



# Impacts of root herbivory on seedlings of three species of boreal forest trees



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## ABSTRACT

Current meta-analysis has identified the shortage of information on responses of woody plants to root damage as the most critical gap in studies of belowground insect herbivory. We explored the impacts of natural and simulated root herbivory on seedlings of three boreal forest-forming trees, *Pinus sylvestris*, *Picea abies* and *Betula pendula*. We compared the effects of natural herbivory and mechanical damage by placing one larva of the common cockchafer, *Melolontha melolontha*, of different instars (to manipulate root loss) into a pot with a one-year-old seedling or we excised a portion of the roots by inserting a 13-mm diameter cork borer into the soil. During the experiment, which lasted from 2 to 8 weeks, the larvae consumed 53–73% of root biomass, whereas the mechanical damage treatment removed 30–40% of roots. Seedling mortality was low (5%) across all treatments, but the aboveground biomass decreased by 3–43% due to natural herbivory and by 6–30% due to mechanical damage. The *M. melolontha* larvae consumed a larger amount of roots from *B. pendula* than from either *P. sylvestris* or *P. abies*, but the larvae showed similar relative growth rates and mass gains, indicating a different efficiency of conversion of ingested food (ECI). The values of ECI calculated for larvae of *M. melolontha* (2.3–3.5%) appeared much lower than the 17% reported earlier for larvae of foliage-feeding beetles, presumably due to the high energetic cost of locomotion in the soil. Consequently, root-feeding insects consume much more plant biomass than leaf-feeding insects do to gain similar body mass, and therefore they inflict relatively more damage to plants per unit of mass gained. Based on the biomass of insect herbivores in European forests, we estimate that they consume 0.5% of the available fine root biomass. The effects of low levels of root damage on growth and reproduction of woody plants remain virtually unknown, emphasising the need for studies of plant- and ecosystem-level effects of minor but chronic root herbivory.

## 1. Introduction

The detrimental effect of belowground insect herbivory in agricultural ecosystems is widely appreciated, because root damaging pests cause great economic losses (Johnson et al., 2016b). At the same time, although many insects are known to feed on the roots of forest trees, quantitative data on root herbivory are almost non-existent for unmanaged forest systems (Hunter, 2008). Consequently, the current review of global patterns in belowground communities (Fierer et al., 2009) has not considered root-feeding insects. Reliable knowledge about the percentage of root biomass consumed by insects in forests is limited to a few estimates (Stevens, 2001; Sun et al., 2011), and this paucity of information on root losses clearly contrasts with the extensive knowledge regarding losses of tree foliage to insects (Turcotte et al., 2014; Kozlov et al., 2015b; Kozlov and Zvereva, 2017). For example, Slansky and Scriber (1982) cited a single paper containing quantitative data on root consumption and utilization by

insects, while listing 118 papers on leaf consumption and utilization. The basic biology and ecology of root-feeding insects, even of many pest species, remains largely unexplored (Frew et al., 2016).

The studies of insect-plant relationships, especially those associated with the effects of global change on herbivores and herbivory, currently focus on exploration of plant defensive responses to damage (Johnson et al., 2016a). New analytical tools provide excellent opportunities for examining the intimate mechanisms underlying these responses, as well as the resulting interactions between insects feeding with aboveground and belowground parts of the same plant (Lankadurai et al., 2013; Robert et al., 2014; Abraham et al., 2015), but the adverse changes in plant fitness caused by insects are often considered as ‘apparent’ or ‘trivial’ (but see Maron, 1998; Tsunoda et al., 2014). As a result, the number of recent studies exploring interactions between aboveground and belowground herbivory (reviewed by Johnson et al., 2012; Papadopoulou and van Dam, 2017) exceeds the number of studies documenting changes in plant growth and reproduction in response to

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root damage. The acute shortage of these ‘trivial’ data hampers the understanding of the ecosystem role of root herbivory and complicates the prediction of the consequences of climate change on forest growth and vitality mediated by root damage due to insects.

The studies that have explored the impacts of root-feeding insects on plant growth have generally been performed on crops. To our knowledge, no quantitative data was ever published on the impacts of many well-known root-damaging forest pests, including the common cockchafer (*Melolontha melolontha*), on tree growth. Consequently, the recent meta-analysis (Zvereva and Kozlov, 2012) identified this shortage of information on responses of forest trees to root damage as the most critical gap in studies of belowground insect herbivory. Still, very little quantitative information on the consequences of root damage of forest trees by insects had been published in the past years (but see Johnson and Riegler, 2013).

Last but not least, the intensity of root damage by insect larvae in experimental studies is difficult to control. This problem can be partially solved by applying mechanical damage; however, the earlier studies concluded that artificial damage does not always mimic the damage caused by insect herbivores (Andersen, 1987; Blossey and Hunt-Joshi, 2003). Earlier we suggested that the simulated root herbivory caused much stronger detrimental effects on aboveground plant traits than the natural herbivory due to different spatial and temporal patterns of root damage: while simulated herbivory usually removes a certain proportion of roots all at once, damage by insects accumulates gradually and is partially counterbalanced by root regrowth (Zvereva and Kozlov, 2012). If this hypothesis is true, then the repeated application of relatively small mechanical root damage should cause the same effects as the natural root herbivory.

The aim of the present multifactorial experiment is to begin to close this research gap by a quantitative exploration of the interactions between larvae of the common cockchafer and the principal forest-forming trees of boreal Europe. We asked whether (i) tree species respond differently to damage to their roots in terms of aboveground growth and biomass allocation; (ii) the effects of natural root herbivory on plants are explained mostly by mechanical damage to the roots; and (iii) larvae of common cockchafer perform differently when feeding on roots of different tree species.

## 2. Materials and methods

### 2.1. Study site and study object

The study was conducted on the premises of the State Forestry Enterprise “Smolevichskij Leskhov” in Belarus (53°50'N, 28°05'E). The common cockchafer is a typical pest of young Scots pine plantations in this region (Kozel et al., 2012). Large (25–30 mm in length) beetles occur in May and early June, feeding mainly on leaves of deciduous trees, and on birches in particular. Mated females dig into the soil to lay their eggs. The larvae hatch in three weeks and remain in soil for a further three years, feeding on plant roots. They are reported to damage several dozen species of woody and herbaceous plants (CABI, 2017).

### 2.2. Experimental design and data collection

A multifactorial pot experiment was carried out with one-year-old seedlings (5–15 cm tall), which suffer strong damage from the common cockchafer larvae in natural environments. On 5 May 2016, 100 seedlings of each species (Scots pine, *Pinus sylvestris*; Norway spruce, *Picea abies* and silver birch, *Betula pendula*), which were obtained from the local forest nursery, were planted individually in 1 L plastic containers (130 mm in diameter) containing local sod-podzolic low fertility soil and grown outdoors for one month prior to the experiment. The bottom of each container was covered by plastic wire mesh. Plants were watered whenever necessary.

On 2 June 2016, we selected 84 healthy seedlings of each study

species (a total of 252 plants), randomly distributed them to treatments (control, natural herbivory and mechanical root damage; 32, 28 and 24 seedlings of each species, respectively) and buried into the soil with their pots in several blocks in a random order. Pots with plants selected for natural herbivory were each infested with one common cockchafer larva, collected from a young Scots pine forest nearby. The larvae were weighed to the nearest 1 mg prior the experiment. We used larvae of the first, second and third instars to achieve different levels of root damage. Mechanical damage was applied by inserting a 13-mm diameter cork borer into the soil in selected pots half-way between the plant stem and the container wall, down to the bottom of the container. After this mechanical damage, the soil was returned to the hole left by the borer. We made a single hole in the soil of the containers selected for low root damage and two holes (on opposite sides of the plant) in containers selected for high root damage. This procedure was repeated at one-week intervals until the end of the experiment. Care was taken to insert the cork borer into a site where the roots were not damaged previously.

To study the effects of the intensity of damage, equal numbers of seedlings from each treatment were collected in 2, 4 and 8 weeks from the beginning of the experiment. The collected seedlings were separated into roots, stem and foliage; the roots were carefully washed to remove soil. The samples were oven-dried (85 °C for 48 h) and weighed to the nearest 1 mg. The surviving larvae were weighed, oven-dried (85 °C for 48 h) and weighed again.

### 2.3. Data analysis

The mortality of seedlings and larvae was analysed using a generalized linear mixed models (procedure GLIMMIX, binomial distribution; SAS Institute, 2009) and the events/trials syntax. Plant species, treatment (for seedlings: control, mechanical damage, and natural herbivory) or instar (for larvae), as well as species × treatment (instar) interactions were considered fixed effects, whereas blocks were considered random effect and duration of the experiment was treated as a covariate.

The final dry masses of 62 surviving larvae, on average, were 0.115 of their fresh masses. Consequently, the initial fresh masses of the larvae were multiplied by 0.115 to obtain an estimate of initial dry masses. All mass data were square-root transformed to meet the normality assumption. The initial (IM) and final (FM) masses of larvae were compared by the paired *t* test. The relative growth rate of larvae (RGR) was calculated as follows:  $RGR = (FM - IM)/(IM \times \text{duration of the experiment})$ .

The efficiency of conversion of ingested food (ECI) was calculated by dividing the biomass gained by the larvae (i.e., FM-IM) by the root biomass lost by the plants. The latter value could not be measured directly at the plant-specific level (because root biomass could not be measured non-destructively at the beginning of the experiment); it was therefore calculated as the species-specific difference in root biomass between control plants and plants exposed to larvae, and adjusted for the duration of the experiment (estimated marginal means, i.e. least-square means in SAS GLIMMIX procedure).

The dry masses of roots, aboveground woody parts and foliage, as well as the root:shoot ratio and the ratio of foliar biomass to aboveground stem biomass, were square-root transformed to meet the normality assumption and analysed using a linear mixed model (procedure GLIMMIX in SAS). Plant species and treatment (control, mechanical damage, and natural herbivory) were considered fixed effects, whereas duration of experiment was treated as a covariate. In addition, we analysed (separately for natural and simulated herbivory) the effects of larval instar and of the intensity of mechanical damage on plant biomass. Finally, we calculated the ratio between the relative decreases in the aboveground and belowground biomass of seedlings which experienced root damage. This was done based on biomass data averaged by species × treatment; the ratios were compared among tree species and among seedlings that received natural and simulated

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