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Effects of experimental warming on competition between *Rhopalosiphum padi* and *Sitobion avenae* mediated by plant water content

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Abstract

Global warming is affecting the severity of yield losses due to increased pest abundances. However, few studies have investigated how warming may affect interspecific competitions in multi-pest systems. Here, we investigated the effects of a 2 °C temperature increase on the population growth and distribution on plants of the aphids *Rhopalosiphum padi* and *Sitobion avenae* in single versus mixed species releases. We also investigated how the distribution of aphids across plant parts (lower leaves, upper leaves and stems) could be explained by plant tissue content in soluble sugars, free amino acids and flavonoids and by plant tissue microenvironment (leaf temperature and water potential). Populations of *R. padi* were higher under increased temperature, which caused increased competition on *S. avenae*. This in turn decreased *S. avenae*'s niche breadth under increased temperature. Contents in soluble sugar, free amino acids and flavonoids were higher in lower and upper leaves compared to stems, but were not affected by temperature. The number of aphids in different plant parts was strongly and negatively correlated with plant tissue water potential, an indicator of reduced content in flavonoids and soluble sugars. Our study shows that even relatively small increases in temperature reflecting climate change may disturb species interactions notably through plant-mediated effects, but consequences for crop productivity are difficult to predict.

Keywords Wheat aphid · Niche competition · Global warming · Water potential · Climate change · Pest management

Introduction

Global temperatures have increased at a rate between 0.15 and 0.20 °C per decade since 1975 and are expected to rise to 1.5–4.5 °C by the end of the century (IPCC 2023), having major implications for all forms of life. Increased temperatures may increase the abundance of pests such as wheat aphids, with negative consequences on agricultural productivity (Han et al. 2019; Wang et al. 2021). Wheat is the third largest grain crop in China, and its production is threatened by global climate change (Xiao et al. 2012; Sun et al. 2022). The aphids *Sitobion avenae* (Fabricius, 1794) and *Rhopalosiphum padi* (Linnaeus, 1758) (Hemiptera: Aphididae) are major wheat pests worldwide and in China, causing in average 10–30% of wheat yield loss and up to 50–60% in severe cases (Zhang et al. 2022).

Field-simulated temperature increases of 2 °C in multiple regions across different latitudes have significantly increased wheat biomass and grain weight (Liu et al. 2020a). However, warming can also increase aphid field abundance and population growth, with negative consequences on wheat yield (Han et al. 2019). Increased temperature may increase plant defences and resistance against herbivore attacks (Dury et al. 1998), but can also decrease plant defences. For instance, Wang et al. (2021) found that increased temperature reduced wheat resistance by reducing the induction of the salicylic and jasmonic acids pathways, which promoted wheat aphid feeding and population growth. Abiotic stress such as increased temperatures and water stress can cause changes in plant content of other metabolites, such as carbohydrates (sugar), nitrogen, water and more generally nutrients such as free amino acids (Aranjuelo et al. 2011; Showler 2013; Fornasiero et al. 2022). These changes affect the nutritional quality of the plant, with direct impacts on the fitness of herbivorous insects (Ryalls et al. 2017; Di et al. 2021). Plants cope with changes in water content caused by temperature changes via osmoregulation to maintain tissue water potential, which may vary greatly among different plant parts (Kutschera and Niklas 2013; Ozturk et al. 2021). Aphids can rapidly respond to these changes through their short generation time and may also prefer specific plant parts (Douglas 2003).

The wheat aphids *S. avenae* and *R. padi* are very often present together on the same wheat plants and have a strong ecological niche similarity, in the sense that they have a very similar biology, use the same plant material and have an optimal development and reproduction under the same temperature window (Wang et al. 2019; Han et al. 2019; Wang et al. 2021). However, they have slightly different habitat / resource preferences, where *R. padi* prefers lower plant parts, while *S. avenae* prefers upper plant parts (Yin et al. 2021). Increased temperatures may affect aphids' behaviour and choice of plant parts, especially if it is related to microenvironmental conditions, and affect the niche competition between aphid species. This could have implications for pest management and is worth exploring. In this study, we investigated how a simulated realistic temperature increase of 2 °C from 19 to 21 °C affected the choice of wheat plant parts by *S. avenae* and *R. padi* as well as their population dynamics. 19 °C was chosen as the control temperature; this is the optimal temperature for wheat aphid development and the mean field temperature during aphid population growth (March to June); in addition, 21 °C was chosen as the elevated temperature treatment, since it is important to measure the effects of gradual climate warming and a + 2 °C warming simulates the expected mean temperature increases by the end of the century (Park et al. 2017; Han et al. 2019; Wang et al. 2021; Sun et al. 2022; IPCC 2023). We also measured the water potential and surface temperature of the different plant parts to tease apart the potential drivers of niche selection and competition between aphids.

Methods

Aphid colonies and experimental wheat

Aphids *S. avenae* and *R. padi* were collected in Langfang, Hebei, China (39°30'N, 116°36'E). They were reared on wheat *Triticum aestivum* L. (variety Hengguan 35) in separate cages at room temperature and a 16:8h light/dark photoperiod, for more than 20 generations. Wheat seeds were placed at cold temperature to lift dormancy, then soaked for 10 min in 0.4% sodium hypochlorite solution, washed with sterile water until odourless, then put into clean petri dishes with filter paper and stored in the dark at 4 °C for 45 days. During the time, we washed the seeds at least three times with sterile water every five days. Then, vernalised seeds were planted in plastic pots (10 cm diameter, 11 cm high) with soil (nutrient soil: vermiculite = 2:1) placed at 19 °C (control temperature) or 21 °C (increased temperature) artificial climatic chambers (60 ± 10% RH; 16:8 light/dark; Ningbo Saifu Experimental Instruments Co., Ltd., Ningbo, China).

Preference of the two aphid species for different parts of wheat plants under increased temperature

We tested the preference of each aphid species for upper leaves, lower leaves or stems of wheat plants, based on the method by Jakobs and Müller (2019). One section of each plant part (of length 10 mm) was cut off and stuck in 1% agar in a 90-mm Petri dish at 5 cm from each other. The Petri dish was then placed in a 150-mm Petri dish filled with water to prevent aphids escaping. Thirty apterous newly emerged adult aphids were then released at the centre of the small Petri dish after having been starved for one hour. Three types of release were established: (1) 30 *S. avenae*; (2) 30 *R. padi*; (3) 15 *S. avenae* and 15 *R. padi* (mixed release). Finally, a white filter paper (60 cm × 60 cm) was rolled around the large Petri dishes to ensure uniform environment light for aphids selecting. The replicates were placed at either 19 °C (control) or 21 °C (increased temperature) for 1 h, after which the position of each aphid was recorded. Three replicates were produced for each release type and each temperature treatment.

Population growth and distribution across plant parts of the two aphid species

Wheat pots were prepared from ten seeds and placed in artificial climate chambers at 19 or 21 °C. Six apterous newly emerged adult aphids were released in each pot when leaves reached a height of 20 cm (wheat growth stage three unfold leaves, 20 days after sowing), with three aphid treatments: (1) 6 *S. avenae*, (2) 6 *R. padi* and (3) 3 *S. avenae* + 3 *R. padi*. Eight pots for each aphid treatments and each temperature treatment were prepared; all had a similar amount of plant biomass. The number of aphids of each species on each plant part (lower leaves, upper leaves or stems) was recorded seven days later and then every three days for a total of five times (total duration 20 days).

Niche breadth and niche overlap index of the two aphid species

The niche breadth B_n and the niche overlap LO between the two aphid species *R. padi* and *S. avenae* were calculated from the population growth data 10 days (early population growth) and 16 days (i.e. when populations started to reach relatively high densities but did not overcrowd the plants) after aphid release for each replicate to assess how population growth (increased population densities) affected species competition, using the formulas by Levins (1968):

$$B_n = \frac{1}{R} \cdot \frac{1}{\sum_i p_i^2}, LO = \frac{\sum_i p_i \cdot p_j}{\sum_i p_i^2},$$

where R is the number of differing environments (here, the three plant parts considered) and p_i and p_j are the proportions of the target species i and of the competitor species j , respectively.

Responses of soluble sugar, free amino acid and total flavonoids contents in different wheat plant parts to increased temperature

Wheat aphid and temperature treatments were the same as the population trials above (Sect. "Population growth and distribution across plant parts of the two aphid species"), but no aphids were released on this set of plants. The upper leaves, stems and lower leaves were cut off after wheat aphid exposure for 16 days (before aphid populations reached saturation in the population growth experiment; see Sect. "Population growth and distribution across plant parts of the two aphid species" and associated results) and were quickly frozen in liquid nitrogen for the test. The

content in soluble sugars, free amino acids and total flavonoids was determined. Soluble sugars and free amino acids are main food sources for aphids, and changes in their content in plant tissues (e.g. as a response to abiotic stress) directly affect aphid development and population growth (Ciepiela et al. 1989; Eleftherianos et al. 2006; Shah & Paulsen 2003). Total flavonoids are plant secondary metabolites conferring resistance to herbivorous attacks, and their content also responds to temperature changes (Lattanzio et al. 2000; Shamloo et al. 2017). The anthrone–sulfuric acid method was used for soluble sugars content (Cao et al. 2018): wheat samples (0.2 g) were grounded, homogenised and transferred into 15-mL centrifuge tubes. Then they were placed into a 87 °C water bath for 10 min. After a centrifugation at 4000 r/ min for 10 min at room temperature, 200 µl of supernatant was collected in 1.5-mL centrifuge tubes, mixed with 800 µl of anthrone reagent and placed in a boiling water bath for 10 min and then cooled to room temperature. Finally, the absorbance value at 620 nm was measured with a full wavelength scanning multifunctional reader (Molecular Devices, Flex Station 3). The kit (G0415W, Suzhou Grace Biotechnology Co. Ltd, Suzhou, China) was used to measure the content of free amino acids (Li et al. 2023): 0.1 g wheat sample was homogenised with ethanol (60%, v/v) at room temperature, centrifuged at 12,000 rpm, 4 °C for 10 min. Then the supernatant was removed, and the reaction mix (1.5 ml anhydrous ethanol, 13.5 ml sodium acetate and 30 mg ninhydrin reagent) and ascorbic acid solution were added. The tubes were placed in boiling water for 15 min, and 320 µl ethanol (95%) was added. After the reaction, the absorbance of the reaction solution was measured at 570 nm. The kit (G0118W, Suzhou Grace Biotechnology Co., Ltd., Suzhou, China) was used to measure the content of total flavonoids (Li et al. 2023): 0.1 g of wheat sample was ground and then shaken at 60 °C for 2 h (Hangzhou Mio Instruments Co., Ltd., China); after that, it was centrifuged at 12,000 rpm for 10 min. Then, the supernatant was removed, and 15 µl sodium nitrite, 30 µl nitric acid and 105 µl sodium hydroxide reagents were added. The absorbance was measured at 510 nm after 15 min of reaction.

Microenvironmental changes in wheat in response to increased temperature

Wheat was treated with the same method as in the population trial above. Ten wheat replicates were prepared for each temperature and each aphid treatment. Three samples (upper leaf, lower leaf and stem) were collected from each pot. The surface temperature of each sample was measured with a handheld temperature and humidity measuring device (TY-YSC, Handan Tengyu Electronic Technology Co., Handan, China). From each sample, a circular section (diameter 7 mm, thickness 2.5 mm) was cut and placed in its respective sample chamber (19 or 21 °C) for 20 min for equilibration. The water potential was then measured with a PSYPRO (Wescor, USA) device.

Data analysis

All statistical analyses were performed using R Core Team (2023) version 4.3.1. For all models, the statistical significance of fixed effects was determined through a stepwise regressive type-II model comparison with an ANOVA and a Chi-square test for generalised linear models (GLMs) or a Fisher test for linear models (LMs). When fixed effects were found to have a significant effect, pairwise mean comparisons between treatments were performed on the best model using the ‘emmeans’ R function (library ‘emmeans’; Lenth 2023). The absence of residual heteroscedasticity and overdispersion was verified in the best model using the functions ‘simulateResiduals()’ (R library ‘DHARMA’; Hartig 2022). The effect of increased temperature and interspecific competition on the preference of *R. padi* and *S. avenae* for different wheat plant parts was assessed using a LM on the number of aphids in each position (lower leaf, upper leaf, stem or no choice) with the position, the release type (single versus mixed species, simulating interspecific competition), the temperature treatment (19 or 21 °C) and the aphid species as fixed effects, as well as all second and third-order interactions between these factors. The effects of increased temperature and interspecific competition on population growth were analysed on the numbers of aphids in each position (lower leaves, upper leaves or stems) after 20 days using a GLM with a negative binomial distribution to account for data overdispersion (R function ‘glm.nb’, R library ‘MASS’; Venables and Ripley 2022). The fixed effects were the same as for the preference test above. The effects of temperature and

release type on the niche breadth and niche overlap were analysed using separate LMs for niche breadth and niche overlap and for each time (10 and 16 days after aphid release), using the temperature treatment, the release type and the aphid species as fixed effects as well as all second and third-order interactions. Finally, the effects of increased temperature on soluble sugar content, free amino acids content, total flavonoids content, water potential and surface temperature in different plant parts were analysed using separate LMs, with the temperature in interaction with the plant part (lower leaf, upper leaf or stem) as fixed effects.

We then performed a linear regression analysis to assess whether the changes in population growth of aphids under increased temperature and their distribution across plant parts could be explained by plant content and microenvironment. For this, we performed a linear regression on the mean values of aphid numbers per plant part 16 days after release for each release type and each aphid species, with the mean values of the five variables: soluble sugar, free amino acids and flavonoids content and surface temperature and water potential. We performed one linear regression for each of the five variables, where it was implemented as a fixed effect in interaction with the species in interaction with the release type, and we recorded the multiple R^2 value of the regression.

Results

Preference of the two aphid species for different wheat plant parts

The proportion of aphids in each plant part (lower leaf, upper leaf, stem or which did not make a choice) was affected by the temperature in interaction with the release type only ($F_{3,79} = 3.22$, $P = 0.027$; Fig. 1), but was not different across species, and the species effect did not change depending on the temperature or the release type (all $P > 0.15$). This was due to a lower proportion of aphids choosing stems under interspecific competition (mixed release) compared to single species release and to a higher proportion of aphids choosing the upper leaf at control temperature and in single species release, relative to mixed release and to higher temperature (Fig. 1).

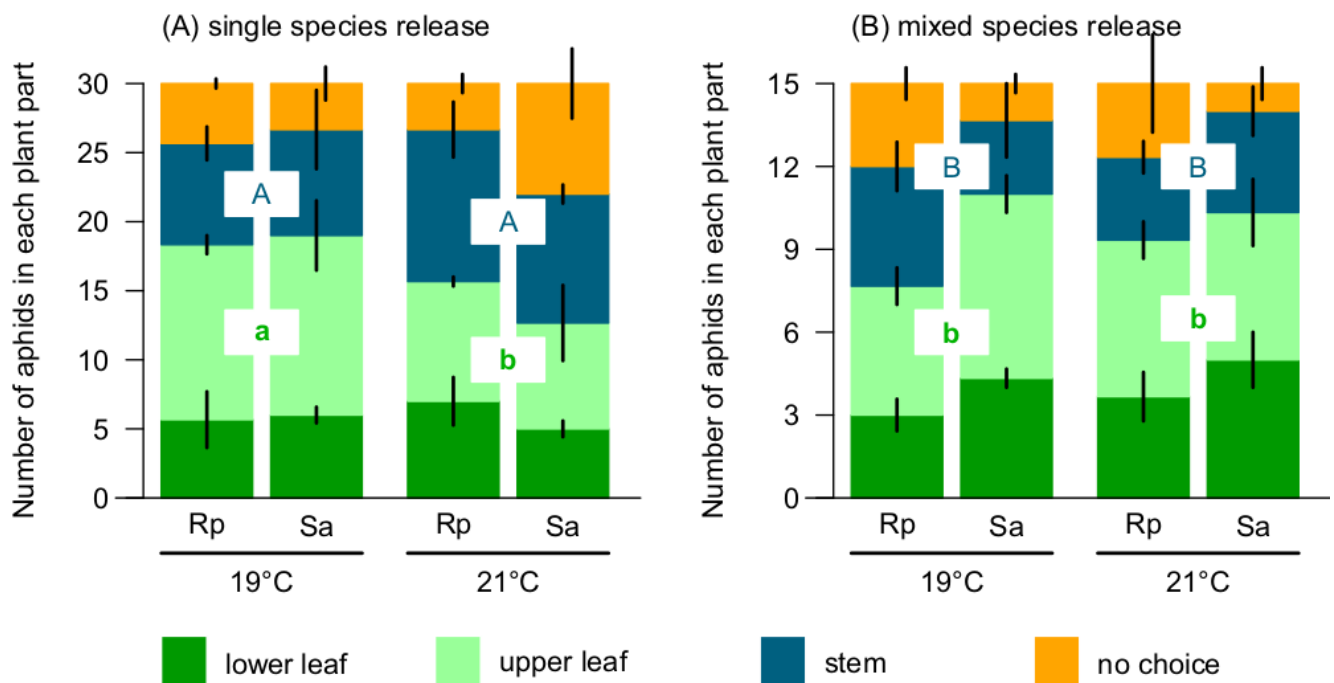


Fig. 1 Effects of increased temperature and interspecific competition on the preference of *S. avenae* and *R. padi* for three different wheat plant parts: mean number \pm SE of aphids on the lower leaf, upper leaf, stem or which did not make a choice, in **a** single species release ($N = 30$ *R. padi* or 30 *S. avenae*) or **b** mixed species release ($N = 15$ *R. padi* + 15 *S. avenae*). $N = 3$ replicates (Petri dishes with three plant parts) per treatment. Different letters show significant differences in numbers on the stem (blue) or the upper leaf (green). Rp *R. padi*; Sa *S. avenae*

Aphid population growth

Overall, populations of *R. padi* grew much faster and to higher densities than those of *S. avenae* (Figs. S1,2). Total numbers of *R. padi* per replicate after 20 days were significantly affected by the temperature in interaction with the release type in interaction with the species (LR = 4.21, df = 1, $P = 0.040$; Fig. 2). Total numbers of *S. avenae* aphids were lower than those of *R. padi* and were reduced in mixed release and under increased temperature. While *R. padi* numbers showed the same trend (lower under mixed release and increased temperature), the effects of the temperature and release treatments on *R. padi* were not significant.

Highest numbers were counted on upper leaves, followed by lower leaves, for both species. Increased temperature in interaction with the species and the release type significantly affected the population growth and distribution of aphids (LR = 18.2, df = 2, $P < 0.001$; Fig. 2). This was due to changes in *S. avenae*, since neither total numbers nor the distribution of *R. padi* was affected by increased temperature or by interspecific competition (release type). Conversely, total numbers of *S. avenae* were lower by 70% in mixed species releases and by 30% under increased temperature, but the relative distribution across plant parts was not different (mean number \pm SE: single release 188 ± 32 , mixed release 56 ± 13 ; control temperature 144 ± 30 , increased temperature 100 ± 24).

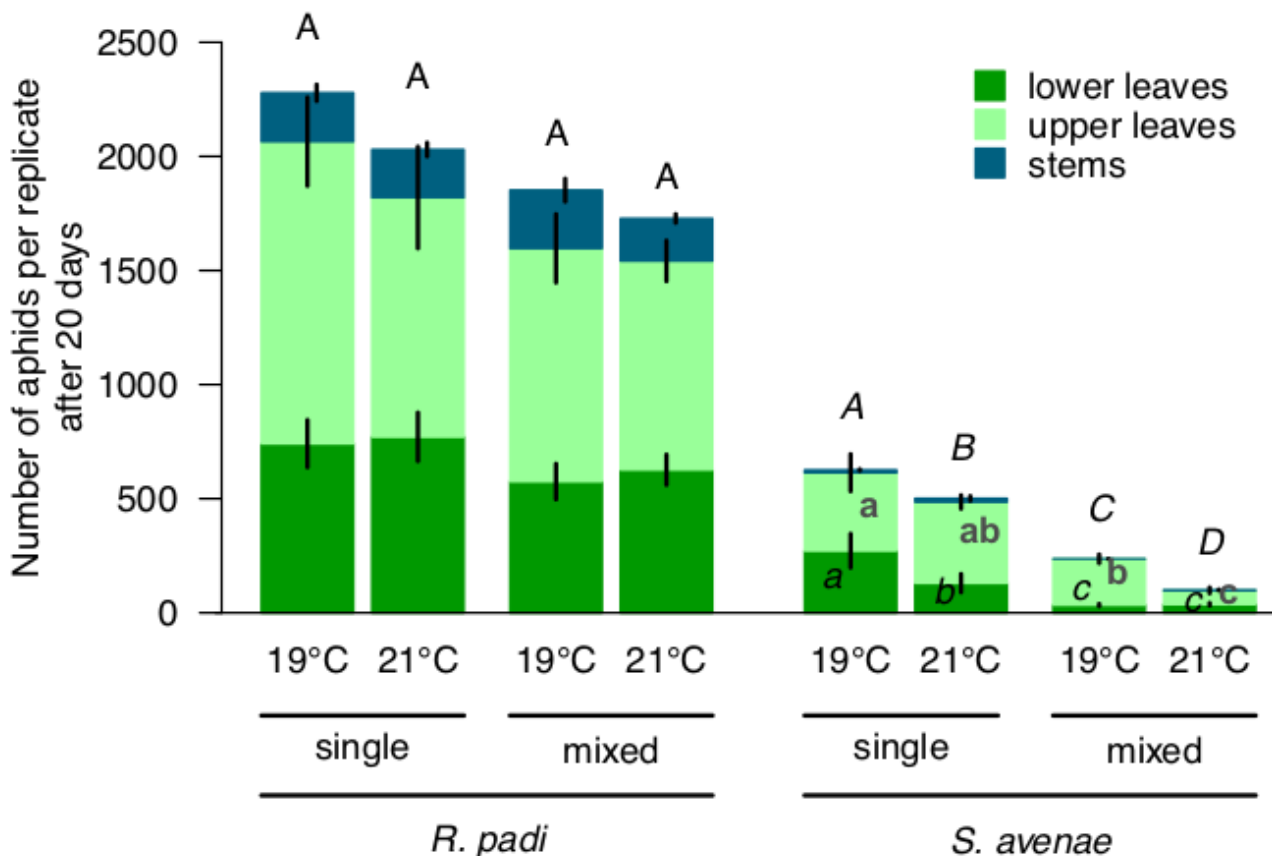


Fig. 2 Population growth (mean number \pm SE) of the two aphid species, *R. padi* and *S. avenae*, after 20 days under control (19 °C) or increased (21 °C) temperatures and in single or mixed species releases. N = 5 replicates (wheat plant pots) per treatment. *Black* and *grey* lowercase letters show significant differences between *S. avenae* numbers in lower and upper leaves, respectively, while uppercase letters show significant differences between total numbers of aphids per plant across treatments

Niche width and niche overlap of the two aphid species

Overall, aphids' niche breadth was comparable between *R. padi* and *S. avenae*, and increased through time, but more importantly in *R. padi* (Fig. 3a, c). Ten days after aphid release, aphids' niche breadth was significantly affected by both the temperature and the release type, each in interaction with the aphid species (temperature/species $F_{1,34} = 14.3$, $P < 0.001$; species/release $F_{1,34} = 6.43$, $P = 0.016$; Fig. 3a). Interspecific competition decreased *R. padi*'s niche breadth, but only at

control temperature, while it increased *S. avenae*'s niche breadth at both control and increased temperatures. Sixteen days after release, aphids' niche breadth was significantly affected by the release type in interaction with the species ($F_{1,36} = 22.7$, $P < 0.001$; Fig. 3c), but not by temperature alone or in interaction with other factors (all $P > 0.25$). Niche breadth was larger in *R. padi* compared to *S. avenae*, and interspecific competition slightly increased *R. padi*'s niche breadth but strongly decreased *S. avenae*'s niche breadth (Fig. 3c).

Similar to niche breadth, niche overlap massively increased through time, up to exceeding 1 in *R. padi* (Fig. 3b, d). Ten days after release, niche overlap was significantly higher in *S. avenae* than in *R. padi* ($F_{1,38} = 5.069$, $P = 0.022$; Fig. 3b), but was not affected by temperature nor by release type and neither by interactions (all $P > 0.3$). Sixteen days after release, niche overlap was significantly affected by the release type in interaction with the species ($F_{1,36} = 13.8$, $P < 0.001$; Fig. 3d), but not by temperature alone or in interaction with the other factors (all $P > 1$). Niche overlap was higher in *R. padi* than in *S. avenae* and was lower in mixed release compared to single species release in *S. avenae* (Fig. 3d).

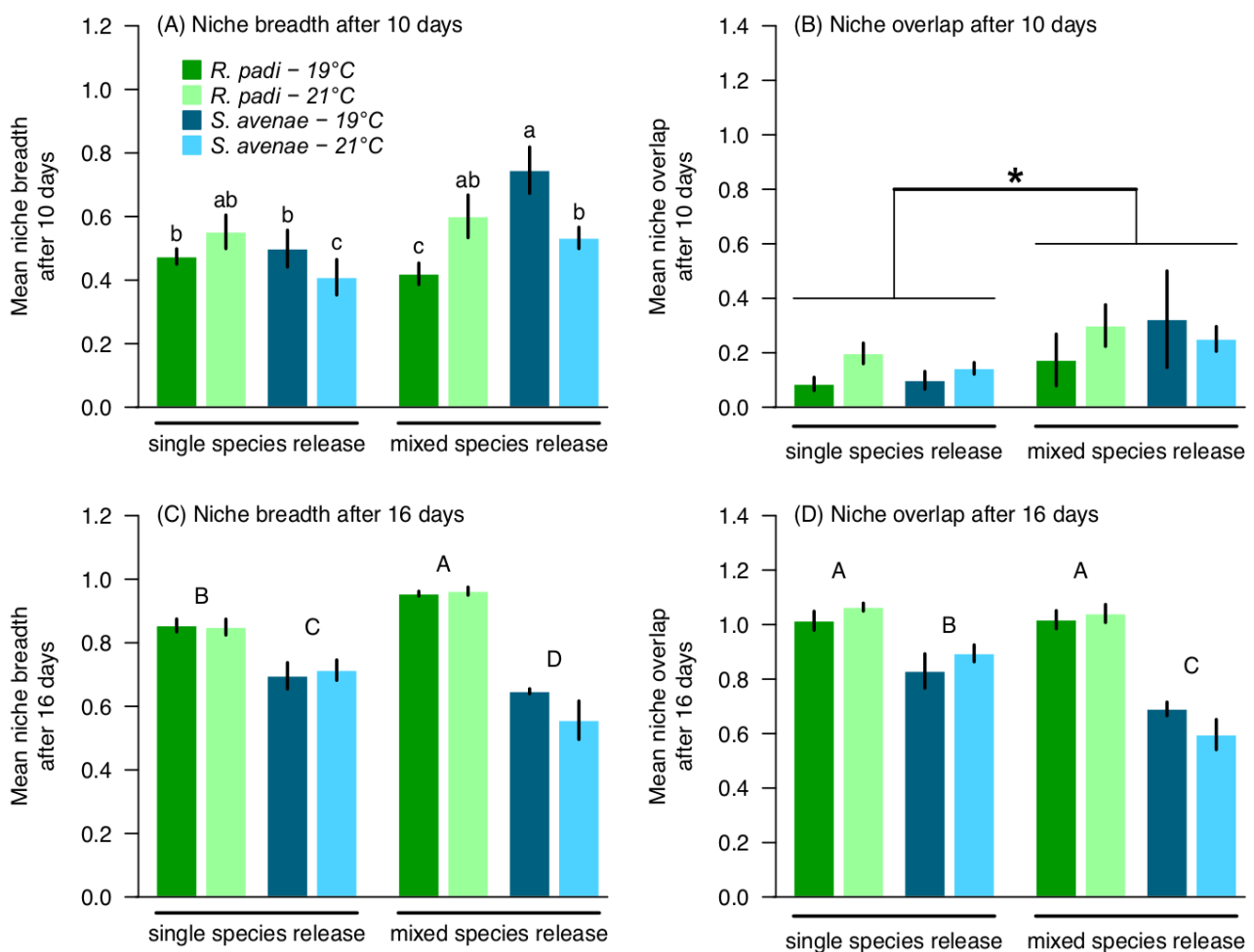


Fig. 3 Niche breadth (a, c) and niche overlap (b, d) of *R. padi* and *S. avenae* calculated across the three different plant parts (lower leaves, upper leaves and stems) 10 days (a, b) or 20 days (c, d) after single versus mixed species release under control (19 °C) or increased (21 °C) temperature. Different letters in a show significant differences between values. Different uppercase letters in c, d show significant differences between species and release types. * in panel b shows a significant difference between single and mixed species releases. N = 5 replicates (wheat plant pots) per treatment

Sugar, amino acids and flavonoids plant content

Sugar content was different across wheat plant parts, but was not affected by temperature nor by the interaction between temperature and plant parts (temperature/plant parts $F_{2,24} = 1.72$, $P = 0.20$, temperature $F_{1,26} = 2.04$, $P = 0.17$, and plant parts $F_{2,27} = 3.96$, $P = 0.031$; Fig. 4a). It was significantly

higher in lower leaves compared to upper leaves. Similarly, free amino acids content was different across plant parts but not affected by temperature (temperature/plant parts $F_{2,23} = 0.390$, $P = 0.68$, temperature $F_{1,25} = 0.855$, $P = 0.36$, and plant parts $F_{2,25} = 3.76$, $P = 0.037$; Fig. 4b). It was also significantly higher in lower leaves compared to upper leaves. Finally, total flavonoids content showed the same trend (temperature/plant parts $F_{2,24} = 1.59$, $P = 0.22$, temperature $F_{1,26} = 1.43$, $P = 0.17$, and plant parts $F_{2,27} = 19.5$, $P < 0.001$; Fig. 4c). It was significantly higher in lower leaves compared to upper leaves and to stems.

Plant microenvironment

not true at 21 °C, and increased temperature significantly increased the water potential of lower leaves (Fig. 5a). Conversely, surface temperature was significantly affected by increased temperature ($F_{1,16} = 360$, $P < 0.001$), but not by the plant parts ($F_{2,14} = 3.62$, $P = 0.054$) and neither by the interaction between temperature and plant parts ($F_{2,12} = 0.550$, $P = 0.59$; Fig. 5b). The surface temperature was increased by 7% at 21 °C compared to 19 °C (mean \pm SE: at 19 °C 21.4 ± 0.06 °C, at 21 °C 22.9 ± 0.05 °C).

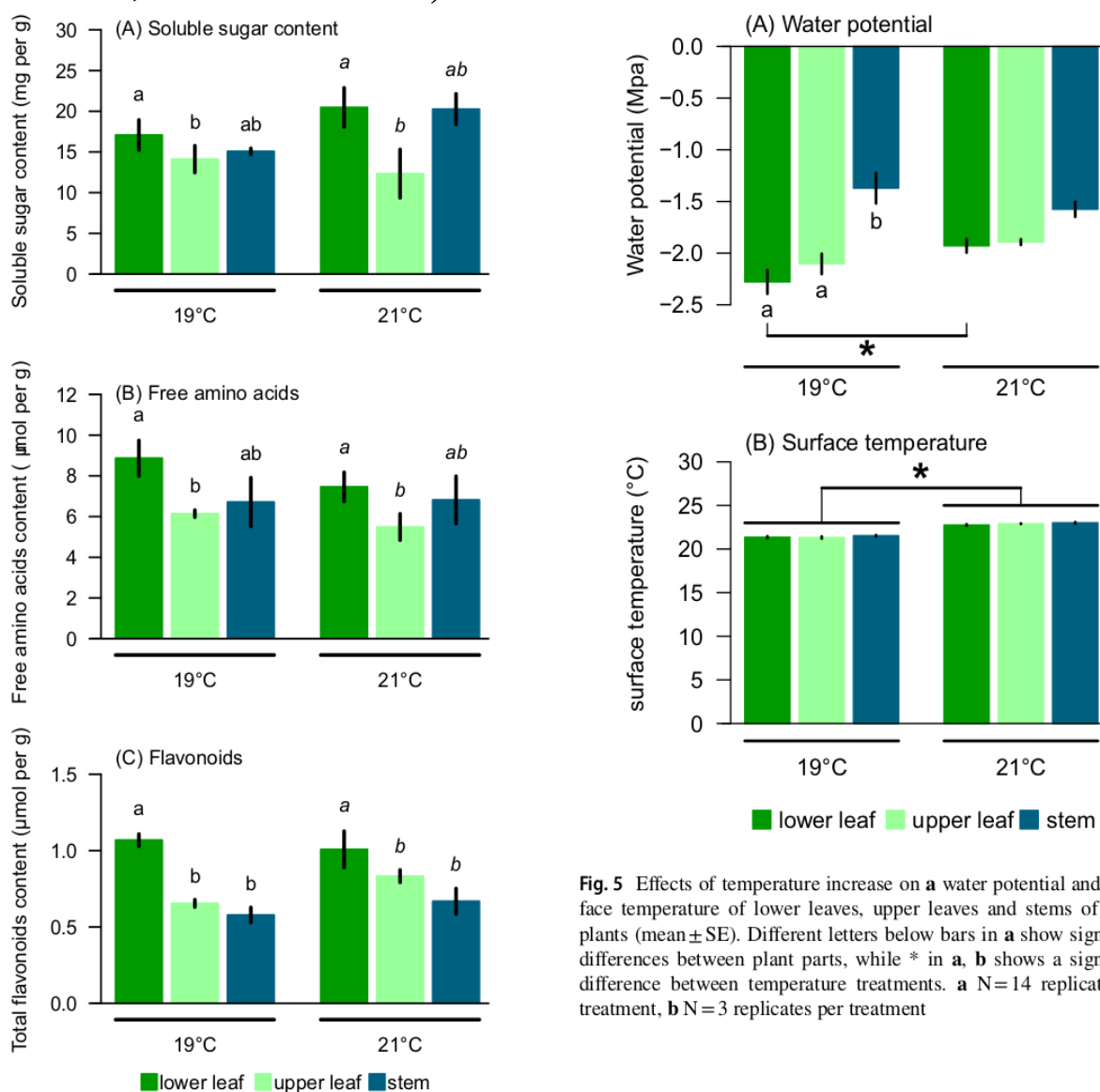


Fig. 4 Effects of temperature increase in soluble sugar (a), free amino acids (b) and flavonoids (c) content in lower leaves, upper leaves and stems of wheat plants. Different letters above bars show significant differences between different plant parts for each temperature treatment. N=10 replicates per treatment

Fig. 5 Effects of temperature increase on a water potential and b surface temperature of lower leaves, upper leaves and stems of wheat plants (mean \pm SE). Different letters below bars in a show significant differences between plant parts, while * in a, b shows a significant difference between temperature treatments. a N=14 replicates per treatment, b N=3 replicates per treatment

Regression analysis between aphid numbers and plant variables

The regression of mean aphid numbers per plant part using mean water potential as explanatory variable in interaction with the aphid species and release type had the highest multiple R^2 value of 0.966 (Fig. 6), compared to regressions using total flavonoids content (multiple $R^2 = 0.853$), surface temperature (multiple $R^2 = 0.812$), free amino acids content (multiple $R^2 = 0.785$) and soluble sugar content (multiple $R^2 = 0.775$). The correlation between aphid number and water potential was strongest in single release in *S. avenae* ($R^2 = 0.923$) followed by *R. padi* ($R^2 = 0.872$) and was flatter and weaker in mixed release in *S. avenae* ($R^2 = 0.661$) followed by *R. padi* ($R^2 = 0.322$; Fig. 6).

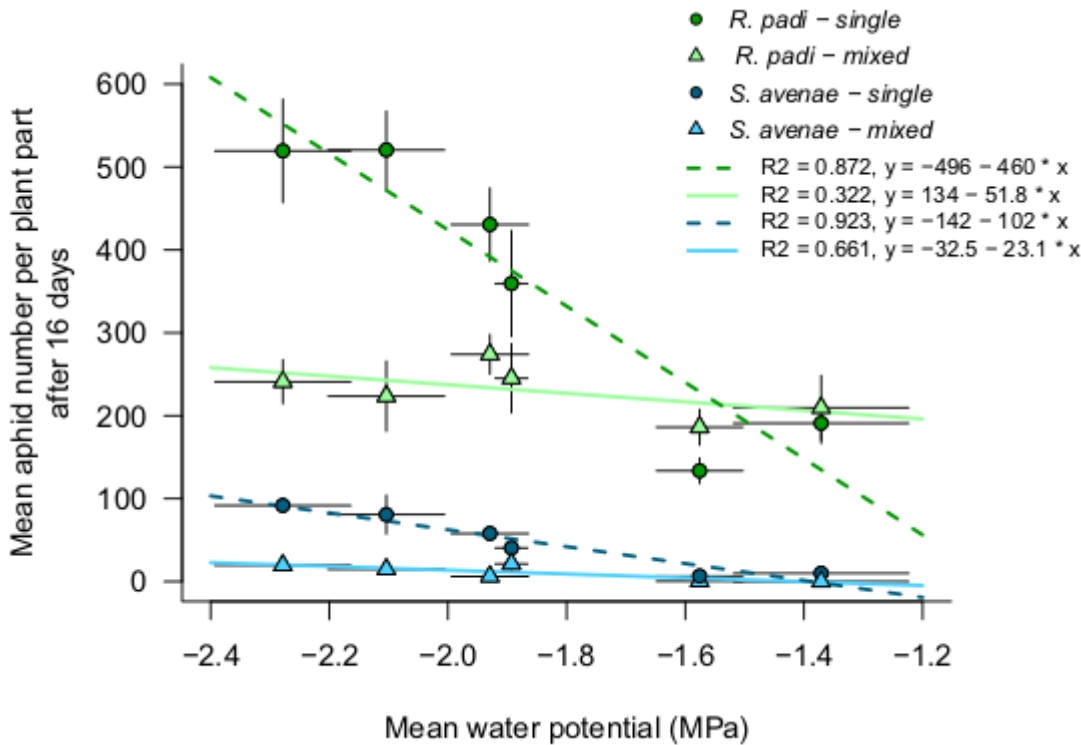


Fig. 6 Regression between mean aphid number per plant part after 16 days and mean water potential per plant part for *R. padi* and *S. avenae* and in single versus mixed species releases

Discussion

Insects, as ectotherms, are sensitive to temperature changes. In this study, we found that a temperature increase from 19 to 21 °C reduced the population growth of *S. avenae*, especially in situations of interspecific competition, and the same trend, although not significant, was observed in *R. padi*. This was confirmed by measures of niche breadth and overlap, showing that *R. padi* was the dominant competitor, able to occupy a larger niche, while *S. avenae* suffered more from interspecific competition. Finally, we found that the preference and niche occupancy (distribution of aphids across plant parts) were best predicted by plant tissue water potential, rather than surface temperature, or soluble sugar, flavonoids and free amino acids content.

We found that 19 °C was more suitable for the population growth of *S. avenae* than 21 °C. However, Acreman and Dixon (1989) found that a temperature increase from 10 to 25 °C increased the development rate of *S. avenae*, both on the ear and the flag leaf of wheat plants, and therefore, populations are expected to grow faster and to higher densities at 21 °C (Lykouressis 1985). Differences with our results may be explained by differences in the wheat variety or the *S. avenae* strain sensitivity used. Increases in *S. avenae* population growth and density under increased mean temperature have also been found in the field (Han et al. 2019; Wang et al. 2021).

Besides temperature, resource competition between insect species may also affect their population growth. Here, we found a strong negative effect of *R. padi* on *S. avenae*'s population growth and a

weak effect of *S. avenae* or *R. padi*'s population growth, similar to Gianoli (2000). We also found that *R. padi* was the dominant competitor, since it had the largest niche breadth and a capacity to expand its niche breadth in the presence of a competing species.

However, the intensity of interspecific competition can be influenced by environmental factors such as temperature (Comeault and Matute 2021). Here, we found that both *R. padi* and *S. avenae* maintained their niche breadth under increased temperatures. Wang et al. (2019) also found that *S. avenae* maintained its niche breadth, but *R. padi* expanded its niche breadth under a temperature increase from 25.7 to 26.3 °C, and in the presence of a third aphid species, *Schizaphis graminum*. The strength of interspecific competition in different environments may be modulated by the ecological niche of each species, where colder and warmer-adapted species will dominate at lower and warmer temperatures, respectively (Kwon 2017). The two temperatures used in our study were within the appropriate temperature range for both aphid species, which had a strong niche overlap under both temperatures. Overall, we found that the competition by *R. padi* on *S. avenae* was stronger at high temperature. We also observed that in mixed species release, increased temperature caused a tendency in *S. avenae* to reduce its niche breadth towards lower leaves and stems, while *R. padi* expanded it and largely occupied upper leaves. Similarly, increased temperature was found to cause *Aphis gossypii* to move downward and *Acyrtosiphon gossypii* to move upward, as a way to reduce interspecific competition (Asin and Pons 2001).

We found that the water potential was higher in stems than in lower or upper leaves under control temperature. The water potential is known to differ across plant parts and at different developmental stages, due to the mechanism of water uptake via a root–stem–leaf decreasing water potential gradient (Kutschera and Niklas 2013). We found a strong correlation between aphid distribution and water potential, where aphids preferred upper and lower leaves than stems. The slopes of the regressions of *R. padi* were significantly bigger than that of *S. avenae*, which indicates a strong response of *R. padi* to water potential. This is consistent

with the results by Yin et al. (2021), who found that *R. padi* was more sensitive to microclimate, while *S. avenae* was more sensitive to limited resources, and indeed, we found that *S. avenae* was the lower competitor in mixed species releases. How aphids select their host plant (or host plant part) may also be affected by ambient temperature and its effects on the host plant. For example, higher temperatures advance the phenology of wheat and thereby boost aphids population growth (Wang et al. 2021).

Aphids feed on plant phloem to obtain nutrients such as carbon and nitrogen necessary to their development and reproduction (Douglas 2003). Saccharide is the main energy source for insect growth and development, and soluble sugars and flavonoids are important metabolites conferring resistance against herbivorous insects in plants; nutrients and secondary metabolites therefore differ in different plant parts due to differential investment in defence (Dury et al. 1998; Liu et al. 2020b; Han et al. 2022). For example, young cabbage leaves contain more thioglucosides and amino acids than mature leaves (Cao et al. 2018), and leaves have higher levels of amino acids and lower concentrations of soluble sugars compared to wheat stems (Yin et al. 2021). In addition, higher temperatures may increase the plant content of secondary plant metabolites, which indirectly and negatively affect insect populations (Dury et al. 1998). Therefore, herbivorous insects may select their host or host plant part as a function of its chemical composition (Sun et al. 2015; Jakobs and Müller 2018; Liu et al. 2020b). In our study, the contents in soluble sugar and flavonoids were correlated (correlation coefficient 0.646), and the flavonoids content was also strongly and negatively correlated with water potential (-0.705). This means that the number of aphids was negatively correlated with flavonoids and soluble sugar content, which may be explained by an avoidance behaviour of aphids for plant tissues better protected against herbivore attacks.

We found that an average temperature increase of 2 °C increased population growth of *R. padi*, the dominant species, and this increased the resource competition over *S. avenae*. This is evidence that pest outbreaks may be bigger under climate change, exacerbating yield losses. Such effects are likely mediated by the intensity of the temperature increase, the host plant response to such

environmental change and heat tolerance capacity of insects, but also initial pest densities. Therefore, it would be important in future studies to investigate the effects of more varied temperature increases, both in intensity and in frequency, and to measure the resistance and recovery of plants and insects after a heatwave (Jeffs and Leather 2014; Wang and Ma 2022). In addition, more subtle changes deserve attention, including the effects of insects on hosts in terms of activation of defences and transmission of pathogens, and the responses of microbial communities in insects and their host plants to climatic changes (Lemoine et al. 2020; Sochard et al. 2021; Luo et al. 2022). Finally, it would be useful to replicate the experiments in more realistic field designs to confirm the results.

Author's contribution

XT conceived the study; WL, YC, JM, JC and YW collected the data; XT and CCJ analysed the data; WL, CCJ and XT wrote the paper; XT secured funding. All authors agreed for publication.

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Data availability Data are available upon reasonable request to corresponding author.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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