Title: The consequences of synthetic auxin herbicide on plant-herbivore interactions

Nia Johnson[1], Grace Zhang[1], Anah Soble[1], Stephen Johnson[1], Regina S Baucom[1*]

[1]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor MI 48109
*Corresponding author, email: rsbaucom@umich.edu

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Glossary

Herbicide drift: The movement of herbicide droplets through the air during or soon after herbicide application to any site other than the intended area.

Dicamba: Dicamba (3,6-Dichloro-*o*-anisic acid), a benzoic acid, is a type of synthetic auxin herbicide that is used to control dicotyledonous weeds. It works by mimicking the action of the natural auxin, indole-3-acetic acid, interfering with plant phytohormone responses. Residues of dicamba can volatilize from plant surfaces and drift to unintended areas.

Dicamba tolerant soybean: Dicamba tolerant crops, such as XTend soybeans are engineered to carry genes from soil bacteria that encode for a mono-oxygenase enzyme that degrades dicamba.

Synthetic auxin herbicide: Synthetic auxin herbicides, including dicamba, **2,4-D** (2,4-Dichlorophenoxyacetic acid), and **MCPA** (4-chloro-2-methylphenoxy acetic acid) work by mimicking the activity of auxin (indole-3-acetic acid). This class of herbicide is commonly used to control broadleaf weeds in grain crops, fallow fields, and rangelands.

Direct effects: Alterations to any plant phenotype or physiological process following exposure to herbicide.

Indirect effects: Herbicide-induced changes of plants that have cascading effects on interacting organisms.

Indole-3-acetic acid (IAA): Also known as auxin, the most common plant hormone. It regulates various aspects of plant growth and development, controls cell division, expansion, and differentiation. It is ubiquitous in plant development and plant processes.

Jasmonic acid: A plant phytohormone that is typically associated with plant stress responses.

Abscisic acid (ABA): A plant hormone that regulates several plant growth, development, and stress responses.

Volatile organic compounds (VOCs): Plant volatile organic carbons (VOCs) are secondary metabolites produced by plants that influence plant-pollinator, plant-herbivore, and plant-plant interactions, among other types of interactions.

Abstract

Although herbicide drift is a common side effect of herbicide application in agroecosystems, its effects on the ecology and evolution of natural communities are rarely studied. A recent shift to dicamba, a synthetic auxin herbicide known for ‘drifting’ to nontarget areas necessitates the examination of drift effects on the plant-insect interactions that drive eco-evo dynamics in weed communities. We review current knowledge of direct effects of synthetic auxin herbicides on plant-insect interactions, focusing on plant herbivory, and discuss potential indirect effects, which are cascading effects on organisms that interact with herbicide exposed plants. We end by developing a framework for the study of plant-insect interactions given drift, highlighting potential changes to plant developmental timing, resource quantity, quality, and cues.

The unknown consequences of changing agricultural practices

Humans have modified the Earth's landscapes for agriculture for nearly 10,000 years [1], with a significant acceleration of extent and impact in the last three hundred [2]. Recent intensive agricultural practices have led to a host of unintended consequences, such as pollinator loss, biodiversity declines, and the evolution of pesticide resistant organisms [3–8]. Herbicide use is a widespread and popular agricultural practice that reduces the impact of crop weeds [9]. However, herbicide use can lead to unintentional outcomes – namely, herbicide resistance [10], changes to weed community structure [11,12], and **herbicide drift**, defined as the exposure of nontarget areas to low doses of herbicide (*i.e.*, ~1-5% of the field dose, [13]). Although drift levels of herbicide are typically well below the threshold for immediate toxicity, exposure to drift can still cause significant plant damage [14–17]. While we have some information on the effect of drift on crop species [18], our knowledge of how drift may impact natural plant communities and the important plant-insect interactions that occur within them is strikingly limited [19,20].

The lack of knowledge about the impact of drift on plant-insect interactions is especially relevant given the increasing use of **dicamba**, a **synthetic auxin herbicide**, in current-day agriculture [21]. **Dicamba tolerant soybean** – a new transgenic tool developed in response to the evolution of resistance to the widely used herbicide glyphosate – has led to a ~500% increased use of dicamba for weed control between 2014 and 2019 in the US [22]. Following initial application, dicamba may 'drift' from target crops, traveling as far as 150 m away and exposing both natural weed communities and ornamental plants in nearby neighborhoods to the herbicide [23–25]. With 40 million acres of dicamba-tolerant soybean now grown in the US [21], and strong evidence that drift is a consistent feature of this herbicide [26,27], a significant amount of land and the natural communities within those areas will likely be exposed to dicamba. How will the recent, large-scale shift to this synthetic auxin herbicide affect natural weed communities in agroecosystems, the insects they support, and the plant-insect interactions that often drive ecological and evolutionary dynamics in agricultural spaces?

One such important plant-insect interaction is herbivory, which is responsible for the movement of energy and nutrients within terrestrial food webs. Understanding how herbivory may be altered given novel stressors like exposure to herbicide has come under recent scrutiny since changes in plant-herbivore dynamics have the capacity to alter subsequent trophic levels, affecting overall community dynamics [28,29]. Because of the recent shift to the use of dicamba, its propensity to drift, and the importance of plant herbivory in natural communities, we anticipate that crucial ecological and evolutionary dynamics will likewise be altered due to the increased use of dicamba in agroecosystems. We propose using this dynamic – the effect of synthetic auxin exposure on plant herbivory – as a model for understanding how changing agricultural regimes may lead to unintended, cascading consequences, and as well, a model for connecting the direct effects of pesticide exposures to subsequent indirect effects that may cascade through natural communities and ecosystems.

Here, we provide a path forward for capturing potential effects of this shift to dicamba by summarizing current knowledge of how synthetic auxin exposure affects natural communities and by developing a framework for future studies of this phenomenon with a focus on plant herbivory. We first briefly review how synthetic auxins act at the biochemical level and function as an herbicide, and we summarize how their application may disrupt or modify the defenses plants employ against herbivores. We then describe **direct effects** as well as **indirect effects** of synthetic auxin exposure, where indirect effects are defined as herbicide-induced changes of plants that have cascading effects on the organisms with which they interact [30]. We end by developing a novel framework for studying both direct and indirect effects of herbicide drift on plants that is relevant to herbicide classes beyond the synthetic auxins. Since dicamba use is rapidly increasing in agriculture, our main interest is in summarizing current knowledge of dicamba exposure in natural systems; however, we include discussion of available studies from the other synthetic auxin herbicides such as **2,4-D** and **MCPA** since these herbicides function in similar ways, allowing us to broaden the scope of this review.

How synthetic auxins affect plants at the biochemical level

Auxins are a class of phytohormones that play a key role in mediating plant growth. As a plant hormone, auxin regulates developmental processes throughout the plant, including in the lateral roots, main root, apical meristem of the shoot, leaves, and reproductive structures [31]. Both auxin signaling and transport have cascading regulatory effects, and the main natural auxin, **indole-3-acetic acid (IAA)**, often interacts with other phytohormones when mediating growth and responding to herbivory. For example, IAA is strongly and rapidly induced in *Nicotiana attenuata* when attacked by the tobacco hornworm (*Manduca sexta*) to regulate a subset of herbivory defense responses that are triggered by **jasmonic acid (JA)**. This suggests IAA plays an independent key role in herbivory defenses against certain herbivores [32,33].

In the past 80 years, synthetic auxins have been used as herbicides to target dicotyledonous crop weeds [34]. When applied at concentrations higher than naturally occurring auxins, synthetic auxins deregulate normal patterns of growth, ultimately causing plant death by leading to distorted cell division and the collapse of tissue structure [35]. Exposure to synthetic auxins may directly impact herbivory defense since auxins in the form of IAA can directly trigger key defense responses, as in the example with herbivory from *M. sexta*. Additionally, auxins interact with other phytohormones that are involved in herbivory defense responses – jasmonic acid, ethylene and **abscisic acid (ABA)**. One response mediated by JA and ethylene is the production of **volatile organic compounds (VOCs)**, which play a number of anti-herbivory roles that include enticing predatory enemies to herbivorous prey and acting as warning signals to nearby plants [36]. Both JA and ethylene engage in phytohormone crosstalk with some auxins during normal plant development and growth processes, creating negative feedback loops [37–39]. In contrast, auxins generally act downstream of ABA in growth and developmental pathways [40]. ABA also mediates herbivory defense responses that are independent of JA and ethylene signaling pathways, and there is evidence that auxins can inhibit some ABA-mediated defenses in tobacco plants [41,42].

Thus, the application of synthetic auxin herbicides may disrupt jasmonic acid and ethylene responses and biosynthesis, potentially hindering the production of VOCs, and potentially suppressing ABA-triggered plant defenses. If the addition of synthetic auxin at drift doses leads to deregulation of normal herbivory responses, we would expect to find a higher rate of herbivory among plants exposed to dicamba drift. There is evidence for increased herbivory in the presence of dicamba in some species [17,43], but whether this is due to the suppression of normal herbivory defense pathways is currently unknown. Because auxins are crucial phytohormones that regulate a host of plant processes at different times in plant development [31], there are many potential effects from exposure to synthetic auxins at drift doses – whether phenotypic or occurring at the biochemical level – and any number of these alterations could underlie changes in herbivore pressure in the presence of drift. We next briefly summarize what is currently known about the direct and indirect effects of synthetic auxin exposure on crop plants and natural communities of weeds and herbivores found within agroecosystems.

Direct effects of synthetic auxins on plants and herbivores

Most current knowledge of the direct effects of nontarget, synthetic auxin exposure on plants comes from studies of crop plants with a focus on non-transgenic soybean [14,15,44], which like other members of the Fabaceae [45], is highly susceptible to synthetic auxins [46]. In fact, due to its sensitivity, recent landscape level dicamba drift events have been captured using soybean as the ‘canary in a coal mine’. The most often reported visual injury to soybean is leaf cupping, where leaves are described as wrinkled on the inner plane, with the edges turning inward to form a cup shape. Affected plants can also show reduced height and yield reduction, the latter depending on the timing of exposure and other environmental conditions [15,44,47,48]. We have comparatively less information on the direct effects of synthetic auxin drift on natural weeds [49], but the phenotypic effects have been described as reduced size and/or height [16,50], greater number of small leaves, leaf cupping, and greener leaves (*i.e.,* increased chlorophyll content in velvetleaf [17]). A study of common weed species in the greenhouse [51] exposed to dicamba drift at 1% the field dose finds similar phenotypes – *i.e.*, leaf cupping, reduced size – but strikingly, finds wide variation in species' damage, biomass, and growth responses, with some species showing leaf damage and reductions in biomass (*Ipomoea hederacea, Solidago canadensis, Persicaria pensylvanica, Daucus carota, Amaranthus palmeri, Trifolium pratense*) whereas others showing limited effects, or even little leaf damage and/or evidence of *increased* size (*Physalis philadelphica*, *Plantago virginica, Sida spinosa*).

Compared to general patterns of growth and damage, there has been more interest in how synthetic auxin drift will impact the flowering of weedy plants since this is one route by which pollinators could be affected. We consider flowering patterns here since florivorous insects – herbivores that feed on floral parts including nectar robbing – could likewise be impacted (Fig 2B). In response to dicamba drift, weedy species can display delayed flowering and/or reduced flower number [17,19,50], a response that is common but not ubiquitous across species [51]. A survey of natural weed communities exposed to low doses of dicamba (1% the field dose) showed a reduction in the abundance and flowering of forbs, but no alteration of overall floral resources within a community, presumably because less-sensitive broadleaved species were able to flower despite the reduction in forb cover [19]. Capturing potential alterations in the quality of floral resources is likewise important, however, very little is known of how synthetic auxins might alter floral rewards such as the quality of pollen and nectar produced. Of the available examples, one study reports no decline in pollen protein content in a weed exposed to dicamba drift (*E. perfoliatum* [50]).

Direct exposure to synthetic auxin likewise appears to negatively impact some insects and insect herbivores but not others [52]. No discernible effect of direct exposure to dicamba at a range of herbicide dosages was identified in the common agricultural pests *Helicoverpa zea* or *Vanessa cardui* when exposed to dicamba [53], and likewise there was no effect on weevil emergence from thistles following exposure to low doses of 2, 4-D [54]. In comparison, the direct exposure of lady beetles (*Coleomegilla maculata*) to the commercial formulation of dicamba at 13% the field dose led to high lethality of larvae whereas dicamba exposure increased mortality of adults; effects of both the active and inactive ingredients were reported

[55]. While not an herbivore, this species is a common and important predator of herbivorous insects in cropping systems such that reductions in lady beetle populations could lead to increased rates of herbivory and potentially subsequent community changes. A survey of weed communities on the edges of crops treated with dicamba showed reductions in three herbivorous pest species (pea aphids, spotted alfalfa aphid, and potato leafhopper), and an increase in one pest (clover root curculio) and one beneficial seed predator (crickets) compared to non-exposed control communities [14]. It is unclear however whether these changes were direct effects of off-target dicamba exposure or indirect effects caused by direct changes to the associated plant communities.

Clearly, the changes to plants and insects summarized here just begin to describe the direct effects of synthetic auxin drift on natural communities. It is important to capture these effects as they may lead to unanticipated consequences. For example, prior to the 1990's, whitefly was a major pest of cotton in Arizona because broad spectrum insecticides used for whitefly control likewise reduced natural whitefly predators [56,57]. Recent work in velvetleaf found increased abundance of whitefly larvae on plants exposed to 0.5% and 1% the field dose of dicamba, showing that herbivory patterns can be altered when plants experience dicamba drift in agricultural systems (see Box 1). It will be interesting to see if more weeds beyond velvetleaf host increased whitefly populations given dicamba drift, and how this might ultimately impact agricultural crops and associated natural communities.

Box 1. How might herbivory be altered in the presence of off-target exposure to synthetic auxins?

Given that there are notable direct effects on some plant and insect species but not others when exposed to synthetic auxins, how might interactions between plants and their herbivores – specifically, herbivory – be altered in the presence of off-target exposure to synthetic auxins? The handful of studies available thus far suggest responses vary according to the plant and herbivore species in question. For example, reduced grasshopper herbivory was uncovered within a grass community exposed to the field rate of 2,4-D and MCPA [34], and in rice, the application of low levels of 2,4-D triggered JA and ethylene pathways [58]. Both results suggest that synthetic auxin exposure may lead to increased herbivory defense responses in monocots.

However, also in rice, larvae of a moth stem borer grew better when plants were sprayed with 2,4-D as a result of higher nitrogen content in the plants [59], and in two separate field experiments, the abundance of whitefly larvae (a sap-sucking insect) increased on velvetleaf plants exposed to dicamba drift (0.5 and 1% of the field dose [17]). These results suggest that because of synthetic auxin exposure, either lowered defenses or altered nutrients in plants can induce herbivory in some species and field contexts.

A field experiment using three common weeds of agriculture – *Abutilon theophrasti* (velvet leaf), *Datura stramonium* (jimsonweed), *Ipomoea purpurea* (common morning glory) – found that both the amount and the type of herbivory differed according to species when exposed to dicamba drift (1% the field dose; [43]). In velvetleaf and jimsonweed, the proportion of chewing herbivory increased in dicamba exposed plants compared to control plants, but the proportion herbivory did not appreciably change in exposed morning glories. Additionally, the type of herbivory shifted from hole-feeding in the control plots to increased margin feeding in the presence of dicamba drift in both morning glory and velvetleaf, but not in jimsonweed [43]. These results again support the idea that herbivory responses will vary among species exposed to synthetic auxins, and provide the finer-grained view that both the type and amount of herbivory may change differently among different species (Fig 1A). It is currently unknown if any such changes are due to differential alterations of herbivory defense mechanisms among plants when exposed to dicamba, or from direct effects of dicamba on the herbivores that may preferentially feed on each plant species. Such a question would be answered by experimentally manipulating dicamba exposure on both plants and herbivores, as shown in Fig 1B.

/End Box 1

Indirect effects of synthetic auxins on plants and their herbivores

Direct effects of synthetic auxin exposure can lead to unintended indirect effects, which are herbicide-induced changes on plants that have cascading effects on interacting organisms [60]. The altered amount and type of herbivory after exposure to herbicide drift (as in Fig 1A) is one such indirect effect that has the potential to lead to changes in insect communities, given that changes in herbivory subsequently leads to changes in herbivore population dynamics. In this section we use current knowledge of direct effects from off-target exposure to synthetic auxins (summarized in Fig 2A), again with a focus on dicamba, to hypothesize about the type of potential indirect effects that could occur and how they may ultimately influence community dynamics.

Both the increased abundance of whitefly larvae on velvetleaf plants exposed to dicamba drift and the altered feeding amount and/or type of herbivory identified in populations of velvetleaf and jimsonweed (Box 1) are examples of indirect effects of dicamba exposure that have the potential to lead to demographic changes of whiteflies and other herbivorous insects. The mechanisms underlying these examples of altered herbivory are currently unknown. There are several ways in which synthetic auxin exposure could lead to changes in plants that may then lead to alterations in herbivory. Natural auxin (IAA) is key to a host of central plant processes including plant development, defense, and reproduction; disruptions to IAA (described above) could directly change immediate defense responses and/or alter the production of volatile organic carbons (VOC) by disrupting plant ethylenes and jasmonic acid signaling (Fig 2B). Furthermore, plant phenotypic changes induced by dicamba drift – *e.g.*, reduced height, and increased chlorophyll in velvetleaf – could lead to indirect consequences for plant herbivores. Reductions in height of some plant species exposed to synthetic auxin drift could lead to herbivores missing their typical plant targets, since plant height is a visual cue for herbivorous insects [63,64], whereas increased chlorophyll in leaves and thus a darker leaf color could likewise be a visual cue associated with typical host plant targets of herbivores.

Just as dicamba-induced phenotypic changes and alterations of plant defenses could influence insect communities that rely on nutrients from above-ground vegetation, there is a strong possibility that populations of florivorous species and root herbivores could likewise be affected by auxin-induced changes (Fig 2B). While very little information is available on root traits – whether morphological, physiological, or chemical – given exposure to low doses of dicamba, roots of grassland species (switchgrass and others) and cultivated pea are reduced in size [65,66], which could indirectly lead to reduced organic matter for root herbivores (Fig 2B). Further, as with other herbicides (glyphosate, fluroxypyr, glufosinate, etc), dicamba drift can delay the onset of flowering in several species (Fig 2B), which has implications for florivorous insects and insects that rob nectar. Delays in flowering stemming from herbicide drift can be substantial, which could lead to a mismatch between flowering peak and seasonal dynamics of insect populations. Such a mismatch in timing, along with reductions in flower number, could reduce population sizes or alter the type of florivorous insect present at any given time (Fig 2B).

Finally, while knowledge of the direct effects of synthetic auxin exposure on insects themselves remains sorely limited, the negative direct consequences of dicamba exposure on lady beetles [55] could lead to consequent indirect effects since lady beetles are natural predators of herbivorous agricultural pests such as Colorado potato beetle, several aphid species, and whiteflies, among others. If predators and parasitoids that normally regulate noxious agricultural pests are removed given herbicide exposure, the population of noxious insects could then increase given lack of natural regulation.

A framework for studying plant-insect interactions and herbicide

Recent and shocking evidence of global declines in insect abundance and diversity [7,67] has captured the attention of scientists, policy makers, and the public. Intensive agriculture has been identified as a significant factor underlying the decline [68,69], although the relative influence of each agricultural practice (*i.e.,* replacing natural land with crops, herbicide, and pesticide use) has yet to be determined on a large scale. Given the link between weed community diversity and insect diversity in agroecosystems [52], the changes in natural weed communities from herbicide exposure are likely to play a significant role in subsequent changes to insect herbivore communities [52,70,71]. In light of the very recent shift in agriculture to the use of dicamba, and concomitant reports of off-target dicamba drift to nontarget organisms and with known effects on some non-target insects, we believe studies of direct and indirect effects of unintentional exposure to herbicide drift on both plants and herbivorous insects are urgently needed.

In Box 2, we propose an organizational framework for studying the direct and indirect effects of off-target herbicide drift on plant interactions in natural communities. This framework is applicable to off-target exposure to any herbicide class and has applicability to other plant-insect interactions beyond that of plants and their herbivores (*e.g.,* plant-pollinator interactions) as well as exposures to other toxins. Essentially, based on work examining dicamba drift exposure in natural plant communities [19,50] and work observing plants exposed to glyphosate [72–74], we propose that researchers interested in plant-insect interactions in light of herbicide exposure focus on the timing of plant development, the quantity and quality of resources that plants produce, and plant cues (Fig 3). Each of these four categories reflect types of plant traits that influence interactions with other species which may show changes post herbicide exposure. Capturing indirect effects of toxin exposure on community members has proven difficult since it requires examining interactions between organisms and relies on preliminary information – whether from empirical or observational studies – about direct changes that may lead to indirect consequences with potential cascading effects. Thus, the organizational framework is designed to help researchers focus on categories of traits that govern plant interactions that may be affected by herbicide.

Box 2. Depending on the innate sensitivity of each plant species, non-lethal herbicide exposure leads to a recovery period such that the ***timing*** of plant phenological development is significantly offset from normal conditions over the growing season. Typical responses of plants exposed to herbicides at drift rates are reduced size (caused by herbicide damage itself and/or stunted growth following application) and a significant time-lag before flowering (as discussed previously). In sensitive plants, delays in flowering can occur anywhere between days to weeks later compared to non-exposed plants (personal observation, RS Baucom). This can impact important downstream plant traits that underlie plant-insect interactions (*i.e.*, plant cues, the quantity of resources, and their quality). Due to the centrality of this delay, we draw arrows in Fig 3 from timing to quality, quantity, and cues.

Delays in development may also impact the ***quantity*** of resources plants produce – due to a shortened growing season, plants may not grow to the size they would normally (*i.e.,* reduced biomass) nor might they produce the same number of flowers as non-exposed plants. Lowered resource quantity may thus impact the population size of interacting community members. Delayed development from herbicide drift exposure may likewise impact plant ***cues*** that insects respond to such as floral displays and plant defense cues. If the ability of plants to produce volatile organic carbons (VOCs) when damaged by herbivory is influenced by interactions between herbicide-induced developmental delays and environments (*e.g.,* environments that may not be ideal due to an offset growing season), the signaling of beneficial predators or parasites that protect plants from further herbivory may be disrupted. Delays in developmental timing may likewise lead to important environmental effects on quality-related traits, such as the nutrient content of leaf tissue, sap, pollen, and nectar.

Beyond considerations of timing and the potential that offset development could influence plant traits important for interactions, herbicide drift can lead to direct effects on plant cues, resource quantity, and quality central to indirect effects (as reviewed in the previous section). For example, the increased chlorophyll content of dicamba-exposed velvetleaf [17] may be an important visual cue for herbivores (*e.g.,* whiteflies attracted to greener leaves), and increased nitrogen content in some plant species exposed to dicamba drift likely reflect higher quality resources from the perspective of herbivores [75,76]. Many plant traits are aligned with each of the broad categories presented, and researchers must first capture direct changes given herbicide exposure to then develop and test hypotheses about how such effects may lead to indirect changes in bi-trophic and ideally tri-trophic interactions. /End Box 2

Concluding Remarks and Future Perspectives

We are currently at a critical point in time where use of a relatively novel selective agent – the herbicide dicamba – is rapidly increasing across agricultural fields, during a time in which insect populations are already on the decline [7,67]. Unfortunately, crop monocultures do not support insect communities as well as more diverse plant communities [77], and agriculture is increasingly dominated by monocultures [78]. Considering the push to use crop margins as areas that can support natural organisms, there is an urgent need to accurately capture how the dynamics of species' interactions in crop margins may be impacted by herbicide drift with a specific focus on dicamba drift. The organizational framework presented here extends current norms of study to highlight categories of plant traits that are crucial for species interactions and as such may be disrupted given drift exposure. Much of the previous work has focused solely on the number of flowers or floral resources produced following dicamba drift, with little emphasis on resources for herbivores and/or pathways in which herbicide exposure may influence plant cues and the quality of resources. A major gap thus exists in understanding how herbicide drift may impact important herbivorous insects as well as predators and parasites of noxious crop insects (see Outstanding Questions). Overall, the potential for cascading effects from novel use of an herbicide in agriculture is high, especially an herbicide which has consistently been reported to drift to off-target areas. The work summarized here highlights the necessity of deepening our study of this dynamic while broadening the scope of investigations to traits responsible for community interactions and provides a guiding framework for doing so.

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Author contributions

RSB, NJ, AS, GZ, and SJ each contributed to the design, writing, and editing of this manuscript.

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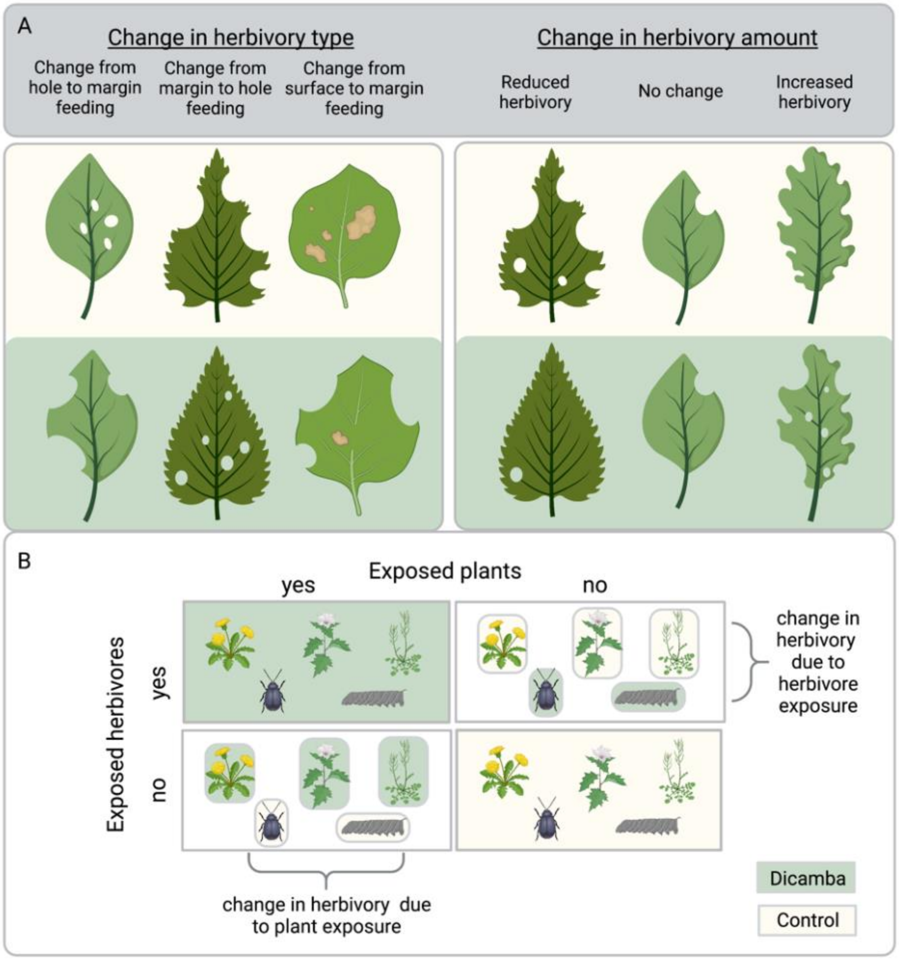
Figure Legends

Fig 1. Exposure to synthetic auxin herbicides, such as dicamba, can alter normal patterns of herbivory. (A) Non-exhaustive examples of how dicamba may affect the type of herbivory (*e.g.,* a change from hole or surface feeding to largely leaf margin feeding) as well as predictions of how the amount of herbivory may be altered (reduced herbivory, no change, or increased herbivory). (B) To determine if changes to herbivory are due to the direct effects of dicamba on either plants or herbivores, a researcher would need to experimentally manipulate which actor – the plant or the herbivore – was exposed to the herbicide, and then compare the amount and type of herbivory to environments where both plants and herbivores are exposed to the herbicide as well as a non-exposed control environment. Prior to direct tests, initial surveys of exposed versus non-exposed communities would be required to identify appropriate plant and herbivore species for manipulation. Figure created with biorender.com.

Fig 2. Direct and indirect effects of synthetic auxin exposure on plants. Plants exposed to synthetic auxin drift show (A) vegetative and flowering phenology changes. Such direct changes to plants lead to observed indirect effects like (B) increases in chewing herbivory and greater abundance of sap-sucking insects and potential indirect effects such as reduced root quality, changes to the production of volatile organic carbons (VOCs) and missed interactions with herbivores due to changes in plant height or delayed timing of peak flowering. If synthetic auxins directly negatively affect beneficial predators or parasitoids (as in [55,61]), their absence in weed communities could lead to an overabundance of pest herbivores such as aphids [62]. Figure created with biorender.com.

Fig 3. A visual representation of four intersecting categories of potential responses when plants are exposed to herbicide drift. A delay in development following herbicide exposure can alter normal life-history **timing**, influencing traits responsible for **quantity** or amount of resource, the **quality** of such resources, and the normal timing of plant **cues**. Traits within each category intersect and can be considered in light of each other or in isolation. For example, a researcher could design an experiment focused solely on the quantity of a particular resource produced following herbicide exposure, and how this might impact interacting species, or could examine the production of the resource in light of delayed development from herbicide exposure and how this delay alters overlaps in plant resources and insect community dynamics. Figure created with biorender.com.

Figures



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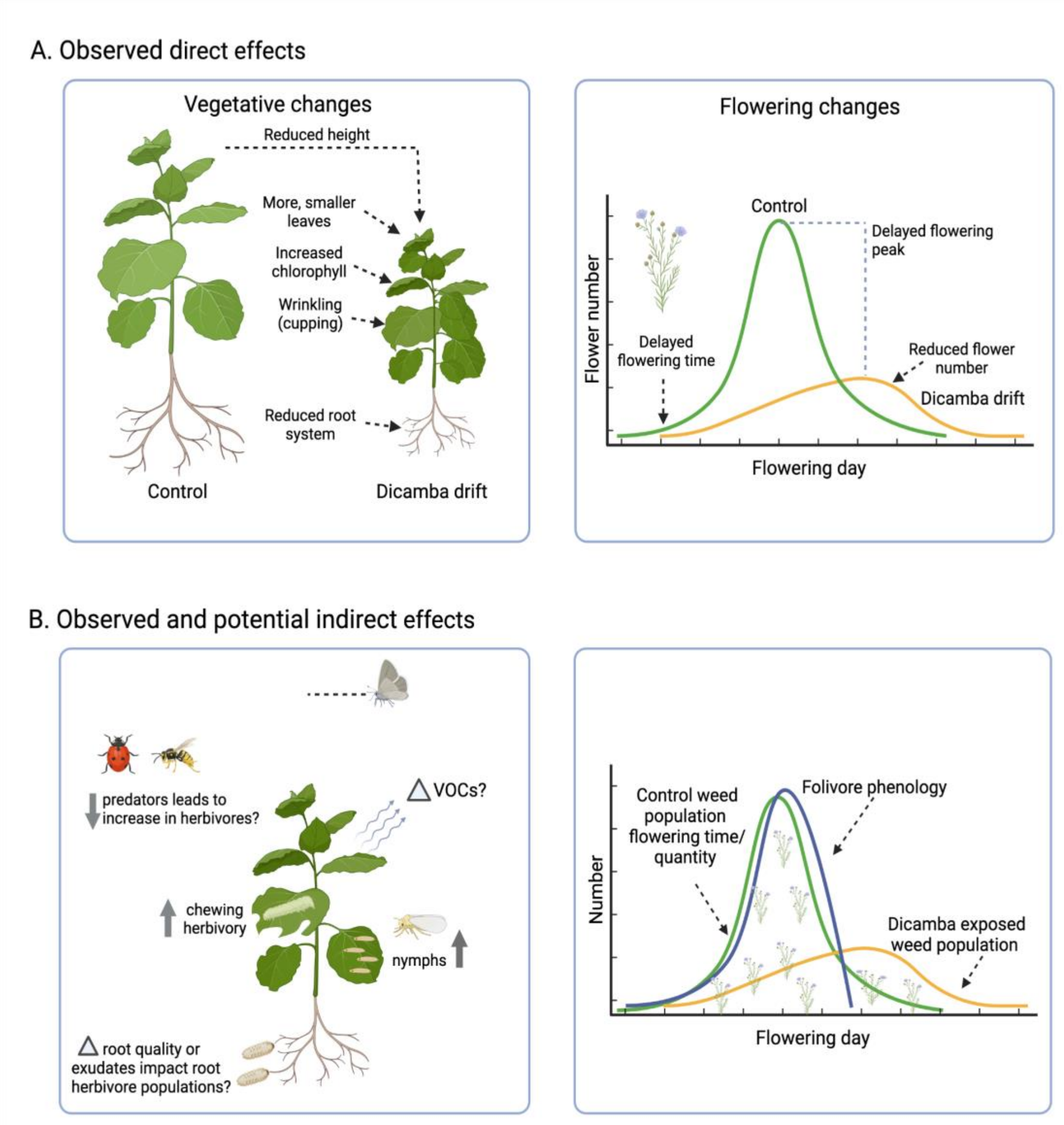

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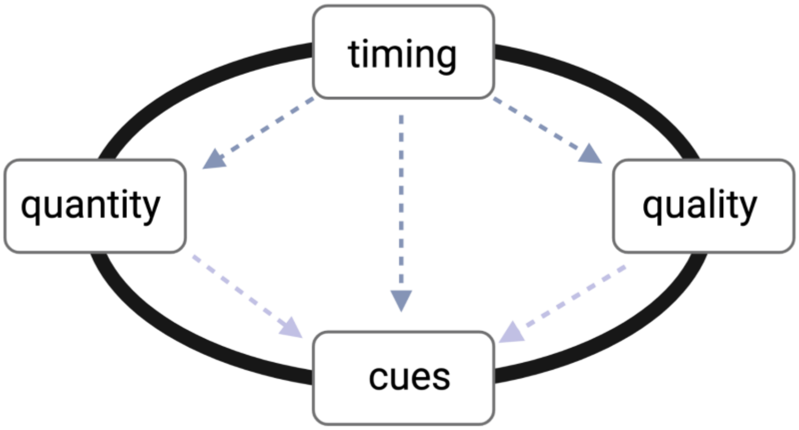

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