

SHORT COMMUNICATION

# Desiccation of *Pinus* foliage induced by conifer sawfly oviposition: effect on egg viability

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**Key words.** Desiccation, hypersensitivity, *Neodiprion*, plant–insect interactions, sawfly.

## Introduction

Plant responses to insects may affect various stages of herbivore life histories. Plant responses may disrupt adult behaviours such as host recognition and oviposition, or inhibit larval feeding and development (Rosenthal & Berenbaum, 1992; Bernays & Chapman, 1994). Some plants can also confine or remove herbivores by destroying the leaf tissue in which they reside (Faeth *et al.*, 1981), often by desiccation or abscission (Williams & Whitham, 1986; Stiling & Simberloff, 1989; Balbyshev & Lorenzen, 1997).

Conifer sawflies (Hymenoptera: Diprionidae) comprise a small family of folivores that are mostly associated with Pinaceae (Wagner & Raffa, 1993). Females oviposit directly into needle tissue by cutting egg slits using serrated ovipositors (Griffiths, 1960; McCullough & Wagner, 1993). In most species, the eggs are deposited in clusters that occupy the 1-year-old terminal shoots, or, later in the season, the current-year growth (Benjamin, 1955; Ghent, 1955). These clusters are often the clutch of a single female (Griffiths, 1960; but see Codella & Raffa, 1995; Blümke & Anderbrant, 1997). The emerging larvae feed gregariously and overwinter in the soil as prepupae within cocoons. Several diprionid species are important economic pests.

The redheaded pine sawfly *Neodiprion lecontei* (Fitch) feeds on all species of two-needled pines within its range in eastern North America. In the Great Lakes region, *N. lecontei* usually produces one generation per year, with a flight period extending from late May to early July (Benjamin, 1955). Females typically carry about 100 eggs (Codella & Raffa, 1995) and oviposit in only one needle per paired pine fascicle (Benjamin, 1955; Griffiths, 1960). *Neodiprion lecontei* undergoes lengthy periods of low population density followed by extensive eruptions that

persist for several years (Benjamin, 1955; Averill *et al.*, 1982), however the underlying factors affecting the population dynamics of this species are not understood well (Haack & Mattson, 1993; Larsson *et al.*, 1993).

There have been several references to diprionid egg hatch failure associated with the desiccation of needle tissue (Warren & Coyne, 1958; Martineau, 1959; Kapler & Benjamin, 1960), however such descriptions have been largely anecdotal. In the work presented here, pine needle desiccation and subsequent egg mortality were quantified in relation to oviposition by *N. lecontei*.

## Materials and methods

Observations were made in a young plantation of red pine *Pinus resinosa* Ait. as a preliminary to a larger study of egg distribution patterns and larval survival reported by Codella and Raffa (1995). The site was located near Winter, Wisconsin (45°45'N, 91°00'W) and consisted of 8-year-old trees ( $n = 352$ ) planted at 1.8-m spacing on level, sandy terrain. *Neodiprion lecontei* had been at outbreak levels for several years prior to the study (Prey *et al.*, 1985). The site was first visited on 13 May 1987, at which time oviposition was already in progress. As this is about 2 weeks earlier than expected (Benjamin, 1955), it was probably very close to the start of adult activity. All trees were examined for eggs. All shoots with eggs were clipped from the trees and transported to the laboratory with the stems in water. The site was revisited about once a month during the 1987 field season, and all trees in the stand were re-examined for eggs at each visit. Any new egg-bearing shoots were harvested on discovery. Therefore, egg-bearing shoots collected during the first site visit had probably been on the trees for a few days at most, while shoots collected during subsequent visits were on the pines for up to 1 month. In the laboratory, collected foliage was maintained using the methods of Knerer (1984), and observations were made of egg hatch and needle desiccation.

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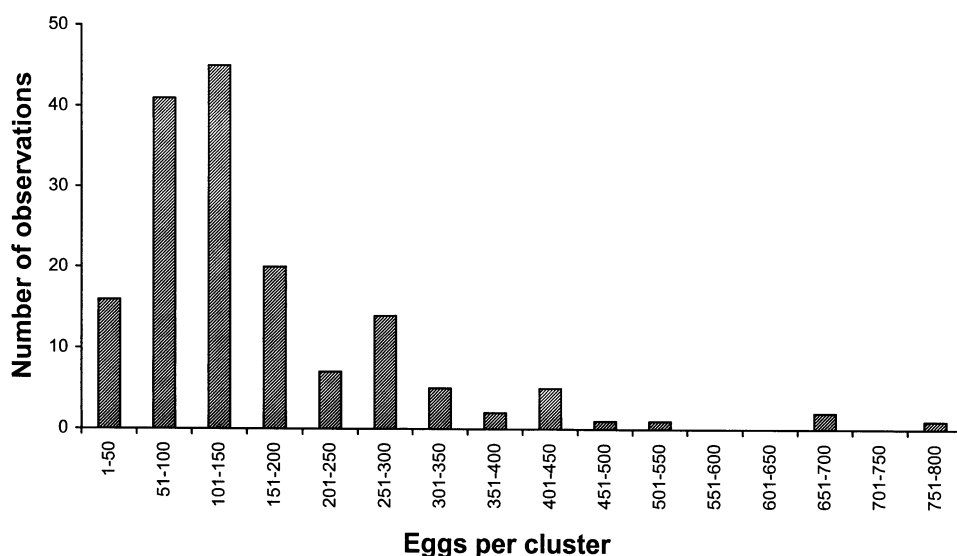


Fig. 1. *Neodiprion lecontei* egg cluster size distribution on *Pinus resinosa*.

## Results and discussion

A total of 157 egg-bearing shoots was recovered from 50 trees during the field season, with a combined egg count of 26 047. These trees averaged  $3.2 \pm 0.3$  ( $\pm 1$  SE) egg-bearing shoots (range = 1–10) and  $520.9 \pm 57.6$  eggs (range = 24–1778). Egg-bearing shoots averaged  $162.8 \pm 99.7$  eggs (range = 8–773). Some egg-bearing needles had been consumed partially by larvae during the previous season, as noted by Wilkinson (1971) for *Neodiprion merkei* Ross. The distribution of egg cluster sizes (Fig. 1) was consistent with variable oviposition behaviour, with some females dividing their clutches among several shoots and others adding their eggs to pre-existing clusters (Codella & Raffa, 1995; Blümke & Anderbrant, 1997).

Shoots ( $n=107$ ) that received eggs after the first collection showed extensive needle desiccation. Affected needles were brown and brittle, and eggs deposited in such tissue did not hatch. A random subsample ( $n=53$ ) of these shoots was examined in detail. Of 13 279 eggs ( $250.6 \pm 22.4$  eggs per shoot), only 3281 hatched (24.7%). In contrast, egg-associated desiccation was not observed in the first collection's shoots, i.e. those removed from the host plants within several days of oviposition. The hatch rate from this group was  $\approx 39\%$  in the laboratory ( $\approx 2000$  of 5143 eggs from 50 shoots on 25 trees).

Needle desiccation was associated strongly with the presence of eggs (Fig. 2). Of 1055 egg-bearing needles within the subsample, 897 (85.0%) were desiccated. In contrast, desiccation occurred in only 52 of 2048 needles (2.5%) that lacked eggs. In the few cases where both needles in a *P. resinosa* fascicle received eggs and only one needle was desiccated, the desiccated needle had a significantly longer proportion of its length occupied by eggs (desiccated:  $41.2 \pm 2.6\%$  of needle length; undesiccated:  $24.0 \pm 2.5\%$ ; Wilcoxon signed ranks test,  $T^+ = 16$ ,  $P = 0.0012$  for  $n = 19$  fascicles).

These results suggest that conifer sawfly oviposition can induce pine needle desiccation, and that this reaction can be an important source of mortality to natural *N. lecontei* populations. McCullough and Wagner (1993) found that oviposition slits made by *Neodiprion fulviceps* (Cresson) severed the resin canals of *Pinus ponderosa* Dougl. needles but avoided the vascular bundle. *Neodiprion nigroscutum* Middleton, which cuts unusually large egg slits, however, commonly suffers from desiccation of egg-bearing needles (Knerer & Atwood, 1973). Some severing of vascular tissue during oviposition also occurs in the *N. virginianus* Rohwer species complex (Wilkinson, 1961). The probability of needle damage probably varies with needle thickness

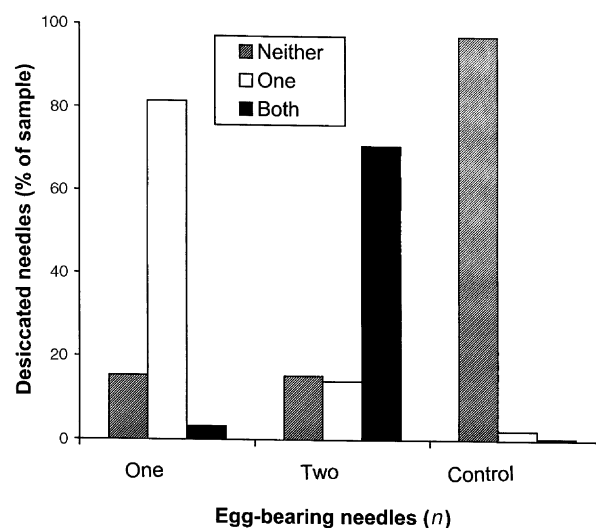


Fig. 2. Effect of egg presence on needle desiccation. Control needles were sampled from adjacent shoots that lacked eggs ( $3 \times 3$  contingency table,  $\chi^2 = 2157.9$ ,  $P < 0.001$ ).

(Wilkinson, 1961) and extent of oviposition. In this study, desiccated needles bore significantly more eggs (as measured by the proportion of needle length occupied by eggs) than needles that were not desiccated. Each oviposition event constitutes an additional chance that a female will cut too deeply or from a less suitable aspect, and thereby induce desiccation and subsequent egg mortality. The prolonged and stereotypic nature of diprionid oviposition (Ghent, 1959; Griffiths, 1960) and the defensive benefits of group feeding (Codella & Raffa, 1993, 1995, 1996) may constrain these sawflies from laying fewer eggs per needle, which might otherwise be a viable evolutionary strategy for reducing needle damage and increasing progeny survival.

Both density-dependent and density-independent factors may affect desiccation of egg-bearing tissue. As female density increases, there is a greater likelihood of multiple females ovipositing in the same needle (Warren & Coyne, 1958) or shoot (Codella & Raffa, 1995), which could increase the probability of damage to the vascular bundle and consequent desiccation. In addition, drought probably contributes to needle desiccation. McCullough and Wagner (1993) noted high desiccation and egg mortality in *N. fulviceps* ovipositing in *P. ponderosa* during a severe drought, and Heikkinen *et al.* (1986) triggered needle loss in ponderosa pine through experimentally induced water stress. In 1988, extensive desiccation of egg-bearing needles was observed in a stand 0.4 km SE of the present study area. The region was experiencing severe drought, and sawfly egg mortality was extremely high (>99%; Codella & Raffa, 1995).

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