in a monitoring station (66; Fig. 3A). At the 2-wk recapture, blue-stained termites were collected in six other monitoring stations (35, 40, 63, 69, 71, and 78); marked foragers were found on three sides of the structure (Table 1; Fig. 3A). Blue-stained termites were also found in one Sentricon station (Sentricon-5) that was ≈30 cm from the monitoring station where blue termites were originally released (Fig. 3A; Haverty et al. 2000). From this we concluded that this colony (Marin-3) occupied a total of seven monitoring stations and Sentricon-5, and comprised a foraging population estimated at 71,483–132,106 (Haverty et al. 2000). The distance between the two monitoring stations that were furthest apart (35 and 78) was 25.3 m (Haverty et al. 2000; Fig. 3B). Agonistic behavior studies corroborated our contention that all seven Marin-3 monitoring stations and the single Sentricon-5 station were all used by the same colony (Haverty et al. 1999a, Getty et al. 2000). Cuticular hydrocarbon analyses confirmed all stations were phenotype A′ (Haverty and Nelson 1997, Haverty et al. 2000).

On 16 June 1996, Sentricon-5 was baited with Recruit II termite bait with ≈50 termites for the Self-Recruitment procedure (Table 1; Figs. 3A and 4). During the inspection on 9 July 1996, termites in all stations in the Marin-3 colony showed signs of a hexaflumuron-exposed and suppressed colony (workers with a bloated and distorted abdomen with irregular margins and opaque or ivory white in color rather than translucent). During this 23-d period, termites removed ≈50% of the bait matrix. Although termites were present in all Marin-3 monitoring stations, including the Sentricon-5 station, population numbers were approximately half that of the previous month (Fig. 4). By 7 August 1996, 2 mo after baiting with Recruit II termite bait, termites removed ≈40% of the bait matrix and all monitoring stations in the Marin-3 colony and the Sentricon-5 station were devoid of foraging termites (Fig. 3C). This continued until 8 January 1998.

On 8 January 1998, ≈18 mo after baiting, termites were found occupying one monitoring station (78) previously occupied by the Marin-3 colony (Fig. 3D). By characterizing the cuticular hydrocarbons of this group of termites (Haverty and Nelson 1997) we determined that monitoring station 78 was occupied by phenotype A′ *Reticulitermes*, the same phenotype as the baited Marin-3 colony. However, because termites were collected and maintained in the laboratory from each monitoring station before baiting the Marin-3 colony, agonistic behavior studies were conducted pairing the newly discovered phenotype A′ termites with termites from each of the monitoring station cultures in the laboratory previously occupied by the baited A′ phenotype Marin-3 colony (Getty et al. 1999b, 2000). The newly discovered termites responded aggressively with the laboratory cultures of all of the former Marin-3 colony (Getty et al. 1999b, 2000). Agonistic bioassays were conducted between the termites now occupying monitoring station 78 and termites in a colony in nearby monitoring stations (57, 87, and 80; Fig. 3D). There was no aggression displayed, and all termites survived after 24 h in all 18 tests (Getty et al. 2000). From these studies we concluded that this monitoring station (78) was occupied by a different colony of *Reticulitermes* than the one

using it before baiting, thus a different colony had moved into the Marin-3 territory from monitoring stations nearby (Fig. 3D).

On 27 March 1998, another monitoring station (35) previously occupied by Marin-3 was found occupied by termites (Fig. 3D). This monitoring station was farthest from the other reinvaded monitoring station (78). Using cuticular hydrocarbon analysis, we determined these termites to be phenotype D *Reticulitermes* and, therefore, from a different colony.

On 30 March 1999, a third monitoring station (63) in the territory formerly occupied by Marin-3, was found occupied by termites (Fig. 3D). With agonistic bouts, pairing the newly discovered termites and termites from each of the laboratory cultures from monitoring stations previously occupied by Marin-3, the newly discovered termites responded aggressively with the laboratory termites in all tests (Getty et al. 2000). The newly discovered termites were then paired with termites from monitoring stations in the vicinity and from existing laboratory cultures. These termites did not react aggressively with any of the termites from one particular phenotype D monitoring station (St21) ≈10 m away. Hydrocarbon analysis confirmed that the newly discovered termites were, in fact, phenotype D *Reticulitermes*, as well. For a third time, we determined that a different termite colony (now a total of three separate colonies) moved into the territory formerly occupied by Marin-3 (Fig. 3D).

The seasonal foraging trends and wood consumption rates of both baited and nonbaited colonies were empirically compared. Foraging activity of *Reticulitermes* (numbers of termites collected and wood consumption) was observed at the two sites on a monthly basis (Haverty et al. 1999b; Figs. 2 and 4). We found that the estimated number of termites was low in the late fall through the early spring and peaked from June to October at the wildland site and peaked from June to November or December at the residential site. Wood consumption by *Reticulitermes* followed similar trends at both sites. Wood consumption was minimal during the winter, increased slightly in the spring and early summer, peaked in the summer and early fall, then declined in the late fall. These data and subsequent collections of termites after 1996 explained the drop in termite numbers and wood consumption seen in the Marin-2 colony from July to December 1996 (Fig. 4). Observations and collections of termites of the Marin-2 colony were made regularly. As expected, this colony increased in the number of foragers in the late spring and continued to have large numbers of termites present as late as October 1997. By June 1999 the Marin-2 colony appeared to have abandoned one station but was foraging into the Marin-3 territory (Figs. 3D and 4).

In summary, we followed the trends in foraging and feeding of four colonies of phenotype A *Reticulitermes* at our wildland site near Placerville, CA, and three colonies of phenotype A′ *Reticulitermes* at our residential site in Novato, CA, for 3 and 2 yr, respectively (Haverty et al. 1999b). For research purposes, it is extremely important to associate the termites in a bait delivery device (such as a Sentricon station) with the means (monitoring stations) for observing the baited colony with some sort of mark-release-recapture scheme. We baited two phenotype A colonies with prototype Baitube devices with 0.1% hexaflumuron. The colony (IFG-2) that was known to be foraging at the Sentricon station was active for 14 mo, but showed signs of suppression during that time. We did not find termites in the monitoring stations occupied by this colony 15 mo after baiting. This trend continued until the stations were inspected again on 7 October 1997. Thus, we infer that the colony was destroyed by baiting with the prototype 0.1% hexaflumuron bait.

At the Novato site, we baited one colony (Marin-1) with a prototype Baitube device without a known connection between the monitoring stations and the nearby Sentricon station. This colony remained active during this baiting period. Replacement of the prototype Baitube devices with a Recruit II termite bait Baitube device resulted in what appeared to be the destruction of the colony after 6 mo; however, this large colony may only have been suppressed. A second colony (Marin-3) at Novato was baited with Recruit II termite bait and all evidence of termite activity ceased within 58 d. We feel that this colony, composed of 71,483–132,106 foragers, was successfully eradicated. The territory (monitoring stations) occupied by the eradicated colony was subsequently invaded by three other colonies of *Reticulitermes* over a 29-mo period. This observation emphasizes the need for continual monitoring of the structure and the termite susceptible perimeter after successful elimination of one or more colonies of *Reticulitermes*. This is necessary to determine whether reinvasion has occurred, and whether additional or supplemental baiting or other remedial measures are necessary.

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