

AN ABSTRACT OF THE THESIS OF

Lorna C. Youngs for the degree of Doctor of Philosophy in Entomology
presented on December 14, 1983.

Title: Ant Predators of the Western Spruce Budworm (*Choristoneura*
occidentalis Freeman): Species Composition and Patterns of
Occurrence in Eastern Oregon and Western Montana

Abstract approved: Redacted for privacy
Robert W. Campbell

The identity and distribution of ant species preying on the western spruce budworm (*Choristoneura occidentalis* Freeman) was investigated in eastern Oregon and western Montana. A sticky trap was developed to index ant foraging activity in the canopy by intercepting ants falling from the tree as they traveled between canopy and ground. For all common ant species, trap catches were highly correlated with the average number of ants moving up the tree bole. Thus, traps indexed both species composition and density of ants foraging in the canopy.

Ant species preying on pupae of the budworm were investigated on 2 sites in eastern Oregon in 1981, and 4 sites in eastern Oregon and 6 sites in western Montana in 1982. Predation was observed by checking pupae stocked on trees actively foraged by ants.

The following ant species and numbers were collected as they fed on budworm pupae: *Camponotus modoc* Wheeler, 160; *C. laevigatus* (Smith), 53; *C. vicinus* Mayr, 48; *Formica obscuripes* Forel, 174; *F. podzolica* Francoeur, 43; *F. accreta* Francoeur, 32; *F. neorufibarbis* Emery 12; *F. lasioides* Emery, 1; *F. sp. (microgyna group)*, 1. *Camponotus* species dominated the Oregon collections, and *F. obscuripes* dominated the collections in Montana.

The distribution of canopy foraging ant species was studied on 24 sites in Montana and 24 sites in Oregon. Sites were selected along a moisture-temperature gradient indexed by vegetational composition

(habitat type). Ant foraging activity was measured using sticky traps, and several site and stand variables were correlated with the abundance of ants collected at each site.

Nine species of Formica and Camponotus were collected in Montana and 11 species in Oregon. Four species were common in both states--C. modoc, C. vicinus, F. neorufibarbis, and F. podzolica. In addition, C. herculeanus (L.) was common in Montana and F. accreta was common in Oregon. The distribution of these species varied among habitat types and between states and the abundance of each was correlated with a different set of environmental variables. At least one ant species predaceous on the western spruce budworm was common in each habitat type in either state. Across almost all habitat types, each common species was more abundant in stands where average canopy coverage was less than 90%. The distribution of ant foragers in the canopy on each plot was highly aggregated in all species in either state.

Ant Predators of the Western Spruce Budworm
(Choristoneura occidentalis Freeman):
Species Composition and Patterns of Occurrence
in Eastern Oregon and Western Montana

by

Lorna C. Youngs

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed December 14, 1983

Commencement June 1984

APPROVED:

Redacted for privacy

Courtesy Professor of Entomology in charge of major

Redacted for privacy

Head of department of Entomology

Redacted for privacy

Dean of Graduate School

Date thesis is presented December 14, 1983

Typed by Marta Eriksen for Lorna C. Youngs

ACKNOWLEDGEMENTS

I thank Marie Dillon, Steve Shattuck and JoAnne Vrilakas for their valuable assistance.

Work leading to these publications was funded by the USDA Forest Service, Canada/United States Spruce Budworms Program, Washington D.C.

Table of Contents

Introduction	1
Chapter I. Predaceous ants in the biological control of insect pests of North American Forests	3
Introduction	4
Research on the role of ant predation in forest protection	4
History of the use of ants in biological control of forest pests	6
Possible disadvantages to using ants in biological control	8
Conclusion	9
Chapter II. Sampling Canopy Foraging Ants with Sticky Traps	12
Introduction	13
Methods	13
Results	16
Discussion and Conclusion	20
Chapter III. Ants preying on pupae of the western spruce budworm <u>Choristoneura occidentalis</u> Freeman in eastern Oregon and western Montana	23
Introduction	24
Materials and Methods	25
Results and Discussion	27
Conclusion	34
Chapter IV. The distribution of ant predators of the western spruce budworm, <u>Choristoneura occidentalis</u> Freeman in eastern Oregon and western Montana	35
Introduction	36
Site Description - Montana	37
Site Description - Oregon	41
Materials and Methods	44
Results - Montana	48
Results - Oregon	58
Discussion	68
Conclusion	77
Bibliography	79

List of Figures

<u>Figure</u>		<u>Page</u>
IV.1	Plot scores on the first two axes of the DCA ordination of tree and understory vegetation for plots 1-24 in Montana in 1982	49
IV.2	Mean number of ants of the five common species in each habitat type in Montana in 1982	52
IV.3	Plot scores on the first two axes of the DCA ordination of tree and understory vegetation for plots 1-24 in Oregon in 1982	59
IV.4	Mean number of ants of the five common species in each habitat type in Oregon in 1982	62

List of Tables

<u>Table</u>	<u>Page</u>
II.1 Percent of total ants caught within 0.5 m of the tree trunk on radial boards in each direction in Montana and Oregon in 1981	17
II.2 Correlation between sticky trap catches and average number of ants collected on tree trunks per 3 minute count in Oregon and Idaho in 1981	17
II.3 Correlations between sample periods of total ants (by species) caught on traps beneath each of 96 sample trees in Montana and 96 sample trees in Oregon in 1982	19
II.4 Values of the slope (b), intercept (a) and coefficient of determination (R^2) from Taylor's power law analysis of plot means and variances of ants collected from traps on 24 plots in Montana and 24 plots in Oregon in 1982	19
III.1 Plot totals by species of ants caught on sticky traps during 3 days and feeding on budworm during 14, 10-min observations in 1981 in Oregon	28
III.2 Plot and species totals of ants collected on sticky traps under 10 study trees per plot, over 3 days in Oregon and Montana in 1982	30
III.3 Plot and species totals of ants preying on western spruce budworm pupae during 24, 5-min observations on 10 trees per plot in Oregon and Montana in 1982	31
IV.1 Site characteristics for habitat types in Montana	40
IV.2 Site characteristics for habitat types in Oregon	42
IV.3 Habitat variables significantly correlated with plot scores on the first two DCA ordination axes of tree and understory vegetation in Montana in 1982	50
IV.4 Habitat variables significantly correlated with the abundance of each common <u>Camponotus</u> over all plots and sample periods, and on only those plots where the species was collected in Montana in 1982	54
IV.5 χ^2 test of differences in ant abundance between plots with open and closed canopies in Montana in 1982	56

<u>Table</u>	<u>Page</u>
IV.6 Habitat variables significantly correlated with the abundance of each common <u>Formica</u> over all plots and sample periods, and on only those plots where the species was collected in Montana in 1982	57
IV.7 Habitat variables significantly correlated with plot scores on the first two DCA ordination axes of tree and understory vegetation in Oregon in 1982	60
IV.8 Habitat variables significantly correlated with the abundance of each common <u>Camponotus</u> over all plots and sample periods, and on only those plots where the species was collected in Oregon in 1982	64
IV.9 Chi ² test of differences in ant abundance between plots with open and closed canopies in Oregon in 1982	65
IV.10 Habitat variables significantly correlated with the abundance of each common <u>Formica</u> over all plots and sample periods, and on only those plots where the species was collected in Oregon in 1982	67

ANT PREDATORS OF THE WESTERN SPRUCE BUDWORM
(CHORISTONEURA OCCIDENTALIS FREEMAN):
SPECIES COMPOSITION AND PATTERNS OF OCCURRENCE IN
EASTERN OREGON AND WESTERN MONTANA

INTRODUCTION

The role of ant predators in the biological control of forest pests has a long history of research in Europe, but has only recently come to the attention of North American workers. European research has focused exclusively on the thatching ants of the Formica rufa group (Cotti 1963, Adlung 1966). North American research has been sporadic, devoted either to documenting ant predation on a forest defoliator (e.g. Jennings 1971) or to efforts to transplant or import species of the Formica rufa group (Bradley 1972, Finnegan 1971, 1975).

There have been few attempts to identify the complex of native ant species preying on a forest defoliator and to determine the effects of that predation on the population dynamics of the pest. One such study was initiated by Campbell and Torgersen (1982) to determine the role of ant predation in the generation survival of the western spruce budworm (Choristoneura occidentalis Freeman). They found that ant predation was a major source of budworm mortality in the late larval and pupal stages (Campbell et al. 1983).

The present study is designed to identify the ant species complex preying on budworm in several sites in eastern Oregon and western Montana, and to determine how these species are distributed over a range of environmental conditions inhabited by the budworm.

A comprehensive review of North American research on ant predators of forest insect pests is given in Chapter I. The advantages and disadvantages of the use of ants as biological control agents in coniferous forests is discussed and approaches for further research are suggested.

The development of a sticky trap used to index ant foraging activity in the canopy of conifers is detailed in Chapter II. The within-stand pattern of distribution of foraging ants is also discussed.

In Chapter III, the results of investigations on the identity of ant species preying on budworm pupae are presented. The relative importance of each species is discussed in relation to the range of sites on which each was encountered.

The distribution of ant predators of the budworm over a range of environmental conditions is discussed in Chapter IV. The common species are identified and their abundance correlated with several site and stand variables on 24 plots in eastern Oregon and 24 plots in western Montana.

Chapter 1. Predaceous Ants in the
Biological Control of Insect Pests
of North American Forests

by

LORNA C. YOUNGS

Introduction

Ants are common and usually ignored members of forest communities, yet their activities affect forests in many ways. Their nesting in soil aids soil aeration, movement of soil particles to the surface, accumulation and breakdown of organic matter, and nutrient recycling (Petal 1978). Ants influence vegetation patterns by dispersing seed while foraging, and by creating favorable or unfavorable microhabitats for plant growth near ant mounds. Ant foraging, whether for plant or animal material, can affect both the population dynamics and the distribution of species commonly included in the ants' diet. Although ants feed on a wide range of organic material, my discussion is confined to those ant species that habitually prey on other insects--species that can play an important role in the biological control of forest insect pests.

The development of sociality has enabled ants to interact with their environment in ways unavailable to solitary insects. Group foraging and food sharing supply ant colonies with sufficient resources to support large populations, which in turn, through division of labor, permit the simultaneous performance of all the tasks a solitary insect usually performs sequentially. Ants can modify the microhabitat at the nest site, thus reducing losses of the vulnerable brood stage to environmental stress. The longevity of ant queens and the presence of supplementary reproductives, in many species, confers a kind of immortality on ant colonies. Ant colonies are long-term residents of forest stands.

Research on the Role of Ant Predation in Forest Protection

Research on ant predation on forest pests has been conducted in Europe for well over 100 years (Cotti 1963). This research has concentrated almost exclusively on the mound-building species of the Formica rufa group, commonly called red wood ants. This group of species has been singled out because the workers are large and aggressive, colony populations frequently reach the hundreds of

thousands, a wide variety of prey is taken, and colony activity can extend up to 200 days per year in favorable climates (Finnegan 1974). A comprehensive review of the usefulness of ants in European forest protection can be found in Adlung (1966).

Until recently, predaceous ants have received little attention from North American forest entomologists. A few investigators have encountered species of both Formica and Camponotus feeding on the larvae or pupae of defoliating caterpillars and sawflies, but have not quantified the effects of ant predation on forest pests (Silver 1960, Ilnitzky and McLeod 1965, Bradley and Hinks 1968, Allen et al. 1970, Jennings 1971, Otvos 1977).

Research in the western United States on the population dynamics of the western spruce budworm has revealed an important role for predaceous ants (Campbell and Torgersen 1982, Campbell et al. 1983). Using exclusion techniques, the investigators measured the predation rates of insectivorous birds, predaceous ants (both Camponotus spp. and Formica spp.), and both groups on budworm larvae and pupae across a range of budworm densities. At low budworm densities, budworm numbers were 10- to 15-fold greater on trees protected from ant and bird predation, compared to trees accessible to both predator groups. At high budworm densities, protected trees had twice as many budworm as accessible trees. Either birds or ants caused similar budworm mortality in the absence of the other group, and predation by either or both groups was the major source of mortality to the budworm in the late larval and pupal stages (Campbell et al. 1983).

The work of Campbell and Torgersen quantifies the effect of ant predation on budworm survival and thus verifies the earlier investigation of Bain (1974). He found a high rate of budworm larval predation by both Formica obscuripes Forel and F. criniventris Wheeler although he did not quantify the effect of ant predation on budworm survival. The conclusions of Campbell et al. (1983) on the importance of ant predation are contrary to those of Markin (1979), who examined the number of budworm larvae and pupae and the amount of defoliation on trees where ants were excluded and on trees routinely foraged by ants. Except at very high ant densities, he found no significant

differences between trees, in budworm numbers or defoliation. Because predation by birds was not prevented in his experiments, the compensatory mortality from bird predation demonstrated by Campbell et al. (1983) may have masked differences in budworm mortality between ant-free and ant-foraged trees.

History of the Use of Ants in Biological Control of Forest Pests

European efforts to use ants in biological control of forest pests have concentrated on augmenting native species of the F. rufa group. Considerable research has been devoted to methods of quantifying the minimum number of colonies per hectare necessary to promote forest protection and on methods of mass rearing, transplantation, and protection of key ant species (Gosswald 1951). Using the criteria of large aggressive workers, large colony size, colonial nest formation, and multiple queens per colony, researchers have selected F. polychteta (Foerster) as the primary candidate for augmentation (Cotti 1963). Another species of the F. rufa group, F. lugubris Zetterstedt, has been augmented to a lesser extent, primarily in alpine forests where F. polychteta is less common and possibly less successful (Pavan 1960).

In North America, researchers have closely followed European techniques in their attempts to use ants in biological control of forest pests. In the early 1950's, colonies of three Formica species, F. fusca L., F. subnuda Emery, and F. integroides Emery, were transplanted in New Brunswick forests to assess their effects on the spruce budworm, C. fumiferana (Clemens) (Morris 1963). The colonies did not become established, and the experiments were not repeated.

Finnegan (1974), in Quebec, has been a strong supporter of using ants in biological control. Using the European criteria for potentially effective ant species, he (1971) surveyed the indigenous ant fauna of Quebec and concluded that none possessed the necessary characteristics for augmentation programs like those in Europe. Therefore, Finnegan (1975) imported F. lugubris from Italy and successfully established colonies in two sites in Quebec.

Subsequently, Finnegan (1978) found up to 20% less defoliation by C. fumiferana on trees near F. lugubris mounds compared to distant trees. McNeil et al. (1978) studied the seasonal predatory activity of F. lugubris and found that C. fumiferana was the most common prey of this ant during peak budworm abundance.

Transplantation of indigenous ant species was attempted later. Formica obscuripes colonies were successfully moved from Manitoba into Quebec (Finnegan 1977). Previous work in Manitoba had shown that colonies of F. obscuripes could be transplanted from one part of a stand to another (Bradley 1972, 1973).

Attempts to transplant indigenous Formica species in the United States have not been successful. Wilkinson et al. (1980) moved F. integra Nylander colonies from Georgia into Florida slash pine plantations. Competition between F. integra and a local carpenter ant C. abdominalis floridanus (Buckley) resulted in the destruction of the Formica colonies. The investigators concluded that because C. abdominalis floridanus dominated the stand and is also predaceous, its potential in biological control should be investigated.

How much forest protection is afforded by ants is still a subject of controversy. Numerous accounts have been published in Europe of red wood ants feeding heavily on defoliating caterpillars and sawflies (for example, Adlung 1966, Petal 1978), but many studies lack data on the effects of ant predation on pest populations. Some work in England, in hardwood forests, showed a significant reduction in wintermoth larvae and their damage, on trees foraged on by red wood ants (Skinner and Whittaker 1981). Red wood ants were also effective in reducing populations of pine-defoliating caterpillars in southern Sweden (Wellenstein 1980). Studies frequently document the number of insects captured by ant colonies (Horstman 1970, 1972) or the amount of defoliation occurring at various distances from ant mounds (Laine and Niemela 1980).

Possible Disadvantages to Using Ants in Biological Control

Those that question the value of ant predation in the control of forest pests do not deny that ants eat large numbers of pest species. They point out, however, that ants do not feed exclusively on pests. Beneficial insects such as parasitic wasps and flies are included in their diet (Adlung 1966). The impact of ant activity on other beneficial insects is likely to be localized near ant colonies, however, and would depend on the extent that the trees in the area are foraged on by ants, and the extent that ant activity interferes with other beneficial insects.

The tendency for ant colonies to be clumped rather than randomly distributed has supplied critics with an additional objection to their usefulness in biological control of forest pests. Ants establish foraging territories near their nests, and they are frequently faithful to their foraging routes from year to year (Rosengren 1971, David and Wood 1980). Thus, the scope of their effectiveness may be limited to areas near the nest, producing patches of trees free from insect damage, a so-called "green island" effect (Laine and Niemela 1980). European augmentation programs have been primarily aimed at reducing the degree of patchiness in ant distributions.

The association of many predaceous ants with tree-feeding homopterans has added to the controversy over the benefits of ant predation on forest pests. Honeydew, primarily from aphids, is probably the most widely exploited carbohydrate source of many ant species. The association between ants and aphids has led to various degrees of mutualism (Way 1963). Aphids that allow ants to solicit honeydew frequently increase honeydew production when tended by ants. In turn, ants may provide some degree of protection for the aphids against natural enemies (Flanders 1951).

Aphids tended by ants are often able to maintain higher populations on trees foraged on by ants (Bradley and Hinks 1968, McNeil et al. 1977). High aphid numbers may adversely affect tree growth. Dixon (1971a, b) found a reduction of sycamore sapling growth and a reduction of root growth in lime samplings associated with high

aphid populations. He did not, however, link aphid numbers to the degree of ant tending.

The association of ants with aphids may indirectly benefit forest protection. Honeydew is a fairly stable food source that ant colonies can exploit in periods of low arthropod abundance. Other insect predator/prey systems demonstrate that honeydew provides an alternate food source that sustains predator populations during low prey density (Price et al. 1980).

The effects of aphids cannot be easily evaluated, because detrimental effects on tree growth depend not only on aphid density, but also on time of feeding and the part of the tree under attack. The relation between ants and aphids can be complex. Aphids themselves may become ant prey (Ayre 1959, Horstman 1970, Skinner 1980b) or one aphid species may be protected and another consumed (Skinner and Whittaker 1981). Ant predation on other insects may also be a direct result of aphid protection. Forest tent caterpillars were attacked by Formica and Camponotus species when larvae ventured too near ant-tended aphid colonies (Green and Sullivan 1950).

The habit of some carpenter ant species of nesting in both living and dead wood may limit the potential use of those species in biological control. Sanders (1964) found three Camponotus species infesting live balsam fir and spruce in New Brunswick and reported an attack rate in New England and the Maritime Provinces of between 0.5 and 4.0% in balsam fir and between 0.5 and 1.0% in spruce. Thus, the degree to which tree-infesting carpenter ant species prey on forest pests would need careful study before their use in biological control could be recommended.

Conclusion

Do predaceous ants have a future in biological control of North American forest pests? European research and augmentation efforts have been extensive, yet even there the verdict is not in. Campbell and Torgersen have shown, for the western spruce budworm, that ant predation is a major mortality factor; this is one of the few

instances in North America where the effect of ant predation on the population of a forest insect has been studied in depth. Although McNeil et al. evaluated the predatory activity of the introduced ant species, F. lugubris, very little is known about the native ant species inhabiting North American forests. The work with western spruce budworm shows that research directed toward quantifying the effects of native ant predation clearly could yield fruitful results.

What approach should we take to investigate the potential use of ants in forest protection? Finnegan (1974) has advocated the European approach of colony transplantation and the importation of Formica rufa species. The silviculture practiced in European forests is different from that practiced--or, often, not practiced--in North American forests. Centuries of manipulation have created intensely managed European stands, where the augmentation of ant populations by colony transplant or mass releases of laboratory-reared queens is possible. North American forests, especially western forests, are frequently unmanaged, inaccessible, and represent an extremely variable environment. Finding a single Formica species comparable to F. polyctena in Europe that can be successfully established over such a wide range of conditions is unlikely.

We need much more information about the ant species native to North American forests, their habitat requirements, their geographic distribution, and--most important--the degree to which they prey on forest insect pests. From the limited information available for this review, both Formica and Camponotus apparently contain predaceous species that may have potential for biological control. Many of these species, especially the boreal Camponotus species, are found over a range of forest conditions and their distribution could be extended by augmentation programs. Perhaps a complex of ant species would provide more effective control of forest pests than a single dominant species, and different complexes may be more successful in controlling pests that are widely distributed, such as the spruce budworm. Perhaps also, silvicultural manipulations--such as those that open the stand or create more woody debris for nesting sites--can augment ant

populations without costly colony transplantation. But all of these possibilities remain mere speculation until more research is done.

Chapter II. Sampling Canopy Foraging Ants with Sticky Traps

by

Lorna C. Youngs

and

Robert W. Campbell

Introduction

Sticky traps have been used extensively to index insect populations, either by passively intercepting insects as they walk, fly or fall onto the trap, or by actively attracting them with color, shape or olfactory cues (Southwood 1978). In this paper we describe a passive sticky trap used to index ant foraging activity in the canopy of conifers. The trap was developed in the course of investigations of ant predators of the western spruce budworm.

We observed that ants frequently fell from the bole, limbs and foliage of conifers as they moved about the tree. Thus, we developed a sticky trap that intercepted falling ants. We conducted a series of experiments to determine the placement of traps that would consistently yield the largest catch, the relation between trap catch and the rate of movement of ants from the ground into the tree canopy, and the relation between trap catch and physical characteristics of the tree. We then used the traps to determine distribution and abundance of ants foraging in the canopy of conifers in several western sites.

Methods

Trap Placement

In 1981, we conducted trials on 2 plots, one in western Montana near Salmon Lake and the other in eastern Oregon ca. 24 k S.E. of Union. On the Montana plot, we selected 15 open-grown Douglas-firs (Pseudotsuga menziesii var. glauca [Beissn.] Franco) ranging in height from 6.7-18.6 m and in crown radius from 1.5-3.0 m. On the Oregon plot, we selected 10 open-grown trees, 5 Douglas-firs and 5 grand firs (Abies grandis [Dougl.] Lindl.), ranging in height from 8.8-25.5 m and in crown radius from 1.7-3.3 m.

We placed 8 (2.5 x 15.2 cm) boards in a radial pattern beneath each tree. The boards were oriented along compass lines, and each board was marked with its compass direction. Boards were nailed to

surveyor's stakes which were driven into the ground, suspending the boards ca. 0.25 m from the ground and ca. 0.15 m from the tree bole. The surveyor's stakes were banded with Tanglefoot to prevent ants from moving from the ground onto the upper surface of the board. All boards extended ca 0.5 m beyond the crown radius. The boards were marked in 0.25 m increments and coated with Tanglefoot.

In each trial, boards were left in place for 1 week. We conducted a single trial in Montana (June 10-17) and 3 trials in Oregon (June 26 - July 2, August 1-11 and September 4-11). At the end of each trial we counted all ants caught in each 0.25 m linear increment of each board. For each tree, we totaled the number of ants caught in each 0.25 m increment from the tree bole and converted that number to a percent of the total catch. We then determined the mean number of ants caught on boards in each direction across all trees in each trial.

Trap Description

We constructed the traps from sheets of 0.6 cm plywood (0.3 x 0.6 m) with 0.3 m strips of 2.5 x 5.0 cm stock nailed to the underside of each end. Two 0.6 m surveyor's stakes were nailed to the ends of the trap to support the trap surface horizontally above the ground. We placed the traps ca 0.25 m from the tree bole and pushed the stakes in the ground until the upper surface was ca. 0.5 m above ground. Sheets of butcher paper were tacked to the trap upper surface and coated with Tanglefoot. At the end of each trial, the paper was covered with a layer of clear plastic wrap to facilitate removal.

Comparisons of Trap Catches with Bole Counts

A series of trials was conducted in 1981 on 2 plots near Union in eastern Oregon, and on 3 plots near McCall in northcentral Idaho. On each plot, we selected both open-grown trees and trees that were part of an interlaced cluster. All trees were either Douglas-fir or grand fir, and were foraged on by ants. We selected 10 trees in each of the

Idaho plots and 33 and 29 trees on the 2 Oregon plots for a total of 92 trees. The following information was recorded for each tree: species, height, d.b.h., average crown radius and the height to the lower crown.

During each trial, 3 traps were placed at the base of each sample tree and left in place for 3 days. In the same time period, 3 min collections were made throughout the day of ants moving up the tree bole into the foliage. We banded each tree bole ca 1.5 m from the ground with surveyor's tape, divided the circumference into thirds, and collected ants crossing each circumference third for 1 min, to insure a representative sample of ant activity on all sides of the tree. Observations were made on each tree once every 1 or 2 hours, depending on the number of trees in the trial and the time required to make a complete circuit. Several trials were required to survey all 92 trees and the number of bole observations varied between trials. The mean number of ants collected per observation period per tree was used in correlation analyses with trap catches. We also correlated trap catches with tree variables to determine if tree dimensions affected trap catches.

Sampling Ant Activity in the Tree Canopy

In 1982, we used sticky traps to sample ant foraging activity in the canopy of conifers on 24 sites in eastern Oregon and 24 sites in western Montana (Chapter IV). On each site we measured ant activity for a 3 day period on 4 trees randomly selected from within a 0.1 ha circular plot. We sampled ants 3 times in Montana (on July 7-12, August 5-13, and August 16-19) and 2 times in Oregon (on July 9-13 and July 29-August 7). During the second sample period in Oregon, we delayed sampling 8 plots until August 17-19.

The number of ants of each species caught on sticky traps was recorded during each sample period. For all species combined and for the 6 common species, totals for each tree were used to test for correlations between sample periods. Plot means and variances per tree were calculated for each ant species for each sampling period.

Taylor's power law (Taylor 1961) was used to determine the mean-variance relation for each species. Taylor's power law is given by: $\hat{S} = a\bar{x}^b$, where the coefficients are estimated by regressing the log of the variance on the log of the mean.

A linear regression model was fitted to data for each common species, in each sample period and for all sample periods combined, in both states. We used an F test to determine if regression parameters calculated for each sample period differed significantly ($P < 0.05$) from those calculated for all sample periods combined.

Results

Trap Placement

In all 4 trials, 43-68% of the ants were collected within 0.5 m of the tree bole (mean % caught: Montana - 67.8 ± 19.4 , Oregon trial 1 - 43.4 ± 18.9 , Oregon trial 2 - 43.8 ± 21.7 and Oregon trial 3 - 54.2 ± 16.6). Thus, regardless of tree size, the area close to the tree bole consistently intercepted a large proportion of falling ants. On average, more ants were caught close to the tree bole on the east side of the tree and differences among the percent caught in each direction were significant for all 4 trials (Table II.1). We observed, however, that when more than one species was present on tree boles, species tended to avoid contact by traveling up different sides of the tree. We also observed that ants changed the side of the bole most heavily traveled as the angle of the sun changed during the day. For these reasons, traps were placed on all sides of the tree to insure a representative sample of all ant species throughout the trap period. We used 3 traps per tree, placed on the west, northeast and southeast sides.

Comparisons of Trap Catches with Bole Counts

Correlations across all plots, between the mean number of ants moving up the bole and 3 day trap catches were highly significant for all

Table II.1 Percent of total ants caught within 0.5 m of the tree trunk on radial boards in each direction in Montana and Oregon in 1981.^{/a}

Trial	Direction								Chi ²
	N	NE	E	SE	S	SW	W	NW	
Montana (n=15)	9	20	25	15	17	6	5	3	35.2
Oregon - Trial 1	8	12	13	24	18	9	10	6	19.5
(n=10) Trial 2	10	28	28	9	10	6	3	6	54.5
Trial 3	14	22	24	9	11	8	5	7	27.7

^{/a} Significant differences ($P < 0.01$) among directions in each trial

Table II.2. Correlation between sticky trap catches and average number of ants collected on tree trunks per 3 minute count in Oregon and Idaho in 1981.

Species	Number of trees	Correlation Coefficient
All ants	92	.79
<u>Camponotus modoc</u>	71	.67
<u>C. vicinus</u>	68	.74
<u>C. laevigatus</u>	17	.80
<u>Formica accreta</u>	78	.68
<u>F. podzolica</u>	79	.69
<u>F. neorufibarbis</u>	35	.85

ants combined and for the 6 commonly collected species (Table II.2). The remaining species were collected on too few trees for meaningful analysis. No significant correlations were found between trap catches and tree dimensions for either all species combined or for any of the 6 common species. Thus, because the major source of variation in trap catch was the density of the ant traffic on the tree bole, traps can be used to index ant foraging activity without adjustments for tree characteristics.

Sampling Ant Activity in the Tree Canopy

Correlations between the number of ants caught at each sample period varied greatly among species (Table II.3). Only 1 species, Camponotus modoc Wheeler, was consistently collected on the same trees over all sample periods in either state. Formica accreta Francoeur numbers were fairly highly correlated between sample periods, but collections in Montana were too few for comparisons between states. In Montana the greatest variation for most species occurred between the numbers collected in the early July sample and in the early August sample, although there were generally high correlations between tree totals for the second and third samples (both in August). The 2 samples in Oregon were collected about the same time of year as the first 2 samples in Montana, however, for C. vicinus Mayr and F. podzolica Francoeur, correlations between Oregon samples 1 and 2 were much higher than between Montana samples 1 and 2. Numbers of ants caught declined from the first to the second sample in both states. The decline continued to a lesser extent in Montana in the third sample period.

Despite the variation in abundance per tree between sample periods, the dispersion pattern indexed by Taylor's mean-variance model remained relatively stable for most species (Table II.4). There were no significant differences ($P < 0.05$) between the regression models developed for each sample period and the model of all periods combined for any common species in either state. Four out of 6 species were common in both states. Differences between state models

Table II.3. Correlations between sample periods of total ants (by species) caught on traps beneath each of 96 sample trees in Montana and 96 sample trees in Oregon, in 1982.

Ant Species	Montana Sample Periods			Oregon Sample Periods 1-2
	1-2	2-3	1-3	
<u>Camponotus modoc</u>	.94	.97	.83	.81
<u>C. herculeanus</u>	.55	.90	.74	---
<u>C. vicinus</u>	.07	.88	.03	.52
<u>Formica accreta</u>	---	---	---	.75
<u>F. neorufibarbis</u>	.21	.70	.16	.17
<u>F. podzolica</u>	.38	.66	.46	.71

Table II.4. Values of the slope (b), intercept (a) and coefficient of determination (R^2) from Taylor's power law analysis of plot means and variances of ants collected on 24 plots in Montana and 24 plots in Oregon in 1982.

	Montana			Oregon			Montana and Oregon/ ^a		
	a	b	r^2	a	b	r^2	a	b	r^2
<u>Camponotus modoc</u>	3.22	1.99	0.97	1.98	1.89	0.92			
<u>C. herculeaus</u>	3.14	1.87	0.97	--	--	--			
<u>C. vicinus</u>	3.13	1.83	0.99	1.39	1.93	0.89			
<u>Formica accreta</u>	--	--	--	2.45	1.96	0.96			
<u>F. neorufibarbis</u>	2.52	1.72	0.94	2.88	1.83	0.98	2.70	1.81	0.96
<u>F. podzolica</u>	2.69	1.86	0.97	2.22	1.82	0.90	2.54	1.86	0.95

^a data from both states pooled if no significant difference ($P < .05$) between state regressions

were significant for 2 species, Camponotus modoc and C. vicinus (Table II.4), although there was no significant difference between the slopes of the regression lines of the state models for C. modoc.

Discussion and Conclusion

A major problem in measuring ant foraging activity is the tendency for forager density to vary with time of day and temperature. Thus comparisons between areas are hampered by the need to make either simultaneous measurements or to calibrate activity by temperature or time. Our sticky traps can be used to index foraging activity on several trees and in several areas simultaneously. Once traps are in place, the application of sticky coated paper to the trap surface requires relatively little time. Traps can be used to index changes in foraging activity over time and can be correlated with changes in temperature.

The disadvantages of sticky traps are discussed by Southwood (1978), who stresses the need for some measure of trap efficiency. Correlations between trap catches and average ant movement up tree boles showed that the traps were effective indicators of the density of ant foragers on a tree. Even at very low densities, traps detected all the species caught on tree boles. We were unable to determine a specific catch rate for each species because our collections from the tree boles were limited to daylight hours. Since some species forage at night as well as day, our tree bole counts may not be a totally representative sample of average ant movement into the tree canopy for each species. We did find some differences in catch rates between species, although the differences were not large.

Our field trials in 1982 revealed that timing of sampling is important in determining the intensity of forager activity in the tree canopy, because numbers caught change with time. Post and Jeanne (1982) also found considerable change among several canopy foraging ant species in the numbers caught on baits when sampled at weekly intervals over a period of 8 months. They also found differences among species in their foraging patterns over time. Thus, depending

on the objectives of the investigators, several sample periods may be required to completely identify the species complex foraging in the canopy of a stand. Frequent sampling may also be required to determine changing patterns of tree use by foraging ants as indicated by the low correlations among sample periods for some species (Table II.3).

Timing of sampling does not appear to be critical in determining the pattern of dispersion over a 0.1 ha plot, as indexed by the parameter b in the Taylor mean-variance model. Taylor (1965) and Taylor et al. (1978) consider b a measure of aggregation that is relatively stable for a species, where values greater than 1.0 indicate an aggregated distribution. The values of b are greater than 1.0 for all common ant species collected in both states (Table II.4), indicating a high degree of aggregation in forager activity across the range of forager species, forager densities, and environmental conditions encountered in our studies.

There is remarkably little difference among species in the parameter b , even between states. This uniformly high degree of aggregation of ant foragers of all species may reflect the limited availability of suitable nesting sites in many forest stands, hence a patchy distribution of ant colonies. Although environmental conditions were fairly uniform on the plots in this study, the plots were small (0.1 ha) and may have intersected portions of foraging territories of colonies not located on the plots.

Aggregation of both ant colonies and foragers in the tree canopy is reported for other species of Formica (Sudd et al. 1977, Skinner 1980a). Bernstein and Gobbel (1979) consider that the pattern of soil insolation exerts a major influence on the dispersion of ant colonies. They found that colonies of ants from a range of genera tend to aggregate in higher elevations where favorable temperature conditions can be limited by slope, aspect and canopy cover.

Aggregated patterns of ant foraging have been found in relatively uniform environments. Ant species formed a mosaic of foraging territories in Ghanaian cocoa plantations and many trees were unoccupied (Majer 1976). Reilly and Sterling (1983) also found

relatively high values for the b parameter of Taylor's model for the red imported fire ant, Solenopsis invicta Buren foraging in cotton fields. In these environments, where suitably warm nesting sites are more abundant, aggregated patterns of foraging activity may be due to a patchy distribution of food together with the ability of ants to recruit nestmates to new food sources, thus quickly increasing forager density in that area.

The highly aggregated dispersion pattern of all the common ant species collected in Oregon and Montana indicate that a large number of trees must be sampled in a given area to obtain a precise estimate of the mean number of foragers that fall onto sticky traps per tree.

Chapter III. Ants Preying on Pupae of
the Western Spruce Budworm,
Choristoneura occidentalis Freeman,
in Eastern Oregon and Western Montana

by

Lorna C. Youngs

and

Robert W. Campbell

Introduction

In 1979, a study of the natural-enemy complex of the western spruce budworm suggested that predation by ants may be an important factor in budworm population dynamics (Campbell and Torgersen 1982). At one site in northcentral Washington, Camponotus vicinus, C. laevigatus (Smith), and Formica haemorrhoidalis Emery were observed eating budworm pupae.

Ant predation on Choristoneura occidentalis and C. fumiferana has been observed by other researchers. Mathers (1932) in British Columbia and Thomson (1957) in Ontario considered ants important budworm predators, although they did not identify the species involved. The investigation of ant predation on budworm has focused on the genus Formica. F. obscuripes and F. criniventris were identified as the major ant predators of the western spruce budworm in Montana (Bain 1974). Markin (1979) listed F. obscuripes, F. subnuda, F. podzolica, and F. argentea Wheeler as possible predators of the western spruce budworm in Idaho.

In eastern North America, efforts have been made to transplant Formica species that may prove valuable budworm predators. Colonies of F. fusca, F. subnuda, and F. integroides were moved to New Brunswick in the early 1950's, but failed to establish (Morris 1963). A European red wood ant, F. lugubris, was successfully introduced into Quebec (Finnegan 1975) from Italy and has been observed preying on C. fumiferana (Finnegan 1978; McNeil et al. 1978).

As possible budworm predators, ants in the genus Camponotus have received less attention than Formica. Sanders (1964) recorded C. novaeboracensis (Fitch) carrying a Choristoneura fumiferana larva, in eastern Canada. Silver (1960) observed many Camponotus vicinus attacking Choristoneura occidentalis larvae in British Columbia. Markin found significantly lower C. occidentalis pupal densities on trees with large forager populations of Camponotus herculeanus (L.).

In 1981, we began a 2-year study in eastern Oregon and western Montana to identify ant species preying on western spruce budworm and to rank the relative importance of the individual species. We

investigated whether the species complex preying on budworm or the predation activity of individual species varied geographically. We identified 3 Camponotus and 6 Formica species predaceous on budworm pupae, and found considerable variation among sites in ant species composition and predation rates of individual species.

Materials and Methods

1981 Trials

The experiments were conducted on 2 sites on Frazier Mountain in eastern Oregon, in the Union Ranger District of the Wallowa-Whitman National Forest. Both sites had fairly open stands of Douglas-fir and grand fir with mixtures of ponderosa pine (Pinus ponderosa Laws.), lodgepole pine (Pinus contorta Dougl.), and Engelmann spruce (Picea engelmannii Parry). Both sites had been selectively harvested for overstory trees. Douglas-fir was more common on 1 site (Raven); grand fir dominated the second site (Frazier).

Twelve open-grown trees ranging from 8-18 m in height (avg. 15.5) were selected: 6 grand fir on Frazier and 6 Douglas-fir on Raven. The criteria for selection were abundant ant activity in the foliage and branches easily observable from the ground. We tried to select trees foraged on by the range of ant species on the site.

To increase the likelihood of observing ant predation on budworm pupae and of determining the relative importance of each observed species as budworm predators, trees with foraging ant populations were stocked with budworm pupae concentrated on a few branches. Predation rates recorded on the study trees should not be considered to represent of the average predation rates for the plot. Twigs bearing pupae were collected from nearby populations and wired to lower crown branch tips of study trees. Each tree was stocked with 30 pupae concentrated on 4 branches. The pupae on each tree were examined for 10 min every 1.5 h from 0730 h to 1800 h. Observations on Raven were made 1 and 3 days after placement of pupae. Frazier was observed the second and fourth day. Each pupae not removed was thus observed 14

times. Observations were terminated after the fourth day; by that time 70-75% of the pupae were missing. All ants feeding on budworm pupae were collected for later identification.

To determine the ant species foraging on the study trees, ants falling from the trunk and foliage were caught on Tanglefoot-coated boards. Three boards (0.6 x 0.3 m) were placed around the trunk of each tree, and supported by surveyor's stakes. In an earlier study, we found that ants frequently fall from the trunk and foliage while moving up and down the tree; the rate of falling is proportional to the density of traffic on the trunk (Chapter II). Thus the catch on sticky traps is a reasonable index of both the species composition and the density of ants foraging in the canopy. Sticky traps were placed under each tree at the end of the pupal observation period and left for 5 days in 1981 and 3 days in 1982.

1982 Trials

The experiments were expanded to 10 sites, 4 in Oregon and 6 in western Montana. The Oregon sites included Raven and Frazier, another site (Lower Raven) on Frazier Mountain with stand characteristics similar to Raven, and a site (Starkey) on the Starkey Experiment Forest also in the Willowa-Whitman National Forest. The Starkey site, in a stand with no previous history of logging, was dominated by grand fir mixed with Douglas-fir and ponderosa pine.

In Montana, two sites (Lubrecht 1 and Lubrecht 2) were in the Lubrecht Experimental Forest, 25 miles east of Missoula in stands dominated by Douglas-fir mixed with ponderosa pine and western larch (*Larix occidentalis* Nutt.). The Lubrecht 1 site had been selectively logged for overstory trees; the Lubrecht 2 site was along an abandoned road cut. Three sites were on Champion International Paper lands, two near Salmon Lake (Cozy Corners and Camp Utmost) and the third (Arkansas Creek) near Potomac. Both the Cozy Corners and Camp Utmost sites were in stands heavily logged for overstory trees with mixed Douglas-fir, ponderosa pine, and lodgepole pine. The Arkansas Creek site was mixed Douglas-fir, lodgepole pine, ponderosa pine, and

western larch. The final Montana site (Archibald) was near Seeley Lake in the Seeley Lake Ranger District of the Lolo National Forest in a mixed stand of Douglas-fir, subalpine fir (Abies lasiocarpa (Hook.) Nutt.), ponderosa pine, lodgepole pine, Engelmann spruce, and western larch.

The experimental procedure was slightly modified in 1982. Ten Douglas-firs were selected on each plot and stocked with 20 pupae, 5 per branch. Pupae on each tree were observed for 5 min on hourly schedules for 3 days after placement. Observations were made 8 h per day, and the schedule was adjusted to cover the period between 0700 h and 2100 h at least once. Each pupa that was not removed was thus observed 24 times.

Voucher specimens were identified by David Smith, U.S. National Museum, Beltsville, Maryland. The remaining ants were identified by Steven Shattuck, Department of Entomology, Oregon State University, Corvallis, Oregon. All specimens are at the Forestry Science Laboratory, Corvallis, Oregon.

Results and Discussion

Because of differences in experimental design, 1981 and 1982 results are presented separately. In 1981, 8 ant species were collected from sticky traps under study trees; 7 species preyed on budworm (Table III.1). Camponotus vicinus and Formica accreta Francoeur were the dominant budworm predators on the Raven plot; C. modoc dominated the Frazier plot. Differences in predation rate among species was not correlated with their abundance: F. podzolica was the most commonly encountered ant, but was captured feeding on budworm proportionally less often than C. modoc (ratio of total budworm predators to sticky-trap totals: C. modoc, 0.10; F. podzolica, 0.01). Species also differed in predation rates from tree to tree; the differences were not correlated with density of the species on the tree.

The sticky-trap catches for the 10 plots in the 1982 trials are given in Table III.2. Twelve species foraged on the 100 study trees,

Table III.1. Plot totals by species of ants caught on sticky traps during 3 days and feeding on budworm during 14, 10-min. observations in 1981 in Oregon.

Plot	Camponotus			Formica				
	<u>vicinus</u>	<u>modoc</u>	<u>laevigatus</u>	<u>accreta</u>	<u>podzolica</u>	<u>neurufibarbis</u>	<u>lasioides</u>	<u>rasilis</u>
Raven								
Sticky trap	306	104	3	436	625	--	3	14
Budworm predator	12	--	1	10	4	--	--	--
Frazier								
Sticky trap	55	74	--	174	237	169	26	--
Budworm predator	1	17	2	--	3	2	1	--

an average of seven species in the Oregon plots and 5 species in the Montana plots. C. vicinus, F. podzolica and, to a lesser extent, C. modoc were common on most plots. The remaining species were abundant in only 1 of the 2 states.

The number of ants preying on budworm pupae in the 1982 trials are given in Table III.3. C. modoc, C. laevigatus and F. obscuripes are the dominant predators with ratios of total budworm predators to sticky-trap totals across all plots of 0.15, 3.5, and 0.12, respectively. C. laevigatus is difficult to catch on sticky traps: thus, its foraging density in the study trees is underestimated. We have observed few C. laevigatus on our research plots, however; it is an active budworm predator, but not an abundant species. C. vicinus, although present on all plots, was not as active a predator as the other Camponotus species. The ratio of total budworm predators to sticky-trap totals across all plots for C. vicinus was 0.07. Although lower than the ratios for the other Camponotus species, it is still greater than the ratios of the remaining Formica species (range 0.005-0.02). Thus the Camponotus species and F. obscuripes represented 85% of all ants observed preying on budworm pupae. The Camponotus species dominated the Oregon predator complex, but Formica species--especially F. obscuripes--dominated the Montana plots.

We eliminated F. lasioides Emery and F. sp. (microgyna group) from consideration as potential budworm predators because they were encountered feeding on budworm only once.

The dominance of F. obscuripes among the Formica species preying on western spruce budworm is not unexpected. It is the sole representative of the F. rufa species group, members of which have been extensively used in European forest protection because of the aggressiveness of the workers and the large populations found in most colonies. F. obscuripes has been considered as a possible biological control agent in Canadian forests; it has been transplanted to protect young pine stands in Manitoba (Bradley 1972) and introduced into Quebec (Finnegan 1977). The remaining Formica species we encountered are from the F. fusca group; they are relatively docile, commonly enslaved by other Formica. Ayre and Hitchon (1968) compared the

Table III.2. Plot and species totals of ants collected on sticky traps under 10 study trees per plot, over 3 days in 1982 in Oregon and Montana.

Species	Plot										
	Oregon				Montana						
	Raven	Frazer	Lower Raven	Starkey	Archibald	Cozy Corners	Camp Utmost	Arkansas Cr.	Lubrecht 1	Lubrecht 2	Total
<u>Camponotus</u>											
<u>vicinus</u>	153	67	154	72	1	11	34	6	11	8	517
<u>modoc</u>	33	97	13	81	--	--	--	576	133	1	934
<u>laevigatus</u>	2	8	3	1	--	--	--	--	--	--	14
<u>herculaneus</u>	--	--	--	--	--	--	--	--	17	--	17
<u>Formica</u>											
<u>accreta</u>	495	139	527	452	2	2	--	--	3	--	1620
<u>podzolica</u>	593	99	323	336	241	--	50	1736	100	14	3492
<u>neorufibarbis</u>	2	305	--	86	14	--	--	--	--	--	407
<u>obscuripes</u>	--	--	--	--	343	606	265	--	19	189	1422
<u>sp. (microgyna group)</u>	--	--	--	--	--	157	--	--	18	--	175
<u>lasioides</u>	--	15	5	--	--	--	--	--	--	--	20
<u>hewitti</u>	--	--	--	--	--	30	--	270	113	--	413
<u>argentea</u>	12	--	8	--	--	--	--	--	--	--	20
Total	1290	730	1033	1028	601	806	349	2588	414	212	9051

Table III.3. Plot and species totals of ants preying on western spruce budworm pupae during 24, 5-min observations on 10 trees per plot in 1982 in Oregon and Montana.

Species	Plot										Total
	Oregon				Montana						
	Raven	Frazer	Lower Raven	Starkey	Archibald	Cozy Corners	Camp Utmost	Arkansas Cr.	Lubrecht 1	Lubrecht 2	
<u>Camponotus</u>											
<u>vicinus</u>	7	4	10	4	--	--	6	--	4	--	35
<u>modoc</u>	66	68	--	--	--	--	--	2	7	--	143
<u>laevigatus</u>	36	8	2	1	--	--	3	--	--	--	50
<u>Formica</u>											
<u>accreta</u>	1	1	5	2	13	--	--	--	--	--	22
<u>podzolica</u>	1	1	2	--	19	--	10	1	1	1	36
<u>neorufibarbis</u>	--	8	--	--	2	--	--	--	--	--	10
<u>obscuripes</u>	--	--	--	--	64	16	2	--	26	66	174
<u>sp. (microgyna group)</u>	--	--	--	--	--	1	--	--	--	--	1
Total	111	90	19	7	98	17	21	3	38	67	471

predatory activity of F. obscuripes, F. fusca, and F. lasioides on eastern tent caterpillars (Malacosoma americana (F.)) and found that F. obscuripes removed the most caterpillars and F. lasioides the least.

The high predation activity among all the Camponotus species (except for C. herculeanus, found on only 1 tree), especially C. modoc, is evidence of a largely unexpected role of this genus as a natural enemy of forest defoliators. Studies focused on foraging activity at the nest or along trails have not found large numbers of insects transported to the nest (Sanders 1964, 1972; Fowler and Roberts 1980). Ayre (1963b) suggests that because Camponotus workers are unable to ingest solid particles larger than 100µm, prey may be consumed in the field and transported in the crop as soluble protein and haemolymph. Ayre (1963a) conducted laboratory feeding studies on C. herculeanus; 98% of all live insects offered to the workers were killed and at least partially consumed. Observations of Camponotus foraging activity at the site of the prey have given clearer evidence of the predatory behavior of this genus. Green and Sullivan (1950) counted 1,800 forest tent caterpillar larvae (M. disstria Hbn.) removed by C. novaeboracensis workers, and Allen et al. (1970) listed C. novaeboracensis among the most common predators of the jack pine budworm (Choristoneura pinus Freeman). Otvos (1977) observed Camponotus herculeanus feeding on blackheaded budworm (Accleris variana (Fern.)) larvae.

In the 1982 trials, as in 1981, predation rates of a given species differed among plots. Once again this variation was not related to the abundance of the species; individual tree totals of ants feeding on budworm were not correlated with sticky-trap catches for any species. We concluded that factors other than ant density affect the predation rate of a given species.

We investigated the possibility that tree size may influence the total catch of budworm predators, using only 1982 data. Although all the trees were Douglas-fir, they ranged in height from 1.5 m-25.0 m (avg. 10.38 m). Tree sizes were not evenly distributed among plots. Archibald, Camp Utmost, and Lubrecht 2 had relatively smaller trees (average sample tree height, 4.58 m, 5.15 m, and 3.71 m, respectively)

and Frazier and Starkey had taller trees (average sample tree height, 17.48 m and 16.25 m, respectively). When the total numbers of ants preying on budworm for each species are correlated with tree dimensions (height, dbh, crown volume) only F. accreta and F. podzolica numbers were significantly ($P < .05$) negatively correlated with tree size. All other species displayed a slightly negative, but insignificant, correlation between tree size and total budworm predators. This tendency toward a negative correlation may be a dilution effect of larger tree size; more foliage area must be searched before the stocked pupae are encountered. Differences in tree size, however, are poorly correlated with differences in predation rates of the dominant budworm predators, the Camponotus species and F. obscuripes.

Campbell et al. (1983) found an increasing rate of budworm survival from ant predation with increasing budworm density in several western sites. Although their data were from randomly selected trees and our trees were chosen with the bias of high ant activity, the same phenomenon may explain our observed differences in species predation rates among plots. High budworm densities undoubtedly reduce the attractiveness of stocked pupae to ants, because of abundant alternative food. Late larval densities of the budworm per square meter of foliage were estimated on all sites but Lower Raven, Lubrecht 1, and Lubrecht 2. Because all ant species were not present on the seven remaining plots, we were unable to examine the relation of individual species predation rates to budworm density. Instead, we divided the species into two groups, the Camponotus species and F. obscuripes, and the remaining Formica species. We first correlated the ant catches on sticky traps for all ants and the two subgroups with budworm densities to determine if ant populations were related to budworm populations. We found no significant correlations. We then correlated budworm densities with plot totals for all ants preying on budworm, all Camponotus and F. obscuripes, and all remaining Formica species and obtained these Pearson product moment correlation coefficients: $r = -0.6711$ ($P < 0.10$), $r = -0.5587$ ($P < 0.20$), and $r = -0.6737$ ($P < 0.10$), respectively. The negative correlation

between budworm density and number of ants preying on budworm is weakest for the dominant predator complex, C. modoc, C. vicinus, C. laevigatus, and F. obscuripes. Clearly, additional factors must be examined before we fully understand the patterns of foraging activity of these potential budworm predators.

Conclusion

Species of both Camponotus and Formica preyed on pupae of the western spruce budworm. Although any given stocked budworm pupae was observed for only 3 h of 48 h in 1981 and 2 h of 72 h in 1982, large numbers of ants were observed preying on the pupae. The budworm predator complex differed geographically. Camponotus species especially C. modoc, dominated the Oregon plots; F. obscuripes dominated the Montana plots. Predation on budworm pupae by a given ant species also varied geographically, was unrelated to ant abundance, and was only slightly related to prey abundance. Further study is needed on the factors influencing the foraging activity of the dominant budworm predators before their effectiveness in control of the western spruce budworm can be predicted.

Chapter IV. The Distribution of Ant Predators
of the Western Spruce Budworm,
Choristoneura occidentalis Freeman
in Eastern Oregon and Western Montana

by

Lorna C. Youngs

and

Robert W. Campbell

Introduction

Predation by insectivorous birds and foliage-foraging ants is a significant mortality factor in the population dynamics of the western spruce budworm. These two groups of predators are the source of most of the mortality of budworm during the late larval and early pupal period, and may be the principal factor responsible for maintaining budworm populations at sparse densities (Campbell 1984).

Species of both Formica and Camponotus were active budworm predators in eastern Oregon and western Montana (Chapter III). The following species were identified as predators of budworm pupae: C. modoc, C. laevigatus, C. vicinus, F. obscuripes, F. podzolica, F. accreta, F. neorufibarbis, and F. lasioides. The dominant predators were the Camponotus species, especially C. modoc, together with F. obscuripes. Additional species of Formica and Camponotus have been observed or implicated as budworm predators - F. haemorrhoidalis in north-central Washington (Campbell and Torgersen 1982), F. criniventris in western Montana (Bain 1974) and F. subnuda, F. argentea and C. herculeanus in Idaho (Markin 1979).

Together, these studies show that the species complex of predaceous ants varies geographically. Any given site may have none or only a few of the species listed above. For the most part, these species were identified on sites selected for study of the population dynamics of the western spruce budworm. Thus, these studies reveal little about the distribution of these budworm predators throughout the range of the budworm.

There exists little information in the literature as well. Beyond broad geographic ranges gleaned from collection records and general descriptions of biology (Wheeler 1917, Mallis 1941, Cole 1942, Wheeler and Wheeler 1978), little is known about many of these species. Wheeler and Wheeler (1963) and Gregg (1963) give comprehensive reviews of the biology and distribution of ants in North Dakota and Colorado respectively, but similar treatments are lacking for many areas of the west.

We initiated this study to provide information about the distribution of ants predaceous on the budworm, at least for 2 areas in the western United States. We wished to determine if the species complex of ants foraging in the forest canopy changed over the range of environmental conditions inhabited by the budworm, to describe the distribution of each species, and to determine if these distributional patterns are related to environmental variables. We also wished to know if the density of ants foraging in the tree canopy changed along environmental gradients.

We conducted the study in eastern Oregon in the Elkhorn and Blue Mountains of the Willowa Whitman National Forest and in western Montana in the Lolo National Forest near Seeley Lake and the Lubrecht Experimental Forest, northeast of Missoula. These areas are well within the range of the budworm. In each state, we examined the pattern of distribution of potential budworm predators over a range of conditions represented by a moisture-temperature gradient. We selected 24 sites of varying environmental conditions in each state and sampled the foliage-foraging ant species as well as several site and stand variables on each site.

Site Description - Montana

We chose the 24 sites to represent both mesic conditions and extremes of moisture and temperature. Environmental conditions at each site were indexed by vegetation. We used the habitat type vegetational classification system of Pfister et al. (1977) for site selection and to determine the relative position of each site on a moisture-temperature gradient. In this region of Montana, the general progression of climax tree species with increasing moisture and decreasing temperature (increasing elevation) is as follows: ponderosa pine, Douglas-fir, grand fir, subalpine fir.

The 24 sites were divided among 4 habitat types, 6 sites per type. The habitat types were: Pseudotsuga menziesii/Symphoricarpos albus (PSME/SYAL h.t.) representing the warm-dry extreme of the moisture-temperature gradient; Pseudotsuga menziesii/Vaccinium

globulare (PSME/VAGL h.t.) and Abies lasiocarpa/Clintonia uniflora (ABLA/CLUN h.t.) representing mesic conditions; and Abies lasiocarpa/Menziesia ferruginea (ABLA/MEFE h.t.) representing the cold-wet extreme of the moisture-temperature gradient. All 4 habitat types are within the range of types inhabited by western spruce budworm (Fellin et al. 1983).

The following general description of these 4 habitat types is given by Pfister et al. (1977). The PSME/SYAL h.t. is common in Montana and found on moderately warm slopes and benches. Ponderosa pine is a major seral dominant, while lodgepole pine and western larch are essentially absent. The PSME/VAGL h.t. is found on relatively cool sites in the Douglas-fir series and is usually bordered upslope by the subalpine fir series. PSME/VAGL h.t. is a major type on the Lolo National Forest, occurring on well drained soils. Lodgepole and ponderosa pine and western larch are major seral dominants. The ABLA/CLUN h.t. is a relatively warm, moist type in the subalpine fir series, and is found extensively in northwestern Montana in river drainages. It is a very diverse habitat type with 5 distinct phases. The major seral tree species are Engelmann spruce, Douglas-fir, western larch and lodgepole pine. The ABLA/MEFE h.t. occurs on cool, moist exposures at higher elevations and is frequently bordered downslope by ABLA/CLUN h.t. in northwestern Montana. Lodgepole pine, Douglas-fir and Engelmann spruce are the common seral components of this type, while subalpine fir dominates old growth stands.

The 24 sites were located in 3 areas: the University of Montana Lubrecht Experimental Forest (25 miles northeast of Missoula), the valley floor near Seeley Lake, and the lower slopes of the Mission Range near Grouse Creek (ca. 15 miles west of Seeley Lake). All plots in the PSME/SYAL and PSME/VAGL h.t.'s were on the Lubrecht Experimental Forest. The plots in the ABLA/CLUN h.t. were located near Seeley Lake and those in the ABLA/MEFE h.t. were located near Grouse Creek. Both areas are in the Lolo National Forest. A north-south moisture gradient exists between Seeley Lake, which is on the upper end of the Clearwater River drainage and the Lubrecht Experimental Forest located near the juncture of the Clearwater and

Blackfoot Rivers. Mean annual precipitation is 56.5 cm at Seeley Lake and 45.5 cm at the lower elevations of the Lubrecht Experimental Forest. Thus the subalpine fir series is encountered at much lower elevations near Seeley Lake than at the Lubrecht Experimental Forest.

The 6 sites within each habitat type were chosen to represent a range of site and stand conditions that may affect ant abundance. In particular, we wished to test the effect of varying degrees of canopy coverage, by selecting sites with similar slopes and aspects, but differing in percent canopy coverage. Thus within each habitat type, 3 sites were designated open stands and 3 sites were designated closed stands, although all stands were within the range of normal stocking for the habitat type.

General site and stand characteristics for each habitat type are summarized in Table IV.1. Sites in the PSME/SYAL h.t. were located in an area where the major portion of the overstory had been removed in the 1930's. Designated open stands had undergone subsequent selection cuts. Shrub and herb cover was generally low. Stands in the PSME/VAGL h.t. were dominated by Douglas-fir. Designated closed stands were undisturbed; designated open stands had undergone either selection cuts, or in one case, an overstory removal (resulting stand was 60 years old). Shrub and herb cover was high in all but the very dense stands. Most of the stands in the ABLA/CLUN h.t. were in early successional stages dominated by seral species and varied considerably among sites in percent species composition. Designated closed stands were mature with considerable deadfall. Designated open stands were either thinned or had undergone an overstory removal. Understory vegetation was extensive and diverse. Most stands in the ABLA/MEFE h.t. contained overmature lodgepole pine, much of it windthrown. Designated open stands had either been thinned or severe windthrow of lodgepole pine had opened the canopy. Shrub species dominated the understory vegetation with little variation in species composition among sites.

Table IV.1. Site characteristics for habitat types in Montana.

Habitat Type - PSME/SYAL		PSME/VAGL	ABLA/CLUN	ABLA/MEFE
Elevation (m)	1220 - 1325	1575 - 1650	1220 - 1250	1860 - 1890
Slope	5 - 14°	5 - 14°	0 - 5°	16 - 45°
Aspect	SE - SW	SW - NW	---	NW - NE
Stand age	60 - 90	60 - 300	150 - 200	120 - 180
Tree species	<i>Pseudotsuga menziesii</i> <i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i> <i>Pinus ponderosa</i> <i>Pinus contorta</i> <i>Larix occidentalis</i>	<i>Pseudotsuga menziesii</i> <i>Pinus contorta</i> <i>Larix occidentalis</i> <i>Abies lasiocarpa</i> <i>Picea engelmannii</i>	<i>Pseudotsuga menziesii</i> <i>Pinus contorta</i> <i>Larix occidentalis</i> <i>Abies lasiocarpa</i> <i>Picea engelmannii</i>
Common understory species	<i>Carex geyeri</i> Boott <i>Calamagrostis rubescens</i> Buckl. <i>Spirea betulifolia</i> Pall. <i>Symphoricarpos albus</i> (L.) Blake	<i>Arnica cordifolia</i> Hook. <i>Berberis repens</i> Lindl. <i>Calamagrostis rubescens</i> <i>Carex geyeri</i> <i>Chimaphila umbellata</i> (L.) Bart. <i>Linnaea borealis</i> L. <i>Xerophyllum tenax</i> (Pursh) Nutt. <i>Vaccinium globulare</i> Rydb.	<i>Arnica cordifolia</i> <i>Berberis repens</i> <i>Calamagrostis canadensis</i> (Michx.) Beauv. <i>Clintonia uniflora</i> (Schulz.) Kunth. <i>Chimaphila umbellata</i> <i>Cornus canadensis</i> L. <i>Fragaria</i> spp. <i>Linnaea borealis</i> <i>Smilacina</i> spp. <i>Symphoricarpos albus</i> <i>Thalictrum occidentale</i> Gray <i>Vaccinium caespitosum</i> Michx. <i>V. globulare</i>	<i>Alnus sinuata</i> (Regel) Rydb. <i>Arnica cordifolia</i> <i>Chimaphella umbellata</i> <i>Menziesia ferruginea</i> Smith <i>Pachistima myrsinitis</i> (Pursh) Raf. <i>Vaccinium globulare</i> <i>V. scoparium</i> Leiberg <i>Xerophyllum tenax</i>
Soil texture surface/subsurface	loam/clay - clay loam	loam - silt loam/sandy loam	loam - sandy loam/clay loam or silty - fine sandy alluvium	sandy - clay loam/sandy - clay loam
% gravels-soil	5 - 35	10 - 70	5 - 20	40 - 60

Site Description - Oregon

We chose 24 sites in Oregon to represent varying conditions along a moisture-temperature gradient, using the habitat type concept. Habitat types in the Douglas-fir, grand fir and subalpine fir series represented (in the order given) increasingly cooler, moister conditions. We chose 8 sites in each tree series, again with varying site and stand conditions, with one half of the stands designated as open and half designated closed. All sites were within the range of conditions inhabited by the western spruce budworm ^{/1}.

The 8 sites in the Douglas-fir series were in the Pseudotsuga menziesii/Symporicarpos albus (PSME/SYAL) habitat type described for the northern Willowa-Whitman National Forest as a warm, dry type with Douglas-fir and ponderosa pine in the overstory and a generally impoverished understory (Daubenmire and Daubenmire 1968, Johnson 1982). Sites in this type were all located ca. 10 miles southeast of Medical Springs in the Willowa-Whitman National Forest. General site characteristics are summarized in Table IV.2. Stands had undergone varying amounts of overstory removal. Understory vegetation was sparse, the percent cover of S. albus increased with increasing Douglas-fir.

The Douglas-fir series is poorly represented in the Willowa-Whitman National Forest (Franklin and Dyrness 1973). It is confined to a narrow band between ponderosa pine sites too dry to support Douglas-fir and sites with sufficient soil moisture for grand fir to establish. The 8 sites in the PSME/SYAL h.t. were located at the upper elevational limits of the type near the transition zone between the Douglas-fir and grand fir series.

The grand fir series covers extensive areas of midslope forests in the Willowa-Whitman National Forest (Franklin and Dyrness 1973). The 8 plots in this series are evenly divided between two habitat types, Abies grandis/Linnaea borealis (ABGR/LIBO) and Abies

^{/1} Daniel B. Twardus, Forest Pest Management, USDA Forest Service, Portland, Oregon. Personal communication.

Table IV.2. Site characteristics for habitat types in Oregon.

	Habitat Type - PSME/SYAL	ABGR/LIBO - ABGR/VAME	ABLA/VAME
Elevation (m)	1340 - 1435	1275 - 1535	1700 - 1760
Slope	5 - 20°	3 - 15°	5 - 25°
Aspect	SW - NW	N - SW	W - N
Stand age	75 - 90	80 - 120	110 - 180
Tree species	<i>Pseudotsuga menziesii</i> <i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i> <i>Abies grandis</i> <i>Pinus contorta</i> <i>Picea engelmannii</i> <i>Larix occidentalis</i>	<i>Pseudotsuga menziesii</i> <i>Abies grandis</i> <i>Abies lasiocarpa</i> <i>Pinus contorta</i> <i>Picea engelmannii</i> <i>Larix occidentalis</i>
Common understory species	<i>Arnica cordifolia</i> <i>Carex geyeri</i> <i>Fragaria</i> spp. <i>Symphoricarpos albus</i>	<i>Arnica cordifolia</i> <i>Adenocaulon bicolor</i> Hook. <i>Chimaphila umbellata</i> <i>Hieracium albiflorum</i> Hook. <i>Linnaea borealis</i> <i>Lonicera utahensis</i> Wats. <i>Osmorhiza chilensis</i> H.&A. <i>Thalictrum occidentale</i>	<i>Arnica cordifolia</i> <i>Cerocarpus ledifolius</i> Nutt. <i>Pyrola</i> spp. <i>Vaccinium membranaceum</i> Dougl. <i>V. scoparium</i>
Soil texture surface/subsurface	sandy - clay loam	loam - silt loam/silt loam	silt loam/loam - silt loam
% gravels-soil	10 - 70	5 - 30	10 - 60

grandis/Vaccinium membranaceum (ABGR/VAME). Both are mesic habitat types located on bottom to midslopes, with stands dominated by grand fir with varying mixtures of Douglas-fir, western larch, lodgepole and ponderosa pine and Englemann spruce. Understory vegetation is diverse and density depends on density of the tree cover (Hall 1973). Johnson (1982) considered the ABGR/VAME h.t. seral to ABGR/LIBO h.t. in the northern region of Willowa-Whitman National Forest. He found in paired stands, that V. membranaceum, coverage was reduced and that of L. borealis increased with increasing crown closure.

Six out of 8 sites in the grand fir series were located on Mount Emily Road, 2 at Simerson Spring, 2 at Drumhill Ridge and 2 at Green Mountain. The remaining 2 sites were located on the Indian Creek Road near Grey's Mountain. All sites were in the Willowa-Whitman National Forest. General site characteristics are found in Table IV.2. Stand densities varied with the degree of past overstory removal. Three out of 4 designated open stands were in the ABGR/VAME h.t. and 3 out of 4 designated closed stands were in the ABGR/LIBO h.t. Understory species were diverse. Thus in the study area, the ABGR/VAME and ABGR/LIBO h.t.'s integrated depending largely on canopy closure and are treated as a single unit for the purposes of this study.

The remaining 8 sites, in the subalpine fir series, were in the Abies lasiocarpa/Vaccinium membranaceum h.t. (ABLA/VAME) described by Hall (1973) as located on mid to upper slopes on generally northern aspects. The type is dominated by subalpine fir, major seral components are Englemann spruce and western larch. Presence of V. membranaceum indicates that this type has the warmest soils in upper forest zone. Density and composition of understory vegetation is again directly related to tree cover.

Six out of 8 ABLA/VAME h.t. sites were located on Indian Creek Road ca. 5 miles north of Point Prominence. The remaining 2 sites were located on Mt. Emily Road near Conklin Spring. All sites were in the Willowa-Whitman National Forest. Sites near Point Prominence were located in a cold air drainage indicated by the presence of V. scoparium Leiberg, which is common in colder habitat types at higher elevations and not usually associated with the ABLA/VAME h.t. General

site characteristics are found in Table IV.2. Stand composition varied considerably among sites and stand density depended on the intensity of previous logging.

Materials and Methods

Field Procedures

We established a 0.1 ha circular plot at each site and recorded the following data for each plot: elevation, slope, aspect, and ground configuration. Ground configuration was coded in 4 classes: convex, straight, concave and undulating; increasing values of configuration classes indicate potential for increasingly moist conditions. We ocularly estimated ground cover in 5 cover classes for: the combination of exposed mineral soil, bed rock, and loose rock, and for moss or lichens. Litter depth was estimated to the nearest cm.

On each plot, we tallied all trees over 1 m tall by species, height (2 m classes) and d.b.h. (10 cm classes). These data were used to generate two measures of stand density - basal area (m^2 of all trees and by species) and crown competition factor (all trees and by species). Crown competition factor (Krajicek et al. 1961) is a relative measure of stand density and is a summation over all trees of the percent of the area of the plot that would be covered by each trees crown if the tree were open grown.

We also measured canopy coverage of all trees with a spherical densiometer at plot center and at 8 equally spaced points, midway between plot center and perimeter. The mean and standard deviation of the 9 percent tree cover scores were recorded for each plot. Stand age was either recorded from available stand records or from increment bores of dominant and codominant trees.

We tallied all exposed woody debris over 10 cm in diameter by length (1 m classes) and diameter (10 cm classes) and assigned a decay class from 1 to 5 based on a classification system developed for Douglas-fir (Fogel et al. 1973). Decay class was based on condition

of the bark, texture and color of the wood, and presence of epiphytes, invading roots and fungi. We calculated a cylindrical overestimation of volume for each piece and totaled the volume for each decay class and for all woody debris.

Snags and stumps were also tallied by diameter (10 cm classes) and height (1 m classes) of exposed wood and assigned one of 9 decay classes (Maser et al. 1979) based on the presence of branches or bark and on the condition of the wood. In this classification, as in that for woody debris, increasing class values indicate increasing decay. Volume of snags and stumps was accumulated by decay class, then totaled.

We identified all understory shrub and herb species and assigned them a cover class by ocular estimation. Cover classes were: rare - 1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, and 95-100% (Pfister et al. 1977). Tree species were assigned cover classes on the same scale.

We dug 1 soil pit at each site to a depth of 70 cm, and recorded depth of the organic layer and the surface soil. The moist consistence and percent gravels (> 2 mm dia.) for the surface and subsurface soils were estimated in the field and soil samples were taken midway in the surface soil and at 70 cm for later texture analysis by the hygrothermometer technique. We recorded texture in 11 classes from sandy (class 1) to increasingly clayey (class 11) soils, and moist consistence in 6 classes from loose (class 1) to extremely firm (class 6) soils.

Aspect, slope and geographic position of each site was used to generate the potential solar radiation in megajoules/m² accumulated over the year on each plot ^{/2}. This variable replaced aspect in subsequent analyses because aspect is a circular rather than linear function, and because changes in aspect are reflected in corresponding changes in the potential solar radiation received on the plot.

We used sticky traps to sample ants foraging in the canopy on 4 trees in each plot. We divided plots into 8 wedges of equal area and

^{/2} Stuart Childes, Department of Soil Science, Oregon State University, Corvallis, Oregon. Personal communication.

randomly selected 4 wedges and a sample tree from each wedge. All sample trees were hosts for the budworm. We placed 3 (0.3 x 0.6 m) boards around the trunk of each sample tree ca 15 cm from the trunk supported on surveyor's stakes ca 0.5 m from the ground. We placed Tanglefoot-coated paper over each board to intercept ants falling from the trunk and foliage. Ants frequently fall from the tree while moving up and down the trunk and the falling rate is proportioned to the density of the traffic on the trunk (Chapter II.). Catches on sticky traps placed near the trunk are thus an index of both species composition and density of ants foraging in the canopy.

Ants were sampled 3 times on the Montana sites and 2 times on the Oregon sites. We left sticky papers on the sample boards for 3 days at each sample period to insure that both nocturnal and diurnal species were represented in the samples. Sampling was confined to periods of warm, dry weather to minimize the possible adverse effects of cool, wet weather on ant foraging activity. It was not possible to sample all 24 plots in each state simultaneously, but we tried to limit the time required to sample all plots. We sampled the Montana plots on July 7-12, August 5-13 and August 16-19, and the Oregon plots on July 9-13 and July 29-August 7. Sampling of 8 plots in the second sample period in Oregon was delayed to August 17-19.

All ants caught on sticky traps were freed from Tanglefoot by solvent and identified to species. Voucher specimens were identified by David Smith, Systematic Entomology Laboratory, U.S. National Museum, Beltsville, Maryland. The remaining ants were identified by Steven Shattuck, Oregon State University, Corvallis, Oregon. All specimens are stored at the Forestry Sciences Laboratory, Corvallis, Oregon.

Analytical Methods

We used detrended correspondence analysis (DCA) (Hill 1979) to ordinate plots by tree and understory species for each state. This ordination method generates axes relatively free from distortion or

compression of axis ends (Gauch 1982). This ordination served as a check on the accuracy of site selection by habitat type. Clustering of plots along ordination axes and the position of each plot with clusters would confirm that vegetation on the plots could be separated into groups and that plots had been accurately classified to groups. Ordination of plots provided unique scores (ordination score) for each plot along a continuous variable (ordination axis) enabling the examination of differences among plots within groups (habitat types). As an aid to interpretation of the axes, the ordination scores for each plot on the first two DCA axes were correlated with the site and stand variables measured on the plot.

The abundance of each common ant species (collected on $\geq 20\%$ of the plots) was graphed against habitat type for each state to determine the general pattern of species occurrence over the moisture-temperature gradient. We then correlated each common ant species (X ants/sample tree/sample period/plot) with site and stand variables over all plots to determine which variables were significantly related to the abundance of each ant species in the state. We undertook a second correlation analysis on only those plots where the species had been collected to determine which variables were significantly related to changes in ant abundance where the species was detected. All correlations were judged significant at the 0.05 level of probability.

The following site and stand variables were used in both correlation analyses: site variables - elevation, slope, ground configuration, total potential solar radiation (radiation), percent cover of mineral soil (% mineral soil), percent cover of moss or lichen (% moss), and average litter depth; stand variables - stand age, total basal area, crown competition factor (CCF) and % canopy cover; dead wood variables - total volume of downed woody debris (woody debris) and total volume of snags and stumps (snags and stumps); soil variables - depth of organic layer (organic depth), depth of surface soil (surface depth), moist consistence surface soil (consistence-surface), texture of surface soil (texture-surface), percent gravels of surface soil (% gravel-surface), moist consistence

of subsurface soil (consistence-subsurface), texture of subsurface soil (texture-subsurface) and % gravels of subsurface soil (% gravel-subsurface).

We also correlated the abundance of each ant species with subsets of the above variables. The abundance of each ant species was correlated with the cover class of each understory species and the cover class of each tree species, to determine if the distribution of individual plant species was more closely related to that of the ant species than the pattern generated by ordination of all plant species. We also correlated the abundance of each ant species with the volume of woody debris and snags and stumps by decay class to determine if information had been lost when total volume was used in the analyses. We again determined significance at the 1.15 probability level.

To test the hypothesis that ants of all species are more common in stands with open canopies, we conducted a Chi^2 test of independence on the total number of ants collected of each species in each habitat in each state in the designated open and closed stands. Additional Chi^2 tests were performed on the number of ants of certain of the wood inhabiting species collected on plots categorized by volume of woody debris and snags and stumps.

Results - Montana

Site Ordination by Vegetation Composition

In the DCA ordination of plots by tree and understory vegetation, most of the variation was captured in the first 2 axes (eigenvalues for axes 1 and 2 were 1.545 and 1.219 respectively; eigenvalues of all subsequent axes were < 1.18). When plot scores on the first 2 axes are graphed (Fig. IV.1) the plots fall into 4 distinct clusters corresponding to the 4 habitat types.

Correlations between plot scores on the first ordination axis (DCA axis 1) show that total potential solar radiation increases with increasing plot scores, while elevation, slope and percent of the

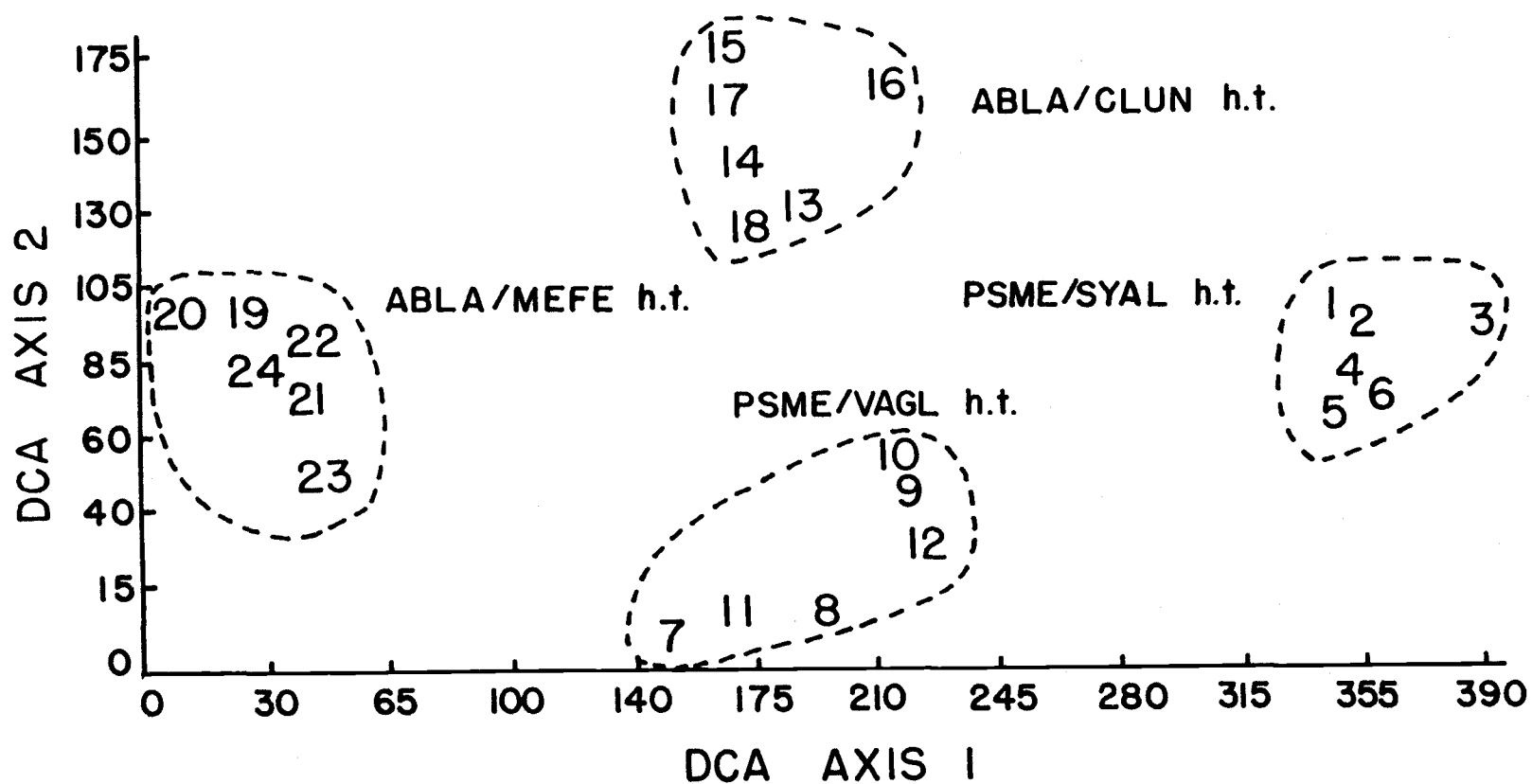


Figure IV.1. Plot scores on the first two axes of the DCA ordination of tree and understory vegetation for plots 1-24 in Montana in 1982.

Table IV.3. Habitat variables significantly correlated with plot scores on the first two DCA ordination axes of tree and understory vegetation in Montana in 1982.

Habitat Variable	Correlation Coefficient (r) ^{/a}	
	Axis 1	Axis 2
Elevation	-.775	-.489
Slope	-.512	--
Ground Configuration	--	.677
Radiation	.863	--
Δ Moss	-.482	--
Litter depth	-.689	--
Organic depth	-.817	--
Surface depth	--	-.475
Consistence - surface	.811	--
Consistence - subsurface	.678	--
Δ gravel - surface		-.552
Δ gravel - subsurface	.504	-.493
texture - surface		-.514
texture - subsurface	.461	--

^{/a} n = 24, p = .05 when r = .404

ground covered by moss decreases (Table IV.3). Litter depth and depth of the organic soil layer also decrease as site scores increase. Thus the first DCA axis can be interpreted as a temperature-moisture gradient. Plots on the hot-dry end of the axis (PSME/SYAL h.t.) are lower in elevation, have high potential radiation values, and less accumulated litter or moss. Plots on the cool-wet end of the axis (ABLA/MEFE h.t.) are higher in elevation, have lower potential solar radiation values, and more moss and litter.

The second DCA ordination axis (DCA axis 2) separates the plots in the ABLA/CLUN h.t. from those in the PSME/VAGL h.t. which are intermingled on the first ordination axis (Fig. IV.1). Because of the north-south moisture gradient between Seeley Lake and the Lubrecht Experimental Forest, subalpine fir grows at much lower elevations at Seeley Lake. Thus mean elevation of the plots in the ABLA/CLUN h.t. are actually lower than those of all other habitat types. Mean potential solar radiation is the same for plots in both PSME/VAGL and ABLA/CLUN habitat types, as is litter depth and depth of the organic layer of the soil.

Plot scores on the second DCA axis are primarily correlated with soil characters and with ground configuration. Plots in the ABLA/CLUN h.t. are either concave or undulating and characterized by soils of varying silty to fine sandy alluvium which were generally poorly drained (Table IV.3). Thus the second DCA axis can be interpreted as a soil moisture gradient, with plots in the ABLA/CLUN h.t. on the wet end of the axis.

Distribution of Ant Species

Nine ant species were collected in sticky traps beneath sample trees, 4 Camponotus species - C. herculeanus, C. laevigatus, C. modoc and C. vicinus and 5 Formica species - F. accreta, F. curiosa Creighton, F. hewitti Wheeler, F. neorufibarbis and F. podzolica. The most commonly encountered species (collected on 20% or more of the plots) were C. herculeanus, C. modoc, C. vicinus, F. neorufibarbis and F. podzolica. C. laevigatus, F. curiosa and F. hewitti were each

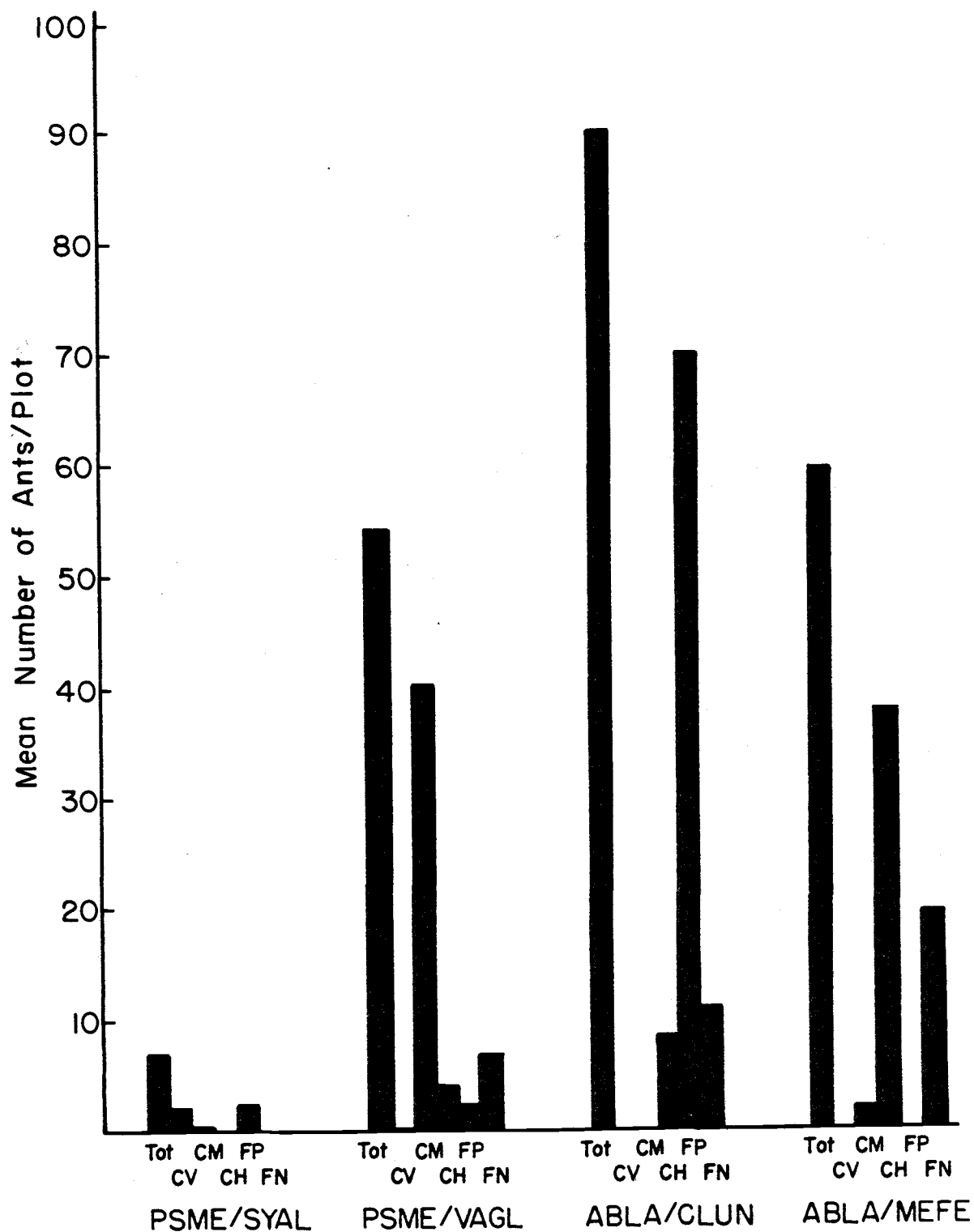


Figure IV.2. Mean number of ants of the five common species in each habitat type in Montana in 1982 (tot= all species, CV= *C. vicinus*, CM= *C. modoc*, CH= *C. herculeanus*, FP= *F. podzolica*, FN= *F. neorufibarbis*).

collected on only 1 plot in the PSME/VAGL h.t. and F. accreta was collected on one plot in each Douglas-fir habitat type.

The most species were collected in the PSME/VAGL h.t. where all 9 were present. Three species were collected in both habitat types of the subalpine fir series and 4 species in the PSME/SYAL h.t. The fewest individuals were collected in the PSME/SYAL h.t. and the most in the ABLA/CLUN h.t., although F. podzolica was 78% of the total collected (Fig. IV.2).

With the exception of C. vicinus, the abundance of all species increased with increasingly moist and cool conditions (Fig. IV.2). C. vicinus was collected on 4 out of 6 plots in the PSME/SYAL h.t. but only 1 plot in the PSME/VAGL h.t. C. modoc was collected on 2 plots in PSME/SYAL h.t., all plots in the PSME/VAGL h.t., and 4 plots in the ABLA/MEFE h.t. C. herculeanus was collected on two plots in the PSME/VAGL h.t., 5 plots in the ABLA/CLUN h.t., and on all ABLA/MEFE plots. F. podzolica was collected on 4 plots in the PSME/SYAL h.t., one in the PSME/VAGL h.t. and 5 plots in the ABLA/CLUN h.t. F. neorufibarbis was collected on 4 plots in the PSME/VAGL h.t., and in both subalpine fir habitat types.

The abundance of F. neorufibarbis (\bar{X} ants/plot/sample) was correlated with that of C. herculeanus ($r=.7337$ $P < .001$). There were no significant correlations among the abundances per plot of any of the other common species.

More ants of all the common species were caught in the first sample period (July 7-12) than the remaining two periods. The percents of the total caught in each sample period in order of the sample period were: C. modoc - 46%, 42%, 12%; C. herculeanus - 63%, 25%, 12%; C. vicinus - 44%, 37%, 19%; F. neorufibarbis - 59%, 25%, 16%; and F. podzolica - 66%, 18%, 16%.

Correlations Between Common Ant Species and Environmental Variables

Significant correlations between habitat variables and the abundance of C. vicinus are given in Table IV.4. Analysis of the relation between the abundance of C. vicinus over all plots and

Table IV.4. Habitat variables significantly correlated with the abundance of each common Camponotus over all plots and sample periods, and on only those plots where the species was collected in Montana in 1982.

Habitat variables	<u>Correlation coefficient (r)</u>					
	<u>C. vicinus</u>		<u>C. modoc</u>		<u>C. herculeanus</u>	
	All plots/ <u>a</u>	Where collected/ <u>b</u>	All plots/ <u>a</u>	Where collected/ <u>c</u>	All plots/ <u>a</u>	Where collected/ <u>d</u>
Elevation	-.268	---	---	---	.238	---
Radiation	.378	---	---	---	---	---
% Mineral soil	.246	---	---	-.354	.366	.428
Litter depth	-.375	---	---	---	---	---
Stand age	---	---	.351	---	---	---
% Canopy cover	---	---	---	---	-.407	-.436
Snags & stumps	---	---	---	.422	---	---
Organic depth	-.340	---	---	---	---	---
Surface depth	---	---	.300	.590	---	---
Consistence-surface	.339	---	---	---	-.301	-.443
Consistence-subsurface	.311	---	---	---	-.449	---
% gravel-surface	---	---	.337	---	.309	---
% gravel-subsurface	---	---	.304	---	.298	---
texture-subsurface	.394	---	---	---	---	---

/a n = 72, p = .05 when r = .233

/b n = 15, p = .05 when r = .514

/c n = 36, p = .05 when r = .329

/d n = 39, p = .05 when r = .316

subsets of the environmental variables showed no significant correlations between C. vicinus and the volume of woody debris in any decay class. However, C. vicinus was significantly correlated with the percent cover of ponderosa pine and 3 understory species: Achillea millefolium L., Balsamorhiza sagittata (Pursch) NuH., and Festuca scabrella Torr. Significantly, more C. vicinus were collected in designated open plots than closed plots (Table IV.5).

Significant correlations between habitat variables and the abundance of C. modoc are given in Table IV.4. The abundance of C. modoc was not correlated with the volume of dead wood in any decay class. The percent cover of Douglas-fir and the understory species Antennaria racemosa Hook., and Berberis repens were significantly correlated with the abundance of C. modoc. Significantly more C. modoc were collected in designated open plots in both PSME/VAGL and the ABLA/MEFE h.t.s (Table IV.5).

Significant correlations between the abundance of C. herculeanus and habitat variables are shown in Table IV.4. C. herculeanus was not correlated with the volume of dead wood in any decay class or with the percent cover of any tree species. Its abundance was correlated with the percent cover of the understory shrubs, Menziesia ferruginea and Vaccinium scoparium. More C. herculeanus were collected on open plots in the ABLA/MEFE h.t. but the reverse occurred in the ABLA/CLUN h.t. (Table IV.5).

Habitat variables significantly correlated with the abundance of F. podzolica are shown in Table IV.6. Formica podzolica nests in the soil, thus correlations with volume of woody debris by decay class were not tested. F. podzolica was significantly correlated with the total basal area of Pinus contorta and negatively correlated with % cover of Pseudotsuga menziesii. F. podzolica was positively correlated with the % cover of 13 understory species; highest correlations were with, Anaphalis margaritacea (L.) B & H, Calamagrostis canadensis, Clintonia uniflora, Cornus canadensis, Equisetum sp., Galium boreale, Osmorhiza chilensis, Prunella vulgaris L., and Smilacina stellata (L.) Desf. More F. podzolica were

Table IV.5. χ^2 test of differences in ant abundance between plots with open and closed canopies in Montana in 1982.

Ant Species	Habitat type	No. ants in each canopy class		P
		Open	Closed	
<u>C. vicinus</u>	PSME/SYAL	18	8	<.05
<u>C. modoc</u>	PSME/VAGL	138	105	<.05
<u>C. modoc</u>	ABLA/MEFE	12	1	<.01
<u>C. herculeanus</u>	ABLA/MEFE	217	12	<.005
<u>C. herculeanus</u>	ABLA/CLUN	4	48	<.005
<u>F. podzolica</u>	PSME/SYAL	3	12	<.05
<u>F. podzolica</u>	ABLA/CLUN	241	183	<.01
<u>F. neorufibarbis</u>	PSME/VAGL	38	3	<.005
<u>F. neorufibarbis</u>	ABLA/CLUN	30	37	N.S.
<u>F. neorufibarbis</u>	ABLA/MEFE	111	7	<.005

Mean and Standard Deviation of tree density variables in each density class in each habitat type in Montana in 1982.

Habitat Type	% Canopy Cover		Basal Area (m ² /ha)	
	Open	Closed	Open	Closed
PSME/SYAL	83.7 ± 3.8	90.3 ± 2.3	23.6 ± 7.1	36.3 ± 7.5
PSME/VAGL	81.0 ± 9.5	93.3 ± 2.3	23.7 ± 5.9	41.6 ± 4.1
ABLA/CLUN	87.7 ± 5.8	94.7 ± 3.2	30.5 ± 6.2	56.5 ± 2.3
ABLA/MEFE	78.7 ± 10.4	87.7 ± 8.4	23.2 ± 5.7	33.3 ± 4.6

Table IV.6. Habitat variables significantly correlated with the abundance of each common Formica over all plots and sample periods, and on only those plots where the species was collected in Montana in 1982.

Habitat variables	<u>Correlation coefficient (r)</u>			
	<u>F. podzolica</u>		<u>F. neorufibarbis</u>	
	<u>All plots/a</u>	<u>Where collected/b</u>	<u>All plots/a</u>	<u>Where collected/c</u>
Elevation	-.243	---	---	---
Slope	-.287	-.532	---	---
Ground configuration	.538	.565	---	---
% Mineral soil	---	---	.278	.405
Stand Age	.354	.402	---	---
% Canopy cover	---	---	-.361	---
Organic depth	---	---	---	-.430
Surface depth	-.580	-.591	---	---
Consistence - subsurface	---	-.507	-.409	-.463
% gravel-surface	-.270	---	---	---
% gravel-subsurface	-.278	---	---	---
Texture-surface	-.549	-.655	---	---
Texture-subsurface	-.373	-.527	---	---

/a n = 72, p = .05 when r = .233

/b n = 30, p = .05 when r = .361

/c n = 36, p = .05 when r = .329

collected on open plots in the ABLA/CLUN h.t. while the reverse occurred in the PSME/SYAL h.t. (Table IV.5).

The abundance of F. neorufibarbis was significantly correlated with just 4 habitat variables (Table IV.6). Although the abundance of this species was not significantly correlated with any category of wood or decay class, significantly more ($\chi^2=76$) were collected on plots with high volumes of woody debris (mean 130 m³/ha), than low volumes (mean 66 m³/ha) in the ABLA/MEFE h.t. The reverse was true in the ABLA/CLUN h.t. where significantly more ($\chi^2=35$) were collected on plots with low volumes of woody debris (mean 24 m³/ha) than plots with high volumes (mean 130 m³/ha).

The abundance of F. neorufibarbis was not significantly correlated with the percent cover of any tree species and with only one understory species - Vaccinium scoparium. More individuals were collected in open stands in all but the ABLA/CLUN h.t. (Table IV.5).

Results - Oregon

Site Ordination by Vegetation Composition

In the DCA ordination of plots by tree and understory species cover classes, most of the variation was captured in the first two axes (eigen values were 0.650 and 0.192 respectively, eigen values for all subsequent axes were < 0.09). When plot scores on the first two axes are graphed (Fig. IV.3), plots fall into 3 clusters corresponding to habitat types in the 3 tree series. The tight clustering of plots in the grand fir series justifies the grouping of the two grand fir habitat types in this study. Plots 17 and 18 in the ABLA/VAME h.t. were on Mt. Emily and had a more heterogenous understory than the remaining subalpine fir sites located ca. 25 miles to the east on Indian Creek Road.

The first DCA axis was positively correlated with total potential solar radiation and percent of the plot covered by exposed mineral soil and negatively correlated with percent area covered by moss or lichen and elevation (Table IV.7). Thus plots become progressively

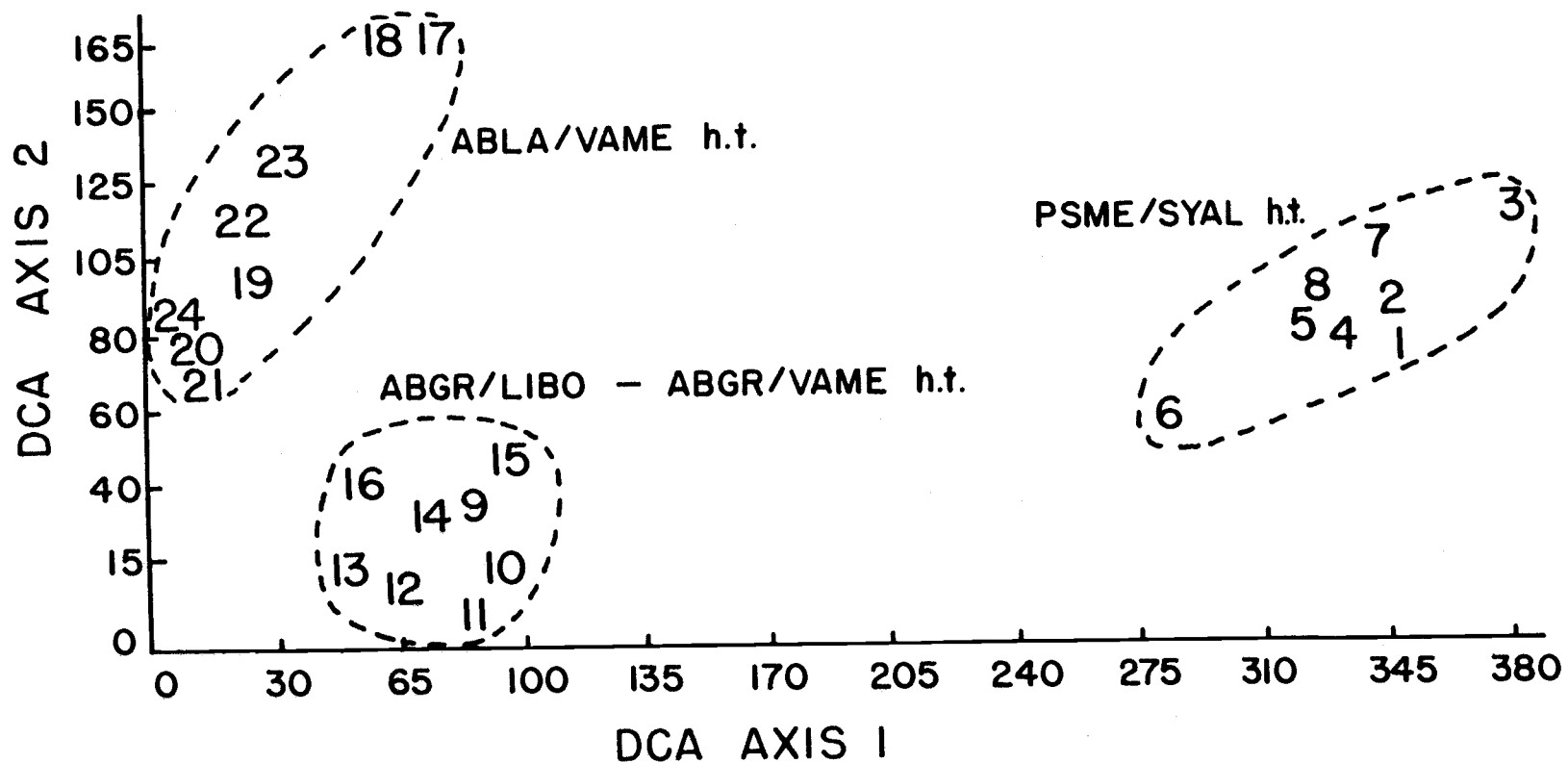


Figure IV.3. Plot scores on the first two axes of the DCA ordination of tree and understory vegetation for plots 1-24 in Oregon in 1982.

Table IV.7. Habitat variables significantly correlated with plot scores on the first two DCA ordination axes of tree and understory vegetation in Oregon in 1982.

Habitat variable	<u>Correlation Coefficient (r)/a</u>	
	Axis 1	Axis 2
Elevation	-.509	.546
Radiation	.434	-.560
% Mineral soil	.412	---
% Moss	-.438	---
Stand age	-.568	.535
Organic depth	-5.23	.463
Surface depth	-.664	-.571
Consistence - surface	.444	---
Consistence - subsurface	---	-.434
% gravel - surface	---	.643

/a $n = 24$, $p = .05$ when $r = .404$

warmer and drier with increasing site scores and this axis can be interpreted as a moisture-temperature gradient. The hot-dry end of the axis is once again represented by plots in the PSME/SYAL h.t.

The second DCA axis further separates the plots in the subalpine fir series from those in the grand fir series. Correlations with elevation and potential solar radiation but not with percent area covered by moss (Table IV.7) indicate that this axis can be interpreted more as a temperature gradient than a temperature-moisture gradient.

Distribution of Ant Species

Eleven species were collected on sticky traps beneath sample trees: 4 Camponotus species--C. herculeanus, C. laevigatus, C. modoc and C. vicinus--and 7 Formica species--F. accreta, F. argentea, F. haemorrhoidalis, F. lasioides, F. neorufibarbis, F. obscuripes, and F. podzolica. The most commonly encountered species (collected on 25% or more of the plots) were C. modoc, C. vicinus, F. accreta, F. neorufibarbis and F. podzolica. F. haemorrhoidalis was collected on 1 plot and F. argentea on 2 plots in the PSME/SYAL h.t. C. laevigatus and F. lasioides were collected on 1 plot in the PSME/SYAL and ABGR/LIBO - ABGR/VAME h.t.s. F. obscuripes was collected on 1 plot in the grand fir and subalpine fir habitat types and C. herculeanus was collected on 1 plot in the subalpine fir habitat type.

The most species were collected in the PSME/SYAL h.t., where all but C. herculeanus and F. obscuripes were collected. The greatest number of ants were also collected in that habitat type. The fewest species (5) and fewest individuals were collected in the subalpine fir habitat type. Eight species were collected in the grand fir habitat types.

With the exception of F. neorufibarbis, there was a general decrease in the number of individuals collected of the 5 common species with increasingly cool and moist conditions (Fig. IV.4). C. vicinus was collected on all plots in the Douglas-fir habitat type and 1 plot in the grand fir habitat types. C. modoc was collected on 7 plots in the Douglas-fir habitat type, all plots in the grand fir

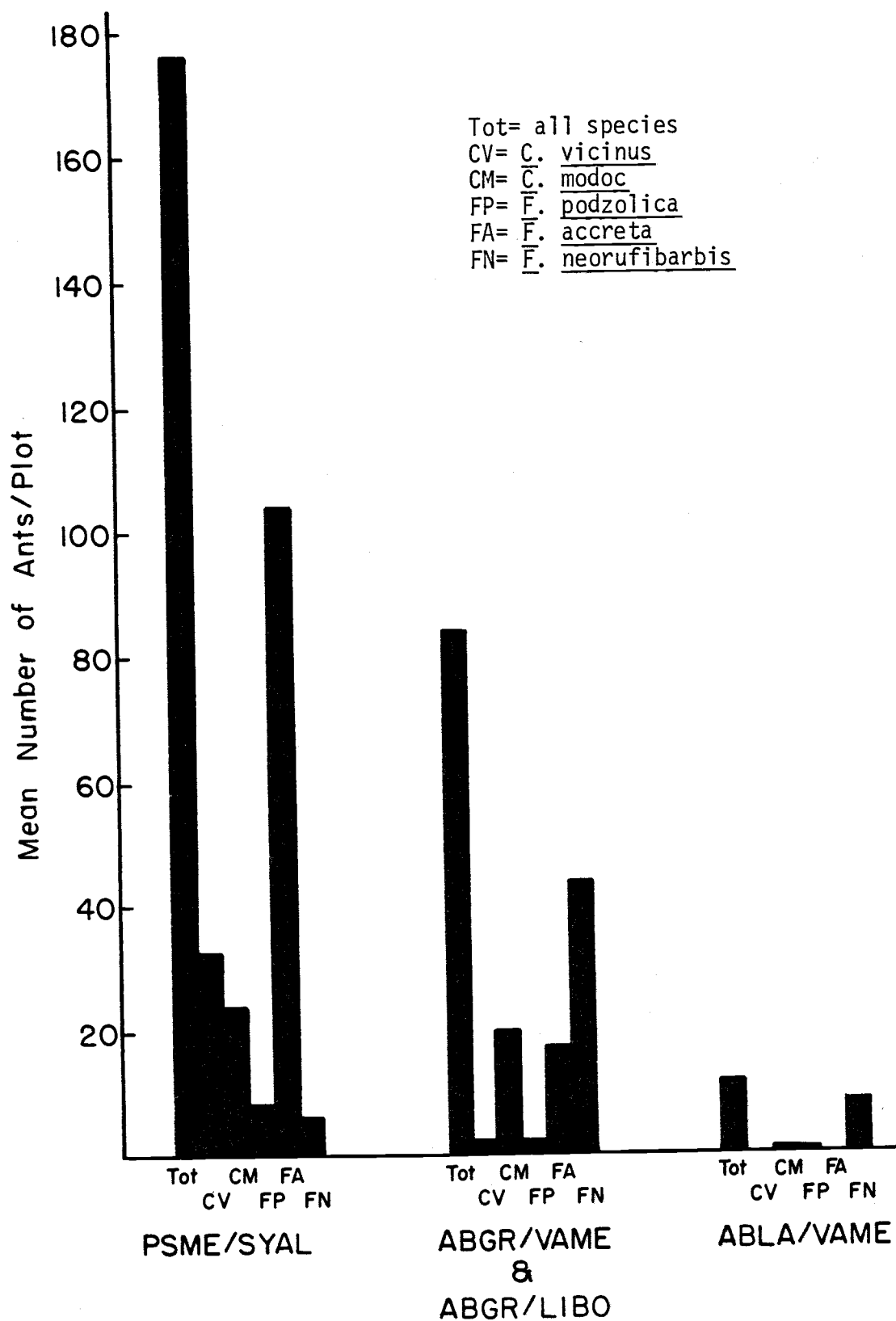


Figure IV.4. Mean number of ants of the five common species in each habitat type in Oregon in 1982.

types and 2 subalpine fir plots. F. accreta was collected on all Douglas-fir plots, and 4 plots in the grand fir habitat types. F. neorufibarbis was collected on 3 Douglas-fir, 7 grand fir plots and 5 subalpine fir plots.

The mean number of C. modoc per sample per plot was correlated ($r=.631$, $P < .05$) with the mean number of F. neorufibarbis and with the mean number of F. accreta ($r=.730$, $P < .05$). There were no significant correlations among the abundances of any other species.

More ants were caught in the first sample period (July 9-13) in the following species: C. modoc - 63%, F. accreta - 54%, and F. neorufibarbis - 80%. More C. vicinus (63%) and F. podzolica (65%) were caught in the second sample period (July 29 - August 7).

Correlations Among Common Species and Environmental Variables

Significant correlations between the abundance of C. vicinus and habitat variables are shown in Table IV.8. C. vicinus was also correlated with the percent cover of ponderosa pine and 4 understory species: Achillea millefolium, Carex geyeri, Cerocarpus ledifolius, and Symphoricarpos albus. The abundance of C. vicinus was not significantly correlated with the volume of wood in any decay class. There was no difference in the number of ants collected in open or closed stands (Table IV.9).

The abundance of C. modoc over all plots was correlated with few site and stand variables (Table IV.8). The volume of dead wood in any decay class was not significantly correlated with the abundance of C. modoc. When the volume of woody debris and of snags and stumps were classified into 2 groups on the grand fir plots, significantly more C. modoc were collected in the high volume classes ($\text{Chi}^2 = 44.4$ and $\text{Chi}^2 = 62.9$, mean volume for woody debris = $169 \text{ m}^3/\text{ha}$ and $63 \text{ m}^3/\text{ha}$ for snags and stumps) than in the low volume classes (mean volume = $54 \text{ m}^3/\text{ha}$ and $28 \text{ m}^3/\text{ha}$ respectively). The reverse occurred on the Douglas-fir plots. More C. modoc were collected in the low volume classes ($\text{Chi}^2 = 163$ for woody debris and for snags and stumps). Mean volume of woody debris for low and high classes was

Table IV.8. Habitat variables significantly correlated with the abundance of each common Camponotus over all plots and sample periods, and on only those plots where the species was collected in Oregon in 1982.

Habitat variables	<u>Correlation coefficient (r)</u>			
	<u>C. vicinus</u>		<u>C. modoc</u>	
	All plots/ <u>a</u>	Where collected/ <u>b</u>	All plots/ <u>a</u>	Where collected/ <u>c</u>
Elevation	-.299	-.582	-.299	---
Ground configuration	.317	---	---	---
Radiation	.417	.566	---	---
% Moss	.459	-.523	---	---
Basal area	---	---	-.235	---
CCF	---	---	-.262	---
Organic depth	-.349	---	---	---
Surface depth	-.402	---	---	---
Consistence-surface	.495	.544	---	-.345
Consistence-subsurface	.293	.562	---	---
Texture-surface	.300	.486	---	---
Texture-subsurface	.318	---	---	---

/a n = 48, p = .05 when r = .285

/b n = 18, p = .05 when r = .468

/c n = 34, p = .05 when r = .339

Table IV.9 Chi² test of differences in ant abundance between plots with open or closed canopies in Oregon in 1982.

Ant species	Habitat type	Number of ants in each canopy class		P
		Open	Closed	
<u>C. vicinus</u>	PSME/SYAL	142	122	N.S.
<u>C. modoc</u>	PSME/SYAL	153	36	<.005
<u>C. modoc</u>	ABGR/LIBO/VAME	117	42	<.005
<u>F. accreta</u>	PSME/SYAL	614	225	<.005
<u>F. accreta</u>	ABGR/LIBO/VAME	136	1	<.005
<u>F. neorufibarbis</u>	PSME/SYAL	48	6	<.005
<u>F. neorufibarbis</u>	ABGR/LIBO/VAME	311	37	<.005
<u>F. neorufibarbis</u>	ABLA/VAME	47	22	<.005

Mean and Standard Deviation of tree density variables in each density class in each habitat type in Oregon.

Habitat Type	% Canopy Cover		Basal Area (m ² /ha)	
	Open	Closed	Open	Closed
PSME	85.0 ± 2.6	92.8 ± 1.5	28.0 ± 5.5	58.2 ± 15.4
ABGR	74.5 ± 11.2	93.8 ± 4.2	26.6 ± 5.3	49.6 ± 15.8
ABLA	75.3 ± 7.4	89.0 ± 6.1	34.3 ± 11.1	46.6 ± 6.1

38 m³/ha and 90 m³/ha and mean volume for snags and stumps for low and high classes was 4 m³/ha and 28 m³/ha. Significantly, more C. modoc were collected in plots with open canopies in both the Douglas-fir and the grand fir habitat types (Table IV.9).

Significant correlations between the abundance of F. accreta and habitat variables are given in Table IV.10. The abundance of F. accreta was correlated with the percent cover of ponderosa pine and with 3 understory species: Berberis repens, Carex geyeri, and Hieracium albiflorum. Significantly more F. accreta were collected in open stands in both the Douglas-fir and grand fir plots (Table IV.9).

Habitat variables correlated with the abundance of F. podzolica are shown in Table IV.10. The abundance of F. podzolica was correlated with the percent cover of ponderosa pine and 4 understory species - Achillea millefolia, Arnica cordifolia, Collomia grandiflora Dougl., Nutt. and Symphoricarpos albus. Although more F. podzolica were collected in closed stands in both the Douglas-fir and grand fir habitat types, the species was collected in so few plots in each habitat type, that a Chi² analysis was not attempted.

The abundance of F. neorufibarbis over all plots was significantly correlated with only one habitat variable (Table IV.10). The abundance of F. neorufibarbis was not significantly correlated with the volume of dead wood in any decay class. However, if the volume of woody debris and of snags and stumps on each plot in the grand fir habitat type are divided into 2 classes, then the number of ants collected the high volume class of woody debris (mean volume - 169 m³/ha) and of snags and stumps (mean volume - 63 m³/ha) is significantly greater (Chi² = 172 and Chi² = 94 respectively) than in the low volume class of woody debris (mean volume 54 m³/ha) and snags and stumps (mean volume = 28 m³/ha). The reverse situation occurred on the plots in the subalpine fir series. Significantly more ants were collected in the low volume class of woody debris (mean volume = 59 m³/ha, Chi² = 5.8) and of snags and stumps (mean volume = 26 m³/ha, Chi² = 48.8) than in the high volume classes (mean volume = 233 m³/ha and 132 m³/ha respectively).

Table IV.10 Habitat variables significantly correlated with the abundance of each common Formica over all plots and sample periods, and on only those plots where the species was collected in Oregon in 1982.

Habitat variables	<u>Correlation coefficient (r)</u>					
	<u>F. podzolica</u>		<u>F. acreta</u>		<u>F. neorufibarbis</u>	
	All plots/ <u>a</u>	Where collected/ <u>b</u>	All plots/ <u>a</u>	Where collected/ <u>c</u>	All plots/ <u>a</u>	Where collected/ <u>d</u>
Ground configuration	---	---	.451	.623	---	---
Radiation	---	.584	---	---	---	---
% Mineral soil	---	.761	.406	.492	---	---
% Moss	---	---	---	---	.309	---
Stand age	---	---	-.312	---	---	---
Basal area	.448	.591	---	---	---	---
Organic depth	---	---	-.313	---	---	---
Surface depth	---	---	-.296	---	---	---
Consistence-surface	.454	.657	---	---	---	---
Texture-surface	.570	.613	---	---	---	---

/a n = 48, p = .05 when r = .285

/b n = 12, p = .05 when r = .576

/c n = 24, p = .05 when r = .404

/d n = 30, p = .05 when r = .361

The abundance of F. neurufibarbis was not significantly correlated with the percent cover of any tree species, but it was significantly correlated with the percent cover of 8 understory species - Bromus sp., Chimaphila umbellata, Galium triflorum, Linnaea borealis, Ranunculus uncinatus D. Don, Ribes sp., Rosa sp. and Smilicina stellata. Significantly more F. neurufibarbis were collected in stands in the low canopy cover class in all habitat types (Table IV.9).

Discussion

Distribution of Common Species

With the exception of a few individuals of the genera Lasius and Myrmica, the complex of ants foraging in the canopy on the plots in both states was composed of species of either Camponotus or Formica. Although 9 species of these two genera were collected in Montana and 11 species were collected in Oregon, only 6 species could be considered common. All of the common species prey on budworm.

Four out of the 6 species were common to both states. Some correlations exist between the pattern of distribution of a few species, but the correlations are unique to one or the other state. In a state, each species had a unique distributional pattern across the range of habitat types we studied, and the pattern usually differed between states. The average abundance per plot of each species also differed between states as well as among habitat types. For most species, there was also considerable variation within habitat types. Thus the pattern of distribution of each species and the environmental variables that may be associated with this pattern must be evaluated individually.

Camponotus vicinus

With one exception in each state, C. vicinus was collected in only the warmest, driest habitat type - PSME/SYAL h.t. (This does not

imply that this habitat type is found under exactly the same conditions in both states. Although the name is used in several western states to describe the same general association of tree and understory species, regional differences exist in the environmental conditions represented by the type.) It is not surprising that the presence of C. vicinus is negatively correlated with elevation and positively correlated with total potential solar radiation in both states. The negative correlation with percent of plot covered by moss or lichen in Montana and depth of the litter layer in Oregon also indicate conditions found on warmer, drier sites. Although the soils in this habitat type differ between states (soils in Montana were generally firmer with a higher clay content and less coarse fragments) C. vicinus was consistently more abundant on plots with firmer soils of high clay content.

The positive correlation between the abundance of C. vicinus and the percent cover of ponderosa pine is to be expected since that tree species is also more common on warm-dry sites. The same can be said for the correlations with understory species. Although, except for Achillea millefolium, the species differ between states, in general, all are found more commonly in the PSME/SYAL h.t. than in the other habitat types examined.

Since few C. vicinus were collected on the Montana plots, and numbers varied little among plots compared to Oregon, discussion of factors related to abundance of this species is confined to the Oregon data. Within the range of conditions on the Douglas-fir plots, C. vicinus is still most abundant on the warmest-driest plots with the highest clay content. Unlike the other common species, the abundance of C. vicinus was not related to stand density.

Camponotus vicinus is member of the subgenus Tanaemyrmex Ashmead, most of the species of which nest in the soil or, rarely, buried wood. Members of this subgenus are generally found in the southern states, although C. vicinus has been recorded throughout the American Rocky Mountains and into Canada. Other researchers have also found it more common in warmer, drier forest sites (Wheeler 1917, Cole 1942, Wheeler and Wheeler 1963). Gregg (1963) reported that in Colorado C.

vicinus was collected in both open and wooded land, primarily deciduous or ponderosa pine - Douglas-fir stands but never in dense forests. He also found a correlation between the presence of C. vicinus and clay soils. Nesting sites were usually under rocks. Thus it appears that C. vicinus is limited to the warm-dry end of the range of conditions inhabited by the western spruce budworm.

Camponotus herculeanus

Camponotus herculeanus was the most commonly encountered species in Montana but virtually absent from Oregon. It was most abundant in the subalpine fir series in Montana, and the only Oregon collection was also in that series. Although the abundance of C. herculeanus was significantly correlated with elevation, the species was also common on the ABLA/CLUN h.t. plots which were at the lowest elevations. This probably reflects the adaptation of C. herculeanus to cooler-moister conditions (usually found at higher elevations) rather than to a relation with elevation alone. C. herculeanus nests in wood not in soil, thus the correlations with more friable soils of high gravel content reflect the occurrence of soils of this type in the ABLA/MEFE h.t. where C. herculeanus was most abundant.

Both the correlation analyses and the Chi^2 tests of numbers caught in open and closed stands show that C. herculeanus is more abundant in stands of lower canopy coverage. Canopy coverage may have a greater effect on the abundance of C. herculeanus than the amount of available dead wood for nesting sites. It is also possible that the lack of correlation between the abundance of this species and the volume of dead wood is due to a threshold effect. The function may not be linear. Since no plot was completely lacking in woody debris, it may be that the availability of nesting sites was not a limiting factor.

C. herculeanus is a dominant ant in boreal and alpine forests of North America (Wheeler and Wheeler 1963). Gregg (1963) found this species abundant in cold coniferous forests in Colorado. Its upper range terminated at the timberline, where he stated that they were

limited by nesting sites. From collection records, he noted that C. herculeanus was found in wood of all stages of decay, but he did not quantify a preference for wood of a certain stage or the relation between ant abundance and amount of available nesting material.

Sanders (1964) investigated the biology of C. herculeanus in New Brunswick and noted that the species occupied diverse habitats and that its occurrence was not correlated with any discernable environmental variables. In later work in 3 successional stages of spruce-fir forest (Abies balsamea (L.) Mill. - Picea glauca (Moench, Voss), Sanders (1970) found more C. herculeanus in immature stands, where he speculated that the availability of woody debris made these stands attractive colonization sites.

Our work shows that, as in other areas, C. herculeanus is adapted to cold forests. Although rarely collected in Oregon, its distribution in Montana was sufficiently broad to prevent further conclusions about its habit preferences based on our data. We did find that its abundance at site is inversely related to stand density. We were not able to show a linear relationship with the abundance of available nesting material, due possibly to the threshold effect discussed above.

Camponotus modoc

Camponotus modoc was common in both states and was collected on more plots in Oregon than any other species. In both states it was most abundant in the more mesic habitat types although it was collected throughout the entire range. The one exception is its absence from the samples in the ABLA/CLUN h.t. Our data offered us no explanation for this and we can only speculate that this habitat type may be too wet for C. modoc.

The abundance of C. modoc is correlated with few environmental variables in either state and those that are significantly correlated vary between states. In both states the abundance of C. modoc is related to stand density and to the amount of dead wood available for nesting sites. Significantly more C. modoc were collected in more

open stands in all habitat types where it was common, and in Oregon both stand basal area and crown competition factor were negatively correlated with the abundance of C. modoc over all plots. In Montana, the abundance of C. modoc on plots where it was collected was significantly correlated with the volume of snags and stumps, while in Oregon more ants were collected in stands categorized as having high volume of dead wood, at least on the grand fir plots. Since the reverse was true on the Douglas-fir plots, it is possible that the effects of stand density and amount of available nesting material are so interrelated that our data are insufficient to clearly separate the two. The same phenomenon of a threshold effect for dead wood discussed above in C. herculeanus may also occur with C. modoc.

Several authors have reported C. modoc over a wide range of forest conditions (Wheeler 1917, Wheeler and Wheeler 1963, Gregg 1963, Cole 1942). Gregg (1963) reported that although the ranges of C. herculeanus and C. modoc overlap, C. modoc is generally found at lower elevations, a situation confirmed by our Montana data and to some extent our Oregon data. The distribution of C. modoc, like that of C. herculeanus is also too broad to produce strong correlation with most of the variables we measured. Where it was present, the abundance of C. modoc was directly related to the amount of available nesting sites (woody debris) and inversely related to stand density.

Formica accreta

Formica accreta was common in Oregon but rarely encountered in Montana. It was not collected in the cool subalpine fir habitat types in either state. The correlations between the abundance of F. accreta and environmental variables in Oregon are difficult to interpret. Although it undoubtedly nests in soil, only the analysis over all plots showed any significant correlation with soil variables (Table IV.10). Since the average values for depth of the organic and surface soil layers are lowest for the PSME/SYAL h.t. and F. accreta is most abundant in that type, correlations between soil variables and F. accreta may not be indicative of an association with shallow soils

with little accumulated organic matter. The negative correlation with stand age may also be due to the fact that stands in the PSME/SYAL h.t. were younger.

More ants were collected on plots with open stands than closed stands (Table 1V.9) and those plots in general had more area covered by exposed mineral soil. Thus from our data we can conclude only that F. accreta is more abundant in the mesic to somewhat xeric range of environments inhabited by the budworm, and that factors such as stand density and soil depth may be related to changes in abundance.

Formica accreta was separated from F. fusca L., and raised to species rank in a taxonomic revision of the F. fusca species group (Francoeur 1973). Thus, there is very little information on the biology of F. accreta that can be separated from that recorded for F. fusca.

Formica podzolica

Formica podzolica was collected in both states on all but the coldest habitat type (ABLA/MEFE). Its distribution in all habitat types but the ABLA/CLUN is so scattered that it is difficult to determine factors related to that distributional pattern. This is especially so in Oregon where the numbers collected were generally low and the 6 plots where it was detected were scattered through all 3 tree series. The scarcity of the Oregon data makes the analysis in that state difficult and we will confine our discussion to the pattern of occurrence in Montana.

Certainly the high numbers of F. podzolica collected in the ABLA/CLUN h.t. created high correlations with the range of environmental variables in that type. Hence, high numbers of F. podzolica are associated with plots of low elevation, gentle slopes, sandy soils, and concave ground configuration - all characteristics of the ABLA/CLUN h.t. Even the majority of species significantly correlated with F. podzolica are more common in that habitat type. However, the negative correlation with stand age may reflect a relation independent of the influence of the high numbers of this

species in the ABLA/CLUN h.t., since average stand age in that type is mid range for all types. Thus, F. podzolica may be a pioneer species in Montana and more common in younger stands.

Francoeur (1973) also found F. podzolica widely distributed in many forest types and noted that the species was common in secondarily successional stands. He speculated that F. podzolica penetrated forested lands following silvicultural activity and was frequently found along forest roads. The greater number of ants found in open stands in Montana (Table IV.5) is in agreement with his general conclusion.

Francoeur also recorded a greater abundance of nests from sandy soils. The presence of high numbers of F. podzolica in the ABLA/CLUN h.t. may be related more to the nature of soils in that habitat type than other environmental variables. Thus, our data indicate that F. podzolica may be present throughout most of the range of habitat types examined, but that abundant populations are more common in open stands or younger stands with sandy soils.

Formica neorufibarbis

Although F. neorufibarbis is very common in both Oregon and Montana, little useful information resulted from the attempt to relate distribution and abundance to environmental variables. The lack of linear correlation with practically all the environmental variables in Oregon results from the high densities collected on the grand fir plots, which represent mesic conditions for most of the variables. In Montana, even though the numbers collected increase in increasingly cooler wetter habitat types, few variables are significantly correlated with ant abundance.

One of the few clear relations between F. neorufibarbis and environmental characteristics is with stand density; in all habitat types in Oregon and 2 out of 3 in Montana, significantly more F. neorufibarbis were collected in open stands. The percent canopy coverage was also negatively correlated with the abundance of F. neorufibarbis over all plots in Montana.

Wheeler and Wheeler (1963) and Francoeur (1973) consider F. neorufibarbis a dominant ant of boreal and alpine forests. Gregg (1963) reported the species from a wide range of forest types and found the species common even at high elevations. He considered F. neorufibarbis extremely cold tolerant. Our findings in Montana were consistent with his observations; highest numbers were collected in the coldest, highest elevational habitat type (ABLA/MEFE).

Francoeur also states that F. neorufibarbis is essentially a forest species. It nests commonly in rotten wood or organic material although it has been reported nesting in soil in western North America. Letendre et al. (1971) considers that distribution of the species at least in some areas of Quebec, may be limited by the availability of suitable nesting sites - woody debris. Although we found no significant correlations between the abundance of F. neorufibarbis and the volume of dead wood in any category or decay class, in both Montana and Oregon more individuals were collected on plots with high volumes of woody debris in the two habitat types where the species was most abundant (ABLA/MEFE and ABGR/LIBO - ABGR/VAME).

Thus we found F. neorufibarbis distributed throughout both areas where we worked and tolerant of the cold, wet conditions found in subalpine fir habitat types. Its abundance is inversely related to stand density and may be influenced by the availability of nesting material.

Distribution of All Species

In both Oregon and Montana, the mesic habitat types were richer in ant species and total numbers collected. While the number of species was reduced in habitat types representing more extreme conditions, the number of ants collected remained comparatively high, usually due to the dominance of one species. The collections in the PSME/SYAL h.t. in Montana and the ABLA/VAME h.t. in Oregon are exceptions to this trend. The plots in the ABLA/VAME h.t. were located in a cold air drainage where the number of frost free days are usually less than on surrounding slopes. Thus, prolonged periods of

cool temperatures may limit the suitability of this area to many species of ants.

Much fewer species and individual ants were collected in the PSME/SYAL h.t. in Montana compared to that habitat in Oregon. As discussed earlier, the average conditions in this habitat differed between states. In general the plots in Montana had more ponderosa pine than Douglas-fir in the overstory, fewer understory species and lower cover, less woody debris and less accumulated organic matter. Thus the Montana plots represented a more xeric extreme for this habitat type. The greater richness and environmental diversity of the plots in Oregon may also explain why more species and more individual ants were collected there. Whitford and Gentry (1981) working in southern longleaf pine plantations considered the mature stands rather sterile environments and found the greatest number of ant species in newly planted areas where increased understory vegetation and open canopies increased the diversity of the site.

The occurrence of only a few species throughout the range of habitat types is not surprising, considering that as a whole ants are more common in tropical conditions. Several genera, such as Formica, are adapted to temperate zones or have members that are adapted to cooler conditions while the majority of the genus is tropical (eg. Camponotus). The number of species that can survive in boreal and alpine forests is not large, however, due not to a lack of moisture but to fewer frost free days. Researchers who have done extensive collecting in North American coniferous forests have also commented on the monotony of ant species (Gregg 1963, Wheeler 1917).

The 3 Formica species collected commonly in Oregon and Montana are all members of the Formica fusca species group. Although our research (Chapter III) showed that all were predators on western spruce budworm pupae, all were less active predators than either members of the Formica rufa species group or the genus Camponotus. The use of species in the Formica rufa group as biological control agents of forest pests has a long history in Europe (Adlung 1966) and has been investigated in eastern Canada (Finnegan 1971). The F. rufa group is favored over other species groups in the genus because the

workers are large, aggressive, take a wide variety of prey and because colonies are usually very populous. However, our studies show that member of this group are not commonly found throughout the range of habitat types examined in Oregon and Montana. Only 2 species of this group (F. haemorrhoidalis and F. obscuripes) were collected in Oregon, and these were only taken from a total of 3 plots. In general, species of the F. rufa group are found in very open stands, forest meadows, road edges and other areas where the ground receives considerable solar radiation. They are apparently not adapted to closed stands, even within the warm-dry extreme of the moisture-temperature gradients we examined.

Conclusion

Although the species complex varied, ant predators of the western spruce budworm foraged in the canopies of host trees throughout a wide range of forest conditions suitable for the budworm. Absolute numbers of ants collected were low in only 2 types--PSME/SYAL h.t. in Montana and ABLA/VAME h.t. in Oregon--and both represent (although for different reasons) conditions unfavorable for ants. All common ant species were also most active in the canopy during the period when budworm larvae and pupae were present in the foliage (first sample period).

The abundance of all the common species varied considerably among plots over the range of habitat types where they were collected, and the abundance of each species was correlated with a slightly different set of environmental variables. However, in both states, most species were more abundant in less dense stands. Thus it appears that silvicultural manipulations that open up stands would also create conditions more favorable for the colonization of ant predators of the budworm. Reducing stand density is also recommended for silvicultural control of the budworm (Cates and Wulf 1984), and for increasing the suitability of the stands for insectivorous birds that also prey on budworm (Takekawa et al. 1982).

Finally, although members of the Formica rufa species group have been shown to be active budworm predators (Bain 1974, McNeil et al. 1978, Chapter III) their usefulness in the biological control of the western spruce budworm is limited unless stands are greatly manipulated to create conditions favorable to their colonization. It is not likely that the kinds of modifications necessary to promote colonization by members of F. rufa group would be compatible with silvicultural practices in western North America. The abundance of members of the genus Camponotus throughout a range of stand conditions, coupled with the active predation demonstrated by some members (Markin 1979, Chapter III), make this group a more promising subject for further study as possible biological control agents of the western spruce budworm.

Bibliography

- Adlung, K. G. 1966. A critical evaluation of the European research on use of red wood ants (Formica rufa group) for the protection of forests against harmful insects. Z. Angew. Entomol. 57: 167-189.
- Allen, D. C., F. B. Knight, and J. L. Foltz. 1970. Invertebrate predators of the jack-pine budworm, Choristoneura pinus, in Michigan. Ann. Entomol. Soc. Am. 63: 59-64.
- Ayre, G. L. 1959. Food habits of Formica subnitens Creighton (Hymenoptera: Formicidae) at Westbank, British Columbia. Insectes Sociaux 6: 105-114.
- Ayre, G. L. 1963a. Laboratory studies on the feeding habits of seven species of ants (Hymenoptera: Formicidae) in Ontario. Can. Entomol. 95: 712-715.
- Ayre, G. L. 1963b. Feeding behavior and digestion in Camponotus herculeanus (L.) (Hymenoptera: Formicidae). Entomol. exp. appl. 6: 165-170.
- Ayre, G. L. and D. E. Hitchon. 1968. The predation of tent caterpillars, Malacosma americana (Lepidoptera: Lasiocampidae) by ants (Hymenoptera: Formicidae). Can. Entomol. 100: 823-826.
- Bain, O. G. 1974. Two wood ant species attacking western spruce budworm, Choristoneura occidentalis (Lepidoptera: Tortricidae) in western Montana. Unpubl. M.S. Thesis. School of Forestry, University of Montana, Missoula, MT.
- Bernstein, R. and M. Gobbel. 1979. Partitioning of space in communities of ants. J. Anim. Ecol. 48: 931-942.
- Bradley, G. A. 1972. Transplanting Formica obscuripes and Dolichoderus tashenbergi (Hymenoptera: Formicidae) colonies in jack pine stands of southeastern Manitoba. Can. Entomol. 104: 245-249.
- Bradley, G. A. 1973. Interference between nest populations of Formica obscuripes and Dolichoderus tashenbergi (Hymenoptera: Formicidae). Can. Entomol. 105: 1525-1528.
- Bradley, G. A. and J. D. Hinks. 1968. Ants, aphids and jack pine in Manitoba. Can. Entomol. 100: 40-50.
- Campbell, R. W. 1984. Population Dynamics. In M. H. Brookes [ed.], Western Spruce Budworm. U.S. Dept. Agric. Tech. Bull. (in press).
- Campbell, R. W. and T. R. Torgersen. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. Environ. Entomol. 11: 111-114.

- Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *For. Sci.* (in press).
- Cates, R. G. and N. W. Wulf. 1984. Site and Stand Characteristics. In M. H. Brookes [ed.], *Western Spruce Budworm*. U.S. Dept. Agric. Tech. Bull. (in press).
- Cole, A. C. 1942. The Ants of Utah. *Amer. Midl. Nat.* 28: 358-388.
- Cotti, G. 1963. Bibliografia ragionata 1930-1961 del Gruppo Formica rufa in Italiano, Deutsch, English. Minist. Agric. For. Roma, Coll. Verde 8. 413 pp.
- Daubenmire, R. and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. *Wash. St. Univ. Agric. Exp. Stn. Tech. Bull.* 60. 104 pp.
- David, C. T. and D. L. Wood. 1980. Orientation to trails by a carpenter ant, Camponotus modoc (Hymenoptera: Formicidae). *Can. Entomol.* 112: 993-1000.
- Dixon, A. F. G. 1971a. The role of aphids in wood formation. I. The effect of the sycamore aphid, Drepanosiphon platanoides (Schr.) (Aphididae), on the growth of sycamore, Acer pseudoplatanus (L.). *J. Appl. Ecol.* 8: 165-179.
- Dixon, A. F. G. 1971b. The role of aphids in wood formation. II. The effect of the lime aphid, Eucallipterus tiliae L. (Aphididae), on the growth of the lime, Tilia x vulgaris Hayne. *J. Appl. Ecol.* 8: 393-409.
- Fellin, D. G., R. C. Shearer, and C. E. Carlson. 1983. Western spruce budworm in the northern Rocky Mountains. *W. Wildl.* 9: 2-7.
- Finnegan, R. J. 1971. An appraisal of indigenous ants as limiting agents of forest pests in Quebec. *Can. Entomol.* 103: 1489-1493.
- Finnegan, R. J. 1973. Diurnal foraging activity of Formica sublucida, F. sanguinea subnuda and F. fossiceps (Hymenoptera: Formicidae) in Quebec. *Can. Entomol.* 105: 441-444.
- Finnegan, R. J. 1974. Ants as predators of forest pests. *Entomophaga* 7: 53-59.
- Finnegan, R. J. 1975. Introduction of a predacious red wood ant Formica lugubris (Hymenoptera: Formicidae) from Italy to eastern Canada. *Can. Entomol.* 107: 1271-1274.
- Finnegan, R. J. 1977. Establishment of a predacious red wood ant Formica obscuripes (Hymenoptera: Formicidae) from Manitoba to eastern Canada. *Can. Entomol.* 109: 1145-1148.

- Finnegan, R. J. 1978. Predation by Formica lugubris (Hymenoptera: Formicidae) on Choristoneura fumiferana (Lepidoptera: Tortricidae). Can. For. Serv. Bi-Mon. Res. Note 34: 3-4.
- Flanders, S. E. 1951. The role of the ant in the biological control of homopterous insects. Can. Entomol. 83: 94-98.
- Fogel, R., M. Ogawa, and J. M. Trappe. 1973. Terrestrial decomposition: A synopsis. Coniferous For. Biome. US/IBP. Rep. 135. 12 pp.
- Fowler, H. G. and R. B. Roberts. 1980. Foraging behavior of the carpenter ant, Camponotus pennsylvanicus, (Hymenoptera: Formicidae) in New Jersey. J. Kans. Entomol. Soc. 53: 295-304.
- Francoeur, A. 1973. Révision taxonomique des especes néarctiques du groupe Fusca, genre Formica (Formicidae, Hymenoptera). Soc. Entomol. du Quebec. Mem. no. 3. 316 pp.
- Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-8. 417 pp.
- Gauch, H. G. 1982. Multivariate Analysis in Community Ecology. Cambridge Univ. Press. New York. 298 pp.
- Gösswald, K. 1951. Die rote Waldameise im Dienste der Waldhygiene. Forstwirtschaftliche, Bedeutung, Nutzung, Lebensweise, Zucht, Vermehrung und Schutz. M. Kinau Verlag, Lüneburg. 160 pp.
- Green, G. W. and C. R. Sullivan. 1950. Ants attacking larvae of the forest tent caterpillar, Malacosoma disstria Hbn. (Lepidoptera: Lasiocampidae). Can. Entomol. 82: 194-195.
- Gregg, R. W. 1963. Ants of Colorado. Univ. Colo. Press. Boulder. 792 pp.
- Hall, F. C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southwestern Washington. U.S. Dep. Agric. For. Serv. Reg. 6 Reg. Guide 3-1. 62 pp.
- Hill, M. O. 1979. DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Sect. Ecol. and Syst. Cornell Univ. Ithaca. 52 pp.
- Horstman, K. 1970. Untersuchungen über den Nahrungserwerb der Waldameisen (Formica polyctena Foerster) im Eichenwald. I. Zusammensetzung der Nahrung, Abhängigkeit von Witterungsfaktoren und von der Tageszeit. Oecologia 5: 138-157.

- Horstman, K. 0972. Untersuchungen über den Nahrungserwerb der Waldameisen (Formica polycтена Foerster) im Eichenwald II. Abhängigkeit von Jahresverlauf und von Nahrungsangebot. *Oecologia* 8: 371-390.
- Il'nitzky, S. and J. M. McLeod. 1965. Notes on ants associated with Neodiprion swainei Midd. in jack pine stands in Quebec. *Can. Dep. For. Bi-Mon. Prog. Rep.* 21: 1-2.
- Jennings, D. T. 1971. Ants preying on dislodged jack-pine budworm larvae. *Ann. Entomol. Soc. Am.* 64: 384-385.
- Johnson, C. G. 1982. An interpretation of synecologic relationships in the Billy Meadows area of the Willowa Whitman National Forest. Unpubl. Ph.D. Thesis Dept. Rng. Res. Oreg. St. Univ. 380 pp.
- Krajicek, J., K. Brinkman, and S. Gingrich. 1961. Crown competition - a measure of density. *For. Sci.* 7: 35-42.
- Laine, K. J. and P. Niemela. 1980. The influence of ants on the survival of mountain birches during an Oporinia autumnata (Lep., Geometridae) outbreak. *Oecologia* 47: 39-42.
- Letendre, M., A. Francoeur, R. Béique and J. G. Pilon. 1971. Inventaire des fourmis de la station de biologie de L' Université de Montréal, St. Hippolyte, Quebec. *Natur. Can.* 98: 591-606.
- Majer, J. D. 1976. The ant mosaic in Ghana cocoa farms: further structural consideration. *J. Appl. Ecol.* 13: 145-55.
- Mallis, A. 1941. A list of the ants of California with notes on their habits and distribution. *S. Calif. Acad. Sci. Bull.* 40: 61-96.
- Markin, G. P. 1979. Ants as predators of the western spruce budworm. Paper presented at 1979 Entomol. Soc. Am. annual meeting, Denver, Col.
- Maser, C., R. G. Anderson, K. Cromack, J. T. Williams, and R. W. Martin. 1979. Dead and Down Woody Material, pp 78-95. In J. W. Thomas [ed.], *Wildlife Habitats in Managed Forests - the Blue Mountains of Oregon and Washington*. U.S. Dept. Agric. For. Serv. Agric. Handbook 553.
- Mathers, W. G. 1932. The spruce budworm in British Columbia. *For. Chron.* 8: 154-157.
- McNeil, J. N., J. Delisle, and R. J. Finnegan. 1977. Inventory of aphids on seven conifer species in association with the introduced red wood ant Formica lugubris (Hymenoptera: Formicidae). *Can. Entomol.* 109: 1199-1202.

- McNeil, J. N., J. Delisle, and R. J. Finnegan. 1978. Seasonal predatory activity of the introduced red wood ant, Formica lugubris (Hymenoptera: Formicidae) at Valcartier, Quebec, in 1976. Can. Entomol. 110: 85-90.
- Morris, R. F. 1963. Predation and the spruce budworm, pp 244-248. In R. F. Morris [ed.], The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31.
- Otvos, I. S. 1977. Some parasites and insect predators of the blackheaded budworm in Newfoundland. Can. For. Serv. Bi-Mon. Res. Note 33: 11-12.
- Pavan, M. 1960. Les transplantations de Formica lugubris sur les Apennins de la province de Pavie. Italy Minist. Agric. For. Coll. Verde 7: 161-169.
- Petal, J. 1978. The role of ants in ecosystems, pp 293-325. In M. C. Brian [ed], Production ecology of ants and termites. Cambridge University Press, Cambridge.
- Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest Habitat Types of Montana. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-34. 174 pp.
- Post, D. C. and R. L. Jeanne. 1982. Rate of exploitation of arboreal baits by ants in an old-field habitat in Wisconsin. Amer. Midl. Nat. 108: 88-95.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on herbivores and natural enemies. Ann. Rev. Ecol. Syst. 11: 41-65.
- Reilly, J. J. and W. L. Sterling. 1983. Dispersion patterns of the red imported fire ant (Hymenoptera: Formicidae), aphids, and some predaceous insects in east Texas cotton fields. Environ. Entomol. 12: 380-385.
- Rosengren, R. 1971. Route fidelity, visual memory and recruitment behavior in foraging wood ants of the genus Formica (Hymenoptera: Formicidae). Acta Zool. Fennica 133: 1-102.
- Sanders, C. J. 1964. The biology of carpenter ants in New Brunswick. Can. Entomol 96: 894-909.
- Sanders, C. J. 1970. The distribution of carpenter ant: colonies in the spruce-fir forests of north-western Ontario. Ecology 51: 865-873.

- Sanders, C. J. 1972. Seasonal and daily activity patterns of carpenter ants (Camponotus spp.) in northwestern Ontario. Can. Entomol 104: 1681-1687.
- Silver, G. T. 1960. Notes on a spruce budworm infestation in British Columbia. For. Chron. 36: 362-374.
- Skinner, G. J. 1980a. Territory, trail structure, and activity patterns in the wood-ant Formica rufa (Hymenoptera: Formicidae) in limestone woodland in northwest England. J. Anim. Ecol. 49: 381-394.
- Skinner, G. J. 1980b. The feeding habits of wood ants Formica rufa (Hymenoptera: Formicidae), in limestone woodland in northwest England. J. Anim. Ecol. 49: 417-433.
- Skinner, G. J., and J. B. Whittaker. 1981. An experimental investigation of interrelationships between the wood ant (Formica rufa) and some tree-canopy herbivores. J. Anim. Ecol. 50: 313-326.
- Southwood, T. R. E. 1978. Ecological Methods. John Wiley and Sons. New York. 524 pp.
- Sudd, J. H., J. M. Douglas, T. Gaynard, D. M. Murray and J. M. Stockdale. 1977. The distribution of wood-ants (Formica lugubris Zelterstedt) in a northern English forest. Ecol. Entomol. 2: 301-313.
- Takekawa, J. Y., E. O. Garton, L. A. Langelier. 1982. Biological control of forest insect outbreaks: the use of avian predators. Trans. 47th N. Amer. Wildlife & Nat. Res. Conf. Wash. D.C. 1982: 393-409.
- Taylor, L. R. 1961. Aggregation, variance and the mean. Nature, Lond. 189: 732-735.
- Taylor, L. R. 1965. A natural law for the spatial disposition of insects. Proc. XIIth Int. Cong. Entomol. 1964: 396-397.
- Taylor, L. R., I. P. Woiwod, and J. N. Perry. 1978. The density-dependence of spatial behavior and the rarity of randomness. J. Anim. Ecol. 47: 383-406.
- Thomson, H. M. 1957. A note on the predation of spruce budworm pupae. Can. For. Serv. Bi-Mon. Res. Notes 13: 2.
- Way, M. J. 1963. Mutualism between ants and honeydew producing Homoptera. Ann. Rev. Entomol. 8: 307-344.
- Wellenstein, G. 1980. Ausirkung hügelbauender Waldameisen der Formica rufa - Gruppe auf forstschädliche Raupen und das Wachstum der Waldbäume. Z. für Ange. Entomol. 89: 144-157.

- Wheeler, G. C. and J. Wheeler. 1963. The Ants of North Dakota. Univ. N. Dakota. Grand Forks. 326 pp.
- Wheeler, G. C. and J. Wheeler. 1978. Mountain ants of Nevada. Great Basin Nat. 38: 379-396.
- Wheeler, W. M. 1917. The mountain ants of western North America. Proc. Amer. Acad. Arts & Sci. 52: 457-569.
- Whitford, W. G., and J. B. Gentry. 1981. Ant communities of southeastern long leaf pine plantations. Environ. Entomol. 10: 183-185.
- Wilkinson, R. C., A. P. Bhatkar, W. H. Whitcomb, and W. J. Kloft. 1980. Formica integra (Hymenoptera: Formicidae). 3. Trial introduction into Florida. Fla. Entomol. 63: 142-146.