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# Adaptations to water gradient in three *Rorippa* plant species correspond with plant resistance against insect herbivory under drought and waterlogged conditions

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## Abstract

1. Plants live in environments where they are constantly, and often simultaneously, exposed to different types of biotic and abiotic stress, such as insect herbivory and water availability. How plants are adapted to abiotic conditions may determine how a surplus or shortage of water affects plant resistance to insect herbivory. Moreover, this effect may vary depending on the feeding mode of the herbivore.
2. We explored how three closely related *Rorippa* plant species that vary in adaptations to different water levels, resist herbivory by four different insects (aphids: *Myzus persicae*, *Lipaphis erysimi*, and caterpillars: *Pieris brassicae*, *Plutella xylostella*) under waterlogging or drought conditions. We hypothesized that plants that are differently adapted to water availability will be disparately affected by water availability in their resistance to insect herbivory.
3. On the semi-aquatic plant species *Rorippa amphibia*, both aphid species reached a larger colony size under drought conditions. This indicates that *R. amphibia* was compromised in resistance to aphid feeding when under drought conditions, to which it is less well adapted. Water conditions did not affect aphid performance on the floodplain species *Rorippa palustris*. On the terrestrial plant species *Rorippa sylvestris*, aphids performed worse on waterlogged than drought-treated plants. Neither caterpillar species was significantly affected by the water availability of their food plant.
4. Our findings suggest that water availability can have distinct effects on plant–insect interactions. We propose that plant adaptations to water conditions can be a major predictor towards explaining the variation of effects that water availability can have on plant–insect interactions.

**KEYWORDS**
biotic and abiotic stress, drought, herbivory, plant defence, plant–insect interactions, waterlogging

## INTRODUCTION

Plants live in environments where they are often exposed to several types of biotic and abiotic stress simultaneously. Two devastating stressors are sub-optimal water availability and insect herbivory (Boyer et al., 2013; Liliane & Charles, 2020; Raderschall et al., 2021; Tian et al., 2021). The spectrum of water availability may range from flooding, to waterlogging, to drought periods. The intensity of insect

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herbivory may vary among plant organs and the type of damage inflicted by the feeding mode of the herbivore, such as sap-feeding aphids and leaf-chewing caterpillars. To maximize its fitness, a plant must optimize its responses to deal with this range of stress conditions (Ben Rejeb et al., 2014; de Bobadilla et al., 2022). Depending on the plant's habitat, the availability of water may be highly variable. To increase their plasticity and resilience towards variabilities in water availability, plant species have evolved adaptations to navigate changes in water availability (Akman et al., 2012; Colmer & Voesenek, 2009). Plants can, for example, mitigate the drought by investing resources in deeper roots to reach new water sources (Kuster et al., 2013; Sponchiado et al., 1989; Uga et al., 2013) or they can endure drought by slowing down their metabolism and reducing water loss to a minimum (Tamang et al., 2021; Zhao et al., 2015). Adaptations to flooding may include enhancing gas transport to flooded organs (Akman et al., 2014; Laan et al., 1989; Sasidharan & Voesenek, 2015). Importantly, responses or adaptations to sub-optimal water conditions can have consequences for plant defence responses to insect herbivory (Lin, Liu, Hsu, et al., 2021; Lin, Liu, Ou, et al., 2021).

Several studies have shown that water availability can affect plant–insect interactions (Khan et al., 2011; Leybourne et al., 2021; Lin, Liu, Hsu, et al., 2021; Lin, Liu, Ou, et al., 2021; Mewis et al., 2012; Mody et al., 2009; Pineda et al., 2016; Pons et al., 2020). Responding to simultaneous sub-optimal water availability and insect herbivory can have different consequences for the plant and is captured by two contrasting hypotheses. The 'plant stress hypothesis' states that water stress has a positive effect on insect herbivores due to increased nutrient concentration (Mattson & Haack, 1987), whereas the 'plant vigour hypothesis' states that plant performance is enhanced under well-watered conditions and provides higher quality food for insect herbivores (Price, 1991). However, these hypotheses are not framed in the context of plant adaptations to sub-optimal water availability. A major knowledge gap is how plant adaptations to water availability in its habitat correspond with their resistance to insect attack under various water regimes.

Plant species widely differ in their adaptations to sub-optimal water availability. In some plant species, drought has been shown to lead to smaller but thicker leaves to reduce evaporation (Chaves et al., 2003). Because more sturdy thicker leaves enhance morphological resistance against leaf-chewing insect herbivory, this adaptation indirectly leads to better protection against certain insect herbivores (Grubb, 1986; Hanley et al., 2007). Under waterlogging conditions, some plants have evolved the ability to create aerenchymous tissue allowing better gas exchange to the roots (Akman et al., 2014; Laan et al., 1989; Sasidharan & Voesenek, 2015). The changes in cell-layer composition may affect how an aphid can navigate its stylets to reach the phloem. Moreover, plants regulate responses to abiotic and biotic stress through signalling cascades that involve the same phytohormones (Ullah et al., 2018). The hormone ethylene, for example, builds up in waterlogged roots and is a signal for the plant that it is waterlogged (Sasidharan & Voesenek, 2015; Voesenek & Sasidharan, 2013). Ethylene also plays a role in regulating defence responses to leaf-chewing herbivores (Winz & Baldwin, 2001). Similarly, jasmonic acid and salicylic acid regulate the signalling of both plant responses to sub-optimal water availability and herbivory-induced responses (Koramutla et al., 2022; Riemann et al., 2015; Smith et al., 2009). The signal-transduction routes regulated by these phytohormones cross talk (Hickman et al., 2019; Thaler et al., 2012; Zhang et al., 2015). This cross talk allows plants to integrate and fine-tune responses to biotic and abiotic stress separately, but might also provide a way for abiotic stress to affect how plants deal with biotic stress (Nguyen et al., 2016). Additionally, sub-optimal water availability is known to have a big metabolomic impact on the plant. Under sub-optimal water availability, some plant species start mobilizing stored resources to respond to the stress (Krasensky & Jonak, 2012; Mewis et al., 2012). These resources can then be utilized by insect herbivores, increasing their performance (Barber & Müller, 2021; Irfan et al., 2010; Lothier et al., 2020). In *Brassica oleracea*, waterlogging has been correlated with a decrease in plant defence compounds (Barber & Müller, 2021). Contrarily, other studies have found that sub-optimal water availability causes an increase in defensive compounds which can hamper insect herbivore performance (Schreiner et al., 2009). This demonstrates the complexity of predicting the effect of sub-optimal water availability on plant–insect interactions.

A comparative study on related plant species may reveal how plants that are differently adapted to abiotic conditions, such as water availability, are disparately affected in their resistance against insect herbivory under various levels of water availability. In this study we characterize how well three closely related *Rorippa* plants adapted to different water gradients resist insect herbivory under drought, well-watered and waterlogged conditions. *Rorippa amphibia* grows in semi-aquatic conditions along the edges of lakes and swamps. It is adapted to waterlogging and we, therefore, hypothesize it will be able to resist insect herbivory to a similar degree in waterlogged and moderate water conditions. As being semi-aquatic, drought conditions are hypothesized to result in more severe stress that may interfere with the plant's resistance against insect herbivores. *Rorippa palustris* grows in wetlands and floodplains and is often exposed to large variation in water conditions by flooding and drought. To escape large fluctuations in water availability, its life-history strategy is to flower and set seeds fast to complete its life cycle before stresses get too severe. We hypothesize that prioritizing resources to reproduction comes at the cost of defence against herbivory (Lind et al., 2013; Lucas-Barbosa et al., 2013). Since its defensive capabilities are expected to be limited, the effect of watering regime on these defensive capabilities might also be limited. *Rorippa sylvestris* grows in drier habitats than the other two plant species—in sandy, disturbed soils and may thus better cope with drought conditions. It is known to adopt an enduring strategy under flooding conditions where it lowers its metabolism to the minimum while waiting for conditions to improve (Akman et al., 2012). Therefore, we hypothesize that this strategy might interfere with mounting a defence response against insect herbivory under sub-optimal water availability. This will cause insect herbivores to perform better on waterlogged *R. sylvestris* plants while remaining unaffected by drought conditions. How plants deal with insect herbivory under

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different water regimes may also depend on the feeding mode of the herbivore. Aphids that feed on phloem sap are likely affected by changes in the nutritional value of phloem sap after drought or waterlogged conditions. Drought-stressed plants have a lower water potential (Mewis et al., 2012). This lower water potential might lead to an increase in concentration of nutrients in the phloem. Therefore, we hypothesize aphids will perform better on drought-stressed plants (but see Pompon et al., 2011 for an alternative hypothesis that osmotic pressure may reduce phloem intake by aphids). At the same time, plant responses to aphids are predominantly regulated through salicylic acid, whereas the responses to caterpillar attacks are predominantly regulated by jasmonic acid (Erb et al., 2012; Koornneef & Pieterse, 2008). Since abiotic stress by sub-optimal water availability induces abscisic acid that often enhances jasmonic acid signalling, sub-optimal water availability might positively affect the plant's resistance against caterpillars while not affecting the plant's resistance against aphids (Erb et al., 2012; Howe & Jander, 2008; Marquis et al., 2020; Vos et al., 2013).

In this study, we discuss how plant adaptations to water conditions can help predict their capacity to deal with aphid or caterpillar attacks under different watering regimes.

## METHODS

### Plants and insects

We selected three closely related plant species of the *Rorippa* genus that are well studied for their difference in adaptation to water conditions (Akman et al., 2012; Sasidharan et al., 2013). We explicitly test whether, for these three plant species, their adaptations correspond with differences in how water availability affects insect herbivory. Seeds of the terrestrial *R. sylvestris*, the flood-plain inhabiting *R. palustris* and rhizomes of the semi-aquatic *R. amphibia* were collected around Wageningen, the Netherlands (51°57′38.2″N 5°39′41.9″E). Seeds were sown and rhizomes were planted in trays with Arabidopsis potting soil (Lentse Potgrond B.V.), watered and kept under greenhouse conditions (22 ± 2°C, 60%–70% relative humidity, 16L:8D). Five weeks after sowing the seeds and 2 weeks after planting the rhizomes, plants were transplanted into pots (ø 12 cm, 1 litre) containing 1:1 Arabidopsis potting soil and sand (Lentse Potgrond B.V.). Plants were allowed to acclimatize and grow in pots for 1 week prior to the watering regime and subsequent insect infestation.

The insect species for which performance was assessed were the phloem feeders *Myzus persicae* (green peach aphid), *Lipaphis erysimi* (wild crucifer aphid) and the leaf-chewing caterpillars of *Plutella xylostella* (diamondback moth) and *Pieris brassicae* (large cabbage white). In our own additional field experiments not reported here, all insect herbivores have been confirmed to naturally occur on the plant species tested (Kamps unpublished data; Mertens et al., 2021). The insects were reared under greenhouse conditions (22 ± 2°C, 60%–70% relative humidity, 16L:8D). The phloem feeders *M. persicae* and *L. erysimi* were both reared on *Raphanus sativus* (Raddish) plants. The leaf chewers *P. xylostella* and *P. brassicae* were reared on *Brassica oleracea* (Brussels sprout) plants. The four insect species were originally collected from cabbage in the same experimental field location around Wageningen. Each of the cultures has been routinely reared for more than 3 years at the Laboratory of Entomology of Wageningen University.

### Experimental setup

To assess how different water regimes affect resistance to insect attack for the three *Rorippa* plant species, an experiment was conducted in a climate controlled greenhouse (22 ± 2°C, 60%–70% relative humidity, 16L:8D). Plants were first randomly appointed to one of the three water treatments: drought, well-watered and waterlogged. These water treatments approximate 8 ± 4%, 20 ± 5% soil moisture content and a submerged waterlogged soil, respectively. The well-watered treatment is an intermediate water condition under which all three plant species show no signs of water stress in their growth or morphology. To achieve drought stress based on soil water content measurement, we assessed in pilot experiments that 8% soil water content is close to the permanent wilting point of all three plant species (Figure S1, Table S1). The water content was maintained by measuring soil water content daily with an electronic water potential meter (Extech MO750) and adding water accordingly. The probe was inserted at the side of the pot on a new spot every day to most accurately measure soil moisture content. To achieve the water regimes, all pots were placed inside buckets (ø 21 cm, 2.75 L) and for the waterlogged treatments these buckets were filled with water up to the soil line (Figure 1). The water treatments were maintained for the entirety of the experiment.

One week after the onset of the water treatment, plants were infested with one of the four insect herbivores (Figure 1): the aphids *M. persicae*, or *L. erysimi*, or the caterpillars *P. xylostella* or *P. brassicae*. Each of the four herbivores was tested in separate experiments in the same greenhouse where plants and treatments were completely randomized over the greenhouse space. To assess aphid performance, per aphid species 90 plants of each of the three *Rorippa* species were potted. These plants were equally divided over the three water treatments (drought, well-watered, waterlogged). This resulted in a total of 30 plants per plant species, water treatment and aphid combination. Per plant, five adult aphids were placed on a young fully expanded leaf, and the plant was covered with a mesh bag to prevent aphids from wandering to other plants. After 2 weeks the number of aphids was counted for each plant as a proxy for plant resistance to aphid attack. In 2 weeks time, the aphid populations grew exponentially and treatment effects on population growth became visible.

To assess caterpillar performance, per caterpillar species 45 plants of each of the three *Rorippa* species were potted. These plants were equally divided over the three water treatments (drought, well-watered, waterlogged). This resulted in a total of 15 plants per plant species, water treatment and caterpillar species combination. Per plant five freshly hatched (L1) caterpillars of similar size were placed

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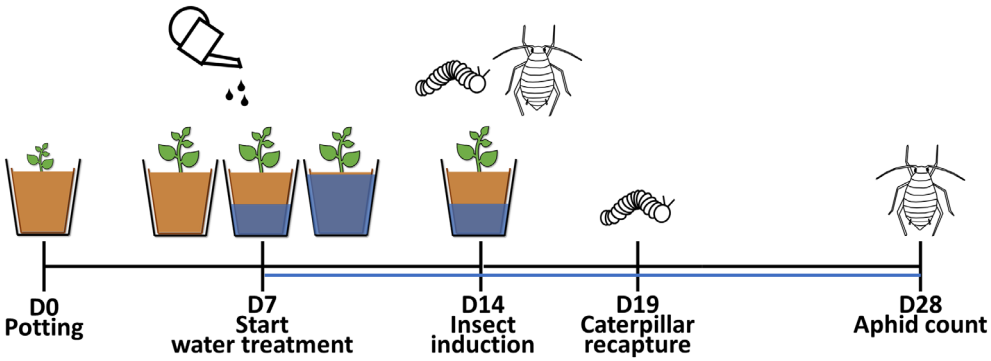



**FIGURE 1** Workflow of experiments. On day 0 (D0) plants of all the three plant species (*Rorippa amphibia*, *Rorippa palustris*, *Rorippa sylvestris*) were potted. Pots were placed in buckets to retain all water of the water treatment. Day 7 marks the start of the water treatment (drought, well-watered, waterlogged). This water treatment was maintained for the rest of the experiment. On day 14, plants were infested with one of the four insect species (*Myzus persicae*, *Lipaphis erysimi*, *Pieris brassicae*, *Plutella xylostella*). On day 19 caterpillars were recaptured and weighed. On day 28 aphid population size was measured.

on a young fully expanded leaf and the plant was covered with a mesh bag to prevent caterpillars from wandering to other plants. After 5 days the caterpillars were recaptured and weighed. Their weight was used as a proxy for how well a plant was able to resist the specific caterpillar. We selected a five day growth period to avoid that the fastest developing species (*P. xylostella*) would reach pupation which coincides with mass reduction.

## Statistical analyses

All statistical analyses were performed using RStudio (Allaire, 2012) under R 3.6.3 (R Core Team, 2013), with packages *lme4* (Bates et al., 2015) *emmeans* (Lenth et al., 2019), and *ggplot2* (Wickham, 2016). Aphid colony size data was analysed using a Generalized Linear Model (GLM) with gamma distribution including the full factorial interaction for plant species and water treatment followed by a Tukey's HSD post-hoc test for each factor. Since multiple caterpillars were measured per plant, caterpillar weight data was analysed using a Generalized Linear Mixed Model (GLMM) adding plant ID as a random factor to accommodate for the variance in both the caterpillars and replicated plants (Pineda et al., 2016; Walter et al., 2012) and including the full factorial interaction of plant species and water treatment followed by a Tukey's HSD post-hoc test for each factor. Performance of each herbivore was analysed with a separate model, because experiments were conducted during different moments in time.

# RESULTS

## Aphid performance

The population development of the aphid species, *Myzus persicae* and *Lipaphis erysimi*, after 14 days of feeding was significantly affected by the water conditions their food plants were exposed to (*M. persicae*: GLM, $\chi^2 = 47.9$, $df = 2$, $p < 0.001$ and *L. erysimi*: $\chi^2 = 41.7$, $df = 2$, $p < 0.001$). Both aphid species generally performed better on plants growing under drought conditions than on waterlogged plants (Figure 2). Moreover, the plant species affected the performance of the two aphid species (*M. persicae*: GLM, $\chi^2 = 212.6$, $df = 2$, $p < 0.001$ and *L. erysimi*: GLM, $\chi^2 = 432.7$, $df = 2$, $p < 0.001$). Both aphid species had the smallest population growth on the semi-aquatic *R. amphibia* plants. The poor performance on this plant species was accompanied by high mortality of *L. erysimi*, with only 11 well-watered and 16 waterlogged *R. amphibia* plants out of 30 supporting an aphid population. The performance of *M. persicae* was similar on the flood-plain species *R. palustris* and the terrestrial *R. sylvestris*, whereas *L. erysimi* performed better on *R. palustris* than on *R. sylvestris* (Figure 2). The effect of the water condition interacted with plant species for the performance of both aphid species (*M. persicae*: GLM, $\chi^2 = 24.8$, $df = 4$, $p < 0.001$ and *L. erysimi*: GLM, $\chi^2 = 37.6$, $df = 4$, $p < 0.001$). On the semi-aquatic species *R. amphibia*, both aphid species reached a larger colony size under drought conditions than on well-watered and waterlogged plants. Performance of *M. persicae* was similar on well-watered and waterlogged *R. amphibia*, whereas the performance of *L. erysimi* was poorer on waterlogged than on well-watered plants. Water conditions did not affect aphid colony size on the flood-plain species *R. palustris*. On the terrestrial species *R. sylvestris*, aphid colony size of *M. persicae* and *L. erysimi* was similar on drought-exposed and well-watered plants, whereas the population size reached was smallest on waterlogged plants but not significantly different from well-watered plants for both aphid species (Figure 2).

## Caterpillar performance

*Pieris brassicae* caterpillar weight after 5 days of feeding was not significantly affected by the water conditions their food plants were exposed to (GLMM, $\chi^2 = 3.2$, $df = 2$, $p = 0.19$) (Figure 3a). Contrarily, *Plutella xylostella* caterpillar weight was significantly affected by water

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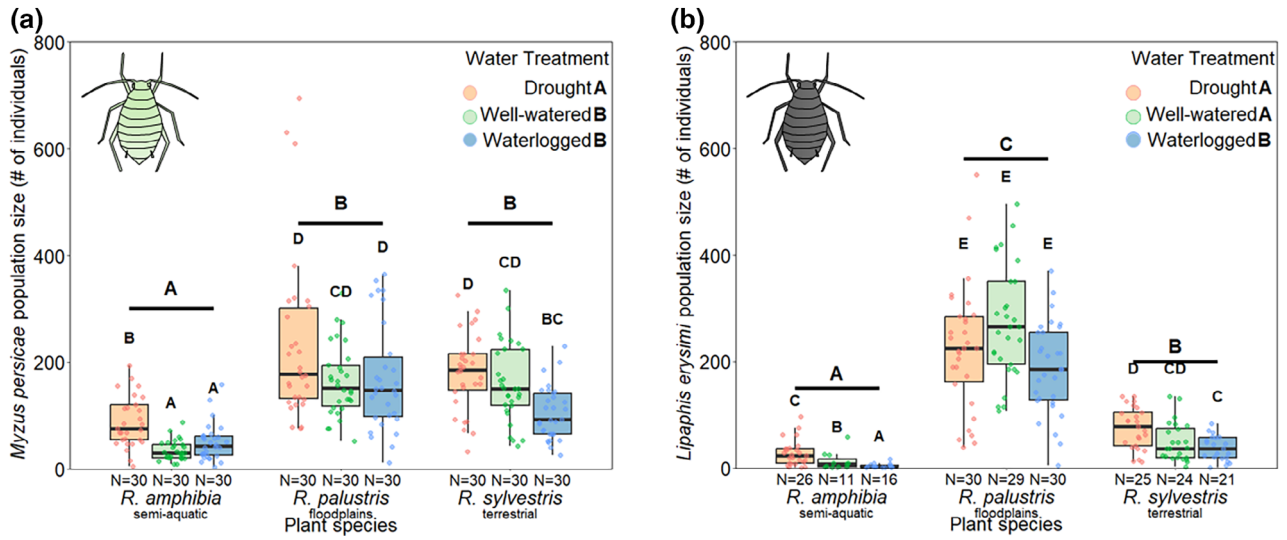



**FIGURE 2** Population size of the aphids (a) *Myzus persicae* and (b) *Lipaphis erysimi* after feeding for 14 days on one of the three plant species from the genus *Rorippa* that were subjected to different water treatments (drought, well-watered and waterlogged). The three plant species (*Rorippa amphibia*, *Rorippa palustris* and *Rorippa sylvestris*) are ordered on the x-axis for their habitat along the water gradient from semi-aquatic to fully terrestrial. Letters in the legend show main effects of water treatment, letters above each plant species show main effects of plant species and letters above each bar show significant differences among each treatment for the performance of aphids (Generalized Linear Model, Gamma distribution, $\alpha = 0.05$).

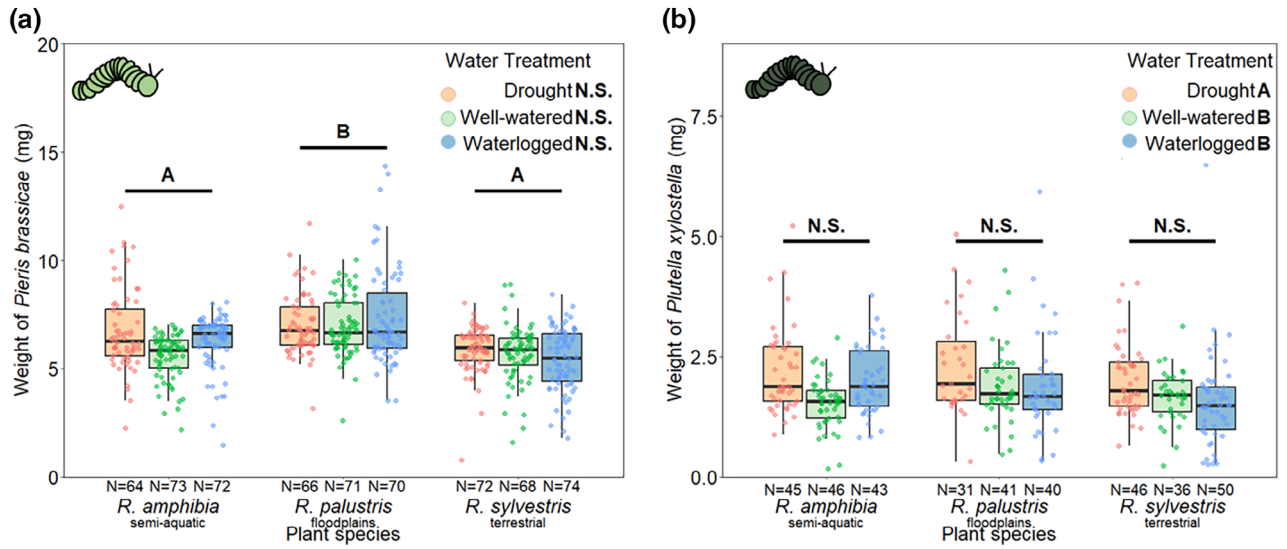



**FIGURE 3** Weight (mg) of (a) *Pieris brassicae* (b) *Plutella xylostella* after feeding for 5 days on one of the three plant species from the genus *Rorippa* that were subjected to different water treatments (drought, well-watered, waterlogged). The three plant species (*Rorippa amphibia*, *Rorippa palustris* and *Rorippa sylvestris*) are ordered on the *x*-axis for their habitat along the water gradient from semi-aquatic to fully terrestrial. Letters in the legend show main effects of water treatment, letters above each plant species show main effects of plant species. No significant effects were found between water treatments within a single plant species (Generalized Linear Mixed Model, Gamma distribution, $\alpha = 0.05$).

treatment (GLMM, $\chi^2 = 14.3$, $df = 2$, $p < 0.001$) (Figure 3b). Similar to the aphids, *P. xylostella* performed slightly better when feeding on drought-treated plants than on well-watered or waterlogged plants. While *P. brassicae* performance was unaffected by the water conditions of its food plant, *P. brassicae* performance was affected by plant species (Figure 3a). It grew bigger on the flood-plain species *R. palustris* than on the semi-aquatic *R. amphibia* or the terrestrial *R. sylvestris* (GLMM, $\chi^2 = 27.0$, $df = 2$, $p < 0.001$). On the other hand, *P. xylostella* performance was not significantly different between the three plant species (GLMM, $\chi^2 = 3.5$, $df = 2$, $p = 0.17$) (Figure 3b). There was no significant interaction between water regime and plant species on caterpillar performance (*P. brassicae* GLMM, $\chi^2 = 4.3$, $df = 4$, $p = 0.366$ and *P. xylostella*: GLMM, $\chi^2 = 5.2$, $df = 4$, $p = 0.257$).

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## DISCUSSION

Our results show that plant species are differently affected by watering regime in their resistance to herbivore attack. We demonstrate that the more terrestrial plant species *R. sylvestris* is not hampered in its resistance against insect herbivores when faced with drought. In contrast, the waterlogging adapted plant species *R. amphibia* was not affected in its resistance against herbivore attack under waterlogging conditions. Both aphid species *M. persicae* and *L. erysimi* generally performed worse on waterlogged plants and better on drought-treated plants. A surplus or shortage of water had less effect on the caterpillar species *P. brassicae* and *P. xylostella*. However, similar to aphids, *P. xylostella* performed better on drought-treated plants.

The better performance of aphids under drought conditions contrasts with the observations of other studies of poorer performance under drought (Huberty & Denno, 2004; Leybourne et al., 2021; Simpson et al., 2012). Generally, poorer aphid performance under drought stress is correlated with a reduction in plant vigour and an increase in chemical defence in drought-stressed plants (Beetge & Krüger, 2019; Inbar et al., 2001; Simpson et al., 2012; Xie et al., 2020). Yet ours is not the only study that shows a better performance of aphids on drought-stressed plants (Mewis et al., 2012; Oswald & Brewer, 1997). Better aphid performance on drought-stressed plants may be explained by increased concentration of amino acids in phloem (Barber & Müller, 2021; Mewis et al., 2012; Xie et al., 2020). Additionally, drought can interrupt the production of defensive compounds when plants are attacked by aphids, as was found in *Brassica oleracea* var. *italica* and *Arabidopsis thaliana* (Khan et al., 2010, 2011; Mewis et al., 2012). Moreover, aphids may benefit from increases in phloem sugar concentrations under drought stress as identified in the plant species *Triticum aestivum* and *A. thaliana* (Mewis et al., 2012; Xie et al., 2020). At the other end of the water-stress spectrum, waterlogging of plants in our study reduced aphid performance. This pattern is more consistent across the few studies on plant responses to waterlogging and may be explained by the effects of waterlogging on primary and secondary metabolites in the phloem sap (Khan et al., 2010; Lin, Liu, Hsu, et al., 2021; Lin, Liu, Ou, et al., 2021; Mewis et al., 2012). In *A. thaliana*, waterlogging led to lower total amino acid and sugar concentration in the phloem sap compared to drought (Mewis et al., 2012). Additionally, concentrations of defensive compounds after waterlogging in *A. thaliana* or *B. oleracea* were not significantly different from well-watered plants and in some cases even increased, in contrast to drought which decreased the concentration of defensive compounds in phloem sap (Khan et al., 2010; Mewis et al., 2012). Another explanation might be the fact that some plant species produce aerenchymous tissue under waterlogged conditions (Akman et al., 2012). This tissue might hamper aphids in reaching the phloem, reducing their performance. However, to our knowledge, no studies have yet been done to investigate the effect of aerenchyma on aphid feeding behaviour. Additionally, leaf water content in waterlogged *A. thaliana* was even lower than in drought-stressed plants (Mewis et al., 2012). Possibly the water content of the plant can deplete to a level where aphids will have difficulty feeding. Even the severity of the stress, such as the duration of drought or waterlogging as well as the stress pattern, that is, continuous versus pulsed, may affect the outcome of water stress on aphid performance. For example, a moderate level of water stress might increase amino acid concentrations and decrease defensive compounds, while a severe level of stress might lower the water content of the leaf so much that aphids are struggling to feed (Kansman et al., 2020; Mody et al., 2009; Rai et al., 2018; Sconiers & Eubanks, 2017).

Caterpillars that are feeding on the leaf tissues were not significantly affected by sub-optimal water conditions such as drought or waterlogging in our study. Other studies have found both positive and negative effects of sub-optimal water conditions on caterpillar performance (Faustino et al., 2021; Gutbrodt et al., 2011; Pineda et al., 2016; Rai et al., 2018; Walter et al., 2012). This seems to correlate with the level of defensive compounds under drought or waterlogged conditions. The increase in defensive compounds mainly affected generalist caterpillars negatively while it had no or a positive effect on specialists (Gutbrodt et al., 2011; Pineda et al., 2016; Rai et al., 2018). Both caterpillar species investigated in this study are specialists on Brassicaceae. They are therefore adapted to cope with the defensive compounds produced by the plants (Ratzka et al., 2002; Smallegange et al., 2007). Any alterations in defensive compounds might thus not have a significant effect on the performance of these caterpillars compared to generalist caterpillars.

Our results show that plant species differ in how they cope with insect herbivory under various water conditions. For these three plant species, the adaptations to their habitat corresponded with their capability to maintain resistance to insect herbivory under sub-optimal water conditions. This emphasizes that taking into account plant evolutionary differences may be imperative in explaining the variation of outcomes of herbivore performance on plants with water stress. These evolutionary differences may govern whether the host quality of a plant to insect herbivores changes under different water levels. We show that in the semi-aquatic plant species *R. amphibia*, waterlogging had little effect on herbivore performance compared to well-watered plants. *R. amphibia* is well adapted to waterlogging and is known to quickly attempt to escape the stress caused by flooding (Akman et al., 2012; Sasidharan et al., 2013). Since plants were already waterlogged for 7 days before herbivores were added, the *R. amphibia* plants might have already resolved the stress and returned to a normal physiological state. This could explain why herbivore performance on waterlogged plants was similar to well-watered plants for most insect species tested. Drought on the other hand might be particularly stressful for the semi-aquatic *R. amphibia* and therefore had a significant effect on the performance of both *M. persicae* and *L. erysimi* aphids. Which of the plethora of responses to drought causes the increase in aphid performance, however, requires further research. In contrast, on the terrestrial plant species *R. sylvestris*, aphids performed similarly on drought-treated and well-watered plants. *Rorippa sylvestris* is more accustomed to drier environments than *R. amphibia* and could thus be less challenged by drier conditions (Stift et al., 2008). Performance on drought-treated *R. sylvestris* could therefore be indistinguishable from well-watered plants. Waterlogging on the other hand

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significantly reduced the performance of both aphid species tested. *Rorippa sylvestris* is known to reduce its metabolism to a minimum when faced with flooding (Akman et al., 2012, Sasidharan et al., 2013). This way it endures rather than escapes the stress. Perhaps by reducing its metabolism it also reduces the sap stream and amount of mobile nutrients reducing its quality as a host for aphids. However, further research into the phloem composition is necessary to confirm this. On the floodplain-inhabiting plant species *R. palustris*, both aphid species, and the caterpillar *P. brassicae* generally performed well regardless of water treatment. This could also be explained by the plant's adaptations. *R. palustris* has a much shorter life cycle than the other two species. *R. palustris* plants were already flowering and setting seeds weeks before the other two *Rorippa* plant species. Perhaps this takes resources away from defence to reallocate them for reproduction allowing herbivores to perform better. This strategy, named 'reproductive escape', is already observed in other plant species (Lind et al., 2013; Lucas-Barbosa et al., 2013). By investing in reproduction under stress, the plant can escape the stress by completing its life cycle before stresses get too severe.

Our study contributes to the understanding of the effects of abiotic stress on plant–insect interactions by showing that plant evolutionary differences correspond with their capacity to deal with variation in combinations of water stress and herbivore attack. Our study thereby suggests that the two major hypotheses predicting herbivore performance on water stressed plants, that is, the 'plant stress hypothesis' and 'plant vigour hypothesis', may align with the context of plant evolutionary variation due to water availability in their habitat. Comparing closely related plant species that differ in adaptation to abiotic conditions for their plasticity in responses to combinations of abiotic and biotic stress, provides a strong tool to further unravel how plants adapt to managing stress combinations. To draw strong conclusions on how to generalize these relationships, broader sampling across plant families as well as more in-depth phylogenetic comparisons for the role of plant adaptations will be imperative. At the same time, we should understand how the ecological context of plant interactions with insects is altered by the water availability in the environment. Soil water content available to plants not only affects the oviposition preference of herbivores (Helmberger et al., 2016; Showler & Castro, 2010), but also the recruitment of natural enemies that reduce the impact of herbivore attack on plants (Kansman et al., 2021; Martini & Stelinski, 2017; Salerno et al., 2017; Weldegergis et al., 2015). Water availability may thus have profound effects on the insect community assembly on plants. Results of water regime on plant–insect interactions under controlled greenhouse conditions should therefore be further explored with field experiments to understand how these interactions are shaped under more natural conditions. We report on the effects of watering regime on plant–insect interaction in the field for the *Rorippa* plant species studied here in forthcoming publications. Moreover, unravelling the plant physiological responses to water availability is a key aspect of understanding insect herbivore responses to plant water stress and the consequences for insect ecology (Ben Rejeb et al., 2014). Understanding how different plant species have evolved to simultaneously respond to abiotic and biotic stress will aid us in predicting how the ecological context matches physiological adaptations to manage multi-stress situations. These insights will provide important guidelines for plant breeding to develop crops that are resilient to more extreme and frequent combinations of abiotic stress and insect herbivore attack in agroecosystems under predicted climate change.

## AUTHOR CONTRIBUTIONS

**Bram B.J. Kamps:** Conceptualization; methodology; investigation; funding acquisition; writing – original draft; formal analysis. **Erik H. Poelman:** Conceptualization; methodology; supervision; writing – review and editing; funding acquisition.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Data S1.** Supporting information.

**Data S2.** Supporting information.

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