Insecticide application did not reveal any impact of herbivory on plant roots in boreal forests

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ABSTRACT

The levels of belowground herbivory in natural ecosystems remain practically undetermined, and nothing is known regarding the geographic and/or climatic variations in belowground herbivory. We endeavoured to narrow this knowledge gap by exploring the latitudinal changes in the intensity of background root herbivory in boreal forest ecosystems by conducting a herbivore exclusion experiment in 10 forested sites from 60°N to 69°N in northwestern Russia. We found no statistically significant differences in fine root biomass between diazinon-treated and control plots, nor did the differences show any latitudinal change. From biomass of root-feeding macrofauna we estimated that root herbivory in our sites averages 0.57 %. This low level of root herbivory could not be quantified reliably by herbivore exclusion experiments; therefore, we suggest that macroecological patterns in root herbivory are invoked from simultaneous measurements of the biomasses of fine roots and of root-feeders. More data on the efficiency of conversion of the food ingested by root-feeding invertebrates is needed to increase the accuracy of the suggested method of estimation of root herbivory.

1. Introduction

The substantial contribution of belowground herbivory to shaping ecosystem structure and functions is widely appreciated (Blossey and Hunt-Joshi, 2003; Johnson and Murray, 2008). Nevertheless, the levels of root herbivory in natural ecosystems remain practically undetermined (Hunter, 2008), in contrast to the thousands of published estimates of leaf area losses to insects (Turcotte et al., 2014; Kozlov et al., 2015; Mendes et al., 2021). Most importantly, nothing is apparently known regarding the geographic and/or climatic variations in belowground herbivory, as we have been unable to identify any study addressing root losses to insects along latitudinal gradients (Zvereva and Kozlov, 2021). This knowledge gap requires immediate attention from entomologists and plant ecologists.

The paucity of empirical data on this topic stems primarily from the methodological difficulties (Brown and Gange, 1990). The direct measurements of root losses require installation of rhizotrons, followed by a period of root recovery from the disturbance associated with this process (Joslin and Wolfe, 1999) and then by repeated recording of visible roots and analysis of their appearance and disappearance (Dawson and Byers, 2008). This limits rhizotron-based studies to safe sites, due to the risk of vandalism, and extends data collection period to several months or even

years. Furthermore, even the rapid disappearance of a root cannot be attributed unequivocally to herbivory (Stevens et al., 2002). Not surprisingly, the work by Stevens et al. (2002) remains the only study to have assessed root herbivory in natural ecosystems using rhizotrons.

The exclusion of belowground herbivores by pesticide application, followed by comparison of fine root biomass in pesticide-treated and control plots (Dawson and Byers, 2008), remains the only practicable method for measuring root herbivory (Stevens and Jones, 2006; Hishi and Takeda, 2008; Sun et al., 2011). In this study, we use this method to test the hypothesis that the intensity of background root herbivory in boreal forest ecosystems decreases from low to high latitudes, in line with general pattern observed in aboveground herbivory (Kozlov et al., 2015; Zvereva and Kozlov, 2021).

2. Material and methods

2.1. Study sites

This study comprises a part of broader research addressing latitudinal changes in structure and functions of boreal forest ecosystems (Finér et al., 2019; Zvereva et al., 2020; Kozlov et al., 2022). The ten forested sites were selected as being closest to the rounded degrees of

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latitude (from 60°N to 69°N) along the road connecting St Petersburg and Murmansk, Russia. All sites (Table 1) are located in uneven-aged, unmanaged, old-growth forests (maximum site-specific tree age ranging from 50 to 300 years). These forests consist of Scots pine (*Pinus sylvestris*), birches (*Betula pubescens* and *B. pendula*) and Norway spruce (*Picea abies*). The field layer vegetation is dominated by dwarf shrubs (primarily *Vaccinium myrtillus* and *V. vitis-idaea*), except for the north-ernmost site, where the herb *Cornus suecica* predominates (Kozlov et al., 2022). The soils in all study sites are gleyic albic podzols and folic albic podzols formed on sandy material. The volumetric stone content of the mineral soil increased towards the north, whereas other soil character-istics, including the thickness of the organic layer and content of mac-ronutrients, did not correlate with the latitude of study site (Finér et al., 2019). The main root-feeding insects in the study region are Coleoptera (Curculionidae, Scarabaeidae), Hemiptera (Cydnidae, Lygaeidae, Ortheziidae, Tingidae) and Lepidoptera (Hepialidae) (Kozlov et al., 2022).

2.2. Experimental setup

We systematically established 5 pairs of plots (25 cm in diameter) in each site along a 100 m long straight line, with 25 m intervals between blocks and 5 m intervals between two plots within a block, at least 1 m from the nearest tree trunk. The centre of each plot was marked with a plastic stick, and the plots within a block were randomly assigned to treatment or control. Based on the effect sizes reported in previously published studies (Stevens and Jones, 2006; Sun et al., 2011), we esti-mated (using power analysis: Zar, 1984) that this level of replication would be sufficient to detect effects of root herbivory on standing biomass of live fine roots with a reasonable degree of statistical confi-dence ($\alpha = 0.05$, $\beta = 0.20$).

We eradicated soil-dwelling herbivores from the treatment plots by application of insecticide (Zemlin®, 50 mg kg^{-1} diazinon; Tekhnoexport Ltd., Russia). On 27–30 June, 5–6 August 2015 and 28–29 June 2016, we applied 0.04 g of this insecticide (mixed with dry sand) to the soil surface and 0.03 g to each of two holes (15 mm diameter, 250 mm depth) made in the soil on opposite sides of a plot. Control plots received equivalent amounts of pure sand applied in the same way as in the treatment plots.

The fine root biomass was measured in samples collected 24–26 August 2016 from the centres of all plots using a cylindrical metal corer 3.6 cm in diameter. As in our previous study (Finér et al., 2019), we divided each core into three subsamples: the organic soil layer and the two mineral soil layers at 0–10 cm and 10–20 cm depths. The thickness of the organic soil horizon was measured to the nearest 5 mm; the deepest sampled layer often had a thickness < 10 cm due to the high stone content in the soil. The cores were transported to the laboratory, where all living fine roots (i.e. roots with diameter ≤ 2 mm), including mycorrhizae and rhizomes, were separated by hand from dead roots based on root morphology, including elasticity and toughness (Persson,

1983), washed to remove the adhered soil, dried for 48 h at 105 °C and weighed to the nearest 0.1 mg.

2.3. Data analysis

The fine root density (i.e. biomass per unit of soil volume in mg cm^{-3}) was calculated by dividing the root weight in a subsample by the thickness of the respective soil layer (in cm) and then by 10.17 (i.e. the number of cm^3 in a 1 cm layer of a soil core 3.6 cm in diameter). We compared fine root density in the treatment and control plots using a linear mixed model (SAS GLIMMIX procedure, type 3 tests; SAS Insti-tute, 2009). We considered treatment (insecticide or control) and soil layer (organic, 0–10 cm mineral, and 10–20 cm mineral soils) as fixed effects, latitude as a covariate and block nested within site as a random effect. We facilitated accurate *F* tests of the fixed effects by adjusting the standard errors and denominator degrees of freedom using the latest version of the method by Kenward and Roger (2009). The significance of random effects was explored by a likelihood ratio test (Littell et al., 2006); the estimated marginal means were compared with a *t*-test embedded into the GLIMMIX procedure (SAS Institute, 2009). We also explored the latitudinal variation in the effect of insecticide on fine root density by meta-regression of the response ratios, calculated from the site-specific means and standard deviations of the fine root density in the treatment and control plots (Rosenberg et al., 1997). The power analysis (Zar, 1984) was performed using a sample size calculator (https://clinca lc.com/stats/samplesize.aspx; $\alpha = 0.05$, $\beta = 0.20$).

3. Results

We found no differences in fine root density (Supplemental Data 1) between insecticide-treated and control plots (Table 2). This result was similar across all soil layers (Fig. 1) and showed no latitudinal variation (Table 2). Consistently, the response ratio did not change with latitude (Fig. 2).

The power analysis demonstrated that our experimental design would allow detection of the effect of root herbivory on fine root biomass only if root-feeding invertebrates consumed at least 19 % of the standing crop of live fine roots.

Table 2
Sources of variation in fine root density (SAS GLIMMIX procedure, type 3 tests).

Effect type	Source of variation	Test statistics	P value
Fixed	Treatment (insecticide vs. control)	$F_{1,\,202.1} = 0.35$	0.56
	Layer	$F_{2,\,200.1} = 2.47$	0.09
	Latitude	$F_{1,\,44.8} = 6.44$	0.01
	Treatment × Latitude	$F_{1,\,202.0} = 0.29$	0.59
	Treatment × Layer	$F_{2,\,197.8} = 0.17$	0.84
	Treatment × Layer × Latitude	$F_{4,\,198.9} = 1.84$	0.12
Random	Block (site)	$\chi^2_1 = 11.43$	0.0004

Table 1
Characteristics of study sites.

Latitude, N	Longitude, E	Mean annual temperature[a], °C	Annual precipitation[a], mm	Stand basal area[b], m² ha^{-1}	Fine root biomass[b], g m^{-2}
59° 58′	32° 11′	3.88	850	18.4	560
61° 00′	33° 03′	2.90	912	21.2	988
61° 58′	34° 14′	2.29	796	23.4	738
63° 00′	34° 22′	1.37	850	12.2	716
64° 01′	34° 04′	1.16	796	18.2	1080
65° 01′	34° 00′	0.84	745	12.6	843
66° 01′	32° 59′	0.55	741	14.2	1157
66° 56′	32° 12′	−0.31	792	18.6	850
68° 01′	32° 57′	−1.55	829	9.0	893
68° 52′	33° 07′	−0.84	792	12.2	605

[a] The long-term (1990–2019) mean annual air temperature and precipitation extracted from NASAPOWER archive (power.larc.nasa.gov).
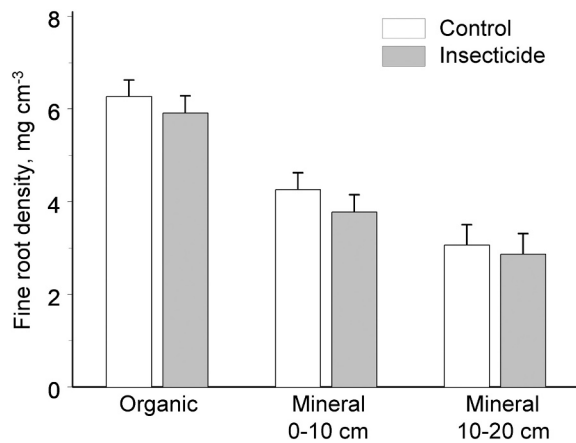[b] After Finér et al. (2019).

Fig. 1. Effect of insecticide application (estimated marginal means + SE) on fine root density in different soil layers. The differences between insecticide-treated and control plots are not statistically significant ($P > 0.30$) in any layers.
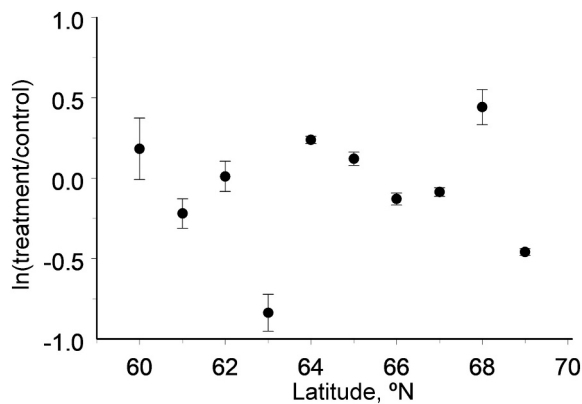

Fig. 2. Geographic variation in the effect of insecticide application (mean response ratio ± variance) on fine root density in the organic soil layer. The response ratio is independent of the latitude of the study site (meta-regression: $Q = 0.13$, df = 1, $P = 0.72$).

4. Discussion

Based on previous studies (Stevens and Jones, 2006; Hishi and Takeda, 2008; Sun et al., 2011), we expected to find greater fine root density in the insecticide-treated plots than in control plots due to the removal of the root-feeding invertebrates. However, these expectations were not met, as we found no statistically significant differences between the experimental and control plots. This 'negative' result could indicate that (1) the applied insecticide did not assure root protection from root-feeding invertebrates, or (2) the insecticide eradicated the root herbivores but also depressed root growth, thereby preventing the plants from using enemy free space, or (3) root herbivory in our plots was smaller than 19 % and therefore it could not be reliably detected with our experimental setup.

The insecticide used in our study was specifically designed for the protection of agricultural plants from root-feeding pests, including wireworms (Elateridae) and cabbage fly (*Delia brassicae*) (www.techno export.ru; accessed 26 May 2022). The half-life of diazinon is 21 to 103 days, depending on the soil type (Hornsby et al., 1996). Diazinon has been used effectively as a soil drench underneath host plants to control peach fruit fly (*Bactrocera zonata*) larvae in Florida (El-Gendy et al., 2021) and root aphids (*Pachypuppa* spp. and *Pachypuppella* spp.) on Sitka spruce in the UK (Straw et al., 1996). The overall soil micro-arthropod density in an abandoned field was depressed almost to zero after a single application of diazinon (Malone, 1969). Therefore, we

reject explanation (1) and conclude that the plant roots on the insecticide-treated plots were protected from soil-dwelling herbivores during the two consecutive growth seasons.

Several studies have reported either no effect of diazinon on root growth of some agricultural plants (Burpee and Cole, 1978; Moore and Kröger, 2010) or an increase in root growth, especially when diazinon was applied at concentrations exceeding those recommended for pest control (Mallyabaeva et al., 2020). Although we found no data on the direct impact of diazinon on the root growth of forest plants, this insecticide had no effects on the stem and shoot growth of Sitka spruce (Straw et al., 1996). Therefore, we consider explanation (2) unlikely.

Verification of explanation (3) requires an independent estimate of the amount of plant roots consumed by root-feeders in our study region. This estimate could be obtained by dividing the biomass of root-feeders by their efficiency of conversion of ingested food (ECI) (Kozlov and Zvereva, 2017). The data on the ECI of root herbivores (based on dry weight) are limited to larvae of three beetle species: *Diabrotica virgifera* (from -7 to 4 %: Moeser and Vidal, 2004), *Melolontha melolontha* (2.3–3.5 %: Kozel et al., 2017) and *Dermolepida albohirtum* (0.5 %: Johnson et al., 2018; recalculated from fresh weight). Thus, the average ECI of the root-feeding beetle larvae was approximately 1.3 %.

The biomass of root-feeding macrofauna averaged across our study plots (Fig. 3c in Kozlov et al., 2022) was (mean ± S.E.) 62.3 ± 18.8 mg m^{-2}. Assuming that the ECI of other root-feeding insects is of the same order of magnitude as the ECI of the beetle species mentioned above, we estimated that the root-feeders would have to consume 4.79 ± 1.45 g m^2 of roots during their lifetime to attain this biomass. The average biomass of the fine roots in our study sites (calculated from Table 1) is 834 ± 62 g m^{-2}; therefore, the average root herbivory, quantified as the percentage of the standing fine root biomass consumed by insects, was 0.57 ± 0.21 %. Therefore, we accept explanation (3) and conclude that our experimental plan did not allow detection of the effect of belowground herbivores on fine root biomass, because this effect appeared astonishingly small relative to the average loss of root biomass across experimental studies (36.3 %: Zvereva and Kozlov, 2012). The power analysis suggested that about 63,800 control and 63,800 treatment soil cores should be analysed to detect such a small effect of insect herbivory on fine root biomass with reasonable confidence.

We used the data by Stevens and Jones (2006) collected in South Carolina, USA to test for the reliability of our method used to estimate root herbivory. The average fine root density in the control cores in South Carolina was 0.38 mg cm^{-3}, whereas the biomass of the root-feeders was 0.79 μg cm^{-3}. Dividing this latter value by 0.013 (i.e. by the ECI = 1.3 %), we estimate that these animals consumed 0.061 mg cm^{-3} of fine root biomass. Consequently, in the absence of herbivores, the fine root density should be 0.44 g cm^{-3}. Thus, the estimated root herbivory in South Carolina is 13.9 %, whereas the herbivory based on direct comparison of fine root density between insecticide-treated and control cores was 41 % (Stevens and Jones, 2006), i.e. three times greater than could be expected from the biomass of the root-feeding invertebrates. However, the density of root-feeders decreased seven-fold between the two collection dates, and we therefore suggest that herbivore biomass averaged between these dates underestimates root herbivory. Alternatively, this discrepancy could indicate that ECI of root herbivores is smaller than 1.3 %. More data on the ECI of root-feeding invertebrates is needed to increase the accuracy of the suggested method of estimation of root herbivory.

In conclusion, our experiment did not reveal any statistically significant differences in fine root biomass between insecticide-treated and control plots in boreal forests, neither we found any latitudinal changes in these differences from 60°N to 69°N. This result is explained by the unexpectedly small (0.57 %) estimate of root herbivory based on the biomass of root-feeding macrofauna.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2022.104554.

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