



Aphids Response to Drought Stress Hypothesis Vary between Species

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Abstract

Aphids possess flexible life cycles and are therefore capable of acclimatizing to various environmental changes. Their physiological, biochemical, and behavioral responses can easily withstand a wide range of biotic and abiotic stressors. This adaptability trait, however, appears to be highly dependent on the specific aphid species and crop types and varieties. Drought stress can alter the chemical composition of host plants, which can have positive or negative effects on aphid performance or in some cases have no effect. Plants also contain secondary metabolites such as alkaloids, phenolic compounds, and terpenoids that can affect aphid survival. In view of these, the response of aphids to drought stress can be too complex to be deduced from a single hypothesis. The differences in findings among studies are most likely due to variations in plant responses to drought stress and subsequent insect variations in drought stress responses. This can be a major focus of future research to broaden our understanding of plant resistance under changing resource-supply conditions as a result of climate change.

Subject Areas

Agricultural Science

Keywords

Aphids, Drought Stress, Adaptation, Secondary Metabolites,

1. Introduction

Over the last decade, researchers have focused on the mechanisms of aphid survival and host plant responses to aphids under drought stress [1]. The presence of abiotic factors and host quality have been attributed to the performance of insects by the majority of researchers [2]. Other studies have found that the adaptation of insect herbivores is highly dependent on their life cycle and ability to compensate for nutritional inadequacy caused by abiotic factors [3]. Drought is one of the most significant challenges in crop production, and approximately 40% of the world's agricultural land is located in arid or semi-arid regions [4]. Drought stress can result in cellular water deficits, membrane damage, decreased enzyme activity, crop yield and even plant death [5]. Drought can also indirectly affect the performance of insect pests by influencing the physiology of host plants. Several studies have found that as the severity of drought increases, so do the populations of insect pests [6]. However, a recent study found that well-watered plants had more aphids than drought-stressed plants [7]. Other studies have proposed that the drought-stress effect on aphids is dependent on plant variety, drought tolerance level, stress intensity and duration, type of damage, and chemical composition of the host plant [8] [9] [10].

Host plants with varying levels of tolerance to drought stress have been reported to respond differently to aphid attack [7]. This suggests that the biochemical and morphological traits that confer drought tolerance in host plants do not always confer resistance to aphids. This could be due to differences in host plant nutrition, palatability, and herbivore resistance. Variations in the physical and chemical composition of the host plant can have a significant impact on herbivore population dynamics [11]. Host plant chemical composition can be modified as a result of drought stress [12] [13], which can affect aphid performance positively [14] or negatively [12] [15] or in some cases have no effect [16]. Moreover, plants are known to contain secondary metabolites that can affect aphid survival [11]. However, only host plants with a higher level of secondary metabolites may be able to accumulate enough to protect themselves from aphid attack [13] [17]. Aphids have dynamic life cycles and, thus, acclimatize to a variety of environmental changes. Their physiological, biochemical, and behavioral responses can easily withstand a wide range of biotic and abiotic stresses. The adaptability trait, however, appears to be highly dependent on the specific aphid species and crop types or varieties. Therefore, the purpose of this study is to review the mechanisms of aphid survival and host plant responses to aphids under drought stress.

2. Aphids' Response to Drought Stress Hypothesis

Due to the complexities involved in understanding aphids' response to drought

stress, researchers have developed three hypotheses: the plant–vigor hypothesis, the pulsed-stress hypothesis, and the plant–stress hypothesis [12]. According to the first hypothesis, osmotic stress from feeding on severely drought hosts would impair aphid performance due to aphids’ relocation of growth and reproduction energy into osmoregulatory mechanisms. The pulsed-stress hypothesis also states that water stress increased nitrogen content availability. Thus, plant turgor increases when plants recover from stress. Sup-sucking insects can access the excess nitrogen content due to the increased turgor pressure associated with plant recovery from stress. Consequently, pulsed-stress improves the quality of host plants for sup-sucking insects. The plant stress hypothesis, on the other hand, proposes that host plants under drought stress may be more vulnerable to aphid attack due to drought-induced primary metabolites that are beneficial to aphids [18]. Although most researchers agree that drought stress renders host plants defenseless, a number of researchers believe that allocating resources to osmoregulatory mechanisms as a result of feeding on drought-stressed hosts would have a significant impact on aphid performance [19] [20]. The most supported hypothesis, the plant-stress hypothesis, asserts that drought stress increases insect population abundance [12]. Only a few field experiments, in particular, support the idea that aphid populations increase on drought-stressed plants; however, experimentally imposed drought stress frequently has a negative impact on aphid population abundance. This suggests that the response of aphids to drought stress is too complex to be attributed solely to a single hypothesis. The differences in findings from different studies are most likely to be due to variations in plant responses to drought stress and subsequent variations in insects’ response to drought stress. Furthermore, levels of drought stress in previous studies were not well-defined in a way that could easily be replicated or compared to other similar studies. This demonstrates that the level of stress defined in previous studies significantly contributes to the differences reported in their findings.

3. Morphological and Physiological Response to Drought and Aphids Infestation

Host plants exhibit a variety of physiological changes, including physical, metabolic, and chemical changes. Some drought avoidance and tolerance mechanisms have been reported to be species-specific, as they are determined by the host plant’s resistance mechanisms. These mechanisms are divided into three categories: escape, avoidance, and tolerance [21]. In the drought escape strategy, host plants avoid drought by completing their life cycle with the limited water available. Drought avoidance is the ability of plants to maintain water potential and increase root hydraulics to maximize water uptake in order to avoid tissue dehydration. Such plants reduce water loss by closing stomata, lowering cuticular conductance, and shedding leaves, while utilizing water storage [22]. Drought tolerance is achieved by host plants avoiding dehydration through consistent water transport through osmotic adjustment. Under low water potentials, this

process prevents meristem cells from dying [23]. Drought avoidance and tolerance mechanisms have been shown to have a significant impact on aphid survival mechanisms, as physiological changes in drought-stressed plants stimulate secondary metabolites that benefit aphid population growth. Water potential is typically regarded as the prospective variable for measuring drought stress by researchers. Other scientists, however, argue that relative water content (RWC) is the best indicator of water potential because water potential varies between cultivars [24] [25]. These opinions suggest that plants respond differently to biotic and abiotic stress. Other morphological and physiological changes, including hydraulic conductance, chlorophyll content, water use efficiency, stomatal conductance, abscission, leaf angle, and photosynthetic rates play major roles in the tolerance of plants to stress conditions [26]. Morphological features of host plants such as leaf shape, texture, and hairiness could also be determinants of insect pest population growth [27].

Trichomes (leaf hairs) are reported to be conducive to the development of insect pests because they provide convenient habitats for them. Alternatively, leaves lacking trichomes may be more resistant to pest attack than rough and hairy leaves. This is due to wind disruption, which makes the insects less comfortable in their development [28]. Cotton (*Gossypium hirsutum*) leaf hairs increased the population of *Bemisia tabaci* on the plants [29]. The population of jassids (*Amrasca devastans*) on cotton varieties with hairy leaves, on the other hand, decreased when compared to those with smooth leaves [30]. Drought also has an effect on stomata size, with smaller stomata observed in drought-stressed plants. The reduction in stomata size allows plants to prevent excess water loss or to enhance their water use efficiency [31]. This is done by altering stomata density and size [32]. This condition is highly dependent on the severity and duration of the stress [33].

4. Biochemical Adaptations of Plants to Drought and Aphid Stress

Plants' natural defense systems evolved to protect them from insect pests and pathogen attacks. In response to insect feeding, host plants can induce signal transduction, which then activates the corresponding physiological and biochemical reactions. Increases in reactive oxygen species (ROS), malondialdehyde (MDA), and proline are common early signal events during plant defense responses [32] [34]. Over accumulation, of ROS can cause cell malfunction and eventually damage to the host plant's biological structures [35]. However, oxidative stress is more than just a symptom of cellular dysfunction; it can also be interpreted as an indication of host plant adaptation mechanisms [32] [35].

Superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and polyphenol oxidase are antioxidant enzymes that play important roles in host plant defense reactions [32] [35]. They can stimulate the transport of insect resistance signals during the defense response and induce the production of related compounds and enzymes in the aftermath of insect invasion through cascade reac-

tions [36]. Insect feeding has been linked to host resistance and has been shown to influence the activities of plant defense enzymes [37].

Proline accumulation is one of the early signal measures in plants under drought stress. Under stress conditions, proline acts as an osmotic intermediary in plants [38]. Proline accumulation in host plants is attributed to protein denaturation prevention, enzyme structure defense, and protection from reactive oxygen species damage [29]. Changes in Pro content have been shown to influence aphid performance in ways other than changing the quality of their diet [38]. Proline content increases have also been linked to host plant resistance to aphid attack [39].

5. Glycoalkaloid and Phytohormones Response to Drought Stress and Aphid Infestation

Drought stress is a significant agricultural challenge that improves the performance of herbivorous insects by altering the nutrition and palatability of host plants [5]. Drought-induced stomatal aperture reduction improves the host plant's natural resistance to aphids by inducing secondary metabolites [40] [41]. Plants in the family of Solanaceae produce a variety of secondary metabolites containing glycoalkaloids, which have a negative impact on aphid reproductive potential and population growth [42]. The main glycoalkaloids found in commercially grown potato cultivars are α -chaconine and α -solanine [43]. The concentrations of glycoalkaloids in different parts of the potato vary greatly [43]. Preferably, high glycoalkaloid concentrations in the leaves of potato plants act as a natural defense against sucking insects, whereas low concentration in tubers also decreases the health risks of consumers [43]. It is speculated that the modification of host plant secondary metabolites against aphid attack may be due to phytohormone synthesis [44].

Plants adaptation to stress is controlled by the synthesis of phytohormones, which include jasmonic acid (JA), salicylic acid (SA), and abscisic acid (ABA), which can cross-talk to induce plant natural defenses against aphids [45]. The accumulation of ABA resulted in abscission and a reduction in stomatal aperture, both of which increased water use efficiency and resulted in the modification of some secondary metabolites [46]. SA inhibited the population growth and reproduction potential of *Bemisia tabaci* (silverleaf whitefly) on *Arabidopsis*, according to research. Plant defense mechanisms against insect pests have been reported to include phytohormones such as JA and its precursor cis (+) 12-oxophytodienoic acid (OPDA) [47]. Other studies showed that the performance of aphids under drought stress may vary depending on the type of plant, resistance mechanism, level of stress, and type of insect species [8] [10]. Many host plants may activate phytohormones to synthesize secondary metabolites, under drought stress; however, only host plants with a greater level of secondary metabolites may be able to defend against aphid attack.

A number of studies were evaluated on aphid responses to host plants and

plant resistance mechanisms to aphid infestation under drought stress (Table 1). The studies investigated how drought stress affects host plant morphology, physiology, and biochemistry, as well as how these changes influence aphid attack. According to the data (n = 27), 33.3, 44.4, and 22.2 percent demonstrated higher, lower, and no change, respectively (Table 1). It is worth noting that some plant species exhibit a wide range of variable drought-induced resistance traits, which

Table 1. Aphids-plant interactions under varying host plants.

Plant species	Aphid species	Effect of drought on plant resistance to aphids	Reference
Apple (<i>Malus domestica</i>)	Apple aphid (<i>Aphis pomi</i>)	Depends on the stress intensity	[8]
Arabidopsis (<i>Arabidopsis thaliana</i>)	Green peach aphid (<i>Myzus persicae</i>)	Higher resistance	[49]
	Green peach aphid	Lower resistance	[44]
	Cabbage aphid (<i>Brevicoryne brassicae</i>)	No change	[44]
Barley (<i>Hordeum vulgare</i>)	Greenbug (<i>Schizaphis graminum</i>)	Higher resistance	[50]
	Russian wheat aphid (<i>Diuraphis noxia</i>)	Lower resistance	[19]
	Corn leaf aphid (<i>Rhopalosiphum maidis</i>)	No change	[19]
	Russian wheat aphid	Higher resistance	[51]
Cabbage (<i>Brassica oleraceae var. capitata</i>)	Green peach aphid	Lower resistance	[53]
	Green peach aphid	Lower resistance	[54]
	Cabbage aphid	Lower resistance	[54]
Canola (<i>Brassica napus</i>)	Cabbage aphid	Higher resistance	[16]
	Mustard aphid (<i>Lipaphis erysimi</i>)	No change	[16]
Cowpea (<i>Vigna sp.</i>)	Cowpea aphid (<i>Aphis craccivora</i>)	Higher resistance	[55]
Norway spruce (<i>Picea abies</i>)	Galling aphid (<i>Adelges abietis</i>)	Higher resistance	[55]
Oatgrass (<i>Arrhenatherum elatius</i>)		Lower resistance	[12]
Orchard grass (<i>Dactylis glomerata</i>)		Higher resistance	[12]
Pea (<i>Pisum sativum</i>)	Pea aphid (<i>Acyrtosiphon pisum</i>)	Lower resistance	[56]
Peach (<i>Prunus persica</i>)	Green peach aphid	Lower resistance	[57]
Poplar (<i>Populus sp. double hybrid</i>)	Poplar aphid (<i>Chaitophorus leucomelas</i>)	Lower resistance	[58]
Sitka spruce (<i>Picea sitchensis</i>)	Green spruce aphid (<i>Elatobium abietinum</i>)	Lower resistance	[59]
Velvet grass (<i>Holcus lanatus</i>)		Higher resistance	[12]
Wheat (<i>Triticum aestivum</i>)	Grain aphid (<i>Sitobion avenae</i>)	Higher resistance	[60]
Wheat (<i>Triticum durum</i>)	Grain aphid	Lower resistance	[61]
	Bird cherry-oat aphid	Lower resistance	[61]

vary depending on the aphid species studied. This suggests that in response to aphid attack, plants may synthesize secondary metabolites; however, the amounts of secondary metabolites accumulated may determine the plant's resistance to aphids. To draw unambiguous conclusions about the effect of drought on plant resistance to aphids, experimental factors such as drought level, evaluation time, and aphid density, among others, must be standardized. This lends support to the long-held belief that herbivorous insects, particularly aphids, exhibit enhanced performance and outbreak dynamics on water-stressed plants [10]. It should be noted that phloem-feeding insects perform poorly on continuously stressed plants that may exist in experimental conditions, whereas these insects may respond positively on intermittently stressed plants in natural conditions [48].

6. Aphid Osmoregulatory Mechanisms

Aphids survive and increase in population through osmoregulatory mechanisms. This is an important mechanism that can potentially increase their population growth by repelling host plant metabolites [62]. Previous research linked aphid survival to an increase in sucrose respiration rate; however, varying sucrose concentrations in an artificial diet proved otherwise [20]. Moreover, aphids' reliance on the xylem sap of host plants and metabolic water production via flight have been identified as potential osmoregulatory mechanisms [63]. Nonetheless, similar studies found a consistent decrease in the abundance of energy metabolism enzymes, which was interpreted as a mechanism for preserving energy for survival [62]. The water metabolic mechanism as a mechanism for aphids' survival under drought stress is still not fully understood. As a result, some studies propose that aphids survive drought stress by relying entirely on other osmoregulatory mechanisms, such as sugar polymerisation or xylem water acquisition [64]. Another study found that *Sitobion fragariae* had improved xylem feeding on wheat and oats during drought [58]. Several studies have confirmed that water acquisition from the xylem is a potential osmoregulatory mechanism for aphids, as starved aphids feed more on xylem sap [63] [65]. It has also been reported that alate aphids reduce their weight before flight, which provides them with aerodynamic assistance. They do, however, prioritize xylem feeding for post-flight rehydration. As a result, feeding on unfavorable hosts becomes a significant challenge to their performance [66].

7. The Simultaneous Effects of Drought Stress and Plant Resistance on Herbivorous Insects

Drought's impact on aphid survival could be direct (water-stressed insect traits) or indirect (effects of drought stressors on host plants) [48]. This observation, however, is uncertain because the effects of drought stress on aphids appear to be species specific [67]. Aphids appear to undergo physiological changes when feeding on drought-resistant plants, indicating that they have adapted to survive

on resistant host plants [68]. Aphids are sap-sucking insects that feed on plant phloem, which contains high sugar but lower amino acid concentration. Thus, the phloem offers an unstable diet due to osmotic pressure, which is considerably higher than that of the aphid body fluids. Host plants nutrients obtainable by aphids are synthesized by drought stress through turgor pressure effects [68] and sap composition [12]. The performance of aphid on drought stressed plants may improve [68], decline [12] [53] or remain unchanged [45]. The increase in aphid performance under drought stress has been attributed to the elevation of amino acid concentrations in the phloem of host plants, while decreased performance has been attributed to an increased need for osmoregulation as phloem solutes increased. However, drought stressed plants are reported to modify secondary metabolites against aphid attack [48].

8. Plant Resistance and Tolerance Mechanisms

Plants that perform well in the face of aphid attack are referred to as being resistant or tolerant, whereas those that perform poorly are referred to as being susceptible [69]. Resistance traits are economically advantageous because they may provide a more sustainable alternative to the use of synthetic pesticides, which can have adverse effects on consumers and the environment. Plant resistance refers to the chemical and physical mechanisms that plants use to defend themselves against pest attack by reducing herbivory (antibiosis) and/or insect preference (antixenosis) [70]. This kind of mechanism can be divided into two types: constitutive and induced resistance. Constitutive resistance occurs independently of the attack, whereas induced resistance occurs directly when the plant is stressed as a result of the attack [71]. Plant tolerance refers to a host plant's ability to regrow and produce yield regardless of the degree of damage caused by an insect attack [72]. External factors such as high nutrient availability and stressed environments have been linked to host plant tolerance in some studies [70] [73]. Others, on the other hand, predict non-exclusive factors, which limit host plant fitness and thus contribute to plant tolerance against herbivores [74] [75]. Under biotic and abiotic stress, resistance and tolerance may coexist [76]. Aphids are regarded as one of the most important pests due to their unique ability to overcome plant natural defenses [77].

Several studies have confirmed that drought stress increases host plant secondary metabolites that inhibit aphid growth and development [78] [79]. However, few studies have evaluated how different drought tolerant levels of host plants respond to different aphid species under drought stress. Only five of the papers reviewed reported on mechanisms involved in aphid survival on susceptible and resistant host plants [80] [81] [82] [59], with the remaining one focusing solely on aphid responses on resistant plants [83]. Furthermore, three studies assessed the responses of three different drought tolerant levels of plants (drought-tolerant, moderately-tolerant, and drought-sensitive) to aphid attack [84] [85], and one studied the mechanism involved in aphid survival on drought tolerant

hosts under drought stress [86]. These few studies suggest that research into the mechanisms involved in different aphid responses to resistant and drought-tolerant plants is limited and needs to be empirically investigated. Some of the findings from these studies indicate that aphid performance increase on well-watered plants compared with drought-stressed plants [7] [17]. This is because sap-sucking insects like aphids thrive on host plants with high water content [7] [82]. A number of studies have shown that drought stress increases the population of insect pests by influencing the physiology of host plants [80] [81]. These findings support previous hypotheses, including the plant vigor and plant stress hypotheses, which do not account for potential differences in plant susceptibility to herbivorous insect pests. It appears that both the inherent resistance of plants to aphids and the water status of the growing medium play important roles in influencing aphid performance. As a result, aphids' responses to plants may differ depending on aphid (aphid fitness) and plant species (plant vigor), plant water potential, and host plant chemical composition variations (high level of defense). Drought stress can alter the chemical composition of the host plant. These findings suggest that, while aphid responses to drought-stressed plants have been studied, there are still many unknowns. Understanding these is paramount for sustainable pest management in areas where multiple stressors are of major concern.

9. Effect of Drought Stress on Aphid Host Selection and Feeding Behavior

Phloem feeding aphids have also been shown to pierce the plant's xylem and extract water and ions. The majority of studies have shown xylem feeding in dehydrated aphids [82] [69]; under these conditions, aphids would require the cibarial pumping action in watered stressed plants to acquire xylem sap. Aphid feeding preferences are strongly influenced by host plant morphology and physiology, such as access to plant phloem, which serves as a source of aphid nutrients. During the early stages of feeding, plant secondary metabolites either protect or disrupt aphids' olfactory orientation. The cross-talk of phytohormones biosynthesis of these secondary metabolites is especially noticeable under drought stress [83]. The ability of the aphids to probe the leaf substrate, infiltrate cells to "taste" a leaf, and reach the phloem, the site of resistance to several aphid species, then determines host acceptance [84] [85]. Aphids secrete calcium-binding proteins that shield stylet probing from clogging sieve elements at phloem feeding sites where volatiles accumulate [86]. The levels of secondary metabolites vary greatly between plant species. Depending on the efficacy of the defense mechanism, feeding on these secondary metabolites may improve or decrease aphid growth, development, survival, and fecundity. The process of host acceptance and utilization results in either a compatible interaction in which an aphid successfully deploys and exploits a susceptible host plant or an incompatible interaction in which an aphid is unable to feed on a resistant plant [87]. During the early stages of feeding, aphids secrete gelling saliva to form a feeding sheath and later watery

digestive saliva capable of eliciting plant defenses [88]. The minimal tissue damage caused by aphid “stealth” feeding and the prolonged duration of aphid feeding suggest that aphid saliva elicits plant defense responses that are very different from mandibulate mouthpart saliva [89]. Aphids secrete salivary proteins containing signal peptide sequences [90], some of which promote or delay growth and colonization [91] [92]. These and other findings suggest that aphid effectors are important in aphid host plant selection and that effectors may be the first factor determining plant resistance or susceptibility to aphid herbivory [93] [94]. This suggests that aphid responses to plants under drought stress differ depending on the aphid and plant species (Figure 1).

10. Drought Induced Decrease in Aphid’s Abundance and Its Effects on Terrestrial Trophic Interactions

Aphids form a significant group of sup-sucking insects from an ecological standpoint because of the diverse community of higher trophic groups they support. Aphids are cosmopolitan insects that are considered primary producers in many ecosystems, providing food for many trophic groups [91]. The majority of the studies reviewed strongly support the notion that the severity of drought stress inhibits aphid growth and development, though the extent of this may be due to an unpalatable host plant as an aphid’s food source. As a result, the severity of the drought is likely to have an impact on the terrestrial trophic interactions that aphids support. This indicates that drought stress will reduce the population of aphids thereby reducing food availability for aphid predators [95]. Furthermore, aphids secrete honeydew, which attracts ants [96]. These ants protect the plant from other herbivore insect pests [96]. Although aphid population reduction due to drought severity may reduce plant damage, it is also likely to reduce plant protection by ants, as reduced honeydew quantity or quality may reduce ant attendance. Ecosystem interaction is mostly stable [97] [98], with variations in the richness of one species or functional group causing fluctuations in the network’s richness and diversity [98]. A reduction in aphid performance due to drought may reduce

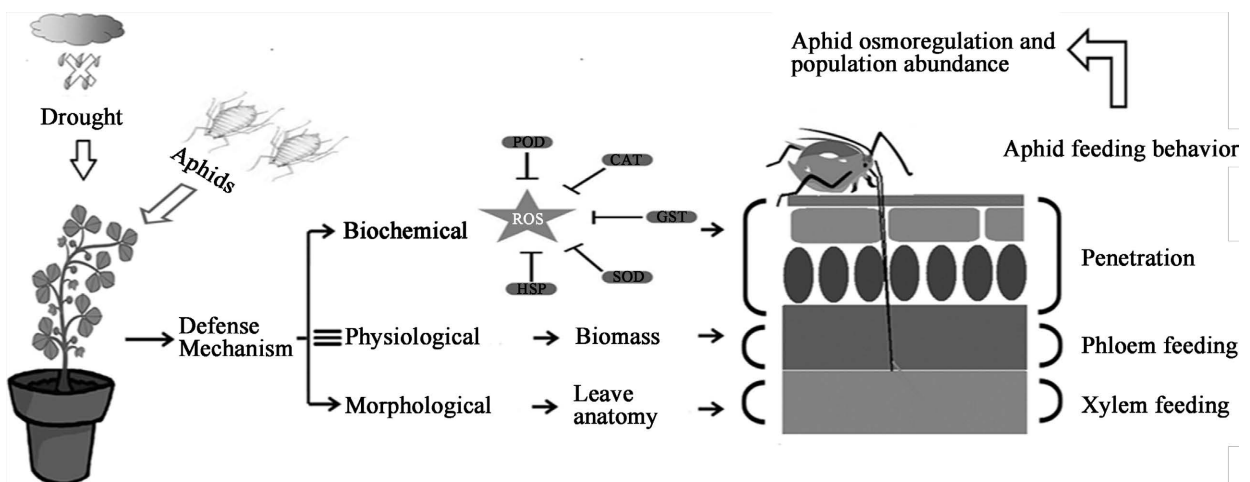


Figure 1. Conceptual diagram showing the links and feedbacks of aphid-plant interaction under drought and aphid stress [80].

richness, which may be available to support other trophic levels. According to a recent study, drought-induced destruction of aphid-parasitoid interactions altered insect population succession [99]. Drought-induced aphid fecundity reductions [100] may also reduce aphid abundance for aphid-natural enemies. However, because only a few of the studies reviewed were field studies, more research into the drought-aphid interaction need to be conducted under field conditions.

11. Conclusion

Drought stress appears to have a mixed effect on aphid resistance but generally, most studies reported that drought decreases plants resistance to aphids. Interestingly, recent research indicates that this is not the case for *M. persicae*. The present study shows that how the availability of resources affects plants susceptibility and resistance to aphid damage still remains to be discovered. This suggests that the response of aphids to drought stress is too complex to be deduced from a single hypothesis. The differences in findings among studies are most likely to be due to variations in plant responses to drought stress and subsequent insect variations in drought stress responses. This can be a major focus of future research to broaden our understanding of plant resistance under changing resource-supply conditions under our changing climate.

Conflicts of Interest

The authors declare no conflicts of interest.

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