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Nutritional physiology of the eastern spruce budworm, *Choristoneura fumiferana*, infected with *Nosema fumiferanae*, and interactions with dietary nitrogen

L.S. Bauer [1] **and G.L. Nordin** [2]

[1] North Central Forest Experiment Station, USDA Forest Service, 220 Nisbet Building, 1407 South Harrison Road, East Lansing, MI 48823, USA
[2] Department of Entomology, University of Kentucky, Lexington, KY 40546, USA

Summary. Female eastern spruce budworm larvae, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), inoculated with a medium lethal spore dosage of the microsporidium *Nosema fumiferanae* (Thomson) exhibited significant reductions in consumptive index (CI), nitrogen consumptive index (NCI), relative growth rate (RGR), and gross (ECI) and net (ECD) production efficiencies when compared to microsporidian-free larvae. Diseased larvae also exhibited significant increases in approximate digestibility (AD), N utilization efficiency (NUE), and larval moisture content. Both healthy and diseased insects were reared on 2.5% N and 4.5% N diets. Those on the 2.5% N diet showed significant increases in CI, although NCI was still lower than NCI measured for larvae reared on 4.5% N. NUE was also higher on the 2.5% N diet. Diseased cohorts reared on 2.5% N diet had significantly greater mortality than those reared on 4.5% N diet. Pupal weight and development time of infected individuals did not respond to dietary N concentration. However, healthy insects achieved greater pupal weights in a shorter time on the 4.5% N diet than those on the 2.5% N diet. Mortality of healthy insects was unaffected by dietary N.

Key words: *Choristoneura fumiferana* – Eastern spruce budworm – *Nosema fumiferanae* – Dietary nitrogen – Digestive efficiency

The eastern spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), a prominent pest of large contiguous tracts of mature balsam fir (*Abies balsamea* L. Mill) and white spruce (*Picea glauca* (Moench) Voss) experiences cyclical population outbreaks (Mott 1963; Blais 1965). The microsporidium *Nosema fumiferanae* (Thom.) (Microsporida), causal agent of a chronic and prevalent disease of spruce budworm in field populations, has been implicated in playing a major role in population collapse (Thomson 1958a; Royama 1984). Sublethal infections result in a prolonged larval development and reductions in pupal weight, adult longevity, and fecundity (Thomson 1958b; Wilson 1983; Bauer 1987). Numerical proliferation of *N. fumiferanae* in host tissues (Thomson 1958b), energy store depletion (Nolan and Clovis 1985), and disruption of nutritional physiology causing a loss of assimilation efficiency (Thomson 1958b) are suggested mechanisms of disease expression.

The importance of food quality to budworm population dynamics has received considerable attention (Blais 1952; Kimmins 1971; Harvey 1974), and dietary nitrogen (N) is considered to be the primary beneficial component (Shaw and Little 1977; Shaw et al. 1978; Mattson and Koller 1983; Koller 1987). The amount of N available varies with host species (Kimmins 1971), flowering conditions (Koller 1987), phenology (Shaw and Little 1977; Koller 1987), and fertilization (Shaw et al. 1978).

The objectives of this study were to quantify the impact of *N. fumiferanae* on spruce budworm nutritional physiology and to determine the interaction of dietary N on the expression of disease caused by *N. fumiferanae*.

Materials and methods

Pathogen

Fresh spores were obtained by the culture of *N. fumiferanae* in spruce budworm larvae to produce (Wilson 1976). The triangulation method of purification (Cole 1970) produced a pure spore suspension. Spore concentration in the stock suspension was determined using a Petroff-Hausser counting chamber, and dosages were prepared using serial dilutions made with sterile distilled water.

Insect

We obtained microsporidia-free, second-instar eastern spruce budworm larvae in hibernacula and held them in refrigerated storage ($6 \pm 2°$ C). Following emergence from diapause, larvae were established in 30 ml clear polystyrene cups either on a diet containing 4.5% N or 2.5% N (Table 1). All larvae were reared at an initial density of eight larvae per cup at $20 \pm 1.5°$ C, L16:D8.

Bioassay

Female larvae were selected from the cohorts reared on 4.5% and 2.5% N diet within 24 h following fourth-instar ecdysis. The bioassay procedure described by Bauer and Nordin (1988) was used to inoculate the larvae with an LD_{50} dosage (2×10^4 spores per larva in 24 h or less). Control larvae were treated with sterile distilled water. Larvae were reared individually on their respective diets following dose consumption.

Offprint requests to: L.S. Bauer

Table 1. Formulation for standard and reduced dietary nitrogen diet with micro-Kjeldahl nitrogen concentration determined at 4.5% and 2.5% dry weight, respectively

Diet ingredients	% Dietary nitrogen	
	4.5[a]	2.5[b]
Water (ml)	168.0	168.0
Agar (g)	5.0	5.0
Casein (g)	7.0	1.75
Alphacel (g)	1.0	3.0
Salt mix-W (g)	2.0	2.0
Sucrose (g)	7.0	7.0
Wheat germ (g)	6.0	6.0
Choline chloride (g)	0.2	0.2
Ascorbic acid (g)	0.8	0.8
Vitamin solution (ml)	2.0	2.0
KOH 4M (ml)	1.0	1.0
Formalin (ml)	0.1	0.1
Methyl paraben (g)	0.3	0.3

[a] Standard diet from McMorran (1965)
[b] Modified diet with reduced casein and increased alphacel

These four cohorts of larvae (4.5% control and diseased, 2.5% control and diseased) provided the source material for the survival assay and the nutritional physiology assay. At least 30 larvae were randomly selected as 1-day-old sixth instars for inclusion in each assay group.

Survival assay. On each diet type, one group of diseased larvae and its corresponding control, were reared to pupation. Pupae were weighed the day following pupation. Developmental time, mortality, and days until death were monitored for the final three instars (IV–VI).

Nutritional feeding bioassay. Another group of diseased larvae and its corresponding control on each diet type were reared in vials with a previously weighed quantity of diet. This allowed for measurements of rates of consumption and growth and efficiencies of food conversion. These larvae were weighed before being placed individually in vials fitted with perforated polypropylene culture tube caps that allowed gas exchange and excess moisture evaporation. After 6 days (prior to the prepupal stage) each larva was removed from its vial, weighed, lyophilized, and reweighed. Uneaten diet and frass were frozen and lyophilized in the vial, then sorted and weighed. A subsample of insects and fresh diet in vials was used for the estimation of initial moisture contents. The initial dry weight of the 4.5% N and 2.5% N diet was $15.2 \pm 0.08\%$ and $14.8 \pm 0.06\%$, respectively. Errors in estimating dry weight consumption were minimized by providing each larva with as little excess diet as possible for the feeding duration. Total N content of diet, frass, and insects were determined by the micro-Kjeldahl method.

Efficiencies of utilization and indices of growth and consumption were calculated gravimetrically on a dry weight basis (Waldbauer 1968). The following equations describe each index:

$$\text{Consumption (C)} = \text{initial diet weight} - \text{final diet weight}$$

$$\text{Consumptive Index (CI)} = \frac{C}{\text{mean weight} \times \text{days}}$$

$$\text{Production (P)} = \text{final larval weight} - \text{initial larval weight}$$

$$\text{Relative Growth Rate (RGR)} = \frac{P}{\text{mean weight} \times \text{days}}$$

$$\text{Assimilation (A)} = C - \text{frass}$$

$$\text{Approximate Digestibility (AD)} = \frac{A}{C} \times 100$$

$$\text{Net Production Efficiency (ECD)} = \frac{P}{A} \times 100$$

$$\text{Gross Production Efficiency (ECI)} = \frac{P}{C} \times 100$$

$$\text{N Consumption (NC)} = C \times \% \text{ dietary N}$$

$$\text{N Frass (NF)} = \text{frass weight} \times \% \text{ rejecta N}$$

$$\text{N Relative Consumption Index (NCI)} = \frac{NC}{\text{mean weight} \times \text{days}} \times 100$$

$$\text{N assimilation (NA)} = NC - NF$$

$$\text{N Utilization Efficiency (NUE)} = \frac{NA}{NC} \times 100$$

Statistics

The Chi-square procedure was used to compare differences in percent mortality. Student's t-test was used to determine the significance of disease or nitrogen effects on insect response variables. The significance of paired multiple comparisons among healthy, sublethally, and lethally responding individuals was based on Duncan's multiple-range test. The Statistical Analysis System was used for all statistical analyses (SAS Institute 1982).

Results

Mortality, lethal time, pupal weight, development time

Cohorts inoculated with an LD_{50} dosage of *N. fumiferanae* spores had 60% higher mortality when reared on 2.5% N diet than when reared on 4.5% N diet ($P \leq 0.05$) (Table 2). Mortality was <3% for control larvae reared on either diet. All mortality occurred during the sixth larval stadium.

Control insects reared on the 4.5% N diet achieved 16% greater pupal weight in 89% of the time required for the group reared on the 2.5% N diet (Table 2). Both differences were significant. The response of sublethally infected individuals, i.e., those successfully inoculated but surviving to reach the pupal stage, was similar at both levels of dietary N. These sublethally infected individuals had average 28.1% lower pupal weights ($P \leq 0.01$) than healthy insects on both diet types, but took significantly longer (18.2%) to develop only on the 4.5% N diet (Table 2).

Consumption, digestibility, growth rate, and efficiency indices

Consumptive index (CI) is a measure of the relative rate at which nutrients enter the digestive tract, reflecting the

Table 2. The response (mean ± S.E.) of female spruce budworm larvae reared on meridic diet containing two levels of dietary N and inoculated as newly molted fourth-instar larvae with 2×10^4 spores of *Nosema fumiferanae*/larva. Data were collected from the fourth stadium to pupation

Variable	% Dietary nitrogen level			
	4.5		2.5	
	Control	Diseased	Control	Diseased
Mortality (%)[a]	0	41.9[b]	2.8	66.7[b]
Pupal dry weight (mg dw)	41.5 ± 1.29[c]	28.4 ± 1.89[d]	35.7 ± 1.19	26.9 ± 2.53[d]
Developmental time (days)	20.3 ± 0.32[c]	24.0 ± 0.77[d]	22.9 ± 0.56	23.1 ± 0.74
Lethal time (days)	–	19.2 ± 2.4	–	22.7 ± 2.9
Initial numbers	29	31	36	31

[a] Chi-square analysis, $\chi^2 = 4.17$
[b] significantly different at the $P \leq 0.05$ level of significance
[c] 4.5% control significantly different from 2.5% control at the $P \leq 0.01$ level of significance, Student's t-test
[d] Disease significantly different from control at the $P \leq 0.01$ level of significance, Student's t-test

Table 3. The response of female spruce budworm larvae reared on meridic diet containing two levels of dietary N and inoculated as newly molted fourth-instar larvae with 2×10^4 spores of *Nosema fumiferanae*/larva. All response variables (mean ± S.E.) were measured for 6 days during instar VI. All diseased individuals within each level of dietary N were pooled

Parameter	% Dietary nitrogen level			
	4.5		2.5	
	Control	Diseased	Control	Diseased
CI (mg/mg/day)	0.78 ± 0.01[a]	0.62 ± 0.04[b]	0.92 ± 0.01	0.72 ± 0.05[b]
RGR (mg/day)	0.22 ± 0.00	0.12 ± 0.02[b]	0.22 ± 0.00	0.12 ± 0.02[b]
AD (%)	54.6 ± 0.0[a]	58.2 ± 0.0[b,c]	47.3 ± 0.0	51.2 ± 0.0[b]
ECI (%)	27.6 ± 0.0[a]	13.7 ± 0.0[b]	24.5 ± 0.0	16.4 ± 0.4[b]
ECD (%)	50.6 ± 0.0	24.2 ± 0.0[b]	51.8 ± 0.0	33.3 ± 0.1[b]
NUE (%)	48.2 ± 0.0[a]	61.9 ± 0.0[b,c]	53.3 ± 0.0	71.6 ± 0.0[b]
NCI (μg/mg/day)	22.4 ± 0.0[a]	17.1 ± 0.0[b,c]	13.9 ± 0.0	10.8 ± 0.0[b]
Moisture (%)	75.8 ± 0.0	82.6 ± 0.0[b]	74.6 ± 0.0	81.7 ± 0.0[b]
Nosema ($\times 10^6$ spores/mg)	–	4.7 ± 0.7	–	3.7 ± 0.6
Number	30	27	30	24

[a] 4.5% control significantly different from 2.5% control, Student's t-test ($P \leq 0.01$)
[b] Disease significantly different from control, Student's t-test ($P \leq 0.01$)
[c] 4.5% disease significantly different from 2.5% disease, Student's t-test ($P \leq 0.01$)

insect's physiological and behavioral response to the food provided. Diseased insects had a 21% lower CI ($P \leq 0.01$) at both levels of dietary N when compared to healthy controls (Table 3). Both healthy and diseased cohorts reared on the 2.5% N diet had 17% higher CIs ($P \leq 0.01$) than the corresponding cohorts reared on the 4.5% N diet.

Approximate digestibility (AD) estimates the efficiency of food assimilation. Budworm larvae infected with *N. fumiferanae* had significantly higher AD when compared to healthy controls at both levels of dietary N (average increase 7.4%) (Table 3). Significant improvement in larval AD (average increase 14.6%) occurred at 4.5% dietary N when compared to the group reared at 2.5% dietary N for both healthy and diseased treatments.

Gross production efficiency (ECI) is an index that expresses the efficiency of conversion of ingested food to insect biomass (Table 3). Diseased cohorts had ECIs that were 50% less than controls at 4.5% N and 33% less than controls at 2.5% N. ECI was not altered by the concentration of dietary N ($P \leq 0.05$).

Net production efficiency (ECD) estimates the efficiency of conversion of digested (assimilated) food to insect biomass production. The response of ECD for diseased insects was similar to that described for ECI, a 52% decline on the 4.5% N diet and a 36% decline on the 2.5% N diet (Table 3).

The relative growth rate (RGR) of diseased budworm was depressed by 45% compared with controls ($P \leq 0.01$). Dietary N was not a significant factor in altering RGR during the sixth stadium in either the healthy or diseased cohorts (Table 3).

Nitrogen consumption index (NCI) and nitrogen utilization efficiency (NUE) were compared across treatments because higher dietary N improved survival of individuals infected with *N. fumiferanae* (Table 2). NCI was 36.8% lower and NUE was 15.7% higher for diseased larvae reared on 2.5% N compared with those on 4.5% N (Table 3). Diseased cohorts had significantly lower NCI (average 22.9%) and higher NUE (average 31.4%) relative to controls on the same diet.

Table 4. The response of female spruce budworm larvae reared on meridic diet containing two levels of dietary N and inoculated as newly molted instar IV larvae with 2×10^4 spores of *Nosema fumiferanae*/larva. All response variables (mean ± S.E.) were measured for 6 days during instar VI. The diseased individuals within each nitrogen treatment were sorted on the basis of final larval dry weight. Diseased larvae not achieving greater than 12 mg dw were expected to have lethal infections and those greater than 12 mg dw were expected to have sublethal infections

Parameter[a]	% Dietary nitrogen level					
	4.5			2.5		
	Disease response			Disease response		
	Control	Sublethal	Lethal	Control	Sublethal	Lethal
CI (mg/mg/day)	0.78 ± 0.01a[c]	0.77 ± 0.02a	0.42 ± 0.05b	0.92 ± 0.01a	0.86 ± 0.06a	0.55 ± 0.06b
RGR (mg/day)	0.22 ± 0.00a	0.20 ± 0.01a	0.02 ± 0.02b	0.22 ± 0.00a	0.19 ± 0.01b	0.04 ± 0.02c
AD (%)	54.6 ± 0.0a[c]	57.1 ± 0.0a[d]	59.5 ± 0.0a	47.3 ± 0.0a	48.6 ± 0.0a	54.3 ± 0.0b
ECI (%)	27.6 ± 0.0a[c]	26.2 ± 0.0a	−1.8 ± 0.1b	24.5 ± 0.0a	26.8 ± 0.1a	4.0 ± 0.1b
ECD (%)	50.6 ± 0.0a	46.2 ± 0.0a	−3.3 ± 0.1b	51.8 ± 0.0a	54.2 ± 0.1a	8.6 ± 0.1b
NUE (%)	48.2 ± 0.0a[c]	58.0 ± 0.0b[d]	67.2 ± 0.0c	53.3 ± 0.0a	68.8 ± 0.0b	74.9 ± 0.0c
NCI (μg/mg/day)	22.4 ± 0.0a[c]	22.1 ± 0.0a[d]	12.1 ± 0.0b	13.9 ± 0.0a	13.1 ± 0.0a	8.4 ± 0.0b
Moisture (%)	75.8 ± 0.0a	80.1 ± 0.0b	85.6 ± 0.0c	74.6 ± 0.0a	77.6 ± 0.0b	86.5 ± 0.0c
Nosema ($\times 10^6$ spores/mg)[b]	–	2.5 ± 0.4[e]	7.6 ± 0.9	–	1.9 ± 0.3[e]	5.7 ± 0.9
Final larval wgt (mg dw)	37.5 ± 1.6a	23.8 ± 1.8b	6.1 ± 0.7c	32.4 ± 1.2a	19.2 ± 1.6b	5.5 ± 0.8c
n	30	15	12	30	13	11

[a] Within each level of dietary nitrogen, means followed by the same letter are not significantly different, Duncan's multiple-range test ($P \leq 0.0001$)
[b] Within each level of dietary nitrogen, means followed by the same letter are not significantly different, Student's t-test, ($P \leq 0.004$)
[c] 4.5% control significantly different from 2.5% control, Student's t-test ($P \leq 0.0001$)
[d] 4.5% sublethal significantly different from 2.5% sublethal, Student's t-test ($P \leq 0.0001$)
[e] Sublethal significantly different from lethal within each level of dietary N, Student's t-test ($P \leq 0.001$)

Disease, at both levels of dietary N, caused a significant increase in moisture content of larvae by approximately 10% (Table 3). Spore load, an indicator of disease level, was not different between nitrogen treatments.

Survivorship in the cohorts reared through to pupation (Table 2) showed that approximately half of the diseased larvae in the nutritional physiology bioassay would be expected to die during the sixth instar. This bioassay lasted only 6 days so we could not determine the ultimate fate of the larvae. The frequency distribution of final larval dry weights for diseased insects included in the nutritional bioassay groups was bimodal. Larvae that were <12 mg dw were presumably responding lethally to *Nosema*. Subsetting the diseased insects, using final larval dry weight as a criterion, showed that these smaller larvae were responsible for many of the measured differences in consumption, growth, and utilization efficiencies (Table 4). The other subset of larvae with final larval dry weights >12 mg and presumably responding sublethally to *Nosema*, showed similar trends to lethally infected individuals, but most response variables were not significantly different from the controls. NUE and moisture content were exceptions, showing elevated levels in the sublethally infected group.

Insects with lethal infections contained a significantly higher *N. fumiferanae* spore load per mg fresh weight than sublethally infected individuals (Table 4). There was a consistent trend for larvae reared on the higher N diet to contain more spores per mg, regardless of the extent of the larval disease response. The magnitude of the difference, however, was not significant. Larval moisture content was greater in the groups with lethal infections when compared to the groups with sublethal infections. Dietary N alone was not a significant factor in altering moisture content.

Discussion

General

The physiological response of spruce budworm larvae infected with *N. fumiferanae* included several important components: reductions in consumption rate (CI), growth rate (RGR), and gross (ECI) and net (ECD) production efficiencies, contrasted by a rise in digestibility (AD), N utilization efficiency (NUE), and larval moisture content. Similar nutritional physiology studies have been performed for other insect/pathogen systems but measured responses suggest that the pathophysiology of each was sufficiently different to prevent direct comparisons of results (Harper 1973; Ramakrishnan and Chaudhari 1974; Subrahmanyam and Ramakrishnan 1981; Tatchell 1981; Mohamed 1982; Mohamed et al. 1982; Bozeman 1983; Sareen et al. 1983).

Consumption, digestibility, efficiency of conversion, and growth

The increases in both AD and NUE refute Thomson's (1958b) suggestion that reduced midgut AD was responsible for the debilitating effects of *N. fumiferanae* in spruce budworm. Similar improvements in AD resulted following *Bacillus thuringiensis* Berliner treatment of *Spodoptera litura* (Fabricius) (Sareen et al. 1983) and *Nourmaea rileyi* (Farlow) Samson infection of *Heliothis zea* (Boddie) (Mohamed et al. 1982). This effect may be due in part to suppressed CI. The inverse relationship between AD and CI has been reported in the literature (Soo Hoo and Fraenkel 1966; Waldbauer 1968) and may be caused by a slowed passage

of food, which creates an opportunity for better absorption.

The effect of *Nosema* on AD suggests that there is surprisingly little damage to overall absorptive capabilities by the midgut epithelial cells, even in individuals responding lethally to the dosage. Nolan and Clovis (1985) found that the nucleic and cytoplasmic structure of infected cells appeared to be unaffected by *Nosema* unless infection was heavy or until larvae died. Overt symptomology associated with *Nosema* infection, therefore, is not caused by a breakdown in abdorptive capabilities, but by a failure of the digestive material to be utilized effectively for growth.

The small RGR in larvae infected with *Nosema* could not be accounted for solely by the lower CI. Because AD and NUE were higher in diseased groups, the decline in RGR was caused by a reduction in the utilization of assimilated food for larval biomass production, ECD. Increased metabolic expenditures experienced by diseased larvae may result from host cell damage during pathogen growth and proliferation. This would necessitate an increased need for cellular repair and replacement. In addition, efficient function of organ systems may be disrupted, leading to a breakdown of pathway coordination and a harmful buildup of intermediate products. Selective diversion of nutrients and changes in active transport across membranes to support pathogen growth and reproduction may also disrupt larval growth physiology and cause decreased efficiency of biomass conversion.

Dietary nitrogen

Healthy and diseased insects reared on 2.5% N obtained needed N by increasing CI relative to the corresponding treatment on 4.5% N. This enabled attainment of comparable production efficiencies (ECD and ECI) and RGR. Insects reared on nutritionally deficient diets have been reported to compensate by increased rates of consumption (House 1965; Soo Hoo and Fraenkel 1966). Spruce budworm reared on 2.5% N, however, did not achieve the NCI realized by insects reared on 4.5% N. Since the greater NCI on 4.5% N compared with 2.5% N produced a lower NUE, N consumed from the diet richer in N probably was in excess of extraction capability and was excreted in the frass. These results suggest that optimal dietary N is at a level between those used in this study.

Increasing the concentration of dietary N improved the overall performance of healthy spruce budworm larvae and significantly improved survival following inoculation with *Nosema*. This improved survival may have resulted from the shorter developmental time for larvae reared on 4.5% N (Bauer and Nordin 1988). The results also suggest that the pathogen may be causing a shortage of N resources that the 4.5% N diet provides in greater quantity. The increases in larval moisture content and NUE suggest that Malpighian tubule functions were disrupted, causing edema and interference with N waste excretion.

Ecological considerations

Price et al. (1980) stressed the need for a holistic approach to plant/herbivore interactions. They suggested that a better understanding of the third trophic level (enemies of herbivores), would facilitate current research on plant defense strategies. An increasing body of literature supports the importance of nutrition and dietary stress on the interaction between insect and parasite (Price et al. 1980) and between insect and predator (Brower et al. 1967). The interaction between pathogen, herbivore, and nutritional quality of the host plant was also recognized as potentially important (Steinhaus 1958). The role of insect nutrition in disease susceptibility was often demonstrated by various responses to invading organisms based on host plant species or variety (Burleigh 1975; Stubblebine and Langenheim 1977; Hare and Andreadis 1983; Hou and Chiu 1986), allelochemic factors (Felton and Dahlman 1984), nutritional components (Harvey and Gaudet 1977; Thompson 1983), or plant moisture content (Biever and Wilkinson 1978). The causes of these observed differences in response to entomopathogens is rarely investigated.

In the field, more spruce budworm larvae infected with *Nosema* were collected from balsam fir trees than from white spruce (Burke 1980). A similar response to host plant species was found following *N. fumiferanae* field tests (Wilson 1978). The phenology of balsam fir, in conjunction with moisture stress and flowering induced by warm, dry spring conditions, has been implicated in budworm population release (Wellington et al. 1950; Pilon and Blais 1961; Greenbank 1963). These conditions were associated with increased availability of foliar N and improved budworm survival and development rates (Koller 1987). The present study isolated N as a variable from other plant nutritional constituents, and showed that higher dietary N improved both larval survival and the proliferation of *N. fumiferanae* in larval tissues. Even with greater survival, however, the prolonged larval periods and slowed rates of consumption induced by *Nosema* could reduce shoot damage.

On both fertilized balsam fir trees (Shaw et al. 1978) and in natural stands (Koller 1987), variations in N concentrations have been correlated with spruce budworm growth. Over several generations, however, the apparent benefits to larvae from N-rich diets may actually lead to population collapse induced by *N. fumiferanae*. The increase in spore load displayed on the 4.5% N diet was expressed as greater spore concentration in sublethally infected larvae. This concentration would ensure that greater numbers of larvae would be infected through transovarial means in the next generation. Harvey and Gaudet (1977) found that budworm larvae naturally infected with *N. fumiferanae* experienced differential survival depending on the level of dietary nitrogen. The greatest tolerance (survival) of *Nosema* infection occurred when larvae were reared on the highest concentration of dietary N (4.5%) (Harvey and Gaudet 1977).

Spruce budworm larvae feed primarily on emergent balsam fir foliage in which, over the larval period, N concentrations naturally decline from approximately 6% to 1% (Koller 1987). The average dietary N level was 1.6% for 80% of total consumption (Koller and Leonard 1981). At this concentration of dietary N the impact of slight natural variations, perhaps due to tree phenology, should be greater than what we have demonstrated in comparing 2.5% to 4.5% N concentrations.

The results of this study suggest that, in the short term, spruce budworm with sublethal *Nosema* infections may require more foliage to complete development because of a prolonged larval period induced by infection. However, a lagging larval developmental rate results in a shift to feeding on expanded shoots that are at a more advanced stage of

development. Such shoots give insects a poorer N source which, presumably, would result in poorer performance. Damage to balsam fir shoots by larval feeding is also substantially reduced because later in the growing season feeding is restricted to needles (Koller 1987). The effects of *Nosema* and N on spruce budworm are opposing, yet not entirely independent. It appears that elevated levels of dietary N improves the growth and survival of both pathogen and insect. Optimal nutritional conditions over several generations, that may lead to an outbreak of the insect, could also induce its collapse by sustaining higher levels of *Nosema*.

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