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The role of nitrogen in the feeding strategy of *Strophosomus melanogrammus* (Forster) (Col., Curculionidae) in a mixed woodland habitat

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Abstract

In the study area adults of the polyphagous weevil *Strophosomus melanogrammus* fed mainly on *Picea sitchensis*, *Betula pubescens* and *Pteridium aquilinum*. Leaf total N and water content were high in the spring in the first two and declined during the summer at which time the levels in the fronds of *P. aquilinum* were higher. Water soluble tannin levels in *B. pubescens* increased from bud-burst onwards reaching peak values just prior to leaf fall. Frass production by weevils feeding on the trees, a measure of leaf consumption, was initially low, increased during July and August, and decreased thereafter. In *P. sitchensis* frass production was negatively correlated with leaf water content; in *B. pubescens* with leaf total N in 1983 and with time, leaf total N and frass total N in 1985. Artificially changing *B. pubescens* leaf total N levels using amino acid solutions demonstrated that increasing N values up to c. 1.5 % were associated with decreasing leaf consumption, above this level N had no effect. Leaf total N was a poor predictor of leaf consumption by adults with the roles of other variables requiring investigation.

1 Introduction

During the last 15 to 20 years our concept of plant/insect interactions has gradually moved away from the classic theory of passive plant defences against herbivores expounded by e.g. FRAENKEL (1959). Many studies have shown that a variety of factors may combine to modify plant chemistry and thus change the nutritional quality of the plants for feeding insects (JERMY 1984; LEVIN 1976; RHOADES 1983; ZUCKER 1983). These factors include environmental stress, mechanical damage by feeding animals and temporal, seasonal and genetic variability. The importance of nitrogen in the plant/insect feeding interaction has been frequently demonstrated (MATTSON 1980; WHITE 1984; MCNEILL and SOUTHWOOD 1978). Consequently any study on a plant/insect relationship must involve monitoring and evaluating the effects of a large number of variables (REDAK and CATES 1984).

Most studies on the effects of plant food quality have concentrated on the feeding behaviour of larval stages. These are usually limited in their choice of feeding site by the oviposition behaviour of the female. This restriction is lacking in many adults which are able to exercise a choice and thus add a further dimension to the relationship. JERMY (1984) classifies insects into four feeding groups in which polyphagous insects, those able to feed and exist on plant species belonging to different families or orders, are the least common. Polyphagy enables an insect to feed on several plant species but entails the necessity of acquiring physiological or behavioural mechanisms to overcome a wide range of plant defences in order to be able to exploit the nutritional qualities of the hosts.

Strophosomus melanogrammus is one of a small group of weevils whose adults feed on a wide variety of plants, particularly trees, in NE Scotland (PARRY 1981). The aim of the present study was to evaluate the role of foliar nitrogen in the feeding strategy of this insect in a mixed deciduous/coniferous woodland in NE Scotland.

2 Materials and methods

The study area was situated in Countesswells forest (PARRY 1974) in a small area of mixed woodland containing *Picea sitchensis* (Bong.) Carr., *Pseudotsuga menziesii* (Mirbel) Franco, *Betula pubescens* Ehrh., *Fagus sylvatica* L. and *Abies grandis* Lindl. over a ground cover of grasses (Gramineae), *Pteridium aquilinum* L. and small quantities of *Calluna vulgaris* L. Tree height ranged from 0.5 m regenerating *B. pubescens* to 6–7 m *P. sitchensis* and mature *F. sylvatica*. Littlejohn Wood (PARRY 1976) was used for supplementary observations in 1985.

Leaf consumption was measured either by weighing the amount of frass produced over a time period or by direct measurement of the leaf area consumed. In the field the frass was collected by enclosing branches containing 10 or 20 introduced weevils, collected from the same host whenever possible, within pollination bags constructed of porous non-woven terylene to minimise condensation. Any dead or missing weevils were replaced on the following sample date on the rare occasions when this proved to be necessary. In the laboratory frass was collected in an excentric polythene cone placed around the plant stem beneath the unenclosed feeding insects. These were emptied at 24 h intervals, the frass being stored in a freezer prior to drying, weighing and analysing.

Laboratory foliar feeding on individual leaves was monitored by measuring the area of leaf consumed by 2 weevils enclosed in cages on attached leaves or on short conifer shoots for 24 h. Following feeding the outline of the leaves was photocopied on to high quality tracing paper, the outlined missing areas being cut out and weighed as an estimate of leaf consumption. Alternatively the frass falling on to the cage floor was collected and weighed.

The nitrogen (N) level of individual leaves was artificially elevated by enclosure in a small twin-chambered plastic box with the petiole inserted into a sponge saturated with amino acid solutions (PARRY 1976), or, when enhancement was not required, with water. Individual insects were then allowed to feed on the leaves in the upper part of the box, the sponge being contained in the smaller, lower part. The apparatus was stored in cabinets at $15 \pm 1^\circ\text{C}$ and 16L:8D photoperiod. Measurements of lamina consumption and/or frass production were made after 48 h at which time the leaves and frass were preserved for analysis.

All plant and frass material used for biochemical analysis was temporarily stored in flasks of liquid nitrogen prior to long term storage in a freezer set at -21°C . Both plant and frass material used for N estimations were dried to a constant weight at 85°C and kept under vacuum until analysis. Total and soluble N levels were evaluated using the micro-Kjeldahl method (PARRY 1974, 1976) and a Technicon automatic N analyser. The digestibility of the leaves was calculated as described by MATTHEW (1980) and expressed as the Digestibility Index AD.

Hot water soluble tannins were extracted from birch leaves dried to constant weight at 35°C . The levels were assessed using Folin-Dennis reagent with tannic acid as a standard (ALLEN 1974).

3 Results

3.1 Field observations

Repeated observations over several seasons revealed that *S. melanogrammus* fed extensively on mature *P. sitchensis* needles only during early spring and late autumn (PARRY 1981). During tree extension growth in spring the weevil fed on current year needles and moved on to newly emerged *B. pubescens* foliage. In late July and August it moved down from the trees on to the fronds of *P. aquilinum*. Newly emerged adults also began feeding on *P. aquilinum*. All the weevils moved back on to tree foliage, particularly *P. sitchensis*, in late autumn; the majority being weevils newly emerged in the summer. Occasional weevils were found feeding on a variety of herbaceous plants during the summer months.

3.2 Nitrogen levels

Total N levels in both *P. sitchensis* and *B. pubescens* were initially high following bud burst. They subsequently fell to a more or less constant level from mid-July through to October when leaf fall occurred in the latter (fig. 1). This pattern was repeated in 1983 in foliage gathered at Countesswells and in 1985 in foliage gathered at Littlejohn Wood, the levels in the latter being generally lower than those in the former (fig. 1a). At Countesswells in 1983 the total N level in *P. sitchensis* foliage from July to August (fig. 1b) was generally lower than that in adjacent *B. pubescens* foliage (fig. 1a).

Soluble N levels were comparable in *P. sitchensis* and *B. pubescens* (table 1) thus giving higher proportions of total N in the former (table 1).

Total N levels in *P. aquilinum* from the time when the weevils moved on to their fronds from late July onwards were generally higher than those recorded on nearby *P. sitchensis* (fig. 1b) although the high variability of the measurements may have obscured the difference on two occasions. The total N levels were not significantly different from those on *B. pubescens* (fig. 1).

Table 1. Soluble nitrogen levels in *B. pubescens* leaves and *P. sitchensis* needles in 1983

Date	Birch N (mg/g)	Sol. N (%) Total	Sitka N (mg/g)	Sol. N (%) Total
13.5	—	—	0.430	13.0
19.5	0.250	7.0	—	—
17.6	—	—	0.160	10.8
8.7	0.086	2.7	0.097	8.2
10.8	0.103	4.7	—	—
5.1	0.064	—	0.130	13.0

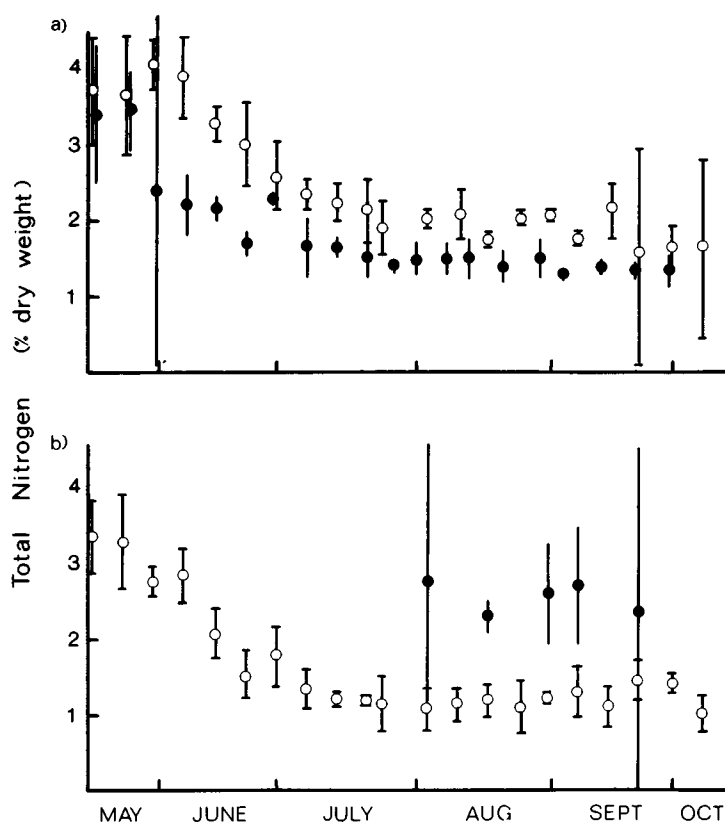


Fig. 1. Total nitrogen levels in relation to time of a) birch leaves at Countesswells in 1983 (○) and at Littlejohn Wood in 1985 (●), b) Sitka spruce needles (○) and bracken fronds (●) at Countesswells in 1983. (Confidence limits at $P = 0.05$)

3.3 Leaf water content

Leaf water content was higher in *P. sitchensis* than in *B. pubescens* from late May to the end of July, thereafter levels remained similar (fig. 2). At the time when the weevils fed preferentially on *P. aquilinum* fronds their water level was higher than that of the tree foliage, the values falling to a similar level by September and October (fig. 2).

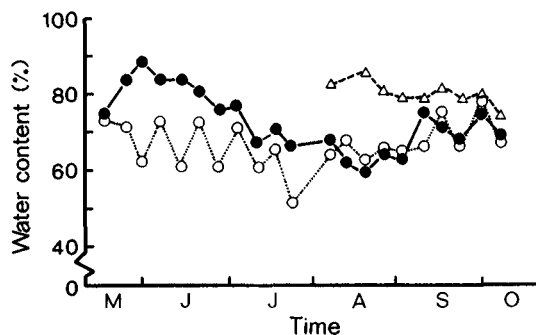


Fig. 2. Leaf water content of birch leaves (\circ), Sitka spruce needles (\bullet) and bracken fronds (Δ) in relation to time at Countesswells in 1983.

3.4 Soluble tannin levels in *B. pubescens* foliage

Tannin levels increased from a post bud-burst low level in early May to reach a plateau from mid-June to mid-August following which levels again increased as the leaves began to senesce (fig. 3).

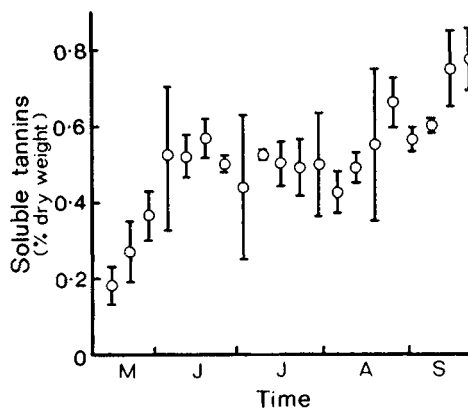


Fig. 3. Water soluble tannin levels in relation to time of birch leaves at Littlejohn Wood in 1985. (Confidence limits at $P = 0.05$)

3.5 Frass production

Frass production by weevils constrained on *P. sitchensis* and *B. pubescens* plants from which they would normally migrate during the summer months showed a characteristic low production in spring and autumn with an intervening period of high production (fig. 4). The amount of frass produced by weevils feeding on *B. pubescens* in Littlejohn Wood (fig. 4c) was lower during the summer months than the amount produced at Countesswells during the same period (fig. 4a).

Total N levels in frass were constant throughout the field observation period on both *P. sitchensis* and *B. pubescens* (fig. 5). The amounts in the former were lower than those in the latter on several occasions, particularly during August (fig. 5).

The measured potential predictors of the amount of frass produced by feeding weevils: time (T), leaf water content (Lw), leaf total N (Ln), total N in frass (Fn), a measure of N unavailability, and, in *B. pubescens* in 1985, soluble tannin level (St), were entered into a multiple linear regression model in a stepwise manner.

In *P. sitchensis* the leaf water content was negatively correlated with frass production (table 2), the remaining variables not being incorporated as their F values were insufficient to justify stepping.

By contrast *B. pubescens* leaf N levels were found to be main predictors of frass production in both 1983 and 1985 (table 2). In 1983 the proportion of the variance attributable to leaf N was only 20 % which indicates that this was a poor predictor of total frass production. In 1985 leaf tannin levels were added to the model (table 2). However, leaf tannin was not recorded as a predictor, leaf N being the initial variable entered into the analysis but with time eventually accounting for the highest proportion of the variance. 53 % of the variance was accounted for by the three factors incorporated into the equation (table 2).

As leaf N was associated with changes in frass production in *B. pubescens* the effects of artificially manipulating the levels was investigated.

Firstly, weevils were fed on shoots dipped in amino acid solutions. This increased the total leaf N and also the proportion of soluble to total N as suggested by the increasing digestibility index AD (table 3). In this case weevil numbers were small and the decrease in frass production can only tentatively be associated with increasing N levels (table 3).

Secondly individual weevils were fed on single leaves from either heavily fertilised or unfertilised *B. pubescens* plants in order to test the hypothesis that total N levels contributed to the amount of leaf consumed as suggested by the field observations. Leaves with high total N (> 1.5 %) were obtained from the former, with lower total N (< 1.5 %) from the latter. Total N levels of around 1.5 % were considered to be important as the weevils emigrated from trees when leaf N levels decreased below this in July (fig. 3).

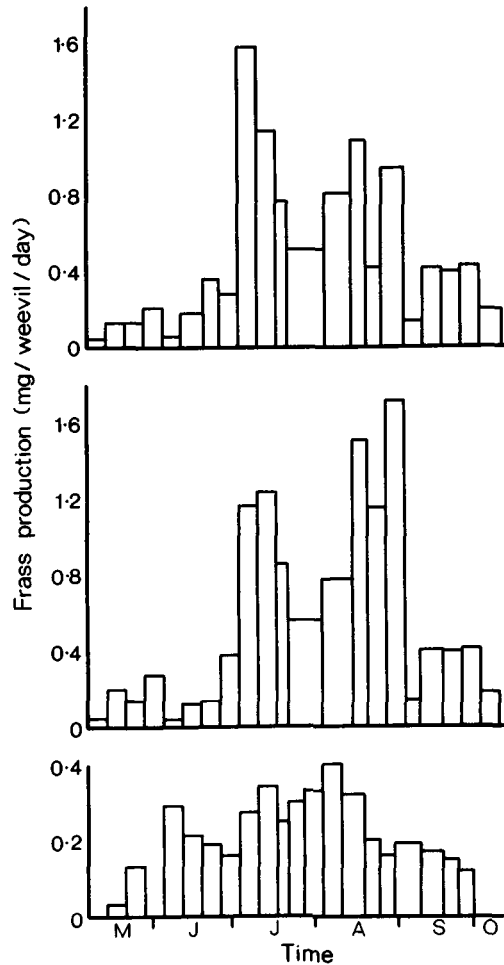


Fig. 4. Frass production by *S. melanogrammus* feeding on a) birch and b) Sitka spruce at Countesswells in 1983 and c) birch at Littlejohn Wood in 1985

Table 2. The relationship between frass production on *P. sitchensis* (Sf) and *B. pubescens* (Bf) and dietary factors

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Year Regression equation	F ratio	R ² (adj)
1983 Sf = 2.169 - 0.037 Lw	F _{1, 19} = 22.63	0.52
1983 Bf = 1.367 - 0.329 Ln	F _{1, 19} = 6.06	0.20
1985 Bf = 2.552 - 0.006 T - 0.437 Ln + 0.153 Fn	F _{3, 15} = 7.77	0.53

Table 3. *B. pubescens* digestibility (AD) at different leaf nitrogen concentrations

Amino acid concentration	Leaf N (%)	Mg leaf eaten/weevil/day	Mg frass/weevil/day	Frass (mg)/leaf eaten (mg)	Digestibility AD
0.75	1.71	0.815	0.41	0.50	0.50
1.00	2.25	0.393	0.18	0.47	0.53
1.50	2.35	0.693	0.31	0.44	0.56
2.25	2.45	0.721	0.22	0.31	0.70

Table 4. Regression of weight (mg) changes in relation to time (days) of adult *S. melanogrammus* either starved or fed on fronds of *P. aquilinum*

Fed weevils Initial weight (a)	b	r	P
17.856	-0.065	-0.700	***
13.076	-0.068	-0.804	***
13.975	78E-7	0.001	
17.214	0.029	0.379	
9.995	0.029	0.556	**
14.580	0.036	0.231	
14.103	0.059	0.761	***
16.714	0.046	0.594	**
12.689	0.019	0.384	
11.798	0.039	-0.622	***
Starved weevils Initial weight (a)	b	r	P
12.168	-0.168	-0.975	***
11.780	-0.140	-0.987	***
13.220	-0.167	-0.971	***
16.694	-0.162	-0.970	***
16.207	-0.162	-0.984	***
11.279	-0.141	-0.993	***
9.742	-0.124	-0.983	***
11.761	-0.142	-0.984	***
11.914	-0.185	-0.987	***
13.036	-0.147	-0.995	***

, * indicate significance at P < 0.01 and P < 0.001 respectively

In those *S. melanogrammus* allowed to feed on young, heavily fertilised seedlings there was no relationship between leaf consumption and total N in either replicate 1 (Frass weight = 4651 + 175 Ln; F_{1,18} = 2.34; r² adjusted = 6.6 %) or replicate 2 (Frass weight =

2190 + 256 Ln; $F_{1,18} = 0.66$; r^2 adjusted = 0%). However, in those weevils fed on unfertilised birch seedlings a decrease in total N was correlated with an increase in frass production (Frass weight = 2531 - 849 Ln; $F_{1,48} = 5.68$; r^2 adjusted = 10.6%; fig. 6).

When *S. melanogrammus* commenced feeding on *P. aquilinum* in late July the total N and water levels in the fronds were higher than those of *P. sitchensis* (figs. 1,2) and the total N levels were comparable to those of *B. pubescens* at Countesswells (fig. 1) while frond water content was higher (fig. 2). In order to test the ability of adult *S. melanogrammus* to feed and survive on a potentially hostile host batches of ten weevils were either fed on *P.*

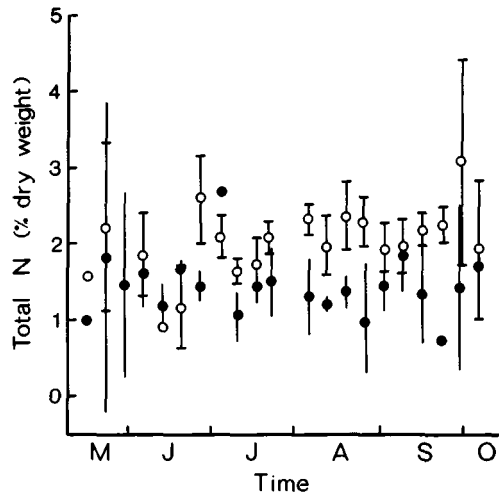


Fig. 5. Total nitrogen levels in relation to time of frass produced by *S. melanogrammus* feeding on birch (○) and Sitka spruce (●) at Countesswells in 1983. (Confidence limits at $P = 0.05$)

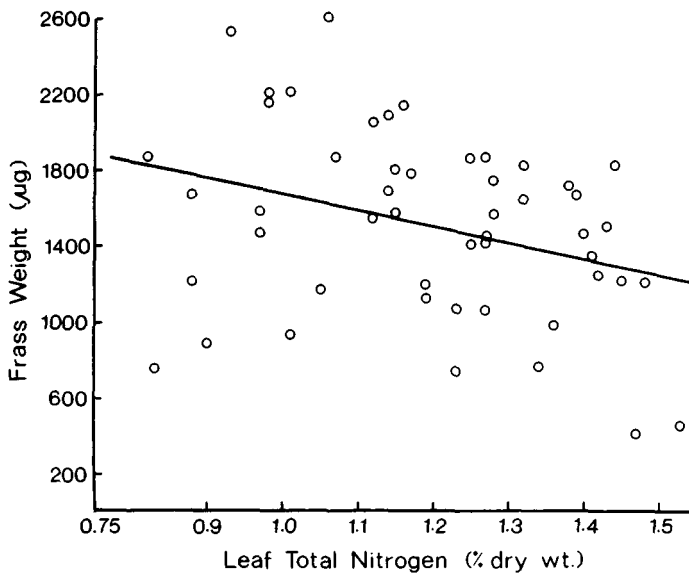


Fig. 6. The relationship between leaf total nitrogen and frass production by *S. melanogrammus* feeding on unfertilised birch with low foliar nitrogen levels

aquilinum fronds renewed daily or starved for the corresponding period. Each individual was weighed daily. Starved weevils produced no frass and consistently lost weight (table 4). By contrast, all the weevils offered food produced frass and of the three that lost weight the loss rate was substantially slower than that of the starved individuals (table 4). The remaining seven either gained or maintained their weights (table 4) thus confirming that *P. aquilinum* can support populations of *S. melanogrammus* from late July onwards with no apparent toxic effects.

4 Discussion

Adult insects primarily require carbohydrates in order to meet energy requirements for flight, reproduction and longevity; some lipids are essential dietary constituents while N in its various forms is necessary for processes such as the production of vitellogenins, egg maturation, growth etc. (ROCKSTEIN 1978). The flightless *S. melanogrammus* has two main feeding periods, one in spring prior to egg production, when high levels of dietary N are necessary, and one in the autumn prior to overwintering in the soil when N levels are less important in the processes of accumulating fat reserves (PARRY 1981, 1983). The first feeding period coincides with the high levels of N extant in the leaves of both *B. pubescens* and *P. sitchensis* (fig. 1; PARRY 1976), the second when N is less accessible as a dietary constituent and it is tempting to speculate that N availability is one of the factors regulating food intake as previously suggested for other insect species (WHITE 1984; MATTSON 1980).

The coincidental movement of *S. melanogrammus* from the trees in the summer and the fall in the N levels of the tree foliage together with the commencement of feeding on *P. aquilinum* fronds with higher levels of N suggest that this may be a regulatory factor. On *B. pubescens* leaves the correlation of food intake with leaf N levels below a threshold of around 1.5% (fig. 6) confirms that this nutrient does act as a weak feeding regulator. However, only a small proportion of the variability is accounted for by this relationship so that other variables, some possibly unidentified in this study, must be involved in the regulation of food intake (table 2). Further confirmation of the regulatory role of leaf N lies in the increase in frass production which occurs in response to decreased available foliar N in those weevils constrained on *B. pubescens* leaves during the summer months (fig. 4). Also, by artificially changing the N levels of *B. pubescens* it was shown that frass production decreased in response to increase in leaf N (table 3). The complexity of the N level/insect feeding relationship is demonstrated by the lower frass production by weevils on *B. pubescens* at Littlejohn than at Countesswells during the summer despite the higher N levels at the latter during this time (fig. 1).

By comparison of all these effects on feeding it becomes apparent that N only affects uptake below c. 1.5% of leaf weight, above this level it ceases to be a regulator. The constant level of N in *S. melanogrammus* frass throughout the season (fig. 5) suggests that under conditions when N acts as a feeding constraint then increasing consumption is the only way in which dietary available N levels can be maintained as it becomes increasingly unavailable in the host foliage. SLANSKY (1982) shows that many insects compensate for a reduction in food quality by increasing ingestion rates. One alternative is to migrate from the inadequate host on to other plants where the N levels are higher, *P. aquilinum* in the case of *S. melanogrammus*. This strategy is adopted by many insect species, particularly Aphididae. Another alternative is to aestivate during the period of summer nutritional inadequacy, a strategy adopted by *Drepanosiphum platanoidis* (Schr.) on *Acer pseudo-platanus* L. (DIXON 1973). No depression in the respiratory rate which accompanies summer aestivation has been measured for *S. melanogrammus* even though this is a strategy adopted by the diapausing adult to conserve stored fat during the winter months (PARRY 1983).

Feeding on grass roots during the summer months by larvae of *S. melanogrammus* and other weevils (GRIMM 1973) is a response to the higher levels of N necessary for insect growth. In the case of the adults the summer represents an interregnum between the appearance of one generation and the next. In the autumn the levels of N are less crucial and feeding is primarily for the purpose of building up food reserves for the overwintering adults. This is important for the overwintering survival of *S. melanogrammus* as those which amass the most food reserves are able to survive longer without supplementary feeding on exposed foliage and consequent subjection to low temperature mortality (PARRY 1983). Feeding on *P. aquilinum* extends this period of reserve accumulation and is of obvious survival importance.

On *P. sitchensis* there was no evidence of a relationship between N levels and frass production; leaf water content being the only correlated variable (table 2). This was not unexpected as feeding on *P. sitchensis* normally commences at a much earlier time than on *B. pubescens* (PARRY 1981) and N levels are generally above the critical threshold at this time (PARRY 1976) and would not be expected to play a critical role. Leaf water level did not contribute to feeding regulation in birch (table 2). It may only be of importance when N levels are high and it may be significant that *P. aquilinum* frond water levels were high at the time that the weevils moved from the *B. pubescens* foliage and that this, and not N, was the most important factor when food reserves were being accumulated in the autumn.

The biochemistry of *P. aquilinum* has been rigorously investigated (JONES 1983) and the large number of putative repellents and toxicants has fuelled the myth of its resistance to insects. *S. melanogrammus* is able to feed and survive on *P. aquilinum* fronds in the field from late July onwards and in the laboratory from an even earlier period (table 4). JONES and FIRN (1979) show that *P. aquilinum* insect deterrence is at its greatest in the period following frond emergence and towards the end of the season. During the intervening period deterrence was less marked and nutritional quantity, if not quality, declined from early May onwards (JONES 1983). The latter coincides with the period when *S. melanogrammus* exploits it as a source of food and is also the period when insect abundance and species diversity reach a peak (LAWTON 1976, 1978).

Although a feeding regulatory role has been demonstrated for foliar N it still remains a poor feeding predictor which indicates that other variables have important roles. The possible effects of feeding deterrents, N availability and tannin production remain enigmatic and much remains to be resolved in the *S. melanogrammus*/plant inter-relationship.

Acknowledgements

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Zusammenfassung

Zum Einfluß von Stickstoff auf die Fraßstrategie von Strophosomus melanogrammus (Forster) (Col., Curculionidae) in einem Mischwaldgebiet

Im Untersuchungsgebiet fraßen die adulten polyphagen Rüsselkäfer, *Strophosomus melanogrammus*, hauptsächlich an *Picea sitchensis*, *Betula pubescens* und *Pteridium aquilinum*. Der Gesamtstickstoff- und Wassergehalt der Nadeln bzw. Blätter der beiden erstgenannten Pflanzen waren im Frühjahr hoch und sanken im Sommer. Zu dieser Zeit waren jedoch die entsprechenden Werte von *P. aquilinum* höher. Der Gehalt an wasserlöslichem Tannin in *B. pubescens* stieg kontinuierlich ab dem Knospenausbruch an und erreichte den Höchstwert kurz vor dem Laubfall. Die Fraßmenge, die über die Kotausscheidung bestimmt wurde, war anfangs niedrig, erhöhte sich im Juli und August, um dann wieder abzufallen. Bei Fraß an *P. sitchensis* war die Kotausscheidung negativ mit dem Wassergehalt der Nadeln korreliert; 1983 war bei *B. pubescens* die Kotausscheidung negativ mit dem Gesamtstickstoffgehalt der Blätter und des Kots korreliert. Bei künstlicher Veränderung des Gesamtstickstoffgehalts der Blätter durch Aminosäurelösungen wurde bei *B. pubescens* ersichtlich, daß eine Steigerung des Stickstoffgehalts von bis zu 1,5 % einen verringerten Fraß zur Folge hatte; eine Steigerung über

diesen Stickstoffwert hinaus blieb jedoch ohne Effekt. Der Gesamtstickstoffgehalt der Blätter erwies sich als schwacher Indikator für den Laubverzehr der adulten Rüsselkäfer. Die Einflüsse der übrigen Variablen bedürfen weiterer Untersuchung.

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