

蜜源食物对节肢动物天敌寿命、繁殖力和控害能力的影响

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摘要: 大多数节肢动物天敌除了寄生或捕食寄主或猎物外, 也会取食蜜源食物, 特别是包括植物花蜜、花外蜜和昆虫蜜露等富含糖分的食物。这些蜜源食物对于提高寄生性和捕食性天敌的飞行和寄主搜索能力、延长寿命、提高繁殖力和增强控害能力都能发挥重要作用。本文重点介绍了农田生态系统中 3 类常见的非猎物性蜜源食物即植物花蜜、花外蜜和昆虫蜜露。其中, 花蜜和花外蜜能够显著延长天敌寿命, 提高天敌繁殖力和控害能力; 蜜露的作用虽次于花蜜和花外蜜, 但仍能促进某些天敌的生态功能。还进一步综述了显花植物和蜜源食物投放在生物防治中的应用, 并从筛选适宜的蜜源植物、蜜源食物中糖成分作用分析和天敌对蜜源食物的搜索和定位等方向开展对蜜源食物的研究利用进行了展望。

关键词: 节肢动物; 天敌; 寿命; 繁殖力; 蜜源食物; 控害能力; 生物防治

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Effects of sugar-rich foods on the longevity, fecundity and pest control capacity of arthropod natural enemies

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Abstract: Most arthropod predators and parasitoids also feed on sugar-rich foods including floral nectar, extrafloral nectar and arthropod honeydew besides preying or parasitizing arthropod hosts. These sugar-rich foods play important roles in enhancing their flight and host foraging ability, prolonging adult longevity, increasing fecundity and improving pest control capacity. In this article, we briefly introduced three common sugar-rich foods in agro-ecosystem including floral nectar, extrafloral nectar and honeydew. Floral nectar and extrafloral nectar could significantly prolong and improve the longevity, fecundity and pest control capacity of most arthropod natural enemies, whereas honeydew could only improve the biological fitness of some natural enemies. The successful applications of planting flowering plants and supplying sugar-rich foods on improving biological control functioning in agro-ecosystem were also reviewed. Furthermore, the further research directions of sugar-rich foods, including screening nectar resource plants, clarifying the effects of sugars in sugar-rich foods and the mechanism of searching and locating the sugar-rich foods by natural enemies, were discussed.

Key words: Arthropods; natural enemies; longevity; fecundity; sugar-rich foods; pest control capacity; biological control

目前我国农业害虫的防治仍然以化学农药为主, 某些情况下农药甚至已经成为害虫防治的唯一

方式。然而, 农药的过量使用不仅杀伤了大量的天敌, 严重削弱天敌对害虫的自然调控功能, 导致害虫

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频繁暴发,而且污染了土壤及水源,影响食品的安全生产,同时也危害人体健康 (Zhang *et al.*, 2011; Qiao *et al.*, 2012; Li *et al.*, 2013)。合理有效地利用天敌控制害虫种群不仅可以减少农药的使用,还可以恢复农田生态系统的自然控害能力,促进农业的可持续发展,取得良好的经济和环境效益(陈学新等,2014)。

天敌昆虫在不同的发育阶段对营养的需求有所差异,大多数寄生性天敌成虫阶段主要或者全部依靠摄取碳水化合物作为能量来源 (Jervis *et al.*, 1993),尽管它们的寿命和产卵率受制于其本身活力,但其搜寻和繁殖行为仍受到营养条件的影响 (Wäckers, 1994; Takasu and Lewis, 1995)。同时,农业生态系统中常见的瓢虫、食蚜蝇、捕食蝽、草蛉、捕食螨、蜘蛛等捕食性天敌的寿命和繁殖力也受到营养条件的显著影响,多数捕食性天敌在捕食猎物的同时也会取食富含糖分的食物作为营养补充 (Zhimo and McMurtry, 1990; McEwen *et al.*, 1993; Taylor and Foster, 1996; Evans, 2000; Belliure and Michaud, 2001; Yong, 2003)。大量的研究结果表明蜜源食物能够促进天敌生长发育、繁殖、迁徙以及搜寻能力 (Fadamiro and Heimpel, 2001; Siekmann *et al.*, 2001; Wäckers, 2001; Winkler *et al.*, 2006),因此合理地补充蜜源食物包括花蜜 (floral nectar)、花外蜜 (extrafloral nectar)、蜜露 (honeydew)、花粉 (pollen)、果实 (fruits)、植物汁液 (plant sap) 等,对于天敌控害功能的发挥具有重要的促进作用 (Wäckers, 2005)。

蜜源食物对节肢动物天敌的作用毋庸置疑,为了最大限度地发挥和提高天敌的控害功能,探索蜜源食物对天敌的作用机理及筛选适宜田间应用的蜜源植物十分必要。本文着重就国内外农田生态系统常见的蜜源食物对节肢动物天敌的影响及其在生物防治中应用等最新研究进展进行总结,以期更有效地进行蜜源食物管理,完善害虫生态防控的技术体系,促进我国农业的可持续发展。

1 农田生态系统中常见的蜜源食物

田间最常见也最重要的蜜源食物为花蜜、花外蜜和蜜露。花内和花外蜜腺分泌的蜜液分布于整个植物王国,如每公顷紫花苜蓿每天可产生 190 L 的蜜液,而棉花和蜜瓜亦可分别产生 2.4 L 和 1.4 L 的蜜液 (Butler *et al.*, 1972)。如果花蜜和花外蜜是定点供应蜜源的话,那么由刺吸式昆虫取食后分泌

的蜜露则广泛零星散布在植物世界的各个角落,为节肢动物天敌提供了丰富的蜜源食物。

1.1 花蜜

花蜜由花内蜜腺分泌。植物开花时韧皮部筛管把汁液运送到蜜腺特化薄壁组织中,汁液经过细胞内酶的作用,发生了一系列变化而形成花蜜。花内蜜腺分泌的花蜜中糖分含量高,主要为蔗糖和己糖 (葡萄糖和果糖)。在 20 世纪初,花蜜最先以蔗糖和己糖的数量比率进行分类, Percival (1961) 对 889 种植物花蜜分析后,依据含量比重的不同,将花蜜分为三大类: (1) 蔗糖为主; (2) 蔗糖、葡萄糖、果糖含量均衡; (3) 己糖 (葡萄糖和果糖) 为主。除了蔗糖、葡萄糖和果糖等主要成分外,有些花蜜中还含有半乳糖、甘露糖、鼠李糖、麦芽糖等 (表 1)。此外,氨基酸也普遍存在于花蜜,但是含量很少,一般只占干重的 0.3% (Heinrich, 1975; Baker and Baker, 1977)。同一种花蜜内含有的氨基酸种类往往是稳定的,但是浓度波动很大 (Gardener and Gillman, 2001)。节肢动物天敌能够取食花蜜 (Lundgren, 2009),但天敌能否成功获得花蜜还与花的结构 (Patt *et al.*, 1997)、颜色 (Begum *et al.*, 2004)、花期 (Segoli and Rosenheim, 2013) 和花蜜气味 (Nicolson and Thornburg, 2007) 等有关。

表 1 花蜜、花外蜜和蜜露中糖分组分比较
Table 1 Comparison of sugar components in floral nectar, extrafloral nectar and honeydews

	花蜜 Nectar	花外蜜 Extrafloral nectar	蜜露 Honeydew
单糖 Monosaccharides			
葡萄糖 Glucose	+ 6, 9, 12, 13, 14	+ 1, 4, 14	+ 5, 7, 8, 10, 11
果糖 Fructoses	+ 6, 9, 12, 13, 14	+ 1, 4, 14	+ 5, 7, 8, 10, 11
半乳糖 Galactose	—	—	+ 10
甘露糖 Mannose	+ 14	—	+ 10
鼠李糖 Rhamnose	—	+ 3	+ 10
二糖 Disaccharides			
蔗糖 Sucroses	+ 6, 9, 12, 13, 14	+ 1, 3, 4, 14	+ 5, 7, 8, 11
海藻糖 Trehalose	+ 14	—	+ 8, 10
麦芽糖 Maltose	+ 13	+ 4	+ 10, 11, 8
蜜二糖 Melibiose	+ 6, 13	—	+ 10
乳糖 Lactose	+ 13	+ 2	—
三糖 Trisaccharides			
蜜三糖 Raffinose	+ 14	+ 1, 3, 4	+ 5, 10
松三糖 Melezitose	—	+ 2	+ 5, 7, 8, 10
吡喃葡萄糖基蔗糖 Erlase	—	—	+ 8, 10

数据出处 Data source: ¹Baskin and Bliss (1969); ²Beattie (1985); ³Bentley (1977); ⁴Bowden (1970); ⁵Byrne *et al.* (2003); ⁶Churchill and Christensen (1970); ⁷Costa *et al.* (1999); ⁸Fischer and Shingleton (2001); ⁹Galletto and Bernardello (2004); ¹⁰Holldobler and Wilson (1990); ¹¹Irvin *et al.* (2007); ¹²Kaczorowski *et al.* (2005); ¹³Petanidou (2005); ¹⁴Watt *et al.* (1974)。

1.2 花外蜜

花外蜜由花外蜜腺分泌,主要成分与花蜜相似,也以葡萄糖、果糖和蔗糖为主。同一种植物的花外蜜中总糖度的变化明显高于花蜜中的,并受蜜腺周围环境的影响,在潮湿的气候下总糖含量只有5%~10%(重量百分比),而在干热的气候下常常超过50%(Lundgren, 2009)。同时,Baker等(1978)比较了33种植物的花外蜜和248种植物花蜜的氨基酸组分,发现花外蜜中的非蛋白质氨基酸的平均种类数显著高于花蜜中的非蛋白质氨基酸的平均种类数。

相对于花蜜,花外蜜腺多分布于植物器官上(叶、茎、苞片、果实),且可稳定存在,因而更易被天敌昆虫获得(Koptur, 2005; Wäckers, 2005)。矢车菊 *Centaurea cyanus* 开花前两周,位于花萼的蜜腺就开始分泌花外蜜,而且在整个花期中,花外蜜腺会持续分泌花外蜜(Géneau *et al.*, 2013)。因此,花外蜜以存在时间长、容易被取食等特点可以作为适宜的非猎物性蜜源食物(Röse *et al.*, 2006; Géneau *et al.*, 2013; Jamont *et al.*, 2013)。现已报道的花外蜜腺植物有109科702属约3766种(Elias, 1983)。不同地区花外蜜腺植物丰富度不同,总体上看,热带地区比温带地区拥有更丰富的花外蜜腺植物(Bentley, 1977; Oliveira and Freitas, 2004),然而也有研究发现在热带高海拔地区群落中花外蜜腺植物较稀少(Keeler, 1979)。目前已有文献报道许多节肢动物天敌具有取食花外蜜的行为,包括蜘蛛(Taylor and Foster, 1996)、捕食螨(Pemberton, 1993)、草蛉(Limburg and Rosenheim, 2001)、瓢虫(Pemberton and Vandenberg, 1993)、多种寄生蜂(Röse *et al.*, 2006)等。

1.3 昆虫蜜露

蜜露是指半翅目或鳞翅目昆虫分泌的一种含糖液体(Maschwitz *et al.*, 1986; Delabie, 2001)。而一般所说的蜜露是指由半翅目中的胸喙亚目和头喙亚目的昆虫在吸食含高浓度的糖和氨基酸含量的植物韧皮部汁液后,为平衡其自身的营养需要而排出的一些含糖的液体(Wäckers, 2000)。蜜露源于寄主植物韧皮部汁液,其主要成分为蔗糖,且糖分占蜜露干重的80%(Ewart and Metcalf, 1956; Lamb, 1959)。植物汁液在被昆虫吸入后,糖分的种类和相对的量都会在肠道内产生变化。一方面,汁液里的糖会被肠道里的酶水解,比如蔗糖和麦芽糖被分解为葡萄糖和果糖;另一方面,一些复杂的三糖和二糖会在相应细胞中合成,比如松三糖、蜜三糖、吡喃

葡糖基蔗糖和海藻糖等(Hendrix *et al.*, 1992; Völkl *et al.*, 1999)。Hogervorst等(2007)通过比较饲养在土豆 *Solanum tuberosum* 和小麦 *Triticum aestivum* 上3种蚜虫蜜露的化学成分发现,3种蜜露都含有大量的蔗糖及其分解产物葡萄糖和果糖,3种糖占总糖量的74%~89%。同时,通过HPLC测定了大豆蚜虫 *Aphis glycines* 蜜露糖成分,发现其蜜露中寡糖含量依次是蔗糖(26%)、葡萄糖(23%)、果糖(21%)、吡喃葡糖基蔗糖(21%)、麦芽糖(5%)、海藻糖(3%)。

蜜露作为一种广泛分布的蜜源,通常以液滴和薄膜的形式存在而被节肢动物广泛利用。调查发现,在生物多样性丰富的巴伐利亚森林中有246种昆虫取食过蚜虫蜜露,在缺少花蜜的农业系统中,蜜露已被证实是节肢动物重要的替代糖源(Wäckers, 1994; Lee *et al.*, 2004)。在卷心菜田,80%的粉蝶盘绒茧蜂 *Cotesia glomerata* 和55%的中红侧沟茧蜂 *Microplitis mediator* 曾取食过蜜露(Wäckers and Steppuhn, 2003)。蜜露能够增加天敌的迁徙、搜寻、捕食或寄生能力(Wäckers, 1994)。

2 蜜源食物对天敌寿命和繁殖力的促进作用

蜜源食物对于天敌控害能力的提高具有十分重要的作用(Witting-Bissinger *et al.*, 2008; Sivinski *et al.*, 2011; Díaz *et al.*, 2012; Rosa García and Mifiarro, 2014),主要表现在延长寿命(Williams and Hendrix, 2008)、提高繁殖力(Masetti *et al.*, 2010)、保持繁殖潜能(Balzan and Wäckers, 2013)甚至提高其子代种群的生态适应性(朱平等, 2013b)等方面。蜜源食物对寄生性天敌和捕食性天敌具有同等重要的意义(Lundgren, 2009)。

2.1 对寄生性天敌的作用

寄生蜂取食蜜源食物后最为显著的效果就是延长了成虫的寿命,同时提高繁殖寄生能力;其中寿命最多可延长8.5倍,而繁殖力最高可提高10.5倍(表2)。研究表明荞麦 *Fagopyrum esculentum* 花花蜜能显著延长寄生蜂的寿命;陆地棉 *Gossypium hirsutum* 和矢车菊 *C. cyanus* 的花外蜜也能显著提高寄生蜂的寿命和繁殖力。一些种类的蚜虫蜜露能显著提高寄生蜂的寿命和繁殖力,但作用较次于花蜜和花外蜜。综合来看,通过蜜源食物延长寄生性天敌寿命和提高繁殖寄生能力,可更有效控制靶标害虫的种群数量(van Rijn and Sabelis, 2005)。

表 2 蜜源食物对寄生性天敌的寿命和繁殖力的影响

Table 2 Effects of sugar-rich foods on longevity and fecundity of parasitoids				
蜜源食物 Sugar-rich foods	寄生性天敌 Parasitoids	天敌寿命 Longevity of parasitoids	天敌繁殖力 Fecundity of parasitoids	参考文献 References
荞麦花蜜 Floral nectar of <i>Fagopyrum esculentum</i>	窗弯尾姬蜂 <i>Diadegma fenestrale</i>	显著延长 Prolonged significantly	—	Géneau <i>et al.</i> , 2012
荞麦花蜜 Floral nectar of <i>F. esculentum</i>	粉蝶盘绒茧蜂 <i>Cotesia glomerata</i>	延长 4 倍 Prolonged by 4 times	—	Lee and Heimpel, 2008
荞麦花蜜 Floral nectar of <i>F. esculentum</i>	赤眼蜂 <i>Trichogramma exiguum</i>	延长 8.4 倍 Prolonged by 8.4 times	提高 6.4 倍 Increased by 6.4 times	Witting-Bissinger <i>et al.</i> , 2008
荞麦花蜜 Floral nectar of <i>F. esculentum</i>	群聚盘绒茧蜂 <i>Cotesia congregata</i>	延长 8.5 倍 Prolonged by 8.5 times	—	Witting-Bissinger <i>et al.</i> , 2008
荞麦花蜜 Floral nectar of <i>F. esculentum</i>	阿维蚜茧蜂 <i>Aphidius ervi</i>	延长 4 ~5 倍 Prolonged by 4 – 5 times	—	Araj <i>et al.</i> , 2006
荞麦花蜜 Floral nectar of <i>F. esculentum</i>	菜蚜大痣细蜂 <i>Dendrocerus aphidum</i>	延长 5 ~6 倍 Prolonged by 5 – 6 times	—	Araj <i>et al.</i> , 2006
荞麦花蜜 Floral nectar of <i>F. esculentum</i>	岛弯尾姬蜂 <i>Diadegma insulare</i>	延长 6 倍 Prolonged by 6 times	—	Lee <i>et al.</i> , 2004
香雪球花蜜 Floral nectar of <i>Lobularia maritime</i>	长绒茧蜂 <i>Dolichogenidea tasmanica</i>	延长 7.1 倍 Prolonged by 7.1 times	提高 7.6 倍 Increased by 7.6 times	Berndt and Wratten, 2005
陆地棉花外蜜 Extrafloral nectar of <i>Gossypium hirsutum</i>	侧沟茧蜂 <i>Microplitis croceipes</i>	—	显著提高 Increased significantly	Stapel <i>et al.</i> , 1997
矢车菊花外蜜 Extrafloral nectar of <i>Centaurea cyanus</i>	中红侧沟茧蜂 <i>Microplitis mediator</i>	延长 6.4 倍 Prolonged by 6.4 times	提高 10.5 倍 Increased by 10.5 times	Géneau <i>et al.</i> , 2012
棉蚜蜜露 <i>Aphis gossypii</i> honeydew	小盾长径蚜茧蜂 <i>Lipolexis scutellaris</i>	—	显著提高 Increased significantly	Singh <i>et al.</i> , 2000
烟粉虱和绣线菊蚜蜜露 Honeydew of <i>Bemisia tabaci</i> and <i>Aphis spiraeicola</i>	丽蚜小蜂 <i>Encarsia formosa</i>	—	显著提高 Increased significantly	Belliure and Michaud, 2001; Burger, 2002
褐飞虱蜜露 <i>Nilaparvata lugens</i> honeydew	稻虱缨小蜂 <i>Anagrus nilaparvatae</i>	延长 1.7 倍 Prolonged by 1.7 times	提高约 2.7 倍 Increased by ca. 2.7 times	郑许松等, 2003
大豆蚜虫蜜露 <i>Aphis glycines</i> honeydew	岛弯尾姬蜂 <i>Diadegma insulare</i>	延长约 3 倍 Prolonged by ca. 3 times	—	Lee <i>et al.</i> , 2004
几种蚜虫蜜露 Honeydew of several aphid species	阿维蚜茧蜂 <i>A. ervi</i>	延长 4 ~8 倍 Prolonged by 4 – 8 times	—	Hogervorst <i>et al.</i> , 2007

—: 文献并没有提供明确的信息 Such information is not available in references. 表 3 和 4 同 The same for Tables 3 and 4.

2.2 对捕食性天敌的作用

花蜜和花外蜜也是捕食性天敌较为容易获得的蜜源,取食花蜜和花外蜜可显著提高其生态适应性,其中寿命最多可延长 7.9 倍,繁殖力可提高 1.7 倍(表 3)。目前,花蜜和花外蜜对捕食性天敌寿命和繁殖力的影响主要集中在田间作物本身蜜腺提供的蜜源对捕食性天敌的研究,如棉花、蚕豆等蜜源植物的花蜜和花外蜜对捕食性天敌寿命和繁殖力都有促进效果。蜜露作为广泛存在的蜜源食物,对延长捕食性天敌寿命、提高繁殖能力也具有积极的作用。同时,捕食性天敌取食蜜露和花蜜能够促进其产卵和幼虫的发育(Lundgren, 2009),对某些天敌还能缩短产卵前期和提高搜索能力(Sheldon and MacLeod, 1971; Schuster and Calderon, 1986),同时可以提高捕食能力(朱平阳等,2013b)。

3 蜜源食物对天敌控害的促进作用

蜜源是大部分节肢动物不可或缺的食物,在农业生态系统中发挥着重要作用,如果能以合适的方式及时提供给天敌,可增强天敌的控害作用,提高生物防治的效果。此外,蜜源食物管理不仅可以提高天敌释放的效果,还能起到对天敌种群的保育作用。目前国际上已经开展了较多蜜源食物应用的研究,主要体现在显花植物的应用(Robinson, 2009; Jacometti *et al.*, 2010; Scheid *et al.*, 2011; Díaz *et al.*, 2012; 朱平阳等,2012; Lu *et al.*, 2014; 陈学新等,2014)和蜜源食物直接投放(Hausmann *et al.*, 2005; Winkler *et al.*, 2006; Evans *et al.*, 2010; Seagraves *et al.*, 2011)这两方面。

表 3 蜜源食物对捕食性天敌寿命和繁殖力的影响

Table 3 Effects of sugar-rich foods on longevity and fecundity of predators

蜜源食物 Sugar-rich foods	捕食性天敌 Predators	天敌寿命 Longevity of predators	天敌繁殖力 Fecundity of predators	参考文献 References
棉花花蜜 Floral nectar of cotton	小花蝽 <i>Orius</i> spp.	—	提高 Increased	Naranjo and Gibson, 1996
香雪球花蜜 Floral nectar of <i>Lobularia maritime</i>	小花蝽 <i>Orius majusculus</i>	延长 2.3 倍 Prolonged by 2.3 times	提高 1.7 倍 Increased by 1.7 times	Pumariño and Alomar, 2012
野外花蜜 Nectar in field	瘤蝽 <i>Phymata pennsylvanica</i>	延长 Prolonged	—	Yong, 2003
蓖麻子花蜜 Floral nectar of <i>Ricinus communis</i>	捕食螨 <i>Iphiseius degenerans</i>	延长 7.9 倍 Prolonged by 7.9 times	提高 1.6 倍 Increased by 1.6 times	van Rijn and Tanigoshi, 1999
棉花花外蜜 Extrafloral nectar of cotton	草蛉幼虫 <i>C. plorabunda</i> larvae	延长 Prolonged	—	McEwen <i>et al.</i> , 1993; Limburg and Rosenheim, 2001
蚕豆花外蜜 Extrafloral nectar of <i>Vicia faba</i>	瓢虫 <i>Coleomegilla maculata</i>	延长 1.5 倍 Prolonged by 1.5 times	提高 1.4 倍 Increased by 1.4 times	Lundgren and Seagraves, 2011
蚕豆花外蜜 Extrafloral nectar of <i>Vicia faba</i>	猎蝽 <i>Macrolophus pygmaeus</i>	延长 4 倍 Prolonged by 4 times	提高 1.7 倍 Increased by 1.7 times	Portillo <i>et al.</i> , 2012
褐飞虱蜜露 Honeydew of <i>Nilaparvata lugens</i>	黑肩绿盲蝽 <i>Cyrtorhinus lividipennis</i>	延长 Prolonged	提高 Increased	Matsumura and Suzuki, 1999; 吕仲贤等, 2005
豌豆蚜和麦无网长管蚜蜜露 Honeydew of <i>Acyrtosiphon pisum</i> and <i>Metopolophium dirhodum</i>	黑带食蚜蝇 <i>Episyrphus balteatus</i>	延长 Prolonged	提高 Increased	Budenberg and Powell, 1992
蜜露 Honeydew	斯氏钝绥螨 <i>Amblyseius swirskii</i>	延长 Prolonged	提高 Increased	Ragusa and Swirski, 1977; Zhimo and McMurtry, 1990; Bruce-Oliver <i>et al.</i> , 1996; Nomikou <i>et al.</i> , 2003

3.1 显花植物的应用

显花植物可以通过花蜜补充天敌的非猎物性营养源和为天敌提供栖息地,提高寄生蜂对害虫的寄生率,抑制靶标害虫的种群密度,从而提高天敌的控害作用(Gallego, 1983; 朱平阳等, 2012; Lu *et al.*, 2014)。早在 1958 年,在果园中种植钟穗花属 *Phacelia* 和刺芹属 *Eryngium* 显花植物提高了天敌对蚜虫的寄生率(Powell, 1986)。甘蔗田中利索寄蝇 *Lixophaga sphenophori* 在取食大戟科植物 *Euphorbia geniculata* 花蜜后提高了其对几内亚甘蔗象 *Rhabdoscelus obscurus* 的寄生率(Topham and Beardsley, 1973)。而在燕麦田中间作蚕豆 *Vicia faba* 同样可以提高寄生蜂对禾谷缢管蚜的寄生率(Helenius, 1990)。在马铃薯田种植琉璃苣 *Borago officinalis* 提高了跳小蜂 *Copidosoma koehleri* 对马铃薯块茎蛾 *Phthorimaea operulella* 的寄生率,而且靠近蜜源植物的土豆植株上马铃薯块茎蛾幼虫的被寄生率显著高于离蜜源植物 20 m 以外土豆植株上的幼虫(Baggen and Gurr, 1998; Gurr *et al.*, 1998)。在棕榈林中种植毛蔓豆 *Calopogonium* 和距瓣豆 *Centrosema* 属的显花植物可以提高多种寄生蜂对椰子缢胸叶甲 *Promecotheca cumingii* 的寄生率,并能显

著抑制靶标害虫的种群数量(Gallego, 1983)。在葡萄园中种植荞麦提供天敌食物和庇护所,并结合喷洒水杨酸甲酯(MeSA)和邻苯甲酸甲酯(MeA)以吸引天敌,有效提高了园区内捕食性蓟马和姬小蜂的数量(Simpson *et al.*, 2011)。芝麻花可以延长稻虱缨小蜂 *Anagrus nilaparvatae* 的寿命和提高缨小蜂的功能,在稻田田埂上种植芝麻可以提高稻虱缨小蜂的数量,从而有效地控制了稻飞虱种群(Zhu *et al.*, 2013a; Lu *et al.*, 2014)。

3.2 蜜源食物的投放

另一个常见的把蜜源食物应用于农田生态系统的策略是蜜源食物的直接投放。蜜源食物的直接投放多以直接喷洒蔗糖为主,同时也可辅以酵母或色氨酸等联合投放以提高效果(表 4)。与种植显花植物相比,蜜源食物直接投放更为简便,且可以根据大田实际情况自由控制投放时间,更可以与蜜源植物联合应用帮助度过蜜源植物的无蜜期。研究表明,在多种农田系统中,蜜源食物直接投放可以提高天敌数量,提高控害效果。目前蜜源食物直接投放应用最多的是在紫花苜蓿、玉米和棉花上,投放相应蜜源食物可以提高靶标天敌的数量和繁殖力,从而降低靶标害虫种群的密度,减轻作物的被害程度(表 4)。

表 4 投放蜜源食物成功控制害虫的实例

Table 4 Successful cases of supplying sugar-rich foods in insect pest management

作物 Crops	投放的蜜源食物 Sugar-rich foods supplied	靶标天敌 Target natural enemies	天敌数量 Population of natural enemy	天敌繁殖力 Fecundity of natural enemy	靶标害虫 Target pests	害虫种群密度 Pest density	作物被危害程度 Plant damage	参考文献 References
紫花苜蓿 Alfalfa	蔗糖 Sucrose	草蛉 <i>Chrysoperla carnea</i> ; 苜蓿叶象甲姬蜂 <i>Bathyplectes curculionis</i>	增加 Increased	提高 Improved	豌豆蚜 <i>Acyrtosiphon pisum</i> ; 苜蓿叶象甲 <i>Hypera postica</i>	-	-	Carlson and Chiang, 1973; Evans and Swallow, 1993; Evans and England, 1996; Canas and O'Neil, 1998; Jacob and Evans, 1998
苹果 Apple	蔗糖 Sucrose	捕食性天敌 Predators	没有影响 No effect	没有影响 No effect	-	-	减小 Reduced	Hagley and Simpson, 1981
玉米 Corn	蔗糖 Sucrose	草蛉、瓢虫类等捕食性天敌 Predators, including <i>C. carnea</i> and coccinellids	增加 Increased	仅草蛉提高 Only <i>C. carnea</i> improved	玉米螟 <i>Ostrinia nubilalis</i> ; 草地贪夜蛾 <i>Spodoptera frugiperda</i>	降低 Decreased	减小 Reduced	Carlson and Chiang, 1973; Canas and O'Neil, 1998;
棉花 Cotton	蔗糖 + 酵母蛋白 Sucrose + yeast hydrolysate	草蛉等捕食性天敌 Predators, including <i>C. carnea</i>	增加 Increased	提高 Improved	实夜蛾亚科 <i>Heliothine</i> moths; 棉蚜 <i>Aphis gossypii</i>	降低 Decreased	减小 Reduced	Hagen <i>et al.</i> , 1970, 1976; Slosser <i>et al.</i> , 2000
橡树枫树林 Oak-maple forest	蔗糖 Sucrose	蚂蚁 Ants	增加 Increased	-	舞毒蛾 <i>Lymantria dispar</i>	降低 Decreased	-	Weseloh, 1993
橄榄树 Olive tree	蔗糖 + 啤酒酵母 + 色氨酸 Sucrose + Brewer's yeast + tryptophan	草蛉 <i>C. carnea</i>	增加 Increased	-	油橄榄巢蛾 <i>Pray solae</i>	降低 Decreased	减小 Reduced	Liber and Niccoli, 1988; McEwen <i>et al.</i> , 1994
辣椒 Pepper	乳清酵母 + 酵母混合物 + 糖 Wheat + yeast hydrolysate + sugar	草蛉 <i>C. carnea</i>	增加 Increased	提高 Improved	桃蚜 <i>Myzus persicae</i>	降低 Decreased	-	Hagen and Hale, 1974
马铃薯 Potato	蜂蜜 + 乳清酵母 + 糖浆 Honey + wheat + molassess	草蛉 <i>C. carnea</i> ; 瓢虫 Coccinellids	增加 Increased	提高 Improved	桃蚜 <i>M. persicae</i>	降低 Decreased	-	Ben and Bishop, 1976
小麦 Wheat	槐花蜂蜜 Acacia honey	捕食性天敌 Predators	增加 Increased	-	玉米蚜 <i>Rhopalosiphum maidis</i>	没有影响 No effect	-	Monstad and Toft, 1999

虽然有大量蜜源食物投放成功应用的例子,但是在实际生产中也有一些蜜源食物投放的应用未能收到预期的效果(Lundgren, 2009)。蜜源食物投放对鳞翅目害虫种群增长的风险性可能是造成应用失败的原因之一,因为鳞翅目害虫同样可以取食投放的蜜源食物从而提高生态适应性。因此,虽然蜜源食物投放简便易行,但在应用之前应掌握其投放风险,同时考虑蜜源食物投放成本、成效以及投放后对环境的影响。

4 小结与展望

随着人们对生活品质要求的提高,绿色农业和有机农业已成为今后的发展趋势。如何提高农田自身生态系统的控害功能、减少化学农药的使用一直是研究的热点(陈学新等, 2014)。目前我国在蜜源食物的应用上已取得一定进展,主要体现在蜜源植物的间种套作,如在水稻田田埂种植芝麻(朱平阳等, 2012)、果园套种不同显花植物(油菜)(丁瑞丰等, 2008)等。我国蜜源食物在农田系统的应用尚处于起步阶段,仍须多借鉴国外的经验,同时应该进一步开展相关研究,以提高蜜源食物的利用率及丰富蜜源食物的利用方式,完善害虫生态防控的技术体系,支撑我国农业的可持续发展。

4.1 筛选适宜的蜜源植物

筛选适宜的蜜源植物是提高天敌控害功能的基础工作之一。值得注意的是并不是所有蜜源植物都对天敌具有促进作用,有些甚至具有不利的影响。如转雪花莲凝集素(*Galanthus nivalis* agglutinin, GNA)基因作物的花蜜中会分泌GNA蛋白,而取食GNA蛋白对多种天敌包括草蛉*C. carnea*、二星瓢虫*Adalia bipunctata*、七星瓢虫*Coccinella septempunctata*等都具有不利的作用(Hogervorst *et al.* 2006; Lawo and Romeis, 2008; Li and Romeis, 2009)。同时花蜜作为天敌合适的蜜源食物来源也可能给害虫提供适宜的食物,恶化潜在的害虫问题。大部分的鳞翅目害虫成虫也能取食花蜜(Kevan and Baker, 1983),田间所提供的蜜源食物可能增加害虫的寿命和产卵率(Wäckers *et al.*, 2007)。挖掘并明确既能提高天敌的控害功能,同时又不会增强害虫适应性的蜜源植物是田间应用的关键。目前已有许多蜜源植物筛选的研究,如在对荞麦*F. esculentum*、箭筈豌豆*V. sativa*、矢车菊*C. cyanus*、大阿米芹*Ammi majus*和蜂室花*Iberis amara* 5种蜜源植物筛选中发

现,荞麦、箭筈豌豆和矢车菊可以显著提高中红侧沟茧蜂的寿命和寄生力,但没有促进甘蓝夜蛾*Mamestra brassicae*的寿命和产卵。因此,荞麦、箭筈豌豆和矢车菊适合作为蜜源植物应用于甘蓝夜蛾发生的田间(Géneau *et al.*, 2012)。芝麻花可以显著地延长螟黄赤眼蜂*Trichogramma japonicum*、稻虱缨小蜂*A. nilaparvatae*、二化螟盘绒茧蜂*Cotesia chilonis*和螟蛉绒茧蜂*Apanteles ruficrus*成虫的寿命,并提高螟黄赤眼蜂和稻虱缨小蜂的寄生力,但是芝麻花并不会增强稻田主要鳞翅目害虫二化螟*Chilo suppressalis*、大螟*Sesamia inferens*和稻纵卷叶螟*Cnaphalocrocis medinalis*的寿命和繁殖力(Zhu *et al.*, 2013a; 吕仲贤等,未发表数据),因此十分适合在稻田系统中应用。然而,目前国内已验证可应用的蜜源植物资源十分有限,更多的筛选工作值得进一步开展。

4.2 蜜源食物中糖成分作用分析

同一天敌取食不同蜜源食物后却往往表现出不同的效果(Lee *et al.*, 2004),开展蜜源食物中糖成分的深入研究分析,将有助于探明害虫及其天敌对蜜源中不同糖成分的选择和利用,筛选出利于天敌而无益于害虫的关键糖。前人研究表明寄生蜂在合适的糖上即使只有一次取食就能显著延长寄生蜂的寿命(Hausmann *et al.*, 2005),很多天敌和害虫都会对蔗糖、葡萄糖、果糖有积极的味觉反应(Wäckers, 1999; Winkler *et al.*, 2005),并能促进其生态适应性(Wäckers *et al.*, 2007)。然而,目前对于蜜源食物中其他寡糖和其他成分(氨基酸等)对于天敌和害虫影响的研究开展得较少。Winkler等(2005)对花蜜和蜜露中常见糖的研究发现海藻糖、蜜二糖和麦芽糖对半闭弯姬蜂的寿命具有延长效果,而棉子糖、蜜二糖、松三糖和麦芽糖能延长小菜蛾的寿命,其结果表明害虫和天敌所利用的寡糖具有一定的区别。进一步开展相关研究阐明天敌和害虫对糖利用的差异性将有助于蜜源食物合理高效的应用。

4.3 天敌对蜜源食物的搜索和定位

昆虫天敌和蜜源食物在长期的自然演化中会形成相互的适应机制,天敌对花蜜的探索已经有很多的研究,如天敌可以通过颜色(Begum *et al.*, 2004)、形状(Patt *et al.*, 1997)、形态(Gumbert, 2000)、气味(Nicolson and Thornburg, 2007)等辨别花朵以获得蜜源,蜜源植物也可以通过提供花蜜和花外蜜吸引天敌(Wäckers and Bonifay, 2004)。蜜露的挥发性物质能够帮助天敌定位寄主,由于蜜露一般是由

半翅目的害虫分泌, 寄生蜂在定位蜜露的同时会搜寻到寄主, 使其节约了寄主及食物搜寻上的时间和能量 (Wäckers, 2005); 蜜源植物在遭受植食性害虫危害后, 通过调节自身的生理生化变化, 释放次生挥发性化学物质以引诱害虫天敌。目前天敌对蜜源食物的搜索和定位的研究主要集中在蜜源食物的挥发物对于天敌的引诱作用, 而对于其他因素对天敌的吸引作用则很少涉及, 尤其是视觉颜色 (蜜源植物的颜色) 对于天敌昆虫的吸引是非常重要的因素 (Begum *et al.*, 2004)。进一步开展不同天敌在视觉和味觉方面对蜜源食物搜索过程中主导作用的研究将有助于针对不同农田生境应用不同的蜜源食物, 提高蜜源食物对天敌的促进作用。

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