

The pollination of *Canavalia virosa* by Xylocopid and Megachilid bees

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ABSTRACT

The floral morphology of *Canavalia virosa* (Roxb.) Wight & Arn. is discussed in relation to pollination by *Xylocopa flavorufa* De Greer and *Megachile combusta* Sm. It was found that the relationship between size of flower and bee influenced the type of pollinating strategy and its success. Bees smaller than *M. combusta* proved ineffective pollinators.

RESUME

LA POLLINISATION DE CANAVALIA VIROSA PAR LES ABEILLES XYLOCOPIDES ET MEGACHILIDES

La morphologie florale de *Canavalia virosa* (Roxb.) Wight & Arn. est discutée en rapport avec sa pollinisation par *Xylocopa flavorufa* De Greer et *Megachile combusta* Sm. On a constaté que la relation entre dimensions de l'abeille et de la fleur influence la technique de pollinisation et son succès. Des abeilles plus petites que *M. combusta* se sont avérées inefficaces pour la pollinisation.

INTRODUCTION

Canavalia virosa (Roxb.) Wight & Arn. has been commonly known in South Africa as *Canavalia ferruginea* Piper. Although often confused with *C. ensiformis* (L.) DC. and *C. glochidiata* (Jacq.) DC., it is usually kept separate (Sauer, 1964, Verdcourt, 1971). However, it has been recently suggested that these three species may belong to one species. *C. ensiformis*, which includes wild and cultivated types (Westphal, 1974). The existence of this complex is not surprising if one considers the widespread cultivation of these plants in modern times as vegetables, fodder and cover crops. *C. virosa* is used here in the sense of Westphal (1974).

GEOGRAPHICAL DISTRIBUTION

C. virosa extends southwards from Arabia, Socotra and India through tropical Africa into north-east South Africa (Westphal 1974). Its distribution south of the Limpopo River is shown in Fig. 1.

FLORAL MORPHOLOGY

The general morphology of *C. virosa* has been adequately reviewed by Piper & Dunn (1922), Sauer (1964), Verdcourt (1971), and Westphal (1974). Piper *et al.* (1922) and Scott Elliot (1891) have written generalized accounts of the structural relationships of the various flower parts of *C. maritima* (Aubl.) Thours. and *C. ensiformis* (L.) DC. respectively. Vogel (1954) drew attention to analogies between the flowers of *C. maritima* and *Salvia africana* L. and also discussed pollination in both species. No account appears to have been given of the pollination of *C. virosa*. However, since, as Sauer (1964) has commented, *Canavalia* spp. generally have monotonous corollas and broad flowering schedules, it is to be expected that the genus is probably minimally adapted to specific pollinators. This implies that pollination is similar in most cases.

The flower structure of *C. virosa* hardly differs from the majority of known *Canavalia* spp. Flowers are generally held in an upright position with the standard facing downwards (e.g. Fig. 4 in Westphal, 1974). But, as Piper *et al.* (1922) pointed out, the flowers are commonly inverted i.e. standard below and facing upwards (e.g. Fig. 2 in Vogel, 1954). So far only inverted flowers have been observed in the

Transvaal. A front view of such a flower is shown in Fig. 2: 1. An outstanding feature of this flower is the longitudinal bulging along the upper surfaces of the two wings (arrowed in Fig. 2: 1). This feature plays a prominent rôle in pollination and it is surprising that very little attention has previously been drawn to it. In Fig. 2: 2 and 3 the bulges are arrowed relative to their position to the standard (S) and keel (K). The two peglike callosities at the base of the standard (S) rest on the portion of wing tissue between the bulges and auricles of the wings. The auricles of the wings articulate with the standard at the point marked * in Fig. 2: 4. This articulation allows the keel and wings of both upright and inverted flowers to return to their original position after being depressed by a visiting insect.

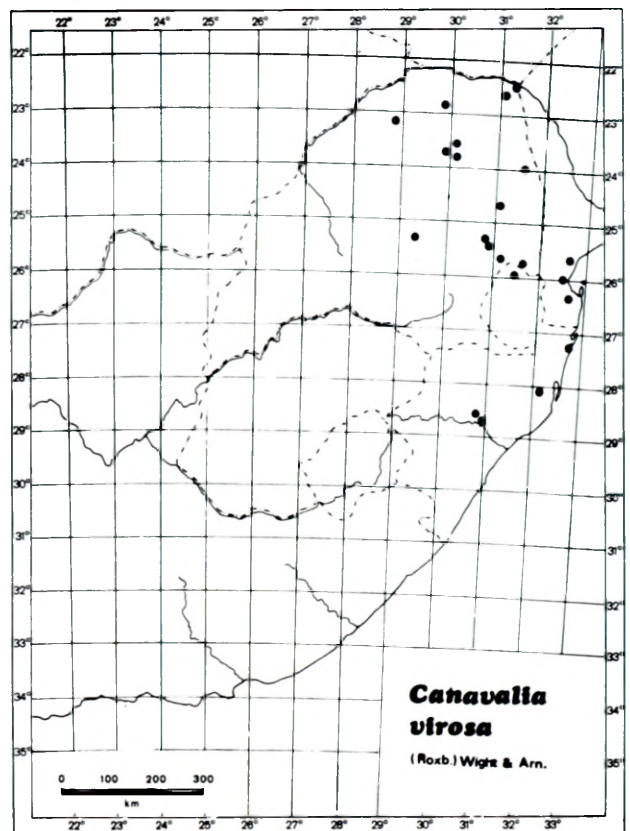


FIG. 1.—Known distribution of *Canavalia virosa* south of the Limpopo River (based on collections housed at the National Herbarium, Pretoria).

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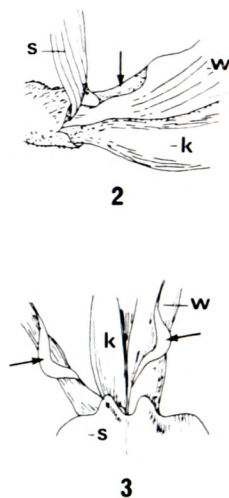
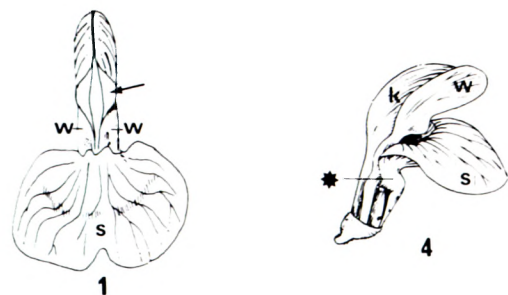


FIG. 2.—*Canavalia virosa* showing various views of the flower: 1, front view of flower with an arrow indicating the opening caused by the bulging of the upper wing margins; 2, side view of flower with one wing and keel blade removed to show relative position of standard, wing and keel; 3, enlargement of centre portion of 2 showing wing pulled aside from the upper margin of the keel; 4, side view of opening flower to show relative position of wing and standard auricles. (K = keel, S = standard, W = wing). Arrows indicate longitudinal bulging of upper wing margins.

POLLINATING VECTORS AND THEIR STRATEGIES

In 1964 Sauer wrote that the available information on pollinating insects in *Canavalia* was meagre. Xylocopid bees have been reported to pollinate *C. maritima* e.g. *Xylocopa violacea* (Scott-Elliott, 1891) and *X. aestuans* (Piper *et al.* 1922). Vogel (1954) reported that *Anthophora* sp. also pollinates this species. Lepidoptera may also visit *C. maritima* (Scott-Elliott, 1891).

Recent field studies in the Nelspruit District of the eastern Transvaal, revealed that only two types of bees were able to depress the keel of *C. virosa* effectively. These bees differed markedly in size and adopted different pollinating strategies.

Xylocopa flavorufa De Greer (Fig. 3: 1) is a noisy fast-flying solitary bee found in coastal bush, montane savanna woodland, fynbos and dry savanna woodland (Watmough, 1974). Both male and female bees were caught feeding on the flowers of *C. virosa* in the Nelspruit Botanical Gardens. The bee lands on the inverted standard with some force causing the whole inflorescence to shudder. This insect fits snugly into the area presented by the standard and maintains a hold by grasping the standard mainly near the peg-like callosities. Its head lies near the opening formed by the longitudinal bulges of the wings of the flower (Fig. 4: 1). To trip the mechanism the bee raises its abdomen and thorax and then thrusts its head against the opening. This movement forces the keel and wings away from the staminal sheath thereby exposing the stigma and anthers, which dust the back of the bee's thorax. This sequence is identical to that shown in Fig. 2 of Vogel (1954) in which he depicts *Anthophora* sp. visiting flowers of *C. maritima*.

Megachile combusta Sm. (Fig. 3: 2) is a smaller and lighter bee than *Xylocopa flavorufa*. It is incapable of landing and maintaining its position as does *X. flavorufa*. This bee lands more or less on the side of the standard and after repeatedly slipping on the shiny area above the callosities, it eventually manoeuvres its body into a position that brings its abdomen into line with the tip of the keel (Fig. 4: 2). When it pushes its head against the opening (Fig. 2: 1) it depresses the keel and wings and causes its abdomen to brush against the exposed stigma and anthers. The wings and keel retract when the insect alights.

Apis mellifera L. and other bees smaller than *M. combusta* were common visitors to flowers of *C. virosa*. These bees were unable to depress the keel. They collected loose pollen and in flowers damaged

by beetles that fed on nectar. Lepidoptera were common visitors.

DISCUSSION

In his discussion of the process of speciation in *Canavalia* Sauer (1964) noted that almost nothing was known about pollination or sterility barriers that could protect the divergent adaptations of subpopulations of diverging species. From his observations that isolated greenhouse plants could set seed, he deduced that facultative self-pollination

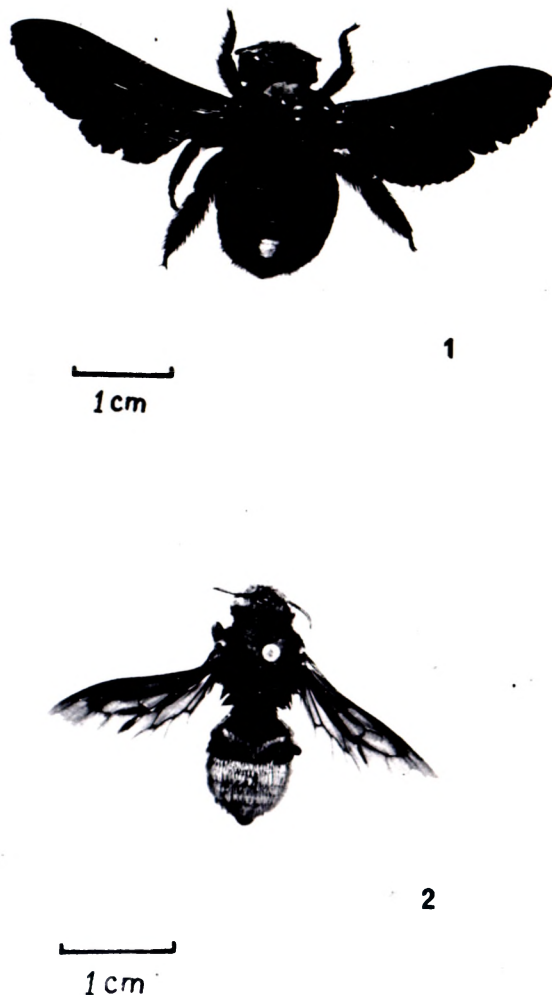


FIG. 3.—Photographs of bees. 1, *Xylocopa flavorufa*; 2, *Megachile combusta*.

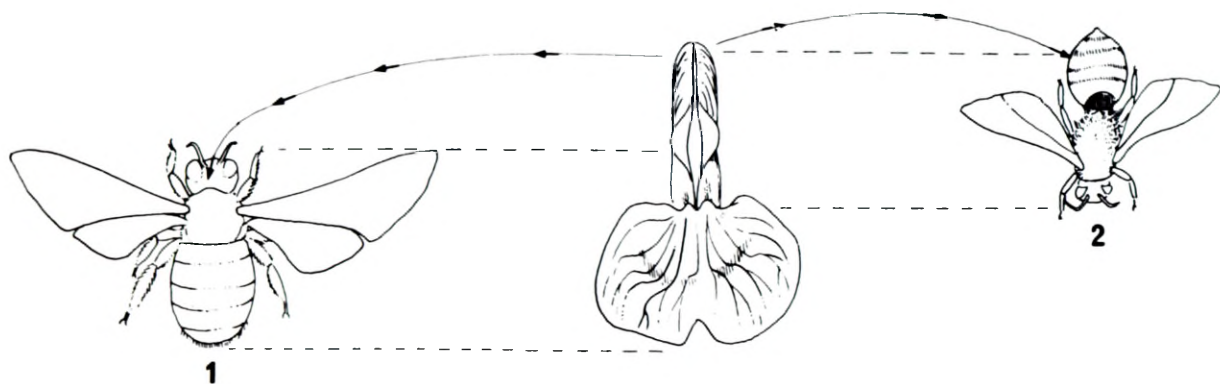


FIG. 4.—Positions adopted by *X. flavorufa* (1) and *M. combusta* (2) when operating the pollination mechanism of *Canavalia virosa*. Arrows indicate that pollen is dusted onto the thorax of *X. flavorufa* and onto the underside of the abdomen of *M. combusta*.

was possible, but he pointed out that the attractiveness of flowers to bumble bees and butterflies indicated cross-pollination.

Watmough (1974) noted that many indigenous Papilionaceae in Southern Africa apparently have no regular effective pollinators other than carpenter bees, which alone possess the power and weight necessary to operate the floral mechanisms. *Canavalia* appears, from the available evidence, to fall into such a class of plants. Plants of *C. virosa* in the eastern Transvaal tend to set between 2–4 seed pods per inflorescence, a factor which could indicate outbreeding as bees did not forage in inclement weather. If inbreeding was operative, one would expect a much higher seed set. It may, therefore, be advantageous to breed and release xylocopid bees in those areas where *C. virosa* and *C. ensiformis* are being cultivated. Watmough (1974) cites a number of references, which indicate that the introduction of these bees has improved the pollination and/or yield of a number of other agricultural crops.

Of the bees studied in this paper, *X. flavorufa* seems a more “natural” pollinator, whereas *M. combusta* and other bees smaller than it show every sign of being opportunists. *M. combusta* has “developed” a method whereby it can utilize nectar and pollen, but one which is not always successful.

Since few bees appear to be large enough to pollinate *C. virosa* successfully, it would appear that the large inverted flowers of this species constitute a possible isolating mechanism. *M. combusta* is the smallest known bee, which can operate the floral mechanism. A comparative study of sympatric *Canavalia* spp. with respect to pollinating vectors could give a better insight into the mechanisms which protect the divergent adaptations of subpopulations of diverging species, particularly those in complexes such as that of *C. ensiformis*.

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UITTREKSEL

Die blomorfologie van Canavalia virosa (Roxb.) Wight & Arn. word bespreek in verhouding tot bestuiwing deur Xylocopa flavorufa De Greer en Megachile combusta Sm.. Dit is gevind dat die verhouding tussen grootte van blom en by die tipe bestuiwingstrategie en die sukses daarvan beïnvloed. Bye kleiner as M. combusta het ondoeltreffende bestuiwers blyk te wees.

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