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Megachile sculpturalis, the giant resin bee, overcomes the blossom structure of sunn hemp (*Crotalaria juncea*) that impedes pollination

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Abstract. Bee species that are effective pollinators of sunn hemp (*Crotalaria juncea* L.: Fabaceae: Crotalarieae) are few in number because of the large size and papilionaceous structure of the plant's blossom. Seed for this potentially valuable cover crop is largely unavailable due to the paucity of pollinators and to the plant's self-incompatibility. The introduced *Megachile* (*Callomegachile*) *sculpturalis* Smith (Megachilidae: Megachilinae), the giant resin bee, has the anatomy and behavior to be a most effective pollinator. While holding onto the upper vexillum petal of the blossom with her mandibles, this bee has the strength to depress the lower keel causing pollen to be expelled by the style through the small opening at the end. The bee is long enough for its metasoma to extend over the end of the keel, and, as a member of the family Megachilidae, has scopal hairs on the venter of the metasoma, which are thus in an optimal position to contact the pollen. Honey bees (*Apis mellifera* L.: Apidae) are common visitors to sunn hemp flowers but are too small to be effective pollinators. A honey bee worker robs the pollen by inserting her proboscis into the end of the keel and extracting the adhering pollen. Possible problems could result from mutual enhancement of populations of an exotic bee and an exotic plant.

INTRODUCTION

Sunn hemp (*Crotalaria juncea* L.: Fabaceae) is an excellent weed and root-knot nematode suppressive cover crop which can contribute to soil improvement by providing nitrogen and organic matter (Cook & White, 1996; USDA NRCS, 1999; Wang *et al*., 2001; Balkcom & Reeves, 2005; Adler & Chase, 2007; Schomberg *et al*., 2007). This potential has not yet been fully realized in the United States because the seed is imported, resulting in high cost and limited availability. Lack of pollinators is a major impedi-

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ment to seed availability and, hence, to more widespread use of this plant as a cover crop (Free, 1993). Although sunn hemp is dependent on bee pollination, relatively few species of bees have the anatomy and behavior necessary to achieve effective pollination, which is discouraged by the structure of the plant's blossom (Westerkamp, 1997). Even in parts of sunn hemp's native India the plant produces little seed, evidently due to a paucity of effective pollinating bees (Free, 1993).

Sunn hemp has a papilionaceous or "keel" blossom (Westerkamp, 1997), characteristic of many Fabaceae (Fig. 1). The blossom has a large central dorsal "flag", also called "standard" or "banner" petal (vexillum), and two lateral "wing" petals (alae). Two lower additional "keel" petals (carina) join along the top and bottom edges to enclose a cavity around the sporophyll column and tapers as a rostrum with a small opening at the distal end. The column is formed by stamen filaments fused at the base, five with elongate anthers alternating with five with ovate anthers, an androecium enclosing the gynoecium. The uppermost filament is not fused to one of the adjacent filaments, and the groove between widens basally to form a nectar access opening. Nectar collects inside the enlarged base of the column, around the base of the ovary within the column. The pistil has an elongate style with the stigma at the terminus. Pollen released from the anthers is confined by the keel petals. The downward flexing of the keel relative to the vexillum causes the style to extend out of the orifice at the end of the keel and to expel the surrounding pollen.

Weight alone on the keel will only cause the entire blossom, the keel along with the vexillum, to tilt forward, and the style will not extend (Westerkamp, 1997). Effective bee pollinators must be sufficiently strong to depress the keel, while immobilizing the vexillum, and long enough so that their metasomata extend over the end of the keel and come into contact with the pollen pushed out by the style. The keel length is about 1.5 cm. Pollen grains are then transferred to the stigma of other plants exposed the same way.

In India and South America, members of the families Megachilidae and Apidae, particularly large nectar-gathering carpenter bees of the genus *Xylocopa* Latreille, as well as honey bees, *Apis mellifera* L., are the most common visitors to species of *Crotalaria* (Westerkamp, 1997; Purseglove, 1968; Nogueira-Couto *et al.*, 1992; Free, 1993; Etcheverry *et al.*, 2003). Species of *Xylocopa* can depress the keel of sunn hemp to some extent, pushing their heads against the vexillum and inserting their proboscides along the channel at the base of the vexillum, through the nectar access opening and into the nectar reservoir. They have abdominal hairs to which pollen can adhere and can be incidental pollinators of subsequently visited plants. Smaller bees, such as the honey bee, can obtain nectar but are unable to release and come into contact with the pollen and thus are unable to be even incidental pollinators.

The most effective bees would be large megachilid females (Westerkamp, 1997; Etcheverry *et al.*, 2003). Bees of this family have the pollen-collecting and transporting hairs (scopae) on the venter of the metasoma, rather than on the hind legs or propodeum as do most other bees. For those species long enough for their metasomata to extend over the end of the keel of the sunn hemp blossom, the location of the scopae is optimal for gathering pollen as it is released. Species of Megachilidae visiting *C. micans* Link in Argentina, lock their mandibles onto the base of the flag petal and repeatedly depress the keel (Etcheverry *et al.*, 2003). The introduced *Megachile* (*Callomegachile*) *sculpturalis* Smith, the giant resin bee, was first detected in the United Sates in 1994 (Mangum & Brooks, 1997), and has since spread through the eastern states, into the central part of the country, and into Canada (Parys *et al.*, 2015). We first recognized this species in Florida during a bee survey of natural areas (Hall & Ascher, 2010). This

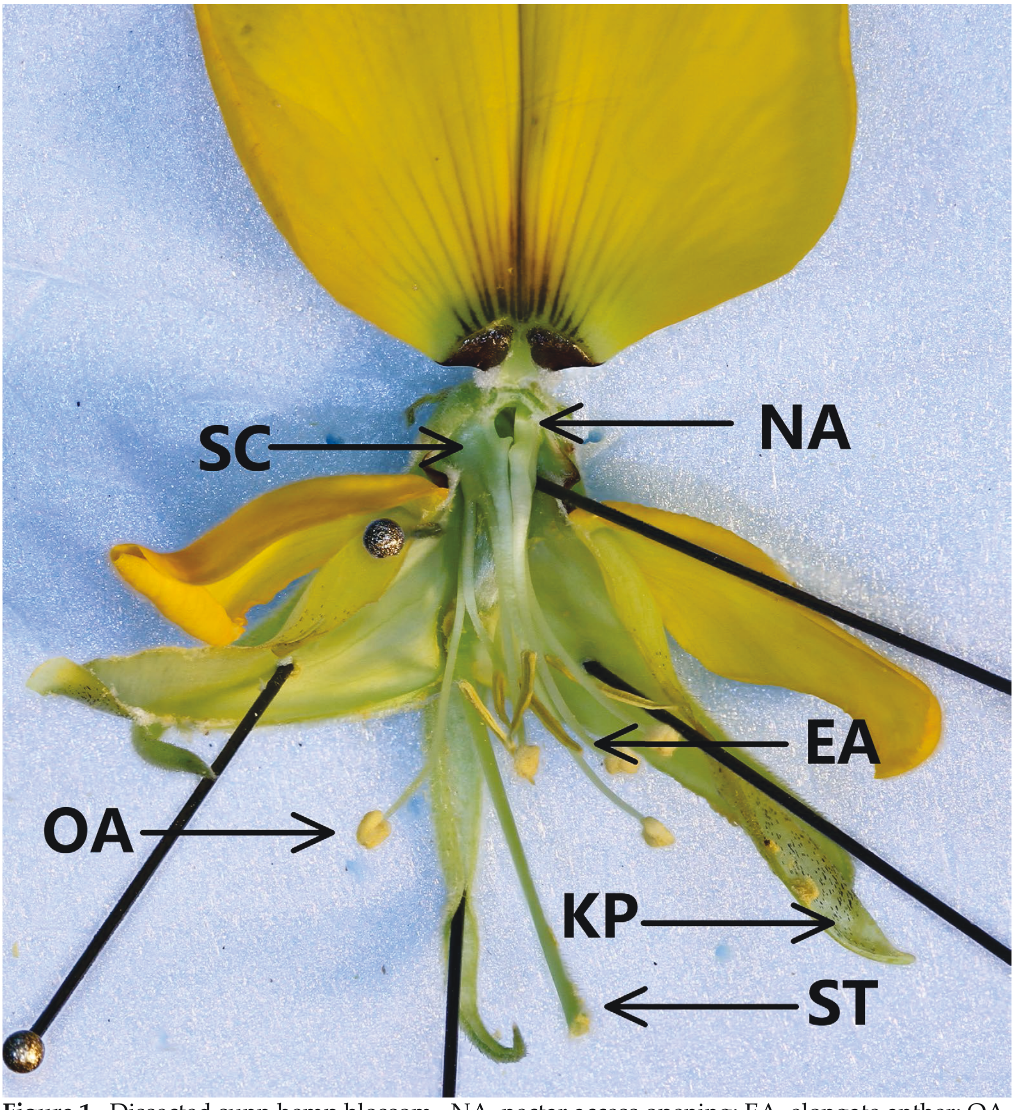

Figure 1. Dissected sunn hemp blossom. NA, nectar access opening; EA, elongate anther; OA, ovate anther; SC, sporophyll column; KP, keel petal; ST, stigma at end of style.

large exotic bee has the size, anatomy, and behavior to be a most effective pollinator of sunn hemp. Images and descriptions of this bee gathering pollen from sunn hemp are presented here, but the amount of seed set resulting from visits by the bee was not determined.

Many species of *Crotalaria* L. are self-pollinated (Koul *et al*., 1983; Etcheverry *et al*., 2003). The flowers' dimorphic anthers dehisce at different times. *Crotalaria micans* has delayed self-compatibility (Etcheverry *et al*., 2003). The first set of elongate anthers dehisce, and the pollen surrounds the stigma. The filaments of a second set of ovate anthers grow and extend past the first set. The stigma becomes receptive after the first set of anthers and before the second set of anthers dehisce. Thus, the flower is initially self-incompatible, and the early pollen is available for out-crossing. It then becomes self-compatible and produces seed from its own pollen. Despite *C. juncea*

Figure 2. Female of *Megachile* (*Callomegachile*) *sculpturalis* Smith on sunn hemp blossom. The bee holds onto the vexillum with her mandibles. Proboscis is not extended into the tongue guide of the vexillum. The style is touching the sternal scopae.

having a similar structure of dimorphic anthers, all anthers dehisce well before the blossom opens, and the stigma, whenever it becomes receptive, is surrounded by pollen from both sets. The plant does not exhibit delayed self-compatibility and requires cross-pollination (Kundu, 1964; Free, 1993). The flower can be cross-pollinated if the metasoma of a visiting insect has pollen from a previous visit to another blossom. However, some investigators report that the plant becomes self-compatible after mechanical stimulation, by brushing the stigma, for example by a bee. Once the stigma has been stimulated, the flower then becomes self-pollinated (Howard *et al*., 1919: *cf*. Free, 1993; Kundu, 1964; Purseglove, 1968).

MATERIAL AND METHODS

Initial observations of *M. sculpturalis* on sunn hemp reported here were made at Rose Koenig's organic farm in Gainesville, Florida (included in bee survey: Hall &

Ascher, 2011), during a USDA SARE project (Southern Region Sustainable Agriculture Research and Education) to investigate accessions of sunn hemp that have the greatest potential as a cover crop in the southeastern USA (Purseglove, 1968; Cook & White, 1996; USDA NRCS, 1999; Schomberg *et al*., 2007). Four faculty members in the University of Florida Department of Horticulture (Carlene Chase, P.I.), investigators in Georgia and Puerto Rico, and H.G.H. were involved in this project in 2008 and 2009 (Cho *et al*., 2010, 2015, 2016). Recently, a smaller plot of sunn hemp was established at a different location in Archer, Florida, from which additional photographs were taken and key bee behavior was observed.

Outdoor bee photographs were taken with a Nikon D50 camera and a Nikkor telephoto or macro lens. Focal plane images of dissected sunn hemp blossoms were obtained by incremental manual focusing of an EFS 60mm macro lens on a Canon 7D camera using two remote 430EXII speedlights. Images were combined with Helicon Focus software.

In late summer and fall 2009, at Rose Koenig's organic farm, we tested whether sunn hemp is self-compatible or incompatible and responds to mechanical stimulation. Unopened inflorescences were covered with mesh bags, preventing insects from accessing flowers, and pollen later transferred by a small artists' paint brush to stigmas. Plants were divided into groups for five treatments: control, no manipulations; keel pulled down so that the style was pushed out and then allowed to retract (without mechanical stimulation of the stigma); keel pulled down so that the style was pushed out, the flower's pollen brushed on the stigma, and then the style allowed to retract (mechanical stimulation of the stigma); pollen of blossoms brushed onto stigmas of others on the same plant; and a mixture of pollen from eight plants, each of a different accession (out-crossing). A total of 39 plants were used for the experiment, 50 racemes (two or three for some plants) with 218 flowers. Ten or more racemes and an average of 55 flowers were used for each of the four treatments. The plants belonged to a total of nine accessions, seven to eight of which were represented among the plants used for each treatment. Accessions come from single plants collected from different locations, each assigned a number. They are propagated in the open, as a group of accession progeny separated at a distance from other accessions, thus largely inbred but subject to some outcrossing.

RESULTS & DISCUSSION

Megachile sculpturalis was an unanticipated visitor to our experimental plots, because we discovered this introduced species first in Florida only a few weeks before, at a location several miles away (Hall & Ascher, 2010). The bee was present during a limited flight period, mainly in June and July. It was not abundant but was present in numbers larger than any other bee, except the honey bee. The bee is large and strong enough to depress the keel of the flower to extrude the style and long enough for the metasoma to contact the pollen pushed out. As a megachilid, the scopal hairs are on the underside of the metasoma, thereby enabling efficient pollen collecting and increasing the likelihood of adhering pollen contacting the stigma of subsequently visited flowers. The observed visits to flowers appeared to be intentionally for pollen collecting. As the bee alights on the front of the blossom, its head is positioned at the base of the vexillum, and, as reported for a *Megachile* (*Pseudocentron*) sp. in Argentina (Etcheverry *et al*., 2003), the mandibles clamp onto the base of the vexillum (Fig. 2). Damage to flower petals from mandibles of *M. sculpturalis* has been observed

Figure 3. Female of *Megachile* (*Callomegachile*) *sculpturalis* Smith on sunn hemp blossom. Keel is held down between the bee's hind legs and directed toward sternal scopal hairs holding pollen. Keels of nearby blossom are more horizontal.

(Mangum & Sumner, 2003). The proboscis is not seen extending into the nectar access opening of the flower, as would be expected if the bee were there to collect nectar. Evidently holding with the mandibles provides the anchor needed to depress the keel with the metasoma and/or the legs. The forelegs and middle legs hold onto the wing petals, and the narrow distal end of the keel is held between the tarsi of the hind legs, thus positioning the extruded pollen directly onto the sternal scopae (Fig. 3). In figure 3, the end of the keel is being held away from the metasoma at that instant, but figure 2 shows it in direct contact with the scopae, which can be seen already to have a large amount of imbedded pollen.

At least one native species of *Megachile* Latreille was seen on sunn hemp at the experimental plots but visited too infrequently and was too small to be an effective pollinator. Small numbers of large carpenter bees, *Xylocopa* (*Xylocopoides*) *virginica* (L.) and *X.* (*Schonnherria*) *micans* Lepeletier, were seen drawing nectar from the flowers and releasing pollen. Honey bees were the most common visitors (colonies were nearby). The foragers were either pollen robbers, a behavior seldom reported in the literature, or nectar robbers. Bees inserted their proboscis into the keel opening to extract pollen (Fig. 4). Pollen was also taken from wilted flowers, made more accessible by separation of the upper edges of the keel petals (Fig. 5). The bees appear to clean their proboscides of pollen grains before visiting additional flowers. Honey bees not collecting pollen were seen pushing their heads up close to the vexillum and extending their proboscides into the channel of the petal. They were behaving as nectar robbers, but we did not determine how successful they were. As with the pollen robbers, they also visited wilted flowers, which, as with the pollen, would make the nectar more accessible.

In past studies evaluating sunn hemp as a cover crop, no seed pods were produced (Mansoer *et al*., 1997: Alabama), or were produced only after hand pollination (Keatinge *et al*., 1998: Brazil), presumably due to the absence of pollinating insects. Whereas in our experimental plots, an average ratio of the number of mature seed pods to the number of flowers was about 60% (Cho *et al*., 2016). The period when pod formation was measured included the short period when *M. sculpturalis* was present, along with *Xylocopa*. Work was not conducted to determine the amount of seed set that could clearly be attributed to each of these different bees. Nevertheless, the much larger number of *M. sculpturalis* and their effective ability collecting pollen suggest that this bee was the major pollinator of the plants. Seed pods were not formed on the many plants visited by abundant numbers of honey bees. Thus, their pollen-robbing behavior results in little or no pollination.

Self-incompatibility of sunn hemp (Kundu, 1964; Koul *et al*., 1983) is apparent from the overall low production of seeds, when few pollinating bees are present, and from our artificial pollination experiments. No seed was produced by flowers from their own pollen or from pollen from other flowers on the same plant, even after mechanical stimulation (brushing) of the stigma. Our results are in contrast to findings by others who have reported that sunn hemp becomes self-compatible after mechanical stimulation by contact with the body of a bee or by a brush, with as much as 18–35% seed set (Howard *et al*., 1919: *cf*. Free, 1993; Kundu, 1964; Purseglove, 1968). Crosses among plants within accessions, using mixtures of pollen from several plants, were made, which resulted in seed pod formation (89% average of number of flowers pollinated) in eight out of nine accessions tested. Even in the presence of bee pollinators, separate plants of highly inbred accessions may not produce seed and may need to be planted together with other accessions to allow cross-pollination.

Megachile sculpturalis pollinating *C. juncea* could result in mutual enhancement of populations of this exotic bee and exotic plant, and activities that encourage population growth of either may not be desirable. Super generalist alien species can reduce native generalist interactions (Aizen *et al*., 2008). The paucity of data regarding the foraging preferences and abundance of this bee makes it impossible, at this time, to pre-

Figure 4. Worker of *Apis mellifera* L. on sunn hemp blossom. Proboscis is inserted into the end of the keel to extract pollen.

dict its effect on the native bee-plant networks. A few studies have listed several plants visited by this bee in the USA and Italy, most of which are of Asian origin (Mangum & Sumner, 2003; Quaranta *et al*., 2014). *Megachile sculpturalis* has been reported to aggressively displace large carpenter bees from nesting burrows (Laporte & Minckley, 2012; Roulston & Malfi, 2012). The flight period of carpenter bees in Florida extends through most of the year, whereas the flight period of *M. sculpturalis* is much shorter. A short flight period, large size, and a greater preference or ability to forage on different plants are factors that may lessen the impact of this bee on native bee populations, but more studies are needed. Conceivably, sunn hemp pollination and seed production could be accomplished by confining the bees and plants in enclosed large cages or greenhouses. We have had *M. sculpturalis* occupy trap nests near the experimental plots. Nests brought from areas where this bee is already abundant would be a source of emerging, young bees.

The genus *Crotalaria* is generally classified as an invasive weed (USDA NRCS Plants Database, 2016), and *C. juncea* is classified as such on many Pacific islands [US

Figure 5. Worker of *Apis mellifera* L. on sunn hemp blossom. In wilted blossoms, pollen in the keel is more accessible to the bee, and pollen is seen adhering to the proboscis.

Forest Service, Pacific Island Ecosystems at Risk (PIER), 2013], but levels of undesirable traits vary among species of the genus. For example, many species of *Crotalaria* are toxic to livestock, whereas a cultivar of sunn hemp is not (USDA NRCS, 1999). Sunn hemp is not considered an invasive threat in the continental USA, precisely because it produces little seed (USDA NRCS, 1999). Due to its many desirable characteristics, interest in sunn hemp's use as a cover crop will likely persist and expand. The ability to spread beyond cultivated areas would be reduced if all seed used for agriculture were produced in confinement, but greater seed availability would result in more widespread presence of the plant. With an increase in planting, sunn hemp could become increasingly successful at propagating, by benefiting natural populations of the very bees that pollinate it. If so, success as an invasive may also increase, but now it cannot be known how problematic that might become. Management practices would need to be developed and implemented to keep the plant under control as much as possible.

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