NUTRITIONAL BASIS FOR FEEDING ZONE PREFERENCE OF *ARHOPALUS FERUS* (COLEOPTERA : CERAMBYCIDAE)

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ABSTRACT

The inner bark and sapwood of **Pinus radiata** are compared regarding their nutritional value to larvae of the cerambycid **Arhopalus ferus**. Larvae feeding in the inner bark, for which they show a strong preference under field conditions, had a relative growth rate four times that of sapwood-fed individuals (48.7 and 11.3 mg/g/day respectively). Nitrogen concentration was much higher in the inner bark than in the sapwood, as were soluble carbohydrate levels. Food consumption, growth, and food utilisation indices are presented for bark-fed larvae as well as estimated nitrogen assimilation.

INTRODUCTION

The subcortical zone of forest trees provides an environmentally stable and protected ecological niche for the development of a wide variety of forest insects, including scolytids, cerambycids, curculionids, and buprestids as well as certain Lepidoptera and Diptera. Most subcortical insects confine themselves to dead or dying trees and logging debris and are innocuous or even beneficial, but some, including *Dendroctonus* Erichson, *Ips* DeGeer, and *Scolytus* Geoff. are destructive forest pests. The probability of such pests becoming established in New Zealand pine forests cannot be lightly dismissed.

The present study was aimed at establishing a nutritional basis for feeding preference of the cerambycid beetle, *Arhopalus ferus* (Mulsant), which attacks dead and freshly felled pines. Its general biology (Hosking and Bain, 1977) and the influence of temperature on larval growth and pupation (Hosking, 1977) have recently been studied. The insect utilises two distinct feeding zones, the inner bark and the sapwood, but clearly prefers the former. Accordingly, the feeding preference and the growth rates of larvae feeding in these two distinct zones were compared. This study relates, from a nutritional viewpoint, the observed differences in larval feeding and growth rates with the chemical composition of the two zones. The efficiency of conversion of ingested material by larvae from the inner bark has also been examined.

Most studies of insect nutrition deal with foliage feeders and stored products pests (House, 1974; Waldbauer, 1968), in environments very different both mechanically and nutritionally from the subcortical zone. The limited studies dealing with subcortical species have almost exclusively resulted from projects associated with artificial rearing programmes (Balogun, 1969; Bedard, 1966; Scott and Berryman, 1971) and cannot be directly related to the natural feeding zone.

MATERIALS AND METHODS

Rectangular (190 × 110 × 7 mm) slices of (a) bark (comprising phloem, cambium and some cortex) and (b) outer sapwood, were cut from the bole of a 7-year-old *Pinus radiata* D. Don. The samples were taken in midwinter from a tree felled 4 weeks previously. Subsamples 20 × 110 × 7 mm were cut from each end of the slices and their moisture content determined by drying at 80°C to constant weight. The main samples were sandwiched between two 5 mm plexiglass sheets which were held firmly together with PVC tape (Fig. 1).

Larvae of *A. ferus* were hatched from a single egg mass and reared in bark nurse sandwiches until they weighed 10 to 20 mg. They were weighed and placed in an appropriate sized hole drilled in the end of the experimental slices. A total of 15 bark and 15 sapwood sandwiches were placed in a rearing chamber at 18.5 ± 1°C and 55 ± 5% RH. The bark sandwiches were incubated for 48 days and the sapwood for 63 to 68 days, periods considered adequate to allow satisfactory estimates of growth rates. The moisture content of each sandwich was estimated from the mean of the two subsamples.

After incubation the samples were opened and the larvae weighed. The frass and uneaten material were separated, dried at 80°C and ground in a Wiley mill. Of the 30 samples, 2 bark and 1 sapwood samples were discarded because the larvae did not establish.

Eight additional larvae were reared in bark sandwiches for 40 days, after which the frass was removed from the clearly defined galleries, dried, and weighed. Impressions of the galleries were taken with oil-based modelling clay and their volumes accurately

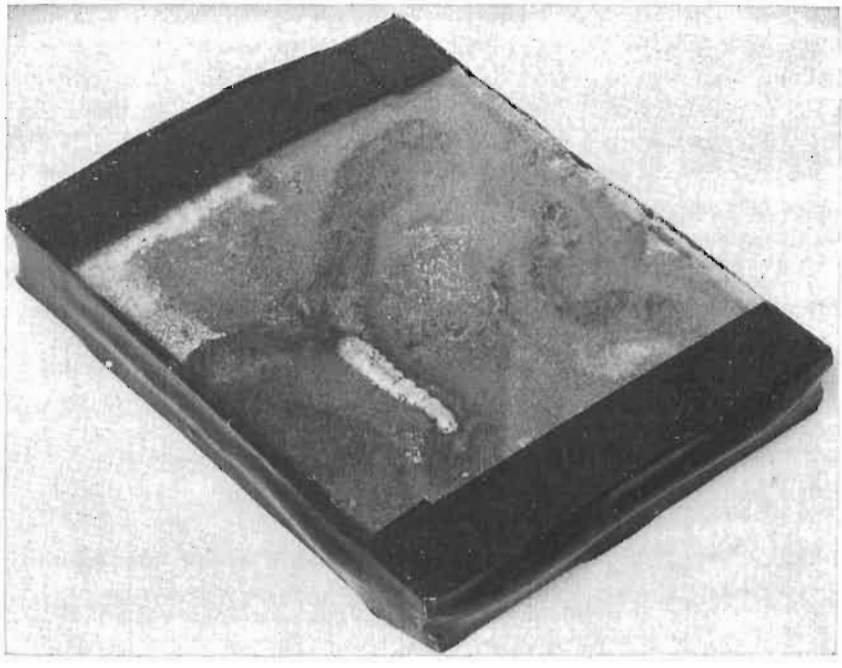

FIG. 1—Well developed larva of **A. ferus** in bark rearing sandwich.

measured by a water displacement method described by Burdett (1979). Frass density was calculated from frass weight and gallery volume for each larva and a mean value (269 mg/ml, SD = 13.8) used to calculate gallery volumes for the remaining 13 bark-fed larvae. No method was devised to estimate the volume of the sapwood galleries which were completely enclosed, irregular in shape, and packed with frass.

The density of 4-week-old inner bark (hereafter referred to as "fresh") was determined from seven samples, the volumes of which were initially determined by liquid displacement and weights obtained after oven drying. The mean of these seven determinations was used for estimating the nitrogen content of the larval food. Calorific values were determined in an adiabatic calorimeter. Total nitrogen was measured by the micro-Kjeldahl method (McKenzie and Wallace, 1954).

RESULTS

Larval Growth Rates

Absolute weight gain is an unsatisfactory basis for comparing the growth rates of larvae, particularly when the growth periods differ.

Accordingly relative growth rate (RGR) was used as the measure of growth rate, this being calculated (Gordon, 1968) as shown in Table 1.

To avoid destructive sampling live larval weights were used in all growth calculations. A very close relationship (R = .981) was found between live and dry weights for 50 larvae ranging from 3.5 mg to 480.5 mg live weight. The gut contents of feeding larvae contributed only 7.1% of live larval weight.

The relative growth rate of the bark-reared larvae was more than 4 times that of the sapwood feeders (Table 1). Frass production per mg increase in fresh body weight for sapwood larvae was more than twice that of the bark feeding individuals and their average daily frass production was less than one-fifth that of the bark-fed larvae. The larvae in bank sandwiches always fed against the plexiglass on the cambial side of the substrate.

Two larvae feeding in sapwood had weight gains about twice the average for larvae in sapwood and were found to be feeding in a band of resin-impregnated wood. Each larva fed in a single narrow band, 1 mm wide and 7 mm thick, until this zone had been completely consumed. The growth rates and frass production of these two larvae were intermediate between the bark-fed and sapwood-fed individuals (Table 1).

No relationship was found between moisture content of the feeding material and larval growth rate. The bark moisture content ranged from 79 to 192% and the sapwood from 159 to 250%, almost certainly well above any lower limits for this insect (Hosking and Bain, 1977).

Nitrogen Concentrations and Assimilation

Total nitrogen per unit dry weight in the fresh bark samples was almost ten times that of similar aged sapwood samples, and although it declined to about half this level over the 48-day larval feeding period it was still six times higher than in sapwood samples of the same age (Table 2). The nitrogen content of aged resin impregnated wood was almost twice that of aged sapwood.

TABLE 1—Mean larval growth rates and frass production by **A. ferus** larvae feeding in bark (13 samples), resin zone (2 samples), and sapwood (12 samples)

	BARK		RESIN ZONE		SAPWOOD	
	Mean	SD	Mean	SD	Mean	SD
Initial larval weight (mg)	14.9	3.0	18.2	3.0	14.7	2.8
Final larval weight (mg)	154.4	33.5	68.5	3.4	31.6	11.1
Feeding days	48		65		63-68	
Fresh weight gain during feeding period (mg)	139.5	32.1	50.2	0.4	16.9	9.0
1. Exponential mean live weight during feeding period (mg)	59.5	11.0	38.0	3.7	22.0	5.9
Fresh weight gain (mg/day)	2.9	0.66	0.76	0.03	0.26	0.14
2. Relative growth rate (mg/g/day)	48.7	3.9	20.3	2.9	11.3	3.2
Dry weight of frass (mg)	1134	311	520	211	303	147
Frass production (mg/day)	23.6	6.5	7.9	2.8	4.9	2.4
Mg frass per mg fresh body weight	8.1	1.4	10.3	4.2	19.1	6.5

1. Exponential mean live weight (A) $= \dfrac{W_2 - W_1}{\log_e W_2 - \log_e W_1}$

2. Relative Growth Rate (RGR) $= \dfrac{\log_e W_2 - \log_e W_1}{T}$

Where W_1 = initial live larval weight
W_2 = final live larval weight
T = duration of feeding period

TABLE 2—Total nitrogen, as a percent of dry weight, of larval food and frass with associated larval growth rates for **A. ferus**

Sample	% Total N			Relative Growth Rate (RGR)[2]	
	n	mean	SD	mean	SD
[1] Bark — Fresh	5	0.867	0.069	48.7	3.9
— Aged	2	0.440	0.042		
Sapwood — Fresh	5	0.088	0.007	11.3	3.2
— Aged	5	0.072	0.001		
Resin zone — Aged	2	0.136	0.018	20.3	2.9
Bark frass	5	0.608	0.059		
Sapwood frass	5	0.084	0.009		

[1] Fresh = condition at time larvae placed in material
Aged = condition at time larvae taken from material
[2] For definition see Table 1.

An estimate of nitrogen assimilation by *A. ferus* could only be made for bark-fed larvae where the change in density between food taken in and frass ejected could be calculated for measured gallery volumes. Using a value of 0.6535% (mean of fresh and aged bark) for the nitrogen content of larval food, larval assimilation was estimated to be 27% (Table 3). The relationship of this figure to protein utilisation is discussed later in this paper.

TABLE 3—Apparent nitrogen assimilation by **A. ferus** larvae feeding in bark (n = 7)

	Mean	SD
Fresh feeding zone density (mg/ml)	342	8.7
Frass density (mg/ml)	269	13.8
[1] Estimated N consumed (mg/ml)	2.24	0.06
Estimated N excreted (mg/ml)	1.64	0.08
% N assimilated	26.8	

[1] Mean nitrogen content of fresh and aged bark (Table 2).

Consumption and Utilisation of Food

The consumption index (CI), relative growth rate (RGR) and conversion of ingested food (ECI), as defined by Gordon (1968), were determined for the 8 bark-fed larvae for which the gallery volume, and hence the weight of ingested material, could be calculated (Table 4).

TABLE 4—Consumption, growth, and utilisation indices of 8 **A. ferus** larvae feeding in bark

			Mean	SD
	(T)	Feeding period in days	48	
	(F)	Dry weight of food consumed (mg)	1495	513
1.	(A)	Exponential mean live weight during T	59.5	11.0
	(CI)	Consumption index $\frac{F}{TA}$	0.68	0.21
	(G)	Fresh weight gain during T (mg)	135.4	27.5
1.	(RGR	Relative growth rate (mg/g/day)	48.4	3.8
	(ECI)	Conversion of ingested food $\frac{RGR}{F}$ (%)	3.4	1.2

1. See Table 1 for definition.

The mean exponential weight of individual larva during the feeding period (A) was generally related within treatments to the initial larval weight. The consumption index (CI), conversion of ingested food (ECI), food ingested (F), and weight gain (G) all showed considerable variability between individuals. However, relative growth rate (RGR) was much more uniform (Table 4).

A net food use efficiency (Hosking and Knight, 1976; Odum, 1971), derived from the measurement of the energy contents of food and frass, was determined for the bark-fed larvae by the following formula:

$$\frac{(\text{Food Density})\ (\text{Input; Joules/g}) - (\text{Frass Density})\ (\text{Output; Joules/g})}{(\text{Food Density})\ (\text{Input; Joules/g}).} \times \frac{100}{1}$$

The energy content and density of the relevant components were calculated to be 18406 joules/g and 0.342 g/ml for food and 18561 joules/g and 0.269 g/ml for frass, giving a net use efficiency of 23.7%.

DISCUSSION

Hosking and Bain (1977) demonstrated that larvae of *A. ferus* preferred feeding in the inner bark of pines compared with the sapwood, which was only used when the bark had been consumed. The present study was designed to eliminate the influences of temperature and critical variations in moisture content from the comparison of larval development in sapwood and bark. Under field conditions microclimate does have a strong influence on the rate of growth (Hosking, 1977).

The importance of nitrogen in the nutrition of larvae has been demonstrated by Slansky and Feeny (1977), Medrano and Brassani (1977), and Becker (1963). It is known to affect larval growth rates, as well as longevity, fecundity and reproductive rates of the adults.

Becker (1963) found a linear relationship between larval growth rate and protein concentration for the cerambycid *Hylotrupes bajulus* L. from 0.1 to 0.6% dry weight of food. If 64% of the total nitrogen is assumed to be in the form of protein (Baker *et al.*,

1970) the protein content of bark and sapwood of radiata pine fall within and just below these limits at 0.56% and 0.06% respectively. The growth rate of larvae in the resin zone (Table 2) is 37% below that expected from the above relationship. However, the resin zone was very narrow and the larvae fed in normal sapwood after the zone had been exhausted.

Nitrogen as a limiting factor in larval growth is likely to be evident in wood- and bark-feeding insects. Insects ingesting herbaceous tissue utilise a substrate which typically contains 1 to 5% N by weight compared with woody tissues with only 0.03 to 0.1% N (Cowling and Merrill, 1966). Low nitrogen levels may well be responsible for the low ECI of bark-fed larvae compared with values for foliage feeders listed by Gordon (1968). Nevertheless, the fact that the sapwood frass contains roughly the same proportion of N as ingested sapwood would suggest that the total concentration of N was not decisive in this case.

Carbohydrates as an energy source have been shown to have a major influence on the development rate of insects (Burton *et al.*, 1977; Hirano and Ishi, 1962; Becker, 1963) although considerable variation exists in the range of carbohydrates that individual species can utilise. Barras and Hodges (1969) showed the bark beetle *Dendroctonus frontalis* Zimm. to be utilising sucrose, glucose and fructose present in the phloem of *Pinus taeda* L.

Cranswick (unpubl.) measured the carbohydrate content of various tissues of *Pinus radiata* and showed bark : outer sapwood ratios of 6.5 : 1 for both glucose and fructose and 2.3 : 1 for sucrose. The bark clearly offers significant advantages over sapwood in terms of readily assimilated carbohydrates.

Marked differences in ingestion, assimilation and frass production rates between bark- and sapwood-fed larvae are likely to be intimately related to mechanical and chemical constraints on the degradation of woody tissue in the insect gut. The present study suggests that for *A. ferus* these constraints are more severe in the utilisation of sapwood compared to inner bark.

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