Universidad de Concepción
Dirección de Postgrado
Facultad de Ciencias Naturales y Oceanográficas
Programa de Magíster en Ciencias con mención en Zoología

IMPACTO DEL USO DE MALLAS FOTO-SELECTIVAS (MPS) SOBRE LA ACTIVIDAD DE ENEMIGOS NATURALES DE INSECTOS PLAGA

Tesis presentada a la Facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción para optar al grado académico de Magíster en Ciencias con mención en Zoología

POR MARÍA JOSÉ YÁÑEZ DÍAZ
Diciembre 2020
Concepción – Chile

Profesora Guía: Dra. Marcela Rodríguez García
Departamento de Zoología
Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Chile
Profesor Co-Guía: Dr. Eric Lucas
Département des Sciences Biologiques, Université du Québec à Montréal, Canadá

AGRADECIMIENTOS

Agradezco profundamente a mi profesora guía, Dra. Marcela Rodríguez, por haberme acogido como su alumna durante estos casi tres años en los que trabajé en el laboratorio. Gracias por todos los conocimientos entregados, por creer en mí, por las oportunidades que me entregó durante mi estancia en el Magíster y por enseñarme a ser una mejor científica. La admiro como persona, profesora e investigadora.

A mi co-tutor de tesis, Dr. Eric Lucas, por haberme acogido en su hogar y por la oportunidad de haber hecho la pasantía en su laboratorio, la cual me permitió desarrollar la primera parte de esta tesis. Sin duda, eres un ejemplo de científico que recordaré durante el resto de mi desarrollo profesional. Agradezco también a Marc Fournier, por el apoyo técnico y logístico durante mi estancia en el laboratorio de la UQAM, así como a todos los miembros que forman parte del laboratorio.

A mi comisión evaluadora, Dra. Lucila Moreno y Dr. Gonzalo Silva, por haber revisado esta tesis y por sus valiosos comentarios entregados durante la presentación de avances y del proyecto de tesis que, sin duda, aportaron al desarrollo de esta investigación.

Agradezco también a todos los docentes del Magíster en Ciencias mención Zoología por su contribución a mi desarrollo académico y científico.

Así mismo, agradezco a las personas que de alguna u otra manera, aportaron y enriquecieron el desarrollo de esta investigación:

A Selim Musleh, por su inmensa paciencia al momento de enseñarme a llevar a cabo los análisis de datos, gracias también por tus comentarios y sugerencias respecto al desarrollo del escrito de la tesis.

Al Dr. Richard Bastías de la Facultad de Agronomía de la Universidad (Chillán) por facilitarnos las mallas utilizadas en esta tesis.

A la Dra. Luisa Bascuñán del Laboratorio de Fisiología Vegetal de la Facultad por facilitar los equipos de medición de luz.

A Luis Devotto del INIA (Chillán) por facilitar el material necesario para llevar a cabo la segunda parte de esta investigación, gracias también por tus comentarios en el manuscrito del segundo capítulo de esta tesis.

A Carolina Mella del Laboratorio de Control Biológico (INIA), por preparar semanalmente el material y por haberme enseñado la parte técnica relacionada a *M. ridens*.

A Patricia Loyola, por traer semanalmente el material de trabajo desde Chillán, te lo agradezco infinitamente.

Agradezco también a mi familia, por apoyarme durante todo el desarrollo del Magíster, por su paciencia, sus palabras de apoyo y su infinito amor.

A todos mis compañeros del Magíster, por los buenos momentos que pasamos dentro y fuera de la Universidad, les deseo éxito en todas las metas que se propongan de aquí en adelante, no podría haber pedido mejores compañeros con los cuáles pasar estos dos años, sin duda los extrañaré.

A mis amigos y amigas, gracias por estar ahí cada vez que los necesitaba, por esos eternos almuerzos compartiendo risas, por sus palabras de ánimo, a todos ustedes, muchas gracias.

Finalmente, agradezco a la Dirección de Postgrado de la Universidad de Concepción, por permitirme la oportunidad de haber estudiado estos dos años, así como a los proyectos de la Vicerrectoría de Investigación y

Desarrollo (VRID) Multidisciplinaria 219.113.095-M de la Universidad de Concepción y a Comisión Nacional de Investigación Científica y Tecnológica (CONICYT) PCI-MEC 80170017, por haber hecho posible el desarrollo de esta investigación.

TABLA DE CONTENIDOS

ÍNDICE DE TABLAS

ÍNDICE DE FIGURAS

RESUMEN

En los últimos años ha aumentado la utilización de mallas protectoras en agricultura como un método de producción para reducir el estrés sobre los cultivos, provocado por condiciones climáticas desfavorables. Además de mejorar la calidad y producción de cultivos, debido a la protección física para las que fueron diseñadas inicialmente, las mallas protectoras han tenido efectos positivos sobre algunos aspectos fisiológicos de los cultivos. Es por esto que se han desarrollado mallas con propiedades foto-selectivas de distintos colores y factores de sombreo utilizadas en producción comercial, con el objetivo de promover respuestas fisiológicas específicas de las plantas. La mayoría de los estudios que utilizan mallas foto-selectivas (MPS) se han centrado en los efectos que éstas tienen en la fisiología o morfología de las plantas, así como en las condiciones micro-climáticas del huerto bajo MPS (cantidad y calidad de luz, humedad relativa, temperatura, etc.). Secundariamente, se han estudiado los efectos de estos sistemas de producción sobre las poblaciones de insectos plaga. Sin embargo, estudios de los efectos de MPS sobre el gremio de enemigos naturales de estas plagas, aún son escasos. El objetivo de esta tesis fue evaluar el desempeño de dos enemigos naturales de insectos plaga bajo cubiertas de MPS (color perla y roja), mallas estándar (ME) negra y sin ningún tipo de malla (control), en condiciones de laboratorio. Se seleccionaron dos modelos de estudio pertenecientes a dos grupos funcionales de enemigos naturales: primero, un depredador, *Harmonia axyridis* (Coleoptera: Coccinellidae), y segundo, un parasitoide, *Mastrus ridens* (Hymenoptera: Ichneumonidae). Se seleccionaron estos dos enemigos naturales ya que, aunque ambos cumplen el rol de controlar eficientemente a los insectos plaga, son funcionalmente distintos en el agroecosistema: uno es un parasitoide especialista que depende de un solo hospedador para reproducirse y el otro es un depredador generalista afidófago que necesita de varias presas para alimentarse.

En el primer capítulo, se evaluó el efecto de distintas MPS y ME negra sobre el comportamiento, localización de presa y eficiencia de depredación de larvas de tercer estadio (L3), machos y hembras del depredador *H. axyridis*. Los resultados mostraron que entre tratamientos hubo diferencias en el comportamiento de búsqueda sólo para L3 y no para los adultos. Además, dentro de cada tratamiento, para los tres tipos de depredadores, hubo un mayor tiempo destinado a la búsqueda de su presa, comparado con las otras etapas de comportamiento. La localización de presa de los adultos fue potenciada bajo MPS perla y retrasada bajo ME negra, probablemente porque en el caso de los adultos los estímulos visuales son importantes para encontrar a su presa. La eficiencia de depredación no fue afectada por la presencia de MPS o ME negra para ningún depredador.

En el segundo capítulo, se evaluó el efecto de distintas MPS y ME negra sobre el comportamiento, localización de hospedador y parasitismo del parasitoide *M. ridens*. Respecto al comportamiento del parasitoide, independiente del color de las mallas, las hembras pasaron la mayor parte del tiempo en la etapa de pre-contacto. Dentro de la etapa de pre-contacto, excepto bajo MPS roja, las hembras pasaron una mayor cantidad de tiempo en la etapa de grooming comparada a la etapa de búsqueda de hospedador. Atributos biológicos como parasitismo, fertilidad, fecundidad realizada y proporción sexual de la descendencia no fueron afectados por la presencia de MPS o ME negra. Sin embargo, la localización de hospedador fue mayor bajo MPS perla y roja, y se vio retrasada bajo ME negra. Similar a *H. axyridis* los estímulos visuales son relevantes para el parasitoide al momento de localizar a su hospedador.

Para ambos enemigos naturales se puede concluir que en condiciones de laboratorio el uso de MPS y ME negra influencian el comportamiento y la capacidad de localizar a su presa/hospedador, sin embargo, no afectan la eficiencia de depredación o de parasitismo. Es por esto que es necesario en el futuro realizar estudios de campo a una mayor escala, tanto espacial como temporal, para evaluar el potencial efecto del uso de estos sistemas de producción sobre distintos atributos biológicos de enemigos naturales.

Palabras clave: mallas foto-selectivas, control biológico, calidad de luz, cantidad de luz, depredador, parasitoide.

ABSTRACT

In recent years there has been an increase in netting utilization in agriculture as a production method to reduce stress on crops, against adverse climatic conditions. In addition to improve crop quality and yield, due to the physical protection for which they were designed, protective nets have had positive effects on some physiological aspects of crops. Therefore, nets with photo-selective properties of different colors and shading factors have been developed and used in commercial production, to promote specific plant physiological responses. Most of the research on the use of photo-selective nets (PSN) have focused on the effects on plant physiology or morphology, as well as on the crop microclimatic conditions underneath PSN (light quantity and quality, relative humidity, temperature, etc.). Additionally, studies have been carried out to assess the effect of these production systems on insect pest populations. However, studies about the effects of PSN on the natural enemies guild, are still lacking. This thesis aimed to evaluate the performance of two natural enemies of insect pest under PSN (pearl and red), black standard net (SN) and without any type of net (control), in laboratory

conditions. Two study models were selected belonging to the two main natural enemies functional groups: first, a predator, *Harmonia axyridis* (Coleoptera: Coccinellidae), and second, a parasitoid, *Mastrus ridens* (Hymenoptera: Ichneumonidae). These two natural enemies were selected because, although both fulfill the role of efficiently controlling insect pests, they are functionally different in the agroecosystem: one is a specialist parasitoid that depends only on one host for reproduction and the other is a generalist aphidophagous predator that needs several preys to feed.

In the first chapter, the effect of different PSN and black SN on the behavior, prey localization, and predation efficiency of third-instar larvae (L3), males, and females of the predator *H. axyridis* was evaluated. The results showed that there were differences among treatments in the foraging behavior only for L3, but not for adults. Also, within each treatment, for the three types of predators, there was a higher amount of time allocated for prey searching, compared to the other foraging behaviors. Adults prey localization was enhanced under pearl PSN and delayed under black SN, probably because, for adults, visual stimuli are important for prey finding. Predation efficiency was not affected by the presence of PSN or black SN, for any predator.

In the second chapter, the effect of different PSN and black SN on the behavior, host localization, and parasitism of the parasitoid *M. ridens* was evaluated. For the behavior of the parasitoid, regardless of net color, females spent most of the time in the pre-contact behavior. Within the pre-contact, except under red PSN, females spent a higher amount of time grooming, compared to searching. Biological attributes like parasitism, fertility, realized fecundity, and offspring sex ratio were not affected by PSN or black SN. However, host localization was enhanced under pearl and red PSN and delayed under black SN. Similar to *H. axyridis*, visual stimuli are relevant for the parasitoid to locate their host.

For both natural enemies it can be concluded that in laboratory conditions PSN and black SN influence their behavior and prey/host localization ability, however, they do not influence predation or parasitism. Therefore, is necessary to carried out future field studies at a higher scale, both spatially and temporally, to evaluate the potential effects of these production systems on different biological attributes of natural enemies.

Keywords: photo-selective nets, biological control, light quality, light quantity, predator, parasitoid.

INTRODUCCIÓN GENERAL

Agroecosistemas y servicios eco-sistémicos

Los agroecosistemas son necesarios para la producción de alimentos suficientes para cubrir las necesidades de la creciente población humana, sin embargo, se requieren sistemas sostenibles que consigan la producción requerida sin dañar el medio ambiente en el proceso (Pretty and Bharucha 2014; Reganold and Wachter 2016). En este sentido, la inclusión de nuevas prácticas dirigidas a la reducción del uso de agro-químicos que disminuyan el impacto sobre la biodiversidad, la salud humana y el medioambiente, son fundamentales (Wratten et al. 2013; Barański et al. 2014; Tubiello et al. 2015). En los últimos años, se han propuesto sistemas agrícolas de base agroecológica (Kremen et al. 2012; Gurr et al. 2016) centrados en estudiar algunas prácticas agrícolas para mejorar los servicios eco-sistémicos (SES) relevantes para la productividad agrícola como el control biológico de plagas (Tomich et al. 2011; Wratten et al. 2012; Wezel et al. 2014). Los SES son servicios que las personas obtienen de los ecosistemas y que pueden ser culturales (recreación y valor estético), de apoyo (ciclo de nutrientes y fotosíntesis), provisión (producción de alimentos) y de regulación (polinización, regulación de plagas) (Millennium Ecosystem Assesment 2005; Wezel et al. 2014), siendo estos últimos dos los relevantes en este estudio. De esta manera, han tomado mayor importancia los cultivos orgánicos, los cuales son sistemas de producción que mantienen la salud de los suelos, ecosistemas y personas al promover los procesos ecológicos, la biodiversidad y ciclos adaptados a condiciones locales sin la utilización de insumos externos que tengan efectos adversos (Lernoud and Willer 2017). A pesar de estos esfuerzos en investigación, todavía hay una falta de implementación de éstas prácticas ecológicas en los sistemas agrícolas convencionales (Reganold and Wachter 2016). La falta de estudios a escala local de cómo se estructura la red alimentaria en distintos sistemas agrícolas y que afecta directamente al control biológico de plagas (González-Chang et al. 2016), y de estudios que consideren la diversidad de las interacciones que ocurren en ambientes naturales (Wirta et al. 2014), contribuyó en el pasado al fracaso en la implementación de programas de control biológico (Gurr and Wratten 2000). Esta falta de conocimientos también puede ocasionar resultados inesperados e indeseados como efectos negativos sobre depredadores nativos, parasitoides y plantas por introducción de especies exóticas (Louda et al. 2003). Por lo tanto, para reducir el impacto del manejo de cultivos sobre los servicios ecosistémicos es necesario estudiar la influencia de cada decisión agrícola, en nuestro caso, la implementación del uso de cubiertas de mallas.

Uso de cubiertas de mallas en agroecosistemas

En los últimos años, ha aumentado la utilización de mallas protectoras en agricultura como un método de producción para reducir el estrés sobre los cultivos provocado por condiciones climáticas desfavorables como alta radiación solar, viento y granizadas (Iglesias and Alegre 2006; Alaphilippe et al. 2016). Las mallas de exclusión representan uno de los medios más accesibles para proteger a los cultivos contra el ataque de plagas, actuando como una barrera física que previene su llegada a los cultivos (Chouinard et al. 2016). Las mallas de exclusión son típicamente transparentes (se ven blancas a la vista) y con orificios de tamaño 0,5 mm – 1,9 mm (Briassoulis et al. 2007; Chouinard et al. 2017). Éstas se pueden disponer en sistemas de exclusión completos o incompletos: en los sistemas incompletos el suelo no está excluido del área encerrada, permitiendo que varias especies plaga completen su ciclo de vida y permanezcan dentro del cultivo. Sin embargo, en las mallas de exclusión completas, el suelo si está excluido del área encerrada; este es el caso para algunos sistemas “fila por fila” (Chouinard et al. 2016; Manja and Aoun 2019). El uso de mallas de exclusión constituye una estrategia ambientalmente aceptable contra insectos plaga (Lloyd et al. 2005). Sin embargo, se debe considerar que el efecto de exclusión de las mallas es no-selectivo, es decir, en el caso de aves pueden impedir el paso tanto de especies frugívoras como de especies beneficiosas que juegan un rol importante en el control de insectos plaga (Twedt 1978; Rigden 2008). Debido a que las mallas pueden causar mortalidad en aves y murciélagos al quedar enredados en la malla o por el impacto del choque (Twedt 1978), se ha planteado el uso de mallas plásticas más rígidas que puede evitar que las aves se enreden en ellas (Fuller-Perrine and Tobin 1993), o bien, que los orificios de éstas no sean mayores a 40 mm (Rigden 2008). Otra estrategia adoptada es que fuera de temporada, algunos agricultores toman la decisión de dejar las mallas de exclusión abiertas, enrollarlas a los lados del huerto para permitir el paso de aves, o almacenarlas cuando no se están usando, maximizando su duración (Fuller-Perrine and Tobin 1993; Rigden 2008). Los murciélagos frugívoros juegan un rol ambiental importante al actuar como polinizadores de flores y dispersores de semillas, por lo tanto, se podrían beneficiar con la medida de abrir las mallas durante ciertos periodos en la temporada (Rigden 2008).

Las mallas de exclusión causan un impacto importante en la fauna debido a que cubren completamente los cultivos (Rigden 2008; Sauphanor et al. 2012; Alaphilippe et al. 2016). La diferencia de las mallas de exclusión con las mallas de sombreo es que éstas últimas se disponen en forma de “túnel” o se ubican directamente sobre los cultivos de forma horizontal y con los lados no cubiertos, ofreciendo una protección sólo parcial contra aves, murciélagos frugívoros e insectos (Chouinard et al. 2016; Ilić and Fallik 2017), lo que permite que tengan libre acceso al lugar. Además, las mallas de sombreo se caracterizan por ser de diferentes colores y tener orificios de tamaño 1,7 mm – 7 mm, dependiendo del factor de sombreo (Castellano et al. 2008).

Dentro de las mallas de sombreo, las más comúnmente utilizadas son las mallas de color negro, ya que son económicas para el agricultor, siendo las mallas estándar en estudios realizados principalmente en cultivos de hortalizas (Shahak 2008; Selahle et al. 2015; Ayala-Tafoya et al. 2018), así como en estudios que evaluaban el efecto del uso de cubierta de mallas sobre poblaciones de áfidos en cultivos vegetales (Ben-Yakir et al. 2012). Esto con el objetivo de disminuir los efectos de la radiación solar excesiva y prevenir daños físicos en los cultivos, ya que aumentan el sombreado en el huerto y en algunos casos controlan el daño causado por granizo (Iglesias and Alegre 2006). Las mallas estándar (ME) negras, al mismo tiempo, disminuyen la disponibilidad de radiación fotosintéticamente activa y de radiación ultravioleta en los cultivos, sin embargo, no afectan la calidad de la luz ni modifican su composición espectral, o su contenido relativo de luz dispersada (Shahak 2008). En cultivos frutales, los daños provocados por el sol afectan directamente a los frutos y pueden disminuir la producción comercial de los cultivos, ya que el color del fruto es importante al momento de determinar su valor en el mercado (Iglesias and Alegre 2006). Respecto a esto, el uso de mallas ha mostrado tener un efecto positivo en la disminución de frutos afectados por quemaduras de sol mediante una reducción en la incidencia directa de radiación sobre el fruto y de la temperatura de la fruta bajo las mallas (Iglesias and Alegre 2006). En hortalizas se ha utilizado ME negra principalmente para controlar la cantidad de luz y la temperatura que llega a los cultivos (Ben-Yakir et al. 2012), con resultados positivos en cuanto a la reducción de la cantidad de radiación incidente y una consecuente menor temperatura en las hojas de las plantas (Ayala-Tafoya et al. 2015, 2018; Ilić et al. 2017). Como se mencionó anteriormente, las ME negras han sido las más comúnmente utilizadas en agricultura. Sin embargo, debido a las nuevas necesidades de los productores de mejorar la calidad de los cultivos y la producción, además de la protección física, es que a lo largo de los años se han ido desarrollando mallas de distintos colores y entramados, con propiedades foto-selectivas con el objetivo de promover características deseadas de la planta y que han comenzado a ser cada vez más utilizadas en producción comercial (Shahak et al. 2004a; Duduzile et al. 2016).

Uso de mallas foto-selectivas (MPS)

Las mallas foto-selectivas (MPS) han sido diseñadas para filtrar varios componentes de la radiación solar y/o transformar luz directa en luz difusa (Antignus 2014), al incorporar aditivos cromáticos o elementos que reflejan la luz o que absorben radiación UV en el material de polietileno (Antignus 2000; Ilić et al. 2017). Éstas comenzaron a ser utilizadas para mejorar la producción ya que combinan protección física del cultivo junto con filtración diferencial de la radiación solar, modificando las condiciones micro-climáticas del huerto como por ejemplo la intensidad y calidad de la luz, temperatura del suelo, velocidad del viento y humedad relativa (Iglesias and Alegre 2006; Rigden 2008; Mupambi et al. 2018). Esto para promover respuestas fisiológicas específicas de la planta que utiliza la luz para regular procesos involucrados en su crecimiento y desarrollo (Shahak et al. 2004b, c; Racsko and Schrader 2012; Mupambi et al. 2018). Las mallas se han desarrollado con el objetivo de ir en favor de la producción tanto de hortalizas (pimiento, tomate, pepino) (Shahak 2008; Papaioannou et al. 2012; Ayala-Tafoya et al. 2015; Ilić et al. 2017) como de especies frutales (arándanos, granada, manzanos) (Shahak et al. 2008b; Bastías and Corelli-Grappadelli 2012; Lobos et al. 2013; Meena et al. 2016). Las MPS están diseñadas para modificar la luz en el rango espectral del ultravioleta (UV), visible o rojo lejano (Shahak 2008; Ilić et al. 2017). Aquellas que absorben radiación UV, bloquean la transmisión de ésta en el rango de 200-400 nm, pero no interfieren con la transmisión del rango visible del espectro de luz (Antignus et al. 1996). Las mallas de colores pueden ser rojas, azules, amarillas, naranjas, grises, blancas y perlas, entre otras. Estas últimas tres no parecen tener color al ojo humano, sin embargo, modifican el espectro no visible y/o aumentan la dispersión de la luz (Shahak et al. 2004c). Las de color azul tienen un peak de transmitancia en la región azul-verde (400-540 nm) absorbiendo en las regiones de radiación UV, amarillo, rojo y rojo lejano; y las de color amarillo transmitiendo luz desde 500 nm hacia arriba. Las MPS de color perla no enriquecen ninguna longitud de onda en particular, pero sí reducen la cantidad de luz UV y están diseñadas para dispersar la luz más que otras mallas de colores (Shahak et al. 2004c; Ilić et al. 2017). Debido a estas modificaciones espectrales, la utilización de MPS perla aumenta el tamaño de la fruta y su firmeza, rendimiento total y reduce la pérdida de peso del fruto después del almacenaje (Shahak 2008; Shahak et al. 2008b, 2016; Selahle et al. 2015). Por otro lado, las MPS de color rojo absorben UV, azul y verde, transmitiendo desde 590 nm hacia arriba en la región del rojo y rojo lejano (Shahak 2008). Esta malla puede potenciar el proceso de fotosíntesis y aumentar la biomasa de la planta, el crecimiento vegetativo, así como el peso promedio de frutos lo que puede llevar a una mejor producción (Shahak 2008; Ayala-Tafoya et al. 2018).

El costo de mallas de sombreo, incluyendo las de color negro, puede ir desde 2500 a 8500 dólares por hectárea dependiendo del material (De Vilder et al. 2015). Esto sin considerar los costos asociados a la instalación, mano de obra, o tipo de construcción, lo que eleva sustancialmente la inversión asociada a utilizar estos método de producción (Iglesias and Alegre 2006; Rigden 2008).

Las MPS de colores tienen un mayor valor costando alrededor de 10.000 dólares por hectárea (Richard Bastías, comunicación personal). Otro aspecto importante a tener en cuenta es la vida útil de las mallas. Las mallas de polietileno de alta densidad (HDPE) tienen buena durabilidad y deberían durar al menos 10 años (Rigden 2008), por ejemplo la malla de color negro anti-granizo puede tener una duración de hasta 15-20 años (Iglesias and Alegre 2006; Brglez Sever et al. 2015). Las mallas de otros colores, incluyendo las fabricadas por Polysack Industries, utilizadas en este estudio, pueden durar entre 5 a 9 años (Shahak et al. 2004a; Brglez Sever et al. 2015).

Otro aspecto relevante de la utilización de mallas en agricultura es el uso de plástico como principal material de fabricación de estos sistemas de producción. El uso de mallas en agricultura es común en muchos lugares del mundo, por lo tanto, se espera que sigan siendo utilizadas en el futuro. Se plantea que al momento de diseñar y fabricar las mallas se debe llegar a un balance entre la efectividad para proteger a los cultivos, junto con la sustentabilidad y durabilidad del material del cual están constituidas (Maraveas 2020). Esto es muy relevante considerando los desafíos que supone la gran cantidad de plástico utilizado hoy en nuestro planeta, en particular, en agricultura (Tudor et al. 2019; Cascone et al. 2020). Los plásticos que no poseen las propiedades mecánicas estándar para aplicaciones en agricultura pueden mejorar sus características mecánicas y su durabilidad al agregarle ciertos aditivos al material (Castellano et al. 2008), sin embargo, se compromete su capacidad de biodegradación y reciclaje (Maraveas 2020). Todas las mallas fabricadas de polietileno de alta densidad son reciclables (Castellano et al. 2008), sin embargo, las nuevas tecnologías deberían enfocarse en fabricar mallas biodegradables que estén libres de sustancias químicas que comprometan su sustentabilidad, al mismo tiempo que continúen protegiendo a los cultivos (Maraveas 2020).

Uso de mallas en Chile

Al igual que en otros lugares del mundo como por ejemplo Israel, Estados Unidos, España e Italia (Bastías et al. 2012; Shahak 2014; Kalcsits et al. 2017; Lopez-Marín et al. 2019), el uso de mallas en Chile busca reducir el estrés causado por alta radiación solar y altas temperaturas, que en especies frutales se manifiesta como golpe de sol en los frutos el cual es el principal problema para los agricultores representando alrededor del 40% de pérdidas económicas (Moggia and Yuri 2003; Bastías 2016). Los estudios llevados a cabo en Chile han utilizado MPS ubicadas horizontalmente sobre los cultivos los cuales se han enfocado en plantas de la vid (Corvalán et al. 2016), arándanos (Retamales et al. 2008; Lobos et al. 2012) y manzanos (Umanzor et al. 2016; Olivares-Soto and Bastías 2018). Se ha estudiado el efecto de mallas de distintos colores y factores de sombreo sobre las condiciones ambientales del cultivo, distintos aspectos relacionados a la calidad de los frutos (golpe de sol, color), crecimiento vegetativo, rendimiento del cultivo, así como aspectos fisiológicos de la planta misma. La utilización de estas mallas ha tenido efectos positivos en cuanto a la reducción de la cantidad de radiación directa que llega al cultivo y, en consecuencia, la cantidad de frutos afectados por golpe de sol (Retamales et al. 2008; Corvalán et al. 2016; Umanzor et al. 2016; Olivares-Soto and Bastías 2018). Sumado a esto, se ha visto que las MPS, en particular de color rojo y perla, mejoran características fotosintéticas así como rasgos físicos de la planta (tamaño foliar) y de los frutos (color y peso) (Corvalán et al. 2016; Umanzor et al. 2016).

Efecto de mallas sobre la fauna

La mayoría de los estudios que utilizan MPS o ME negra se centran en los efectos que éstas tienen en la fisiología de las plantas y en mejorar la eficiencia de luz para potenciar la calidad de los cultivos (Shahak et al. 2004b, c; Shahak 2008; Ilić and Fallik 2017; Mupambi et al. 2018). Las mallas protectoras además, independiente de si son de exclusión o de sombreo, funcionan como una barrera mecánica que detiene el paso de plagas de insectos, aves y murciélagos, siendo las mallas de exclusión las que tienen un efecto más pronunciado sobre la fauna, como se mencionó anteriormente (Lloyd et al. 2005; Rigden 2008; Sauphanor et al. 2012; Chouinard et al. 2016, 2017).

En el caso de abejas polinizadoras es poco probable que se vean afectadas ya que son capaces de atravesar orificios de 12 mm en las mallas, sin embargo, en el caso que los orificios sean más pequeños, las colmenas pueden ser introducidas exitosamente durante el periodo de floración (Rigden 2008). Otra medida adoptada es la apertura de mallas (de exclusión y de sombreo) en ciertos momentos de la temporada para ayudar al movimiento de abejas y permitir mejorar el flujo de aire si es que la polinización por viento es un factor importante (Rigden 2008; Chouinard et al. 2017). En el caso de los murciélagos frugívoros, en Australia, además de ser considerados plaga, éstos juegan un rol ambiental importante al actuar como polinizadores de flores y dispersores de semillas (Rigden 2008), por lo tanto, esta acción se podría ver beneficiada con la medida de abrir las mallas durante ciertos momentos del año.

Sumado a esto, se ha visto que la utilización de mallas diseñadas para mejorar la producción, pueden interferir con la capacidad de los insectos de poder visualizar a sus plantas hospedadoras y de diferenciarlas de su entorno (Ben-Yakir et al. 2012), ya que el componente UV del espectro de luz juega un rol importante en el comportamiento del insecto, incluyendo su orientación y alimentación (Antignus 2000). Por ejemplo, las mallas con propiedades absorbentes en el rango UV-A y UV-B tienen un efecto positivo en disminuir la llegada de insectos como áfidos, ácaros y moscas blancas en comparación a mallas estándar (Chiel et al. 2006; Ben-Yakir et al. 2012; Legarrea et al. 2012a; Antignus 2014). Basado en estos resultados, se sugiere que bajo condiciones de deficiencia de luz UV los insectos no pueden orientarse en el cultivo, y como consecuencia, disminuyen su movimiento y/o alimentación (Antignus et al. 1996; Antignus 2000). En comparación a mallas de color negro y rojas, las MPS de color amarillo y perla han demostrado ser más eficientes en reducir el nivel de infestación de áfidos y moscas blancas, así como de distintas enfermedades virales asociadas a estas plagas (Shahak et al. 2008a; Antignus 2010; Ben-Yakir et al. 2012). Aparentemente el mecanismo de protección de las mallas está asociado con la repelencia de insectos por la alta reflexión de la luz que tienen las MPS amarilla y perla en el rango visible del espectro, comparada con la baja reflexión de las MPS roja y negra (Ben-Yakir et al. 2012). Por lo tanto, la protección de los cultivos mediante el uso de mallas que excluyen, repelen o arrestan plagas, también puede contribuir a disminuir la utilización de insecticidas para su control y a disminuir los costos debido a una menor frecuencia de aplicaciones (Ben-Yakir et al. 2012; Sauphanor et al. 2012; Alaphilippe et al. 2016; Chouinard et al. 2016; Candian et al. 2019). Si hacemos una comparación entre el uso de insecticidas para el control de plagas y el uso de mallas, la segunda opción es una alternativa más sustentable y amigable con la salud humana y el medioambiente (Castellano et al. 2008), especialmente si se desea disminuir la entrada de insumos externos a los cultivos y evitar efectos secundarios asociados al uso de insecticidas en agricultura (Aktar et al. 2009).

El arreglo de barreras ópticas está basado en la habilidad de los insectos de percibir señales de luz que afectan drásticamente su orientación de vuelo y su aterrizaje, así como su interacción con las plantas hospedadoras en términos de alimentación y tasas de propagación (Antignus 2014). Esto debido a que los insectos son capaces de percibir la luz a través de un par de ojos compuestos que facilitan la visión (Antignus 2014). Los pigmentos visuales ubicados en los omatidios son proteínas unidas a membrana conocidas como opsinas que están conjugadas con un cromóforo, y que permiten la visión al transformar la energía lumínica en una señal bioeléctrica que llega al sistema nervioso (Antignus 2014). La capacidad de los insectos de percibir señales lumínicas en el rango UV (300-400 nm) está asociada con la presencia de fotorreceptores específicos en su ojo compuesto (Antignus 2014).

Efecto de mallas sobre enemigos naturales (EN)

Debido a que las áreas cubiertas por mallas de exclusión son inaccesibles, esto significa un impacto para distintos grupos de animales, como por ejemplo, parasitoides y depredadores, en cuanto a su dispersión, búsqueda de alimento y reproducción (Maraveas 2020). Así mismo, en el caso de mallas de sombreo estándar y MPS, éstas influyen en la actividad del gremio de enemigos naturales (EN) de los insectos plaga. Estudios que hablan de la relación que existe entre el uso de mallas UV-absorbentes y el desempeño de parasitoides reportan que el comportamiento de búsqueda de su hospedador no se ve afectado por la deficiencia de luz UV en el ambiente (Chiel et al.

2006; Sal et al. 2008; Legarrea et al. 2014; Dáder et al. 2015). Por otro lado, también se ha observado que en algunos casos los parasitoides parecen desempeñarse bien en condiciones de baja luz UV, reflejado en mayores tasas de parasitismo (Dáder et al. 2015). De esta manera, se sugiere que existen respuestas especie-específicas a la luz UV y que el resultado del uso de materiales UV-absorbentes no se debe generalizar a otras especies (Chiel et al. 2006; Legarrea et al. 2012b; Dáder et al. 2015). En los casos en que los parasitoides no se ven afectados por la falta de luz UV se sugiere que éstos utilizan señales olfativas más que visuales para localizar a su hospedador (Chyzik et al. 2003; Chiel et al. 2006). Y, al contrario, para las especies que se desempeñan mal en ambientes deficiente de UV, los estímulos visuales son importantes para localizar a su hospedador y las longitudes de onda UV son esenciales para que el insecto pueda percibir estas señales (Chiel et al. 2006). Al igual que el grupo de los parasitoides, los depredadores también han mostrado una preferencia por ambientes sin ningún tipo de malla, en comparación a mallas de exclusión o MPS (Dib et al. 2010; Cramer et al. 2019), o ambientes donde esté disponible todo el espectro de luz (similar a condiciones de luz del sol) (Omkar et al. 2005). En el estudio de Cramer et al. (2019), además de la deficiencia de luz UV en el ambiente, los autores le atribuyeron la disminución del movimiento del escarabajo a una mayor proporción de luz difusa presente en el ambiente, ya que esta especie en particular prefiere luz directa. Esto porque al igual que especies parasitoides del orden Hymenoptera, depredadores del orden Coccinellidae también tienen fotoreceptores en el rango del UV, azul y verde y, por lo tanto, se ven atraídas a este rango espectral (Lin 1993; Nabli et al. 1999; Zhou et al. 2013). Sin embargo, existen estudios que hablan del efecto neutro que tienen las MPS sobre algunas especies de depredadores (Dáder et al. 2015). Debido a las inconsistencias en estos resultados, tanto para parasitoides como depredadores, es importante seguir realizando investigaciones a nivel local de los posibles efectos que tendrían estos sistemas de producción de cultivos (MPS y ME negra) sobre el servicio ecosistémico entregado por estos controladores biológicos (depredadores y parasitoides), de regulación de poblaciones de insectos plaga.

Cultivos frutícolas y hortícolas

Los cultivos frutícolas y hortícolas son propensos a sufrir daños provocados por factores climáticos como radiación solar, granizadas y altas temperaturas, o bien por la acción de insectos plaga en distintos cultivos (Lloyd et al. 2005;

Ben-Yakir et al. 2014). Así, la protección de la producción contra plagas es uno de los pilares fundamentales de los programas orientados a la seguridad de los recursos alimenticios para la población mundial (Mazzi and Dorn 2012). Actualmente, las exigencias de los mercados internacionales van dirigidas a la producción de frutas y vegetales con altos estándares de calidad para exportación, que no exhiban ningún tipo de daño provocado por insectos plaga (Díaz et al. 2006; Pajac et al. 2011; Papaioannou et al. 2012) y procedentes de cultivos orgánicos o comerciales sujetos a un régimen de manejo integrado de plagas (MIP) y enfermedades. En agricultura, un insecto se considera una plaga si se presenta en tal cantidad que le causa daño a un cultivo y este es suficiente para reducir la cosecha y/o la calidad del producto (van Lenteren 2006). Por lo tanto, la búsqueda de alternativas de control para lograr una cosecha de calidad y buena condición en post-cosecha es un gran desafío.

Dentro del orden Lepidoptera (mariposas y polillas) existen especies importantes que causan grandes pérdidas económicas en agricultura debido a que atacan a los frutos (Sorensen 2009). Uno de los ejemplos más reportados en la literatura es la polilla de la manzana *Cydia pomonella* (Linneo) (Lepidoptera: Tortricidae) que ataca a distintos árboles frutales (pomáceas principalmente) y es considerada la plaga clave del manzano a nivel mundial (Welter 2009). Esta especie ha alcanzado prácticamente una distribución global debido a su gran potencial de adaptación convirtiéndola en uno de los insectos plaga más exitosos conocidos (Thaler et al. 2008). Esta plaga es difícil de controlar debido al corto intervalo de tiempo que existe entre la eclosión de la larva neonata y su entrada al fruto donde causa el daño, por lo tanto, ese es el momento crucial para aplicar métodos de control lo que requiere de mucha precisión (Hughes et al. 2003). Debido al daño directo que ocasiona en los frutos, *C. pomonella* ha sido tradicionalmente controlada mediante la aplicación de insecticidas (Reyes et al. 2007; Rodríguez et al. 2010). Sin embargo, esta especie ha desarrollado resistencia a la mayoría de las materias activas de insecticidas disponibles en el mercado para su control, situación que dificulta la efectividad de las estrategias de control (Sauphanor et al. 2000; Fuentes-Contreras et al. 2007; Knight 2008; Rodríguez et al. 2012; Bosch et al. 2018). Debido a las exigencias del mercado de reducir el uso de insecticidas en los agroecosistemas, proteger la salud humana y del medio ambiente, y evitar la pérdida de biodiversidad, es que han tomado importancia las estrategias de manejo integrado de plagas (MIP) incluyendo el uso de controladores biológicos de insectos plaga. Para *C. pomonella* se han estudiado distintos enemigos naturales para su control, incluyendo entomopatógenos, depredadores y parasitoides (Lacey and Unruh 2005). Dentro de este último grupo, *M. ridens* Horstmann (Hymenoptera: Ichneumonidae) es un ectoparasitoide idiobionte gregario específico de larvas de quinto estadio o pre-pupas de *C. pomonella* (Bezemer et al. 2005). Es un parasitoide importante de la polilla de la manzana en su región de origen en Asia Central (sur de Kazajstán y norte de China) (Hougardy et al. 2005; Mills 2005) que ha sido utilizado en programas de control biológico clásico contra esta plaga en países como Estados Unidos, Chile y Argentina (Mills 2005; Devotto et al. 2010; Tortosa et al. 2014). Se han realizado estudios de especificidad de este parasitoide utilizando alrededor de 15 especies de lepidópteros como potenciales hospedadoras de *M. ridens*, dentro de las cuales, cuatro especies fueron ocasionalmente atacadas y sustentaron el desarrollo de algunas larvas hasta el estado adulto (Department of Agriculture Fisheries and Forestry 2013). Sin embargo, el número de potenciales hospedadores atacados por *M. ridens* y de larvas que alcanzaron la adultez fue significativamente menor que en *C. pomonella*, por lo tanto, se plantea que este parasitoide es un enemigo natural específico de esta plaga (Department of Agriculture Fisheries and Forestry 2013).

Por otro lado, y también considerados insectos plaga, especies del orden Hemiptera (áfidos) pueden causar serios daños en muchos cultivos debido a su forma de alimentación polífaga, provocando daños físicos directos, transmisión de patógenos virales hacia las plantas de las cuáles se alimentan y causando enormes pérdidas económicas por reducción de la producción (Sorensen 2009; Tian et al. 2017). Uno de los áfidos más importantes es *Myzus persicae* (Hemiptera: Aphididae), un insecto plaga extremadamente polífago (se alimenta de más de 400 especies de plantas pertenecientes a más de 50 familias) y con un gran rango de relaciones hospedador-planta (Völkl et al. 2007; Tian et al. 2017). La gran importancia de *M. persicae* radica en su alta eficiencia como vector de virus, transmitiendo más de 100 virus hacia las plantas incluyendo cultivos de papa, tabaco, y tomates (Völkl et al. 2007; Tian et al. 2017). Al igual que *C. pomonella*, esta especie ha tratado de ser controlada mediante la utilización de insecticidas. Sin embargo, existen poblaciones que han exhibido distintos mecanismos de resistencia (Sorensen 2009; Li et al. 2016), por lo tanto, el uso de controladores biológicos contra esta especie juega un rol fundamental en su control. Para áfidos, se han utilizado parasitoides y depredadores pertenecientes a los órdenes Hymenoptera (Braconidae), Diptera (Syrphidae y Cecidomyiidae) y

Coleoptera (Coccinellidae) (Gomes et al. 2018; Yi et al. 2019). Dentro de este último grupo, la chinita asiática o chinita arlequín *Harmonia axyridis* (Pallas 1773) (Coleoptera: Coccinellidae) es un depredador generalista afidófago nativo de Asia (Dobzhansky 1933) que juega un rol importante en el control de *M. persicae* (Gomes et al. 2018). Este coccinélido ha sido utilizado en programas de control biológico clásico, aumentativo y de conservación contra insectos plaga (Roy et al. 2006), debido a que las larvas y adultos son depredadores voraces de moscas blancas y áfidos, permitiendo regular sus poblaciones en agroecosistemas y bosques (Ahmed et al. 2017).

El control biológico es una alternativa al uso de insecticidas tradicionales para el control de insectos plaga que ha tomado mucha relevancia en los últimos años para regular los niveles poblacionales de especies como *M. persicae* y *C. pomonella*. Para ambas especies, se ha estudiado y aplicado el uso de enemigos naturales, incluyendo a *H. axyridis* y *M. ridens*, respectivamente, los cuales juegan un rol importante para su control.

Por lo tanto, y en base a los antecedentes recién mencionados, podemos apreciar que existen numerosos estudios que dan cuenta del efecto que tienen las MPS y ME negra en la fisiología de las plantas, en la producción de cultivos, así como en poblaciones de insectos dañinos. Sin embargo, las investigaciones respecto a las consecuencias de la utilización de estos sistemas de producción sobre el gremio de enemigos naturales de insectos plaga son escasas. Debido a que el uso de estos sistemas de producción se está generalizando en Chile y en otros países, es importante realizar investigaciones que permitan comprender los efectos que tienen los distintos tipos de mallas actualmente en uso sobre el desempeño de enemigos naturales utilizados (un depredador y un parasitoide) a nivel local.

HIPÓTESIS

En base a la información expuesta anteriormente que reportan (1) el efecto de mallas foto-selectivas (MPS) perla y roja, y mallas estándar (ME) negra sobre aspectos físicos y fisiológicos de plantas, sobre el microclima de los cultivos donde son utilizadas, debido a una alteración en la cantidad y calidad de la luz que llega a la superficie, y (2) considerando además los efectos sobre poblaciones de insectos plaga y sus enemigos naturales que indican los mismos antecedentes, se propone la siguiente hipótesis general de investigación:

- Las cubiertas de MPS perla y roja y ME negra alteran la actividad del depredador *Harmonia axyridis* sobre su presa, y del parasitoide *Mastrus ridens* sobre su hospedador, disminuyendo la eficacia de búsqueda de presa/hospedador así como la depredación y el parasitismo, debido a la diferencia de disponibilidad y calidad de luz.

En particular, se propone abordar las siguientes preguntas de investigación específicas sobre la actividad de depredación y parasitismo de estos dos enemigos naturales:

- ¿Las mallas foto-selectivas (MPS) perla y roja, y malla estándar (ME) negra, retrasan la localización de la presa o del hospedador de los enemigos naturales, en comparación a la no utilización de mallas?
- ¿Las mallas foto-selectivas (MPS) perla y roja, y malla estándar (ME) negra, disminuyen la eficiencia de depredación y parasitismo de los enemigos naturales, en comparación a la no utilización de mallas?
- ¿Las mallas foto-selectivas (MPS) perla y roja, y malla estándar (ME) negra, alteran el comportamiento inicial de búsqueda de presa y hospedador de los enemigos naturales, en comparación a la no utilización de mallas?
- ¿Los efectos medidos sobre los enemigos naturales serán influenciados diferencialmente por el color de malla utilizada (MPS perla, MPS roja y ME negra)?

Predicción: Se espera que la ME negra tenga un efecto más negativo sobre la localización de presa y hospedador, la depredación y parasitismo, así como el comportamiento inicial de ambos enemigos naturales, debido al mayor factor de sombreo que posee, disminuyendo una mayor cantidad y calidad de luz en comparación a MPS roja y perla.

Justificación para la hipótesis

Cantidad de luz

Algunas especies de los órdenes Hymenoptera y Coleoptera son sensibles a la disponibilidad de luz presente en el ambiente, cuya actividad se ha asociado positivamente con la cantidad de luz (Tan et al. 2014; Chen et al. 2016). Esto se ha reflejado en mayores tasas de parasitismo (parasitoides), o mayor velocidad y capacidad de búsqueda de presa (depredadores) bajo una mayor intensidad de luz (Bahlai et al. 2008; Schirmer et al. 2008; Tan et al. 2014). Debido a que las MPS y la ME negra disminuyen la cantidad de luz disponible en el ambiente (Bastías et al. 2012; Lobos et al. 2012; Arthurs et al. 2013; Acero 2015; Zhou et al. 2018), la actividad de los enemigos naturales disminuirá en presencia de estas mallas, en comparación a la no utilización de mallas.

Calidad de luz

En especies de los órdenes Hymenoptera y Coleoptera se identifican fotorreceptores espectrales con sensibilidad máxima en la región del UV, azul y verde del espectro de luz (Peitsch et al. 1992; Lin 1993; Sun and Liu

2018), mostrando una capacidad de responder positivamente a estas longitudes de onda (Zhou et al. 2013; Chen et al. 2014, 2016; Tan et al. 2014). Debido a que las MPS y la ME negra disminuyen la disponibilidad de ciertas longitudes de onda del espectro de luz (Shahak et al. 2004c, b; Shahak 2008; Arthurs et al. 2013; Ilić and Fallik 2017; Zhou et al. 2018), las cuales coinciden con sus fotorreceptores, la actividad de los enemigos naturales disminuirá en presencia de estas mallas, en comparación a la no utilización de mallas.

OBJETIVOS

Para abordar la hipótesis general y preguntas de investigación, se propone un enfoque experimental de observación en los siguientes objetivos:

Objetivo General

Evaluar el desempeño de dos enemigos naturales, un depredador, *Harmonia axyridis* (Coleoptera: Coccinellidae) y un parasitoide, *Mastrus ridens* (Hymenoptera: Ichneumonidae), bajo cubiertas de MPS perla y roja, ME negra y sin ningún tipo de malla, en condiciones de laboratorio.

Objetivos Específicos

- Caracterizar el comportamiento inicial de búsqueda de presa y hospedador para cada enemigo natural bajo cubiertas de MPS perla y roja, ME negra y sin cubierta de malla.
- Determinar el tiempo necesario de cada enemigo natural para localizar a su presa y hospedador bajo cubiertas de MPS perla y roja, ME negra y sin cubierta de malla.

- Determinar la eficiencia de depredación y parasitismo para cada enemigo natural bajo cubiertas de MPS perla y roja, ME negra y sin cubierta de malla.
- Comparar los efectos de mallas de diferentes colores sobre el desempeño de ambos enemigos naturales.

Para responder a los objetivos planteados se desarrollaron experimentos de laboratorio con la finalidad de estudiar la actividad de depredación de *Harmonia axyridis* sobre ninfas de *Myzus persicae* y la actividad de parasitismo de *Mastrus ridens* sobre larvas de *Cydia pomonella*, bajo mallas de color (MPS perla y roja, y ME negra), comparado con un control sin malla. Los resultados encontrados sobre el parasitismo y la depredación, incluyendo el efecto sobre el tiempo de localización de la presa/hospedador y sobre el comportamiento inicial de los enemigos naturales para ambos casos, se presentan a continuación en los dos capítulos que componen esta tesis.

CAPÍTULO I

Impact of photo-selective nets (PSN) systems on Coccinellid predation

Impact of photo-selective nets systems (PSN) on Coccinellid predation

Yáñez-Díaz, María-José[1], Rodríguez, Marcela A.[1], Musleh, Selim[1, 2], Silva, Gonzalo[3], Lucas, Eric[4]

[1] Laboratorio de Entomología Aplicada, Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Barrio Universitario s/n, Casilla 160-C, Concepción, Chile;
[2] Núcleo Milenio INVASAL, Concepción, Chile;
[3] Laboratorio de Entomología, Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Concepción, Av. Vicente Méndez 595, Casilla 537, Chillán, Chile;
[4] Laboratoire de Lutte Biologique, Département des Sciences Biologiques, Université du Québec à Montréal, 141 Avenue du Président-Kennedy, Montréal, QC H2X 1Y4, Canada;

E-mail corresponding author: marcela.arg@gmail.com

María José Yáñez Díaz (ORCID ID: 0000-0003-4006-1679)

Marcela A. Rodríguez (ORCID ID: 0000-0002-2431-3701)

Selim Musleh (ORCID ID: 0000-0003-3211-585X)

Gonzalo Silva (ORCID ID: 0000-0002-2463-5540)

Eric Lucas (ORCID ID: 0000-0003-4126-4988)

Artículo enviado a: Journal of Pest Science

Abstract

Photo-selective nets (PSN) increase agricultural crop production, by modifying light quantity and quality that reaches the focal plant. Furthermore, PSN also affects arthropod pest populations and potentially their natural enemies. The present study aimed to assess the impact of PSN systems on coccinellid predation. Experiments were carried out in microcosm conditions to evaluate the efficiency (prey localization and predation) of the multi-spotted Asian ladybeetle *Harmonia axyridis*, when preying on the green peach aphid *Myzus persicae* on potato plants. Four treatments were compared and tested (black SN (standard net), pearl PSN, red PSN, and no PSN (control)) on three different ladybeetle stages and sexes (third-instar larvae (L3), females and males). We hypothesize that PSN and black SN alter the predator behavior, by delaying the time until the aphid colony localization, or by reducing the overall aphid predation. Our results showed that in the absence of predators, the aphid colony was not affected by any treatment. Aphid colony localization by adult coccinellids was delayed under black SN and favored under pearl PSN. The overall aphid predation was not affected by net type. Among treatments, initial foraging behavior was different for L3, but not for adults. Within treatments, predators allocated a higher amount of time to prey searching, regardless of net type. We conclude that in laboratory conditions, pearl PSN, red PSN, and black SN affect aphid colony localization and ladybeetle foraging behavior, but do not affect the predation efficiency. Subsequent trials have to be carried out in the field.

Keywords: Biological control, Coccinellidae, light intensity, light quality, photo-selective nets, prey localization.

Key Message

- Photo-selective nets (PSN) are used to protect crops from climatic adversities and they can potentially influence insect pests and their natural enemies.
- This study aims to evaluate the effect of PSN on *Harmonia axyridis* predation.
- Prey localization by adults was delayed under black standard net (SN) and favored by pearl PSN.
- Predation efficiency was not affected by the use of nets.
- Initial foraging behavior differed among treatments and predators.
- Our results may be relevant to develop control strategies under PSN.

Introduction

Photo-selective nets (PSN) have been developed to improve crop production since combining physical protection of the orchards and differential filtration of solar radiation can promote certain physiological responses in focal plants (Shahak et al. 2004a, b). PSN can reduce light quantity reaching the crop and transform direct light into diffused light, through the incorporation of chromatic or light-dispersive additives into the plastic material (Shahak et al. 2008a; Antignus 2014). In agriculture, shade nets are used as a production method to reduce stress in crops due to adverse climatic conditions such as high solar radiation, wind, and hail (Alaphilippe et al. 2016). Traditionally, black standard nets (SN) have been used in countries like Chile, Israel, and South Africa due to their lower cost compared to other colored nets (Shahak et al. 2008b; Tinyane et al. 2013; Bastías 2016). They increase the shading factor, lowering the availability of photosynthetically active radiation (PAR) and UV radiation under the net (Shahak 2008; Ayala-Tafoya et al. 2011). Black SN lowers the light quantity through the whole light spectra but does not modify the spectral composition and the relative content of diffused light (Shahak 2008). In the case of colored PSN that do affect the spectral light composition, pearl PSN absorbs light in the UV region and is designed to disperse more light than other colored nets (Shahak 2008). Due to these spectral modifications, the utilization of pearl PSN increases fruit size, firmness, plant productivity, total yield, and reduces fruit weight loss after storage (Shahak 2008; Shahak et al. 2008b, 2016; Selahle et al. 2015). On the other hand, red PSN absorbs UV, blue, and green light, while increasing wavelength transmission in the red, and far-red range (Shahak 2008). This PSN enhances the photosynthesis process and increases plant biomass, vegetative growth, vigor, and average fruit weight, leading to increased production (Shahak 2008; Ayala-Tafoya et al. 2018).

Beyond direct advantages reported for crop production, the use of PSN and black SN can also influence the behavior of agricultural pests and their natural enemies. Negative effects on pest populations have been reported. PSN can lower the arrival of pests to different crops by optical manipulation (deterring host landing because of the high light reflection provided by the PSN, and causing difficulties for host plant recognition) or by mechanical protection (Antignus et al. 1996, 1998; Shahak et al. 2008a; Ben-Yakir et al. 2012, 2014). In general, insects have photoreceptors with maximal sensitivity in the UV, blue, and green range of the light spectra (Menzel 1979; Briscoe and Chittka 2001). Photoreceptors play an important role in the insect vision (Goldsmith and Bernard 1974), therefore, a UV light deficiency in the environment can affect the insect behavior (Antignus et al. 1996, 2001). As a result the insect fails to orientate inside the crop decreasing its flight activity and dispersion capability (Antignus et al. 2001; Miranda et al. 2015). As was mentioned, natural enemies like parasitoids and predators, including coccinellids, have three types of spectral photoreceptors, showing a positive response to maxima sensitivity in 360 nm (UV light), 420 nm (blue light), and 520 nm (green light) (Peitsch et al. 1992; Lin 1993; Chen et al. 2012; Zhou et al. 2013). If PSN and black SN interferes with these light spectra the activity of natural enemies will be affected. Predatory insects depend on a visual search when seeking prey (Nakamuta 1984). Some Coleopteran species prefer environments with light over dark conditions for feeding or with unfiltered light (Harmon et al. 1998; Cramer et al. 2019). In particular, coccinellids are more active when exposed to high light intensity. The higher speed of movement under these conditions could be an adaptation for more effective prey consumption (Tan et al. 2014). However, few studies assess the effects of PSN and black SN on the activity of predatory beetles, in particular, ladybird beetles (Pajaĉ et al. 2018; Cramer et al. 2019).

The multicolored Asian ladybeetle *Harmonia axyridis* (Pallas 1773) (Coleoptera: Coccinellidae) is an aphidophagous predator native to Asia (Dobzhansky 1933). This coccinellid has been used worldwide as a biological control agent of pest insects due to their high voracity against whiteflies and aphids leading to the regulation of pest populations in agro-ecosystems and forests (Roy et al. 2006; Ahmed et al. 2017). *H. axyridis* is a natural predator of the green peach aphid *Myzus persicae* (Sulzer 1776) (Hemiptera: Aphididae), a highly polyphagous insect pest that feeds on a wide variety of plants including agricultural and horticultural crops (Tian et al. 2017).

The present study aims to assess the impact of PSN and black SN on the predation of an aphidophagous coccinellid. More specifically, the predation efficiency of *H. axyridis* on *M. persicae* was compared under four treatments (black SN, pearl PSN, red PSN, and no PSN (control)), by measuring the time until aphid colony localization, and the voracity of the predator. We hypothesize that PSN and black SN alter the predator behavior, by delaying the time until the aphid colony localization, or by reducing the overall aphid predation. The mechanism proposed is the decrease of light quantity under the PSN and black SN and the change of light quality under the PSN (Shahak et al. 2008b; Arthurs et al. 2013; Ilić and Fallik 2017; Zhou et al. 2018) alter the behavior of the predator *H. axyridis*, including both aphid colony localization and predation rate.

Materials and Methods

Laboratory bioassays were carried out to assess whether PSN and black SN influence *H. axyridis* predation. In particular, if prey localization and predation efficiency would be affected by the nets. Also we evaluated, by visual observations, if PSN and black SN would influence the foraging behavior of predators.

Insects and plants

We chose the green peach aphid *M. persicae* and the multi-spotted Asian ladybeetle *H. axyridis* to conduct the bioassays. Both species were obtained from rearings available at the Laboratoire de Lutte Biologique, UQAM (Montréal, Canada). The adults *H. axyridis* were collected in Québec, Canada at Sainte-Agathe (46°23′0.3″N and 71°24′33.5″W) in 2017, and *M. persicae* was collected near Montréal, Canada. The *M. persicae* colony was established in 2010, and every year new individuals were added. *M. persicae* was reared on potato plants and *H. axyridis* was maintained with *M. persicae* colonies in a growth chamber at 24°C, 16L: 8D, and 70% RH. Insecticide-free potato plants *Solanum tuberosum* L. 1753 (var Nordland) grown in a greenhouse at 22 ±1 °C, 60% RH, and 16:8 (L:D) photoperiod, were used as a substrate for the bioassays.

Bioassays were carried out to study the influence of PSN and black SN on prey localization and predation of *H. axyridis* on an aphid colony (Table 1). Additionally, a foraging behavior bioassay was performed during the first 30 minutes to assess the time spent by predators on different foraging behaviors. As an experimental unit (microcosm), a 12L box (22.6 x 23 x 20.5 cm, high/length/width, respectively) (Figure 1) was built using two plastic boxes of 6L each, both cages were attached with adhesive gum, one inverted on top of the other. Each cage had holes covered with transparent muslin to allow ventilation inside the cage. For all bioassays, four treatments were used: black SN, pearl PSN, and red PSN above the cage, and no PSN were used as control (cages without nets). These treatments were chosen because i) black SN is commonly used by growers for crop protection in Chile and, ii) pearl and red PSN have been recently introduced to improve crop production in Chile (Umanzor et al. 2016). These treatments were put directly above each cage stuck with adhesive tape to modify the light quantity and quality inside the experimental unit. Inside each cage, there were six potato plants (~15 cm height). As a light source, two tubes of 32 Watts (E-lume 50K/ G13/ 32W / T8 Daylight) were located 50 cm above the cage surface. Different stages of the predator were submitted to the four treatments: a single *H. axyridis* individual, either 1) third-instar larvae (L3), 2) adult female, 3) adult male, alongside a colony of 20 *M. persicae* nymphs (body length: one mm). The predators (L3 and adults) were individually isolated in a Petri-dish and starved for 24 hours before the bioassays. Inside the Petri-dish, water was provided to *H. axyridis* with water-soaked cotton inserted into an Eppendorf tube, and ventilation was maintained through holes covered with a transparent muslin (Chimney Petri). With a clip-cage (modified from MacGillivray and Anderson 1957), the colony of 20 aphids was established in a leaf of a potato plant located in the corner of the cage (Focal plant), and after two hours, the clip-cage was removed. In a leaf of a potato plant located in the opposite corner of the cage (diagonally) (Initial plant), the predator was individually introduced. Each bioassay was replicated 15 times under the four treatments for each predator stage and sexes. All experiments were carried out at 22 ± 1°C and 65 ± 5% RH.

Aphid colony without predators

To assess the aphid natural mortality, and also the potential impact of the PSN and the black SN on aphid displacement, the aphid colony (n=20 aphids) without predators was observed and the number of aphids was counted every 30 minutes for four hours and at 24 hours after the beginning of the experiments.

Prey localization

For prey localization, once the predator was individually introduced inside the cage, the time required until colony localization was recorded every 30 minutes for four hours and at 24 hours after the beginning of the experiments.

Predation

For predation efficiency, once the predator was individually introduced inside the cage, the number of aphids in the plant where the colony was established was counted every 30 minutes for four hours and at 24 hours after the beginning of the experiments.

Foraging behavior

Continuous observations of *H. axyridis* (L3 and adults) foraging behavior were done during the first 30 minutes of the experiments. These observations were cataloged according to the localization of the predator: i) “Initial plant” (corresponds to the time spent by the predator on the plant where it was introduced), ii) “Focal plant” (corresponds to the time that each predator remained on the plant where the colony of aphids was located), iii) “Other” (corresponds to the time that each predator changed to another plant or moved through the experimental cage).

Data analysis

Before the analysis, to assess if the data were normally distributed and the variances were homogeneous, a Shapiro-Wilks test and a Bartlett test were performed (Bartlett 1937; Shapiro and Wilks 1965). To determine if the PSN and the black SN influenced on the time required by each *H. axyridis* predator (L3 and adults) to find the aphid colony, a generalized linear model (glmm) with binomial distribution was performed using the statistical package glmmTMB (Brooks et al. 2017). For the analysis, the dependent variable was if the predator located the aphid colony at each of the nine time intervals (binary data: 1 when the predator find the aphid colony, and 0 when the predator does not find the aphid colony), and the independent variables were the four treatments and time intervals. To determine if the PSN and the black SN influenced the predation efficiency at each time interval, a repeated-measures ANOVA was performed separately for each predator (L3 and adults). To test the effect of the PSN and the black SN on the mortality of the aphid colony without predators, a repeated-measures ANOVA was also performed. The dependent variables were the number of aphids consumed and the number of aphids on the colony, respectively, and the independent variables were the four treatments and the time intervals. Finally, to test if there were significant differences among treatments for the time spent by each predator separately (L3 and adults) on each foraging behavior, a Kruskal-Wallis test was performed. If there were significant differences among treatments, the Wilcoxon test with Bonferroni correction was used. Additionally, to evaluate if there were significant differences within each treatment for the time spent on each foraging behavior, a Wilcoxon Signed-Rank test for paired observations was used. All analyses were conducted using R version 3.6.0 (R Core Team 2019).

Results

Aphid colony without predators

To standardize natural aphid mortality, the number of aphids in the colony was counted in the absence of predators at continuous time intervals under each treatment. Our results showed that the natural mortality of the *M. persicae* colony was low (≤ 6%), and it was not affected by the PSN and the black SN treatments in any of the time intervals (df=3, P=0.845) (Figure 2, Online Resource 1). Considering the low mortality, and because aphids did not move from the plant where they were introduced, we did not correct for natural aphid mortality in the analyses.

Prey localization

To assess the effect of the PSN and the black SN on prey localization, the time it took the predator (L3 and adults) to find the aphid colony was recorded under the four treatments. Our results showed that the PSN and the black SN significantly affected the three types of predators (Figure 3; Online Resource 2 and 3).

For L3: overall prey localization time was shorter under the black SN throughout the four hours after its introduction to the cage when compared to the other treatments. We observed significant differences between the black SN and red PSN (df=535, P=0.025), and between the black SN and no PSN (df=535, P=0.003), with overall prey localization being shorter under black SN in both cases.

For females: the shortest prey localization occurred under the pearl PSN, and there were significant differences compared to the black SN (df=535, P=1.27e-08), the red PSN (df=535, P=0.0003), and the no PSN (df=535, P=0.0002). There were also significant differences between the black SN and the red PSN (df=535, P=0.015) and between the black SN and the no PSN (df=535, P=0.022), with prey localization being shorter under the red PSN and the no PSN, respectively.

For males: the shortest prey localization occurred under the pearl PSN and was delayed under the black SN, being significantly different from each other (df=535, P=0.010).

However, at 24 hours there were no significant differences in the time required for prey localization among treatments for any of the three types of predators (Online Resource 4).

Predation

In this bioassay we assessed if the PSN and the black SN influenced the predation efficiency of different stages and sexes of the ladybeetle *H. axyridis* on the *M. persicae* colony. Our results showed that the PSN and the black SN treatments did not affect *H. axyridis* predation at any of the time intervals tested for none of the predators (L3: df=3, P=0.885; female: df=3, P=0.201; male: df=3, P=0.855) (Figure 4; Online Resource 5). However, there were significant differences in predation between adult sexes (P=0.033). Females consumed significantly more aphids than males, considering all time intervals. Also, 24 hours after the introduction of predators inside the cage, there were no significant differences in the number of aphids consumed among treatments (L3: df=3, P=0.984; female: df=3, P=0.549; male: df=3, P=0.820).

Foraging behavior

A foraging behavior bioassay was performed during the first 30 minutes of the experiment to assess the effect of the PSN and the black SN on the time that the predator stayed in the initial plant, walked through other substrates, and found the focal plant. Our results showed that for L3 there were no significant differences among treatments in the time spent in the foraging behaviors "Initial plant" (x^2=4.00, df=3, P=0.261) and "Focal plant" (x^2=3.42, df=3, P=0.332) (Figure 5, Online Resource 6). However, we found significant differences among treatments for the time spent in "Other" (x^2=8.77, df=3, P=0.032). L3 spent significantly more time searching the prey under the black SN and the no PSN, compared to the pearl PSN (W=57.5, P=0.022, and W=172, P=0.014, respectively). Regarding both the female and the male, there were no significant differences among treatments for the time spent in each foraging behavior.

Within each treatment, our results showed that the PSN and the black SN affected the time allocated by the predators to different foraging behaviors (Figure 5, Online Resource 6).

L3: Under all four treatments L3 spent significantly more time in the "Initial plant" and "Other" compared to the time spent in the "Focal plant". There were no significant differences between the time spent in the “Initial plant” and “Other” in any of the four treatments.

Females: Under the black SN, the red PSN, and the no PSN, there were significant differences among the three foraging behaviors. For these three treatments the female spent significantly more time in “Other”, followed by the time in the “Initial plant” and lastly in the “Focal plant”. For the pearl PSN there were no significant differences between the time spent in the “Initial plant” and “Other” (V=23, df=14, P=0.068), but the time spent in the “Focal plant” was significantly lower than in the “Initial plant” (V=104, df=14, P=0.013) and “Other” (V=99, df=14, P=0.004).

Males: Under the no PSN males spent less time on the “Focal plant” compared to the time spent in the “Initial plant” (V=105, df=14, P=0.001) and “Other” (V=91, df=14, P=0.001). Under the red PSN and the black SN, there were significant differences among the three foraging behaviors. The male spent most of the time in “Other”, followed by “Initial plant” and spent the lowest time in the “Focal plant”. Under the pearl PSN, the time spent in “Other” was significantly higher than the time spent in the other two foraging behaviors. No differences were found between the “Initial plant” and “Focal plant” under the Pearl PSN (V=82.5, df=14, P=0.06).

Discussion

In this study we assessed the effect of the PSN and the black SN on prey localization, predation efficiency, and foraging behavior of *H. axyridis* on an *M. persicae* colony under laboratory conditions. The results support our hypothesis that the PSN and the black SN have a significant impact on prey localization and the behavior of the ladybeetle *H. axyridis*. However, in our microcosm conditions, these effects did not modify the predation efficiency of the predator.

Aphid colony without predators

We found that the PSN and the black SN treatments did not have any significant effect on aphid colony survival. Aphid mortality was very low and aphids did not modify their behavior in the presence of the PSN and the black SN. Aphids mainly stayed in the initial plant on the same leaf. The fact that the PSN and the black SN do not affect the aphid colony without predators has to be verified also in field studies over a longer time.

Prey localization

Predators were directly affected by the treatments regarding the time required to encounter their prey. Coccinellid larvae, contrary to adults, do not appear to rely only on visual stimuli to find their prey (Banks 1954; Stubbs 1980; Hattingh and Samways 1995). Larvae and adults coccinellids have different visual systems. The stemmata present in larvae are simple low-resolution optical units and poor image formers, whereas adults have high-resolution compound eyes with a more accurate vision (Prokopy and Owens 1983; Lambin et al. 1996; Klowden 2007). Therefore light intensity may have a stronger effect on adults compared to larvae. Others factors than light quality and quantity could also influence prey localization by larvae as, for example, olfactory cues (Stubbs 1980). These factors could be involved in the fact that the black SN somehow increased L3 prey localization compared to the red PSN and the no PSN. Nonetheless, if the black SN somehow influences these other factors requires further research. Physical contact and random movements are also important for the larvae to locate their prey (Kawai 1976). Thus, it is possible that under our experimental conditions, light quantity and light quality did not influence prey localization by L3. Adults

H. axyridis use visual and olfactory cues to detect prey from a distance (Obata 1986, 1997). Based on our results, it appears that visual cues played an important role in finding the *M. persicae* colony. In this case, the black SN, contrary to L3, has a negative effect on aphid localization by females and males, by delaying the time needed for finding the prey. When compared to the other PSN, the black SN lowers the amount of light intensity throughout the whole light spectra (Shahak 2008). Therefore the prey localization is negatively affected under low light conditions because adults coccinellids rely on visual stimuli to orientate towards their prey (Nakamuta 1984; Harmon et al. 1998). Under the pearl PSN, adults reached the aphid colony faster than under the black SN. Due to the *H. axyridis* positive phototaxis it is possible that under the pearl PSN, where there is a similar amount of light compared to no PSN, this coccinellid found more suitable conditions inside the cage (microenvironment) for prey finding. Also, in terms of light quality, under the pearl PSN there is a higher amount of dispersed light when compared to the other treatments (Shahak 2008), which can help females and males in colony localization. The pearl PSN improves light penetration into the most shaded canopies compared to direct light (Hemming et al. 2008). When compared to the other treatments, the light under the pearl PSN is more available within the canopy and more evenly distributed in the environment (Hemming et al. 2008; Kong et al. 2013). It is possible that under our experimental conditions, the coccinellid preferred more indirect light conditions provided by the pearl PSN vs direct light. Taking our results into account, it is unlikely that prey localization is affected by light quality, since prey localization for the three predators was similar under the red PSN and no PSN. Rather, it appears that light quantity has a more evident effect with a positive relationship between light quantity and prey localization, at least for the adult stage.

Predation

Overall predation efficiency on aphids is a key factor when considering the biocontrol value of the predator. Our results on the predation activity indicate that the PSN and the black SN do not influence the predatory voracity of *H. axyridis*. Despite the influence of the PSN and the black SN on prey localization the predation was not affected by the treatments. This means, that in 24h in microcosm conditions, the delayed predator can recuperate its predation impact. Also, we may expect that the PSN and the black SN would not alter biocontrol services provided by ladybeetles in the field, although we have to verify it in real conditions. In this sense, once the predator has successfully located the aphid colony, the PSN and the black SN do not impede aphid consumption.

Foraging behavior

During the first 30 minutes we only found significant differences among treatments for L3 regarding the time spent searching the prey, moving from one plant to the other, or walking around the arena ("Other"). Under the pearl PSN, the L3 spent less time searching the prey when compared to the black SN and the no PSN. This shorter time spent walking around the arena is directly related to the fact that under the pearl PSN, the L3 spent more time in the "Initial plant". Frequent movements of *H. axyridis* larvae moving between plants and on the ground while searching for an aphid colony, have been described before (Kawai 1976). A coccinellid larva can spend a good amount of time in one plant, due to its tendency to visit most parts of the plant, and be led back to leaves it has already visited wasting time and energy (Banks 1957). The extensive search by coccinellids is characterized by fast and linear movements in the habitat where the prey may be present, while intensive search involves slow and turning movements (Bond 1980; Ettifouri and Ferran 1993). After predators encounter their prey, they change the patterns of searching behavior from extensive search to an area-restricted search, and if further prey is not encountered, they can resume the extensive search behavior (Carter and Dixon 1982; Nakamuta 1985). Also, for the L3, and under the four treatments, there was a general trend of a higher amount of time spent in the “Initial plant” and prey searching when compared to the time in the “Focal plant”. Similarly, under all treatments, and for adults, there was a higher amount of time allocated for prey searching, walking around the cage, and moving between plants with a very low number of predators climbing to the focal plant with aphids during the first 30 minutes. This can be explained by the need of the predator to start the search for prey immediately after its introduction inside the cage. For this reason, the higher amount of time in “Other” is motivated by prey encounters and consumption. The amount of time allocated to prey searching was high compared to the other foraging behaviors, regardless of the treatment. After 30 minutes we already see differences in the foraging behavior among and within the different PSN and the black SN. It is worth mentioning that here we are describing an initial behavior, and based on our prey localization results these differences can be more accentuated among treatments given more time.

The PSN utilization has become relevant in agro-ecosystems as a production system in different crops worldwide on the grounds that it combines physical protection and differential filtration of the solar radiation to promote certain physiological responses in plants (Shahak et al. 2004b). In consequence, these changes affect arthropod pests and their natural enemies (Chiel et al. 2006; Doukas and Payne 2007; Legarrea et al. 2012). Studies about the use of PSN and their potential effect on arthropod communities, in particular, natural enemies like predators, are still scarce. To our knowledge, this is the first study assessing the effect of PSN on ladybeetle activity, in particular, on the prey localization, predation, and foraging behavior. More studies should be carried out involving PSN of different colors and shading factors, at larger temporal and spatial scales, on various life-history traits (e.g. fecundity, reproduction, dispersal) of several groups of insects, in particular biocontrol agents (predators and parasitoids), their natural enemies (spiders, hyperparasitoids), and ants tending aphids (Tayeh et al. 2015; Plouvier and Wajnberg 2018). Therefore, and continuing with our PSN research, another ongoing experiment is taking place in similar laboratory conditions, this time evaluating the effect of the PSN and the black SN on the behavior, parasitism, and host localization of the codling moth parasitoid *Mastrus ridens*

(Hymenoptera: Ichneumonidae). Furthermore, our results are very relevant due to the current climate change events on the planet, potentially boosting the demand for the use of these production systems in the field.

Conclusion

Our results indicate that the presence of the PSN and the black SN affect prey localization and foraging behavior of predators. Despite this, they do not affect the biological control of their prey. We conclude that once the predator finds the prey, the PSN and the black SN do not affect predation efficiency. This could have a significant implication for natural biocontrol provided by ladybeetles in the field, due to their important role in regulating aphid populations. We propose that the utilization of biological control agents can be compatible with the use of PSN in agro-ecosystems, in particular, the pearl PSN. They could and should be considered in integrated pest management (IPM) strategies. Studies have to be carried out to evaluate the effect of these production systems on inundative or inoculative releases of biological control agents. It is worth to point out that protective nets constitute a non-chemical pest control tool and a sustainable alternative to favor crop protection against insect pests.

Acknowledgments

We thank the Laboratoire de Lutte Biologique, UQAM, Montréal, Canada, for providing the insect, the plant material, and the space to carry out the experiments. Special thanks to Marc Fournier for technical and logistic assistance, and to all members of the laboratory. Also, thanks to Dr. Richard Bastías from Facultad de Agronomía, Universidad de Concepción, Chillán, Chile for providing the pearl and red PSN. Finally, to Dirección de Postgrado, Universidad de Concepción, Chile, to Vicerrectoría de Investigación y Desarrollo (VRID) Multidisciplinaria 219.113.095-M and to Comisión Nacional de Investigación Científica y Tecnológica (CONICYT) PCI MEC 80170017 Grants for supporting this research.

References

Ahmed K, Majeed MZ, Rafi M, et al (2017) Biodiversity and Species Distribution of Coccinellids (Coccinellidae: Coleoptera) in District Sargodha (Punjab), Pakistan. Pak J Zool 49:1749–1759. doi: 10.17582/journal.pjz/2017.49.5.1749.1759

Alaphilippe A, Capowiez Y, Severac G, et al (2016) Codling moth exclusion netting: an overview of French and Italian experiences. IOBC-WPRS Bull 112:31–35

Antignus Y (2014) Management of Air-Borne Viruses by “Optical Barriers” in Protected Agriculture and Open-Field Crops. In: Maramorosch K, Mettenleiter TC, Murphy FA, et al. (eds) Advances in Virus Research. pp 1–33

Antignus Y, Lapidot M, Hadar D, et al (1998) Ultraviolet-Absorbing Screens Serve as Optical Barriers to Protect Crops from Virus and Insect Pests. J Econ Entomol 91:1401–1405. doi: 10.1093/jee/91.6.1401

Antignus Y, Mor N, Ben Joseph R, et al (1996) Ultraviolet-Absorbing Plastic Sheets Protect Crops from Insect Pests and from Virus Diseases Vectored by Insects. Environ Entomol 25:919–924. doi: 10.1093/ee/25.5.919

Antignus Y, Nestel D, Cohen S, Lapidot M (2001) Ultraviolet-Deficient Greenhouse Environment Affects Whitefly Attraction and Flight-Behavior. Environ Entomol 30:394–399. doi: 10.1603/0046-225X-30.2.394

Arthurs SP, Stamps RH, Giglia FF (2013) Environmental modification inside photoselective shadehouses. HortScience 48:975–979. doi: 10.21273/HORTSCI.48.8.975

Ayala-Tafoya F, Yañez Juárez M, López Orona C, et al (2018) Sunlight transmitted by colored shade nets on photosynthesis and yield of cucumber. Cienc Rural 48:1–9. doi: 10.1590/0103-8478cr20170829

Ayala-Tafoya F, Zatarain-López DM, Valenzuela-López M, et al (2011) Crecimiento y rendimiento de tomate en respuesta a radiación solar transmitida por mallas sombra. Terra Latinoam 29:403–410

Banks CJ (1954) The searching behavior of coccinellid larvae. Br J Anim Behav 2:37–38. doi: 10.1016/S0950-5601(54)80082-7

Banks CJ (1957) The behavior of individual coccinellid larvae on plants. Br J Anim Behav 1:12–24. doi: 10.1016/S0950-5601(57)80039-2

Bartlett MS (1937) Properties of Sufficiency and Statistical Tests. Proc R Soc London A 160:268–282. doi: 10.1098/rspa.1937.0109

Bastías RM (2016) Malla sombra en Manzanos. Boletín Técnico Pomáceas, Univ. Talca 16:2–4

Ben-Yakir D, Antignus Y, Offir Y, Shahak Y (2014) Photoselective nets and screens can reduce insect pests and diseases in agricultural crops. Acta Hortic 1015:95–102. doi: 10.17660/ActaHortic.2014.1015.10

Ben-Yakir D, Antignus Y, Offir Y, Shahak Y (2012) Colored shading nets impede insect invasion and decrease the incidences of insect-transmitted viral diseases in vegetable crops. Entomol Exp Appl 144:249–257. doi: 10.1111/j.1570-7458.2012.01293.x

Bond AB (1980) Optimal foraging in a uniform habitat: the search mechanism of the green lacewing. Anim Behav 28:10–19. doi: 10.1016/S0003-3472(80)80003-0

Briscoe AD, Chittka L (2001) The Evolution of Color Vision in Insects. Annu Rev Entomol 46:471–510. doi: 10.1146/annurev.ento.46.1.471

Brooks ME, Kristensen K, van Benthem KJ, et al (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J 9:378–400. doi: 10.32614/RJ-2017-066

Carter MC, Dixon AFG (1982) Habitat quality and the foraging behavior of coccinellid larvae. J Anim Ecol 51:865–878. doi: 10.2307/4011

Chen Z, Kuang R, Zhou J, Liu X (2012) Phototactic behaviour in *Aphidius gifuensis* (Hymenoptera: Braconidae). Biocontrol Sci Technol 22:271–279. doi: 10.1080/09583157.2012.655261

Chiel E, Messika Y, Steinberg S, Antignus Y (2006) The effect of UV-absorbing plastic sheet on the attraction and host location ability of three parasitoids: *Aphidius colemani*, *Diglyphus isaea* and *Eretmocerus mundus*. BioControl 51:65–78. doi: 10.1007/s10526-005-8667-z

Cramer ME, Demchak K, Marini R, Leskey T (2019) UV-blocking High-tunnel Plastics Reduce Japanese Beetle (*Popillia japonica*) in Red Raspberry. HortScience 54:903–909. doi: 10.21273/HORTSCI13820-18

Dobzhansky T (1933) Geographical Variation in Lady-Beetles. Am Nat 67:97–126. doi: 10.1086/280472

Doukas D, Payne CC (2007) The use of ultraviolet-blocking films in insect pest management in the UK ; effects on naturally occurring arthropod pest and natural enemy populations in a protected cucumber crop. Ann Appl Biol 151:221–231. doi: 10.1111/j.1744-7348.2007.00169.x

Ettifouri M, Ferran A (1993) Influence of larval rearing diet on the intensive searching behavior of *Harmonia axyridis* (Col.: Coccinellidae) larvae. Entomophaga 38:51–59. doi: 10.1007/BF02373138

Goldsmith TH, Bernard GD (1974) The visual system of insects. In: Rockstein M (ed) The Physiology of Insecta: Volume II, Second Edi. Academic Press, inc., pp 165–272

Harmon JP, Losey E, Ives AR (1998) The role of vision and color in the close proximity foraging behavior of four coccinellid species. Oecologia 115:287–292. doi: 10.1007/s004420050518

Hattingh V, Samways MJ (1995) Visual and olfactory location of biotopes, prey patches, and individual prey by the ladybeetle *Chilocorus nigritus*. Entomol Exp Appl 75:87–98. doi: 10.1111/j.1570-7458.1995.tb01914.x

Hemming S, Dueck T, Janse J, van Noort F (2008) The Effect of Diffuse Light on Crops. Acta Hortic 1293–1300. doi: 10.17660/ActaHortic.2008.801.158

Ilić ZS, Fallik E (2017) Light quality manipulation improves vegetable quality at harvest and postharvest: A review. Environ Exp Bot 139:79–90. doi: 10.1016/j.envexpbot.2017.04.006

Kawai A (1976) Analysis of the aggregation behavior in the larvae of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) to prey colony. Res Popul Ecol 18:123–134. doi: 10.1007/BF02754087

Klowden MJ (2007) Physiological Systems in Insects. Elsevier Academic Press, Oxford, UK

Kong Y, Avraham L, Perzelan Y, et al (2013) Pearl netting affects postharvest fruit quality in 'Vergasa' sweet pepper via light environment manipulation. Sci Hortic (Amsterdam) 150:290–298. doi: 10.1016/j.scienta.2012.11.029

Lambin M, Ferran A, Maugan K (1996) La prise d'informations visuelles chez la coccinelle *Harmonia axyridis*. Entomol Exp Appl 79:121–130. doi: 10.1111/j.1570-7458.1996.tb00817.x

Legarrea S, Weintraub PG, Plaza M, et al (2012) Dispersal of aphids, whiteflies and their natural enemies under photoselective nets. BioControl 57:523–532. doi: 10.1007/s10526-011-9430-2

Lin J-T (1993) Identification of Photoreceptor Locations in the Compound Eye of *Coccinella septempunctata* Linnaeus (Coleoptera, Coccinellidae). J Insect Physiol 39:555–562. doi: 10.1016/0022-1910(93)90037-R

MacGillivray M, Anderson G (1957) Three Useful Insect Cages. Can Entomol 89:43–46

Menzel R (1979) Spectral Sensitivity and Color Vision in Invertebrates. In: Autrum H, Bennet MF, Diehn B, et al. (eds) Comparative Physiology and Evolution of Vision in Invertebrates. Springer Berlin Heidelberg, pp 503–580

Miranda MP, Dos Santos FL, Felippe MR, et al (2015) Effect of UV-blocking plastic films on take-off and host plant finding ability of *Diaphorina citri* (Hemiptera: Liviidae). J Econ Entomol 108:245–251. doi: 10.1093/jee/tou036

Nakamuta K (1984) Visual Orientation of a Ladybeetle *Coccinella septempunctata* L ., (Coleoptera : Coccinellidae), toward Its Prey. Appl Entomol Zool 19:82–86. doi: 10.1303/aez.19.82

Nakamuta K (1985) Mechanism of the switchover from extensive to area-concentrated search behavior of the ladybird beetle, *Coccinella septempunctata* Bruckii. J Insect Physiol 31:849–856. doi: 10.1016/0022-1910(85)90102-7

Obata S (1997) The influence of aphids on the behaviour of adults of the ladybird beetle, *Harmonia axyridis* (Col: Coccinellidae). Entomophaga 42:103–106. doi: 10.1007/BF02769885

Obata S (1986) Mechanisms of prey finding in the aphidophagous ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). Entomophaga 31:303–311. doi: 10.1007/BF02373340

Pajaĉ I, Kos T, Lemić D, et al (2018) Exclusion nets influence on the abundance of ground beetles (Coleoptera: Carabidae) in apple orchards. Appl Ecol Environ Res 16:3517–3528. doi: 10.15666/aeer/1603_35173528

Peitsch D, Fietz A, Hertel H, et al (1992) The spectral input systems of hymenopteran insects and their receptor-based colour vision. J Comp Physiol A 170:23–40. doi: 10.1007/BF00190398

Plouvier WN, Wajnberg E (2018) Improving the efficiency of augmentative biological control with arthropod natural enemies: A modeling approach. Biol Control 125:121–130. doi: 10.1016/j.biocontrol.2018.05.010

Prokopy RJ, Owens ED (1983) Visual detection of plants by herbivorous insects. Annu Rev Entomol 28:337–364. doi: 10.1146/annurev.en.28.010183.002005

R Core Team (2019) R: A Language and Environment for Statistical Computing. R Found. Stat. Comput. Vienna, Austria URL https//www.r-project.org/

Roy H, Brown P, Majerus M (2006) *Harmonia axyridis*: a successful biocontrol agent or an invasive threat? In: Eilenberg J, Hokkanen HMT (eds) An Ecological and Societal Approach to Biological Control, Springer. pp 295–309

Selahle KM, Sivakumar D, Jifon J, Soundy P (2015) Postharvest responses of red and yellow sweet peppers grown under photo-selective nets. Food Chem 173:951–956. doi: 10.1016/j.foodchem.2014.10.034

Shahak Y (2008) Photo-Selective Netting for Improved Performance of Horticultural Crops. A Review of Ornamental and Vegetable Studies Carried Out in Israel. Acta Hortic 161–168. doi: 10.17660/ActaHortic.2008.770.18

Shahak Y, Gal E, Offir Y, Ben-Yakir D (2008a) Photoselective shade netting integrated with greenhouse technologies for improved performance of vegetable and ornamental crops. Acta Hortic 797:75–80. doi: 10.17660/ActaHortic.2008.797.8

Shahak Y, Gussakovsky EE, Cohen Y, et al (2004a) ColorNets: A new approach for light manipulation in fruit trees. Acta Hortic 609–616. doi: 10.17660/ActaHortic.2004.636.76

Shahak Y, Gussakovsky EE, Gal E, Ganelevin R (2004b) ColorNets: Crop protection and Light-Quality Manipulation in One Technology. Acta Hortic 659:143–151. doi: 10.17660/ActaHortic.2004.659.17

Shahak Y, Kong Y, Ratner K (2016) The wonders of yellow netting. Acta Hortic 1134:327–334. doi: 10.17660/ActaHortic.2016.1134.43

Shahak Y, Ratner K, Giller YE, et al (2008b) Improving Solar Energy Utilization, Productivity and Fruit Quality in Orchards and Vineyards by Photoselective Netting. Acta Hortic 772:65–72. doi: 10.17660/ActaHortic.2008.772.7

Shapiro SS, Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52:591–611. doi: 10.2307/2333709

Stubbs M (1980) Another look at prey detection by coccinellids. Ecol Entomol 5:179–182. doi: 10.1111/j.1365-2311.1980.tb01139.x

Tan X, Zhao J, Zhang F, Wang S (2014) Light dependency of life trails, reproduction, locomotion, and predation in the polyphagous ladybird *Hippodamia variegata*. Entomol Exp Appl 152:200–208. doi: 10.1111/eea.12217

Tayeh A, Hufbauer R, Estoup A, et al (2015) Biological invasion and biological control select for different life histories. Nat Commun 6:1–5. doi: 10.1038/ncomms8268

Tian M, Wei Y, Zhang S, Liu T (2017) Suitability of *Bemisia tabaci* (Hemiptera: Aleyrodidae) biotype-B and *Myzus persicae* (Hemiptera: Aphididae) as prey for the ladybird beetle, *Serangium japonicum* (Coleoptera: Coccinellidae). Eur J Entomol 114:603–608. doi: 10.14411/eje.2017.073

Tinyane PP, Sivakumar D, Soundy P (2013) Influence of photo-selective netting on fruit quality parameters and bioactive compounds in selected tomato cultivars. Sci Hortic (Amsterdam) 161:340–349. doi: 10.1016/j.scienta.2013.06.024

Umanzor C, Bastías R, Wilckens R, Quezada C (2016) Influencia del uso de malla perla y roja en las condiciones micro-climáticas, daño por sol y desarrollo de color de frutos en huertos de manzanos cvs. gala y fuji. Rev Bras Frutic 39:1–13. doi: 10.1590/0100-29452017930

Zhou J, Kuang R, Chen Z, et al (2013) Phototactic Behavior of *Coccinella septempunctata* L . (Coleoptera : Coccinellidae). Coleopt Bull 67:33–39. doi: 10.1649/072.067.0108

Zhou K, Jerszurki D, Sadka A, et al (2018) Effects of photoselective netting on root growth and development of young grafted orange trees under semi-arid climate. Sci Hortic (Amsterdam) 238:272–280. doi: 10.1016/j.scienta.2018.04.054

Tables

Table 1.1 Light intensity measured as photosynthetic active radiation (PAR) and shading factor provided by photo-selective and black standard nets (PSN and SN, respectively) used in the experiments.

Treatments	Supplier	Specifications	PAR* (µmol m^{-2} s^{-1})	Shading factor (%)
No PSN (control)	-	-	7	0
Pearl PSN	ChromatiNet®, Polysack Industries, Negev, Israel	HDPE monofilament, mesh size 5 x 2 mm	6	20
Red PSN	ChromatiNet®, Polysack Industries, Negev, Israel	HDPE monofilament, mesh size 5 x 2 mm	5	20
Black SN	Polytex S.A., Chile	HDPE raschel, mesh size 3 x 1 mm	1	80

Figures

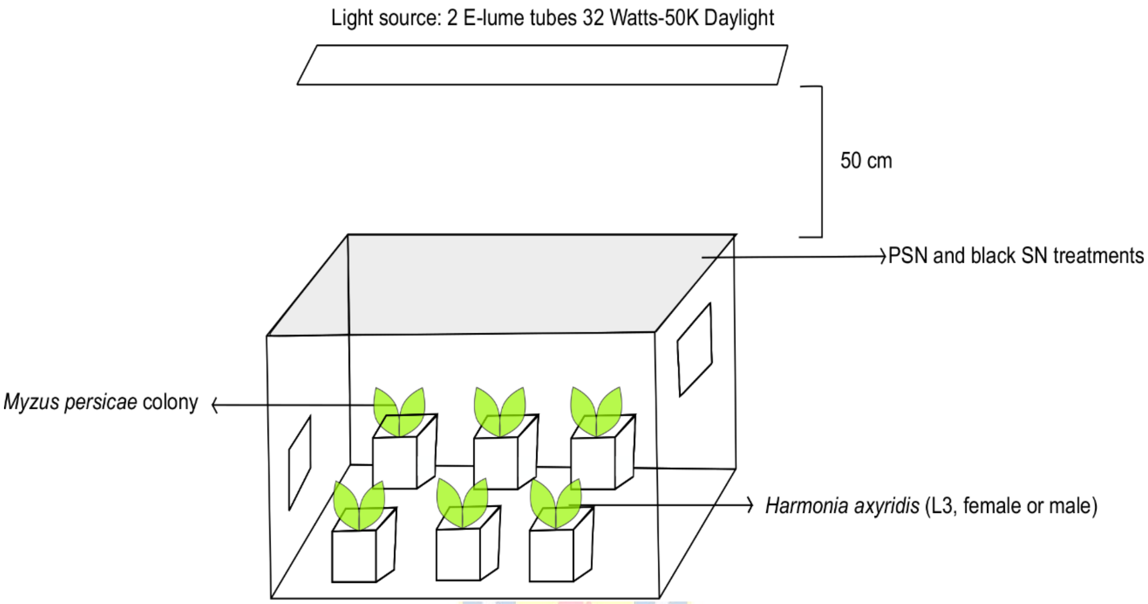


Figure 1.1 Experimental design (22.6 x 23 x 20.5 cm high/length/width) used for the experiments performed. In one plant at one extreme of the cage the *M. persicae* colony was placed (prey) (n=20) and at the other extreme we introduced *H. axyridis* (predator).

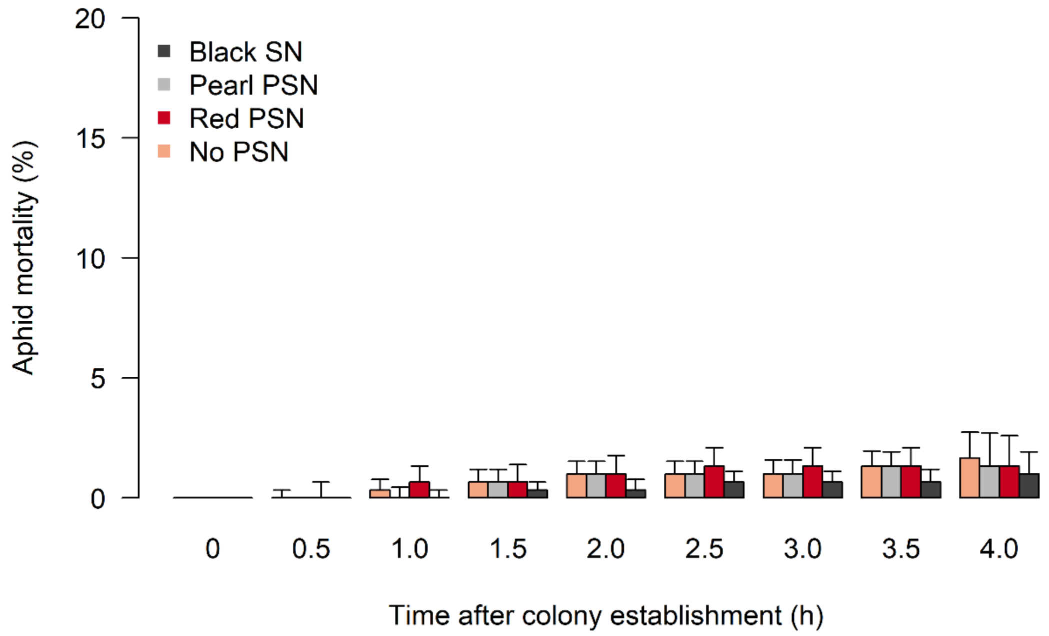
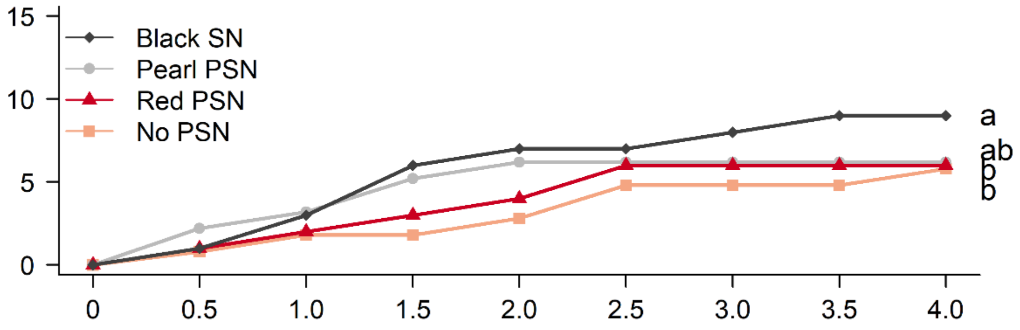
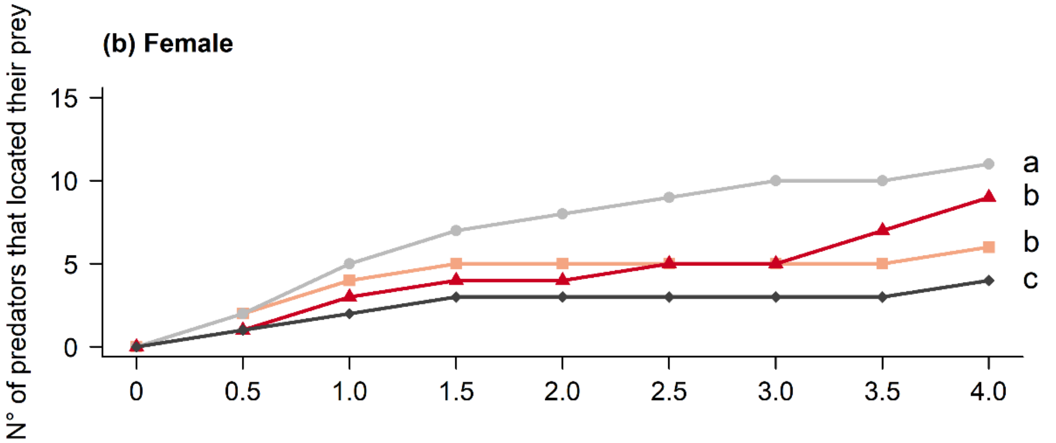


Figure 1.2 Natural mortality of *M. persicae* colony, under photo-selective and black standard nets (PSN and SN, respectively) throughout the time observations after aphid colony establishment (mean % ± SE; n=20 aphids).

(a) Third-instar larvae (L3)



(b) Female



(c) Male

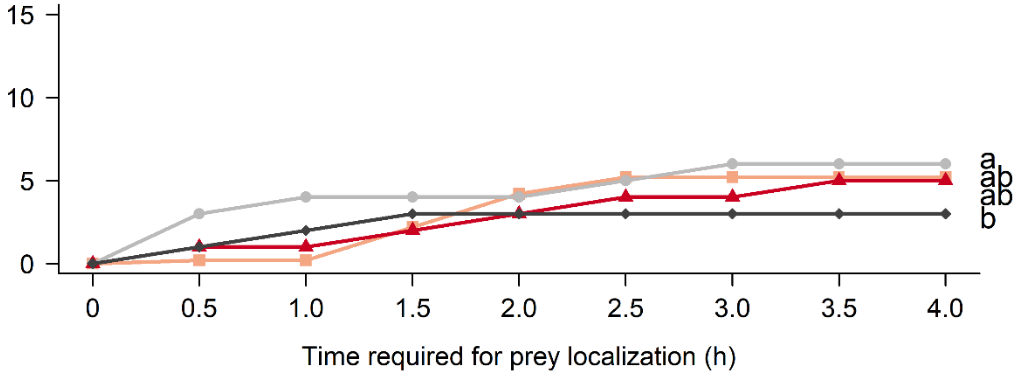
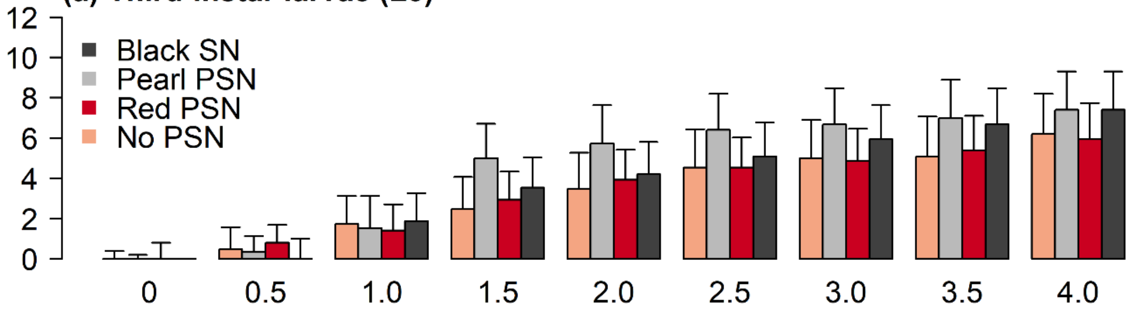
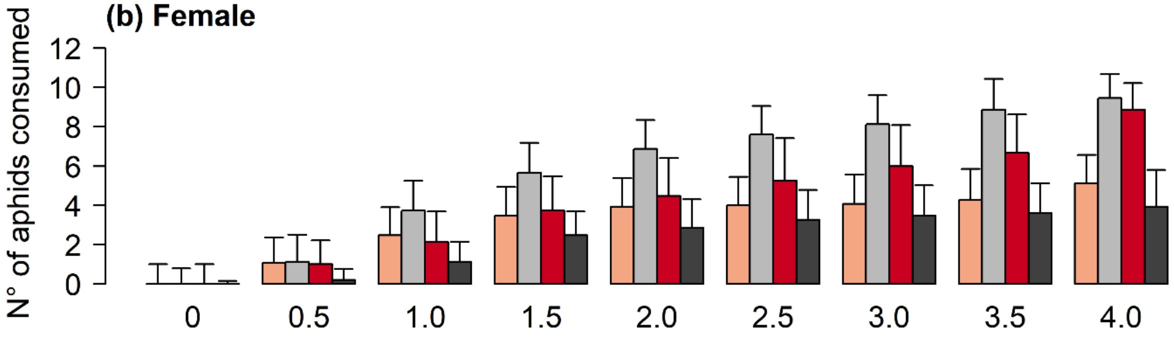


Figure 1.3 Accumulated number of *H. axyridis* (a) third-instar larvae (L3), (b) females, and (c) males that located the aphid colony under photo-selective and black standard nets (PSN and SN, respectively) along the first four hours of observation. Different letters indicate significant differences among treatments.


(a) Third-instar larvae (L3)


(b) Female

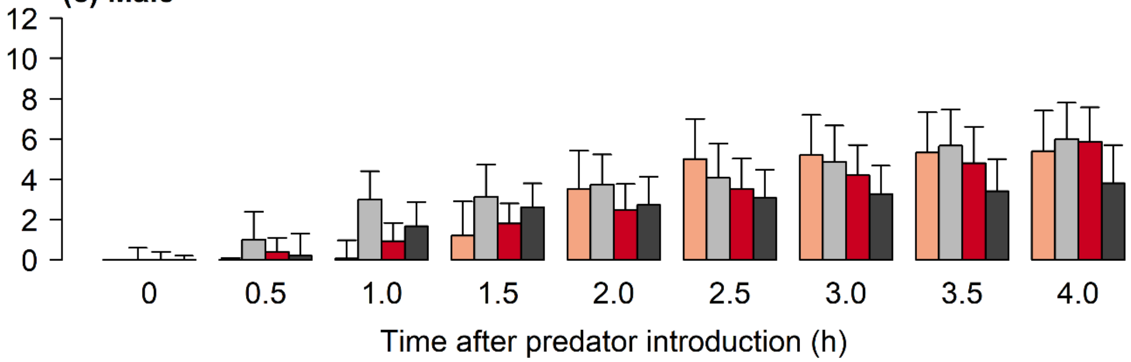

(c) Male

Figure 1.4 Number of aphids consumed by *H. axyridis* (a) third-instar larvae (L3), (b) female and, (c) male, under photo-selective and black standard nets (PSN and SN, respectively) along the first four hours of observation. The initial aphid number=20.

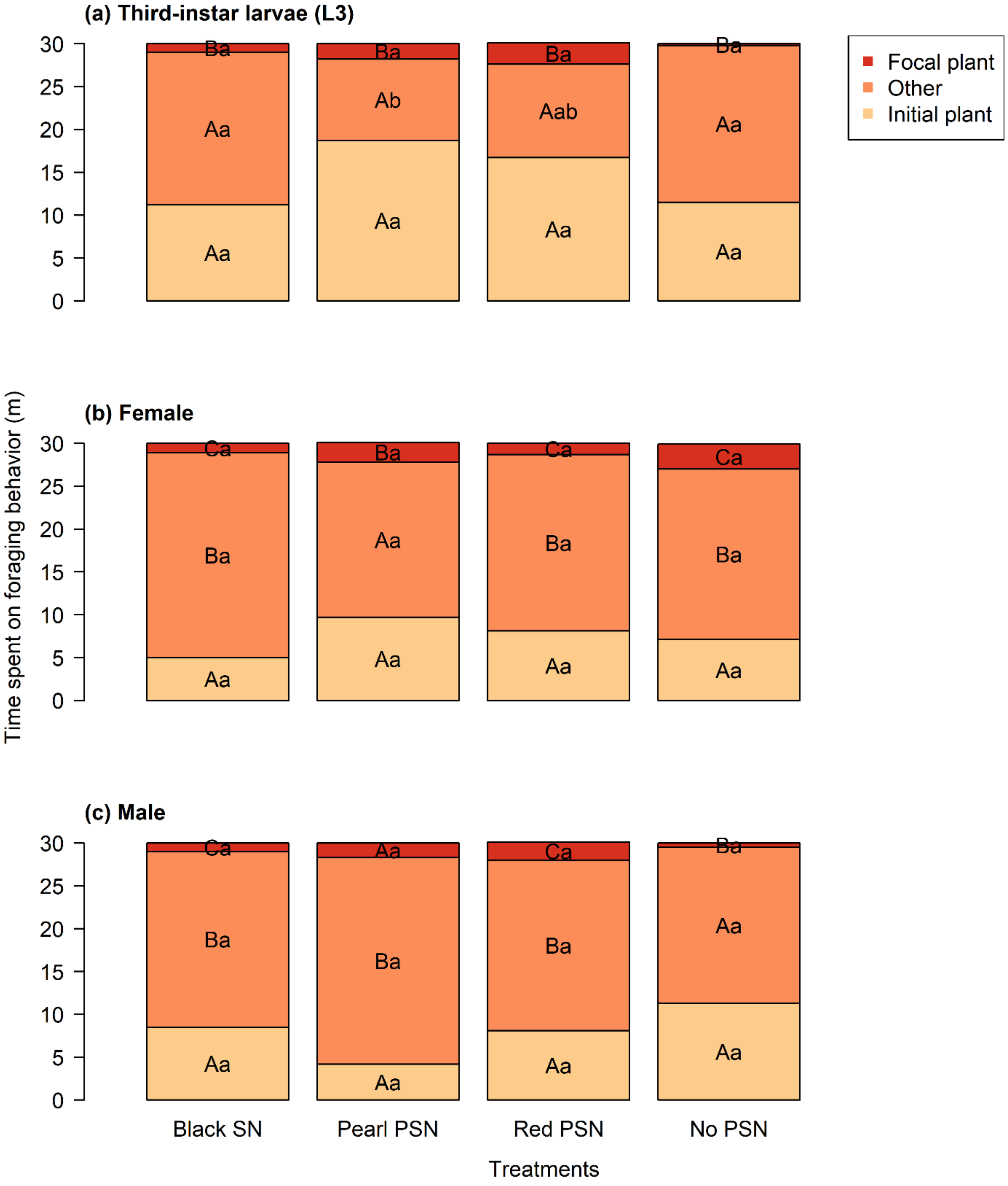

(a) Third-instar larvae (L3)
Focal plant
Other
Initial plant
Ba
Aa
Aa
Ba
Ab
Aa
Ba
Aab
Aa
Ba
Aa
Aa
(b) Female
Ca
Ba
Aa
Ba
Aa
Aa
Ca
Ba
Aa
Ca
Ba
Aa
(c) Male
Ca
Ba
Aa
Aa
Ba
Aa
Ca
Ba
Aa
Ba
Aa
Aa
0
5
10
15
20
25
30
Time spent on foraging behavior (m)
Black SN
Pearl PSN
Red PSN
No PSN
Treatments

Figure 1.5 Effect of photo-selective and black standard nets (PSN and SN, respectively) on the time spent by *H. axyridis* (a) third-instar larvae (L3), (b) females and, (c) males on different foraging behaviors. Different lowercase letters indicate significant differences among treatments for each foraging behavior for each predator separately. Uppercase letters indicate significant differences among foraging behaviors within each treatment for each predator separately. Total observation time = 30 minutes.

CAPÍTULO II

Photo-selective nets and pest control: activity of the codling moth parasitoid *Mastrus ridens* (Hymenoptera: Ichneumonidae) under varying light quantity and quality

Photo-selective nets and pest control: activity of the codling moth parasitoid *Mastrus ridens* (Hymenoptera: Ichneumonidae) under varying light quantity and quality

María-José Yáñez-Díaz[a], Marcela Rodríguez[a*], Selim Musleh[a, b], Luis Devotto[c], Gonzalo Silva[d], Eric Lucas[e]

[a] Laboratorio de Entomología Aplicada, Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Barrio Universitario s/n, Casilla 160-C, Concepción, Chile;

[b] Núcleo Milenio INVASAL, Concepción, Chile;

[c] Instituto de Investigaciones Agropecuarias (INIA), Centro Tecnológico de Control Biológico, Centro Regional de Investigación Quilamapu, Avda. Vicente Méndez 515, postal box 426, Chillán, Chile;

[d] Laboratorio de Entomología, Departamento de Producción Vegetal, Facultad de Agronomía, Universidad de Concepción, Av. Vicente Méndez 595,Casilla 537, Chillán, Chile;

[e] Laboratoire de Lutte Biologique, Département des Sciences Biologiques, Université du Québec à Montréal, 141 Avenue du Président-Kennedy, Montréal, QC H2X 1Y4, Canada;

E-mail addresses: mariajoseyd@gmail.com (MJ. Yáñez-Díaz), marcela.arg@gmail.com (M. Rodríguez), semusleh@gmail.com (S. Musleh), ldevotto@gmail.com (L. Devotto), gosilva@udec.cl (G. Silva), lucas.eric@uqam.ca (E. Lucas).

*Corresponding author

E-mail address: marcela.arg@gmail.com (M. Rodríguez)

Artículo será enviado a: Biological Control

Abstract

Photo-selective nets (PSN) are widely used to manipulate the physiology of fruit crops. Besides their advantages to the crop, the PSN can also affect insect pests and potentially their natural enemies. We aimed to assess the effect of these production systems on the activity of the codling moth parasitoid, *Mastrus ridens*. We hypothesize that the PSN and the black standard net (SN) affect the behavior of the parasitoid by delaying host localization and reducing parasitism. Laboratory experiments were carried out in closed cages evaluating the activity of the parasitoid under four treatments: black SN, pearl PSN, red PSN, and no PSN used as control (uncovered cages). Our results showed that *M. ridens* host localization was delayed under the black SN and enhanced by the pearl and the red PSN. The PSN and the black SN did not affect traits like parasitism, fertility, realized fecundity, and offspring sex ratio. The initial behavior of the parasitoid during the first 30 minutes of the bioassays was not affected by treatments. However, females spent most of the time walking aimlessly around the arena, grooming or resting (pre-contact), regardless of the color of the nets. Our results are relevant because if the PSN and black SN affect *M. ridens* host localization in a microcosm, the same could happen once the parasitoid is released at a larger spatial scale, so further studies in real field conditions must be carried out.

Keywords: biological control, *Cydia pomonella*, host localization, light quality, parasitism, photo-selective nets

1. Introduction

The increased UV radiation observed after the weakening of the ozone layer and the increasing occurrence of unexpected climatic events (rain, hail, frosts, etc.) are challenging to the global food production, particularly in fruit growing (Moretti et al., 2010; Wheeler and von Braun, 2013). In response, agriculture under netting is increasing, becoming one of the main strategies for protection against climatic stressors (Kalcsits et al., 2017; Mupambi et al., 2018). Among other benefits, netting provides a reduction in the incidence of direct radiation by keeping the suited temperature for the crop, leading to decreased fruit damage (Iglesias and Alegre, 2006). At present, the black standard nets (SN) have been the most used by growers in several countries like Chile, Israel, and South Africa (Lobos et al., 2012; Shahak et al., 2008; Tinyane et al., 2013), mainly due to their low cost, and because they provide a higher shading factor, compared to other nets (Ben-Yakir et al., 2012; Elad et al., 2007). The black SN reduces the amount of light (PAR and UV) throughout the whole light spectra but does not affect the light quality (Shahak, 2008). In addition to light quantity, the light quality that passes through the nets into the crop has been manipulated to promote certain physiological responses in target plants and to improve fruit quality. For this purpose, photo-selective nets (PSN) of different colors have been developed to provide physical protection and differential filtration of the solar spectra. Different types of netting are used depending on the goals that the grower or the researcher wants to reach (Bastías and Corelli-Grappadelli, 2012; Mupambi et al., 2018; Shahak et al., 2004). Through the incorporation of light reflective or chromatic elements into the plastic material, the modification of light spectra in the UV (200-400 nm), visible (400-700 nm) or red regions (600 nm and up) is possible (Ilić et al., 2017; Shahak, 2008). For example, the pearl PSN reduces the light quantity (PAR, 400-700 nm), and, at the same time, affects the light quality, lowering the transmission of UVA and UVB regions (280-400 nm) (Arthurs et al., 2013; Shahak, 2008). Compared to other PSN and black SN, under the pearl PSN, there is a higher amount of diffuse light, which improves the light penetration into the inner, most shaded canopies inside the crop (Hemming et al., 2008). This light manipulation provided by the pearl PSN increases fruit size, improves plant productivity, and total yield in target plants (Selahle et al., 2015; Shahak, 2008; Shahak et al., 2008). Similar to the pearl PSN, the red PSN also enhances the light scattering throughout the crop, although to a lesser extent (Shahak, 2008). The red PSN is specifically designed to absorb three light bands (UV, blue, and green), and to enhance light transmission in the red, and far-red range (600 nm and up) (Ilić et al., 2017; Shahak, 2008). This light manipulation results in increasing biomass, vegetative growth, and average fruit weight in target plants (Shahak, 2008).

At present, most of the studies on UV-absorbing nets and insect responses have focused on agricultural pests, including aphids, whiteflies, and mites (Antignus et al., 1998; Chyzik et al., 2003; Dáder et al., 2014). Based on the available results, a general pattern has been raised in UV-deficient environments, showing negative effects in both, insect vision and orientation, lowering their flight and dispersion capability, and delaying their arrival to the crop (Antignus et al., 2001; Chyzik et al., 2003; Legarrea et al., 2012a). The knowledge of the effect of the PSN on the activity of natural enemies is very limited, and the response of predators, parasitoids, or both to netting has been studied very little. One of the few studies related to parasitoids in greenhouse trials established that by using UV-absorbing plastic sheets, some hymenopteran parasitoids were not affected in their capability to locate hosts (Chiel et al., 2006). However, other parasitoids used UV light for long-range host location, and therefore their fitness was affected by changes in the amount of UV light. It has been proposed that parasitoids that were not affected by reduced UV light used mainly olfactory signals instead of visual cues for host finding; and species with bad performance under UV-deficient environments used mainly visual stimuli for host finding (Chiel et al., 2006; Chyzik et al., 2003).

In the present study, to assess the effect of the black SN, the pearl PSN, and the red PSN on the activity of a biological control agent, we selected the codling moth *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) and its natural enemy *Mastrus ridens* Horstmann (Hymenoptera: Ichneumonidae). Apple is one of the most important fruit crops in Chile, and the use of netting in apple cultivars has widened in the last years, especially in Fuji and related varieties. The PSN and the black SN used in this study were chosen because i) the black SN is commonly used in Chile by growers and, ii) the pearl and the red PSN have been recently introduced for crop protection in Chile (Umanzor et al., 2016). *C. pomonella* is the main pest insect of apple, pear, and walnut worldwide (Welter, 2009). The area of origin of *C. pomonella* is in Eurasia and it is present in all main temperate fruit growing areas of the world (Wearing et al., 2001). Because *C. pomonella* larvae cause direct damage to fruits, its control relies heavily on frequent insecticide sprays, which is against consumer preference and increases the risk of insecticide resistance (Bosch et al., 2018; Rodríguez et al., 2011; Sauphanor et al., 1999). To reduce the use of insecticides, several natural enemies have been evaluated for *C. pomonella* control, including pathogens, predators, and parasitoids (Lacey and Unruh, 2005). Early in the 90s, not only mankind but science benefited from the end of the Cold War, as US researchers were granted access to *C. pomonella* center of origin in the former USSR territory. Several hymenopteran parasitoids were found, and some brought to the US for further evaluation including *M. ridens*, a gregarious idiobiont ectoparasitoid of fifth-instar larvae or pre-pupal *C. pomonella* (Bezemer et al., 2005). Later, this parasitoids was introduced to Chile and Argentina under a classical biological control approach (Devotto et al., 2010; Mills, 2005; Retamal et al., 2016).

For some hymenopteran parasitoids, phototactic activity has been positively associated with the light quantity, reflected in higher parasitism rates (Chen et al., 2016; Schirmer et al., 2008). Additionally, the visual systems of hymenopteran species is mainly composed of blue, green, and UV photoreceptors, so the parasitoids respond to different wavelengths, showing preferences for certain colors and light intensities (Chen et al., 2016, 2014; Peitsch et al., 1992). The fitness of *M. ridens* in netted orchards has not been studied in any of the countries where the parasitoid has been introduced. Therefore, our research aimed to assess the effect of the PSN and the black SN on the activity of the parasitoid *M. ridens* in laboratory conditions. Specifically, we will measure the time needed by *M. ridens* for host localization and we will compare the parasitism rates under the PSN and the black SN. We hypothesize that the presence of the PSN and the black SN affects the behavior of *M. ridens*, by delaying host localization and reducing parasitism on fifth-instar *C. pomonella* larvae. We expect that the lower light levels and the different light spectra range under PSN and the black SN, compared to no PSN, will diminish the activity of *M. ridens*.

2. Materials and Methods

Laboratory bioassays were carried out to assess the effect of the PSN and the black SN on the activity of *M. ridens*. In particular, if the PSN and the black SN influence the host finding capability and parasitism rates. Also, we evaluated if these nets influence the initial behavior of the parasitoid in terms of searching and host finding.

2.1. Insects

To conduct the bioassays, the host chosen was the fifth-instar *C. pomonella* larvae and the ectoparasitoid *M. ridens*, specialized in attacking *C. pomonella* larvae (Bueno et al., 2017). Both fifth-instar *C. pomonella* larvae and *M. ridens* pupae were obtained from colonies maintained on the Entomology Laboratory, Center for Biological Control Technology, INIA Quilamapu, (Chillán, Chile). The parasitoid was imported from the United States in 2004, and subsequently maintained for sixteen years. The colony of *C. pomonella* has been maintained for over fourteen years with wild individuals added periodically mainly from apple orchards (Devotto et al., 2010). *C. pomonella* eggs and larvae were reared on round plastic containers (8 cm high and 12 cm diameter) with 80-100 ml of agar-based diet. Both *C. pomonella* and *M. ridens* were brought to the Applied Entomology Laboratory, Universidad de

Concepción, and maintained at 26°C and 16:8 (L: D) photoperiod in a growing chamber. *M. ridens* adults that emerged from the pupae were kept in wood and glass cages (31.5 x 21.5 x 23 cm) and provided with honey and water *ad libitum*.

2.2. Host localization

To study the effect of the PSN and the black SN treatments on *M. ridens* host localization, bioassays were conducted inside an experimental unit, consisting of a 12 L plastic box (22.6 x 23 x 20.5 cm, high/length/width, respectively) built using two 6 L plastic boxes attached with clay, one inverted on top of the other. Each cage had holes on the side covered with transparent muslin to allow ventilation inside the cage. For all bioassays, four treatments were used: black SN, pearl PSN, and red PSN above the cage, and no PSN were used as control (uncovered cages) (Table 1). The PSN and the black SN were put directly above each cage to modify light quantity and quality inside the experimental unit. Inside each cage, there were six apple plants (~10 -15 cm height) put on top of a green foam base inside a plastic pot. As a light source, two 36 Watts tubes (SERA Daylight Brilliant 36W 60K T8) were located 57 cm above the surface of the cage. One *M. ridens* couple (aged 24 - 48 hours) was used alongside four fifth-instar *C. pomonella* larvae on individual cardboard pieces, based on the attack rate registered by this parasitoid (1 - 4 hosts/day in the laboratory) (Sandanayaka et al., 2011). The day before the bioassays, the fifth-instar *C. pomonella* larvae were put individually on cardboard pieces to allow them to spin their cocoon. *M. ridens* adults were fed *ad libitum* with honey and water before and during the bioassays. In one plant at one extreme of the cage, four fifth-instar *C. pomonella* larvae were attached to the trunk of the plant with a double-sided adhesive. The *M. ridens* couple was introduced by the ventilation hole on the other extreme of the cage. Each treatment was replicated 15 times. The experiments were carried out at 27±1°C, 16:8 (L: D) photoperiod, and 60% RH. To assess the effect of the PSN, the black SN, and no PSN on the host localization capability of the parasitoid, the time spent finding the host was recorded every 30 minutes for six hours and at 24 hours after the beginning of the bioassays.

2.3. Parasitism

We tested if the PSN and the black SN affects the parasitism activity of *M. ridens*. For this purpose, the *M. ridens* couple and the four fifth-instar *C.

pomonella larvae were introduced in the same experimental unit described in 2.2. After 24 h of exposure to the female *M. ridens*, the cardboard pieces containing the fifth-instar *C. pomonella* larvae were placed on a Petri dish (5 cm diameter) on a growing chamber at 26°C, and 16:8 (L:D) photoperiod until adult emergence. Each treatment was replicated 15 times. We recorded i) the parasitism rate (number of parasitized larvae by female out of the four larvae offered), ii) the female fertility (total parasitoid larvae on an attacked host/day), iii) the realized fecundity (total emerged adults by a female/day), and iv) the sex ratio (percentage of female offspring respect to the total adult offspring). Regarding the fertility data, we counted the number of larvae laid by a female, instead of counting the number of eggs laid, to avoid the unnecessary manipulation and risk of mortality on eggs due to the handling process. Finally, to assess the natural mortality of *C. pomonella* larvae, we placed four fifth-instar larvae on individual cardboard pieces on a Petri dish. This was replicated 7 times (each time we carried out a set of parasitism bioassays). After 24 hours, we moved them to a growing chamber under the same conditions established in 2.3 until adult emergence. As the mortality of *C. pomonella* larvae on the Petri dishes was low, we did not correct the parasitism data in the analysis.

2.4. Parasitoid behavior

We assessed the effect of the PSN and the black SN on the behavior of the female parasitoids during the first 30 minutes after their introduction to the experimental unit. These observations were used to describe the parasitoid responses to the experimental unit. Parasitoid behavior was cataloged based on behavioral categories modified from Charles et al. (2013). The parasitoid responses were categorized into two phases. Phase 1 (localization and examination) consisted of the sub-phases 1.1) pre-contact (walking aimlessly around the arena, grooming or resting), 1.2) mating (copulation behavior between male and female), 1.3) examination (walking around the cocoon, with a continuous examination by antennae and ovipositor), and 1.4) acceptance (host acceptance and stinging, terebra insertion). Phase 2 of our observations (Pre-contact) focused on the pre-contact sub-phase described in Phase 1. Phase 2 was divided into two sub-phases, 2.1) searching (walking around the arena) and, 2.2) grooming (resting but moving antennae, legs, abdomen, or ovipositor). Observations of parasitoid behavior were replicated 15 times under each treatment.

2.5. Data analysis

To determine if the PSN and the black SN influence the time required by females *M. ridens* to find the fifth-instar *C. pomonella* larvae, a generalized linear model (GLM) with binomial distribution was performed using the statistical package glmm TMB (Brooks et al., 2017). For the analysis, the dependent variable was if the parasitoid located the fifth-instar *C. pomonella* larvae at each given time (binary data: 1 when the parasitoid finds the host, and 0 when the parasitoid does not find the host), and the independent variables were the four different treatments, and the 13 time intervals. To determine if the PSN and the black SN treatments had a significant effect on traits like influence parasitism, fertility, realized fecundity, and offspring sex ratio, and because they were not normally distributed, a non-parametric Kruskal-Wallis test for multiple comparisons was performed. Finally, to test if the PSN and the black SN influenced the time allocated by the females to different behaviors (phase 1 and phase 2 described in 2.4), and since the data was not normally distributed, a non-parametric Kruskal-Wallis was performed. Additionally, to evaluate if there were significant differences within each treatment for the time spent by females on each behavior sub-phase (phase 1 and phase 2), a Wilcoxon Signed-Rank test for paired observations was used. All analyses were carried out in R version 3.6.0 (R Core Team, 2019).

3. Results

3.1. Effect of the PSN and the black SN on the host localization capability of *M. ridens*

The host localization capability of *M. ridens* differed significantly depending on the color of the PSN and the black SN used in our experimental cages (Figure 1). Under the black SN, *M ridens* host localization was delayed compared to the other treatments, being significantly different from the pearl PSN (df=775, P=0.0003) and the red PSN (df=775, P=0.0001). However, no significant differences were observed along the observation time between the host localization capabilities of the parasitoids under the black SN compared to parasitoids under no PSN (df=775, P=0.072). The observed response of the parasitoids under the pearl PSN was similar to the parasitoids under the red PSN (df=775, P=0.0750) and under no PSN (df=775, P=0.052). Under the red PSN, the host localization capability by females was enhanced, with a higher proportion of females reaching the host, compared to the control (df=775, P=0.0003). At 24 hours after the bioassay started, there were no significant differences in the host localization among treatments (data not shown).

3.2. Effect of the PSN and the black SN on the parasitism rate of *M. ridens*

A Kruskal-Wallis analysis of the parasitism percentage revealed that the color of the nets did not affect the parasitism rate of the parasitoid females in laboratory conditions (Figure 2). Larval parasitism ranged from 5% to 10% depending on the color of the nets, but no significant differences were detected (df=3, P=0.668).

3.3. Effect of the PSN and the black SN on the fertility of *M. ridens*

The mean number of parasitoid larvae on each parasitized host varied from 0.7 larvae under the red PSN to 1.4 larvae under the black SN. However, the Kruskal-Wallis analysis showed that the color of the nets did not influence the number of parasitoid larvae left by the female *M. ridens* (df=3, P=0.702) (Figure 3).

3.4. Effect of the PSN and the black SN on the realized fecundity of *M. ridens*

The mean number of *M. ridens* offspring that reached the adult stage varied from 0.53 adults under the red PSN to 0.8 adult parasitoids under the pearl and the black SN (Figure 4). Similarly for both, parasitism and fertility, the analysis showed no significant differences among treatments for this trait (df=3, P=0.769).

3.5. Effect of the PSN and the black SN on the offspring sex ratio of *M. ridens*

The sex ratio of *M. ridens* offspring showed a strong bias towards males, regardless of the color of the nets. The proportion of females is the most important indicator in biological control agents and ranged from 17% under the black SN to 33% in emerged parasitoids under the pearl PSN (Figure 5), but no significant differences among treatments were detected (df=3, P=0.392).

3.6. Effect of the PSN and the black SN on the behavior of females *M. ridens*

We observed the behavior of females *M. ridens* to assess the effect of the PSN and the black SN during the first 30 minutes immediately after their release inside the experimental units. We found no significant differences in the time spent on phase 1 of behavior among treatments (Figure 6a). Regardless of the nets color, all females spent most of their time in the pre-contact sub-phase (df=3, P=0.523), which accounted for more than 95% of the total time among treatments, especially under the black SN where the females spent the whole 30 minutes of observation on this behavior sub-phase. The time spent on pre-contact was significantly higher than the time spent on the other three behavior sub-phases under all four treatments (V=120, P<0.05). The analysis of mating also showed no differences among treatments (df=3, P=0.565). It is important to state that we only observed mating under the pearl PSN and under no PSN. The mating between the male and the female lasted no longer than one minute, and after termination, the male moved away from the female. The female stayed still for a few seconds before resuming the host search. The examination process, where the female finds the host and taps the cardboard with the antennae, was a very rare event and was not affected by the treatments (df=3, P=0.792). No hosts were reached under the black SN. A single female reached the host during the first 30 minutes under the pearl PSN, the red PSN, and no PSN. Although some females reached the host during this time, acceptance was not registered in any of the four treatments tested. Furthermore, for phase 2 of behavior

(Figure 6b), the results showed no differences among treatments for searching (df=3, P=0.301) and grooming (df=3, P=0.382). In terms of the behavior within each treatment, except under the red PSN (V=32, P=0.117), the time spent on grooming was significantly higher than the time spent searching (Black SN: V=12.5, P=0.007; Pearl PSN: V=19, P=0.038; No PSN: V=4.5, P=0.003).

Discussion

Our study demonstrated that the presence of the PSN and the black SN significantly affected some traits of *M. ridens* parasitoid activity. For *M. ridens* host localization, our results showed that the PSN and the black SN had a significant effect. Females *M. ridens* are attracted to kairomones emitted by the cocoons to locate potential hosts (Jumean et al., 2005), therefore we offered four fifth-instar *C. pomonella* larvae that have recently spun cocoons (≤ 24 hours) to a single female. For effective parasitism, the parasitoid first must find the environment where the potential host is, and then properly locate the host for reproduction (Salt, 1935). In our study, we placed the parasitoid and the host in the same environment. Once the parasitoid and host share the same environment, the chemical, visual, tactile, and olfactory senses are used as short-range cues (Wajnberg and Colazza, 2013). We were interested, in particular, on the visual stimuli which are relevant for the process of host finding (Koul and Dhaliwal, 2003). The PSN and the black SN can modify the light quantity and quality and potentially interfere with the behavior of both pests and parasitoids (Chiel et al., 2006). Our results indicate that under the black SN, host localization was delayed, supporting our hypothesis about the negative effects on the host finding capabilities of the parasitoid in low light conditions. This should be considered whenever this net is used simultaneously with biological control agents in the field. The highest host localization occurred under the pearl and the red PSN. The pearl and the red PSN increase the amount of diffused light in the environment, compared to the other treatments, which can improve light penetration inside the canopy (Shahak, 2008). Based on our host localization results, we suggest that a higher light availability enhances the host finding capability of *M. ridens*. Although visual cues are important in host finding, chemical cues associated with the host also play a major role in host localization (Vinson, 1976). Under our experimental conditions, we cannot say the extent to which, visual or chemical cues influenced *M. ridens* host localization because the success of locating a host depends on multiple mechanisms (Vinson, 1976; Wajnberg and Colazza, 2013), and we cannot separate them. Other ichneumonid parasitoids use antennal tapping, olfaction, and visual contrast for host localization (Flores-Prado and Niemeyer, 2012; Sandlan, 1980). According to Chiel et al. (2006) and Chyzik et al. (2003), the parasitoids *Aphidius colemani* Viereck (Hymenoptera: Braconidae), *Diglyphus isaea* Walker (Hymenoptera: Eulophidae), and *Aphidius matricariae* (Haliday) (Hymenoptera: Braconidae) were not affected in terms of host localization capability under UV-filtered environments. Probably because these parasitoids use different cues for host localization or because their visual capabilities are not significantly affected under UV-deficient light. Nevertheless, our results showed that during the first six hours of the bioassays, the capability of the parasitoid to find a host was delayed under the black SN, suggesting that during the initial host finding process, the visual stimuli are relevant for *M. ridens*.

The parasitism, the fecundity, and the sex ratio are some of the most relevant factors when rearing parasitoid wasps (Bueno et al., 2017). Our results showed that the PSN and the black SN did not have a significant effect on parasitism, fertility, realized fecundity, and offspring sex ratio. These results suggest that, under our experimental setup, the light quantity or quality are not the main factors influencing parasitism. It has been established that in laboratory conditions, the parasitoid attacks a maximum of four hosts a day (Sandanayaka et al., 2011). In our study, females *M. ridens* did not parasitize more than one host per day. A similar result was observed by Hougardy et al. (2005) who also found that *M. ridens* parasitize just one or two hosts a day. Our results showed that the fertility (larvae hatched) and the realized fecundity (adults emerged) were not affected by the utilization of the PSN and the black SN, meaning that the treatments do not influence the number of descendants left by a female. Similar results of fecundity were obtained by Devotto et al. (2010) in laboratory conditions at 25°C (0.54 parasitoids/female/day). Finally, regarding the offspring sex ratio, there were no differences among treatments, and the emergence was sex-biased towards males. In *M. ridens*, like most hymenopterans, sex determination is linked to arrhenotoky, where females are diploid and develop from fertilized eggs, and males are haploid and develop from non-fertilized eggs, but males can also be diploids due to complementary sex determination in ichneumonids parasitoids (Heimpel and de Boer, 2008). Our male-biased sex ratio results agree with the studies of Bueno et al. (2017) and Zaviezo et al. (2018), where inbred lines of *M. ridens* produced fewer daughters than outbred lines. They attributed this result to the production of diploid males. Sex ratio is an important subject in insect rearing for future use in biological control programs (Heimpel and Lundgren, 2000). Since females are the ones with the reproductive capability, and ultimately, responsible for pest control (Bueno et al., 2017).

In terms of the female behavior during the first 30 minutes, our results showed that for phase 1 of the observations (pre-contact, mating, examination, acceptance), the PSN and the black SN did not influence the time spent by the female on each sub-phase. The fact that there were no differences in the time spent on each sub-phase shows that light quantity and quality do not influence significantly the time allocation decision by a female, at least during the first 30 minutes. Once the female and host are on the same habitat, the searching behavior is accomplished by walking, oriented by physical, visual, olfactory, and chemical cues (Koul and Dhaliwal, 2003; Vinson, 1976). The latter can guide the flight of the parasitoid to the habitat where the host is located (long-range cues), a fact well known in the attraction of *M. ridens* to *C. pomonella* (Jumean et al., 2005). Therefore, the volume of our experimental units and the enclosed environment could have saturated the cage with cues, causing the female to spend similar times on each sub-phase, regardless of the color of the nets. However, under all four treatments, the time spent on the pre-contact sub-phase was significantly higher than the other three sub-phases. In phase 2, the pre-contact behavior is dominated by walking around the experimental cage with continuous antennae movement, sporadically interrupted by grooming, or resting (Charles et al., 2013). Indeed, we observed all of these behaviors inside the experimental unit, with the time spent grooming being significantly higher than the time spent searching and walking around the cage, except under the red PSN where the times between these sub-phases were similar. Possibly, the females spent more time grooming (moving antennae, abdomen, and ovipositor) to detect some chemical cues that help them orient towards the *C. pomonella* cocoons (Jumean et al., 2005). Even though some females were observed examining the host on the cardboard within the first 30 minutes, the acceptance behavior was never registered under any treatment. It is possible that under our experimental conditions the parasitoid needed more time to find and accept the host.

The PSN and the black SN have been used as a protection tool and as a crop production method worldwide, with the majority of research focused on their influence on plant physiology and fruit quality (Bastías et al., 2012; Ilić et al., 2015; Lobos et al., 2013; Shahak, 2008). We must consider that the utilization of PSN and the black SN can also influence insect pests and their natural enemies (Legarrea et al., 2012b). Overall, our results show that under laboratory conditions, the PSN and the black SN affect *M. ridens* host localization but do not influence other traits like parasitism, fertility, realized fecundity, or offspring sex ratio. As it was mentioned earlier, there are contrasting results in the literature for host localization, where it has been proposed that host finding capability is not influenced by the presence of the PSN, with host-plant signals and olfactory cues rather than visual, being the main drivers for host finding (Chyzik et al., 2003; Dáder et al., 2015). On the other hand, some hymenopteran parasitoids species have difficulties locating their host under UV-light deficiency preferring unfiltered light (Chiel et al., 2006; Cochard et al., 2017). In this sense, we agree with the statement of Legarrea et al. (2012b) and Chiel et al. (2006) that suggest that the responses of parasitoids to UV-light deficiency are species-specific, therefore, the result of the utilization of PSN on host finding capability should not be generalized to every species. Our results indicate that the utilization of PSN, specifically the pearl and the red PSN, is compatible with the activity of the parasitoid *M. ridens*. Nevertheless, studies in natural conditions are also necessary to verify if host localization is also affected in real field conditions as it was in a microenvironment of a laboratory.

Conclusion

The fitness of parasitoids can be determined by several factors, but reproduction and host location capability are some of the most important. The results of our study showed that *M. ridens* host localization was enhanced by the pearl and the red PSN and delayed under the black SN. However, traits like parasitism, fertility, realized fecundity, and offspring sex ratio were not affected by the PSN and the black SN. The use of PSN (pearl and red) and biological control agents are compatible strategies included in integrated pest management (IPM) programs. Both strategies can play a role in reducing pest populations as well as reducing the use of insecticides in agro-ecosystems. Our results are relevant because if the PSN and the black SN affect *M. ridens* host localization in a microcosm, the same could happen once the parasitoid, reared for biological control purposes, is released at a larger scale, so further field studies are also necessary.

Acknowledgments

We would like to thank the Entomology Laboratory, Center for Biological Control Technology, INIA Quilamapu (Chillán, Chile), for providing us with the *C. pomonella* larvae, the *M. ridens* pupae, and the wood and glass cages for the emergence of parasitoids in our laboratory. Thanks to Patricia Loyola and Carolina Mella for the weekly shipping of the insect material. Also, we would like to thank Dr. Richard Bastías from Facultad de Agronomía, Universidad de Concepción, Chillán, Chile for providing us with the pearl and the red PSN, and Dr. Luisa Bascuñán from Laboratorio de Fisiología Vegetal, Universidad de Concepción for providing the Quantum sensor device for light measurements. Finally, thanks to Universidad de Concepción, VRID Multidisciplinaria 219.113.095-M and MEC 80170017 (PIC-CONICYT) Grants for financially supporting this research.

References

Antignus, Y., Lapidot, M., Hadar, D., Messika, Y., Cohen, S., 1998. Ultraviolet-Absorbing Screens Serve as Optical Barriers to Protect Crops from Virus and Insect Pests. J. Econ. Entomol. 91, 1401–1405. https://doi.org/10.1093/jee/91.6.1401

Antignus, Y., Nestel, D., Cohen, S., Lapidot, M., 2001. Ultraviolet-Deficient Greenhouse Environment Affects Whitefly Attraction and Flight-Behavior. Environ. Entomol. 30, 394–399. https://doi.org/10.1603/0046-225X-30.2.394

Arthurs, S.P., Stamps, R.H., Giglia, F.F., 2013. Environmental modification inside photoselective shadehouses. HortScience 48, 975–979. https://doi.org/10.21273/HORTSCI.48.8.975

Bastías, R.M., Corelli-Grappadelli, L., 2012. Light Quality Management in Fruit Orchards: Physiological and Technological Aspects. Chil. J. Agric. Res. 72, 574–581. https://doi.org/10.4067/S0718-58392012000400018

Bastías, R.M., Manfrini, L., Corelli Grappadelli, L., 2012. Exploring the Potential Use of Photo-Selective Nets for Fruit Growth Regulation in Apple. Chil. J. Agric. Res. 72, 224–231. https://doi.org/10.4067/S0718-58392012000200010

Ben-Yakir, D., Antignus, Y., Offir, Y., Shahak, Y., 2012. Colored shading nets impede insect invasion and decrease the incidences of insect-transmitted viral diseases in vegetable crops. Entomol. Exp. Appl. 144, 249–257. https://doi.org/10.1111/j.1570-7458.2012.01293.x

Bezemer, T.M., Harvey, J.A., Mills, N.J., 2005. Influence of adult nutrition on the relationship between body size and reproductive parameters in a parasitoid wasp. Ecol. Entomol. 30, 571–580. https://doi.org/10.1111/j.0307-6946.2005.00726.x

Bosch, D., Avilla, J., Musleh, S., Rodríguez, M.A., 2018. Target-site mutations (AChE and kdr), and PSMO activity in codling moth (*Cydia pomonella* (L.) (Lepidoptera: Tortricidae)) populations from Spain.

Pestic. Biochem. Physiol. 146, 52–62. https://doi.org/10.1016/j.pestbp.2018.02.010

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. R J. 9, 378–400. https://doi.org/10.32614/RJ-2017-066

Bueno, E., Romero, A., Osorio, I., Zaviezo, T., 2017. Laboratory rearing methods that promote inbreeding have a negative impact on the fitness of *Mastrus ridens* Horstmann (Hymenoptera: Ichneumonidae), a parasitoid used to control the codling moth. Chil. J. Agric. Res. 77, 413–419. https://doi.org/10.4067/S0718-58392017000400413

Charles, J.G., Sandanayaka, W.R.M., Chhagan, A., Page-Weir, N.E.M., 2013. Host selection behaviour in *Mastrus ridens*, a gregarious ectoparasitoid of codling moth, *Cydia pomonella*. BioControl 58, 493–503. https://doi.org/10.1007/s10526-013-9517-z

Chen, Z., Liu, X., Zhou, J., Dou, H., Kuang, R., 2014. Phototactic behavior of *Pachyneuron aphidis* (Hymenoptera: Pteromalidae) – hyperparasitoid of *Myzus persicae* (Hemiptera: Aphidiae). Biocontrol Sci. Technol. 24, 1469–1480. https://doi.org/10.1080/09583157.2014.945901

Chen, Z., Xu, R., Kuang, R., Sun, R., 2016. Phototactic behaviour of the parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae). Biocontrol Sci. Technol. 26, 250–262. https://doi.org/10.1080/09583157.2015.1099071

Chiel, E., Messika, Y., Steinberg, S., Antignus, Y., 2006. The effect of UV-absorbing plastic sheet on the attraction and host location ability of three parasitoids: *Aphidius colemani*, *Diglyphus isaea* and *Eretmocerus mundus*. BioControl 51, 65–78. https://doi.org/10.1007/s10526-005-8667-z

Chyzik, R., Dobrinin, S., Antignus, Y., 2003. Effect of a UV-Deficient Environment on the Biology and Flight Activity of *Myzus persicae* and

Its Hymenopterous Parasite *Aphidius matricariae*. Phytoparasitica 31, 467–477. https://doi.org/10.1007/BF02979740

Cochard, P., Galstian, T., Cloutier, C., 2017. Light Environments Differently Affect Parasitoid Wasps and their Hosts ' Locomotor Activity. J. Insect Behav. 30, 595–611. https://doi.org/10.1007/s10905-017-9644-y

Dáder, B., Gwynn-Jones, D., Moreno, A., Winters, A., Fereres, A., 2014. Impact of UV-A radiation on the performance of aphids and whiteflies and on the leaf chemistry of their host plants. J. Photochem. Photobiol. B Biol. 138, 307–316. https://doi.org/10.1016/j.jphotobiol.2014.06.009

Dáder, B., Plaza, M., Fereres, A., Moreno, A., 2015. Flight behaviour of vegetable pests and their natural enemies under different ultraviolet-blocking enclosures. Ann. Appl. Biol. 167, 116–126. https://doi.org/10.1111/aab.12213

Devotto, L., del Valle, C., Ceballos, R., Gerding, M., 2010. Biology of *Mastrus ridibundus* (Gravenhorst), a potential biological control agent for area-wide management of *Cydia pomonella* (Linneaus) (Lepidoptera: Tortricidae). J. Appl. Entomol. 134, 243–250. https://doi.org/10.1111/j.1439-0418.2009.01412.x

Elad, Y., Messika, Y., Brand, M., David, D.R., Sztejnberg, A., 2007. Effect of colored shade nets on pepper powdery mildew (*Leveillula taurica*). Phytoparasitica 35, 285–299. https://doi.org/10.1007/BF02981163

Flores-Prado, L., Niemeyer, H.M., 2012. Host Location by Ichneumonid Parasitoids is Associated with Nest Dimensions of the Host Bee Species. Neotrop. Entomol. 41, 283–287. https://doi.org/10.1007/s13744-012-0048-6

Heimpel, G.E., de Boer, J.G., 2008. Sex Determination in the Hymenoptera. Annu. Rev. Entomol. 53, 209–230. https://doi.org/10.1146/annurev.ento.53.103106.093441

Heimpel, G.E., Lundgren, J.G., 2000. Sex Ratios of Commercially Reared Biological Control Agents. Biol. Control 19, 77–93. https://doi.org/10.1006/bcon.2000.0849

Hemming, S., Dueck, T., Janse, J., van Noort, F., 2008. The Effect of Diffuse Light on Crops. Acta Hortic. 1293–1300. https://doi.org/10.17660/ActaHortic.2008.801.158

Iglesias, I., Alegre, S., 2006. The effect of anti-hail nets on fruit protection, radiation, temperature, quality and profitability of “Mondial Gala” apples. J. Appl. Hortic. 8, 91–100. https://doi.org/10.37855/jah.2006.v08i02.22

Ilić, Z.S., Milenković, L., Šunić, L., Barać, S., Mastilović, J., Kevrešan, Ž., Fallik, E., 2017. Effect of shading by coloured nets on yield and fruit quality of sweet pepper. Zemdirbyste-Agriculture 104, 53–62. https://doi.org/10.13080/z-a.2017.104.008

Ilić, Z.S., Milenković, L., Šunić, L., Fallik, E., 2015. Effect of coloured shade-nets on plant leaf parameters and tomato fruit quality. J. Sci. Food Agric. 95, 2660–2667. https://doi.org/10.1002/jsfa.7000

Jumean, Z., Unruh, T., Gries, R., Gries, G., 2005. *Mastrus ridibundus* parasitoids eavesdrop on cocoon-spinning codling moth, *Cydia pomonella*, larvae. Naturwissenschaften 92, 20–25. https://doi.org/10.1007/s00114-004-0581-1

Kalcsits, L., Musacchi, S., Layne, D.R., Schmidt, T., Mupambi, G., Serra, S., Mendoza, M., Asteggiano, L., Jarolmasjed, S., Sankaran, S., Khot, L.R., Zúñiga Espinoza, C., 2017. Above and below-ground environmental changes associated with the use of photoselective protective netting to reduce sunburn in apple. Agric. For. Meteorol. 237–238, 9–17. https://doi.org/10.1016/j.agrformet.2017.01.016

Koul, O., Dhaliwal, G.S., 2003. Predators and Parasitoids, 1st ed. Taylor & Francis.

Lacey, L.A., Unruh, T.R., 2005. Biological Control of Codling Moth (*Cydia pomonella*, Lepidoptera: Tortricidae) and Its Role in Integrated Pest Management, With Emphasis on Entomopathogens. Vedalia 12, 33–60.

Legarrea, S., Betancourt, M., Plaza, M., Fraile, A., García-Arenal, F., Fereres, A., 2012a. Dynamics of nonpersistent aphid-borne viruses in lettuce crops covered with UV-absorbing nets. Virus Res. 165, 1–8. https://doi.org/10.1016/j.virusres.2011.12.012

Legarrea, S., Weintraub, P.G., Plaza, M., Viñuela, E., Fereres, A., 2012b. Dispersal of aphids, whiteflies and their natural enemies under photoselective nets. BioControl 57, 523–532. https://doi.org/10.1007/s10526-011-9430-2

Lobos, G.A., Retamales, J.B., Hancock, J.F., Flore, J.A., Cobo, N., del Pozo, A., 2012. Spectral irradiance, gas exchange characteristics and leaf traits of *Vaccinium corymbosum* L. "Elliott" grown under photo-selective nets. Environ. Exp. Bot. 75, 142–149. https://doi.org/10.1016/j.envexpbot.2011.09.006

Lobos, G.A., Retamales, J.B., Hancock, J.F., Flore, J.A., Romero-Bravo, S., Del Pozo, A., 2013. Productivity and fruit quality of *Vaccinium corymbosum* cv. Elliott under photo-selective shading nets. Sci. Hortic. (Amsterdam). 153, 143–149. https://doi.org/10.1016/j.scienta.2013.02.012

Mills, N., 2005. Selecting effective parasitoids for biological control introductions: Codling moth as a case study. Biol. Control 34, 274–282. https://doi.org/10.1016/j.biocontrol.2005.02.012

Moretti, C.L., Mattos, L.M., Calbo, A.G., Sargent, S.A., 2010. Climate changes and potential impacts on postharvest quality of fruit and vegetable crops : A review. Food Res. Int. 43, 1824–1832. https://doi.org/10.1016/j.foodres.2009.10.013

Mupambi, G., Anthony, B.M., Layne, D.R., Musacchi, S., Serra, S., Schmidt, T., Kalcsits, L.A., 2018. The influence of protective netting on tree physiology and fruit quality of apple: A review. Sci. Hortic. (Amsterdam). 236, 60–72. https://doi.org/10.1016/j.scienta.2018.03.014

Peitsch, D., Fietz, A., Hertel, H., de Souza, J. De, Ventura, D.F., Menzel, R., 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. J. Comp. Physiol. A 170, 23–40. https://doi.org/10.1007/BF00190398

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput. Vienna, Austria URL https//www.r-project.org/.

Retamal, R., Zaviezo, T., Malausa, T., Fauvergue, X., Le Goff, I., Toleubayev, K., 2016. Genetic analyses and occurrence of diploid males in field and laboratory populations of *Mastrus ridens* (Hymenoptera: Ichneumonidae), a parasitoid of the codling moth. Biol. Control 101, 69–77. https://doi.org/10.1016/j.biocontrol.2016.06.009

Rodríguez, M.A., Bosch, D., Avilla, J., 2011. Resistance of Spanish codling moth (*Cydia pomonella*) populations to insecticides and activity of detoxifying enzymatic systems. Entomol. Exp. Appl. 138, 184–192. https://doi.org/10.1111/j.1570-7458.2010.01088.x

Salt, G., 1935. Experimental Studies in Insect Parasitism. III. Host Selection. Proc. R. Soc. B Biol. Sci. 117, 413–435. https://doi.org/10.1098/rspb.1935.0037

Sandanayaka, W.R.M., Chhagan, A., Page-Weir, N.E.M., Charles, J.G., 2011. Colony optimisation of *Mastrus ridens* (Hymenoptera : Ichneumonidae), a potential biological control agent of codling moth in New Zealand. New Zeal. Plant Prot. 64, 227–234. https://doi.org/10.30843/nzpp.2011.64.5959

Sandlan, K., 1980. Host location by *Coccygomimus turionellae* (Hymenoptera: Ichneumonidae). Entomol. Exp. Appl. 27, 233–245. https://doi.org/10.1111/j.1570-7458.1980.tb02970.x

Sauphanor, B., Bouvier, J.C., Brosse, V., 1999. Effect of an ecdysteroid agonist, tebufenozide, on the completion of diapause in susceptible and resistant strains of the codling moth, *Cydia pomonella*. Entomol. Exp. Appl. 90, 157–165. https://doi.org/10.1046/j.1570-7458.1999.00434.x

Schirmer, S.T., Sengonca, C.E., Blaeser, P.E., 2008. Influence of abiotic factors on some biological and ecological characteristics of the aphid parasitoid *Aphelinus asychis* (Hymenoptera: Aphelinidae) parasitizing *Aphis gossypii* (Sternorrhyncha: Aphididae). Eur. J. Entomol. 105, 121–129. https://doi.org/10.14411/eje.2008.017

Selahle, K.M., Sivakumar, D., Jifon, J., Soundy, P., 2015. Postharvest responses of red and yellow sweet peppers grown under photo-selective nets. Food Chem. 173, 951–956. https://doi.org/10.1016/j.foodchem.2014.10.034

Shahak, Y., 2008. Photo-Selective Netting for Improved Performance of Horticultural Crops. A Review of Ornamental and Vegetable Studies Carried Out in Israel. Acta Hortic. 161–168. https://doi.org/10.17660/ActaHortic.2008.770.18

Shahak, Y., Gussakovsky, E.E., Gal, E., Ganelevin, R., 2004. ColorNets: Crop protection and Light-Quality Manipulation in One Technology. Acta Hortic. 659, 143–151. https://doi.org/10.17660/ActaHortic.2004.659.17

Shahak, Y., Ratner, K., Giller, Y.E., Zur, N., Or, E., Gussakovsky, E.E., Stern, R., Sarig, P., Raban, E., Harcavi, E., Doron, I., Greenblat-Avron, Y., 2008. Improving Solar Energy Utilization, Productivity and Fruit Quality in Orchards and Vineyards by Photoselective Netting. Acta Hortic. 772, 65–72. https://doi.org/10.17660/ActaHortic.2008.772.7

Tinyane, P.P., Sivakumar, D., Soundy, P., 2013. Influence of photo-selective netting on fruit quality parameters and bioactive compounds in selected tomato cultivars. Sci. Hortic. (Amsterdam). 161, 340–349. https://doi.org/10.1016/j.scienta.2013.06.024

Umanzor, C., Bastías, R., Wilckens, R., Quezada, C., 2016. Influencia del uso de malla perla y roja en las condiciones micro-climáticas, daño por sol y desarrollo de color de frutos en huertos de manzanos cvs. gala y fuji. Rev. Bras. Frutic. 39, 1–13. https://doi.org/10.1590/0100-29452017930

Vinson, S.B., 1976. Host selection by insect parasitoids. Annu. Rev. Entomol. 21, 109–133. https://doi.org/10.1146/annurev.en.21.010176.000545

Wajnberg, E., Colazza, S., 2013. Chemical Ecology of Insect Parasitoids. Wiley-Blackwell. https://doi.org/10.1002/9781118409589

Wearing, C.H., Hansen, J.D., Whyte, C., Miller, C.E., Brown, J., 2001. The potential for spread of codling moth (Lepidoptera: Tortricidae) via commercial sweet cherry fruit: a critical review and risk assessment. Crop Prot. 20, 465–488. https://doi.org/10.1016/S0261-2194(01)00023-0

Welter, S.C., 2009. Codling Moth, in: Resh, V.H., Cardé, R.T. (Eds.), Encyclopedia of Insects. Elsevier Inc., pp. 174–175.

Wheeler, T., von Braun, J., 2013. Climate Change Impacts on Global Food Security. Science (80-). 341, 508–513. https://doi.org/10.1126/science.1239402

Zaviezo, T., Retamal, R., Urvois, T., Fauvergue, X., Blin, A., Malausa, T., 2018. Effects of inbreeding on a gregarious parasitoid wasp with complementary sex determination. Evol. Appl. 11, 243-253. https://doi.org/10.1111/eva.12537

Tables

Table 2.1 Light intensity measured as photosynthetic active radiation (PAR) and shading factor provided by photo-selective and black standard nets (PSN and SN, respectively) used in the experiments

PSN color	Supplier	Specifications	PAR (µmol m^{-2} s^{-1})	Shading factor (%)
No PSN (control)	-	-	7	0
Pearl PSN	ChromatiNet®, Polysack Industries, Negev, Israel	HDPE monofilament, mesh size 5 x 2 mm	6	20
Red PSN	ChromatiNet®, Polysack Industries, Negev, Israel	HDPE monofilament, mesh size 5 x 2 mm	5	20
Black PSN	Polytex S.A., Chile	Polyethylene, mesh size 3 x 1 mm	2	80

Figures

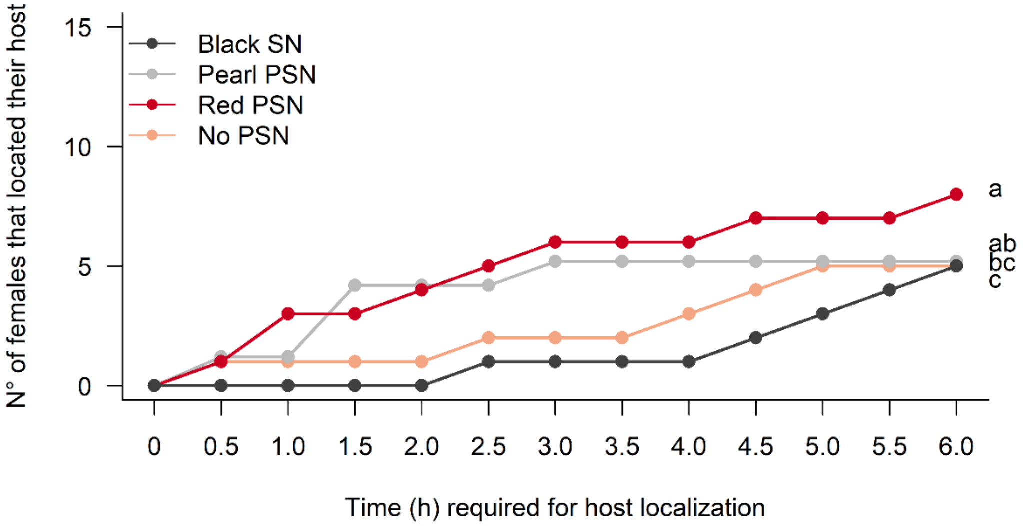


Figure 2.1 Accumulated number of females *M. ridens* that located the fifth-instar *C. pomonella* larvae under the PSN and the black SN along the first six hours of observation. Different letters next to each line indicate significant differences among treatments according to the glmm test

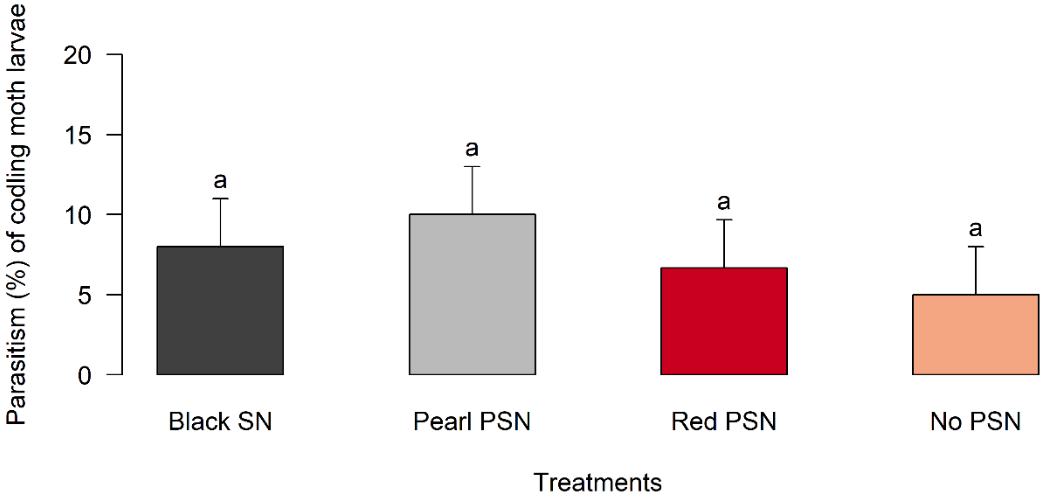


Figure 2.2 Effect of the PSN and the black SN on the parasitism (%) (Mean ± SE, n=15) of *M. ridens* on fifth-instar *C. pomonella* larvae. The same letters above bars and SE indicate no significant differences among treatments according to the Kruskal-Wallis test

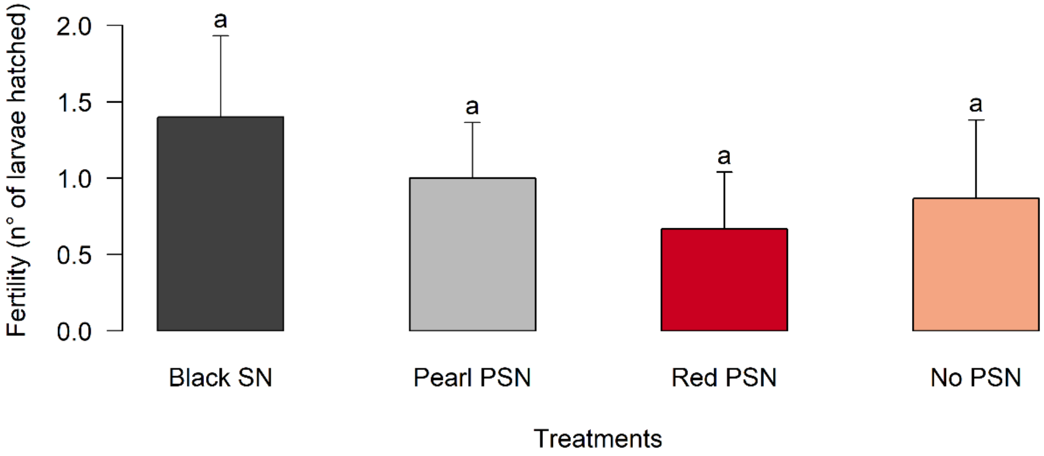


Figure 2.3 Effect of the PSN and the black SN on the fertility (n° of larvae hatched) (mean ± SE, n=15) of *M. ridens* on fifth-instar *C. pomonella* larvae. The same letters above bars and SE indicate no significant differences among treatments according to the Kruskal-Wallis test

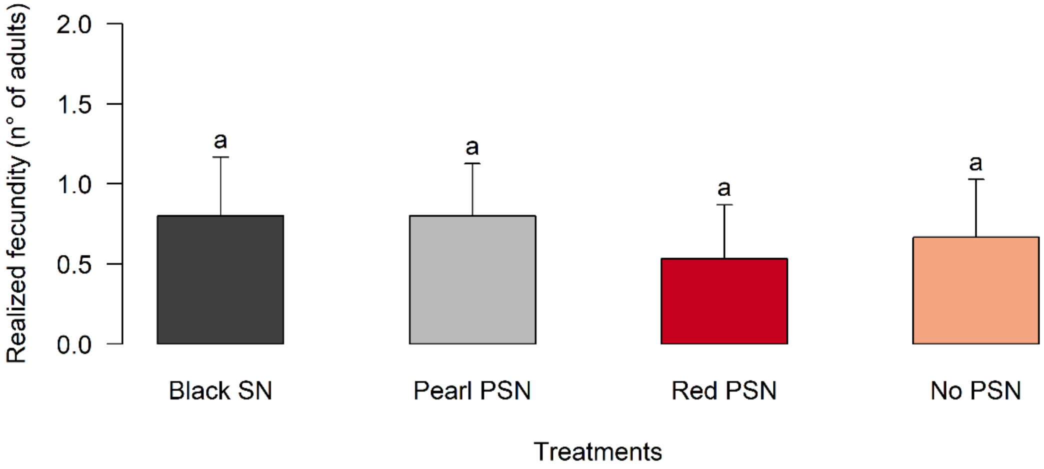


Figure 2.4 Effect of the PSN and the black SN on the realized fecundity (n° of adults emerged) (mean ± SE, n=15) of *M. ridens* on fifth-instar *C. pomonella* larvae. The same letters above bars and SE indicate no significant differences among treatments according to the Kruskal-Wallis test

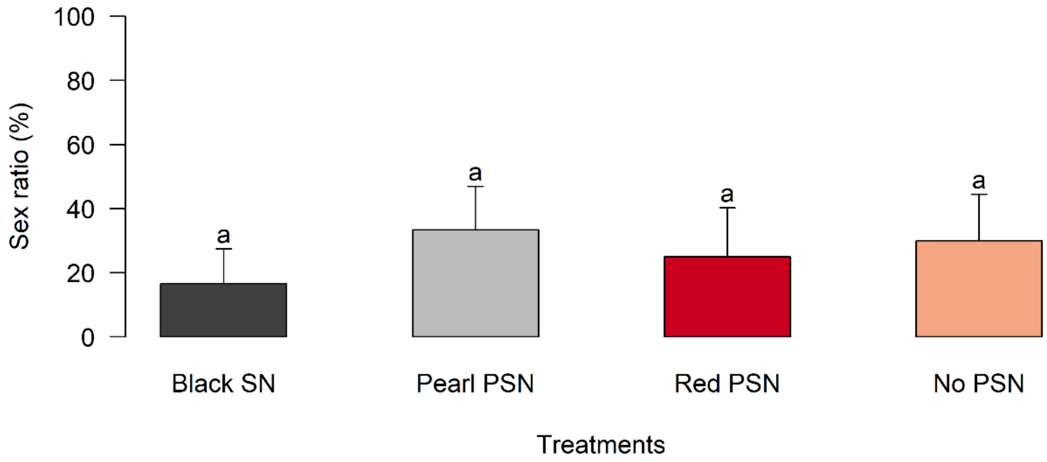
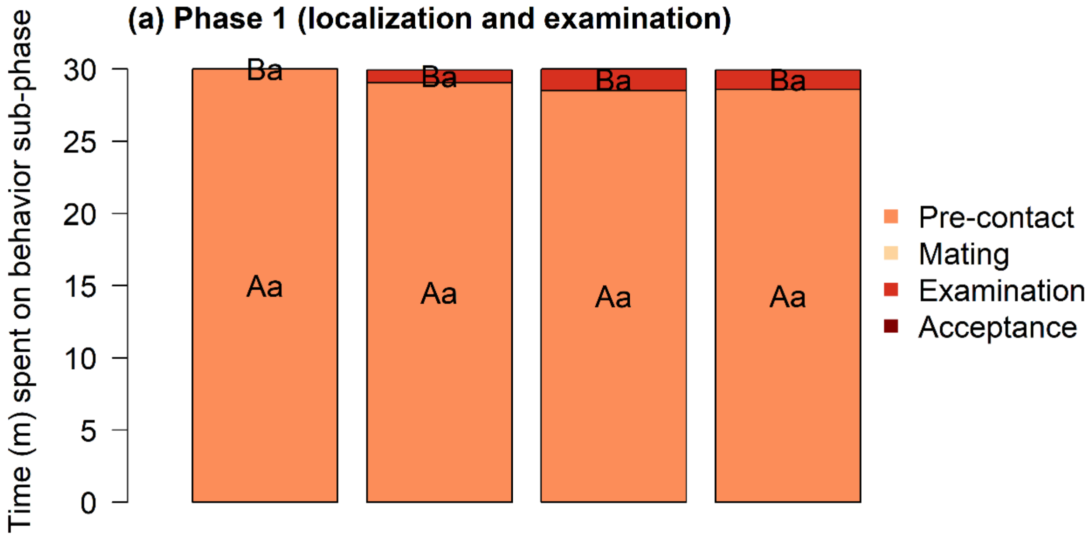


Figure 2.5 Effect of the PSN and the black SN on the offspring sex ratio (% of females) (mean ± SE, n=15) of *M. ridens* emerged from fifth-instar *C. pomonella* larvae. The same letters above bars and SE indicate no significant differences among treatments according to the Kruskal-Wallis test


(a) Phase 1 (localization and examination)

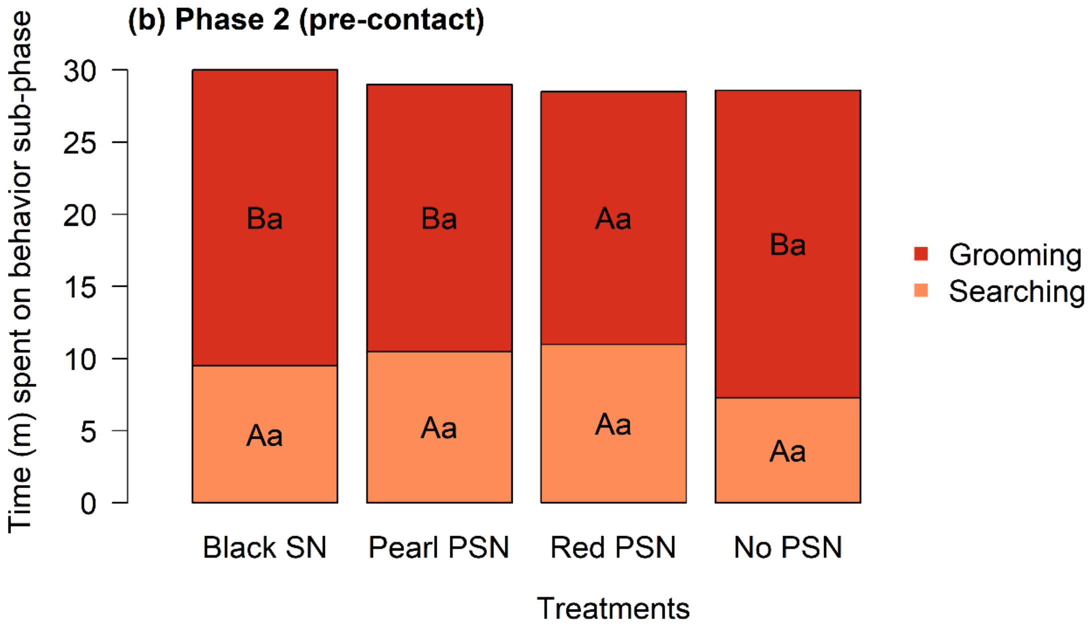

(b) Phase 2 (pre-contact)

Figure 2.6 Effect of the PSN and the black SN on the mean time (minutes) allocated by females *M. ridens* to the different behavior categories. a) Phase 1 (localization and examination): 1.1) pre-contact, 1.2) mating, 1.3) examination, and 1.4) acceptance*, (b) Phase 2 (pre-contact): 2.1) searching, and 2.2) grooming. The total observation time was 30 minutes. Different lowercase letters in bars indicate significant differences among treatments for each sub-phase according to the Kruskal-Wallis test. Uppercase letters in bars indicate significant differences among sub-phases within each treatment according to the Wilcoxon Signed-Rank test for paired observations. *Time spent by females *M. ridens* on the sub-phases mating and acceptance of phase 1 were so low that are not shown on the graphic

DISCUSIÓN GENERAL

Estudios acerca del efecto de las MPS en agricultura han ido en aumento en los últimos años en Chile (Umanzor et al. 2016; Olivares-Soto and Bastías 2018) y en países como Israel, Estados Unidos, España e Italia, con el objetivo principal de proteger a los cultivos de condiciones climáticas adversas (Bastías et al. 2012; Shahak 2014; Kalcsits et al. 2017; Lopez-Marín et al. 2019). Las MPS tienen una variedad de efectos complejos tanto directos como indirectos sobre todo el sistema, es decir, sobre la planta focal (protección), las plagas, y los enemigos naturales de estas plagas (depredadores, parasitoides y patógenos). La mayoría de los estudios publicados se referían al efecto de las MPS sobre el microclima del huerto, sobre aspectos fisiológicos y morfológicos de las plantas, o bien, sobre poblaciones de insectos plaga presentes en los cultivos. Sin embargo, estudios acerca de los efectos de las MPS sobre el gremio de enemigos naturales de insectos plaga eran escasos. Por lo tanto, esta tesis tuvo por objetivo estudiar los efectos directos de éstos sistemas de producción sobre atributos biológicos específicos de enemigos naturales.

En el capítulo I se estudió el efecto de las MPS perla, roja y malla estándar (ME) negra sobre el comportamiento, depredación y localización de presa del coccinélido generalista *Harmonia axyridis* en presencia de una colonia de áfidos *Myzus persicae*, en condiciones de laboratorio. Para esto se estudió el efecto de las mallas tanto en larvas (tercer estadio) como en adultos del depredador (machos y hembras), ya que éstos son consumidores voraces de distintos insectos plaga incluyendo áfidos. Los resultados mostraron que el comportamiento de búsqueda de presa se vio afectado diferencialmente dentro de cada tratamiento para larvas y para adultos. La eficiencia de depredación no se vio influenciada por las MPS perla y roja y ME negra para ningún estadio/sexo. Sin embargo, la localización de presa en adultos se vio afectada negativamente bajo la ME negra, con un retraso en el tiempo para localizar a la colonia de áfidos. En el caso de la larva, la diferencia en la calidad y cantidad de luz pareciera no haber influido significativamente, probablemente por los diferentes aparatos visuales entre larvas y adultos, siendo más simples y menos eficientes en las larvas. En el caso de los adultos, la localización de presa fue influenciada positivamente bajo MPS perla tanto para machos como para hembras, probablemente por la mayor cantidad de luz difusa bajo este tratamiento que podría haber ayudado a los adultos a localizar a su presa.

En el capítulo II se evaluó el efecto de las MPS perla, roja y ME negra sobre el comportamiento, parasitismo y localización de hospedador del parasitoide de la polilla de la manzana *Cydia pomonella* (plaga clave del manzano), *Mastrus ridens*. En cuanto a *C. pomonella*, la única información que existía acerca del efecto de mallas de exclusión (no MPS) sobre esta plaga era que las mallas impedían su llegada a los cultivos y, en consecuencia, disminuía la cantidad de frutos de manzanos dañados y la cantidad de insecticidas necesarios para su control (Sauphanor et al. 2012; Baiamonte et al. 2015; Alaphilippe et al. 2016). Nuestros resultados mostraron que las MPS perla y roja y ME negra no influenciaron en parámetros biológicos como el parasitismo, fertilidad, fecundidad realizada y proporción sexual de su descendencia. En cuanto a su comportamiento, el parasitoide se caracterizó por pasar un mayor tiempo en la etapa de "pre-contacto" en comparación a las otras etapas de comportamiento, independiente del color de la malla. Similar a *H. axyridis*, la localización de su hospedador se vio retrasada bajo la ME negra, sin embargo, fue influenciada positivamente bajo las MPS perla y roja. Basado en esto, podemos decir que las diferentes cantidades y calidades de luz en el ambiente si influyen en la capacidad del parasitoide de encontrar a su hospedador.

Esta investigación es una de las primeras en evidenciar los efectos de los sistemas de producción de MPS (perla y roja) y ME negra sobre dos grupos funcionales de enemigos naturales, un depredador y un parasitoide, en un sistema cerrado en condiciones de laboratorio. Bajo nuestras condiciones experimentales (sistema cerrado y límites de espacio y de tiempo) tanto el depredador como el parasitoide en algún momento iban a encontrar a su presa y a su hospedador, respectivamente. Ahora, en condiciones de campo, influyen factores bióticos y abióticos cuya complejidad y variación es muy difícil de replicar en un ambiente controlado de laboratorio. No podemos afirmar qué es lo que ocurrirá exactamente con los enemigos naturales bajo las MPS y ME negra en el campo, pero sí podemos suponer que si en el laboratorio las mallas tienen efectos significativos sobre la actividad de depredadores y parasitoides, esto también ocurrirá en el campo. Es así como el paso siguiente en esta investigación debe enfocarse en experimentos de campo a mayor escala espacial y temporal evaluando el efecto de las MPS y ME negra sobre la actividad de enemigos naturales especialistas y generalistas para comprender de mejor manera las estrategias que utilizan para lidiar con la variabilidad propio de los ambientes dentro de cadenas tróficas (Wäschke et al. 2013), incluyendo variaciones relacionadas al cambio climático (Holopainen et al. 2013).

Las diferencias entre las condiciones de laboratorio y las condiciones complejas en el campo pueden afectar el comportamiento de los enemigos naturales. En el caso de depredadores, los estudios de laboratorio son valiosos para identificar protagonistas claves y los peores escenarios posibles: una especie que no es atacada por *H. axyridis* en el laboratorio es poco probable que esté en riesgo en el campo (Pell et al. 2008). *H. axyridis* puede atacar a presas no-objetivo así como a otros miembros del gremio de afidófagos (Majerus et al. 2006; Lucas 2012), sin embargo, en condiciones naturales, se podrían observar comportamientos de escapes, reduciendo el riesgo de depredación intragremio de *H. axyridis* sobre otras especies (Ware and Majerus 2008). Los adultos de *H. axyridis* responden hacia señales visuales (vista de hojas verdes) y señales olfativas de plantas sanas y del olor de áfidos, haciendo que su búsqueda sea más efectiva (Obata 1997; Adedipe and Park 2010), incluso cuando las densidades poblacionales de áfidos son bajas (Feng et al. 2018). Estas diferentes señales pueden variar en importancia a distintas escalas, por ejemplo, a una mayor distancia espacial (más allá de los confines del laboratorio) las señales visuales parecen ser más importantes para encontrar los hábitats donde las presas están presentes (Bahlai et al. 2008).

En el caso de las hembras parasitoides, para lograr encontrar a sus hospedadores éstas deben seguir una secuencia de pasos que incluyen la localización del hábitat donde se encuentran los hospedadores, localización del hospedador, aceptación del hospedador, idoneidad del hospedador y regulación del hospedador (Vinson 1975). En el campo, las señales volátiles pueden guiar a *M. ridens* hacia el hábitat donde se encuentran sus hospedadores (Vinson 1975) mientras que las señales químicas de contacto y las señales físicas (forma y tamaño del hospedador, textura de la planta hospedadora) son importantes a corto alcance (Turlings et al. 1993; Hilker and Mcneil 2008). Las señales visuales consisten en el color del objetivo, claridad, forma, dimensión y contraste con su fondo, y pueden guiar al parasitoide durante la localización del hábitat así como en las etapas finales de localización del hospedador (Chiel et al. 2006). Sin embargo, las señales olfativas serían más efectivas en los casos en que la visión se vea reducida (doseles densos, baja iluminación o cuando se establecen barreras físicas y ópticas) (Chiel et al. 2006). Las hembras buscan los hábitats adecuados considerando factores físicos como temperatura, humedad, viento e intensidad de luz (Vinson 1975). Por lo tanto, el uso de MPS y ME negra puede dificultar el proceso de localización al interferir con la capacidad del parasitoide de responder a estímulos visuales que les ayuden a encontrar el hábitat donde se encuentran sus potenciales hospedadores.

Las hembras de *M. ridens* también son atraídas a kairomonas volátiles asociadas con el capullo de las larvas de *C. pomonella* (Jumean et al. 2005) y a kairomonas no volátiles de contacto de larga duración presentes en el capullo, las cuales ayudan al parasitoide a encontrar a *C. pomonella* en el campo (Charles et al. 2013a). El uso de MPS puede disminuir la velocidad del viento en la copa de los árboles que se encuentran bajo las mallas comparado a árboles descubiertos (Wachsmann et al. 2014). Sin embargo, la disminución de la velocidad del viento bajo mallas dependen del factor de sombreo de ésta (densidad de los hilos), del diseño de construcción y de su ubicación física en relación a las plantas (Shahak et al. 2004c; Stamps 2009; Mupambi et al. 2018). La ubicación de mallas sobre los cultivos también puede causar un aumento de temperatura si la velocidad del viento es reducida en más de un 25% (McCaskill et al. 2016). Al mismo tiempo, los cambios en el microclima, resultado del posicionamiento de mallas encima de los cultivos, pueden afectar los procesos de transpiración, fotosíntesis y respiración de las plantas (Stamps 2009; McCaskill et al. 2016). El hecho de que las mallas disminuyan la velocidad del viento puede afectar la volatilidad de las kairomonas asociadas a las plantas hospedadoras o a los hospedadores del parasitoide por una menor dispersión de los compuestos volátiles ya que las señales olfativas son llevadas en dirección del viento (Elkinton and Cardé 1984). La detección de estímulos olfativos por parte de un insecto es influenciado, entre otros, por la tasa de emisión de moléculas de olor transmitidos como plumas, distancia entre el insecto y la fuente del olor, y la velocidad del viento (Turlings et al. 1993). Por lo tanto, un cambio en la velocidad del viento en un cultivo bajo mallas, junto con la presión del aire y la temperatura, pueden afectar la liberación de volátiles tanto de las plantas como de los hospedadores, así como el comportamiento del parasitoide incluyendo su vuelo (Gu and Dorn 2001; Hilker and Mcneil 2008).

Además, la reproducción de los parasitoides podría verse limitada por la longevidad y por las tasas de encuentro con su hospedador en el campo. Como resultado, la reproducción exitosa esperada puede ser menor que en el laboratorio, donde existe una mayor expectativa de reproducción futura, por lo tanto, en condiciones de campo, la capacidad de encontrar a sus hospedadores puede dar una representación más acertada del éxito reproductivo (Bezemer and Mills 2003).

Tanto depredadores como parasitoides no están solos en un agroecosistema, existe un gremio de enemigos naturales acompañando a las plagas y, al mismo tiempo, existen muchas plagas por cultivos. Un gremio de enemigos naturales se define como todas las especies que explotan un recurso similar y que por lo tanto pueden competir entre ellos, independiente de su modo de nutrición o posición taxonómica (Polis and Holt 1992). Por ejemplo, los gremios de especies afidófagas son muy diversificados y la mayoría de las colonias de áfidos son atacadas por una gran variedad de depredadores como escarabajos, sírfidos, cecidómidos (depredadores furtivos), crisópidos, hemípteros depredadores, arañas (depredadores emboscadores), parasitoides idiobiontes y koinobiontes y patógenos (Bell 1990; Ehler 1996; Lucas et al. 2007; Völkl et al. 2007; Mills 2009; Guénard et al. 2018). Uno de los fenómenos que pueden ocurrir dentro de un gremio, debido a que las especies coexisten y compiten entre ellas, es la depredación intragremio (DIG) donde uno de los miembros mata y se alimenta de otro miembro del mismo gremio (Polis and Holt 1992). Esta interacción involucra a los dos depredadores donde uno actúa como un competidor o agresor (depredador intragremio), el otro como un depredador víctima (presa intragremio) y su presa en común (presa extragremio) (Devee et al. 2018). La DIG está influenciada por factores intragremios (interacción entre miembros del gremio), factores asociados a la presa extragremio (tamaño de colonia de áfidos, sitio, edad), a la planta hospedadora (tamaño, fenología, defensas), factores antrópicos (tipo de control biológico utilizado) y factores abióticos (perturbaciones) (Lucas 2005). Por lo tanto, el uso de mallas en campo (MPS y ME negra) entendida como una perturbación en las condiciones naturales de cantidad y calidad de luz, velocidad del viento, humedad, temperatura, etc., pueden afectar la dinámica de los gremios de enemigos naturales presentes en un cultivo y en consecuencia el servicio ecosistémico de control biológico de plagas entregado por estas especies.

Considerando todas las interacciones que ocurren en los agroecosistemas es difícil predecir cómo será la respuesta del gremio de enemigos naturales en presencia de MPS. Estudios que hablan del efecto de MPS (UV-bloqueadoras) en campo indican que en sistemas de túneles (6.5 m ancho, 8 m largo y 2.6 m alto) durante 6 semanas, las larvas del depredador *Sphaerophoria rueppellii* Wiedemann (Diptera: Syrphidae) se dispersaron más bajo malla estándar (Amorós-Jiménez et al. 2020). Los autores hipotetizaron que debido a que la malla estándar no afecta la dispersión de áfidos, el depredador encontró colonias de áfidos más pequeñas lo que lo motivó a moverse entre plantas buscando nuevos parches. Además, no hubo diferencias en la capacidad del depredador de encontrar plantas con flores como fuente de alimento. Sin embargo, los resultaron no fueron concluyentes en cuanto a si las mallas UV-absorbentes afectaron la percepción visual hacia las flores, ya que los depredadores son capaces de utilizar otros sentidos para localizar sus fuentes de alimentos, como por ejemplo las señales olfativas que también juegan un rol importante en la detección de sitios de ovoposición. Dáder et al. (2015) tampoco encontraron que las MPS afectaran el vuelo de *S. rueppellii* en túneles más pequeños que los utilizados por Amorós-Jiménez et al. (2020). Estos autores concluyeron que los ambientes deficientes de UV no tienen efectos negativos en las dinámicas poblacionales de sírfidos en el campo, ya que estos aún son capaces de encontrar parches de áfidos en ambientes con baja radiación UV (Dáder et al. 2015; Amorós-Jiménez et al. 2020).

Para parasitoides, se ha estudiado el efecto de mallas UV-absorbentes dispuestas en túneles (1-2 m largo x 0.6 m ancho x 0.6 m alto; 6.5 m x 8 m x 2.6 m alto) en el desempeño y en la actividad de vuelo de especies del género

Aphidius. Las MPS (no mencionaron el color utilizado) no afectaron el parasitismo ni el comportamiento de búsqueda de hospedador del parasitoide, implicando que el uso de señales volátiles (olfativas) provenientes de los complejos hospedador-planta atacados por plagas son más relevantes que las señales visuales en el proceso de atracción, aterrizaje y oviposición (Sal et al. 2008; Legarrea et al. 2014; Dáder et al. 2015). El uso de films UV-absorbentes de polietileno en túneles "walk-in" (15 m x 6 m x 2.7 m) no afectó la fecundidad y comportamiento de búsqueda de hospedador de *Aphidius matricariae*, comparado a films estándar (Chyzik et al. 2003). Similar a estudios anteriores, los autores explican esto como resultado de la utilización de señales olfativas más que visuales como mediadores para la atracción de parasitoides hacia sus hospedadores. El uso de láminas de plástico UV-absorbentes en invernaderos de 250 m^2 tampoco afectó la capacidad de *Aphidius colemani* y *Diglyphus isaea* de localizar a su hospedador, ya sea porque estas especies encuentran a sus hospedadores usando señales distintas a las visuales o porque su capacidad visual no se ve afectada por la deficiencia de luz UV (Chiel et al. 2006). Sin embargo, en este último estudio el parasitoide *Eretmocerus mundus* fue incapaz de localizar plantas infestadas ubicadas al centro del invernadero, debido a que, en cierta medida, esta especie depende de estímulos visuales como señales de largo alcance para localizar a su hospedador, por lo que se recomienda que este parasitoide sea liberado en múltiples puntos dentro del invernadero para facilitar el proceso de localización (Chiel et al. 2006).

Debido a que en condiciones naturales de campo existen factores bióticos (interacciones intragremio e interacciones con plantas hospedadoras) (Romeis et al. 2005; Majerus et al. 2006) y abióticos (estímulos químicos, perturbaciones climáticas) (Jumean et al. 2005; Hilker and Mcneil 2008; Holopainen et al. 2013) que son difíciles de replicar en un sistema controlado, y debido a que las condiciones de laboratorio pueden limitar la capacidad de búsqueda natural de presas u hospedadores de los enemigos naturales (Abrams 1982; Feng et al. 2018), se hipotetiza que en condiciones de campo:

- El uso de MPS perla y roja y ME negra disminuyen la eficacia de búsqueda de presa de *Harmonia axyridis* y búsqueda de hospedador de *Mastrus ridens* así como la depredación y el parasitismo, debido al aumento de la escala espacial (en un campo) y temporal (mayor tiempo de exposición), donde el enemigo natural va a tardar más tiempo en encontrar a sus presas/hospedadores debido a una mayor cantidad de estímulos provenientes del medio ambiente y por encontrarse en una mayor superficie sobre la cual realizar la búsqueda.

Predicción: Al igual que en condiciones de laboratorio, se espera que la ME negra tenga un efecto más negativo sobre la localización de presa y hospedador, la depredación y parasitismo, por el mayor factor de sombreo que posee, disminuyendo una mayor cantidad y calidad de luz, en comparación a las MPS perla y roja.

CONCLUSIÓN

La presente tesis ha evaluado los efectos del uso de mallas foto-selectivas (MPS) y ME negra en condiciones de laboratorio sobre el comportamiento de dos enemigos naturales, un depredador y un parasitoide, estudiados para el control de insectos plaga. En base a los resultados obtenidos, la hipótesis general de trabajo se rechaza ya que solo la ME negra disminuyó la eficacia de búsqueda de presa/hospedador y ninguna de las mallas utilizadas tuvieron efecto sobre la depredación y el parasitismo de los enemigos naturales. Los resultados de esta investigación son, en primer lugar, un aporte al conocimiento fundamental de la biología de coccinélidos depredadores e himenópteros parasitoides, y de cómo éstos responden a estímulos lumínicos bajo distintas cubiertas de MPS y ME negra, utilizadas para la producción de cultivos en varios países del mundo. Y, en segundo lugar, constituyen un conocimiento base que en el futuro podrá ser aplicado en experimentos de campo los cuales son necesarios ya que en nuestro sistema cerrado de laboratorio tanto el enemigo natural como la presa/hospedador no podían elegir irse, lo cual si es posible en condiciones naturales. En un sistema abierto en campo es difícil predecir cómo responderá el gremio de enemigos naturales, ya que por ejemplo podrían evitar un cultivo cubierto con ME negra, seleccionar mallas de distintos colores, o bien, elegir cultivos sin ningún tipo de malla.

Si estos sistemas de producción de cultivos son utilizados en conjunto con enemigos naturales de plagas en el contexto de Manejo Integrado de Plagas (MIP), las modificaciones espectrales proporcionadas por las mallas deben ser compatibles con la actividad de controladores biológicos y polinizadores, así como con las condiciones óptimas para el crecimiento y desarrollo del cultivo. Por lo tanto, estudios futuros realizados en campo deben investigar el efecto de MPS de distintos colores y factores de sombreo sobre rasgos de historia de vida (fecundidad, reproducción, dispersión) de agentes de control biológico (depredadores y parasitoides) y sus enemigos naturales (arañas, hiperparasitoides) a una mayor escala espacial y temporal en huertos que utilizan estas mallas para proteger a los cultivos contra factores climáticos adversos y contra insectos dañinos.

BIBLIOGRAFÍA

Abrams PA (1982) Functional responses of optimal foragers. Am Nat 120:382–390. doi: 10.1086/283996

Acero A (2015) Influencia de mallas antigranizo en producción de manzana ecológica. Universidad de Zaragoza

Adedipe F, Park Y (2010) Visual and olfactory preference of Harmonia axyridis (Coleoptera : Coccinellidae) adults to various companion plants. J Asia Pac Entomol 13:319–323. doi: 10.1016/j.aspen.2010.07.004

Ahmed K, Majeed MZ, Rafi M, et al (2017) Biodiversity and Species Distribution of Coccinellids (Coccinellidae: Coleoptera) in District Sargodha (Punjab), Pakistan. Pak J Zool 49:1749–1759. doi: 10.17582/journal.pjz/2017.49.5.1749.1759

Aktar W, Sengupta D, Chowdhury A (2009) Impact of pesticides use in agriculture: Their benefits and hazards. Interdiscip Toxicol 2:1–12. doi: 10.2478/v10102-009-0001-7

Alaphilippe A, Capowiez Y, Severac G, et al (2016) Codling moth exclusion netting: an overview of French and Italian experiences. IOBC-WPRS Bull 112:31–35

Amorós-Jiménez R, Plaza M, Montserrat M, et al (2020) Effect of UV-Absorbing Nets on the Performance of the Aphid Predator Sphaerophoria rueppellii (Diptera: Syrphidae). Insects 11:1–12

Antignus Y (2014) Management of Air-Borne Viruses by “Optical Barriers” in Protected Agriculture and Open-Field Crops. In: Maramorosch K, Mettenleiter TC, Murphy FA, et al. (eds) Advances in Virus Research. pp 1–33

Antignus Y (2000) Manipulation of wavelength-dependent behaviour of insects: an IPM tool to impede insects and restrict epidemics of insect-borne viruses. Virus Res 71:213–220. doi: 10.1038/sj.eye.6700752

Antignus Y (2010) Optical Manipulation for Control of *Bemisia tabaci* and its vectored viruses in the greenhouse and open field. In: Stansly PA, Naranjo SE, Brown JK, et al. (eds) Bemisia: Bionomics and Management of a Global Pest. pp 1–540

Antignus Y, Mor N, Ben Joseph R, et al (1996) Ultraviolet-Absorbing Plastic Sheets Protect Crops from Insect Pests and from Virus Diseases Vectored by Insects. Environ Entomol 25:919–924. doi: 10.1093/ee/25.5.919

Arthurs SP, Stamps RH, Giglia FF (2013) Environmental modification inside photoselective shadehouses. HortScience 48:975–979. doi: 10.21273/HORTSCI.48.8.975

Ayala-Tafoya F, Yáñez-Juárez MG, Partida-Ruvalcaba L, et al (2015) Producción de pepino en ambientes diferenciados por mallas de sombreo fotoselectivo. ITEA Inf Tec Econ Agrar 111:3–17. doi: 10.12706/itea.2015.001

Ayala-Tafoya F, Yañez Juárez M, López Orona C, et al (2018) Sunlight transmitted by colored shade nets on photosynthesis and yield of cucumber. Cienc Rural 48:1–9. doi: 10.1590/0103-8478cr20170829

Bahlai CA, Welsman JA, Macleod EC, Schaafsma AW (2008) Role of Visual and Olfactory Cues from Agricultural Hedgerows in the Orientation Behavior of Multicolored Asian Lady Beetle (Coleoptera : Coccinellidae). Behavior 37:973–979

Baiamonte I, Raffo A, Nardo N, et al (2015) Effect of the use of anti-hail nets on codling moth (Cydia pomonella) and organoleptic quality of apple (cv . Braeburn) grown in Alto Adige Region (northern Italy). J S. doi: 10.1002/jsfa.7313

Barański M, Średnicka-Tober D, Volakakis N, et al (2014) Higher antioxidant and lower cadmium concentrations and lower incidence of pesticide residues in organically grown crops: A systematic literature review and meta-analyses. Br J Nutr 112:794–811. doi: 10.1017/S0007114514001366

Bastías RM (2016) Malla sombra en Manzanos. Boletín Técnico Pomáceas, Univ. Talca 16:2–4

Bastías RM, Corelli-Grappadelli L (2012) Light Quality Management in Fruit Orchards: Physiological and Technological Aspects. Chil J Agric Res 72:574–581. doi: 10.4067/S0718-58392012000400018

Bastías RM, Manfrini L, Corelli Grappadelli L (2012) Exploring the Potential Use of Photo-Selective Nets for Fruit Growth Regulation in Apple. Chil J Agric Res 72:224–231. doi: 10.4067/S0718-58392012000200010

Bell WJ (1990) Searching behavior patterns in insects. Annu Rev Entomol 35:447–467

Ben-Yakir D, Antignus Y, Offir Y, Shahak Y (2012) Colored shading nets impede insect invasion and decrease the incidences of insect-transmitted viral diseases in vegetable crops. Entomol Exp Appl 144:249–257. doi: 10.1111/j.1570-7458.2012.01293.x

Ben-Yakir D, Antignus Y, Offir Y, Shahak Y (2014) Photoselective nets and screens can reduce insect pests and diseases in agricultural crops. Acta Hortic 1015:95–102. doi: 10.17660/ActaHortic.2014.1015.10

Bezemer TM, Harvey JA, Mills NJ (2005) Influence of adult nutrition on the relationship between body size and reproductive parameters in a parasitoid wasp. Ecol Entomol 30:571–580. doi: 10.1111/j.0307-6946.2005.00726.x

Bezemer TM, Mills NJ (2003) Clutch size decisions of a gregarious parasitoid under laboratory and field conditions. Anim Behav 66:1119–1128. doi: 10.1006/anbe.2003.2296

Bosch D, Rodríguez MA, Avilla J (2018) Monitoring resistance of Cydia pomonella (L.) Spanish field populations to new chemical insecticides and the mechanisms involved. Pest Manag Sci 74:933–943. doi:

10.1002/ps.4791

Brglez Sever M, Tojnko S, Unuk T (2015) Impact of various types of anti-hail nets on light exposure in orchards and quality parameters of apples– a rewiev. Agricultura 12:25–31. doi: 10.1515/agricultura-2016-0004

Briassoulis D, Mistriotis A, Eleftherakis D (2007) Mechanical behaviour and properties of agricultural nets. Part II: Analysis of the performance of the main categories of agricultural nets. Polym Test 26:970–984. doi: 10.1016/j.polymertesting.2007.06.010

Candian V, Pansa MG, Santoro K, et al (2019) Photoselective exclusion netting in apple orchards : effectiveness against pests and impact on beneficial arthropods , fungal diseases and fruit quality. Pest Manag Sci 76:179–187. doi: 10.1002/ps.5491

Cascone S, Ingrao C, Valenti F, Porto SMC (2020) Energy and environmental assessment of plastic granule production from recycled greenhouse covering films in a circular economy perspective. J Environ Manage 254:1–11. doi: 10.1016/j.jenvman.2019.109796

Castellano S, Russo G, Briassoulis D (2008) Plastic Nets in Agriculture: A General Review of Types and Applications. Appl Eng Agric 24:799–808. doi: 10.13031/2013.25368

Charles JG, Sandanayaka WRM, Chhagan A, Page-Weir NEM (2013a) Host selection behaviour in Mastrus ridens, a gregarious ectoparasitoid of codling moth, Cydia pomonella. BioControl 58:493–503. doi: 10.1007/s10526-013-9517-z

Charles JG, Sandanayaka WRM, Chhagan A, Page-Weir NEM (2013b) Host selection behaviour in *Mastrus ridens*, a gregarious ectoparasitoid of codling moth, *Cydia pomonella*. BioControl 58:493–503. doi: 10.1007/s10526-013-9517-z

Chen Z, Liu X, Zhou J, et al (2014) Phototactic behavior of *Pachyneuron aphidis* (Hymenoptera: Pteromalidae) – hyperparasitoid of *Myzus persicae* (Hemiptera: Aphidiae). Biocontrol Sci Technol 24:1469–1480.

doi: 10.1080/09583157.2014.945901

Chen Z, Xu R, Kuang R, Sun R (2016) Phototactic behaviour of the parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae). Biocontrol Sci Technol 26:250–262. doi: 10.1080/09583157.2015.1099071

Chiel E, Messika Y, Steinberg S, Antignus Y (2006) The effect of UV-absorbing plastic sheet on the attraction and host location ability of three parasitoids: *Aphidius colemani*, *Diglyphus isaea* and *Eretmocerus mundus*. BioControl 51:65–78. doi: 10.1007/s10526-005-8667-z

Chouinard G, Firlej A, Cormier D (2016) Going beyond sprays and killing agents: Exclusion, sterilization and disruption for insect pest control in pome and stone fruit orchards. Sci Hortic (Amsterdam) 208:13–27. doi: 10.1016/j.scienta.2016.03.014

Chouinard G, Veilleux J, Pelletier F, et al (2017) Impact of exclusion netting row covers on arthropod presence and crop damage to ‘Honeycrisp’ apple trees in North America: A five-year study. Crop Prot 98:248–254. doi: 10.1016/j.cropro.2017.04.008

Chyzik R, Dobrinin S, Antignus Y (2003) Effect of a UV-Deficient Environment on the Biology and Flight Activity of *Myzus persicae* and Its Hymenopterous Parasite *Aphidius matricariae*. Phytoparasitica 31:467–477. doi: 10.1007/BF02979740

Corvalán N, Bastı RM, Umanzor C, Serra I (2016) Grapevine root and shoot growth responses to photoselective nets: preliminary results. In: Proc. I Int. Symp. on Grapevine Roots. pp 89–94

Cramer ME, Demchak K, Marini R, Leskey T (2019) UV-blocking High-tunnel Plastics Reduce Japanese Beetle (*Popillia japonica*) in Red Raspberry. HortScience 54:903–909. doi: 10.21273/HORTSCI13820-18

Dáder B, Plaza M, Fereres A, Moreno A (2015) Flight behaviour of vegetable pests and their natural enemies under different ultraviolet-blocking enclosures. Ann Appl Biol 167:116–126. doi: 10.1111/aab.12213

De Vilder I, Buyle G, Virgo V (2015) Materials for shade nets. 20

Department of Agriculture Fisheries and Forestry A (2013) Final Risk Analysis Report for the release of Mastrus ridens for the biological control of codling moth (Cydia pomonella). 42

Devee A, Arvaniti K, Perdikis D (2018) Intraguild predation among three aphidophagous predators. Bull Insectology 71:11–19

Devotto L, del Valle C, Ceballos R, Gerding M (2010) Biology of *Mastrus ridibundus* (Gravenhorst), a potential biological control agent for area-wide management of *Cydia pomonella* (Linneaus) (Lepidoptera: Tortricidae). J Appl Entomol 134:243–250. doi: 10.1111/j.1439-0418.2009.01412.x

Díaz BM, Biurrún R, Moreno A, et al (2006) Impact of ultraviolet-blocking plastic films on insect vectors of virus diseases infecting crisp lettuce. HortScience 41:711–716. doi: 10.1006/abbi.2000.1936

Dib H, Sauphanor B, Capowiez Y (2010) Effect of codling moth exclusion nets on the rosy apple aphid, Dysaphis plantaginea, and its control by natural enemies. Crop Prot 29:1502–1513. doi: 10.1016/j.cropro.2010.08.012

Dobzhansky T (1933) Geographical Variation in Lady-Beetles. Am Nat 67:97–126. doi: 10.1086/280472

Duduzile MN, Soundy P, Jifon J, Sivakumar D (2016) Spectral quality of photo-selective nets improves phytochemicals and aroma volatiles in coriander leaves (Coriandrum sativum L .) after postharvest storage. J Photochem Photobiol B Biol 161:328–334. doi: 10.1016/j.jphotobiol.2016.05.032

Ehler LE (1996) Structure and Impact of Natural Enemy Guilds in Biological Control of Insect Pests. In: Polis GA, Winemiller KO (eds) Food Webs: Integration of Patterns and Dynamics, 1st edn. Springer-Science+Business Media, B. V., p 93

Elkinton JS, Cardé RT (1984) Odor Dispersion. In: Bell WJ, Cardé RT (eds) Chemical Ecology of Insects. Chapman and Hall Ltd., pp 73–91

Feng Y, Zhou Z, An M, et al (2018) The effects of prey distribution and digestion on functional response of Harmonia axyridis (Coleoptera : Coccinellidae). Biol Control 124:74–81. doi: 10.1016/j.biocontrol.2018.04.009

Fuentes-Contreras E, Reyes M, Barros W, Sauphanor B (2007) Evaluation of Azinphos-Methyl Resistance and Activity of Detoxifying Enzymes in Codling Moth (Lepidoptera: Tortricidae) from Central Chile. J Econ Entomol 100:551–556. doi: 10.1603/0022-0493(2007)100

Fuller-Perrine L, Tobin M (1993) A Method for Applying and Removing Bird-Exclusion Netting in Commercial Vineyards. Wildl Soc Bull 21:47–51

Gomes E, Almeida A, Sá E De, et al (2018) Coccinellidae, Syrphidae and Aphidoletes are key mortality factors for Myzus persicae in tropical regions : A case study on cabbage crops. Crop Prot 112:288–294. doi: 10.1016/j.cropro.2018.06.015

González-Chang M, Wratten SD, Lefort MC, Boyer S (2016) Food webs and biological control: A review of molecular tools used to reveal trophic interactions in agricultural systems. Food Webs 9:4–11. doi: 10.1016/j.fooweb.2016.04.003

Gu H, Dorn S (2001) How do wind velocity and light intensity influence host-location success in *Cotesia glomerata* (Hym., Braconidae)? J Appl Entomol 125:115–120. doi: 10.1046/j.1439-0418.2001.00520.x

Guénard B, Dumont F, Fréchette B, et al (2018) May furtive predation provide enemy free space in ant-tended aphid colonies ? PLoS One 13:1–14

Gurr G, Wratten S (2000) Biological Control: Measures of Success

Gurr GM, Lu Z, Zheng X, et al (2016) Multi-country evidence that crop diversification promotes ecological intensification of agriculture. Nat Plants 2:22–25. doi: 10.1038/NPLANTS.2016.14

Hilker M, Mcneil J (2008) Chemical and behavioral ecology in insect parasitoids: how to behave optimally in a complex odorous environment. In: Wajnberg E, Bernstein C, van Alphen J (eds) Behavioral Ecology of Insect Parasitoids. pp 92–111

Holopainen JK, Himanen SJ, Poppy GM (2013) Climate Change and its Effects on the Chemical Ecology of Insect Parasitoids. In: Wajnberg E, Colazza S (eds) Chemical Ecology of Insect Parasitoids, First Edit. John Wiley & Sons, Ltd., pp 168–190

Hougardy E, Bezemer TM, Mills NJ (2005) Effects of host deprivation and egg expenditure on the reproductive capacity of *Mastrus ridibundus*, an introduced parasitoid for the biological control of codling moth in California. Biol Control 33:96–106. doi: 10.1016/j.biocontrol.2005.01.013

Hughes WOH, Gailey D, Knapp JJ (2003) Host location by adult and larval codling moth and the potential for its disruption by the application of kairomones. Entomol Exp Appl 106:147–153. doi: 10.1046/j.1570-7458.2003.00020.x

Iglesias I, Alegre S (2006) The effect of anti-hail nets on fruit protection, radiation, temperature, quality and profitability of “Mondial Gala” apples. J Appl Hortic 8:91–100. doi: 10.37855/jah.2006.v08i02.22

Ilić ZS, Fallik E (2017) Light quality manipulation improves vegetable quality at harvest and postharvest: A review. Environ Exp Bot 139:79–90. doi: 10.1016/j.envexpbot.2017.04.006

Ilić ZS, Milenković L, Šunić L, et al (2017) Effect of shading by coloured nets on yield and fruit quality of sweet pepper. Zemdirbyste-Agriculture 104:53–62. doi: 10.13080/z-a.2017.104.008

Jumean Z, Unruh T, Gries R, Gries G (2005) *Mastrus ridibundus* parasitoids eavesdrop on cocoon-spinning codling moth, *Cydia pomonella*, larvae. Naturwissenschaften 92:20–25. doi: 10.1007/s00114-004-0581-1

Kalcsits L, Musacchi S, Layne DR, et al (2017) Above and below-ground environmental changes associated with the use of photoselective protective netting to reduce sunburn in apple. Agric For Meteorol 237–

238:9–17. doi: 10.1016/j.agrformet.2017.01.016

Knight AL (2008) Codling Moth Areawide Integrated Pest Management. In: Koul O, Cuperus G, Elliott N (eds) Areawide Pest Management: Theory and Implementation. pp 159–190

Kremen C, Iles A, Bacon C (2012) Diversified Farming Systems: An Agroecological, Systems-based Alternative to Modern Industrial Agriculture. Ecol Soc 17:44–62. doi: 10.5751/ES-05103-170444

Lacey LA, Unruh TR (2005) Biological Control of Codling Moth (*Cydia Pomonella*, Lepidoptera: Tortricidae) and Its Role in Integrated Pest Management, With Emphasis on Entomopathogens. Vedalia 12:33–60

Legarrea S, Diaz BM, Plaza M, et al (2012a) Diminished UV radiation reduces the spread and population density of Macrosiphum euphorbiae (Thomas) [Hemiptera: Aphididae] in lettuce crops. Hortic Sci 39:74–80. doi: 10.17221/79/2011-HORTSCI

Legarrea S, Velázquez E, Aguado P, et al (2014) Effects of a photoselective greenhouse cover on the performance and host finding ability of *Aphidius ervi* in a lettuce crop. BioControl 59:265–278. doi: 10.1007/s10526-014-9564-0

Legarrea S, Weintraub PG, Plaza M, et al (2012b) Dispersal of aphids, whiteflies and their natural enemies under photoselective nets. BioControl 57:523–532. doi: 10.1007/s10526-011-9430-2

Lernoud J, Willer H (2017) The World of Organic Agriculture 2017: Summary

Li Y, Xu Z, Shi L, et al (2016) Insecticide resistance monitoring and metabolic mechanism study of the green peach aphid , Myzus persicae (Sulzer) (Hemiptera : Aphididae), in Chongqing , China. Pestic Biochem Physiol 132:21–28. doi: 10.1016/j.pestbp.2015.11.008

Lin J-T (1993) Identification of Photoreceptor Locations in the Compound Eye of *Coccinella septempunctata* Linnaeus (Coleoptera, Coccinellidae). J Insect Physiol 39:555–562. doi: 10.1016/0022-1910(93)90037-R

Lloyd A, Hamacek E, George A, et al (2005) Evaluation of Exclusion Netting for Insect Pest Control and Fruit Quality Enhancement in Tree Crops. In: Drew R (ed) Proc. IS on Hort. in Asian-Pacific Region. pp 253–258

Lobos GA, Retamales JB, Hancock JF, et al (2013) Productivity and fruit quality of *Vaccinium corymbosum* cv. Elliott under photo-selective shading nets. Sci Hortic (Amsterdam) 153:143–149. doi: 10.1016/j.scienta.2013.02.012

Lobos GA, Retamales JB, Hancock JF, et al (2012) Spectral irradiance, gas exchange characteristics and leaf traits of *Vaccinium corymbosum* L. “Elliott” grown under photo-selective nets. Environ Exp Bot 75:142–149. doi: 10.1016/j.envexpbot.2011.09.006

Lopez-Marín J, Galvez A, Otalora G, del Amor FM (2019) Photoselective shade nets for pepper cultivation in southeastern Spain. Acta Hortic 1252:183–189. doi: 10.17660/ActaHortic.2019.1252.24

Louda SM, Pemberton RW, Johnson MT, Follett PA (2003) Nontarget Effects - The Achille’s Heel of Biological Control? Retrospective Analyses to Reduce Risk Associated with Biocontrol Introductions. Annu Rev Entomol 48:365–396. doi: 10.1146/annurev.ento.48.060402.102800

Lucas É (2012) Intraguild Interactions. In: Hodek I, van Emden H, Honek A (eds) Ecology and Behaviour of the Ladybird Beetles (Coccinellidae), First Edit. Blackwell Publishing Ltd., pp 343–374

Lucas É, Labrie G, Vincent C, Kovach J (2007) The Multicoloured Asian Ladybird Beetle: Beneficial or Nuisance Organism? In: Vincent C, Goettel MS, Lazarovits G (eds) Biological Control a global perspective. pp 38–52

Lucas ÉRIC (2005) Intraguild predation among aphidophagous predators. Eur J Entomol 102:351–364. doi: 10.14411/eje.2005.052

Majerus M, Strawson V, Roy H (2006) The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera:

Coccinellidae), in Britain. Ecol Entomol 31:207–215

Manja K, Aoun M (2019) The use of nets for tree fruit crops and their impact on the production : A review. Sci Hortic (Amsterdam) 246:110–122. doi: 10.1016/j.scienta.2018.10.050

Maraveas C (2020) The Sustainability of Plastic Nets in Agriculture. Sustainability 12:1–24

Mazzi D, Dorn S (2012) Movement of insect pests in agricultural landscapes. Ann Appl Biol 160:97–113. doi: 10.1111/j.1744-7348.2012.00533.x

McCaskill MR, McClymont L, Goodwin I, et al (2016) How hail netting reduces apple fruit surface temperature: A microclimate and modelling study. Agric For Meteorol 226–227:148–160. doi: 10.1016/j.agrformet.2016.05.017

Meena VS, Kashyap P, Nangare DD, Singh J (2016) Effect of coloured shade nets on yield and quality of pomegranate (*Punica granatum*) cv. Mridula in semi-arid region of Punjab. Indian J Agric Sci 86:500–505

Millennium Ecosystem Assesment A (2005) Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC., Island Pre. Washington, DC.

Mills N (2005) Selecting effective parasitoids for biological control introductions: Codling moth as a case study. Biol Control 34:274–282. doi: 10.1016/j.biocontrol.2005.02.012

Mills N (2009) Parasitoids. In: Encyclopedia of Insects. pp 748–751

Moggia C, Yuri JA (2003) Apple postharvest practices in Chile. In: Washington Tree Fruit Postharvest Conference. Washington, pp 1–9

Mupambi G, Anthony BM, Layne DR, et al (2018) The influence of protective netting on tree physiology and fruit quality of apple: A review. Sci Hortic (Amsterdam) 236:60–72. doi: 10.1016/j.scienta.2018.03.014

Nabli H, Bailey WC, Necibi S (1999) Beneficial Insect Attraction to Light Traps with Different Wavelengths. Biol Control 16:185–188

Obata S (1997) The influence of aphids on the behaviour of adults of the ladybird beetle, <i>Harmonia axyridis<i/> (Col: Coccinellidae). Entomophaga 42:103–106. doi: 10.1007/BF02769885

Olivares-Soto H, Bastías RM (2018) Photosynthetic efficiency of apples under protected shade nets. Chil J Agric Res 78:126–138. doi: 10.4067/S0718-58392018000100126

Omkar, Mishra GE, Singh KA (2005) Effects of different wavelengths of light on the life attributes of two aphidophagous ladybirds (Coleoptera : Coccinellidae). Eur J Entomol 102:33–37. doi: 10.14411/eje.2005.005

Pajac I, Pejic I, Baric B (2011) Codling Moth, Cydia pomonella (Lepidoptera: Tortricidae) – Major Pest in Apple Production: an Overview of its Biology, Resistance, Genetic Structure and Control Strategies. Agric Conspec Sci 76:87–92. doi: 10.1080/09583150802267046

Papaioannou C, Katsoulas N, Maletsika P, et al (2012) Effects of a UV-absorbing greenhouse covering film on tomato yield and quality. Spanish J Agric Res 10:959. doi: 10.5424/sjar/2012104-2899

Peitsch D, Fietz A, Hertel H, et al (1992) The spectral input systems of hymenopteran insects and their receptor-based colour vision. J Comp Physiol A 170:23–40. doi: 10.1007/BF00190398

Pell JK, Baverstock J, Roy HE, et al (2008) Intraguild predation involving *Harmonia axyridis*: A review of current knowledge and future perspectives. BioControl 53:147–168. doi: 10.1007/s10526-007-9125-x

Polis GA, Holt RD (1992) Intraguild predation: The dynamics of complex trophic interactions. Trends Ecol Evol 7:151–154. doi: 10.1016/0169-5347(92)90208-S

Pretty J, Bharucha ZP (2014) Sustainable intensification in agricultural systems. Ann Bot 114:1571–1596. doi: 10.1093/aob/mcu205

Racsko J, Schrader LE (2012) Sunburn of Apple Fruit: Historical Background, Recent Advances and Future Perspectives. CRC Crit Rev Plant Sci 31:455–504. doi: 10.1080/07352689.2012.696453

Reganold JP, Wachter JM (2016) Organic agriculture in the twenty-first century. Nat Plants 2:1–8. doi: 10.1038/nplants.2015.221

Retamales JB, Montecino JM, Lobos GA, Rojas LA (2008) Colored Shading Nets Increase Yields and Profitability of Highbush Blueberries. In: Proc. XXVII IHC - Cultiv. Utiliz. Asian, Sub-Trop., Underutilized Hort. Crops. pp 193–198

Rigden P (2008) To net or not to net?

Rodríguez MA, Bosch D, Avilla J (2012) Azinphos-methyl and carbaryl resistance in adults of the codling moth (Cydia pomonella (L.), Lepidoptera: Tortricidae) from Northeastern Spain. Pestic Biochem Physiol 103:43–48. doi: 10.1016/j.pestbp.2012.03.002

Romeis J, Babendreier D, Wäckers FL, Shanower TG (2005) Habitat and plant specificity of *Trichogramma* egg parasitoids - Underlying mechanisms and implications. Basic Appl Ecol 6:215–236. doi: 10.1016/j.baae.2004.10.004

Roy H, Brown P, Majerus M (2006) *Harmonia axyridis*: a successful biocontrol agent or an invasive threat? In: Eilenberg J, Hokkanen HMT (eds) An Ecological and Societal Approach to Biological Control, Springer. pp 295–309

Sal J, Velázquez E, Legarrea S, et al (2008) Influence of UV-absorbing nets in the population of *Macrosiphum euporbiae* Thomas (Homoptera: Aphididae) and the parasitoid *Aphidius ervi* (Haliday) (Hymenoptera: Aphididae) in lettuce crops. In: Proceedings of the Third International Symposium on Biological Control of Arthropods. pp 329–337

Sauphanor B, Brosse V, Bouvier JC, et al (2000) Monitoring resistance to diflubenzuron and deltamethrin in French codling moth populations (Cydia pomonella). Pest Manag Sci 56:74–82. doi: 10.1002/(SICI)1526-4998(200001)56:1<74::AID-PS96>3.0.CO;2-C

Sauphanor B, Severac G, Maugin S, et al (2012) Exclusion netting may alter reproduction of the codling moth (Cydia pomonella) and prevent associated fruit damage to apple orchards. Entomol Exp Appl 145:134–142. doi: 10.1111/j.1570-7458.2012.01320.x

Schirmer ST, Sengonca CE, Blaeser PE (2008) Influence of abiotic factors on some biological and ecological characteristics of the aphid parasitoid *Aphelinus asychis* (Hymenoptera: Aphelinidae) parasitizing *Aphis gossypii* (Sternorrhyncha: Aphididae). Eur J Entomol 105:121–129. doi: 10.14411/eje.2008.017

Selahle KM, Sivakumar D, Jifon J, Soundy P (2015) Postharvest responses of red and yellow sweet peppers grown under photo-selective nets. Food Chem 173:951–956. doi: 10.1016/j.foodchem.2014.10.034

Shahak Y (2008) Photo-Selective Netting for Improved Performance of Horticultural Crops. A Review of Ornamental and Vegetable Studies Carried Out in Israel. Acta Hortic 161–168. doi: 10.17660/ActaHortic.2008.770.18

Shahak Y (2014) Photoselective netting: An overview of the concept, R&D and practical implementation in agriculture. Acta Hortic 1015:155–162

Shahak Y, Gal E, Offir Y, Ben-Yakir D (2008a) Photoselective shade netting integrated with greenhouse technologies for improved performance of vegetable and ornamental crops. Acta Hortic 797:75–80. doi: 10.17660/ActaHortic.2008.797.8

Shahak Y, Ganelevin R, Gussakovsky E, et al (2004a) Efectos de la modificación de la calidad de la luz mediante mallas de sombreo fotoselectivas (Chromatinet) sobre la fisiología , mejora del rendimiento y calidad de las cosechas. In: Producción Hortícola y Seguridad Alimentaria. Cámara de Comercio de Almería, Universidad de Almería, pp 117–137

Shahak Y, Gussakovsky EE, Cohen Y, et al (2004b) ColorNets: A new approach for light manipulation in fruit trees. Acta Hortic 609–616. doi: 10.17660/ActaHortic.2004.636.76

Shahak Y, Gussakovsky EE, Gal E, Ganelevin R (2004c) ColorNets: Crop protection and Light-Quality Manipulation in One Technology. Acta Hortic 659:143–151. doi: 10.17660/ActaHortic.2004.659.17

Shahak Y, Kong Y, Ratner K (2016) The wonders of yellow netting. Acta Hortic 1134:327–334. doi: 10.17660/ActaHortic.2016.1134.43

Shahak Y, Ratner K, Giller YE, et al (2008b) Improving Solar Energy Utilization, Productivity and Fruit Quality in Orchards and Vineyards by Photoselective Netting. Acta Hortic 772:65–72. doi: 10.17660/ActaHortic.2008.772.7

Stamps RH (2009) Use of colored shade netting in horticulture. HortScience 44:239–241

Sun Y-X, Liu T-X (2018) *Harmonia axyridis* Does Not Have Obvious Fitness Gain and Preference to the Red Morph of *Acyrthosiphon pisum* : A Case Study on a Laboratory Strain. Front Ecol Evol 6:1–7. doi: 10.3389/fevo.2018.00001

Tan X, Zhao J, Zhang F, Wang S (2014) Light dependency of life trails, reproduction, locomotion, and predation in the polyphagous ladybird *Hippodamia variegata*. Entomol Exp Appl 152:200–208. doi: 10.1111/eea.12217

Thaler R, Brandstätter A, Meraner A, et al (2008) Molecular phylogeny and population structure of the codling moth (*Cydia pomonella*) in Central Europe: II. AFLP analysis reflects human-aided local adaptation of a global pest species. Mol Phylogenet Evol 48:838–849. doi: 10.1016/j.ympev.2008.05.027

Tian M, Wei Y, Zhang S, Liu T (2017) Suitability of *Bemisia tabaci* (Hemiptera: Aleyrodidae) biotype-B and *Myzus persicae* (Hemiptera: Aphididae) as prey for the ladybird beetle, *Serangium japonicum* (Coleoptera: Coccinellidae). Eur J Entomol 114:603–608. doi: 10.14411/eje.2017.073

Tomich TP, Brodt S, Ferris H, et al (2011) Agroecology: A Review from a Global-Change Perspective. Annu Rev Environ Resour 36:193–222.

doi: 10.3109/10428199709068284

Tortosa O, Carmona A, Martínez E, et al (2014) Liberación y establecimiento de Mastrus ridens (Hymenoptera : Ichneumonidae) para el control de Cydia pomonella (Lepidoptera : Tortricidae) en Mendoza , Argentina. Rev la Soc Entomológica Argentina 73:109–118

Tubiello FN, Salvatore M, Ferrara AF, et al (2015) The Contribution of Agriculture, Forestry and other Land Use activities to Global Warming, 1990-2012. Glob Chang Biol 21:2655–2660. doi: 10.1111/gcb.12865

Tudor V, Smedescu D, Fintineru G, et al (2019) Plasticulture : Diffusion of Plastic Materials in the Agricultural Sector. Mater Plast 56:730–734

Turlings TCJ, Wackers FL, Vet LEM, et al (1993) Learning of Host-Finding Cues by Hymenopterous Parasitoids. In: Papaj DR, Lewis AC (eds) Insect Learning-Ecological and Evolutionary Perspectives. Springer Science+Business Media Dordrecht, pp 51–78

Twedt DJ (1978) Control Netting as a Hazard to Birds. Environ Conserv 217–218

Umanzor C, Bastías R, Wilckens R, Quezada C (2016) Influencia del uso de malla perla y roja en las condiciones micro-climáticas, daño por sol y desarrollo de color de frutos en huertos de manzanos cvs. gala y fuji. Rev Bras Frutic 39:1–13. doi: 10.1590/0100-29452017930

van Lenteren JC (2006) Ecosystem services to biological control of pests: why are they ignored? Proc Netherlands Entomol Soc Meet 17:103–111

Vinson SB (1975) Biochemical coevolution between parasitoids and their hosts. In: Price PW (ed) Evolutionary Strategies of Parasitic Insects and Mites. Plenum Press, New York, pp 14–48

Völkl W, Mackauer M, Pell JK, Brodeur J (2007) Predators, Parasitoids and Pathogens. In: van Emden HF, Harrington R (eds) Aphids as Crop Pests. CAB International, pp 187–233

Wachsmann Y, Zur N, Shahak Y, et al (2014) Photoselective Anti-Hail

Netting for Improved Citrus Productivity and Quality. Acta Hortic 2015:169–176

Ware RL, Majerus MEN (2008) Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird Harmonia axyridis. In: Roy HE, Wajnberg E (eds) From Biological Control to Invasion: the Ladybird Harmonia Axyridis as a Model Species, Springer. pp 169–188

Wäschke N, Meiners T, Rostás M (2013) Foraging Strategies of Parasitoids in Complex Chemical Environments. In: Wajnberg E, Colazza S (eds) Chemical Ecology of Insect Parasitoids, First Edit. John Wiley & Sons, Ltd., pp 37–63

Welter SC (2009) Codling Moth. In: Resh VH, Cardé RT (eds) Encyclopedia of Insects, Second Edi. Elsevier Inc., pp 174–175

Wezel A, Casagrande M, Celette F, et al (2014) Agroecological practices for sustainable agriculture. A review. Agron Sustain Dev 34:1–20. doi: 10.1007/s13593-013-0180-7

Wirta HK, Hebert PDN, Kaartinen R, et al (2014) Complementary molecular information changes our perception of food web structure. Proc Natl Acad Sci 111:1885–1890. doi: 10.1073/pnas.1316990111

Wratten S, Sandhu H, Cullen R, Costanza R (2013) Ecosystem Services in Agricultural and Urban Landscapes

Wratten SD, Gillespie M, Decourtye A, et al (2012) Pollinator habitat enhancement: Benefits to other ecosystem services. Agric Ecosyst Environ 159:112–122. doi: 10.1016/j.agee.2012.06.020

Yi XY, Fu FW, Liu YST (2019) Intraguild predation between *Harmonia axyridis* and Aphidius gifuensis : effects of starvation period , plant dimension and extraguild prey density. BioControl 64:55–64. doi: 10.1007/s10526-018-09913-1

Zhou J, Kuang R, Chen Z, et al (2013) Phototactic Behavior of *Coccinella septempunctata* L . (Coleoptera : Coccinellidae). Coleopt Bull 67:33–39. doi: 10.1649/072.067.0108

Zhou K, Jerszurki D, Sadka A, et al (2018) Effects of photoselective netting on root growth and development of young grafted orange trees under semi-arid climate. Sci Hortic (Amsterdam) 238:272–280. doi: 10.1016/j.scienta.2018.04.054