

The effect of defoliation history on photosynthetic rates in mountain birch

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PRUDHOMME, THOMAS I. The effect of defoliation history on photosynthetic rates in mountain birch. Rep. Kevo Subarctic Res. Stat. 18: 5 – 9. 1982. – The effect of defoliation history on the rate of $^{14}\text{CO}_2$ uptake was studied in natural populations of mountain birch near the Kevo Subarctic Research Station in Northern Finland. Birches protected from outbreaks of *Epirrita autumnata* by colder winter temperatures at low elevations photosynthesized at a rate 42 % slower than trees at the middle elevation on fell Jesnivaara which were undamaged in the outbreak in 1960s. Surviving trees defoliated in this outbreak photosynthesized 63 % faster than undamaged trees at the same elevation. Therefore, the hypothesis that increases in allocation to defensive chemicals after defoliation decrease resource use in other areas of metabolism is not supported with respect to carbon uptake rates in trees experiencing cyclical outbreaks.

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Introduction

Forest trees typically lose a percentage of their leaf biomass each season due to the feeding of phytophagous insects. Host populations subject to periodic outbreaks of defoliating insects have the additional problem of recovering from the loss of an entire season's leaf biomass during the peak of each herbivore cycle. Mediating this interaction are the herbivore's requirements for energy and nutrients set against a variety of defensive mechanisms employed by the plant plus its own resource requirements for growth and storage (Prudhomme 1982). Recent studies have demonstrated short term responses to leaf damage as well as other forms of stress (Haukioja & Niemelä 1977, 1979; topic reviewed by Rhoades

1979). However, large scale fluctuations in the herbivore population would require a long term strategy in the host species to ensure the re-establishment of equilibrium conditions following an outbreak. Therefore, a consistent local variation in the intensity of such outbreaks would represent a strong selection pressure in the development of a plant species' survival strategy.

In northern Fennoscandia, the mountain birch, *Betula pubescens* ssp. *tortuosa*, is periodically defoliated by the geometrid moth, *Epirrita* (= *Oporinia*) *autumnata* (Tenow 1972, Kallio & Lehtonen 1973). Outbreaks occur at ten year intervals, the most recent being in 1960s which removed more than 90 % of the foliage on half of the trees in the Fennoscandian subarctic birch forest zone (Kallio & Lehtonen 1975). However, many birches at lower elevations and in the river valleys

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were not affected since cold air drainage during the winter destroyed many of the egg masses in these areas (Niemelä 1979, Haukioja 1980a). Thus, the montane birches have survived both low level attack by a diverse herbivore fauna (Koponen 1973a, b) as well as the massive defoliations caused by *E. autumnata*. While the river valley birches may have been defoliated by this herbivore, such attacks would have occurred less frequently on trees growing at lower elevations. These differences would have important implications in the natural selection of strategies for the acquisition and allocation of resources in each population. Haukioja et al. (1978) found the total phenolic content to be lowest in leaves at the lowest elevation, hence the steady-state carbon allocation to these allelochemicals was higher in the zone with a higher frequency of defoliation.

Employing current assumptions on the allocation of limited resources derived from Pimentel (1968) and Mooney (1972), such an emphasis on phenolic compounds would manifest itself in reduced priorities for other metabolic functions. However, the central premise is that, in the long term, the available resource bases for the two populations are equal, hence for reductions to be effected in non-defense related areas of carbon use the annual uptake rates for this resource must be similar. Therefore, the metabolic machinery used in CO_2 fixation should be exempted from reductions in carbon allocation due to an increase in the emphasis on phenolic compounds since a significant reduction in photosynthetic rates would reduce the size of the resource base.

The objective of this study was to elucidate the effects of defoliation history on the rate of carbon fixation in mountain birch. For the long term effects of cyclical defoliation it was hypothesized that although the allocation of fixed carbon might be different, the uptake rates would be equivalent. It was further hypothesized that trees which were defoliated in the previous outbreak of *E. autumnata* would have lower carbon uptake rates than nearby undamaged trees as a consequence of a further increase in allocation to phenolic compounds in the damaged trees (Haukioja, unpublished data). While potentially

decreasing the annual uptake of CO_2 by these trees, the highly defended leaves would be less vulnerable to herbivore attack. This strategy would provide for conservative but consistent growth and a slow replacement of stored reserves lost in resprouting. Adequate preparation would increase the probability of surviving the next herbivore cycle peak.

Materials and methods

In July-August 1979, the carbon uptake rates for mountain birch from near the Kevo station (low elevation) were compared with trees from the middle elevation of fell Jesnalvaara (MJ). On Jesnalvaara, individuals which had not previously been sampled were marked to represent either trees defoliated in the last outbreak (O population) or those protected by winter temperatures at a nearby site and therefore undamaged (U population). Both study areas were situated near the MJ site used by Haukioja et al. (1978). The O individuals were predominantly root sprouts, and although U trees were polycormic relative to trees at the base of the fell, there was usually one dominant stem. For each population, approximately one third of the individuals measured were of the non-dominant form. Due to the physical separation of these two populations paired measurements were impossible, however morning and afternoon periods were alternated giving equivalent sample numbers and time periods during which measurements were made. Near the Kevo station, individuals were marked to represent the C (control) population. The O and U individuals were labelled during 25–31 July followed by the C individuals from 1–4 August.

Carbon uptake rates were estimated using $^{14}\text{CO}_2$ labelling techniques of Oechel & Mustafa (1979). Birch leaves were incubated for 45 seconds in a 1 cm^3 chamber with $^{14}\text{CO}_2$ in air circulating around the leaf surface at a rate of 60 ml/min. Air temperature was monitored using a shaded, type T (Cu-Cn) thermocouple read with an Omega Instruments analog laboratory thermometer. Incident photosynthetically active radiation (PhAR, 400–700 nm) was measured during each labelling using a Li-Cor model LI-185 light meter with a model LI-170 quantum sensor. Immediately after labelling, a 0.32 cm^2 disk was taken from each leaf, stored in dry ice (solid carbon dioxide), and a few hours later oven-dried at 80°C for 24 hours. The disks were then weighed for calculation of leaf density, combusted in an Intertechnique (Model IN 1401) Oxymat sample oxidizer, and assayed for ^{14}C activity. Uptake rates were calculated on an area basis.

Mean uptake rates ($\text{mg CO}_2/\text{dm}^2/\text{h}$) for populations were compared by Student's *t* test using the Statistical Analysis System (version 79.4) GLM procedure for analysis of covariance (LSMEAN option) with temperature, PhAR, and leaf density

Table 1. Mean $^{14}\text{CO}_2$ uptake rates (\pm S.E.) in relation to earlier damage for *Betula pubescens* ssp. *tortuosa* taken from the middle elevation on fell Jesnalvaara (damaged (O), undamaged (U)) and from near the Kevo research station (undamaged control (C)) between 25 July and 4 August 1979. For the statistical probabilities t test was used.

Site	mg $\text{CO}_2/\text{dm}^2/\text{h}$	Probability	n
Kevo station (C)	4.5 ± 0.2	$p < 0.0001$	150
Jesnalvaara (U)	6.4 ± 0.2	$p < 0.0001$	193
Jesnalvaara (O)	10.4 ± 0.2		193
leaves from root sprouts	9.8 ± 0.2	$p < 0.05$	120
leaves from old branches	10.8 ± 0.2		73

as covariates. This analysis was chosen in order that the responses of photosynthesis to the covariates would be compared rather than simple means of the data which were taken on different days and under slightly different conditions.

Results and discussion

The mean uptake rate for each population is presented in Table 1. Rather than being equal, the undamaged (U) trees from Jesnalvaara fixed CO_2 at a rate 42 % faster than the undamaged trees from the C population. The difference was highly significant ($p < 0.0001$). At the middle elevation on Jesnalvaara, the damaged (O) birches fixed CO_2 at a rate 63 % higher ($p < 0.0001$) than the undamaged (U) trees despite a greater concentration of phenolic compounds in the O population.

Haukioja (1975, 1980b) has described the dichotomy between the responses to leaf damage in birch populations at different elevations. On fell Jesnalvaara, trees at low elevations demonstrated rapid decreases in leaf quality after damage, but had a poor ability to recover after complete defoliation. At middle and higher elevations the immediate response to damage was slower, but survival was better following defoliation. That the uptake rates were higher on Jesnalvaara is consistent with these results. At MJ, the slow reduction in leaf quality coupled with a rapid recovery of lost biomass suggested that the priority for carbon allocation to storage may be high in these birches. Due to an increase in the size of the carbohydrate sink size, such a constant drain on the photosynthate pool in the leaf would stimulate higher uptake rates (Kramer & Kozlowski 1979: 219–221).

In the temporal framework of natural selection individuals with higher photosynthetic rates and a large storage capacity would have an additional advantage.

The results presented for the Jesnalvaara populations demonstrate the importance of photosynthate production after severe herbivore damage. The magnitude of the differences strongly suggests an increase in the allocation of resources to photosynthetic metabolism in the leaves of damaged trees, however other physiological phenomena may also contribute. The strain of post-outbreak carbon requirements on stored reserves could again result in the maintenance of near maximum rates due to an increased rate of photosynthate translocation out of the leaf. In addition, leaves on young shoots tend to have higher photosynthetic rates than leaves from mature stems (Kramer & Kozlowski 1979: 215–216). However, when the data were grouped into leaves from root sprouts versus those from older branches, the mean uptake rate for the former group was actually slightly lower, although the difference was barely significant (Table 1, $p = 0.044$). Therefore, this tendency could not be responsible for the observed enhancement of photosynthetic rates in the damaged (O) population.

Clearly, populations of mountain birch which undergo periodic defoliation by *E. autumnata* not only have a greater allocation of resources to the production of allelochemicals, but they also possess a greater capacity to fix the necessary carbon. Thus, the hypothesis that the photosynthetic rates would be equal in the U and C populations is not supported. Further, maintenance of the photosynthetic

machinery in the MJ birches is not adversely affected by changes in carbon allocation priorities following defoliation. Hence, in the carbon economics of mountain birch, the assumption that allocation to the carbon fixation apparatus and to allelochemicals are related in a "guns and butter" fashion is an oversimplification. Rather, the survival strategy for the birches in the zone of high incidence of damage (MJ) appears to be more inclined toward an increase in the use of carbon to support photosynthesis which then provides the resource for an increase in defensive chemical production while at the same time providing for the replacement of storage reserves used in resprouting after defoliation.

Evidence for compensatory responses to cyclical reductions in photosynthetic biomass due to herbivore feeding exists for certain grazing systems (McNaughton 1982), and reflects the importance such events may have in natural selection and therefore species composition in these communities. The results presented here also support the hypothesis that selection is acting on ecophysiological processes within a species. Future research in the area of plant-herbivore interactions should consider the effects of both defoliation history and changes in the overall carbon balance of the plant in assessing its short term responses to herbivore attack.

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