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Ovule abortion – a rivalry action or dispersal strategy?

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ABSTRACT

Abortion of ovule leading to lowering of seed set or seedlessness. A number of mechanisms have been suggested to occur side by side, creating a sort of "genetic sieve" which leads to development of certain embryo genotypes preferentially. These include lack of pollination, Parent-offspring conflict and sibling rivalry as internal. Several species invariably practicing obligate ovule abortion. *Hyptis suaveolens* (L.) Poit. (family-Lamiaceae) falls in this category. It is known by several vernacular names (American Mint, Ganga Tulsi, Vilaiyti Tulsi, Bustrena and Kallu Thumbai); an important invader of the tropical and sub-tropical regions of the world. The species behaves as a self-pollinated plant in the tropical climes of study area i.e., Jammu province of UT of J&K, India. Present work is done to explore the details of the process of ovule abortion and its implications for the invasiveness of this species.

Key words*: Seedlessness, Genetic sieve, Sibling rivalry, Invader*

Introduction

Though abortion of ovules leading to lowering of seed set or seedlessness is reported in a number of plant species, the phenomenon has been studied in depth in only a few (Ganeshaiah and Uma Shaanker (1988); Rocha and Stephenson (1991); Weins (1984) and Dhar *et al*. (2006)). A number of mechanisms, i.e. pre and post fertilization have been suggested to occur side by side, creating a sort of "genetic sieve" which leads to the development of certain embryo genotypes preferentially (Dhar *et al*., 2006). These include lack of pollination and sufficient resources among external factors and parent-offspring conflict and sibling rivalry as internal. Several species practicing obligate ovule abortion are however interesting that in spite of being highly self-pollinated and growing in a nutritionally rich areas, they invariably show a definite pattern of ovule abortion across all the individuals of population as also across different populations. *Hyptis suaveolens* (L.) Poit. falls in this category.

Hyptis suaveolens (L.) Poit, (family-Lamiaceae) known by several vernacular names (American Mint, Ganga Tulsi, Vilaiyti Tulsi, Bustrena and Kallu Thumbai) is an important invader of the tropical and sub-tropical regions of the world. A noxious weed, native of tropical America, it has naturalized in various parts of world including Indian subcontinent (Singh *et al.* 2010). It is an annual or perennial herb of aggressive nature that grows wildly in dry barren areas, waste land, along roadsides and railway tracks (Padalia *et al.*, 2015). The plant is highly invasive as it propagates through seed bank available in the soil and behaves as annual. It also acts as a perennial as it can perpetuate through root stock of previous years also (Sharma and Sharma, 2019).

The species behaves as a self-pollinated plant in the tropical climes of study area i.e., Jammu province of UT of J&K, India (Sharma and Sharma, 2019). Plants are peculiar in showing extremely high (>90%) fruit set both on open pollination as well as

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in bagged flowers. Average seed set is however low (approximately 45%) in both the conditions as more than 50% of the ovules invariably abort. Present work is done to explore the details of the process of ovule abortion and its implications for the invasiveness of this species.

Materials and Methods

Plant material and study area

The work compiled in this manuscript includes detailed studies on three population's of *Hyptis suaveolens* (L.) Poit. tagged at 3 different sites of Jammu province of J&K (U.T), India having an altitude variation of 272-431 masl and a set of plants (n=10) acclimatised under controlled conditions in Botanical Garden of University of Jammu, J&K, India (Table 1).

The plants were studied in field for their detailed plant and floral features including plant height, number of leaves/branch, leaf size and number of inflorescences and flowers/branch. Flowers were collected randomly in the field and studied later for various floral features such as length of sepals, petals, length of carpel and stamens, size of ovary etc. by using stereomicroscope.

Anthesis and Anther dehiscence

Anthesis and dehiscence of anthers were observed at regular intervals of time. Plants were regularly monitored in the field throughout the day in order to record the time taken by individual flower, individual inflorescence and full plant to bloom. Dehiscence of anthers was studied in the field and later confirmed under the stereomicroscope (SMZNIKON) in flowers of different developmental stages.

Stigma receptivity

At different developmental stages of flower, Carpels were removed and mounted on clear glass slide in a drop of mixture of 4 ml of 1% aqueous acid fuchsin, 2 ml of 1% light green, 40 ml of lactic acid and 46 ml of distilled water. These were then observed under the microscope to record the amount of the pollen load on stigma. For counting the number of pollen grains germinating on the stigma, carpels of different developmental stages were fixed in Carnoy´s fixative (3:1 absolute alcohol: acetic acid) for 24 hrs and were later washed in distilled water and then stained in mixture elaborated above.

Fluorescence microscopy

Carpels were fixed in Carnoy's fixative (3 alcohol:1 acetic acid) for 24 hours and then transferred to 70% ethanol. These were thoroughly washed in distilled water after 24 hours and placed in 4N NaOH in an oven maintained at 60 °C for 2 hours and then shifted to room temperature and kept as such for 24 hours to allow complete clearing of pistils. The cleared carpels were washed in distilled water and kept in decolorized aniline blue (DAB) overnight. The stained carpels were later mounted in DAB and glycerol in the ratio of 1:1 and scanned under fluorescence microscope (Nikon eclipse 80i) to trace the path of pollen tubes.

Pollen-ovule ratio

To estimate pollen – ovule ratio, mature undehisced anthers (n =15) were squashed one at a time in a drop of 1% acetocarmine on a clean glass slide. The slide was scanned under the microscope to count the number of pollen grains. Ovules were counted by gently dissecting them out from each locule of the ovary. From the values so recorded, P/O ratio was estimated for individual flower.

Insect monitoring

To observe the presence of visitors, plants were regularly monitored in the field throughout the day. Their time of visitation and duration of the visits on the flower were properly recorded.

Ovule abortion

Pistils were dissected out from the flowers and

Table 1. Site description and GPS location of populations of *Hyptis suaveloens*

S.No.	Plant species	Site description	Latitude (N)	Longitude (E)	Altitude (masl)
1	*Hyptis suaveolens*	Ban (Waste land)	33.385–	75.561–	431
2		Samba (Waste land)	32.946–	74.170–	384
3		Chadwal (Ravine)	32.790–	75.522–	324
4		Botanical garden (Under controlled conditions)	33.208–	75.437–	272

scanned for the position and number of ovules within a carpel under microscope. Also, the percentage of pistils showing ovule abortion was calculated in different populations scanned as follows:

Total number of pistils with ovule abortion/Total number of pistils scanned *100

Pollination studies

1. Open pollination

Mature and unopened flowers (n=30) were tagged and left as such for allowing pollination as it occurs in nature.

2. Bagging

Mature and unopened flowers (n=30) were bagged and left undisturbed to check the extent of selfing.

Fruit and seed set

Percentage fruit and seed set on open pollination and bagging was calculated as under:-

$$\frac{\text{Total number of fruits formed}}{\text{Total number of flowers}} \times 100$$

$$\frac{\text{Total number of seeds formed}}{\text{Total number of flowers} \times \text{Number of ovules in each flower}} \times 100$$

Results and Discussion

Habit and plant morphology

Plants of *Hyptis suaveolens* are scented annual or perennial herb having rough, angular, pubescent stem that varies in height at different sites (Table 2). Plants in all populations are highly branched. Leaves are arranged in opposite decussate manner, these are ovate or cordate, velvety and sticky on both the sides. Plants maintained in Botanical Garden are the tallest reaching to a maximum height of 2.69 mtrs. These are vigorous and exceed plants of other populations in all vegetative features. Plant morphology shows significant difference with respect to height, no. of branches, no. of flower/cluster etc. Morphometric details of individual flowers however display non-significant differences.

Floral morphology

Flowers are aggregated in verticillate cymes (2-5) in the axil of leaves. The flower is bilabiate (Figure 1a). The upper lip is divided into two lobes having dark purple nectar guides, and the lower lip is divided into three lobes with central lobe (carinal lobe) having flattened appearance. This carinal lobe encloses four epipetalous, basifixed, didynamous stamens arranged in 2+2 pattern. Filaments of two stamens are long, while that of other two are short (Figure 1b). Each of these stamens are reddish brown to dark brown having bilobed anther and hairy white filaments. Due to the formation of false septum, ovary is tetralocular and each locule carries one ovule (Figure 1c). Style is long and terminates into a

Table 2. Plant morphology of *H. suaveolens* at different sites

S.No.	Characters (n=30)	Ban	Samba	Chadwal	Botanical garden	p-Value
1.	Height of the plant (Cm)	26.7±5.77 (8.5-57)	32.13±4.26 (13.6-48.2)	55.36±4.68 (29.6-75)	214.7±13.98* (137-269)**	1.073E-18^{S}
2.	Length of internode(Cm)	2.75±0.28 (1.5-4)	2.53±0.22 (1.1-3.7)	4.49±0.27 (3-5.7)	9.6±0.22 (8-10)	4.892E-16^{S}
3.	Number of branches/ plant	7.9±1.94 (0-18)	3.7±0.61 (1-6)	11.5±1.80 (4-17)	23.3±3.67 (5-35)	4.44E-06^{S}
4.	Number of leaves/ plant	48.9±9.70 (10-112)	311.2±28.91 (150-412)	228.2±31.20 (115-381)	1010.2±81.02 (651-1390)	2.588E-16^{S}
5.	Length of leaf (Cm)	2.22±0.28 (1-3.9)	3.37±0.17 (2.6-4.3)	2.83±0.26 (1.8±4.4)	11.7±0.47 (10-14)	1.798E-22^{s}
6.	Width of Leaf (Cm)	1.82±0.24 (0.7-3)	2.89±0.14 (2.3-3.6)	2.19±0.18 (1.5-3.5)	9±0.33 (8-11)	1.385E-22^{S}
7.	Length of petiole (Cm)	1.76±0.24 (0.4-3)	1.95±0.11 (1.3-2.5)	1.42±0.25 (0.8-2.7)	9.4±0.22 (8-10)	8.016E-26^{S}
8.	Number of flower cluster/ branch	12.2±0.97 (7-16)	11±1.96 (4-24)	14.5±0.99 (9-21)	16.9±3.87 (5-38)	0.7896^{NS}
9.	Number of flowers/ cluster	3.9±0.45 (2-6)	5.1±0.50 (2-7)	4.1±0.52 (2-6)	4.8±0.41 (2-6)	0.2865^{NS}

Mean± Standard error* Range** ^{S}Significant at p<0.05

Table 3. Data on Floral morphology of *H. suaveolens*

S.No.	Characters (n=30)			Ban	Samba	Chadwal	Botanical garden	P-Value
1.	Length of peduncle (cm)			0.86±0.071 (0.5-1.2)	0.86±0.01 (0.8-0.9)	0.68±0.1 (0.4-1.2)	0.76±0.01 (0.7-0.8)	0.1564^{NS}
2.	Length of complete flower (cm)			0.75±0.01 (0.7-0.8)	0.64±0.01 (0.6-0.7)	0.81±0.01 (0.7-0.9)	0.86±0.01 (0.8-0.9)	9.195E-10s
3.	Calyx	Length of sepal (cm)		0.40±0.002 (0.4-0.42)	0.30±0.004 (0.3-0.35)	0.28±0.01 (0.2-0.3)	0.29±0.01 (0.2-0.3)	8.362E-12^{S}
		Length of bristles (cm)		0.12±0.013 (0.1-0.2)	0.21±0.006 (0.2-0.25)	0.21±0.01 (0.2-0.3)	0.19±0.004 (0.15-0.2)	3.928E-08^{S}
4.	Corolla (cm)	Large petal	Length	0.40±0.004 (0.4-0.45)	0.38±0.01 (0.3-0.4)	0.38±0.01 (0.3-0.4)	0.40±0.004 (0.4-0.45)	0.1235^{NS}
			Width	0.30±0.002 (0.3-0.32)	0.28±0.04 (0.2-0.3)	0.30±0.005 (0.3-0.35)	0.30±0.004 (0.3-0.35)	0.05906^{NS}
		Length of Wing	w_1	0.30±0.0009 (0.3-0.31)	0.20±0.015 (0.2-0.25)	0.29±0.006 (0.25-0.3)	0.20±0.004 (0.2-0.25)	3.379E-19^{S}
			w_2	0.30±0.0009 (0.3-0.31)	0.20±0.015 (0.2-0.25)	0.29±0.00 6(0.25-0.3)	0.20±0.004 (0.2-0.25)	3.379E-19^{S}
		Corolla tube		0.41±0.009 (0.4-0.42)	0.40±0.015 (0.4-0.45)	0.40±0.001 (0.4-0.41)	0.40±0.004 (0.4-0.45)	0.4897^{NS}
5.	Androecium	Length of lower stamens	length× width of anther (um)	292.16 ±17.35 × 740 ±964.36 (315.4-348.6)× (713.8-747)	504.64±4.42× 851.58±7.02 (498-531.2)× (813.4-879.8)	371.84±6.63× 856±4.42 (332-381.8)× (796.8-863.2)	295.48±8.5× 628.52±8.69 (249-315.4)× (597.6-674.4)	2.2956E-18^{S}& 5.632E-07^{S}
			Length of filament (um)	1123±21.96 (1032-1260)	1113.3±32.09 (998-1162)	1137.1±24.89 (1079-1328)	1136.6±22.07 (1080-1301)	1.129E-08^{S}
		Length of upper stamens	Length×width of anther (um)	330.34±3.87× 725.42±3.54 (315.4-348.6)× (713.8-730.4)	502.98±6.57× 878.14±10.62 (4464.8-531.2)× (846.6-929.6)	385.12±5.42× 829.92×6.56 (365.2-415)× (796.8-863.2)	350.0±-10.2× 813.4±28.32 (265.6-381.8)× (647.4-879.8)	7.847E-17^{S}& 2.258E-22^{S}
			Length of filament (cm)	0.31±0.008 (0.3-0.37)	0.36±0.01 (0.3-0.4)	0.30±0.005 (0.3-0.35)	0.44±0.01 (0.4-0.5)	0.8592^{NS}
6.	Gynoecium	Length of stigma (um)		292.16±7.9 (249-315.4)	272.08±3.7 (249-282.2)	272.24±13.59 (199.2-315.4)	305.44±5.07 (265.6-315.4)	0.0201^{S}
		Length of style (cm)		0.55±0.005 (0.5-0.65)	0.47±0.01 (0.4-0.5)	0.55±0.01 (0.5-0.6)	0.57±0.02 (0.5-0.7)	0.001811^{S}
		Size of ovary (um)		1067.38±18.19 (996-1145.4)	1117.18±13.56 (1029.2-1145.4)	1113.92±17.6 (1045.4-1195.8)	1168.64±5.64 (1145.4-1195.2)	0.00032^{S}

Mean± Standard error* Range** ^{S}Significant at p<0.05

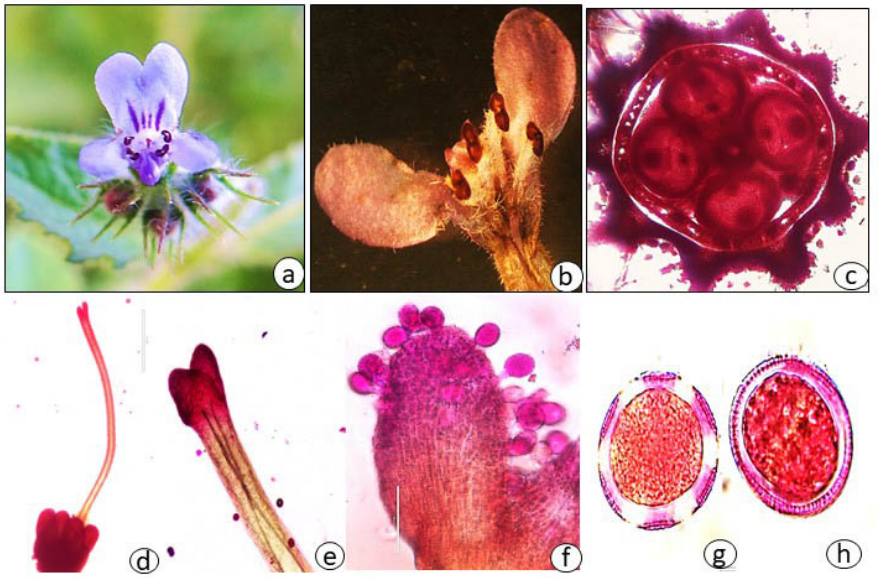


Fig. 1. Floral features of H. suaveolens
a. Bilabiate flower
b. didynamous anthers
c. tetralocular ovary carrying one ovule each
d-e. long style with bifid stigma
f. pollen load on the stigma
g-h. colpate and noncolpate pollen grains

bifid stigma (Figure 1d-e). A fleshy nectary disc is presentat the base of ovary. Stigma and lower stamens are present almost at the same level in mature flower. Upper stamens are present slightly above the level of both of these. Details of flower morphometry are given in Table 3.

Another dehiscence, stigma receptivity and pollen-Ovule ratio

Flowers are weekly protandrous with dehiscence of anthers taking place approximately 2:00 hrs before anthesis when the bud size reaches around 08 mm. Dehiscence is extrorse and release of cloud of sticky yellow coloured pollen occurs by the formation of longitudinal slit.

Stigma attains maximum receptivity after 5-6 hrs of the anthesis of flower, when the flower attains its maximum size (approximately 8.5 mm). At this time, the stigma shows an average pollen load of 56.3±2.8 (45-67), with percentage germination of 79.57%. Number of pollen grains is copious on stigmatic surface (Figure 1f) Most of the pollen tubes

Table 4. Data on pollen characteristics and pollen- ovule ratio

S.No.	Charactersn=30		Ban	Samba	Chadwal	Botanical garden
1.	Total pollen count/ anther		418.9±1.98 (405-428)	364.81±2.71 (356-381)	437.9±2.47 (428-445)	644.8±3.33 (624-657)
2.	Total pollen count/ flower		1675.6	1459.27	1751.6	2579.2
3.	Percentage pollen viability (FDA)		76.2	78.1	79.9	78.6
4.	Percentage pollen stainability (Acetocarmine)		91.74	93.23	94.38	93.29
5.	Ovule size (um)	Length (um)	750.32±15.61 (713.8-813.4)	595.94±18.25 (514.6-680.6)	686.38±26.58 (498-780.2)	781.86±7.19 (763.6-813.4)
6		Width (um)	393.42±11.62 (348.6-431.6)	285.52±8.13 (265.6-332)	297.14±10.33 (215.8-332)	368.52±4.82 (348.6-381.8)
7.	Ovule count /flower		4	4	4	4
8.	Pollen/ ovule ratio		418.9:1	364.81:1	437.9:1	644.8:1

Table 5. Percentage of seed set/ fruit

S. No.	Number of seeds/ fruit	%age of fruits having different number of seeds
1.	0	2.78
2.	1	22.22
3.	2	72.22
4.	3	2.78
5.	4	0

traverse through the stylar tissue and reach the ovule without any kind of hinderance throughout their pathway (Figure 2a-f).

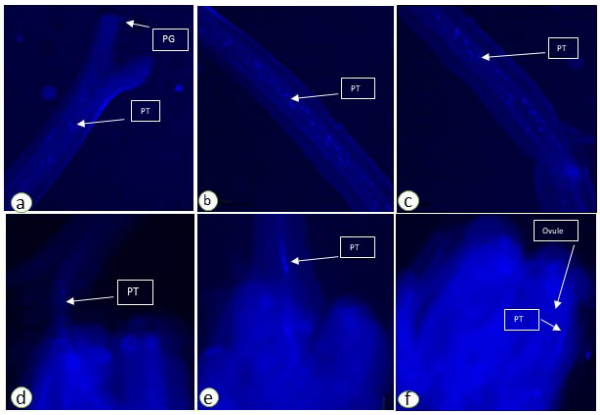


Fig. 2. Fluorescence microscopy showing pathway of pollen tubes from stigma toward ovary
PG: pollen grain; PT: pollen tube

Pollen are of two types, *i.e* colpate and non-colpate (Figure 1g-h). The pollen production per anther averages 364.81±2.71 (356-381) to 601.3±3.15 (583-612) in different populations (Table 4). The number of ovules in all flowers is invariably 4, so the pollen ovule ratio ranges from 364.81:1 to 644.8:1.

The pollen stainability in 1% acetocarmine is high and averages between 91.74 to 94.38%. Viability as revealed by FDA is slightly low and ranges between 76.2-79.9%.

*Mean ±Standard error

**Range

Ovule abortion

Each flower has 4 ovules, of which only one/two or rarely three develop into seeds (Figure 4). Only one ovule in each half or single ovule in the whole ovary develops into seed while the others abort. The number of aborted ovules/ovary averages 2.46±0.13 (2-4). Majority of fruits are 2 seeded (Table 5) followed by the ones with one seed. Approximately 3% fruits bear 3 seeds, while none if the fruits have 4 seeds.

Fruit and seed set

Open pollination

Percentage fruit set on open pollination ranges from

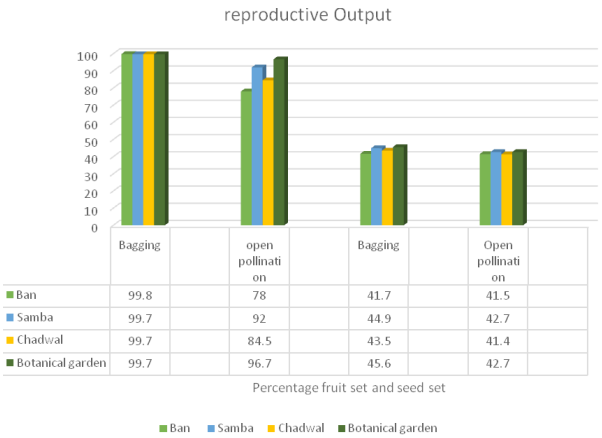
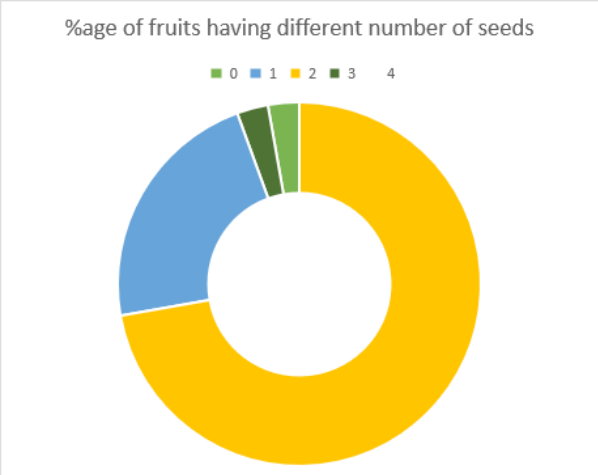


Fig. 3. Reproductive output in *H.suaveolens* in different populations

Table 6. Reproductive output in *H. suaveolens*

S. No.	Characters (n=30)		Ban	Samba	Chadwal	Botanical garden (control condition)	P-value
1	Percentage fruit set	Bagging	99.8±0.13 (99-100)	99.7±0.15 (99-100)	99.7±0.16 (99-100)	99.7±0.15 (99-100)	0.9514 ^{NS}
		Open pollination	78±0.14 (77-79)	92±0.14 (91-93)	84.5±0.16 (84-85)	96.7±0.15 (96-97)	8.152E-43^{S}
2	Percentage seed set	Bagging	41.7±0.26 (40-43)	44.9±0.17 (44-46)	43.5±0.16 (43-44)	45.6±0.05 (45-46)	1046E-15^{S}
		Open pollination	41.5±0.16 (41-42)	42.7±0.15 (42-43)	41.4±0.16 (41-42)	42.7±0.15 (42-43)	5.842E-08^{S}

Mean± Standard error* Range** ^{S}Significant at p<0.05



78±0.14 (77-79)- 96.7±0.15 (96-97) in different populations. However, seed set in all the population is low and hovers around 42% (Table 6).

Bagging

Individual in florescences (n=30) were bagged in bud condition to check fruit and seed set on unassisted selfing. Fruit set in these flowers is nearing 100 %at all the sites. Here also, Seed set is low and ranges from 41.7 to 45.6% (Table 6).

Discussion

Despite having all contrivances for cross pollination, *Hyptis suaveolens* is predominantly selfer in area of study though it is reported to practice mixed mating system by other authors (Aluri (1990) and Aluri and Reddi (1996)). From the data on reproductive output (Figure 3), it is clearly seen that there is around 100% fruit set on bagging (self-pollination) and very high amount on open pollination as well (96.7%). Percentage seed set albeit is quite low in all the populations.

Parameters like availability of maternal resources, competitiveness among embryos for maternal resources or active female choice are known to be largely responsible for the low seed set in many species (Arathi *et al.*, 1999). In *H. suaveolens* however it is a regular feature in all populations including under controlled conditions.

It is clearly seen that the plants of the species never produces seed more than 50% seed/fruit and this abortion of ovule is congruous throughout the various populations explored. It is unlikely that the pattern of ovule abortion is related to phenotypic response of plant towards different environmental

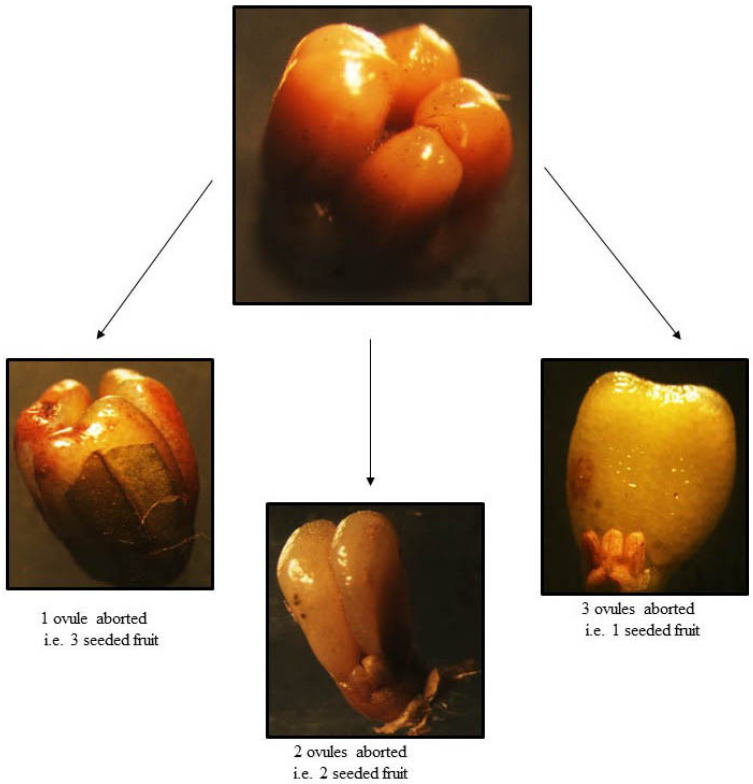


Fig. 4. Pattern of ovule abortion in *H. suaveolens*

conditions. It is confirmed experimentally that even in controlled conditions, this plant species shows abortion of ovules. Pattern of ovule abortion in *H. suaveolens* leads to conclusion that consistent ovule abortion in each flower may not result from lack of pollination or maternal resources. The onset of abortion occurs after the pollination event as is evident from florescence microscopy. This may be an adaptive strategy of this species for the successful dispersal of seeds. When flower of *Hyptis* is mature, corolla abscises and calyx dries and remains intact to the plant. Therefore, it acts as a vehicle for the dispersal of seeds. Abortion of ovules may be a strategy of the plant for long distance dispersal as it makes the fruit light. Examples of ovule abortion related to seed dispersal exist in Lamiaceae family (Caspers and Wiens, 1981). For example, *Salazaria mexicana* (Lamiaceae) also produces 4 ovules/ovary (a typical characterstic of mint family). In this species, preliminary data suggest that frequency of flowers producing single nutlet is twice of that producing double nutlet and 8 times higher than with 3 nutlets. It occasionally produces 4 nutlets (Casper and Weins, 1981).

Invariable ovule abortion across all populations including plants which are raised in botanical garden points toward the involvement of genetic factors in spite of adequate pollination. Ovule abortion in *H. suaveolens* is may be helping to increase the dispersal distance of seeds in this species to larger areas and this may be one of the contributing factors for theaggressive nature and invasiveness of this species.

Conclusion

Ovule abortion in *H. suaveolens*, where some ovules fail to develop into mature seeds, potentially aids in the dispersal of seeds over larger areas. With fewer seeds competing for resources within the parent plant's vicinity, mature seeds have a better chance to thrive and are dispersed over greater distances by wind, water, or animals. This wider dispersal range allows the species to colonize new areas more effectively, contributing to its aggressive nature and invasiveness as it can outcompete native vegetation and dominate ecosystems, thus causing ecological imbalances.

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Conflict of interest

We hereby declare that we have no known conflict of interest or personal relationships that could have appeared to influence the work reported in this paper.

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