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Review Article

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Insect responses to drought events and salinity stress: unveiling direct and indirect effects

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ABSTRACT- The future holds a projection of escalated occurrences of extreme climate events, which are expected to affect insect life substantially. Extensive research efforts in this field have witnessed rapid expansion despite significant gaps in knowledge. This review article addresses a deeper understanding of the impacts of severe climate events on insects that outline promising avenues for future research in this field. Drought has emerged as one of the predominant forms of extreme climate events that have extensively influenced insects, as frequently documented in the literature. The significance of drought occurrences on insects is crucial within the climate change scenario. Furthermore, the increasing occurrence and intensity of drought episodes, which are associated with changes in the climate, can result in elevated salinity levels in water bodies and soils. These changes have far-reaching implications for ecosystems, including impacts on biology, survival, and insect behavior. This review aims to analyze developments in information acquisition with anticipated climate change implications, particularly drought and salinity, on various aspects of insect life.

INTRODUCTION

Over the past few decades, there has been a noticeable surge in climate variability, and future projections indicate that this trend will persist. Extreme events are anticipated to intensify in duration, magnitude, and frequency. Compared to plants and vertebrates, insects are more likely to react quickly to changes in climate due to their short lifespans and high reproduction rates. (Sharma, 2014). The impacts of extreme climate events on insects are intricate and multifaceted (Filazzola et al., 2021). Insects are highly susceptible to the effects of climate change since their development, reproduction, and survival are heavily influenced by environmental conditions. This includes insect pest and their natural enemies (Sharma, 2014). Insect communities exhibit species-specific responses to extreme climate events, with some species demonstrating varying degrees of resilience or sensitivity to these climatic extremes.

Drought is a frequently investigated form of extreme climate events in ecology (Marques et al., 2014; Forister et al., 2018). With climate change as the main driver, future projections suggest that both the frequency and intensity of droughts are anticipated to rise (Liu et al., 2023), which can highly affect growth, morphology, and physiology in plants. These changes can then have a cascading impact on the populations and outbreaks of insect pests. The effects of drought on insects hold great importance, and the response of various feeding guilds to drought stress varies (Anderegg et al., 2015; Gely et al., 2020).

The increasing intensity and frequency of drought occurrences, linked to changes in climate conditions, can increase salinity levels in water bodies and soils. The problem of salinization of water/soil is pervasive worldwide. Plant development, food uptake, ion regulation, tolerance mechanisms, and water relations can all receive stimuli from salt stress. Furthermore, this stress can alter direct and indirect defense chemicals in plants. These modifications may subsequently have bottom-up consequences on herbivore fitness (Dasgupta et al., 2015; Munns & Tester 2008; Forieri et al. 2016; Quais et al., 2019). The effect of salt stress on insect herbivores is unpredictable and highly dependent on the kind of plant and insect species and stress severity (Quais et al., 2019).

To enhance our present knowledge regarding the effects of drought and salinity on insects, we conducted a comprehensive review of the available literature. These stressors affecting insects have far-reaching implications. Examining how salinity and drought impact insect survival, reproduction, and behavior can help us to identify resilient species. It may inform conservation efforts, ensuring the preservation of insect diversity can aid in climate change mitigation and adaptation. Moreover, by studying the impacts of these stressors on insects, researchers aim to understand the ecological consequences of these stressors to develop strategies to mitigate pest damage and improve agricultural productivity. It is crucial for designing efficacious conservation strategies for protecting and preserving insect diversity and ecosystem serv

Furthermore, understanding the impacts of these stressors on insect dynamics is essential to optimize ecological balance, agricultural productivity, and ecosystem functions.

Direct effects of drought on insects

The occurrence of drought can have a direct impact on aquatic insects or insects that undergo life stages in aquatic habitats, mainly by increasing the vulnerability to dehydration (Filazzola et al., 2021). Moreover, substantial evidence from terrestrial environments suggests that extreme droughts can have a direct impact on insects, which involves an elevated risk of desiccation for *Lepidopteran pupae* and collembolans (Elnitsky et al., 2008; McDermott Long et al., 2017). A comparative analysis of three butterfly species, characterized by different levels of susceptibility to climate change, demonstrated the significance of stress tolerance during the initial stages of development. The species deemed the most prone to vulnerability displayed the most substantial decrease in the successful hatching of eggs when subjected to elevated temperatures and aridity-induced stress. Additionally, a parallel trend occurred in mortality rates among the newly hatched individuals. The augmented fatality proportions in the initial stages of development could potentially entail significant implications for the extant biodiversity (Klockmann & Fischer, 2017). Generally, terrestrial insects are expected to encounter higher mortality rates and food stresses, owing to the adverse ramifications of drought periods affecting water resources and the quality of plants. These alterations are deemed a significant hazard to biodiversity (Hoffmann et al., 2013).

Impact of drought on insect damage to plants

Drought stress can modify how plants respond to insect damage, potentially resulting in an elevation or reduction in the extent of insect damage.

The damage of sorghum shoot fly, namely *Atherigona soccata* (Rond.), was mitigated due to severe drought stress (Soman et al., 1994). Gall-forming insects, such as sawflies and cecidomyiid flies, reportedly had reduced performance on drought-stressed plants and caused less damage under drought-stress conditions (Price, 1991; Huberty and Denno, 2004).

Drought-stressed plants of sorghum exhibited heightened vulnerability to the spotted stem borer, *C. partellus*, and the sugar-cane aphid, *Melanaphis sacchari* (Zehnt.), resulting in greater levels of damage compared to the plants cultivated under irrigated conditions. It was demonstrated that the combination of drought stress and aphid herbivory had an interactive influence on faba bean yield. Under drought stress, yield loss caused by black bean aphid (*Aphis fabae* Scopoli) herbivory was lower in faba beans (*Vicia faba* minor L.) (Price, 1991; Raderschall et al., 2021).

Since drought stress affects the behavior of insect herbivores, it is likely to determine whether the yield loss due to insect herbivory is reduced or heightened in drought-stressed plants. It is still unclear how the combination of drought stress and insect herbivory affects crop yield (Raderschall et al., 2021).

Impact of drought on insect outbreak

In particular, the increasing frequency of drought is understandable as a significant contributing factor that can cause insect outbreaks. Its primary cause is the direct influence on the dynamics of insect populations and the indirect consequences on plant growth and defense mechanisms (Bao et al., 2019). Additionally, sample research has shown that protracted or severe droughts are detrimental to tree development and survival and can lead to more frequent or severe outbreaks of forest pests (Netherer et al., 2015). However, drought can cause a series of physiological reactions in plants, some of which can limit insect herbivory (Kansman et al., 2022). For instance, the hypothesis of plant stress-insect performance posits that drought conditions promote the outbreak of phloem-feeding insects. It is attributable to the induction of plant stress responses, which subsequently enhance nitrogen availability for these insects. Nevertheless, the empirical evidence presents a contradictory stance towards this hypothesis, as it indicates that the response of herbivores to changes in plants induced by drought cannot be consistent in predictions based solely on nitrogen availability (Khan et al., 2010; Banfield-Zanin & Leather, 2016; Kansman et al., 2022).

Impact of drought on insect performance

Severe drought studies have been conducted to investigate how drought stress impacts insect populations and various aspects of their performance and life history characteristics (Verdugo et al., 2015; Aleosfoor et al., 2023; Rad et al., 2023). Multiple studies have indicated that insect performance rises in response to plant stress as the investment in chemical defenses dwindles. These findings gain support from frequent anecdotal reports of insect outbreaks during droughts (Mattson et al., 1978; Van Bael et al., 2004; Allen et al., 2010). Plants might reduce their production of chemical defenses during drought, which could be advantageous for most feeding groups. However, the toughness of leaves may also rise, affecting insect groups that chew on leaves (Gely et al. 2020).

Cabrera et al. (1995) found that *Schizaphis graminum* Rondani feeding on wheat experienced a drop in growth rate after being subjected to continuous drought stress. By feeding *Myzus persicae* Sulzer on well-watered and

drought-stressed susceptible and resistant peach cultivars (*Prunus persica*), the survival and ability to colonize resistant cultivars were higher under drought-stress conditions (Verdugo et al., 2015). Moderate and severe drought stress had a neutral impact on *Metopolophium dirhodum* (Walker, 1849) (Hemiptera: Aphididae) in tolerant-wheat cultivars but negatively affected drought-susceptible ones. Compared to aphids raised on wheat plants without drought stress, those raised under severe drought stress had lower net reproductive rates and finite and intrinsic rates of increase (Aleosfoor et al., 2023). The western flower thrips, *Frankliniella occidentalis* (Pergande), performed worse on drought-stressed tomato plants. Severe drought stress in host plants led to a reduction in the population of *F. occidentalis.* This reduction resulted from lower longevity, fecundity, and other population parameters of the thrips (Rad et al., 2023).

The fertility of insects can be affected by drought stress, and if the environmental humidity is too low, it can also impact the rate at which insects lay eggs and emerge from their pupae (Liu et al., 2023). Low humidity levels caused decreased pupal weight in *Spodoptera litura* and impaired spawn ability in female adults (Guohong et al., 2001). Drought stress caused weight reduction in adult *Nilaparvata lugens* insects, their egg-laying rates, and the hatching of their eggs (Luo et al., 2012). The death rate of Holotrichia oblita Fald increased significantly in high-humidity environments (Dang et al., 2009).

While generalist pests seem to reproduce better under more severe water deficit stress, specialists typically suffer more from severe drought conditions while benefiting from moderate stress levels (Dale & Frank, 2017; Gely et al., 2020).

Impact of drought on plant nutritional quality and chemical defenses

Water availability is altered by climate change, thereby indirectly influencing the growth of plants and insect-plant interactions. When plants experience drought stress, they undertake various physiological changes to support their growth and reproductive capacities. These alterations subsequently impact the performance of herbivorous insects (Kansman et al., 2022).

During drought, soluble sugar levels and polyols in the phloem tend to rise more than normal (Marček et al., 2019). Elevating concentrations of soluble sugars, notably sucrose, may exert an adverse impact on the reproductive capacity of some phloem-feeding insects (Douglas, 2006). Additionally, drought stress causes plants to produce specific chemical components and physical structures and activate their phytohormone defenses, which may increase their resistance to herbivory (Ahmed et al., 2015; Pineda et al., 2016; Lin et al., 2021; Rad et al., 2023).

Plant tissue contents of carbon and nitrogen compounds increase in response to moderate drought circumstances, but decrease in severe drought conditions, supported by the available literature (Farooq et al., 2009; Gely et al., 2020). Plants under moderate drought stress may have higher carbon and nitrogen levels, thus increasing the availability of nutrients for herbivorous insects. Potential benefits from this phenomenon on plant nutritional quality are outweighed by the concurrent effects of reduced vegetative growth and amplified plant defense mechanisms (Gely et al., 2020). It is crucial to emphasize that there could be a non-linear pattern in how drought affects plant defenses and nutritional quality. In the early phases of a drought event, there is an increase in the synthesis of substances for defense mechanisms and nitrogen compounds. However, if the drought persists and intensifies, a subsequent decline in these factors may follow (Gely et al., 2020; Kansman et al., 2022).

Impact of drought on insect pest natural enemies

Although drought stress has an impact on natural enemies, there is limited evidence regarding the anticipated effects of climate change on them. Understanding the predatory potential of natural predators when facing drought stress relies on assessing the impact on their phytophagous prey. Drought stress can modify the performance and survival of phytophagous insect pests, leading to changes in demographic characteristics. These changes can then affect population and parasitization rates by influencing the suitability of prey and host relationships (Aslam et al., 2013; Banfield Zanin & Leather, 2016). Host plants change insect herbivore quantity, typically through modifications in plant secondary metabolites. These alterations have reportedly played a role in mediating tritrophic interactions, causing adjustments in consumption rates and function responses due to changes in the quality of the host plant (Timms et al., 2008; Banfield-Zanin & Leather, 2015).

The combination of extended droughts, and then substantial rainfall, can contribute to an upsurge in oriental armyworm populations, primarily attributed to the adverse impact of drought on the activity and abundance of natural enemies that play a vital role in controlling this pest (Sharma et al., 2010). Aslam et al. (2013) observed that parasitism rates decreased in the bird cherry-oat aphid, i.e., *Rhopalosiphum padi* L., on *Hordeum vulgare* when subjected to drought stress. According to Weldegergis et al. (2015), the presence of water-deficit stress did not affect the parasitoids of *Mamestra brassicae* caterpillars feeding on Brussels sprout (*Brassica oleracea* L. var. Gemmifera). The

impact of various levels of intensity and frequency of drought on the rate at which aphids are consumed by the two coccinellid species was investigated by Banfield-Zanin and Leather (2016). Their results proposed that under drought stress, prey-mediated impacts can change predator consumption and subsequently affect biocontrol efficiency. According to Shehzad et al. (2021), aphid performance was highest on plants experiencing medium drought stress; however, the parasitoids only consistently responded to treatments involving severe drought stress, prompting a decrease in their performance. Colorado potato beetle fertility and life parameters suffered after being fed on drought-stressed potato plants, while adult natural enemies of *Arma chinensis* Fallou experienced a decline in survival rate (Liu et al., 2023).

Overall, the impacts of drought stress on insect natural enemies can be intricate and context-dependent. It is crucial to comprehend these consequences to devise effective pest management strategies and conserve beneficial insect populations in facing climate change.

Impact of drought on pollinators

Insect pollination is necessary for about 75% of crop species that are grown for human consumption globally. Drought may alter a plant species flowering time, geographic range, or both, which could lead to temporal and spatial mismatches among plant species and pollinating insects. Phases of plant reproduction and pollination are vulnerable to this abiotic stress. Drought will alter the interactions between plants and pollinators by affecting insect-favoring cues or signals, such as flower appearance, plant height, flower counts per plant, flower color, shape, size, the composition of scent molecules, and the rewards offered by flowers such as volume of nectar, concentration, and the sugar composition, pollen amount and chemical composition. Drought has the potential to harm both plants and their pollinators due to their interdependence, leading to a decrease in reproductive success for both partners in these interactions (Descamps et al., 2021).

Impact of drought on bark beetles and wood borers

When trees experience moderate drought stress, they may utilize excess carbon to synthesize resin and create ducts, which helps in making them more resistant to attacks from beetles and wood borers (Muilenburg & Herms, 2012; Gely et al., 2020). Extreme drought conditions can attract bark beetles and wood borers to trees. However, drought-stressed trees may have reduced nutritional value, which can hinder the development of bark beetles, similar to what reportedly occurred in other feeding guilds (Huberty & Denno, 2004). Nonetheless, most research has demonstrated that mild drought has negative effects on bark beetle populations and wood borer, and severe drought has favorable effects. In other words, there is a positive correlation between bark beetle populations, performance, attack success, and the severity of drought (Wotherspoon et al., 2014; Anderegg et al., 2015; Kolb et al., 2016; Netherer et al., 2019; Müller et al., 2022).

Wood borers *Tomicus destruens* (Coleoptera: Scolytidae) preferred adequately-watered pine trees, and it also had a greater survival rate on such trees than those experiencing drought stress. Severe drought conditions can contribute to the proliferation of bark beetle populations, whereas trees experiencing moderate stress levels may exhibit more resilience/resistance to bark beetle infestations (Netherer et al., 2015; Netherer et al., 2019).

Impact of host plant salinity stress on insects

Water salinity is a fundamental factor of habitat appropriateness and a primary driver of aquatic insect species distribution (Carbonell et al., 2017). The rise in salt levels in water resources may harm an expanding number of aquatic organisms (Cañedo-Argüelles et al., 2019).

The outcomes of salinity stress on insect herbivores when interacting with host plants appear to lack a clear pattern and are predominantly influenced by factors such as the type of the plant, the insect species, and the intensity of the stress level (Quais et al., 2019). Variations in host plant quality due to salinity stress may have neutral, adverse, or positive effects on herbivore insects (Bowdish & Stiling 1998; Polack et al. 2011; Han et al. 2016; Renault et al. 2016; Sienkiewicz-Paderewska et al. 2017; Quais et al., 2019; Rad et al., 2024). In a study by Dong et al. (2020), the performance of two insect species, *Macrosiphum euphorbiae* and *Tuta absoluta*, was examined on tomato plants exposed to drought and salt stresses. According to their findings, water and salt stresses affected plant growth, thus changing both herbivores via bottom-up effects.

M. euphorbiae survival and fertility were adversely affected by salinity stress. Larval development of *T. absoluta* was also negatively influenced by water limitation caused by salinity stress. In another study, Rad et al. (2023) investigated the impacts of salinity stress on demographic traits of the western flower thrips (WFT), *Frankliniella occidentalis* (Pergande). Their study highlighted that WFT could pose challenges in regions experiencing moderate salinity. However, severe salinity stress conditions caused significant fitness costs on the thrips. Salinity stress also affects freshwater insects, threatening their health and ecosystem dynamics (Silver & Donini, 2021).

CONCLUSION

Despite numerous uncertainties surrounding climate change stressors, there is widespread consensus that they affect plants and insects associated with them. Due

to the diversity of insect species and their interactions with host plants, insect species exhibit varied responses to climate change elements, including drought and salinity. The impacts of drought and salinity on insects are multifaceted, as these stressors can favor certain insect species while inhibiting others. Additionally, these stressors can affect insect distribution, diversity, abundance, development, and growth. As climate change factors create favorable conditions for pest infestations and crop damage, there is a substantial risk of experiencing significant economic losses and encountering challenges in ensuring an adequate human food supply. Addressing this issue will necessitate a proactive and evidence-based approach. It entails the need for meticulous planning and the development of adaptation and mitigation strategies, such as modified IPM techniques. These strategies should incorporate climate and pest monitoring with modeling tools and relevant utilization strategies.

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مقاله مروری

پاسخ حشرات به رویدادهای خشکسالی و تنش شوری: آشکار کردن اثرات مستقیم و غیر مستقیم

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چکیده – در آینده پیش‌بینی می‌شود رخدادهای شدید آب و هوایی افزایش یابد و انتظار می‌رود که این رخدادها اثرات قابل‌توجهی بر حشرات داشته باشند. تلاش های تحقیقاتی گسترده در این زمینه در حال انجام است با این حال، شکاف های قابل توجهی در دانش وجود دارد. برای به دست آوردن بینش در مورد اثرات رویدادهای آب و هوایی شدید بر حشرات و ترسیم راه های امیدوارکننده برای تحقیقات آینده در این زمینه، این مرور انجام شد. همانطور که در بررسی منابع دیده می‌شود خشکسالی به عنوان یکی از اشکال غالب رویدادهای شدید آب و هوایی است که به طور گسترده بر حشرات تأثیر می‌گذارد. تأثیر خشکسالی بر حشرات در زمینه تغییرات آب و هوایی مهم است. علاوه بر این، فراوانی و شدت فزاینده رویدادهای خشکسالی، که با تغییرات آب و هوایی مرتبط است، باعث افزایش سطح شوری در بدنه‌های آبی و خاک می‌شود. این تغییرات پیامدهای گسترده ای برای اکوسیستم‌ها، از جمله تأثیرات بر زیست شناسی، بقا و رفتار حشرات دارد. این بررسی با هدف تجزیه و تحلیل پیامدهای تغییر اقلیم ، به ویژه خشکسالی و شوری، بر جنبه های مختلف زندگی حشرات انجام شده است.