Ivyleaf morningglory (Ipomoea hederacea Jacq.) competition is not intensified by drought in silage corn in central New York State, USA

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Article

Ivyleaf morningglory (*Ipomoea hederacea* Jacq.) competition is not intensified by drought in silage corn in central New York State, USA

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Abstract

Ivyleaf morningglory (IMG, *Ipomoea hederacea* Jacq.) is a summer annual vine that is native to the Americas and invasive globally. This species decreases field crop yields through competition and interference with harvesting. Here, we explore the potential of IMG to compete with silage corn (*Zea mays* L.) in New York State, USA. In a 2-year field study, we measured silage yield at five IMG planting densities (0–8 plants m^{-2}) under no-drought conditions and a drought treatment established with rainout shelters. Volumetric water content was 26%–28% lower in the drought treatment than the no-drought treatment. Drought reduced fresh corn silage yield ($P = 0.003$). Fresh silage yield was 21 600 $\pm$ 700 kg ha^{-1} in the no-drought treatment in 2016, 19 100 $\pm$ 900 kg ha^{-1} in the drought treatment in 2016, 30 500 $\pm$ 900 kg ha^{-1} in the no-drought treatment in 2017, and 28 200 $\pm$ 700 kg ha^{-1} in the drought treatment in 2017. Silage yield was not strongly responsive to IMG density, regardless of drought. These data suggest that the risk of corn silage yield losses due to IMG is relatively low in New York State and unlikely to be affected by drought. The risk posed by IMG may differ in other cropping systems or regions and under climate change.

Key words: annual vine, Convolvulaceae, rainout shelter, soil moisture deficit, weed–crop competition

Résumé

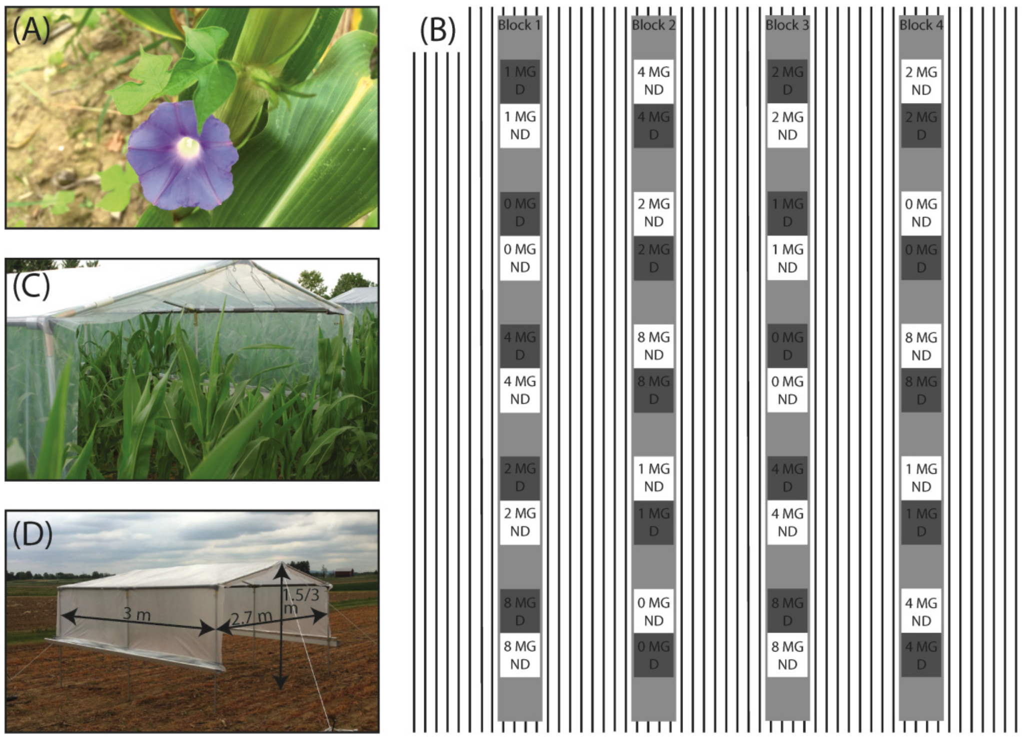
Le liseron bleu (LB, *Ipomoea hederacea* Jacq.) est une annuelle grimpante estivale indigène dans les Amériques, mais envahissante ailleurs dans le monde. L'espèce diminue le rendement des cultures industrielles en leur livrant concurrence et en nuisant à leur récolte. Les auteurs ont examiné la capacité du LB à concurrencer le maïs d'ensilage (*Zea mays* L.) dans l'État de New York (É.-U.). Lors d'une étude de deux ans, ils ont mesuré le volume d'ensilage obtenu à cinq densités de peuplement du LB (de 0 à 8 plants par m2), en régime pluvial et en régime aride, sous des abris contre la pluie. Le volume d'eau dans le régime aride était 26 à 28 % plus faible que celui dans le régime pluvial. La sécheresse diminue le rendement du maïs d'ensilage frais ($P = 0{,}003$), qui se chiffrait à 21 600 $\pm$ 700 kg par hectare pour le régime pluvial en 2016, à 19 100 $\pm$ 900 kg par hectare pour le régime aride la même année, à 30 500 $\pm$ 900 kg par hectare pour le régime pluvial en 2017 et à 28 200 $\pm$ 700 kg par hectare pour le régime aride en 2017. Le rendement du maïs d'ensilage ne réagit pas énormément à la densité de peuplement du LB, qu'il y ait sécheresse ou pas. Ces résultats laissent croire que les risques d'une baisse de rendement du maïs d'ensilage attribuable au LB sont relativement minces dans l'État de New York et que le rendement est peu affecté par la sécheresse. Les risques que pose le LB pourraient néanmoins être différents pour d'autres cultures ou régions, en raison du changement climatique. [Traduit par la Rédaction]

Mots-clés : annuelle grimpante, Convolvulaceae, abri contre la pluie, carence en eau, concurrence adventice-culture

Introduction

Ivyleaf morningglory (IMG, *Ipomoea hederacea* Jacq.) is a summer annual twining or climbing vine with three-lobed leaves and funnel-shaped flowers (Fig. 1A; Uva et al. 1997). This species is native to the Americas (Bright and Rausher 2008) and invasive globally. It has been recorded as invasive in 21 countries and is especially problematic in East Asia and the USA (Global Biodiversity Information Facility 2021). Morningglories (*Ipomoea* spp.) including IMG were collectively ranked as the most troublesome weed of corn (*Zea mays* L.) in the southern USA in 2008 (Webster and Nichols 2012) and have consistently been among the most troublesome weeds in all crops in that region (Webster and Coble 1997). Morningglories are also a problem for field crops, including

Fig. 1. Methods for research on drought and ivyleaf morningglory (IMG) competition in silage corn in Ithaca, NY, USA in 2016 and 2017. (A) IMG in corn. (B) Experimental design. Four blocks (replicates) each containing 5 plots (IMG planting densities), each of which contained two subplots (no-drought and drought treatments). Plot arrangement for 2016 is shown; plots were re-randomized in 2017. Vertical lines represent corn rows. (C, D) Rainout shelter for drought treatment, 2.7 m wide by 3 m long by 1.5 (early season) to 3 m (late season) tall.



corn, in the mid-Atlantic USA (Wallace et al. 2018; Teasdale et al. 2019).

Several traits contribute to IMG interference with agricultural production. Tall morningglory (*Ipomoea purpurea* (L.) Roth), closely related to IMG, exhibits at least nine traits from Baker's list of ideal weed characteristics (Baker 1974; Chaney and Baucom 2012). Annual morningglories are often difficult to control with herbicides (Van Etten et al. 2016; Asami et al. 2021). Other challenges in the management of IMG stem from its long seed viability and capacity for emergence from depths exceeding 10 cm (Wilson and Cole 1966; Gomes et al. 1978; Whigham 1984; Burnside et al. 1996). Lastly, this vine readily climbs on field crop plants and interferes with harvesting (Wilson and Cole 1966; Price and Wilcut 2007).

IMG is present in New York State, USA (USDA NRCS 2021) but not yet causing the severe yield losses observed in the southeastern USA. It is unclear whether IMG poses a substantial threat to field crop production in New York State under current climatic conditions. It is also unclear how climate change will affect the competitiveness of IMG relative to crops such as corn. For example, climate change is increasing the risk of agricultural droughts (periods of soil moisture deficit) throughout the northeastern USA (Hayhoe et al. 2007; USGCRP 2017). Understanding the effect of drought on competition between IMG and corn will provide insight into the potential impact of IMG on corn in New York State under climate change. More generally, research on interactions between drought and IMG may be relevant to weed risk assessments in arid regions of the world.

The effect of drought on competition between IMG and crops is not well characterized. In a greenhouse study of soybean [*Glycine max* (L.) Merr.], Holloway and Shaw (1996) reported that IMG generally consumed more water (per plant) than soybean when planted in single-species pots. Treating mixed-species pots with selective herbicides increased water availability to soybean by eliminating IMG water use. In a field study, soybean yield losses due to IMG occurred only in a year with intermittent drought stress (Holloway and Shaw 1995). In contrast, Mosier and Oliver (1995) found that irrigation increased soybean yield losses due to entireleaf morningglory (*I. hederacea*), a different form of the same species. In tall morningglory, Mason et al. (2015) reported that drought had a greater effect on reproduction than on vegetative growth. The authors identified high plasticity as an explanation for their findings and a strategy for drought tolerance and competitiveness in the southeastern USA.

The objective of this study was to evaluate competition between IMG and silage corn under no-drought or drought conditions. We hypothesized that increasing IMG densities would cause increasing silage corn yield losses, and that drought would exacerbate the effect of IMG on yield.

Materials and methods

Site and experimental design

The experiment was conducted at the Caldwell Field Research Facility in Ithaca, NY, USA (42°27′N, 76°27′33″W). The soil was predominantly a Williamson very fine sandy loam (USDA NRCS 2018). Silage corn (FS 38R08SS) was planted on 27 May 2016 and 17 May 2017. Planting (four-row John Deere 7000, 71 660 plants ha^{-1}, 76 cm rows) and fertilization (banded at planting, 22.4 kg N ha^{-1}, 44.8 kg P ha^{-1}, 44.8 kg K ha^{-1}) were carried out according to Cornell's guidelines for field crop management (Cornell University Cooperative Extension 2016). Experimental plots were arranged in a randomized complete block design with four blocks (Fig. 1B). Each block (replicate) contained five plots corresponding to IMG planting densities of 0, 1, 2, 4, and 8 plants m^{-2}, for a total of 20 plots. These densities were selected because they represent the range of IMG densities observed in New York State crop fields (A. DiTommaso, personal observation). Blocks (replicates) were separated by 8 corn rows and plots (IMG planting densities) were separated by 3 m. Each plot (6 m by 4 corn rows) was split into drought and no-drought subplots (3 m by 4 corn rows).

Experimental method

IMG seeds were collected from a greenhouse experiment in 2014, which used seeds collected from a corn field in Delaware, USA, in 2013. In the 2016 and 2017 growing seasons, seeds were pre-germinated and grown in a greenhouse (for 7 days in 2016 and 15 days in 2017) until the seedlings were approximately as large as the corn (7–10 cm, 1–2 true leaves). IMG seedlings were transplanted into corn rows on 9–10 June 2016 and 8 June 2017. Transplanting was generally successful; occasional dead seedlings were replaced for up to 7 days after transplanting. Non-IMG weeds were controlled with pre-transplant glyphosate applications (1.12 kg ai ha^{-1}, 8 June 2016 and 5 June 2017), interrow cultivation (June 2016 only), and hand weeding as needed.

Rainout shelters (Figs. 1C and 1D) were installed on 21 July 2016 and 16 July 2017. The shelters were 2.7 m wide by 3 m long by 1.5 m tall and constructed with steel electrical conduit and capped with 6 MIL high-clarity greenhouse film (Sun Master® Pull and Cut, Growers Supply, Dyersville, IA). The shelters were extended to 3 m tall as the corn approached 1 m in height. Runoff was captured by gutters at the base of the greenhouse film. The gutters were attached to 10 cm drainage tile (minimum 3 m long), which diverted the water away from the plots and into adjacent rows or to the edge of the field. A noteworthy lesson from this project was the importance of reinforcing shelter legs and footings to maintain stability during high wind events. Microclimate effects have been minimal in other studies using rainout shelters (Gray et al. 2013; Kant et al. 2017). In a previous study using the same rainout shelters used in this study (greenhouse film was replaced between experiments), the shelters did not affect mid-canopy air temperature and only increased mean pre-dawn corn leaf temperature by 0.9 °C (Hunter et al. 2021). The rainout shelters did reduce irradiance (12%–20% reduction), but the authors concluded that shading probably did not contribute much to the observed reduction in corn growth under the rainout shelters because light availability was still near saturating levels (Hunter et al. 2021).

Due to a regional drought in 2016, no-drought plots were irrigated (2.5 cm on each of 1, 8, and 15 July). The decision to irrigate was based on the historic severity of this drought (Sweet et al. 2017). Fixed-in-place time-domain reflectometer (TDR) probes, buried in the center of 15 plots in 2016 and all 20 plots in 2017, were used to determine volumetric water content of each plot. The probes were custom-built by Robert Schindelbeck (Cornell University) and were 30 cm long and buried at a 30° angle so that the tip of the probe reached a ~15 cm depth. Other studies have determined that rainout shelters also reduce volumetric water content deeper in the soil (Gray et al. 2013; Hunter et al. 2021). Readings were taken weekly using a Tektronix 1502B cable tester (Beaverton, OR). Measurements of volumetric water content are reported as means of block–plot–date combinations from early/mid-July to late August. Corn and IMG stems were counted and harvested in mid-September 2016 and late August 2017 from 2.28 m^2 quadrats in the center of each subplot (1.5 m by two 76 cm corn rows). The fresh weight of corn stems was determined immediately after harvest. Corn was dried for 14 days under hot, dry late-summer conditions in a greenhouse without climate control. IMG was dried in an oven (55 °C, 48 h). After drying, dry biomass was measured.

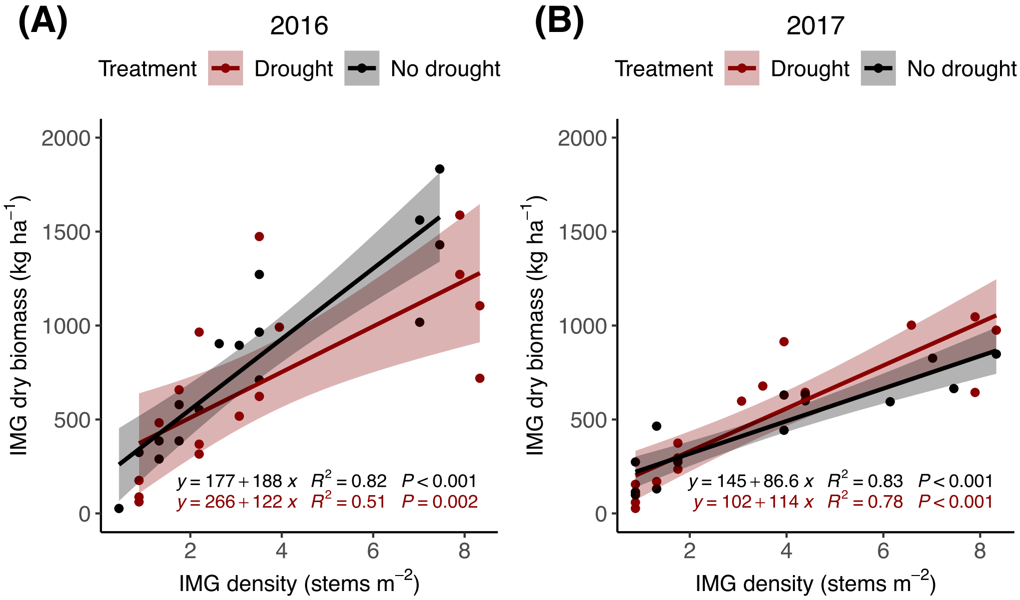
Data analysis

Data analysis was performed in R version 4.0.2 (R Core Team 2021). Unless otherwise noted, measures of error are standard error and $\alpha = 0.05$ for tests of significance. We tested the fixed effects of drought, observed IMG density, year, and all interactions in linear mixed models (packages "lme4" and "lmerTest") of corn yield or IMG biomass. Block and corn stem density in the sampled area were included as random effects. From these full models, we selected reduced models by backward elimination of random-effect terms followed by backward elimination of fixed-effect terms (package "lmerTest", Satterthwaite's method, $\alpha = 0.1$ for random effects and $\alpha = 0.05$ for fixed effects). Both full and reduced model residuals were checked for normality and heteroskedasticity by visual inspection of residual plots and histograms. Quadrats without IMG were excluded from the analysis of IMG biomass. Figures 2 and 3 (created with packages "ggplot2", "ggpubr", and "ggpmisc") include linear regressions with 95% confidence intervals. R^2 and P values in the figures refer to these regressions (run individually for each combination of treatment and year), not to the full or reduced models described in the text.

Results

In 2016, no-drought plots received 29 cm of water (21 cm rainfall plus 8 cm irrigation) and drought plots received 6 cm of rainfall. These totals represented 81% and 18%, respectively, of 36 cm, the 30-year (1981–2010) average for rainfall between the 2016 planting and harvest dates (Northeast Regional Climate Center 2021). In 2017, no-drought plots

Fig. 2. Effects of ivyleaf morningglory (IMG) density and drought treatments on IMG dry biomass in (A) 2016 and (B) 2017 in Ithaca, NY, USA. Fitted lines represent linear regressions with 95% confidence intervals.



received 36 cm of rainfall and drought plots received 15 cm. These totals represented 109% and 44%, respectively, of 33 cm, the 30-year average for the 2017 growing season (Northeast Regional Climate Center 2021). TDR measurements of volumetric water content showed that soil water content in 2016 was 26% lower in drought plots (0.086 ± 0.003 cm^3 water cm^{-3} soil) than in no-drought plots (0.116 ± 0.003 cm^3 water cm^{-3} soil). In 2017, soil water content was 28% lower in drought plots (0.176 ± 0.006 cm^3 water cm^{-3} soil) than in no-drought plots (0.246 ± 0.007 cm^3 water cm^{-3} soil). These data demonstrate that the rainout shelters imposed a drought stress while unsheltered plots remained well watered.

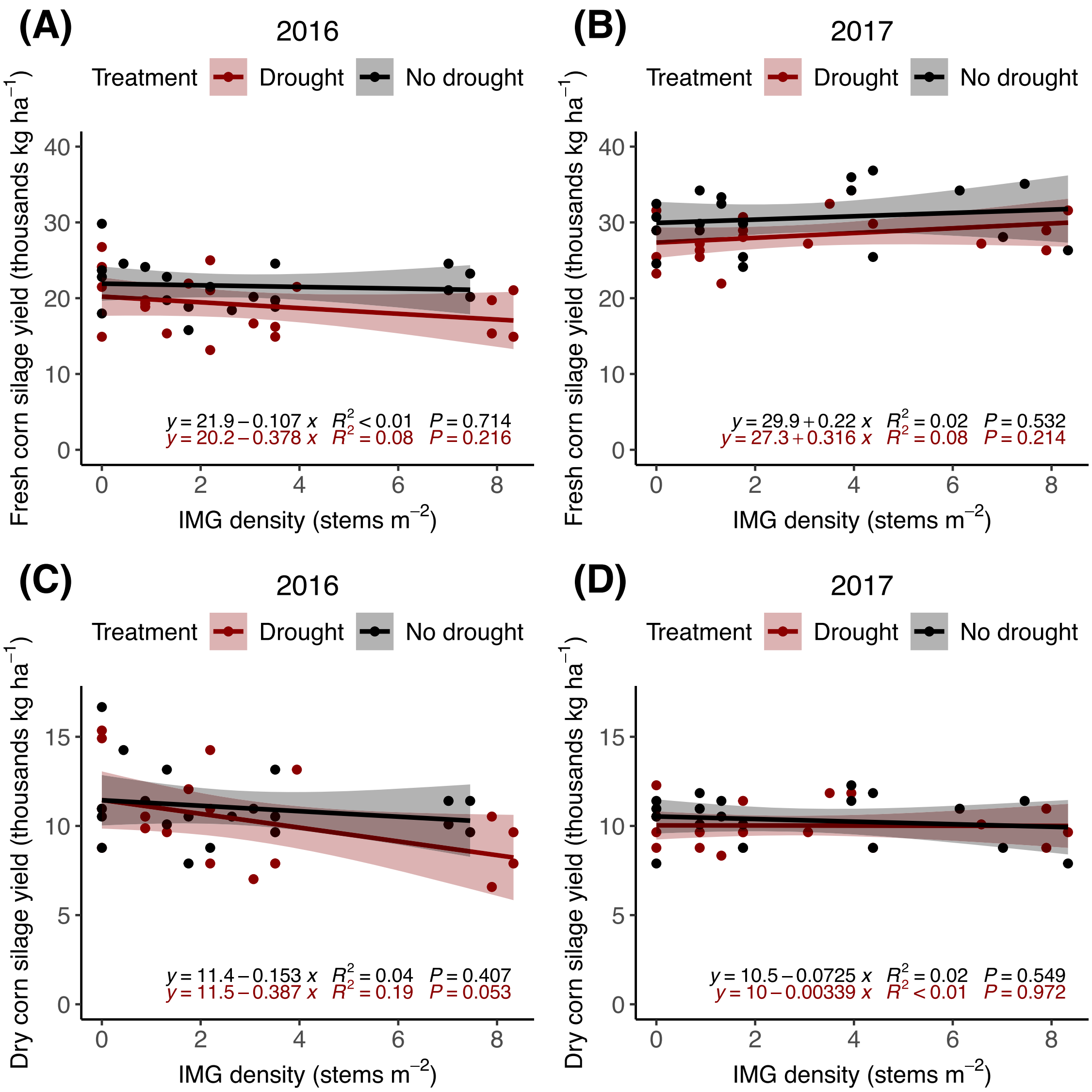
The reduced model of IMG biomass contained the fixed effects of IMG density, year, drought, and all interactions, but no random effects. IMG biomass increased with IMG density ($P < 0.001$) and was higher in 2016 than in 2017 ($P < 0.001$; Fig. 2). IMG biomass increased more slowly with IMG density in 2017 (two-way interaction, $P = 0.03$), especially under no-drought conditions (three-way interaction, $P = 0.04$). Fresh corn silage yield was significantly reduced by the drought treatment (Fig. 3). Drought reduced fresh corn silage yield by 12% in 2016, from $21\,600 \pm 700$ kg ha^{-1} (across IMG densities; mean ± standard error) in the no-drought treatment to $19\,100 \pm 900$ kg ha^{-1} in the drought treatment. In 2017, the no-drought treatment resulted in a fresh silage yield of $30\,500 \pm 900$ kg ha^{-1} and the drought treatment was 8% lower at $28\,200 \pm 700$ kg ha^{-1}. The reduced model of fresh silage yield contained drought ($P = 0.003$) and year ($P < 0.001$) as fixed effects and no random effects. Trends in dry silage yield (treatment-by-year means between 10 000 and 11 100 kg ha^{-1}) were less consistent and the reduced model contained only the random effect of corn stem density.

Discussion

IMG biomass may have been largely unaffected by drought because both treatments provided adequate water in the soil profile for this species. We are unaware of any published work on the typical rooting depth of IMG. IMG has a taproot (Diamond 2021; University of Missouri n.d.), although the degree of branching varies considerably (Colom and Baucom 2020). Scott and Oliver (1976) reported that the roots of tall morningglory extended deeper than soybean roots but did not identify a maximum rooting depth because they only sampled the top meter of soil. Monks et al. (1988) found that tall morningglory roots reached 110 cm by 9 weeks after emergence (soybean roots were longer at 160 cm). Annual morningglories, unlike some deep-rooted perennial Convolvulaceae species, have high root densities in the upper soil layers (Leonie et al. 2014). Maximum rooting depth in corn often reaches 1.5 m or more (Feldman 1994; Ordóñez et al. 2018). Taking all these reports into account, we consider it unlikely—though not impossible—that IMG roots grew deeper than the roots of the (larger) corn plants in our experiment. If water was available deep in the soil profile of the drought treatment (not measured), it seems more probable that corn plants accessed this water.

If IMG plants did not avoid drought by accessing water deep in the soil profile, they might have achieved drought resistance through other mechanisms. In tall morningglory, Mason et al. (2015) described significant plasticity in ecophysiological traits and increased water-use efficiency under recurring water limitation. Tall morningglory tolerates dry soils (Defelice 2001). Annual morningglories can cause significant soybean yield losses under dry conditions (Wilson and Cole 1966), which may be decreased under higher moisture conditions (Howe and Oliver 1987). When rainfall is abundant,

Fig. 3. Effects of ivyleaf morningglory (IMG) density and drought treatments on corn fresh silage yield and dry silage yield in (A, C) 2016 and (B, D) 2017 in Ithaca, NY, USA. Fitted lines represent linear regressions with 95% confidence intervals. Low R^2 values and high *P* values are consistent with the insignificant effect of IMG density on corn yield (see text).



IMG may not be a strong competitor for soil moisture (Cordes and Bauman 1984). Applied to our experiment, these reports are consistent with the explanation that IMG tolerated water limitation better than corn, contrary to the generalization that C_4 plants achieve greater water-use efficiency than C_3 plants (Ehleringer and Monson 1993). IMG or corn may also have been limited by resources other than water. However, strong nutrient limitation was unlikely because fertilizer inputs were typical for corn production and neither species showed visible nutrient deficiency symptoms. IMG may have been shaded by corn after canopy closure.

Contrary to expectations, IMG did not substantially reduce corn yield. Major influences on morningglory competitiveness include density and interference time. The planting densities tested in this experiment, up to 8 plants m^{-2}, would be high enough for annual morningglories to cause yield losses in soybean (Wilson and Cole 1966; Cordes and Bauman 1984). It is possible that corn is vulnerable only to very high IMG densities, although this possibility seems unlikely because morningglories are a serious threat to corn in the southern USA (Webster and Nichols 2012). Morningglory densities of approximately 10 plants m^{-2} are common in some corn fields in southern Georgia, USA; however, more morningglory seedlings often emerge in late summer when light availability at the soil surface increases as corn matures (Eric Prostko, personal communication, University of Georgia, 13 December 2021). Like other annual weeds, annual morningglories are more competitive when established earlier (Buchanan et al. 1980; Keeley et al. 1986). In our experiment, IMG seedlings (7 days after emergence in 2016 and 15 days in 2017) were transplanted into corn 13–22 days after corn planting, which protected young corn seedlings from competition without preventing strong IMG establishment. In addition to competing for resources, early-season weeds alter the red-to-far-red ratio (Page et al. 2010). This change to light quality can trigger a shade-avoidance response that reduces crop yield. This resource-independent interference may contribute to the onset of the critical period for weed control, which often begins a few weeks after corn emergence (Page et al. 2009). In our experiment, earlier transplanting of larger seedlings (or early seeding directly into the corn rows) would probably have increased the negative effect of IMG on corn yield.

Two additional factors could help explain why we did not observe significant yield losses due to IMG interference. First, silage corn is harvested earlier than grain corn. This weed species may be a greater concern in grain corn, particularly if climbing vines interfere with grain harvesting. Second, temperatures may have been too cool for rapid IMG growth, especially early in the season. We used IMG seeds collected from Delaware corn fields, which may not have been adapted to the New York climate. Even if we had been able to acquire seeds from New York populations, we would expect initial IMG growth and development to occur later in the season in New York State relative to warmer areas. Cordes and Bauman (1984) found that soybean yield losses were greatest when warm early-season temperatures facilitated rapid IMG development. A high relative growth rate can help tall morningglory tolerate competition from corn (Chaney and Baucom 2014). The effects of temperature on IMG growth and development could help explain why this weed has caused more damage in the southeastern USA than in the northeastern USA, although its range covers both regions (USDA NRCS 2021). If so, increased temperatures due to climate change might increase the competitiveness of IMG in the northeastern USA and other relatively cold regions of IMG's global distribution.

Our findings demonstrate that drought can reduce fresh corn silage yield. However, they provide little evidence that IMG has a competitive effect on corn or that drought alters the competitive relationship between these two species. These results were observed in both a dry year (2016) and a wetter year (2017), indicating that they may be generalizable. We therefore reject the hypothesis that IMG will pose an increased threat to corn silage yield under drought stress. The data instead support the view that IMG does not compete strongly against corn in New York State under current climatic conditions, regardless of water availability. However, IMG might still cause yield losses through interference with mechanical harvesting. Future research should explore the effects of IMG in grain corn and under warmer conditions. Future research should also evaluate whether early-season interference from IMG (excluded by our study design) could reduce corn yield. Until more information is available, growers should seek to control IMG, particularly in warm areas or years, and prevent seed set. Preventing seed set is a good way to impede the development of herbicide resistance and keep IMG from reaching densities high enough to threaten crop yield.

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Author notes

The authors declare there are no competing interests.

Author contributions

Conceptualization: AD; formal analysis: ASW, KMA; funding acquisition: AD; methodology: AD, KMA, SHM; project administration: AD, KMA; resources: AD, MCH; writing—original draft: ASW, KMA; writing—review and editing: AD, ASW, KMA, MCH, SHM.

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References

Asami, H., Tachibana, M., and Homma, K. 2021. Chemical and cultural control of *Ipomoea hederacea* var. *integriuscula* in narrow-row soybean in southwestern Japan. Weed Biol. Manage. **21**: 135–145. doi:10.1111/wbm.12232.

Baker, H.G. 1974. The evolution of weeds. Annu. Rev. Ecol. Evol. Syst. **5**: 1–24. doi:10.1146/annurev.es.05.110174.000245.

Bright, K.L., and Rausher, M.D. 2008. Natural selection on a leaf-shape polymorphism in the ivyleaf morning glory (*Ipomoea hederacea*). Evolution, **62**: 1978–1990. doi:10.1111/j.1558-5646.2008.00416.x. PMID: 18462212.

Buchanan, G.A., Street, J.E., and Crowley, R.H. 1980. Influence of time of planting and distance from the cotton (*Gossypium hirsutum*) row of pitted morningglory (*Ipomoea lacunosa*), prickly sida (*Sida spinosa*), and redroot pigweed (*Amaranthus retroflexus*) on competitiveness with cotton. Weed Sci. **28**: 568–572. doi:10.1017/S0043174500061245.

Burnside, O.C., Wilson, R.G., Weisberg, S., and Hubbard, K.G. 1996. Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. Weed Sci. **44**: 74–86. doi:10.1017/S0043174500093589.

Chaney, L., and Baucom, R.S. 2012. The evolutionary potential of Baker's weediness traits in the common morning glory, *Ipomoea purpurea* (Convolvulaceae). Am. J. Bot. **99**: 1524–1530. doi:10.3732/ajb.1200096. PMID: 22922396.

Chaney, L., and Baucom, R.S. 2014. The costs and benefits of tolerance to competition in *Ipomoea purpurea*, the common morning glory. Evolution, **68**: 1698–1709. doi:10.1111/evo.12383. PMID: 24611886.

Colom, S.M., and Baucom, R.S. 2020. Belowground competition can influence the evolution of root traits. Am. Nat. **195**: 577–590. doi:10.1086/707597. PMID: 32216668.

Cordes, R.C., and Bauman, T.T. 1984. Field competition between ivyleaf morningglory (*Ipomea hederacea*) and soybeans (*Glycine max*). Weed Sci. **32**: 364–370. doi:10.1017/S0043174500059142.

Cornell University Cooperative Extension. 2016. Cornell guide for integrated field crop management. Cornell University, Ithaca, NY.

Defelice, M.S. 2001. Tall morningglory, *Ipomoea purpurea* (L.) Roth—flower or foe? Weed Technol. **15**: 601–606. doi:10.1614/0890-037X(2001)015[0601:TMIPLR]2.0.CO;2.

Diamond, A.R. 2021. *Ipomoea hederacea*. *In* Alabama plant atlas. University of West Alabama. *Edited by* B.R. Keener, A.R. Diamond, L.J. Davenport, P.G. Davison, S.L. Ginzbarg, C.J. Hansen, C.S. Major, D.D. Spaulding, J.K. Triplett and M. Woods. Livingston, AL. Available from http://www.floraofalabama.org/Plant.aspx?id=1607[accessed 11 January 2021].

Ehleringer, J.R., and Monson, R.K. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annu. Rev. Ecol. Syst. **24**: 411–439. doi:10.1146/annurev.es.24.110193.002211.

Feldman, L. 1994. The Maize Root. *In* The maize handbook. *Edited by* M. Freeling and V. Walbot. Springer, New York, NY. pp. 29–37.

Gomes, L.F., Chandler, J.M., and Vaughan, C.E. 1978. Aspects of germination, emergence, and seed production of three *Ipomoea* taxa. Weed Sci. **26**: 245–248. doi:10.1017/S0043174500049808.

Gray, S.B., Strellner, R.S., Puthuval, K.K., Ng, C., Shulman, R.E. Siebers, M.H., et al. 2013. Minirhizotron imaging reveals that nodulation of field-grown soybean is enhanced by free-air CO_2 enrichment only when combined with drought stress. Funct. Plant Biol. **40**: 137–147. doi:10.1071/FP12044. PMID: 32481094.

Hayhoe, K., Wake, C.P., Huntington, T.G., Luo, L., Schwartz, M.D. Sheffield, J., et al. 2007. Past and future changes in climate and hydrological indicators in the US Northeast. Clim. Dyn. **28**: 381–407. doi:10.1007/s00382-006-0187-8.

Holloway, J.C., Jr., and Shaw, D.R. 1995. Influence of soil-applied herbicides on ivyleaf morningglory (*Ipomoea hederacea*) growth and development in soybean (*Glycine max*). Weed Sci. **43**: 655–659. doi:10.1017/S0043174500081789.

Holloway, J.C., Jr., and Shaw, D.R. 1996. Herbicide effects on ivyleaf morningglory (*Ipomoea hederacea*) and soybean (*Glycine max*) growth and water relations. Weed Sci. **44**: 836–841. doi:10.1017/S0043174500094790.

Howe, O.W., III, and Oliver, L.R. 1987. Influence of soybean (*Glycine max*) row spacing on pitted morningglory (*Ipomoea lacunosa*) interference. Weed Sci. **35**: 185–193. doi:10.1017/S0043174500079030.

Hunter, M.C., Kemanian, A.R., and Mortensen, D.A. 2021. Cover crop effects on maize drought stress and yield. Agric. Ecosyst. Environ. **311**: 107294. doi:10.1016/j.agee.2020.107294.

Kant, S., Thoday-Kennedy, E., Joshi, S., Vakani, J., Hughes, J. Maphosa, L., et al. 2017. Automated rainout shelter's design for well-defined water stress field phenotyping of crop plants. Crop Sci. **57**: 327–331. doi:10.2135/cropsci2016.08.0677.

Keeley, P.E., Thullen, R.J., and Carter, C.H. 1986. Influence of planting date on growth of ivyleaf morningglory (*Ipomoea hederacea*) in cotton (*Gossypium hirsutum*). Weed Sci. **34**: 906–910. doi:10.1017/S0043174500068089.

Leonie, W., Krähmer, H., Santel, H.-J., Claupein, W., and Gerhards, R. 2014. Thiencarbazone-methyl efficacy, absorption, translocation, and metabolism in vining weed species. Weed Sci. **62**: 512–519. doi:10.1614/WS-D-14-00005.1.

Mason, C.M., Christopher, D.A., Rea, A.M., Eserman, L.A., Pilote, A.J., Batora, N.L., and Chang, S.-M. 2015. Low inbreeding depression and high plasticity under abiotic stress in the tall morningglory (*Ipomoea purpurea*). Weed Sci. **63**: 864–876. doi:10.1614/WS-D-15-00005.1.

Monks, D.W., Oliver, L.R., and Bozsa, R.C. 1988. Seedling growth of soybeans (*Glycine max*) and selected weeds. Weed Sci. **36**: 167–171. doi:10.1017/S0043174500075809.

Mosier, D.G., and Oliver, L.R. 1995. Common cocklebur (*Xanthium strumarium*) and entireleaf morningglory (*Ipomoea hederacea* var. *integriuscula*) interference on soybeans (*Glycine max*). Weed Sci. **43**: 239–246. doi:10.1017/S0043174500081133.

Northeast Regional Climate Center. 2021. Climod 2. Available from http://climod2.nrcc.cornell.edu/[accessed 25 January 2021].

Ordóñez, R.A., Castellano, M.J., Hatfield, J.L., Helmers, M.J., Licht, M.A. Liebman, M., et al. 2018. Maize and soybean root front velocity and maximum depth in Iowa, USA. Field Crops Res. **215**: 122–131. doi:10.1016/j.fcr.2017.09.003.

Page, E.R., Tollenaar, M., Lee, E.A., Lukens, L., and Swanton, C.J. 2009. Does the shade avoidance response contribute to the critical period for weed control in maize (*Zea mays*)? Weed Res. **49**: 563–571. doi:10.1111/j.1365-3180.2009.00735.x.

Page, E.R., Tollenaar, M., Lee, E.A., Lukens, L., and Swanton, C.J. 2010. Shade avoidance: an integral component of crop–weed competition. Weed Res. **50**: 281–288. doi:10.1111/j.1365-3180.2010.00781.x.

Price, A.J., and Wilcut, J.W. 2007. Response of ivyleaf morningglory (*Ipomoea hederacea*) to neighboring plants and objects. Weed Technol. **21**: 922–927. doi:10.1614/WT-06-146.1.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Scott, H.D., and Oliver, L.R. 1976. Field competition between tall morningglory and soybean. II. Development and distribution of root systems. Weed Sci. **24**: 454–460. doi:10.1017/S0043174500066443.

Sweet, S.K., Wolfe, D.W., DeGaetano, A., and Benner, R. 2017. Anatomy of the 2016 drought in the Northeastern United States: implications for agriculture and water resources in humid climates. Agric. For. Meteorol. **247**: 571–581. doi:10.1016/j.agrformet.2017.08.024.

Teasdale, J.R., Mirsky, S.B., and Cavigelli, M.A. 2019. Weed species and traits associated with organic grain crop rotations in the mid-Atlantic region. Weed Sci. **67**: 595–604. doi:10.1017/wsc.2019.38.

University of Missouri. n.d. Ivyleaf morningglory. Weed Id Guide. Division of Plant Sciences, Columbia, MO. Available from https://weedid.missouri.edu/weedinfo.cfm?weed_id=138 [accessed 11 January 2021].

USDA NRCS. 2018. Web Soil Survey. USDA Natural Resources Conservation Service, Washington, DC. Available from https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm[accessed 14 May 2018].

USDA NRCS. 2021. PLANTS Database. USDA Natural Resources Conservation Service, Washington, DC. Availabe from https://plants.usda.gov/java [accessed 2 March 2021].

USGCRP. 2017. Climate Science Special Report: Fourth National Climate Assessment. U.S. Global Change Research Program, Washington, DC, USA.

Uva, R.H., Neal, J.C., and DiTomaso, J.M. 1997. Weeds of the Northeast. Cornell University Press, Ithaca, NY.

Van Etten, M.L., Kuester, A., Chang, S.-M., and Baucom, R.S. 2016. Fitness costs of herbicide resistance across natural populations of the common morning glory, *Ipomoea purpurea*. Evolution **70**: 2199–2210. doi:10.1111/evo.13016.

Wallace, J.M., Keene, C.L., Curran, W., Mirsky, S., Ryan, M.R., and VanGessel, M.J. 2018. Integrated weed management strategies in cover crop–based, organic rotational no-till corn and soybean in the mid-Atlantic region. Weed Sci. **66**: 94–108. doi:10.1017/wsc.2017.53.

Webster, T.M., and Coble, H.D. 1997. Changes in the weed species composition of the southern United States: 1974 to 1995. Weed Technol. **11**: 308–317. doi:10.1017/S0890037X00043001.

Webster, T.M., and Nichols, R.L. 2012. Changes in the prevalence of weed species in the major agronomic crops of the southern United States: 1994/1995 to 2008/2009. Weed Sci. **60**: 145–157. doi:10.1614/WS-D-11-00092.1.

Whigham, D.F. 1984. The effect of competition and nutrient availability on the growth and reproduction of *Ipomoea hederacea* in an abandoned old field. J. Ecol. **72**: 721–730. doi:10.2307/2259527.

Wilson, H.P., and Cole, R.H. 1966. Morningglory competition in soybeans. Weeds, **14**: 49–51. doi:10.2307/4041122.