Population dynamics of European pine sawfly *Neodiprion sertifer* (Fourcroy) (*Hym., Diprionidae*)

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This article reviews the factors affecting population dynamics of European pine sawfly *Neodiprion sertifer*. It was concluded that predation of the small mammals on cocoon stage is the most important factor in population regulation of *N.sertifer*. Other natural enemies can cause rapid population decline towards the end of outbreaks. Stand nutritive state may have an effect on insect population, and induced plant response may play a role when population reach eruptive levels.

Keywords: population, dynamics, *Neodiprion Sertifer*, hemisphere, pirethroids

Introduction

The European pine sawfly *Neodiprion sertifer* (Fourcroy) (*Hymenoptera, Diprionidae*) is one of the most harmful insects found in the coniferous forests on the Northern hemisphere. The mass outbreaks of this species in Latvia have been recorded since last century. Outbreaks appeared periodically with 10-12 year intervals (Ozols 1985). In former Soviet Union the *N.sertifer* outbreaks usually were controled by using the pirethroids, that have great impact on environment (Зубкова 1988, Ozols 1985). *N.sertifer* larvae feeds on needles of young pine trees but large mass outbreaks can cover also mature stands (40-50 years) (Ozols 1985). All pine species can serve as a host for *N.sertifer* (Kolomiets *et al.* 1979), but in Latvia the main host is *Pinus sylvestris* L. Under normal conditions the host tree does not die from the damage, but the growth loss may be considerable. After heavy infestation of pine stand in Norway wood production decreased by 1/3 in the following 9 years (Austarå *et al.* 1987).

It is much discussed why some sawfly species reach outbreak level while others never cause considerable defoliation (Larsson, Björkman 1993, Hanski 1987). The aim of this paper is to evaluate factors affecting population dynamics of European pine sawfly and find the key factors responsible for natural control of pest populations.

N.sertifer is univoltine, larvae hatch at the beginning of May, and pass through 4 (males) or 5 (females) instars. Larvae feed gregariously. In the middle of June the fully developed larvae enter the prepupae stage which spins the cocoon in the soil. Pupation takes place in cocoon and in September-October adults emerge. Females lay 60-80 eggs in clusters, unfertilised eggs becoming males and 2/3 of fertilised eggs becoming females. *N.sertifer* overwinters as an egg. For more details of life history see Juutinen 1967; Kolomiets *et al.* 1979, Griffiths 1959.

Factors affecting population dynamics of *Neodiprion sertifer*

The natural control by Huffaker's *et al.* (1971) definition is "the maintenance of population numbers within certain upper and lower limits by the action of the whole environment, necessarily including an element that is density-induced, i.g. regulating, in relation to the conditions of the environment and the properties of the species".

There are different patterns in population dynamics of phytophagous insects. Turnock (1977) studied 13 native pest species of Canadian prairie ecosystems and found three population patterns: (i) opportunistic populations with two equilibrium states; (ii) populations with a single, unstable state, apparently lacking effective natural enemies; and (iii) populations with single, stable equilibrium and effective natural enemies. Population patterns of *Neodiprion sertifer* perhaps can be characterised as single, stable equilibrium where outbreaks appear after some disturbances (e.g. weather, plant stress). In Northern Europe 6 out of 11 sawfly species feeding on pine have gregarious larval stages. To five of these 6 species outbreaks are recorded (Hanski 1987). Outbreaks often start in pine stands on poor soils and are often preceded by a dry, hot weather (Kolomiets *et al.* 1979, Ozols 1985). The *N.sertifer* populations suffer large fluctuations in density between endemic and outbreak levels (Olofsson 1987). There are 4 major hypotheses that tend to explain patterns of sawfly dynamics where the regulatory factors are:

- microparasite (pathogen) caused mortality;
- macroparasite (parasitoid) caused mortality;
- predation on hibernating cocoons,
- plant defence mechanisms and induced plant response to defoliation;

Further we analyse the hypotheses mentioned above.

Pathogens

The polyhendrosis virus (NPV) of *N.sertifer* was discovered at the beginning of this century (Escherich 1913). This virus can cause epizootics in sawfly populations. The NPV agent was succesfully tested for control of the *N. serrifer* (Заринь 1973, 1976).

Anderson and May (1980; 1981) showed that pathogens may control insect populations. The proposed model is based on very simple assumptions with dynamic elements drawn from predator-pray studies. It describes how high pathogenic infections, with long-lived infectious stages, tend to produce cyclic behaviour in their host populations. This model shows the slow increase of pest population and rapid decline caused by virus induced mortality. The frequent outbreaks of *N. sertifer* in Northern Europe, however, appear to start abruptly (Juutinen 1967; Olofsson 1987).

The model by Anderson and May suggested that the parasite has a long living and long survival infectious stage, so it can survive low pest densities between outbreaks. In the soil the NPV reimains active at least 13 years (Olofsson 1988b) and can be dispersed to pine foliage by dust and further transmitted to larval colonies (Olofsson 1988a). The horisontal transmission of virus within and between larval colonies is well described (e.g. Bird 1955, Olofsson 1988c). The virus disease can be carried from colony to colony by sawfly natural enemies and spread in pest population (Olofsson 1989a). The vertical transmission of virus is also described. Virus is transmitted from one year to the next chiefly through eggs of infected adults (Bird 1955, Olofsson 1989b).

During the outbreak the NPV can cause the main population mortality (Bird 1953,1955). Nevertheless, in many cases epizootics developed slowly and many sawfly outbreaks ended before high mortality caused by NPV had been reached (Olofsson 1987). There were some cases also in Northern America when sawfly populations reached high densities but showed no evidence of virus infection (Mohamed *et al.* 1982). During 4 year studies by Olofsson (1987) at moderate *N.sertifer* densities the killing power of NPV was rather small and did not exceed 0.12. Furthermore, larval mortality caused by virus disease showed a signifficant negative correlation with population size of the same year. Unfortunately the study period was too short to evaluate delayed density dependence. In Southern Sweden, the virus was found during most sawfly outbreaks but only in a few larval colonies.

It seems that virus disease becomes an important mortality factor mainly during prolonged outbreaks and it is unlikely that microparasites are responsible for regulation of *N.sertifer* populations under moderate population densities.

Some other pathogens are known to infect the *N.sertifer* larvae (e.g. bacteria *Bacillus septicimiae lophyri*, fungus *Beauveria bassiana*, protozoa *Nosema* sp.) but these parasites are less frequent (Kolomiets *et al.* 1979).

Parasitoids

There is much literature dealing with parasites of endemic species and the role of parasitoids in population regulation. In many cases introduction of parasitoids of introduced pest species led tu successful biological control (Greathead 1986). Hassell and Varley (1969) derived an inductive population model for insect parsites that served as the background for assumption that parasitoids can control herbivore populations.

European pine sawfly have a wide array of parasitoids that attack egg, larval and cocoon stages. Altogether about 40 parasitoid species have been reported (Pschorn-Walcher 1965). The parasitism can be high, especially during the outbreaks and in following years. In Southern Sweden the levels of egg parasitism have usually been below 30% in the early phase of outbreaks. However, towards the end of outbreaks more than 90% parasitism has been recorded (Olofsson 1987). The delayed mortality in early larval stages due to usually heavy reduction of colony size of parasitized sawfly clusters must be added to mortality in the egg stage caused by parasitism (Pschorn-Walcher 1973). During the 4 year studies by Olofsson (1987) the level of egg parasitism varied between 19% and 34%. This study period was too short to analyse delayed density dependent mortality. The main egg parasitoid species in Swden are *Chrysotomyia ruforum* (Krauss) (Eulophidae) and *Dipriocampa elongata* (Edr.) (*Tetracampidae*) (Olofsson 1987).

The long term studies on principal larval parasitoids of *N.sertifer* were carried out by Pschorn-Walcher (1987). During 10 year study period two outbreaks of this pest appeared. Two larval parasitoids (*Exenterus abruptorius* and *Lophyroplectus luteator* (Hym., Ichneumonidae)) show strong delayed density dependcence and were partly responsible for suppressing pest populations during the outbreaks. The killing power varied from 0.1 to 1.4 (20% and 96% parasitism respectively). During 4 year studies by Olofsson (1987) parasitism varied from 8% to 30%. The parasitoids are the most active during the 4th and 5th instars, while virus induced mortality occured during 3rd and 4th larval instars. Further more, the parasitoids seemed to avoid colonies with diseased larvae. Olofsson also pointed out that parasitoids of sawfly larvae in Sweden rarely cause high mortality. Most parasitoids overvinter in the sawfly cocoons in the litter where they are exposed to predation and other mortality factors for about 8 months.

It seems that the importance of parasitoids in population regulation of European pine sawfly vary in different regions. In Northern America, total parasitism is generally lower than in European populations (Griffiths 1959). The parasitoids can affect the pest population by spreading virus between larval colonies (Olofsson 1989b). As Pschorn-Walcher (1977) has summarised, the potentially successful natural enemy is one that has:

1. high searching ability,
2. high reproductive rate,
3. high degree of host specificity,
4. good sincronisation with the host, and
5. high degree of adaptability to a wide range of eco-climatic conditions.

Most of *N.sertifer* parasitoids, however, are polyphagous (Pschorn-Walcher 1965), but in pure pine stands they may act as monophagous because of the absence of other hosts. To test the parasitoid hypothesis it is also important to have a detailed information on spatial distribution of parasitism (Hassell 1985). Parasitoids can also affect the pest populations indirectly e.g. by attracting predators (Roland 1988).

Predators

The winter moth *Operoptera brumata* L. is a good example where tha predation play a major role in insect population regulation (Varley 1971). Hence *N.sertifer* pupates in the middle of summer when all cocoon predators are active and cocoons are located on the ground one could expect a high predation rate on sawfly cocoons. In 4 year studies by Olofsson (1987) the main pest population mortality was caused by predation on sawfly cocoons (mainly by small mammals). The killing power varied from 0.5 to 1.4 (68% to 96% mortality) and were strongly density dependent. The functional as well as numerical response to prey density may have occured. The average predation rate of small mammals seems to be smaller in Russia and Northern America (Kolomiets *et al.* 1979; Griffiths 1959). Predation on sawfly cocoons by invertebrate predators (mainly by elaterid larvae) is also observed to some extent (Juutinen 1967; Kolomiets *et al.* 1979).

Predation caused mortality appears also in other developmental stages. There is little predation in egg stage by aphid lion (*Crisops ventralis*) and other insect predators. Larval stages are attacked by a number of coleoptera species, ants and birds (Kolomiets *et al.* 1979). The red forest ants *Formica* spp. may cause high mortality af sawfly larvae near ant nests. Beyond 40 m from the nest larval survival increases sharply (Olofsson 1992). By introducing red forest ant nests in forest defoliation can be reduced to minimum (Михельсон 1975).

The predation by forest ants can affect the sawfly population also indirectly. The larvae are able to defend themselves from smaller predators (e.g. ants) by regurgitating a sticky droplet when attacked. This droplet consist mainly of resin acids and, therefore, especially if predation pressure is high, the larvae will actively search for tissues to feed on which is rich in resin acids (Björkman 1991). However, larvae feeding on tissues with high concentrations of resin acids will grow slower and, in the absence of predators, also suffer a higher mortality than larvae feeding on tissues with low concentrations (Larsson *et al.* 1986). Thus the sawfly larvae here faces a dilemma, whether to have a good defence or a fast growth. it has been shown that when the predation pressure is high, the larvae feed more on tissues with higher concentrations of resin acids (Björkman and Larsson 1991). Also during the decline of an outbreak, when predation pressure is supposedly high, the females choose to oviposit on needles with high concentrations of resin acids (Björkman 1991).

The other group of generalist predators are birds. It is well known that forest pests consist a significant part of songbirds nourishment (Cramp 1993; Priedītis 1958; Tinbergen 1960, Òèià 1958), but *N.sertifer* larvae are often refused by the most songbirds (Михельсон 1964). There are little studies on impact of birds on pest population dynamics. Latvian forestry has long time experience in attracting birds to forest stands. First attempts to increase the bird densities in forest stands started in 1946-47 (Тауриньш 1954). The density of pied flycatcher – *Ficedula hypoleuca* can be increased even 72 times (Михельсон 1958).

Hence small mammals cause main population mortality and this effect is strongly density dependent, it seems that they can regulate the pest population to some extent. The three trophic level interaction is characteristic for predation by forest ants. Forest ants can be localy important predators. Other predators are less important.

Plant defence

One of the theories about factors limiting population growth in *N.sertifer* deals with food quality. The concept food quality can either be spoken of in a positive way, e.g. high nitrogen concentrations may increase population growth, or in negative way, e.g. the presence of secondary componds may decrease population growth.

In the case of *N.sertifer* it has been observed that outbreaks often are preceeded by dry years and mostly occur in stands growing on soils poor in nutrient and with a low water-holding capacity. This pattern indicates a correlation between outbreaks and stressed host plant. However, one should be careful with drawing such a conclusion since the same factors causing environmental stress in host plants also influence the insects directly (e.g. weather) (Mattson and Haack 1987).

Larsson and Tenov (1984) studied the areal distribution of a *N.sertifer* outbreaks on Scots pine as related to stand condition. Following the pattern mentioned earlier the outbreak was preceded by dry years and was limited to infertile soils. They also found that pine stands aged 20-40 yr. (accumulating biomass fast thus needing large amounts of nutrients) suffered most and that it was less severe in trees benefiting from a reduced inter-tree competition and less severe in a fertilased stand. Larsson and Tenov drew the conclusion that stand nutritive state has an effect on the insect populations.

Later, Larsson *et al.* (1986) studied the response of *N.sertifer* larvae to variation in needle resin acid concentration in Scots pine. Resin acids are generally considered to act as a major defence sistem in conifers (e.g. Hanover 1975). Larsson *et al.* (1986) found that the early instars of *N.sertifer* suffered higher mortality and developed slower when fed on needles with high concentrations of resin acids than when fed on needles with low concentrations. However, late instar larvae were not affected in the same way. In fact, late instar larvae seemed to actively search for tissues rich in resin acids.

When Björkman *et al.* (1991) studied the effects of nitrogen fertilisation on pine needle chemistry and sawfly performance, no difference in performance between larvae reared on fertilased trees and larvae reared on control trees was achieved. The authors explained this with the simultane increase of both nitrogen (positively affecting performance) and resin acids (adversly affecting performance) that took place in the needles of fertilased trees.

Can the *N.sertifer* larvae themselves cause changes in the needles through their damage thus changing their own food resourse, or in other words, can the host plant – Scots pine – respond to the atack? Lyytikäinen (1992) studied the influence of artifical damage to *Pinus sylvestris* on the performance of inter alia *N.sertifer* larvae. He found that a higher damage level resulted in lower larval and cocoon weights and delayed relative growth rate. However, in the case of *N.sertifer*, no significant differences were seen until the year after the damage.

In conclusion, many observations indicate some correlation between stand nutritive state and outbreaks. When outbreaks occur, plant defence is induced and will give a delayed negative effct on larval performance especially in the first instars.

The key factors in population regulation of N.sertifer

The study by Olofsson (1987) shows that populations of *N. sertifer* can be regulated at population levels where competition for food does not have a significant effect. However, the frequent occurance of outbreaks causing severe defoliation indicates that such regulation is often insufficient.

The main regulating factor seems to be predation of small mammals in the cocoon stage. Hence regulation based on a functional response operates only at moderate prey densities (Holling 1959) the other mortality factors can play an important role. When favourable conditions have a positive impact on larvae developement the pest population can escape regulation. During the outbreak the food shortage reduce the population growth rate. In the following years the other factors such as induced plant response and increased mortality caused by natural enemies lead to rapid population decline.

In conclusion it seems that predation of small mammals on cocoon stage is the most important factor in population regulation, ond other natural enemies (e.g. egg parasitoids, virus disease) can be responsible for population crash after outbreak. Stand nutritive state may have an effect on insect population, and induced plant response may play a role when population reach eruptive levels. Resin acids affect larvae both positively and negatively, by improving defence abilities and by delaying developement.

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Популяционная динамика рыжего соснового пилильщика *Neodiprion sertifer*

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Резюме

В статье рассмотрены факторы, влияющие на популяционную динамику рыжего соснового пилильщика *Neodiprion sertifer*. Авторы пришли к выводу, что важнейшим фактором регулирующим популяции пилильщика является хищничество малых млекопитающих. Другие естественные враги вредителя могут вызвать упад численности к концу массового размножения. Плодородность почвы лесных насаждений может влиять на популяции вредителя, так как массовое размножение рыжего соснового пилильщика обычно начинается в малоплодовитых насаждениях. Индуцированная реакция растения (сосны) может быть важным фактором, когда популяция достигает Эруптивного уровня.

Ключевые слова: популяции, динамика, *Neodiprion sertifer*, пиретройды.