

Seasonal patterns in the incidence of specialism: Macrolepidopteran larvae on Finnish deciduous trees

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Deciduous trees exhibit seasonal variation in the production of new leaves. The trees of the so-called *Quercus*-type (e.g. *Quercus robur* and *Prunus padus*) produce new leaves mainly in spring, while new foliage in the trees of *Populus*-type (e.g. *Populus*, *Betula*, *Alnus*) is also produced in late season.

According to optimal defence theory, specialist (monophagous) herbivores should prefer young leaf tissue while generalist (polyphagous) species should grow better on mature leaf tissue. This difference gives rise to the prediction that the proportion of specialists will be highest on the trees of *Quercus*-type mainly early in the season, while on the trees of *Populus*-type their seasonal distribution will be more even.

This assumption was tested using data on the Finnish macrolepidopteran fauna. The observed trends were as predicted: the proportion of specialists was significantly highest in spring on *Quercus*-type, while on *Populus*-type the proportion was more constant over the season as a whole. However, on both tree types 70-85 % of macrolepidopteran fauna consisted of generalized feeders early in the season, which disagrees with the prediction of the optimal defence theory. It was suggested that the seasonal species richness patterns of herbivores are also affected by the differences in the seasonal production of allelochemicals between these two tree types.

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1. Introduction

Feeny (1970) in his classical work showed that the seasonal species richness pattern of the lepidopteran herbivores on the oak (*Quercus robur*) in Britain had a peak in spring. He was also able to demonstrate that the quality of leaves for winter moth (*Operophtera brumata*) larvae was optimal at the same time (high nitrogen and water content, low tannin content). It was shown later that this kind of species richness distribution of the Lepidoptera observed on oak seems not to apply to all deciduous trees (Niemelä & Haukioja 1982, Niemelä et al. 1982). Among Finnish deciduous trees thus far studied, only the oak and the bird cherry (*Prunus padus*) have spring-peaking species richness distributions, while the other trees have a peak more or less in autumn. Niemelä & Haukioja (1982) proposed that this variation among deciduous trees in the species richness pattern of Lepidoptera is connected with the differences in the length of the annual shoot-growth periods and in the timing of seasonal leaf production. The trees of the so-called *Quercus*-type (*sensu* Hoffman & Lyr 1973) produce new leaves mainly during

the springtime (for example the oak and the bird cherry) while the trees of *Populus*-type (*sensu* Hoffmann & Lyr) produce them throughout the growing season (e.g. aspen, birches and alders) (Kikuzawa 1982).

As a consequence of this variation in the timing of new leaf production, there are two potential food resources for herbivores (new and old leaves) on the trees of *Populus*-type during the late season but only one (mature leaves) on the *Quercus*-type. If greater heterogeneity of available resources allows of a greater number of coexisting species (e.g. MacArthur 1968), then late in the season the species richness of herbivores on the trees of *Populus*-type can theoretically be much higher than that of the *Quercus*-type. This hypothesis presupposes differences among herbivores in their utilisation of new and mature leaves. According to the optimal defence theory (Feeny 1976, Rhoades and Cates 1976, Rhoades 1979), young leaves defend themselves against herbivores by using cheap toxic-like compounds. This is thought to be effective against generalist herbivores and counteradaptation of herbivores is, therefore, specialization. The defensive armour of mature leaves

consists of dose-dependent digestibility-reducing substances and toughness. This should be effective against all kinds of herbivores, including specialists.

On this basis the following predictions can be made:

1) On the trees of *Quercus*-type, where the production of new leaves occurs mainly in spring, the proportion of specialized herbivores should also be higher in early, than in late, summer.

2) On the trees of *Populus*-type, which also produce new leaves in the latter half of the season, the proportion of specialists should be more or less constant throughout the season.

In the following I will test these predictions using the available data on Finnish macrolepidopterans.

2. Materials and methods

The data on larval phenology and host-plant relations are taken from Seppänen's (1970) extensive work, "The Food Plants of the Larvae of the Macrolepidoptera of Finland". Seasonal distributions of species richness on the host trees were calculated by using the timing of larval periods. A more detailed description of these calculations is given by Niemelä et al. (1982).

Seppänen's work also reports which lepidopteran species use particular plant species as their preferred food plants and which species not exhibit such strict preferences. The division between specialized and generalized feeders is based on this information. Lepidopteran species using certain plant(s) as their preferred food plants are considered specialists on this host. Other lepidopteran species on the same host are considered generalist feeders.

In most studies, the criterion of this classification has been the number of plant genera or families in the diet of the lepidopteran concerned. A disadvantage of this method is that rare or poorly studied species are too easily classified as specialists due to under-recording of their host plants. The criterion used in this study includes the assumption that herbivores are specialists of their main food plants and there are some cases when a specialist is also classified as generalist when using another non-preferred food plant. However, I regard the present method as a more reliable criterion of specialism than the mere number of food plants. The difference between these two criteria though is not great because specialists are generally monophagous in nature (see also Niemelä et al. 1982).

The seasonal production of new leaves is measured as the duration of the shoot-growth period. The reason for this is that new leaves are mainly produced at the tops of growing shoots. Thus, the longer the shoot-growth lasts, the longer is the period when new leaves are available. The seasonal patterns in the shoot-growth of Finnish deciduous trees are based on studies by Raulo and Leikola (1974) at Punkaharju (61°47'N, 29°19'E) in 1965, except the oak (*Quercus robur*), which was measured at Turku in 1980 (Niemelä and Haukioja 1982). The length of the shoot-growth period is calculated as degree days (i.e. as the sum of daily mean temperatures over 5° C). This eliminates annual variation in growth phenology due to the weather.

3. Results

Figure 1 compares the seasonal distributions of the incidence of specialism in the *Quercus*- and the

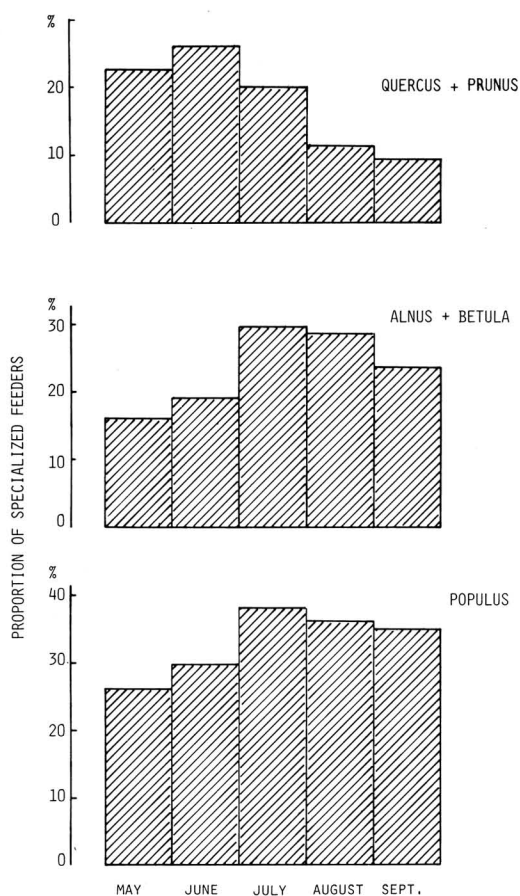


Fig. 1. Proportion of specialized feeders from the total macrolepidopteran fauna on the *Quercus* type (*Quercus*, *Prunus*) and on the *Populus* type (*Populus*, *Betula*, *Alnus*).

Populus-type. According to prediction 1 the proportion of specialist feeders on the *Quercus*-type should be highest in spring. The trend is as expected, the distribution of specialists differing from that of the macrolepidopteran fauna as a whole (Brandt-Snedecor $\chi^2 = 9.83$, $df = 4$, $p < 0.05$).

Prediction 2 stated that the incidence of specialism on the trees of *Populus*-type should be more even because of the occurrence of new leaves during the late season. The results (Fig. 1) indicate that the proportion of specialized feeders even increases towards the late season on the *Populus*-type. There is, however, no statistically significant difference between distributions of specialists and generalists (χ^2 -tested), which accords with prediction 2.

When the seasonal species richness patterns of total macrolepidopteran fauna were analysed,

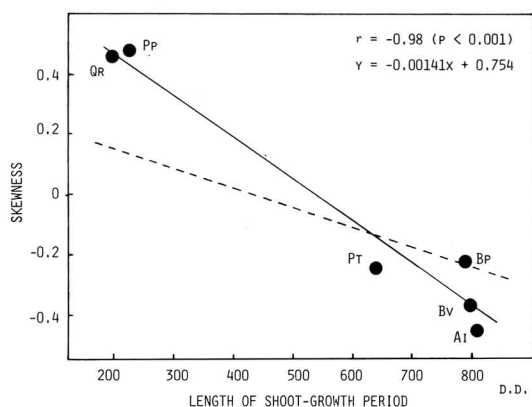


Fig. 2. Relationship between the length of the shoot-growth period and the skewness values of seasonal species richness of specialist feeders on those Finnish deciduous trees from which data about shoot-growth periods are available. Qr = *Quercus robur*, Pp = *Prunus padus*, Pt = *Populus tremula*, Bp = *Betula pubescens*, Bv = *B. verrucosa*, Ai = *Alnus incana*. Dotted regression line ($Y = -0.00064X + 0.237$) is for total macrolepidopteran fauna (Niemelä & Haukioja 1982).

there was a good correlation between the skewness values of species richness distributions and the length of the annual shoot-growth periods of host trees, which obviously measures the period when new leaves are available (Niemelä & Haukioja 1982). Fig. 2 shows that there is a similar correlation with specialized feeder too. The species richness distribution of specialists peaks in spring (a positive skewness value) on trees with a short shoot-growth period like *Quercus robur* and *Prunus padus*. Similarly, the longer the shoot growth period, the more negatively skewed is the distribution.

4. Discussion

The observed trends in the seasonal incidence of specialism are, to a limited extent, in accordance with the predictions derived from the optimal defence theory. Also, seasonal species distribution of specialists is correlated with the seasonal production of new leaves. It is, however, obvious that neither all specialized herbivores are obligatorily limited to new leaves, nor are generalized herbivores similarly, limited to mature leaves. Otherwise it would be difficult to explain why there are specialists on the oak and bird cherry during the late season when the amount of new foliage is minimal, or how generalist herbivores can manage during spring-time when only new leaves are available.

The proportion of generalists in early season is particularly difficult to explain on the basis of optimal defence theory. If young leaves defend themselves against herbivores by using toxic-like compounds, as theory predicts, then the majority of herbivores ought to be specialists. As a matter of fact, on both tree-types 70–85 % of the macrolepidopteran fauna consists of generalized feeders early in the season (Fig. 1). Hence it would seem that, at least among those deciduous trees considered in this study, there is no “effective” defence against generalized herbivores in young leaves early in the season.

According to Mattson (1980), there are differences in the seasonal production of allelochemicals between these two tree types. These differences are connected with the seasonal resource allocation tactics of trees. The observed variation in the seasonal species richness patterns of the herbivore fauna can be, at least partially, a consequence of this variation of the allelochemical profile of the plant.

In trees which undergo a single, large, synchronized growth flush (like the *Quercus*-type) each growing season there will be a low allelochemical production (especially carbon-based compounds) against herbivores early in the season (Mattson 1980). The reason for this is the tremendous and widespread carbon and nutrient demands for purposes other than that of allelochemicals. When leaf and shoot-growth is completed, carbon and nutrients can be invested in the allelochemicals and the amount of tannins and phenolics for example, increases (Fig. 3). This superior leaf quality in spring easily explains why most herbivore species, and also generalized feeders (Feeny 1970, Niemelä et al. 1982), are concentrated in the early season in the trees of

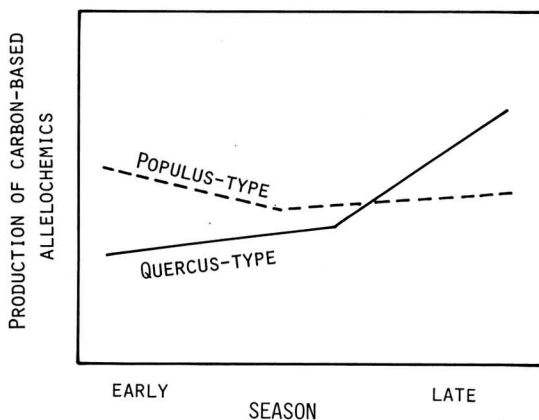


Fig. 3. Seasonal patterns in the production of carbon-based allelochemicals. Generalized from Feeny (1970) and Shultz et al. (1982).

Quercus-type and why there are so few species late in the season. It is worth noting in this context that oak and bird cherry are the only deciduous trees which have frequent large-scale defoliations in South Finland. These defoliations occur only in spring and are caused by *Tortix viridiana* (Lep., Tortricidae) on oak and *Yponomeuta evonymellus* (Lep., Yponomeutidae) on bird cherry.

Trees (such as the *Populus*-type) which undergo smaller-scale and continuous flushing also possess smaller carbon and nutrient demands and consequently this allows more stable seasonal production of allelochemicals (Mattson 1980). During the late season the amount of allelochemicals does not increase (Fig. 3) because resources are invested in growth. For example, in yellow birch (*Betula allegheniensis*) the phenolic content was highest in young growing leaves (Schultz et al. 1982). The consequence of this "stable" production

of allelochemicals is that there is no clear optimal period in leaf quality (except perhaps in the very young leaves) for herbivores, and it also allows high species richness late in the season.

The above reasoning does not specify the role of "positive" factors (nitrogen and water content, toughness) nor how different types of allelochemicals affect specialized and generalized herbivores. Recent studies indicate that the effect of "digestibility-reducers", for example phenolics, may be very specific (see e.g. Fox 1981) and we require more knowledge about allelochemicals and their impact in herbivores to enable more detailed hypotheses to be formulated.

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