

Can sunspot activity and ultraviolet-B radiation explain cyclic outbreaks of forest moth pest species?

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Cyclic outbreaks of forest moth pest species have long remained a puzzle for foresters and ecologists. This paper presents time-series exhibiting a strong negative relationship between sunspot numbers and population indices of autumnal and winter moths, both in a mountain birch forest in central Norway and in a mixed lowland forest in southern Norway. In the latter area, also the population level of a moth species feeding entirely on lichens was negatively related to sunspot numbers. Low sunspot activity leads to a thinner ozone layer and thus higher surface ultraviolet (UV)-B radiation. As winter moth larvae prefer leaves subjected to enhanced UV-B radiation, we suggest that the causal relationship between sunspots and moths is that the metabolic costs of producing UV-B-protective pigments during periods of low sunspot activity reduce trees' and lichens' resistance to herbivores, and thus increase the survival of moth larvae. Higher peak densities of moth cycles in mountain forests could be explained by the general higher UV-B radiation at higher altitudes.

Keywords: herbivore resistance; moth cycles; pest species; sunspots; ultraviolet-B

1. INTRODUCTION

The influence of climate change and ozone layer depletion on global biodiversity and agricultural systems is largely acknowledged, but the potential additional impact of natural fluctuations in sunspot activity is still debated. In the Northern Hemisphere, densities of forest moths often peak when sunspot numbers are low (Myers 1998; Ruohomäki *et al.* 2000), a pattern that has been difficult to explain. Because defoliation by moth pest species is costly to forestry, knowledge about the impact of both natural and human-induced environmental fluctuations on moth performance would be of great value to forecast and prevent damage.

At the maxima of the 11-year solar cycle, the dose of surface ultraviolet (UV)-B may be 4–13% lower than at the minima, because high UV-C radiation leads to a thicker ozone layer, and thus reduced surface UV-B fluxes (Rozema *et al.* 2002). Thus, production of UV-B-protective phenolics in trees (e.g. Harborne & Williams 2000; Lavola *et al.* 2000) should be highest when solar activity is low. As this production probably represents a metabolic cost (Hessen 1996), it may occur at the expense of herbivore resistance, either because resources are allocated to leaf phenolics that protect against UV-B rather than against herbivores (Tegelberg *et al.* 2003) or because increased transport of essential amino acids in UV-B-stressed trees benefits growth and survival of leaf-chewing insects (White 1984, 1993).

In Norway, the autumnal moth (*Epirrita autumnata*), winter moth (*Operophtera brumata*) and northern winter moth (*O. fagata*) are pest species in mountain birch (*Betula*

pubescens) forests, with regular outbreaks at *ca.* 10-year intervals (Tenow 1972). Survival and egg production of autumnal moths are lower at higher temperatures (Virtanen & Neuvonen 1999), but lack of outbreaks in the lowland could also be explained by lower doses of surface UV-B, because the UV-B radiation increases by *ca.* 20% per 1000 m elevation (Blumthaler *et al.* 1997). There may also, however, be regular, but low-amplitude and therefore unnoticed, population fluctuations of forest lepidoptera in the lowland.

Outbreaks of forest lepidoptera are usually associated with mature trees (Bylund 1997). We have previously found a relationship between autumnal moth population growth and birch mast seeding (Selås *et al.* 2001), suggesting that high seed crops increase the nutritional value of birch leaves (Selås 1997). However, as masts were usually produced when sunspot activity was high (Selås *et al.* 2001), the relationship between seed production and moth populations may be an artefact caused by a simultaneous effect of sunspots on both flowering and larval performance. But any interaction between seed production and moth population levels may confound effects of sunspot activity, especially in the lowlands, where the impact of UV-B radiation should be less.

We have investigated the relationship between sunspot activity and population levels of autumnal and winter moths both from a mountain birch forest in central Norway and from a lowland mixed forest in southern Norway. Because we lacked detailed information on birch seed production in the lowland, we also studied population fluctuations of the pale November moth (*E. christyi*), which feeds mainly on rowan (*Sorbus aucuparia*) leaves. By use of long-term data series on rowanberry production, we were able to adjust for any effects of fluctuating seed production

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Table 1. Results from regression analyses with autoregressive errors on moth population indices (year t) from a mountain birch (*Betula pubescens*) forest in Central Norway (Budal) and a lowland mixed forest in Southern Norway (Nesodden). (All moth–sunspot relationships were negative, whereas the rowan (*Sorbus aucuparia*) index (pooled rowanberry production year $t-1$ and $t-2$) contributed through a positive effect. The residuals of the regression models were all uncorrelated and normally distributed. AIC, Akaike's information criterion; AR, autoregressive.

species and area	explanatory variable	r^2	p	AIC	significant ^a
					AR-terms
<i>Epirrita autumnata</i> , Budal	none	—	—	107.10	1, 3
	sunspots year t	0.84	< 0.001	52.96	—
	sunspots year $t-1$	0.56	< 0.001	82.89	—
<i>Operophtera</i> spp., Budal	none	—	—	135.36	1, 2
	sunspots year t	0.42	< 0.001	120.14	1
	sunspots year $t-1$	0.41	0.002	118.02	1, 2
<i>Epirrita autumnata</i> , Nesodden	none	—	—	66.87	1
	sunspots year t	0.02	0.600	68.56	1
	sunspots year $t-1$	0.15	0.090	65.59	1
<i>Operophtera</i> spp., Nesodden	none	—	—	61.39	1
	sunspots year t	0.12	0.168	61.18	—
	sunspots year $t-1$	0.31	0.016	56.66	—
<i>Epirrita christyi</i> , Nesodden	none	—	—	31.42	—
	sunspots year t	0.25	0.026	27.73	—
	sunspots year $t-1$	0.45	0.001	21.61	—
	sun $t-1$ and rowan	0.61	< 0.001	16.76	—
<i>Eilema lurideola</i> , Nesodden	none	—	—	60.62	1, 3
	sunspots year t	0.61	< 0.001	44.03	—
	sunspots year $t-1$	0.45	0.001	50.73	—

^a Significance was established at $p < 0.05$.

when analysing for relationships between population levels of the pale November moth and sunspot numbers.

Recently, UV-B-induced production of sun-screening pigments has also been documented for lichens (Solhaug *et al.* 2003). As there is no annual variation in resource allocation caused by variable seed production in lichens, caterpillars feeding on lichens could be expected to respond more directly to fluctuations in sunspot activity than those feeding on trees. From the lowland area, we therefore also present data on the common footman (*Eilema lurideola*), which feeds entirely on lichens (e.g. *Parmelia*) growing on tree trunks or rocks.

2. MATERIAL AND METHODS

The study was carried out in an unmanaged mountain birch forest in Budal, central Norway (62°45' N, 10°30' E; 780–900 m elevation), during 1972–2003 and in a managed lowland mixed forest in Nesodden, southern Norway (59°44' N, 10°36' E; 70 m elevation), during 1984–2003. In Budal, oligotrophic 'heath' birch forests predominate (Hogstad 1997). The study area in Nesodden consists of coniferous and temperate deciduous forests stands of different ages intermixed with agricultural and developed areas. Both winter moths, which were not distinguished in the analyses, and the autumnal moth feed on birch, but in the lowlands also on other deciduous tree species.

Because of the exponential nature of population growth, and in order to meet the assumption of normal distribution, all moth series were log-transformed before analyses. In Budal, autumnal and winter moth caterpillars were collected at random from the lowest 4 m of birch branches by use of a sweep-net. Each year, 5–15 collections, each of 100 sweeps, were taken in the first days of July, when the larvae were in their fourth to fifth instars. The annual population index from Budal is the mean number of larvae

of instar 4 and 5 collected per 100 sweeps. Because there were several years when no caterpillars were found, the data from Budal were $\log(x+1)$ transformed.

In Nesodden, population levels of adult moths were estimated by use of light-trapping. The trap used was of a simple funnel type with a 160 W mixed light bulb (Osram HWL 160 W/235 V). The trap was hung with the bulb 1 m above the ground at precisely the same location each year. The trap was operated on the three first nights of every week from late June to late October. For each moth species, the average number from nine nights with the highest average abundance (three nights in each of three consecutive weeks) was used as a population-level index (Kobro 1991). Light-trapping is probably less reliable than larvae counts because the weather may influence trapping efficiency (Kobro 1991), but larvae counts are too time consuming in areas of intermixed forest stands with no outbreaking populations.

Indices of rowanberry production were provided by the apple fruit moth forecasting service at The Norwegian Crop Research Institute, Ås, Norway. In our lowland study area, as well as in two areas situated ca. 1.2 km southeast of this area, the number of flower clusters was counted annually on 20 tagged trees or branches. We used the mean of the annual index calculated from each of these areas. Rowanberry production has usually been high at 2–3-year intervals (Kobro *et al.* 2003). Because of a predicted positive effect of seed production in the previous year on moth performance (Selås 1997, 2000; Selås *et al.* 2001), we used either the mean rowanberry production of the previous year or the pooled mean production of the two previous years in the analyses.

Cyclic fluctuations in insect populations could be caused either by delayed density dependence or by autocorrelated exogenous factors (Williams & Liebhold 1995; Hunter & Price 1998). After having examined the time-series for presence of general and structural dependences by calculating sample autocorrelation and

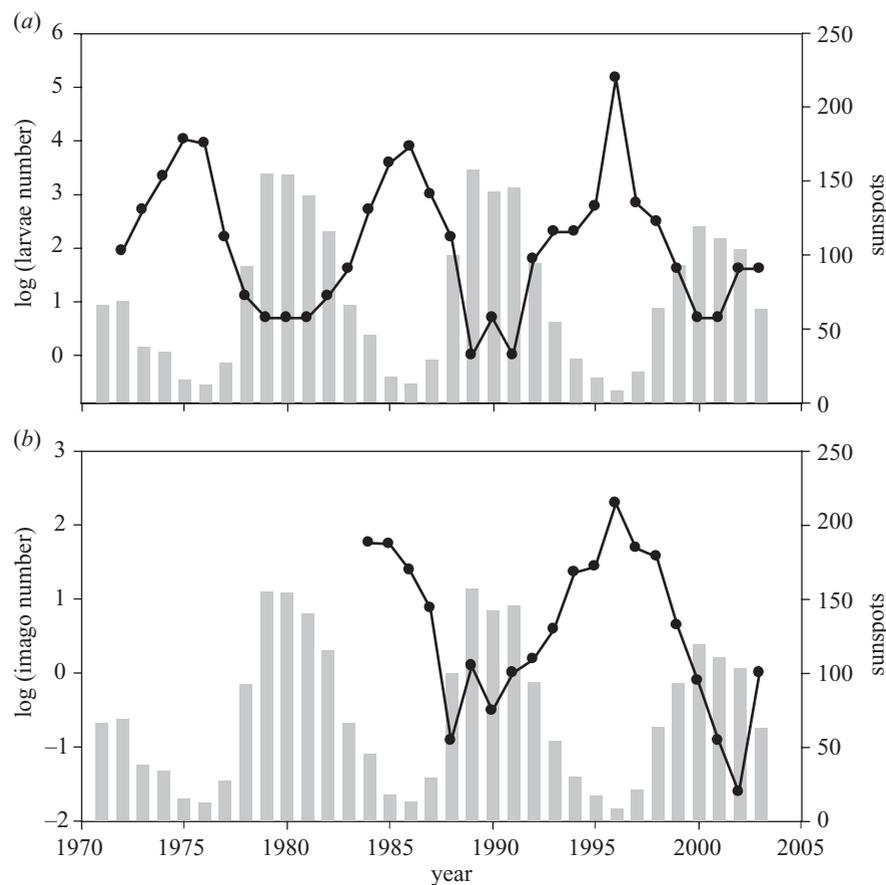


Figure 1. Annual fluctuations in the population level of two moth species (solid line) compared with fluctuations in sunspot numbers (bars). (a) Data on the autumnal moth (*Epirrita autumnata*) from a mountain birch (*Betula pubescens*) forest in central Norway (Budal) ($r^2 = 0.84$); and (b) data on the common footman (*Eilema lurideola*) from a lowland mixed forest in southern Norway (Nesodden) ($r^2 = 0.61$). The former moth feeds on birch leaves in spring, the latter on lichens growing on tree trunks and rocks.

partial autocorrelation functions, we fitted regression models with autocorrelated errors (PROC AUTOREG in SAS), both with and without the sunspot data included. Our prediction was that higher-order feedback terms, indicating delayed density dependence, should disappear from the time-series model with the sunspot data included. The sunspot series used were the yearly means calculated as the average of the daily means (available at ftp://ftp.ngdc.noaa.gov/STP/SOLAR_DATA/SUNSPOT_NUMBERS/YEARLY).

3. RESULTS

For all moth species, we found a negative relationship between population-level indices and sunspot numbers in the same or the previous year (table 1). Sample partial autocorrelation functions indicated the presence of first-, second- and third-order structural dependences in the two moth series from the mountain forest and in the common footman series from the lowland forest. Adding sunspot data from the same year as a covariate had the effect that the higher-order structural dependences in these moth data disappeared (table 1). This may indicate that the higher-order structural dependences in the moth series were caused by this exogenous factor.

In the mountain forest, sunspot activity in the current year explained statistically 84% of the variation in the population index of autumnal moth (table 1; figure 1) and 42% of that of the less common winter moths (table 1). In

the lowland forest, the population levels of the common footman also exhibited a relationship with sunspot numbers in the same year (table 1; figure 1), whereas populations of the autumnal moth, pale November moth and winter moths in the lowland area displayed a stronger covariance with sunspot numbers of the previous year (table 1). The relationship was significant for the pale November moth and winter moths, but not for the autumnal moth (table 1).

For the population level of the pale November moth, there was an additional positive effect of the pooled rowanberry production of the two previous years ($p = 0.017$). When this variable was entered, the explanatory power of the regression model increased from 45% to 61% (table 1; figure 2). For the other moth species, there were no significant relationships between population levels and rowanberry production.

4. DISCUSSION

The population level of all moths studied was negatively related to sunspot numbers, a pattern that is in accordance with the hypothesis that high UV-B radiation in periods of low sunspot activity reduces the herbivore resistance in host trees and lichens. Moreover, our study confirmed the assumption of a 10-year low-amplitude moth cycle in lowland forests, almost synchronous to the

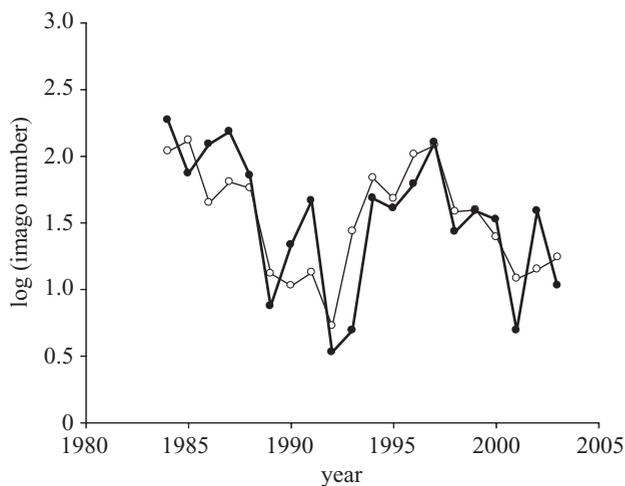


Figure 2. Population fluctuation of the pale November moth (*Epirrita christyi*) in a lowland mixed forest in southern Norway (Nesodden) (filled circles, thick line) and the population fluctuation predicted from a multiple regression model (open circles, thin line). The explanatory variables used were sunspot numbers in the previous year (negative effect) and rowan (*Sorbus aucuparia*) seed production of the two previous years (positive effect). $r^2 = 0.61$. The pale November moth feeds on rowan leaves in spring.

well-documented cycle of autumnal and winter moths at higher altitudes. The time lag of 1 year between sunspots and population indices of forest moths in the lowland could be because these moths respond more slowly to the environmental changes responsible for the population fluctuations. As mentioned in the introduction, the peak levels of UV-B may affect lowland trees less than mountain trees because of the higher UV-B levels at high altitudes.

Myers (1998) suggested that weather conditions associated with the sunspot cycle might act as a Moran effect by synchronizing fluctuating moth populations. If so, the driving force behind moth cycles could be factors other than UV-B. Among mechanisms commonly suggested to create delayed density dependence, and thus population cycles, are maternal effects (Ginzburg & Taneyhill 1994) and trophic interactions such as delayed effects of enemies (Myers 1993; Berryman 1996) and delayed induced effects of defoliation on plant chemistry (Kaitaniemi *et al.* 1998). However, the lack of delayed feedback terms in our regression models (with sunspot variables included) does not support any of the above delayed density dependence hypotheses.

There are also experimental studies that support the suggested direct effect of UV-B radiation on herbivore resistance in trees. Caterpillars of the winter moth preferred silver birch (*B. pendula*) leaves that had been subjected to artificially increased UV-B radiation (Lavola *et al.* 1998). A similar preference has been reported for cottonwood beetles (*Chrysomela scripta*) feeding on black cottonwood (*Populus trichocarpa*) (Warren *et al.* 2002), and for different insect herbivores feeding on willows (*Salix* spp.) (Veteli *et al.* 2003). For the winter moth, the preference was not related to the observed increase in sun-screening pigments (Lavola *et al.* 1998).

An alternative explanation for the sunspot–moth relationship is that sunspot-induced fluctuations in climate (e.g. Tsiropoula 2003) affect moth performance by influencing plant phenology rather than plant chemistry. For the tree-feeding moths investigated (but not for the common footman), it is probably important that the eggs hatch as soon after budburst as possible (Hunter 1992). However, in a 50-year time-series (1928–1977) on the timing of budburst in birch and sessile oak (*Quercus petraea*) from two study areas in southern Norway, no significant statistical effects of sunspots were found (V. Selås, unpublished data). As also shown by Post & Stenseth (1999), there was a highly significant relationship between tree phenology and the North Atlantic Oscillation (NAO). The NAO was related to spring temperatures in the study areas, but not to the number of sunspots ($r^2 < 0.01$, $p = 0.70$).

Only for the autumnal moth in our lowland study area was the relationship between sunspots and population indices not significant. This could be a result of the generally low population level, making population indices less reliable, or of confounding effects of variations in seed production of birch or other deciduous trees. The relationship between rowanberries and the pale November moth suggests that seed production is an important additional factor that should be considered when forest moth population fluctuations are analysed. At lower altitudes, this factor may be even more important than effects of sunspot activity for tree species that occasionally produce especially high seed crops, such as oak (*Quercus* spp.) and beech (*Fagus* spp.).

For moths in general, the number of eggs laid per female is so high that outbreak levels would be reached in a few years if most larvae survived. The main reason why this usually does not happen appears to be high mortality in the nutrition-demanding early-instar larvae, possibly caused by the general low availability of essential amino acids in plants (White 1993). Most forest moth pest species are flush feeders, i.e. their early-instar larvae feed on developing leaves. Even a slight increase in the nutritional value of such leaves, caused, for example, by some environmental stress factors that require increased metabolic activity in the plant, may significantly enhance larvae survival, and thus initiate population outbreaks (White 1993).

Moth performance is most probably a result of the combined effect of nutritive and defensive compounds in plants (Haukioja 2003). In host trees, the levels of herbivore-protective phenolics, which are different from UV-B-screening phenolics, increase during the decline phase of a moth cycle (Kaitaniemi *et al.* 1998; Ivashov *et al.* 2001), but the driving force behind the changes in leaf chemistry and moth numbers has remained unknown. We suggest that these fluctuations are initiated by the direct effect of solar activity, and modified by the synchronizing effect of both sunspots and climate on the endogenous flowering cycle in trees (Sork & Bramble 1993; Piovesan & Adams 2001; Selås *et al.* 2002). The hypothesis about the positive effects of UV-B-induced plant stress on herbivore performance should now be addressed in controlled laboratory experiments, with focus on different ecological categories of both plants and herbivorous animals.

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