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Organic soils promote the efficacy of entomopathogenic nematodes, with different foraging strategies, in the control of a major forest pest: A meta-analysis of field trial data

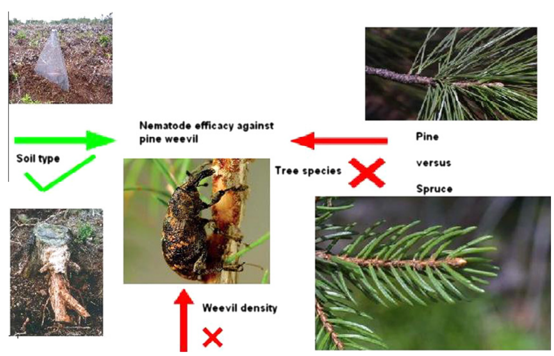
Christopher D. Williams [a,*], Aoife B. Dillon [b], Robbie D. Girling [a,1], Christine T. Griffin [a]

[a] Behavioural Ecology and Biocontrol Laboratory, Department of Biology, National University of Ireland Maynooth, Co. Kildare, Ireland
[b] Coillte Teoranta, Newtownmountkennedy, Co. Wicklow, Ireland

HIGHLIGHTS

- A meta-analysis of field trials for the control of pine weevil by EPN was conducted.
- EPN are more effective controls of pine weevil on peat than mineral substrates.
- Efficacy was independent of host density and tree species.
- Results are robust for both a 'cruiser' and an 'ambush' foraging EPN.
- The 'cruiser' is more efficacious than the 'ambush' forager.

GRAPHICAL ABSTRACT



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ABSTRACT

The large pine weevil, *Hylobius abietis*, is a serious pest of reforestation in northern Europe. However, weevils developing in stumps of felled trees can be killed by entomopathogenic nematodes applied to soil around the stumps and this method of control has been used at an operational level in the UK and Ireland. We investigated the factors affecting the efficacy of entomopathogenic nematodes in the control of the large pine weevil spanning 10 years of field experiments, by means of a meta-analysis of published studies and previously unpublished data. We investigated two species with different foraging strategies, the 'ambusher' *Steinernema carpocapsae*, the species most often used at an operational level, and the 'cruiser' *Heterorhabditis downesi*. Efficacy was measured both by percentage reduction in numbers of adults emerging relative to untreated controls and by percentage parasitism of developing weevils in the stump. Both measures were significantly higher with *H. downesi* compared to *S. carpocapsae*. General linear models were constructed for each nematode species separately, using substrate type (peat versus mineral soil) and tree species (pine versus spruce) as fixed factors, weevil abundance (from the mean of untreated stumps) as a covariate and percentage reduction or percentage parasitism as the response variable. For both nematode species, the most significant and parsimonious models showed that substrate type was consistently, but not always, the most significant variable, whether replicates were at a site or stump level, and that peaty soils significantly promote the efficacy of both species. Efficacy, in terms of percentage parasitism, was not density dependent.

1. Introduction

The large pine weevil, *Hylobius abietis* (L.), is the most serious pest of reforestation in Europe costing the forestry sector millions

* Corresponding author.
E-mail address: chris.david.williams@gmail.com (C.D. Williams).
[1] Current address: Centre for Biological Sciences, University of Southampton, Southampton, UK.

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of euro per annum e.g. €2.57 million ($3.36 million) a year in the UK and up to €30 million ($38.84 million) annually in Sweden (Weslien, 1998; Leather et al., 1999; Långström and Day, 2004). If no chemical control measures were used against the pine weevil, the most recent estimate for the economic damage that would result across Europe was €140 million ($181.26 million) (Långström and Day, 2004). Adult weevils are attracted to volatile chemical cues which are emitted when coniferous trees are felled. Females oviposit in the stump, with larvae and pupae developing in or under the bark (Leather et al., 1999) often at depths in excess of 20 cm. On emergence, adults feed on the bark of young trees planted on the clearfelled site, which can result in death through 'ring barking'. Without control measures, weevils can destroy up to 100% of newly planted trees, with a UK national average estimate of 50% mortality within the first few years at untreated sites (Heritage and Moore, 2001).

The most popular current control measure involves treating young plants prior to planting with alpha cypermethrin or cypermethrin, with an additional top-up spray the year after planting (Coillte, 2012; Willoughby et al., 2004). However, with concerns over environmental impacts, cypermethrin is being phased out across Europe (E.C., 2012). Forest certification schemes require that alternatives to chemical control be sought wherever possible, and one of these bodies, the Forest Stewardship Council (FSC), specifically classifies cypermethrin and alpha-cypermethrin as 'highly hazardous' chemicals, requiring that certificate holders possess a derogation to continue using these chemicals (FSC, 2011). These chemicals have been noted to have a repellence effect on the pine weevil and whereas this protects young plants, it does little to impact on the local populations of the pest (Torr et al., 2005; Leather et al., 1999). Current management practices, in addition to chemical control, include silviculture methods such as mounding, planting later in the season and leaving sites fallow (Von Sydow, 1997; Örlander and Nilsson, 1999; Örlander and Nordlander, 2003). Landscape level mitigation includes managing felling dates using decision support systems integrated with GIS to minimize weevil impacts (Wainhouse et al., 2001; Evans et al., 2004).

Entomopathogenic nematodes (EPN) have been used as an alternative method of controlling pine weevils (Dillon et al., 2007). Nematodes are applied as inundative biological control agents (biopesticides) targeted against pine weevil larvae, pupae and callow adults developing within the stumps. EPN are described as exhibiting different foraging strategies ranging from highly motile 'cruisers', which actively seek out insect hosts, to extreme 'ambushers', which tend to remain near the soil surface until hosts approach (Lewis et al., 1992, 2006; Grewal et al., 1994). We have previously shown that *Heterorhabditis downesi* (Stock, Griffin, and Burnell), a 'cruiser' forager, was best at controlling the subterranean cryptic pest, but *Steinernema carpocapsae* (Weiser), an 'ambusher', was also effective (Dillon et al., 2006). At operational level, *S. carpocapsae* is applied by pressure hose, from a tank mixer mounted on a modified forwarder, at an average rate of 3.5 million nematodes per stump (Torr et al., 2005). These operations are conducted by growers in the UK and Ireland, mainly the Forestry Commission and Coillte, respectively. For experiments, however, nematodes are usually applied by hand as a sub-surface drench. Entomopathogenic nematodes are harmless to humans, other warm blooded animals and plants (Boemare et al., 1996). They are also generally environmentally safe (Ehlers and Hokkanen, 1996) and have been shown to have little impact on non-target Coleoptera abundance, species richness, diversity or community composition when applied in clear-felled plantation forest ecosystems (Dillon et al., 2012).

The aim of the present study was to provide a meta-analysis of field trials which have tested the efficacy of entomopathogenic nematodes in the control of the large pine weevil. We focus on the only two species of nematode that have been commonly and repeatedly applied in such field trials: *S. carpocapsae* and *H. downesi*. The advantages of focusing on these species is that *S. carpocapsae* is the species widely used at an operational level, but *H. downesi* has shown the best results to date (Dillon et al., 2006, 2007) and the two species represent two different foraging strategies, namely that of an 'ambusher' and that of a 'cruiser', respectively. Specifically we sought to investigate the importance of tree species and soil type on nematode efficacy, and whether the levels of control achieved were related to the size of the host population (density dependent).

2. Materials and methods

We collated data from published field studies which used EPN as biopesticides to control the large pine weevil in Britain and Ireland (Table 1) and also included our own unpublished data. We contacted workers of published studies to request unpublished data and have also included unpublished data from Evans et al. (Table 1). In total 28 trials were analysed in this meta-analysis (Table 1). Exact locations of study sites and methods can be found in the relevant papers cited in Table 1. Locations (latitude and longitude), altitude and year of application of our twelve previously unpublished trials are presented in Appendix A. The following description of methods relates only to our previously unpublished data, but similar methods were used in the published studies of Table 1.

2.1. Nematode application

In July 2007, *S. carpocapsae* was applied to approximately 150 ha (5 sites) of forests in the estate of Coillte, the Irish state-owned forestry company. All of these trials involved a single tree species except Lackenrea, which included both Lodgepole pine (*Pinus contorta* Douglas) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) stumps. Each tree species was treated as a separate trial in this case. In each trial, the majority of the stumps were treated with *S. carpocapsae* by pressure hose from a tank mixer mounted on a modified forwarder at an average rate of 3.5 million nematodes per stump, which is the standard operational protocol. A small number of stumps received *H. downesi* (5 trials) or were left untreated (all trials). *H. downesi* was applied by hand as a subsurface drench at the same rate as *S. carpocapsae*, using the same methods as Dillon et al. (2006). Also in July 2007 both nematode species were applied by hand at a sixth site (Knockeen). In June 2008 *S. carpocapsae* was applied by pressure hose to three further sites with untreated stumps left as controls. In June of 2010 and 2011, stumps at two additional sites (Summerhill and Kilduff) were treated with *S. carpocapsae* by hand using a sub-surface drench giving a total of twelve trials on eleven sites (Appendix A). *Steinernema carpocapsae* was supplied by Becker Underwood whereas *H. downesi* strain K122 was mass reared in wax moths according to the methods of Dillon et al. (2006).

2.2. Assessment methods and experimental design

Stumps were either destructively sampled 3–4 weeks after nematode application or covered with insect traps designed to catch emerging adults using a modified design based on Owen (1989). Untreated (control) and nematode-treated stumps were arranged in a randomized block design with one stump of each treatment per block. There were 10–20 blocks for each assessment method at each site (Appendix A).