RESISTANCE OF DOUGLAS FIR TO PSEUDOCOREMIA SUAVIS

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ABSTRACT

The resistance of a 70-year-old **Pseudotsuga menziesii** (Mirb.) Franco (Douglas fir) to a major geometrid defoliator has been investigated. The resistance was largely confined to the current-year foliage and **Pseudocoremia suavis** (Butler) (Lepidoptera : Geometridae) larvae feeding on this exhibited high mortality and reduced growth rates and final weights.

INTRODUCTION

The selection of host plants by insects involves discrimination between physical and chemical cues proffered by the plant in the form of nutrients, attractants, and repellents. Variation within and between plants dictates which plants, or plant parts, are eaten (Hsiao 1969; Feeny 1970; Schoonhoven 1972).

Physical and chemical variation within Douglas fir has been well documented (Maarse & Kepner 1970; von Rudloff 1972; van den Driessche 1973; Rehfeldt 1974; Zarvarin & Snajberk 1975), and varietal resistance to some herbivores has been noted. Dimock *et al.* (1976) demonstrated browsing preferences by deer and hare among different Douglas fir genotypes. Resistance to the Douglas fir woolly aphid (*Gillettlla cooleyi* Gill.) was found in a survey of 59 populations of Douglas fir by Mejnartowicz & Szmidt (1978), and McDonald (1979) found relative feeding differences, within seven populations of Douglas fir seedlings, by Western spruce budworm (*Choristoneura occidentalis* Freeman).

This report evaluates Painter's (1958) "antibiotic" and "non-preference" resistance of a 70-year-old Douglas fir to the larvae of *Pseudocoremia suavis,* an indigenous geometrid with a host range which includes indigenous and exotic hardwoods and softwoods. Epidemics of *P. suavis* have been recorded on pines (*Pinus* spp.) in the 1950s and 1960s, and on Douglas fir in 1970, 1972, and 1978 (Kay 1982).

METHODS

The apparently resistant tree was discovered quite fortuitously during the sampling of about 20 trees in an energy flow study of *P. suavis* on Douglas fir. It was an edge tree in a 44.6-ha stand planted in 1905 in Whakarewarewa State Forest (38° 10′S, 176° 15′E) and was phenotypically indistinguishable from its neighbours. The seed source for the stand is unknown, but was probably coastal north-west America. Foliage up to 3 m above ground level was sampled from the resistant tree (*R*) and adjacent trees (*NR*).

Caterpillars were reared from eggs laid by moths caught in a Rothamsted pattern light trap about 1 km from the stand. Conditions maintained during the experiments were 14 h light/10 h dark, 20° ± 1°C, and 80% ± 5% RH, and insects were caged in glass jars capped with thin, punctured, plastic film. Foliage was collected from the trees on the day of an experiment and sprigs of foliage fed to caterpillars were individually supplied with a vial of water to maintain turgor. Shoots were changed before complete defoliation to prevent cambial chewing.

Feeding Preference

Newly moulted fifth-instar larvae were caged individually with shoots of current-year *R* and *NR* foliage. The shoots were cut and their foliage thinned to similar proportions and they were bound together at the base so that their needles entwined. The needles removed were dried (60°C) and weighed to determine a mean dry weight per needle per shoot.

The shoots were examined 2, 4, and 6 days after the introduction of the caterpillar and the number of missing and chewed needles recorded. The partly chewed needles and the petiole stubs remaining from the missing needles were then removed, dried, and weighed. Consumption was estimated by subtracting their combined weight from that estimated from the product of the mean needle weight plus the number of missing and chewed needles. Needles were removed from shoots, where necessary, to maintain approximately equal amounts of foliage on the two sprigs being compared. Dropped needle fragments of indeterminable origin were collected, dried, and weighed.

Antibiosis

(1) The development of individually caged fifth-instar larvae, fed current-year *R* and *NR* foliage or starved (20 larvae per treatment), with water available to caterpillars from a cotton wick, was recorded at 2-day intervals till death or pupation.

(2) Newly hatched first-instar larvae were placed at 10 per shoot on current-year, 1-year-old, and 2-year-old *R* and *NR* foliage, with three replicates (caterpillars were caged individually from the fourth instar). Developmental time, survival, and pupal weights were recorded.

(3) Newly moulted fifth-instar larvae were caged individually on shoots of current, 1-year-old, and 2-year-old foliage. Caterpillars had been fed only foliage from a 23-year-old Douglas fir, growing about 1 km from the study trees, which had been used previously to rear *P. suavis*. Developmental time, growth rate, and mortality were recorded.

Statistical tests applied included t-test, ANOV, and S.N.K. multiple range test.

RESULTS

The consumption of foliage by fifth-instar larvae in a free choice situation was significantly greater on nonresistant than on resistant foliage (Table 1). The difference was least marked during the initial feeding period. Foliage fragments of indeterminable origin collected during the free choice experiment averaged less than 8% of the total foliage consumed and were ignored during statistical comparisons.

TABLE 1—Dry weight of foliage, from resistant (**R**) and nonresistant (**NR**) trees, consumed by fifth-instar larvae over 2-day intervals during the first 6 days of feeding in a free-choice situation

	Days 1 & 2	Days 3 & 4	Days 5 & 6
Mean **NR** foliage consumed (mg)	15.8 ± 5.5	56.9 ± 5.7	83.1 ± 10.7
Mean **R** foliage consumed (mg)	6.4 ± 2.3	13.8 ± 4.1	24.7 ± 6.4
n	10	10	10
Σ **NR** - **R**	94.6	430.8	584.2
s.d.	13.4	17.7	47.6
t	2.23	7.70	3.88
p	<0.10	<0.001	<0.01

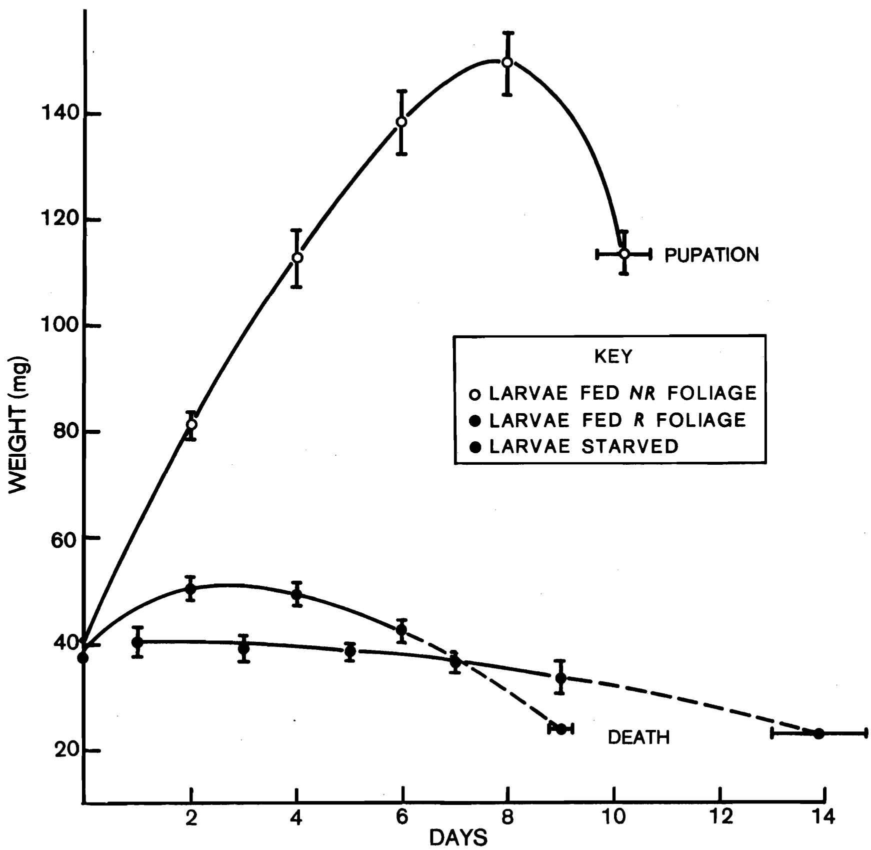

FIG. 1—Weight gain or loss by fifth-instar **P. suavis** larvae fed nonresistant foliage, resistant foliage, or starved. Bars indicate the magnitude of the standard error in weight or time, and dashed lines indicate the period over which caterpillar mortality was recorded.

In a comparison of fifth-instar larvae starved or fed resistant or nonresistant foliage in a no choice situation (Fig. 1), those feeding on resistant foliage initially gained weight, although to a much lesser extent than those fed nonresistant foliage, but subsequently died before the caterpillars that were starved.

There was over 90% mortality for caterpillars fed current-year resistant foliage from hatching to pupation (Table 2) and developmental time from hatching to pupation tended to be longer, although not significantly so. Pupal weights of those surviving, however, were significantly lower than those of larvae fed nonresistant or 3-year-old resistant foliage. No female pupae were reared from larvae fed current *R* foliage. The bulk of the mortality in all treatments was in the early instars (Table 3), but a high proportion of early instar survivors on resistant foliage died in later instars.

All caterpillars transferred from apparently salubrious Douglas fir foliage to current-year *R* foliage died (Table 4). Of those transferred to 1-year-old *R* foliage, 20% succumbed; the survivors had a significantly lower growth rate and a longer developmental time than those caterpillars fed 2-year-old *R,* or any age *NR,* foliage.

TABLE 2—A comparison of developmental times, pupal weights, and mortality of **P. suavis** reared, from hatching, on resistant and nonresistant foliage of different ages

Foliage type	Foliage age	n	Development time (days)	Pupal weights (mg)		Mortality (%)
				Male	Female	
Nonresistant	Current	29	37.1 ± 0.8a	89.2 ± 1.4b	97.6 ± 4.3d	10.3
	1-year-old	29	39.3 ± 0.8a	*	95.7 ± 4.0d	17.2
	2-year-old	27	41.3 ± 2.3a	91.3 ± 4.1b	103.9 ± 4.9d	11.1
Resistant	Current	29	45.5 ± 3.5a	69.4 ± 6.2c	*	93.1
	1-year-old	27	37.9 ± 0.8a	82.3 ± 3.4bc	90.7 ± 3.8d	7.4
	2-year-old	29	36.9 ± 0.5a	81.0 ± 1.8b	99.8 ± 3.6d	10.3

Means not followed by a common letter are significantly different ($p = 0.05$).
* No individuals of this gender reared from this treatment.

DISCUSSION

Tree *R* clearly shows some considerable resistance to *P. suavis* manifested as mortality, increased development time, decreased growth rates, and lower final weights of caterpillars that fed on the resistant foliage. Where a choice was offered, *P. suavis* showed a preference for nonresistant foliage and this preference appeared to be accentuated with previous experience of *R* foliage. The preference was not so strong as to deter the insects from feeding, and they fed, albeit slowly, until they succumbed to some toxic factor rather than starvation.

When fed resistant foliage from the time of hatching, *P. suavis* exhibited some tolerance of this toxic factor, although mortality was very high over the entire larval period. In contrast, those larvae fed resistant foliage only in their final instar succumbed rapidly. This may indicate the presence of an induced enzymatic detoxification system in larvae with early experience of the resistance factor (Brattsten *et al.* 1977). This defence appears to wane in later instars not exposed to the resistance.

TABLE 3—Developmental times and mortality, by instar, of larvae fed from hatching on resistant (**R**) and nonresistant (**NR**) foliage of various ages (n as in Table 2)

Foliage age		Instars 1		2		3		4		5	
		NR	**R**	**NR**	**R**	**NR**	**R**	**NR**	**R**	**NR**	**R**
Current-yr	Devel. time (days)	6.0 ± 0.1	8.14 ± 0.7	5.6 ± 0.2	5.9 ± 1.9	5.7 ± 0.2	7.6 ± 1.1	5.7 ± 0.2	11.0 ± 1.3	14.1 ± 0	10.3 ± 3.5
	Mortality (%)	3.5	51.7	3.6	28.6	0	40.0	0	0	0	33.3
1-yr	Devel. time (days)	6.5 ± 0.2	7.2 ± 0	5.2 ± 0.2	5.9 ± 0.3	6.1 ± 0.2	5.8 ± 0.1	6.7 ± 0.6	5.5 ± 0.7	14.7 ± 0.8	14.2 ± 0.8
	Mortality (%)	10.3	7.4	3.8	0	0	0	0	0	5.0	0
2-yr	Devel. time (days)	7.1 ± 0.4	6.1 ± 0.2	5.6 ± 0.1	6.0 ± 0.5	5.9 ± 0.2	5.8 ± 0.4	6.5 ± 0.4	5.6 ± 0.9	16.2 ± 2.3	12.7 ± 0.5
	Mortality (%)	7.4	3.5	0	7.1	0	0	0	0	0	0

TABLE 4—Mortality, growth, and development of last instar **P. suavis larvae** fed foliage of different ages from resistant and nonresistant trees

Foliage type	Foliage age	n	Mean body weight (mg) Initial	Final (pre pupa)	Development time (days)	Growth rate	Mortality (%)
Nonresistant	Current	10	38.0 ± 1.6a	111.3 ± 2.4b	9.2 ± 0.3c	10.8 ± 0.6d	0
	1-yr-old	10	39.0 ± 0.7a	119.6 ± 2.3b	8.9 ± 0.2c	11.5 ± 0.4d	0
	2-yr-old	10	38.5 ± 0.8a	118.4 ± 3.5b	9.5 ± 0.3c	10.8 ± 0.5d	0
Resistant	Current	10	38.1 ± 1.6a	39.5 ± 4.4	9.8 ± 0.6c*	-0.5 ± 1.0	100
	1-yr-old	10	37.2 ± 1.5a	106.5 ± 8.4b	14.7 ± 2.8	8.2 ± 1.5	20
	2-yr-old	10	36.2 ± 1.6a	119.5 ± 3.0b	8.6 ± 0.2c	12.5 ± 0.4d	0

* Time of death.

Means not followed by a common letter are significantly different ($p = 0.05$).

The resistance is largely confined to current-year foliage, with some expression in 1-year-old foliage. Seasonal and temporal change in chemical composition has been noted in the foliage of many plants, including Douglas fir (Maarse & Kepner 1970). Herbivore response has also been noted to vary with foliage age, with insects generally showing a preference for young foliage (Coley 1980; Reichle *et al.* 1973). Beckwith (1976) found that the tussock moth (*Orgyia pseudotsugata* (McDunnough)) preferred young Douglas fir foliage. However, there are instances in conifers where young foliage is not preferred, or contains antibiotic agents toxic to insect defoliators (Henson *et al.* 1970; Ikeda *et al.* 1977; Wagner *et al.* 1979). The obvious advantage to these plants is that the considerable energy investment in photosynthetically more efficient young foliage is protected. Moreover, by maintaining a non-toxic forage resource in the form of mature foliage, the host diminishes the selective pressure on the insect to overcome the resistance.

Host plant resistance as a method of insect pest control is compatible with, and often additive to, other controls. Its specificity and persistence contrast with current insecticides and its low cost to the grower make it ideally suited to crops with a low value per hectare, such as managed forests. Many examples of host plant resistance are utilised in agriculture, even though the basis of the resistance is largely unknown (Chapman 1974).

The resistance reported here is undoubtedly an example of allopatric resistance, probably in the form of a toxin present in the current-year foliage. It is effective against the major indigenous defoliator of Douglas fir, *P. suavis,* and in less rigorous tests the closely related but rarer *P. fenerata* (Feld) which is also found in the complex of insect defoliators of Douglas fir (unpubl. data). Further work is under way to determine its heritability and its occurrence in Douglas fir provenances held at the Institute.

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