Temperature modifies the magnitude of a plant response to Collembola presence

Matthieu Chauvat, Estelle Forey

▶ **To cite this version:**

Matthieu Chauvat, Estelle Forey. Temperature modifies the magnitude of a plant response to Collembola presence. Applied Soil Ecology, 2021, 158, 10.1016/j.apsoil.2020.103814 . hal-03124482

HAL Id: hal-03124482
https://hal.science/hal-03124482

Submitted on 7 Nov 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

Version of Record: https://www.sciencedirect.com/science/article/pii/S0929139320307435
Manuscript_3b814b5b6cfbcb30333f521fbee38ef7

Temperature modifies the magnitude of a plant response to Collembola presence

Matthieu Chauvat* and Estelle Forey

Normandie Univ, UNIROUEN, INRAE, ECODIV, 76000 Rouen, France

*Corresponding author

matthieu.chauvat@univ-rouen.fr

© 2020 published by Elsevier. This manuscript is made available under the CC BY NC user license
https://creativecommons.org/licenses/by-nc/4.0/

Abstract

Soil properties and the growth and maturation of herbaceous plants are known to be influenced by the soil fauna (Collembola) and by the temperature. But little is known about how these two factors interact. We hypothesized that the vegetative and reproductive responses of *Poa annua* L. to the presence of soil Collembola density will change according to temperature. *P. annua* was grown in microcosms with or without Collembola at two different air temperature conditions, 16°C as a Low T° vs. 19°C as a High T°. Both factors "Collembola" and "Temperature" significantly influenced several plant and soil variables. The number of flowers, the root biomass of *P. annua* were higher either in presence of Collembola or under elevated temperature. The same applied for soil ergosterol or K content for example. Soil nitrate content was exclusively affected by the presence/absence of Collembola and not by the temperature. Finally, significantly interactive effects between temperature and Collembola upon several plant or soil variables (root biomass, number of flowers, soil K and Mg content) were shown. Our study suggests that biotic factors (here soil fauna) may strongly interact with climatic variables in regulating plant growth through changes in soil nutrient availability. We provide experimental evidence that climate warming modifies the effect of soil Collembola on the reproduction strategy of the plant.

Key words: above-belowground interactions; soil fauna; plant growth; facilitation

1. Introduction

A biotic response to climate warming remains one of the greatest challenges in ecology in terms of predicting how ecosystems will respond to the currently high rates of warming (Blois et al., 2013). How plant growth responds to temperature has been well documented over the last decades (see metanalysis of Lin et al., 2010) with a general increase of biomass (+12.3%) associated with warming, without differences of increased patterns between shoots or root biomasses. Furthermore, plants experiencing elevated temperatures have a different phenology and physiology, as they may, for example, flower significantly earlier (Fitter and Fitter, 2002; Menzel et al., 2006; Anderson et al., 2012) or increase their root exudation rate (Yin et al., 2013), although this last point has mainly been documented for trees. Furthermore, according to the metabolic scaling theory, metabolism increasing with temperature drives ecological processes at different levels of biological organisation (West et al., 1997; Brown et al., 2004). Thus, in a context of global warming that affects plant performance, it seems necessary not only to focus on the direct effect of the temperature factor upon plants but also on its indirect effect on other biotic factors to deepen our understanding of the effect of climate change on biotic responses.

Within this framework, while above-ground responses to climate changes have elicited the most attention, the responses of biota below-ground and their consequences on above-ground organisms are notoriously understudied (West et al., 2006; Bardgett and Wardle, 2010), despite the acknowledged importance of above-ground/below-ground links in ecosystem functioning (Bardgett and Wardle, 2010) . Soil biota encompasses a wide array of organisms both directly (e.g. pathogens, symbionts, rhizophages) and indirectly (e.g. detritivores, predators) by interacting physically with plant roots. To date, most of studies have investigated the interactive effects between temperature and soil biota upon plant growth, with a focus on soil microorganisms (Van Grunsven et al., 2010; Thakur et al., 2017), and very few have considered soil fauna (Walther, 2004; Cornelissen et al., 2007). These few papers, rather, have suggested a change in interactions between plants and the soil faunal community as a result of global climate change, but without focusing on mechanisms.

Soil faunal activity exerts a strong influence on the composition, structure and functioning of above-ground communities (De Deyn et al., 2003). For example, Collembola, a dominant soil microarthropod group, is known to regulate flows of nutrients to plants by shaping the biomass and activity of the microbial community (both bacteria and fungi), either directly, through feeding, or indirectly, through the comminution of organic matter and dissemination of microbial propagules (Moore et al., 1988; Coulibaly et al., 2019). Furthermore, various Collembolan species have been shown to act upon plant root biomass without any clear pattern, either directly, by exerting rhizophagous pressure (Endlweber et al., 2009), or indirectly, by interacting with microbes as detailed above. In previous studies, we were able to show that the presence of Collembola stimulates plant growth and accelerate flowering, potentially through increasing nutrient availability and uptake by plants (Forey et al., 2015; Winck et al., 2020).

Collembola, ectothermic organisms, may exhibit greater activity and higher growth and reproductive rates with moderate warming, resulting in elevated metabolic demands (Gillooly et al., 2001, Mallard et al., 2020). A few studies focusing on the fate of the Collembola community have tried to disentangle the effects of temperature from those of soil moisture (Wolters, 1998; Xu et al., 2012; Santonja et al., 2018; Mallard et al., 2020). These studies generally reported an increase in the growth rate, abundance and diversity of Collembola in warmer soil conditions if soil humidity remained favourable. Indeed, as described above, many factors may explain the changes in plant performance following an increase in temperature (Fig. 1), ranging from the direct effects of temperature upon plants to its indirect effects through changes in the soil-available nutrients regulated by the interactions between microbes and their consumers (e.g. Collembola).

Thus, in a microcosm experiment, we explored the interaction of temperature and Collembola on the growth of one of the most common grass species in the world, *Poa annua* L. As Figure 1 shows, we hypothesised that the positive effect of Collembola on *P. annua* growth and flowering would be stronger under a higher air temperature (+3°C), mimicking climate warming compared to the actual temperature. Indeed, we expected that a higher

temperature would stimulate Collembola metabolism and growth, leading to an increase in their number and a shift in their community composition and structure. This increase in Collembola activities would result in a higher amount of nutrients (N, P and K) available in the soil for plants (see Fig.1), ultimately promoting plant growth (biomasses) and eventually flowering. In other words, we assumed that there was a strong interaction of Collembola and temperature that affected soil nutrient status and plant performance (both growth and reproductive investment).

2. Material and Methods

In a microcosm experiment performed in October 2017, four treatments were established corresponding to the presence ('Coll.') or absence ('None') of Collembola, with two air temperature levels: Low T° (16°C) and High T° (19°C). The low temperature represents the mean air temperature of the growing season of *P. annua* in late spring and summer (from May through August) in Normandy (the mean data from 1981 to 2010 registered by a local weather station at Boos-Rouen; https://www.infoclimat.fr). The high temperature level (19°C) mimics what could be expected in the near future in Normandy during spring and summer according to the different climate change scenarios (RCP 6.0 and RCP 8.5) presented in the fifth report of the IPCC (2014).

Each treatment was replicated 15 times in microcosms (10x9x9cm PVC pots), where individuals of *P. annua* were grown. The soil was a rendosol (organic matter content = 6.17%; pH_{H2O} = 7.79) collected in September 2017 from a chalk grassland (1°703000E, 49°2202200N) in Normandy, France. Part of the soil was defaunated by deep-freezing and thawing over the course of one week and then repeated the following week, as described in Forey et al. (2015). The 60 microcosms were meshed (0.250mm) to prevent any escape of Collembola and filled with approximately 245g FW of previously sieved (5mm) and defaunated soil. The soil density obtained at the start of the experiment was of 0.47g.cm^{-3}, which is particularly light but may result from using a 2mm-sieved soil and not compacting the soil when filling in the microcosms in order to leave available pore space for Collembola

116 (especially large species).

117 From the remaining soil, microorganisms (fungi and bacteria) were extracted and re-
118 inoculated in the 60 microcosms prior to setting the different treatments (see Forey et al.,
119 2015, for further details). Re-inoculation of microorganisms in all microcosms was followed
120 two weeks later by the addition of Collembola only in the 15 'High T°-Coll' and 15 'Low T°-
121 Coll' microcosms. This time lap of two weeks was applied in order to let the microbial
122 components colonise the soil and not suffer from, for example, overgrazing. Each microcosm
123 of the Low T°-Coll and High T°-Coll was reinoculated with natural Collembola assemblages
124 extracted from 150g of fresh soil. To do this, we first extracted, using the Berlese-Tullgren
125 device (Tullgren, 1918), the Collembola of each 150g of fresh soil into pots filled with moist
126 plaster. Under a stereomicroscope, we captured and transferred Collembola with pooters into
127 the different microcosms. These specific and manual transfers ensured that only introduce
128 Collembola and no other mesofauna groups were transferred. As Collembola species could
129 only be determined with certainty under a microscope, we selected under the
130 stereomicroscope different morphospecies, i.e. species distinguished from others only by
131 their morphology, that were easily recognisable. This allowed us to introduce the same set of
132 species in each microcosm. To obviate for too much discrepancy between number of
133 individuals introduced per species or morphospecies under the stereomicroscope, we
134 selected 3 to 5 individuals per morphospecies except for the dominant morphospecies (later
135 identified as *Parisotoma notabilis*), of which 10 to 15 individuals were introduced. As mortality
136 may have occurred during the re-inoculation process, making it difficult to estimate the
137 number of individuals that establish themselves, Collembola were extracted from 5
138 microcosms of each treatment at the end of the experiment using the Berlese-Tullgren
139 device (Tullgren, 1918), allowing us to confirm that no contamination was observed in the
140 treatment without Collembola, as none was found in either the treatment 'Low T°-None' nor
141 in 'High T°-None'. It also allowed us to compare Collembolan communities between
142 treatments at the end of the experiment.

143 Within each microcosm, a single seedling of *P. annua* was transplanted into each microcosm

144 according to the methods used by Forey et al. (2015). All the seedlings were obtained from
145 seeds collected at a single spot in a calcareous grassland in Moult, Normandy.
146 The microcosms dedicated to the low-temperature treatments (Low T°-None and Low T°-
147 Coll) were incubated in climate chambers (temperature: 16°C; daily light/dark 16h/8h), while
148 the microcosms dedicated to the high temperature treatments (High T°-none and High T°-
149 Coll) were incubated in similar climatic chambers with the same photoperiod but at a 19°C air
150 temperature. For all microcosms, the soil moisture was kept to 60% of the soil's water-
151 holding capacity during the experiment by weighing the microcosms every 3 days and adding
152 water accordingly. This process was stopped after 13 weeks, when more than 80% of *P.*
153 *annua* were flowering.
154 At the end of the experiment, several plant traits were measured. On ten replicates, root
155 traits (root length and number of root tips) were assessed using WinRHIZO™ image-analysis
156 software (V. reg. 2009c, Regent Instruments, Canada), as described by Forey et al. (2015).
157 On ten replicates, plant height, the number of leaves, the number of spikelets (thereafter
158 'flowers') and the number of ramets were measured. To estimate plant biomass allocation,
159 both root (R) and shoot (S) biomasses were measured after drying them at 65°C for 48 h.
160 The S/R ratio was then calculated. Finally, the carbon and nitrogen content of leaves was
161 measured by chromatography with a CHN pyrolysis micro-analyser (Flash 2000 Series,
162 CHNS/O Analysers Thermo Scientific, France). Mineral elements (Mg, Mn and P, n = 8) in
163 the leaves were analysed by atomic absorption spectrophotometry (AAS, ICE 3000 SERIES,
164 Thermo Scientific, China; see Forey et al., 2015, for methods). We also determined for each
165 microcosm the first flowering date, calculated as the number of days between the seedling
166 transplantation into the microcosms and the flowering.
167 Correlation tests between plant traits were performed in order to avoid autocorrelative
168 parameters in further analyses. According to the results, we only kept the shoot and root
169 biomasses and their ratio as markers of vegetative growth and thus excluded plant height,
170 number of leaves and number of ramets. The number of flowers and the first flowering date
171 were kept as markers of reproductive status. Finally, the root length was used as a marker of

172 root architecture, and we therefore excluded the number of root tips for further analyses.
173 Soil properties were also investigated at the end of the experiment; these included fungal
174 biomass (i.e. ergosterol concentration), determined according to the method of Gong et al.
175 (2001), microbial carbon biomass (C_{mic}), determined using the fumigation-extraction method
176 (Jenkinson and Powlson, 1976) and mineral N ($N–NO_3^-$ and $N–NH_4^+$), determined
177 colourimetrically (Sequential Analyser Gallery, Thermoscientific). All these variables were
178 measured on only ten replicates per treatment, and were not investigated in the five
179 microcosms per treatment dedicated to the extraction of soil Collembola. Furthermore,
180 nutrient content (Mg, Mn, P and K), pH_{H2O} and soil water content (see Forey et al., 2015, for
181 full methods) were also investigated in all microcosms (n = 15) in each treatment. To answer
182 our main hypothesis on the joint effects of temperature and Collembola in determining the
183 response of *P. annua* and soil variables, we used a Generalised Linear Model (GLM)
184 approach with the presence or absence of Collembola and the two levels of temperature as
185 fixed factors. We fitted the model according to the distribution of the data (details in Tables 1
186 and Fig. 1 and 2). A Bonferroni correction for multiple tests was applied for both plant and
187 soil variables. Differences in Collembola communities between treatments were tested using
188 a Permanova test with 9999 permutations, Bray–Curtis distance, and Bonferroni's correction
189 applied to the p-values. Wann–Whitney U tests were used to depict differences in the
190 abundance of each Collembolan species between both temperature treatments. Finally, to
191 test whether the response of reproduction simply results from the effect on plant biomass or
192 whether the temperature also affects reproductive investments, we tested the residual of the
193 number of flowers~plant biomass by means of a GLM. All tests were computed using
194 Statistica software package (version 10.0, Statsoft, Tulsa, 2010).
195
196 **3. Results**
197 *3.1 Effect of temperature and springtails on plant variables*
198 Three plant variables—the number of flowers, the first flowering date (number of days to
199 flower emergence) and the root biomass—were significantly affected by the interactive term

200 'Temperature * Collembola' (Fig. 2 a-c).

201 The number of flowers per plant was significantly higher in the 'High T°-Coll' treatment than
202 in the other three treatments, with an increase ranging from +120% compared to the 'Low T°-
203 None' treatment to +150% compared to the 'Low T°-Coll' treatment (Fig. 2a). The number of
204 flowers was also significantly affected by the factor 'Temperature' (+67% in the High T°
205 treatments compared to the Low T° treatments) and by the factor 'Collembola' (+75% in the
206 treatments with Collembola compared to the treatments without Collembola (Fig. 2a).
207 Furthermore, the reproductive investment of *P. annua* influenced by the interactive term
208 'Collembola * Temperature' was independent of the plant biomass (GLM, $F = 0.08$; $p = 0.78$).
209 The number of days to emergence was significantly reduced, by approximately one week for
210 a growth period of around 7–8 weeks in 'High T°-Coll' compared to both 'Low T°-Coll' and
211 'High T°-None', 'Low T°-None' had an intermediate value (Fig. 2b and Fig. S1). This variable
212 was influenced neither by the temperature nor by the presence of Collembola alone (Fig. 2b).
213 The shoot biomass and the P of the leaves showed higher values in the 'High T°' treatments
214 compared to the 'Low T°' treatments (by 64% and by 15%, respectively; Fig. 2d). In parallel,
215 the P content in the leaves was also higher (+23%) in the presence of Collembola. On the
216 other hand, the shoot/root ratio (-49%), the C/N (-6%) and the Mg content (-16%) of the
217 leaves were all significantly lower in the treatments with Collembola compared to those
218 without (Table 1). The root biomass was significantly higher in the 'High T°-Coll' treatment
219 compared to all other treatments, with an increase ranging from +62% compared to the 'Low
220 T°-Coll' to +153% compared to the 'Low T°-None'. These last two treatments also differed
221 significantly, with +56% of root biomass in 'Low T°-Coll' compared to 'Low T°-None'. Both
222 factors 'Temperature' and 'Collembola' affected the root biomass, with mean values 41%
223 higher in the 'High-T°' treatments and 87% higher in the presence of Collembola (Fig. 2c).
224 The root length was not influenced by both factor or their combination (Fig. 2f).
225

226 *3.2 Effect of temperature and Collembola on soil properties*

227 The concentrations of two soil nutrients, Mg and K, were affected by the interaction between

228 'Temperature' and 'Collembola' (Fig. 3a-b), with approximately 10% less Mg in the 'High T°-
229 Coll' soil compared that of both 'Low T°-Coll' and 'Low T°-None'. In parallel, soil Mg content
230 was also significantly but slightly lower (-5%) in the presence of Collembola (Fig. 3a). Soil K
231 content was higher in 'High T°-Coll' compared to all other treatments: +22% compared to
232 both 'High T°-None' and 'Low T°-None' and +17% compared to 'Low T°-Coll'. This variable
233 was also affected by both the 'Temperature' and 'Collembola' factors, with +9% and +13% of
234 soil K content under high temperature and in the presence of Collembola, respectively (Fig.
235 3b).
236 Besides soil Mg and K content, several other soil variables were affected by either the
237 'Temperature' or 'Collembola' factor. The microbial biomass (+29%; Table 2), the ergosterol
238 content (+20%; Table 2) and the soil NH_4^+ content (+79%; Fig. 3c) had higher mean values
239 under high temperature. The presence of Collembola, regardless of temperature, significantly
240 increased the ergosterol (+16%; Table 2), NO_3^- (+95%; Fig. 3d), and P (+23%; Fig. 3e) and
241 content (Table 2). The concentration of Mn into the soil was not affected by both factors of
242 their interactions (Fig. 3f).
243
244 *3.3 Effect of Temperature on Collembola communities*
245 The total amount of Collembola was significantly higher: 79% higher in the 'High T°'
246 compared to the 'Low T°' soils (Table 2). The significant PERMANOVA showed that both
247 communities were different from each other (Table 2). Of the eleven taxa found at the end of
248 the experiment, three species occurred only in the 'Low T°' treatments, while two were found
249 only in the 'High T°'. The abundance of only one species, *Isotomurus palustris*, however, was
250 significantly affected by the factor 'Temperature', with 8.7 times more individuals in the 'High-
251 T°' compared to the 'Low-T°' groups (Table 2). Finally, *Parisotoma notabilis* was the
252 dominant species in both treatments, constituting a 60.5% and 46.6% share of the 'Low-T°'
253 and 'High-T°' groups, respectively.
254
255 **4. Discussion**

As expected, we observed joint effects of both the 'Temperature' and 'Collembola' factors on *P. annua* reproductive (flowering) or vegetative (root biomass) variables, as well on as soil Mg and K content. This clearly demonstrates the interactive effect of temperature and Collembola on plant growth and development. To our knowledge, our study is the first to examine and demonstrate experimentally such interactive effects among soil fauna, Collembola and temperature upon plant growth and reproduction. We also expected that the interactions between 'Collembola' and 'Temperature' would result in a shift of the Collembolan assemblage (species and abundances) at high temperature compared to the low-temperature treatment. We effectively found different assemblages of Collembola between the two temperatures that partly explained the interactive effects observed. Indeed, increasing temperature can have strong direct effects on Collembola demographic parameters (e.g. fecundity, reproduction, development; Hopkin, 1997), thereby affecting their densities. In fact, our results lend insights into the Collembola response to warming that have often been found to be more species-specific than general (e.g. Wolters, 1998; Makkonen et al., 2011). Drought has often been reported as the main negative factor explaining a decrease in Collembola experiencing global warming (Kennedy, 1994; Jucevica and Melecis, 2006; Makkonen et al., 2011; Petersen, 2011). In contrast to these studies, we only manipulated soil temperature, with soil moisture maintained as constant. Although we do not have the exact number of individuals introduced at the beginning of the experiment, the higher total abundance of Collembola found in our case within the 'High T°-Coll' group supports the results of other studies focusing on temperature increase (Day et al., 2009; Kardol et al., 2010; Xu et al., 2012; Santonja et al., 2019). Only one Collembola species, however, had a significantly different abundance between the two temperatures of incubation. It is unlikely that an increase in temperature will increase the survival of arthropods, so the overall higher density is probably due to increased fecundity and reduced generation time at the higher temperature. Recently, Mallard et al. (2020) found that the growth rate of a Collembolan species increased with temperature but that this thermal reaction was modulated by intraspecific competition. This, when taken into account along

with interspecific competition, may explain why in our case only one species benefited from an increased temperature. Three species with a low number of individuals were found only at low temperature, but as we did not introduce the same number of individuals to each microcosm, it is difficult to draw a conclusion from this finding. Nevertheless, as found in previous research (Hodkinson et al., 1998; Makkonen et al., 2011, Petersen, 2011), our results support the role of temperature as a determinant of Collembolan communities. In the literature, deep-living small euedaphic species were found to have difficulties coping with an increase in temperature, unlike larger epedaphic species living on top of the soil (Jucevica and Melecis, 2006; Makkonen et al., 2011). Our results showed an increase of only one epedaphic species, partly supporting the previous findings.

Changes in Collembolan communities under increasing temperature might also be mediated by plant–soil feedbacks (PSFs). Indeed, increasing temperature is known to affect almost every biological processes in a plant, including morphogenesis, respiration and photosynthesis (Quint et al., 2016; Dusenge et al., 2019). Generally, these metabolic processes, such as photosynthesis, occur between 20°C and 30°C depending on species (Berry and Björkman, 1980). As a consequence, elevated temperatures may increase the amount and nature of compounds transferred to the rhizospheric soil by plants through increasing root respiration and root exudation (Atkin et al., 2000; Yin et al., 2013). These changes in soil carbon dynamic and inputs can stimulate soil microbial communities from the rhizosphere (Lange et al., 2014), thereby potentially modifying through bottom-up control Collembola communities. Our experiment was not designed to test or quantify the importance of these PSFs. Many questions, however, need to be addressed to understand how climate change will alter PSFs and their potential consequences for ecosystem functioning. In a recent meta-analysis on this topic, Pugnaire et al. (2019) stressed the need to understand how warming affects these PSFs through the importance of rhizodeposits, which are often overlooked in the literature.

We further hypothesised that an increase of Collembola with increasing temperature would result in higher amount of nutrients available in the soil for plants and ultimately higher plant

312 growth and faster flowering. While we effectively found an effect of the interaction between
313 temperature and Collembola on several soil nutrients (Mg and K), this was not the case for
314 all Collembola. Furthermore, even if the interactions between 'Collembola' and 'temperature'
315 affected the concentration of several soil nutrients, plant nutrients were not affected. The
316 temperature-associated potential changes in the specific needs for nutrients (stoichiometry)
317 of microbial components, Collembola and plants may partly explain the discrepancies found
318 in the nutrient responses either in the soil (with only K and Mg affected) or within the plants to
319 the interaction of 'Collembola' and 'Temperature'. The factor 'Collembola' alone, however,
320 has been found to affect soil and plant nutrients strongly, as found by Forey et al. (2015) and
321 Winck et al. (2020). This suggests that Collembola might first stimulate mineralisation
322 performed by microorganisms, leading to an increase in soil nutrients, but also that they
323 might limit the ability of the microbial biomass to grow and compete with plants for N and P,
324 even if they do not reduce the total microbial biomass. This could probably be achieved
325 through selective grazing by promoting (in relative proportion) different microbial components
326 that may be less competitive for N and P acquisition and also for other nutrients (Ngosong et
327 al., 2014; Kutáková et al., 2018, Coulibaly et al., 2019). We did not find, however, the
328 interactive effect upon microbial variables that we might have expected regarding the
329 conceptual scheme (Fig. 1). It could be that the coarse parameters used to describe the
330 microbial component were not sensitive enough to detect changes that may have occurred
331 within the assemblages according to the interaction between 'Collembola' and 'temperature'.
332 Alternatively, PSFs might also have masked these interactive effects on the microbial
333 variables. Our design did not allow us to clearly separate a Collembola effect due to an
334 increase of either their abundance or their metabolism or through a change in their
335 community composition and structure with temperature, which may have prevented us from
336 detecting such interactive effect on nutrients. An intriguing but very challenging project would
337 be to disentangle how these variables may participate in causing the joint effects observed of
338 temperature on plant growth.

In general, the functional consequences for soil functioning and ultimately the plant growth of trophic interactions between soil invertebrates and microbial components remain poorly understood (Kutáková et al., 2018). Nevertheless, in microcosms, selective grazing of microarthropods upon micro-organisms has been proven to regulate plant development (see Friberg et al., 2005, for a review). Furthermore, the recent results obtained by a field study by Schuldt et al. (2017) support the view that top-down regulation below ground might be more important than previously thought, operating through feedbacks among the different microbial components, detritivores and plant communities, adding complexity to the PSFs.

Interestingly, even if the nutrient status of the plant was not affected by the interaction between the two treatments, both plant reproduction and a marker of plant growth were. This suggests that, besides regulating nutrient availability through microbial grazing in a temperature-dependent manner, Collembola may also interact through other mechanisms with plants and that those synergistic interactions or mechanisms are partly temperature-dependent. In a review paper, Puga-Freitas and Blouin (2015) highlighted that very different soil organisms, such as bacteria or Collembola, may activate similar hormone signalling pathways, leading to mutual consequences upon plant growth or defence. This should be further investigated, but may likely play a role in the interaction pathways between plants and soil. For example, in a different context, Rodríguez-Echeverría et al. (2013) showed that belowground biota (specifically microbial communities) shaped by nurse (or benefactor) plant species play an important role in the facilitation of other plant (or beneficiary) species. They hypothesised that such PSF effects could be related to the increased nutrient availability promoted by soil microbes and/or to production of phytohormones by plant growth, promoting bacteria.

The shoot biomass, as opposed to root biomass, did not respond to the interaction between ‘Temperature’ and ‘Collembola’. This difference in the response of shoot and root biomass was also found in our case regarding the simple effect of the factor ‘Collembola’ and may result from the close physical relationship between Collembola and roots. For example, several Collembola are known to feed on roots occasionally (Endlweber et al. 2009), which

may lead to a compensatory growth of roots. Lin et al. (2010), however, in a meta-analysis found that shoot and root biomass of grasses exposed to climate warming increased by 5% and 33%, respectively, showing a different response of above- or below-ground plant parts independently of soil fauna. In our case, while root biomass increased to the same magnitude (+41%) with temperature, the shoot biomass increased much more (+64%) than the mean values reported in the meta-analysis (+5%). Such a discrepancy may be explained by the absence of plant competition in our experiment and by our choice to maintain constant soil moisture rather than limiting moisture throughout the whole experiment. Several authors also pointed to the fact that root traits are species-specific and highly plastic to abiotic or biotic (i.e. microorganisms) environmental factors (Eissenstat et al., 2000; De Kroon et al., 2012; Hendriks et al., 2015). We also cannot exclude the possibility that the size of our microcosms may have restricted the growth of the roots.

The reproductive success of *P. annua* (i.e. its number of flowers) was doubled in presence of both elevated temperature and Collembola. Most importantly, only the joint effect of high temperature coupled with the presence of Collembola led to influence the flowering phenology of *P. annua*, with the number of days to flower emergence being reduced by 14% compared to both the 'Low T°-Coll' and 'High T°-None' groups. Other studies have demonstrated a positive influence of arthropods on plant reproduction or on phenology (Ando et al., 2017; Forey et al., 2015), but have focused on temperature as an interactive factor. As noticed by Forey et al. (2015), changes induced both in soil chemistry and within the soil microbial community may lead shorten flowering emergence. Without being able to disentangle these mechanisms, our findings of higher soil K and ergosterol content in parallel with shorter flowering emergence and higher flowering numbers in 'High T°-Coll' support this assertion.

Therefore, any suggestions about the mechanisms involved would be rather speculative. Although these points were beyond the scope of our study, they would certainly be worth addressing. The results of temperature on plant growth via soil biota are supported by a

recent study that found soil warming to affect the relationship between plants and soil biota, e.g. nematodes feeding on microbes (Thakur et al., 2017).

5. Conclusion

The effects of soil invertebrates upon plants are of high importance when considering their specific responses to global warming. For example, *P. annua* is a Eurasian species from a temperate climate that is invasive on sub-Antarctic islands (Molina-Montenegro et al., 2012). Understanding the dynamic and adaptation of this alien species in northern regions experiencing climate warming requires the integration of both climate change and changes in below-ground compartments, as suggested by our study and demonstrated by the significant interactive terms 'Collembola' * 'Temperature' regarding several plant and soil variables.

Few Species Distribution Models include biotic interactions, and even fewer include the role of soil fauna in plant growth. We thus strongly recommend testing the effect of climate change with more complex plant communities and soil fauna groups, as our results for temperature effects on plant growth via soil biota confirm previous results (Thakur et al., 2017, Heinze et al., 2017). It remains unclear, however, whether the effects found in our case in a simplified model system are relevant within natural complex soil food webs. Furthermore, other factors, such as changes in precipitation patterns or elevated atmospheric CO_2, must also be taken into account, as they may regulate the activities of below-ground organisms and plants.

Acknowledgments

The authors would like to thank the Botanical Garden of Caen for providing seeds. The authors are grateful to Philippe Delporte and Marthe Akpa-Vinceslas (Ecodiv lab, University of Rouen Normandy) and the FR SCALE CNRS 3730 for technical assistance. This study was financially supported by GRR TERA and SFR SCALE (Région Haute-Normandie, France). The authors would like to thanks two anonymous reviewers for their comments

improving an earlier version of this manuscript.

References

Anderson, J. T., Inouye, D. W., McKinney, A. M., Colautti, R. I., Mitchell-Olds, T., 2012. Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change. Proc. Royal Soc. B: Biol. Sci., 279, 3843-3852.

Ando, Y., Utsumi, S., Ohgushi, T., 2017. Aphid as a network creator for the plant-associated arthropod community and its consequence for plant reproductive success. Funct. Ecol. 31, 632-641.

Atkin, O.K., Edwards, E.J., Loveys, B.R., 2000. Response of root respiration to changes in temperature and its relevance to global warming. New Phytol. 147, 141-154.

Bardgett, R.D., Wardle, D.A., 2010. Aboveground-belowground linkages: biotic interactions, ecosystem processes, and global change. Oxford University Press, Oxford.

Berry, J., Bjorkman, O., 1980. Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physio. 31, 491-543.

Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C., Finnegan, S., 2013. Climate change and the past, present, and future of biotic interactions. Science 341, 499-504.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771-1789.

Cornelissen, J. H., Van Bodegom, P. M., Aerts, R., Callaghan, T. V., Van Logtestijn, R. S., Alatalo, J., et al. 2007. Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. Ecol. Lett. 10, 619-627.

Coulibaly, S.F.M., Winck, B.R., Akpa-Vinceslas, M., Mignot, L., Legras, M., Forey, E., Chauvat, M., 2019. Functional Assemblages of Collembola Determine Soil Microbial Communities and Associated Functions. Front. Env. Sci. 7, 52.

Day, T.A., Ruhland, C.T., Strauss, S.L., Park, J.H., Krieg, M.L., Krna, M.A., Bryant, D.M., 2009. Response of plants and the dominant microarthropod, *Cryptopygus antarcticus*, to

warming and contrasting precipitation regimes in Antarctic tundra. Glob. Change Biol. 15, 1640-1651.

De Deyn, G.B., Raaijmakers, C.E., Zoomer, H.R., Berg, M.P., de Ruiter, P.C., Verhoef, H.A., Bezemer, T.M., van der Putten, W.H., 2003. Soil invertebrate fauna enhances grassland succession and diversity. Nature 422, 711-713.

De Kroon, H., Hendriks, M., van Ruijven, J., Ravenek, J., Padilla, F.M., Jongejans, E., Visser, E.J., Mommer, L., 2012. Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity. J. Ecol., 100, 6-15.

Dusenge, M.E., Duarte, A.G., Way, D.A., 2019. Plant carbon metabolism and climate change: elevated CO2 and temperature impacts on photosynthesis, photorespiration and respiration. New Phytol. 221, 32-49.

Eissenstat, D.M., Wells, C.E., Yanai, R.D., Whitbeck, J.L., 2000. Building roots in a changing environment: implications for root longevity. New Phytol. 147, 33-42.

Endlweber, K., Ruess, L., Scheu, S., 2009. Collembola switch diet in presence of plant roots thereby functioning as herbivores. Soil Biol. Biochem. 41, 1151-1154.

Ericsson, T., 1995. Growth and shoot: root ratio of seedlings in relation to nutrient availability, in: Nilsson, L.O., Hüttl, R.F., Johansson, U.T. (Eds), Nutrient Uptake and Cycling in Forest Ecosystems. Developments in Plant and Soil Sciences 62. Springer, Dordrecht, pp. 205-214.

Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flowering time in British plants. Science 296, 1689-1691.

Forey, E., Coulibaly, S.F.M., Chauvat, M., 2015. Flowering phenology of a herbaceous species (*Poa annua*) is regulated by soil Collembola. Soil Biol. Biochem. 90, 30-33.

Friberg, H., Lagerlöf, J., Rämert, B., 2005. Influence of soil fauna on fungal plant pathogens in agricultural and horticultural systems. Biocontrol. Sci. Tech. 15, 641-658.

475 Gange, A., 2000. Arbuscular mycorrhizal fungi, Collembola and plant growth. Trends Ecol.
476 Evol. 15, 369-372.
477 Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size
478 and temperature on metabolic rate. Science 293, 2248–2251.
479 Gong, P., Guan, X., Witter, E., 2001. A rapid method to extract ergosterol from soil by
480 physical disruption. Appl. Soil Ecol. 17, 285-289.
481 Heinze, J., Gensch, S., Weber, E., Joshi, J., 2017. Soil temperature modifies effects of soil
482 biota on plant growth. J. Plant Ecol. 10, 808-821.
483 Hendriks, M., Ravenek, J.M., Smit-Tiekstra, A.E., van der Paauw, J.W., de Caluwe, H., van
484 der Putten, W.H., de Kroon, H., Mommer, L., 2015. Spatial heterogeneity of plant–soil
485 feedback affects root interactions and interspecific competition. New Phytol. 207, 830-840.
486 Hopkin, S. P., 1997. Biology of the springtails:(Insecta: Collembola). Oxford University Press,
487 Oxford.
488 Hodkinson, I.D., Webb, N.R., Bale, J.S., Block, W., Coulson, S. J., Strathdee, A.T., 1998.
489 Global change and Arctic ecosystems: conclusions and predictions from experiments with
490 terrestrial invertebrates on Spitsbergen. Arct. Alp. Res. 30, 306-313.
491 IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II
492 and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change,
493 Core Writing Team, R.K. Pachauri and L.A. Meyer (Eds.). IPCC, Geneva, Switzerland.
494 Jenkinson, D.S., Powlson, D.S., 1976. The effects of biocidal treatments on metabolism in
495 soil-V: A method for measuring soil biomass. Soil Biol. Biochem. 8, 209-213.
496 Jucevica, E., Melecis, V., 2006. Global warming affect Collembola community: A long-term
497 study. Pedobiologia 50, 177-184.
498 Kardol, P., Cregger, M.A., Campany, C.E., Classen, A.T., 2010. Soil ecosystem functioning
499 under climate change: plant species and community effects. Ecology 91, 767-781.
500 Kennedy, A.D., 1994. Simulated climate change: a field manipulation study of polar
501 microarthropod community response to global warming. Ecography 17, 131-140.

Lange, M., Habekost, M., Eisenhauer, N., Roscher, C., Bessler, H., Engels, C., Oelmann, Y., Scheu, S., Wilcke, W., Schulze, E.D., Gleixner, G. 2014. Biotic and abiotic properties mediating plant diversity effects on soil microbial communities in an experimental grassland. PLoS ONE 9, e96182

Lin, D., Xia, J., Wan, S., 2010. Climate warming and biomass accumulation of terrestrial plants: a meta- analysis. New Phytol. 188, 187-198.

Kutáková, E., Cesarz, S., Münzbergov., Z., Eisenhauer, N. 2018. Soil microarthropods alter the outcome of plant-soil feedback experiments. Sci. Rep. 8, 11898.

Makkonen, M., Berg, M. P., Van Hal, J. R., Callaghan, T. V., Press, M. C., Aerts, R. 2011. Traits explain the responses of a sub-arctic Collembola community to climate manipulation. Soil Biol. Biochem. 43, 377-384.

Mallard, F., Le Bourlot, V., Le Coeur, C., Avnaim, M., Péronnet, R., Claessen, D., T., Tully. 2020. From individuals to populations: How intraspecific competition shapes thermal reaction norms. Funct. Ecol. 34, 669-683.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavska, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mage, F., Mestre, A., Nordli, Ø., Penuelas, J., Pirinen, P., Remisova, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.- E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Glob. Change Biol. 12, 1969-1976.

Molina-Montenegro, M.A., Carrasco-Urra, F., Rodrigo, C., Convey, O., Valladares, F., Gianoli, E., 2012. Occurrence of the non-native annual bluegrass on the Antarctic mainland and its negative effects on the native plants. Conserv. Biol. 26, 717-723.

Moore, J. C., Walter, D. E., Hunt, H. W., 1988. Arthropod regulation of micro-and mesobiota in below-ground detrital food webs. Annu. Rev. Entomol. 33, 419-435.

Ngosong, C., Gabriel, E., Ruess, L., 2014. Collembola grazing on arbuscular mycorrhiza fungi modulates nutrient allocation in plants. Pedobiologia 57, 171-179.

529 Partsch, S., Milcu, A., Scheu, S., 2006. Decomposers (Lumbricidae, Collembola) affect plant
530 performance in model grasslands of different diversity. Ecol. 87, 2548-2558.
531 Petersen, H., 2011. Collembolan communities in shrublands along climatic gradients in
532 Europe and the effect of experimental warming and drought on population density,
533 biomass and diversity. Soil Organisms 83, 463-488.
534 Puga-Freitas, R., Blouin, M. 2015. A review of the effects of soil organisms on plant hormone
535 signalling pathways. Environ. Exp. Bot. 114, 104-116.
536 Pugnaire, F.I., Morillo, J.A., Peñuelas, J., Reich, P.B., Bardgett, R.D., Gaxiola, A., Wardle,
537 D.A., van der Putten, W.H., 2019. Climate change effects on plant-soil feedbacks and
538 consequences for biodiversity and functioning of terrestrial ecosystems. Sci. Adv. 5,
539 eaaz1834.
540 Quint, M., Delker, C., Franklin, K.A., Wigge, P.A., Halliday, K.J., van Zanten, M., 2016.
541 Molecular and genetic control of plant thermomorphogenesis. Nature Plants 2, 15190.
542 Rodríguez-Echeverría, S., Armas, C., Pistón, N., Hortal, S., Pugnaire, F. I., 2013. A role for
543 below-ground biota in plant–plant facilitation. J. Ecol. 101, 1420-1428.
544 Santonja, M., Aupic-Samain, A., Forey, E., Chauvat, M., 2018. Increasing temperature and
545 decreasing specific leaf area amplify centipede predation impact on Collembola. Eur. J.
546 Soil Biol. 89, 9-13.
547 Schuldt, A., Bruelheide, H., Buscot, F., Assmann, T., Erfmeier, A., Klein, A.M., Ma, K.,
548 Scholten, T., Staab, M., Wirth, C., Zhang, J., Wubet, T., 2017. Belowground top-down and
549 aboveground bottom-up effects structure multitrophic community relationships in a
550 biodiverse forest. Sci. Rep. 7, 4222.
551 Thakur, M. P., Reich, P. B., Wagg, C., Fisichelli, N. A., Ciobanu, M., Hobbie, S. E., Rich,
552 R.L., Stefanski, A., Eisenhauer, N., 2017. Effects of soil warming history on the
553 performances of congeneric temperate and boreal herbaceous plant species and their
554 associations with soil biota. J. Plant Ecol. 10, 670-680.

555 Tullgren, A., 1918. Ein sehr einfacher Ausleseapparat fur terricole Tierformen. Z. Angew.
556 Entomol. 4, 149–150.
557 Van Grunsven, R.H.A., Van der Putten, W.H., Bezemer, T.M., Veenendaal, E.M., 2010.
558 Plant–soil feedback of native and range-expanding plant species is insensitive to
559 temperature. Oecologia 162, 1059-1069.
560 Walther, G.R., 2004. Plants in a warmer world. Perspect Plant Ecol Evol Syst 6, 169–185.
561 West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of allometric
562 scaling laws in biology. Science 276, 122–126.
563 West, J.B., Hobbie, S.E., Reich, P.B., 2006. Effects of plant species diversity, atmospheric
564 CO_2, and N addition on gross rates of inorganic N release from soil organic matter. Glob.
565 Change Biol. 12, 1400-1408.
566 Winck, B.R., Chauvat, M., Coulibaly, S.F.M., Santonja, M., Saccol de Sá, E.L., Forey, E.,
567 2020. Functional collembolan assemblages induce different plant responses in *Lolium*
568 *perenne*. Plant Soil 452, 347-358.
569 Wolters, V., 1998. Long-term dynamics of a collembolan community. Appl. Soil Ecol. 9, 221-
570 227.
571 Xu, G.L., Kuster, T.M., Günthardt-Goerg, M.S., Dobbertin, M., Li, M.H., 2012. Seasonal
572 exposure to drought and air warming affects soil Collembola and mites. PLoS One 7, 8.
573 Yin, H., Li, Y., Xiao, J., Xu, Z., Cheng, X., Liu, Q. 2013. Enhanced root exudation stimulates
574 soil nitrogen transformations in a subalpine coniferous forest under experimental warming.
575 Glob. Change Biol. 19, 2158-2167.
576

577 **Tables**

578 Table 1. Means (± SD) of plant leaves chemistry and soil variables according to the factor "Temperature – T°" (High or Low) and the combined
579 presence of "Collembola" (Coll.) or not (None). Means and SD were calculated per treatment. Results of Glms with the two factors are given. F
580 or W and P-values are given. n.s: p> 0.05; *: p < 0.05; **: p < 0.01; ***: p < 0.001. For clarity, significant results are in bold. In case of a
581 significant interactions, different letters denote significantly different values. Cmic: microbial biomass; DW: dry weight.

						Statistical tests					
		Low T°		High T°		T° effect		Coll effect		T° x Coll	
	N	None	Coll	None	Coll	F or W	P-value	F or W	P-value	F or W	P-value
Leaves chemistry											
C/N	10	11.0 (0.6)	10.9 (0.6)	12.0 (0.6)	10.8 (0.4)	6.66†	n.s	**10.3**	*	0.40	n.s
Mg (mg.g^{-1} DW)	8	1.60^{AB} (0.21)	1.45^{BC} (0.13)	1.66^{A} (0.09)	1.29^{C} (0.1)	1.97†	n.s	**37.6**	***	5.61	n.s
Mn (mg.g^{-1} DW)	8	0.06 (0.01)	0.07 (0.01)	0.07 (0.02)	0.07 (0.01)	0.62†	n.s	0.51	n.s	0.02	n.s
P (mg.g^{-1} DW)	8	0.94 (0.08)	1.10 (0.12)	1.02 (0.11)	1.32 (0.21)	**8.78**‡	*	**22.7**	**	1.68	n.s
Soil variables											
Cmic (mgC.g^{-1}DW)	10	357.9 (48)	383.8 (69)	466.4 (50)	490.6 (92)	**19.9**†	**	1.52	n.s	0.11	n.s
Ergosterol (µg.g^{-1}DW)	10	1.35 (0.1)	1.48 (0.2)	1.53 (0.1)	1.86 (0.2)	**28.5**†	***	**22.3**	***	3.69	n.s
Water content (%DW)	15	21.2 (1.2)	21.57 (2.0)	21.8 (1.5)	22.5 (0.8)	2.12†	n.s	3.13	n.s	0.67	n.s

582 † Gaussian distribution
583 ‡ Poisson distribution
584

585 Table 2. Means and standard deviations (SD) of collembolan species abundance (number of
586 individuals) in microcosms (650ml of soil) under two different temperatures with a seedling of
587 *Poa annua* at the end of the 13 weeks of experiment. Species are ordered according to their
588 abundance in the Low T° treatment. Results of two-sided Mann-Whitney U test Z and P-level
589 of significance are given. n.s: $p > 0.05$; *: $p < 0.05$. Low T°: 16°C; High T°: 19°C; n=5. Hemi:
590 Hemiedaphic species; Ep: Epedaphic species; Eu: Euedaphic species.

591

Life-forms	Species	Mean Abundance (± SD)			
		Low T°	High T°	Z	P-level
Hemi	*Parisotoma notabilis* (SCHÄFFER 1896)	24.2 (12.9)	33.4 (6.0)	1.04	n.s
Hemi	*Folsomia fimetaria* (LINNE 1758)	8.8 (5.5)	24.0 (18.9)	1.78	n.s
Hemi	*Pseudosinella octopunctata* (PACKARD 1873)	2.2 (1.9)	3.6 (3.6)	0.42	n.s
Hemi	*Folsomia decemoculata* (STACH 1946)	1.2 (1.8)	0.0 (0.0)	1.04	n.s
Ep	*Isotomurus palustris* (LUBBOCK 1862)	0.8 (1.1)	7.0 (6.2)	2.24	*
Eu	*Protaphorura armata* (TULLBERG 1869)	0.8 (1.1)	0.0 (0.0)	1.04	n.s
Eu	*Mesaphorura sp.*	0.8 (1.1)	2.0 (2.0)	0.90	n.s
Eu	*Megalothorax minimus* (WILLEM 1900)	0.8 (0.8)	0.0 (0.0)	1.57	n.s
Ep	*Lepidocyrtus lanuginosus* (TULLBERG 1871)	0.4 (0.9)	0.4 (0.9)	0.01	n.s
Hemi	*Folsomia quadrioculata* (FABRICIUS 1783)	0.0 (0.0)	0.8 (1.8)	0.52	n.s
Ep	*Sminthurinus elegans* (FITCH 1863)	0.0 (0.0)	0.4 (0.9)	0.52	n.s
	Total	40.0 (15.8)	71.6 (17.8)	-2.4	*

592

593 **Figure Captions**

594

595 **Fig. 1.** Hypothesized effect of Collembola presence coupled to an increase of temperature
596 upon plant growth. Increase of temperature stimulates metabolic activity of ectotherms
597 organisms [1] and [2] (Gillooly et al., 2001; Mallard et al., 2020) as well as stimulates plant
598 shoot and root biomasses [3] (Lin et al., 2010). Furthermore, presence of Collembola may
599 directly interact with roots by consuming them [4] (Endlweber at al. 2009), but this trophic
600 interaction usually does not detrimentally affect plant performance, as plants seems to rather
601 to increase shoot and root growth in presence of Collembola (Gange, 2000, Partsch et al.,
602 2006, Endlweber and Scheu, 2006, Endlweber and Scheu, 2007), and indirectly through
603 regulation of microflora [5] (Ngosong et al., 2014; Coulibaly et al., 2019; Winck et al., 2020),
604 enhancing mineralization and therefore increasing the pool of soil nutrients [6] (Forey et al.,
605 2015) available for plants or by reducing plant pathogens [7] (Endlweber et al., 2009).
606 Collembola may also directly increase the pool of soil nutrients through their faeces [8]
607 (Hopkin, 1997). An increase pool of soil nutrients may favour shoot biomass over root
608 biomass [9] (Ericsson, 1995).

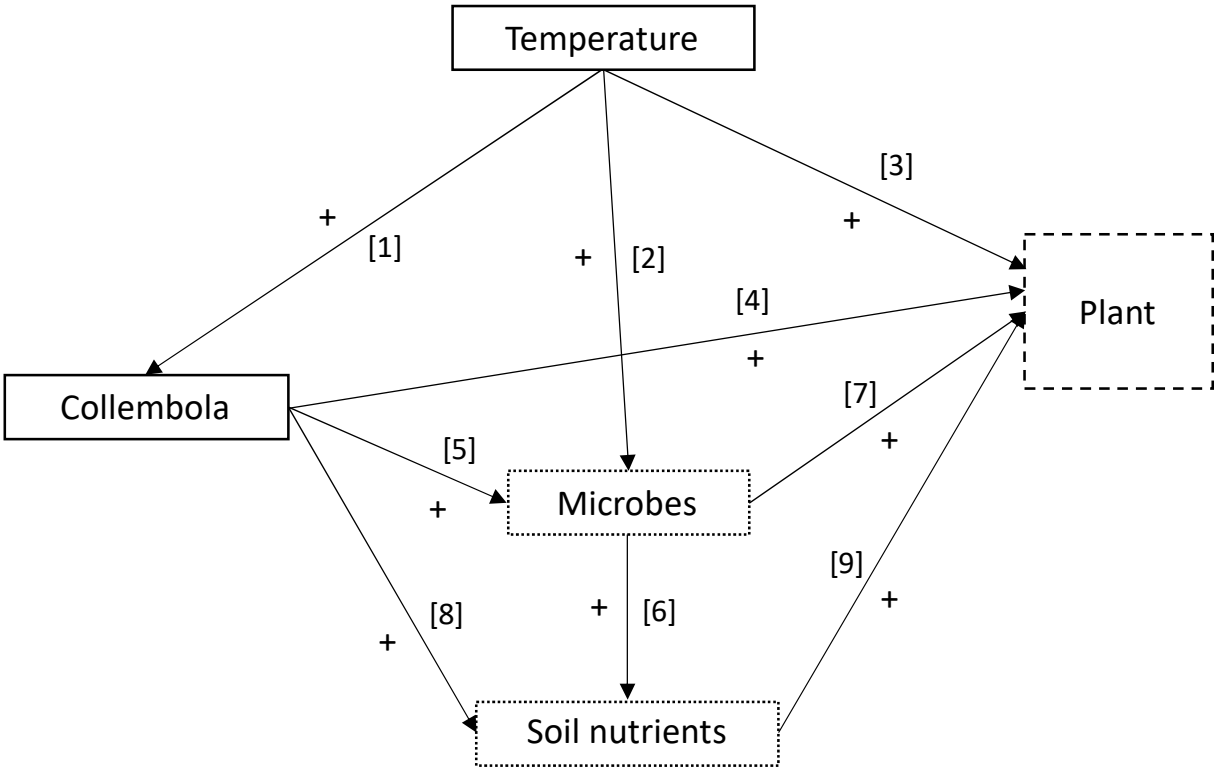
609

610 **Fig. 2a-f.** Mean (and SD) of morphological variables of *Poa annua* : a) Number of flowers, b)
611 First flowering date, c) Root biomass d) Shoot biomass, e) Shoot/root ratio, f) Root length,
612 grown with Collembola ("Coll") or without ("None") under two temperatures conditions (Low
613 T° = 16°C; High T° = 19°C). For a single variable, results of two-ways GLMs are given with
614 the factor "Temperature", "Collembola" and their interactive terms. In case of a significant
615 interactions different letters denote significant differences between the treatments (Tukey
616 HSD test). For all variables, except the number of flowers with a poisson distribution, a
617 gaussian distribution was used in the GLMs. Temp: Temperature; Coll: Collembola.

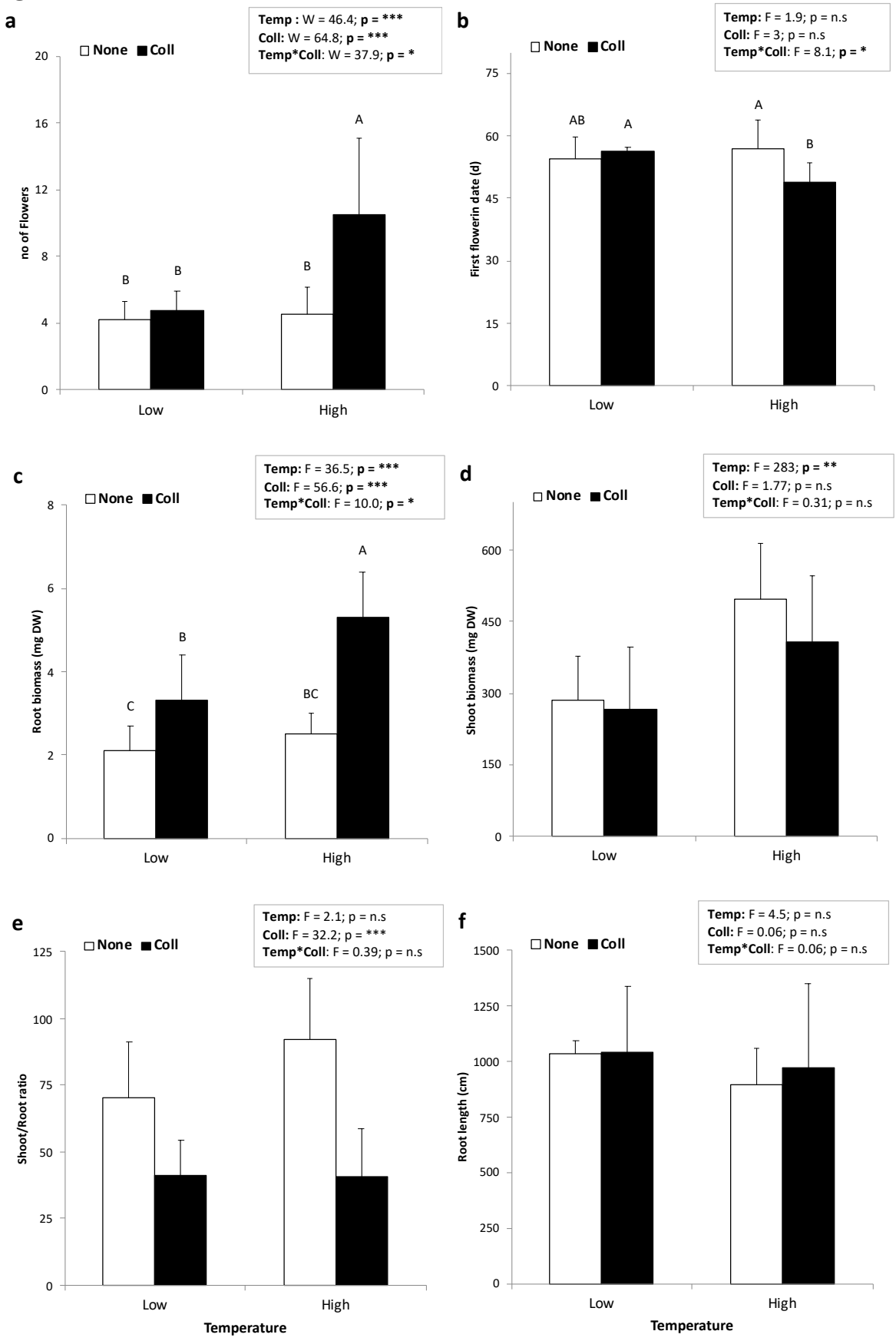
618

Fig. 3a-f. Mean (and SD) of soil nutrients content a) Mg, b) K, c) NH_4^+, d) NO_3^-, e) P, f) Mn, in presence of Collembola ("Coll") or in absence ("None") under two temperatures conditions (Low T° = 16°C; High T° = 19°C). For a single variable, results of two-ways GLMs are given with the factor "Temperature", "Collembola" and their interactive terms. In case of a significant interactions different letters denote significant differences between the treatments (Tukey HSD test). An inverse gaussian distribution was used in the GLMs for both the soil K content and the soil NH_4^+ content. A gaussian distribution was used for the other variables. Temp: Temperature; Coll: Collembola.

Figure 1:

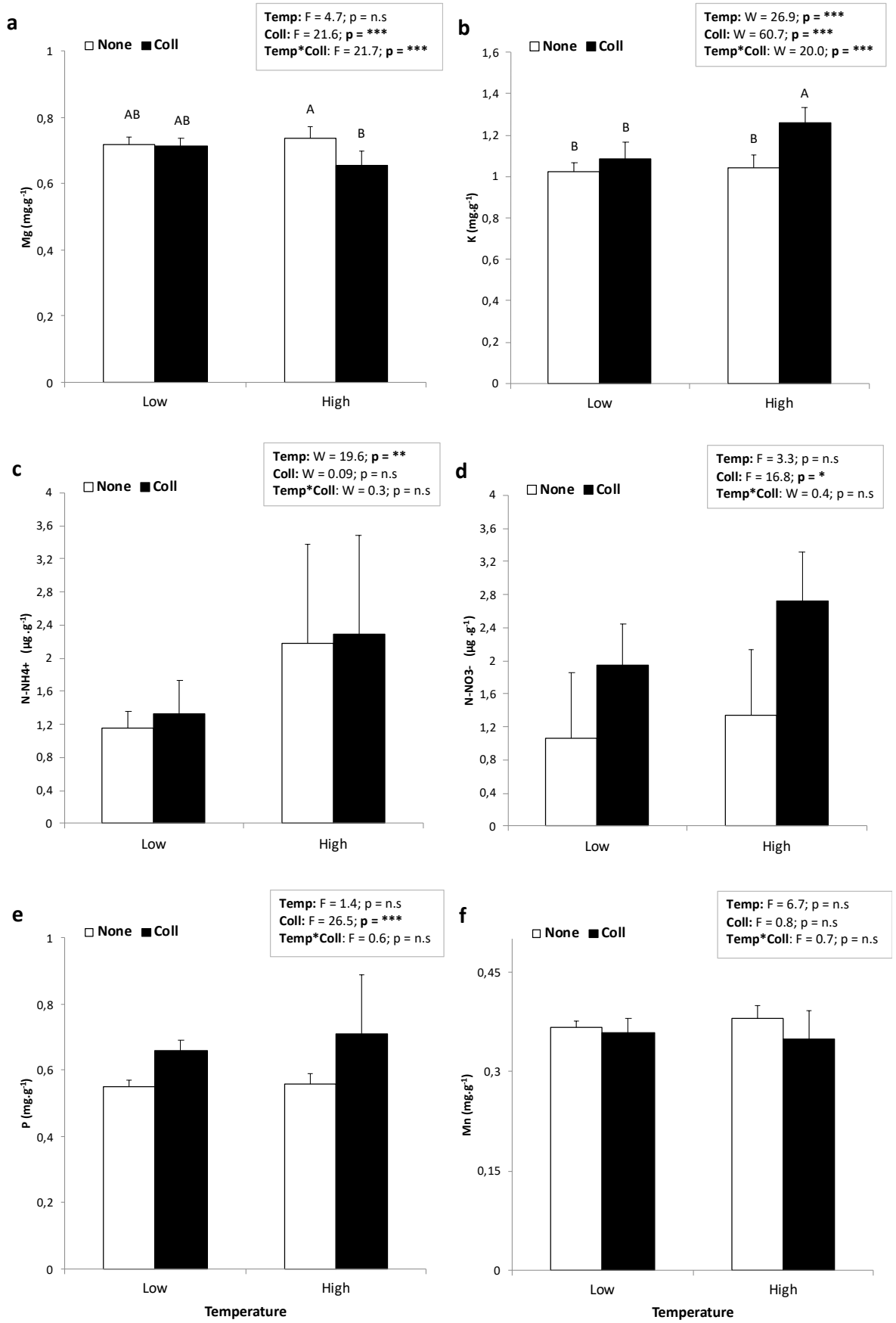

Temperature
[1]
[2]
[3]
[4]
Plant
Collembola
[5]
Microbes
[7]
[8]
[6]
[9]
Soil nutrients
+

632 **Figure 2:**



633
634

635 **Figure 3:**



636
637