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扶桑绵粉蚧与长角立毛蚁的互惠关系及其对寄主棉花叶片叶绿素荧光特性的影响

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摘要:【背景】草食动物对寄主植物的取食或损伤会诱导改变植物的光合作用,从而直接影响植株的健康生长。产蜜昆虫与蚂蚁的互惠关系是物种相互促进的一种重要的生态学现象,能够促进产蜜昆虫的种群数量,然而这种互惠关系及其对寄主植物光合生理的影响还知之甚少。【方法】在室内条件下,运用叶绿素荧光动力学技术研究了外来入侵害虫扶桑绵粉蚧与长角立毛蚁的互惠对寄主棉花叶片叶绿素荧光特性的影响。【结果】随着扶桑绵粉蚧危害时间的延续,寄主植物上蚂蚁和扶桑绵粉蚧的数量均呈现显著上升的趋势,而在危害后期,蚂蚁存在情况下扶桑绵粉蚧的数量要明显低于无蚂蚁处理;在扶桑绵粉蚧取食寄主棉花 20 d 后,有、无蚂蚁存在的棉花叶片的光合利用率 α 值较无虫处理分别下降了 53.5%和37.0%;存在蚂蚁或扶桑绵粉蚧危害后期对棉花叶片最大相对电子传递效率 $rETR_{max}$ 有显著影响,然而扶桑绵粉蚧单独取食或与蚂蚁互作的情况下未显著影响棉花叶片对强光的耐受能力(E_k)。【结论与意义】研究明确了扶桑绵粉蚧与长角立毛蚁的互惠关系对寄主棉花叶片的光合生理产生了一定的负面效应,为进一步解释扶桑绵粉蚧入侵、扩散及暴发的生态学过程提供了科学依据。

关键词: 互惠; 光合活性; 快速光曲线; 扶桑绵粉蚧; 长角立毛蚁; 生物入侵

Mutualistic interaction between *Phenacoccus solenopsis* and tending ant *Paratrechina longcornis* and their effects on chlorophyll fluorescence in cotton leaves

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Abstract:【Background】Herbivore injury has a direct effect on the growth and performance of host plants through photosynthetic suppression. However, changes in the photosynthetic activity of host plants affected by mutualism between honeydew-producing hemipterans and tending ants remain poorly understood.【Method】The effects of interaction between an invasive mealybug *Phenacoccus solenopsis* and its tending ant *Paratrechina longicornis* on chlorophyll characteristics of infested cotton *Gossypium hirsutum* leaves were observed through a chlorophyll fluorescence measurement system under greenhouse conditions.【Result】*P. longicornis* numbers increased with *P. solenopsis* numbers. However, over time, plants infested with had a lower number of mealybugs than uninfested plants. Changes in light utilization efficiency were induced by *P.solenopsis* feeding of infested cotton leaves. After *P.solenopsis* feeding injury for 20 d, the light utilization efficiency compared with the control was reduced by 37.0% and 53.5% for without- and with-ant treatments, respectively. Changes in maximum relative electron transport rate were also induced by *P.solenopsis* feeding injury, and the influence was more obvious after 20 d or with tending ant infestation. However, the light saturation coefficient describing the resistant capacity of a sample to glare was not influenced by *P.solenopsis* with or without ants.【Conclusion and significance】The interactions between *P.solenopsis* and *P.longicornis* and their negative effects on the photosynthetic activity of cotton leaves could have been caused by *P.solenopsis* feeding rate by *P.longicornis*.

Key words: mutualistic interaction; photosynthetic activity; rapid light curves; *Phenacoccus solenopsis*; *Paratrechina longicornis*; biological invasion

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互惠关系(Mutualism)是物种相互促进的一种重要生态学现象,是物种多样性、生态系统结构与功能得以维持的重要机制(Bronstein,1994)。蚂蚁与产蜜半翅目昆虫(Honeydew-producing hemipterans)的互惠是动物界中的经典例子,也是近年研究的热点问题之一(Grinath *et al*.,2012; Kaplan & Eubanks,2005; Tena *et al*.,2013; Way,1963; Wimp & Whitham,2001)。二者互惠对寄主植物的生理生长也具有深远影响(Styrsky & Eubanks,2007),如蚂蚁取食产蜜半翅目昆虫排放的蜜露,同时也保护后者免受天敌伤害(Huang *et al*.,2011; Zhou *et al*.,2013),并且通过刺激产蜜半翅目昆虫的取食率、繁殖力和扩散力从而加重对寄主植物的危害(Stadler & Dixon,1998; Yao *et al*.,2000; Yao & Akimoto,2002),在此过程中蚂蚁也会对植物上其他为害的食草动物进行捕食或驱赶(Buckley,1987; Delabie,2001; Way & Khoo,1992)。

扶桑绵粉蚧 *Phenacoccus solenopsis* Tinsley 属半翅目 Hemiptera 粉蚧科 Pseudococcidae(Cockerell,1902),是一种典型的产蜜半翅目昆虫,通过刺吸取食和排泄蜜露对大田作物、园林观赏植物、果树和蔬菜等经济作物造成严重危害,且极易随人为活动而远距离快速扩散传播(武三安和张润志,2009)。该虫原产于北美,最初被发现于美国新墨西哥州的热带火蚁 *Solenopsis geminata* (Fabricius)的蚁巢内(Tinsley,1898),该粉蚧较容易与蚂蚁如入侵性红火蚁 *Solenopsis invicta* Buren(Zhou *et al*.,2012)和双针棱胸切叶蚁 *Pristomyrmex pungens* Mayr(Huang *et al*.,2012)形成互惠关系。目前关于扶桑绵粉蚧与蚂蚁的互惠对寄主植物光合生理的影响等方面还知之甚少。

光合作用为植物生长提供所需能量和同化物,是植物生理学研究的核心(Lawlor,2009)。而草食动物对植物的取食或损伤会导致对后者光合生理产生直接影响(Kempema *et al*.,2007; Nabity *et al*.,2009; Samsone *et al*.,2012)。叶绿素是一类与光合作用有关的最重要色素,是影响光合作用的物质基础(Krause & Weis,1991)。由于活体叶绿素具有荧光现象,因此通过叶绿素荧光动力学技术(Chlorophyll fluorescence kinetics technique)能测定叶片光合作用过程中光系统对光能的吸收、传递、耗散、分配等(Ni *et al*.,2009)。该技术具有快速、灵敏且对植株不造成损伤的特点,已开始应用于昆虫学领域。通过对叶绿素荧光动力学参数的测定和分析,发现俄罗斯小麦蚜虫 *Diuraphis noxia* (Kurdjumov)(Burd & Elliott,1996)、二斑叶螨 *Tetranychus urticae* (Koch)(Bounfour *et al*.,2002; Iatrou *et al*.,1995)、松大锯角叶蜂 *Diprion pini* L.(Schroder *et al*.,2005)、一种蜡蚧 *Coccus* sp.(Retuerto *et al*.,2004)等通过取食诱导寄主植物光合生理发生改变。Huang *et al*.(2013)应用该技术测定了不同密度扶桑绵粉蚧危害下番茄叶片的光合活性,结果表明,该粉蚧初始高密度处理 38 d 后,番茄 *Solanum lycopersicum* L.叶片的相对叶绿素含量和光合利用效率分别下降了 57.3%和 42.4%,最大相对电子传递速率和光饱和参数分别下降了 82.0%和 69.7%。本试验以扶桑绵粉蚧、长角立毛蚁 *Paratrechina longicornis* (Latreille)和棉花 *Gossypium hirsutum* L.为试材,利用叶绿素荧光动力学技术及快速光曲线的测定与分析方法,明确扶桑绵粉蚧的危害是否会影响棉花叶片叶绿素荧光特性,以及蚁—蚧互惠对棉花叶片光合生理活性的影响,为进一步解释扶桑绵粉蚧入侵、扩散及暴发的生态学过程提供科学依据。

1　材料与方法

1.1　供试植物

盆栽棉花:浙棉 607。棉花栽种于装有灭菌泥炭土的塑料盆(上口径 16 cm)内,放置在温室大棚内,温度(30±2)℃,相对湿度(75±5)% RH,水肥按常规管理,待植株长至 6~8 片叶展开时供试。

1.2　供试昆虫

扶桑绵粉蚧于 2011 年 8 月采自浙江省杭州市萧山区市郊的大花马齿苋 *Portulaca grandiflora* (Hook)上,室内以盆栽棉花为寄主饲养继代至今。供试虫态为 3 龄若虫,虫体从室内饲养种群中随机挑取,用毛笔将其小心转移至供试棉花上。

供试蚂蚁为长角立毛蚁,蚂蚁种类鉴定参照《广西蚂蚁》(周善义,2001)和《中国蚂蚁》(吴坚和王常禄,1995)。该种蚂蚁在温室大棚内外的大花马齿苋、夏堇 *Torenia fournieri* L.、番茄、辣椒 *Capsicum annuum* L.、牛筋草 *Eleusine indica* Gaertn.上广泛存在,并且在植株上有扶桑绵粉蚧的地方活动更为频繁。

1.3 试验设计

挑选 15 盆生长状况一致的棉花植株,随机分成 3 组并搭配不同处理:(1)扶桑绵粉蚧+长角立毛蚁;(2)单独存在的扶桑绵粉蚧;(3)无虫害植株。扶桑绵粉蚧的初始虫量为 15 头 · 株$^{-1}$,每个处理重复 5 次。试验前,对供试植株进行仔细检查,在确保无其他节肢动物存在的情况下,放入蚂蚁活动范围内。通过装满水的瓷盘(60 cm×45 cm×5 cm)隔绝蚂蚁访问植株,将砖块(25 cm×10 cm×5 cm)堆放在瓷盘中间,植株放置在砖块上,每天往瓷盘里添加水。分别在 0、5、10、15、20 d 进行棉花叶片叶绿素荧光参数的测定,测试叶片在植株上部叶片中随机挑取;0、10、20 d 测定前还需分别统计植株上扶桑绵粉蚧和长角立毛蚁的数量。

1.4 叶绿素荧光参数测定

通过 PAM-2500 型便携式调制叶绿素荧光仪(Walz 公司,德国)连体测定棉花叶片的快速光曲线。使用叶夹 2030-B 直接进行测定,光化光强度梯度及持续时间按操作手册说明设置。测定最终得到 *ETR*(光合电子传递速率)随 *PAR*(光合有效辐射)的变化图,即为光响应曲线,并采用 Platt *et al*.(1980)方法对快速光曲线进行拟合,拟合公式为 $P = P_m \times (1-e^{-\alpha\times PAR/P_m}) \times e^{-\beta\times PAR/P_m}$,各参数符号和定义如表 1 所示。

表 1 快速光曲线拟合公式中参数符号和定义

Table 1 Parameter abbreviations used in the text

符号 Notation	定义 Definition
P	光合速率 Photosynthetic rate(*rETR*)
P_m	光饱和能力 Photosynthetic capacity at saturation($rETR_{max}$)
α	起始斜率,描述光合利用率 Initial slope: describes the light utilization efficiency
β	光抑制参数 Photoinhibition parameter
$E_k = P_m/\alpha$	光饱和参数,描述一个样本对闪光的抵抗能力 Light-saturation parameter: describes the resistant capacity of a sample to glare
ETR_m	快速光曲线中的最大相对电子传递效率(无量纲) Maximum relative electron transport rate in a RLC (dimensionless)
PAR	光合有效辐射 Photosynthetic active radiation

1.5 数据分析

采用单因素方差分析比较扶桑绵粉蚧不同危害时间下植株上访问蚂蚁的数量;重复测量方差分析比较扶桑绵粉蚧危害过程中有、无蚂蚁存在的情况下粉蚧数量的差异性,以及比较扶桑绵粉蚧不同危害时间下各处理之间叶绿素荧光参数的差异性,Tukey 检验比较区分各处理间的差异显著性。所有数据采用 SPSS 14.0 软件进行统计分析,Excel 2003 软件作图,数据以平均数±标准误(means±*SE*)表示。

2 结果与分析

在扶桑绵粉蚧的整个危害过程中,有、无蚂蚁存在的处理中扶桑绵粉蚧数量均呈显著上升趋势($F_{2,16} = 329.06$, $P < 0.001$);扶桑绵粉蚧危害 20 d 后,有蚂蚁访问的粉蚧数量(343.6 头 · 株$^{-1}$)约为起始阶段的 22.9 倍,而无蚂蚁访问的情况下,粉蚧数量(499.8 头 · 株$^{-1}$)约为起始阶段的 33.3 倍。有、无蚂蚁处理对扶桑绵粉蚧数量的影响也存在显著差异($F_{1,16} = 7.19$, $P = 0.028$),但是处理和危害时间对粉蚧数量无交互影响($F_{2,16} = 14.38$, $P<0.001$)。随着扶桑绵粉蚧危害时间的延长,访问蚂蚁的数量呈极显著上升趋势($F = 61.80$, $df = 2$, $P < 0.001$)(图 1)。

图 2 和表 2 显示了各处理棉花叶片的叶绿素荧光参数(α, ETR_{max} 和 E_k)随时间的变化情况。结果表明,各处理之间 α 值有显著差异($F_{2,48} = 13.35$, $P<0.001$),然而危害时间($F_{4,48} = 4.45$, $P = 0.0039$)以及二者的交互($F_{8,48} = 4.0013$, $P = 0.0011$)对 α 值无显著影响(图 2A)。处理和危害时间对 ETR_{max} 值均有显著影响(图 2B, $F_{2,48} = 34.24$, $P<0.001$; $F_{4,48} = 2.57$, $P = 0.04$),然而,二者交互对该值无显著影响($F_{8,48} = 1.79$, $P = 0.10$)。处理和危害时间以及二者的交互对 E_k 值无显著影响(图 2C, $F_{2,48} = 3.55$, $P = 0.061$; $F_{4,48} = 1.059$, $P = 0.39$; $F_{8,48} = 1.47$, $P = 0.19$)。

3 讨论

大量研究表明,互惠能同时促进产蜜半翅目昆虫和访问蚂蚁数量的增长(Eubanks *et al*., 2002; Huang *et al*., 2010; Lach, 2003)。本研究也得到一致结果,即棉花上长角立毛蚁的数量随扶桑绵粉蚧数量的增加而增加;但在扶桑绵粉蚧危害后期,有蚂蚁访问的粉蚧数量要低于无蚂蚁访问,这可能是由于蚂蚁的访问影响了扶桑绵粉蚧个体的存活及

繁殖力。从营养角度考虑,蚂蚁可能更倾向于能排泄大量蜜露的高龄粉蚧个体,由此导致粉蚧个体产卵的延迟,相关研究还有待进一步试验验证。

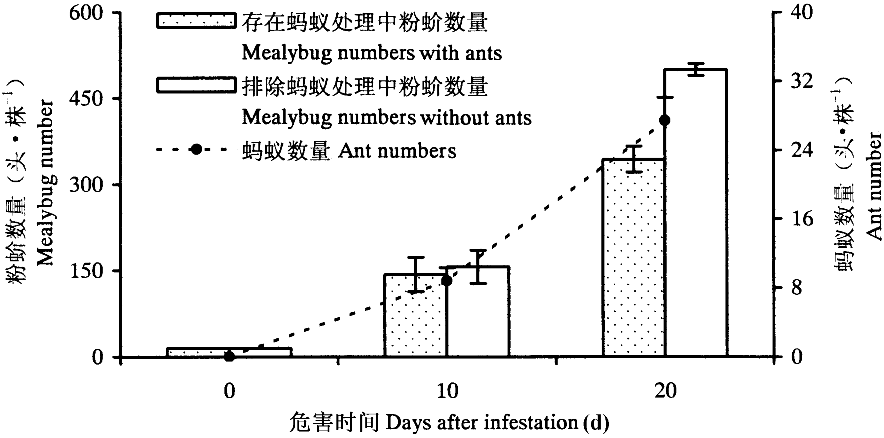

图 1　不同处理、不同危害时间下扶桑绵粉蚧及长角立毛蚁的数量

Fig.1　Mean numbers of *P.longicornis* per plant in the presence of ants, and effects of ant tending by *P.longicornis* on *P.solenopsis* numbers in the with-ants and without-ants treatments

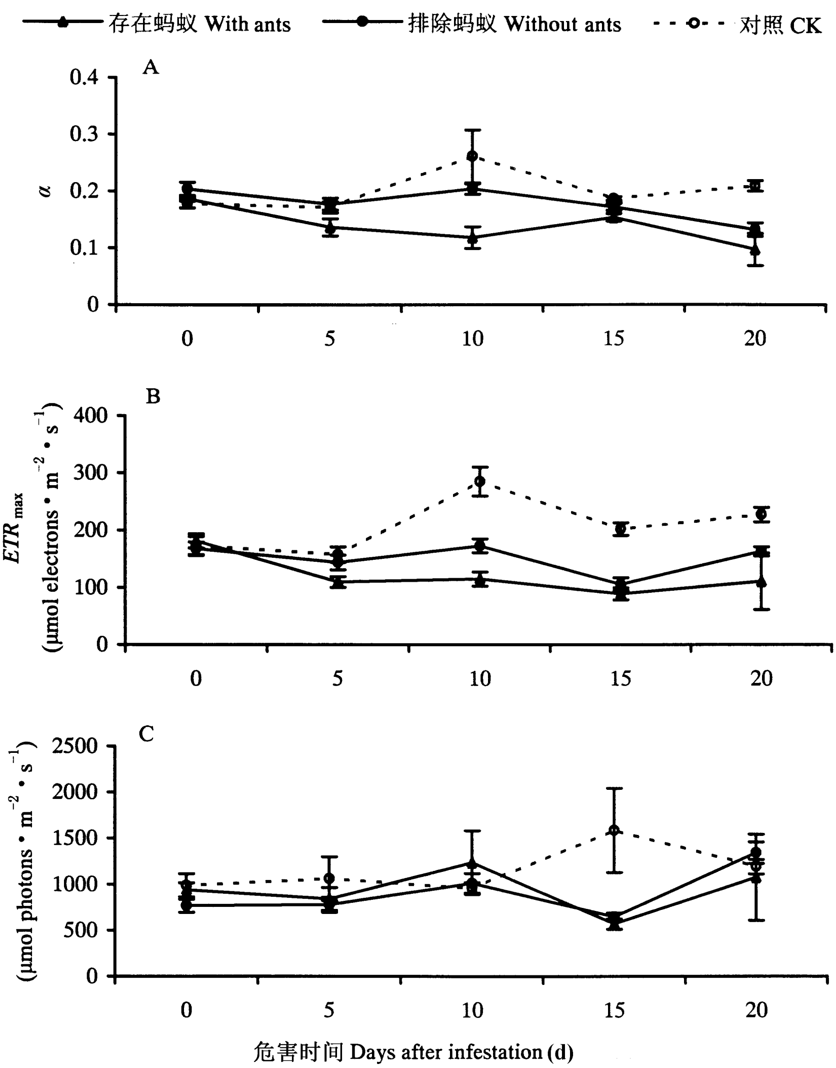

图 2　不同处理棉花叶片的叶绿素荧光参数随扶桑绵粉蚧危害时间的变化趋势

Fig.2　Effects of *P.longicornis* and feeding-injury time on (A) light utilization efficiency (α), (B) maximum relative electron transport rate ($rETR_{max}$), and (C) light saturation coefficient (E_k) of infested cotton leaves

表 2 扶桑绵粉蚧不同危害时间及蚂蚁访问对棉花叶片叶绿素荧光参数(α,ETR_{max}和 E_k)的影响

Table 2 Results of repeated measures ANOVA on the effects of *P. longicornis* (Treatment), feeding-injury time (Time), and their interaction on the data of chlorophyll fluorescence parameters (α, ETR_{max}, E_k)

拟合参数 Fitting parameters	因素 Factors	自由度(分子,分母) *df* (numerator, denominator)	均方 Mean squares	*F*	*P*
α	处理 Treatment	2,48	0.025	13.35	<0.001
	时间 Time	4,48	0.0060	4.45	0.0039
	处理×时间 Treatment×time	8,48	0.0054	4.0013	0.0011
ETR_{max}	处理 Treatment	2,48	49830.72	34.24	<0.001
	时间 Time	4,48	9395.82	2.57	0.04
	处理×时间 Treatment×time	8,48	6569.72	1.79	0.10
E_k	处理 Treatment	2,48	464476.73	3.55	0.061
	时间 Time	4,48	270267.01	1.059	0.39
	处理×时间 Treatment×time	8,48	376159.23	1.47	0.19

植物叶片叶绿素荧光特性的测定和分析是植物生理学研究中的一个重要途径。Welter(1989)和Zangerl *et al*.(2002)研究表明,食叶动物的取食会影响未受损叶片的有效量子产率和电子传递速率,但是不会影响最大量子产率。介壳虫的危害使得花叶冬青光合速率显著提高,并且高温和光照会对这种光合补偿效果产生促进作用(Retuerto *et al*., 2004)。扶桑绵粉蚧危害番茄植株 38 d 后,高虫口密度处理下番茄叶片的 α、$rETR_{max}$和 E_k 值分别下降了 42.4%、82.0%和 69.7%(Huang *et al*.,2013)。本研究表明,扶桑绵粉蚧的危害导致棉花叶片的光合利用效率发生了变化,并且其最小值出现在有蚂蚁访问的情况下。例如,在粉蚧危害 20 d 后,无蚂蚁和有蚂蚁处理组的 α 值与对照组相比分别下降了 37.0%和 53.5%。$rETR_{max}$ 的变化同样由扶桑绵粉蚧危害而诱导产生,这种影响在危害后期或在有蚂蚁访问的情况下尤为明显。有研究表明,蚜虫会根据访问蚂蚁的需求而改变自身的取食行为和蜜露排泄量,这或许是蚂蚁与蚜虫互惠诱导寄主植物有机挥发性化合物产生变化的一种机制(Paris *et al*.,2011)。有些蚜虫种类还会根据蚂蚁需求而改变它们排泄蜜露的成分(Yao & Akimoto,2002; Yao *et al*.,2000)。因此,长角立毛蚁也可能通过刺激扶桑绵粉蚧刺探取食而加速影响棉花叶片的部分光合活性,因为蚂蚁访问并未影响叶片的光饱和参数,今后有必要就该方面进行深入研究。

大量事实证明,蚂蚁访问通常会使它们互惠的同伴获益(Stadler & Dixon, 2005)。Daane *et al*. (2007)发现加利福尼亚沿海的葡萄园中,暗色粉蚧 *Pseudococcus viburni* (Signoret)由于受到阿根廷蚁 *Linepithema humile* (Mayr)的悉心照料而使其数量显著上升;在阿根廷蚁存在的情况下,葡萄园中寄生性天敌 *Pseudaphycus flavidulus* (Brèthes)和 *Leptomastix* nr. *epona* (Walker)的数量显著下降。在本研究中,明确了长角立毛蚁和扶桑棉粉蚧的互惠对受危害的棉花叶片的叶绿素荧光特性有负面影响。而且在调查中也发现,蚂蚁存在的受危害叶片比无蚂蚁的受危害叶片凋落得更快。因此,在扶桑绵粉蚧发生区域对蚂蚁进行管理,或许能有效降低粉蚧的暴发。

本研究只考虑了长角立毛蚁和扶桑绵粉蚧同时存在的情况,然而大田情况更为复杂,其他草食动物、产蜜昆虫以及它们的自然天敌的存在,也会对寄主植物造成直接或间接影响。因此,下一步研究还应考虑以上因素,从而综合评价蚁—蚧互惠对寄主植物光合生理活性的影响。

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