

The Explosive Floral-mechanism and Pollination in the Genus *Hyptis* (Lamiaceae)

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Hyptis is a New World genus with a few of its species occurring in the Old World. It is characterised by the sexual floral organs enclosed in the carinal-like lower lip which slips explosively or non-explosively upon landing of the appropriate forager seeking floral reward. The principal pollinating agents include bees, wasps and hummingbirds. Very few species have been studied compared to the vast number of species listed in the genus. The species contain flag-shaped blossoms and adapted to sternotribic mode of pollination. This paper reviews information on the floral mechanisms and pollination in the genus and also compares the same with similar floral mechanisms found in other members of Lamiaceae and also with the members of other angiospermic families.

Key words : Lamiaceae, *Hyptis*, Explosive mechanism, Bees, Wasps and hummingbirds

Introduction

The Neotropical genus *Hyptis* is one of the largest genera of Lamiaceae with about 400 species of annuals or perennials (Hickey & King 1988). The genus extends from the southern United States through the Caribbean region and Central America, South to Argentina. A few species of this genus are weeds and have become naturalised in warmer parts of the Old World (Harley 1988, Nowicke & Epling 1969; Hickey & King 1988). *Hyptis* is a member of the subfamily Nepetoideae tribe Ocimeae subtribe Hyptidinae (Cantino & Harley 1991). Flowers

of the members of this subfamily have the sexual floral organs always extend ventrally in the corolla tube, proximate to or along the lower flower lip, and not along the upper lip as in the majority of the Lamiaceae. It is characterised by sternotribic flowers in which the stamens are held in the lower lip of the corolla, which in most species is strongly compressed to form an explosive pollination mechanism. Such a floral mechanism is unique for the genus *Hyptis* and appears to be a parallel to the papilionaceous type in which the sex organs are set free explosively from the lower lip

when this is triggered (Burkart 1937, Harley 1971, 1976, Brantjes & De Vos 1981, Aluri 1990). However, the complexity and homogeneity of the floral mechanism in correlation with independent morphological features distinguish the genus *Hyptis* from allied genera with similar or parallel floral mechanisms. The explosive mechanism exists in *Aellonthus* (Hedge 1972), *Eriope* (Harley 1971, 1976), *Marsipianthes*, *Peltodon*, *Raphiodon* and *Homalocheilos* (Harley 1976) and non-explosive mechanisms in *Plectranthus* and *Coleus* (Scott-Elliot 1891, Blake 1971, Tanaka 1972, Faegri & van der Pijl 1979).

In this paper, we present a review of the available information of the function of flower-mechanisms and pollination in *Hyptis* species scattered in the literature. We also compare the same with similar and parallel floral-mechanisms found in some genera of other families. This will be a source of background information for extensive investigations on the form and function of floral mechanisms in all other species in this genus that have not been worked out thus far.

Review of Pollination in *Hyptis*

The members of *Hyptis* occur as herbs, undershrubs or trees in soils profoundly disturbed or undisturbed places in tropical and subtropical parts of the world (Nowicke & Epling 1969). Some species such as *H. suaveolens* (L.) Poit. and *H. capitata* Jacq. are normally restricted to disturbed places comprising rubbish, waste or poor lands and in this sense they are considered to be 'ruderal' species (Aluri & Subba Reddi 1989; Aluri 1990; Keller & Armbuster 1989). The genus is remarkable for the wide variation in inflorescence type : paniculate of cymes, either verticillate or of numerous small

bracteate heads and uninterrupted spikes or globose heads usually solitary on terminal or axillary peduncles. The floral colours include blue, purple, red, and white and also occur in combination of these colours. The blue and purple-flowered species occur predominantly.

H. suaveolens is an annual or perennial undershrub and flowers between October and April in the New World (Adams 1972). In Asia, this species flowers throughout the year in Taiwan (Anonymous 1978) and from September to December in India (Aluri 1990). *H. suaveolens* produces aerial growth from the previous root stock or the seed following heavy rains in June after a 3-4 month dry season (Aluri & Subba Reddi 1989). The plant produces small, odourless blue flowers each day from dawn to dusk. The period of anthesis strongly coincides with the period of diurnally active foragers. The floral carinal structure formed by the middle lobe of corolla lower lip conceals the stamens and stigma and does not open following the natural anthesis. Upon anthesis, the carinal lobe is under tension which is later released by wind or bees of various species but only *Xylocopa latipes*, *Thyreus histrio* and *Amegilla* trip the explosive floral mechanism effectively in a single foraging visit resulting in pollen release from the stamens and subsequent pollen deposition on the stigma and on the forager in sternotribic manner. It results in both self - and cross-pollination. The wind-activated flower-tripping is subjected to the wind speed above 0.8 m/ sec. and brings about self-pollination only (Aluri 1990). The plant reproduces through autogamy and allogamy. Both require explosion of carinal lobe for pollination. The flexibility of the mating system is shown as a safeguard ensuring its ruderal nature for

weediness. Besides, the plant exhibits asexuality by vegetative propagation from the perennating root stalk. The dual reproductive behaviour ensures the plant to perpetuate in any habitat of disturbed soils in subtropics or tropics (Aluri 1990).

H. capitata is a ruderal species and found its way into the warmer parts of the Old World including India. Heide (1927) noted that this species was abundantly pollinated by *Stilbum cyanurum* var. *splendidum* in East Indies. Five decades later, Keller and Armbruster (1989) made a detailed study on this species in Panama. They describe that *H. capitata* antheses between 0700 and 1615 h and its white flowers produced in globose heads on long peduncles are visited by wasps, bees, lepidopterans and other insects for nectar. The explosive mechanism involves the sudden release of the stamens from the sac-like petal lobe as in *H. suaveolens*. Here, the tripping of floral mechanism is completely an act of disturbance caused by the forager. Of the visitors, only wasps of *Omicron flavonigrum* trip the flowers open and collect nectar nototribically. The nototriby in the reverse gullet blossoms is surprising as it is thought to be the norm in the gullet blossoms (van der Pijl 1972; Stirton 1977). Unlike in *H. suaveolens*, fruits mature in non-tripped flowers and thereby indicating self compatibility and self-pollination in *H. capitata* (Keller & Armbruster 1989).

H. pauliana Epling is another ruderal species and grows in xeric habitats in Brazil. Brantjes and De Vos (1981) speculate that its flowers with explosive mechanism are pollinated by hummingbirds. The authors show that the floral characters such as flower size, absence of odour, brick-red coloured

corolla, tubular shape and horizontal position of the corolla, and large quantity of nectar are adapted to a hummingbird-pollination syndrome in agreement with Faegri & van der Pijl (1979). The explosion of floral-carina causes disposition of pollen grains on the chin of a drinking hummingbird. They report that the pressure in large epidermal cells of the suspensor plate, in combination with the stiffness of collenchymatic, deeper cell layers of the carina formed from the middle lower lip produces the force for the explosion which makes the anthers to slip violently from the carina, swing up and eject the pollen on the flower visitor. *H. mutabilis* Briq. and *H. fasciculata* Benth. with similar floral details have been shown to exhibit explosive pollen presentation by tripping (Burkart 1937). *H. emoryi* is a characteristic bee-flower with explosive labellum and occasionally visited by hummingbirds (Grant & Grant 1968). *H. alata* occurs as a native of mainland United States and extends to all parts of North America and Pacific Islands. It occupies wet habitats such as damp savannas, swamps and marshes. It produces white flowers with purple dots in elongate racemes of pedunculate capitula. The flowers appear to possess explosive mechanism but further study needed to confirm this (Harley 1983). *H. paradisi* Harley is a moderate-sized shrub seen in Brazil. Its flowers are lilac with pale area at the base of upper lip. A black bumblebee, *Bombus brevivillus* is a frequent visitor to this species. The bee triggers the flowers and removes the pollen (Harley 1974). *H. siphonantha* Harley, a herb with pale violet flower is frequently visited by bees of *Centris tarsata* and *Hypanthidium rubriventre*. The bees trip flowers and collect pollen (Harley 1974). The Brazilian *H. subrosea* Harley with red

flowers is expected to be pollinated by hummingbirds but field observations show that a small solitary bee species, and females of *Exomalopsis auropilosa* regularly trigger the explosive mechanism and remove pollen (Harley 1974).

H. cruciformis Epling is a small shrub, found in the wettest parts of the marshes and stream margins in Brazil. Its close species *H. pachyphylla* Epling in striking contrast is a tree and restricted to drier areas, inhabiting among outcropping rocks that are in close proximity to the marshes and stream margins in Brazil. Flowers of the two species, unlike most members of the genus, do not have a compressed lower lip and explosive pollination mechanism (Harley 1986). Instead, the lower lip is spoon-shaped and not held under tension by the stamens, which are exposed as soon as the flower opens. With such a floral situation, the position of both anthers and stigma ensures contact with foragers probing in an orthodox manner. The foragers comprise only bees of different species. *H. cruciformis* is visited by worker *Apis mellifera adansonii*, worker and male *Bombus brevivilus* and female *Euglossa melanotricha*. *H. pachyphylla* is visited by the first species and *Xylocopa* sp. (Harley 1986). Further, the putative hybrids from these two species naturally cooccur in the transition zone from the drier ground to the marsh. The hybrid individuals appear intermediate in habit, leaf and floral characters and are visited by *A. mellifera adansonii* only. Whether the hybrids survive or not, will depend on the extent to which the F₁ and subsequent generations are both physiologically adapted to the environment and sufficiently fertile to ensure the continuation of the line (Harley 1986). The red-flowered *H. macrantha*, an undershrub

also has similar non-explosive floral mechanism. It has large tubular corolla, with a lower lip relatively much too small to enclose and retain the stamens under pressure for explosive pollen release (Harley 1971).

The floral descriptions of the following species - *H. tagetifolia* Harley, *H. hamatidens* Epling and Jativa, *H. peduncularis* Benth, *H. nitidula* Benth, *H. dictyodea* Pohl ex-Benth, *H. verticillata* Jacq., *H. pectinata* (L.) Poit. *H. spicigra* Lam., *H. atrorubens* Poit. *H. brevipes* Poit. and *H. rhomboides* Mart. & Gal. show that they possess explosive mechanism and appear to exhibit bee-pollination syndrome (Harley 1974). *H. guanchezii* R. Harley is a newly reported species, found in Venezuela. It produces white flowers in capitula on spiciform inflorescence. Its floral illustrations indicate that it has explosive pollination mechanism (Harley 1989).

Discussion and Conclusions

Pollination biology of only a few species of *Hyptis* is studied compared to the vast number of species in the genus. This genus is characterised by flag-shaped blossoms morphologically adapted to sternotribic pollination. The morphological adaptation is such that the anthers remain in tension after anthesis in the lower lip and are explosively released upon a slight external disturbance. A recent report on *H. capitata* by Keller and Armbruster (1989) shows that this species with explosive mechanism is functionally adapted to nototribic pollination. This report underscores the inadequacy of inferring pollination modes from floral morphology alone.

The explosive mechanism occurs with slightest deviations in several allied genera

such as *Aeollanthus* (Hedge 1972), *Eriope* (Harley 1971, 1976), *Marsiphanthes*, *Peltodon*, *Raphiodon* and *Homalocheilos* (Harley 1976). Parallel floral mechanisms causing pollination as a result of the violent movement of anthers/stamens and style alone or together with restraining petals are reported for some members of the Loranthaceae, Urticaceae, Ericaceae, Leguminosae, Fumariaceae, Musaceae, Onagraceae, Rhizophoraceae, Cornaceae, Stylidiaceae, Acanthaceae and Marantaceae. But, only the Leguminosae members, *Cytisus scoparius* and *Medicago sativa* exhibit more or less similar explosive mechanism that found in *Hyptis* species (Meeuse and Morris 1984).

Although *Hyptis* is unique to possess explosive pollination mechanism, a few species such as *H. cruciformis*, *H. pachyphylla* and *H. macrantha* St. Hil. ex benth. have non-explosive mechanisms by which they expose anthers non-violently as soon as their flowers open. Similar non-explosive floral mechanism has been noted for the allied genera, *Coleus* (See Faegri and van der Pijl 1979) and *Plectranthus* (Nilsson et al. 1985).

The explosive pollen presentation is frequently encountered in the subfamily Ocimoideae. The frequent occurrence of this mechanism does not necessarily imply a phylogenetic link between genera within the sub-family but suggests that this might have evolved independently several times in the different genera. The development of explosive nature of floral mechanism might have been made possible by the dominance of the lower lip. The lip was probably of adaptive value as a landing platform or stamen protector before the explosive mechanism evolved. Moreover, the position

of the anthers in the lower lip in the bud is common to the whole sub-family. The anthers position in the upper lip is phylogenetically and ontogenetically secondarily attained in connection with a change towards nototriby (van der Pijl 1972). Evidence for a phylogenetic origin of the explosion mechanisms comes from the diversity of the associated structures (see for details Brantjes & De Vos 1981).

The pollination agents of different species of *Hyptis* comprise bees, wasps, butterflies, long-tongued flies and humming birds, but butterflies and flies play a meagre role in causing pollination. The red-flowered species are pollinated by hummingbirds, while the species with other colours are pollinated by different groups of insects. The biotic visitors obtain pollen and/or nectar from the flowers. In *H. suaveolens*, the violent slipping of the anthers and style from the lower lip upon landing of small bees, *Trigona*, *Ceratina* and *Pithitis* causes a disturbance to the bees and makes them move a little away from the flower. After a few successive visits to these flowers, the bees change their flower-approaching behaviour. They first touch the carinal lobe with their proboscides to make sure it is exploded and then probe the flower for floral reward (Aluri 1990).

Anemophily was not reported earlier either in *Hyptis* or in any other member of Lamiaceae. Our studies (Aluri & Subba Reddi 1989, Aluri 1990) report for the first time the active role of wind in triggering pollination mechanism in *H. suaveolens* thus warranting extensive studies on the role of wind in flower tripping in other species of *Hyptis* that have been studied and in those that have not been worked out yet (Aluri 1990).

Although *Hyptis* is a neotropical genus, a few members, particularly the weedy species are able to grow successfully in paleotropics. The weeds such as *H. rhomboides*, *H. spicigera*, *H. brevipes*, *H. suaveolens*, *H. capitata*, *H. pectinata*, etc. have found their way into Asia from the New World. The last four species occur in India but only *H. suaveolens* is widespread. These species are highly successful as weeds being able to perpetuate by vegetative and sexual methods (Anonymous 1978, Aluri & Subba Reddi

1989, Aluri 1990). The dual reproductive behaviour enables propagation of these species in various habitats (Aluri 1990).

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