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INFLORESCENCE MODIFICATION AND FLORAL BIOLOGY OF SOME *COMMIPHORA* SPECIES

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ABSTRACT: The present paper stipulates the inflorescence branching pattern and their presumed evolutionary trend, the floral biology with the possible explanation on the evolution of floral sex, sexual systems and sex distribution, phenology and pollination mechanics in *Commiphora* species of NE and E Tropical Africa. It conveys the apparent trend in the process of inflorescence modification in *Commiphora* and draws the phylogenetic information based on the different patterns of inflorescence branching mechanisms. Five different types of inflorescence are identified within the studied species, with their presumed modification trends. In terms of sex distribution, the majority of the studied species is found to be dioecious vis-à-vis hermaphrodite and monoecious and other intermediate forms verifying out crossing as a norm within the group. With regard to evolution of floral sex the hermaphrodite flower is considered to be an ancestral condition giving rise to other forms that finally has lead to dioecy. Data on phenology has suggested that most species of *Commiphora* are active twice a year following a bimodal rainfall pattern of the environment in which they grow.

Key words/phrases: *Commiphora*, **inflorescence, phenology, pollination**

INTRODUCTION

The genus *Commiphora* is one of the most diverse genera of the family Burseraceae. It is largely represented in Africa where it is confined to arid and semi-arid areas. *Commiphora* also occurs in Iran, Pakistan, Peninsula India, Sri Lanka and Brazil. The genus is co-dominant with *Acacia* over the huge areas of the Horn of Africa and supports the large livestock populations of pastoral and agro pastoral communities. Of the 190 or so species in the genus, more than half of the species are native to the Horn of Africa. This might support the notion that the center of genetic diversity of the genus is in this part of the world.

In former days attempts have been made to circumscribe the genus, among others, Engler (1913 and 1931), Sprague (1927), Chiovenda (1932), Vollesen (1985, 1986 and 1989), Gillett (1991) and Thulin (1999) are the ones to be mentioned. However, information on the general reproductive biology of *Commiphora* such as the inflorescence modification and architecture, floral biology and evolution of sex, sexual systems and sex distribution, phenology and pollination mechanics have not been studied. Thus, the present paper deals with the aforementioned information of the genus *Commiphora*.

MATERIALS AND METHODS

Studies on seventy three NE and E Tropical African *Commiphora* species were made. The investigations were based on the living materials, plant parts fixed in the field or from plants grown in the green house or preserved as herbarium specimens. Data were gathered from the intensive field works and from various literatures. Flowers fixed in alcohol: acetic acid (3:1) were gathered during the field works and studied under microscope. Dried flowers were usually softened by heating in water and studied. Drawings were made under Camera Lucida. The inflorescence architecture has been studied and determined by comparing with the standard terminologies as in Hedberg and Edwards (1989). The phenological data were gathered from field and herbarium specimens and finally compiled. Floral visitors were extensively observed in the field and the particular visitors were captured and photographed.

The seventy-three species of NE and E Tropical African *Commiphora* that have been dealt with in the present study is given in Table 1. Note that C. *wightii* (from India) was included for discussion purposes.

Table 1. List of *Commiphora* species included in the study.

No.	Scientific name of taxa	No.	Scientific name of taxa
1	*C. acuminata* Mattick	38	*C. merkeri* Engl.
2	*C. africana* Engl.	39	*C. mildbraedii* Engl.
3	*C. alaticaulis* Gillett and Vollésen	40	*C. mollis* Engl.
4	*C. albiflora* Engl.	41	*C. mombassensis* Engl.
5	*C. baluensis* Engl.	42	*C. monoica* Vollesen
6	*C. boranensis* Vollesen	43	*C. mossambicensis* Engl.
7	*C. bruceae* Chiov.	44	*C. myrrha* Engl.
8	*C. caerulea* B.D. Burtt	45	*C. oblongifolia* Gillett
9	*C. campestris* Engl.	46	*C. obovata* Chiov.
10	*C. chaetocarpa* Gillett	47	*C. oddurensis* Chiov.
11	*C. ciliata* Vollesen	48	*C. ogadensis* Chiov.
12	*C. confusa* Vollesen	49	*C. ovalifolia* Gillett
13	*C. corrugata* Gillett and Vollesen	50	*C. paolii* Chiov.
14	*C. cyclophylla* Chiov.	51	*C. pedunculata* Engl.
15	*C. danduensis* Gillett	52	*C. pteleifolia* Engl.
16	*C. edulis* Engl.	53	*C. quadricincta* Schweinf.
17	*C. ellenbeckii* Engl.	54	*C. rostrata* Engl.
18	*C. eminii* Engl.	55	*C. samharensis* Schweinf.
19	*C. engleri* Guillaumin	56	*C. sarandensis* B.D. Burtt
20	*C. erlangeriana* Engl.	57	*C. schimperi* Engl.
21	*C. erosa* Vollesen	58	*C. sennii* Chiov.
22	*C. fulvotomentosa* Engl.	59	*C. serrata* Engl.
23	*C. gileadensis* C. Chr.	60	*C. serrulata* Engl.
24	*C. glandulosa* Schinz	61	*C. spathulata* Mattick
25	*C. gowlello* Sprague	62	*C. sphaerocarpa* Chiov.
26	*C. gracilispina* Gillett	63	*C. sphaerophylla* Chiov.
27	*C. guidottii* Chiov.	64	*C. staphyleifolia* Chiov.
28	*C. gurreh* Engl.	65	*C. stolonifera* B.D. Burtt
29	*C. habessinica* Engl.	66	*C. suffruticosa* Teshome
30	*C. hildebrandtii* Engl.	67	*C. swynnertonii* B.D. Burtt
31	*C. hodai* Sprague	68	*C. terebinthina* Vollesen
32	*C. hornbyi* B.D. Burtt	69	*C. truncata* Engl.
33	*C. horrida* Chiov.	70	*C. ugogensis* Engl.
34	*C. kataf* (Forssk.) Engl.	71	*C. unilobata* Gillett and Vollesen
35	*C. kua* Vollesen	72	*C. velutina* Chiov.
36	*C. lindensis* Engl.	73	*C. wightii* Bhandari
37	*C. madagascarensis* Jacq.	74	*C. zanzibarica* Engl.

The geographical areas included under the present investigation were NE (North East which refers to Ethiopia and Eritrea) and E (East referring to Kenya, Tanzania and Uganda) Tropical Africa. Because of the transgressing nature of *Commiphora* species to the adjacent Somalia, Somalia was also included in the map for discussion purposes. The description of the regional floristic divisions of the flora areas (*i.e.*, Ethiopia, Eritrea, East Africa and Somalia) followed Hedberg and Edwards (1989), Polhill (1988) and Thulin (1999) as given in Fig. 1 below.

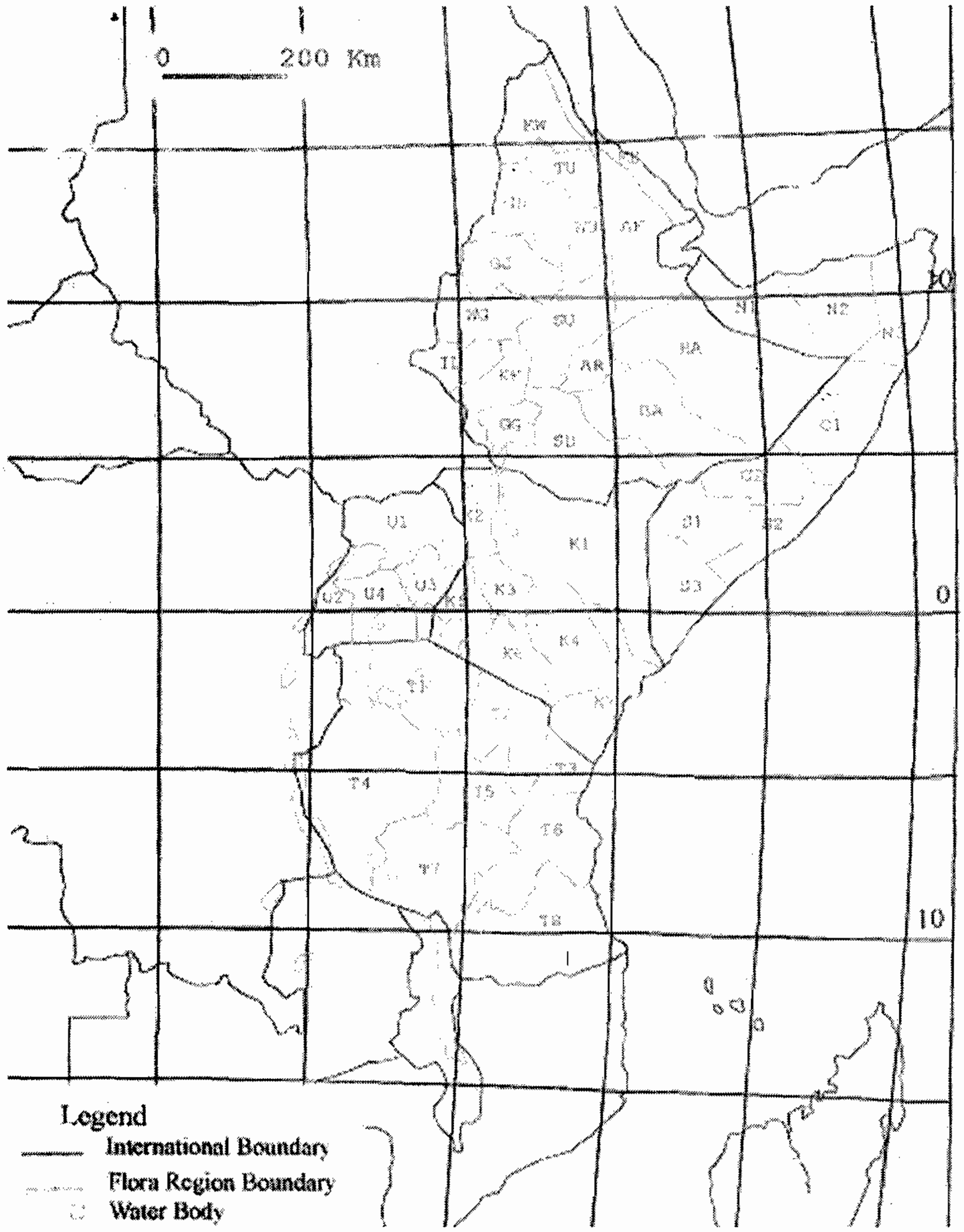

Fig. 1. Regional floristic divisions of Ethiopia, Eritrea, East Africa and Somalia.

RESULTS AND DISCUSSIONS

Nature of inflorescences in Commiphora

The inflorescence system in *Commiphora* commonly involves different levels of organization that differ qualitatively in pattern of branching and development. Both anthotelic and blastotelic inflorescence types *sensu* Briggs and Johnson (1979) occur in *Commiphora* species. Briggs and Johnson (1979) attest that those terms that were previously used such as closed or determinate are special applications of words that do not necessarily convey any notion of termination by flower. As a result Briggs and Johnson (1979) coined the term anthotelic (a Greek word, ending in a flower) and blastotelic (Greek word, ending in a bud or sprout) with further distinction of the later.

The major inflorescence types in the *Commiphora* species occurring in NE and E Tropical Africa belong to one of the following: panicle, raceme, cymes, fascicle and uniflorous. The majority of the species possess cymes and fascicle types. Of all the species investigated for inflorescence types, 29 species possess various types of cymes, 19 species possess a fasciculate type, 2 species a racemose type, 3 species a paniculate type, 10 species have uniflorous type and 11 species have a combination of different types based possibly on variation between male and female plants (as in *C. unilobata* and *C. suffruticosa)* or within the species as in *C. africana*. *C. erlangeriana* and *C. staphyleifolia* are the only species with raceme type inflorescence and *C. zanzibarica*, *C. guidottii*, *C. engleri* the only ones with a panicle type inflorescence (see Table 2 and Fig. 2 for the details). Most species occurring in the drier parts such as lowlands of Borana, Ogaden, the adjacent Somalia (S1 & S2), northern Frontier of Kenya (K1) largely posses fasciculate or uniflorous inflorescence. In most fasciculate inflorescence, the individual flowers are so small in size and pubescent, while the uniflorous ones appear to be longer and glabrous in nature. This trend coupled with the smaller leaves of these species, might be an adaptation to conserve water.

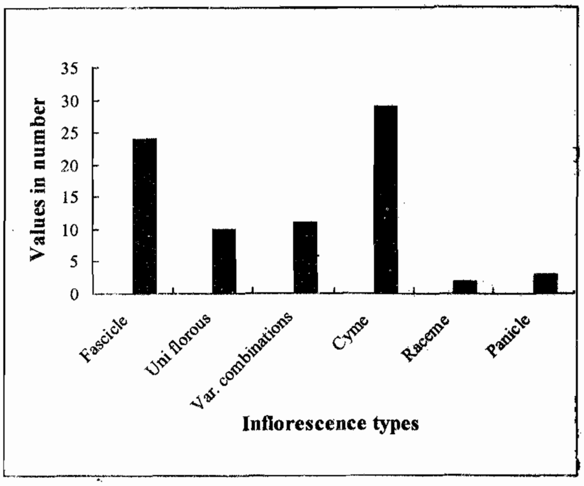

Fig. 2. Proportions of inflorescence types.

Table 2. Major inflorescence types in *Commiphora* species occurring in NE and E Tropical Africa.

No.	Scientific name of taxa
	Cyme
1	*C. albiflora* Engl.
2	*C. baluensis* Engl.
3	*C. boranensis* Vollesen
4	*C. caerulea* B.D. Burtt
5	*C. campestris* Engl.
6	*C. ellenbeckii* Engl.
7	*C. erosa* Vollesen
8	*C. fulvotomentosa* Engl.
9	*C. gileadensis* C. Chr.
10	*C. glandulosa* Schinz
11	*C. habessinica* Engl.
12	*C. hornbyi* B.D. Burtt
13	*C. kataf* (Forssk.) Engl.
14	*C. mildbraedii* Engl.
15	*C. mollis* Engl.
16	*C. mombassensis* Engl.
17	*C. monoica* Vollesen
18	*C. myrrha* Engl.
19	*C. obovata* Chiov.
20	*C. paolii* Chiov.
21	*C. pedunculata* Engl.
22	*C. quadricincta* Schweinf.
23	*C. rostrata* Engl.
24	*C. schimperi* Engl.
25	*C. serrulata* Engl.
26	*C. sphaerocarpa* Chiov.
27	*C. sphaerophylla* Chiov.
28	*C. stolonifera* B.D. Burtt
29	*C. velutina* Chiov.
	Various Combinations
1	*C. acuminata* Mattick
2	*C. africana* Engl.
3	*C. ciliata* Vollesen
4	*C. confusa* Vollesen
5	*C. edulis* Engl.
6	*C. eminii* Engl.
7	*C. kua* Vollesen
8	*C. merkeri* Engl.
9	*C. mossambicensis* Engl.
10	*C. suffruticosa* Teshome
11	*C. unilobata* Gillett and Vollesen
	Fascicle
1	*C. alaticaulis* Gillett and Vollesen
2	*C. chaetocarpa* Gillett
3	*C. corrugata* Gillett and Vollesen
4	*C. danduensis* Gillett
5	*C. gracilispina* Gillett
6	*C. hildebrandtii* Engl.
7	*C. lindensis* Engl.
8	*C. madagascarensis* Jacq.
9	*C. oblongifolia* Gillett
10	*C. ogadensis* Chiov.
11	*C. pteleifolia* Engl.
12	*C. sarandensis* B.D. Burtt
13	*C. sennii* Chiov.
14	*C. serrata* Engl.
15	*C. spathulata* Mattick
16	*C. swynnertonii* B.D. Burtt
17	*C. truncata* Engl.
18	*C. ugogensis* Engl.
19	*C. wightii* Bhandari
	Uniflorous
1	*C. bruceae* Chiov.
2	*C. cyclophylla* Chiov.
3	*C. gowlello* Sprague
4	*C. gurreh* Engl.
5	*C. hodai* Sprague
6	*C. horrida* Chiov.
7	*C. oddurensis* Chiov.
8	*C. ovalifolia* Gillett
9	*C. samharensis* Schweinf.
10	*C. terebinthina* Vollesen
	Racemose
1	*C. erlangeriana* Engl.
2	*C. staphyleifolia* Chiov.
	Panicle
1	*C. engleri* Guillaumin
2	*C. guidottii* Chiov.
3	*C. zanzibarica* Engl.

An overview of the different types of inflorescence in *Commiphora* species from NE and E Tropical Africa is given in Fig. 3. In a panicle, where the main axes of the inflorescence is terminated by flower (e.g. *C. guidottii*), or an inflorescence derived from it, as well as in tymes (*e.g., C. baluensis*; see also Fig. 3 III for some inflorescences in some species), the terminal flowers assume a dominating position and it is that flower which attains maturity before the other lateral flowers. This had been augmented by Weberling (1992) in the sense that ontogenetically the terminal flower holds the lead over the upper lateral flowers. The length of the pedicels of the terminal flowers of these inflorescence types are different among the different species of *Commiphora* providing either a loose, as in *C. baluensis* and *C. unilobata* for the peduncle is long, or a congested (*e.g.,* in *C. confusa*) nature of the inflorescence.

Racemes or botrytic inflorescences characteristically have the internodes of their main axis well developed as in *C. erlangeriana* (Fig. 3 II); all flowers appearing on the inflorescence axis have short stalks. Such an inflorescence does not terminate with a flower, as seen in Fig. 3 II. The arrangement of the flowers on the inflorescence axis is primarily alternate. In these inflorescences the flowers that attain maturity first are the ones on the lowermost part proceeding upward and this also corresponds to the order in which the flowers usually open.

The branching pattern of the cymes or the thyrse inflorescence could occur either in a blastotelic type (Fig. 3 III a) that is observed in some secondary axes and in the main terminal axes or anthotelic type (Fig. 3 III b) that is prevalent in most of the secondary axes. It is also remarkable to note another interesting feature of the branching pattern of the inflorescence type in *C. baluensis* (Fig. 3 III c), where the branches originating in the axils of the prophylls continue the same manner of branching and mostly exceed the parent axis (Fig. 3 III d) thereby producing a dichasium pattern. In this inflorescence type in general the terminal flower seems to be the one that attains maturity before the lateral ones or where the terminal is reduced then the two lateral flowers will eventually equally develop.

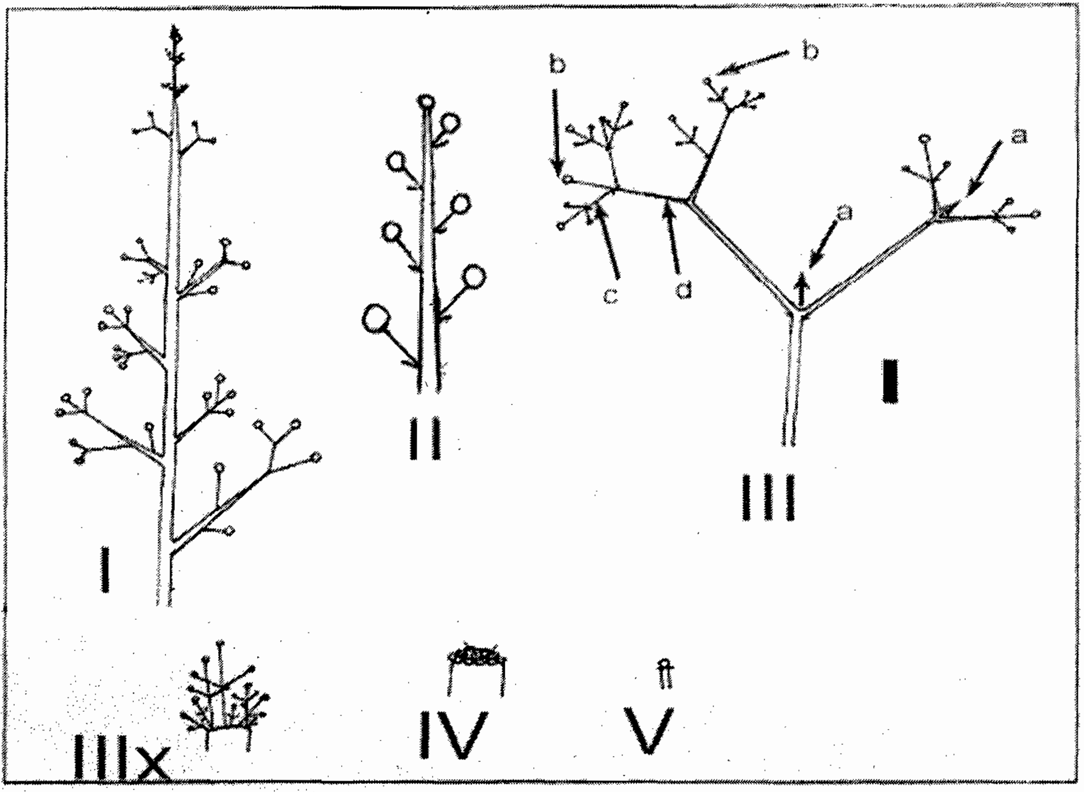

Fig. 3. Inflorescence types in NE and E Tropical African *Commiphora* species. I, panicle; II, raceme; III, cymes; III x, congested cymes; IV, fascicle and V, uniflorous. See text for further explanations. Scale bars I-II, 1 cm and the rest 1 mm.

Fasciculate (Fig. 3 IV) and uniflorous (Fig. 3 V) inflorescence types seems to be the result of the evolutionary reduction that in one way or the other had taken place from one of the inflorescence types above. In some species of *Commiphora* like *C. corrugata* and *C. ogadensis*, the fasciculate inflorescences are head like and the older flowers occupy the lower portion and the younger ones the central position. At times leaves could emerge or proliferate from within the inflorescence itself. Evolutionarily, such type of inflorescence could be a contracted thyrse.

Taking the nature of inflorescence architecture into consideration, one can draw phylogenetic information based on the different patterns of branching within the group under discussion. Within *Commiphora*, the basic or ancestral condition seems to be a paniculate type, a type recorded from *C. zanzibarica*. Furthermore, Troll (1964), Briggs and Johnson (1979) and Weberling (1992) in their work considered the basic condition as frondobracteose panicle. The diversity of other aforementioned inflorescence types seems to be the result of reduction of panicles often accompanied by aggregation.

Presumably, the apparent trend in the process of inflorescence modification in *Commiphora* could possibly follow one or more of the following conditions as depicted in Fig. 4: reduction in number of nodes on the different axes, reduction in the degree of branching and reduction in the number of flowers possibly by abortion without affecting or reducing the degree of branching. Following this hypothesis, a paniculate inflorescence could give rise to a raceme by reduction in a number of nodes and degree of branching followed by abortion of some flowers. On the other line a paniculate inflorescence could give rise to cymes through reduction by affecting number of nodes and to some extent axes of different orders, as seen in Fig. 4, see also Fig. 3 for comparison. It is interesting to note that populations of *C. unilobata* possess both raceme and panicle type of inflorescence (Gillett, 1991) and some of the populations of this species could possibly represent transitional stages. Similarly, *C. eminii* and *C. ciliata* might be transitional between paniculate and cymes types of inflorescences for the reasons stated above.

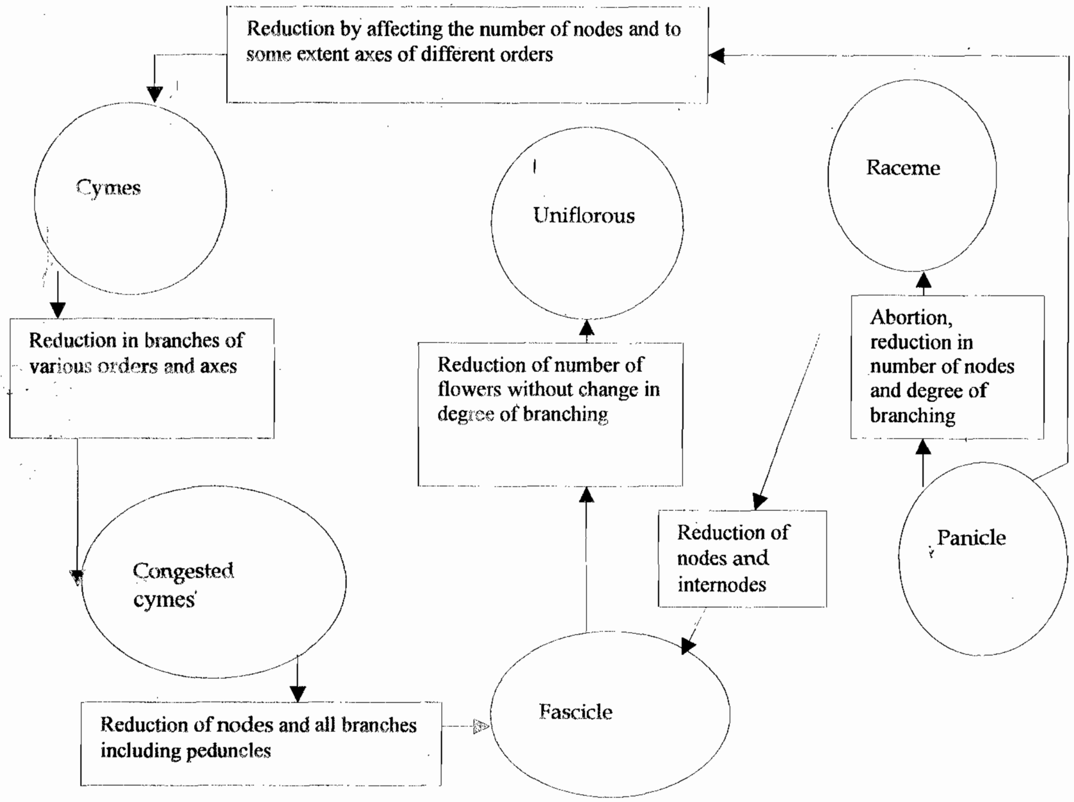

Fig. 4. Presumed trends of inflorescence modification in *Commiphora*. Compare this trend with Fig. 3. See explanation in the text.

By the same token cymes undergo reduction in branches of various orders and axes giving rise to congested cymes, as in the case of *C. confusa* (in populations of this species both congested and fasciculate types of inflorescence were recorded; see Fig. 3 III x).

If congested cymes in turn undergo further reduction of nodes and of all branches including the peduncles, a fasciculate type inflorescence results. Another modification toward a fasciculate type is when a raceme inflorescence might undergo reduction in its various nodes and internodes. Evidently it is interesting to note here that the blastotelic raceme inflorescence of, for example, *C. erlangeriana* in this case, gave rise to a fasciculate type like *C. corrugata* where the bud eventually developed to leafy shoots which appears in between the group of flowers in such species. However, such leafy shoots are not common in all species possessing a fasciculate inflorescence type. Similarly, a fasciculate type of inflorescence could undergo reduction in flower number (here by abortion) without changes in degree of branching (Fig. 4) to give rise to a uniflorous inflorescence. Populations of *C. suffruticosa* and *C. merkeri* might be transitional between fasciculate and uniflorous type.

Flowers of Commiphora

The flowers of *Commiphora* species occurring in NE and E Tropical Africa are either bisexual or unisexual, with the unisexual species being abundant. The latter are dioecious except for *C. monoica*, which is the only monoecious species. The flowers are generally four- and very rarely five-merous.

The calyx is either cup shaped or tubular. It is quadrangular in some species like *C. kua* (Fig. 5A). The longest calyx is that of *C. baluensis* ranging from 3-6 mm in both sexes; while the shortest is that of *C. velutina* and *C. albiflora* which is about 1mm in both species.

In *Commiphora* species of NE and E Tropical Africa, corolla shapes and corolla tips vary considerably between the species. The shapes could be oblong as in *C. baluensis* or linear in most cases as in *C. unilobata*. The tips can be recurved as in *C. ogadensis* (Fig. 5B); curved out ward as in *C. baluensis* (Fig. 5C); curved inward as in *C. monoica* (Fig. 5D); reflexed as in *C. corrugata* (Fig. 5E) and *C. hildebrandtii* (Fig. 5F) or elliptic straight as in *C. albiflora* (Fig. 5G). Corolla size in male is always longer than the size in females. Thus, male and female flowers of a given species are sexually dimorphic. The longest corolla was recorded from *C. suffruticosa* that ranges from 4.7-7.2 mm in both sexes and the shortest is that of *C. velutina* which ranges from 1-2 mm.

The stamens in *Commiphora* species are mainly eight in the majority of the species or rarely four. When the stamens are eight in a given flower, four are normally short and four are long showing staminal dimorphism. In the studied species, the filament length ranges from 0.5 to 5.5 mm, the longest record being from *C. suffruticosa*. Staminodes have been recorded in female flowers of most species.

The gynoecium of *Commiphora* species currently dealt with is syncarpous and superior. The styles are conduplicate to terete in most species. The longest style was that of *C. kua* measuring about 2 mm and the shortest style is that of *C. mollis* measuring 0.2 mm. The stigmas are obscurely four lobed, subcapitate, or capitate. The ovaries of pistillate flowers are usually 2-locular. However, three-locular ovaries recorded by Vollesen (1989), Gillett (1991) and four-locular ovaries by Chithra and Henry (1997) are also known, though they are rare. Of the two ovary locules commonly seen in most species of *Commiphora*, it is only one that remains fertile in which one seed develops.

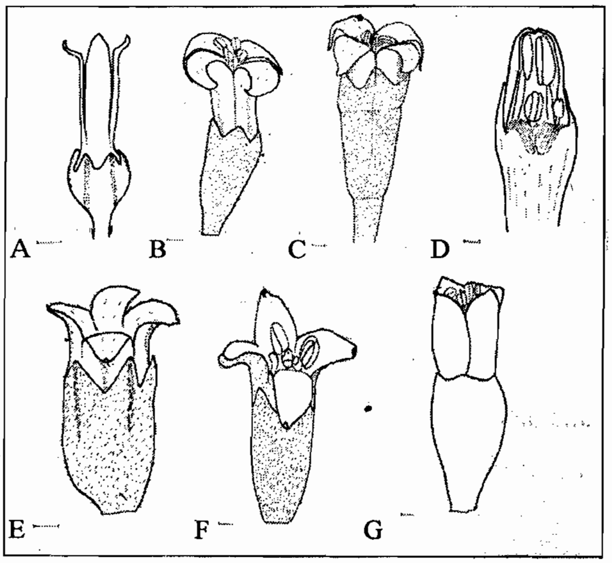

Fig. 5. Flowers of some NE and E Tropical African *Commiphora* species. A- *C. kua*; B- *C. ogadensis*; C- *C. baluensis*; D- *C. monoica*, E- *C. corrugata*; F- *C. hildebrandtii*; and G- *C. albiflora*. Scale bars all 0.5 mm.

Sexual systems and sex distribution

Most species of *Commiphora* in NE and E Tropical Africa are dioecious. Only a few species such as *C. schimperi*, *C. samharensis* and *C. obovata* appear to have bisexual flowers and one species, *C. monoica*, is monoecious. Therefore, of the 74 species of *Commiphora* species currently dealt with, about 95 percent are dioecious and about 4 percent are hermaphrodite. One Indian species, *C. wightii*, which is included here for discussion purposes, is andromonoecious (Gupta *et al.*, 1998) and another NE African species is monoecious (*C. monoica*) that makes about 1% of the total. In addition, Van der Walt (1973) recorded the polygamous and dioecious nature of some South African *Commiphora* species. Of these, *C. pyracanthoides* may have androdioecious or gynodioecious populations next to typical dioecious ones.

In the dioecious species of *Commiphora*, out crossing must be the norm. There are, however, indications that selfing may occur in non-dioecious species such as the Indian *C. wightii* (Gupta *et al.*, 1996). Gillett (1991) also suggested that self pollination may sometimes occur in the hermaphrodite *C. samharensis* with cross pollination as a norm in the genus. Apart from the possible reproduction potential of *Commiphora* species by seed, the majority can easily reproduce by branch cuttings.

Contrary to the normal situation in most sexually reproducing species Gupta *et al.* (1996) reported the following for *C. wightii*: 1) formation of seeded fruits from female flowers with no access to pollen or even after emasculation and bagging, 2) failure of the pollen tubes to enter the ovule following hand pollination, 3) occurrences of nucellar polyembryony and 4) autonomous development of endosperm. Based on the aforementioned information Gupta *et al.* (1996) concluded that autonomous apomixis and polyembryony in *C. wightii* could be a strategy for reproduction and survival in the absence of male plant. Moreover, the same authors (Gupta *et al.*, 1998) reported that their study established the male and andromonoecious plants of *C. wightii* have normal pollen development and bear viable.

Evolution of floral sex

Bawa and Beach (1981) attest that after the development of the synthetic theory of evolution, the genetic implications of the diversity in sexual systems emerged as a major issue in the evolutionary biology of plants, and selective pressure for an optimal amount of recombination came to be viewed as the essential force in the evolution of sexual systems. Different models and evolutionary pathways have been proposed for floral sexes, notably by Carlquist (1966), Arroyo and Raven (1975), Charlesworth and Charlesworth (1978), Bawa (1980), Beach and Bawa (1980), Bawa and Beach (1981), Bawa (1984), Baker *et al.* (2000 a and 2000 b), Vassiliadis *et al.* (2000) and Pannell (2002). The fact that *Commiphora* species are composed of different forms of floral sex, the evolution of those sex forms might have presumably taken place via different pathways, i.e. the evolution from hermaphroditism to both monoecy and dioecy.

Charlesworth and Charlesworth (1978) suggested that monoecy has evolved from hermaphroditism and it must be separated by at least two genetic changes from hermaphroditism, gynomonoecy (plant bearing bisexual and female flowers) or andromonoecy (plant bearing bisexual and male flowers) occurring as intermediate stages. These genetic changes according to these authors are mutations converting some flowers into females and then two or more mutations reducing the female fertility of the remaining hermaphrodite flowers. Although study on the complete sex structure of populations in different species of *Commiphora* species are lacking, it is reasonable to assume that a hermaphrodite species like *C. schimperi* gave rise to a monoecious species like *C. monoica* through the intermediate group either via gynomonoecy or andromonoecy. The presence of andromonoecy, as reported for *C. wightii* by Gupta *et al.* (1996), might support the hypothesis that intermediates were in between hermaphroditism and monoecy in the process of floral evolution (see Fig. 6).

Furthermore, Bawa and Beach (1981) proposed that evolution of monoecism represents the continuation of the trend seen in andromoecious species towards the specialization of flowers into pollen donors and pollen recipients which is partly due to sexual selection and partly due to the mechanics of pollination and it can arise in one step from andromonoecism by the sterilization or abortion of the stamens from hermaphrodite flowers.

Dioecy has been presumed to have evolved via different routes. Many attempts have been made to explain the evolutionary basis of dioecy and most evolutionary models have dealt with the genetic benefits of out crossing as the selective forces of most importance (Charlesworth and Charlesworth, 1978 and literature cited therein). According to Bawa (1980 and 1984) who had eloquently discussed floral evolution, dioecy have evolved through five distinct routes directly from hermaphroditism and via androdioecy, gynodioecy, monoecy and heterostyly with the population genetic models for almost all pathways assuming selective pressure against inbreeding as the major driving forces. This author further suggested that dioecy for example would evolve from gynodioecy if male sterility mutation were to be followed by another mutation causing complete female sterility in hermaphrodites. Similar procedure could be assumed for the evolution of dioecy from androdioecy. It appears reasonable to assume that dioecy in *Commiphora* species might have evolved via the four evolutionary lines mentioned (the fifth, heterostyly, does not occur in *Commiphora*). This can be corroborated by the fact that *Commiphora* species have species with hermaphrodite (*e.g.*, *C. schimperi*), androdioecious and/or gynodioecious (*e.g.*, *C. paracanthoides*) and monoecious (*e.g.*, *C. monoica*) flowers. A presumed route of dioecy evolution is also presented in Fig. 6.

Taking androdioecy as one of the possible evolutionary routes of dioecy, Bawa (1980) hinted that theoretically, dioecy could be established via androdioecy as an intermediate step in the same manner as via gynodioecy, but no such evolutionary pathway is known in extant taxa. He further argued that if out breeding advantage were invoked for the maintenance of females in gynodioecious populations, it could not be invoked for the persistence of males in androdioecious populations because it is assumed that the hermaphrodites can self and the selfed flower are not available to be fertilized by males.

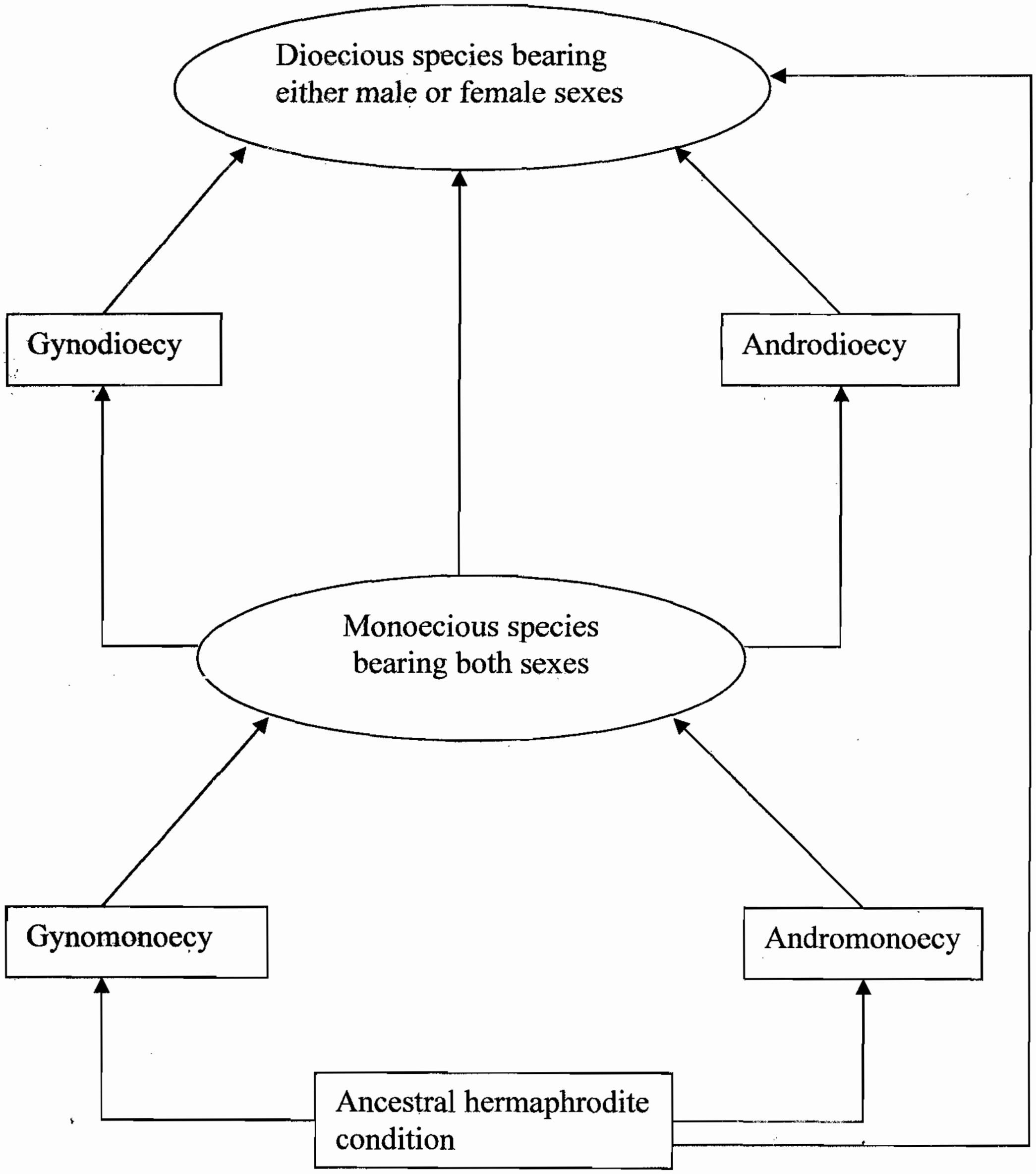

Fig. 6. Possible evolution of floral sexes in *Commiphora* species. Note that gynomonoecy, andromonoecy, gynodioecy and andromonoecy are intermediate steps in the process. The arrow indicates the direction of evolutionary lines (see explanation in the text).

Close observations of the female flowers of most dioecious taxa (such as *C. baluensis*) could enable to witness the presence of rudimentary stamens, while the corresponding male flowers lack any rudimentary style of the opposite sex. Still in other species such as *C. africana*, both rudimentary sexes are observed making the presumptuous decision as to whether dioecy evolved from androdioecy or gynodioecy lines difficult.

Phenology

Most species of *Commiphora* in NE and E Tropical Africa occur in places experiencing bimodal or erratic rainfall. In a bimodal regime, rains fall in the months between March to May and between the periods of September and November (Daniel Gamachu, 1977). As a result of the bimodal rainfall situation, most species of *Commiphora* tend to flower and fruit twice in a year, although there are some exceptions. The most interesting behaviour of some species of *Commiphora* (*e.g.*, *Commiphora africana*) is that they start flowering before the beginning of the actual rain. Most species produce leaves, flowers and fruits between September and December and between March and June.

The phenological information gathered from fieldwork and herbarium specimens is compiled and presented in Table 3. In some of the cases, however, information is inconclusive because too few data (field observation or herbarium specimens) were available. A good example for such a case is *Commiphora campestris* (Table 3). As alluded to earlier, the general phenological trend in most species of *Commiphora* is between September and December and between March and June concomitant to the highest rainfall that occurs in the months of October and April. Species like *Commiphora africana*, *C. boranensis*, *C. serrulata* and *C. terebinthina* start flowering in the month of September, possibly around the end of the month.

Some species flower and fruit only once in a year. Field observation at different periods of the year in different places showed that *Commiphora baluensis* was phenologically inactive (*i.e.*, no flower and fruit) in the months between April-June, while it was leafy elsewhere. Of 53 herbarium specimens of *Commiphora baluensis* checked for phenology, however, two were in fruit and flower in the months of January and February respectively. In addition to such anomalous behaviour of species deviating from the general trend, prolonged drought could also have an impact on the phenological condition of a particular species.

Table 3. The phenology of some NE and E Tropical African *Commiphora* species. Note that fruit is abbreviated as fr., flower as fl. and leaf as lf. and are used to make distinctions in some species, otherwise all occur in the seasons.

Species	Phenology (lf., fl. and fr.)
C. africana	Sept.-Dec. and March-June
C. alaticaulis	Sept.-Dec. and March-June
C. albiflora	March-June
C. baluensis	Oct.-Dec. and lf. in April-June
C. boranensis	Sept.-Dec. and March-June
C. bruceae	Sept.-Dec. and Feb.-May
C. campestris	Fr. and lf. in May
C. ciliata	Nov.-Feb. and May-August
C. confusa	Oct.-Dec. and April-June
C. corrugata	Oct.-Dec. and April-June
C. cyclophylla	Oct.-Dec. and April-June
C. danduensis	Oct.-Dec. and April-June
C. edulis	Oct.-Dec. and Feb.-May
C. ellenbeckii	May-July
C. erlangeriana	Oct.-Dec. and April-June
C. erosa	Oct.-Dec. fr. and lf. and April-June
C. gileadensis	March-June
C. gowlello	Oct.-Dec. and April-June
C. guidottii	Oct.-Dec. lf. and May-August
C. gurreh	Oct.-Dec. and April-June
C. habessinica	Oct.-Dec. and April-June
C. hildebrandtii	Oct.-Dec. and April-June
C. hodai	April-June
C. kua	Oct.-Dec. and April-June
C. monoica	Oct.-Dec. and April-June
C. myrrha	Sept.-Dec. and March-June
C. obovata	Oct.-Dec. and April-June
C. ogadensis	Oct.-Dec. fl. and lf. and April-June
C. rostrata	Oct.-Dec. and April-June
C. samharensis	Oct.-Dec. and April-June
C. schimperi	Oct.-Dec. and April-July
C. serrulata	Sept.-Dec. and April-July
C. suffruticosa	Sept.-Dec. and April-July
C. terebinthina	Sept.-Dec. and March-June
C. velutina	Oct.-Dec. and April-June

Pollination

The pollination mechanics in the genus *Commiphora* was not studied well in the past. Gillett (1991) indicated that the mechanism by which the pollination takes place is obscure since the genus does not seem to be adapted to wind pollination adding that the only insect visitors recorded seems to be ants, seen by P. Scholte visiting the flower of *C. kataf* in north Yemen in the year 1988. It is clear that ants could climb trees of various heights and visit any organ of the plant. However, it seems unrealistic to consider ants as a pollinator of a dioecious species like *C. kataf* for the following reasons: firstly assume that the ant climbs the male plant of *C. kataf* and visited its flower (takes pollen on its body). The same ant has to walk down to visit the female plant which could be some distance far (up to 500 m) from the male plant. While walking down along the tree trunk, then on the ground and climb (as opposed to the flying animals) the trunk of the female plant, the chance that the ant could still harbour the pollen is almost negligible. Secondly, the flower of C. *kataf* is as large as that of C. *baluensis* that is pollinated by sunbird (see below). A sunbird with its long beak is capable of reaching the base of a long tubular corolla like that of C. *baluensis* to suck the nectar. As a result, the idea that ants are pollinators of C. *kataf* most likely is erroneous [see also Bawa (1990) for similar observation].

According to field observations, the flowers of C. *hildebrandtii* were visited by a beetle, *Stychothyria picticollis* Kr. (see Fig. 7 D-E). On the other hand, flowers of C. *africana* were visited by a fly (see Fig. 7 A-C). Close observation of this fly indicated that the fly was foraging on the pollen of the male plant and also seen while visiting the female plant nearby. Moreover, it was observed that the flowers of C. *baluensis* were repeatedly visited by sunbirds (*Nectarinia senegalensis*) where C. *baluensis* is the most dominant species forming almost a closed canopy.

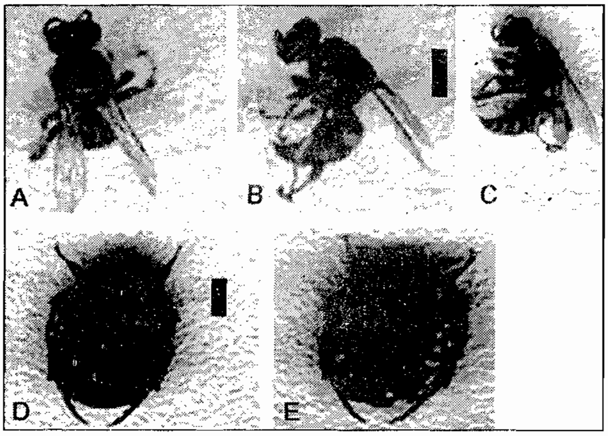

Fig. 7. Some floral visitors of NE and E Tropical African *Commiphora* species. A-C fly visiting *C. africana* A, backside, B, side view, C, front view; D-E *Stychothyria picticollis* Kr. D, front side and E, backside. Scale bar 1 cm. Note that the fly has white strips on its abdomen and the insect has white dots as a diagnostic feature.

CONCLUSIONS

Results from the present study indicated that the major inflorescence types in the *Commiphora* species occurring in NE and E Tropical Africa belong to panicle, raceme, cyme, fascicle and uniflorous with the majority of the species possessing cymes and fascicle types. In terms of phylogeny, the basic or ancestral condition in *Commiphora* seems to be a paniculate type and the others are the results of presumed modification of the basic type, resulting in an advanced uniflorous ones.

Most species of *Commiphora* in NE and E Tropical Africa are dioecious with few bisexual/hermaphrodite and monoecious taxa. In the dioecious taxa, out crossing is the norm for the formation of fruits while selfing could be an additional possibility in non-dioecious species. Besides the reproductive potentials by seeds, *Commiphora* species can easily and readily reproduce by branch cuttings. Phenologically, most species of *Commiphora* are active twice a year following the bimodal rainfall pattern of the environment in which they grow. Thus, the general phenological trend is between Septembers to December and between Marchs to June.

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