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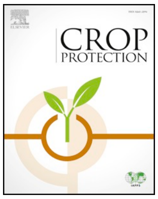

Imidacloprid is compatible with control provided by the predator *Jalysus wickhami* Van Duzee (Hemiptera: Berytidae) in flue-cured tobacco (*Nicotiana tabacum* L.)

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ABSTRACT

Jalysus wickhami Van Duzee is the most abundant predator in North Carolina flue-cured tobacco production but information on the effect of contemporary pest management practices and interactions with other arthropods is lacking. We measured the effect of systemic imidacloprid on *J. wickhami* in field experiments during 2015 and 2016 by surveying its abundance, the abundance of its prey; the pests *Heliothis virescens* (Fabricus), *Manduca sexta* L., and *Manduca quinquemaculata* (Haworth, 1803); and other predatory arthropods in the agro-ecosystem. Systemic imidacloprid applications did not reduce *J. wickhami* abundance nor increase the abundance of *H. virescens*, *M. sexta*, and *M. quinquemaculata*, indicating natural control was not affected. *J. wickhami* abundance was positively correlated with the abundance of prey and predators from another feeding guild, suggesting species interactions have significant implications for the predators.

1. Introduction

Flue-cured tobacco (*Nicotiana tabacum* L.) is the most valuable crop produced in North Carolina (NC), grown on over 67,000 ha with a total value of ca. $647 million USD in 2016 (USDA NASS, 2018). Insecticides represent a significant cost for tobacco growers (Bullen and Fisher, 2018), and are applied to the soil as prophylactic systemic treatments targeting early-season pests and foliar treatments targeting mid and late season pests (Burrack and Toennisson, 2018). Recent research has revealed that unnecessary insecticide applications are often made by tobacco growers when treatment thresholds are not observed, which increases pest management costs and reduces the abundance of natural enemies (Slone and Burrack, 2016). These unnecessary applications may, therefore, potentially increase tobacco pest populations.

Tobacco has a relatively small group of associated herbivores (Burrack and Toennisson, 2018) and natural enemies (Jackson et al., 1989). *Jalysus wickhami* Van Duzee (Hemiptera: Berytidae) is the most abundant predatory arthropod in NC flue-cured tobacco fields and feeds on the pests *Myzus persicae* (Sulzer, 1776) (Hemiptera: Aphididae), *Heliothis virescens* (Fabricius, 1777) (Lepidoptera: Noctuidae), and *Manduca* spp. (Lepidoptera: Sphingidae): *M. sexta* (Linnaeus, 1763) and *M. quinquemaculata* (Haworth, 1803) (Elsey and Stinner, 1971; Lawson, 1959). *J. wickhami* can consume up to 1000 *Manduca* spp. eggs and 2000 *H. virescens* eggs during an 80-day lifetime (Elsey and Stinner, 1971; Jackson and Kester, 1996), potentially providing a massive amount of natural control. The basic biology of *J. wickhami* has been studied (Elsey, 1974a, 1974b; 1973; Elsey and Stinner, 1971), but there is a paucity of information regarding its compatibility with contemporary tobacco pest management practices and interactions with other arthropods.

Conservation biological control, the practice of enhancing reproduction, survival, and efficacy of natural enemies (DeBach, 1964; Ehler, 1998; Jonsson et al., 2008), has the potential to contribute to management of arthropod pests within the framework of integrated pest management programs (Naranjo et al., 2015; Romeis et al., 2018; Stern et al., 1959). Conservation biological control (CBC) can be implemented by modifying pesticide use patterns or manipulating the environment to favor natural enemies (Eilenberg et al., 2001; Gentz et al., 2010; Tscharntke et al., 2016; Varenhorst and O'Neal, 2012; Veres et al., 2013). For CBC to be effective in improving pest management, knowledge of the life-histories of natural enemies of interest is required, including the biology and ecology of the organisms within a select agro-ecosystem (Foti et al., 2017; Letourneau, 1998; Schmitz and Barton, 2014; Sigsgaard et al., 2013). Similarly, information detailing the effects of crop management tactics, including insecticide use, on natural enemies is required for management decisions promoting biological control (Barbosa, 1998; Biondi et al., 2015; Croft, 1990; Jonsson et al., 2008; Tamburini et al., 2016).

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Systemic applications of neonicotinoid insecticides have been widely adopted by flue-cured tobacco growers for early-season pest management over the last 20 years (Toennisson and Burrack, 2017). Applied as a greenhouse tray drench prior to transplant, imidacloprid is frequently used as a prophylactic against *M. persicae* (Merchán and Burrack, 2017*),* *Epitrix hirtipennis* (Melsheimer) (Coleoptera: Chrysomelidae) (Burrack and Toennison, 2018), and *Frankliniella fusca* (Hinds) (Thysanoptera: Thripidae), the primary vector of tomato spotted wilt virus in NC (Groves et al., 2001). The xylem-mobile insecticide is translocated throughout the plant, and target pests are exposed when they consume the treated plant tissue and sap. *J. wickhami* also facultatively feed on tobacco plants in addition to insect prey, taking drinks of sap. *J. wickhami* may be exposed to carbamate (aldicarb, aldoxycarb) and organophosphate (disulfoton, fostheitane) insecticides when applied systemically (Semtner, 1979), but these are no longer used in tobacco production and similar exposure to imidacloprid has not been confirmed.

Understanding the ecology and biology of natural enemies, as well as their interaction and compatibility with pest management tactics, is key when incorporating conservation biological control strategies into integrated pest management programs. We conducted small plot experiments over two years in two locations with the goal of determining whether a common pest management tactic in North Carolina flue-cured tobacco production, systemically applied imidacloprid, was compatible with *J. wickhami*. We measured the abundance of *J. wickhami* and its prey, *H. virescens*, and *Manduca* spp., to assess possible effects of imidacloprid on *J. wickhami* biological control. We also evaluated the potential for other arthropods to explain *J. wickhami* abundance.

2. Methods

2.1. Experimental design

We conducted field experiments in 2015 and 2016 at the North Carolina Department of Agriculture and Consumer Services Lower Coastal Plain Research Station (Lenoir County, North Carolina 35.297404, −77.574259) and Upper Coastal Plain Research Station (Edgecombe County, North Carolina, 35.894264, −77.680346). Organically produced tobacco seedlings (var. NC 196) were used to ensure plant material was free of imidacloprid residues. Plants were left untreated or treated with Admire Pro (42.8% imidacloprid) (Bayer CropScience, Research Triangle Park, North Carolina) at a rate of 17.76 ml/1000 plants using one of two systemic application methods: (1) a greenhouse tray drench less than two days prior to transplant, immediately rinsed into growing media; and (2) a soil water drench applied at transplant. Plots consisted of eight 15.24 m long rows with 25 plants per row, spaced 1.22 m apart, arranged in a randomized complete block design with four replicates per treatment.

We transplanted tobacco seedlings on 4 May 2015 (Lenoir County), 8 May 2015 (Edgecombe County), 25 April 2016 (Lenoir County), and 27 April 2016 (Edgecombe County) and followed standard agronomic practices for flue-cured tobacco production in North Carolina (Brown et al., 2018), with the exception that no insecticides, aside from systemic imidacloprid treatments, were applied.

2.2. Insect assessment

We surveyed plots weekly for focal insects (*J. wickhami* adults and nymphs, *H. virescens* larvae, and *Manduca* spp. larvae), and any other predatory arthropods by inspecting entire tobacco plants. We inspected all plants in rows four and five early in the season (15 May to 27 June 2015, 23 May to 22 June 2016), when plants were small and insect abundance was low. Thereafter, all plants in row five were inspected through the first week of August (1 August 2015, 1 August 2016), at which point North Carolina flue-cured tobacco harvest is underway. We deployed yellow sticky traps in 2015 to monitor *J. wickhami,* but they proved to be ineffective (see Appendix A).

2.3. Statistical analyses

We standardized all insect counts (focal insects and other predatory arthropods) from plant inspections by row to account for the different number of rows inspected earlier (two) and later (one) in the season. Season-long abundance and weekly means were log-transformed (log +1) for analysis, but non-transformed data are presented for clarity. All statistical analyses were performed in SAS v. 9.4 (SAS Institute, Cary NC). Degrees of freedom for all analysis of variance tests were calculated using the procedure described by Kenward and Roger (1997).

The influence of imidacloprid treatments (tray drench, transplant drench, untreated control) on focal insect season-long abundance was analyzed independently using a linear mixed model (PROC MIXED). For each focal species, a full model was developed with the season-long abundance of the insect as the response variable, insecticide treatment as the fixed variable, and with the following random effects: year, location, the interaction of year and location, and block nested within location.

To assess the influence of insecticide treatment on focal insect abundance throughout the growing season, we used a linear mixed model (PROC MIXED) with repeated measures. We fit the following model for each focal species: weekly mean insect abundance as the response variable, insecticide treatment, week after treatment, and their interactions as fixed variables, and the following random variables: year, location, the interaction of year and location, and block nested within location. The repeated statement utilized compound symmetry structure and the subject was the interaction of the plot by location by year.

We performed stepwise regression (PROC GLMSELECT) to determine the influence of other arthropods on *J. wickhami* season long abundance. We included the following predictor variables: “chewing” predators, the sum of Chrysopidae (Neuroptera) and Coccinellidae (Coleoptera); “piercing-sucking” predators, the sum of hemipteran families Anthocoridae, Geocoridae, Nabidae, and Reduviidae; Oxyopidae; *H. virescens*; *Manduca* spp. The variables were assessed with full interactions and *J. wickhami* season long abundance was log-transformed. Stepwise model selection was used, and effect inclusion in the model ended when none of the effects outside of the model had significant *F*-tests (Cohen, 2006). The default select and stop criterion, based on Schwarz Bayesian information criterion, was used for the model, and the model with the lowest Akaike's information criterion values was chosen (SAS Institute, 2012). We quantified the relationship between predictor variables and *J. wickhami* abundance chosen by stepwise regression through linear regression using PROC REG. We calculated variance inflation factor (VIF) scores for each term to ensure our model was not confounded by multicollinearity.

3. Results

During 2015, 2016, we counted a total of 3885 *J. wickhami,* which was 80.4% and 82.8%, respectively, of all predatory arthropods surveyed (Table 1, Fig. 1). Other predatory taxa surveyed included members of the families Chrysopidae (Neuroptera), Coccinellidae (Coleoptera), Anthocoridae (Hemiptera), Geocoridae (Hemiptera), Nabidae (Hemiptera), Reduviidae (Hemiptera) and Oxyopidae (Aranae), (Table 1, Fig. 1). We counted a total of 1599 *H. virescens* and 1469 *Manduca* spp. larvae during 2015 and 2016.

There were no differences between imidacloprid treatments in the season-long abundance of *J. wickhami* ($F = 1.19$; df = 2, 35.8; $P = 0.3156$), *H. virescens* ($F = 0.13$; df = 2, 35.7; $P = 0.8798$), and *Manduca* spp. ($F = 2.03$; df = 2, 36; $P = 0.1464$) (Table 2).

Imidacloprid treatment throughout the season was not significant

Table 1
Summary of North Carolina flue-cured tobacco predatory arthropods from plant inspections in 2015 and 2016.

Predator Taxa	Count (Proportion)	
	2015	2016
Anthocoridae (Hemiptera)	3 (0.0026)	3 (0.00084)
Jalysus wickhami (Berytidae: Hemiptera)	939 (0.80)	2946 (0.83)
Chrsyopidae (Neuroptera)	3 (0.0026)	18 (0.0051)
Coccinellidae (Coleoptera)	20 (0.017)	357 (0.10)
Geocoridae (Hemiptera)	169 (0.14)	171 (0.048)
Nabidae (Hemiptera)	7 (0.0060)	27 (0.0076)
Oxyopidae (Aranae)	9 (0.0077)	25 (0.0070)
Reduviidae (Hemiptera)	15 (0.013)	0 (0)
Sum	1168	3557

Table 2
Combined 2015, 2016 season-long mean (± SEM) focal insect abundance in response to imidacloprid treatments. Means within rows were not significantly different from each other ($P > 0.05$).

Insect	Imidacloprid Treatment		
	Untreated Control	Tray Drench	Transplant Water
Jalysus wickhami	107.8 ± 28.1	61.1 ± 9.1	69.2 ± 10.6
Heliothis virescens	30.3 ± 3.5	30.0 ± 3.1	31.1 ± 4.1
Manduca spp	33.1 ± 9.3	22.4 ± 4.5	34.0 ± 11.3

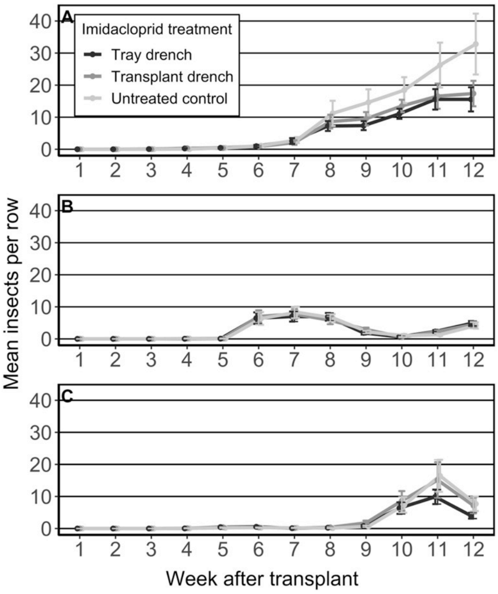

Fig. 1. Combined 2015, 2016 *Jalysus wickhami* (A), *Heliothis virescens* (B), and *Manduca* spp. (C) weekly mean (± SEM) abundance.

for all focal insects (*J. wickhami*: $F = 1.36$; df = 2, 531; $P = 0.2570$), (*H. virescens*: $F = 0.24$; df = 2, 531; $P = 0.7865$), (*Manduca* spp.: $F = 0.461$; df = 2, 531; $P = 0.4601$), and there were no significant treatment by week interactions. Abundance of all focal insects varied significantly over time (*J. wickhami*: $F = 146.96$; df = 11, 531; $P < 0.0001$), (*H. virescens*: $F = 63.07$; df = 11, 531; $P < 0.0001$), (*Manduca* spp.: $F = 99.34$; df = 11, 531; $P < 0.0001$). *J. wickhami* abundance was highest 10 through 12 weeks after treatment (WAT), while *H. virescens* abundance peaked eight WAT and *Manduca* spp. abundance was greatest 11 WAT (Fig. 1).

The model selection process for stepwise regression was stopped at the third step with the final model including *H. virescens, Manduca* spp., and "chewing" predators (AIC = −73.63994). The linear regression model including *H. virescens, Manduca* spp., and "chewing" predators was significant ($F = 14.77$, df = 3,44; $P < 0.0001$), explaining 50.2% of *J. wickhami* season long abundance variance. All predictor variables were positively correlated with *J. wickhami*, with *Manduca* spp. explaining the greatest amount of variability, followed by "chewing" predators and *H. virescens* explaining the least amount (Table 3).

4. Discussion

Modifying insecticide use to conserve natural enemies is one approach to conservation biological control (Biondi et al., 2012; Newsom et al., 1976; Roubos et al., 2014), and thus it is necessary to understand how insecticide use affects natural enemies. Systemic insecticide applications generally reduce the risk of exposure to non-target organisms compared to other application methods, but natural enemies feeding on pollen and nectar may ingest insecticides translocated to those tissues (Barbosa et al., 2017; Cloyd and Bethke, 2011; Smith and Krischik, 1999). *J. wickhami* must consume plant sap for long-term survival (Jackson and Kester, 1996) and therefore may be exposed to xylem-mobile imidacloprid (Jeschke et al., 2011). Laboratory research demonstrates that exposure to tobacco leaves treated systemically with imidacloprid reduces *J. wickhami* survival (Nelson, 2018). This study incorporated the two most commonly used application methods for imidacloprid in tobacco: a greenhouse tray drench prior to transplant (most common) and an in furrow application (less common). Foliar imidacloprid applications in tobacco are extremely rare. *J. wickhami* abundance in either imidacloprid treatment did not differ from untreated controls (Table 2) nor did *H. virescens* and *Manduca* spp. larval abundance, indicating that the method of systemic application does not influence the potential for exposure to those insects. Absolute *J. wickhami* means trended higher in untreated controls but were not significantly different from imidacloprid treatments due to interplot variability.

J. wickhami populations did not increase appreciably until seven weeks after transplant, at which point imidacloprid titers in plants may be reduced to concentrations incapable of producing acute toxicity. Likewise, imidacloprid efficacy against *Myzus persicae* eventually decreases post-transplant (Semtner and Srigiriraju, 2005), as titers of imidacloprid probably decrease throughout the season as observed in

Table 3
Results of linear regression evaluating arthropod influence on *Jalysus wickhami* abundance.

Variable	Partial R^2	Estimate (SE)	*t*	*P*	VIF
Manduca spp. season-long abundance	0.319	0.0051 (0.0012)	4.41	< 0.0001	1.04727
"chewing" predators season-long abundance	0.132	0.0053 (0.0020)	2.62	0.0119	1.14952
H. virescens season-long abundance	0.051	0.062 (0.030)	2.11	0.0403	1.10742

VIF: variance inflation factor.

studies on other crops (Huseth et al., 2014).

Early-season imidacloprid applications are not used to manage lepidopteran tobacco pests due to limited toxicity (Lagadic et al., 1993; Wink and Theile, 2002). Therefore, any differences in *H. virescens* or *Manduca* spp. abundance between treatments is unlikely to be the direct result of systemically-applied imidacloprid. We found the abundance of *H. virescens* and *Manduca* spp. did not differ between insecticide treatments, indicating that other factors regulating pest caterpillar populations were unaffected by imidacloprid. As no other pest management tactics were used in our experiments, it is reasonable to conclude that biological control provided by natural enemies was not affected. Visual inspections of plants in 2015 and 2016 confirmed that *J. wickhami* is the most abundant predator in North Carolina tobacco agro-ecosystems, therefore we infer that the predator's role in regulating *H. virescens* and *Manduca* spp. was not influenced by imidacloprid.

Predator populations may respond to variations in prey abundance, typically exhibiting positive numerical responses through population growth as prey abundance increases (Costa et al., 2017; Midthassel et al., 2014; Solomon, 1949). Season long abundance of *H. virescens* and *Manduca* spp. were two effects retained in a model resulting from stepwise multivariate regression, and our results indicate that *J. wickhami* abundance was positively correlated with the abundance of *H. virescens* and *Manduca* spp. larvae (Table 3). It is important to note that both variables were derived from larval counts, while *J. wickhami* typically consumes eggs (Elsey and Stinner, 1971). However, we can assume that most lepidopteran larva surveyed originated from eggs laid within the same plots, thus increasing caterpillar abundance should correlate with increased *J. wickhami* prey abundance.

Generalist predators are thought to exhibit a weak functional response to target prey densities (Holling, 1966; Luck, 1984; Prasad and Snyder, 2006; Van Maanen et al., 2012), but alternative food resources can help overcome this by causing a positive numerical response and increasing the number of predators consuming prey (Eubanks et al., 2000; Eubanks and Denno, 1999; Leman and Messelink, 2015; Oveja et al., 2016). Numerical responses are driven by predator aggregation (Döbel and Denno, 1994; Mausel et al., 2017) and reproduction (Amiri-Jami and Sadeghi-Namaghi, 2014; Dixon and Guo, 1993). Our results indicate that *J. wickhami* respond positively to the presence of prey and that *Manduca* spp. abundance explained more variance than *H. virescens* abundance (Table 3). This may be due to the fact that peak *J. wickhami* abundance coincided with peak *Manduca* spp. abundance (Fig. 1). Future research should investigate the potential of providing alternative foods earlier in the season to increase *J. wickhami* abundance.

Interactions between predators may be antagonistic, additive, or synergistic, and their outcomes can have significant biological control implications. *J. wickhami* abundance was also positively correlated with “chewing” predators (Table 3). Investigating the interaction between *J. wickami* and “chewing” predators was not one of our explicit research goals and future efforts could clarify this by assessing whether the predators respond to prey abundance in a manner similar to *J. wickhami,* the potential for intra-guild predation (Arim and Marquet, 2004; Gagnon et al., 2011; Polis et al., 1989) or synergistic interactions between the predators (Finke and Snyder, 2010; Losey and Denno, 1998).

Our efforts presented herein were partially focused on determining the effects of early-season systemic imidacloprid applications on *J. wickhami* and predation on *Heliothis virescens* and *Manduca* spp. To accomplish this, systemic imidacloprid treatments were the only pest management tactic employed and thus our results are not representative of North Carolina commercial flue-cured tobacco production. Preventing tobacco caterpillar pests from surpassing economic thresholds typically requires 1–3 foliar insecticide applications per year; these are linked to declines in *J. wickhami* abundance (Slone and Burrack, 2016). Our plots received no foliar insecticide applications and therefore the abundances of caterpillars and *J. wickhami* were higher than those typical in commercial tobacco fields. Future efforts assessing the toxicity of commonly used foliar insecticides to *J. wickhami* could be utilized in developing recommendations for insecticides compatible with the predators.

Plant-feeding can enhance predator arthropod life-history traits or may be required for development and survival, as in the case of *J. wickhami.* Systemically applied insecticides have the potential to cause effects detrimental to the predator, but our results indicate that imidacloprid applications are compatible with *J. wickhami.* As such, this research should function as a starting point for improving conservation biological control with *J. wickhami* in contemporary flue-cured tobacco production, as detailed knowledge of the life systems of natural enemies is required for successful implementation.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cropro.2018.12.002.

Appendix A

During 2015 we deployed Pherocon® Unbaited AM yellow sticky traps (Trece, Inc., Adair, OK, USA) to monitor predatory arthropods including *J. wickhami.* Two traps were placed equidistant from each other between rows four and five of replicate plots and were suspended directly above the canopy of tobacco plants by attaching them to wooden stakes with binder clips, adjusting their height throughout the season. We deployed and changed traps weekly from 15 May to 5 August. Yellow sticky traps captured a total of seven *J. wickhami* during 2015. Other predatory taxa captured included Chrysopidae (4) (Neuroptera), Coccinellidae (66) (Coleoptera), Anthocoridae (4) (Hemiptera), Geocoridae (18) (Hemiptera), Nabidae (5) (Hemiptera), and Oxyopidae (5) (Aranae). While retrieving yellow sticky traps used to monitor arthropods in tobacco fields for another project in 2016, we observed multiple *J. wickhami* walking across the surface of the sticky traps without becoming entrapped (see Supplementary Material: j wickhami sticky trap video). This may help explain the ineffectiveness of yellow sticky traps for monitoring *J. wickhami* in 2015, although similar monitoring methods have been effective in monitoring the predators in tomatoes (Pease and Zalom, 2010).

Reported hosts of *J. wickhami* are predominantly characterized as “glandular-hairy” (Wheeler and Henry, 1981), and their propensity for association with such plants may be partially explained by their anatomy. *Jalysus wickhami* have two morphological features which have been postulated to be involved in their ability to travel across “sticky plant” surfaces without becoming entrapped. In his monograph of Berytidae of the Western hemisphere, Henry (1997) postulated that the dentate claws may allow berytids to “tip-toe” on sticky plant surfaces or grip trichome stems, facilitating their radiation to plants covered in trichomes. Similarly, Southwood (1986) speculated that the elongate legs and swollen femoral tips provide “enlarged tibia-femoral articulation”, causing an “increase in the leverage to swing the apex of the leg.” Given that the surface of a yellow sticky trap is considerably more uniform than the surface of a tobacco leaf or other plant covered and glandular trichomes, we speculate that elongated legs and enlarged tibia-femoral articulation provide *J. wickhami* the ability to maneuver on "sticky plants". Assessing the mechanics of *J. wickhami* locomotion on sticky plant surfaces may help elucidate other potential mechanisms used by insects for movement, like those reported by Voigt et al. (2007) and Voigt and Gorb (2010, 2008).

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