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

Running title: Aphid-plant interactions under drought stress

Daniel J Leybourne [1,2,3Ŧ], Katharine F Preedy [4], Tracy A Valentine [2,], Jorunn IB Bos [1,3] & Alison J Karley [2*]

[1] Division of Plant Science, School of Life Science. Dundee University, Dundee. UK

[2] Ecological Science, The James Hutton Institute. Invergowrie, Dundee. UK

[3] Cell and Molecular Science, The James Hutton Institute. Invergowrie, Dundee. UK

[4] Biomathematics and Statistics Scotland. Invergowrie, Dundee. UK

Ŧ Current address: ADAS High Mowthorpe, Duggleby, Malton, North Yorkshire, YO17 8BP, UK

[*] Author for correspondence

Funding

DJL was funded by the James Hutton Institute and the Universities of Aberdeen and Dundee through a Scottish Food Security Alliance (Crops) PhD studentship. The James Hutton Institute is supported by the Scottish Government Rural and Environment Science and Analytical Services.

Author contributions

AJK, DJL, and KFP conceived and designed the study. DJL extracted and analysed the data, with input from KFP. All authors contributed to data interpretation. DJL wrote the manuscript with input from all authors. All authors read and approved the final manuscript.

Conflict of interest

The authors declare no conflict of interest.

Abstract

Aphids are a common and widely distributed group of phloem-feeding insects and are abundant components of insect communities in natural and managed ecosystems. It is anticipated that a changing climate will lead to more frequent periods of drought, which will have consequences for the biology and ecology of these ubiquitous species and the foodwebs they support. To date there has been no comprehensive assessment of the literature to determine the extent to which drought negatively affects aphid fitness. For the first time, we qualitatively and quantitatively assess the literature to determine whether drought stress has an overall negative, positive, or null effect on aphid fitness in terms of development, fecundity, survival and abundance. The underlying causes of changes in aphid fitness are assessed by examining measures of plant growth, nutrition, and defence in relation to the predictions of the plant vigour hypothesis. The meta-analysis indicates that aphid fitness is typically reduced under drought stress, and this is mediated by a reduction in plant vigour and an increase in allocation to defence in drought-stressed plants. We discuss the ecological consequences of increased drought frequency for aphid success, plant resistance against aphids, and aphid-trophic interactions in natural and agricultural systems.

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 et al., 2016). For areas which do not regularly experience prolonged periods of water deprivation, such as temperate regions, prolonged drought conditions can have severe consequences on plant physiology, often leading to reduced growth and photosynthetic capacity (Osakabe et al., 2014; Zeppel et al., 2014). Changes in plant physiology in response to drought stress can directly influence the population dynamics, fitness, phenology, and biology of herbivorous insects (Huberty & Denno 2004; Mody et al., 2009; Aslam et al., 2013), with consequences that cascade through trophic networks (Johnson et al., 2011; Rodríguez-Castañeda 2013).

Previous meta-analyses have examined drought effects by comparing responses of herbivorous insect species with different feeding strategies (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 due to their near-worldwide distribution, ability to colonise most habitat types, and capacity to vector plant viruses (Van Emden & Harrington 2017). There are over 4400 known species of aphid (Blackman & Eastop 2000) and many of these are major agricultural and horticultural pests, making them an economically important group of herbivorous insects. Aphids are abundant components of insect communities in diverse ecosystems across the globe (Messelink et al., 2012; Roubinet et al., 2018). In many ecosystems, aphids sustain several higher trophic groups, including the primary consumers of aphids, such as parasitoid wasps, spiders, ladybirds, and carabid beetles (Staudacher et al., 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 a range of 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 (Romo & Tylianakis 2013; Teixeira et al., 2020)

The effect of drought stress on aphid fitness has been investigated experimentally across many aphid-plant systems (Pons & Tatchell 1995; Agele et al., 2006; Mody et al., 2009; Aslam et al., 2013; Grettenberger & Tooker 2016; Foote et al., 2017), with numerous studies indicating that aphids are negatively affected by drought stress. To date, there has been no

comprehensive analysis of the causes of decreased aphid fitness under drought stress, although several studies suggest that it is mediated through reduced plant fitness (Hale et al., 2003; Banfield-Zanin & Leather, 2015; Dai et al., 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) assessed the responses of herbivorous insects from different feeding guilds to drought stress conditions and found limited 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); conversely, their analysis showed that drought stress typically has negative effects on herbivorous insect fitness and abundance. Second, Cornelissen et al., (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 or plant tissues. These findings lead us to hypothesise that the effects of drought stress on aphid fitness and abundance are driven by decreased plant vigour rather than stress-related changes in plant nutritional quality.

Although the majority of studies have reported reduced aphid fitness when exposed to drought stressed host plants (Banfield-Zanin & Leather, 2015; Dai et al., 2015; Foote et al., 2017), several studies have reported null (Mewis et al., 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 (1997) a positive effect of drought stress on aphid fitness was detected in the Russian wheat aphid, *Diuraphis noxia*, and a negative effect was reported for the corn leaf aphid, *Rhopalosiphum maidis*. Although both of these 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 et al., 2018). The findings of Oswald and Brewer (1997) suggest that differences in aphid biology and/or life history could underlie contrasting responses to drought stress. Additionally, the specific aphid-plant combination could further influence the effects of drought stress on aphid fitness. For example, multiple aphid species exhibit contrasting responses to drought stress on a common plant host (Mewis et al., 2012) and a single aphid species can display contrasting responses to drought stress on several related host plant species (Hale et al., 2003). These findings suggest that the specific aphid-plant combination could be a key factor in mediating aphid responses to drought stress, with differences likely to be driven by plant species-specific responses to drought (i.e. the

availability of nutrients, the abundance and concentration of defensive compounds, resource allocation to new tissue growth). Understanding these mechanisms is necessary to predict the outcomes of plant-insect interactions under changing climatic conditions.

Here, we take the novel approach of analysing data on aphid fitness and host plant physiology, in 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 with decreased plant vigour under reduced water availability irrespective of 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 stress 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 any data reporting on plant physiological responses to drought stress, including measurements of plant growth and/or mass, 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 stress effects on plant physiology in parallel with aphid fitness responses. A secondary aim of the meta-analysis was to determine whether 1) aphid tribe and/or 2) the aphid-plant system (i.e. species combinations) explain variation in aphid fitness responses to drought stress. The mechanistic understanding provided by our study allows the effects of drought stress on herbivore success to be anticipated for phloem-feeding insects under future climatic conditions.

Literature search and meta-analysis

Criteria for inclusion in analysis

The search terms “Drought” AND “Aphid” were used to conduct a literature search of the Web of Science database (with a publication cut-off date of March 2020). A total of 188 papers was identified. A previous meta-analysis which examined insect responses to drought undertaken by Huberty and Denno (2004) was screened for further studies, and an additional 16 studies were identified. This produced a pool of 204 studies published between 1958 and 2020. To be considered for inclusion in the analysis, papers had to satisfy the following criteria: 1) to be primary literature (not a review or opinion article) presenting data on the responses of at least one aphid species to drought stress relative to an unstressed control treatment; 2) to report aphid responses as the effect of drought stress on a measure of aphid fitness (detailed below); 3) present the responses so that an estimation of the

treatment differences could be determined alongside an estimate of the variation. Field studies were included in the analysis, but only when drought was empirically investigated. A total of 46 studies satisfied these criteria. A further 23 studies reported data for aphid fitness but either did not display the data or did not present an indication of the variation of the data; these studies were excluded from the meta-analysis but included in preliminary "vote-counting" assessment. The full range of studies in relation to publication year are displayed in Fig. 1 and detailed in Supplementary File 1 and Supplementary File 2.

Data extraction and pooling: aphid responses

Aphid fitness data were extracted from drought stress and controlled (unstressed) treatments. Where reported, the mean value and an indication of the variation around the mean were extracted directly from the reported data or determined from figures using WebPlotDigitizer v.4.2 (A. Rohatgi, 2019. Weblink: https://automeris.io/WebPlotDigitizer). Where median and interquartile ranges were reported, means and standard deviation were estimated by following Luo et al. (2018) and Wan et al. (2014). Data were extracted for any of the following aphid fitness parameters: fecundity (including 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 (including time until adulthood and time until first reproduction), aphid biomass, or aphid lifespan. The effect size (Hedges' g; Cooper et al., 2019) was calculated from aphid responses under drought conditions relative to aphid responses under control conditions. Where multiple drought stress treatments were imposed, data were extracted from the control and the most severe drought stress treatment imposed.

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 for these 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) data for drought and control conditions were pooled across the three CO_2 treatments), and within aphid species at the clone/genotype level to provide one data point per aphid species per fitness parameter. Data were collated separately for each host plant species tested. This pooling method produced 78 unique data points over the 46 studies.

Two datasets were compiled based on these extracted data: in the first dataset ("global"), data were pooled within each study across multiple fitness parameters, plant hosts, and

aphid species to produce 46 data points, i.e. one pooled effect size per study, reporting the overall aphid responses to drought stress. 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 done 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). For the second dataset ("expanded"), effect sizes were calculated separately for each fitness parameter measured and aphid - host plant combination included in the study. To ensure that the direct comparison ("expanded" dataset) of different aphid fitness parameters were justified for inclusion in the analysis, the calculated hedges' g values for each data point were plotted (Supplementary Fig. 1) to confirm that data were evenly distributed and not clustered into observable 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 carried out on the "expanded" dataset.

Grouping of extracted data: aphid responses

Extracted data contained information on 20 aphid species (Table 1). To disentangle any potential taxonomic differences in aphid responses to drought stress, data were categorised into two groups described in detail below: a "Tribe" grouping based on the taxonomic tribe of the aphid species; and a "Plant-Aphid" group based on the plant-aphid system examined. Several aphid tribes, and one subfamily, were represented in the dataset (Aphidini, Chaitophorini, Eulachnini, Macrosiphini, Panaphidina, Hormaphidini, and Phloemyzinae). However, for all tribes apart from Aphidini and Macrosiphini, the level of replication was $n = 1$. As a result of this low representation in other tribes, the final grouping used consisted of Aphidini, Macrosiphini, and other ($n = 5$). One study (Oswald & Brewer, 1997) was omitted from the "Tribe" analysis when using the "global" dataset as the pooled effects size for this study included a combination of data from the Macrosiphini and Aphidini tribes. In the "expanded" dataset, Macrosiphini ($n = 54$) and Aphidini ($n = 20$) were still overrepresented compared with the others ($n = 6$).

The extracted aphid fitness data, all fitness parameters across all aphid species over all studies, covered 22 host plant species: *Arrhenatherum elatius* (Ae, $n = 1$), *Malus domestica* (Md, $n = 2$), *Arabidopsis thaliana* (At, $n = 4$), *Brassica oleracea* (Bo, $n = 8$), *B. napus* (Bn, $n = 2$), *Chenopodium sp.* (Cs, $n = 1$), *Dactylis glomerata*, *(Dg,* n = *1), Festuca arundinacea* (Fa, $n = 1$), *Glycine max* (Gm, $n = 1$) *Holcus lanatus* (Hl, $n = 1$), *Hordeum vulgare* (Hv, $n = 9$), *Lolium perenne* (Lp, $n = 1$), *Medicago sativa* (Ms, $n = 4$), *Picea abies* (Pa, $n = 1$), *P.*

sitchensis (Ps, *n = 6*), *Pisum sativum* (Psat, *n = 1*), *Populus sp.* (Psp, *n = 2*), *Rumex sp.* (Rs, *n = 1*), *Solanum tuberosum* (St, *n = 8*), *S. lycopersicum* (Sl, *n = 1*), and *Triticum aestivum* (Ta, *n = 24*). To facilitate comparison between plant-aphid combinations, data were grouped into the following plant host categories: Brassicas (comprising Bo, Bn: *n = 4* and *10* from the "global" and "expanded" datasets, respectively), Cereals (comprising Ae, Dg, Hl, Hv, Ta: *n = 18* and *36*), Forage species (comprising Ms, Lp, Cs: *n = 5* and *7*), Legumes (comprising Psat, Gm: *n = 2* for both datasets), Model species (comprising At: *n = 3* and *4*), *Solanum sp.* (comprising: St, Sl: *n = 4* and 9), and Tree systems (comprising Md, Pa, Ps, Psp, Rs: *n = 10* and *12*).

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

The full range of studies incorporated into the meta-analysis of aphid responses to drought stress (Supplementary File 2) were screened for inclusion in an additional meta-analysis to determine the impact of drought stress at the plant level. To be considered for inclusion in this subsequent analysis, studies had to satisfy the following criteria: 1) present data on the responses of at least one plant species to drought stress conditions relative to plant responses under a controlled condition; 2) to report plant responses as the effect of water stress on either a measure of vigour (including mass, height, and growth), a measure of tissue nitrogen (N) or amino acid concentration, or a measure of the plant defensive response (e.g. secondary metabolite or phytohormone concentration); 3) present the responses so that an estimation of the differences could be determined alongside an estimate of the variation. From the pool of 46 studies included in the aphid meta-analysis, 25 studies reported a plant vigour response, ten reported a measure of tissue N or amino acid concentration, and six 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 sub-datasets: vigour, nutritional, and defensive.

Measuring publication bias: aphid and plant datasets

A funnel plot was created to test for publication bias in the 46 studies represented in the meta-analyses and a rank correlation test was carried out to test for funnel plot asymmetry (Fig. 2A). 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 = 271* and *n = 1765* 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 Studio Desktop version 1.0.143 running R version 3.5.3, with additional packages ggplot2 (Wickham, 2016), meta v.4.9-7, and metafor v.2.1-0. A total of 69 and 46 studies were included in the vote counting and meta-analysis, respectively (detailed in Supplementary File 1 and Supplementary File 2).

To account for variation between analysed studies with regards to different methodologies used to implement drought stress, 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 in order to determine that different methodologies used to initiate drought stress did not vary substantially in their effects (Supplementary Fig. 2).

Aphid response analysis: Vote counting procedure

To examine the proportion of publications which reported either a positive, negative, or null response of aphids to drought stress, a “vote counting” method was employed. Briefly, the included studies were screened for whether a significant effect of drought stress on aphid fitness was detected, and if so 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 (46 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 measured, giving multiple pooled effect sizes per study (78 data points).

For the first meta-analysis ("global" dataset), data were analysed using a random linear mixed effects model fitted with restricted maximum likelihood distribution. The difference between aphid tribes and the plant-aphid systems were examined in two subsequent models by incorporating these two factors as fixed terms. 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 and the differences between aphid tribes and the plant-aphid system was assessed in two models. In a further model, the responses of the specific aphid fitness parameters were tested.

Plant response analysis: Meta-analysis procedure

From the pool of studies which reported aphid responses to drought stress, 25, ten, and six studies also reported the effect of drought stress 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 three individual models, divided into "vigour", "nutritional", and "defensive" models.

Results

Aphid fitness is reduced under drought stress

The vote counting procedure (Fig. 3) indicated that aphid fitness is reduced when exposed to drought stressed host plants. To investigate the size of this effect, a full meta-analysis was employed. The meta-analysis was based on data extracted from 46 papers (published 1988 – 2020), reporting studies of 20 aphid species, covering six aphid tribes (grouped into the Aphidini, Macrosiphini, and others) and seven plant-aphid systems (Brassica, Cereal, *Solanum,* Model species, Forage, Tree, and Legume). Data provided information on five aphid fitness parameters (aphid biomass, development, fecundity, lifespan, and population size) and for the global analysis, all responses variables were pooled to produce one effect size per study.

These pooled data were determined to be significantly heterogeneous, as indicated by Cochran's Q (Q_E = 292.86; df = 43; p = <0.001). 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, 2008) . Analysis of the pooled data indicated that aphid fitness is generally reduced under drought stress (Q_M = 30.60; p = <0.001; Fig. 4; Supplementary Fig. 3). Subsequent comparisons were carried out after separating the data into biologically relevant categories, i.e. aphid tribe and the plant-aphid system. These further comparisons indicated that aphid fitness was broadly reduced under drought stress for aphid tribe categories examined (Q_M = 26.87; p = <0.001; Fig. 5) and across plant-aphid systems (Q_M = 27.48; p = <0.001; Fig. 6). However, due to low levels of replication for some groups a comprehensive comparative analysis was not possible.

To analyse the effect of drought stress on specific fitness parameters, a second dataset comprising 78 data observations over the 46 studies was compiled (the “expanded” dataset). Meta-analysis of this expanded dataset indicated that aphid fitness was still reduced under drought stress (Q_M = 18.96; p = 0.002; Fig. 7 insert). However, these data were significantly asymmetric (T = -0.29; p = <0.001; Fig. 2B), which limits the extent to which these data can be analysed. Data did, however, indicate that the majority of aphid fitness parameters examined, especially parameters intrinsically associated with aphid abundance (fecundity and population size), were negatively affected by drought stress conditions (Q_M = 83.37; p = <0.001; Fig. 7).

Drought stressed plants show reduced vigour and increased tissue concentrations of defensive compounds

Meta-analysis of the pooled plant responses to drought stress (Supplementary Fig. 4 – 6) indicated that exposure to drought conditions has an overall negative effect on plant vigour (Q_M = 49.75; p = <0.001; Fig. 8) and, on average, results in more chemically-defended plant tissues (Q_M = 29.58; p = <0.001; Fig. 8). However, tissue N and amino acid concentrations were not found to be increased consistently (Q_M = 4.59; p = 0.204; Fig. 8). 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 Figure 7.

Discussion

This study provides the first comprehensive assessment of aphid and host plant responses to drought stress conditions, analysed in terms plant vigour, nutritional quality, and plant defence. The meta-analysis supported our prediction that drought stress 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.

Plant vigour could explain drought stress effects on aphid fitness

The primary finding that aphid fitness is reduced when feeding on drought stressed plant 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 likely due to the negative effects of drought on host plant physiology, including plant growth and plant tissue concentrations of defensive or defence signalling compounds. It should be noted that, out of the studies included in our meta-analysis, around half measured plant vigour (25 studies) while only a few measured tissue concentrations of defensive compounds (n = 7). 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 (see Supplementary Fig. 7). This finding is consistent with our prediction and is supported by a large body of literature reporting elevated plant defence and decreased plant growth and vigour under drought stress (Templer et al., 2017; Beetge & Krüger 2019; Xie et al., 2020), indicating that these plant responses mediate the impact of drought stress on sap-feeding insect herbivores. These changes could be caused by increased contact between aphids and plant defensive compounds, a reduction in the availability of nutrients in the phloem sap, or/and a reduction in the growth and development of new plant tissue which is often the preferred feeding site for many aphid species, although this can differ between aphid-plant combinations (Leather & Dixon, 1981).

A secondary aim of this meta-analysis was to examine the consistency of drought stress effects across aphid groups and aphid-plant systems in order to identify factors which could explain differential effects observed in several studies (Oswald & Brewer, 1997; Hale et al., 2003). All aphid tribes assessed here showed decreased aphid fitness in response to drought stress. However, there was an overrepresentation of the Aphidini and Macrosiphini tribes (41 out of the 46 studies), probably because many empirical studies focus on agriculturally or ecologically important aphid species, which are widely represented in these two aphid tribes (Kim & Lee 2008; Choi et al., 2018), this limits the extent to which differences can be detected. Further experimental work would be needed to determine whether drought responses vary between aphid groups. For example, it could be hypothesised that aphid species which actively remobilise plant nutrients (e.g. *Diuraphis*

noxia; see Sandström et al., 2000) or species that are able to sequester plant defensive chemicals (e.g. *Brevicoryne brassicae;* see Kazana et al. 2007) are less affected by drought stress than species that are unable to maintain a sufficient supply of plant nutrients or lack the mechanisms to sequester or tolerate toxic plant chemicals.

When data were assessed across several aphid-plant groups, namely Brassica, Cereal, Forage, Legume, Model, *Solanum,* and Tree, aphid fitness was generally reduced on drought stressed plant hosts across all plant groups assessed, but again 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 stress 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 stress

Although based on a relatively small number of studies, our analysis indicated that host plant defence is elevated under drought stress, 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 altered environmental conditions. From the 46 studies assessed in this meta-analysis, only four included observations of aphid responses on both susceptible and (partially)-resistant plant types (Oswald & Brewer, 1997; Dardeau et al., 2015; Verdugo et al., 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 et al., 1995; Rousselin et al., 2018; Quandahor et al., 2019) and only one study examined the interactive effects of aphid resistance and drought tolerance (Grettenberger & Tooker, 2016). This low level of representation means that the interactive effect between plant resistance and drought stress could not be investigated empirically using meta-analysis approaches. These three studies report similar findings: aphid fitness is reduced on both susceptible and resistant plant hosts (Oswald & Brewer, 1997; Dardeau et al., 2015; Guo et al., 2016), with a smaller reduction in fitness the resistant host plant than on the susceptible host plant (Oswald & Brewer, 1997; Dardeau et al., 2015). These findings indicate that while aphid fitness is lower on resistant plants under benign conditions, it decreases to similarly low values on susceptible and resistant plants under drought stress, highlighting a significant knowledge gap in our

understanding of how plant resistance traits are affected by environmental stress, which is increasingly important to understand 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 stress in relation to altered host-plant resistance, termed the Plant Resistance Hypothesis (Fig. 9). 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). Plant-mediated responses to drought stress are likely to cause a reduction in plant vigour and a decrease in plant palatability for the aphid, characterised by elevated concentrations of plant defensive compounds (Inbar et al., 2001; Ozturk et al., 2002), as confirmed in this study, leading to differential changes in the abundance of defensive compounds in the susceptible (from low abundance to high abundance) and resistant (continually high abundance) plants. Under drought stress, aphid fitness is reduced due to decreased plant vigour and increased plant defence, but differential levels of basal fitness between the two plant types leads to differences in the extent to which aphid fitness is affected 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

The central finding of our meta-analysis is that exposure to drought-stressed host plants is detrimental to aphid fitness; although the extent of this is likely affected by host plant resistance/decreased suitability as an aphid food source, the effect of drought stress on aphid populations is overwhelmingly negative. Consequently, higher incidences of drought will have a detrimental effect on the terrestrial trophic levels that are supported by aphids: aphids are widespread across temperate regions, are abundant consumers of primary production in many ecosystems, and provide a food source for many different trophic groups (Gilbert 2005; Messelink et al., 2012; Roubinet et al., 2018). Our findings that individual and population level measures of aphid fitness are typically reduced by drought stress suggests that drought will have cascading consequences for host plant consumption by aphids and,

therefore, impact on the abundance of aphid-centric trophic systems. These consequences will likely include reduced population density of aphid parasites and pathogens, as there will be fewer viable aphid hosts under drought conditions (Nguyen et al., 2007; Ahmed et al., 2012; Aslam, et al., 2013) and reduced abundance of aphid predators, as a direct consequence of a decrease in food source quality and availability (Wade et al., 2017). Similarly, many aphids, including a high proportion of Aphidini and Macrosiphini species, are tended by ants who farm aphids for their honeydew secretions (Stadler et al., 2003). These ants also provide protective services to plants by deterring herbivory by other insect pests (Offenberg et al., 2004; Rosumek et al., 2009). A reduction in aphid abundance, or decreased honeydew quantity or quality, could result in decreased ant attendance (higher ant attendance is observed in denser aphid colonies; see Stadler et al., 2003), compromising the protective services delivered by ants, thereby exacerbating the detrimental effects of drought on plant physiology by increasing exposure to additional biotic stressors.

Ecological networks often exist in stable equilibria (McQuaid & Britton, 2015; Landi et al., 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 will decrease the overall abundance, mass, or quality of aphids available to support other trophic levels, which can destabilise population equilibria; a recent modelling study illustrated the destabilising effects of drought stress on aphid-parasitoid interactions leading to altered insect population cycles (Preedy et al., 2020). A key finding of this meta-analysis was that plant resistance to aphids can influence the extent to which aphids are negatively affected by drought stress. The negative consequences of plant resistance for aphids generally include decreased fecundity and a reduction in aphid mass (Greenslade et al., 2016; Leybourne et al., 2019A). Reduced aphid abundance and quality could have negative consequences for aphid natural enemies; indeed, we recently observed that resistant plants negatively affect the success of an aphid parasitoid (Leybourne et al., 2019B). Analysing the interactive effects of drought and plant defence for aphid-natural enemy interactions and the composition and function of ecological networks would be an important avenue for future research. This approach will improve our understanding of how drought, along with other changing climate factors, and insect-host plant combinations of contrasting suitability contribute to the increased rates of species loss and population declines observed in recent decades (Sánchez-Bayo & Wyckhuys, 2019).

Conclusion

In conclusion, aphid fitness is adversely affected under drought stress conditions. This negative effect was apparent across the different categories examined here (aphid and plant groups), although the limited number of studies in some aphid and plant groups limits our ability to conclude whether these findings are universally true. As drought stress has an overall negative effect on aphid fitness it is anticipated that drought-induced reductions in aphid fitness will confer far-reaching negative consequences across a range of ecological systems, specifically in relation to trophic levels which are supported by aphids (i.e. impacts on spiders, parasitoids, beetles, and hyperparasitoids). In addition, one key knowledge gap was identified in this study: the overall effect of drought stress on aphid fitness can be mediated by the extent of host plant resistance against aphids. We propose a conceptual model describing the anticipated effects of drought on aphid fitness due to changes in plant vigour and defence allocation depending on the level of plant resistance against aphids, which provides a basis for stimulating further research on insect herbivore responses to a changing climate.

Figures and Tables

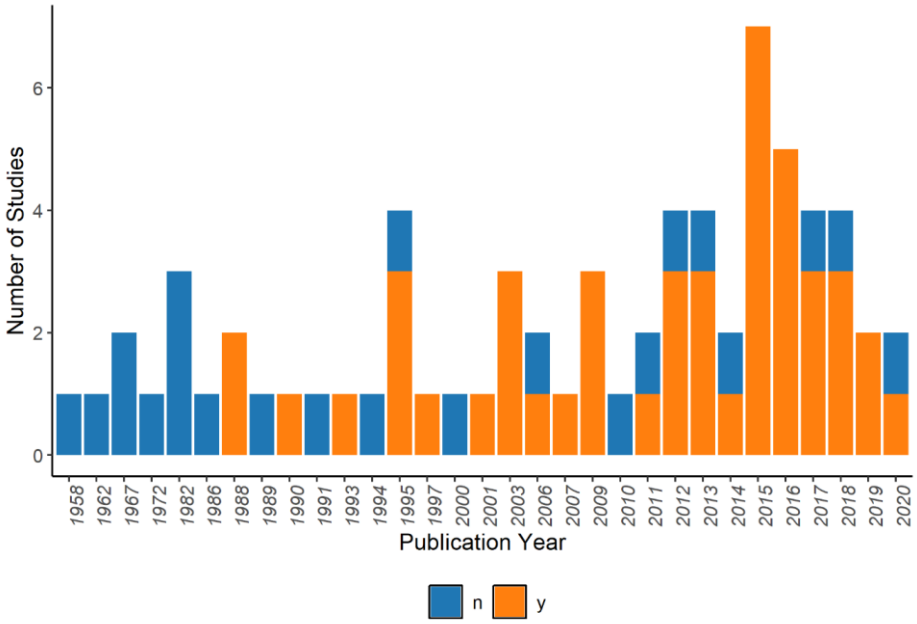

Fig. 1: Histogram of studies included in the analysis, colour-coded to indicate whether the study was included in the full meta-analysis (orange) or the vote-counting analysis (blue).

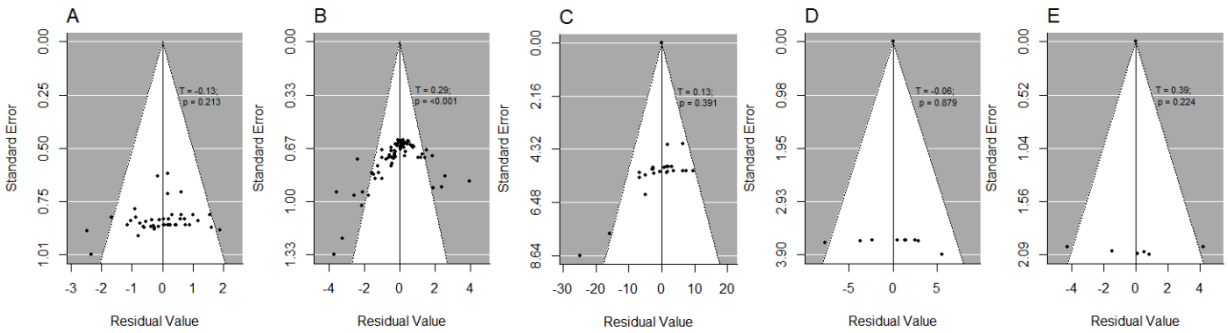

Fig. 2: Funnel plots testing for publication bias in the studies included in all meta-analyses. A) Studies included in the aphid meta-analysis (“global” dataset). B) Studies included in the aphid meta-analysis (“expanded” dataset). C) Studies included in the plant meta-analysis (“*Vigour*” subdataset). D) Studies included in the plant meta-analysis (“Nutritional” subdataset). E) Studies included in the plant meta-analysis (“Defensive” subdataset). Publication bias was tested using a rank correlation test for funnel plot asymmetry.

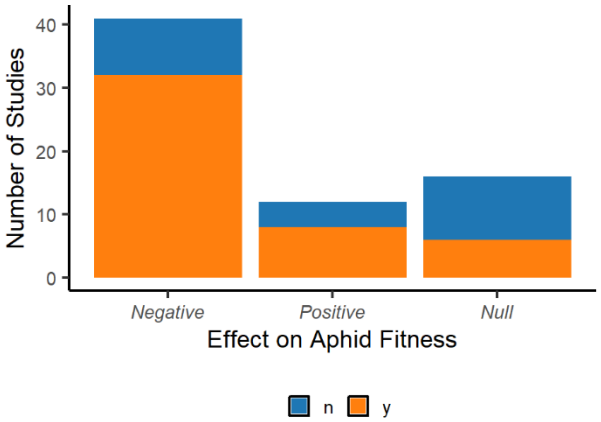

Fig. 3: Bar graph displaying the number of studies reporting negative, positive, or null effects of drought stress on aphid fitness. Bars are coloured to indicate the proportion of studies in each category that were included in the full meta-analysis (y) vs those in the complete dataset (n).

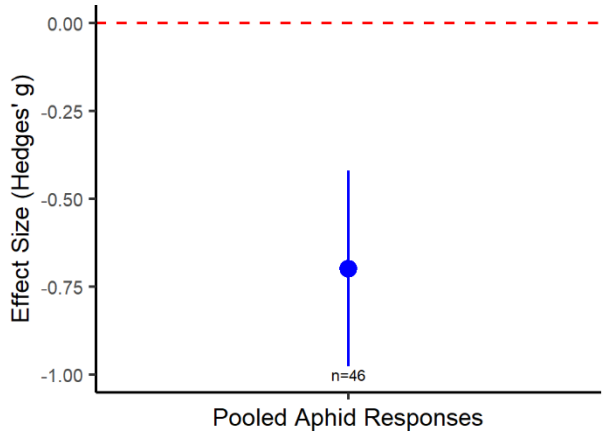

Fig. 4: Overall responses of aphids to drought stress using data from the “global” dataset. Data were pooled across variables reported in each study to produce a single effect size per study. Graph displays the mean effect size (Hedges’ g) and the 95% confidence interval. Red dashed line represents zero effect size.

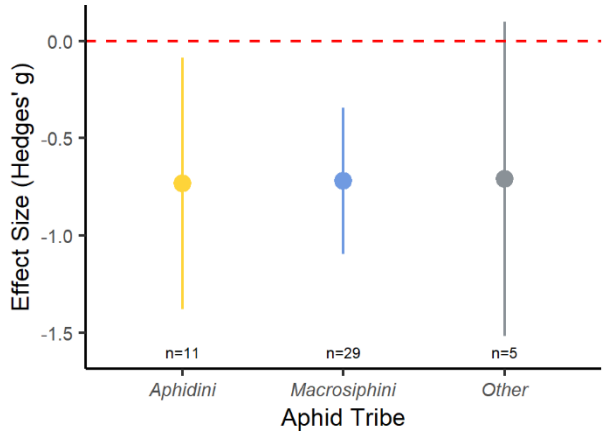

Fig. 5: Pooled responses of aphid tribes to drought stress conditions using the “global” dataset where response variables were pooled to produce one effect size per study. Graph displays the mean effect size (Hedges’ g) and the 95% confidence intervals for the different aphid tribes identified from the extracted data. Red dashed line represents zero effect size.

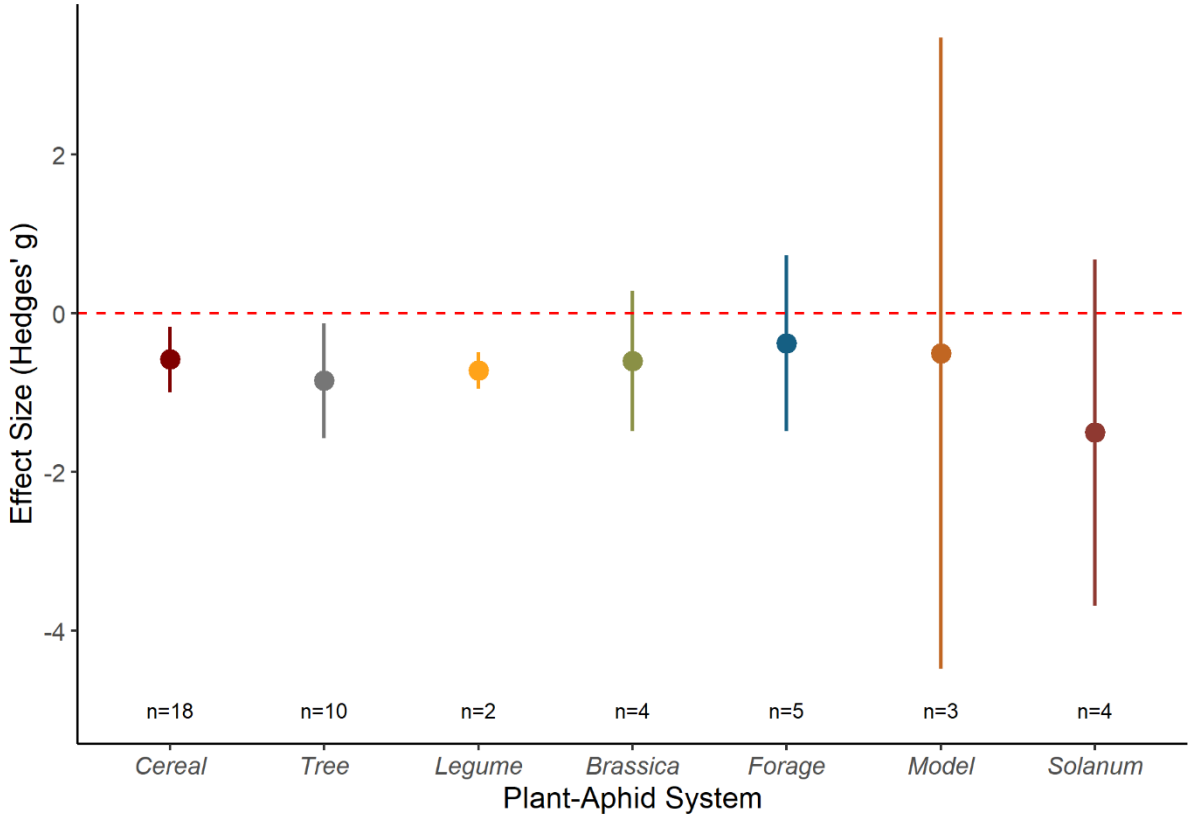

Fig. 6: Effect of the plant-aphid system on overall aphid responses to drought stress conditions using the "global" dataset where response variables were pooled to produce one effect size per study. Graph displays the mean effect size (Hedges' g) and the 95% confidence intervals for the different plant-aphid systems identified from the extracted data. Red dashed line represents zero effect size.

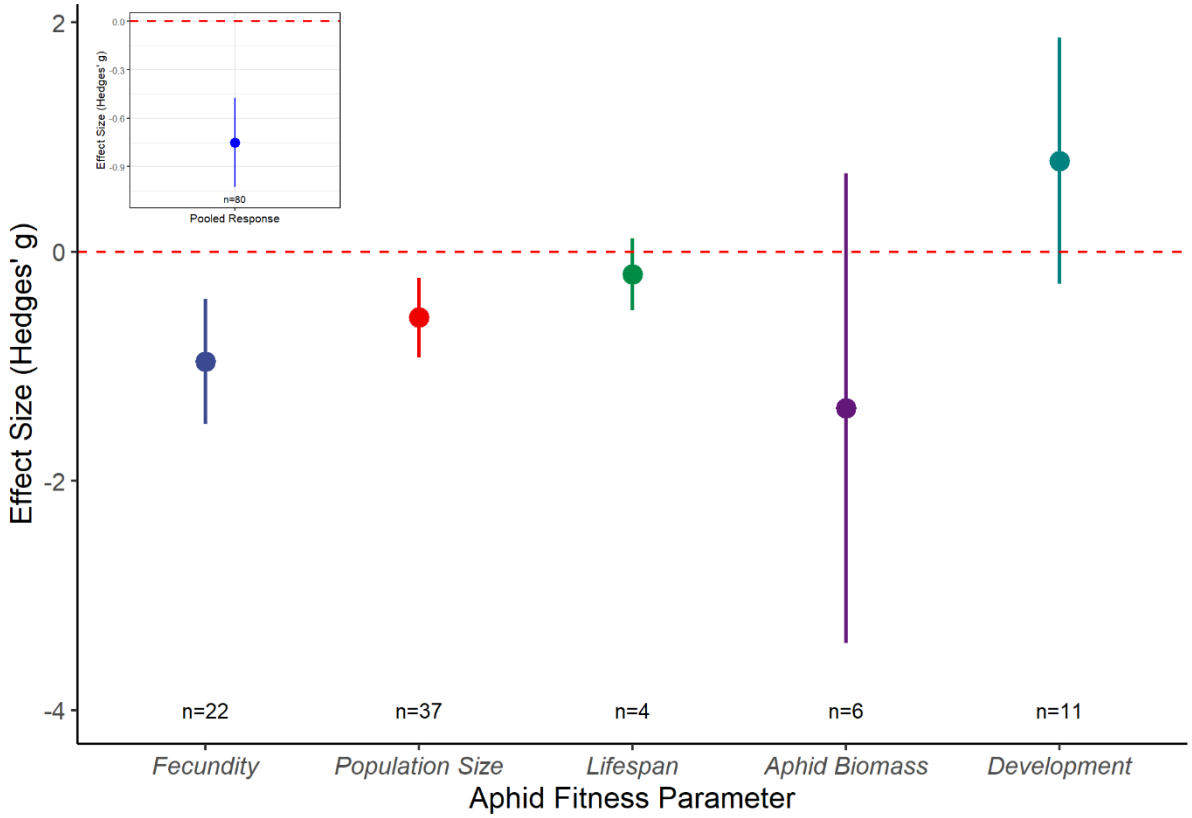

Fig. 7: Responses of aphids to drought stress using the "expanded" dataset which included an effect size per response variable and for each aphid species measured in each study. Main graph displays the mean effect size (Hedges' g) and the 95% confidence intervals for the different plant-aphid systems 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.

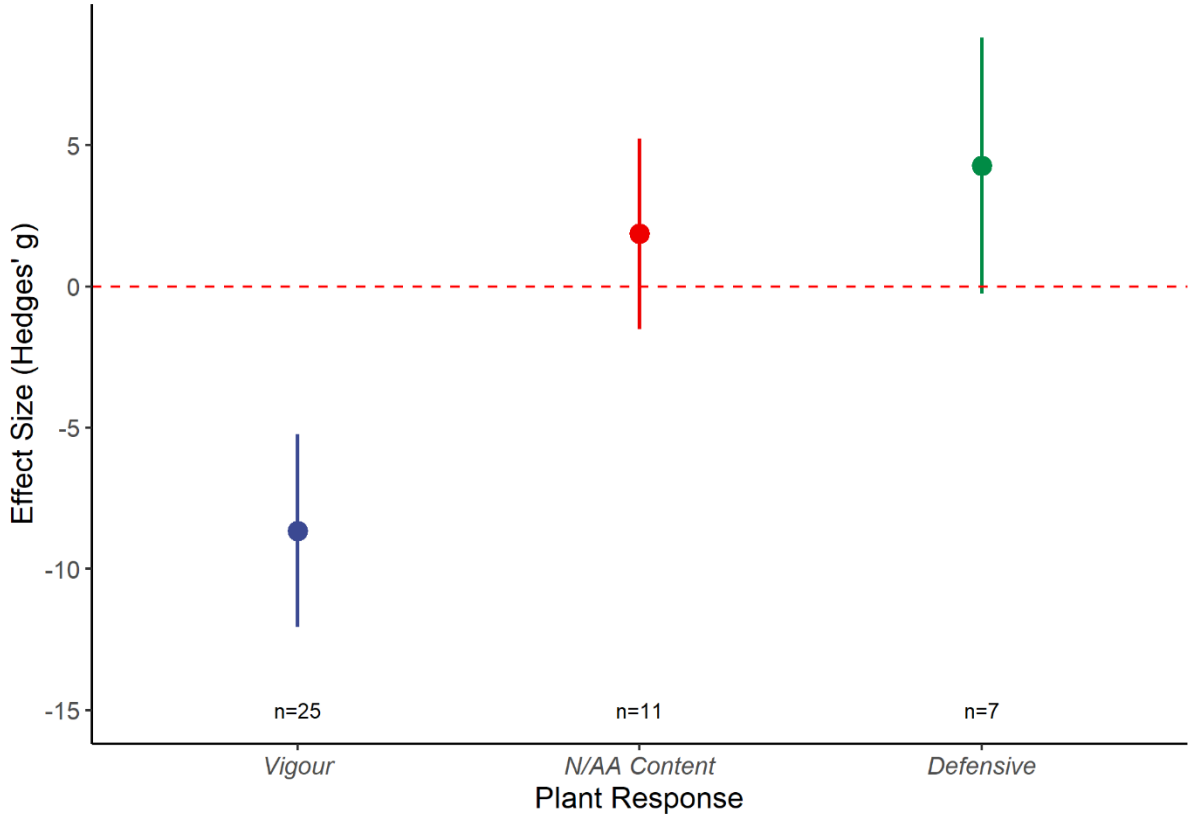

Fig. 8: The effect of drought stress on plant vigour using the “plant” dataset where measures of plant vigour (vigour), N or amino acid (AA) concentration (N/AA Content), or tissue concentrations of defensive compounds (Defensive) were reported. Graph displays the mean effect size (Hedges’ g) and the 95% confidence intervals for the different plant-aphid systems identified from the extracted data. Red dashed line represents zero effect size.

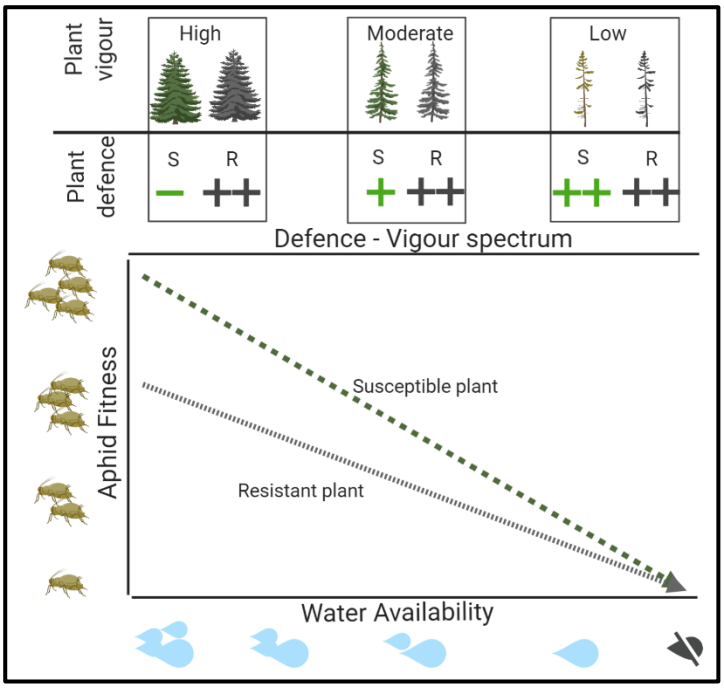

Fig. 9: Conceptual representation of the Plant Resistance Hypothesis (PRH). As water availability decreases plant defence increases and plant vigour declines, leading to reduced aphid fitness. Basal levels of aphid fitness under conditions of ample water availability differ between the susceptible (S, 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

Tables

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	Agricultural and ecological importance	Number of data points: "Expanded" dataset and study from which data were extracted Ŧ
Aphis glycines	Soybean aphid	Aphidini	Significant pest of soybean across North America and Asia	1 datapoint from study 28
A. Pomi	Apple aphid	Aphidini	Significant pest of apple trees, specifically on nursery stock. Colonies can be attended by ants	1 datapoint from study 26
Acyrthosiphon pisum	Pea aphid	Macrosiphini	Widespread in temperate regions. Serious pest of the Fabaceae. Vector of over 30 plant viruses	4 datapoints from studies 7, 18, 24, 37
Brevicoryne brassicae	Cabbage aphid	Macrosiphini	Wax-covered aphid. Widely distributed throughout Europe, major pest of Brassicaceae	5 datapoints from studies 21, 40, 41
Cinara costata	Mealy spruce aphid	Eulachnini (Other)	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 22
Chaitophorus leucomelas	Black polar leaf aphid	Chaitophorini (Other)	A widely distributed pest of poplar. Colonies can reside in the galls formed by other insects and can occassionally be attended by ants.	1 datapoint from study 33
Diuraphis noxia	Russian wheat aphid	Macrosiphini	A significant cereal pest in South Africa and North America. Vector of barley yellow dwarf virus.	3 datapoints from studies 2, 14, 30
Dysaphis plantaginea	Rosy apple aphid	Macrosiphini	Widely distributed across temperate regions and a significant pest of apples. Colonies develop in galls and are attended by ants.	1 datapoint from study 35
Elatobium abietinum	Green spruce aphid	Macrosiphini	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	Wild crucifer aphid	Macrosiphini	Can feed on various Brassicaceae crops.	1 datapoint form study 21
Macrosiphum euphorbiae	Potato aphid	Macrosiphini	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, 29, 34
Metopolophium festucae subsp. *Cerealium*	Fescue aphid	Macrosiphini	A subspecies of *M. festucae* which can be a significant pest of cereals and grasses.	2 datapoints form study 16
Myzus persicae	Peach-potato aphid	Macrosiphini	Significant pest with worldwide distribution. Broad host range. Can cause significant economic damage through the transmission of over 40 plant viruses.	10 datapoints from studies 25, 31, 32, 38, 40, 41, 42
Pemphigus betae	Sugarbeet root aphid	Hormaphidini (Other)	Root-feeding aphid, a main economic pest of sugar beet.	2 datapoints from study 27

Phloeomyzus passerinii	Poplar woolly aphid	Phloeomyzinae (Other)	Distributed in temperate regions. Significant economic pest of poplar.	1 datapoint from study 12
Rhopalosiphum maidis	Green corn aphid	Aphidini	Widely distributed worldwide. A significant pest of cereals. Commonly attended by ants. Vector of several plant viruses.	2 datapoints from studies 30, 36
R. padi	Bird cherry-oat aphid	Aphidini	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 and wasps.	15 datapoints from studies 3, 9, 13, 16, 17, 19, 45
Sitobion avenae	Wheat aphid	Macrosiphini	Widespread pest of cereals with worldwide distribution. A vector of several economically important plant viruses.	15 datapoints from 1, 11, 15, 23, 39, 43, 46
Schizaphis graminum	Spring green aphid	Aphidini	Widely distributed pest of cereals. Can vector a range of plant viruses.	1 datapoint from study 10
Therioaphis trifolii (*T. maculate*)	Spotted alfalfa aphid	Panaphidina (Other)	Widespread pest of Fabaceae.	1 datapoint from study 7

Ŧ Full study references are contained in Supplementary File 2

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