UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ÉVALUATION DE L'EFFICACITÉ DU SYRPHE D'AMÉRIQUE (DIPTERA: SYRPHIDAE) EN SYSTÈME DE PLANTES RÉSERVOIRS POUR LE CONTRÔLE DU PUCERON DU MELON (HEMIPTERA: APHIDIDAE) SUR LE CONCOMBRE DE SERRE.

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

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AVANT-PROPOS

Ce mémoire est le résultat d'un projet de maîtrise réalisé au laboratoire de lutte biologique de l'UQAM, encadré par Éric Lucas (Université du Québec à Montréal) et António Onofre Soares (University of the Azores). Le projet a été financé par le Ministère de l'Agriculture, des Pêcheries et d'Alimentation du Québec (MAPAQ), à travers le programme Prime-Vert 18-009-UQAM.

Les chapitres 2 à 4 de ce mémoire sont sous forme d'article scientifique. Le deuxième chapitre visait à établir un outil simple pour la distinction morphologique des stades larvaires du syrphe d'Amérique qui sont très peu décrits dans la littérature. Il a été publié dans la revue *Phytoprotection* en décembre 2022 sous la forme d'une note scientifique. Une fois cet outil disponible, une collaboration a été établie avec Noémie Gonzalez, doctorante au laboratoire de lutte biologique de l'UQAM, afin d'étudier les préférences de ponte du syrphe d'Amérique. Cela a mené à la rédaction d'un article qui sera soumis à la revue *Insects* en février 2023. Celui-ci se retrouve en ANNEXE A puisque j'ai agi à titre de co-autrice. Le troisième chapitre, traitant du développement et de la voracité du syrphe d'Amérique sera publié sous peu à la revue *Insect Science*. Enfin, le quatrième chapitre, traitant du potentiel de trois espèces végétales en tant que plantes réservoirs, sera soumis sous peu, cette fois à la revue *Biocontrol*.

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m	Mètre
m^2	Mètre carré
cm	Centimètre
mm	Millimètre
g	Gramme
mg	Milligramme
°C	Degré Celsius
%	Pourcentage
®	Marque enregistrée
$CAD	Dollar canadien
n	Nombre de répétitions

RÉSUMÉ

Les infestations par le puceron du melon, *Aphis gossypii* Glover 1877, dans les serres de concombres sont problématiques. Ce ravageur a un taux de croissance très important sur les cucurbitacées, est un vecteur pour de nombreux phytopathogènes et développe rapidement une résistance aux pesticides. Actuellement, la majorité des producteurs en régie biologique utilisent une combinaison de guêpes parasitoïdes *Aphidius colemani* Viereck 1912 ou *Aphidius matricariae* Haliday 1834 et de la cécidomyie prédatrice, *Aphidoletes aphidimyza* Rondani 1847 pour lutter contre le puceron du melon. Cette méthode n'est toutefois pas toujours efficace puisque les guêpes parasitoïdes sont susceptibles d'être hyperparasitées en milieu d'été et que le système n'est pas toujours performant en lâchers inondatifs.

Le syrphe d'Amérique, *Eupeodes americanus* (Wiedemann 1830), diptère Néarctique dont la larve est aphidiphage, présente un bon potentiel en tant qu'agent de lutte pour complémenter les méthodes déjà existantes. Il dispose de caractéristiques favorables telles qu'une voracité élevée, une bonne capacité de vol, une bonne capacité à détecter les colonies de pucerons ainsi qu'une importante fécondité. Son efficacité pour le contrôle du puceron de la digitale, *Aulacorthum solani* Kaltenbach 1843, sur le poivron a d'ailleurs déjà été démontrée par le laboratoire de lutte biologique. De plus, l'utilisation du syrphe d'Amérique en système de plantes réservoirs pourrait être une avenue intéressante, la lutte inondative n'étant pas toujours envisageable à coûts raisonnables et efficace. Ce système permet d'assurer l'action immédiate des agents de lutte dès l'arrivée des ravageurs. Cette méthode est donc particulièrement adaptée pour les pucerons à reproduction rapide comme le puceron du melon.

Le but du projet est d'évaluer le potentiel du syrphe d'Amérique, en système de plantes réservoirs, pour lutter contre le puceron du melon en serres de concombres. Pour atteindre cet objectif, un outil d'identification des stades larvaires du syrphe d'Amérique a d'abord dû être développé puisque ces derniers sont très peu décrits dans la littérature et que la suite du projet dépendait de cette information. Ensuite, afin de vérifier que l'agent de lutte puisse être adéquat dans le système à l'étude, le développement et la voracité du syrphe d'Amérique en fonction d'une alimentation composée de la proie focale ou de la proie réservoir ont été évalués. Finalement, une fois cet aspect validé, trois espèces candidates de plantes réservoirs ont été évaluées afin de déterminer leurs avantages respectifs et ainsi permettre l'optimisation du système à l'étude.

Le présent projet a permis de mettre en lumière une méthode de lutte biologique intégrant un nouvel agent de lutte et ayant un potentiel important pour complémenter les approches déjà existantes pour le contrôle du puceron du melon. Les résultats ont aussi permis d'élargir les connaissances sur un insecte indigène qui fournit un double service écosystémique par le contrôle des ravageurs et la pollinisation. Finalement, le projet a contribué à l'augmentation des connaissances sur les systèmes de plantes réservoirs qui sont encore peu utilisés.

Mots clés : Syrphe d'Amérique, plantes réservoirs, concombre, serres, lutte biologique.

ABSTRACT

Melon aphid, *Aphis gossypii* Glover 1877, infestations in cucumber greenhouses are problematic. This pest has a very high growth rate on cucurbits, is a vector for many phytopathogens and quickly develops resistance to pesticides. Currently, most organic growers use a combination of the parasitoid wasps *Aphidius colemani* Viereck 1912 or *Aphidius matricariae* Haliday 1834 and the predatory midge, *Aphidoletes aphidimyza* Rondani 1847 to control the melon aphid. However, this method is not always effective since the parasitoid wasps are likely to be hyperparasitized in mid-summer and the system is not always efficient under inundative releases.

The American hoverfly, *Eupeodes americanus* (Wiedemann 1830), a Nearctic dipteran whose larvae are aphidiphagous, has good potential as a biocontrol agent to complement the existing methods. It has favorable characteristics such as high voracity, good flight capacity, good ability to detect aphid colonies and high fertility. Its efficient control of the foxglove aphid, *Aulacorthum solani* Kaltenbach 1843, on peppers has already been demonstrated by the biological control laboratory. In addition, the use of the banker plant system for the American hoverfly could be an interesting avenue, as inundative control is not always possible at reasonable and effective cost. This system ensures the immediate action of biocontrol agents as soon as the pests arrive. This method is therefore particularly suitable for rapidly reproducing aphids like the melon aphid.

The goal of the project is to assess the potential of the American hoverfly, in a banker plant system, to control the melon aphid in cucumber greenhouses. To achieve this objective, a tool for identifying the larval stages of the hoverfly had to be developed first since they are scarcely described in the literature and the rest of the project depended on this information. Then, to verify if the biocontrol agent could be adequate in the system studied, the development and voracity of the hoverfly according to a diet composed of either the focal prey or the banker prey were evaluated. Finally, once this aspect was validated, three candidate species of banker plants were compared in order to determine their respective advantages and thus allow the optimization of the system studied.

This project has brought to light a method of biological control integrating a new biocontrol agent, and having a significant potential for complementing existing approaches for the control of the melon aphid. The results also broadened knowledge about a native insect that provides a dual ecosystem service through pest control and pollination. Finally, the project has contributed to increasing knowledge on banker plant systems which are still too little used.

Keywords : American hoverfly, banker plants, cucumber, greenhouse, biological control.

INTRODUCTION

1.1 Problématique

La consommation de légumes de serre est en essor en Amérique du Nord et particulièrement au Canada (MAPAQ, 2018). Le concombre de serre est l'une des trois productions les plus importantes des cultures sous abris au Québec et au Canada (Statistiques Canada, 2022b). Le marché biologique prend également une part de marché de plus en plus grande au Québec, en particulier en culture sous abri. Vingt-trois pourcent de la production en serres était en régie biologique en 2016, en faisant le secteur avec la plus importante proportion de producteurs en régie biologique (Keable, 2018; MAPAQ, 2018). Malgré la barrière physique que procure la serre, permettant généralement de réduire l'utilisation de pesticides, la culture du concombre de serre présente de nombreux défis phytosanitaires (Singh et al., 2017). L'un des principaux ravageurs de ces cultures est le puceron du melon (*Aphis gossypii* Glover 1877). La combinaison d'*Aphidius colemani* Viereck 1912 avec *A. aphidimyza* est considérée parmi les plus efficaces pour lutter contre le puceron du melon (Messelink et al., 2020). Cette approche ne convient toutefois pas toujours entre autres parce que les parasitoïdes peuvent être sujets à l'hyperparasitisme en milieu d'été et que *A. aphidimyza* est peu efficace à basse température (moins de 20°) (Alotaibi, 2008; Bonsignore et Vacante, 2018).

Le Syrphe d'Amérique (*Eupeodes americanus* (Wiedemann 1830)), première espèce de syrphe commercialisée au Canada, présente également un bon potentiel pour la lutte contre les pucerons. Les espèces aphidiphages de cette famille présentent effectivement plusieurs caractéristiques qui les prédisposent à être de bons agents de lutte telles qu'une importante voracité, une bonne capacité de vol et de localisation des colonies de pucerons ainsi qu'une fécondité élevée (Putra et Yasuda, 2006; Almohamad et al., 2009; Dunn et al., 2020). Le laboratoire de lutte biologique de l'UQAM a d'ailleurs récemment démontré l'efficacité du syrphe d'Amérique pour le contrôle du puceron de la digitale (*Aulacorthum solani* Kaltenbach 1843) sur le poivron en système de plantes réservoirs (Bellefeuille et al., 2021). En Europe, trois espèces de syrphe, *Episyrphus balteatus* De Geer, 1776, *Sphaerophoria rueppellii* Wiedemann, 1830 et *Eupeodes corollae* Fabricius, 1794, sont déjà couramment utilisées pour la lutte contre les pucerons.

Le puceron du melon, en particulier, nécessite une gestion alternative à la lutte chimique qui soit aussi rapide que cette dernière puisque ce ravageur développe facilement une résistance aux pesticides et prolifère rapidement sur le concombre. Les plantes réservoirs, qui assurent la présence des agents de lutte avant les infestations, peuvent donc être intéressantes pour lutter contre ce puceron (Ebert et Cartwright, 1997; Fischer et Leger, 1997; Kianpour et al., 2010; AAC, 2020; Messelink et al., 2020).

Dans cette optique, le syrphe d'Amérique a été étudié comme agent de lutte en système de plantes réservoirs contre le puceron du melon en contexte de serres de concombres. Ce projet a donc pour but non seulement d'évaluer l'efficacité de cet insecte à contrôler le puceron du melon, mais aussi d'élargir les connaissances sur la biologie de cette espèce indigène et sur les systèmes de plantes réservoirs.

1.2 Lutte biologique

1.2.1 Définition et historique

Plus d'une trentaine de définitions existent pour la « lutte biologique » (Suty, 2010; IOBC, 2012; Heimpel et Mills, 2017). Certains points de divergences dans les définitions sont l'intégration dans la lutte biologique des produits dérivés d'organismes vivants, des processus naturels de contrôle ainsi que des processus d'élimination ou de contrôle de populations qui ne sont pas nuisibles aux humains (Suty, 2010; Heimpel et Mills, 2017). L'une des définitions communes est la suivante : « l'utilisation d'organismes vivants pour diminuer la densité d'une population ou l'impact d'un organisme nuisible spécifique, le rendant moins abondant et moins dommageable qu'il ne le serait autrement » (traduit de Eilenberg et al., 2001). La définition proposée par Hoy (2008) dans *Encyclopedia of Entomology* est légèrement différente, incluant l'action des ennemis naturels et ne visant pas nécessairement les organismes nuisibles à l'humain : « action de parasites, prédateurs ou pathogènes dans le maintien des densités de population d'un autre organisme à un niveau globalement plus bas qu'il n'arriverait s'ils n'étaient pas présents. La lutte biologique peut se produire naturellement (on parle alors de lutte naturelle) ou provenir de manipulations ou de l'introduction d'agents de lutte biologique » (adapté de Hoy, 2008). La lutte biologique peut être utilisée contre différentes cibles telles que les ravageurs invertébrés, les mauvaises herbes et les phytopathogènes (Eilenberg et al., 2001). Le présent projet sera axé particulièrement sur la lutte aux ravageurs invertébrés et acceptera la définition de la lutte biologique proposée par l'organisation internationale de la lutte biologique : « l'utilisation d'un organisme pour réduire la population d'un autre organisme » (IOBC, 2012).

Il existe trois grandes branches de lutte biologique, soit la lutte classique, augmentative et conservative. La lutte classique est définie comme l'introduction d'un nouvel agent de lutte, souvent exotique, dans un environnement dans le but qu'il s'y implante de façon permanente et qu'il effectue un contrôle à long terme des ravageurs. La lutte augmentative est décrite par l'introduction de petites ou grandes quantités d'agents de lutte pour contrôler des populations de ravageurs sur le court à moyen terme. Finalement la lutte conservative est caractérisée par la modification de l'environnement ou des pratiques culturales pour favoriser la présence et l'action des ennemis naturels d'un milieu (Eilenberg et al., 2001; Vincent et al., 2007; Driesche et Bellows, 2012; IOBC, 2012).

La première réussite documentée de lutte biologique en serre date de 1927 contre l'aleurode des serres, *Trialeurodes vaporariorum* Westwood 1856 (Hemiptera: Aleyrodidae), en lutte augmentative avec la guêpe parasitoïde *Encarsia formosa* (Hymenoptera: Aphelinidae) (Speyer, 1927; Payton Miller et Rebek, 2018). Le développement de nouveaux pesticides de synthèse tels que le dichlorodiphényltrichloroéthane (DDT) dans les années 1940 a momentanément diminué l'intérêt pour la lutte biologique, mais l'apparition de résistances quelques années plus tard a provoqué un retour vers cette approche (Payton Miller et Rebek, 2018). L'inquiétude grandissante des gouvernements face aux effets des pesticides sur l'environnement et la santé humaine ainsi que la parution en 1962 de l'ouvrage Silent Spring de Rachel Carson, dévoilant au grand public les impacts de ces produits, ont également stimulé le développement de la lutte biologique (Andow et al., 1997; Gay, 2012; Riudavets et al., 2020). Au Québec en particulier, c'est dans les années 1985 que la lutte biologique a débuté, et dans les années 90 qu'elle a réellement pris son envol (Lambert, 2000).

1.2.2 Sytème de plantes réservoirs

Dans les régions tempérées la lutte biologique contre les pucerons en serre est majoritairement effectuée par des lâchers inondatifs réguliers d'agents de lutte et ne suffit pas à contrôler les dommages entraînés par les pucerons (Rabasse et van Steenis, 1999; Knapp et al., 2020). Il est donc impératif d'explorer des méthodes alternatives, telles que le système de plantes réservoirs qui intègre des aspects de lutte augmentative et conservative, pour améliorer l'efficacité des agents de lutte (Payton Miller et Rebek, 2018). Cette méthode, relativement récente (datant de la fin des années 70) (Huang et al., 2011; Payton Miller et Rebek, 2018), est encore peu utilisée en Amérique du Nord, particulièrement aux États-Unis (1 à 5% des producteurs utilisaient ce système en 2008), mais aussi au Canada (10 à 25% des producteurs y avaient recours en 2008) (Huang et al., 2011).

1.2.2.1 Définition

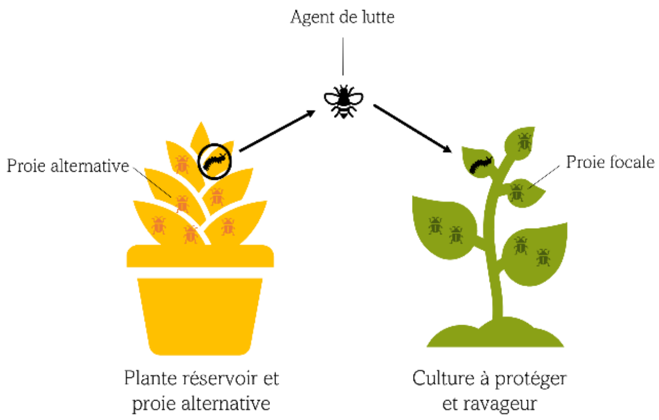

Figure 1.1 Système de plantes réservoirs.

Le système repose sur l'introduction d'une plante dans la culture à protéger, prodiguant une source d'alimentation et un milieu de reproduction pour les ennemis naturels d'un ravageur ciblé (figure 1). La forme d'alimentation que procure la plante réservoir peut être directement un élément de cette dernière, tel que le pollen, ou encore une proie ou un hôte alternatif qu'elle héberge pour l'ennemi naturel (Yano, 2006; Frank, 2010; Huang et al., 2011; Payton Miller et Rebek, 2018; Yano, 2019). Par exemple, un plant de céréale tel que l'orge pourrait héberger un puceron inoffensif (proie alternative) pour la culture d'intérêt, tel que le puceron bicolore des céréales (*Rhopalosiphum padi* L. 1758), et cet ensemble servirait de milieux d'alimentation et de reproduction pour une cécidomyie prédatrice, agent de lutte contre les pucerons. La plante et la proie ou l'hôte alternatif sont généralement différents de la culture d'intérêt et du ravageur ciblé, mais il arrive qu'ils soient identiques. L'introduction préventive d'un ravageur comme proie alternative est appelée « l'approche du premier arrivé » (Huang et al., 2011; Payton Miller et Rebek, 2018). Cette approche peut simplifier les manipulations liées au système, mais implique d'importants risques d'infestation qui peuvent être évités en sélectionnant une proie alternative qui n'est pas dommageable pour la culture d'intérêt. Le système de plantes réservoirs présente de nombreux avantages, tant au niveau de l'efficacité que des coûts par rapport aux lâchers réguliers d'agents de lutte (Boll et al., 2001; Suty, 2010; Huang et al., 2011).

1.2.2.2 Avantages et inconvénients par rapport à la lutte augmentative

L'utilisation de plantes réservoirs offre de nombreux avantages par rapport à la lutte augmentative tels que l'action rapide des agents de lutte grâce à leur présence dans la culture avant les infestations, la réduction des coûts associés à de multiples lâchers grâce à l'établissement des agents de lutte, l'attraction d'autres ennemis naturels, l'augmentation de la qualité des agents de lutte par la diminution du transport et des manipulations liées à la commercialisation, l'atténuation de la dépendance de la croissance démographique des agents de lutte à celle de la population de ravageurs grâce à la proie alternative, ainsi que la possibilité d'agencement de cette méthode aux traitements chimiques en lutte intégrée grâce à l'aspect mobile des plants (Fischer et Leger, 1997; Boll et al., 2001; Yano, 2006; Suty, 2010; Huang et al., 2011; Payton Miller et Rebek, 2018). Parmi ces caractéristiques, la présence précoce des agents de lutte lors d'infestations joue un rôle majeur dans l'efficacité du système. Le délai d'arrivée des agents de lutte est effectivement l'un des principaux enjeux de la lutte augmentative, laissant le temps aux populations de ravageurs non seulement d'effectuer des dommages dans les cultures, mais aussi d'atteindre un seuil de densité de population plus difficile à contrôler (Tenhumberg, 1995b; Fischer et Leger, 1997; Frank, 2010; Payton Miller et Rebek, 2018). Le recours aux lâchers préventifs pour faire face à ce problème n'est pas toujours envisageable, surtout pour les agents de lutte ayant des périodes de reproduction très courtes et nécessitant donc des lâchers trop fréquents (Fischer et Leger, 1997). Les plantes réservoirs pallient facilement ce problème en assurant la présence constante des agents de lutte, et ce, à moindres coûts et en grand nombre (Boll et al., 2001; Huang et al., 2011; Payton Miller et Rebek, 2018). Il existe toutefois quelques désavantages. Les agents de lutte peuvent être sujets à l'hyperparasitisme et ne pas réussir à s'établir. De plus, si la préférence de l'agent de lutte pour le ravageur n'est pas nette, la présence de la proie alternative peut diluer son effet de prédation. Les plantes réservoirs peuvent aussi agir comme puit en attirant fortement d'autres ennemis naturels, réduisant donc l'efficacité de contrôle du ravageur (Huang et al., 2011). De plus, le système, même s'il occupe un espace restreint, prend quand même une place disponible pour la culture et peut donc occasionner une diminution du rendement. Pour ces raisons, il doit être adapté aux différentes cultures à protéger afin d'optimiser son efficacité.

1.2.2.3 Choix de la plante hôte et de la proie alternative

La relation entre la plante hôte, la proie alternative et l'ennemi naturel joue un rôle important dans le contrôle en système de plantes réservoirs. Un équilibre doit être maintenu entre la disponibilité de la proie alternative, la durée de vie des plantes réservoirs et la dispersion des ennemis naturels (qui peut être réduite si la proie alternative est en trop grand nombre ou préférée par l'agent de lutte par rapport au ravageur cible dans la culture protégée) (Frank, 2010; Huang et al., 2011; Yano, 2019).

Pour le choix de la plante hôte, une attention particulière doit donc être portée à sa capacité à soutenir un élevage de proies alternatives de bonne qualité, sa résistance aux dommages engendrés par ceux-ci, sa facilité d'entretien, sa rapidité de croissance, sa susceptibilité aux maladies ainsi qu'à sa compatibilité avec les paramètres de croissance du milieu visé (Frank, 2010; Huang et al., 2011; Jandricic et al., 2014). La quantité de plantes réservoirs est également importante pour le bon fonctionnement du contrôle biologique (Boll et al., 2001). Les études et les entreprises offrant ces produits suggèrent généralement trois à cinq plants par hectare et un peu plus si la serre est petite pour annuler l'effet de bordure (Fischer et Leger, 1997; Koppert biological systems, s.d.; Skinner et al., 2011).

Pour ce qui est de la proie alternative, il est évident que l'innocuité de celle-ci pour la culture d'intérêt doit être vérifiée, mais il est tout aussi important de considérer sa valeur nutritive pour l'ennemi naturel, ainsi que le fait qu'elle ne soit pas choisie préférentiellement par rapport au ravageur ciblé (Boll et al., 2001; Frank, 2010; Huang et al., 2011; Yano, 2019).

1.2.2.4 Systèmes commercialisés et communs

Parmi les systèmes de plantes réservoirs commercialement disponibles au Canada et communément utilisés contre les pucerons, l'un des plus communs est le blé ou l'orge comme support pour le puceron bicolore des céréales en tant que proie alternative pour le parasitoïde *A. colemani* (Suty, 2010; Payton Miller et al., 2017; Payton Miller et Rebek, 2018). Les monocotylédones sont régulièrement utilisées comme plantes réservoirs puisqu'elles représentent des hôtes intéressants pour les proies alternatives des parasitoïdes (Huang et al., 2011). Notamment, le contrôle des pucerons à l'aide des trois espèces de plantes réservoirs étudiées dans le présent projet, soit l'éleusine (*Eleusine coracana* L.) (Poaceae), le maïs (*Zea mays* L.) (Poaceae) et l'orge (*Hordeum vulgare* L.) (Poaceae) avec *R. padi* et des guêpes parasitoïdes principalement, mais aussi des prédateurs comme les syrphes et les cécidomies prédatrices, s'est avéré efficace à plusieurs reprises (Fischer et Leger, 1997; Jacobson et Croft, 1998; Goh et al., 2001; Bellefeuille et al., 2021). L'orge en particulier s'est montrée efficace dans une étude de Bellefeuille et al. (2021) en tant que plante réservoir avec *R. padi* pour le contrôle du puceron de la digitale par *E. americanus*.

1.2.3 Caractéristiques d'un bon agent de lutte en système de plantes réservoirs

Les ennemis naturels les plus couramment utilisés en systèmes de plantes réservoirs sont les prédateurs et les parasitoïdes, les organismes entomopathogènes étant plus rarement employés (Huang et al., 2011). Ultimement l'efficacité d'un agent de lutte contre un ravageur s'évalue empiriquement, mais plusieurs aspects écologiques concernant les deux organismes doivent être vérifiés au préalable (Coppel et Mertins, 1977).

1.2.3.1 Voracité

L'efficacité des agents de lutte prédateurs pour le contrôle d'un ravageur donné est grandement déterminée par la relation entre leur voracité et la croissance de la population de ravageurs (Tenhumberg, 1995b). Pour qu'ils soient efficaces, il faut que le taux des prédation de la population d'agents de lutte, joint à l'effet de l'ensemble des ennemis naturels présents, surpasse le taux de croissance des ravageurs (Coppel et Mertins, 1977). Dans le cas particulier des pucerons, dont la croissance démographique peut être très rapide, il est primordial que les agents de lutte aient une voracité importante (Tenhumberg, 1995b; Lambert, 2010).

1.2.3.2 Spécificité et effets négatifs sur les ennemis naturels

L'importance de la spécificité des agents de lutte est débattue. Certaines études suggèrent que les agents généralistes sont plus efficaces ou que la spécificité des agents de lutte est importante seulement en lutte classique (Stiling et Cornelissen, 2005; Mason et al., 2008). Toutefois, d'autres ouvrages avancent que les agents de lutte monophages ou légèrement oligophages seraient plus efficaces, car ils seraient mieux adaptés à leurs proies ou à leur hôte et seraient alors plus en mesure de répondre aux changements de densités de population de leur proie ou leur hôte (Huffaker et al., 1971; Coppel et Mertins, 1977). Cela favoriserait aussi la concentration de leurs efforts de prédation ou de parasitisme sur la population de ravageurs et éviterait la prédation intraguilde (van Lenteren et Manzaroli, 1999; Lambert, 2010; White, 2019). Dans le cas particulier des pucerons, qui ont une croissance très rapide, le contrôle par des généralistes peut être plus difficile comme ceux-ci sont souvent moins bien adaptés à localiser rapidement les populations que les spécialistes (Dunn et al., 2020). Dans tous les cas, il est nécessaire que l'agent de lutte puisse se développer et se reproduire au moins sur deux espèces de pucerons : la proie réservoir et le ravageur (Frank, 2010).

1.2.3.3 Réponse densité-dépendante : numérique et fonctionnelle

Pour qu'un agent de lutte contrôle efficacement un ravageur, celui-ci doit s'adapter aux populations de ce ravageur en modifiant non seulement sa réponse fonctionnelle, comme son taux de prédation, mais aussi sa réponse numérique, c'est-à-dire sa croissance démographique qui, en serre, repose principalement sur la reproduction (le recrutement étant plus difficile). Ainsi, l'augmentation rapide des infestations de ravageurs devrait entraîner une augmentation rapide des populations d'ennemis naturels et de la pression de prédation ou du parasitisme individuels de ceux-ci (Coppel et Mertins, 1977; van Lenteren et Manzaroli, 1999). La capacité de reproduction de l'ennemi naturel doit être élevée pour qu'une telle relation soit possible (Coppel et Mertins, 1977; White, 2019).

1.2.3.4 Capacité de développement sur le ravageur

Afin de permettre une introduction des prédateurs ou parasites sur une période prolongée, comme c'est le cas en lutte inoculative et en système de plantes réservoirs, il est nécessaire que ceux-ci puissent effectuer l'ensemble de leur développement dans le système culture-ravageur. Un ennemi naturel ne pouvant se développer entièrement en s'alimentant ou en parasitant le ravageur dans la culture d'intérêt ne pourrait pas s'établir convenablement dans celle-ci et de nombreuses réintroductions seraient nécessaires, comme c'est le cas en lutte augmentative (Coppel et Mertins, 1977; van Lenteren et Manzaroli, 1999). Certains éléments peuvent toutefois être ajoutés tels que du pollen ou du nectar pour permettre la survie de phases particulières du développement de l'ennemi naturel (Coppel et Mertins, 1977).

1.2.3.5 Dispersion et capacité de recherche

La dispersion des ennemis naturels est particulièrement importante en système de plantes réservoirs puisque celles-ci sont peu nombreuses par supeficie et que les ennemis naturels sont donc rarement proches des infestations contrairement au cas des lâchers inondatifs où les producteurs peuvent les placer manuellement (Frank, 2010). Il est possible d'atténuer cette contrainte en déplaçant les plantes réservoirs en fonction des foyers d'infestations (Payton Miller et Rebek, 2018). Dans tous les cas, un agent idéal ne devrait être introduit que quelques fois à travers la serre et devrait se disperser assez bien pour effectuer un contrôle dans l'ensemble de la culture (van Lenteren et Manzaroli, 1999). Pour éviter de nombreuses réintroductions, il est important que, malgré sa forte capacité de dispersion, l'agent soit enclin à s'établir et demeurer dans la culture (Crowder et al., 2007). Il est aussi préférable qu'il ait une action à large spectre, en réduisant tous les foyers d'infestation en dessous du seuil économique de dommage, plutôt qu'en décimant complètement seulement quelques foyers d'infestations (van Lenteren et Manzaroli, 1999). Cette caractéristique est également liée à la capacité de recherche, qui doit être excellente pour que les agents de lutte soient en mesure de trouver les populations lorsqu'elles sont encore peu développées et les maintenir à faible densité (van Lenteren et Manzaroli, 1999; White, 2019).

1.2.3.6 Préférence de ponte

Pour que le contrôle des ravageurs fonctionne efficacement, il est primordial que le degré de préférence de ponte de l'agent de lutte soit plus élevé pour le système du ravageur sur la culture principale que pour celui de la proie alternative sur la plante réservoir, et ce, même à faible densité de ravageurs. Autrement, l'effet de prédation par l'agent de lutte serait nettement altéré par une trop faible densité de population dans la culture à protéger (Boll et al., 2001; Yano, 2019).

1.2.3.7 Adaptabilité au climat de la serre

La capacité de l'agent de lutte à se développer efficacement dans les conditions des cultures où le ravageur est présent est primordiale. Un décalage à ce niveau peut faire échouer la tentative de lutte (Coppel et Mertins, 1977; van Lenteren et Manzaroli, 1999; Mason et al., 2008; Lambert, 2010). Les conditions de température et d'humidité dans les serres qui peuvent être particulièrement extrêmes rendent cet aspect encore plus important.

1.2.3.8 Synchronisation saisonnière

La synchronisation saisonnière est particulièrement importante en lutte inoculative où un agent de lutte est introduit dans un écosystème afin qu'il exécute un contrôle à long terme (van Lenteren et Manzaroli, 1999). Il est primordial que l'agent de lutte soit synchronisé au niveau de son cycle de vie avec le ravageur pour qu'il puisse être introduit et actif avant et pendant toute la période d'activité du ravageur (Huffaker et al., 1971). Même si les agents de lutte peuvent être introduits au moment opportun en système de plantes réservoirs, il est essentiel que ces derniers ne perdent pas d'efficacité et n'entrent pas en diapause avant le ravageur (Huffaker et al., 1971).

1.2.3.9 Production de masse

Comme la plupart des agents ne peuvent pas être trouvés en assez grand nombre dans les milieux naturels, il est souvent nécessaire d'en faire des élevages de masse. La simplicité de production est cruciale pour que la commercialisation de l'agent soit réalisable à des coûts raisonnables (Coppel et Mertins, 1977; van Lenteren et Manzaroli, 1999; Mason et al., 2008). Contrairement à la lutte inoculative où l'agent de lutte ne doit être pas être introduit à chaque saison (van Lenteren et Manzaroli, 1999), la production de masse est nécessaire dans un système de plantes réservoirs puisque l'agent doit être introduit en quantité importante à chaque début de saison.

1.3 Système biologique

1.3.1 Culture du concombre de serre

1.3.1.1 Situation au Québec et au Canada

La culture de légumes de serre est un marché important et en constante expansion au Québec et au Canada. En 2021, la recette monétaire de la culture sous abris (toutes catégories confondues) au Canada s'élevait à 3,8 milliards de dollars avec 2993 hectares en production sous abris, dont 23% était de la tomate,16% du concombre et 22% du poivron (Statistique Canada, 2022b; Statistique Canada, 2023a). Le Canada est le deuxième plus important producteur de culture sous abris en Amérique du Nord et le Québec est au troisième rang parmi les provinces productrices avec 13% des ventes en 2021 derrière l'Ontario (55%) et la Colombie britannique (21%) (MAPAQ, 2018; Statistique Canada, 2022a). En 2021, le Québec comptait 167 hectares de production sous abris de fruits et légumes de serre dont les principales cultures étaient la tomate (48%), le concombre (25%) et le poivron (6%) (Statistiques Canada, 2022b)

Le marché biologique est aussi en grande expansion au Canada et au Québec et se concrétise entre autres par la mise en œuvre de certifications biologiques (AAC, 2020; MAPAQ, 2018). Au Canada, en 2022, le marché biologique de fruits et légumes comptais 14 000 hectares en production pour une recette monétaire de 199 millions de dollars (Statistique Canada, 2023b). Le Québec est un acteur important sur la scène canadienne, représentant près de 30% des producteurs biologiques au pays. En 2016, la province se classait effectivement au premier rang au Canada en ce qui concerne le nombre (1 049) et la proportion (3,6%) de producteurs en régie biologique (Keable, 2018). Le secteur de culture de légumes de serres en particulier montre une forte propension à la culture biologique détenant la plus grande proportion de productions biologiques par secteur, soit 23% (Keable, 2018).

1.3.1.2 Paramètres de croissance

La serriculture, même si elle engendre d'importants coûts énergétiques et un investissement en temps et en main-d'œuvre, peut être avantageuse pour les producteurs. Elle permet de contrôler les paramètres environnementaux pour fournir un milieu plus favorable pour les fruits et légumes et d'ainsi augmenter nettement leur qualité et la productivité (Singh et al., 2017). Par le fait que le milieu est relativement fermé, la lutte contre les ravageurs est aussi généralement simplifiée (Singh et al., 2017; Keable, 2018; MAPAQ, 2018). Grâce à ces caractéristiques, le rendement de concombre peut être augmenté jusqu'à 4 fois en serriculture en comparaison avec la culture en champs (Spehia, 2015).

Les paramètres ayant une influence importante sur la culture des concombres en serre sont l'humidité relative, la température, la radiation et la teneur en CO_2 (Singh et al., 2017; AAC, 2020). Les concombres sont particulièrement sensibles à la dessiccation, 85% de leur réseau racinaire étant concentré dans les 30 premiers centimètres de terre. Un suivi de l'hydratation des plants est donc primordial, ceux-ci étant susceptibles tant au manque qu'au surplus d'eau (Singh et al., 2017). La température optimale pour la germination des graines se situe entre 26 et 28 °C, tandis que la température optimale de croissance est de 21 °C pour équilibrer la croissance feuille/fruit (AAC, 2020). Les plants sont parthénocarpiques (ils développent des fruits sans fertilisation) et ne nécessitent donc pas de pollinisation (AAC, 2020). En général, au Canada, comme dans les autres pays en zone tempérée, trois cycles de culture sont effectués en serre pour le concombre, mais certains producteurs peuvent en faire jusqu'à quatre (AAC, 2020; Messelink et al., 2020).

1.3.1.3 Principaux enjeux phytosanitaires

L'un des plus grands défis de la serriculture est le standard de qualité élevé des productions. Dans ce milieu, la lutte aux ravageurs ne doit donc pas servir uniquement à assurer la survie des plants pour garantir une production, mais doit également permettre une qualité élevée des produits (Gullino et al., 2020). Le concombre de serre est sujet à de nombreuses infections, telles que des bactérioses, des mycoses, des viroses, dont les principales sont : la fonte des semis, la pourriture des racines, le flétrissement bactérien, le chancre gommeux, le mildiou, le blanc du concombre (oïdium), la pourriture noire des racines, le virus de la mosaïque jaune de la courgette et le virus de la mosaïque du concombre (Richard et Boivin, 1994, Messelink et al. 2020). Il est également sujet à des infestations par des nématodes, insectes ou acariens (Richard et Boivin, 1994; Messelink et al. 2020).

Les principaux insectes ravageurs des cultures de concombre de serre au Canada sont l'aleurode des serres, le puceron du melon, les mouches des terreaux (Diptera : Sciaridae, principalement des genres *Bradysia* et

Corynoptera), les mouches des rivages (Ephydridae : Diptères, du genre *Scatella*), le thrips des petits fruits (*Frankliniella occidentalis* Pergande 1895), le thrips de l'oignon (*Thrips tabaci* Lindeman 1889), diverses chenilles (Lepidoptera), la chrysomèle maculée du concombre (*Diabrotica undecimpunctata* Mannerheim 1843), la chrysomèle rayée du concombre (*Acalymma vittatum* F. 1775), la mineuse du chrysanthème (*Liriomyza trifolii* Burgess 1880), la mineuse maraîchère (*Liriomyza sativae* Blanchard 1938), les punaises des plantes (Hemiptera : Miridae, majoritairement du genre *Lygus*) et le tétranyque à deux points (*Tetranychus urticae* Koch, 1836) (Richard et Boivin, 1994; AAC, 2020).

1.3.2 Puceron du melon

1.3.2.1 Répartition et plantes hôtes

Le puceron du melon est à ce jour l’un des pucerons ayant la répartition géographique la plus globale et des plantes hôtes et cycles de vie des plus diversifiés (Blackman et Eastop, 2017). Il est présent partout au Canada (Richard et Boivin, 1994) et dans le monde (Kocourek et al., 1994; Blackman et Eastop, 2017; Bonsignore et Vacante, 2018). Il est un important ravageur des cultures maraichères et ornementales surtout dans les régions tempérées (Satar et al., 2005). S’attaquant à plus de 700 espèces de plantes mondialement, il est l’un des ravageurs les plus importants en serriculture (Richard et Boivin, 1994; Hosseinzadeh et al., 2017; Bonsignore et Vacante, 2018; Rodríguez-Gasol et al., 2020) et représente la principale espèce de puceron trouvée sur le concombre, se reproduisant très rapidement sur les cucurbitacées (Messelink et al., 2020) et causant d’importants dommages une fois présent (Capinera, 2004). Parmi les cucurbitacées, il est problématique surtout pour les cultures de concombres, de melons d’eau et de cantaloups et parfois de citrouilles et de courges. Il peut aussi faire des dommages sur les poivrons, les aubergines, les asperges, les citrons, le coton, l’hibiscus, le gombo et plusieurs autres cultures (Capinera, 2004; Bonsignore et Vacante, 2018).

1.3.2.2 Cycle de vie

Le puceron du melon a un cycle de vie variant en fonction du climat. Dans les milieux plus chauds, il ne se reproduit habituellement que par parthénogenèse, tandis que dans les climats plus frais, il a un cycle holocyclique et passe donc par une phase sexuée. Il peut être monœcique (cycle de vie effectué sur une seule plante hôte) ou diœcique (cycle de vie effectué sur deux plantes hôtes différentes) (Van Steenis, 1992; Capinera, 2004; Bonsignore et Vacante, 2018). Au Canada, il passe l’hiver sur son hôte primaire sous forme d’œuf (Blackman et Eastop, 2017; Bonsignore et Vacante, 2018). Au printemps, les œufs éclosent et donnent lieu à des femelles qui peuvent alors se nourrir, se développer et se reproduire par parthénogenèse sur ce même hôte ou sur un hôte secondaire suite à la production d’individus ailés (Capinera, 2004;

Bonsignore et Vacante, 2018). Lorsque la qualité des plants diminue, que les colonies sont trop denses ou que l'automne approche, des individus ailés sont produits pour migrer vers de nouveaux plants intacts ou vers les hôtes primaires (Richard et Boivin, 1994; Capinera, 2004; Bonsignore et Vacante, 2018). À l'automne, des mâles et des femelles ovipares aptères sont générés pour se reproduire de façon sexuée et produire des œufs qui passeront l'hiver (Capinera, 2004). Dans des conditions chaudes (environ 28 °C), le puceron du melon peut compléter son cycle en 7 jours et sa population peut passer de 10 à 12 fois sa taille chaque semaine, chaque adulte produisant 4 larves par jour (Richard et Boivin, 1994; Capinera, 2004).

1.3.2.3 Dommages

Les pucerons du melon envahissent généralement les feuilles du bas en premier et se propagent ensuite dans l'ensemble de la plante (Richard et Boivin, 1994; Bonsignore et Vacante, 2018). Jusqu'à 2000 individus peuvent se retrouver sur une seule feuille (Richard et Boivin, 1994). Ils causent des dommages de manière directe en soutirant les nutriments des plantes par leur sève, mais aussi en étant vecteurs de problématiques secondaires par la production de miellat et la transmission de virus (Ebert et Cartwright, 1997; Capinera, 2004; Bonsignore et Vacante, 2018; Knapp et al., 2020). Le premier symptôme associé à l'arrivée des pucerons du melon est généralement le jaunissement des feuilles (Bonsignore et Vacante, 2018). Avec l'augmentation des populations, les feuilles peuvent être percées, courbées, flétries et affaissées ce qui diminue leur capacité photosynthétique (Capinera, 2004; Bonsignore et Vacante, 2018; AAC, 2020; Muhammad et Sarfraz, 2020). Le miellat que les pucerons produisent en grande quantité peut également favoriser la croissance de fumagine, qui peut nettement diminuer la qualité des fruits, et la capacité photosynthétique de la plante (Capinera, 2004; Bonsignore et Vacante, 2018; AAC, 2020; Muhammad et Sarfraz, 2020). Le miellat peut aussi attirer d'autres ravageurs ou insectes comme les fourmis, qui peuvent protéger les pucerons de leurs ennemis naturels (Bonsignore et Vacante, 2018). Finalement, étant un vecteur de plus de 50 virus mondialement, dont le virus de la mosaïque du concombre et le virus de la mosaïque de la pastèque de type 2, le puceron du melon peut être extrêmement nuisible pour les cultures (Kocourek et al., 1994; Blackman et Eastop, 2017; AAC, 2020; Knapp et al., 2020).

1.3.2.4 Lutte chimique et biologique contre le puceron du melon

Au Canada, en serre de concombre, mis à part l'utilisation de pesticides classiques, diverses approches sont utilisées pour combattre les pucerons, telles que l'utilisation de biopesticides, d'arthropodes comme agents de lutte, de plantes réservoir, de piégeage, de pratiques d'hygiène, de grillage sur les évents ainsi que d'huile de dormance. La diversification des pesticides pour éviter l'acquisition de résistance est également favorisée (AAC, 2020). Les principaux ennemis naturels du puceron du melon incluent les coccinelles (Coleoptera: Coccinellidae), les chrysopes (Neuroptera: Chrysopidae), les cécidomyies (Diptère: Cecidomyiidae), les guêpes parasitoïdes (Hymenoptera), les hémérobes (Neuroptera: Hemerobiidae) et les syrphes (Diptera: Syrpidae) (van Steenis, 1992; Capinera, 2004; Hosseinzadeh et al., 2017; Bonsignore et Vacante, 2018; Muhammad et Sarfraz, 2020). Les chrysopes peuvent être efficaces pour contrôler le puceron du melon (Bonsignore et Vacante, 2018), mais sont difficiles à introduire, puisque seules les plus vieilles larves s'établissent efficacement. Les coûts associés à leur utilisation sont donc plutôt importants (Rabasse et van Steenis, 1999). Les coccinelles ont été beaucoup étudiées pour le contrôle des pucerons, mais le problème réside encore une fois dans l'établissement des individus dans les serres (Rabasse et van Steenis, 1999). Les cécidomyies peuvent aussi être efficaces, mais leur voracité est faible par rapport aux autres prédateurs (Rabasse et van Steenis, 1999). De nombreux producteurs utilisent une combinaison des guêpes parasitoïdes *A. colemani* ou *Aphidius matricariae* Haliday 1834 avec la cécidomyie *A. aphidimyza* pour le contrôle du puceron du melon, mais le système n'est pas toujours assez efficace car les parasitoïdes sont souvent sujets à l'hyperparasitisme en milieu d'été et la cécidomyie n'est pas efficace à basse température (Capinera, 2004; Lambert, 2005; Alotaibi, 2008; Bonsignore et Vacante, 2018; Knapp et al., 2020). Le présent projet se penchera sur le potentiel du syrphe d'Amérique pour complémenter les agents existant pour le contrôle de cet important ravageur.

1.3.3 Syrphe d'Amérique

La famille des Syrphidae est l'une des plus vastes des diptères, détenant plus de 6000 espèces réparties à travers le monde à l'exception de l'Antarctique et de quelques îles océaniques (Pu et al., 2019; Dunn et al., 2020; Rodríguez-Gasol et al., 2020). Elle est divisée en 4 sous-familles : Syrphinae, Pipizinae, Eristalinae et Microdontinae qui regroupent des espèces dont les régimes alimentaires sont très diversifiés, incluant la consommation d'arthropodes, de plantes, de champignons et de matière en décomposition (Skevington et al., 2019; Rodríguez-Gasol et al., 2020). Le syrphe d'Amérique fait partie de la sous-famille Syrphinae et appartient au genre *Eupeodes*. Cette sous-famille ainsi que les Pipizinae et une petite partie des Eristalinae regroupent la majorité des espèces s'alimentant d'arthropodes à corps mou tels que les pucerons (Hemiptera: Aphididae), les thrips (Thysanoptera) et les chenilles (Lepidoptera), qui comptent pour environ 1/3 de toutes les espèces de Syrphidae (Skevington et al., 2019; Dunn et al., 2020).

1.3.3.1 Morphologie et discrimination des stades larvaires

Les syrphes adultes du genre *Eupeodes* sont caractérisés par un métasternum poilu, un abdomen avec marge et la présence de taches ou de bandes jaunes sur le troisième et le quatrième tergite (Gonçalves Miranda et al., 2013; Skevington et al., 2019). Chez *E. americanus*, les tergites trois et quatre sont caractérisés par une bande jaune qui n'atteint pas l'abdomen et qui n'est généralement pas écrasée au centre (Skevington et al., 2019). L'alua dans l'aile n'a pas de poils. Ces traits permettent de distinguer *E. americanus* des autres syrphes du genre *Eupeodes*, à l'exception de l'espèce *Eupeodes pomus* Curran 1921 dont seule la partie génitale du mâle est différente (Skevington et al., 2019). En Amérique du Nord en particulier, les adultes sont beaucoup mieux décrits que les larves et la plupart du temps, les stades larvaires ne sont pas différenciés. Notamment, un guide pour l'identification des espèces américaines détaillé a été publié par Skevington et al. (2019), mais les larves n'y sont pas décrites. En Europe, une clé pour l'identification des larves de troisième stade de la plupart des genres existe toutefois, mais sans différentiation des autres stades larvaires (Láska et al. 2013). Malgré tout, Hartley (1961) ainsi que Rotheray & Gilbert (2011) avancent que la fusion des tubes respiratoires postérieurs est généralement un critère distinctif du troisième stade larvaire chez les Syrphidae, mais cela n'a pas été confirmé pour *E americanus*.

1.3.3.2 Cycle de vie

Les syrphes passent par trois stades larvaires suivis d'une pupaison et de l'émergence d'un adulte qui pond des œufs (Skevington et al., 2019). Les stades larvaires durent de deux à trois semaines (Ree et Knutson, 1997). Chez *E. americanus*, ceux-ci ont une durée totale moyenne de 6,9 jours et la pupaison dure en moyenne 7,14 jours avant l'émergence de l'adulte qui a une longévité moyenne de 18,68 jours (Ouattara et al., 2022). Les syrphes peuvent migrer ou hiberner sous la forme de pupe ou d'adulte dépendant des espèces et des phénotypes (Rodríguez-Gasol et al., 2020). Le comportement d'hivernation du syrphe d'Amérique est méconnu.

1.3.3.3 Principales proies

La larve du syrphe d'Amérique est aphidiphage généraliste (Rojo et al., 2003) tandis que l'adulte s'alimente de pollen et de nectar (Skevington et al., 2019). Plus d'une trentaine d'espèces de pucerons réparties dans plus de 25 genres ont été répertoriées comme des proies du syrphe d'Amérique (Ree et Knutson, 1997; Rojo et al., 2003; Bellefeuille et al., 2017). Une grande partie des Syrphinae s'alimente aussi de proies périphériques, mais ces modes d'alimentation ont généralement un effet négatif sur leur « fitness » (Rodríguez-Gasol et al., 2020). Il est possible que le syrphe d'Amérique ne s'alimente pas uniquement de pucerons, mais aucune information n'est disponible à ce sujet.

1.3.3.4 Principales caractéristiques d'agent de lutte biologique chez le syrphe d'Amérique

Plusieurs traits confèrent un bon potentiel d'agent de lutte aux syrphes. D'abord, leur grande voracité combinée à leur haute fécondité, permettent une forte pression de prédation (Chambers, 1986; Rodríguez-Gasol et al., 2020). De plus, leur tendance à surconsommer les pucerons lorsqu'ils sont abondants ou à éviter de se déplacer vers un autre plant tant qu'il reste des proies fait d'eux de bons candidats en tant qu'agent de lutte (Ambrosino, 2006; Rodríguez-Gasol et al., 2020). Ils sont aussi très habiles pour voler et ont une bonne capacité à localiser les pucerons (Horn, 1981; Tenhumberg, 1995b; Francis et al., 2005; Skevington et al., 2019), qui leur permet de contrôler les populations de ravageurs rapidement, avant que les dommages ne soient trop importants. De nombreuses études ont d'ailleurs démontré le potentiel d'agent de lutte de plusieurs espèces européennes telles que *E. corollae* pour le contrôle de *A. gossypii* (Chambers,1986) et de *Myzus persicae* Sulzer 1776 (Pekas et al., 2020), *E. balteatus* pour le contrôle de *A. solani* (Tenhumberg, 1995a) ou encore *S. rueppellii* pour le contrôle de *M. persicae* (Pekas et al., 2020). Peu d'informations sont toutefois disponibles sur *E. americanus*. Son excellent potentiel pour le contrôle du puceron de la digitale à basse température a toutefois déjà été démontré par Ymilie Bellefeuille du laboratoire de lutte biologique de l'UQAM (Bellefeuille et al., 2017; Bellefeuille et al., 2019; Bellefeuille et al., 2021). *Eupeodes americanus* pourrait donc avoir une synchronisation saisonnière surpassant la plupart des autres agents de lutte par le fait qu'il est actif à basse température et que sa période active de vol se situe entre avril et novembre en Amérique du Nord (Skevington et al., 2019; Bellefeuille et al., 2019; 2021).

1.4 Objectifs et hypothèses

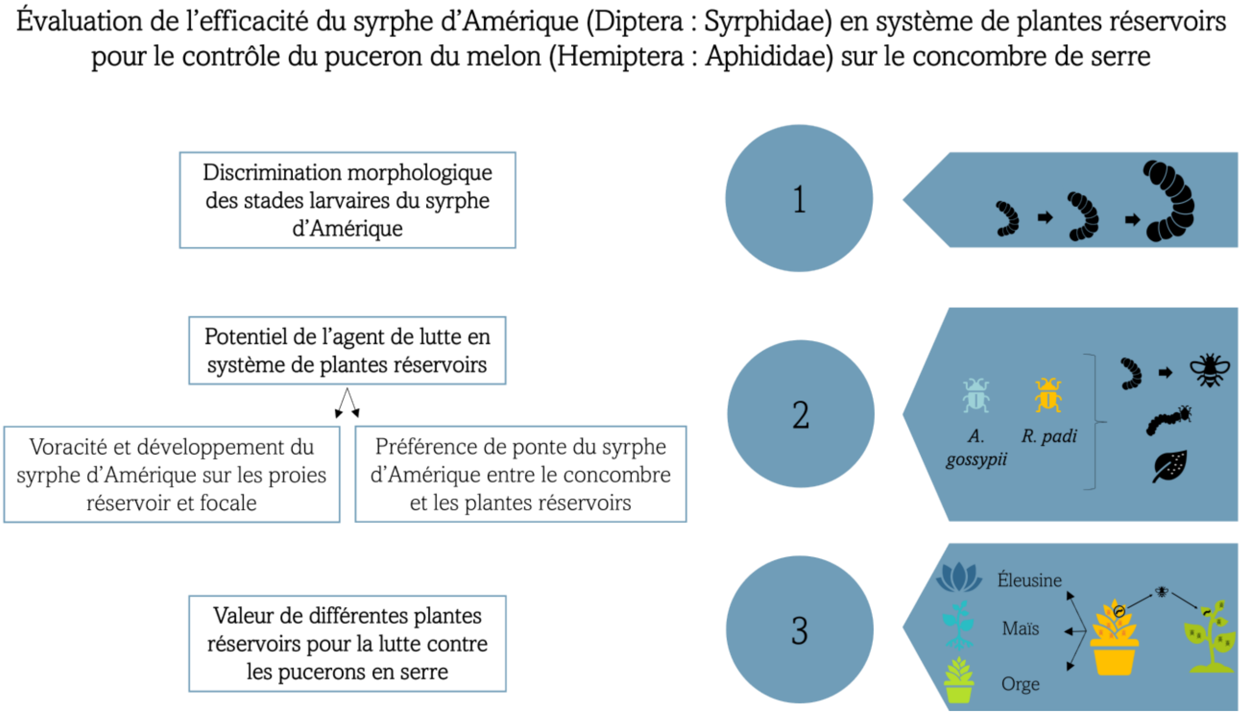

Figure 1.2 Schéma des objectifs du projet

1.4.1 Objectif général

Évaluer l'efficacité du syrphe d'Amérique, *Eupeodes americanus* (Diptera: Syrphidae), en système de plantes réservoirs pour le contrôle du puceron du melon, *Aphis gossypii* (Hemiptera: Aphididae), en concombre de serre.

Afin de répondre à cet objectif général, plusieurs objectifs spécifiques ont été fixés.

1.4.1.1 Discrimination morphologique des stades larvaires d'*Eupeodes americanus* (Wiedemann 1830)

En premier lieu, un outil de travail permettant la discrimination des trois stades larvaires du syrphe d'Amérique a été. développé. Le manque d'information à ce sujet dans la littérature empêchait les étapes futures de l'évaluation de cette espèce en tant qu'agent de lutte. Le premier objectif du projet a donc consisté à décrire morphologiquement les trois stades larvaires et à déterminer des critères permettant de les distinguer.

1.4.1.2 Potentiel de l'agent de lutte en système de plantes réservoirs : voracité et développement du syrphe d'Amérique sur la proie réservoir (dans la plante réservoir, *R. padi*) et la proie focale (ravageur, *A. gossypii*)

En second lieu, la capacité de l'agent de lutte à se développer sur les proies réservoirs (puceron bicolore des céréales, *R. padi*) et focales (puceron du melon, *A. gossypii*) et à effectuer un contrôle de la proie focale est essentielle pour l'efficacité du système. La voracité est un bon indicateur du contrôle par les prédateurs puisqu'elle est directement reliée à la prédation. Dans le cadre de cette expérience, la proie réservoir a été considérée comme un témoin entraînant un bon développement et une importante voracité. Elle est la proie d'élevage du syrphe d'Amérique au laboratoire de lutte biologique de l'UQAM depuis 2014 et elle occasionne de très bons résultats. Le syrphe d'Amérique a également été en mesure de contrôler des colonies de pucerons bicolores des céréales dans des plantes réservoirs sur le terrain en deux à trois semaines à une densité de dix larves/plante réservoir (Fournier M, obs. personnelle). Sa voracité sur ce puceron est donc importante.

Prédictions spécifiques :

1. Les deux pucerons permettront au syrphe d'Amérique de compléter son développement
2. L'agent de lutte aura un meilleur développement en s'alimentant de la proie réservoir, c'est-à-dire qu'il se développera plus rapidement, aura un taux de mortalité et de déformation moindre et générera des adultes de poids supérieur.
3. L'agent de lutte aura une voracité plus importante (totale, quotidienne et en termes de biomasse) lorsqu'il s'alimentera de la proie réservoir.

Justification : Comparativement à la proie réservoir, la proie focale, soit le puceron du melon, devrait occasionner un moins bon développement et une voracité moindre puisque qu'elle se retrouve sur le concombre qui a des trichomes qui peuvent nuire au déplacement des larves (Verheggen et al., 2009; Vosteen et al., 2018). De plus, ce puceron est nettement plus petit que le puceron bicolore des céréales et peut donc engendrer des coûts de capture plus importants (Sadeghi and Gilbert, 2000).

Par ailleurs, il est fondamental que l'agent de lutte préfère aller pondre sur la culture d'intérêt où se retrouve le ravageur cible, même lorsqu'il fait face à un choix entre un système de plante réservoir et cette dernière. Cet aspect a été étudié dans le cadre d'une expérience sur les préférences de ponte du syrphe d'Amérique, dont les résultats sont présentés en annexe A puisque j'y ai participé à titre de co-auteur.

1.4.1.3 Comparison de trois plantes réservoirs pour le contrôle des pucerons: l'orge (*Hordeum vulgare* L.), le maïs (*Zea mays* L.) et l'éleusine (*Eleusine coracana* (L.) Gaertn)

En troisième lieu, une fois l'efficacité de l'agent de lutte dans le contexte à l'étude vérifiée, le système a pu être peaufiné. L'espèce végétale de plante réservoir joue un rôle majeur dans l'efficacité d'un système de lutte. Les trois plantes étudiées dans le cadre de l'expérience sur la préférence de ponte du syrphe d'Amérique ont donc été évaluées en tant que candidates pour la lutte contre les pucerons. Ces trois plantes ont été sélectionnées puisqu'elles présentent chacune des caractéristiques différentes au niveau de leur productibilité et leur résistance aux pucerons et aux conditions de serres.

<u>Prédictions spécifiques</u> :

1. La plante réservoir d'orge sera rapide et peu couteuse à produire, mais ne fournira pas la plus importante quantité de pucerons, car elle aura une mauvaise résistance à la pression d'herbivorie par rapport à l'éleusine et au maïs.
2. La plante réservoir de maïs sera plus longue à produire que l'orge, mais résistera mieux aux dommages causés par les pucerons. Elle fournira tout de même une quantité de pucerons moins importante que l'éleusine à cause de sa structure moins dense.
3. La plante réservoir d'éleusine sera longue et couteuse à produire, mais produira une quantité plus importante de pucerons que les deux autres espèces et résistera mieux à la pression d'herbivorie effectuée par ces derniers.

<u>Justification</u> : Les trois plantes ont été étudiées plusieurs fois en tant que plantes réservoirs pour la lutte contre les pucerons, mais n'ont jamais été comparées dans une même étude (Huang et al., 2011). Elles ont déjà démontré leur potentiel au moins une fois en tant que plante réservoir pour *A. colemani* en association avec *R. padi* pour le contrôle de *A. gossypii* sur le concombre (Fisher et léger, 1997; Jacobson et Croft, 1998; Boll et al., 2001; Goh et al., 2001). Selon ces études, le maïs et l'éleusine ont l'avantage de résister aux dommages causés par les pucerons et n'ont généralement pas ou peu besoin d'être remplacés en une saison de croissance, tandis que l'orge doit être remplacée plus souvent, mais est plus rapide à produire (Fisher et Léger, 1997; Jacobson et Croft, 1998). La structure des plants d'éleusine et d'orge suggère qu'elles puissent supporter une plus grande charge de pucerons, le volume de matière végétale par unité de surface pouvant être très important comparativement au maïs. Toutefois, la plus grande résistance aux pucerons de l'éleusine suggère qu'elle puisse atteindre une plus grande charge maximale que les deux autres plants. Finalement, l'éleusine étant la seule des trois plantes qui n'est pas produite localement, il est fort probable qu'elle coûte plus cher à produire que les deux autres.

CHAPITRE 2

MORPHOLOGICAL DISCRIMINATION OF THE LARVAL INSTARS OF *EUPEODES AMERICANUS* (DIPTERA: SYRPHIDAE)

Arlette Fauteux, Noémie Gonzalez, António O. Soares & Éric Lucas

2.1 Résumé/Abstract

En Amérique du Nord, le potentiel du syrphe d'Amérique, *Eupeodes americanus* (Wiedemann, 1830) (Diptera: Syrphidae), comme agent de lutte biologique a été démontré, notamment contre le puceron de la digitale, *Aulacorthum solani* Kaltenbach, 1843 (Hemiptera: Aphididae). Aucune information n'étant disponible pour distinguer macroscopiquement les stades larvaires de cette espèce, la présente étude a utilisé l'observation semi-continue (photographie image par image et observation à la loupe binoculaire) des trois stades larvaires pour construire un tableau de traits morphologiques et une clé dichotomique pour discriminer les stades larvaires par observation à la loupe binoculaire. Les traits discriminants sont la présence de poils noirs au premier stade et la fusion des tubes respiratoires postérieurs au troisième stade.

Mots clés: Poils noirs, mue, tubes respiratoires postérieurs, photographie image par image, lutte biologique

In North America, the potential of the American hoverfly, *Eupeodes americanus* (Wiedemann, 1830) (Diptera: Syrphidae), as a biocontrol agent has been demonstrated, particularly against the foxglove aphid *Aulacorthum solani* Kaltenbach, 1843 (Hemiptera: Aphididae). Since no information is available to distinguish the larval instars of this species, the present study used semi-continuous observation (time-lapse photography and stereo microscope) of the three larval stages to build a table of morphological traits and a dichotomic key for discriminating the larval instars by observation under stereo microscope. Discriminating traits are black hairs at first instar and fused posterior breathing tubes at third instar.

Key words: Black hairs, molt, posterior breathing tubes, time-lapse photography, biocontrol.

2.2 Introduction

Hoverflies (Diptera: Syrphidae) have proven to play an important role in the ecosystem due to their dual services as pollinators (adult) and biological control agents (larvae) (Dunn et al. 2020). Since 2014, works from the Biocontrol laboratory of University of Quebec in Montreal (UQAM) on the American hoverfly, *Eupeodes americanus* (Wiedemann, 1830) (Diptera: Syrphidae), have shown that this species is able to be active at low temperatures (12-14-18°C), e.g., for: (i) flight, (ii) oviposition, and (iii) feeding activities (Bellefeuille et al. 2017; 2019). Due to those characteristics, this species shows great potential as a biological agent, even under low temperatures. *Eupeodes americanus* can feed on more than 25 aphid species (Rojo et al. 2003; Vockeroth 1992) including several major pests in Quebec greenhouses such as the green peach aphid *Myzus persicae* Sulzer, 1776 (Hemiptera: Aphididae), the foxglove aphid, *Aulacorthum solani* Kaltenbach, 1843 (Hemiptera: Aphididae), the pea aphid *Acyrthosiphon pisum* Harris, 1776 (Hemiptera: Aphididae) and the melon aphid *Aphis gossypii* Glover, 1877 (Hemiptera: Aphididae).

While *E. americanus* appears to be a promising biological control agent, many biological traits remain to be explored such as its voracity, development, and hibernation habits. Regarding their morphological traits, only adults are well described, notably with identification keys (Vockeroth 1992; Skevington et al. 2009). However, for most hoverfly species, larval instars have not been differentiated in most of the earlier works. According to Joshi and Ballal (2013) and Rotheray and Gilbert (2011), this is probably due to the fact that exuviae are not easily visible by being very thin, transparent, and often crumpled and damaged. In Europe, the morphological description of syrphid larvae is more advanced with notably a key for third instar larvae and a color guide of most European genera (Rotheray 1993; Láska et al. 2013). Some studies tend to describe all three larval instars, but they often only provide information on variable traits such as color and body length (Davidson 1919; Bergh & Short 2008). The full development of the posterior breathing tubes is usually a fundamental criterion to identify the third instar larvae of Syrphidae (Hartley 1961; Rotheray & Gilbert 2011), but it has not been confirmed for *E. americanus*. Ouattara et al. (2022) showed that, like most hoverflies (Rotheray 1993; Skevington et al. 2019), *E. americanus* has three larval instars. However, the identification of the larval instars through morphological characters remains incomplete, which is a barrier to further studies on this species. Notably, identification of instars is necessary to evaluate the syrphid's development or voracity since aspects like development time, mortality, or number of prey consumed vary between instars. This study aims to provide a dichotomous key of discriminating morphological traits to differentiate the three larval instars of *E. americanus*.

2.3 Material and methods

2.3.1 Insect rearing

Insect rearing was carried out at UQAM in the Biocontrol laboratory. The melon aphids, *A. gossypii*, were reared on cucumber, *Cucumis sativus* L. (Cucurbitales: Cucurbitaceae), the bird cherry-oat aphid, *R. padi*, on barley plants, *Hordeum vulgare* L. (Poales: Poaceae), and the pea aphid, *A. pisum*, on broad bean plants *Vicia faba* L. (Fabales: Fabaceae) (25°C, 16 L: 8 D photoperiod, and 60% R.H.). *Eupeodes americanus*, rearing was done as described in Bellefeuille et al. (2019). Adults were fed with pollen and sugar water and larvae were fed with *R. padi* reared on barley.

2.3.2 Photography methods for first to second instar differentiation

Eleven larvae were observed from egg hatch to the second instar (during approximately three days) using a time-lapse photography technique to visualize molting, usually difficult to observe. Eggs were allowed to hatch on a broad bean leaf placed on damped cotton in a 5cm diameter opened Petri dish. After hatching, larvae were transferred to cucumber or barley leaves placed on agar gel in the same type of opened Petri dish (21°C, 9 L: 15 D photoperiod, and 45% R.H). Polytetrafluoroethylene insect barrier, PTFE Plus (Formica®) was used to prevent larvae from escaping. Larvae were fed *ad libitum* either with melon aphids or bird cherry-oat aphids. The Petri dish was kept under ambient light during the day and under a LED lightbulb (120 volts, 150 mA, Luminus®PLYB1305D) in a basic reflector lamp with a red filter that was continuously on at night. Exposition time and ISO were the same during day and night (ISO-400 and ¼ second exposition time). Time-lapse was set at 5 min between each shot and a Canon EOS 50D® with a 4x optical zoom was used. The camera was placed at approximately 65 cm above the petri dish. Photos were observed twice a day. Molting was identified by the behavior of the larva (standing still for a moment and then stepping out of its exoskeleton, leaving it on the leaf) and by observing the exuviae using a binocular microscope. Less than 24 hours after molting (after confirming that no other molt took place) larvae were observed under a binocular microscope. A preliminary descriptive grid from the first to the second instar was created assessing principal morphological traits for each instar. ImageJ (an open-source image processing program developed by the National Institutes of Health, Bethesda, Maryland, USA) software was used to measure the length of all larvae less than 10 minutes after hatching or molting (n=13 for first instar and n=11 for second instar).

2.3.3 Observation method for second to third instar differentiation

To confirm if, as claimed by Rotheray & Gilbert (2011) for all Syrphinae larvae, third instar larvae of *E. americanus* could be distinguished by their fused breathing tubes, ten new second instar larvae were placed individually in Petri dishes and fed with *A. pisum* (24°C, 16 L: 8 D photoperiod and 40% R.H). Time-lapse photography could not be used since third instar larvae were too mobile. Larvae were observed twice a day under a stereo microscope until molt. The posterior breathing tubes development was described. Molt of larvae was determined by observation of the exuviae. Less than 24h after molting, the larvae were measured using ImageJ. Thanks to this experiment, the descriptive grid was completed up to third instar.

2.3.4 Confirmation of *E. americanus* larval instars descriptive grid

The grid was confirmed with the daily observation of 13 larvae from 24 hours after hatching until the third instar, reared under controlled conditions (25 °C, 16 L: 8 D photoperiod and 60% R.H.), and given *ad libitum A. gossypii* and *R. padi* aphids.

2.4 Results

Results allowed the determination of primary and secondary traits (Table 2.1). Primary traits are constant over time and among individuals and are used to discriminate the larval instars of *E. americanus.* Secondary traits are more descriptive and may vary significantly over time (at the same instar) or according to the individual.

Table 2.1. Morphological traits grid for discrimination of the three larval instars of *E. americanus*. The primary traits allow the differentiation of the three larval instars by observation under the stereo microscope. The secondary traits are additional information and may vary slightly depending on the individual

		First instar larvae	**Second instar larvae**	**Third instar larvae**
PRIMARY TRAITS	**Hairs**	Dorsal view: 9 transverse rows of 8 **long black hairs** each except for the rows of the two first segments containing 4 to 6 very small **black hairs.** Hairs of the first transverse row are not all the same size.	Translucent hairs at the same places as the 1^{st} instar.	Translucent hairs at the same places as the previous instars.
	Posterior breathing tubes	Separated pale brown circular breathing tubes.	Bigger and lithely darker brown circular breathing tubes. Appearance of more bumps and still separated at base.	**Larger and darker brown circular breathing tubes fused at the base.**
SECONDARY	**Appearance of the integument**	Glossy and translucent.	Progressively more mast and opaque.	Mast and partially opaque.
	Longitudinal dorsal view	Very thin transverse white stripes if they are visible.	Still very thin but more defined transverse white stripes.	Thicker transverse white stripes. Sometimes joined with yellowish stripes.

Spicules at the surface of the integument	No or few very small black spicules evenly distributed over the entire integument except the ventral part.	Few to many black spicules evenly distributed over the entire integument except on the ventral surface. No obvious pattern.	Densification of black spicules in certain places forming defined black spots in a regular pattern.
Body-length after molt (mm)	1,21 ± 0,06	3,08 ± 0,09	7,43 ± 0,37

Two primary traits have been established. The color of the dorsal hairs serves to differentiate the first instar from the two others. Noticeably, only the first instar has long black hairs which become translucent in the second and third instars (Fig.2.1). The fusion of posterior breathing tubes, forming two contiguous circles, is the main trait that discriminates the third from the other instars. In fact, posterior breathing tubes are clearly spaced from each other in the first and second instars (Fig.2.2).

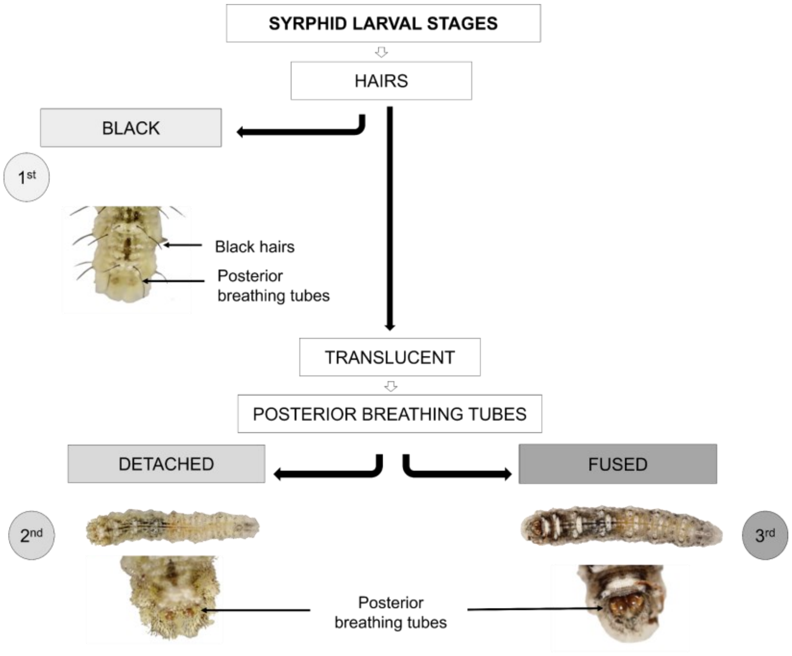

Figure 2.1. Dichotomous key for larval instars identification of *E. americanus*.

Several secondary traits differ between the three instars (Fig.2.3). For example, the number of spicules on the surface of the integument increases and gradually forms a pattern (forming dense groups of spicules distributed regularly among the dorsal surface of the integument). The thickness of the white stripes visible on the dorsal part of the larva also gradually increases over time. The stripes of the third instar larvae can be up to four times as wide as the stripes of the first instar larvae. The appearance of the integument also changes during development, going from glossy and translucent to mast and partially opaque. Finally, the length of the larvae can be used as a general indicator of the instar but varies greatly among individuals and depending on rearing conditions. Less than 24h after hatching or molting, first, second, and third instar larvae measure respectively about 1,23 ± 0,06 mm 3,08 ± 0,09 mm, and 7,43 ± 0,37 mm.

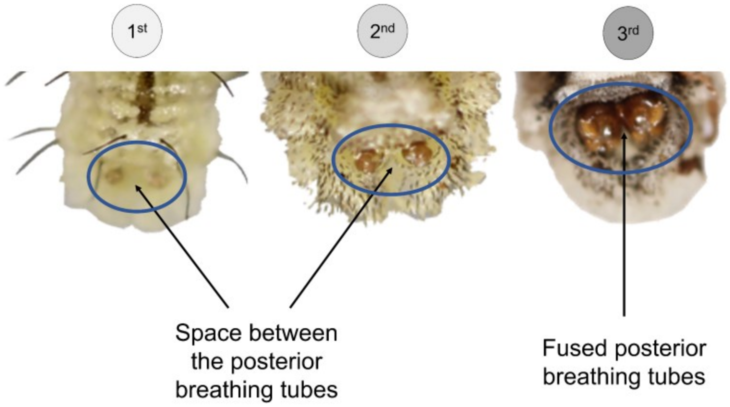

Figure 2.2. Detailed pictures of the posterior breathing tubes of *E. americanus* larvae.

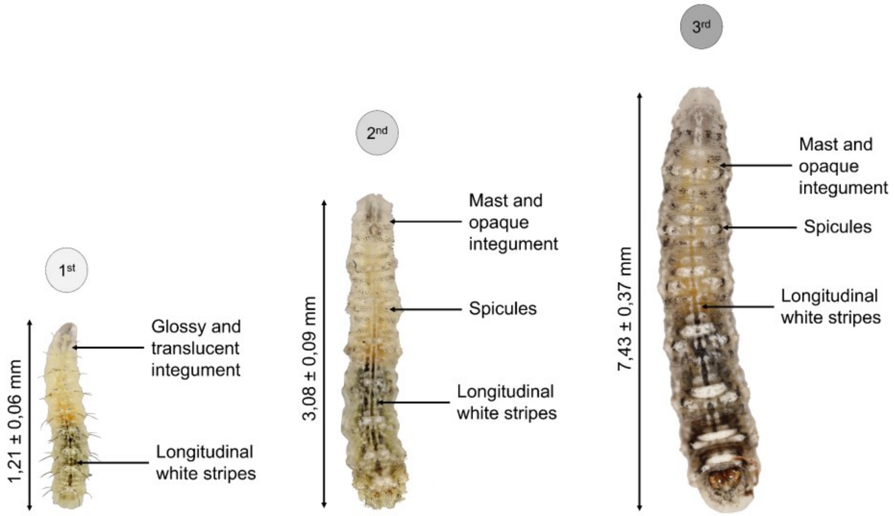

Figure 2.3. Secondary morphological traits of *E. americanus* three larval instars.

2.5 Discussion

The present results allow to clearly discriminate the three larval instars of the American hoverfly, using morphological traits. Even if it was not used as a discriminatory character, the change in the color of hairs from the first to the second instar was previously described with *Eupeodes luniger* (Meigen, 1822) (Diptera: Syrphidae), by Bhatia (1939) and uncolored hairs were also reported for species of the genus *Scaeva* Fabricius,1805 (Diptera: Syrphidae) by Láska et al. (2006). The fused breathing tubes at the third instar were also observed in numerous species (Bhatia, 1939; Hartley 1961). Other secondary characters from our descriptive grid were also reported in the literature. The presence of nine transverse rows of hairs at all stages was ubiquitous among the seven Nearctic, Palearctic and Holarctic species studied by Bhatia (1939). The appearance of the integument transitioning from transparent to opaque among stages as well as the presence of spinules or spicules at the third stage was also reported in numerous species (Bhatia,1939; Hartley 1961; Láska et al., 2006). Nonetheless, variation in those traits is evident as Bathia (1939) showed that *Episyrphus balteatus* De Geer, 1776 (Diptera: Syrphidae) and *Sphaerophoria rueppellii* (Wiedemann, 1830) (Diptera: Syrphidae) integuments were transparent and shiny even at the third instar. The description of these primary and secondary traits of *E. americanus* larvae broadens the morphological knowledge on each instar of this species and makes it possible to easily differentiate them, either in the laboratory or in the field, with a hand lens. Being a promising biological control agent, it is important to assess fundamental characteristics for its use like its voracity, larval development, and mortality rate, wich differ between instars. It is also useful for optimizing the mass rearing of *E. americanus*. Moreover, time-lapse photography has proven to be a useful technique for monitoring the larval development of hoverflies. It allows knowing exactly when the molting process takes place without having to find the exuviae which can be very difficult to see otherwise (Rotheray & Gilbert, 2011; Joshi & Ballal, 2013). Thanks to the high definition of the pictures, time-lapse photography allows observing details on a very small scale while requiring very little data storage compared to video. This little-used method would benefit from being exploited more.

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CHAPITRE 3

LARVAL DEVELOPMENT AND VORACITY OF *EUPEODES AMERICANUS* (DIPTERA: SYRPHIDAE): COMPARISON OF THE FOCAL PREY *APHIS GOSSYPII* (HEMIPTERA: APHIDIDAE) AND THE BANKER PREY *RHOPALOSIPHUM PADI* (HEMIPTERA: APHIDIDAE)

Arlette Fauteux, António O. Soares & Éric Lucas

3.1 Résumé/Abstract

Contrairement aux espèces européennes, le potentiel des syrphes néarctiques en tant qu'agents de lutte biologiques est encore peu étudié. Néanmoins, le syrphe d'Amérique (*Eupeodes americanus*, (Wiedemann 1830)) a récemment produit de bons résultats en tant qu'agent de lutte contre le puceron de la digitale (*Aulacorthum solani* Kaltenbach 1843) sur le poivron. La présente étude vise à élargir les connaissances sur le syrphe d'Amérique, et plus spécifiquement à évaluer son potentiel pour le contrôle du puceron du melon (*Aphis gossypii* Glover 1877) en système de plantes réservoirs. Conséquemment, le développement préimaginal et la voracité de *E. americanus* ont été comparés lorsqu'il s'alimentait de la proie focale (*A. gossypii*) ou la proie réservoir (puceron bicolore des céréales, *Rhopalosiphum padi* L. 1758) par l'observation quotidienne des spécimens de l'éclosion à l'adulte. Le temps de développement préimaginal, le taux de survie et l'occurrence de déformation étaient similaires pour les deux espèces de proies. Toutefois, le poids du troisième stade larvaire et de la pupe était plus élevé lorsque les larves s'alimentaient de la proie réservoir. La voracité maximale des larves de syrphes était similaire pour les deux proies, sauf pour les larves de troisième stade qui consommaient plus de proies focales. Les résultats suggèrent qu'un système de plantes réservoirs impliquant le puceron bicolore des céréales pourrait être adéquat pour que *E. americanus* contrôle efficacement le puceron du melon.

Mots clefs : Lutte biologique, système de plantes réservoirs, concombre de serres, syrphe d'Amérique, puceron du melon, puceron bicolore des céréales.

Unlike European species, the potential of Nearctic syrphids as biological control agents is still poorly studied. Nonetheless, the American hoverfly (*Eupeodes americanus* (Wiedemann 1830)) has recently demonstrated promising traits as a biocontrol agent, notably against the foxglove aphid (*Aulacorthum solani* Kaltenbach 1843) on pepper. The present study aims to extend our knowledge of the American hoverfly, and more specifically to evaluate its potential as a biocontrol agent in a banker plant system, against the melon aphid

(*Aphis gossypii* Glover 1877) in a greenhouse cucumber crop. Consequently, the preimaginal development and voracity of *E. americanus* were compared when preying upon the focal prey/pest (*A. gossypii*) or the banker prey (bird cherry-oat aphid, *Rhopalosiphum padi* L. 1758) by the daily observations of individuals from egg to adult. Preimaginal development time, survival rate and occurrence of deformation were similar on both prey species. However, third instar and pupal weight were higher for larvae fed with the banker prey. The *ad libitum* voracity of the syrphid larvae was similar on both preys except for the third instar larvae which consumed more focal prey. Results suggest that a banker plant system involving the bird cherry-oat aphid could be adequate for *E. americanus* to efficiently control the melon aphid.

Key words: biological control, banker plant system, greenhouse cucumber, American hoverfly, melon aphid, bird cherry-oat aphid.

3.2 Introduction

Infestations by the melon aphid, *Aphis gossypii* Glover 1877 (Hemiptera: Aphididae), in cucumber greenhouses are a major problem in organic and conventional crops (Capinera, 2007; Prado et al., 2015; Gullino et al., 2020). This pest has a high growth rate on cucurbits and is a vector of many phytopathogens (Capinera, 2007; Gullino et al., 2020). Chemical control is rarely effective since the pest rapidly develops resistance to pesticides and the products applied generally do not reach all the individuals who may be hidden in the hollows of the leaves (Capinera, 2007). In organic crops, to control the melon aphid, most Canadian growers use a combination of parasitoid wasps *Aphidius colemani* Viereck 1912 (Hymenoptera: Braconidae) or *Aphidius matricariae* Haliday 1834 (Hymenoptera: Braconidae) and predatory midges, *Aphidoletes aphidimyza* (Rondani 1847) (Diptera: Cecidomyiidae) (Gullino et al., 2020). However, parasitoid wasps are likely to be hyperparasitized (Vacante and Kreiter, 2018) and midges can be victims of intraguild predation (Messelink et al., 2020) in mid-summer. Thus, to control this pest, particularly in cucurbits crops, it is imperative to find new agents to complement existing ones.

The American hoverfly, *Eupeodes americanus* (Wiedemann 1830) (Diptera: Syrphidae), a Nearctic species with a predatory larval stage and pollinating adult stage, could constitute a suitable biological complement for controlling the melon aphid in North American cucurbit crops. Predatory species of the Syrphidae family generally exhibit characteristics that predispose individuals to be successful biocontrol agents, including high voracity, low-temperature activity, good flight ability, rapid finding of aphid colonies, and high voracity and fecundity (Almohamad et al., 2009; Rodríguez-Gasol et al., 2020; Bellefeuille et al., 2021; Van Oystaeyen et al., 2022). Due to its traits, the American hoverfly has demonstrated good potential as a biocontrol agent against the foxglove aphid, *Aulacorthum solani* (Kaltenbach 1843) at low temperatures (Bellefeuille et al., 2019, 2021).

An important limitation for the successful control of fast-growing aphids is the delay in the action of the natural enemies (Fischer and Leger, 1997; Payton Miller and Rebek, 2018). Even when aphid colonies are discovered early, the time lapse between introduction and action of biological control agents frequently allows for pest population to surpass the economic threshold of damage (Fischer and Leger, 1997). The banker plant system can reduce this delay, mostly by ensuring the enduring presence of biocontrol agents in the crop prior to the arrival of the pests, consequently improving their effectiveness (Huang et al., 2011). The system is based on the introduction of a banker plant into the protected crop, providing an alternative food source (banker prey) and an environment for reproduction of the natural enemies of the targeted pest (Frank, 2010; Huang et al., 2011; Payton Miller and Rebek, 2018; Yano, 2019).

The success of a banker plant system is determined by an array of different factors, including compatibility of the system with the greenhouse environment and with the other biological control methods used by growers. One of the key points is the oviposition preference of the predator female for the focal crop/pest versus the banker plant/banker prey systems. As demonstrated by Gonzalez et al. (2023)[1], the American hoverfly has a strong preference for the melon aphid on cucumber when given the choice between this crop/pest system and a banker plant system composed of the bird cherry-oat aphid, *Rhopalosiphum padi* L., 1758 (Hemiptera: Aphididae) on finger millet, *Eleusine coracana* (L.) Gaertn (Poaceae). In a case where the bird cherry-oat aphid would be used as a banker prey for the control of the melon aphid by the American hoverfly, the oviposition preference should not perturbate the control of the pest. The second point, which may affect the first one, is related to the respective nutritional values of the banker prey and the focal prey (Sadeghi and Gilbert, 2000). Indeed, if the focal prey is of lower quality than the banker prey for the development of the biocontrol agent, its arrival in the focal crop can both lower the predator's population growth and potentially orient its egg-laying preference towards other preys. To enable a potential biological control, a good prey should allow rapid development of the predator (for population growth), generate heavy individuals (since it is generally linked to fecundity), as well as a balanced sex ratio (for reproduction) and low deformation and mortality rates (as an indicator of individual fitness and long-term population growth) (Coppel and Mertins, 1977; Tenhumberg, 1995; van Lenteren and Manzaroli, 1999; Almohamad et al., 2009). Also, the voracity of a predatory biological control agent is directly related to its predation rate, which needs to be high for the control of fast-growing pests like the melon aphid (Coppel and Mertins, 1977;

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[1] See Annexe A.

Dunn et al., 2020;). Both development and voracity must ensure that the quantity of prey consumed by the biocontrol agent population exceeds the population growth of the pest (van Lenteren and Manzaroli, 1999).

Several studies have shown that the aphid species consumed by a predator can have an impact on its growth, development, and survival, both in the case of more generalist predators such as lacewings (Neuroptera) (Liu and Chen, 2001) and ladybirds (Coleoptera: Coccinellidae) (Hauge et al., 1998; El-Serafi et al., 2000; Omkar and Srivastava, 2003; Soares et al., 2005; Hodek and Evans, 2012; Sebastião et al., 2015; Rosagro et al., 2020) and in the case of some hoverfly (Diptera: Syrphidae) species such as *Eupeodes corollae* (Fabricius, 1794), *Episyrphus balteatus* (De Geer, 1776) and *Heringia calcarata* (Loew 1886) (Jiang et al., 2022; Putra and Yasuda, 2006; Rüzička, 1975; Rosagro et al., 2020;Short and Berg, 2004). In some cases, certain aphid species can be considered unsuitable for the development of the hoverfly. For instance, Rüzička et al. (1975) and Jiang et al., (2022), respectively showed that the majority (or close) of *E. corollae* larvae died when fed with *Aphis sambuci* L. 1758 or *Megoura crassicauda* Mordvilko, 1919. The voracity of a biocontrol agent also differs between prey species (Short and Berg, 2004; Putra and Yasuda, 2006; Rodríguez-Gasol et al., 2020). For example, *E. balteatus* has a higher predation rate on *Microlophium carnosum* Buckton 1876 (Hemiptera: Aphididae) compared to *Acyrthosiphon pisum* Harris 1776 (Hemiptera: Aphididae) and *Sitobion avenae* F. 1775 (Hemiptera: Aphididae) (Alhmedi et al., 2008).

The aim of the present study was to determine if the American hoverfly can be a suitable biological control agent of the melon aphid in a banker plant system. More specifically, the first objective was to assess if the focal prey (melon aphid = pest) was as adequate as the banker prey (bird cherry-oat aphid = rearing prey) for the development of the American hoverfly. The second objective was to determine if the voracity of the hoverfly was as high when feeding on the focal prey than on the banker prey. For both objectives, the banker prey was considered as the reference prey since it is the rearing prey of the syrphid since 2014 in the Biological Control Laboratory (UQAM) and because syrphid larvae demonstrated a high voracity on this aphid. Indeed, in the field, barley banker plants inoculated with bird cherry-oat aphids were almost emptied in one to two weeks by 10 American hoverfly larvae (Fournier M, pers. comm.). Furthermore, the bird cherry-oat aphid is often used in banker plants and is suitable for an array of biocontrol agents, including other syrphid species (Pineda and Marcos-García 2008; Huang et al., 2011).

We predicted that (1) since the hoverfly is a generalist species, both focal and banker prey will allow the predator to complete its development, (2) since the banker prey is also the rearing prey, and has proven to be of high quality food for the predator, that the development will be optimal when larvae are fed on the banker prey, (3) the voracity of the predator will be superior on the banker prey than on the focal prey.

3.3 Material and methods

3.3.1 Plant material and insect rearings

Plants were grown in the greenhouse complex of the University of Quebec at Montreal (UQAM), under the following conditions: 23°C average temperature, 16L: 8D photoperiod with natural and artificial light (high pressure sodium), and 50% R.H. The barley, *Hordeum vulgare* L. (Poaceae), was sown directly in pots of 13 x 13 x 15cm at a density of approximately 50 seeds per pot. The broad bean, *Vicia faba* L. (Fabaceae) was sown by groups of two seeds per pot of 8 x 8 x 10cm. Cucumber, *Cucumis sativus* L. (Cucurbitaceae), was sown in seed trays and transplanted individually after approximately two weeks in pots of 13 x 13 x 15cm or 8 x 8 x 10cm. Plants were watered two to three times a week and fertilized (N-P-K, 20-20-20) once a week.

Insect rearing was done at the Biological Control Laboratory (UQAM). Melon aphids (focal prey) were reared on cucumber and bird cherry-oat aphids (banker prey) on barley plants (18°C, 16 L: 8 D photoperiod, and 60% R.H). American hoverfly rearing was done following Bellefeuille et al. (2019). Adults were fed with artificial flowers (cotton soaked in sugar water and covered in bee pollen, hung on a wooden stick) and sugar water served in small jars (20g/L approximately) and laid their eggs on broad bean plants. Eggs were allowed to hatch on the broad bean plants and larvae were collected and transferred on 2 weeks old barley plants inoculated with *R. padi*.

3.3.2 Effect of prey species on the development of the American hoverfly

The entire experiment took place under controlled conditions of 25°C and 50% R.H. Hoverfly eggs were allowed to hatch in petri dishes containing several broad bean leaves from the mass rearing, on which females had laid eggs, placed on a humid cotton. Less than 24 hours after the eggs hatched, larvae were placed individually in petri dishes (5cm ø) previously filled with Agar (*bacteriological grade I-tech*, 5.57g / L) and the underside of either cucumber or oat leaves on top with respectively melon aphids or bird cherry-oat aphids. Larvae were fed *ad libitum* for the total length of their development. The stage and weight of the larvae as well as the presence of deformities and mortality were recorded daily until pupation. Duration of pupal stage and sex of adults after emergence were also recorded. Twenty-four to 27 independent replicates were performed for each treatment (34 to 40 replicates when accounting for mortality).

3.3.3 Effect of prey species on the voracity of the American hoverfly

The experiment took place under the conditions previously described. Due to time constraints, the voracity of larvae was evaluated in two temporal blocks (on different groups of individuals for each block). The first temporal block addressed the voracity of larvae from less than 24 hours old to the end of second instar (less than 24 hours after the beginning of stage three). The second temporal block addressed the voracity of larvae less than 24 hours after the beginning of third instar to the beginning of pupal stage. For the first and second block, 150 to 600 aphids and 900 to 1100 aphids were provided every day, respectively. Aphids were between first and third instar to make sure they could not reproduce and to standardise the size of individuals. To control for natural aphid mortality, two control petri dishes were set every day under the same conditions, except for the presence of the larva. The number of aphids provided each day to the larvae was adjusted to the consumption of the larvae by assuming that if a minimum of 15% of the aphids provided daily were not eaten after 24 hours, the larva could eat at maximum capacity. Following this rule, more *A. gossypii* than *R. padi* were given to the larvae (because the prey is smaller, and pretests showed that more were needed to ensure *ad libitum* consumption). Only three larvae did not get enough food during their development (at third instar). Two of those were feeding on the banker prey and one was feeding on the focal prey. Those replicates were taken out of the dataset because it could have biased the results towards less voracious larvae. For the first temporal block, 14 and 13 independent replicates were performed for larvae fed with *R. padi* and *A. gossypii* respectively. For the second temporal block, 10 independent replicates were performed for each prey.

Individual biomass of the two species of aphids was also calculated. For each species, five samples of 200 aphids of stage one to three, representative of the aphids supplied to the larvae, were weighed. The individual biomasses of the two aphid species were then estimated.

3.3.4 Statistical analysis

All statistical analyses were performed using R statistical software version 4.0.3. (R Core Team, 2020). The packages lme4 (Bates et al., 2015) (for linear and logistic mixed models) and emmeans (Lenth, 2022) (for posthoc analysis of mixed models and for estimation of the marginal means presented in the Figures) were used. For all models, the choice of inclusion of the fixed effects and interaction terms was based on the biological pertinence of the terms as well as on the comparison of the AIC (Akaike information criterion, relative indicator of model quality for a given set of data) of the different models. The validation of the models was done with Shapiro-test and Q-Q plots for the normality of residuals. Plots of Pearson residuals against explanatory variables as well as Cooks'distance plots were performed to verify homoscedasticity of variance and leverage of the data.

3.3.4.1 Development

Developmental time of each preimaginal instar and maximal weight of each instar (except for pupal stage which was only weighted less than 24h after pupation contrary to all other instars which were weighted every day) were extracted from the data as well as global survival rate and deformity occurrence. All were used as dependent variables for statistical analysis.

Developmental time and larval weight (after log transformation of developmental time) were evaluated by two distinct linear mixed models with the prey species and the stage of development as fixed effects and the identity of individuals (ID) as random effect. The interaction between stage of development and prey species was included only in the larval weight model for the reasons mentioned above. Different distributions (gamma and Poisson for developmental time, and only gamma for larval weight) were also tested, but the normal distribution, after log transformation for the developmental time, was more appropriate in terms of distribution of residuals (normality and homoscedasticity).

Survival rate was evaluated by a mixed effects logistic regression with the prey species and the stage of development (larva or pupa) as fixed effects and ID as random effect. The larval instar could not be included as an explanatory variable due to the low mortality rate. Logistic regressions assume that less that 20% of the contingency table groups have a frequency of less than five (Josephat and Ame, 2018) and including the larval instar in the model would have generated that problem.

For the same reason, deformities occurred too rarely (2,70%) to be interpreted statistically.

The effect of the prey consumed by the larvae on the differential mortality between males and females was analyzed by looking at the sex ratio of the emerged adults. It was tested by a logistic regression with the prey species as the explanatory variable.

3.3.4.2 Voracity

Statistical analyses of the voracity at first and second instars were done separately from those at third instar since the data for first and second instars were taken from the same individuals, but not those for third instar. Number of aphids eaten by the larva was extracted from the data by subtracting the number of live aphids remaining in the petri dishes from the number of aphids supplied to the larvae (calculated by the number of aphids supplied minus the average natural mortality of the two controls). The daily voracity of larvae was calculated by dividing the voracity at each instar by the duration of each instar (number of days) for every replicate. The biomass consumed for each larval instar was also extracted from that data by multiplying the voracity for each larval instar by the individual biomass of the aphid species concerned.

The effect of the prey species on the voracity, the daily voracity and the biomass consumed by first and second instars larva were evaluated by linear mixed models with the prey species and the stage of development as fixed effects and the identity of the larva as random effect. Interaction between prey species and stage was kept in the model only when significant (in that case, posthoc analysis using emmeans package were done to look at the contrasts of interest. Effect of prey species on voracity and daily voracity of third instar larvae was tested with Student T tests. Effect of prey species on the aphid biomass consumed by third instar larvae was tested with a nonparametric Wilcoxon test.

Biomass difference between the two aphid species was tested with a non-parametric Wilcoxon test due to the low number of replicates.

3.4 Results

3.4.1 Development

3.4.1.1 Developmental time

Larval mean (± standard error) developmental time (from first instar to the end of third instar) was 6.57 ± 0.15 days, all diets combined, ranging from a minimum of five days to a maximum of 10 days. Pupal mean (± standard error) developmental time (from third instar to adult emergence) was 6.64 ± 0.13 days, all diets combined, ranging from a minimum of six days to a maximum of eight days.

Mean larval developmental time was 6.50 ± 0.22 days when the larvae fed on the banker prey and 6.63 ± 0.20 days when larvae fed on the focal prey. When larvae fed on the banker prey, first instar accounted for 25.08 ± 1.68% of the total larval development time, second instar accounted for 22.16 ± 1.72% and third instar duration represented the major part, that is 52.76 ± 1.45% (Figure 3.1). Proportions were similar with larvae fed on the focal prey, that is, 24.53 ± 1.41% for first instar, 22.86 ± 1.47% for second instar, and 52.60 ± 1.40% for third instar. The effect of aphid prey species on hoverfly development time was not significant (Figure 3.1) (n=51, df = 49, t-value = -0.466, p-value = 0.643) and was similar for all stages, (no main effect or interaction term significant and model without interaction between stage and diet best fitted with an AIC of 108.52 versus 121.61 with the interaction).

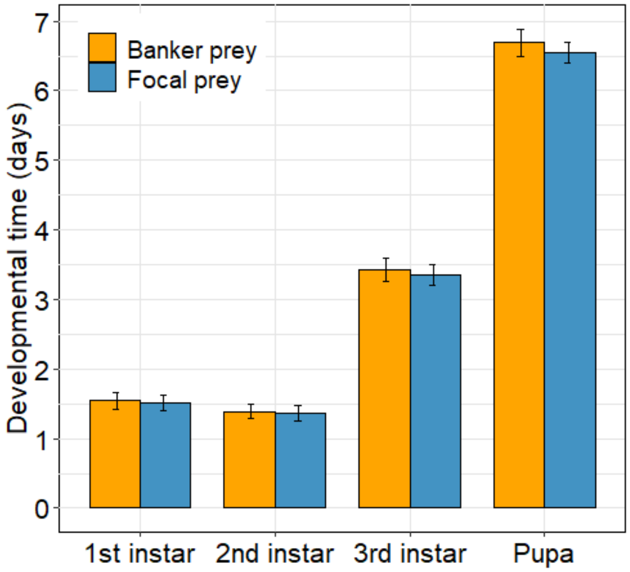

Figure 3.1. Preimaginal developmental time of *E. amerianus* depending on a diet composed of the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the effect of the prey species on the larval development time was determined using a mixed effects linear model with the prey species and the stage of development as fixed effects and the ID as random effect. Means displayed are estimated marginal means derived from the model.

3.4.1.2 Weight

Mean (± standard error) global weight for first, second, third instar and pupa were respectively 0.37 ± 0.03 mg, 3.16 ± 0.17 mg, 38.26 ± 1.06 mg, and 31.67 ± 0,80 mg. The weight increased exponentially from first to third instar and slightly decreased during pupal stage (Figure 3.2). Mean larval weight, when fed on the banker prey, was 0.40 ± 0.04 mg at the end of the first instar, 3.43 ± 0.28 mg at the end of the second instar (7.57 times heavier than first instar), 42.12 ± 1.56 mg at the end of the third instar (11.29 times heavier than second instar) and 34.84 ± 1.07 mg at the beginning of pupal stage (17% lighter than third instar). When fed on the focal prey, mean larval weight was 0.35 ± 0.03 mg at the end of the first instar, 2.93 ± 0.20 mg at the end of the second instar (7.47 times heavier than first instar), 34.83 ± 1.09 mg at the end of the third instar (10.89 times heavier than second instar) and 28.84± 0.87 mg at the beginning of pupal stage (17% lighter than third instar).

Larval weight of third instar larva and pupa was significantly higher when the larvae had been fed on the banker prey than when fed on the focal prey (Figure 3.2) (n = 51, df = 49, t = - 6.222, p-value < 0.001 for third instar and n = 51, df = 49, t-value = -5.095, p-value <0.001 for pupa). When larvae were fed on the banker prey, average third instar larval weight was 20,95% higher and average pupal weight was 20,81% higher than when fed on focal prey. First and second instar larval weight did not differ significantly with a diet composed of the focal or the banker prey (n = 51, df = 49, t = -0.048, p-value = 0.962 and n = 51, df = 49, t = -0.429, p-value = 0.667 for first and second instars respectively).

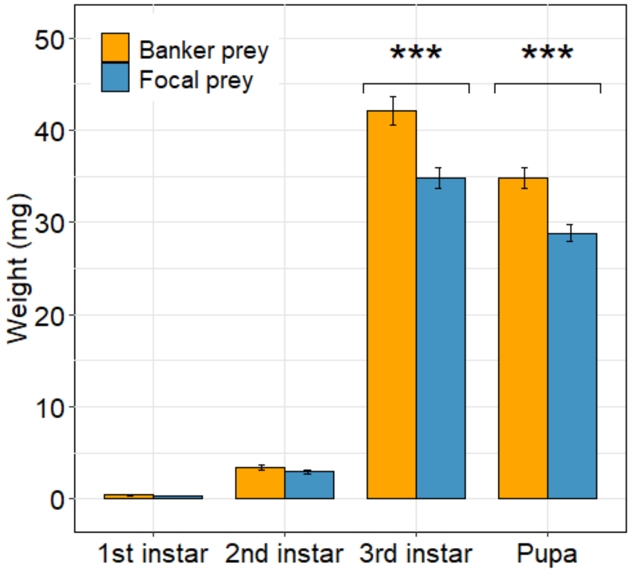

Figure 3.2 Preimaginal weight of *E. americanus* depending on a diet composed of the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the effect of the prey species on preimaginal weight was determined using a mixed effects linear model with the prey species, the stage of development and the interaction between the two factors as fixed effects and the ID as random effect. Means displayed are estimated marginal means derived from the model. The signification of stars is as follows: ***<0.001.

3.4.1.3 Survival

Global larval survival rate was 68.89 ± 5.42% and global pupal survival rate was 68.63 ± 6.56%. Survival did not differ significantly between diets, neither for the larval nor for the pupal stage (Figure 3.3A) (respectively,n = 74, Z= -0.286, p-value = 0.7749 and n=40, Z= 0.562, p-value = 0.5742). Larval survival rate was 70.59 ± 7.81% when larvae were fed with the banker prey and 67.50 ± 7.41% when larvae were fed with the focal prey (Figure 3.3A). Pupal survival (emergence) rate was 66.67 ± 9.62% when larvae were fed on the banker prey and 75.00 ± 10.83% when fed on the focal prey. Although not evaluated statistically due to the low occurrence of mortality, when larvae fed on the banker prey, the survival rates were slightly higher at first and second instar but lower at third instar and pupal stage (Figure 3.3B). Lowest survival rate occurred at pupal stage with both preys.

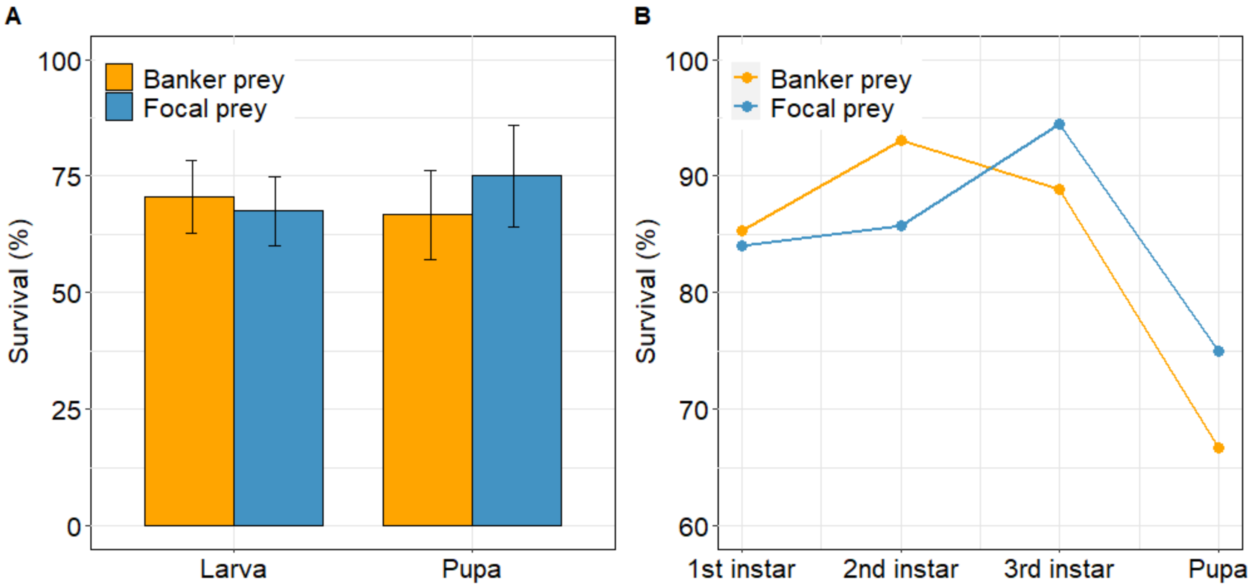

Figure 3.3. Overall survival (A) and survival trajectory (B) depending on the prey species: the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the overall survival was determined using a mixed effects logistic regression with the prey species and the stage of development (larva or pupa) as fixed effects and ID as random effect. Overall survival means (A) displayed are estimated marginal means derived from the model. Survival trajectories (B) displayed are raw data.

3.4.1.4 Deformities

Deformities occurred only with larvae fed on the focal prey, but it happened in only 2.70% (2/74) of all replicates, so no statistical analysis was performed. Both occurences took the form of a growth located on the head of the larvae and only one of the two larvae survived for its entire development.

3.4.1.5 Sex ratio

Adult sex ratio (number of males:number of females emerged) was 1:1 when larvae fed on the banker prey and 7:5 when larvae fed on the focal prey (Figure 3.4). Proportion of females emerged was not significantly related to the prey species consumed by the larvae (Figure 3.4) (n = 28, Z = 0.437, p-value = 0.662).

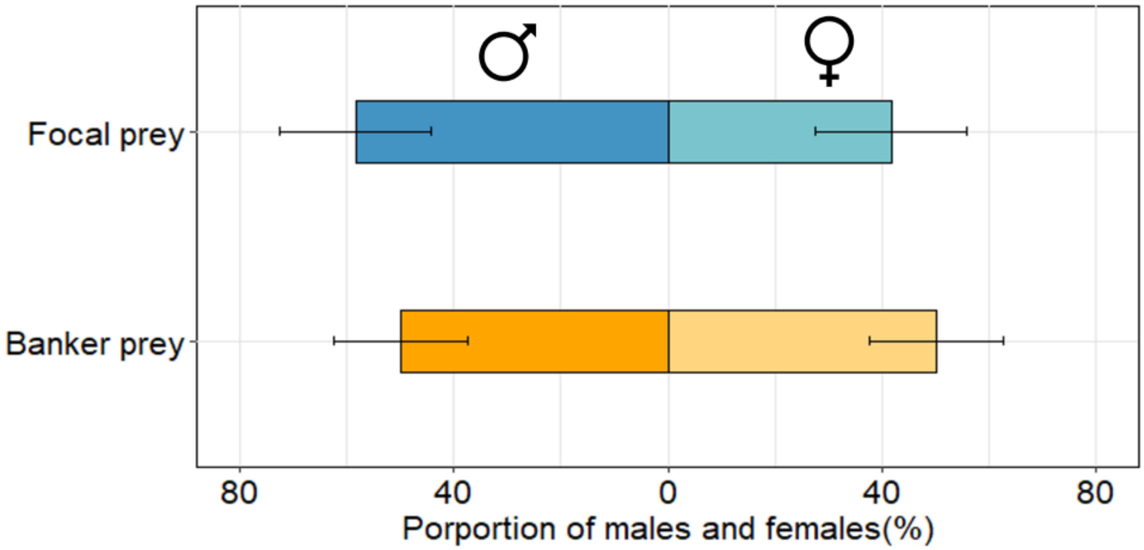

Figure 3.4. Proportion of females emerging from *Eupeodes americanus* pupae depending on the prey consumed by the larvae: the banker prey (bird cherry-oat aphid) or the focal prey (melon aphid). Statistical significance of the proportion of females emerged was determined using a logistic regression with the prey species as the explanatory variable. Means displayed are estimated marginal means derived from the model.

3.4.2 Voracity

3.4.2.1 Total voracity

Total larval voracity (mean number of aphids consumed during the entire larval stage) was 1780.44 banker aphids and 2266.33 focal aphids. Average third instar voracity represented 78.32% and 82.39% of the total voracity with larvae fed on the banker prey and the focal prey respectively (Figure 3.5A).

At third instar, larval voracity (mean number of aphids eaten at each instar) was 33,22% higher when fed on the focal prey than on the banker prey (Figure 3.5A) (n = 20, t-value = 2.440, df = 18, p-value = 0.029). Voracity of the first and second instar did not significantly differ between prey types (n= 27, t-value = -0.354, df = 51, p-value = 0.725).

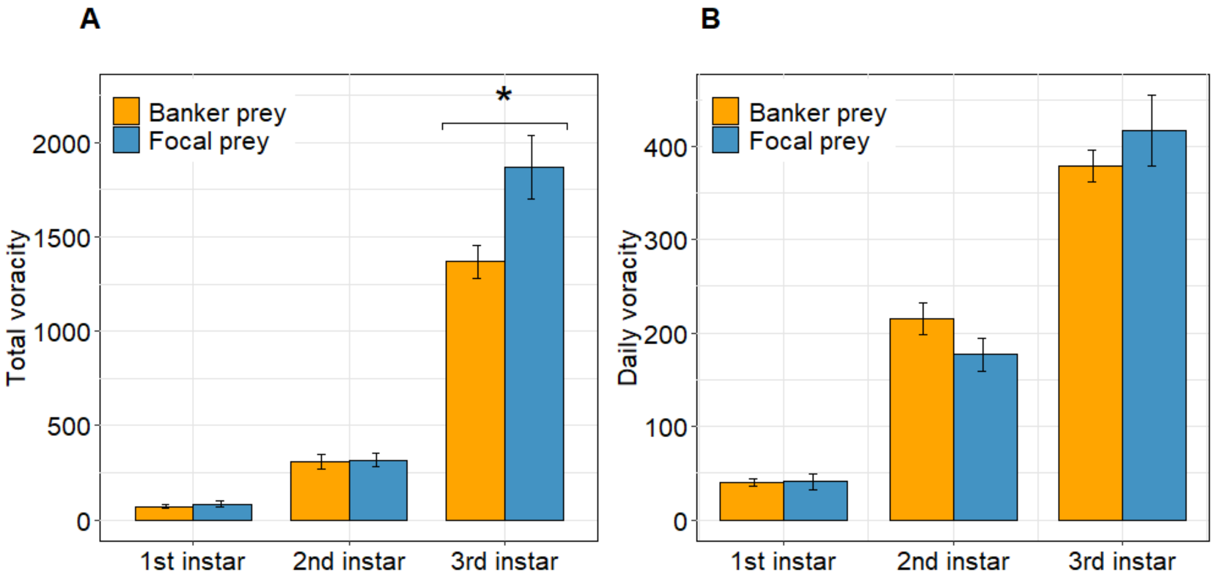

Figure 3.5. Total instar voracity (number of prey consumed by instar) (A) and daily voracity (B) of *E. americanus* depending on the prey type. Statistical significance of the effect of the prey species on the total instar voracity and the daily voracity of first and second instar larvae was determined with a mixed effects linear model with the prey species and larval developmental stage as fixed effects and the ID as random effect. Interaction between prey species and larval developmental stage was also included as a fixed effect for the daily voracity only. Statistical significance of the effect of the prey species on the total instar voracity and daily voracity of third instar larvae was determined with a Student T tests. Means displayed are estimated marginal means derived from the models. The signification of stars is as follows: *<0.05.

3.4.2.1 Daily voracity

As in the case of total voracity of each instar, daily voracity increased during the development (Figure 3.5B). When larvae fed on the banker prey, third instar daily voracity was 843.09% higher than first instar daily voracity and 75.79% higher than second instar daily voracity. When larvae fed on the focal prey, third instar daily voracity was 914.79% higher than first instar daily voracity and 135.30% higher than second instar daily voracity. The daily voracity was similar for both preys at all larval instars (Figure 3.5B) (n = 27, t-value = 0.065, df=47.2, p-value = 0.948; n = 27, t-value = -2.113, df = 47.2, p-value = 0.040 and n = 20, t-value = 0.910, df = 12, p-value = 0.380 for first, second, and third instar, respectively).

3.4.2.2 Biomass consumed by instars

Aphid individual mean biomass was significantly different between the banker and focal species (W = 0, p-value = 0.008). Banker prey's biomass was 2.01 times that of the focal prey. For this reason, voracity was expressed and then also analyzed in terms of biomass consumed.

The total biomass consumed by larvae during their entire development was higher when fed on the banker prey (42.34 mg) than on focal prey (26.88 mg).

At second and third instars, biomass consumed was significantly higher with larvae fed on the banker prey than on the focal prey (Figure 3.6) (n = 27, t-value = -4.468, df = 50, p-value <0.001 and n = 20, W = 11, p-value = 0.002 for second instar and third instar, respectively). Biomass consumed by larvae feeding on the banker prey in comparison to the focal prey was 94.18% higher at second instar and 50.51% higher at third instar. Biomass consumed at first instar was not different depending on the prey species consumed (n = 27, t-value = -0.922, df =50, p-value = 0.361).

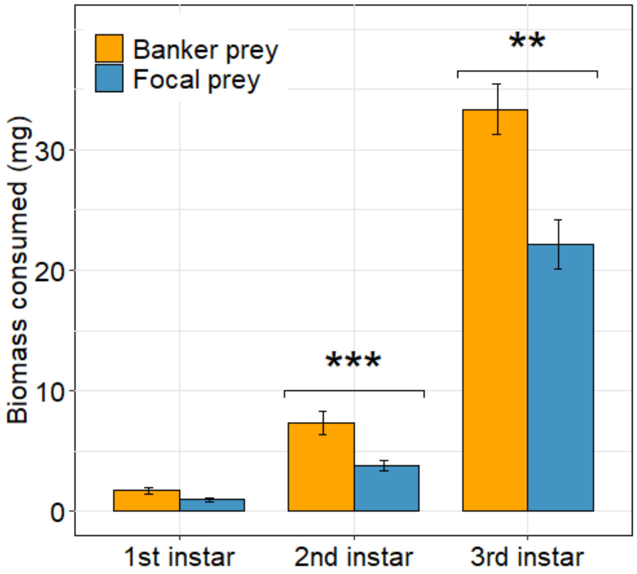

Figure 3.6. Biomass consumed by *E. americanus* depending on the prey species. Statistical significance of the effect of the prey species on the biomass consumed by first and second instar larvae was determined with a mixed effects linear model with the prey species, the larval developmental stage and the interaction between prey species and larval developmental stage as fixed effects and the ID as random effect. Statistical significance of the effect of the prey species on the voracity of third instar larvae was determined with a nonparametric Wilcoxon test. Means displayed are estimated marginal means derived from the model. The signification of stars is as follows: **<0.01 ***<0.001.

3.5 Discussion

Aligned with our first prediction, both focal and banker preys allowed complete preimaginal development of the syrphid predator. However, contrary to the second prediction, the focal and the banker prey engendered a similar development for most of the parameters studied. Finally, in contrast with the third prediction, the third instar voracity, expressed in number of preys eaten in the stage, was higher on the focal prey than on the banker prey and the daily voracity was similar for both preys. Nonetheless, consistently with the third prediction, the biomass consumed was higher on the banker prey.

Considering that the high-quality banker prey *R. padi* sustains a viable colony of *E. americanus* at the Biological Control Laboratory since 2014, this suggests that *A. gossypii* could also be adequate for the development of the predator. Indeed, except for the larval weight, quality of the focal prey was similar to the one of the banker prey for the preimaginal development time, mortality, deformation rates, and sex ratio.

The fact that *E. americanus* development was mostly similar when feeding on the banker prey or the focal prey differs from the results of numerous studies that have demonstrated the influence of prey species on different aspects of the development of predators, like developmental time, mortality, fecundity, etc. (Hodek, 1993; Sadeghi and Gilbert, 2000; Liu and Chen, 2001; Putra and Yasuda, 2006; Hodek and Evans, 2012). However, there is not always consistency among the results. For example, Rüzička (1975) and Du and Chen (1993) found contradictory results concerning the quality of *Brevicoryne brassicae* (L. 1758) (Hemiptera: Aphididae) for *E. corollae*, that is, Rüzička (1975) found that the prey caused a longer development time while Du and Chen (1993) concluded that *E. corollae* was unable to develop on it. Nonetheless, both studies agree on the quality of other common prey species studied, such as *A. pisum* and *Aphis craccivora* Koch, 1854 (Hemiptera: Aphididae). Discrepancy in the results cited in the literature could be explained by the fact that density of aphids and host plant can modulate the impact of the prey species on the predators (Hodek, 1993; Vanhaelen et al., 2002; Putra and Yasuda, 2006). Considering this, investigation of the effect of prey at low density on the present system would be interesting since focal preys tend to be at very low densities on the field.

Contrary to the other aspects of development, focal prey was of lower quality for the predator regarding its larval weight; third instar and pupae being 20,81 and 20,95%, lighter respectively when feeding on it. This result is not surprising since smaller preys (such as the focal prey) may lead to higher capture costs for larvae. (Sadeghi and Gilbert, 2000). Considering that generally, within the same insect species, lighter individuals tend to have lower fecundity (Honěk, 1993), it is possible that the larvae that are fed with the focal prey would have lower fecundity than larvae fed on banker prey. This phenomenon has been demonstrated with *E. balteatus* whose lifetime fecundity and egg production rate were linked to female body size, which was directly related to their somatic dry mass (Branquart et Hemptinne, 2000). Nonetheless, it is possible that this relation does not apply to all hoverfly species. Indeed, Scott and Barlow (1984) demonstrated that female of *E. corollae* could compensate for low body weight by overproducing eggs.

They showed that total eggs produced were the same independently of the number of aphids consumed by the larvae and therefore, the pupal weight.

However, two other studies found opposite results, that is, that total fecundity of *E. corollae* was positively linked with pupal weight (Cornelius and Barlow, 1980; Whittingham, 1991). Nonetheless, both studies suggest that pupal weight has a stronger effect on fecundity when longevity of adults is higher, potentially because compensation takes a lot of resources and shortens the longevity of individuals resorting to this strategy (Cornelius and Barlow, 1980; Whittingham, 1991). If this compensation effect applies to the American hoverfly, even if it concerns only short-lived individuals, it could lessen the effect of the weight on the fecundity. Considering this and the fact that the size of effect is relatively small, we can still conclude that the quality of the focal prey for *E. americanus* is not drastically lower than that of the banker prey, which sustains a viable colony of hoverflies at the Biological Control Laboratory since 2014.

The results concerning voracity are also partly divergent from what the literature reports. Indeed, contrary to our expectations, the number of preys consumed by each larval instar was similar, or higher (at third instar), when larvae fed on the focal prey than on the banker prey. Those results are surprising since syrphid larvae tend to move with more difficulty on surfaces containing trichomes, like cucumber (Verheggen et al., 2009; Vosteen et al., 2018), which could have made the predation more difficult and therefore reduce voracity. Nonetheless, as stated earlier, smaller prey can engender higher capture costs, meaning that the lighter weight of the focal prey probably generated a higher predation rate since more prey were needed to complete development. It could also explain why the difference in voracity only appeared at third instar, where the voracity represented 78.32% to 82.39% of the total number of aphids consumed by a larva so the impact of prey size was emphasised. However, since the biomass consumed by larvae on the focal prey diet was lower at second and third instars—even though the number of aphids consumed was higher at third instar—it seems that the higher predation rate on the focal prey diet did not totally compensate for the smaller weight of the melon aphids. This result is consistent with the fact that *E. americanus* tends to be lighter when feeding on the focal prey.

Overall, our results emphasize the potential of the American hoverfly to control the melon aphid in a banker plant system involving the bird cherry-oat aphid. The fact that, at least at high aphid densities, the focal prey engenders similar results to the banker prey concerning hoverfly development time, survival, deformations, and sex ratio suggests that melon aphids could sustain a viable population of American hoverflies given that the banker prey has been successfully used as a rearing prey at the Biological Control Laboratory since 2014. It also implies that the population growth of the American hoverfly would not be altered by longer development, higher mortality and unbalanced sex ratio with the arrival of the focal prey in the crop. Moreover, even though the focal prey produced lighter individuals, considering that the difference was only about 20% and that hoverfly reproductive performance is also strongly dependent on other factors like available floral resources (Laubertie et al., 2012; van Rijn et al., 2013), arrival of the focal prey in the system would probably not significantly reduce the reproductive performance of individuals.

However, more research is needed to properly assess the impact of the arrival of the focal prey on the population dynamics of the American hoverfly in a banker plant system in the field. Among other things, if the predator does not tend to lay eggs in populations of aphids parasitized or predated by other natural enemies, it could lead to control failure. Apart from the necessity to develop well on its prey, the capacity of biocontrol agents to control pest populations also relies on intrinsic characteristics such as their voracity (Dunn et al., 2020). The huge voracity of the American hoverfly on both the focal and banker preys should generate a high killing rate, which is essential, particularly in the case of fast-growing aphids like the melon aphid.

3.6 Conclusion

In conclusion, the American hoverfly appears well suited to attacking and potentially controlling the melon aphid, as at least in the laboratory, hoverflies on a melon aphid diet developed quickly and with low rates of mortality. In addition, the higher voracity of the predator on the smaller focal prey should maximize the predation impact on the melon aphid population. Moreover, as tested by Gonzalez et al. (2023)[2], the American hoverflies should readily oviposit in melon aphid colonies in the field if it is presented with the right banker plant species, like finger millet or corn, *Zea mays* L. (Poaceae). Nonetheless, future studies should also examine how other factors such as interactions with other natural enemies, the presence of additional alternative prey species, and the more variable weather conditions in the field may alter the effectiveness of the American hoverfly as a biocontrol agent for *A. gossypii*. Due to the small sample sizes used in the experiments, results must also be interpreted with caution. Nevertheless, this study provides novel evidence to suggest that *E. americanus* can be successfully reared on melon aphids in the laboratory, and thus American hoverflies may well be a suitable candidate for development as a biocontrol agent against *A. gossypii* in the future.

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[2] See Annexe A.

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CHAPITRE 4

THE RIGHT BANKER PLANT FOR THE RIGHT APPLICATION: COMPARISON OF THREE CANDIDATES FOR APHID BIOCONTROL, BARLEY (*HORDEUM VULGARE* L.), CORN (*ZEA MAYS* L.), AND FINGER MILLET (*ELEUSINE CORACANA* (L.) GAERTN)

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4.1 Résumé/Abstract

En régions tempérées, la lutte biologique contre les pucerons dans les cultures maraîchères sous abris est principalement réalisée par des lâchers multiples d'agents de lutte biologique, mais cette méthode n’est pas toujours efficace. Du fait de la croissance rapide des populations de pucerons, l'action retardée des agents de lutte biologique permet aux populations de pucerons de dépasser le seuil économique de traitement et de générer des dégâts. Les systèmes de plantes réservoirs compensent ce retard en offrant aux ennemis naturels un environnement de qualité avant l'arrivée des ravageurs. De manière optimale, les plantes réservoirs doivent être faciles à produire, résistantes aux conditions environnementales, fournir une grande quantité de proies alternatives, et enfin, résister à la pression d’herbivorie de ces proies alternatives. La présente étude vise à comparer la valeur de trois espèces candidates de Poaceae, l'orge (*Hordeum vulgare* L.), l'éleusine (*Eleusine coracana* (L.) Gaertn) et le maïs (*Zea mays* L.), par des expériences de laboratoire et en serre. Nos résultats montrent que les trois plantes peuvent convenir à des contextes différents. L'éleusine produit la plus grande biomasse fraîche à sa hauteur optimale, peut détenir la plus grande quantité de proies réservoirs et résiste plus longtemps à la pression d’herbivorie des pucerons que les autres plantes. Néanmoins, elle est 19,16 fois à 829,10 fois plus coûteuse à produire que l'orge et le maïs respectivement. L'orge pousse 2,00 fois plus vite que l'éleusine et 2,20 fois plus vite que le maïs.

Mots clefs : Charge maximale de pucerons, sénescence, caractéristiques de croissance, serres, puceron bicolore des céréales.

In temperate regions, biological control of aphids in greenhouse vegetable crops is mostly achieved by multiple releases of biocontrol agents, but this method is not always effective. Due to the rapid growth of aphid populations, the delayed action of biocontrol agents allows the aphid populations to overpass the economic threshold of treatment and generate damage. Banker plant systems compensate for this delay by providing natural enemies with an environment of quality before the arrival of pests. Optimally, banker plants should be easy to produce, resistant to environmental conditions, provide a large quantity of alternative prey, and finally, resist the herbivory pressure of these alternative prey. The present study aims to compare the value of three candidate Poaceae species, barley (Hordeum vulgare L.), finger millet (Eleusine coracana (L.) Gaertn), and maize, (Zea mays L.), in laboratory and greenhouse experiments. Our results show that the three plants can be suitable for different contexts. Our results showed that finger millet produced the biggest fresh biomass at its optimal height, had the highest peak load of banker prey, and resisted longer to aphid feeding than the other plants. Nevertheless, it is more expensive to produce on a scale of 19.16 times and 829.10 times compared to barley and corn respectively. Barley was 2.00 times faster to grow than finger millet and 2.20 times faster to grow than corn.

Keywords: Maximal charge of aphids, senescence, growth characteristics, greenhouses, bird cherry-oat aphid.

4.2 Introduction

In temperate regions, aphid biological control in greenhouses is often performed through the repeated releases of a high number of mass-reared natural enemies, under an augmentative approach (Knapp et al., 2020). Due to the rapid rate of increase in aphid populations (Dixon, 1998; Borges et al., 2011), these approaches are often inefficient or too costly for growers to ensure the constant presence of beneficial insects inside the greenhouses (Rabasse and van Steenis, 1999). Delay between the arrival of the pest and the introduction and subsequent action of biocontrol agents is indeed a major problem in biological control. It often provides time for aphids to reach high densities and damage crops (Tenhumberg, 1995; Frank, 2010; Payton Miller and Rebek, 2018). The use of banker plants in greenhouses is the ideal tool to overcome this problem by ensuring the enduring presence of biocontrol agents before the arrival of pests (Huang et al., 2010; Payton Miller and Rebek, 2018; Xu et al., 2020). The system relies on the addition of banker plants into the protected crop, providing an alternative food source and a breeding medium for the natural enemies of the target pest. For aphid control by predators and parasitoids, the banker plant is often inoculated with an alternative aphid prey or host which is usually different from the protected crop and targeted pest (Yano, 2006, 2019; Frank, 2010; Huang et al., 2011; Payton Miller and Rebek, 2018). Generally, the banker plants used against aphids are composed of monocotyledons with the bird cherry-oat aphids, *Rhopalosiphum padi* L. 1758, serving as an alternative host for parasitoid wasps such as *Aphidius colemani* Viereck, 1912 and *Aphidius matricariae* Haliday, 1834 or an alternative prey for predatory gall midges such as *Aphidoletes aphidimyza* (Rondani, 1848) (Frank, 2010, Huang et al., 2011; Payton Miller and Rebek, 2018; Pijnakker et al., 2020).

Apart from the reduction of the delay before the action of the biocontrol agents, banker plants present numerous advantages over augmentative biocontrol. Among other things, they ensure high-quality biocontrol agents by avoiding transport and reducing release manipulations, they are cheaper than conventional release of beneficials, and they can promote the recruitment of other natural enemies (Bennison and Corless, 1993; Fischer and Leger, 1997; Yano, 2006; Huang et al., 2011; Payton Miller and Rebek, 2018). Nonetheless, they require an investment of time and space from the growers and can sometimes act as sinks of natural enemies if they are preferred over the focal crop/pest (Huang et al., 2011; Pijnakker et al., 2020).

The selection of a banker plant relies on different aspects related to the system, such as the individual characteristics of the banker plant itself, and the relation between the banker plant, the biocontrol agent, and the crop with its target pest (Huang et al., 2011; Jandricic et al., 2014; Yano, 2019). A suitable banker plant system should be fast-growing, cheap to produce, sustain a high population of alternative prey, resist the feeding of the latter, and be compatible with the growth parameters of the targeted environment (Frank, 2010; Huang et al., 2011; Jandricic et al., 2014). The banker plant species can have an impact on several of those characteristics (Frank, 2010). Among other things, some plants can be better hosts for the banker prey by engendering better development and higher population growth rate (Price et al., 1980; Jacobson and Croft, 1998; Abe et al., 2011). Some plants also have better resistance to the feeding of banker prey (Jacobson and Croft, 1998) and greenhouse conditions (Payton-Miller and Rebek, 2018). For example, Jacobson and Croft (1998) found that control of the melon aphid (*A. gossypii* Glover 1877) could be achieved by three different banker plants, ryegrass (*Lolium perenne* L.), corn (*Zea mays* L.), and wheat (*Triticum aestivum* L.), but considered the corn to be better suited since it required less maintenance. Wheat often succumbed to mildew or other diseases and the banker prey, *R. padi*, did not thrive on ryegrass and needed to be reinoculated often. The banker plant system must also be appropriate for the crop and the targeted biocontrol agent. The latter must be able to develop and reproduce on the banker plant system but choose to lay eggs preferentially on the focal crop/pest system (Frank, 2010; Huang et al., 2011). For example, a study in an experimental greenhouse found that the use of barley banker plants with *R. padi* provided better control of *A. gossypii* on daisies than on pansies and, by contrast, provided better control of *M persicae* on pansies than on daisies (Van Driesche et al., 2008). Therefore, the choice of the right banker plant, including the plant species and the banker prey species, is a key factor for the success of a biocontrol program for a protected crop. (Coppel and Mertins, 1977; van Lenteren and Manzaroli, 1999; Almohamad et al., 2009; Huang et al., 2011).

The most used banker plant system against aphids in protected crops is barley (*Hordeum vulgare* L.) or wheat infested with *R. padi* for the parasitoid wasp *A. colemani* (Yano, 2019). Nonetheless, even if those plants have been efficient at controlling pests in numerous situations (Starý, 1993; Goh et al., 2011; Bellefeuille et al., 2021), their superiority over other monocotyledons has not received much attention (Frank, 2010; Huang et al., 2011) except for a few comparative studies (Jacobson and Croft; 1998; Jandricic et al., 2014; Song et al., 2017). Among other species, corn and finger millet (*Eleusine coracana* (L.) Gaertn) have been effective at controlling different pests including aphids with biocontrol agents such as parasitoid wasps mostly, but also predatory midges (Fischer and Leger, 1997; Jacobson and Croft, 1998; Boll et al., 2001; Xiao et al., 2011). Several characteristics of those plants, and the commonly used barley banker plant, have been mentioned in greenhouse, field, and laboratory experiments. Finger millet was described as needing little maintenance, lasting "several months" according to Boll et al. (2001) under greenhouse conditions and feeding by banker prey. Fischer and Leger (1997) affirmed that this plant has a very dense architecture, suggesting it could sustain a high population of banker prey. It however grows slowly, reaching maturity after three to six months (Dida and Devos, 2006; Kumar and Srivastava, 2020). Corn was also stated as resistant, lasting three months under greenhouse conditions and feeding of banker prey (Jacobson and Croft, 1998). It reaches maturity in approximately three months (García-Lara and Serna-Saldivar; 2019). Barley is fast-growing, reaching the two leaves stage (aimed for banker plant use) in only three weeks (Power et al., 1967). However, it was described as poorly resistant to high temperatures, needing to be replaced every 7 to 14 days under greenhouse conditions by Payton Miller and Rebek (2018). All that information considered, except for anecdotical data scattered in multiple experiments, the individual characteristics predisposing finger millet, corn, and barley as adequate banker plants have never been properly compared.

The present study aimed to characterize barley, finger millet, and corn as banker plants for aphid biocontrol programs in greenhouses. We hypothesized that the plants would have different benefits. According to the information cited previously, we predicted that a) barley would be shorter and easier to produce, but would resist less aphid feeding and sustain a smaller alternative prey population than the two other plants, b) finger millet and corn would be longer to grow but would resist longer to aphid feeding and greenhouse conditions, and c) finger millet would sustain a higher population of banker prey.

4.3 Material and methods

4.3.1 Biological material

Plants were grown in the greenhouses complex of the University of Quebec in Montreal (UQAM), under the following conditions: 23°C average temperature, 16L: 8D photoperiod supplied with artificial light (high-pressure sodium), and 50% R.H. The barley, *H. vulgare* for cattle feeding, and finger millet, *E. coracana* for human consumption, were sown directly in pots of 13 x 13 x 15cm with approximately (or precisely for the growth characteristics experiment) 300 and 800 seeds per pot respectively to ensure maximum density. Corn, *Z. mays* variety P9188 for cattle feeding, was sown in seed trays and after two weeks transplanted individually in pots of 13 x 13 x 15cm. All seeds used were free of pesticide treatment. Plants were watered two to three times a week and fertilized (N-P-K, 20-20-20) once a week.

Insect rearing was done at the Biological Control Laboratory (UQAM). *Rhopalosiphum padi* were provided by Anatis Bioprotection Inc. (https://anatisbioprotection.com/en/) and reared in a growth chamber (Conviron E15) on barley plants (18°C, 16 L:8 D photoperiod, and 60% R.H.), in cages of 36 x 36 x 38 cm covered with muslin.

4.3.2 Maximal aphid charge and resistance to aphid feeding

The experiment took place under controlled conditions (25°C, 16 L:8 D photoperiod, 50% R.H.). Barley, finger millet, and corn were inoculated with 1000 *R. padi* of all stages and placed in cages (25 x 25 x 60 cm for barley and finger millet and 25 x 25 x 95 cm for corn) covered with mousseline. At the time of inoculation, barley measured between 22 cm and 25 cm (23,72 cm on average), finger millet between 21cm and 45cm (28,33 cm on average), and corn between 60 cm and 110 cm (82,67 cm on average). The optimal height of the plant was determined as the optimal compromise between developmental time, space required in a greenhouse, and production of fresh biomass. The plant condition (based on preestablished degradation characters projected on a scale from 100 to 0%, see Table 4.1) and the number of aphids were estimated at the beginning of the experiment and once a week afterward. The number of aphids on each plant was estimated by counting precisely on a portion of the plant and multiplying that count by 1/proportion. In the case of spontaneous parasitism, mummies were counted. It never reached more than 10% of the aphid population. The maximal charge of aphids was defined as the maximum number of aphids reached on each plant. Watering was done two to three times a week and fertilization (N-P-K, 20-20-20) once a week. Seventeen replicates were performed with barley, 15 with finger millet, and 15 with corn.

Table 4.1 Plant condition scale

	100-76%	75-51%	50-26%	25-0%
	Good health, straight and strong leaves, absence or little honeydew.	Sagging of the leaves, presence of honeydew.	Yellowing of the leaves, possible presence of mold.	All or almost all the leaves completely yellow, low

				abundance of aphids.

4.3.3 Plant condition in greenhouses

The experiment took place in two 30 x 7m greenhouses, situated in two different regions (Montérégie, Québec and Lanaudière, Québec) and lasted from June until September 2020. The majority of the crop was cucumber.

Each of the first two weeks, two barley banker plants and two finger millet banker plants, inoculated with *R. padi*, were introduced for a total of four plants per greenhouse per week. In the following weeks, plants were replaced when they died or when there were no more aphids in the plants. The plant condition was evaluated every week (Table 1). Corn was not tested in that experiment since it would have produced too few replicates/plant species for statistical analysis.

4.3.4 Growth characteristics of plants

The experiment took place in the greenhouse complex of UQAM [23°C, 16L: 8D photoperiod supplied with artificial light (high-pressure sodium) and 50% R.H.]. Respectively 300 and 800 seeds per pot (13 x 13 x 15 cm) of barley and finger millet were planted in direct seeding to maximize density. Before sowing, the seeds (300 or 800 by pot) were weighed. The corn kernels were planted in a multi-cell tray and transplanted into larger pots (13 x 13 x 15 cm) one to two weeks later, depending on when the seeds germinated. Plant size was measured once a week and the plants were watered twice a week and fertilized (20-20-20) once a week. When the plants reached the expected size (average size of the banker plants used in the preceding laboratory experiment), the number of strands (representing the number of germinated seeds) was counted, and the fresh biomass was weighed. In this experiment, no aphids were introduced. A total of 18 barley plants, 18 finger millet plants, and 25 corn kernels were planted.

4.3.5 Statistical analysis

All statistical analyses were performed using R statistical software version 4.0.3. (R Core Team, 2020). The packages lme4 (Bates et al., 2015) (for the quadratic mixed model), mgcv (Wood, 2011) (for the general additive models), and emmeans (Lenth, 2022) (for post-hoc analysis of mixed models and estimation of the marginal means presented in the figures) were used. For all models, the choice of inclusion of the fixed effects and interaction terms was based on the biological pertinence of the terms as well as on the comparison of the AIC of the different models. The validation of the models was done with Shapiro tests and Q-Q plots for the normality of residuals. Plots of Pearson residuals against explanatory variables were performed to verify the homoscedasticity of variance.

4.3.5.1 Maximal aphid charge and resistance to aphid feeding

Maximal charge of aphids, after square root transformation, was evaluated by an ANOVA followed by a Tukey multiple comparisons of means test. The difference in the evolution of aphid charge through time between the three plant species was modeled by a generalized additive model with time, plant species, and interaction between time and plant species as fixed effects and replicate identity (ID) as a random effect. The response variable, number of aphids by plant, was transferred on the square root scale for better normality of the residuals. Mean number of weeks before senescence was compared between the three plants by a non-parametric Kruskal-Wallis rank sum test followed by a Dunn's test due to the absence of normality of the residuals even after log, square root, or inverse transformation. The difference between the three plants species in terms of degradation of the plant condition through time was evaluated by a quadratic model with time, square time, plant, and interaction between time and plant as fixed effects and replicate ID as random effect. The response variable, plant condition, was transferred on the square root scale for better normality of the residuals.

4.3.5.2 Plant condition in greenhouses

Since some plants were taken out before senescence (due to space constraints in the greenhouse for example), the analyzes were only carried out over the first 4 weeks after introduction. Analyzing the data beyond that period would have created a bias since, after the fourth week, too many finger millets had been taken out before senescence (five) compared to barley (one) which died more rapidly. Only one replicate (finger millet) was removed before senescence less than four weeks after its introduction and was not included in the analyses. With the two greenhouses combined, 16 barley plants and 11 finger millet plants were included in the analyses. The difference between the two plants in terms of degradation of plant condition through time was evaluated with a generalized additive model with time, plant species, and interaction between plant species and time as fixed effects and ID as well as greenhouse as random effects.

4.3.5.3 Growth characteristics of plants

The average price per weight of barley and corn seeds was calculated as the mean of the annual price of seeds from 2010-2011 to 2015-2016 provided by the annual report of the *Financière Agricole du Québec*, available on the website of *Producteurs de grains du Québec* (2022). The average price of the finger millet was calculated as the mean of the price of four suppliers chosen randomly. As this plant is not produced locally, the price may be more variable. Also, the shipping was not included in the calculation so the price might be underestimated. The price of each barley and finger millet plant of the experiment was estimated by multiplying the weight of the seeds used with the average price per weight of the seeds. For those two plants, the germination rate is considered in the weight of the seeds (germinated and ungerminated seeds were all weighed together before planting). The price was calculated the same way for corn but, as it was sown individually (1 seed/pot), the weight of ungerminated seeds was not considered in the initial calculation. To account for the fact that not all seeds will germinate, the mean price/ plant was divided by the germination rate. For the fresh weight of corn, only leaf biomass was included in the analysis considering that most of the stalk biomass is not accessible to aphids. Differences between the three plants in terms of time before senescence, fresh weight, and price for 100 plants at optimal height were analyzed by non-parametric Kruskal-Wallis tests followed by Dunn's multiple comparison tests, adjusted with the Bonferroni method.

4.4 Results

4.4.1 Maximal aphid charge and resistance to aphid feeding

The average maximal charge of aphids was significantly higher on finger millet, 25806 ± 5228 aphids, than on barley, 13077 ± 2981 aphids (n = 32, p-value = 0.027) (Figure 4.1A). The average maximal charge of aphids on corn, 16526 ± 1758, was not significantly different from the one of the two other plants (n = 30, and p-value = 0.239 for finger millet and n = 32, p-value = 0.591 for barley) (Figure 4.1B). Nevertheless, the temporal dynamics of aphid colonies, number of aphids (± CI 95%) through time, on the banker plants were different between the three species (Figure 4.1B). The maximal charge of aphids was achieved at 2.00 weeks after inoculation for barley (n = 17), 3.00 weeks after inoculation for finger millet (n = 15), and 2.91 weeks after inoculation for corn (n = 15). A 50% diminution in the abundance of aphids in the colony was reached after 2.57 weeks for barley, 3.71 weeks for corn, and 5.51 weeks for finger millet. The abundance of aphids in the colony was similar for the three plants one week after inoculation but significantly lower in barley than in corn and finger millet from two weeks (n = 32, t-ratio = 6.287, and p-value <0.001 for corn and n = 32, t-ratio = 9.327, and p-value <0.001 for finger millet) until three weeks after inoculation (n = 32, t-ratio = 3.906, and p-value <0.001 for corn and n = 32, t-ratio = 10.236, and p-value <0.001 for finger millet). All barley plants reached senescence before the fourth week after inoculation. Aphid colonies on finger millet were significantly larger than on corn from the second week after inoculation until corn senescence (six weeks after inoculation) (n = 30 for all weeks, t-ratio = 3.005, and p-value <0.009 for week two, t-ratio = 6.625, and p-value <0.001 for week three, t-ratio = 8.745, and p-value <0.001 for week four, t-ratio = 7.064, and p-value <0.001 for week five, and t-ratio = 4.270, and p-value <0.001 for week six).

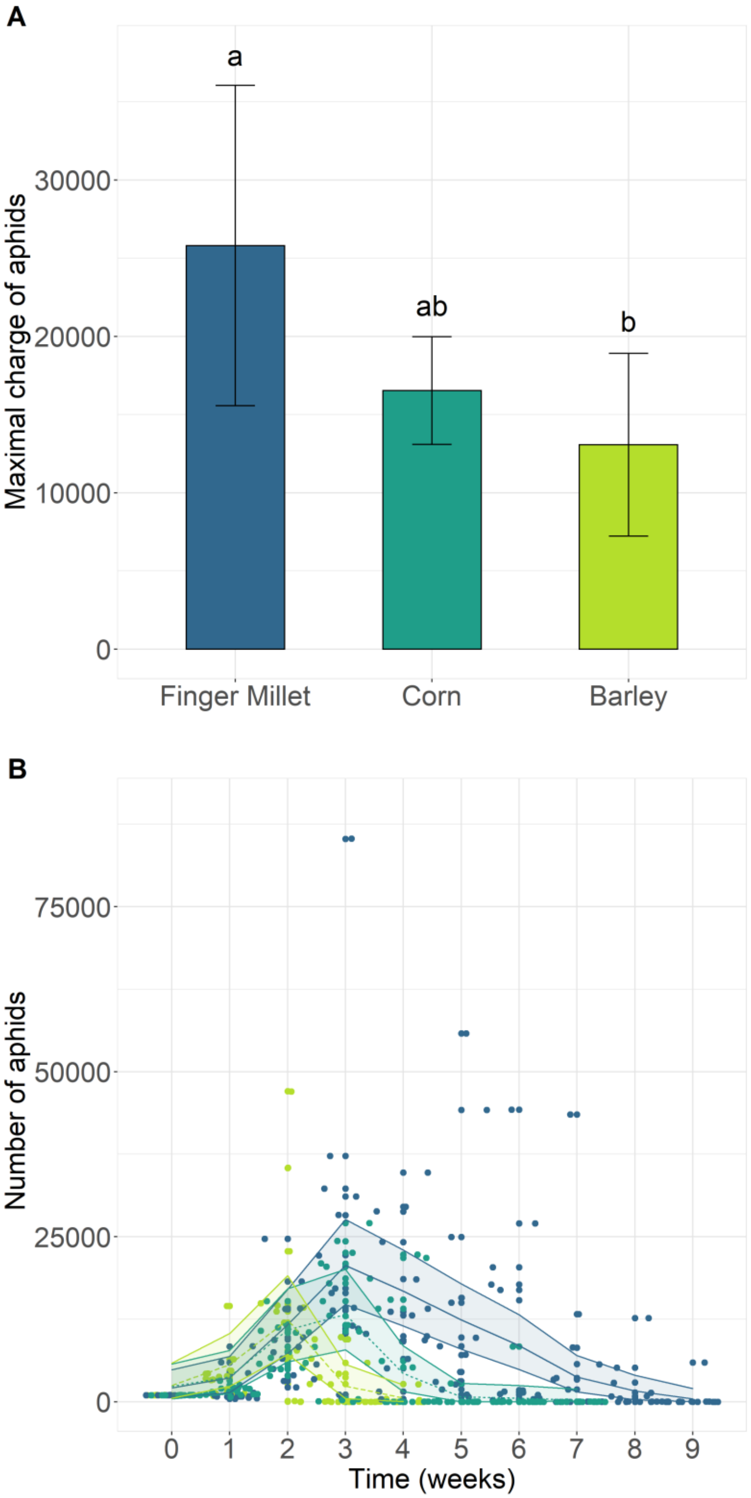

Figure 4.1 Maximal charge of aphids (± CI 95%) (A) and temporal dynamic of the number of aphids (± CI 95%) (B) on three banker plants after inoculation with 1000 *R. padi*. (A) ANOVA followed by a Tukey multiple comparisons of means test. Letters indicate a significant difference (alpha = 0.05) (B) Generalized additive model with time, plant species, and interaction between the two factors as fixed effects and ID as a random effect. Means and CI (95%) displayed are estimated marginal means and CI derived from the model.

Finger millet resisted significantly longer to aphid feeding pressure, with a mean time before senescence of 7.00 ± 0.29 weeks, than corn and barley, which respectively lasted on average 4.27 ± 0.28 weeks and 3.23 ± 0.14 weeks (Figure 4.2A). As presented in Figure 4.2B, contrary to the corn, the condition of finger millet and barley decreased following a linear trend with no statistically significant quadratic effect of time (n = 15, t-value = -0.124, and p-value = 0.901 for finger millet, and n = 17, t-value = 0.910, and p-value = 0.363 for barley). The rate of degradation of barley was more important than the one of finger millet (n = 32, t-value = -2.567, and p-value = 0.011). For corn, the quadratic effect of time was statistically significant (n=15, t-value = 6.811, and p-value < 0,001) with a faster decrease at the start, and the inclination of the slope was significantly more pronounced than the finger millet, but not than barley (n = 30, t-value = 6.259, and p-value < 0.001 for finger millet, and n = 32, t-value = 1.226, and p-value = 0.221 for barley). According to the statistical model, the plant condition had decreased by 50% respectively 2.41 weeks after inoculation for barley, 2.76 weeks for corn, and 5.15 weeks for finger millet.

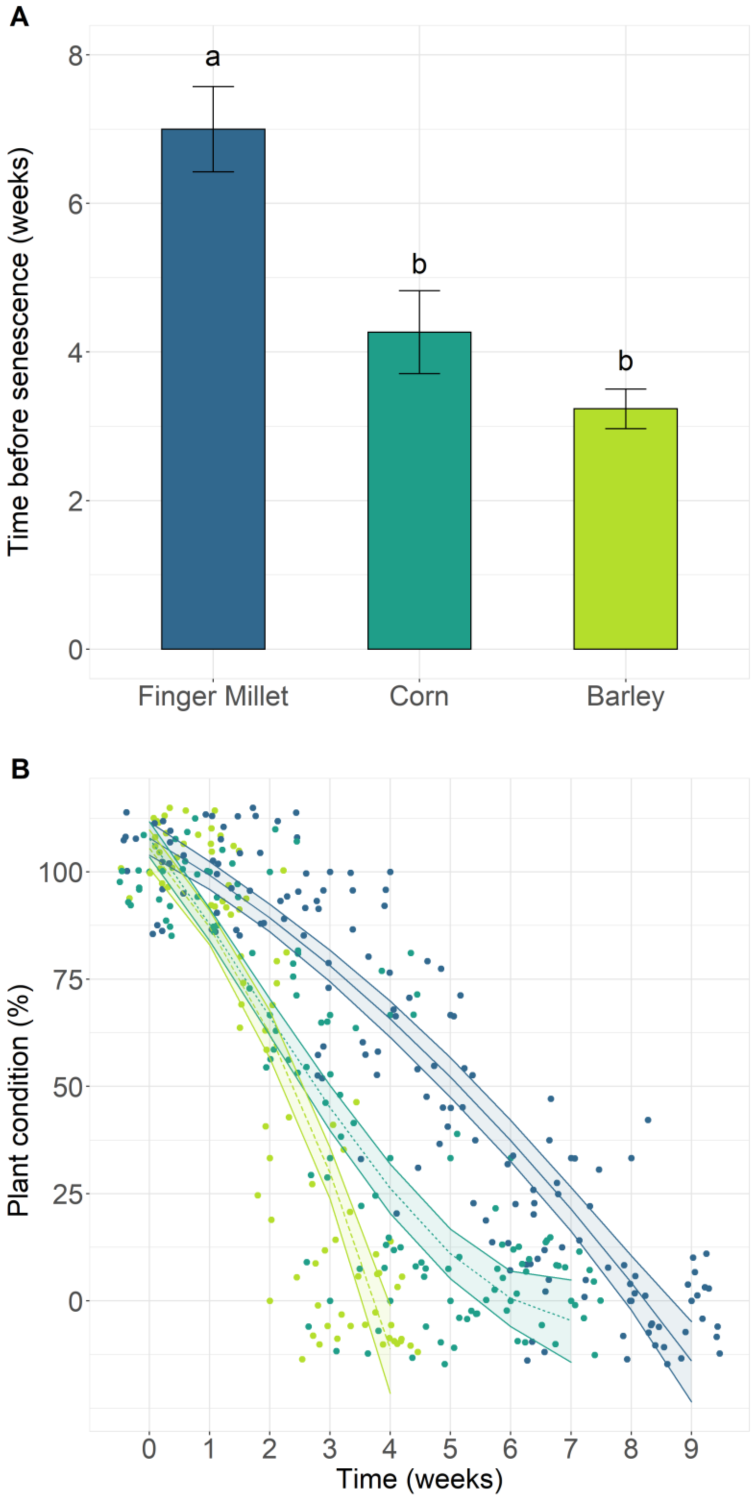

Figure 4.2 Time before senescence (mean ± CI 95%) (A) and temporal evolution of the plant condition (mean plant condition ± CI 95%) (B) of three banker plant species after inoculation with 1000 *R. padi*. (A) Kruskal-Wallis rank sum test followed by a Dunn's test. Letters indicate a significant difference (alpha = 0.05). (B) Quadratic model with time, square time, plant, and interaction between time and plant as fixed effects and replicate ID as random effect. Means and CI (95%) displayed are estimated marginal means and CI derived from the model.

4.4.2 Plant condition in greenhouses

In the greenhouses, the degradation of barley compared to finger millet followed a similar trend to that of the laboratory experiments, the latter maintaining a better condition than barley through time (Figure 4.3). The random effect of the greenhouse in which the plants were (In Montérégie, Québec or Lanaudière, Québec) was not significant (F value = 0.000, p-value = 0.893). The global effect of plant species on the degradation of their condition through time was statistically significant (n = 26, F value = 37.644, and p-value < 0.001). There was a significant difference in mean plant condition between the two species from one to four (limit of the data analyzed) weeks after introduction in the greenhouse (n = 26, t-value = -4.396 and p-value < 0.001 for the first week, n = 26, t-value = -6.041 and p-value < 0.001 for the second week, n = 26, t-value = -6.345 and p-value < 0.001 for the third, and n = 26, t-value = -5.258 and p-value < 0.001 for the fourth week).

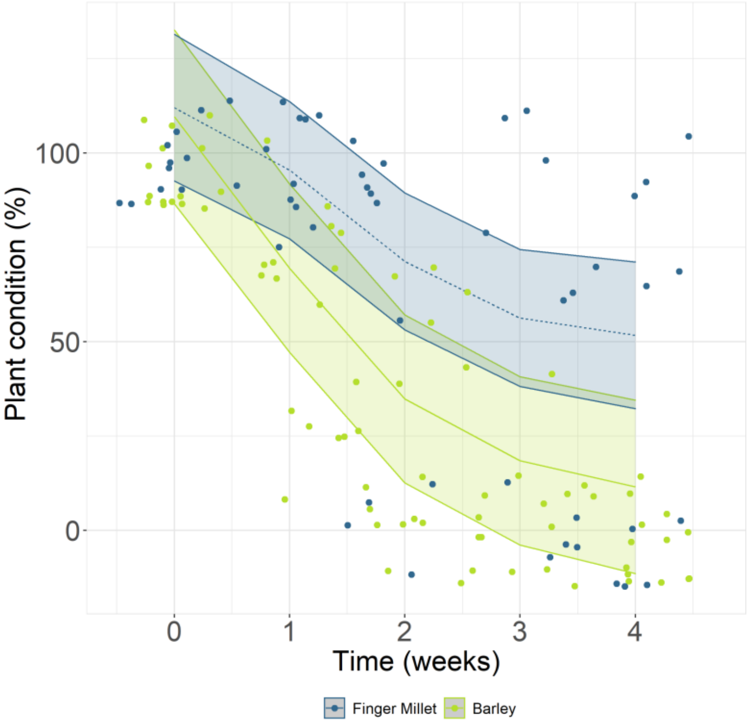

Figure 4.3 Degradation (mean plant condition ± CI 95%) of barley and finger millet condition through time in greenhouse. The difference between the two plants in terms of degradation of condition through time was evaluated with a generalized additive model with time, plant species, and interaction between plant species and time as fixed effects and ID and greenhouse as random effects. Means and CI (95%) displayed are estimated marginal means and CI derived from the model.

4.4.3 Growth characteristics of plants

Barley was 2.00 times faster to grow (2.16 ± 0.09 weeks on average) than finger millet (4.33 ± 0.11 weeks on average) (n = 36, Z value = 4.578, p-value < 0.001) and 2.20 times faster to grow than corn (4.76 ± 0.09 weeks on average) (n=39, Z value = 6.405, p-value < 0.001) (Figure 4.4A). The growth time of corn and finger millet was not significantly different (n=39, Z value = -1.654, p-value = 0.294). Finger millet had a significantly higher fresh weight at its optimal size (96.81 ± 3.50g on average) than barley (58.97 ± 1.32g on average) and corn (52.97 ± 3.63g on average) (n = 36, Z value = 4.458, p-value < 0.001 for barley, and n=39, Z value = 5.622, p-value < 0.001 for corn). Its fresh matter was respectively 1.64 and 1.83 times heavier than the one of barley and corn (Figure 4.4B). No significant difference was found between fresh weight of barley and corn (n = 39, Z value = -0.996, p-value = 0.958). Finger millet was significantly costlier (on average 4.87 ± 0.12$ for 100 plants) to produce than corn (on average 0.01± 0.00$ for 100 plants) (n = 39, Z value = 7.034, p-value < 0.001) and barley (on average 0.25 ± 0.00$ for 100 plants) (n = 36, Z value = 3.25, p-value = 0.003), being 829.10 times more expensive than corn and 19.16 times more expensive than barley (Figure 4.4C). Barley was 43.27 times costlier to produce than corn (n = 36, Z value = -3.66, p-value < 0.001).

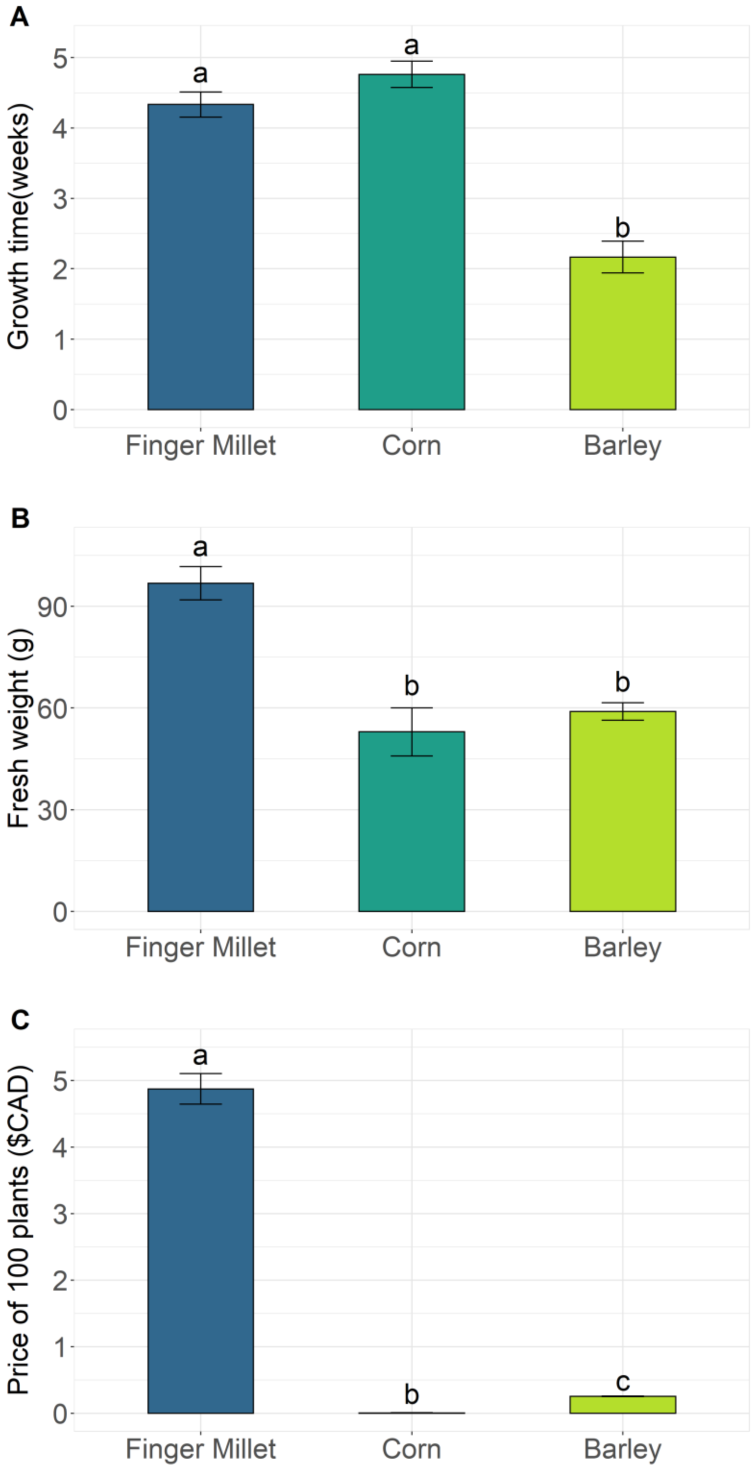

Figure 4.4 Growing parameters of barley, corn, and finger millet. (A) Differences in growth time to reach optimal size, (B) fresh weight at optimal height, and (C) price for 100 plants of the three plant species were analyzed by Kruskal-Wallis tests followed by Dunn's multiple comparison tests for non-parametric data, adjusted with the Bonferroni method. Letters indicate a significant difference (alpha = 0.05)

4.5 Discussion

Overall, the results show that the three plant species are suitable banker plants. However, they have specific characteristics that predispose them to be used in different contexts. Barley had the advantage to grow fast (2.16 ± 0.09 weeks) and at a low cost. Nonetheless, as predicted, it produced less fresh biomass and sustained a smaller maximal charge of aphids for a shorter period (both under controlled conditions and in the greenhouse). Indeed, the results showed that, under controlled conditions, the colony of banker prey and the plant condition decreased very rapidly. Both parameters were reduced by 50% respectively only 2.57 weeks and 2.41 weeks after inoculation. This means that even before reaching senescence, at on average 3.23 ± 0.14 weeks, the plant's capacity to sustain a high population of biocontrol agents was already lessened significatively because of its poor condition and of the low population of banker prey it contained. This implies that barley would need to be changed often, most likely, one or two weeks after inoculation, as stated by Van Driesche et al. (2008). Those characteristics make that plant species more appropriate for rapid crop cycles, like lettuce which only takes 4 weeks to grow before being harvested (Hamza et al., 2022). The fact that this plant is cheap and fast to grow and that it reaches its maximal aphid charge faster than corn and finger millet (after 2.00 weeks) may compensate for its need to be changed often. Nonetheless, the fact that it does not sustain a high banker prey population means it would most probably sustain a smaller population of biocontrol agents than the other plants (Frank, 2010; McClure and Frank, 2015). Moreover, as described by Yano (2006), in closed systems under banker plant biocontrol, the control of a pest population is possible if the initial number and growth rate of the pest population can be compensated by the predator/parasitoid population and its predation/parasitism rate. Therefore, since barley would probably provide a lower population of natural enemies, this banker plant could lead to control failure if it is introduced too late in the season (allowing pests to reach a population threshold impossible to control with few biocontrol agents). It might also not be efficient with aphid pest having a particularly high population growth rate, such as the melon aphid on cucurbits (Messelink et al., 2020) for example, or if it is used with slow-growing crops that allow the population of pests to increase for too long.

The finger millet had opposite benefits to barley. It had the advantage to sustain an abundant population of banker prey (1.97 and 1.56 times higher respectively than barley and corn), partly because the plant has a very dense architecture (Fischer and Leger, 1997), providing important fresh biomass at maturity. Moreover, that population collapsed at a lower velocity on finger millet than on the two other plants (reaching a 50% diminution only 5.51 weeks after inoculation, i.e. 2.14 and 1.49 times slower than on barley and corn respectively). This implies that finger millet could probably sustain a larger population of biocontrol agents (Frank, 2010; McClure and Frank, 2015). It might also be appropriate for a larger range of biocontrol agents including voracious predators, like syrphids or ladybeetles that need a high population of banker prey

(Rabasse and van Steenis, 1999). Again, since bigger and more efficient (voracious or with a high parasitism rate) natural enemies can control faster-reproducing pests (Yano, 2006), finger millet could be appropriate for pests with high rates of increase, like the melon aphid for example (Messelink et al., 2020). Nonetheless, the use of the banker prey by natural enemies also depends largely on the architecture of the plant (Andow and Prokrym, 1990; Clark and Messina, 1998). Indeed, as Prado and Frank (2013) showed in a greenhouse experiment, *A. colemani* reduced *Myzus persicae* (Sulzer, 1776) densities to a lesser extent (52% vs 93%) on denser plants. The dense architecture of finger millet might therefore complicate access to banker prey and reduce the potential production of natural enemies of this plant. However, predators and parasitoids can also have specific searching patterns and the availability of aphids might depend on the natural enemy concerned (Price et al., 1980). Furthermore, finger millet was longer, both to grow and to reach its maximal charge of aphids, and costlier to produce than barley. This means, coherently with the literature (Fischer and Leger, 1997), that this plant needs less maintenance, but more investment for its production.

Corn presents some benefits of the other two plants. Like barley, it was cheap but did not produce important fresh biomass at its optimal height. Like finger millet, it grew at a slow pace. Even though it did not produce a high fresh vegetal biomass, its mean maximal charge of aphids tended to be higher than the one of barley and lower than the one of finger millet but was not significantly different from both plants. It did not, however, tolerate well aphid feeding as aphids and plant condition decreased rapidly, reaching a 50% diminution at 3.71 weeks and 2.76 weeks respectively after inoculation. Those results are different from the findings of previous studies. Jacobson and Croft (1998) stipulated that corn could last around three months under the feeding pressure of aphids under greenhouse conditions (21-24°C). This could be because aphids remained low due to pressure imposed by *A. colemani*. Plants indeed had to be reinoculated once during their experiment. The difference could also come from the fact that plants were potentially not the same height (not mentioned) as in the present experiment. If the corn was allowed to grow more, it might have reached a more resilient state and thus have resisted better to aphid feeding. Nonetheless, in the present case, the poor resistance of corn was similar to the one of barley, meaning it would probably also need to be replaced every one or two weeks after inoculation, making it more appropriate for short crop cycles. As it is cheaper to produce, on a scale of 19.16 and 829.10 times compared to barley and finger millet, even if it involves more maintenance than finger millet, and is longer to produce than barley, it is still an interesting banker plant solution from an economic point of view. Finally, being able to reach a banker prey population somewhat, but not significantly, higher than barley, it might be able to support a slightly bigger population of biocontrol agents (Frank, 2010; McClure and Frank, 2015), or species that are a little more voracious or have a slightly higher parasitism rate. Nonetheless, its use should be concealed to short crop cycles and non-innundative use as it can not control a very high population of pests.

4.6 Conclusion

Overall, each of the three banker plants seems suitable in different specific contexts. Corn, and even more so barley, could be more adapted to short crop cycles and targeted pests with a slower population growth rate than finger millet. Even if they are adequate for similar types of systems, they don't present the same benefits since barley grows faster than corn but is costlier. Finger millet could be more appropriate for long crop cycles with fast reproducing natural enemies, voracious predators, or highly efficient parasitoids and, like corn, would need more planning and investment at the beginning of the growing season.

Nonetheless, other critical aspects must be considered when choosing a banker plant system. Among other things, the biocontrol agents targeted need to oviposit and develop well on the banker plant system (Frank, 2010; Huang et al., 2011). They must have an oviposition preference for the focal crop infested with the pest over the banker plant system, and the plant species of the latter can influence this balance (Huang et al., 2011, Payton Miller and Rebeck, 2018; Gonzalez et al., 2023). Furthermore, as most of the results are from laboratory experiments, future studies should examine the utilization of the banker plants by natural enemies under greenhouse conditions. Investigation of the potential to combine banker plant species for optimization of their use by different beneficials could also be interesting. Chen et al (2022) recently showed that the combination of *Ricinus communis* L.- *Trialeurodes ricini* (Misra, 1924) and *Glycines max* L.- *Megoura crassicauda* Mordvilko, 1919 banker plant systems had a positive impact on the control of two major pests in tomato, *M. persicae* and *Bemisia tabaci* (Gennadius, 1889). The combination allowed the population of two important natural enemies, *Encarsia formosa* Gahan 1924 and *Propylea japonica* (Thunberg, 1781) to increase enough for efficient control of both pests. This aspect is of crucial importance since several pests are often present at the same time in crops so multiple biocontrol agents are needed. Finally, in the present experiment, the height of the plants was determined as the optimal compromise between length of development, space utilization in a greenhouse, and production of fresh biomass, but other experiments using the same banker plant species but with units of different heights would be interesting since, as suggested with corn, it might influence the parameters tested. All those aspects remain to be studied, and the choice of banker plant system should be based not only on the overall aspects of the plant species, but also on its interaction with the crop and natural enemies, and its compatibility with the growth parameters of the targeted crop (Frank, 2010, Huang et al., 2011).

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CONCLUSION

Dans un contexte de changements climatiques et de modification des courants de pensées vers une gestion plus verte de la production maraîchère, de nouvelles alternatives aux pesticides doivent être développées. La gestion des pucerons, ravageurs importants des cultures, sous régie biologique n'est pas encore suffisamment efficace pour être adoptée par la majorité des producteurs (Knapp et al., 2020; Rabasse et van Steenis, 1999). En régions tempérées, le contrôle de ces derniers se fait par de multiples lâchers d'agents de lutte, mais fréquemment cela ne suffit pas puisque les pucerons ont un taux de croissance très élevé et peuvent causer des dommages rapidement (Knapp et al., 2020; Rabasse et van Steenis, 1999). Pour cette raison, le système de plantes réservoirs constitue une alternative particulièrement bien adaptée à ces ravageurs. Ce système assure la présence des agents de lutte avant à l'arrivée des ravageurs, en fournissant des ressources alimentaires et un milieu de reproduction pour les ennemis naturels des ravageurs (Frank, 2010; Huang et al., 2011; Payton Miller et Rebek, 2018; Yano, 2019). Il permet donc de réduire les risques liés à la croissance rapide des populations pucerons puisque celles-ci sont soumises au contrôle des agents de lutte dès leur arrivée (Fischer et Leger, 1997; Frank, 2010; Payton Miller et Rebek, 2018). L'un des pucerons les plus dommageables à travers le monde est le puceron du melon, dont la gamme d'hôtes s'étend à 700 espèces végétales (Richard et Boivin, 1994; Hosseinzadeh et al., 2017; Rodríguez-Gasol et al., 2020; Bonsignore et Vacante, 2018). En Amérique du Nord, le contrôle de ce puceron est effectué majoritairement par l'introduction d'une combinaison d'agents de lutte: une guêpe parasitoïde, telle que *A. colemani* ou *A. matricariae* et la cécidomyie prédatrice, *A. aphidimyza* (Messelink et al., 2020). Les parasitoïdes peuvent toutefois être sujets à l'hyperparasitisme en milieu d'été et ne sont donc pas toujours efficaces (Capinera, 2004). C'est dans ce contexte qu'un nouvel agent de lutte, le syrphe d'Amérique, a été étudié dans ce projet, ce afin d'évaluer son potentiel à complémenter les méthodes existantes dans la lutte contre le puceron du melon, en système de plantes réservoirs.

Tout d'abord, une description morphologique des stades larvaires du syrphe d'Amérique, *Eupeodes americanus* (Wiedemann 1830) a été effectuée afin de combler le manque de connaissances à ce sujet. Les résultats ont permis d'établir deux critères morphologiques permettant la discrimination simple et rapide des stades larvaires à l'aide d'une loupe binoculaire ou d'une loupe de terrain. Le premier stade peut être discriminé des autres par la présence de longs poils noirs sur la partie dorsale du tégument tandis que, tel que décrit par Rotheray et Gilbert (2011) chez de nombreuses espèces européennes, le troisième stade peut être discriminé des autres par la fusion des tubes respiratoires postérieurs. Le deuxième stade est caractérisé par le fait qu'il ne possède aucun de ces deux critères: les poils sont translucides et les tubes respiratoires sont distincts. Plusieurs autres critères (secondaires), qui évoluent progressivement au cours du développement larvaire du syrphe, ont également été décrits. En plus de fournir un outil important pour l'étude de cette espèce indigène, cette démarche scientifique a permis de montrer que la méthode de la photographie image par image peut être pertinente pour la description morphologique des espèces.

Cet outil a rendu possible les étapes suivantes du projet: tout d'abord, l'étude du développement et de la voracité du syrphe d'Amérique en fonction d'une alimentation composée de la proie focale, le puceron du melon, ou de la proie réservoir, le puceron bicolore des céréales. Pour qu'un système de plantes réservoirs soit efficace, il est fondamental que les agents de lutte puissent maintenir une population élevée et donc se développer convenablement sur les deux proies impliquées dans le système. La voracité envers ces derniers doit aussi être assez importante pour pouvoir contrôler la proie focale (ravageur). Dans cette étude, la proie réservoir constituait un témoin permettant un bon développement et générant une importante voracité. La proie réservoir est effectivement utilisée comme proie d'élevage au laboratoire de lutte biologique de l'UQAM depuis 2014 avec d'excellents résultats. L'étude a permis de valider la première prédiction, soit le fait que les deux proies permettaient au prédateur de compléter son développement. La deuxième prédiction, qui supposait que la proie focale serait de moins bonne qualité que la proie réservoir pour le développement du syrphe d'Amérique a été infirmée en grande partie. Excepté le poids des individus qui était significativement moins élevé lorsqu'ils s'alimentaient de la proie focale, aucune différence significative n'a été observée entre les deux diètes concernant le temps de développement, le taux de mortalité et de déformations et le sexe-ratio des adultes. Fondamentalement, la différence de poids des individus pourrait signifier une baisse de fécondité puisque les individus moins lourds auraient moins de ressources à allouer à leur reproduction (Honěk, 1993; Branquart et Hemptinne, 2000). Toutefois, puisque le modèle prévoit une seulement de l'ordre de seulement 20%, cet aspect ne devrait avoir qu'un impact négligeable sur l'efficacité du système de lutte en serre. La troisième prédiction, qui prévoyait que le syrphe d'Amérique serait plus vorace sur la proie réservoir que sur la proie focale a également été infirmée. Les résultats ont plutôt montré une voracité plus élevée au troisième stade sur la proie focale. La biomasse consommée était toutefois, tel que prévu, plus importante lorsque le prédateur consommait la proie réservoir. Cela concorde avec le fait que cette diète engendre des individus légèrement moins lourds, ce qui ne représente qu'un impact mineur sur l'efficacité du système de lutte. Cette étude confirme donc le potentiel prometteur du syrphe d'Amérique pour le contrôle du puceron du melon en système de plantes réservoirs en serre.

Toutefois, d'autres aspects doivent être pris en considération dans l'évaluation d'un tel système, comme la préférence de ponte de l'agent de lutte. Il est fondamental que cette dernière soit dirigée préférentiellement vers la culture focale contenant la proie focale plutôt que vers le système de plantes réservoirs (Frank, 2010; Huang et al., 2011; Yano, 2019). Cet aspect a été vérifié dans le cadre d'une collaboration avec une doctorante du laboratoire de lutte biologique de l'UQÀM, Noémie Gonzalez. Les résultats, présentés en ANNEXE A, montrent que les systèmes de plantes réservoirs de maïs et d'éleusine, avec *R. padi* pourraient être intéressants puisqu'ils engendrent une préférence de ponte, légère dans le cas du maïs et particulièrement marquée dans le cas de l'éleusine, pour la culture de concombre avec le puceron du melon. L'orge avec *R padi*, quant à lui, semble peu approprié puisqu'il est nettement préféré à la culture focale.

En plus de son impact sur la préférence de ponte des ennemis naturels, l'espèce végétale d'une plante réservoir peut jouer un rôle important dans le succès d'un système de lutte (Huang et al., 2011; Jandricic et al., 2014). Dans cette optique, le maïs, l'orge et l'éleusine ont été évaluées en tant que plantes réservoirs pour la lutte contre les pucerons. Celles-ci ont été sélectionnées car elles présentaient des structures végétales différentes et étaient soit utilisées couramment, comme c'est le cas de l'orge, ou avaient déjà été démontré des résultats prometteurs en contexte de plantes réservoirs (Huang et al., 2011, Payton Miller et Rebek, 2018). La première prédiction a été validée, l'orge étant effectivement performante au niveau de la productibilité car elle croît rapidement et occasionne peu de coûts. Elle a toutefois produit une moins grande biomasse végétale fraiche et supporté une moins grande colonie de proies alternatives que l'éleusine, à laquelle elle a aussi moins bien résisté, tant en laboratoire qu'en serre. La deuxième prédiction a aussi été validée en partie, le maïs étant une plante plus longue à produire, mais ayant tendance à mieux résister à la pression d'herbivorie que l'orge (non significatif), mais moins que l'éleusine. La colonie de pucerons fournie par le maïs n'était toutefois pas significativement moins importante que l'éleusine même si une tendance était encore une fois visible. La dernière prédiction a aussi été validée, l'éleusine étant une plante longue et coûteuse à produire, mais fournissant une grande quantité de proies alternatives à cause de sa structure dense (fournissant une importante biomasse végétale fraîche) et sa résistance à l'herbivorie. Par le fait même, elle nécessite peu d'entretien. Les trois plantes sont donc optimales dans différents contextes grâce à leurs caractéristiques individuelles. L'orge et le maïs semblent plus appropriés pour des cycles de culture courts et des agents de lutte moins voraces ou dont le taux de parasitisme de pucerons est bas puisqu'ils fournissent une petite quantité de proies réservoirs. L'orge propose plus de réactivité face aux imprévus, car elle se produit rapidement, tandis que l'avantage du maïs réside dans son coût très bas. L'éleusine paraît optimale pour des cycles de culture plus longs et des prédateurs voraces ou des parasitoïdes efficaces, mais nécessite, comme le maïs, plus de prévision puisqu'elle se produit plus lentement et entraîne des coûts de production plus importants.

En conclusion, ce projet a permis de suggérer et d'évaluer un modèle pour optimiser le potentiel du syrphe d'Amérique pour le contrôle du puceron du melon en serre de concombre. Les différentes étapes du projet ont permis de montrer qu'un système de plantes réservoirs impliquant le puceron bicolore des céréales pourrait être adéquat pour le contrôle du puceron du melon par le syrphe d'Amérique, mais que l'espèce végétale réservoir doit être judicieusement sélectionnée. L'orge ne semble pas être optimale dans le présent contexte parce qu'elle est hautement préférée au système concombre-puceron du melon en ce qui concerne la ponte et fournit moins de proies réservoirs, ce qui peut être problématique pour un agent de lutte aussi vorace que le syrphe d'Amérique. La nette préférence de ponte pour la culture focale avec la proie focale lorsque le syrphe doit choisir entre cette dernière et le système éleusine-proie réservoir est un aspect très avantageux de cette espèce végétale en tant que plante réservoir. Cet équilibre pousse à croire que la plante réservoir d'éleusine favorisera la dispersion de l'agent de lutte vers la culture focale et le ravageur si elle est utilisée dans le contexte à l'étude. Le système maïs-proie réservoir pourrait également être adéquat puisqu'il n'engendre aucune préférence de ponte significative entre lui et la culture focale,. Toutefois, puisque l'éleusine peut soutenir des colonies de proies réservoirs plus importantes pour une plus longue durée, elle serait sans doute plus adéquate pour le syrphe d'Amérique.

Toutes ces conclusions proviennent toutefois presque exclusivement d'expériences de laboratoire et doivent donc être interprétées avec prudence. Deux études en conditions réelles ont été effectuées dans le cadre du présent projet, mais ont donné des résultats trop peu concluants pour être présentés. La première s'est déroulée en serres de concombre (6 au total, réparties chez 3 producteurs et groupées en couples de serres témoin et test). L'objectif était d'installer dans les serres tests des plantes réservoirs d'orge et d'éleusine en début de saison, d'y introduire 40 syrphes par semaine pour les deux premières semaines et ensuite de surveiller l'évolution des colonies de pucerons du melon au fil de la saison de croissance dans toutes les serres (témoins et tests). Plusieurs embûches ont rendu cette expérience infructueuse. D'abord, pour des raisons techniques, l'expérience reposait sur l'infestation naturelle des cultures de concombre par le puceron du melon. Ce dernier n'a infesté que trois serres sur six, rendant les résultats difficilement interprétables. Le principal problème a toutefois été que les colonies de syrphes ne se sont installées dans aucune des serres tests pour une durée de plus de 3 semaines après leur introduction. Afin de résoudre ces problèmes, l'année suivante, un nouveau design expérimental a été établi. Les plantes réservoirs et les syrphes ont cette fois été introduits dans des serres de fines herbes, qui ne sont pas sensibles aux pucerons du melon, suivant la même séquence d'introduction que dans l'expérience précédente. Cette fois, les plants de concombres ont été introduits dans les serres. La moitié d'entre eux étaient en cages (donc inaccessibles aux syrphes) et l'autre moitié était libres d'accès. Tous étaient inoculés de pucerons du melon. L'objectif était encore une fois de faire le suivi des colonies de pucerons du melon et de comparer les colonies des plants sous traitement par les syrphes et à celles des plants témoins. Malheureusement, l'échec de l'établissement des colonies de syrphes a encore mené à l'abandon de l'expérience. Le premier obstacle a été ici la colonisation des plantes réservoirs par la cécidomyie prédatrice *A. aphidimyza*. Les tests ont donc été reportés à la fin de l'été, après l'entrée en diapause de cette dernière. Les résultats n'ont toutefois pas été plus concluants, les colonies de syrphes chutant rapidement après leur introduction. Plusieurs hypothèses pourraient expliquer ce phénomène telles que l'occurrence de parasitisme du syrphe d'Amérique à un taux assez important pour contrôler sa population ou encore la dispersion trop importante des adultes qui ne resteraient pas dans la serre. En effectuant un inventaire des espèces de syrphes en culture de laitue aux États-Unis, Smith et Chaney (2007) ont d'ailleurs trouvé que jusqu'à 57% des larves de syrphes étaient parasitées par les parasitoïdes *Diplazon* sp. (Hymenoptera : Ichneumonidae) ou *Pachyneuron* sp (Hymenoptera : Pteromalidae). Le taux de parasitisme semblait être positivement corrélé avec la maturité des plants. Il est également possible que la présence d'individus ou d'œufs d'autres ennemis naturels dans les plantes réservoirs ait nuit à la ponte des syrphes. Almohamad et al. (2008a) ont effectivement démontré que les femelles *E. balteatus* pondaient significativement moins d'œufs dans les colonies de pucerons où il y avait des momies ou des larves d'*Harmonia axyridis* (Pallas, 1773). Toutefois, l'échec des deux expériences en conditions de serres effectuées dans le cadre de ce projet contraste avec les résultats de Bellefeuille et al. (2021) qui, en suivant un design expérimental presque identique à celui de notre deuxième expérience, ont démontré que le syrphe d'Amérique pouvait contrôler le puceron de la digitale à basse température, en système de plantes réservoirs. L'une des principales différences réside dans le fait que l'expérience a été effectuée à la fin du printemps (avril-mai) au lieu de l'été ou l'automne. Si, tel qu'avancé par Smith et Chaney (2007), le taux de parasitisme augmente avec la maturité des cultures, il est possible que le fait que l'expérience de Bellefeuille et al. (2021) se soit déroulée en début de saison ait contribué au succès d'établissement des populations de syrphes, les parasitoïdes et les cécidomyies étant moins efficaces à ce moment. D'autres expériences en contexte de serre sont nécessaires afin d'étudier cette problématique et de vérifier l'efficacité du syrphe d'Amérique en contexte réel aux différentes périodes de la saison de culture.

Malgré ceci, les résultats ont mis en évidence plusieurs caractéristiques du syrphe d'Amérique qui le prédisposent à être un bon agent de lutte contre les pucerons en général. Étant un aphidiphage généraliste (Rojo et al., 2003), le syrphe d'Amérique a le potentiel d'être utilisé contre d'autres espèces que le puceron du melon. Son importante voracité, démontrée dans le chapitre 3, soit de 1780,44 à 2266,33 proies consommées en approximativement 7 jours, est une caractéristique particulièrement intéressante pour un agent de lutte contre les pucerons, qui ont un taux de reproduction très élevé (Rabasse et van Steenis, 1999). Il pourrait être intéressant, par exemple, d'évaluer son potentiel de lutte contre les diverses espèces de pucerons affectant la laitue. Cette dernière représente une part importante des cultures sous abris au Québec (121 829 m^2 de superficie de culture en 2015 comparativement à 114 496 m^2 pour le concombre) et est souvent sujette aux infestations de pucerons (MAPAQ, 2018; Gard et Giovanna, 2020). Selon Bugg et al. (2008), les syrphes seraient les principaux ennemis naturels impliqués dans le contrôle du puceron de la laitue, *Nasonovia ribisnigri* (Mosley, 1841), qui ravage les cultures de laitue sur la côte centrale de Californie. Le syrphe d'Amérique est d'ailleurs parmi les espèces de syrphes communément retrouvées dans ces cultures (Bugg et al., 2008). Puisque la laitue contient peu de trichomes, il est probable que les larves de syrphes s'y déplacent facilement et que les adultes y pondent des œufs. Dans ce contexte, la plante réservoir qui, tel que montré en ANNEXE A, peut avoir un impact important sur la préférence de ponte du syrphe d'Amérique, devrait être sélectionnée afin d'optimiser la ponte sur la culture focale, soit la laitue avec le puceron ravageur ciblé. Cela dit, de plus amples investigations devraient être menées afin de vérifier la possibilité de commercialisation des laitues malgré la présence de larves de syrphes (faisabilité d'éliminer les larves avant au lavage précédant la commercialisation). Les résultats permettent d'extrapoler sur le potentiel du syrphe pour le contrôle des pucerons en contexte de serre, mais se transposent moins bien aux cultures en champs. Toutefois, de nombreuses études ont également démontré l'efficacité des bandes florales pour l'attraction de plusieurs espèces de syrphes, incluant *E. balteatus*, *Melanostoma sp.* et *Sphaerophoria sp.*, pour le contrôle des ravageurs en milieux ouverts (Hickman et Wratten, 1996; Marshall et West, 2007; Haenke et al., 2009; Tschumi et al., 2014; Serée et al., 2022). Il serait intéressant d'investiguer le potentiel de contrôle du syrphe d'Amérique en grande culture, considérant que celui-ci est très vorace et détient plusieurs autres caractéristiques intéressantes en tant qu'agent de lutte tel qu'une importante fécondité (Ouattara et al., 2022) et une excellente capacité de vol (Bellefeuille et al., 2017).

En plus des conclusions sur le potentiel de lutte du syrphe d'Amérique en système de plantes réservoirs, ce projet a permis d'élargir l'état des connaissances sur plusieurs autres sujets. Entre autres, l'efficacité de la photographie par image par image pour l'étude morphologique des arthropodes a été démontrée. De plus, ce projet a permis d'augmenter les connaissances sur la morphologie de l'importante espèce indigène qu'est le syrphe d'Amérique. Il a également mis en lumière l'impact que peut avoir un régime alimentaire sur le développement des arthropodes. Finalement, il a démontré que les plantes réservoirs sont un système complexe et que les espèces végétales peuvent avoir un impact majeur sur le succès d'un programme de lutte. De nombreuses autres avenues restent toutefois à explorer, telles que la compatibilité du syrphe avec d'autres agents de luttes, l'efficacité de ce dernier à différents moments de l'année, son potentiel en cultures sous lumière artificielle, ou encore son efficacité dans d'autres cultures sous abris sujettes aux infestations de pucerons.

ANNEXE A

OVIPOSITION PREFERENCE OF THE AMERICAN HOVERFLY, EUPEODES AMERICANUS, BETWEEN BANKER PLANTS AND TARGET CROP

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A.1 Résumé/Abstract

L'évaluation des préférences de ponte des syrphes prédateurs est essentielle pour prédire le succès de ces agents de lutte biologique contre les pucerons dans les serres, en particulier lorsqu'un système de plantes réservoirs est utilisé ou lorsque les serres sont en cultures mixte. Dans cette étude, les préférences de ponte du syrphe d'Amérique, *Eupeodes americanus* (Wiedemann, 1830) (Diptères : Syrphidae) ont été évaluées dans des expériences de choix avec différents systèmes plante/pucerons. Les choix de ponte des femelles ont été évalués dans deux contextes : choix entre plantes réservoirs et cultures cibles et choix entre deux cultures (cultures mixtes). Les résultats ont montré que, dans les cultures de concombre, l'espèce de plante réservoir utilisée influence considérablement la préférence de ponte du syrphe. Celui-ci avait une préférence pour l'orge par rapport au concombre et pour le concombre par rapport à l'éleusine. Aucune préférence entre le concombre et le maïs comme plante réservoir n'a été démontrée. Les résultats ont aussi démontré que, contrairement au concombre, la plante réservoir d'orge pourrait être appropriée pour les cultures de poivron, puisque ce dernier est préféré par rapport à la plante réservoir. Dans un contexte de culture mixte, le syrphe d'Amérique n'a pas de préférence entre le concombre et le poivron, ce qui signifie qu'il pourrait être utilisé en serre pour protéger les deux cultures. Cette étude montre que le système de plante réservoir doit être choisi en fonction des cultures/pucerons présents dans la serre afin d'optimiser l'impact du syrphe comme agent de lutte biologique.

Mots clefs : Syrphes aphidophages, Syrphidae, Lutte biologique, *Aphis gossypii*, *Myzus persicae*, *Rhopalosiphum padi*, cultures en serres.

Assessing the oviposition preferences of predatory hoverflies is essential to predict the success of these biological control agents against aphids in greenhouses, especially when using banker plant systems or for greenhouses with mixed crops. In this study, the oviposition preferences of the American hoverfly, Eupeodes americanus (Wiedemann, 1830) (Diptera: Syrphidae) were evaluated in two-choice experiments with different plant/ aphid systems. Female oviposition choices were evaluated in two contexts: choice between banker plants and target crops and choice between two crops (mixed crops). The results showed that in cucumber crops, the species of banker plant used drastically influences the oviposition preference of the hoverfly, with a preference for barley over cucumber and a preference for cucumber over finger millet. However, there was no preference when corn was used as a banker plant. When faced with barley as a banker plant, the oviposition preference is also affected by the type of target crop/ pest. Results indeed showed that this banker plant could be adequate for pepper contrarily to cucumber crops. In a mixed crop context, the American hoverfly has no preference between cucumber and pepper, which means that it can be used in greenhouses to protect both crops. This study shows that the banker plant system should be chosen according to the crops/ aphids present in the greenhouse to optimize the impact of the hoverfly as a biocontrol agent.

Key words: Aphidophagous hoverflies, Syrphidae, Biocontrol, *Aphis gossypii*, *Myzus persicae*, *Rhopalosiphum padi*, Greenhouse crops.

A.2 Introduction

Aphids are major greenhouse pests (Knapp, Palevsky & Rapisarda, 2020; Rabasse & van Steenis, 1999). The use of pesticides against aphids can be problematic because they are resistant to several active ingredients and because hidden individuals are difficult to reach (Rabasse & van Steenis, 1999; Capinera, 2004). In temperate climates, biological aphid control strategies generally include inundative releases of parasitoids of the genus *Aphidius* combined with predators like the aphid midge, *Aphidoletes aphidimyza* Rondani 1847 (Diptera: Cecidomyiidae) (Gullino, Albajes, & Nicot, 2020). However, those biocontrol agents can be subject to hyperparasitism or intraguild predation and are not efficient enough in the middle of summer (Capinera, 2004; Bonsignore et Vacante, 2018; Knapp et al., 2020; Messelink et al., 2020a). Moreover, this method can be too costly, especially when using biological control agents with a short life cycle since they need to be introduced too often (Fischer & Léger, 1997; Boll et al., 2001). Therefore, aphids remain a major concern in several greenhouse crops (Gullino et al., 2020). For example, the melon aphid, *Aphis gossypii* Glover 1877 (Hemiptera: Aphididae) is still today one of the most important pests limiting the production of cucumber (*Cucumis sativus* (L.)) in many countries (Garzo, Diaz, & Fereres, 2003; Polat Akköprü, 2018; Chi, Zhang, Shi, Wang, & Liu, 2019; Alaserhat, Canbay, & Özdemir, 2021; Kahia et al., 2021). The development of new biological control methods is therefore necessary to improve aphid control and prevent crop losses.

The main problem associated with the biological control of aphids is the delayed action of natural enemies (Fischer & Léger, 1997; Payton Miller & Rebek, 2018). Even when aphid colonies are found early, the delay between detection, introduction of biological control agents, and time required for them to take effect often allow pest populations to increase beyond the economical threshold (Fischer & Léger, 1997). Banker plants could constitute a good solution as they ensure the constant presence of biological control agents in the crop by providing an alternative food source and oviposition sites even in the absence of pests (Huang et al., 2011; Frank, 2010). One possible drawback of banker plants is that they may act as a sink for the biocontrol agents and thus divert them from the target crop (Frank, 2010; Huang et al., 2011). The success of banker plants depends largely on the balance between the quality of the banker prey and the oviposition preference of the predator for the target prey. The biological control agent must be able to develop and reproduce well on the banker plant, but choose to leave it, at least partially, when pests invade the crop (Frank, 2010; Yano, 2019). Therefore, when evaluating the efficacy of a biocontrol agent using a banker plant system, it is necessary to investigate its oviposition behavior and more specifically its preference among all plants and aphid species involved (Frank, 2010). Moreover, in greenhouse production, two or three aphid species are often present at the same time. For example, intercropping integrates two crops or more under the same greenhouse (Rezende, Cecílio Filho, Barros Junior, Porto & Martins, 2011; Cecílio Filho, Rezende, Barbosa & Grangeiro 2011; Cecílio Filho, Neto, Rezende, Barros Junior & de Lima, 2015) creating a similar scenario where oviposition behavior is an important factor for biological control efficacy.

Apart from the use of banker plants, new biocontrol agents also need to be investigated for the control of aphids since, as stated earlier, the ones that are commonly used don't suffice for efficient control. Predatory flies of the Syrphidae family (Diptera) generally exhibit characteristics that predispose them to be successful biological control agents. For example, they tend to have a high voracity, a good flight and searching ability, and a high fecundity (Almohamad, Verheggen, & Haubruge, 2009; Rodríguez-Gasol, Alins, Veronesi & Wratten, 2020). The American hoverfly, *Eupeodes americanus* (Wiedemann, 1830) (Diptera: Syrphidae), which as an aphidophagous larval stage and a pollinator adult stage, shows great potential at controlling aphids. Previous research at the Biocontrol laboratory of Université du Québec à Montréal (UQAM) on the American hoverfly has shown that this species is active at low temperatures, e.g., for flight, oviposition, and feeding activities (Bellefeuille, Fournier, & Lucas, 2019), which enables it to efficiently control the foxglove aphid, *Aulacorthum solani* Kaltenbach 1843 (Hemiptera: Aphididae) in greenhouse crops (Bellefeuille, Fournier, & Lucas 2021). Furthermore, *E. americanus* has a longer larval development time (i.e. predacious stage) and longer adult longevity compared to the commercially available aphidophagous predator *A. aphidimyza* (Ouattara et al., 2022). However, knowing that hoverfly larvae do not disperse very well, control by the American hoverfly depends largely on the dispersion and oviposition of the females (Rodríguez-Gasol et al., 2020). Hoverfly oviposition preference is influenced by different factors such as aphid species, nutritional quality, and density (Sadeghi & Gilbert, 2000; Almohamad, Verheggen, Francis, & Haubruge, 2007, Dunn, Lequerica, Reid, & Latty, 2020). For example, female hoverflies of *Episyrphus balteatus* De Geer, 1776, (Diptera: Syrphidae) prefer to lay their eggs in colonies of the green peach aphid, *Myzus* *persicae* Sulzer 1776 (Hemiptera: Aphididae) and the pea aphid, *Acyrthosiphon pisum* Harris, 1773 (Hemiptera: Aphididae) rather than in colonies of the vetch aphid, *Megoura viciae* Buckton 1876 (Hemiptera: Aphididae) on broad beans (*Vicia faba* (L.)) (Vanhaelen, Haubruge, Gaspar & Francis, 2001). Another factor influencing the oviposition preference of syrphid females is host plant species, both in terms of physical traits and chemicals emitted by the plant (Almohamad et al. 2007, Dunn et al., 2020). According to Vanhaelen et al. 2001, *E. balteatus* prefers white mustard (*Sinapis alba* (L.)) to rapeseed (*Brassica napus* (L.)) and broad beans. Finally, predation risk associated with the site as well as the presence of intraspecific or interspecific competitors can have a dissuasive impact on oviposition by syrphid females (Hemptinne, 1993; Pineda, Morales, Marcos-García, & Fereres, 2007; Almohamad, Verheggen, Francis, & Haubruge, 2010; Amiri-Jami, Sadeghi, Gilbert, Moravvej, & Asoodeh, 2016; Dunn et al., 2020).

Therefore, the study aims to evaluate the oviposition behavior of the American hoverfly in different predominant greenhouse contexts in temperate regions, that is, cucumber or pepper (*Capsicum annuum* (L.)) crops, with or without banker plants. Both of those crops are affected by major pests: the melon aphid on cucumber, and green peach aphid on pepper (Messelink et al., 2020a; Messelink et al., 2020b). Three species of banker plants were evaluated in this study: barley (*Hordeum vulgare* (L.)), corn (*Zea mays* (L.)), and finger millet (*Eleusine coracana* (Gaert)). Those plant species were selected because they were either commonly used, such as barley, or had already demonstrated their efficiency as banker plants in previous experiments, such as corn and finger millet (Fischer & Leger, 1997; Jacobson & Croft, 1998; Goh et al., 2001; Frank, 2010; Huang et al., 2011 Bellefeuille et al. 2021). They are also well suited for the experiment since they are all used with the bird cherry-oat aphid, *Rhopalosiphum padi* L. (Hemiptera: Aphididae).

Our first objective was to evaluate if the three banker plant species were adequate for the control of the melon aphid on cucumber. For that, we verified if the American hoverfly laid proportionally more eggs on cucumber than on the banker plants. We also verified if some banker plant species were better suited than the others, i.e. engendering a bigger proportion of eggs laid on the focal crop and a higher number of eggs laid in total.

Our second objective was to verify that the barley banker plant, being the most commonly used, was adequate for the control of the green peach aphid on pepper (proportionally more eggs laid on pepper than barley). We also verified if that banker plant was more appropriate for this crop than for cucumber i.e. engendering a bigger proportion of eggs laid on the focal crop and a higher number of eggs laid in total.

Finally, our third objective was to verify if the oviposition behavior of the American hoverfly was adequate for the control of both the melon aphid on cucumber and the green peach aphid on pepper in a mixed crop greenhouse context (engendering an equal proportion of eggs laid on both focal crops).

A.3 Material and methods

A.3.1 Plants

The crop plants used during the experiment were pepper, *Capsicum annum* L. (Solanaceae) (cv. hybrid Aristotle X3R, Norseco) and cucumber, *Cucumis sativus* L. (Cucurbitaceae) (cv. hybrid Speedway, Norseco). The banker plants used were barley (Sollio agriculture), finger millet (Snake River Seed Cooperative), and corn (Sollio agriculture). All plants were sown and grown in the greenhouses of UQAM at 25°C during the day, 19°C at night, and 60% relative humidity (RH) and 16 L: 8 D under high-pressure sodium lamps. Seedlings of cucumber and pepper were transplanted in plastic pots (9 × 9 cm). The plugs and substrate used were a humus content potting mix enriched with compost (Garden soil, Fafard). The plants were watered as needed and provided weekly with a fertilizer (20–20–20 NPK). No chemical insecticides were applied to the plants.

A.3.2 Insect rearing

All insect colonies were kept at UQAM in the Biocontrol laboratory. *Aphis gossypii* were reared on cucumber and *M. persicae* on pepper in a 35 × 35 × 35 cm cage kept in a growth chamber at 24°C, with a 16 L: 8 D photoperiod and 70% RH. Wild adults of *E. americanus* were collected on Phlox sp. (L.) in Sainte-Agathe-de-Lotbinière (N 46 ° 23'726 "W 71 ° 21'446"), Québec, Canada in 2014. Hoverfly colonies were refreshed yearly with new wild individuals. American hoverfly rearing was done as described in Bellefeuille et al. (2019). In this study, broad bean plants infested with pea aphids were placed in the center of the cage to allow females to lay eggs after mating and the larvae were transferred to barley plants infested with the bird cherry-oat aphid. When needed, *R. padi* were transferred on finger millet or corn before using them for the experiment.

A.3.3 Objective 1: Adequacy of three banker plant species to control *A. gossypii* on cucumber

To evaluate the adequacy of the three banker plants, the oviposition preferences of *E. americanus* between each banker plant and *A. gossypii* on cucumber was verified. Three different choice trials (with barley, finger millet, and corn) were performed (Figure A.1A).

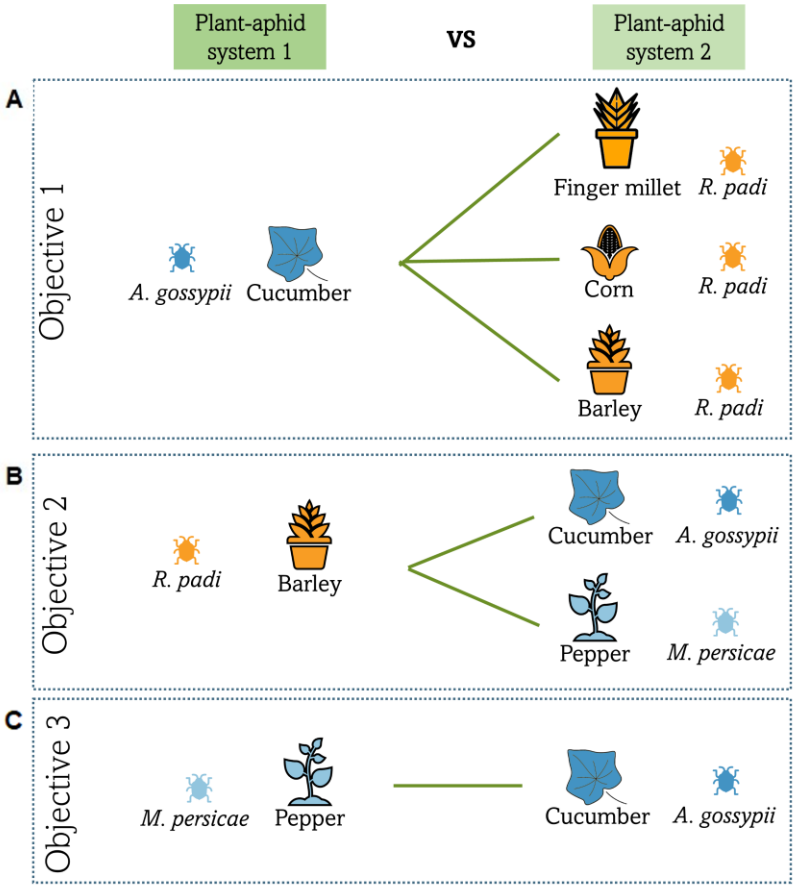

Figure A.1 Composition of the different choice trials as plant/ aphid systems

Each choice trial was done in a 50 x 45 x 58 cm transparent plastic box with a muslin-screened lid and two 20 x 20 cm screened windows (Figure A.2B). One banker plant with *R. padi* (alternative prey) was placed at one end of the box, and one cucumber plant with *A. gossypii* (focal crop and pest) was placed at the opposite end of the box (Figure A.2A). A total of 100 aphids of mixed developmental stages were placed on each plant in the box. Such a high number of aphids was chosen to better study oviposition since hoverflies prefer to lay eggs on plants with high densities of aphids (Almohamed et al., 2009). Each plant was provided with an artificial flower and a mixture of sugar: water (1: 10 v/ v) in a small cup with a roll of dental cotton sticking out of the lid for feeding the adult hoverflies. The artificial flower was made of a wooden stick with a cotton pad at its end, soaked in a mixture of water and honey, and covered with bee pollen (Miel Gauvin Inc.) (Figure A.2A). For each replicate, a female hoverfly was released in the middle of the plastic box between the two plant/ aphid systems (Figure A.2A). The test lasted four days, during which time the box was placed in a Conviron growth chamber at 25°C, 16 L: 8 D photoperiod, and 50% RH (Figure A.2B). After four days, the eggs laid were counted on each plant. Fifteen replicates were performed per choice trial. The quality of the aphid colonies was checked and replicates in which aphids did not develop correctly (abundance less than the initial individuals) were not considered.

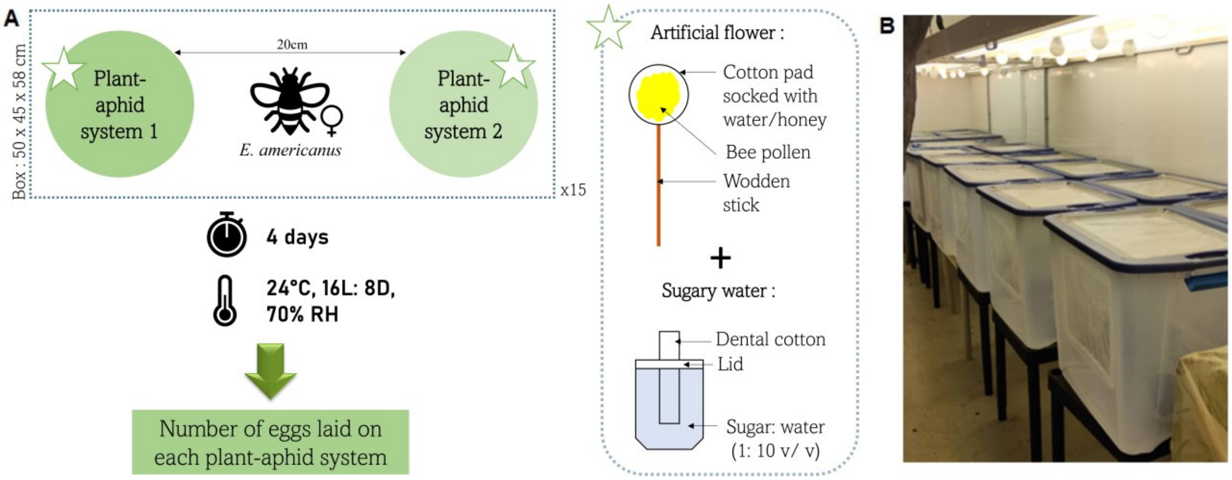

Figure A.2 (A) Experimental design of the choice trial used to identify the oviposition preference *of E. americanus* between two different plant/aphid systems; (B) Plastic boxes used to conduct the choice trials and placed in a Conviron growth chamber.

Female hoverflies used in this experiment were one week old. Before their introduction in the experiments, female hoverflies that newly emerged were put together in a screen cage measuring 30x30x60 cm for one week at a ratio of two males for three females. The hoverflies were left in groups so that each female copulated with several males, which reduced the chances of using an unfertilized female for a test, in the event of a dysfunctional male. They were fed with one artificial flower and sugary water as described above. One broad bean plant infested with pea aphids was also place in the center of the cage because the presence of an oviposition stimulus was proven to be necessary for hoverflies to lay fertile eggs and avoid the resorption of eggs (Branquart and Hemptinne, 2000; Orengo-Green et al., 2022).

A.3.4 Objective 2: Adequacy of barley banker plant species to control *M. persicae* on pepper and comparison with *A. gossypii* on cucumber

To evaluate the adequacy of barley banker plant for the control of *M. persicae* on pepper, the oviposition preferences of *E. americanus* between those two plant/ aphid systems was verified in a choice trial (Figure A.1B). The same methods as for objective 1 was used. Results were compared with the choice trial realized for objective 1 between barley banker plant and *A. gossypii* on cucumber.

A.3.5 Adequacy of the American hoverfly to control aphids in a mixed crop greenhouse context

To evaluate the adequacy of *E. americanus* in mixed crops, its oviposition preferences between *M. persicae* on pepper and *A. gossypii* on cucumber was verified in a choice trial (Figure A.1C). The same methods as for objective 1 was used.

A.3.6 Data analysis

Statistical analyses were carried out with R 4.0.5 software. For all the experiments, the normality and homoscedasticity of the residuals were verified with Shapiro–Wilk tests ($p > 0.05$) and inspection of diagnostic plots (residuals vs fitted, normal QQ plot, scale location, constant leverage). If they could not be obtained, even after square root, log, or inverse transformations, non-parametric tests were used. For each test, the significance level was set at alpha = 0.05.

For the first objective, the difference between the proportion of eggs laid by females on cucumber/*A. gossypii* and on the three banker plant systems was analyzed with non-parametric paired Wilcoxon tests or T test depending on the normality and homoscedasticity of the residuals. Afterward, within each choice trial, the number of eggs laid by females on the target crop cucumber and in total were respectively square root and log transformed. The impact of the banker plant system (corn, barley or finger millet with *R. padi*) on those two parameters was tested by one-way analysis of variance (ANOVAs). Posthoc Tukey's HSD tests were then performed to identify which banker plant systems engendered a significantly different number of eggs laid in total and on the focal crop.

For objective 2, the difference between the proportion of eggs laid on pepper/*M. persicae* and on barley/*R. padi* was tested by a paired T test. To verify if the barley banker plant was more adapted to pepper or cucumber crops, differences in the number of eggs laid during those two choice trials were analyzed (barley vs pepper and barley vs cucumber). The number of eggs laid on the focal crop (pepper or cucumber) was compared, using a non-parametric paired Wilcoxon test. The total number of eggs laid in those choice trials (on the banker plant and on the focal crop) was compared with a T test.

For objective 3, the difference between the proportion of eggs laid by females on pepper/*M. persicae* and cucumber/*A. gossypii* crop systems was analyzed with a non-parametric paired Wilcoxon test.

A.4 Results

A.4.1 Objective 1: Adequacy of three banker plant species to control *A. gossypii* on cucumber

Concerning the three cucumber/ *A. gossypii* and banker plant (barley, finger millet, and corn/ *R. padi*) choice trials, females showed statistically significant oviposition preferences in two out of the three trials (Figure A.3A). Moreover, in some cases, the female chose to lay all her eggs only on one of the two plants. Female hoverflies laid a significantly bigger proportion of eggs on the barley banker plant than on cucumber (respectively 82.00 ± 8.0% and 18.01 ± 8.32%, $n=30$, $V = 8$, p-value = 0.003). In this trial, 46.6% of females laid all their eggs only on barley. In contrast, female hoverflies laid a significantly bigger proportion of eggs on cucumber than on the finger millet banker plant (respectively 94.48 ± 3.57% and 5.51 ± 3.57%, n=30, V = 120, p-value < 0.001) and 53.3 % of females laid all their eggs only on cucumber. Finally, female hoverflies had no oviposition preference between the cucumber and the corn banker plant (respectively 55.35 ± 7.72% and 44,65 ± 7.72% of eggs laid on each plant/aphid system, n=30, t = 0.653, df = 14, p-value = 0.524) but 6.6% of females laid all their eggs only on corn.

All females laid between 92 ± 6.43 and 173 ± 18.71 eggs in total during the trials (Figure A.3B). When females were given the choice between cucumber and different banker plant systems, the total number of eggs laid per females varied significantly according to the banker plant species (n=45, F=10.15, df= 2, p < 0.001). Females laid 38 to 47% less eggs in the choice trial between cucumber and barley. The difference was significant compared to the choice trials between cucumber and finger millet or corn (respectively, p = 0.007 and p < 0.001) (Figure A.3B).

Similarly, in those choice trials, the number of eggs laid on cucumber varied significantly depending on which banker plant system it was paired with (n=45, F= 28.82, df = 2, p = 1.32e-08) (Figure A.3B). The number of eggs laid on the target crop, cucumber, in presence of barley was significantly lower than with finger millet by 93% (p < 0.001) and corn by 90% (p < 0.001) as banker plants. The number of eggs laid on cucumber with finger millet or corn as banker plants was not significantly different (p = 0.122).

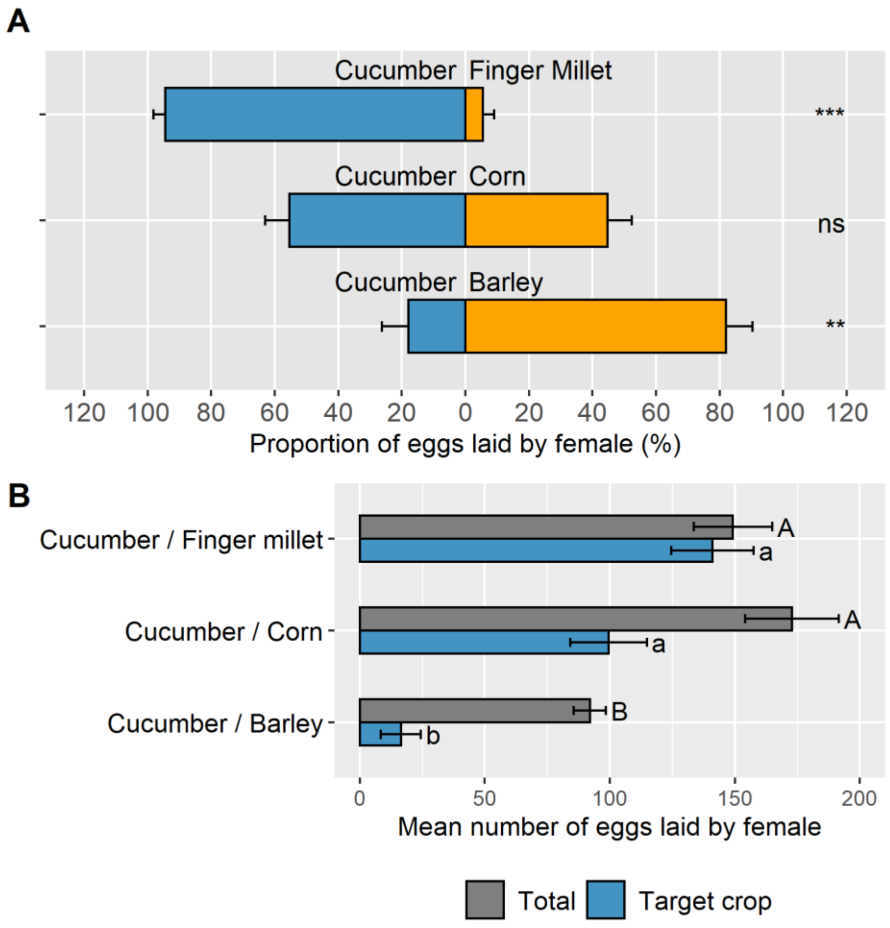

Figure A.3 (A) Proportion of eggs laid by *E. americanus* between cucumber and three banker plant systems. Significant differences between plant-aphid systems are showed by asterisks (alpha = 0.05, paired Wilcoxon test or T test). The signification of stars is as follows: ns>0.05 *<0.05 **<0.01 ***<0.001; (B) Number of eggs laid by *E. americanus* in choice trials involving cucumber and three banker plant systems. Uppercase letters indicate differences between total number of eggs laid in 4 days (alpha = 0.05, ANOVA followed by Tukey's HSD test). Lowercase letters indicate differences between the number of eggs laid on the target crop only (alpha = 0.05, ANOVA followed by Tukey's HSD test). The lines represent the mean ± SE.

A.4.2 Objective 2: Adequacy of barley banker plant species to control *M. persicae* on pepper and comparison with *A. gossypii* on cucumber

Concerning the choice trial with pepper/ *M. persicae* and barley/ *R. padi* banker plant system, female hoverflies laid a significantly bigger proportion of eggs on pepper compared to barley (Figure A.4A) (respectively 66.72 ± 7.32% and 33.28 ± 7.32%, n=30, t = -2.372, df = 14, p-value = 0.032) and 13.3 % of females laid all their eggs only on pepper.

When comparing this trial with the one of cucumber vs barley (objective 1), the total number of eggs laid per female was significantly 66% higher in the choice trial with pepper than in the one with cucumber (n=30, t = 2.2234, df = 15.647, p = 0.041) (Figure A.4B). Moreover, the number of eggs laid on the focal crop was significantly higher on a scale of 8.45 times in the choice trial involving pepper than in the one involving cucumber (n=30, W = 18, p < 0.001) (Figure 4B).

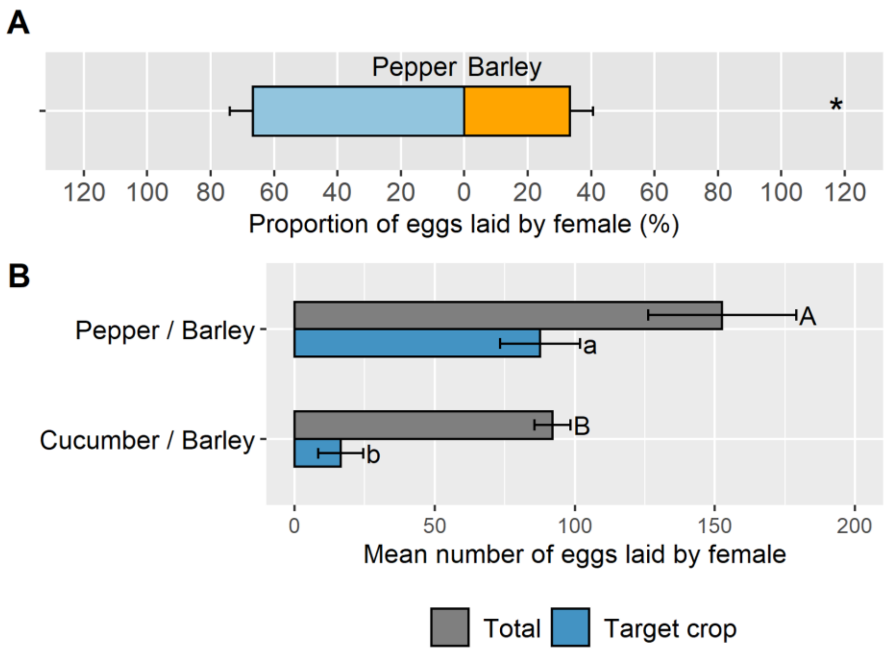

Figure A.4 (A) Proportion of eggs laid by *E. americanus* between pepper and barley banker plant system. Significant differences between plant-aphid systems are showed by asterisks (alpha = 0.05, T test). The signification of stars is as follows: ns>0.05 *<0.05 **<0.01 ***<0.001; (B) Number of eggs laid by *E. americanus* in choice trials involving barley banker plant system and two major crops (cucumber and pepper). Uppercase letters indicate differences between total number of eggs laid in 4 days (alpha = 0.05, T test). Lowercase letters indicate differences between the number of eggs laid on the target crop only (alpha = 0.05, paired Wilcoxon test). The lines represent the mean ± SE.

A.4.3 Objective 3: Adequacy of the American hoverfly to control aphids in a mixed crop greenhouse context

In the mixed crop choice trial, female hoverflies had no oviposition preference between pepper/ *M. persicae* and cucumber/ *A. gossypii* (Figure A.5) (respectively 64.06 ± 7.93% and 35.93 ± 7.93% of eggs laid on each plant/aphid system, n=30, V = 89, p-value = 0.105) but 20 % of females laid all their eggs only on pepper.

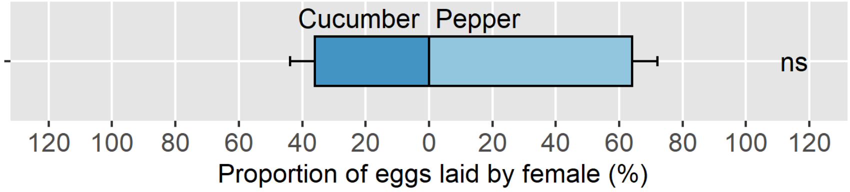

Figure A.5 Proportion of eggs laid by *E. americanus* between pepper and cucumber. Significant differences between plant-aphid systems are showed by asterisks (alpha = 0.05, paired Wilcoxon test). The signification of stars is as follows: ns>0.05 *<0.05 **<0.01 ***<0.001. The lines represent the mean ± SE.

A.5 Discussion

Oviposition preferences of female hoverflies can be influenced by different factors like host plant, aphid species, aphid colony size, visual and chemical stimuli, presence of intra- or interspecific competitors, female age, and food resources for adults (Almohamad et al., 2009). All of these factors must be taken into account when establishing strategies of biological control against aphids using hoverflies. When using a banker plant system, a good biological control agent must prefer the target crop/ prey combination to the banker plant to ensure the success of the biological control strategy (Frank, 2010; Higashida et al., 2016; Yano, 2019). Indeed, *E. americanus* should readily reproduce well both on the banker plants and the target crop, and newly emerged females from banker plants should move quickly to the target crop (Higashida et al., 2016; Huang et al., 2011; Payton Miller & Rebek, 2018; Yano, 2019). In the present case, *E. americanus* should prefer *A. gossypii* on cucumber or *M. persicae* on pepper to *R. padi* on banker plants.

The results showed that when cucumber was the target crop, *E. americanus* oviposition preferences changed drastically depending on which banker plant was presented. In this case, only the host plant species changed between choice trials since they were all carrying the same banker prey, *R. padi*. It is therefore the characteristics of these host plants which influenced the oviposition choice. *Eupeodes americanus* significantly preferred to oviposit on barley banker plant than cucumber (82.00 ± 8.0% compared to 18.01 ± 8.32%), which could be explained by the difference in leaf surface morphology. Indeed, it is known that hoverfly larvae and adults are negatively affected by plants with a high density of trichomes (Almohamad et al., 2009; Verheggen, Capella, Schwartzberg, Voigt, & Haubruge, 2009; Sobhani, Madadi, & Gharali, 2013; Riddick & Simmons., 2014). Sadeghi (2002) and Almohamad et al. (2007) proved that the oviposition preference of female syrphids is correlated with offspring performance on preferred host plants because the aphidophagous larvae have limited dispersal abilities (Chandler 1969; Scholz & Poehling 2000; Ambrosino, Jepson, & Luna., 2007). For example, oviposition of *E. balteatus* was lower on tomato cultivars, with a high density of trichomes, than on broad bean, *Vicia faba* L, which has a smooth surface (Verheggen et al., 2009).

This may explain the preference of the American hoverfly for the smooth-surfaced barley banker plant rather than the pubescent cucumber. Similarly, the American hoverfly did not have any oviposition preferences between cucumber and corn banker plant, potentially because both plants have trichomes. Indeed, various studies have investigated the negative impact of corn leaf trichomes on insects and particularly on oviposition (Durbey & Sarup, 1982; Kumar, 1992; Widstrom, Mcmillian & Wiseman., 1979). In parallel, other host plant characteristics can influence the oviposition of natural enemies, such as their plant chemistry (allelochemicals or secondary plant metabolites), their impact on prey accessibility and availability, or even their supply of food resources (e.g. flowering species) (Cortesero, Stapel, & Lewis, 2000; Almohamad et al., 2009). This could explain why *E. americanus* preferred to oviposit on cucumber compared to finger millet banker plant. Indeed, the dense architecture of the finger millet greatly reduces the prey's accessibility to female hoverflies. *R. padi* were found hiding at the base of finger millet stems (data not shown) and the density of these stems constituting the banker plant left very little access to hoverflies. This strong preference for cucumber makes finger millet an appropriate banker plant for the control *A. gossypii*.

A good banker plant must also maximize female oviposition. Results showed that, when combined with cucumber, corn and finger millet induced a higher total number of eggs laid in each choice trials than barley. Further studies are needed to explain these results. For example, differences in the quantity and composition of honeydew produced on the different banker plants could be an initial step to investigate since it can influence the number of eggs laid by hoverflies (Budenberg & Powell, 1992; Leroy et al., 2014; Scholz & Poehling, 2000; Sutherland, Sullivan, & Poppy, 2001). These results, and the strong preference for barley instead of cucumber, resulted in a significantly lower mean number of eggs laid on the target crop than in the trials with corn and finger millet. In the context of biological control of *A. gossypii* on cucumber by *E. americanus*, both finger millet and corn could constitute better banker plant systems than barley since they maximized both the oviposition of females and the number of eggs laid on the target crop cucumber. They also require less maintenance and have a high longevity due to their resistance to hot greenhouse temperatures and high aphid abundance, especially compared to barley (Fischer & Léger, 1997; Jacobson & Croft, 1998; Payton Miller & Rebek, 2018). Nonetheless, *E. americanus* showed a strong nonpreference only for finger millet over cucumber, which constitutes a good attribute for a banker plant (53.3 % of females laid all their eggs only on cucumber). This is even more important in commercial greenhouses where the density of aphids, at least at the beginning of the infestation, will be higher on the banker plant than on the protected crop. This could redirect the preference towards the banker plant. Indeed, it has been proven that aphid density is also an important factor for hoverfly oviposition (Sutherland et al., 2001; Almohamad, Verheggen, Francis, & Haubruge, 2006; Almohamad et al., 2009; Ambrosino et al., 2007; Nelson, Hogg, Mills & Daane, 2012). For this reason, finger millet seems more appropriate than corn for the control of *A. gossypii* by *E. americanus*.

The efficiency of a banker plant system also depends largely on the target crop it is used with. Indeed, a good banker plant for a specific target crop may not be appropriate for another greenhouse context. Our results concur with that since, contrary to cucumber, barley seems appropriate for pepper. Indeed, females chose to oviposit preferentially on pepper over barley (66.72 ± 7.32% compared to 33.28 ± 7.32%). Moreover, both total number of eggs laid, and eggs laid on the target crop were higher in the pepper vs barley trial, than in the cucumber vs barley trial. This higher total number of eggs laid can be explained by different attributes of the pepper/ *M. persicae* system such as pepper plant morphology (smooth surface), aphid species preference, chemical cues, etc. (Almohamad et al., 2007; Pu et al., 2019; Sadeghi & Gilbert, 2000). Overall, the results suggest that the barley banker plant is more appropriate to control *M. persicae* in pepper crops than to control *A. gossypii* in cucumber crops. This highlights the importance of choosing a banker plant system according to the target crop.

Finally, in a mixed crop context, the results showed that there was no oviposition preference between the two systems: pepper/ *M. persicae* and cucumber/ *A. gossypii*. One might have expected that the American hoverfly would prefer pepper because of its smoother surface than pubescent cucumber, but here aphid population growth differences probably come into play. Indeed, *A. gossypii* has a higher growth rate than *M. persicae* (Parajulee 2007; Satar, Kersting, & Uygun, 2008; Gullino et al., 2020) thus the population density may have been different after the 4 days of experiment. Since the oviposition of hoverflies is positively affected by high aphid densities (Sutherland et al., 2001; Almohamad et al., 2006; Almohamad et al., 2009; Ambrosino et al., 2007; Nelson et al., 2012), the absence of ovipositional preference then may have been caused by changes in the density ratio of aphid species. Nonetheless, considering that females showed no oviposition preference between cucumber/ *A. gossypii* and pepper/ *M. persicae*, results suggest that *E. americanus* could be a good agent to control both pests in mixed crops. However, as discussed earlier, differences in aphid population growth rates could be responsible for the observed results and they should therefore be interpreted cautiously. Also, as demonstrated above, banker plants are not equally suitable for all crops so, in the case of mixed crops, care should be taken to find a banker plant that fits both crops.

Furthermore, in all choice trials, between 6.6% and 53.3% of females chose to lay all their eggs only on one of the two plants involved, even when no significant global preference was found. Those results suggest that at least several females were specialists (Sadeghi & Gilbert, 1999). This begs the question: are American hoverflies generalist aphidophagous individuals, or is the species considered as such since it is composed of multiple specialists with varying targets? Our results do not allow answering this question, but more research should be done as it could have an impact on mass rearing or even on the possibility of using artificial selection to optimize this specie's efficiency as a biocontrol agent (Clercq, 2002).

A.6 Conclusion

This study has clarified the differences in *E. americanus* oviposition preferences not only according to aphid species but also to host plants. Furthermore, it showed the impact of different banker plant systems on oviposition preferences and its maximization in the context of biocontrol against two major aphids. Finger millet banker plant should be more suitable for the control of *A. gossypii* in cucumber crops and barley banker plant for the control of *M. persicae* in pepper crops. Finally, this study confirms that *E. americanus* oviposition may be adapted to the control of aphids in mixed crop of cucumber and pepper. However, it is essential to test these oviposition preferences in a commercial greenhouse, as carried out by Higashida et al., 2016, to validate the recommendations for the choice of banker plant. It is also necessary to determine how aphid density on the focal crop will affect the female oviposition behavior, e.g. at which focal aphid density the predator will start to lay eggs on the focal crop rather than on the banker plant. Finally, other parameters of banker plant systems, such as speed of plant growth, plant longevity in greenhouse contexts, ability to produce enough biological control agents, and cost must be investigated before possible commercialization (Frank, 2010; Huang et al., 2011).

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