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Khodaverdi, Haleh
Fowles, Trevor
Bick, Emily
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Climate Change

Does Drought Increase the Risk of Insects Developing Behavioral Resistance to Systemic Insecticides?

Haleh Khodaverdi,[1] Trevor Fowles,[1] Emily Bick,[1] and Christian Nansen[1,2,3]

[1]Department of Entomology and Nematology, UC Davis Briggs Hall, Room 367, Davis, CA 95616 (haleh.khodaverdi@gmail.com; tmfowles.work@gmail.com; enbick@ucdavis.edu; chrnansen@ucdavis.edu), [2]State Key Laboratory Breeding Base for Zhejiang Sustainable Pest and Disease Control, Zhejiang Academy of Agricultural Sciences, 198 Shiqiao Rd., Hangzhou 310021, China and [3]Corresponding author, e-mail: chrnansen@ucdavis.edu

Abstract

Increases in severity and frequency of drought periods, average global temperatures, and more erratic fluctuations in rainfall patterns due to climate change are predicted to have a dramatic impact on agricultural production systems. Insect pest populations in agricultural and horticultural systems are also expected to be impacted, both in terms of their spatial and temporal distributions and in their status as pest species. In this opinion-based article, we discuss how indirect effects of drought may adversely affect the performance of systemic insecticides and also lead to increased risk of insect pests developing behavioral insecticide resistance. We hypothesize that more pronounced drought will decrease uptake and increase the magnitude of nonuniform translocation of systemic insecticides within treated crop plants, and that may have two concurrent consequences: 1) reduced pesticide performance, and 2) increased likelihood of insect pests evolving behavioral insecticide resistance. Under this scenario, pests that can sense and avoid acquisition of lethal dosages of systemic insecticides within crop plants will have a selective advantage. This may lead to selection for insect behavioral avoidance, so that insects predominantly feed and oviposit on portions of crop plants with low concentration of systemic insecticide. Limited research has been published on the effect of environmental variables, including drought, on pesticide performance, but we present and discuss studies that support the hypothesis described above. In addition, we wish to highlight the importance of studying the many ways environmental factors can affect, directly and indirectly, both the performance of insecticides and the risk of target insect pests developing resistance.

Key words: behavioral insecticide resistance, systemic insecticide, neonicotinoid, climate change, IPM

In this opinion-based article, we discuss how indirect effects of drought may adversely affect both the performance of systemic insecticides and also lead to increased risk of insect pests developing behavioral insecticide resistance. Furthermore, we argue that the possible adverse effects of drought on the performance of systemic insecticides has to be given increased research attention, as climate change will likely lead to increased severity and frequency of drought in many agricultural regions. The Food and Agriculture Organization of the United Nations defines a pesticide as "Any substance or mixture of substances intended for preventing, destroying, or controlling any pest . . . The term includes substances intended for use as a plant growth regulator, defoliant, desiccant, or agent for thinning fruit or preventing the premature fall of fruit." (Anonymous 2002). Systemic insecticides are chemicals absorbed by plants and distributed internally via the vascular system, delivering the insecticide to untreated plant tissues (Bennett 1949). These insecticides have outstanding efficacy in crop protection against a number of pest invertebrates (Laurent and Rathahao 2003), especially piercing–sucking insect herbivores (Stamm et al. 2013). However, neonicotinoids have limited efficacy against lepidopteran and coleopteran pests (Tomizawa and Casida 2005). Advantages associated with systemic insecticides over nonsystemic insecticides include: 1) reduced sensitivity to spray coverage and canopy penetration (Nansen et al. 2015), as the active ingredient translocates within and among plant tissues, 2) high water solubility and xylem mobility of the active ingredients (Simon-Delso et al. 2015), 3) continuous plant protection for an extended period of time without repeated applications (Bonmatin et al. 2015), and 4) protection from direct insect herbivore damage (mainly sap feeding) and reduced indirect crop damage by pathogens they transmit (Simon-Delso et al. 2015). Due to these advantages, systemic insecticides, including neonicotinoids, have been widely adopted across a diverse range of food production systems worldwide since the 1990s (Jeschke and Nauen 2008, Jeschke et al. 2010, Casida and Durkin 2013). Considering the versatility and widespread adoption, pests evolving physiological and behavioral resistance to systemic insecticides should be a concern to global food security.

In this opinion-based article, we hypothesize that drought will increase the likelihood of pests evolving behavioral resistance to systemic insecticides. Moreover, we predict that climate change will increase the likelihood of severe drought events in many agricultural regions and adversely affect the uptake and vascular flow in crop plants treated with systemic insecticides. If so, this may lead to nonuniform distribution of the active ingredient in plant tissues. Under this scenario, pests that can sense and avoid acquisition of lethal dosages of systemic insecticides within crop plants will have a selective advantage. We present and discuss studies supporting this hypothesis. In addition, we wish to highlight the possible effect of drought on the performance of systemic insecticides as a justification for more research into the many ways environmental factors can affect, directly and indirectly, both the performance of insecticides and the risk of target insect pests developing resistance.

Application of Systemic Insecticides

In 1936, a study showed that levels of aphid infestation in wheat plants were negatively associated with soil content of selenium (Hurd-Karrer and Poos 1936). This discovery led to experiments with selenium uptake from soils as a systemic insecticide, giving rise to a new method of insecticide applications (Hurd-Karrer and Poos 1936). In modern crop protection, systemic insecticides are applied to crops in four ways: 1) coating seeds surface prior to planting (seed treatment), 2) spraying of crop foliage or soil, 3) soil drenching after crop emergence, and 4) the addition of the insecticide to starter solutions used at transplanting (Baranowski 1962, Bonmatin et al. 2015). Seed treatment and soil applications are the two preferred methods, representing ~60% of neonicotinoid insecticide applications worldwide (Jeschke et al. 2010). Seed coating is the primary method for delivering neonicotinoid insecticides to agricultural crops throughout the world (Simon-Delso et al. 2015). This method is considered a "safe" alternative to conventionally applied insecticides, because seed coating minimizes drift of pesticides to nontarget surfaces and organisms (Ahmed et al. 2001, Koch et al. 2005). In addition, seed coating significantly decreases the amount of insecticide applied to a crop field area compared with conventional spray methods (Laurent and Rathahao 2003).

Neonicotinoid insecticides and fipronil currently account for approximately one-third of the world insecticide market (monetarily based on 2010 prices; Simon-Delso et al. 2015). Their success is due to high efficacy in arthropod pest management, flexibility of application method, and extended residual effect (Bonmatin et al. 2015). The neonicotinoid class of insecticides is applied to a wide range of agricultural and horticultural crops, including cotton, maize, potato, and oil seed rape (canola; Weichel and Nauen 2003, Van Timmeren et al. 2011, Van Timmeren et al. 2012, Vernon et al. 2013).

Uptake and Translocation of Systemic Insecticides

Absorption and translocation of systemic insecticides are linked to physical and chemical characteristics of the insecticides' octanol water partition coefficient and dissociation constant (Bromilow and Chamberlain 1995, Bonmatin et al. 2015). Once absorbed by crop roots, a high water solubility increases the likelihood of uniform distribution and bioavailability of the active ingredients within plant tissues (Koltzenburg et al. 2008, Pierobon et al. 2008). Typically, the xylem transport system is responsible for translocation of systemic insecticides (Bonmatin et al. 2015), but some systemic insecticides can also move within the phloem, or both (Ahmed et al. 1954, Norris 1967). Radiolabeled imidacloprid has been observed moving toward leaf tips and margins after foliar applications (Bonmatin et al. 2015). However, predicting the translocation of insecticides in treated plants is difficult due to variable plant morphology, physiology, and chemical properties of the specific compounds. Generally, translocation occurs faster in younger stems and leaf tissues (Bennett 1957), but abiotic factors, such as weather conditions and soil properties, may affect the uniformity of systemic insecticide distribution among plant tissues (Cox et al. 1997, 1998).

Abiotic factors, including light intensity (Baur et al. 2006), temperature (Wedding 1953), relative humidity, and wind, influence water transpiration from leaves, thus influencing movement of systemic insecticides in the vascular tissue (Stamm et al. 2013). Depending on environmental conditions, a plant may direct water to certain parts of the plant, which will influence the uniformity of systemic insecticide distribution (Desneux et al. 2007). Additionally, the uptake of a systemic insecticide is affected by the rate of transpiration of water leaving the plant (Cloyd et al. 2011). This was demonstrated through drench tests, which determined that systemic insecticides require specific amounts of water to be most efficacious (Baranowski 1962).

Behavioral Resistance Mechanisms

Insecticide resistance was first reported over 100 yr ago (Melander 1914). Since then, there have been 11,254 separate records of 546 pest species evolving resistance to 331 insecticidal compounds (Tabashnik et al. 2014, Sparks and Nauen 2015). Most of these records refer to "metabolic" or "target-specific" insecticide resistance, which are driven by genetic and physiological selection pressures (Nansen and Ridsdill-Smith 2013). In addition to target-specific insecticide resistance, "behavioral insecticide resistance" has been reported in >30 species of insects (Sparks et al. 1989, Sparks and Nauen 2015) for >40 yr (Georghiou 1972). Insect pests expressing behavioral insecticide resistance avoid contact with or ingestion of a lethal dose of an insecticide, thereby increasing their survivorship (Lockwood et al. 1985, Brattsten 1988, Grieco et al. 2007).

There are a variety of behavioral resistance strategies of pests, and a few are briefly described below. Reduced leaf tissue penetration by piercing–sucking insects has been shown to function as a resistance mechanism to many different insecticides (Price 1991), because it reduces the insecticide acquisition rate (Saha and Mukhopadhyay 2013). For example, the adult tea mosquito bug *Helopeltis theivora* (Hemiptera: Miridae) demonstrated avoidance of multiple insecticidal compounds (organochlorine, organophosphates, synthetic pyrethroids, and neonicotinoids; Roy and Mukhopadhyay 2011, Roy et al. 2011). When exposed to insecticide-treated plants, the tea mosquito bug also shifts its oviposition behavior away from tea shoots, where the insecticide is believed to have the highest concentration (Roy and Mukhopadhyay 2011). Like the tea mosquito bug, diamondback moth *Plutella xylostella* L. (Lepidoptera: Plutellidae) populations have exhibited behavioral avoidance through oviposition site selection (Sarfraz et al. 2005). In a different study, diamondback moths larvae and ovipositing females of two diamondback moths strains (high and low physiological resistance) expressed different behavioral responses when offered cabbage leaves with and without insecticide treatments (Nansen et al. 2016). The latter study showed a clear and positive relationship between the level of physiological susceptibility to the insecticides by diamondback moth strains and each strain's level of

avoidance to the insecticide-treated cabbage leaves (Nansen et al. 2016). In addition, insecticide resistance behavior led to the decline in performance of glucose-based attractants for control of German cockroaches *Blatella germanica* L. (Dictyoptera: Blattellidae) in restaurants and food warehouses in the late 1980s and early 1990s (Hostetler and Brenner 1994, Wang et al. 2004). While high selection pressure favored cockroaches avoiding the attractants, there was a significant fitness cost to German cockroaches of being glucose averse (Shik et al. 2014).

When studying behavioral insecticide resistance, it is a fundamental assumption that arthropod pests can somehow sense the presence of pesticides and therefore adjust their feeding and oviposition behavior to avoid contact with the lethal active ingredient. The specific mechanisms responsible for such ability to sense the presence of pesticides are not well described, and that may be considered a weakness of the hypothesis discussed in this article. However, it is well-established that evolution has led to strong selection pressures on arthropod populations regarding both their selection of both host and oviposition plants. And a large body of research has been published on the evolution and nonrandom host selection by arthropods. We are therefore arguing that some of the basic traits used by arthropods to optimize their selection of feeding and oviposition sites may also enable them to avoid plant tissues with high concentrations of pesticides. Even though not directly linked to the discussion of main hypothesis in this article, we wish to highlight the importance of studying the many ways environmental factors can affect, directly and indirectly, both the performance of insecticides and the risk of target insect pests developing resistance.

Climate Change and Behavioral Insecticide Resistance

Climate change is already predicted to cause significant challenges to agriculture and pest management strategies. Using current greenhouse gas emission scenarios, increases to global temperatures and changes to regional patterns of precipitation and humidity have been predicted (Bloomfield et al. 2006), and a likely scenario is more frequent and also more severe drought conditions (Sheffield and Wood 2008, Dai 2013). An important body of research has demonstrated that elevation of CO_2 concentration in the atmosphere, as a consequence of climate change, may enhance the effectiveness of *Bacillus thuringiensis* (*Bt*) toxins that are applied as foliar applications (Coviella and Trumble 2000). The authors demonstrated that the combination of *Bt* toxins and elevated atmospheric CO_2 concentration led to a reduced nitrogen concentration in leaves, so that herbivorous insects had to consume more leaf material in order to acquire enough nitrogen, and that increased their ingestion of *Bt* toxins. However, regarding expression of *Bt* toxins in genetically modified crops, elevated atmospheric CO_2 concentration appears to reduce the toxin expression (Coviella et al. 2000), which supports the argument articulated in this article that climate change may adversely affect the performance of systemic insecticides. We are unaware of similar reports detailing any of the possible effects of climate change on the performance of non-*Bt* systemic insecticides. However, it seems reasonable to speculate that climate change, through its effect on ambient temperature, humidity, and accessible soil water, will affect the rate of transport in the plant's vascular system (Wedding 1953). If so, this may lead to a reduction in both uptake and vascular flow of systemic insecticide. This phenomenon represents a serious threat to global food security, as most insect pest management is still based on insecticide applications.

Several agricultural systems already demonstrate evolved behavioral resistance, which could be exacerbated by drought. Significant differences in Colorado potato beetle *Leptinotarsa decemlineata* (Say) larval mortality and development among vertical leaf positions provide evidence that the concentration of imidacloprid and its metabolites were unevenly distributed in the potato foliage 8–14 wk post planting (Olson et al. 2004). Olson et al. (2004) indicated that the concentration of imidacloprid was lowest in the younger tissues of the upper leaves and highest in the older, lower leaves. While these leaves act as toxic barriers to susceptible Colorado potato beetles, beetles could easily develop behavioral resistance that would allow the insects to preferentially feed on the lower insecticide concentrations in the upper canopy. Therefore, the risk of behavioral resistance increases in this system, if the younger upper leaves receive a lower concentration of systemic insecticide (through reduced translocation; Olson et al. 2004). Similarly in sugar beet, the concentration of imidacloprid was six times higher in lower leaves compared with the upper leaves 49 d after application (Westwood et al. 1998). A similarly nonuniform distribution pattern was noticed with the carbofuran (systemic insecticide) in Douglas firs (Mrlina et al. 1994), which documented decreasing concentrations of the chemical from the roots to the upper part of the tree. These examples highlight nonuniform systemic insecticide distribution within treated plants, and such within-plant gradients may be exacerbated under the effects of climate change.

Another significant factor which may lead to an increase in behavioral resistance within a pest population is the unequal amount of insecticide between neighbor plants receiving the same treatments. This can be caused by variable amounts of water available in the soil, a situation likely to occur under drought. Higher quantities of soil moisture favor water uptake, and consequently insecticide uptake (Laurent and Rathahao 2003). Castle et al. (2005) observed little difference in imidacloprid concentration between lower and upper sections of citrus trees, but found significant variation among the trees. Variability in the uptake of insecticide for these trees could be explained through different soil moisture contests, with optimal irrigated plants in the field able to incorporate more product than suboptimally irrigated plants. This situation is exacerbated during a drought, creating an opportune situation for populations of pest insects to develop behavioral resistance (Castle et al. 2005).

In conclusion, as we prepare for the effects of climate change and predicted increases in frequency and severity of droughts, food production systems face a wide range of direct and indirect challenges. Climate change will, both directly and indirectly, affect crop maintenance, occurrence of invasive species, and existing pest management practices. Compared to the different types of physiological resistance, behavioral insecticide resistance mechanisms have received considerably less research attention (Saha and Mukhopadhyay 2013). In this article, we discussed potential effects of climate change on the performance of systemic insecticides, and we argue that more research is needed to thoroughly study the likelihood and potential impact of the following scenarios: 1) drought suppression of systemic insecticide uptake and vascular flow rates, 2) the distribution and concentration of systemic insecticide within plant organs (i.e. vertically within the canopy), 3) target insect pests developing the ability to sense and avoid leaf tissues with high concentrations of systemic insecticides (positive evolutionary selection pressure), and 4) behavioral resistance becoming more widespread as consequence of climate change. Comprehensive and interdisciplinary research approaches to direct and indirect effects of climate change on risks of target pests developing resistance to insecticides will most likely be needed as part of establishing sustainable pest

management practices in the 21st century. Pest management decisions could be refined based on more research into the many ways environmental factors can affect, both directly and indirectly, the performance of insecticides and the risk of target insect pests developing resistance.

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