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SHORT COMMUNICATION

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Influence of drought on interactions between *Rhopalosiphum padi* and ground dwelling predators – A mesocosm study

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Abstract

Climate change will lead to extreme droughts, but it is difficult to predict how this will affect crop pests. In particular, it is unclear how interactions between natural enemies and pests will be influenced. In the field, bird cherry-oat aphids (*Rhopalosiphum padi* (L.)) have been observed to reside close to, or below the ground surface during dry conditions. We hypothesized that this will increase the niche overlap between *R. padi* and ground-dwelling predators such as carabid beetles and wolf spiders and that aphid numbers will therefore decline during dry conditions. A fully factorial mesocosm experiment was conducted testing the combined effects of drought and predator presence on aphid position and abundance on barley (*Hordeum vulgare*) plants. In support of our hypothesis, we found that (a) aphids moved below ground during dry conditions, (b) predators reduced aphid numbers, but only during dry conditions, and (c) predators reduced the proportion of aphids below ground in dry conditions. This increased predation effect during dry conditions was, however, compensated for by a corresponding increase in aphid performance on the plants and so the net effect of drought on aphid numbers ended up being neutral. Thus, pests can be affected by drought in complex ways via a combination top-down and bottom-up mechanisms. Predicting how pest populations will be affected by droughts in the future is thus a formidable research challenge.

KEYWORDS
biological control, bottom-up regulation, climate change, niche overlap, plant water stress, top-down regulation

1 | INTRODUCTION

Climate change will result in increased temperatures and more extreme droughts (Rosenzweig et al., 2001). Overall, pest abundances are expected to increase with increasing temperatures in most regions due to faster development (Deutsch et al., 2018). The effects of drought are harder to predict. Plant water stress can have positive or negative effects on herbivore performance and survival (Huberty & Denno, 2004). It can be beneficial since nitrogen levels tend to increase, but it also results in reduced plant turgor and water content which can reduce herbivore performance. A less studied consequence of drought is that it can modify interactions between natural enemies and herbivores in complex ways (Banfield-Zanin & Leather, 2016; Barton & Ives, 2014).

Bird cherry-oat aphid, *Rhopalosiphum padi* L., is a key pest on cereal crops in Europe (Leather et al., 1989). In a field study, *R. padi* declined by 50% in a drought treatment (Wade et al., 2017), but in another study fecundity of *R. padi* increased due to reduced humidity (Leather, 1985). Effects of drought depend on host plant species (Hale et al., 2003) and strength of the drought event (Huberty & Denno, 2004). A couple of studies have investigated the effects of drought on interactions between *R. padi* and parasitoids (Aslam et al., 2012; Johnson et al., 2011), but we are aware of no studies exploring the interactions between *R. padi* and ground-dwelling predators.

In Sweden, it is expected that droughts will become more common and severe during spring and early summer (Spinoni et al., 2018). This coincides with when *R. padi* colonizes and initiates population development on spring sown crops like barley (*Hordeum vulgare*) and oats (*Avena sativa*) (Chiverton, 1987). When conditions are dry in early summer, it has been observed that aphids mainly reside on lower parts of the plants and sometimes below the soil. When *R. padi* has recently colonized the crop, the natural enemy community is dominated by ground-dwelling generalists like carabid beetles and wolf spiders, and there is evidence from molecular gut content analysis that several of those species are key aphid predators (Nyffeler & Benz, 1988; Roubinet et al., 2018). We hypothesized that drought increases niche overlap between *R. padi* and ground-dwelling predators (because the aphids are expected to reside close to the soil surface) and that this leads to stronger top-down regulation of the aphid. To test this hypothesis, we conducted a mesocosm experiment in the green house where we compared *R. padi* population density and distribution on different plant parts under simulated dry and humid conditions in the presence or absence of predators.

2 | MATERIALS AND METHODS

2.1 | Experimental design

A mesocosm experiment was designed to test the influence of drought on top-down regulation of *R. padi* on barley by ground-dwelling carabid beetles and wolf spiders. It was conducted in a greenhouse at SLU, Uppsala, Sweden, in June and July 2019, under ambient light conditions and temperatures between 19°C–28°C. The experiment had a fully factorial design with two factors: dry/wet conditions and with/without predators. Each combination of the two factors was replicated five times. Barley seeds (cultivar Kara) were sown in twenty plastic crates measuring 60 cm × 40 cm × 20 cm with potting soil (S-jord; Hasselfors, Garden Ltd., Örebro, Sweden) to a depth of 15 cm. Thirty seeds were sown per row in four rows with inter-row spacing of 10 cm in each crate. A cage with a mesh size of 0.5 mm × 0.5 mm and resealable on one side to allow aphid counting was fixed on top of each crate.

Eighty *R. padi* were introduced into each cage on the 8th day after sowing on eight Petri dishes placed on the soil surface. At this point in time barley plants were approximately 10 cm high and in Zadoks growth stage 10–12. Two individuals each of the carabid beetles, *Pterostichus melanarius* (Illiger) and *Harpalus rufipes* (De Geer), and representatives from one wolf spider genus, *Pardosa* spp., were added to each cage assigned to the predator treatments on the second day after *R. padi* introductions. Molecular gut content analyses have shown that all three predators regularly feed on *R. padi*, and they are among the most common ground-dwelling predators in Swedish cereal fields (Roubinet et al., 2018). The predators had been collected from oat and barley fields nearby using pitfall traps. To simulate drought, ten crates were watered until germination of the barley plants, after which no further water was added. The drought treatment thus simulated a period without rain of about 21–28 days until aphids were counted (see details below). At the end of the experiment, the plants showed signs of wilting. To simulate wet conditions, crates were watered with 1,520 ml until germination and then every second day from germination until termination of the experiment with a further 762.5 ml each time.

2.2 | Data collection and analysis

Aphids were counted 14, 18 and 21 days after introduction of aphid predators. On each count, sixteen barley seedlings per cage were uprooted carefully one at a time and placed on a tray. Aphids were counted below ground, 0–1 cm above ground on the stem, ≥1 cm above ground on the stem, and on the leaves. General linear mixed effects models were used to analyse effects of drought, presence of predators and the interaction between drought and predators on the total number of aphids on plants, and the proportion of aphids on different plant parts. Blocks nested within sampling day were included as random factors. Aphid numbers were log transformed and proportions on different plant parts arc-sine square root transformed prior to analyses to improve model residuals. Analyses were performed with the lme function in the nlme package in R 3.4.

3 | RESULTS

The effect of drought on aphid numbers depended on predator presence ($t = -2.887$, $p = .006$; Figure 1). Without predators, drought increased the number of aphids, but not when predators were present (i.e. predators reduced aphids only in dry conditions). The effect of drought on the proportion of aphids found below ground was also dependent on predator presence ($t = -4.327$, $p = .0001$; Figure 2a). Drought increased proportion of aphids below ground, when no predators were present, but strongly reduced it when predators were present. Drought had no effect on proportion of aphids 0–1 cm above ground ($t = -1.22285$, $p = .206$), but predators significantly reduced proportion of aphids present there ($t = -2.560$, $p = .0141$; Figure 2b). There were no effects of drought ($t = -0.983$, $p = .331$) and predator presence ($t = -1.05$, $p = .301$) on the proportion of aphids on barley stems ≥1 cm above ground (Figure 2c). On barley leaves, effects of drought depended on predator presence, with

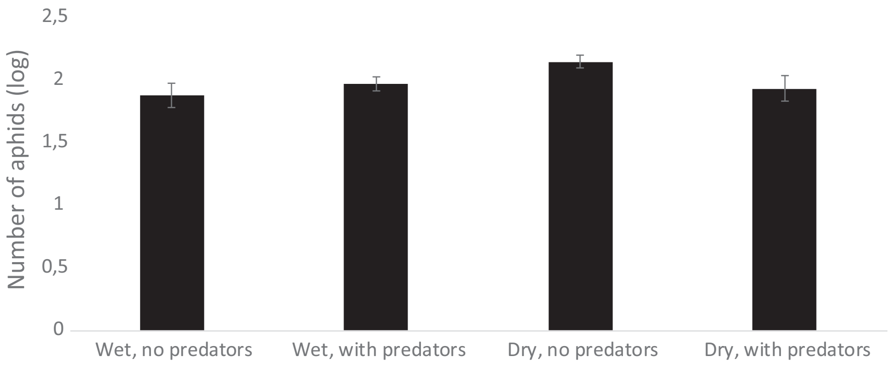

FIGURE 1 Average number (±*SE*) per day of *R. padi* in the different mesocosm treatments. The effect of drought depended on predator presence ($t = -2.887$, $p = .006$), with aphid numbers increasing during dry conditions when predators were absent but not when they were present

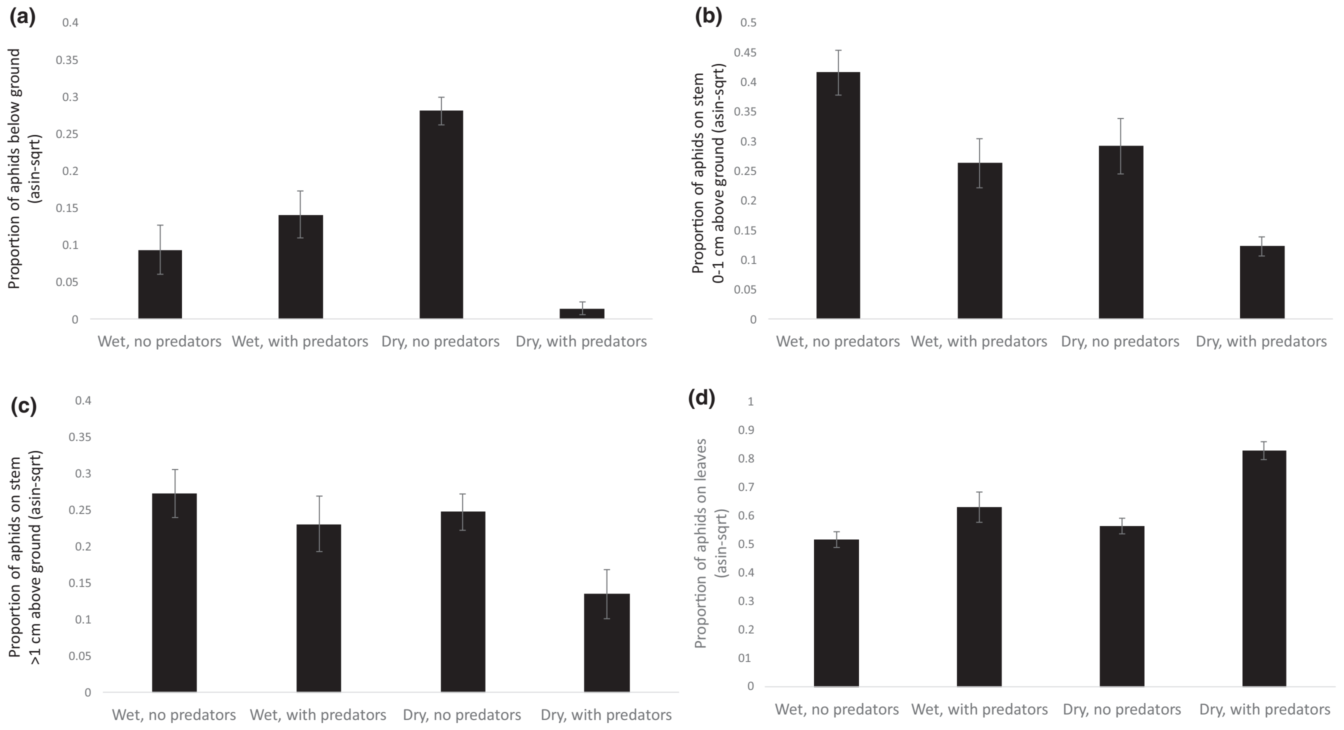

FIGURE 2 Average proportion (±*SE*) per day of *R. padi* residing (a) below ground, (b) 0–1 cm above ground on stem, (c) >1 cm above ground on stem, and (d) on the leaves in the different mesocosm treatments. Drought increased proportion of aphids below ground (a), when no predators were present, but reduced it when predators were present ($t = -4.327$, $p = .0001$). Predators reduced proportion of aphids 0–1 cm above ground (b) ($t = -2.560$, $p = .0141$). There was no difference between treatments in the proportion of aphids on barley stems ≥1 cm above ground (c). On barley leaves (d), effects of drought depended on predator presence, with increased proportion of aphids in dry conditions when predators were present ($t = 2.459$, and $p = .018$)

increased proportion of aphids observed in dry conditions when predators were present ($t = 2.459$, and $p = .018$; Figure 2d).

4 | DISCUSSION

We found partial support for our hypothesis that drought increases top-down regulation of *R. padi* by ground-dwelling predators. It was supported by the fact that during dry conditions (a) aphids moved down below ground, (b) predators reduced aphid numbers, and (c) predators reduced the proportion of aphids found below ground. This increased predation effect during dry conditions was, however, compensated for by a corresponding increase in aphid numbers on plants during dry conditions (evident in treatments without predators). Thus, the net effect of drought on aphid numbers was neutral.

A higher proportion of aphids on below ground plant parts was found in the drought treatment. This supports the field observation that aphids tend to reside close to or below the ground surface during dry conditions. It has been shown that drought can increase the movement of *R. padi* (Bailey et al., 1995). The ultimate reason why aphids move downwards is, however, unknown. It could be to search for more sheltered conditions, because water-stressed barley seedlings are more nutritious or have higher turgor pressure on their lower parts (Wade et al., 2017).

Predators significantly reduced aphid numbers during dry conditions, and the proportion of aphids present below ground declined. This effect seemed to have been driven by higher predation rates below ground. This could either be because predators were looking for shelter against drought, or they were actively searching for aphids that had moved below ground (Luff, 1980). There was a significant impact of predators 0–1 cm above ground (unrelated to drought) and no effect of predators on aphids located higher on plant stems and leaves. Thus, we found support for our hypothesis that drought increases predation rates but only below ground.

Increased predation rates in dry conditions did not result in decreased aphid numbers. This was probably because aphids increased their fecundity during drought (aphids increased in the drought treatment without predators). It has been found that fecundity of *R. padi* can increase during reduced humidity, possibly due to increased transpiration rates of the plants (Leather, 1985). Other work has found that effects of water stress on phloem feeders depend on the strength of the drought event. If the plant is strongly water stressed, aphid performance may decline, but if water stress is moderate, it may increase (Huberty & Denno, 2004). In some cases, however, aphids may decline also during moderate water stress (Mcvean & Dixon, 2001). It is possible that the drought simulated in our experiment only caused moderate water stress in the barley seedlings.

To conclude, we found that drought induced behavioural changes in aphids increasing their niche overlap with ground-dwelling predators on barley seedlings, but the increased top-down effect that resulted was compensated for by increased aphid performance on the water-stressed plants. This experiment illustrated how complex effects of drought on pests can be since it depends on the characteristics of the pest and host plant, intensity of water stress, and on interactions between pests and natural enemies. This complexity needs to be considered to make realistic predictions of how increased frequency of drought will affect pest dynamics in the future.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

MJ conceived research, MM conducted experiments, and MJ and MM analysed data and conducted statistical analyses. MM and MJ wrote the manuscript, with contributions from PM and JN. MJ and JN secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.qz612jmd9 (Njue et al. 2021)

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