

## Effects of nitrogen on bionomics and food consumption of *Cabera pusaria* (Lepidoptera: Geometridae)

Emanuel Kula, Alena Pešlová, Petr Martinek & Pavel Mazal

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Birches, *Betula pendula* Roth, grown in pots were fertilized with ammonium nitrate ( $\text{NH}_4\text{NO}_3$ ) in the amounts of 0 g, 0.5 g, 1 g and 1.5 g per plant four times per season on moist soil surface with subsequent gradual dissolution by watering. *Cabera pusaria* caterpillars from laboratory were fed on leaves with different content of nitrogen ( $19.2\text{--}47.4 \text{ mg}\times\text{g}^{-1}$ ). The excessive content of nitrogen in food appeared to be a stress factor as it increased mortality and development time of the caterpillars, decreased food consumption and weight of larvae and pupae, and caused anomalies at pupation. This is as expected for a summer-feeding caterpillar feeding on foliage with seasonally decreasing concentration of nitrogen.

*E. Kula, A. Pešlová, P. Martinek & P. Mazal, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, 613 00 Brno, Czech Republic; E-mails: kula@mendelu.cz, alenapeslova@seznam.cz, martinekpe@seznam.cz, mazal@mendelu.cz*

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### 1. Introduction

White (1993) and Douglas (1993) presented nitrogen to be the limiting factor for insects. Nitrogen input into plants is associated with nitrogen oxides ( $\text{NO}_x$ ) pollution (Heliövaara & Väisänen 1993) or with fertilization (Butler *et al.* 2012). The quality of food for phytophages is often positively affected by the increased concentration of organic nitrogen in leaves and phloem of plants (Rhoades 1979, White 1984, Mattson & Haack 1987, Haddad *et al.* 2000). On the other hand, depending on species and conditions nitrogen fertiliser does not have only positive effects on insects (Bi *et al.* 2005, Pikul *et al.* 2005), but negative (Salmah *et al.* 1998, Pitan *et al.* 2000) or even no effects at all (Haile & Hofsvang 2001, Srikanth *et al.* 2002). Sucking insects have shown a much

stronger response to the level of nitrogen (fertiliser) than chewing insects (Annan *et al.* 1997, Megahed 2005, Schulz *et al.* 2008, Butler *et al.* 2012). Lepidoptera, Hemiptera and Diptera have shown a significant positive and Coleoptera a negative response to nitrogen fertiliser (Butler *et al.* 2012).

Some spring phytophages, for which the content of nitrogen in diet can be a limiting factor, are able to find plants or parts of plants rich in nitrogen (McNeil & Southwood 1978). In these species, low doses of nitrogen provoke consumption of more food, prolonged feeding period and longer digestion and development. Inadequate N content in diet may be compensated by presence of symbiotic organisms in the digestive system, incidental carnivorousness etc. (Mattson 1980).

Preference of tissues with higher content of

nitrogen in spring species was confirmed for example in *Phyllobius* sp. (Kaňová & Kula 2004), *Pristiphora abietina* (Berger & von Katzensteiner 1994), *Choristoneura fumiferana* (Shaw & Little 1972) and *Choristoneura conflictana* (Bryant *et al.* 1987). Positive reaction of phytophages to increased N content in plant tissues may also be associated with the decrease of the phenolic compound content (Jones 1976, Kiraly 1976, Joseph *et al.* 1993).

For summer species (e.g. *Bupalus piniarius*, *Neodiprion swainei*) appearing at the time of natural decline of N content in needles, oversupply of N may be unfavourable (Smirnoff & Bernier 1973, Katzel & Loffler 1995). In this study, we use the geometrid *Cabera pusaria* as a model species with larvae feeding during summer period, i.e. on leaves with decreasing natural concentration of N.

In air-polluted areas with a high proportion of birch in forest stands, *C. pusaria* is the most abundant species of the moths attracted to light traps in Sněžník (50°47'57.01" N, 14°05'04.74" E) (Děčín Highlands, Czech Republic) (Kula 2007). It is also the most represented species within the fauna of caterpillars in the birch crowns (Kula 2008). Generally, flight activities take place in mid-May to mid-September with culmination in the first half of July (Kula 2007).

Caterpillars of *C. pusaria* rank among disjoint oligophages occurring in crowns of birch trees in the Palaearctic region (Copolovici *et al.* 2011) from the beginning of June till the end of September. The period of caterpillar hatching is long, 4–6 weeks. Caterpillars go through five instars with the lengths of 2–4–8–12–17 mm (Gninenko 1974). They live individually above all in the late summer aspect when they create a dominant component of the birch crown fauna in the Děčín Highlands and Ore Mountains (Czech Republic), their presence till the end of the growing season being not a rarity (Kula 2008). They occur in broadleaved forests on poplar, willow, birch and alder but also on hornbeam or bird cherry (Ladenburger 1989). In Scandinavia, it is mentioned particularly on birch (Nordström *et al.* 1941). The species pupates in humus layer where it also overwinters.

Birch is an unpretentious light-demanding species tolerating only open crown canopy. It is

not sensitive to late frosts and it grows well on poor dry soils as well as on acid sites (pH 3.5–5.0) (Hejný & Slavík 1990). Increased inputs of nitrogen with simultaneous drought stress cause intensive premature summer leaf-fall (Kaňová & Kula 2004) and decreased increment (Kula *et al.* 2012a). Damage to forests by *C. pusaria* has not been reported (Kula 2007). Young, actively growing tissues show the highest concentration of nitrogen (e.g. in birches 30–70 mg×g<sup>-1</sup>) and its decrease is connected with tissue aging (Rodin & Bazilevich 1967, Mattson 1980, Hrdlička & Kula 2001). Throughout the growing season, a wide spectrum of phytophagous species develop on the leaves (Kula 2008), with species composition limited by adaptation to obtaining necessary energy and nutrition, surpassing the defensive reactions of the plant and to other environmental factors (Mattson 1980).

The increased content of nitrogen in the diet of *C. pusaria* caterpillars that in natural conditions develop during summer period on birch leaves with decreasing N content may have a negative impact on their development, food consumption and mortality. Accordingly, the aim of this paper is to describe the response of *C. pusaria* caterpillars to the increased level of nitrogen in birch leaves (*Betula pendula*).

## 2. Material and methods

Birches were grown from one year old seedlings in 10 L pots in a forest nursery (Brno – Řečkovice, altitude 220 m a.s.l.) with soil substrate from the Cambic mineral horizon of a forest soil (Kula *et al.* 2012a). Changes in the content of nitrogen in the substrate were induced by application of ammonium nitrate (NH<sub>4</sub>NO<sub>3</sub>) to the plants in four treatments: 0 g (T0), 0.5 g (T1), 1 g (T2) and 1.5 g (T3). Fertilization was carried out in one month intervals, four times in the year of planting (2006) and five times in 2007 and 2008. The amount of ammonium nitrate applied to a plant was chosen in order to achieve a gradient of N content in the birch leaves ranging from insufficiency to oversupply. The normal concentration of nitrogen in birch leaves according to Bergmann (1988) is 2.5–4%.

In accordance with the methods of ICP Fo-

rests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests operating under the UNECE Convention on Long-range Transboundary Air Pollution), mature leaves (except the four terminal ones) were collected from the upper half of the birch crown annually at the turn of August and September and the content of nitrogen was determined after desiccation at 70 °C for 24 hours by the method of Kjeldahl using the Tecator 2300 Kjeltex Analyzer Unit.

Kula *et al.* (2012a) showed that in birches with similar treatments as in this study there were statistically significant differences in the content of nitrogen in leaves between the treatments T0–T3 at the end of growing season, i.e. that the fertilization was effective. Accordingly, similar differences among treatments are assumed in this study, too.

Laboratory rearing of *C. pusaria* (30 females and 20 males) caught in the Ore Mountains was established in mid-July 2008. When the caterpillars began to hatch from the laid eggs (22 July), the caterpillar rearing on foliage from treatments T0–T3 in Petri dishes began. In each of the dishes (15 repetitions in each treatment), 10 caterpillars of the 1<sup>st</sup> instar were placed (total of 600 caterpillars). The rearing was conducted under controlled conditions of the Climacell 707 thermostat with a simulation of the following daily exposure:

- Daylight 10 h, temperature 19.8 °C, relative humidity 60%
- Without light 6 h, temperature 15 °C, relative humidity 85%
- Transitional light with 20% intensity twice for 4 h with gradual changes of temperature and humidity.

Branches with leaves from several host plants grown in plastic greenhouses under different treatments (T0–T3) were cut in each check-up day and transported to the laboratory in coolers within an hour. The long shoot branches were cut up to short segments (1–2 cm long) with only one mature leaf left. The segments were moistened and then placed into Petri dishes with caterpillars of the corresponding treatments (T0–T3). The interval of food (new leaves) exchange was 48 h. During the food exchange, the instar of each cat-

terpillar was determined, as well as the date of pupating and weight of the pupa. Moreover, mortality of caterpillars was monitored for the particular treatments and evaluated in 10-day intervals.

The consumed leaf area was determined as a difference between the leaf area before and after the experiment using a Leaf Area Meter AM300 (ADC BioScientific, Hoddesdon, England). The area of the leaves with only minor feeding marks by the 1<sup>st</sup> instar caterpillars, which could not be detected by this apparatus, was determined in the biometric laboratory of the Faculty of Forestry and Wood Technology, MENDELU in Brno by means of the system of analysis and processing the NIS – Elements AR image (digital camera 5 Mpix Nikon DS – Fi 1 with macro-objective Navitar, exposure KAISER RB 5000 DL, exciter lamp KAISER Prolite Basic, computer with NIS – Elements AR program, version 2.30, processor X86, 2533 MHz, HD 230 GB, RAM 2 MB). The output of measurements mentioned above was the mean consumed areas of the leaves per one caterpillar in a Petri dish by each check-up day. Food consumption was evaluated in 10-day intervals.

After termination of the caterpillar rearing, the content of N in mixed samples of birch leaves remains was assessed in 14-day intervals in order to determine the change of N content in the individual treatments T0–T3.

Statistica.cz (StatSoft 2007) software was used to analyse the data. Shapiro-Wilks test revealed that most of the data obtained in *C. pusaria* rearing (length of development, weight of larvae and pupae and food consumption) deviated from the normal distribution. Therefore, the non-parametric Kruskal-Wallis ANOVA (K-W test hereafter) was used. Subsequently we performed the Dunn's multiple comparison test. The distribution of the data did not deviate from normal only for the length of 5<sup>th</sup> instar caterpillars' development and the mortality of the 1<sup>st</sup> instar caterpillars. ANOVA with Fisher's multiple comparison (LSD test) was used for these data.

For the variables with measured traits for each individual caterpillar, the averages of the values of all caterpillars reared in each Petri dish were used in statistical tests, i.e. the Petri dishes represented independent replicates within treatments, not the individual caterpillars.

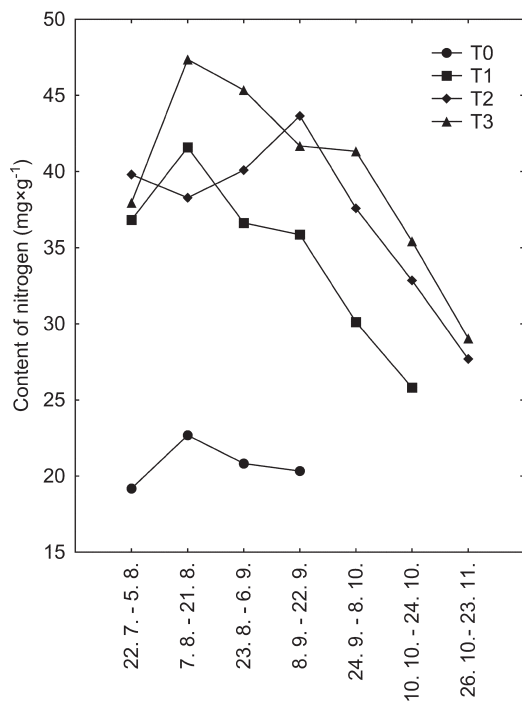


Fig. 1. Average content of nitrogen in leaves of *Betula pendula* fed to *Cabera pusaria* caterpillars in treatments T0–T3 (application of  $\text{NH}_4\text{NO}_3$  as: T0, 0 g; T1, 0.5 g; T2, 1 g; T3, 1.5 g). For T0, caterpillars had pupated by 5<sup>th</sup> period.

### 3. Results

#### 3.1. Content of nitrogen in remains of birch leaves after *C. pusaria* caterpillar rearing

The level of nitrogen in leaves of the control birch trees (T0) was markedly lower compared to the leaves from the fertilized treatments T1–T3 (Fig. 1). From 22 September onwards the gradual decline of nitrogen in leaves due to senescence became evident in treatments T1–T3. In treatment T0, the caterpillars had already pupated by this date and, therefore, there were no leaf remains to be analysed for the content of nitrogen.

#### 3.2. Caterpillar mortality

Mortality (%) of *C. pusaria* caterpillars at the end of the rearing period was assessed separately for each Petri dish, originally containing 10 individuals. The same procedure was chosen to determine

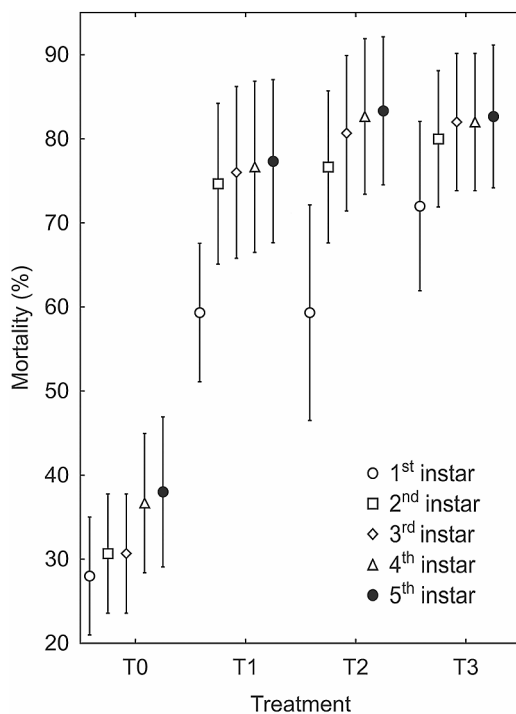


Fig. 2. Means ( $\pm 0.95\%$  confidence intervals) of mortality in *Cabera pusaria* caterpillars (1<sup>st</sup>–5<sup>th</sup> instars and total) reared on *Betula pendula* leaves with increased content of nitrogen, see Fig. 1.

mortality of each instar with the cumulative rise of the dead individuals. Therefore, the mortality in the 5<sup>th</sup> instar equals the mortality assessed for the whole development.

There were significant differences in mortality among the treatments in the first instar (ANOVA,  $F(3, 56)=16.914$ ,  $p<0.001$ ) as well as in other instars (in all K-W tests,  $H(3, N=60) > 30.923$ ,  $p<0.001$ ). The first instar was the most sensitive with the highest frequency of mortality in all treatments (T0–T3). Additional nitrogen in diet (treatments T1–T3) turned out to be the key factor in 1<sup>st</sup> instar mortality (59.3–71.0%) compared to the control (28.0%) (Fig. 2, significant differences between T0 and T1–T3, LSD tests:  $p<0.001$ , no significant differences among T1–T3, LSD tests:  $p>0.054$ ).

During the 2<sup>nd</sup>–5<sup>th</sup> instars, there were significant differences between T0 and other treatments like in 1<sup>st</sup> instar (Dunn's tests:  $p<0.001$ ), but no differences among treatments T1–T3 (Dunn's tests:  $p>0.999$ ). In the 2<sup>nd</sup> and 3<sup>rd</sup> instars, the inten-

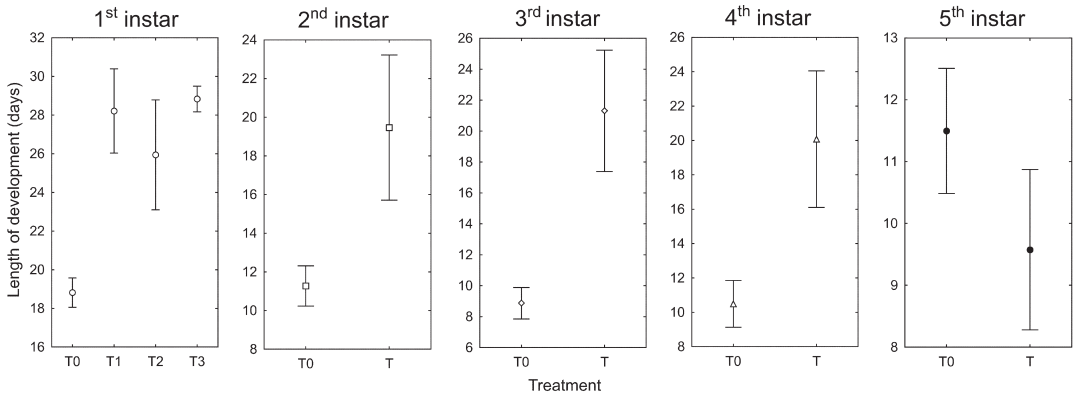


Fig. 3. Means ( $\pm 0.95\%$  confidence intervals) of length of developmental period of each instar of *Cabera pusaria* caterpillars. Treatments T0–T3, see Fig. 1.

sity of mortality decreased and in the 4<sup>th</sup> and 5<sup>th</sup> instars it was minimal in comparison to mortality in the first instar (Fig. 2). In T0, totally 38.0% of the caterpillars did not finish their development while in the treatments with supplemented nitrogen (T1–T3), mortality reached 77.3–83.3% (Fig. 2).

### 3.3. Length of development of caterpillars

Due to high mortality, development of *C. pusaria* caterpillars during the rearing was assessed separately for each instar.

There were significant differences in the duration of the 1<sup>st</sup> instar among the treatments (K-W test  $H(3, N=54)=30.302, p<0.001$ ), with T0 statistically significantly different (shorter development, Fig. 3) from T1–T3 (Dunn's tests,  $p<0.005$ ), but no significant differences among T1, T2 and T3 (Dunn's tests,  $p>0.925$ ).

Due to the limited number of caterpillars (high mortality) in the nitrogen-affected treatments (T1–T3) we decided to merge them together from the 2<sup>nd</sup> instar onwards into a single nitrogen treatment (T). For the 2<sup>nd</sup>–5<sup>th</sup> instars, statistically significant differences between the control (T0) and the individuals reared on nitrogen-enriched food (T) were found (2<sup>nd</sup> instar, K-W test:  $H(1, N=36)=14.607, p<0.001$ ; 3<sup>rd</sup> instar, K-W test:  $H(1, N=28)=18.368, p<0.001$ ; 4<sup>th</sup> instar, K-W test:  $H(1, N=26)=17.898, p<0.001$ ; 5<sup>th</sup> instar, ANOVA:  $F(1, 24)=6.686, p<0.021$ ). The average lengths of the individual instars are shown in Fig. 3.

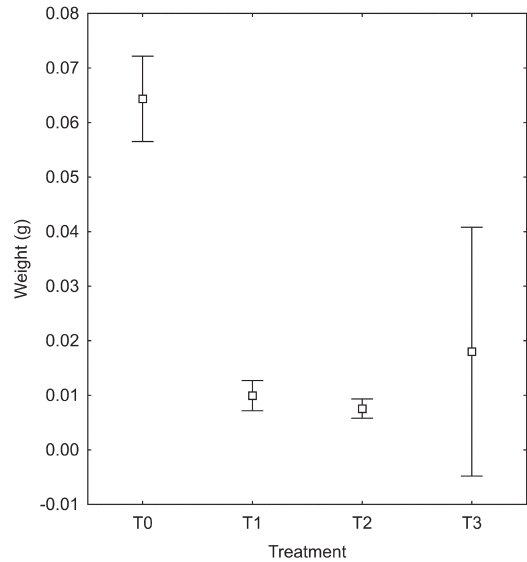


Fig. 4. Means ( $\pm 0.95\%$  confidence intervals) of weight of caterpillars of *Cabera pusaria* after 52 days from the experiment establishment. Treatments T0–T3, see Fig. 1.

### 3.4. Weight of caterpillars and pupae

After 52 days from the begin of the experiment, the weight of every live larva was determined. There were significant differences in weights of caterpillars among the treatments (K-W test:  $H(3, N=107)=72.372, p<0.001$ ). Weight of the caterpillars in control (T0) was significantly higher than that in the treatments with additional nitrogen (T1–T3) (Fig. 4) (Dunn's tests:  $p<0.001$ ).

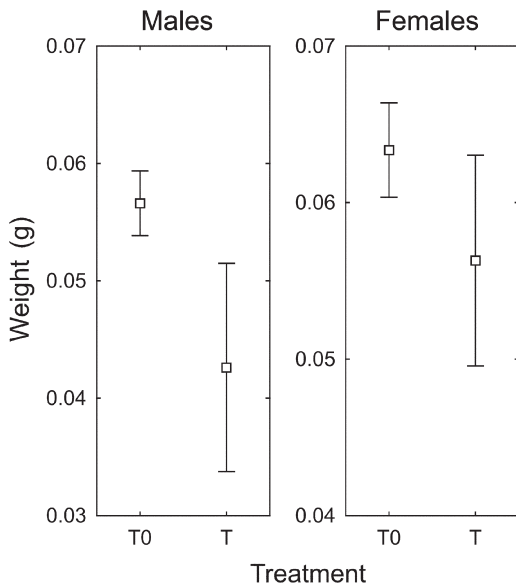


Fig. 5. Means ( $\pm 0.95\%$  confidence intervals) of weight of pupae of males and females of *Cabera pusaria*. Treatments T0 and T (T=T1, T2, T3 combined), see Fig. 1.

Between the treatments T1–T3, statistically significant differences did not occur (Dunn’s tests:  $p > 0.999$ ) (Fig. 4).

The number of pupae obtained in treatments T1–T3 was limited not only by high mortality of the caterpillars, but also by mortalities and abnormalities that occurred during the pupation (41% of the pupae in treatments T1–T3 were deformed). Only 4% of the caterpillars in the treatments T1–T3 completed successfully their development to the pupal stage. Therefore, the treatments with additional nitrogen had to be combined into one treatment (T). Males and females were evaluated separately. The average weight of male (0.053 g) and female (0.062 g) pupae differed significantly (K-W test:  $H(1, N=69) = 14.749, p < 0.001$ ). Only in male pupae a statistically significant difference was found between the control T0 and treatment T (K-W test:  $H(1, N=31) = 8.511, p < 0.004$ ) (Fig. 5). In also female pupae a trend of weight decrease with the increased nitrogen concentrations was noted (Fig. 5) but not quite a statistically significant difference between the treatments T0 and T was found due to the somewhat higher dispersion (K-W test:  $H(1, N=38) = 3.581, p = 0.058$ ).

### 3.5. Food consumption

The different rate of the caterpillar development allowed us to evaluate the differences in the consumption of food between the particular treatments for the first 60 days of rearing (until 20.IX.2008). By this time, most of the caterpillars in the treatment T0 had pupated, hence the statistical group needed for the comparison was not available any more. The average consumption of food by one caterpillar was evaluated in ten-day intervals (Fig. 6). During the first ten days (22.VII.–1.VIII.2008), statistically significant differences between the treatments were not observed (K-W test:  $H(3, N=60) = 5.971, p = 0.113$ ) (max. consumption 1.58 mg in T0 and min. 1.39 mg in T3). During the following five periods of ten days, there were statistically significant differences among the treatments (in all K-W tests:  $H(3, N=(27-59)) > 19.876, p < 0.001$ ). In the con-

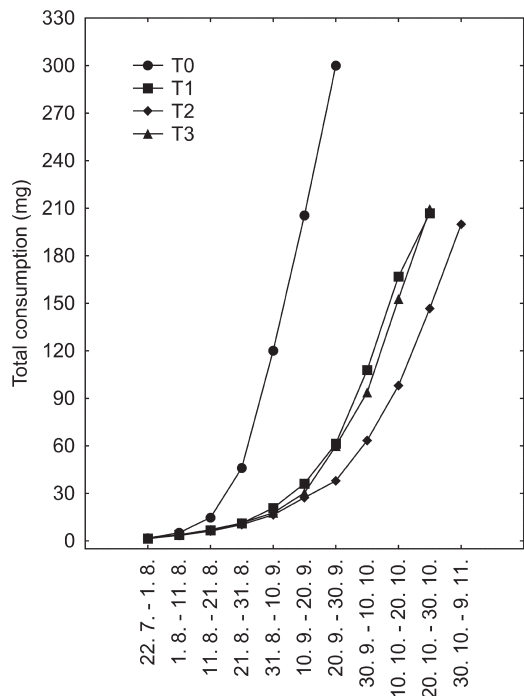


Fig. 6. Cumulative curve of the total consumption of food by caterpillars of *Cabera pusaria* converted per one caterpillar in laboratory rearing with additional nitrogen in food (*Betula pendula*). Treatments T0–T3, see Fig. 1.

trol treatment, feeding gradually increased from 3.36 mg to 83.30 mg while in treatments T1–T3 clearly a slower increase of food consumption was noted, being from 1.89 mg to 18.27 mg. The differences between T0 and other treatments were statistically significant (Dunn's tests:  $p < 0.025$ ), except for the T0 vs. T1 comparison of the period from 31.8. to 10.9., which was not significant (Dunn test:  $p > 0.081$ ). During the whole larval period, the average consumption of food by a caterpillar in T0 reached 300 mg, whereas in treatments T1–T3 it remained close to 200 mg (Fig. 6).

#### 4. Discussion

The increased content of nitrogen in food had markedly negative effects on *C. pusaria* caterpillars. In the Ore Mountains, Hrdlička and Kula (2001) specified the average content of nitrogen in birch leaves in the growing season as  $28.59 \text{ mg} \times \text{g}^{-1}$ . Compared to the period 1995–1998 (Kula & Hrdlička 1998) they stated that air-pollution inputs of nitrogen compounds were thus adequate for normal conditions and their effect receded in the area of the Ore Mountains. According to Hrdlička and Kula (2001), the level of nitrogen in birch leaves declined during the growing season from  $36.36 \text{ mg} \times \text{g}^{-1}$  (May) to  $29.75$  and  $27.49 \text{ mg} \times \text{g}^{-1}$  (July–August) down to  $24.28 \text{ mg} \times \text{g}^{-1}$  (September). In the present study, caterpillars in the control treatment were reared on food with lower level of nitrogen ( $19.19$ – $22.68 \text{ mg} \times \text{g}^{-1}$ ), whereas the treatments with additional nitrogen markedly exceeded the above-mentioned nitrogen content ( $35.85$ – $47.37 \text{ mg} \times \text{g}^{-1}$ ) characterizing the area from where the parental moths for this study had been trapped. Thus, an environment with clearly differentiated food as nitrogen content was created.

Changes in the quality of food may represent a stress situation for phytophages, for example due to production of secondary metabolites by plants (Mattson 1980, White 1984, Bryant et al. 1993). Responses of phytophages to air pollution and increased inputs of nitrogen into plants has been discussed by, e.g., Jansson and Smilowitz (1985), Heliövaara and Väisänen (1993) and Pronos et al. (1999).

In the present study, the 1<sup>st</sup> and 2<sup>nd</sup> instar caterpillars of *C. pusaria* responded most sensitively to the high level of nitrogen in food. Mortality increased continuously through the 3<sup>rd</sup> to the 5<sup>th</sup> instar, being not different among treatments with increased N levels (T1–T3) at the end of larval development. The deviations from the control treatment showed that the higher contents of nitrogen increases caterpillar mortality and prolongs their development. An increase of mortality with the increased content of nitrogen in food was also observed in hymenopterous larvae of *Neodiprion swainei* (Smirnoff & Bernier 1973), the feeding of which culminated in August and at the beginning of September (McLeod 1970). Despite their longer period of development, the caterpillars of *C. pusaria* fed with food with additional nitrogen consumed lower total amount of food than the caterpillars in the control treatment. The caterpillars in treatments with additional nitrogen reached also lower weight than those in control treatment in the comparable period. The same was true for the pupae of the caterpillars that completed their development, though for females this was not quite statistically significant. Moreover, contrary to the treatments with additional nitrogen, no developmental anomalies appeared in pupae of the control treatment. This fact can be related even to toxicity of nitrogen-rich food for larvae ordinarily developing on leaves in the period of naturally declining N content. On the other hand, many early season insect herbivores are known to react positively to increased concentrations of organic nitrogen in leaves and phloem of plants (White 1984, Haddad et al. 2000), for example *Choristoneura fumiferana* (Shaw & Little 1972), *Choristoneura conflictana* (Bryant et al. 1987) and *Lymantria dispar* (Lindroth et al. 1991, 1997, Kula et al. 2012b, Pešlová 2012). Feeding of these phytophages occurs early in spring when the content of nitrogen in leaves is the highest (Rodin & Bazilevich 1967, Hrdlička & Kula 2001, Šrámek et al. 2009).

It is important to take into account the generally different responses of particular plant species, especially to stress, and subsequently the different responses of insects induced by changes in the quality of food (Larsson 1989). Therefore, it is not possible to generalize the detected responses of *C. pusaria* caterpillars. Other species

or even the same insect species can behave differently on another plant species (Heliövaara & Väisänen 1993). On pine (*Pinus ponderosa*), population density of phytophages decreased with increasing content of nitrogen but the species diversity remained the same (evaluated at the level of orders and suborders) (Jones & Paine 2006), indicating that their development was possible even at the increased level of nitrogen, but it was accompanied by increased mortality. Opposite responses to higher inputs of nitrogen were shown in sucking insects; Psylloidea showed a fall of species diversity and increase of abundance (Prestidge 1982), and the plant lice *Metopolophium dirhodum* an increase of abundance (Honek 1991).

In summary, the hypothesis presuming negative responses of caterpillars of the summer phytophagous species *C. pusaria* to increased N content in their food (*Betula pendula*) was supported. Smaller size of caterpillars and especially male pupae (in the case of a female pupae we didn't find a statistically significant difference) and prolonged development of the larvae and their increased mortality were observed.

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