



Warming increased feeding of a root-chewing insect at the soil surface and enhanced its damage on a grass

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ABSTRACT

Air and soil warming influences both plants and root herbivorous insects, but how warming alters their interactions is largely unknown. Because both the intensity of herbivory and plant susceptibility to the herbivory depend on temperature, it is difficult to predict the effects of insect herbivory on plant growth under warming. To analyse changes in belowground plant-insect interaction due to warming, we conducted a pot experiment using one grass species, *Lolium perenne*, and one beetle grub *Anomala cuprea*. Temperature (17 °C or 20.3 °C), presence or absence of a grub, and presence or absence of organic matter (OM) on the surface of the potted soil were manipulated. OM at the soil surface is an important resource for grubs, and contains neutral lipid fatty acids (NLFA) that can serve as a bacterial marker. NLFAs can be used as a tracer to determine whether grubs had fed upon OM, so we evaluated the consumption and vertical movement of a grub in response to warming. In the absence of grubs, plant biomass increased with warming, but was not affected by the OM treatment. In the presence of grubs, plant biomass was significantly decreased. Moreover, the interaction term between the temperature and grub treatments was significant, demonstrating that grub damage was more severe under warmer conditions. Grub mortality was not affected by any treatment. The bacterial NLFAs in a grub were significantly more detectable when OM was added relative to those without OM, and the amount increased with warming treatments. This suggests that the grub fed near the soil surface under both temperature conditions, but increased consumption rates under the warmer condition. The mean relative soil moisture content in the warmer conditions was significantly lower than that in the control conditions. OM additionally increased soil moisture, but it had no effect on herbivory damage, suggesting that plant susceptibility to herbivory was not attributable to soil moisture. These results show the importance of biological-context dependency of warming on a plant. Temperature changes will alter the root-herbivore interactions not by changing the plant susceptibility to herbivory but by increasing the consumption of the grub.

1. Introduction

Global mean temperature is predicted to rise by about 3 °C by the end of this century (Meehl et al., 2007). Terrestrial communities and ecosystems are strongly influenced by temperature, which determines geographic species distributions and behaviour of ectotherms. Therefore, understanding the effects of the warming on primary production is crucial for predicting future community dynamics and their services (Millennium Ecosystem Assessment, 2005). Early studies suggested that belowground communities may be buffered from direct impacts of climate change by soil (Bale et al., 2002; Hodkinson and Bird, 1998). However, there is increasing awareness that the interactions between

plants and soil fauna determine the response of ecosystem services to environmental changes (Ehrenfeld et al., 2005; Bardgett and Wardle, 2010; van der Putten et al., 2016; Hiltbold et al., 2017).

The magnitude of warming on plant productivity is highly biological-context dependent (Rouifed et al., 2010; Way and Oren, 2010; Jamieson et al., 2012; Makoto et al., 2016) because the warming influences both plants and soil fauna (Bardgett et al., 1999; Frey et al., 2008; van der Putten et al., 2016). Therefore, warming would affect plant productivity directly and indirectly. The direct effects of warming on plants have been intensively studied (e.g., Thomas and Norris, 1981; Zhao and Running, 2010), however, the indirect effects of warming via soil fauna are poorly understood owing to their hidden dynamics

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(Makoto et al., 2014). Especially, roles of belowground insect herbivores are largely unknown, although root herbivorous insects have profound effects on plant growth and mortality (Brown and Gange, 1990; Blossey and Hunt-Joshi, 2003; Tsunoda et al., 2014a) as well as on primary production (Gange and Brown, 2002; De Deyn et al., 2003; Schädler et al., 2004; Stein et al., 2010).

Abiotic conditions such as temperature and soil moisture may alter the behaviour and dietary choice of polyphagous root-chewing insects, the dominant root-feeding guilds such as grubs (Coleoptera: Scarabaeidae), wireworms (Coleoptera: Elatridae), and leatherjackets (Diptera: Tipulidae) (Brown and Gange, 1992; Zvereva and Kozlov, 2012; Johnson et al., 2016). These root-chewing insects can feed on roots of various species, as well as organic matter (OM) derived from leaves. Warming and subsequent changes of soil moisture alter the availability of OM for insects because insects move to deep soil to avoid desiccation of the soil surface (Villani and Wright, 1988, 1990). As a result, the insects cannot reach the OM on the soil surface, and their growth does not increase. Warming directly increases the metabolic rates of soil fauna (Ott et al., 2012). Increasing metabolic rates of soil fauna may lead to increases in their consumption, and consequently their growth. Thus, the effects of warming on the growth of polyphagous root-chewing insects are difficult to predict.

The effects of root herbivory on plants will differ depending on temperature and soil moisture (Villani and Wright, 1990; Erb and Lu, 2013; Tsunoda et al., 2014b). If warming reduces soil moisture, the warming affects plant productivity via the changes in vertical distributions of insects. Because of the filament-like morphology of roots, root herbivory at the root base in the top soil layer often causes plant mortality and large biomass reduction. However, herbivory at root tips does not affect plant performance significantly (Davidson and Roberts, 1969; Tsunoda et al., 2014a, 2014b). Therefore, desiccation of the soil surface caused by warming may reduce the negative effects of root herbivory. However, temperature and soil moisture may also alter the relative value of roots for plant fitness (Rasmann et al., 2011; Erb and Lu, 2013). For example, water limitation can dramatically increase the importance of individual roots: under plentiful amounts of water, plants can tolerate the loss of a significant part of their root system (Erb et al., 2009). However, a relatively minor loss of absorptive tissue can decrease growth when the whole root system is needed to acquire sufficient resources from the soil (Dunn and Frommelt, 1998). Thus, it is hard to predict the effects of warming on interactions between roots and root-feeding insects (Hiltbold et al., 2017).

To understand changes in the interaction due to warming, we conducted a microcosm experiment using a well-studied grass species, *Lolium perenne* L. (Poaceae), and a root-chewing insect, an *Anomala cuprea* Hope (Coleoptera: Scarabaeidae) grub (Tsunoda et al., 2014a, 2014c). Warming increases the growth of *L. perenne* directly (Thomas and Norris, 1981), but its indirect effects via root herbivorous insects have not been examined, as far as we know. We manipulated the air temperature, the presence or absence of the grub, and the presence or absence of OM on the soil surface. Moreover, OM contains some specific fatty acids derived from bacteria, which were used in the experiment as diet markers of the grub (Tsunoda et al., 2017). By analysing the growth and fatty acids of the grub, we evaluated the grub's consumption and vertical movement in response to the warming and subsequent changes in soil moisture. Specifically, we tested how temperature and OM addition influence the behaviour of root-chewing insects, and therefore the effects on the growth of *L. perenne*.

2. Materials and methods

2.1. Study species

Lolium perenne cv. 'amazing' seeds were obtained from a commercial supplier (Snow Brand Seed Co., Ltd, Sapporo, Japan). One *Lolium perenne* L. (Poaceae) seedling was grown in each pot, to which we added a

second-instar larva, or grub, of the polyphagous root-chewing insect, *Anomala cuprea* Hope (Coleoptera: Scarabaeidae). The grub feeds on roots of various herbaceous species as well as on OM (Okuno et al., 1978; Sakai and Fujioka, 2007; Tsunoda et al., 2017). Growth of grubs that feed on OM is larger than that of grubs that feed on roots (King, 1977), probably because nitrogen concentration, a limiting factor of the insect growth (van Dam, 2009), is higher in OM than in roots. Grubs were grown from eggs laid by adult *A. cuprea* in the OM (commercial horticulture humus mainly composed of broad leaves, "Kanjukufuyohdo", Hirota-shoten Co., Ltd., Tochigi, Japan). The adult *A. cuprea* on *Fallopia japonica* were manually collected from a floodplain of the Tama River (35°38'N, 139°23'E) in June and July 2015. Leaves of *F. japonica* were used as a diet for the adults.

2.2. Experimental design

We conducted the experiment from February to May 2016 in growth chambers (Koitoiron, Koito Industries, Ltd., Kanagawa, Japan) with a 14-h day/10-h night photoperiod. Plants were grown in 9-cm diameter and 12-cm depth plastic pots, each filled with 500 mL of soil (350–365 g in dry weight). The soil was collected from the experimental garden of Tokyo Metropolitan University (Hachioji, Tokyo: 35°37'N, 139°23'E) in February 2016, and sieved with a 6-mm mesh to eliminate OM and macrofauna. *Lolium perenne* seeds were sown on a tray of peat moss. Ten days after the sowing (27th February), one seedling was transplanted into each pot.

The growth experiment had a three-way randomized factorial design with nine replications. The factors were temperature with two levels (control, 17 °C and warmer, 20.3 °C), presence or absence of OM, and presence or absence of the grub. The OM was sieved to pass through a 6-mm mesh. The control temperature was in the range of soil temperatures of the grub's growing seasons in Tokyo. The temperature increase of 3.3 °C in the warmer conditions represented the predicted increase in air temperature by 2050 in Japan according to Rowlands et al. (2012). All experimental pots received same amount of water during the experiment. Until day 28 after transplantation, 30 mL of water was added every two to three days (i.e., Watered on Monday, Wednesday, and Friday). After day 28, 60 mL of water was added every two to three days because amounts of transpiration increased. We re-randomized the pot arrangement at every watering.

On day 35 after transplantation (2nd April), 150 mL of OM (25–30 g in dry weight) was added on the soil surface. On 12th April, day 10 after OM addition, a weighed grub was introduced to pots of the grub-present treatment. A grub was added to the centre of a pot, and it burrowed into the soil.

On day 85 after transplantation (22nd May, day 40 after introduction of grubs), we harvested plants and divided them into shoots and roots. The shoots and roots were separately dried at 70 °C for three days, and weighed. Plant biomass was defined as the sum of the shoot and root biomass of each plant. At the harvest, we recovered the OM on soil surface for the evaluation of microbial biomass. We recorded the survival of the grubs (Table S1), and weighed a living grub. The surviving grubs were freeze-dried for the fatty acid analysis.

2.3. Soil moisture measurement

After the addition of OM, soil moisture was measured with a soil moisture probe (ECH₂O, Decagon Devices, Inc., Pullman, Washington, USA). The relative soil-moisture content was measured at top soil layer (one cm of soil) and bottom soil layer (seven cm of soil) every two to three days (i.e., Measured on Monday, Wednesday, and Friday) before the watering. The probe was inserted from a slit in the pot in the top and bottom soil layer. Relative soil-moisture content was calculated as the difference between the measured value and the minimum value during the experimental period, divided by the range between the maximum and minimum values during the measurements (James et al.,

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