Stressful times in a climate crisis: how will aphids respond to more frequent drought?

Running title: Aphid-plant interactions under drought stress

Abstract

Aim

Aphids are abundant in natural and managed vegetation, supporting a diverse community of organisms and causing damage to agricultural crops. Using a meta-analysis approach, we aimed to advance understanding of how increased drought incidence will affect this ecologically and economically important insect group, and to characterise the underlying mechanisms.

Location

Global.

Time period

1958–2020.

Major taxa studied

Aphids.

Methods

We used qualitative and quantitative synthesis techniques to determine whether drought stress has a negative, positive, or null effect on aphid fitness. We examined these effects in relation to 1) aphid biology, 2) the aphid-plant. species combination. We compiled two datasets: 1) a “global” dataset (n = 55 from 55 published studies) comprising one pooled effect size per study, and 2) an “expanded” dataset (n = 93) containing multiple datapoints per study, separated into different measures of aphid fitness but pooled across aphid-plant combinations. Where reported, we extracted data on the effect of drought on plant vigour, and plant tissue concentrations of nutrients and defensive compounds, to capture the potential causes of aphid responses.

Results
Across all studies ("global" dataset), drought stress had a negative effect on aphid fitness: Hedges' $g = -0.57$; 95% confidence interval (CI$_{95}$) = ±0.31. The "expanded" dataset indicated that, on average, drought stress reduced aphid fecundity ($g = -0.98$; CI$_{95}$ = ±0.50) and increased development time ($g = 1.13$; CI$_{95}$ = ±1.02). Furthermore, drought stress had a negative impact on plant vigour ($g = -7.06$; CI$_{95}$ = ±2.86) and increased plant concentrations of defensive chemicals ($g = 3.14$; CI$_{95}$ = ±3.14).

Main conclusions

Aphid fitness is typically reduced under drought, associated with reduced plant vigour and increased chemical defence in drought-stressed plants. We propose a conceptual model to predict drought effects on aphid fitness in relation to plant vigour and defence.

Keywords: Climate change, Ecological entomology, Insect-environment interactions, Meta-analysis, Plant-insect interactions
Introduction

The changing climate is anticipated to lead to decreased annual levels of precipitation in some regions, resulting in extended periods of drought (Blenkinsop & Fowler 2007; Santos, Belo-Pereira, Fraga & Pinto 2016). For plants in mesic habitats, prolonged drought can have severe consequences on plant physiology, often leading to reduced growth and photosynthetic capacity (Osakabe, Osakabe, Shinozaki & Trans 2014; Zeppel, Wilks & Lewis, 2014). Plant physiological responses to drought can directly influence the population dynamics, fitness, phenology, and biology of herbivorous insects (Stayley et al., 2006; Huberty & Denno 2004; Mody, Eichenberger & Dorn, 2009; Aslam, Johnson & Karley, 2013), with consequences that cascade through trophic networks (Johnson, Stayley, McLeod & Hartley, 2011; Rodríguez-Castañeda 2013). Meta-analysis provides a useful approach to predict the direction of drought effects on insect herbivores, reporting an overall response that accommodates between-study variation.

Previous meta-analyses have examined drought effects by comparing responses of herbivorous insect species with different feeding strategies (Koricheva & Larsson, 1998; Huberty & Denno 2004). To date, however, there has been no comprehensive assessment of drought effects on a specific herbivore group and the underpinning causes due to physiological changes in the host plant. Aphids are phloem-feeding insects of global ecological importance (Van Emden & Harrington 2017) as abundant components of insect communities in diverse ecosystems across the globe (Messelink, Sabelis & Janssed, 2012; Roubinet et al., 2018). There are over 4,400 known species of aphid (Blackman & Eastop 2000) and around 250 of these are major agricultural and horticultural pests, making them an economically important group of herbivorous insects. In many ecosystems, aphids sustain several higher trophic groups, including their primary consumers, such as parasitoid wasps, spiders, ladybirds, and carabid beetles (Staudacher, Jonsson & Traugott, 2016), the higher-level consumers of these aphid natural enemies, such as hyperparasitoids (Traugott et al., 2008; Lefort et al., 2017), small mammals and birds, and many entomological pathogens and parasites (Hagen & van den Bosch 1968). Examining how climate change, including drought, might influence aphid fitness is a major avenue of current research, specifically with regards to examining how this might affect the productivity and functioning of agricultural, horticultural, and natural
vegetation systems across the globe (Romo & Tylianakis 2013; Teixeira, Valim, Oliveira & Campos, 2020)

Analysis of sap-feeding insects by Huberty & Denno (2004) suggested that drought has an overall negative effect on the fitness of sap-feeding insects. Experimental studies of aphids indicate that this negative effect of drought is observed across many aphid-plant systems (Pons & Tatchell 1995; Agele, Ofuya & James, 2006; Mody et al., 2009; Aslam et al., 2013; Grettenberger & Tooker 2016; Foote, Davis, Crowder, Bosque-Pérez & Eigenbrode, 2017), although this has not been assessed quantitatively. Further, there has been no comprehensive analysis of the causes of decreased aphid fitness under drought, although several studies suggest that it is mediated through reduced plant fitness (Hale, Bale, Pritchard, Masters & Bworn, 2003; Banfield-Zanin & Leather, 2015; Dai, Liu & Shi, 2015). Two meta-analyses conducted in recent decades provide context for constructing a hypothesis to explain variation in aphid fitness under water stress in relation to plant fitness. First, Huberty & Denno (2004) found little evidence for the plant stress hypothesis (i.e. enhanced insect performance on water-stressed host plants due to increased tissue nitrogen availability: White, 1969) amongst sap-feeding insects (phloem and mesophyll feeders). Second, Cornelissen, Fernandes & Vasconcellos-Neto (2008) examined insect fitness in relation to plant vigour and demonstrated that sap-feeding insects are more abundant and show increased fitness when feeding on more vigorously growing plants. These findings lead us to hypothesise that the effects of drought on aphid fitness are driven by decreased plant vigour, such as reduced plant growth rate or mass (Hatier et al., 2014), rather than stress-related changes in plant nutritional quality.

Although many studies have reported reduced aphid fitness when exposed to drought stressed hosts (Banfield-Zanin & Leather, 2015; Dai et al., 2015; Foote et al., 2017), studies have reported null (Mewis, Khan, Glawischnig, Schreiner & Ulrichs, 2012) and positive (Oswald & Brewer, 1997) effects. Multiple factors could explain these contrasting observations, including differences in aphid or plant biology. Indeed, in the study by Oswald & Brewer a positive effect of drought on aphid fitness was detected in the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), and a negative effect was reported for the corn leaf aphid, *Rhopalosiphum maidis* (Fitch). Although both species are cereal-feeding aphids, *D. noxia* and *R. maidis*
belong to two distinct aphid tribes, the Macrosiphini and the Aphidini, respectively (Kim & Lee, 2008; Choi, Shin, Jung, Clarke & Lee, 2018), raising the possibility that differences in aphid biology and/or life history could underlie the contrasting responses. Additionally, the specific aphid-plant combination could further influence the effects of drought on aphid fitness. For example, multiple aphid species exhibit contrasting responses to drought on a common host plant (Mewis et al.) and a single aphid species can display contrasting responses on related host plant species (Hale et al., 2003). These findings suggest that aphid responses to drought could be mediated by plant species-specific responses to drought (i.e. the availability of nutrients, the concentration of defensive compounds, resource allocation to new tissue). Understanding these mechanisms is necessary to predict the outcomes of plant-insect interactions under a changing climate.

Here, we take the novel approach of analysing data on aphid fitness and host plant physiology, using studies comparing drought with unstressed conditions, to examine the hypothesis that changes in aphid fitness are driven by the effects of drought on plant vigour. We predicted that reduced aphid fitness would be associated more strongly with decreased plant vigour (e.g. decreased mass, reduced growth) under drought than with changes in plant nutritional quality or defensive chemistry. Initially, we carry out a literature synthesis and take a “vote-counting” approach to qualitatively determine whether drought has an overall negative, positive, or null effect on aphid fitness. Following this, we use meta-analysis techniques to quantify these effects. Next, we extract data reporting on plant physiological responses to drought, including measurements of plant vigour, and tissue concentrations of plant nutrients and plant defensive compounds. This provides us with data that can be used, for the first time, to quantify drought effects on plant physiology in parallel with aphid fitness responses. A secondary aim of the meta-analysis was to explore patterns in aphid responses to drought in relation to 1) aphid tribe or aphid host range, and 2) the aphid-plant system (i.e. species combinations) to identify any common features of aphid biology that explain variation in aphid fitness responses to drought. The mechanistic understanding provided by our study allows the effects of drought on herbivore success to be anticipated for phloem-feeding insects across different habitats under future climatic conditions.

**Literature search and meta-analysis**
The search terms “Drought” AND “Aphid” were used to conduct a literature search of both the Web of Science and Scopus databases (with a publication cut-off date of September 2020), to maximise the number of studies included (the overlap between them is only 40-50%: Nakagawa, Noble, Senior & Lagisz, 2017). 190 papers were identified from the Web of Science database and 197 from the Scopus database. After removing duplicates, 247 published papers were extracted. A previous meta-analysis which examined insect responses to drought (Huberty & Denno, 2004) was screened and an additional 16 studies were identified. This produced a pool of 263 studies published between 1958 and 2020. See Fig. 1 for the PRISMA flow diagram, constructed following Moher, Liberati, Tetzlaff & Altman (2009). To be considered for inclusion in the analysis, papers had to satisfy the following criteria: 1) to be primary literature presenting data on the responses of at least one aphid species to drought relative to an unstressed control treatment; 2) report aphid responses as the effect of drought on a measure of aphid fitness; 3) present the responses so that an estimation of the treatment differences could be determined alongside an estimate of the variation. A total of 55 studies satisfied these criteria. A further 26 studies reported data for aphid fitness but did not display the data; these studies were excluded from the meta-analysis but included in qualitative “vote-counting” assessment. The full range of studies are detailed in Appendix 1 and Appendix 2.

Heterogeneity is routinely expected and accepted in meta-analyses (Higgins, 2008). Acceptance of heterogeneous data is dependent on whether the inclusion criteria are sound and the underlying data correct (Higgins). Extracted data were assessed for heterogeneity by measuring Cochran’s Q.

Data extraction and pooling: aphid responses

Aphid fitness data were extracted from drought and control (unstressed) treatments. Where reported, the mean value and an indication of the variation around the mean were extracted using WebPlotDigitizer v.4.2 (Rohatgi, 2019. Weblink: https://automeris.io/WebPlotDigitizer). Where median and interquartile ranges were reported, means and standard deviation were estimated following Luo, Wan, Liu & Tong (2018) and Wan, Wang, Liu & Tong (2014). Data were extracted for the following aphid fitness parameters: fecundity (daily, lifetime, and mean fecundity and
life-history parameters related to reproduction, such as the intrinsic rate of increase), population size or aphid density/abundance, aphid development (time until adulthood and time until first reproduction), aphid biomass, or aphid lifespan. The effect size (Hedges’ g; Cooper, Hedges, Valenting, 2019) was calculated from aphid responses under drought relative to aphid responses under control conditions. Hedges’ g was selected as this parameter performs better across studies with a lower sample size, when compared with Cohen’s D or Glass’s Delta. Where multiple drought treatments were imposed, data were extracted from the control and the most severe drought treatment.

Where multiple formats of a fitness parameter were reported (e.g. fecundity reported in terms of mean fecundity and lifetime fecundity) data were pooled across different measures of the core parameter to provide one response per parameter assessed. Data were further pooled across any other experimental treatments imposed in the study (for example, in Xing et al. (2003) drought and control conditions were pooled across three CO₂ treatments), and within aphid species to provide one data point per aphid species per fitness parameter. Data were collated separately for each host plant species. This pooling method produced 93 unique data points over the 55 studies.

Two datasets were compiled based on these data. In the “global” dataset (see Supplementary Fig. 1A for the associated funnel plot), data were pooled within each study across fitness parameters, plant hosts, and aphid species to produce 55 data points, i.e. one pooled effect size per study, reporting the overall aphid responses to drought. Within the “global” dataset, the calculated hedges’ g values for developmental fitness parameters were converted from positive to negative values to align with the net direction of other fitness parameters (this was required because a positive hedges’ g value for development represents a fitness decrease, compared with the other parameters for which a fitness decrease would result in a negative hedges’ g value). In the "expanded" dataset (see Supplementary Fig. 1B for the associated funnel plot), effect sizes were calculated separately for each fitness parameter and aphid-host plant combination in the study. To ensure that the direct comparison of different aphid fitness parameters was justified for inclusion in the analysis, the calculated hedges’ g values for each data point were plotted (Supplementary Fig. 2) to confirm that data were evenly distributed and not clustered
into categories. Furthermore, to avoid potential pseudo-replication resulting from extracting multiple fitness parameters per study, the study number was included as a random term in all analyses of the “expanded” dataset.

**Grouping of extracted data: aphid responses**

Extracted data contained information on 23 aphid species (Table 1). To disentangle any potential taxonomic differences, data were categorised into three groups: a “Tribe” grouping based on the taxonomic tribe of the aphid species; an “Aphid Host Range” category based on whether the aphid species is a specialist or generalist feeder; and a “Plant-Aphid” group based on the plant-aphid system examined. Categorisations for Tribe and Aphid Host Range are detailed in Table 1. The final Tribe grouping used in the “expanded” dataset comprised Macrosiphini \( (n = 60) \), Aphidini \( (n = 23) \), and others \( (n = 10) \), while the aphid host range grouping comprised Specialist \( (n = 62) \) and Generalist \( (n = 31) \) categories.

Extracted data covered 24 host plant species. To facilitate comparison between plant-aphid combinations, data were grouped into the following plant host categories: Brassicas (comprising *Brassica oleracea* and *B. napus*, Bn: \( n = 6 \) and 15 from the “global” and “expanded” datasets, respectively), Cereals (*Arrhenatherum elatius*, *Dactylis glomerate*, *Holcus lanatus*, *Hordeum vulgare*, *Triticum aestivum*: \( n = 20 \) and 38), Forage species (*Chenopodium sp.*, *Festuca arundinacea*, *Medicago sativa*, *Lolium perenne*, *L. multiforum*, *Poa autumnalis*, *Rumex sp.*: \( n = 7 \) and 10), Legumes (*Pisum sativum*, *Glycine max*: \( n = 2 \) for both datasets), Model Arabidopsis species (*Arabidopsis thaliana*: \( n = 3 \) and 4), *Solanum sp.* (*Solanum tuberosum*, *S. lycopersicum*: \( n = 4 \) and 9), and Tree systems (*Malus domestica*, *Picea abies*, *P. sitchensis*, *P. Sylvestris*, *Populus sp.*, \( n = 13 \) and 15).

**Criteria for inclusion in analysis, data pooling, and data grouping: plant responses**

Studies were screened for inclusion in an additional meta-analysis to determine the impact of drought on the host plant. To be considered for inclusion, studies had to satisfy the following criteria: 1) present data on the responses of at least one plant species to drought relative to a controlled condition; 2) report responses as the effect of drought on either a measure of vigour (including mass, height, and growth), tissue nitrogen (N) or amino acid concentration, or plant chemical defence (e.g. secondary
metabolite or phytohormone concentration); 3) report an estimation of the differences alongside the variation. From the pool of 55 studies, 32 reported effects of drought on plant vigour (i.e. dry matter accumulation, plant growth, and leaf/tiller production), 12 reported a measure of tissue N or amino acid concentration, and ten reported tissue defensive compound concentrations. The effect size (Hedges’ g) was calculated as described above. Data were pooled at the study level into measures of vigour, N or amino acid concentration, and defensive compound concentrations, resulting in three plant sub-datasets: vigour, nutritional, and defensive.

Measuring publication bias

Funnel plots were created to test for publication bias and a rank correlation test was carried out to test for funnel plot asymmetry (Supplementary Fig. 1). Additionally, as most null results go unpublished, failsafe analysis using Orwin’s method (Orwin, 1983) was employed to estimate the number of studies reporting a null effect that would be required to reduce the observed average effect size to -0.1. This analysis estimated $n = 261$ and $n = 2228$ null studies required to reduce the observed average effect size to -0.1 in the aphid and plant datasets, respectively.

Analysis of extracted data

Statistical analysis was carried out using R version 4.0.3, with additional packages ggplot2 v.3.3.2 (Wickham, 2016), meta v.4.15-1, and metafor v.2.4-0. A total of 81 and 55 studies were included in the vote counting and meta-analysis, respectively (detailed in Appendix 1 and Appendix 2).

To account for variation between different methodologies used to implement drought, drought methodology was allocated into one of five categories: FC (studies where % reduction in field capacity was used); DI (studies where decreased volume of irrigation was used); GM (studies which used a gravimetric method to adjust irrigation); CC (studies which used a calibration curve to help advise water irrigation regimes); and RW (studies where irrigation was simply restricted or withheld from the drought treated plants). The effect of these drought treatments on aphid fitness was examined to confirm that different methodologies used to initiate drought did not vary in their effects (Supplementary Fig. 3).

Aphid response analysis: Vote counting procedure
Briefly, studies were screened for whether a significant effect of drought on aphid fitness was detected, and whether the direction of the effect was positive or negative. Studies which reported non-significant results were categorised as null response. Data were deemed as significant based on the statistical reporting in each study (significance was determined by \( p = <0.05 \)). For studies measuring the responses of several aphid species (such as Foote et al., 2017), the results of the statistical analysis at the drought treatment level, not the species x drought interaction level, were used to determine whether the observation was significant amongst all aphid species.

**Aphid response analysis: Meta-analysis procedure**

Two meta-analyses were carried out using the two datasets described above: 1) an analysis using the “global” dataset pooled across aphid species and host plant giving one pooled effect size per study (55 data points); 2) an analysis using the “expanded” dataset which was pooled at the aphid species and host plant levels and separated by aphid fitness parameter, giving multiple pooled effect sizes per study (93 data points).

For the first meta-analysis (“global” dataset), data were analysed using a linear mixed effects model fitted with restricted maximum likelihood distribution. The difference between the plant-aphid systems was examined in a subsequent model by incorporating this factor a fixed term. For the second meta-analysis (“expanded” dataset), ‘study’ was incorporated as a random term to account for multiple data points in some studies and to avoid potential pseudo-replication. Data were analysed in a similar way to the method above: briefly, a random linear mixed effects model fitted with restricted maximum likelihood distribution was used to examine differences between aphid tribes, aphid host range, and the plant-aphid system in three models. In a further model, the responses of the different aphid fitness parameters were tested.

**Plant response analysis: Meta-analysis procedure**

32, 12, and ten studies also reported the effect of drought on plant vigour, plant tissue nutrient concentration, and tissue defensive compound concentrations, respectively. Data were analysed using a random linear mixed effects model fitted
with restricted maximum likelihood distribution. Data were analysed in an individual model for each plant response.

**Results**

*Aphid fitness is reduced under drought*

The vote counting procedure (Fig. 2) indicated that aphid fitness is reduced when exposed to drought stressed plants. Analysis of the pooled data indicated that aphid fitness is generally reduced under drought ($Q_M = 26.71; p = <0.001$; Supplementary Fig. 3), average Hedges’ $g = -0.57$; 95% confidence interval ($CI_{95}$) $= \pm 0.31$. Subsequent comparisons were carried out after separating the data into the plant-aphid system. Pooled data were significantly heterogeneous, indicated by Cochrans’ $Q$ ($Q_E = 404.34; df = 54; p = <0.001$). Further comparison indicated that aphid fitness was broadly reduced under drought across plant-aphid systems ($Q_M = 25.81; p = <0.001$; Fig. 3). However, due to low replication for some groups, a comprehensive comparative analysis was not possible. No trends over publication time were observed for pooled aphid responses (Supplementary Fig. 8).

To analyse the effect of drought on aphid fitness in relation to aphid tribe and aphid host range, and to identify any differences between fitness parameters, a second dataset comprising 93 data observations over the 55 studies was compiled (the “expanded” dataset). Meta-analysis of this expanded dataset indicated that aphid fitness was reduced under drought ($Q_M = 18.03; p = 0.003$; Fig. 4 insert). Most aphid fitness parameters examined, especially parameters intrinsically associated with aphid abundance (fecundity and population size) and development, were negatively affected by drought ($Q_M = 91.88; p = <0.001$; Fig. 4). Drought decreased aphid fitness to a similar extent across the different aphid tribes ($Q_M = 19.45; p = 0.002$): Aphidini ($g = -0.55; CI_{95} = \pm 0.38$), Macrosiphini ($g = -0.85; CI_{95} = \pm 0.37$), and Other ($g = -0.32; CI_{95} = \pm 1.18$). Fitness decreases were similar for aphids with contrasting host plant ranges ($Q_M = 14.13; p = 0.001$): specialist ($g = -0.67; CI_{95} = \pm 0.32$), generalist ($g = -0.90; CI_{95} = \pm 0.54$).

*Drought stressed plants show reduced vigour and increased tissue concentrations of defensive compounds*
Meta-analysis of the pooled plant responses to drought (Supplementary Fig. 5 – 7) indicated that exposure to drought has an overall negative effect on plant vigour ($Q_M = 35.97; p < 0.001$; Fig. 5) and, on average, results in more chemically-defended plant tissues ($Q_M = 46.37; p < 0.001$; Fig. 5). However, tissue N and amino acid concentrations did not increase consistently ($Q_M = 4.92; p = 0.178$; Fig. 5). The consistency of the relation between drought effects on aphid fitness, plant vigour and plant chemical defence, but not plant nutritional quality, is shown in Supplementary Fig. 9. No trends over publication time were observed for any plant responses (Supplementary Fig. 8).

**Discussion**

This study provides the first comprehensive assessment of aphid and host plant responses to drought stress, analysed in terms of aphid fitness and plant vigour, nutritional quality, and chemical defence. The meta-analysis supported our prediction that drought reduces aphid fitness, and this effect was linked most consistently with reduced plant vigour rather than altered tissue nutrient concentrations, although increased chemical defence of plant tissues might also play a role. Our study includes data extracted from 81 (qualitative assessment) and 55 studies (quantitative assessment), including 42 papers for quantitative assessment published between 2003 – 2020 that were not included in an earlier meta-analysis across different insect feeding guilds (Huberty & Denno, 2004). Our findings, therefore, represent a significant advance in knowledge on the effects of drought on sap-feeding insects with a novel focus on drought effects on aphids as an ecologically important insect group.

**Plant vigour could explain drought effects on aphid fitness**

The primary finding that aphid fitness is reduced when feeding on drought stressed hosts confirms the findings of Huberty & Denno (2004) for sap-feeding insects. Our study goes further, however, by providing evidence for the underlying mechanisms. We show that decreased aphid fitness is most frequently associated with the negative effects of drought on plant growth (vigour), with some evidence that plant tissue concentrations of defensive chemicals or signalling compounds play an important role. It should be noted that, out of the studies included in our meta-analysis, over half measured plant vigour (32 studies) while only around one-fifth
measured tissue concentrations of defensive compounds ($n = 10$). Most of these studies showed a strong association between decreased aphid performance, reduced plant vigour and increased tissue concentrations of plant defensive compounds, but no clear association with tissue nutrient concentrations. This finding is consistent with our prediction and is supported by a large body of literature reporting elevated chemical defence and decreased plant growth and vigour under drought (Templer et al., 2017; Beetge & Krüger 2019; Xie et al., 2020). As less vigorous plants have a higher concentration of biochemical defences, drought stress could lead to increased aphid exposure to plant defensive compounds, leading to reduced fitness due to feeding deterrence and decreased phloem ingestion.

A secondary aim of this meta-analysis was to examine the consistency of drought effects across aphid groups and aphid-plant systems to identify factors which could explain differential effects (Oswald & Brewer, 1997; Hale et al., 2003). All aphid tribes assessed showed decreased aphid fitness in response to drought and a similar response was observed when aphids were categorised as specialists or generalists. However, there was an overrepresentation of the Aphidini and Macrosiphini tribes (45 out of the 55 studies) because many empirical studies focus on agriculturally or ecologically important aphid species, which are widely represented in these two tribes (Kim & Lee 2008; Choi et al., 2018). This limits the extent to which differences between tribes can be detected and further experimental work would be needed to confirm consistent drought responses across aphid groups. For example, it could be hypothesised that aphid species which actively remobilise plant nutrients (e.g. *D. noxia*; see Sandström, Telang & Moran, 2000) are less affected by drought than species that are unable to maintain a sufficient supply of plant nutrients. Similarly, species that can sequester plant defensive chemicals (e.g. *Brevicoryne brassicae* (Linnaeus); see Kazana et al. 2007) might better tolerate increased concentrations of toxic plant chemicals in response to drought.

Similarly, aphid fitness was generally reduced on drought stressed plants across all plant groups assessed, but there was an overrepresentation of two plant groups (Cereal and Tree groups), which prevents firm conclusions. Nonetheless, these findings confirm that the effect of drought on herbivorous insects is primarily
mediated by general changes in plant physiology, as indicated by Cornelissen et al. (2008).

The role of host plant defence in aphid responses to drought

Although based on a relatively small number of studies, our analysis indicated that plant chemical defence is elevated under drought, and this correlates with reduced aphid fitness. Several studies highlight the effects of anti-herbivore plant resistance strategies on aphid fitness under benign conditions (Guerrieri & Digilio, 2008; Greenslade et al., 2016), but few studies have examined whether host plant resistance against aphids is modified under climate stress. From the 55 studies assessed here, only five included observations of aphid responses on both susceptible and (partially)-resistant plant types (Oswald & Brewer, 1997; Björkman 2000; Dardeau et al., 2015; Verdugo, Sauge, Lacroze, Francis & Ramirez, 2015; Guo et al., 2016) with one further study examining aphid responses on resistant plants only (Ramirez & Verdugo, 2009). Additionally, three studies compared aphid responses on drought tolerant and drought susceptible host plants (De Farias, Hopper, Leclant, 1995; Rousselin et al., 2018; Quandahor, Lin, Gou, Coulter & Liu, 2019) and only one study examined the interactive effects of aphid resistance and drought tolerance (Grettenberger & Tooker, 2016). Such a low level of representation means that the interactive effect between plant resistance and drought could not be investigated empirically using meta-analysis. Of these studies, four report similar findings: aphid fitness is reduced on both susceptible and resistant plant hosts (Oswald & Brewer; Björkman; Dardeau et al.; Guo et al.), with a smaller reduction in fitness on the resistant host plant than on the susceptible host plant (Oswald & Brewer; Dardeau et al.). These findings indicate that while aphid fitness is reduced on resistant plants under benign conditions, under drought it decreases to similarly low values on susceptible and resistant plants. This highlights a significant knowledge gap in our understanding of how plant resistance traits are affected by environmental stress, which is becoming increasingly important for successful pest management in changing climatic conditions.

To stimulate further research into this potentially important interaction between plant resistance, herbivore success, and climatic conditions, we propose a simplified conceptual model to predict how aphids will respond to drought in relation to altered
host-plant resistance, termed the Plant Resistance Hypothesis (Fig. 6). This expands upon previous conceptual models, the plant stress hypothesis and plant vigour hypothesis, which do not consider the potential differences in plant susceptibility to herbivorous insect pests. This new model suggests that under benign conditions the basal level of aphid fitness will differ between the susceptible (high aphid fitness) and resistant (moderate-to-low aphid fitness) plant types, as will the level of plant defence: susceptible (low level of defence) vs. resistant (high level of defence). Drought is likely to cause a reduction in plant vigour and decreased plant palatability for the aphid, characterised by elevated concentrations of plant defensive compounds (Inbar, Doostdar & Mayer, 2001; Ozturk et al., 2002), leading to differential changes in the chemical defence of susceptible (from low to high concentration) and resistant (continually high concentration) plants. Differential levels of basal aphid fitness between the two plant types leads to differences in the extent to which aphid fitness is affected by drought depending on whether the host is a susceptible (from high fitness to low fitness) or resistant (from intermediate fitness to low fitness) plant type.

**Drought-induced reduction in aphid fitness could destabilise aphid-trophic interactions**

Aphids represent an important group of herbivorous insects from both an economic perspective, in relation to agricultural crop protection, and an ecological perspective, regarding the diverse community of higher trophic groups they support. The central finding of our meta-analysis is that exposure to drought-stressed hosts is detrimental to aphid fitness, although the extent of this effect is likely affected by host plant suitability as an aphid food source. Consequently, higher incidences of drought will have a detrimental effect on the terrestrial trophic networks that are supported by aphids: aphids are widespread in vegetation systems globally, are abundant consumers of primary production in many ecosystems, and provide a food source for many trophic groups (Gilbert 2005; Messelink et al., 2012; Roubinet et al., 2018). Our findings, largely based on aphid species in the Aphidini and Macrosiphini tribes, indicate that individual and population level measures of aphid fitness are affected negatively by drought, suggesting that drought will have cascading consequences for host plant consumption by aphids and the abundance of other trophic groups. If these findings translate to other aphid species and tribes, they imply that drought
could reduce the availability of aphid hosts for parasites and pathogens (Nguyen, Michaud & Cloutier, 2007; Ahmed, Liu & Simon, 2012; Aslam, et al., 2013) and decrease food availability for aphid predators (Wade, Karley, Johnson & Hartley, 2017). Similarly, many aphids are tended by ants for their honeydew secretions (Stadler et al., 2003). These ants provide protective services to plants by deterring herbivory by other insect pests (Offenberg, Nielsen, MacIntosh, Havanon & Aksomkoeae, 2004; Rosumek et al., 2009). While reduced aphid fitness might decrease plant consumption, it could also compromise the protective services delivered by ants: lower aphid abundance, or decreased honeydew quantity or quality, could decrease ant attendance (see Stadler, Kindlmann, Šmilauer & Fiedler, 2003), thereby exacerbating the detrimental effects of drought by increasing plant exposure to additional biotic stressors.

Ecological networks often exist in stable equilibria (McQuaid & Britton, 2015; Landi, Minoarivelvo, Brännström, Hui & Dieckmann., 2018), with a change in the abundance of one species or functional group leading to perturbations in abundance and diversity across the network (McQuaid & Britton, 2015). A drought-induced reduction in aphid fitness might decrease abundance, mass, or quality of aphids available to support other trophic levels, with potential to destabilise population equilibria; a recent modelling study illustrated that the destabilising effects of drought on aphid-parasitoid interactions lead to altered insect population cycles (Preedy, Chaplain, Leybourne, Marion & Karley, 2020). A key finding of this meta-analysis was that plant resistance to aphids may influence the extent to which aphids are negatively affected by drought. The negative consequences of plant resistance for aphids generally include decreased fecundity (Greenslade et al., 2016; Leybourne et al., 2019) which could reduce aphid abundance for aphid natural enemies. This could have further consequences for aphid/insect distributions in regions that are experiencing more frequent drought events. Analysing the effects on aphid-natural enemy interactions of drought, and its interactions with other determinants of host suitability, is therefore an important avenue for future research to understand the impacts on the composition and function of ecological networks and species distributions (e.g. Rodríguez-Castaneda, 2013). This will improve our understanding of how drought and plant suitability characteristics might contribute to recent reports of increased rates of species loss and population declines (Saunders, Janes &
O’Hanlon, 2020; Leather, 2018). Our conceptual model of the anticipated effects of drought on aphid fitness in relation to plant resistance, plant vigour, and chemical defence provides a basis for stimulating future research on insect-plant interactions under a changing climate.

References

Agele S., Ofuya T. & James P. (2006). Effects of watering regimes on aphid infestation and performance of selected varieties of cowpea (Vigna unguiculata L. Walp) in a humid rainforest zone of Nigeria. *Crop Protection, 25*, 73-78.

Ahmed S., Liu D. & Simon J.-C. (2012). Impact of water-deficit stress on tritrophic interactions in a wheat-aphid-parasitoid system. *PLoS ONE, 12*, e0186599.

Aslam T., Johnson S. & Karley A. (2013). Plant-mediated effects of drought on aphid population structure and parasitoid attack. *Journal of Applied Entomology, 137*, pp. 136-145.

Banfield-Zanin J. & Leather S. (2015). Reproduction of an arboreal aphid pest, Batabium abietinum, is altered under drought stress. *Journal of Applied Entomology, 139*, pp. 302-313.

Beetge L. & Krüger K. (2019). Drought and heat waves associated with climate change affect performance of the potato aphid *Macrosiphum euphorbiae*. *Scientific Reports, 9*, e3645.

Blackman R. & Eastop V. (2000). Aphids on the world’s crops - an identification and information guide. New York: John Wiley and Sons, Ltd.

Blenkinsop S. & Fowler H. (2007). Changes in European drought characteristics projected by the PRUDENCE regional climate models. *International Journal of Climatology, 27*, pp. 1595-1610.

Björkman C. (2000). Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. *Oecologia, 123*, pp. 223-231

Choi H., Shin S., Jung S., Clarke DJ. & Lee S. (2018). Molecular phylogeny of Macrosiphini (Hemiptera: Aphididae): An evolutionary hypothesis for the Pterocomma-group habitat adaptation. *Molecular Phylogenetics and Evolution, 121*, pp. 12-22.

Cooper H., Hedges L. & Valentin, J. (2019). *The handbook of research synthesis and meta-analysis: The Russel Sage Foundation*.

Cornelissen T., Fernandes G. & Vasconcellos-Neto J. (2008). Size does matter: variation in herbivory between and within plants and the plant vigour hypothesis. *Oikos, 117*, pp. 1121-1130.

Dai P., Liu D. & Shi X. (2015). Impacts of water deficiency on life history of *Sitobion avenae* clones from semi-arid and moist areas. *Journal of Economic Entomology, 108*, pp. 2250-2258.

Dardeau F., Berthier A., Feinard-Duranceau M., Brignolas F., Laurans F., Lieutier F. & Sallé A. (2015). Tree genotype modulates the effects of water deficit on a plant-manipulating aphid. *Forest Ecology and Management, 353*, pp. 118-125.

De Farias A., Hopper K. & Leclant F. (1995). Damage symptoms and abundance of *Diuraphis noxia* (Homoptera, Aphididae) for 4 wheat cultivars at 3 irrigation levels. *Journal of Economic Entomology, 88*, pp. 169-174.

Foote N., Davis T.S., Crowder DW., Bosque-Pérez NA. & Eigenbrode SD. (2017). Plant water stress affects interactions between an invasive and a naturalized aphid species on cereal crops. *Environmental Entomology, 46*, pp. 609-616.
Gilbert F. (2005). Syrphid aphidophagus predators in a food-web context. *European Journal of Entomology, 102*, pp. 325-333.

Greenslade AFC., Ward JL., Martin JL., Corol DL., Clark SJ., Smart LE. & Aradottir GI. (2016). *Triticum monococcum* lines with distinct metabolic phenotypes and phloem-based partial resistance to the bird cherry-oat aphid *Rhopalosiphum padi*. *Annals of Applied Biology, 168*, pp. 435-449.

Grettenberger I. & Tooker J. (2016). Inter-varietal interactions among plants in genotypically diverse mixtures tend to decrease herbivore performance. *Oecologia, 182*, pp. 189-202.

Guerreri E. & Digilio M. (2008). Aphid-plant interactions: a review. *Journal of Plant Interactions, 3*, pp. 223-232.

Guo H., Sun Y., Peng X., Wang Q., Harris M. & Ge F. (2016). Up-regulation of abscisic acid signaling pathway facilitates aphid xylem absorption and osmoregulation under drought stress. *Journal of Experimental Botany, 67*, pp. 681-693.

Hagen KS. & van den Bosch R. (1968). Impact of pathogens, parasites, and predators on aphids. *Annual Review of Entomology, 13*, pp. 325-384.

Hale B., Bale JS., Pritchard J., Masters GJ. & Brown VK. (2003). Effects of host plant drought stress on the performance of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.): a mechanistic analysis. *Ecological Entomology, 28*, pp. 666-677.

Hatier, J-HB., Faville MJ., Hickey MJ., Koolaard JP., Schmidt B-LC. & Jones CS. (2014). Plant vigour at establishment and following defoliation are both associated with responses to drought in perennial ryegrass (*Lolium perenne* L.). *Journal of Experimental Botany, 65*, pp. 5823-5834.

Higgins J. (2008). Commentary: Heterogeneity in meta-analysis should be expected and appropriately quantified. *International Journal of Epidemiology, 37*, pp. 1158-1160.

Huberty A. & Denno R. (2004). Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology, 85*, pp. 1383-1398.

Inbar M., Doostdar H. & Mayer, R. (2001). Suitability of stressed and vigorous plants to various insect herbivores. *Oikos, 94*, pp. 228-235.

Johnson S., Staley J., McLeod F. & Hartley S. (2011). Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions. *Journal of Ecology, 99*, pp. 57-65.

Kazana E., Pope TW., Tibbles L., Bridges M., Pickett JA., Bones AM., ... Rossiter JT. (2007). The cabbage aphid: a walking mustard oil bomb. *Proceedings of the Royal Society B, 274*, pp. 2271-2277.

Kim H. & Lee S. (2008). A molecular phylogeny of the tribe Aphidini (Insecta: Hemiptera: Aphididae) based on the mitochondrial tRNA/COII, 12S/16S and the nuclear EF1α genes. *Systematic Entomology, 33*, pp. 711-721.

Koricheva J. & Larsson S. (1998). Insect performance on experimentally stressed woody plants: A meta-analysis. *Annual Review of Entomology, 43*, pp. 195-216

Landi P., Minoarivelo H.O., Brännström Å., Hui C. & Dieckmann U. (2018). Complexity and stability of ecological networks: a review of the theory. *Population Ecology, 60*, pp. 319-345.

Leather S.R. (2018) "Ecological Armageddon" - more evidence for the drastic decline in insect numbers. *Annals of Applied Biology, 172*, pp. 1-3.

Lefort M-C., Wratten SD., Cusumano A., Varennes Y-D. & Boyer S. (2017). Disentangling higher trophic level interactions in the cabbage aphid food web using high-throughput DNA sequencing. *Meta-bar-coding and Meta-Genomics, 1*, e13709.
Leybourne DJ., Valentine TA., Robertson J., Perea-Fernandez E., Main AM., Karley AJ. & Bos JIB. (2019). Defence gene expression and phloem quality contribute to mesophyll and phloem resistance to aphids in wild barley. *Journal of Experimental Botany*, 70, pp. 4011-4026.

Luo D., Wan X., Liu J. & Tong T. (2018). Optimally estimating the sample mean from the sample size, median, mid-range, and/or mid-quartile range. *Statistical Methods in Medical Research*, 27, pp. 1785-1790.

McQuaid C. & Britton N. (2015). Parasite species richness and its effect on persistence in food webs. *Journal of Theoretical Biology*, 364, pp. 377-382.

Messelin G., Sabelis MW. & Janssen A. (2012). Generalist predators, food web complexities and biological pest control in greenhouse crops. In: M. Larramendi & S. Soloneski, eds. *Integrated pest management and pest control - current and future tactics*: IntechOpen, pp. 191-214.

Mewis I., Khan MAM., Glawischnig E., Schreiner M. & Ulrichs C. (2012). Water stress and aphid feeding differentially influence metabolite composition in *Arabidopsis thaliana* (L.). *PLoS ONE*, 7, e48661.

Mody K., Eichenberger D. & Dorn S. (2009). Stress magnitude matters: different intensities of pulsed water stress produce non-monotonic resistance responses of host plants to insect herbivores. *Ecological Entomology*, 34, pp. 133-143.

Moher D., Liberati A., Tetzlaff J. & Altman DG. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *BMJ*, 339, e2535.

Nakagawa S., Noble WAN., Senior AM. & Lagisz M. (2017). Meta-evaluation of meta-analysis: ten appraisal questions for biologists. *BMC Biology*, 15, e18.

Nguyen T., Michaud D. & Cloutier C. (2007). Proteomic profiling of aphid *Macrosiphum euphorbiae* responses to host-plant-mediated stress induced by defoliation and water deficit. *Journal of Insect Physiology*, 53, pp. 601-611.

Offenberg J., Nielsen MG., MacIntosh DJ., Havanon S. & Aksomkoae S. (2004). Evidence that insect herbivores are deterred by ant pheromones. *Proceedings of the Royal Society B*, 271, pp. S433-S435.

Orwin R. (1983). A fail-safe n for effect size in meta-analysis. *Journal of Educational Statistics*, 8, pp. 157-159.

Osakabe Y., Osakabe K., Shinozaki K. & Trans L-S. (2014). Response of plants to water stress. *Frontiers in plant Science*, 5, p. 86.

Oswald C. & Brewer M. (1997). Aphid-barley interactions mediated by water stress and barley resistance to Russian wheat aphid (Homoptera: Aphididae). *Environmental Entomology*, 26, pp. 591-602.

Ozturk Z., Talamé V., Deyholos M., Michalowski CB., Galbraith DW., Gozukirmiz N., ... Bohnert HJ. (2002). Monitoring large-scale changes in transcript abundance in drought- and salt-stressed barley. *Plant Molecular Biology*, 48, pp. 551-573.

Pons X. & Tatchel G. (1995). Drought stress and cereal aphid performance. *Annals of Applied Biology*, 126, pp. 19-31.

Preedy K., Chaplain MA., Leybourne DJ., Marion G. & Karley AJ. (2020). Learning-induced switching costs in a parasitoid can maintain diversity of host aphid phenotypes although biocontrol is destabilized under abiotic stress. *Journal of Animal Ecology*, 89, pp. 1216-1229.

Quandahor P., Lin C., Gou Y., Coulter J. & Liu C. (2019). Leaf morphological and biochemical responses of three potato (*Solanum tuberosum* L.) cultivars to drought stress and aphid (*Myzus persicae* Sulzer) infestation. *Insects*, 10, 435.
Ramierez C. & Verdujo J. (2009). Water availability affects tolerance and resistance to aphids but not the trade-off between the two. *Ecological Research*, **24**, pp. 881-888.

Rodriguez-Castañeda G. (2013). The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecology and Biogeography*, **22**, pp. 118-130.

Romo C. & Tylianakis J. (2013). Elevated temperature and drought interact to reduce parasitoid effectiveness in suppressing hosts. *PLOS ONE*, **8**, p. e58136.

Rosumek F., Silveira FAO., Never F de S., Barbosa NP de U., Diniz L., Oki Y., ... Cornelissen T. (2009). Ants on plants: a meta-analysis of the role of ants as plant biotic defenses. *Oecologia*, **160**, pp. 537-549.

Roubinet E., Jonsson T., Malsher G., Staudacher K., Traugott M., Ekborn B. & Jonsson M. (2018). High redundancy as well as complementary prey choice characterise generalist predator food webs in agroecosystems. *Scientific Reports*, **8**, p. 8054.

Sandström J., Telang A. & Moran N. (2000). Nutritional enhancement of host plants by aphids-a comparison of three aphid species on grasses. *Journal of Insect Physiology*, **46**, pp. 33-40.

Santos A., Belo-Pereira M., Fraga H. & Pinto J. (2016). Understanding climate change projections for precipitation over western Europe with a weather typing approach. *Journal of Geophysical Research: Atmospheres*, **121**, pp. 1170-1189.

Saunders ME., Janes JK., & O’Hanlon JC. (2020). Moving on from the insect apocalypse narrative: engaging with evidence-based insect conservation. *BioScience*, **70**, pp. 80-89.

Roulain E., Jonsson T., Malsher G., Staudacher K., Traugott M., Ekborn B. & Jonsson M. (2018). High redundancy as well as complementary prey choice characterise generalist predator food webs in agroecosystems. *Scientific Reports*, **8**, p. 8054.

Teixeira N., Valim J., Oliveira M. & Campos W. (2020). Combined effects of soil silicon and drought stress on plant chemical and ultrastructural quality for leaf-chewing and sap-sucking insects. *Journal of Agronomy and Crop Science*, **206**, pp. 187-201.

Templer SE., Ammon A., Pschedt D., Gobotaa O., Schuy C., McCollum C., ... Voll LM. (2017). Metabolite profiling of barley flag leaves under drought and combined heat and drought stress reveals metabolic QTLs for metabolites associated with antioxidant defense. *Journal of Experimental Botany*, **68**, pp. 1697-1713.

Traugott M., Bell JR., Broad GR., Powell W., van Veen FJJ., Vollhardt IMG. & Symondson WOC. (2008). Endoparasitism in cereal aphids: molecular analysis of a whole parasitoid community. *Molecular Ecology*, **17**, pp. 3928-3938.

Van Emden H. & Harrington R. (2017). *Aphids as crop pests*. Wallingford: CABI Publishing.
Data accessibility statement

Data will be uploaded to the Dryad data repository upon acceptance of the manuscript for publication.
### Table 1: information on the aphid species included in the meta-analysis, the agricultural and ecological importance of each species, and the number of data points present in the “Expanded” dataset.

| Aphid species | Common name               | Aphid tribe / Specialism (generalist or specialist) | Agricultural and ecological importance                                                                 | Number of data points: “Expanded” dataset and study from which data were extracted |
|---------------|---------------------------|------------------------------------------------------|----------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------|
| *Adelges abietis* Linnaeus | Eastern spruce gall aphid | Adelgini (Other) / Specialist                        | Common pest of Norway and Sitka spruce. Stem-mother forms pineapple-shaped gall.                        | 2 datapoints from studies 10 and 11                                              |
| *Aphis glycines* Matsumura | Soybean aphid             | Aphidini / Specialist                                | Significant pest of soybean across North America and Asia                                              | 1 datapoint from study 31                                                        |
| *A. pomi* DeGeer | Apple aphid               | Aphidini / Specialist                                | Significant pest of apple trees, specifically on nursery stock. Colonies can be attended by ants       | 1 datapoint from study 29                                                        |
| *Acyrthosiphon pism* (Harris) | Pea aphid                | Macrosiphini / Generalist                            | Widespread in temperate regions. Serious pest of the Fabaceae. Vector of over 30 plant viruses       | 4 datapoints from studies 7, 20, 26, 43                                            |
| *Brevicoryne brassicae* (Linnaeus) | Cabbage aphid             | Macrosiphini / Generalist                            | Wax-covered aphid. Widely distributed throughout Europe, major pest of Brassicaceae                   | 8 datapoints from studies 23, 37, 47, 48, 49,                                      |
| *Cinara costata* (Zetterstedt) | Mealy spruce aphid        | Eulachnini (Other) / Specialist                      | Wax-covered aphid. Can cause damage to spruce trees. Unlike other *Cinara* spp. *C. costata* is not readily attended by ants. | 1 datapoint from study 24                                                        |
| *C. pinea* (Mordvilko) | Large pine aphid          | Eulachnini (Other) / Specialist                      | Forestry pest of Scots pine and other *Pinus* spp. Often found on young pine trees.                   | 1 datapoint from study 32                                                        |
| *Chaitophorus leucomelas* Koch | Black polar leaf aphid    | Chaitophornini (Other) / Specialist                  | A widely distributed pest of poplar. Colonies can reside in the galls formed by other insects and can occasionally be attended by ants. | 1 datapoint from study 39                                                        |
| *Diuraphis noxia* (Mordvilko) | Russian wheat aphid       | Macrosiphini / Specialist                            | A significant cereal pest in South Africa and North America. Vector of barley yellow dwarf virus.     | 3 datapoints from studies 2, 16, 34                                               |
| *Dysaphis plantagin* (Passerini) | Rosy apple aphid          | Macrosiphini / Specialist                            | Widely distributed across temperate regions and a significant pest of apples. Colonies develop in galls and are attended by ants. | 1 datapoint from study 41                                                        |
| *Elatobium abietinum* (Walker) | Green spruce aphid        | Macrosiphini / Specialist                            | Distributed across Europe and North America. Can cause economic and environmental damage by causing needle defoliation on Spruce trees. | 6 datapoints from studies 2, 4, 5, 6                                              |
| *Lipaphis erysimi* (Kaltenbach) | Wild crucifer aphid       | Macrosiphini / Specialist                            | Can feed on various Brassicaceae crops.                                                              | 1 datapoint from study 23                                                        |
| Species                                              | Subspecies                | Aphid Family         | Status          | Description                                                                                                                                                                                                 | Data Points from Studies |
|------------------------------------------------------|---------------------------|----------------------|-----------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------|
| *Macrosiphum euphorbiae* (Thomas)                    | Potato aphid              | Macrosiphini / Generalist | A significant pest species with worldwide distribution. Can cause significant economic damage through the transmission of over 20 plant viruses. | 7 datapoints from studies 8, 33, 40                                                                                                                                   |
| *Metopolophium festucae* subsp. *Cerealium* (Theobald) | Fescue aphid              | Macrosiphini / Specialist | A subspecies of *M. festucae* which can be a significant pest of cereals and grasses. | 2 datapoints from study 18                                                                                                                                         |
| *Myzus persicae* (Sulzer)                            | Peach-potato aphid        | Macrosiphini / Generalist | Significant pest with worldwide distribution. Broad host range. Can cause significant economic damage through the transmission of over 40 plant viruses. | 12 datapoints from studies 27, 35, 38, 44, 47, 48, 49, 50                                                                                                         |
| *Pemphigus betae* Doane                              | Sugarbeet root aphid      | Hormaphidini (Other) / Specialist | Root-feeding aphid, a main economic pest of sugar beet. | 2 datapoints from study 30                                                                                                                                         |
| *Phloeomyzus passerinii* (Signoret)                  | Poplar woolly aphid       | Phloeomyzinae (Other) / Specialist | Distributed in temperate regions. Significant economic pest of poplar. | 1 datapoint from study 14                                                                                                                                         |
| *Rhopalosiphum maidis* (Fitch)                       | Green corn aphid          | Aphidini / Specialist   | Widely distributed worldwide. A significant pest of cereals. Commonly attended by ants. Vector of several plant viruses. | 2 datapoints from studies 34, 42                                                                                                                                       |
| *R. padi* (Linnaeus)                                 | Bird cherry-oat aphid     | Aphidini / Specialist   | Widely distributed worldwide, a significant pest of cereals and a vector of numerous plant viruses. Populations on the primary host can be attended by ants. | 18 datapoints from studies 3, 9, 15, 18, 19, 21, 28, 53, 55                                                                                                          |
| *Sitobion avenae* Fabricius                         | Wheat aphid               | Macrosiphini / Specialist | Widespread pest of cereals with worldwide distribution. A vector of several economically important plant viruses. | 16 datapoints from 1, 13, 17, 25, 36, 46, 51, 54                                                                                                                     |
| *Sipha maydis* Passerini                             | Bristly black grass aphid | Siphini (Other) / Specialist | Widely distributed pest that feeds on numerous Poaceae species, including cultivated crops and perennial grasses. Can be attended by ants. | 1 datapoint from 28                                                                                                                                             |
| *Schizaphis graminum* (Rondani)                      | Spring green aphid        | Aphidini / Specialist   | Widely distributed pest of cereals. Can vector a range of plant viruses. | 1 datapoint from study 12                                                                                                                                         |
| *Theroaphis trifolii* (f. maculate) (Buckton)        | Spotted alfalfa aphid     | Panaphidina (Other) / Specialist | Widespread pest of Fabaceae. | 1 datapoint from study 7                                                                                                                                          |

688 □ Full study references are contained in Appendix 2

689
Figures and Figure Legends

**Fig. 1:** PRISMA diagram
Fig. 2: The number of studies reporting negative, positive, or null effects of drought stress on aphid fitness. Bars are coloured to indicate the proportion of studies in each category that were included in the full meta-analysis (Orange) vs those in the complete dataset (Blue).
**Fig. 3:** Effect of the plant-aphid system on overall aphid responses to drought stress conditions using the “global” dataset where response variables were pooled to produce one effect size per study. Graph displays the mean effect size (Hedges’ g) and the 95% confidence intervals for the different plant-aphid systems identified from the extracted data. Red dashed line represents zero effect size.
Fig. 4: Responses of aphids to drought stress using the “expanded” dataset which included an effect size per response variable and for each aphid species measured in each study. Main graph displays the mean effect size (Hedges’ g) and the 95% confidence intervals for the different plant-aphid systems identified from the extracted data. Insert displays the mean effect size (Hedges’ g) and the 95% confidence intervals for the combined data. Red dashed line represents zero effect size.
**Fig. 5:** The effect of drought stress on plant vigour using the “plant” dataset where measures of plant vigour (vigour), N or amino acid (AA) concentration (N/AA Content), or tissue concentrations of defensive compounds (Defensive) were reported. Graph displays the mean effect size (Hedges’ g) and the 95% confidence intervals for the different plant-aphid systems identified from the extracted data. Red dashed line represents zero effect size.
Fig. 6: Conceptual representation of the Plant Resistance Hypothesis (PRH). As water availability decreases plant defence increases and plant vigour declines, leading to reduced aphid fitness. Basal levels of aphid fitness under conditions of ample water availability differ between the susceptible (S, green line) and the resistant (R, grey line) plant types. Under drought, aphid fitness is reduced on both plant types, however the extent of this reduction is greater for the susceptible plant (high to low fitness) than the resistant plant (intermediate to low fitness). This image made in BioRender © - biorender.com
Appendices

Appendix 1: References for the 25 studies which were included in the “vote-counting” analysis but excluded from the full meta-analysis

1. Agele SO., Ofuya TI. & James PO. (2006). Effects of watering regimes on aphid infestation and performance of selected varieties of cowpea (Vigna unguiculata L. Walp) in a humid rainforest zone of Nigeria. Crop Protection 25, 73-78.

2. Banfield-Zanin JA. & Leather SR. (2014). Frequency and intensity of drought stress alters the population size and dynamics of Elatobium abietinum on Sitka spruce. Annals of Applied Biology 165, 260-269.

3. Björkman C. (2000). Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. Oecologia 123, 223-231

4. Braun S. & Flückiger W. (1984). Increased population of the aphid Aphis pomi at a motorway. Part 2-The effect of drought and deicing salt. Environmental Pollution. Series A, Ecological and Biological, 36, 261-270

5. DeVries NEL. & Manglitz GR. (1982). Spotted alfalfa aphid (Theroiophis maculata (Buckton)) (Homoptera: Aphididae): water stress, amino acid content and plant resistance. Journal of the Kansas Entomological Society 55, 38-42.

6. Forbes AE., Harvey CT. & Tilmon KJ. (2005). Variation in the responses of spotted alfalfa aphids, Theroiophis maculata Buckton (Homoptera: Aphididae) and pea aphids, Acrystosiphon pisum Harris (Homoptera: Aphididae) to drought conditions in alfalfa (Medicago sativa L., Fabaceae). Journal of the Kansas Entomological Society, 78, 387-389

7. Gange AC. & Brown VK. (1989). Effects of root herbivory by an insect on a foliar-feeding species, mediated through changes in the host plant. Oecologia, 81, 38-42.

8. Karley AJ., Emslie-Smith M. & Bennett AE. (2017). Potato aphid Macrosiphum euphorbiae performance is determined by aphid genotype and not mycorrhizal fungi or water availability. Insect Science, 24, 1015 - 1024.

9. Kennedy JS., Lamb KP. & Booth CO. (1958). Responses of Aphis fabae Scop. to water shortage in host plants in pots. Entomologia Experimentalis et Applicata, 1, 274-290.

10. Khan MAM., Ulrichs C. & Mewis I. (2010). Influence of water stress on the glucosinolate profile of Brassica oleracea var. italica and the performance of Brevicoryne brassicae and Myzus persicae. Entomologia Experimentalis et Applicata, 137, 229-236.

11. Khan MAM., Ulrichs C. & Mewis I. (2011a). Drought stress - impact on glucosinolate profile and performance of phloem feeding cruciferous insects. In: Hale C, ed. Xxviii International Horticultural Congress on Science and Horticulture for People, 111-117.

12. Khan MAM., Ulrichs C. & Mewis I. (2011b). Effect of water stress and aphid herbivory on flavonoids in broccoli (Brassica oleracea var. italica Plenck). Journal of Applied Botany and Food Quality-Angewandte Botanik, 84, 178-182.

13. Latimer JG & Oetting RD. (1994). Brushing reduces thrips and aphid populations on some greenhouse-grown vegetable transplants. Hortscience, 29, 1279-1281.

14. McMurtry J. (1962). Resistance of alfalfa to spotted alfalfa aphid in relation to environmental factors. Hilgardia 32, 501-539. DOI:10.3733/hilg.v32n12p501

15. Michels GJ Jr. & Undersander DJ. (1986). Temporal and spatial distribution of the Greenbug (Homoptera: Aphididae) on sorghum in relation to water stress. Journal of Economic Entomology 79, 1221-1225.
16. Miles P., Aspinall D. & Rosenberg L. (1982). Performance of the cabbage aphid, *Brevicoryne brassicae* (L.), on water-stressed rape plants, in relation to changes in their chemical composition. *Australian Journal of Zoology*, **30**, 337-346.

17. Pons X. & Tatchell GM. (1995). Drought stress and cereal aphid performance. *Annals of Applied Biology*, **126**, 19-31.

18. Romo CM. & Tylianakis JM. (2013). Elevated temperature and drought interact to reduce parasitoid effectiveness in suppressing hosts. *PLoS ONE*, **8**.

19. Salas ML. & Corcuera LJ. (1991). Effect of environment on gramine content in barely leaves and susceptibility to the aphid *Schizaphis graminum*. *Phytochemistry*, **30**, 3237–3240.

20. Service PM. & Lenski RE. (1982). Aphid genotypes, plant phenotypes, and genetic diversity: a demographic analysis of experimental data. *Evolution*, **36**, 1276–1282.

21. Teixeira N., Valim J., Oliveira M. & Campos W. (2020). Combining effects of soil silicon and drought stress on host plant chemical and ultrastructural quality for leaf-chewing and sap-sucking insects. *Journal of Agronomy and Crop Science*, **206**, 187-201.

22. Volpe V., Chitarra W., Cascone P., Volpe MG., Bartolini P., Moneti G., … Balestrini R. (2018). The association with two different arbuscular mycorrhizal fungi differently affects water stress tolerance in tomato. *Frontiers in Plant Science*, **9**.

23. Wearing CH. (1967). Studies on the relations of insect and host plant: ii. effects of water stress in host plants on the fecundity of *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.). *Nature*, **213**, 1052-1053.

24. Wearing CH. (1972). Responses of *Myzus persicae* and *Brevicoryne brassicae* to leaf age and water stress in brussels sprouts grown in pots. *Entomologia Experimentalis et Applicata*, **15**, 61-80.

25. Wearing CH. & Van Emden HF. (1967). Studies on the relations of insect and host plant: i. effects of water stress in host plants on infestation by *Aphis fabae* Scop, *Myzus persicae* (Sulz.) and *Brevicoryne brassicae* (L.). *Nature*, **213**, 1051-1052.
Appendix 2: References for the 55 studies which were included in the full meta-analysis. Indicates which studies contained more than one data point when split into the "expanded responses" dataset. * Indicates which studies reported on plant physiological, defensive, or nutritional responses for inclusion in the plant meta-analysis

1. Ahmed SS., Liu D. & Simon J-C. (2017). Impact of water-deficit stress on tritrophic interactions in a wheat-aphid-parasitoid system. *PLoS ONE*, 12, e0186599.

2. Archer TL., Bynum ED., Onken AB. & Wendt CW. (1995). Influence of water and nitrogen fertilizer on biology of the Russian wheat aphid (Homoptera: Aphididae) on wheat. *Crop Protection*, 14, 165-169. *

3. Aslam TJ., Johnson SN. & Karley AJ. (2013). Plant-mediated effects of drought on aphid population structure and parasitoid attack. *Journal of Applied Entomology*, 137, 136-145. *

4. Banfield-Zanin JA. & Leather SR. (2015A). Drought intensity and frequency have contrasting effects on development time and survival of the green spruce aphid. *Agricultural and Forest Entomology*, 17, 309-316. *

5. Banfield-Zanin JA. & Leather SR. (2015B). Reproduction of an arboreal aphid pest, *Elatobium abietinum*, is altered under drought stress. *Journal of Applied Entomology*, 139, 302-313.

6. Banfield-Zanin JA & Leather SR. (2015C). Season and drought stress mediate growth and weight of the green spruce aphid on Sitka spruce. *Agricultural and Forest Entomology*, 17, 48-56. *

7. Barton BT. & Ives AR. (2014). Species interactions and a chain of indirect effects driven by reduced precipitation. *Ecology*, 95, 486-494. *

8. Beetge L. & Kruger K. (2019). Drought and heat waves associated with climate change affect performance of the potato aphid *Macrosiphum euphorbiae*. *Scientific Reports*, 9. *

9. Bultman TL. & Bell GD. (2003). Interaction between fungal endophytes and environmental stressors influences plant resistance to insects. *Oikos*, 103, 182-190. *

10. Björkman C. (2000). Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. *Oecologia*, 123, 223-231 *

11. Björkman C. (1998). Opposite, linear and non-linear effects of plant stress on a galling aphid. Scandinavian *Journal of Forest Research*, 13, 177-183 *

12. Cabrera HM., Argandona VH., Zuniga GE. & Corcuera LJ. (1995). Effect of infestation by aphids on the water status of barley and insect development. *Phytochemistry*, 40, 1083-1088. *

13. Dai P., Liu D. & Shi X. (2015). Impacts of Water Deficiency on Life History of *Sitobion avenae* Clones from Semi-arid and Moist Areas. *Journal of Economic Entomology*, 108, 2250-2258. *

14. Dardeau F., Berthier A., Feinard-Duranceau M., Brignolas F., Laurans F., Lieutier F. & Salle A. (2015). Tree genotype modulates the effects of water deficit on a plant-manipulating aphid. *Forest Ecology and Management*, 353, 118-125. *

15. Davis TS., Bosque-Pérez NA., Foote NE., Magney T. & Eigenbrode SD. (2015). Environmentally dependent host–pathogen and vector–pathogen interactions in the *Barley yellow dwarf virus* pathosystem. *Journal of Applied Ecology*, 52, 1392-1401. *

16. De Farias AMI., Hopper KR. & Leclant F. (1995). Damage symptoms and abundance of *Diuraphis noxia* (homoptera, aphididae) for 4 wheat cultivars at 3 irrigation levels. *Journal of Economic Entomology*, 88, 169-174.
17. Fereres A., Gutierrez C., Del Estal P. & Castañera P. (1988). Impact of the English Grain Aphid, Sitobion avenae (F.) (Homoptera: Aphididae), on the Yield of Wheat Plants Subjected to Water Deficits. *Environmental Entomology, 17*, 596-602.

18. Foote NE., Davis TS., Crowder DW., Bosque-Perez NA. & Eigenbrode SD. (2017). Plant Water Stress Affects Interactions Between an Invasive and a Naturalized Aphid Species on Cereal Crops. *Environmental Entomology, 46*, 609-616.

19. Grettenberger IM. & Tooker JF. (2016). Inter-varietal interactions among plants in genotypically diverse mixtures tend to decrease herbivore performance. *Oecologia, 182*, 189-202.

20. Guo H., Sun Y., Peng X., Wang Q., Harris M. & Ge F. (2016). Up-regulation of abscisic acid signaling pathway facilitates aphid xylem absorption and osmoregulation under drought stress. *Journal of experimental botany, 67*, 681-693.

21. Hale BK., Bale JS., Pritchard J., Masters GJ. & Brown VK. (2003). Effects of host plant drought stress on the performance of the bird cherry-oat aphid, Rhopalosiphum padi (L.): a mechanistic analysis. *Ecological Entomology, 28*, 666-677.

22. Johnson SN., Staley JT., McLeod FAL. & Hartley SE. (2011). Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions. *Journal of Ecology, 99*, 57-65.

23. King C., Jacob HS. & Berlander F. (2006). The influence of water deficiency on the relationship between canola (Brassica napus L.), and two aphid species (Hemiptera : Aphididae), Lipaphis erysimi (Kaltenbach) and Brevicoryne brassicae (L.). *Australian Journal of Agricultural Research, 57*, 439-445.

24. Larsson S. & Bjorkman C. (1993). Performance of chewing and phloem-feeding insects on stressed trees. *Scandinavian Journal of Forest Research, 8*, 550-559.

25. Liu D., Dai P., Li S., Ahmed SS., Shang Z. & Shi X. (2018). Life-history responses of insects to water-deficit stress: a case study with the aphid Sitobion avenae. *BMC Ecology, 18*.

26. McVean RIK. & Dixon AFG. (2001). The effect of plant drought-stress on populations of the pea aphid Acyrthosiphon pisum. *Ecological Entomology, 26*, 440-443.

27. Mewis I., Khan MAM., Glawischnig E., Schreiner M. & Ulrichs C. (2012). Water Stress and Aphid Feeding Differentially Influence Metabolite Composition in Arabidopsis thaliana (L.). *PLoS ONE, 7*, e48661.

28. Miranda IM., Omacini M. & Chaneton EJ. (2011). Environmental context of endophyte symbioses: Interacting effects of water stress and insect herbivory. *International Journal of Plant Sciences, 172*, 499-508.

29. Mody K., Eichenberger D. & Dorn S. (2009). Stress magnitude matters: different intensities of pulsed water stress produce non-monotonic resistance responses of host plants to insect herbivores. *Ecological Entomology, 34*, 133-143.

30. Moran NA. & Whitham TG. (1988). Population Fluctuations in Complex Life Cycles: An Example from Pemphigus Aphids. *Ecology, 69*, 1214-1218.

31. Nachappa P., Culkin CT., Saya PM., Han J. & Nalam VJ. (2016). Water Stress Modulates Soybean Aphid Performance, Feeding Behavior, and Virus Transmission in Soybean. *Frontiers in Plant Science, 7*, 552.

32. Neuvonen S., Routio I. & Haukioja E. (1992). Combined effects of simulated acid rain and aphid infestation on the growth of Scots pine (Pinus sylvestris) seedlings. *Annales Botanici Fennici, 29*, 101-106.

33. Nguyen TTA., Michaud D. & Cloutier C. (2007). Proteomic profiling of aphid Macrosiphum euphorbiae responses to host-plant-mediated stress induced by defoliation and water deficit. *Journal of Insect Physiology, 53*, 601-611.
34. Oswald CJ. & Brewer MJ. (1997). Aphid-barley interactions mediated by water stress and barley resistance to Russian wheat aphid (Homoptera: Aphididae). *Environmental Entomology, 26*, 591-602.

35. Pineda A., Pangesti N., Soler R., van Dam NM., van Loon JJA. & Dicke M. (2016). Negative impact of drought stress on a generalist leaf chewer and a phloem feeder is associated with, but not explained by an increase in herbivore-induced indole glucosinolates. *Environmental and Experimental Botany, 123*, 88-97.

36. Pons C., Voß A-C., Schweiger R. & Müller C. (2020). Effects of drought and mycorrhiza on wheat and aphid infestation. *Ecology and Evolution, 10*, 10481-10491

37. Prill N., Bullock JM., van Dam NM. & Leimu R. (2014). Loss of heterosis and family-dependent inbreeding depression in plant performance and resistance against multiple herbivores under drought stress. *Journal of Ecology, 102*, 1497-1505.

38. Quandahor P., Lin C., Gou Y., Coulter J. & Liu C. (2019). Leaf morphological and biochemical responses of three potato (Solanum tuberosum L.) cultivars to drought stress and aphid (Myzus persicae Sulzer) infestation. *Insects, 10*, 435

39. Ramirez CC. & Verdugo JA. (2009). Water availability affects tolerance and resistance to aphids but not the trade-off between the two. *Ecological Research, 24*, 881-888.

40. Rivelli A., Trotta V., Toma I., Fanti P. & Battaglia D. (2013). Relation between plant water status and Macrosiphum euphorbiae (Hemiptera: Aphididae) population dynamics on three cultivars of tomato. *European Journal of Entomology, 110*, 617-625.

41. Rousselin A., Bevacqua D., Vercambre G., Sauge MH., Lescourret F. & Jordan MO. (2018). Rosy apple aphid abundance on apple is shaped by vegetative growth and water status. *Crop Protection, 105*, 1-9.

42. Rudgers JA. & Swafford AL. (2009). Benefits of a fungal endophyte in Elymus virginicus decline under drought stress. *Basic and Applied Ecology, 10*, 43-51.

43. Ryalls JMW., Moore BD., Riegler M. & Johnson SN. (2016). Above-Below ground Herbivore Interactions in Mixed Plant Communities Are Influenced by Altered Precipitation Patterns. *Frontiers in Plant Science, 7*.

44. Simpson KLS., Jackson GE. & Grace J. (2012). The response of aphids to plant water stress – the case of Myzus persicae and Brassica oleracea var. capitata. *Entomologica Experimentalis et Applicata, 142*, 191-202.

45. Smyrnioudis IN., Harrington R., Karis N. & Clark SJ. (2000). The effect of drought stress and temperature on spread of barley yellow dwarf virus (BYDV). *Agricultural and Forest Entomology, 2*, 161-166

46. Tamburini G., van Gils S., Kos M., van der Putten W. & Marini L. (2018). Drought and soil fertility modify fertilization effects on aphid performance in wheat. *Basic and Applied Ecology, 30*, 23-31.

47. Tariq M., Wright DJ., Bruce TJA & Staley JT. (2013A). Drought and Root Herbivory Interact to Alter the Response of Above-Ground Parasitoids to Aphid Infested Plants and Associated Plant Volatile Signals. *PLoS ONE, 8*.

48. Tariq M., Rossiter JT., Wright DJ. & Staley JT. (2013B). Drought alters interactions between root and foliar herbivores. *Oecologia, 172*, 1095-1104.

49. Tariq M., Wright DJ., Rossiter JT. & Staley JT. (2012). Aphids in a changing world: testing the plant stress, plant vigour and pulsed stress hypotheses. *Agricultural and Forest Entomology, 14*, 177-185.

50. Verdugo JA., Sauge MH., Lacroze JP., Francis F. & Ramirez CC. (2015). Drought-stress and plant resistance affect herbivore performance and proteome: the case of
the green peach aphid *Myzus persicae* (Hemiptera: Aphididae). *Physiological Entomology, 40*, 265-276.

51. Wade RN., Karley AJ., Johnson SN. & Hartley SE. (2017). Impact of predicted precipitation scenarios on multitrophic interactions. *Functional Ecology, 31*, 1647-1658.

52. Warrington S. & Whittaker JB. 1990. Interactions between sitka spruce, the green spruce aphid, sulfur-dioxide pollution and drought. *Environmental Pollution, 65*, 363-370.

53. Xing GM., Zhang J., Liu J., Zhang XY., Wang GX. & Wang YF. (2003). Impacts of atmospheric CO2 concentrations and soil water on the population dynamics, fecundity and development of the bird cherry-oat aphid *Rhopalosiphum padi*. *Phytoparasitica, 31*, 499-514.

54. Xie H., Shi J., Shi F., Wang X., Xu H., He K. & Wang Z. (2020). Aphid fecundity and defences in wheat exposed to a combination of heat and drought stress. *Journal of Experimental Botany, 71*, 2713-2722.

55. Yule KM., Woolley JB. & Rudgers JA. (2011). Water availability alters the tri-trophic consequences of a plant-fungal symbiosis. *Arthropod-Plant Interactions, 5*, 19-27.