Title: Dicamba drift alters plant-herbivore interactions at the agro-ecological interface

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ABSTRACT

Natural populations evolve in response to biotic and abiotic changes in their environment, which shape species interactions and ecosystem dynamics. Agricultural systems can introduce novel conditions via herbicide exposure to non-crop habitats in surrounding fields. While herbicide drift is known to produce a variety of toxic effects in plants, little is known about its impact on non-target wildlife species interactions. In a two-year study, we investigated the impact of herbicide drift on plant-herbivore interactions with common weed velvetleaf (*Abutlion theophrasti*) as the focal species. The findings reveal a significant increase in the phloem feeding silverleaf whitefly (*Bermisia tabaci*) abundance on the plants exposed to herbicide at drift rates of 0.5% and 1% of the field dose. Additionally, we found evidence that drift imposes correlated selection on whitefly resistance and growth rate as well as positive linear selection on herbicide resistance. We also identified a significant phenotypic tradeoff between whitefly resistance and herbicide resistance in addition to whitefly resistance and relative growth rate in the presence of dicamba drift. These findings suggest herbicide exposure to non-target communities can significantly alter herbivore populations, potentially impacting biodiversity and community dynamics of weed populations found at the agro-ecological interface.

Keywords: agroecology, eco-evolution, plant-insect interactions, herbicide drift, weed adaptations

INTRODUCTION

Biotic and abiotic interactions influence species assemblage and evolution throughout ecosystems (Thompson 1999, Klanderud et al. 2015). Often a source of atypical abiotic factors, agricultural practices are largely dependent on pesticide use for increased crop yield and labor efficiency (Gianessi 2013). Despite the economic benefits of herbicides for weed control, however, their use can lead to unintentional impacts on non-target wildlife if the herbicide 'drifts' or migrates outside of the target area during or after the initial application (Freemark and Boutin 1995, Carlsen et al. 2006). Though herbicide drift is known to produce a variety of toxic effects on non-target vegetation (Marrs et al. 1991, Fletcher et al. 1996, Marrs and Frost 1997, Gove et al. 2007, Boutin et al. 2014, Cederlund 2017), and can lead to significant plant phenotypic and compositional changes (Iriart, Baucom, and Ashman 2020), few studies have evaluated how herbicide drift may disrupt or influence the interactions between plants and other community members such as pollinators and herbivores.

Weeds and other non-crop plants found at the edges of crops serve as important reservoirs of insect biodiversity (Egan and Mortensen 2012), which provides crucial ecosystem services for agriculture such as pollination and pest control (Daily 1997). The plant- insect interactions that occur at the agro-ecological interface are key determinants for the movement of energy and nutrients as well as drivers of ecological and evolutionary dynamics (Ehrlich and Raven 1964, Futuyma and Agrawal 2009). However, weed communities at the agro-ecological interface can be exposed to herbicide drift rates between 0.1% and 5% of the normal field application rate of herbicide (Cessna et al. 2005), and we currently understand very little about how this drift may influence ecological interactions and potentially lead to subsequent evolutionary responses. For example, does herbicide drift change herbivore abundance or damage, and/or lead to altered patterns of plant investment in resistance to either herbicide or herbivore damage?

One herbicide known for non-target damage is dicamba (3,6-dichloro-2-methoxybenzoic acid). Dicamba is a broadleaf selective synthetic auxin whose use has increased in recent years in response to the evolution of resistance to the more commonly used herbicide glyphosate (RoundUp). Dicamba is absorbed by plant leaves and mimics the deformative and growth-altering effects caused by overdoses of the natural plant auxin, indole-3-acetic acid (IAA) (Grossman 2010). Dicamba drift can cause a shift in plant and arthropod diversity (Egan et al. 2014), delay the onset of flowering, reduce the number of flowers, and even reduce the amount of pollinator visits (Bohneblust et al. 2016). However, we have very little information on how dicamba drift may impact plant-herbivore interactions. A broad expectation is that exposure to a synthetic auxin, such as dicamba, could alter plant allocation towards growth and defence, and potentially lead to increased vulnerability to herbivores, in line with growth-defense tradeoff framework (Coley, Bryant, Chapin 1985). Recent work has shown that exposure to drift rates of herbicides like dicamba can lead to the evolution of reduced herbicide

sensitivity (Vieria et al. 2020) and recurrent selection of low dose herbicides can lead to non-target site resistance (Busi et al. 2013), however there is little understanding of how this process may influence selection for allocation herbivory defense.

Here we examined the impact of dicamba drift on plant herbivory using the crop weed velvetleaf, *Abutilon theophrasti*. First introduced to the United States from Asia in the late 17th century, this annual species is now one of the most common broad-leaved species in and around corn and soybean agricultural fields located in Canada, Europe, and the United States (Spencer 1984). While past work has shown that lines with evolved herbicide resistance (defined by survival of herbicide at application rate) can exhibit reduced herbivory resistance depending on light availability (Gassman 2005), there is a striking lack of information on how such a phenotypic tradeoff evolves when populations are exposed to drift rates under natural field conditions. We performed field experiments to address this gap in our knowledge, and specifically asked the following questions: Does the application of dicamba drift influence herbivory in the common weed *Abutilon theophrasti* (velvetleaf)? Does the amount of herbicide damage, which reflects resistance to herbicide, influence the amount of herbivory, which reflects resistance to herbivory? (i.e., is there a trade-off between these two forms of defense in the presence of dicamba drift)? Is either herbicide or herbivore resistance negatively correlated with relative growth rate, indicating a growth- defense tradeoff?

METHODS

Experimental Design

We performed two consecutive field experiments to characterize the extent of herbicide drift damage and herbivory response in *A. theophrasti*. In the first experiment, we planted replicate seeds from 23 maternal lines originally sampled from a single population (Dexter, MI) in the summer of 2018. We increased the number of populations from 1 to 8 for a total of 50 maternal lines in the second field experiment, including the population from the first field experiment. All seeds were collected in the Fall prior to each summer in and around soybean fields located in Dexter, MI.

In the first field experiment we scarified and planted 276 total seeds in a randomized block design (23 maternal lines x 3 treatments x 2 replications x 2 blocks). Our three experimental treatments were two levels of a drift exposure (1% and 0.5% of the recommended field dose of dicamba (3,6-dichloro-2-methoxybenzoic acid) (2.8 g ae/ ha dicamba, 5.6 g ae/ha dicamba) and water as the control. For the second field experiment, we scarified and planted 450 total seeds in a randomized block design with the same treatments as the previous field experiment (50 maternal lines x 3 treatments x 3 blocks). We recorded leaf count, height, and largest leaf width for all plants biweekly in both experiments. We recorded flower count weekly and sampled all seeds at the end of the season for an estimate of fitness. Five weeks after seed germination, when the average plant height was 11 cm tall, we applied 1% and 0.5% dicamba to plants in each respective treatment. We assessed herbicide damage two weeks following herbicide application by recording the proportion of leaves exhibiting visual deformation (curling or

cupping), and proportion of the plant damage was determined by evaluating the number of leaves with a cupping or curling pattern divided by the total number of leaves.

To estimate resistance to herbivory in 2018, we assessed both physical damage from chewing insects and the abundance of phloem-feeding insects (dominated by silverleaf whiteflies). Because there was little evidence of chewing insects, only whitefly abundance was assessed in 2019. We assessed chewing herbivory damage five weeks after herbicide application using the imaging software, Fiji ImageJ version 3.0 (Schindelin et al. 2012). To do this, we collected 3 leaves at random from each plant and scanned them using the Canon CanoScan L110. To obtain the total surface area, we converted each image to binary format and used the particle analysis tool which quantifies total pixel number into centimeters. We then used a macro plug-in to place a grid with 0.1cm^2 spacing over each image to estimate the amount of chewing herbivore damage per leaf.

Visual estimates of whitefly abundance were sampled in both field experiments by selecting 10 leaves at random per plant. Because most whiteflies feed and oviposit at the same location (Van Lenteren and Noldus 1990), estimates of percentage of leaf area covered by whitefly oviposits were captured by visually partitioning each leaf into quarters and evaluated for each section, as suggested in Johnson et al 2015. We estimated whitefly abundance on a scale from 0 – 5. A score of 0 meant no whitefly oviposits were present, 1 was 1 - 20% leaf coverage by whitefly oviposits, two was between 21 – 40 % leaf coverage, three was 41 - 60 % leaf coverage, four representing 61 - 80% leaf coverage, and five representing 81 - 100% leaf coverage.

Photosynthetic carbon dioxide response

To determine if there was a link between herbicide resistance and photosynthetic response to dicamba drift, we estimated photosynthetic efficiency by examining variation in photosynthetic carbon dioxide response curves (A-Ci Curve) using the Li-Cor 6400 portable photosynthesis system (Open System Vers, 4.0, Li-Cor, Inc., Lincoln NE). During gas exchange measurements, we maintained cuvette conditions at a photosynthetic photon flux density (PPFD) of 1500 µmol/ m^{2}s, air flow rate at 500 µmol/s, and leaf chamber block temperature being 30°C to match ambient air temperature. In order to measure the gas exchange, we first set the CO_2 concentration reference at 400 µmol/mol, and we maintained the leaf under such conditions for ten minutes for adaptation and stabilization of leaf photosynthesis. We set a loop of changing reference CO_2 concentration at 400, 300, 200, 100, and 50µmol/mol. We controlled CO_2 concentration in the cuvette with a CO_2 mixer across this series and measurements were recorded after equilibration to a steady state. We then set another loop of changing reference CO_2 concentration at 400, 600, 800, 1000, 1300, and 1500 µmol/mol and again logged at each iteration. Between each group of measurements, we set the reference CO_2 concentration back to 400 µmol/mol for 5 minutes. These measurements were made four to five weeks after herbicide application, within a ten-day period. We recorded these data on a leaf area of 2 cm^2, from 2 leaves on each of three plants from each treatment. For plants growing in drift treatments, we included one leaf that developed prior to herbicide application (Leaf 1), and one leaf that developed after herbicide application which as a result exhibited a deformation in shape (Leaf 2). The purpose of taking measurements on leaves with different times of

development was to investigate if potential herbicide sequestration impacts photosynthetic efficiency of leaves exhibiting damage, potentially impacting herbivore resistance mechanisms for the entire plant. Measurements were taken for each leaf per plant were taken on the same day.

DATA ANALYSIS

Herbivory Response to Drift Exposed Host

We conducted all statistical analyses in R studio (version 3.4.1, R Development Core Team). For each type of herbivory measurement (chewing damage and whitefly abundance), we performed analysis of variance to determine whether herbivory resistance differed in response to dicamba application. Prior to performing ANOVAs, we transformed response variables using Tukey's Ladder of Powers in the rcompanion package (Mangiafico 2016) to correct for non-normality of residuals. We fit the following mixed linear model using the lmer4 package (Bates et al. 2011):

$$y = u + \text{treatment} + \text{block} + (\text{treatment x block}) + (1|\text{maternal line}) + (1|\text{maternal line x treatment}) + \varepsilon$$

where, y, the response variable, is chewing damage or whitefly abundance, u is the intercept or mean of the model, treatment and block are fixed-effect terms, maternal line and maternal line by treatment interactions are both random effects, and ε is the error term. We determined the significance of the predictor variables using *F*-statistics for the fixed effects with Kenward-Roger to estimate the degrees of freedom and used a log-likelihood ratio test to estimate χ^2 for the random effect. We then used a Welch two sample t-test to determine if there were significant differences between the two dicamba drift treatments.

Plant Performance in Response to Herbicide Drift

To determine how drift treatments influenced plant performance, we ran mixed linear models as described above. In 2018, we fit separate models for each plant trait (height, leaf count, leaf width, and flower number): $y = u + \text{treatment} + \text{block} + (\text{treatment x block}) + (1|\text{maternal line}) + (1|\text{maternal line x treatment}) + \varepsilon$; where each trait was the response variable, block, treatment, and block by treatment interactions were fixed effects, and maternal line, and maternal by treatment interactions were random effects. In 2019, we nested maternal line into population and added population and population by treatment interactions as random effects to the existing model: $y = u + \text{treatment} + \text{block} + (\text{treatment x block}) + (1|\text{population: maternal line}) + (1|\text{population: maternal line}) \text{ x treatment} + (1|\text{population}) + (1|\text{population}) \text{ x treatment} + \varepsilon$. We transformed each trait again using Tukey's Ladder of Powers to meet the assumptions of normality. We performed separate analyses for each year because preliminary analysis revealed a significant difference in plant growth between years.

Additionally, variance of photosynthetic carbon dioxide response was analyzed for 2018 with treatment and block as well as their interaction as fixed variables and maternal line as a random variable. We performed a similar analysis of variance on those plants growing in drift

treatments to determine if time of leaf development impacted photosynthetic carbon dioxide response among leaves with and without deformation by including leaf developmental time and its interaction with treatment as fixed effects.

Plant Resistance and Genetic Variation

We define herbicide resistance operationally as 1 minus the proportion of leaves exhibiting damage from the herbicide, which was observed as yellowing and curling/deformation of leaves. Because there was limited damage from chewing herbivores, we elected to focus on phloem-feeding herbivory, dominated by whiteflies. Whitefly resistance was defined as 1 minus the amount of whitefly larvae coverage per individual (as described previously). We examined herbivory and herbicide resistance for both years combined and were explicitly interested in determining if there was evidence for genetic variation for either herbicide or herbivory resistance *via* a population or maternal line by treatment interaction. We fit the following separate mixed linear models for each type of resistance: $y = u + \text{treatment} + \text{block} + (\text{treatment} \times \text{block}) + (1|\text{population: maternal line}) + (1|\text{population: maternal line}) \times \text{treatment} + (1|\text{population}) + (1|\text{population}) \times \text{treatment} + \varepsilon$; where each type of resistance was the response variable, block, treatment, and block by treatment interactions were fixed effects, and maternal line, maternal by treatment interactions, population, and population by treatment interactions were random effects. We determined if there was evidence of genetic variation for herbicide resistance and whitefly resistance by performing log-likelihood ratio tests to estimate χ^2 for maternal, maternal line by treatment, population, and population by treatment interactions for each resistance type. Finally, because we are interested in potential growth-defense trade-offs, we used a similar mixed linear model to examine genetic variation in relative growth rate.

Phenotypic Correlations

In order to test for correlations between herbicide resistance and whitefly resistance (defined operationally as above), we performed Pearson's correlation test. We elected to perform tests across both experiments as preliminary analyses revealed similar trends for whitefly resistance.

Phenotypic Selection

In accordance with the Lande–Arnold approach (e.g., Arnold et al. 2001; Arnold 2003; Hereford et al. 2004), we used phenotypic measurements to quantify natural selection on both whitefly resistance and herbicide resistance. We estimated selection gradients within drift environments (0.5% and 1% the field dose of dicamba) by performing multiple regressions with whitefly resistance, herbicide resistance, and relative growth rate (calculated as change in leaf count plus change in height divided by the number of weeks spent growing) as predictor variables and relative fitness as the dependent variable. We also included interactions between whitefly resistance, herbicide resistance, and relative growth rate in the model, as there is evidence of a relationship between plant stress, defense, and growth (Huot et al. 2014, Zust and Agrawal 2017). Relative fitness was calculated as the final seed count divided by mean seed count for each block per year. We elected to perform a joint selection analysis using standardized measurements (i.e., subtracted the mean and divided by the standard deviation) of all plant traits because it allowed us to examine selection acting on each trait while controlling for

environmentally induced biases. Additionally, we examined the potential for both linear and nonlinear selection on herbicide resistance, whitefly resistance, relative growth rate and their interactions within drift environments. Linear selection gradients were estimated in models without the nonlinear effects, while nonlinear effects were estimated with linear effects incorporated into the model. Quadratic regression coefficients were doubled to estimate nonlinear selection gradients. Furthermore, we estimated linear and nonlinear selection on whitefly resistance in the absence of herbicide drift in order to estimate the potential cost associated with herbicide resistance.

RESULTS

Herbivory Response to Drift Exposed Host

We found no evidence that dicamba drift influenced the amount of chewing damage experienced by *A. theophrasti* (STable 1; Fig 1A) but we did find a significant increase in whitefly abundance on treated plants (F-value = 4.15, p-value = 0.02, STable 1; Fig 1B). This effect was also present in the second field season in which we included five more *A. theophrasti* populations (F-value = 5.63, p-value < 0.01, STable 1; Fig 1C). Both levels of dicamba drift -- 0.5% and 1% of the suggested field dose -- exhibited higher whitefly abundance than the controls. Plants exposed to 0.5% dicamba also had significantly higher whitefly abundance than 1% dicamba treatments across both years (2018: t = 2.74, p < 0.01; 2019: t = 2.06, p = 0.04).

Plastic Response to Herbicide Drift on Plants

We examined a number of plant traits in response to dicamba drift in order to determine how drift impacts velvetleaf growth and physiology, which may underscore herbivory responses. Across both experimental years, we found that leaf count increased following the application of dicamba drift (Treatment effect for 2018: F-value = 28.01, p-value < 0.01; 2019: F-value = 5.65, p-value < 0.01, STable 2; Fig 2), whereas leaf width decreased significantly in 2018 but not 2019 (Treatment effect: 2018, F-value = 7.47, p-value < 0.01; 2019: F-value = 1.44, p-value = 0.24, STable 2; Fig 2), which may be a result of significant population variation in 2019 for leaf width ($\chi 2$ = 4.21, p-value = 0.04).

Both plant height and flower count decreased as a result of dicamba drift in both experiments (Treatment effect: Height 2018: F-value = 226.36, p-value < 0.01; Flower Count 2018: F-value = 7.51, p-value < 0.01; Height 2019: F-value = 3.17, p-value = 0.04; Flower Count 2019: F-value = 7.32, p-value < 0.01, STable 2; Fig 2). Typically, plant leaf number was greater, and height and flower number were lower in the 1% dose of dicamba drift compared to the 0.5% dose (Fig 2, STable 2). We found evidence for block effects and block by treatment effects in the first field experiment across most phenotypic traits, but these effects were less evident in the second field experiment (STable 2). Finally, we found no evidence for maternal line or population effects associated with dicamba drift exposure, indicating that at least in this sample of 50 maternal lines, there was no evidence that the plastic response for height, leaf count, leaf width, and flower count varied genetically.

Photosynthetic carbon dioxide response (A-C_i, umol/m2) did not differ across treatments, indicating that dicamba drift did not significantly impact photosynthetic carbon dioxide response overall ($F = 0.92$, $p = 0.40$; SFig 2; STable 3). Within plants grown in drift treatments, however, we found evidence of a significant interaction between treatment and time of leaf development on A-Ci curves ($F = 16.11$, $p < 0.01$; SFig 2; STable 4). In general, leaves exposed directly to 0.5% of the field dose of dicamba exhibited higher A/Ci responses than their counterparts that developed after dicamba treatment (SFig 2; STable 4). In contrast to the lower dosage, leaves treated directly with 1% of the field dose of dicamba exhibited lower A/Ci responses than their counterparts that developed after dicamba exposure (SFig 2; STable 3). We also found significant interactions between block and time of leaf development ($F = 9.08$, $p < 0.01$; SFig 2; STable 3). This result indicates high amounts of photosynthetic plasticity in response to dicamba, potentially associated with altered herbicide translocation and metabolism contributing to resistance. We did not find significant variation among maternal lines among treatments, indicating that within the populations sampled there was no evidence of genetic variation for photosynthetic carbon dioxide response to dicamba drift (STable 3; STable 4).

Genetic variation for whitefly resistance, herbicide resistance, and relative growth rate

We found no evidence of maternal line, maternal line by treatment, population, or population by treatment effects on whitefly resistance (STable 5). For herbicide resistance, we found a significant interaction between population and drift treatment ($\chi^2 = 4.27$, $p = 0.04$; STable 5), but no evidence of maternal line, maternal line by treatment or population effects (STable 5). This suggests that while there is no evidence for maternal line variation in response to dicamba drift, there is evidence that populations show different levels of resistance to dicamba drift. For relative growth rate, we found no evidence of maternal line, maternal line by treatment, population, or population by treatment effect (STable 5).

Phenotypic correlations

Across both experiments, we found evidence of a negative phenotypic correlation between herbicide resistance and whitefly resistance within drift environments ($r = -0.18$, $p = 0.03$), suggesting that both types of resistance are indirectly impacting one another. We also found a negative correlation between whitefly resistance and relative growth rate in the presence of drift but not in the absence (drift environment: $r = -0.16$, $p = 0.05$; control environment: $r = -0.17$, $p = 0.12$), indicating a tradeoff between growth and herbivory defense when exposed to herbicide drift.

Phenotypic selection

We identified positive linear selection on herbicide resistance but no evidence of linear selection on whitefly resistance (herbicide resistance: $\beta = 0.25$, $p = 0.04$; whitefly resistance: $\beta = 0.08$, $p = 0.49$; Figure 3; Table 1) in the herbicide drift environment. Although we detected a significant negative phenotypic correlation between herbicide resistance and whitefly herbivory resistance, indicating a trade-off between them, we found no evidence of correlated selection acting on the two traits ($Y = 1.10$, $p = 0.45$; Table 1).

Moreover, we detected a significant interaction between relative growth rate and treatment environment ($\beta = 6.06$, $p = 0.03$), in which herbicide drift strengthened linear selection on relative growth rate by 36%. We also found evidence of right skewed stabilizing selection on relative growth rate in the presence of drift, but no evidence of stabilizing selection in the absence of drift (drift environment: $Y = 0.732$, $p < 0.001$; Table 1; control environment: $Y = 0.215$, $p = 0.147$), suggesting an optimal growth rate when exposed to dicamba. Further, in comparison to the control environment, herbicide drift imposed correlated selection on relative growth rate and whitefly resistance (control environment: $Y = -0.29$, $p = 0.10$; $Y = -0.39$, $p = 0.01$; Table 1; Figure 4), indicating that drift alters the pattern of phenotypic selection on the interaction between the two traits. We also detected correlated selection acting on relative growth rate and herbicide resistance ($Y = -5.81$, $p < 0.001$; Table 1), signifying an intermediate fitness peak for the cross-product of relative growth rate and each type of resistance in the presence of drift (Figure 5).

DISCUSSION

The purpose of our work was to determine if drift rates of the herbicide dicamba would alter plant-herbivore interactions in natural weed populations found at the agro-ecological interface. Dicamba use is on an upwards trajectory in agriculture due to the adoption of dicamba-tolerant crops (USDA- ERA, 2018). However, this herbicide can drift to non-target areas, causing significant damage to unprotected crops and natural plant populations (Egan et al 2014, Bohnenblust et al 2016, Jones et al 2018, Vieira et al 2020). Currently, we understand little about how the widespread use of dicamba may impact non-target organisms and even less about whether dicamba drift may impact plant-insect interactions.

Our results show that the common weed velvetleaf exhibited a greater abundance of the phloem-feeding silverleaf whitefly when exposed to drift, an effect that was consistent between separate experiments, while also showing limited evidence for changes to chewing herbivory. In an effort to understand the trend of increased whitefly abundance and how this might influence plant investment towards fitness or defense, we examined growth-defense relationships in the presence and absence of herbicide drift. Our initial expectation, based on growth-defense tradeoff theory, was that growth rate would be negatively correlated with resistance to either herbicide or herbivory damage, *i.e.*, individuals with higher growth rates would display lower levels of resistance to damage from either whiteflies or herbicide. We found this expectation to play out for whitefly resistance -- velvetleaf individuals with higher growth rates showed decreased whitefly resistance -- but there was no such trade-off present for resistance to dicamba drift. However, we did find a trade-off between resistance to whiteflies and dicamba, suggesting that velvetleaf invests more in one type of defense or the other.

We also found evidence that velvetleaf, a very common weed found in most midwestern and North American agricultural crops, has the potential to evolve higher levels of resistance to dicamba drift. We uncovered evidence of positive linear selection on herbicide resistance and found that populations varied in their level of resistance to dicamba drift. Additionally, we

found that dicamba drift imposed stabilizing selection on velvetleaf growth rate while also imposing correlated selection on growth rate and whitefly resistance. This suggests that the presence of dicamba disrupts the relationship between plant investment for growth and whitefly resistance while also imposing positive linear selection for dicamba resistance. Overall, our combined ecological and evolutionary work shows that dicamba drift could lead to higher levels of dicamba resistance in velvetleaf and an increased abundance of whiteflies when plants are exposed to dicamba. Below, we discuss our main findings in the context of current literature and link the ecological effects of dicamba use with potential evolutionary outcomes.

Ecological effects -- dicamba drift increases whitefly abundance and alters plant morphology and physiology

Our study provides the first evidence that dicamba drift can increase phloem feeding herbivore abundance in the field, a finding that should be of concern to agriculture more broadly given the negative effects of the silverleaf whitefly on crops (e.g., viral transmission mediated by whitefly, Hogenhout 2008). In two separate field experiments, velvetleaf exposed to dicamba drift showed higher silverleaf whitefly abundance in comparison to their control counterparts. These findings indicate dicamba drift can increase susceptibility to phloem feeding herbivorous insects, potentially due to greater feeding preference, shorter development time, and/ or greater survival on dicamba treated plants. This is consistent with previous work showing increased abundance of english green aphids feeding on dicamba treated barley in a glasshouse experiment (Hintz 1971).

Additionally, we found evidence of significant phenotypic tradeoffs between whitefly resistance and herbicide resistance as well as between whitefly resistance and relative growth rate in the presence of drift. Growth rate has long been linked to investment towards herbivory defense, suggesting that when resources are limited competition favors fast-growing plant species that allocate less towards herbivore defenses (Coley, Bryant, and Chapin 1985). In the literature, this is evident by positive correlations between growth rate and herbivory damage (Coley 1987, Cebrian and Durate 1994, Fine et al. 2006) and negative correlations between biomass accumulation and defense chemicals, such as salicylic acid (Meyer et al. 2007), a plant hormone specifically involved in defense against phloem-feeding silverleaf whiteflies (Kempema 2007). Such negative correlations suggest that pools of herbivore defenses can be depleted as strong growth occurs under certain environmental conditions. While our results reveal no correlation between growth rate and herbicide resistance, a significant correlation between growth rate and whitefly resistance when under drift induced stress supports the growth-defense tradeoff expectations of depleted reservoirs of herbivore defenses in the presence of high growth.

Because plant architecture is known to influence herbivore performance and abundance (Jaenike 1978, Haysom and Coulson 2004, Schlinkert et al. 2015), we assessed the morphological and physiological response of velvetleaf to dicamba drift. While our results indicate dicamba at drift levels stunts the height of velvetleaf, this synthetic auxin also increased the number of leaves produced, although they were typically smaller in size compared to non-sprayed control plants. Additionally, we examined the impact of dicamba on

A/Ci response curves, as photosynthetic capabilities are linked to natural auxin presence (McAdam et al. 2007) and are a key driver for plant metabolism. The pattern of A/Ci response differed between drift treatments and time of leaf development, indicating a high amount of photosynthetic plasticity which varied over herbicide exposure and time. These findings align with a recent study that showed dicamba exposure initially decreased photosynthesis by 22% in *Palmer amaranth* but improved over time (Browne et al. 2020). Moreover, there was no evidence of maternal line nor population variation for morphological or physiological responses to herbicide drift, suggesting a high level of plasticity among all traits measured across individuals.

Evolutionary effects -- correlated evolution between resistance and relative growth rate

In addition to morphological and physiology responses, we also examined the potential that resistance to both dicamba drift and whitefly damage could evolve within these populations. Drift-meditated correlative selection was detected between relative growth rate and herbicide resistance along with relative growth rate and whitefly resistance. While this would imply populations could evolve to an optimum fitness at intermediate values of relative growth rate and both types of resistance, we did not uncover evidence of genetic variation for relative growth rate or whitefly resistance within these populations. We did, however, identify positive selection for resistance to dicamba drift and genetic variation underlying resistance to drift (*i.e.*, population by treatment effects on dicamba resistance), indicating that higher levels of resistance could evolve. Although we did not uncover a significant maternal line by treatment interaction, which is the typical effect that indicates the presence of genetic variation underlying herbicide resistance (Baucom and Mauricio 2008), velvetleaf is a highly selfing species such that population variation should indicate significant genetic variation.

Whether or not increased dicamba resistance will evolve in this species is contingent on current field practices, which include the use of the herbicide glyphosate, the active ingredient in RoundUp. In recent years, crops that can tolerate both dicamba and glyphosate (Roundup Ready 2 Xtend®) have been introduced in the US, and one weed species, kochia (*Bassia scoparia*) has evolved resistance to both the herbicides (Westra et al. 2019). Though resistance to both herbicides can involve numerous mechanisms (Heap 2014), exposure to glyphosate at drift rates has been correlated with increases in the metabolic rate of IAA (indole-3-acetic acid), the natural plant hormone which dicamba mimics (Lee and Dumas 1985). Moreover, increased metabolism is a common non-target resistance mechanism for synthetic auxins, such as dicamba (Jugulam and Shyam 2019). This suggests populations exposed to glyphosate drift may unexpectedly evolve increased metabolism of dicamba. These findings align with unpublished work that indicates the same populations involved in this study are also evolving reduced sensitivity to glyphosate (Johnson and Baucom unpublished data). While the evolution of herbicide resistance in weeds is governed by the interaction of genetic and ecological factors over time, our results suggest that velvetleaf could become dicamba-glyphosate resistant in the coming years.

Given the expected rise in dicamba use, our findings suggest weed populations exposed to dicamba drift at agricultural edges may experience increases in whitefly abundance. While studies have shown dicamba can negatively impact key whitefly predators such as lady beetles (Freydier and Lundgren 2016), further research is needed to determine if this is caused by an increase in herbivore preference or performance/survival, as a result of deterred predators, or a combination of both. In conjunction with the expected increases of whitefly abundance in the presence of drift, the evolutionary trajectory of the traits examined in this study suggest weedy populations exposed to dicamba drift may evolve intermediate levels of growth rates, along with herbicide resistance. Consequently, agricultural systems may experience dramatic upward trends in whitefly abundance proving to be detrimental to agricultural outputs in the long term.

Conclusion

Insect herbivores can significantly impact nutrient cycling and consequently resource availability as well as the assemblage, growth, and productivity of plant communities (Schowalter 2000, Belovsky & Slade 2000). Not only can modifications in insect herbivory impact plant community composition and nutrient dynamics, but these modifications can reciprocally influence insect herbivore populations. Herbicide-induced increases in insect herbivore abundance may result in positive feedbacks where elevated consumption increases nutrient cycling and thus stimulates insect population growth, which can directly affect the abundance of other members of the community such predators and pollinators (Forkner & Hunter 2000, Hunter 2001, Ceulemans 2017).

Our results expand what is currently understood about shifts in insect-plant interactions in responses to abiotic changes in the environment. We show that dicamba drift can significantly increase whitefly abundance on velvetleaf populations, a finding that could mean dicamba-treated weeds act as a reservoir for whitefly populations, potentially leading to negative impacts on agricultural yields. If our results are applicable more broadly, it would suggest that plants can potentially evolve higher levels of resistance to dicamba drift, while concomitantly serving as a preferred host for whiteflies in the presence of dicamba. As agricultural pests that colonize more than 600 host plants globally (Byrne and Bellows 1991), whiteflies are known vectors for transmitting over 70% of the world's plant viruses (Hogenhout 2008). Given the projected expanded use of dicamba, there is a clear and urgent need to examine to what extent community dynamics may shift as a result of dicamba use, especially for communities existing at the intersection of natural and managed vegetative systems.

FIGURES AND TABLES

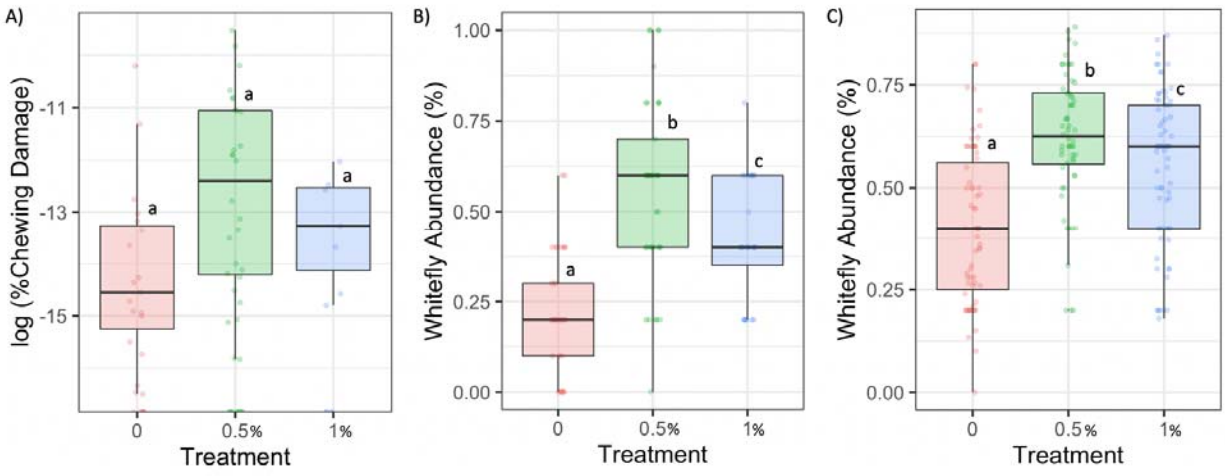

Figure 1. Herbivory measurements in response to dicamba drift: 0% field dose (peach), 0.5% field dose (green), and 1% field dose (blue). A) Chewing herbivory damage summarized by dicamba treatment from the first field experiment in 2018. Damage was measured as area with chewing damage/total leaf surface area. B) Treatment effect on Whitefly abundance summarized by treatment in both the B) 2018 and C) 2019 field experiments. Whitefly abundance was measured as visual estimates of percent larvae area/total leaf surface area.

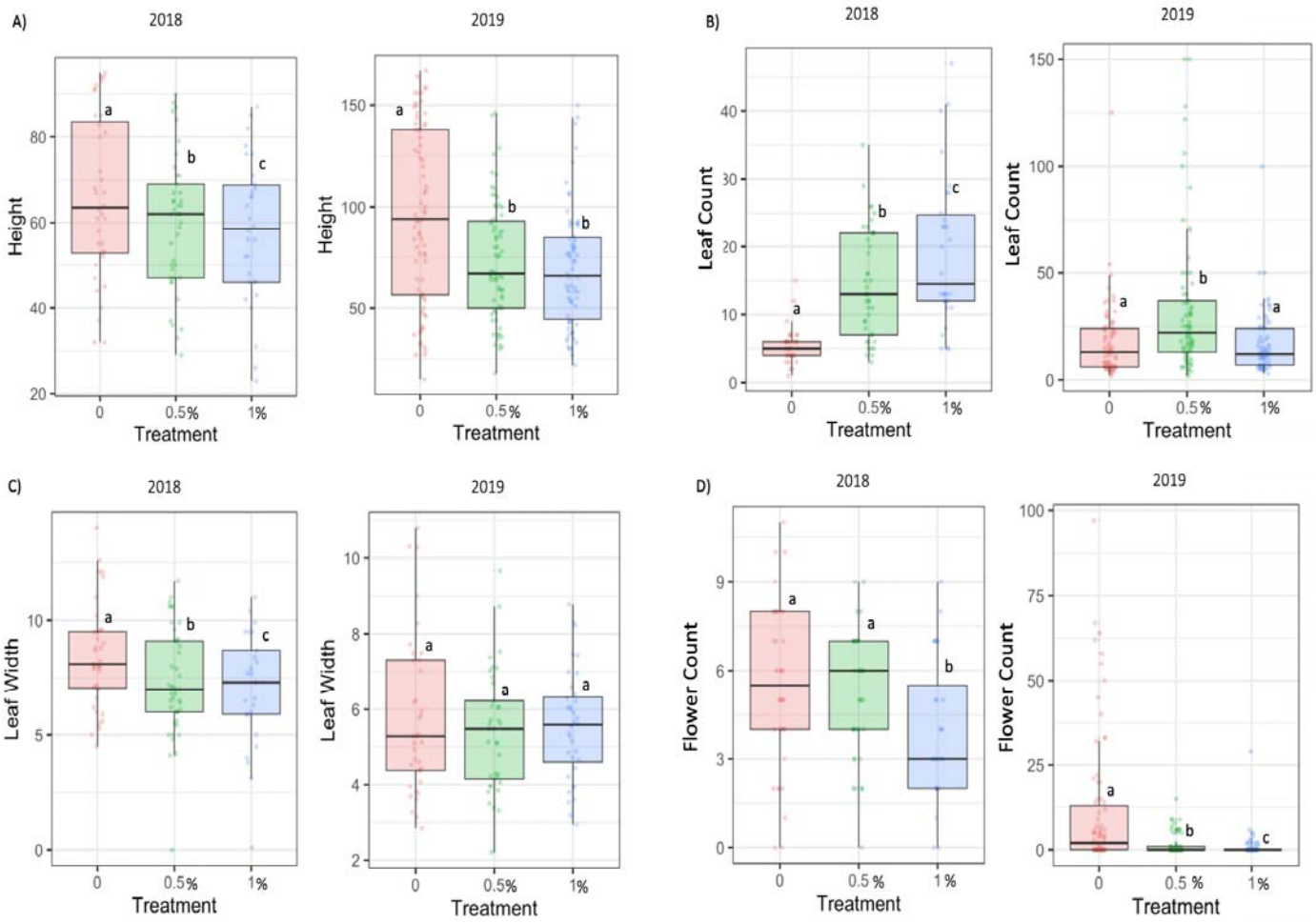

Figure 2. Plant size measurements in response to dicamba drift environments: 0% field dose (peach), 0.5% field dose (green), and 1% field dose (blue). Combines treatment effect for both years on velvetleaf traits: A) height B) leaf count C) leaf width and D) flower count.

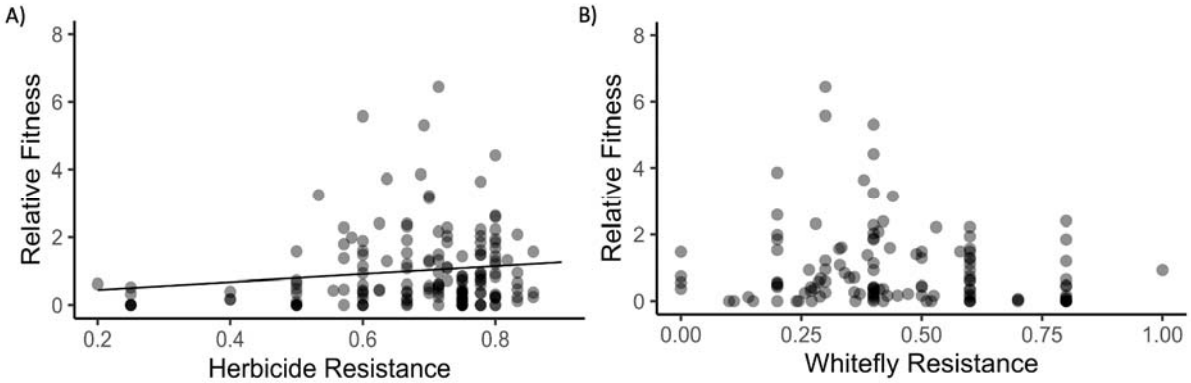

Figure 3. Linear regression of resistance traits onto relative fitness. Resistance traits are reported per individual. There is significant positive selection on herbicide resistance when *A. theophrasti* is in the presence of herbicide drift (A) (β = 0.254, *p-value* = 0.044), but no evidence of selection on whitefly resistance in the presence of drift (B) (β = 0.094, *p-value* = 0.492). ANOVA showed that the Treatment by Population interaction is significant for herbicide resistance (*F* = 5.33, *p-value* = 0.03; STable 3), indicating that herbicide drift levels influence the pattern selection on herbicide resistance among populations.

Trait	β	SE	P	*Y*	SE	P	*r*	P
Whitefly Resistance	0.084	0.122	0.492	0.310	0.114	0.168	-0.130	0.149
Herbicide Resistance	**0.254**	**0.125**	**0.044**	-0.043	0.101	0.832	-0.004	0.955
Relative Growth	**1.168**	**0.117**	**< 0.001**	**0.732**	**1.464**	**< 0.001**	**0.732**	**< 0.001**
Whitefly Resistance X Herbicide Resistance				-0.103	0.068	0.452	**-0.180**	**0.026**
Whitefly Resistance X Relative Growth				**-0.784**	**0.143**	**0.007**	**-0.163**	**0.052**
Herbicide Resistance X Relative Growth				**-0.800**	**0.069**	**< 0.001**	-0.094	0.200
Whitefly Resistance X Herbicide Resistance X Relative Growth				**0.462**	**0.081**	**0.005**		

Table 1. Selection analysis showing direct selection on focal traits: whitefly resistance, herbicide resistance, and relative growth rate. Linear (β) ($R^2 = 0.485$; $p < 0.001$) and quadratic (γ) ($R^2 = 0.621$; $p < 0.001$) selection gradients, and total selection (*r*) with associated standard errors (SE) and *P*-values (*P*). The r column represents correlation coefficients between trait and fitness or between individual plant traits themselves, estimated as Pearson product- moment correlations. Significant selection gradients and correlation coefficients are shown in boldface.

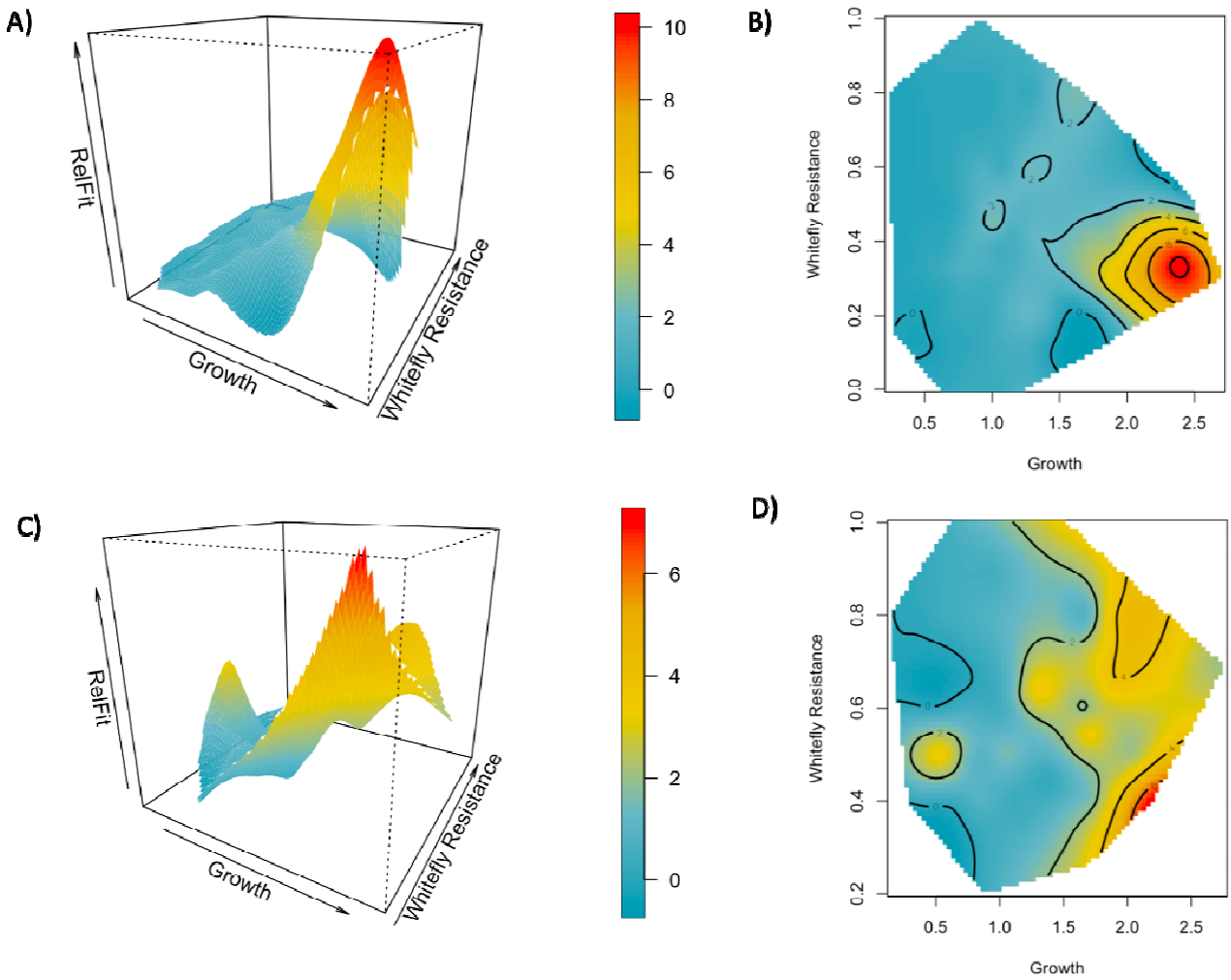

Figure 4. Fitness surfaces for correlated selection on relative growth rate and whitefly resistance in the presence (A and B) and the absence (C and D) of herbicide drift. Relative fitness is expressed through the color gradient (blue, yellow, red). The plots have been smoothed using the thin plate spline using the *Tps* function in the fields package (Nychka et al. 2015).

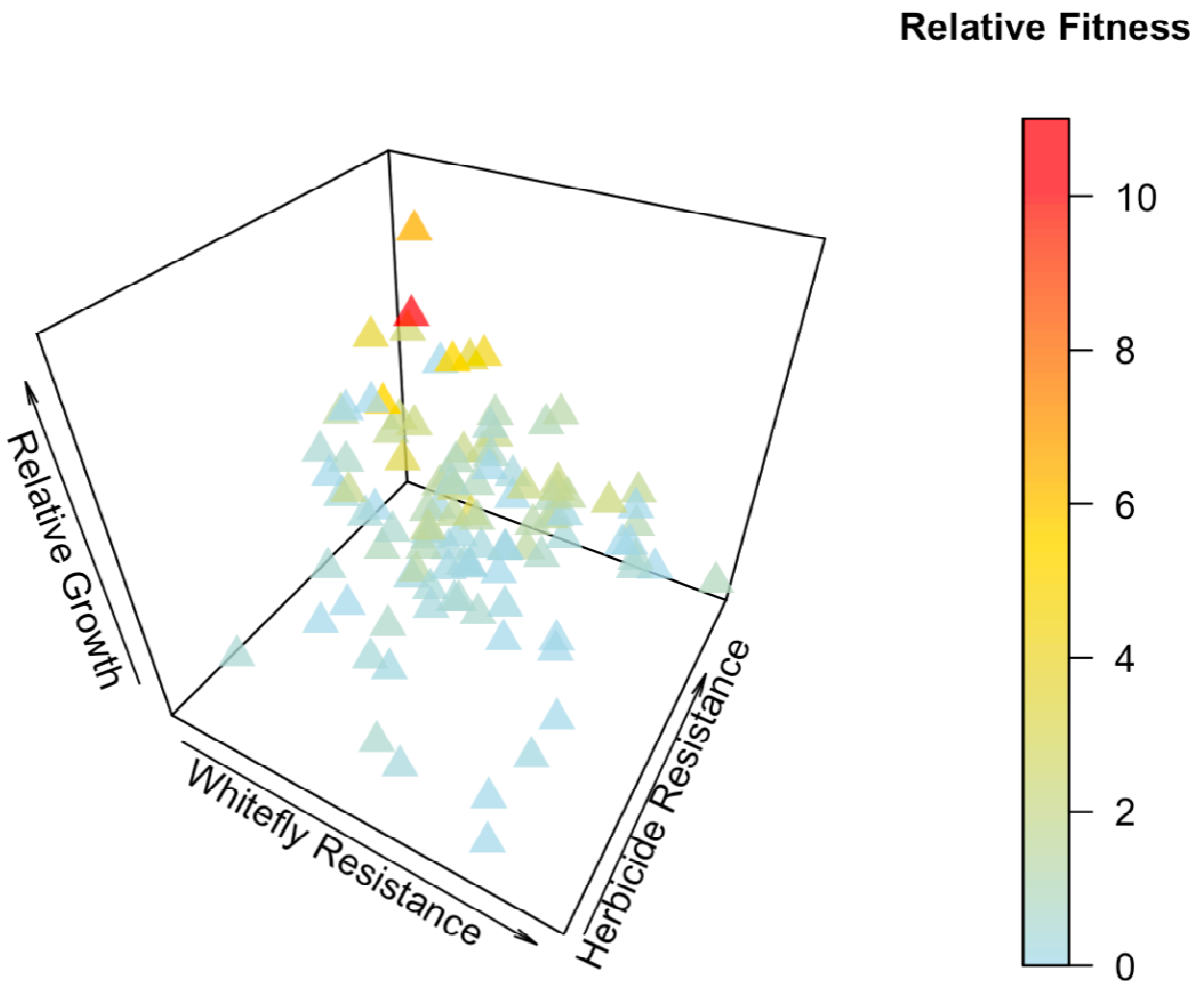

Figure 5. 3D representation demonstrating the relationship between whitefly resistance, herbicide resistance, and relative growth rate as it relates to relative fitness expressed through color gradient (blue, yellow, red).

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