# Reproductive ecology of *Cleome gynandra* and *Cleome viscosa* (*Capparaceae*)

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Received: September 09, 2015 ▷ Accepted: March 06, 2016

**Abstract.** *Cleome* is an important genus for the study of self- and cross-pollination through polymorphism, and adaptations for pollination by both invertebrate and vertebrate pollinators. *Cleome gynandra* is polygamodioecious, representing functionally staminate short gynoecium floral type and functionally hermaphrodite medium and long gynoecium floral types. *Cleome viscosa* is functionally hermaphroditic with short, medium and long gynoecium floral types. Both species are self-compatible and autogamous. *Cleome gynandra* is ambophilous, while *C. viscosa* is entomophilous. In both species, mature and dry pods dehisce septicidally and disperse seeds by wind. The seeds of *C. gynandra* germinate immediately and produce new plants, if soil has moisture, while those of *C. viscosa* remain dormant and germinate only during rainy season. *Cleome viscosa* is a $C_3$ plant growing in cool environments, while *C. gynandra* is a $C_4$ plant growing in warm environments. *Cleome gynandra* is a climate resilient species and suitable for the restoration of ecologically degraded habitats and also habitats with warm conditions.

**Key words:** ambophily, entomophily, hermaphroditism, polygamodioecy

## Introduction

*Cleome* is the largest genus in *Capparaceae*, with over 200 annual or perennial herb and shrub species widely distributed in pantropical and subtropical regions of the world. They are distributed in America, in the Old World, mostly in Africa and the Middle East. In India, about fifteen *Cleome* species have been reported (Jacobs 1960; Iltis 1967; Bruinsma 1985; Raghavan 1993; Aparadh & al. 2012). *Cleome* is a suitable subject for the study of versatile adaptations which permit it to invade and flourish well in diverse habitats due to possession both $C_3$ and $C_4$ photosynthetic mechanisms (Benedito 2007). *Cleome* exhibits polymorphism (Iltis 1967) and "super dioecy" (Murneek 1927). Many *Cleome* species are protandrous, self-compatible and predominantly out-crossing (Iltis 1967). *Cleome spinosa* is polygamodioecious, represented by three floral types – pistillate, hermaphroditic and staminate; bats are its pollinators, while sphingids, bees and hummingbirds are its nectar thieves (Machado & al. 2006). *Cleome lutea* and *C. serrulata* produce staminate and hermaphrodite flowers, the production rate of which varies depending on fruiting rate. Their flowers attract bees, wasps and butterflies during daylight hours (Cane 2008). *Isomeris arborea* (*Capparaceae*) produces greater numbers of hermaphroditic flowers and fewer male flowers per inflorescence, when the flowers are damaged by the nitidulid beetle, *Meligethes rufimanus* (Krupnick & Weis 1998).

*Cleome viscosa* is a common weed found all over India. It is used in Ayurveda and other systems of medicine to cure many diseases, such as liver disease, chronic painful joints and mental disorders (Asolkar & al. 1992; Nadkarni 1998; Chatterjee & Pakrashi 1991). It is used as a source of vitamin-C and iron, and as a green leafy vegetable by poorer segment of the population (Theophilus & Arulanantham 1949).

Seeds are used as a condiment due to their pleasant flavor by the people of the Garhwal Himalaya. Poor people who cannot afford cumin mostly use *Cleome*. Because of its piquant flavor, along with other spices it is now used extensively as a condiment in the preparation of pickling spices, sausages, green and other vegetables, curries and pulses. A kilogram of *Cleome* seed is exchanged for 7 kg of unhusked rice or 4 kg of wheat. Exchange is not merely for economic gain but involves reciprocity relationships among families (Maikhuri & al. 2000). The medicinal uses of *C. gynandra* are not known. The intent of the present study is to understand the functionality of sexual system in the floral types of *Cleome gynandra* and *C. viscosa* with reference to natural fruit set rates and to characterize pollination syndromes functional through pollinating agents. Further, a careful effort is made to highlight their medicinal/economic values and importance in eco-restoration based on the existing relevant literature.

## Material and methods

**Floral biology**: *Cleome gynandra and Cleome viscosa* (*Capparaceae*) growing seasonally in Visakhapatnam (17°42'N and 82°18'E), Andhra Pradesh, India, were selected for study during 2012–2014. Twenty-five fresh flowers were used for each species to record the floral details. Anthesis schedule and anther dehiscence timing were recorded by observing twenty -five marked mature buds in the field. For both species, 20 undehisced anthers from each flower morph on ten plants were used to determine pollen output and study pollen grain characteristics as per the protocols given in Dafni & al. (2005). The protocols stated in Mondal & al. (2009) were followed to identify amino acid types present in the pollen. The protocols described in Sadasivam & Manickam (1997) and Lowry & al. (1951) were followed to estimate protein content in the pollen. The pollen-ovule ratio was determined as per the protocol given in Cruden (1977). In *C. gynandra*, the pollen-ovule ratio was calculated separately for each flower morph, taking into account the constant number of stamens and average number of ovules per flower. In *C. viscosa,* the pollen-ovule ratio was calculated separately for each flower morph, taking into account the average number of stamens and the average number of ovules per flower.

In *C. gynandra*, ten mature buds were bagged and removed three hours after anthesis. Then, micropipette was inserted into the flower base to extract nectar for measurement. The average of nectar of ten flowers was taken as the total volume of nectar/flower and the same sample was used to measure nectar sugar concentration (Dafni & al. 2005). The sugar content/flower is expressed as the product of nectar volume and sugar concentration per unit volume, mg/µl (Dafni & al. 2005). The caloric reward of nectar/flower/day was measured as per the formula given in Heinrich (1975). Paper chromatography method described in Dafni & al. (2005) was followed to identify the amino acid types in the nectar. Ten flowers, each from five individuals of each plant species, were used to test stigma receptivity. It was tested with hydrogen peroxide from mature bud stage to flower closure/drop as per Dafni & al. (2005). Further, the receptivity was also observed visually, whether the stigma is shiny, wet or changing colors, or withering.

**Insect foraging activity and pollination:** The insects were observed visually and by using binoculars; the insect species that could not be identified on spot were captured and later identified with the help of the identified specimens available at the Department of Environmental Sciences, Andhra University. The hourly foraging visits of each insect species on each plant species were recorded on four occasions and the data was tabulated for further analysis. For each species, approximately a patch of five hundred flowers were selected to record the foraging visits of insects. The data obtained was used to calculate the percentage of foraging visits of each category of insects per day in order to understand the relative importance of each category of insects. The insects were observed on a number of occasions on each plant species for their foraging behavior such as mode of approach, landing, probing behavior, the type of forage collected, contact with essential organs and inter-plant foraging activity. The hourly forage collection activity of each species was also recorded to understand whether any relationship exists between standing crop of nectar or pollen and flower visiting activity.

**Fruiting behavior**: Two hundred flowers on twenty individual plants of each plant species were tagged prior to anthesis and followed for fruit and seed set for two weeks. The resulting fruit and seed output were pooled up for calculating fruit and seed set rates for each species. Fruit maturation period, the fruit and

seed characteristics were recorded. Fruit and seed dispersal modes were carefully observed. The aspects of seed germination and establishment of populations were observed briefly.

## Results

### *Cleome gynandra* L.

**Plant phenology and flower morphology:** It is an erect branching annual weedy herb, which grows up to 60 cm, in full sunlight in moist and well drained soils. The plant grows throughout the year, if the soil is moderately wet. The flowering and fruiting events occur throughout the year at population level. However, the vegetative growth, flowering and fruiting events occur simultaneously and they are very prominent during August-September. During rainy season, the plant produces pure stands in well-drained sunlight-exposed soils. The other concurrently growing plants along with this weed include: *Cleome viscosa* (*Capparaceae*), *Boerhaavia diffusa* (*Nyctaginaceae*), *Euphorbia hirta, Phyllanthus niruri*, *Acalypha indica,* (*Euphorbiaceae*), *Cardiospermum halicacabum* (*Sapindaceae*), and *Sida cordata* (*Malvaceae*). It flowers during August–December. The inflorescence is a terminal raceme with many flowers. The flowers are of two types: staminate consisting of residual ovary devoid of ovules, and bisexual consisting of functional ovary and fertile stamens. The bisexual floral type is classified into four different flower morphs based especially on the length of gynoecium: Medium Gynoecium Flowers (MGF), Long Gynoecium Flowers (LGF), Medium Gynoecium Short Stamen Flowers (MGSSF) and Medium Gynoecium Sessile Shortest Stamen Flowers (MGSeSF). The flower morphs, SGF, MGF and LGF are produced in the same individual, while the other two flower morphs are produced singly on different individual plants. At population level, the percentage of plants producing SGF, MGF and LGF is 60 %, of MGSSF 18 % and of MGSeSF 22 %. Morphologically, all flower morphs look alike but closer examination only indicates certain differences in these flower morphs (Tables 1 and 4). The plants producing SGF, MGF and LGF are common, while those producing MGSSF and MGSeSF are uncommon. The percentage of SGF gradually decreased from initial to final phase of flowering while that of MGF and LGF gradually increased from initial to final phase of flowering. But, flower morph-wise, the SGF constituted 48–60 %, MGF 17–22 % and LGF 23–30 % of the total flower production (Table 2).

**Table 1. Morphometrics of floral sex organs in the floral types and morphs of *Cleome gynandra*.**

| Floral structure | Staminate floral type | Hermaphrodite floral type – flower morphs | | | |
|---|---|---|---|---|---|
| | Short Gynoecium flower morph (mean±s.d.) | Medium Gynoecium flower morph (mean±s.d.) | Long Gynoecium flower morph (mean±s.d.) | Medium Gynoecium Short Stamen flower morph (mean±s.d.) | Medium Gynoecium Sessile Shortest Stamen flower morph (mean±s.d.) |
| Gynophore (mm) | 1±0.4 | 11±1 | 8±0.4 | 13±0.4 | 5±0.8 |
| Gynoecium (mm) | 2±0.4 | 18±0.6 | 21±0.6 | 15±0.4 | 13±0.4 |
| Stamen (mm) | 22±0.4 | 25±0.4 | 24±0.4 | 7±0.4 | 2±0.5 |

**Table 4. Ovule number in the floral types/morphs of *Cleome gynandra*.**

| Floral type/ morph | Sample size | Range | Mean±S.D. |
|---|---|---|---|
| SGF | 20 | – | – |
| MGF | 20 | 68–175 | 116±34 |
| LGF | 20 | 66–198 | 120±55 |
| MGSSF | 20 | 21–192 | 130±50 |
| MGSeSF | 20 | 54–168 | 119±25 |

**Table 2. Percentage of common floral types/morphs in *Cleome gynandra*.**

| Floral type/ morph | Initial flowering (July 1st week) | Peak flowering (August – September) | Final flowering (October 2nd week) |
|---|---|---|---|
| SGF | 60 | 55 | 48 |
| MGF | 17 | 20 | 22 |
| LGF | 23 | 25 | 30 |

**Sample size**: 210 flowers from 30 plants at each flowering phase.

In plants producing SGF, MGF and LGF, the inflorescence produces 34 to 40 flowers over a period of two weeks; in those producing only MGSSF, the inflorescence produces 21–24 flowers over a period of about ten days; and in those producing only MGSeSF, the inflorescence produces 18 to 22 flowers over a period of about ten days. The SGF, MGF and LGF are 33 ± 0.56 mm long, while MGSSF and MGSeSF are 21 ± 0.23 mm long. The flower morphs are pedicellate and open-type, with exposed ovary and stamens. They bear androphore and the gynophore. The androphore is the part of thalamus between the sepals, petals and stamens, while the gynophore is an elongated part between the stamens and gynoecium. The two parts are collectively referred to as androgynophore. All flower morphs are white and actinomorphic. The sepals are four, green, lanceolate, connate at the base, 3 mm long

and 2 mm wide. The petals are four, white, free, elliptical to obovate, rounded at the apex, 11 mm long and 5 mm wide. The stamens are six, with long purple filaments and green exserted dithecous anthers; they are 22 ± 0.4 mm long in SGF, 25 ± 0.4 mm long in MGF, 24 ± 0.4 mm long in LGF, 7 ± 0.4 mm long in MGSSF, and 2 ± 0.5 mm long in MGSeSF (Table 1). The ovary is bicarpellary syncarpous, unilocular with numerous ovules on parietal placentation; the bicarpellary state of ovary is due to the development of a false septum during fruit development. The style is short and extends into a purple capitate stigma, which is depressed at apex.

**Floral biology**: The floral characters are similar for all five flower morphs, unless otherwise specified. The immature buds take two weeks to mature into flowers. First sepals develop and elongate fully, followed by petals, stamens, pistil and gynophores. The flowers open at dusk during 15:00–16:00 h, initially signaled by a slight relaxation of petals to create an opening at the bud apex through which first the stigma, and subsequently the entire pistil is exserted, with the convoluted gynophore and stamens still enclosed within the petals. The petals unfold and then the stamens and gynophore become fully turgid and erect. The stigma is receptive to pollen from the time of initial exsertion, while the anthers dehisce when the filaments expand fully which takes place an hour after anthesis suggesting that the flowers are protogynous. The stigma receptivity extends up to 17:00 h of the following day. The pollen output per flower varied with each flower morph and phase of flowering. The SGF, MGF and LGF produce more pollen than the other flower morphs; the total output is almost the same for SGF during initial and final phase, while it is significantly greater during the peak phase of flowering. In case of MGF, the pollen output gradually decreased from initial to final phase of flowering. In case of LGF, the pollen output was slightly less in the initial phase, when compared to that produced during the peak and final phase of flowering. In the other two flower morphs, the pollen output was almost the same during initial and final phase but it was significantly more during peak phase of flowering (Table 3).

In all five flower morphs, the pollen grains are monads, spherical, golden-yellow, powdery, 19.92 ± 4.28 μm, prolate, tricolpate, reticulate, and with incomplete reticulum. The pollen-ovule ratio varied depending on the number of ovules produced, as well as the number of pollen grains produced per flower. SGF morphs totally lack ovules. In the other four flower morphs, pollen-ovule ratio increased from initial to peak and then decreased at final phase of flowering (Table 5).

**Table 3. Pollen output per flower in the floral types/morphs of *Cleome gynandra*.**

| Floral type/ morph | Initial flowering (mean±s.d.) | Peak flowering (mean±s.d.) | Final flowering (mean±s.d.) |
|---|---|---|---|
| SGF | 60949±1572 | 63653±3317 | 61517±3820 |
| MGF | 63422±3292 | 61711±4734 | 59958±4047 |
| LGF | 63230±3636 | 66222±2998 | 65602±3968 |
| MGSSF | 23105±2057 | 24578±13910 | 22790±2303 |
| MGSeSF | 38308±4656 | 43220±1521 | 37825±4186 |

**Sample size**: Ten anthers from five plants at each flowering phase.

**Table 5. Pollen-ovule ratio in the floral types/morphs of *Cleome gynandra*.**

| Floral type/ morph | Initial flowering (mean±s.d.) | Peak flowering (mean±s.d.) | Final flowering (mean±s.d.) |
|---|---|---|---|
| SGF | – | – | – |
| MGF | 546:1 | 531:1 | 516:1 |
| LGF | 526:1 | 551:1 | 546:1 |
| MGSSF | 177:1 | 189:1 | 175:1 |
| MGSeSF | 321:1 | 363:1 | 317:1 |

In all five flower morphs, the pollen contains six essential amino acids and nine non-essential amino acids. The essential amino acids are threonine, methionine, lysine, histidine, arginine and tryptophan. The non-essential amino acids include alanine, amino-butyric acid, aspartic acid, cysteine, cystine, glycine, hydroxyproline, proline and serine. The total protein content per 1 mg of pollen is 231.25 μg in all five flower morphs. All five flower morphs are nectariferous and the nectar is secreted by the nectar glands situated at the base of each sepal; it can be seen as four minute droplets, one each at the base of the sepal which glistens against sunlight. The flowers present nectar by the time the flower opens; it is 0.26 ± 0.1 μl with 60 ± 0.5 % sugar concentration. The sugar content is 15.52 mg, which is equivalent to 2.59 Joules of energy. The nectar contains five essential and nine non-essential amino acids. The essential amino acids are threonine, lysine, histidine, arginine and tryptophan, while the non-essential amino acids are alanine, amino-butyric acid, aspartic acid, cysteine, cysteine, glutamic acid, glycine, proline, and serine. In two-day flowers, the stamens coil and contact the stigma facilitating autogamy. Further-

more, the powdery pollen is driven away by wind on sunny days, it is visible to the naked eye; this is considered to be affecting both self- and cross-pollination. The petals and stamens fall off on the third day, while sepals fall off after ten days.

**Flower visitors and pollination**: All five flower morphs were indiscriminately visited by insects as soon as they are open during dusk hours. They were foraged during 15:00–18:00 h and again during 07:00–09:00 h on the second day of anthesis. The insects recorded were bees (*Apis cerana, Trigona iridipennis, Anthophora cingulata* and *Anthophora*), an ant (*Crematogaster* sp.), one unidentified fly, and a butterfly (*Pachliopta aristolochiae*) (Table 7; Fig. 1). Of these, bees as regular and consistent visitors and the fly as an irregular visitor foraged during dusk hours on the day of anthesis and also on the following day during morning hours; the former for pollen and/or nectar, while latter for nectar only. The ant was a resident forager and gathered nectar continually moving between flowers mostly on the same or nearby plants during daylight hours. The butterfly was a regular nectar forager, but it collected nectar only during the dusk hours on the day of anthesis. The data collected on the foraging visits of insects showed that 69 % of the total visits were made during dusk hours and the remaining percentage during the morning hours of the following day. Bees constituted 90 %, the fly 7 % and butterflies 3 % of total visits made. The insects approached the flowers in upright position for probing the forage. The bees either held the staminal filaments or hovered at the anthers to collect pollen; while doing so, they did not distinguish the stamens from the stigma and tried to collect pollen from the stigma also. Such a behavior contributed to effecting pollination. They descended to the flower base and probed the flowers for collecting nectar droplets during which they never had any contact with the flower sex organs. The bees first collected pollen and then gathered nectar in the same visit; the pollen-collecting behavior effected pollination, while nectar-collecting behavior simply labeled them as nectar robbers. The fly directly descended to the petal area, landed on petals and then collected nectar droplets from the base of sepals. Its flower probing behaviour never facilitated the contact between the stamens and stigma to effect pollination and, hence, it acted as nectar robber. Similarly, the butterfly also came for collecting nectar, in so doing, its upper parts of wings always had contact with the stamens and stigma contributing to pollination. The duration of stigma receptivity period was found to be in tune with the foraging activity schedules of pollinator bees and the butterfly. The pollen being dry and powdery, it easily deposited on the dorsal surface of the pollen-probing bees and on the upper parts of wings of the nectar-feeding butterfly species. Bees moved very swiftly from flower to flower on the same or closely or distantly spaced individual plants in quest of more pollen; the absence of landing place for pollen collection appeared to be driving these bees to make visits to a number of flowers in quick succession across population(s) to promote cross-pollination. The butterfly also visited the flowers of different conspecific plants for want of nectar as there was competition for the same resource from bees and the fly.

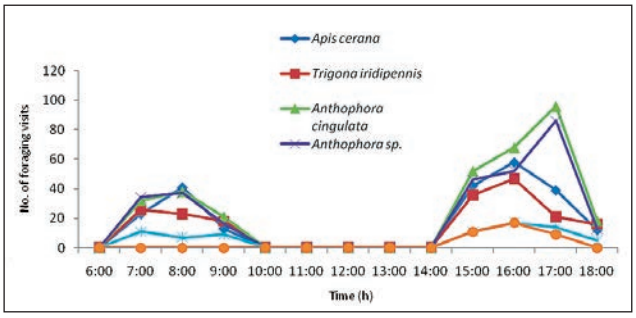


**Fig. 1.** Hourly foraging activity of insets on *Cleome gynandra* (average foraging visits recorded on four different days during wet season in 2012 and 2013).

**Table 7. List of insect foragers on *Cleome gynandra*.**

| Order | Family | Genus | Species | Common name | Forage sought |
|---|---|---|---|---|---|
| Hymenoptera | Apidae | *Apis* | *cerana* F. | Indian Honey Bee | P+N |
| | | *Trigona* | *iridipennis* Smith | Stingless Honey Bee | P+N |
| | Anthophoridae | *Anthophora* | *cingulata* F. | Blue Banded Bee | P+N |
| | | *Anthophora* sp. | – | – | P+N |
| | Formicidae | *Crematogaster* sp. | – | – | N |
| Diptera | | Fly (unidentified) | – | – | N |
| Lepidoptera | Papilionidae | *Pachliopta* | *aristolochiae* L. | Common Rose | N |

**P** = Pollen, **N** = Nectar.

**Fruiting ecology and seed dispersal**: The fruit growth and development begins immediately after pollination and fertilization, during which the ovary elongates. The fruits mature, shifting colour from green to brown within a week. The short style and capitate stigma remain so until fruit dehiscence. The natural fruit set is 98 % in both MGF and MGSeSF morphs, 99 % in LGF morphs and 96 % in MGSSF morphs (Table 6). The mature and dry fruits vary in length with each flower morph. The fruits produced by MGF are 6.20 ± 0.40 cm, those by LGF 6.80 ± 0.60 cm, those by MGSSF 3.14 ± 0.56 cm, and those by MGSeSF 2.30 ± 0.35 cm. The mature and dry fruit is a long-stalked, linear, suberect, and cylindric capsule tapering at both ends. The dry fruits dehisce septicidally releasing seeds into the air. The seeds are brown, subglobose or orbicular, 1.5 mm in diameter, with many concentric ribs and irregular cross-ribs. The seed output per fruit varies with the flower morph; it is 82.8 ± 5.51 in MGF, 148 ± 49.85 in LGF, 134.6 ± 8.40 in MGSSF, and 126.2 ± 19.12 in MGSeSF. Seed set rate varies with each flower morph; it is 71 % in MGF, 81 % in LGF, 97 % in MGSSF, and 95 % in MGSeSF (Table 6). The seeds are non-dormant and germinate within a week, if the soil is wet. But, seed germination rate is high during rainy season; then the plant forms pure stands or grows intermingled with other herbaceous flora in open, full sunlight. Seeds are minute, light in weight and disperse by wind during dry season and by rain water during rainy season. The plant reproduces exclusively by seed.

**Table 6. Fruit set and seed set in the floral types/morphs of *Cleome gynandra*.**

| Floral type/ morph | No of flowers sampled | Fruit set (%) | Seed set (%) |
|---|---|---|---|
| SGF | 100 | 0 | 0 |
| MGF | 100 | 98 | 71 |
| LGF | 100 | 99 | 81 |
| MGSSF | 100 | 96 | 97 |
| MGSeSF | 100 | 98 | 95 |

## *Cleome viscosa* L.

**Plant phenology and flower morphology**: It is an erect branching annual weedy herb, which grows up to 1 m in full sunlight, in wet or semi-wet soils at roadsides, in waste places, ruderal locations, and open places. The plant appears during early monsoon season. The lush vegetative growth occurs by July and flowering occurs during August-November based on the extent of rainfall. The plant forms pure stands in certain areas and grows as scattered individuals along with other plants, such as *Cleome gynandra, Boerhaavia diffusa* (*Nyctaginaceae*), *Euphorbia hirta, Phyllanthus niruri, Acalypha indica* (*Euphorbiaceae*), *Cardiospermum halicacabum* (*Cardiospermaceae*), *Sida cordata* (*Malvaceae*), and *Pedalium murex* (*Pedaliaceae*). The inflorescence is a lax, corymbose, 30 cm long few-flowered raceme (13.72 ± 1.34). The flowers are also borne solitary in leaf axils.

The flowers are bisexual and represent three flower morphs: Short Gynoecium Flowers (SGF), Medium Gynoecium Flowers (MGF) and Long Gynoecium Flowers (LGF); all three morphs occur on the same plant. The SGF consist of 4 mm long gynoecium, with 100 ovules and 7 mm long stamens, MGF has 8 mm long gynoecium, with 113 ovules and 8 mm long stamens, and LGF has 10 mm long gynoecium, with 162 ovules and 11 mm long stamens (Tables 8 and 11). The stamen number is 19.65 ± 3.39 in SGF, 17.35 ± 6.22 in MGF and 16.1 ± 4.99 in LGF. The production rate of these flower morphs is almost constant throughout the flowering phase; the percentage of SGF is 18–19 %, of MGF 60–62 % and of LGF 20–21 % (Table 9). All three flower morphs are pedicellate (20 mm long) and inverted-bell shaped, exposing the ovary and stamens. The pedicel is 20 mm long during flowering phase and 35–40 mm long during fruiting phase.

**Table 8. Morphometrics of gynoecium and stamens in the floral morphs of *Cleome viscosa*.**

| Floral structures | Short Gynoecium flower morph (mean±s.d.) | Medium Gynoecium flower morph (mean±s.d.) | Long Gynoecium flower morph (mean±s.d.) |
|---|---|---|---|
| Gynoecium (mm) | 4±1 | 8±1 | 10±1 |
| Stamen (mm) | 7±1 | 8±1 | 11±1 |

**Table 11. Ovule number in the floral morphs of *Cleome viscosa*.**

| Floral morph | Sample size | Range | Mean±S.D. |
|---|---|---|---|
| SGF | 20 | 62–128 | 100±72 |
| MGF | 20 | 96–143 | 113±18 |
| LGF | 20 | 89–215 | 162±44 |

**Table 9. Percentage of floral morphs of *Cleome viscosa* at different phases of flowering.**

| Floral morph | Initial flowering (July 1st week) (mean±s.d.) | Peak flowering (August–September) (mean±s.d.) | Final flowering (October 4th week) (mean±s.d.) |
|---|---|---|---|
| SGF | 19 | 18 | 18 |
| MGF | 60 | 62 | 61 |
| LGF | 21 | 20 | 21 |

The flower morphs are yellow and actinomorphic. The sepals are four, green but purple outside at the base, lanceolate, free but connate at the base, glabrous inside, glandular hairy outside, 5–6 mm long and 1–2 mm wide. The petals are four, yellow, free, oblong-spathulate, base cuneate with a 5 mm long claw at base, rounded at the tip, glabrous, 7–12 mm long and 3–5 mm wide. The stamens vary in number as mentioned above for all three flower morphs. They are free, glabrous, filaments almost filiform, anthers linear, green, exserted and dithecous. The ovary is sessile, oblong-cylindric, glandular-pubescent, bicarpellary syncarpous, unilocular with numerous ovules on parietal placentation; the bicarpellary state of ovary is due to the development of a false septum during fruit development. The style is short (2–5 mm long), slender and extends into a capitate stigma.

**Floral biology**: The floral characters are similar for all three flower morphs unless otherwise specified. The mature buds begin to open at 02:30 h by showing slits between petals and after half an hour, the stamens protrude through the slits. After a short while, anthesis is complete and the petals reflex, exposing the stamens and stigma. The anthesis occurs during 03:00–04:00 h and anther dehiscence occurs by longitudinal slits simultaneously. The stigma is receptive to pollen two hours after anthesis and ceases its receptivity by noontime of the same day. During receptive period, it is shiny and glistens against sunlight. The pollen output per flower in all three flower morphs slightly varied at initial, peak and final phase of flowering. Among these morphs, the SGF morphs produce the highest number of pollen grains followed by MGF and LGF morphs, and the same trend is evidenced throughout the flowering season (Table 10).

**Table 10. Pollen output per flower in the floral morphs of *Cleome viscosa*.**

| Floral morph | Initial flowering (mean±s.d.) | Peak flowering (mean±s.d.) | Final flowering (mean±s.d.) |
|---|---|---|---|
| SGF | 78140±893 | 76281±3270 | 75707±2285 |
| MGF | 68022±1960 | 68019±1744 | 69098±3301 |
| LGF | 63386±848 | 63476±1760 | 62165±2763 |

The pollen grains are identical and possess similar characters in all three flower morphs. They are monads, triangular, yellow, slightly sticky, prolate, tricolpate, lobate, with veiculate ornamentation and tectum reticulated. The pollen grain size varied with each flower morph, it is 19.80 ± 4.20μm in SGF, 27.45 ± 5.23μm in MGF and 23.62 ± 5.71μm in LGF. The pollen-ovule ratio varies depending on the number of ovules produced and the number of pollen grains produced per flower. The ratio is the highest in SGF and the lowest in LGF morphs; almost the same trend exists throughout the flowering season (Table 12).

**Table 12. Pollen-ovule ratio in three floral morphs of *Cleome viscosa*.**

| Floral morph | Initial flowering (mean±s.d.) | Peak flowering (mean±s.d.) | Final flowering (mean±s.d.) |
|---|---|---|---|
| SGF | 782:1 | 763:1 | 757:1 |
| MGF | 602:1 | 602:1 | 610:1 |
| LGF | 391:1 | 392:1 | 384:1 |

In all three morphs, the pollen contains six essential amino acids and nine non-essential amino acids. The essential amino acids are threonine, methionine, lysine, histidine, arginine, and tryptophan. The non-essential amino acids include alanine, amino-butyric acid, aspartic acid, cysteine, cystine, glycine, hydroxyproline, proline, and serine. The total protein content per 1 mg of pollen is 90.45 μg in all three flower morphs. All three flower morphs are nectariferous and the nectar is secreted in traces or minutely by the nectar glands situated at the flower base around the ovary. The flowers present nectar by the time the flower opens and is covered by the hairs around the ovary. The petals fold back by noon on the day of anthesis, enclosing the stamens and stigma. The closure of petals facilitates the contact between the stamens and stigma and effects autogamy. The flowers remain in that state, wither away the next day and drop off on the 3rd day.

**Flower visitors and pollination**: The floral buds of all three morphs provide breeding site for two species of thrips (unidentified). These thrips occurred during bud and flower phase, and fed on nectar and pollen during and after anthesis. Insect foragers were found to visit all three flower morphs indiscriminately during 07:00–12:00 h, with peak activity during 08:00–09:00 h (Figs. 2, 3). The insects recorded were bees (*Apis dorsata, A. cerana, A. florea, Trigona iridipennis* (*Apidae*), *Halictus* sp., *Nomia* sp. and one unidentified bee (*Halictidae*), a fly (*Helophilus* sp.) and butterflies (*Pachliopta hector, Catopsilia pomona, C. pyranthe*, *Eurema hecabe, Pieris canidia, Cepora nerissa* and *Anaphaeis aurota*, *Acraea violae* and *Danaus chrysippus, Castalius romison* and *Chilades laius* (Table 13).

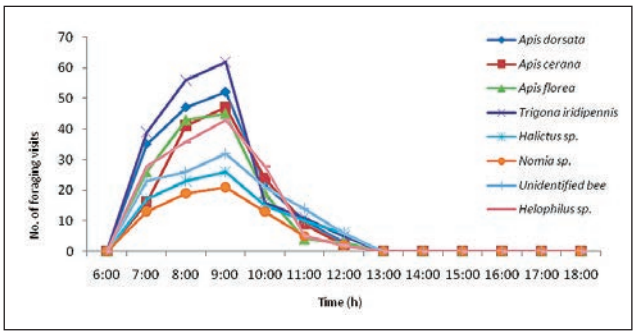


**Fig. 2.** Hourly foraging visits of been and flies on *Cleome viscosa* (average foraging visits recorded on four different days during wet season in 2012 and 2013).

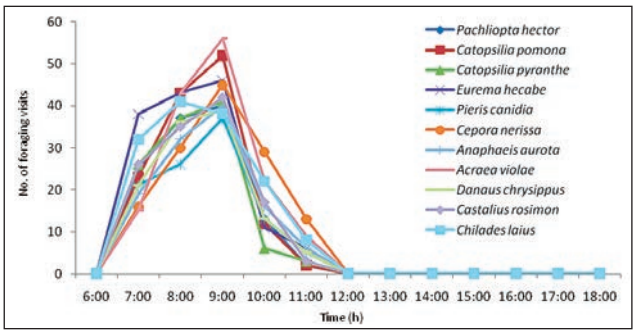


**Fig. 3.** Hourly foraging activity of butterflies on *Cleome viscosa* (average foraging visits recorded on four different days during wet season in 2012 and 2013).

**Table 13. List of insect foragers on *Cleome viscosa*.**

| Order | Family | Genus | Species | Common name | Forage sought |
|---|---|---|---|---|---|
| Hymenoptera | Apidae | *Apis* | *dorsata* F. | Rock Honey Bee | P+N |
| | | *Apis* | *cerana* F. | Indian Honey Bee | P+N |
| | | *Apis* | *florea* F. | Dwarf Honey Bee | P+N |
| | | *Trigona* | *iridipennis* smith | Stingless Honey Bee | P+N |
| | Halictidae | *Halictus* sp. | – | – | P+N |
| | | *Nomia* sp. | – | – | P+N |
| | | Bee (unidentified) | – | – | P+N |
| Diptera | Syrphidae | *Helophilus* sp. | – | – | P |
| Thysanoptera | Thripidae | Thrips (unidentified) | – | – | P+N |
| | | Thrips (unidentified) | – | – | P+N |
| Lepidoptera | Papilionidae | *Pachiliopta* | *hector* L. | Crimson Rose | N |
| | Pieridae | *Catopsilia* | *pomona* F. | Common Emigrant | N |
| | | *Catopsilia* | *pyranthe* L. | Mottled Emigrant | N |
| | | *Eurema* | *hecabe* L. | Common Grass Yellow | N |
| | | *Pieris* | *canidia* L. | Indian Cabbage White | N |
| | | *Cepora* | *nerissa* F. | Common Gull | N |
| | | *Anaphaeis* | *aurota* F. | Pioneer | N |
| | Nymphalidae | *Acraea* | *violae* F. | Tawny Coster | N |
| | | *Danaus* | *chrysippus* L. | Plain Tiger | N |
| | Lycaenidae | *Castalius* | *rosimon* F. | Common Pierrot | N |
| | | *Chilades* | *laius* Stoll | Lime Blue | N |

Of these, bees and butterflies were the regular foragers during the entire flowering season. The bees foraged for both pollen and nectar, the fly for only pollen and butterflies only for nectar. Bees made 38 %, the fly 6 % and butterflies 56 % of total visits on any given day. Among butterflies, pierids made 62 %, nymphalids 20 %, lycaenids 10 % ,and papilionids 8 % of total visits. These insects approached the flowers in upright position, landed on the petals and probed the flowers for pollen and/or nectar. While collecting pollen from the anthers, the bees gained contact with their forehead and ventral side, due to which pollen was transferred from the anthers to their body. They did not show any discriminatory behavior between the stamens and the stigma and, hence, attempts to collect pollen from both sex organs were considered to be resulting in pollination. While collecting nectar, the bees reached the nectar location and in so doing, their ventral as well as dorsal surface had contact with the stamens and stigma and this nectar probing behavior also contributed to pollination. While collecting pollen, the fly species contacted the stamens and stigma with its forehead only and such a contact was considered to be effecting pollination. While collecting nectar, the butterflies contacted the stamens and stigma with their proboscis and forehead effecting pollination. The bees spent relatively more time per flower while collecting pollen, as compared to nectar collection. While collecting nectar, both bees and butterflies moved quickly between flowers and plants within and between populations.

**Fruiting ecology and seed dispersal**: The fruit growth and development begins immediately after pollination and fertilization, during which the ovary elongates. The fruits mature within a week shifting colour from green to brown. The natural fruit set is 98 % in SGF, 100 % in MGF and 99 % in LGF (Table 14).

**Table 14. Fruit set and seed set in the floral morphs of *Cleome viscosa*.**

| Floral morph | Flowers sampled | Fruit set (%) | Seed set (%) |
|---|---|---|---|
| SGF | 100 | 98 | 90 |
| MGF | 100 | 100 | 99 |
| LGF | 100 | 99 | 94 |

The mature and dry fruits vary in length with each flower morph. The fruits produced from SGF are 5.30 ± 0.51 cm, those from MGF 6.30 ± 0.32 cm and those from LGF 7.40 ± 0.40 cm. The dry fruits are long-stalked, linear, hairy, suberect, and cylindric capsules tapering at both ends, the upper end forms 3 mm long stipe. They dehisce septicidally from the tip to the base by the separation of false septum formed in ovary and release seeds into the air. The seeds are brown, subglobose or orbicular with narrow cleft, 1–1.5 mm diameter, with strong cross-ribs and weak concentric ribs. The seed output per fruit varies with the flower morph: it is 89.80 ± 28.48 in SGF, 114.23 ± 19.80 in MGF and 152.61 ± 40.37 in LGF. Seed set rate varies with each flower morph: it is 90 % in SGF, 99 % in MGF, 94 % in LGF (Table 13). The seeds are dormant and germinate during rainy season. Seeds are minute and light in weight and disperse by wind during dry season and by rain water during rainy season. The plant reproduces exclusively by seed.

## Discussion

The flowering phenology of *Cleome viscosa* and *C. gynandra* suggests that it represents a modified steady state flowering (Gentry 1974). Both species produce flowers in high numbers at plant level. They occur together and flower concurrently; they show patchy distribution as pure stands in open sites and also scattered occurrence in other areas, which are occupied predominantly by *Sida* and *Triumfetta* along with other herbaceous flora. The steady state flowering and patchy distribution of plants enhance attraction to flower visitors and maximize fruit/seed set in these two species.

In *Capparaceae*, andromonoecy (*Capparis herbacea*, *Cleome lutea* and *C. serrulata*), trimonoecy (*Cleome rosea*) and polygamodiecy (*Cleome spinosa*) sexual systems have been reported (Inocencio & al. 2006; Carvalho 2002; Machado & al. 2006; Cane 2008). In the present study, *Cleome gynandra* is polygamodioecious, consisting of andromonoecious individuals producing both staminate and fertile hermaphrodite floral types and fertile hermaphrodite individuals. In andromonoecious individuals, short gynoecium floral type is functionally staminate, while hermaphrodite flowers represent medium and long gynoecium floral types. The hermaphrodite individuals produce either medium gynoecium short stamen floral type, or medium gynoecium sessile stamen floral type. This polygamodioecious sexual system supported by highest fruit and seed set rates in hermaphrodite floral types indicates that *C. gynandra* is self-compatible and autogamous. Wind causes self- and cross-pollination due to liberation of light and powdery pollen grains on sunny days during rainy season. Further, intra-plant foraging activity of insects results in self-pollination, while inter-plant foraging activity across the population(s) brings about cross-pollination. The success of these pollination modes is associated with the rate of pollen production and, in line with this, pollen is produced in huge amount at flower and plant level. The pollen production rate is very high and it is almost similar in all three floral types of andromonoecious individuals, while it is far less in the floral types of hermaphrodite individuals, thus needing the latter to receive pollen from andromonoecious individuals, especially for cross-pollination. The simultaneous production of functionally male and hermaphrodite flowers in andromonoecious individuals increases the pollen flow, leading to elevated pollen-ovule ratio, which further enhances the chance of a sufficient pollen charge on pollinators body and, consequently, on stigmatic surface (Heithaus & al. 1974). The staminate or male-biased sex ratio throughout the flowering season appears to be due to the need for pollen overproduction to ensure successful pollination (Inocencio & al. 2006). Therefore, the complex sexual system observed in *C. gynandra* seems to be favouring its reproductive success with a high fruit and seed set.

*Cleome viscosa* is a hermaphroditic species producing short gynoecium, medium gynoecium and long gynoecium floral morphs, with fertile pollen and functional ovaries in 1:3:1 ratio on the same individual almost throughout the flowering season. This sexual system, coupled with highest fruit and seed set rates in all three floral morphs, indicates that the plant is self-compatible and autogamous. The closure of petals facilitates the coiling stamens to contact the capitate stigma and effect autogamy. Furthermore, intra-plant foraging activity of insects results in self-pollination, while inter-plant foraging activity across the population(s) brings about cross-pollination. The success of these pollination modes is associated with the rate of pollen production and, in line with this, pollen is produced in huge amount at flower and plant level. The pollen production rate in the medium gynoecium floral morphs is almost three times greater than that produced in the other two floral morphs; it is almost the same throughout the flowering season. Such a high rate of pollen production at plant level increases the pollen flow, leading to elevated pollen-ovule ratio and further enhances the chance of a sufficient pollen charge on pollinators body and, consequently, on stigmatic surface (Heithaus & al. 1974). Pollen overproduction appears to be the need for maximizing cross-pollination (Inocencio & al. 2006). Therefore, the hermaphroditic sexual system with trimorphic floral forms observed in *C. viscosa* seems to be favouring its reproductive success with a high fruit and seed set.

Some studies have shown that plants will alter their sexual expression when resources, such as nutrient or light (Solomon 1985), become limited and when conditions become more severe (Wells & Lloyd 1991), or when biotic changes to the plant take place (foliar herbivory or pathogenic infestion) (Lokesha & Vasudeva 1993). In both *C. gynandra* and *C. viscosa*, floral sex is not labile and the ratios of floral types remain almost unchanged throughout the flowering season, since there is only slight change in pollen and ovule production rate during different phases of flowering. The consistency in the expression of functional floral sex could be related to the availability of adequate nutrients, light and also their ability to outcompete with the co-occurring and co-flowering herbaceous flora. Therefore, the two *Cleome* species are not exposed to environmental stress in the study areas.

In genus *Capparis*, apomixis is reported in *C. frondosa* (Mauritzon 1935), self-compatibility in *C. flexuosa, C. verrucosa* (Ruiz & Arroyo 1978), *C. pittieri* (Bawa & al. 1985), *C. atamisquea* (Aizen & Feinsinger 1994), and *C. retusa* (Bianchi & Gibbs 2000). The members of genus *Cleome* have been reported to be polymorphic, protandrous and cross-pollinated; but many species are self-compatible (Iltis 1967). *Cleome gynandra* and *C. viscosa* in the present study can be considered as facultative autogamous species, ripening fruits and viable seeds even in the absence of pollinators. *C. gynandra* is protogynous, while *C. viscosa* is protandrous, but both are self-compatible. Their floral characteristics, such as low investment in attractive structures as showy petals, nectar and pollen, brief anthesis schedule, self-compatibility, brief period of stigma receptivity (extended to the 2$^{nd}$ day in *C. gynandra* due to evening anthesis), and delayed autonomous selfing, confirm that they are facultative autogamous with the option kept open for allogamy (Faegri & van der Pijl 1979; Cruden & Miller-Ward 1981). Delayed autonomous selfing is regarded to be adaptive, because it apparently assures seed production, when pollinators are scarce or absent, yet allows outcrossing to predominate, when they are abundant (Wyatt 1983). Such a breeding system is a "fail-safe system" to assure the plant to achieve pollination and set fruit and seed in the absence of insects.

*Cleome gynandra* and *C. viscosa* flowers are actinomorphic; the petals are conspicuously white in the former and yellow in the latter species. Despite the existence of four nectaries at the base of ovary in both species, nectar is secreted in minute volume in *C. gynandra* and in traces in *C. viscosa*. The presence of this level of nectar appears to be a strategy to conserve the nutrient energy and attract insect visitors for pollination. Furthermore, the pollen production rate is significantly high in *C. gynandra,* as compared to the pollen production rate in *C. viscosa*. Actinomorphy with free petals allows easy access for the insects to pollen and nectar resources in both species. However, *C. gynandra* with a good volume of nectar and high amount of pollen is able to attract only bees as consistent foragers, while *C. viscosa* with traces of nectar and comparably less amount of pollen is able to attract both bees and butterflies as consistent foragers, suggesting that the white floral colour of *C. gynandra* and the yellow floral colour of *C. viscosa* are equally attractive to bees, while only the

yellow floral colour of *C. viscosa* appears to be attractive to butterflies.

Machado & al. (2006) reported that *Cleome spinosa* is visited by bats, sphingids, bees, and hummingbirds, but only bats are the effective pollinators, while all others are nectar thieves. Cane (2008) reported that in *Cleome lutea* and *C. serrulata*, the flowers do not attract nocturnal visitors but attract plentiful bees, wasps and butterflies during daylight hours. Chweya & Mnzava (1997) stated that *C. gynandra* is pollinated especially by honeybees, spiders and the wind. The present study shows that in *C. gynandra*, the flower-opening occurs during dusk hours and it is pollinated principally by bees during dusk hours and again during the forenoon period of the next day. Anemophily occurs on clear sunny days due to freely dispersed dry, powdery pollen grains from the anthers. It is important in the afternoon period, since insects do not visit the second-day flowers. The ability of the plant to use both bees or insects and wind is indicative of ambophily. In *C. viscosa*, anthesis occurs during morning hours and it is pollinated principally by bees and butterflies; in the latter category, pierids are prominent pollinators. Wind has no role in the pollination of this species, since its pollen is sticky and does not disperse in powdery form. Therefore, it is exclusively entomophilous, and if categorized specifically, it is both melittophilous and psychophilous. Aparadh & Karadge (2011) described pollen characteristics for these two species and the present study confirms the same regarding pollen features. Ruiz & al. (1997) reported that the pollen morphology and exine sculpturing of *Cleome* species do not indicate any relationship with pollination syndromes. It appears to be true in the present study also for *Cleome* species, especially *C. gynandra*, which has mixed characteristics adapted for versatile pollination syndrome, anemophily and entomophily.

*Cleome gynandra* and *C. viscosa* produce pollen in copious amount and in both species it is a source of six essential amino acids and nine non-essential amino acids *sensu* DeGroot (1953). The protein content is relatively higher in *C. gynandra* than in *C. viscosa*. Therefore, the pollen of these two species is nutritionally important for bees. Since pollen production rate is huge at plant and population level in both species, their pollen collection activity may not significantly reduce the pollen availability for pollination purpose. The nectar of *C. gynandra* is also a source of five essential amino acids and nine non-essential amino acids. As the bees also collect nectar along with butterflies and other insects, the presence of minute volume of nectar in *C. gynandra* and traces of nectar in *C. viscosa* compel them to visit the flowers of several plants promoting cross-pollination. In *C. gynandra*, the pollen and nectar-feeding activity of thrips may further drive the pollinating bees and butterflies to visit a number of conspecific plants for the floral rewards, due to which cross-pollination is maximized.

Ekpong (2009) reported that *Cleome* plants are mainly propagated by seed. Keller & Kollmann (1999) observed that seed germination in *Cleome* is erratic and may take up to one year to reach maximum germination. Chweya & Mnzava (1997) have also opined that seed germination is poor and delayed in *Cleome,* due to dormancy and this is one of the major problems in the propagation of these plants. Aziz & Shaukat (2012) reported that *C. viscosa* completes its life from seed germination to seed set in 12 weeks. In the present study, *C. gynandra* and *C. viscosa* release seeds from the pods explosively and they are dispersed by wind due to their light weight; they germinate immediately and produce new plants, if soil has moisture in case of *C. gynandra,* but remain dormant and germinate only during rainy season in case of *C. viscosa*. Furthermore, the seeds of both species also disperse during early rainy season by rain water. Kokwaro (1976) reported that *C. gynandra* is spread by birds, and by dispersal owing to capsule dehiscence. Therefore, the dispersal modes recorded in these species enable them to migrate and colonize new areas.

Baker & Stebbins (1965) stated that *Cleome* species possess pollination traits that have long been considered favourable for colonists. Cane (2008) reported that self-fertility enables the first individual that colonizes a site to produce viable seed. If pollinators are absent, perhaps following some ecological perturbation such as fire or flood, they are capable of autogamy and facilitate self-pollination. In *C. gynandra* and *C. viscosa*, pollination traits are expected to favour self-fertility, when pollinator services might be unreliable. The ability of these plants to use a facultative autogamous breeding system is advantageous, as the delayed autogamy would enable them to set fruit and spread rapidly onto new sites without precluding the ability to exchange genes within the

population at large, when one develops through outcrossing (Klips & Snow 1997).

Krupnick & Weis (1998) reported that *Isomeris arborea* (*Capparaceae*) produces greater numbers of hermaphroditic flowers and fewer male flowers per inflorescence, when the flowers are damaged by the nitidulid beetle, *Meligethes rufimanus*. Even though more hermaphroditic flowers are produced per inflorescence, damage to the ovaries by the flower-feeding insects is so extensive that fruit production is lower among plants exposed to herbivory, as compared to plants protected from herbivory. Under low-herbivore conditions in natural habitats, this alternation of sexes is apparent in *I. arborea* and also in *Cleome spinosa*. Herbivory damage thus affects male and female reproductive success in ways beyond its effect on resource allocation to sex. In this context, Strauss & Irwin (2004) stated that herbivore damage can indirectly affect plant fecundity by influencing interactions between plants and pollinators. In the present study, *C. gynandra* and *C. viscosa* are not exposed to herbivory, despite the presence of certain beetles which commonly feed on the flowers of herbaceous flora, such as *Mylabris phalerata* feeding on the occurring species *Sida acuta* and *S. cordifolia*. Therefore, *Cleome* species appear to be resistant to floral herbivory and, hence, are insulated from floral herbivores that affect their reproductive success.

The genus *Cleome* is a suitable subject for the study of versatile adaptations, which permit it to invade and flourish well in diverse habitats, due to possession of both $C_3$ and $C_4$ photosynthetic mechanisms (Benedito 2007). The $C_4$ plants have advantages, when limitation on carbon acquisition is imposed by high temperature, drought and salinity stress, and show high rates of photosynthesis and efficient use of water and nitrogen, while $C_3$ plants are relatively inefficient because oxygen competes with $CO_2$ for the active sites of Rubisco enzyme and some of the fixed carbon is lost by photorespiration (Brown 1999; Voznesenkaya & al. 2001). Higher photosynthetic nitrogen use efficiency in the $C_4$ and $C_3$ species is linked with greater investment in sexual reproduction and storage, and the avoidance of nitrogen limitations on leaf growth, suggesting advantages of the $C_4$ pathway in disturbed and infertile ecosystems (Ripley & al. 2008). $C_4$ plants increase photosynthesis particularly in warmer climates (Jordan & Ogren 1984) and this photosynthetic pathway is an adaptational mechanism that enables them to survive in drier and hot environments, such as semiarid, subhumid and humid climates consisting of many soil types (Osborne & Freckleton 2009; Mishra & al. 2011). Despite increasingly higher atmospheric $CO_2$ levels, warmer global temperatures are expected to promote the expansion of $C_4$ species range in the near future and such a situation could represent $C_4$-dominated systems in warm regions (Sage 2004). *Cleome viscosa* is a $C_3$ species, while *Cleome gynandra* is a $C_4$ species. The former predominates in cool environments, while the latter predominates in warm environments. Such versatility enables *C. gynandra* to invade and flourish well in diverse environments and extend its distribution range (Silva & al. 2011). *Cleome gynandra* is a suitable plant for consideration in the restoration of ecologically degraded and warm habitats. Kumar & al. (1984) have experimentally proved that this plant is tolerant and resistant to salt and water stress, which is important for erosion control and, hence, is an ideal weed in both warm and cool environments. Apart from these advantages, they have a unique role to play in plant community restoration, bloom quickly and sustain diverse insect pollinator, as well as herbivore communities (Cane 2008). *Cleome* species are used as leafy vegetables in many regions (Theophilus & Arulanantham 1949; Ekpong 2009). Therefore, these species are important ecologically, medicinally and economically, and are essential constituents of tropical ecosystems by their interactions with local insects/animals and serve their part as constituents of biodiversity.

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