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Response of Horseweed (*Erigeron canadensis*) from New York Vineyards and Orchards to Paraquat and Diquat

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Abstract. **Horseweed (*Erigeron canadensis* L.) is a troublesome species in specialty crops, including orchards and vineyards. Some growers in New York have adopted paraquat [photosystem I (PSI) electron diverter] for in-season weed control as an alternative to glyphosate. This change was facilitated by concerns about possible crop injury and herbicide resistance to glyphosate. In response to weed control failures following paraquat applications in a vineyard (NY-Gr) and apple orchard (NY-Ap), whole-plant dose–response assays were conducted to confirm putative resistance. The paraquat rates required to reduce NY-Gr and NY-Ap biomass by 50% (GR_{50}) were 0.63 and 0.56 kg a.i./ha, respectively; these values were 31- and 28-fold greater than the mean estimated GR_{50} value (0.02 kg a.i./ha) for the paraquat-susceptible checks from a roadside (NY-Ro) and a soybean field (NY-So). The diquat rates required to reduce the biomass of the NY-Gr and NY-Ap populations by 50% were 0.019 and 0.052 kg a.i./ha, respectively. Conversely, the mean rate required to reduce the biomass of the NY-Ro and NY-So populations was ≤0.004 kg a.i./ha. The photosynthetic efficiency (CO_2 assimilation and chlorophyll *a* fluorescence) of resistant individuals remained unaltered, suggesting that the resistance mechanisms may not be directly related to the target site. All horseweed populations were effectively controlled by glufosinate and saflufenacil applied at 0.05 and 0.98 kg a.i./ha, respectively. These findings confirm that paraquat resistance is present in two New York horseweed populations. The NY-Gr and NY-Ap populations were less sensitive to diquat than the NY-Ro and NY-So populations, which could suggest emerging resistance to another PSI active ingredient. The extent of paraquat resistance in New York state is not known and requires additional investigation. Given the wind-dispersed nature of horseweed seeds, growers should be vigilant for paraquat escapes to prevent the spread of resistant biotypes. This should include the use of effective, alternative chemistries when resistance is suspected.**

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Weeds pose a significant challenge in orchards and vineyards, particularly during establishment, flowering, and fruiting (Alcorta et al. 2011; Breth and Tee 2013; Breth et al. 2016; MacRae et al. 2007; Majek et al. 1993; Mitchem and Lockwood 2017; Parker and Meyer 1996; Shrestha et al. 2010; Weller et al. 1985). In addition to competition for water and nutrients, dense weed populations can create habitats for pests, impede the application of crop protection chemicals, delay harvest operations, and increase labor costs (Belding et al. 2004; Derr 2001a, 2001b; Killian and Meyer 1984). Herbicides are widely used to manage unwanted weeds beneath tree and vine canopies due to their high efficacy and relatively low cost compared with alternative weed control strategies. However, repeated herbicide use exerts selection pressure that promotes the proliferation of herbicide-resistant (HR) biotypes within weed populations (Heap 2024; Norsworthy et al. 2012; Westwood et al. 2018). Currently, more than 100 cases of HR weeds have been reported in orchard and grape (*Vitis* spp.) production systems worldwide; this includes multiple confirmed occurrences in North America from California, Michigan, New Mexico, and Oregon, as well as from Ontario (Canada) and Mexico (Heap 2024).

Horseweed (*Erigeron canadensis* L.) is a small-seeded, erect, facultative winter annual native to North America. This species is frequently found in agricultural fields, along roadsides, and in areas where tillage is not routinely practiced (Alcorta et al. 2011; Bajwa et al. 2016; Mohler et al. 2021; Shrestha et al. 2010; Van Wychen 2022). Reports of HR horseweed frequently originate from agronomic crops, although cases of resistance have been documented in orchard and grape systems (Heap 2024). Globally, horseweed populations have evolved resistance to active ingredients in several herbicide groups as defined by the Weed Science Society of America, including group 2 (acetolactate synthase inhibitors), group 5 [photosystem II (PSII) inhibitors], group 9 (5-enolpyruvylshikimate 3-phosphate synthase inhibitors), and group 22 [photosystem I (PSI) electron diverters] (Eubank et al. 2012; Heap 2024; Moretti et al. 2016; Smisek et al. 1998; VanGessel et al. 2006; Weaver et al. 2004). The reproductive capacity of horseweed enables the spread of herbicide resistance on a regional scale. Under optimal growing conditions, horseweed plants can produce 200,000 to 400,000 wind-dispersed seeds capable of traveling long distances via atmospheric currents (Dauer et al. 2007; Liu et al. 2018; Shields et al. 2006).

In tree and vine crops, the use of glyphosate is often limited to dormant applications to minimize the perceived risk of crop injury (Rosenberger et al. 2013; Rosenberger 2019; Singh et al. 2019). Consequently, paraquat has become an important in-season postemergence herbicide for many producers, placing selection pressure on weeds repeatedly exposed to this active ingredient (Moretti et al. 2015, 2016; US Geological Survey 2024). Paraquat and diquat, a related active ingredient that is also registered for use in some perennial crops, are PSI electron diverter herbicides in the pyridinium chemical family (Pesticide Properties DataBase 2024). Both chemistries provide broad-spectrum control with contact and desiccant activity (Pesticide Properties DataBase 2024). They act by accepting electrons from iron–sulfur proteins near ferredoxin on the stromal side of photosystem I, forming unstable free radicals that generate reactive oxygen species (Cobb and Reade 2010). Although resistance to paraquat has been extensively studied for many decades, the mechanisms of resistance remain unclear for many species. However, evidence suggests that vacuolar sequestration (Brunharo and Hanson 2017; Lasat et al. 1997; Yu et al. 2007), reduced translocation (Ndou et al. 2024; Tehranchian et al. 2018), or enhanced antioxidative activity (Chiang et al. 2008) could be involved.

In 2020, two perennial crop producers in western New York reported inadequate control of horseweed following paraquat applications. In 2021, preliminary trials were conducted to assess the response of four horseweed populations to paraquat at rates of 0.73 and 1.46 kg a.i./ha (Maloney and Sosnoskie 2022). Horseweed collected from a vineyard and an apple orchard survived the paraquat applications, while horseweed from a roadside site and a soybean field were completely controlled. These results supported the need for formal evaluation of PSI responses. Greenhouse and laboratory studies were conducted in 2022 to (1) confirm and characterize paraquat resistance, (2) evaluate potential cross-resistance to diquat, (3) investigate potential mechanisms of resistance, and (4) evaluate alternative herbicides for managing paraquat-resistant horseweed populations.

Materials and Methods

Plant materials. Greenhouse trials were conducted at Cornell AgriTech in Geneva, NY (42.8 N, 77.0 W) to investigate suspected resistance to paraquat in horseweed. In Aug and Sep 2020, mature seeds were collected from natural populations from a vineyard (hereafter referred to as NY-Gr; 42.6 N, 77.4 W), an apple orchard (NY-Ap; 42.3 N, 77.2 W), along a roadside (NY-Ro; 42.9 N, 77.9 W), and in a soybean field (NY-So; 43.0 N, 78.4 W) located in western New York. The grape and apple sites had received at least two applications of paraquat per growing season for at least 2 years before seed collection (Sosnoskie LM, personal communication). Conversely, the soybean population had not been directly exposed to paraquat (Sosnoskie LM, personal communication). No data are available regarding herbicides applied to the roadside population. Following collection, seed samples were stored in paper envelopes and stratified at 4 °C until use.

Whole plant paraquat and diquat dose–response studies. Horseweed seeds were surface planted into 7.67-cm-diameter pots containing a commercial potting media that was composed of 80% to 90% Lambert LM-111 Canadian sphagnum peatmoss (Lambert peat moss; Riviere-Ouelle, QC, Canada) plus an equal mix of horticultural pearlite, calcitic limestone, and dolomitic limestone. The greenhouse was set to a constant temperature of 25 °C with a 16-h light/8-h dark photoperiod. Natural daylength was supplemented with 2000-K high-pressure sodium bulbs to deliver a photosynthetically active radiation (PAR) flux density of 640 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The pots were gently watered to prevent seed movement and fertilized as needed. Horseweed seedlings were hand-thinned to one plant per pot once they had produced two or three true leaves. Herbicide applications were made when plants reached the 7- to 11-leaf stage and were approximately 30 to 50 mm in diameter.

In the paraquat dose–response study, horseweed plants were treated with Gramoxone® SL 2.0 (Syngenta Crop Protection, LLC, Greensboro, NC, USA) at rates of 0 [untreated control (UTC)], 0.14, 0.38, 0.56, 1.12, 2.24, 4.48, and 8.96 kg a.i./ha. The recommended paraquat application rates in tree and vine crops range from 0.7 to 1.12 kg a.i./ha, depending on weed species and size at the time of application. In the diquat dose–response study, horseweed plants were initially treated with Reglone® (Syngenta Crop Protection, LLC) at rates of 0, 0.091, 0.183, 0.365, 0.73, 1.46, 2.92, and 5.84 g a.i./ha. However, these diquat doses resulted in nearly complete control (99% mortality) of all treated plants (data not shown). Therefore, to more accurately assess population variations in response to diquat, a second series of two experimental runs was initiated. In this follow-up study, the plants were treated with Reglone® at rates of 0, 0.016, 0.031, 0.063, 0.125, 0.25, and 0.5 kg a.i./ha. The recommended label rates for diquat in perennial crops range from 0.5 to 1 kg a.i./ha. All paraquat and diquat treatments included a nonionic surfactant at 0.25% (v/v) (WETCIT®; Rovensa Next, Fresno, CA, USA).

Herbicides were applied using a cabinet track sprayer (DeVries Manufacturing, Hollandale, MN) equipped with a single XR8002VS nozzle (TeeJet Technologies, Glendale Heights, IL), delivering 187 $L \cdot ha^{-1}$ at 276 kPa. Aboveground plant biomass was harvested 21 d after treatment (DAT), dried at 60 °C for 7 d, and weighed. The experimental design was completely randomized, with each population-by-herbicide-by-rate combination replicated 12 times. The paraquat and diquat dose–response studies were each conducted twice.

Maximum quantum yield of PSII (F_v/F_m). Chlorophyll fluorescence *a* is an indicator of the efficiency and functionality of the photosynthetic machinery. Measurements of chlorophyll fluorescence provide insights into plant stress responses, including herbicide damage; this response variable has been extensively used to quantify paraquat damage in plants (Brunharo and Hanson 2017). Seed from the suspected resistant (NY-Gr and NY-Ap) and susceptible (NY-So) populations were sown in trays and transplanted at the seedling stage to 400-mL square pots (6.7 × 6.7 × 8.9 cm) filled with commercial media (Pro-Mix BX; PRO-MIX, Quakertown, PA, USA). Seeds of NY-Ro were not available for this trial. Consequently, a second population derived from another soybean field (hereafter referred to as "Pop 10": lat. 42.9100 N, long. 76.5660 W) was included as a substitute. Pop 10 was also completely controlled by paraquat at 0.73 kg a.i./ha (Maloney and Sosnoskie 2022). Five plants of each horseweed population were sprayed at the mature rosette stage (100-mm diameter) at rates of 0 (UTC), 0.035, 0.07, and 0.14 kg a.i./ha of paraquat. Treatments were applied using a commercial track sprayer (DeVries Manufacturing, Inc.) equipped with an 8002EVS nozzle (TeeJet; Spraying Systems Co., Denver, CO) calibrated to deliver 187 $L \cdot ha^{-1}$. Following treatment, the plants were returned to the greenhouse under previously described environmental conditions. The pots were arranged in a completely randomized design, and the experiment was conducted twice.

The plants were dark adapted for 30 min before F_v/F_m measurements were collected at 0, 3, 6, 9, 24, and 48 h after application (HAA). Measurements were taken from the second youngest fully expanded leaf using a portable photosynthesis analyzer (LI-6800; LI-COR Inc., Lincoln, NE). The measuring light beam was set to provide a dark modulating rate of 50 Hz, rectangular flash set with red target of 8000 $\mu mol \cdot m^{-2} \cdot s^{-1}$, duration of 1000 ms, and output rate of 100 Hz. The leaves were marked with a pen to ensure that measurements were captured from the same sites over time.

CO_2 response curves (A–C_i). CO_2 assimilation estimates (A) were computed to describe the efficiency of the photosystem in resistant and susceptible populations. Four individuals (100- to 150-mm rosette diameters) per horseweed population were analyzed for this study. A–C_i regression curves were built by applying different concentrations of CO_2 to selected leaves and subsequently measuring A. A LI-6800 photosynthesis analyzer was used to build A–C_i curves following the method described by Ruiz-Vera et al. (2022). Briefly, the CO_2 concentration was first decreased to 0 and then increased up to 2500 $\mu mol \cdot mol^{-1}$ (i.e., 400, 200, 100, 50, 0, 600, 800, 1000, 1500, 2000, and 2500 $\mu mol \cdot mol^{-1}$). The chamber air temperature was set to ambient, relative humidity at 50%, air flow rate of 500 $\mu mol \cdot s^{-1}$, fan speed of 10,000 rpm, and saturating light of 1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$. A light response curve pilot was run previously to set the PAR requirement. The gas-exchange systems were matched before each curve and leaf temperature, and the assimilation rate and intercellular CO_2 concentration (C_i) were recorded. The A–C_i models were used to calculate key photosynthesis estimates. First, the rate of RUBISCO activity ($V_{c,\max}$) was derived to test whether resistant plants could have physiological alterations that affect the pool of Calvin cycle intermediates. Second, the maximum rate of electron transport ($J_{\max}$) was calculated to test whether resistant individuals exhibited reduced efficiency in electron transport. Finally, the rate of dark respiration was quantified to assess whether there were greater metabolic costs to paraquat resistance compared with susceptible plants. The experiment was conducted twice.

Response to alternative chemistries. The sensitivity of the New York horseweed populations to two alternative postemergence chemistries was also evaluated. Treatments consisted of 0.05 kg a.i./ha saflufenacil (Treevix®; BASF Corporation, Research Triangle Park, NC, USA) and 0.98 kg a.i./ha glufosinate (Rely 280 ®; BASF Corporation). Both herbicides were tank mixed with 1% ammonium sulfate (v/v) (Brandt Magnify®; Brandt Consolidated Inc., Tampa, FL) and 1% methylated seed oil (v/v) (Brandt MSO®; Brandt Consolidated Inc.) and applied using the cabinet sprayer. A UTC was also included for comparison. The plants were grown in the greenhouse and treated as previously described. The pots were arranged in a completely randomized design, and each population-by-herbicide combination was replicated 12 times. The alternate herbicide screening study was conducted twice. Aboveground plant biomass was harvested at 21 DAT, dried at 60 °C for 7 d, and subsequently weighed.

Data analysis. Dry plant biomass data from the paraquat and diquat dose–response studies were expressed as percentages of the UTC to standardize responses across populations. The data were arcsine square root transformed to improve normality and subjected to analysis of variance (ANOVA) in SAS 9.4 (SAS Institute, Cary, NC, USA) using PROC MIXED. The ANOVA results indicated no significant differences between the experimental runs in both studies. As a result, the data were combined across runs for further analysis. The dose–response data were analyzed using PROC NLIN in SAS 9.4 and fitted to the three-parameter log-logistic regression model shown in Eq. [1] (Seefeldt et al. 1995) for the suspected PSI-resistant horseweed populations and the two-parameter exponential decay function shown in Eq. [2] (Smisek et al. 1998; Weaver et al. 2004) for the PSI-sensitive populations:

$$Y = a/\{1 + \exp^{[b(\log(x) - \log(x_0))]}\} \quad [1]$$

$$Y = a/2^{(x/x_0)} \quad [2]$$

where Y is the relative dry biomass at herbicide rate x, a is the estimated maximum horseweed relative weight, b is the relative slope around x_0, and x_0 is the herbicide dose required to reduce dry plant biomass by 50% (GR_{50}) relative to the UTC. The slope of the response curve (b) for the exponential decay function shown in Eq. [3] was calculated as follows:

$$b = \ln(2)/x_0 \quad [3]$$

Each horseweed population by herbicide combination were analyzed separately. Model fits were evaluated using the root mean square error (RMSE) and modeling coefficient of efficiency (EF) values (Heneghan and Johnson 2017; Sarangi et al. 2016). The RMSEs were computed using Eq. [4]:

$$\mathrm{RMSE} = \left[\frac{1}{n}\sum_{i=1}^{n}(P_i - O_i)^2\right]^{\frac{1}{2}} \quad [4]$$

where P_i is the value predicted by the models, O_i is the observed value, and n is the total number of observations. Smaller RMSE values indicate a better fit to the model (McMaster et al. 1992). The EF values were calculated based on the following:

$$\mathrm{EF} = 1 - \left[\sum_{i=1}^{n}(O_i - P_i)^2 / \sum_{i=1}^{n}(O_i - \bar{O}_i)^2\right] \quad [5]$$

where O_i represents the observed values, P_i represents the values predicted by the models, $\bar{O}_i$ represents the mean observed values, and n is the number of observations. The EF values can range from $-\infty$ to 1, with values closer to 1 indicating a better fit of the model. Parameter estimates were compared using an F-test ($\alpha = 0.05$) to perform a parallel curve analysis, following the method described by Seefeldt et al. (1995). The resistance level, expressed as the R/S ratio, was calculated by dividing each of the GR_{50} values of the suspected paraquat-resistant population by the average GR_{50} value of the susceptible populations. The curves were generated using SigmaPlot version 14.5 (Systat Software Inc., San Jose, CA, USA).

The F_v/F_m data were pulled across experimental runs and analyzed using a linear model with interactions between data collection time and population as fixed effects. We analyzed each paraquat rate separately as we were primarily interested in comparing the differences among populations rather than the effects of increasing paraquat rates. F_v/F_m was calculated with the following equation:

$$\frac{Fv}{Fm} = \frac{(Fm - Fo)}{Fm} \quad [6]$$

where F_o is the minimal level of fluorescence, F_m is maximum fluorescence in the light in dark-adapted leaves, and F_v is variable fluorescence at any given time during induction.

The A–C_i curves were created for individual plants and analyzed using the *fitaci* function from the *plantecophys* R package (Duursma 2015). After building the regressions, we extracted the estimated maximum rate of RUBISCO carboxylation ($V_{c,\max}$), the maximum rate of electron transport at 25C ($J_{\max}$), and the dark respiration rate at reference temperature (R_d) with the following equation:

$$A_n = \min(A_c, A_j) - R_d \quad [7]$$

where A_n is the net rate of CO_2 assimilation, A_c is the gross photosynthesis rate when RUBISCO activity is limiting, and A_j is the rate when ribulose 1,5-bisphosphate regeneration is limiting. The details of these functions and the temperature dependence of the various parameters are described elsewhere (Duursma 2015; Long and Bernacchi 2003). The F_v/F_m and A–C_i parameters were analyzed using *emmeans* package with Šidák ad-hoc correction in RStudio version 2023.06.1 (RStudio Team, Boston, MA, USA).

For the statistical analysis of the alternative chemistry evaluations, the dry plant biomass data were expressed as percentage of the UTC to standardize responses across populations. An ANOVA was conducted using the generalized linear mixed model (GLIMMIX) procedure in SAS version 9.4 (SAS Institute). Herbicide treatments, populations, and interactions between these two factors were considered fixed effects, whereas run and replication nested within run were designated as random factors in the model. Mean comparisons for the fixed effects were performed using Tukey's honestly significance test when the F values were statistically significant ($P \leq 0.05$).

Results and Discussion

Under greenhouse conditions, paraquat injury symptoms were evident on susceptible NY-Ro and NY-S horseweed plants 1 to 3 DAT (Fig. 1). The NY-Ro and NY-So populations exhibited pronounced necrosis resulting in plant death. In contrast, symptom development for the putative resistant NY-Gr and NY-Ap populations progressed more slowly and was less severe. When observed, injury for the NY-GR and NY-Ap populations was primarily characterized by water soaking and chlorosis, which was sometimes followed by necrosis that did not systematically kill the meristem. Smisek et al. (1998) reported that paraquat-resistant horseweed from Ontario displayed localized bleaching of leaf tips and older leaves with the apical meristem of resistant plants remaining green and undamaged. Leal et al. (2022) noted that paraquat-resistant Sumatran fleabane (*Erigeron sumatrensis* Retz.) from Turkey exhibited only a few necrotic spots on treated leaves.

Paraquat dose–response analyses confirmed differences in dry biomass accumulation among the tested horseweed populations (Fig. 2). The results showed that the estimated doses required to reduce the relative dry biomass of the susceptible NY-Ro and NY-So populations by 50%, relative to the UTC, were 0.021 and 0.022 kg a.i./ha, respectively (Table 1). The estimated paraquat rates required to reduce the relative dry biomass of the suspected resistant NY-Gr and NY-Ap populations by 50%, relative to the UTC, were 0.62 and 0.56 kg a.i./ha, respectively (Table 1). The calculated R/S values indicate that the NY-Gr and NY-Ap populations were 26- to 29-fold more resistant than the susceptible checks.

Although the estimated GR_{50} values for the NY-Gr and NY-Ap populations were lower than the recommended use rate range for perennial crops, it is important to note that plant survival ranged from 75% to 96% (data not shown). Eubank et al. (2012) reported a GR_{50} value of 0.67 kg a.i./ha for a paraquat-resistant horseweed population in Mississippi, which was 9-fold greater than the GR_{50} value for the susceptible check. VanGessel et al. (2006) determined that the GR_{50} value for a paraquat-resistant horseweed population in Delaware was 0.78 kg a.i./ha, which was 22-fold greater than the control population. Smisek et al. (1998) reported that paraquat rates ranging from 2.8 to 3.7 kg a.i./ha were required to reduce by 50% the biomass of a paraquat-resistant horseweed population in Ontario; these rates were 25- to 35-fold greater than the

Fig. 1. New York horseweed populations following an application of paraquat at a rate of 0.73 kg a.i./ha at 1 d after treatment. (Top left) Paraquat-resistant population collected from a New York vineyard (NY-Gr); (top right) paraquat-susceptible population collected from a New York roadside site (NY-Ro); (bottom left) paraquat-resistant population collected from a New York apple orchard (NY-Ap); and (bottom right) paraquat-susceptible population collected from a New York soybean field (NY-So).

doses for the susceptible populations. A paraquat-resistant horseweed population in California with a GR_{50} value of 1.4 kg a.i./ha was determined to be 323-fold more resistant than a susceptible check (Moretti et al. 2016). Variations in plant growth responses among studies are likely influenced by genetic differences among populations, as well as factors such as plant size and environmental conditions at the time of treatment. These factors can also affect horseweed biomass accumulation and survival in the absence of resistance (Harre et al. 2021; Mellendorf et al. 2013; Montgomery et al. 2017).

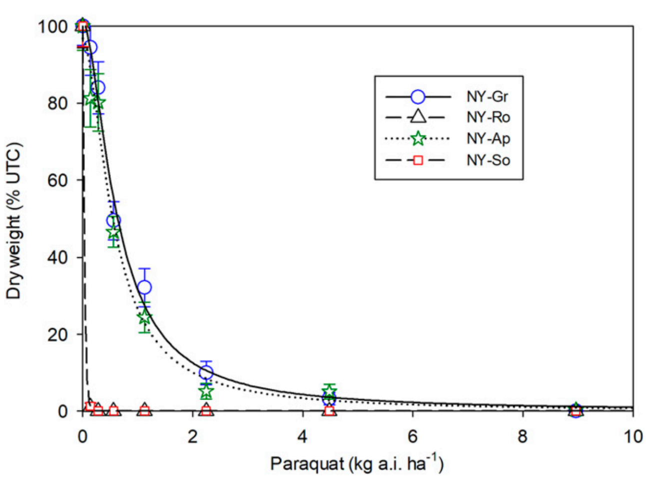

Fig. 2. Dose–response curves of paraquat-resistant (NY-Gr and NY-Ap) and paraquat-susceptible (NY-Ro and NY-So) horseweed populations showing dry plant biomass adjusted as a percentage of the nontreated check 21 d after paraquat treatments. NY-Ap = paraquat-resistant population collected from a New York apple orchard; NY-Gr = paraquat-resistant population collected from a New York vineyard; NY-Ro = paraquat-sensitive population collected from a New York roadside site; NY-So = paraquat-sensitive population collected from a New York soybean field.

Diquat injury symptoms on horseweed were like paraquat. The NY-Ro and NY-So populations displayed water soaking followed by rapid necrosis. Meristem survival and plant regrowth were more frequently observed in the NY-Gr and NY-Ap populations. Dose–response analyses revealed distinct differences in the dry biomass accumulation responses among the tested horseweed populations (Table 1; Fig. 3). The GR_{50} values for the susceptible populations, NY-Ro and NY-So, were estimated at 0.004 and 0.001 kg a.i./ha, respectively. In contrast, the diquat rates required to reduce the relative dry biomass of the NY-Gr and NY-Ap populations by 50% were 0.019 and 0.052 kg a.i./ha, respectively. These findings correspond to R/S ratios of 8 to 22. Weaver et al. (2004) documented cross-resistance to diquat in paraquat-resistant horseweed populations from an Ontario peach orchard. The researchers observed that GR_{50} values increased with plant size. Paraquat-resistant plants had diquat GR_{50} values of 0.014 kg a.i./ha at 8 weeks and 0.135 kg a.i./ha at 10 weeks, whereas susceptible populations had GR_{50} values of 0.002 and 0.023 kg a.i./ha at the same growth stages. Moretti et al. (2021) reported that paraquat-resistant horseweed populations from California exhibited 11- to 16-fold resistance to diquat. Additionally, paraquat-resistant populations of hairy fleabane (*Erigeron bonariensis* L.) were found to be 44- to 90-fold more resistant to diquat compared with susceptible checks.

Under nonstress conditions, the F_v/F_m ratios were similar across all populations (Table 2; Fig. 4). The putative susceptible populations, Pop 10 and NY-So, showed a significant decrease in PSII efficiency within 6 HAA of paraquat at rates between 0.035 and 0.140 kg a.i./ha; the values remained low throughout the assessment period. In contrast, resistant populations (NY-Gr and NY-Ap) maintained higher F_v/F_m ratios compared with the susceptible populations following paraquat treatment (Table 2; Fig. 4). While resistant populations experienced a temporary reduction in F_v/F_m within the first 9 HAA at the lowest paraquat rate, they were able to recover over time.

Similar trends were observed by Brunharo and Hanson (2017) in Italian ryegrass [*Lolium perenne* L. spp. *multiflorum* (Lam.) Husnot], suggesting a lag-time between stress perception and activation of defense mechanisms at the cellular level. Resistance mechanisms that exclude paraquat away from the target site, such as vacuolar sequestration in the chloroplast, could provide similar trends in F_v/F_m (Brunharo and Hanson 2017). Overall, our findings are similar to those previously reported for other weed species. Susceptible populations of horseweed and Italian ryegrass exhibited significant reductions in chlorophyll

Table 1. Regression model parameter and model goodness-of-fit estimates describing the responses of four New York horseweed populations to paraquat and diquat at 21 d after treatment.

Population	a[i]	b	GR_{50} (kg a.i./ha)	RMSE	EF	R/S[ii]
Paraquat						
NY-Gr	101.4 ± 4.19	1.7 ± 0.22	0.62 ± 0.063	23.16	0.74	28.7
NY-Ap	96.9 ± 4.36	1.7 ± 0.24	0.56 ± 0.061	23.70	0.71	26.0
NY-Ro	100.0 ± 1.98	32.6 ± 13.60	0.0213 ± 0.0089	9.67	0.92	—
NY-So	100.0 ± 1.85	31.3 ± 10.59	0.0221 ± 0.0075	9.03	0.93	—
Diquat						
NY-Gr	99.9 ± 2.81	1.3 ± 0.13	0.019 ± 0.0015	13.67	0.86	7.7
NY-Ap	99.3 ± 3.90	1.5 ± 0.18	0.052 ± 0.0052	20.09	0.76	21.5
NY-Ro	100.0 ± 3.24	171.2 ± 29.84	0.004 ± 0.0007	15.77	0.83	—
NY-So	100.0 ± 3.05	839.7 ± 97.35	0.001 ± 1.2006	14.84	0.85	—

[i] Parameters for the resistant (NY-Gr and NY-Ap) and susceptible (NY-Ro and NY-So) populations were computed using the three parameter log logistic regression model $Y = a/\{1+\exp^{[b(\log(x)-\log(x_0))]}\}$ and the exponential decay regression model $Y = a/2^{(x/x_0)}$, respectively, where Y is the relative dry biomass at herbicide rate x; a is the estimated maximum horseweed relative weight; and b is the relative slope around x_0, which is also the GR_{50} value. b parameters for the NY-Ro and NY-So populations were computed using the formula $b = ln\ (2)/bx_0$.

[ii] The resistance level was calculated by dividing the GR_{50} values of the paraquat-resistant population by the average GR_{50} value of the NY-Ro and NY-So populations.

a = estimated maximum horseweed relative weight; b = relative slope; EF = coefficient of efficiency; GR_{50} = herbicide dose required to reduce dry plant biomass by 50% relative to the nontreated control; NY-Ap = paraquat-resistant population collected from a New York apple orchard; NY-Gr = paraquat-resistant population collected from a New York vineyard; NY-Ro = paraquat-sensitive population collected from a New York roadside site; NY-So = paraquat-sensitive population collected from a New York soybean field; RMSE = root mean square error; R/S = resistance level.

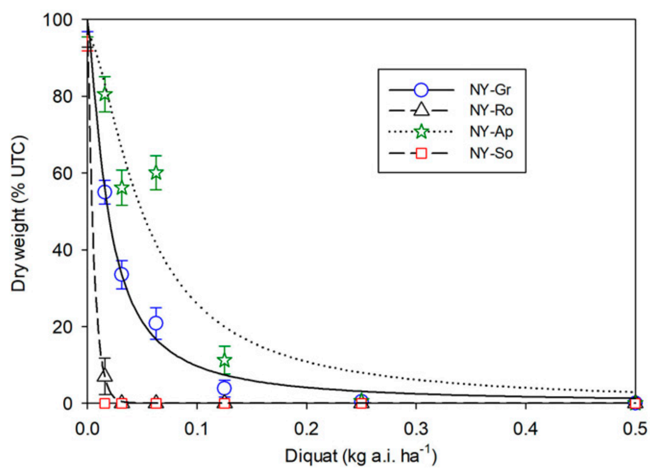

Fig. 3. Dose–response curves of paraquat-resistant (NY-Gr and NY-Ap) and paraquat-susceptible (NY-Ro and NY-So) horseweed populations showing dry plant biomass adjusted as a percentage of the nontreated check 21 d after diquat treatments. NY-Ap = paraquat-resistant population collected from a New York apple orchard; NY-Gr = paraquat-resistant population collected from a New York vineyard; NY-Ro = paraquat-sensitive population collected from a New York roadside site; NY-So = paraquat-sensitive population collected from a New York soybean field.

a fluorescence (over 60%) within 10 HAA at paraquat rates higher than 105 g a.i./ha, with complete reduction by 24 HAA (Leal et al. 2023) and 48 HAA (Brunharo and Hanson 2017). Notably, paraquat-resistant Italian ryegrass populations retained PSII efficiency after paraquat treatment (Brunharo and Hanson 2017), as observed in our study. Studies suggested vacuolar sequestration of paraquat in Italian ryegrass (Brunharo and Hanson 2017) and antioxidative activity in Sumatran fleabane (Chiang et al. 2008) can mitigate oxidative damage in resistant populations. While enzymatic studies were not conducted in our study, the patterns of chlorophyll a fluorescence response with paraquat application indicates a potentially similar resistance mechanism. Although the genetic changes conferring paraquat resistance in weeds remain unknown, candidate genes have been recently identified (Brunharo et al. 2024). The genes *VATP-P1* and *NPF5.10*, a V-type proton ATPase and a nitrate transporter, respectively, are membrane-bound transporters that could be involved in the recognition of paraquat and enhanced vacuolar sequestration in weeds, although more research is needed to functionally validate these genes (Brunharo et al. 2024).

Additionally, we conducted studies to investigate the physiological impacts on the photosynthetic apparatus associated with the evolution of paraquat resistance (Table 2; Fig. 5) and to determine whether the resistance mechanisms are associated to

Table 2. Parameters of assimilation CO_2 response curves (A–C_i) of New York horseweed paraquat-resistant (NY-Gr and NY-Ap) and paraquat-susceptible (Pop 10 and NY-So) populations.

Parameter	NY-Gr	NY-Ro	Pop 10	NY-So	P value
$V_{c,\max}$	49.74 ± 15.55	56.59 ± 19.03	52.36 ± 7.52	47.46 ± 4.74	ns
$J_{\max}$	77.47 ± 19.88	82.46 ± 22.26	77.94 ± 11.74	74.63 ± 8.70	ns
R_d	1.24 ± 0.27	1.15 ± 0.11	1.32 ± 0.38	1.30 ± 0.28	ns
Γ	54.35 ± 1.42	54.34 ± 1.06	54.01 ± 0.89	55.27 ± 1.04	ns
K_m	1072.42 ± 48.90	1072.07 ± 36.34	1073.40 ± 33.91	1104.13 ± 36.18	ns
$A_c \times A_j$	469.25 ± 90.07	430.48 ± 127.04	416.74 ± 76.04	475.63 ± 59.85	ns

Means are followed by confidence interval at 95%. Estimates followed by the same letters within lines represents no significant (ns) differences at 5% of probability. Γ = CO_2 compensation point in the absence of dark respiration (mmol·mol^{-1}); A_c = gross photosynthesis rate when Rubisco activity is limiting; A_j = when ribulose 1,5-bisphosphate regeneration is limiting; K_m = Michaelis–Menten constant for CO_2 and O_2; NY-Gr = paraquat-resistant population collected from a New York vineyard; NY-Ro = paraquat-sensitive population collected from a New York roadside site; NY-So = paraquat-sensitive population collected from a New York soybean field; Pop 10 = second population derived from another soybean field; $J_{\max}$ = maximum rate of electron transport at 25 °C (μmol·m^{-2}·s^{-1}); R_d = dark respiration rate at reference temperature 25 °C (μmol·m^{-2}·s^{-1}); $V_{c,\max}$ = maximum rate of Rubisco carboxylation (μmol·m^{-2}·s^{-1}).

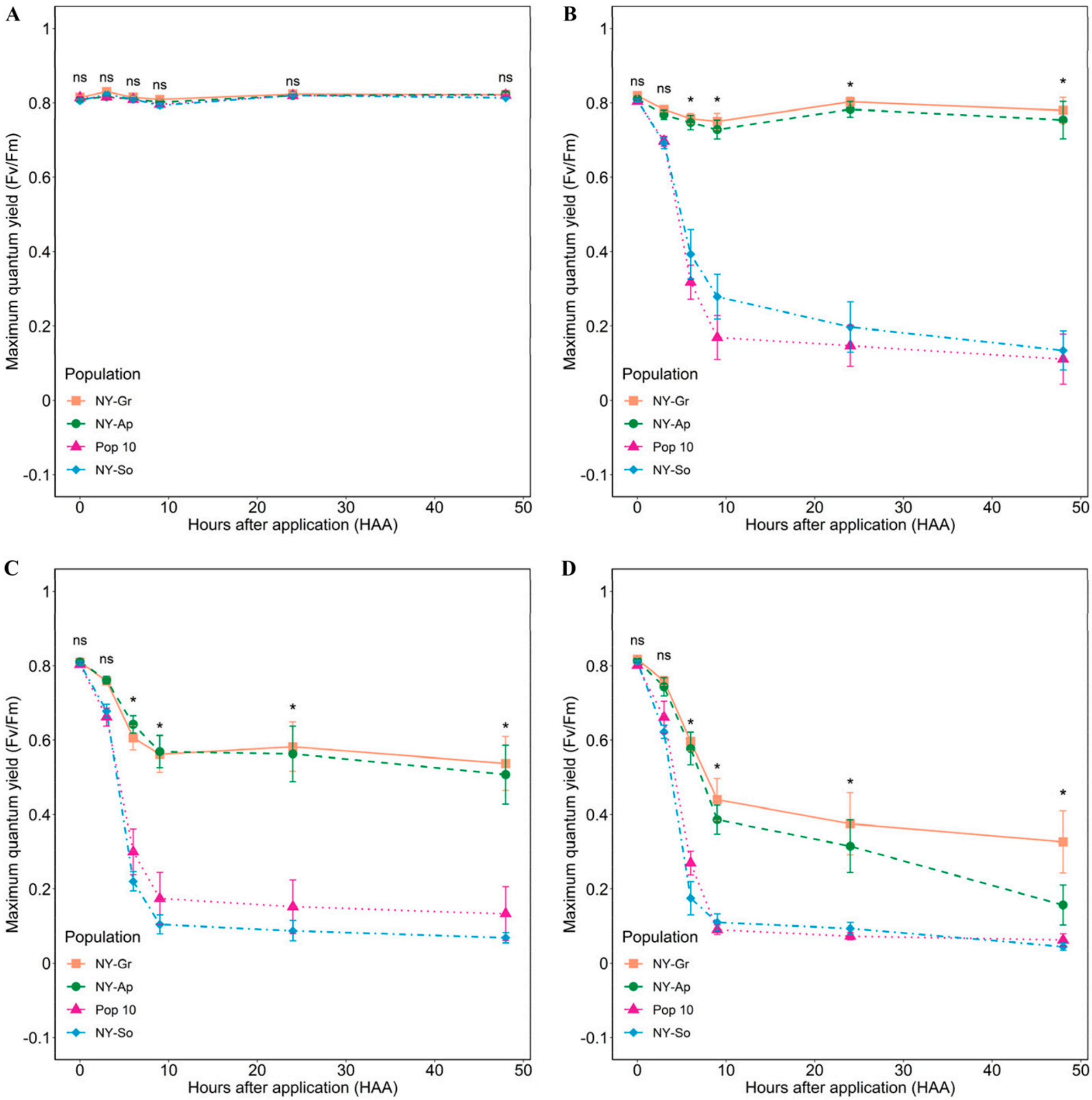

Fig. 4. Maximum quantum yield (F_v/F_m) of New York horseweed populations sprayed at 0 (**A**), 35 (**B**), 70 (**C**), and 140 (**D**) g a.i./ha of paraquat. The means are followed by standard errors, and significant differences ($P < 0.05$) among populations within HAA were followed by asterisks (*). HAA = hours after application; ns = not significant; NY-Ap = paraquat-resistant population collected from a New York apple orchard; NY-Gr = paraquat-resistant population collected from a New York vineyard; NY-So = paraquat-sensitive population collected from a New York soybean field; Pop 10 = second population derived from another soybean field.

alterations in the photosynthetic machinery. In other weed species, resistance evolution to herbicides that target the photosystem can be accompanied by lower-photosynthetic-efficiency (Bajkán et al. 2010; Váradi et al. 2000) A–C_i models for C_3 plants to allow us to understand the photosynthetic efficiency between resistant and susceptible horseweed populations. The A–C_i modeling results indicated no differences in photosynthetic capacity in terms of CO_2 assimilation among populations (Table 2; Fig. 5). The similar photosynthetic efficiency among the horseweed populations suggests that resistance to paraquat has not compromised the photosynthetic apparatus.

All New York horseweed populations evaluated in this study were controlled >98% following glufosinate applied at 0.98 kg a.i./ha (Table 3). Response to saflufenacil applied at 0.05 kg a.i./ha was less consistent, with >94% control for NY-Ap, Ny-Gr, and NY-So populations but only 67% control for NY-Ro population. Previous studies have reported that glufosinate alone is an effective herbicide for managing glyphosate-resistant *Erigeron* populations (Eubank et al. 2008; Moretti et al. 2013, 2021). However, its efficacy can vary and is influenced by specific environmental factors, including air temperature (Kumaratilake and Preston 2005), relative humidity (Coetzer et al. 2001), and sunlight exposure (Takano and Dayan 2020). Eubank et al. (2013) reported 71% to 89% control of glyphosate-resistant horseweed when saflufenacil was applied at 0.025 kg·ha^{-1}, with greater efficacy observed when 2% (v/v) methylated seed oil was included in the spray mixture. Moretti et al. (2013, 2021) demonstrated effective

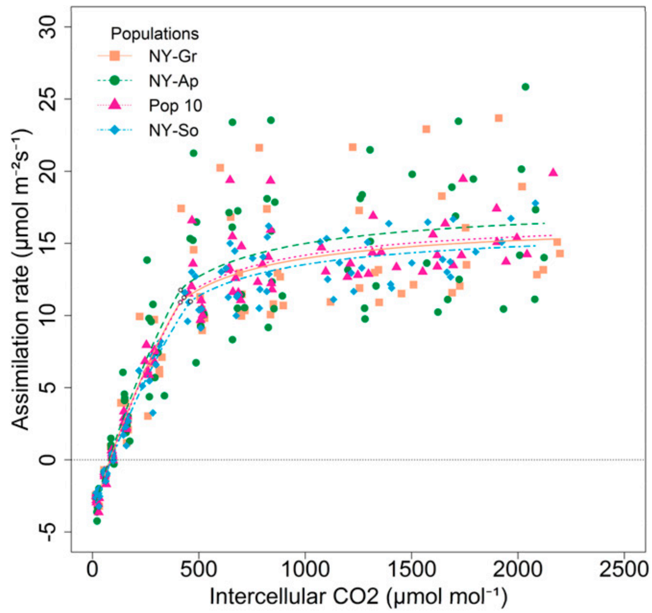

Fig. 5. Assimilation CO_2 response curves (*A–Ci*) of *Erigeron* populations resistant and susceptible to paraquat. Gray points in the model fitted represents $A_c \times A_j$ intersection. NY-Ap = paraquat-resistant population collected from a New York apple orchard; NY-Gr = paraquat-resistant population collected from a New York vineyard; NY-So = paraquat-sensitive population collected from a New York soybean field; Pop 10 = second population derived from another soybean field.

control of *Erigeron* species with saflufenacil under greenhouse and field conditions. In contrast to glufosinate, saflufenacil demonstrated greater herbicidal activity under low light intensity (300 $\mu mol \cdot m^{-2} \cdot s^{-1}$) compared with high light intensity (1000 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Mellendorf et al. 2015). To date, no instances of horseweed resistance to glufosinate or saflufenacil have been reported either in the United States or internationally (Heap 2024). The reduced control observed for the NY-Ro population in response to saflufenacil could be due to genetic variation among populations, which may influence plant susceptibility to this herbicide, as well as suboptimal plant size and environmental conditions at the time of application. This is consistent with previous research on factors affecting saflufenacil efficacy in controlling glyphosate-resistant horseweed (Budd et al. 2017; Mellendorf et al. 2013, 2015).

Table 3. Dry biomass 21 d after treatment response responses of four New York horseweed populations to saflufenacil and glufosinate.

	Herbicide (% UTC)	
Population	Saflufenacil	Glufosinate
NY-Gr	5.7 b	0
NY-Ap	2.5 b	0
NY-Ro	33.1 a	1.6
NY-So	4.2 b	1.9

Saflufenacil and glufosinate were applied at 0.05 and 0.98 kg a.i./ha, respectively, and mixed with 1% ammonium sulfate (v/v) and 1% methylated seed oil (v/v). The data were pooled across runs, and means followed by the same letter within in a column are not significantly different based on Tukey's honestly significant difference test (α = 0.05). NY-Ap = paraquat-resistant population collected from a New York apple orchard; NY-Gr = paraquat-resistant population collected from a New York vineyard; NY-Ro = paraquat-sensitive population collected from a New York roadside site; NY-So = paraquat-sensitive population collected from a New York soybean field; UTC = untreated control.

Currently, eight reports from the International Herbicide Resistant Weeds database describe paraquat or paraquat and diquat resistance in weed species belonging to the *Erigeron* genus (Heap 2024). Results from our trials demonstrated 26- to 29-fold differences between the paraquat-resistant and -susceptible horseweed populations with respect to dry biomass accumulation, relative to the UTC, following paraquat applications. Photosynthetic efficiency, including CO_2 assimilation and chlorophyll a fluorescence, remained unaffected in paraquat-resistant biotypes, suggesting that the resistance mechanisms may not be directly related to the herbicide's target site. Although all horseweed populations were effectively controlled at diquat rates (0.5 to 1 kg a.i./ha) labeled for use in perennial crops, notable differences in dry biomass accumulation were observed between the paraquat-resistant and paraquat-susceptible populations following diquat application. These results are consistent with findings by Vaughn et al. (1989), who reported that hairy fleabane populations showed a 10-fold greater resistance to paraquat compared with diquat. Although paraquat-resistant populations can be effectively controlled with labeled rates of diquat, evidence of variation in control efficacy among populations at lower treatment rates suggests the potential for emerging resistance. Horseweed is a prolific seed producer with small, plumed seeds that enable long-distance dispersal. Liu et al. (2018) reported that horseweed seeds could travel over 185 km by the end of the seed-shedding season. Shields et al. (2006) observed seeds at altitudes of 41 to 140 m, confirming their ability to enter the planetary boundary layer. Within this layer, wind speeds often exceed 20 m per second, allowing seeds to travel up to 500 km in a single event. These studies highlight the potential for local horseweed infestations to spread regionally via wind currents, underscoring the risk of novel resistance traits dispersing over large areas. The management of resistant horseweed populations should include a diversity of control measures, including effective alternative chemistries such as glufosinate and saflufenacil.

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