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Full Length Research Paper

Breeding system and pollination biology of the semi-domesticated fruit tree, *Tamarindus indica* L. (Leguminosae: Caesalpinioideae): Implications for fruit production, selective breeding, and conservation of genetic resources

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In this paper, we provide data on the breeding system of *Tamarindus indica*, examining fruit production as well as pollen tube growth under different controlled pollination experiments (open, cross and self pollination). We discuss implications of the results for management for fruit production in Tamarind, conservation of genetic resources and the potential for selective breeding. Observation of the germination and the pollen tubes growth under various pollination modes show that the tamarind is an incompatible species partially. This incompatibility appears at the pre level zygotic (IE on the level of the stigmatic, style and ovary) and post zygotic by the abortion of seeds.

Keys words: *Tamarindus indica*, caesalpinioideae, breeding system, self-incompatibility, pollination system.

INTRODUCTION

Many tropical fruit trees are not the objects of large world markets, but still have considerable importance in local and national economies, being harvested by rural populations for local consumption and commercialisation on a small scale. With increasing recognition of their importance, these tree species are beginning to attract attention as renewable natural resources that are possibly under threat. Managing their populations, and improving the quality and regularity of fruit production are perceived as priorities for the economic development of rural populations (Bonkoungou et al., 1998). However, efforts in this direction are limited by lack of information about the population biology of most of these locally important fruit trees. Genetic diversity at the local level and population processes such as mating systems, pollination biology, seed dispersal, and establishment of juveniles, are poorly studied. Thus little information is available about the factors that limit fruit production, the potential for genetic improvement via selective breeding, the degree of genetic and ecological vulnerability, and many other aspects important in the management of these resources.

Tamarind, *Tamarindus indica* L. (Leguminosae: Caesalpinioideae), is an example of an economically important but little studied tropical fruit tree. The seeds in its indehiscent pods are enveloped by dark brown pulp with a pleasantly sweet and acid flavour, much appreciated in condiments and used to juice. The composition and nutritional quality of tamarind pulp have been determined by many authors (Kerkaro and Adam, 1974; Lumen et al., 1986; Mateo et al., 1992; Bhattacharya et al., 1994; Grant et al., 1995; Ibrahim et al., 1995). It is especially important in the semi-

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arid regions of Africa and south Asia, where it has long been present. Its origin remains a subject of controversy, some authors favouring India (Poupon and Chauvin, 1983; Wunderlin, 1992; Bärtel, 1994), others favoring Africa (Oliver, 1871; Hooker, 1879; Lefèvre, 1971; Grollier et al., 1998; Diallo, 2007), and still others favoring Madagascar (Aubréville, 1950; Giffard, 1974; Maydell, 1990; Grovel, 1993). The tree has been widely introduced throughout the tropics over the last 400 years (Dalziel, 1937). Tamarind fruits reached Europe in the middle ages via Arab traders, and commerce in these fruits has continued. For example, tamarind orchards in Mexico covered 8000 ha in the 1960's and produced about 250 000 tons per year, of which 3 000 were exported to Europe (Lewis and Neelakantou, 1964).

In the Sahelian region of Africa, as in numerous other regions throughout the tropics (Aubréville, 1950; Maydell, 1990; Arbonier, 2000) tamarind fruits, collected from 'natural' populations or from individual trees that have been preserved, encouraged or planted, are important components of the non-monetarised 'hidden harvest' of wild resources, for which assessment of their economic importance requires estimating how much local populations would have to pay to replace these 'free' resources. Tamarind fruits are also locally commercialised, being sold in markets or supporting small industries such as the manufacture of tamarind juice (Diallo et al., 2000; Lamien and Bayala, 1996). Tamarind ranks fourth on the list of 15 species considered most important by rural populations of the Soudano-sahelian zone of Africa (Bonkoungou et al., 1998). The tree has multiple uses, including uses in traditional medicine (Tybirk, 1993).

Despite its economic importance, very little is known about the reproductive ecology and population genetics of tamarind. Interviews with local residents in the study area in Burkina Faso who harvest tamarind fruits showed that these users voiced several management concerns that could be addressed by research on the plant's reproductive ecology. Low fruit production by many trees was listed as the principal problem. The small size of many fruits, containing few seeds and hence little pulp, was also a frequently mentioned concern. Erratic and low productivity are also cited by El-Siddig et al. (1999) as limiting the scope for commercial cropping. Caesalpinioid legume trees, like many other tree species, are often self-incompatible or at least preferentially allogamous (Gibbs et al., 1999; Lewis and Gibbs, 1999; Arista et al., 1999). Many caesalpinioid legumes are pollinated by single bees, and social bees, especially *Apis* spp., are often predominant among floral visitors (Eynard and Galetto, 2002). Because visits by social bees often result in a high proportion of geitonogamous pollinations, especially on trees, which bear large numbers of flowers, the availability of cross pollen may often limit fruit set (Lewis and Gibbs, 1999; Arista et al., 1999). In semi-arid areas, water stress may contribute to resource limitation of fruit set (Tybirk, 1993; Hartley et al., 2002).

As in other caesalpinioid legume trees, tamarind flowers appear principally bee-pollinated, and honeybees are frequent visitors (Thimmaraju et al., 1988; Radhamani et al., 1993; Nagarajan et al., 1997; Diallo, 2001). Although nothing is known in detail about its breeding system, tamarind also appears to be at least preferentially allogamous. Flowers are hermaphroditic, but stamens are shorter than the style, so that the spatial arrangement of anthers and stigma may tend to limit automatic autogamous and insect-mediated self-pollination (Diallo, 2001). According to Bajpai et al. (1968), flowers are protogynous, with stigmatic receptivity occurring one day before anthesis. This poses an additional barrier to self-pollination. A combination of facultative or obligate allogamy and frequent geitonogamous pollinations by social bees could thus be responsible for low fruit set and low fruit quality. However, in this semi-arid habitat, resources might also frequently limit fruit set and fruit development. Data on the relative importance of pollen limitation and resource limitation could provide important information to guide recommendations for management.

Little is known about genetic diversity of tamarind at different geographical scales (El-Siddiq et al., 1999). However, recent work based on neutral molecular-genetic markers (Diallo et al., 2007) has defined three major groups constituted by populations from West Africa, East Africa, and Cameroon. The high genetic diversity revealed in West African populations indicates that there is no immediate risk of genetic erosion in this region, as long as ecological conditions continue to permit regeneration. In West Africa, the maintenance of regeneration is by no means assured. Tamarind is a semi-domesticated species, and has long been planted in some areas. Vestiges of orchards dating from 400 B.C. are known from Egypt (Aubréville, 1950). In several Asian countries, including India, Thailand and Pakistan, selection has resulted in the creation of distinct varieties varying in taste of the pulp (sour, sweet, or bitter) and size of the pod (long or short) (Swaminathan and Ravindrau, 1989). In the Sahel zone of Africa, however, tamarind trees are rarely planted, because they are slow-growing and it is said that "the planter will die before the tree bears fruit". Elsewhere, tamarind has been documented to bear fruit as early as 4 or 5 years after planting, although the juvenile phase usually lasts a dozen or more years (El-Siddig et al., 1999). In the Sahel region, all trees appear to result from natural regeneration, and there is little or no management of individual trees beyond sparing them from other, destructive uses. Any young tree spotted is systematically spared and allowed to grow. This dependence on natural regeneration further underscores the interest of understanding the tree's reproductive ecology, in order to maintain not only fruit production in the short term, but also for the long-term maintenance of the tree's populations. Fruit production is often low, and in some populations one gains the impression that natural regeneration is virtually non-existent. Because mature trees are long-lived, there could be a long lag time between a strong reduction in recruitment of juveniles and its perception as a problem.

Tamarind populations in the Sahel zone of West Africa are usually small, and often isolated from other populations. Individual trees also occur, relatively isolated in the landscape, the product of seed dispersal by humans and domesticated or wild mammals on frugivory and seed dispersal (Aubréville, 1950). While fruit production appears to be higher in trees located near conspecific individuals, even isolated trees sometimes produce fruits. This suggests that trees might be self-compatible. The consesquences of selfing, both for fruit quality and for survival, growth and fruit production of the progeny are unknown.

To gain information crucial to the management of fruit production and the maintenance of viable populations of this valuable and poorly studied tree, we undertook a study of the pollination biology of tamarind, focussing on questions shown by interviews with local residents who harvest tamarind fruits to be pertinent to management concerns they consider important:. (1) Is fruit production in 'natural' populations limited by pollination? (2) Is the tree self-compatible? (3) If so, do fruit set and fruit size (an important aspect of fruit quality) depend on pollen source (auto- or allopollen)?

MATERIALS AND METHODS

Study species

Tribal classification of Caesalpinioideae based on the leguminous cladistic analysis modified from Polhill et al. (1994) placed *Tamarindus* genera in the *Amhertia* group of the Detarieae Tribal. In the Sudano-sahelian region of West Africa, the flowering seasons of tamarind and other numerous plants is the end of the long dry season and its flowering can extend over five months (De Bies et al., 1999). Each yellow hermaphroditic flower contains three stamens and a pistil with up to 14 ovules. Pollen grains are compacted together and sticky. According to Oswald (1984) pollen grains is (14 u < t < 100 u). In sudanian and sahelian zone pollinators were identified by Diallo (2001) appartend to hymenoptera group dominate by social bees (*Apis mellifera*, *Polistes fastidious*, *Trigona* sp.) and single bees (*Xylocopa olivacea*, *Megachile* sp.) Period of fruit maturation is December to January. The fruit is a pod with 1 to 10 brown seeds. Fruits were collected from tree. Animals eat tamarind fruits and disperse their seeds (Aubréville, 1950; Arbonier, 2000).

Field study site

The study of pollination biology was conducted in western Burkina Faso, in the village of Souroukoudinga 11°14 N and 4° 26 W, west of Bobo-Dioulasso (2nd town of Burkina Faso). The climate of this region is described as sudanian (Guinko, 1984), i.e., less arid than Sahelian climate.

Pollination experiments

Five phenological stages were defined for this study: (1) stage A: flower bud; (2) stage B: elongated flower; (3) stage C: open flower with closed anthers; (4) stage D: open flower with dehiscent anthers; and (5) stage E: fully opened flower starting to wilt. To determine the floral stage at which pollen viability is highest, we performed viability tests, using carmine red (Hauser and Morrison, 1964; Kearns and Inouye, 1993). For each floral stage, these tests were performed on 100 anthers collected on a total of 80 flowers from three different individuals (n = 8 trees, x and 10 flowers per individual). Anthers were sectioned with a razor blade, sections were placed on microscope slides, and pollen grains were counted and scored for viability. From 20 to 40 pollen grains were scored per anther. Cytoplasm of viable pollen grains stained red, whereas unviable grains appeared orange, as the staining fluid simply filled up the empty cells. Based on results of these viability tests, pollen used for the crossing experiments was collected on flowers at C and D stages. Allo-pollen was collected on 8 different individuals (15 flowers per individual), all from the single studied population. Auto-pollen was collected from a mix of 100 different flowers of each focal individual. Prior to the crossing experiments, flowers were placed within mesh bags to prevent pollinator visits. C-stage flowers (anthers still closed) were castrated and pollen (auto or allo-pollen) was deposited onto the stigma using a camel-hair brush. D-stage flowers in neighbouring inflorescences were used as open-pollinated controls. We performed auto and allo hand pollinations on eight different individuals of the population. Autopollen was collected from flowers on other inflorescences spread through the crown of the plant. Pollination experiment was run on 5 non-rainy days for each of the three treatments (open, cross and self pollination). The fruits obtained in each experiment were collected upon maturity. We counted the number of fruits produced, and for each fruit the number of ovules that had begun to develop, and the number of ovules that had developed into mature seeds. These numbers reflect proportions, because the number of ovules per ovary in *Tamarindus* varied extremely little around a mean of 14 (based on counts performed on a total of 148 ovaries from a total of 4 individual trees).

Observation of pollen tube growth under controlled pollination experiments

During the previous breeding experiments, flowers were collected 5 days after hand pollination to examine pollen tube growth under different pollination regimes. Because flower abortion was highly variable among trees and treatments and across phenological stages, the number of flowers in which pollen tube growth could be examined was also variable. Flowers were preserved in FAA and transported to the laboratory (Centre d'Ecologie Fonctionnele et Evolutive, Montpellier, France). Flowers preserved in FAA were rinsed in 70% ethanol and then placed in a vial containing aniline blue (Kearns and Inouye, 1993). Vials were then put in a water bath at 60°C for 45 min. The flowers were then placed again in ethanol for 72 h. This treatment renders pollen tubes fluorescent, permitting their observation under a fluorescence microscope equipped with a yellow filter. Pollen tube growth was estimated using the following indices: 0 = no pollen tube; 1 = 1-3 pollen tubes; 2 = 4-6 pollen tubes; 3 = more than 6 pollen tubes. The pollen tubes were counted in three different parts of the flower: on the stigma, within the style and within the ovary. For each flower we also counted the total number of ovules per ovary.

Data analysis

A preliminary analysis has shown the normality of our data. We transformed the variable number of the fertilisation ovules into arc sinus and used percentage data to do the analysis. A Khi-2 test allowed us to know the evolution of the pollen tubes inside each compartment of the pistil. Then an ANOVA test has been done by the General linear Model (GLIM) and we compared the quotation means by the DUNCAN test (5%). Then a second data analysis has concern-

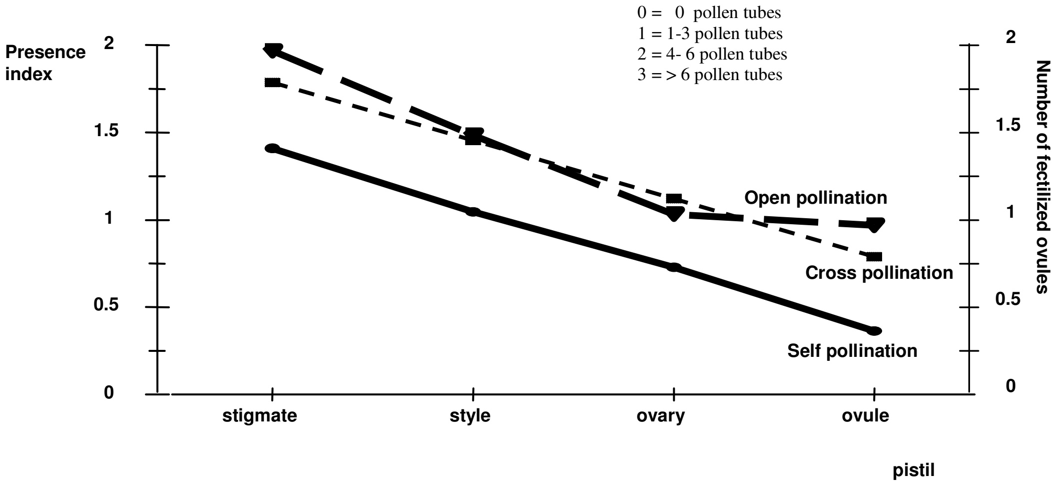

Figure 1. Effect of three pollination mode (open, cross, self) on the number of germinated pollen on stigmate, the proportion of pollen tubes that had reached the style and in the ovary and the proportion of fertilised ovules.

ed fruit productions. We had considered two hypotheses in our experiment. The first one had concerned the impact of the pollen nature on the development of fruit and seed set. The second one had treated the limitative effect of the pollen distribution on the fruit production. The models used for each variable analysis are the following:

Variable number of fruit set: We considered two models for this variable. First model is the effect of the pollination and the second is the effect of tree. The effect of the pollination model is: $Y_{ijk} = \mu + P_i + E_{ijk}$. The effect of tree is: $Y_{ijk} = \mu + A_j + E_{ijk}$ where Y_{ijk} = fruit number; μ = field mean; P_i = pollination mode effect i, i = (self, cross, open); and A_j = tree effect j, j = (1,2,.....,6).

Loges number and seed number: $Y_{ijk} = \mu + P_i + A_j + (PA)_{ij} + E_{ijk}$ where Y_{ijk} = variables; μ = field mean; P_i = pollination mode effect i, i = (self, cross, open); A_j = tree effect j, j = (1,2,.....,6); $(PA)_{ij}$ = interaction between pollination mode and tree; and E_{ijk} = error.

RESULTS

Pollen tubes quantification

In D-stage flowers, some pollen tubes had reached the ovules, whereas in flowers at stage C, no pollen tubes were present in the style or in the ovary, nor had any pollen germinated on the stigma. All comparisons thus concern the two modes of hand pollination, and open pollination, in flowers at stage D. The Figure 1 shows that with all three modes of pollination, pollen grains had germinated on the stigma, pollen tubes were present in the style and the ovary, and ovules had been fertilised by pollen tubes. However, the proportion of pollen that germinated, the growth of pollen tubes (proportions that had reached the style and ovary), and the proportion of ovules fertilised all depended strongly on the mode of pollination, as shown by ANOVA (Table 1). Values for all of these three variables were much lower in self-pollinated flowers than in the other two treatments. Except for the proportion of pollen tubes that had reached the style, there were highly significant differences among individual trees in these variables. There were no significant interaction effects between mode of pollination and individual tree for any of the variables ($P > 0.05$ in all cases). Comparison of means for the three pollination modes using the Duncan 5% test (Table 2) showed that there were no significant differences in any variable examined between hand cross-pollination and open pollination. In contrast, differences between hand self-pollination and each of the other two treatments were highly significant for all variables tested.

Pollen tube growth

Figure 2 illustrates the germination of pollen grains on the stigma, the growth of pollen tubes in the style and the ovary, and the fertilisation of ovules, respectively for hand self-pollination (a), open pollination (b), and hand cross-pollination (c). The greater number of pollen tubes in the open-pollination and hand cross-pollination treatments than in the hand self-pollination treatment is evident from these photographs. Once arrived in the style, as the pollen tubes continue to grow toward the ovary, and the formation of callose (stained by the aniline treatment) intensifies as pollen tubes near the ovules. In the ovary, pollen tubes examined showed three outcomes. Some had penetrated into an ovule and fertilised it; others had reached an ovule but had been unable to penetrate it, as shown by others had not yet approached an ovule. Whereas in open-pollinated flowers and hand cross-

Table 1. Analyse of variance on the number of pollen grains germination on stigmate (general linear model).

Source	Ddl	Sum of square	Means square	F Value	Proba P>F
Pollination	2	22.450513	11.225256	15.06	0.0001 ***
Tree	7	91.390260	13.055751	17.52	0.0001 ***
Pollin x Tree	14	15.684595	1.120328	1.50	0.1048 NS

* Significant; ** very significant ; *** highly significant; NS, non significant.

Table 2. Analyse of variance on the number of pollen tubes growth in style (general linear model).

Source	Ddl	Sum of Square	Means Square	F Value	Proba P>F
Pollination	2	19.109246	9.554623	12.62	0.0001 ***
Tree	7	16.282033	2.326005	3.07	0.0034 **
Pollin x tree	14	12.272344	0.876596	1.16	0.3040 NS

* Significant; ** very significant ; *** highly significant; NS, non significant.

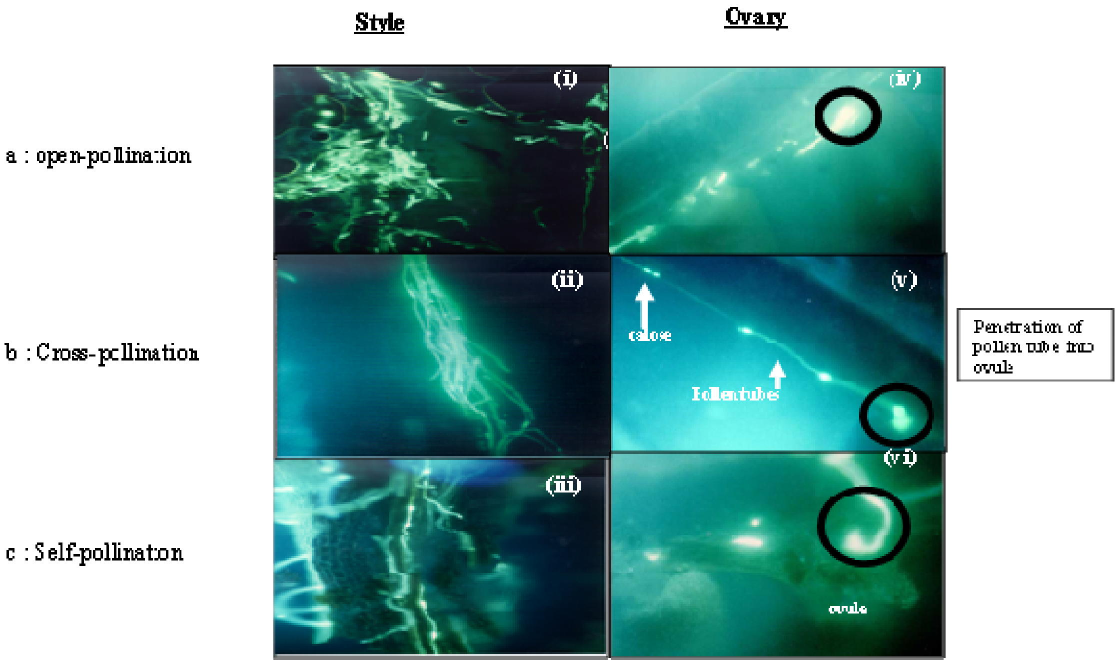

Figure 2. Pollen tubes intensity in the style and the ovary for the three pollination odes. (a) open pollination; (b) cross pollination; and (c) self pollination. (i), (ii) and (iii) = pollen tubes growing through the style. (iv), (v) and (vi): pollen tube into ovary.

pollinated flowers, pollen tubes had penetrated perpendicularly into the ovule, in hand self-pollinated flowers there was sometimes an "elbow" at the point of contact, indicating the rejection of the pollen tube by the ovule (Figure 2).

Fruit set and seed set

The ANOVA showed that for each of the three variables, (proportion of flowers yielding mature fruit, proportion of ovules that had begun to develop, and proportion of ovules that yielded mature seeds), were highly significant effects of mode of pollination (P < 0,001). However there were no significant effects of tree. The loges or fruits number and seed number can be examined on the ANOVA table (Table 3).

Comparison of means for the three pollination modes (Table 4) showed the same results as we got with the proportion of pollens tubes: on the one hand there were

Table 3. Analyse of variance on the number of pollen tubes growth in ovary (general linear model).

Source	Ddl	Sum of Square	Means Square	F Value	Proba P>F
Pollination	2	34.366993	17.183496	21.06	0.0001 ***
Tree	7	9.618325	1.374046	1.68	0.1099 NS
Pollin x tree	14	12.660478	0.904320	1.11	0.3465 NS

* Significant; ** very significant ; *** highly significant; NS, non significant.

Table 4. Analyse of variance on the number of ovules fecundated in ovary (general linear model).

Source	Ddl	Sum of square	Means square	F value	Proba P>F
Pollination	2	49.212875	24.606437	17.27	0.0001 ***
Tree	7	36.980488	5.282927	3.71	0.0006 ***
Pollin x arbre	14	13.366684	0.954763	0.67	0.8046 NS

* Significant; ** very significant ; *** highly significant; NS, non significant.

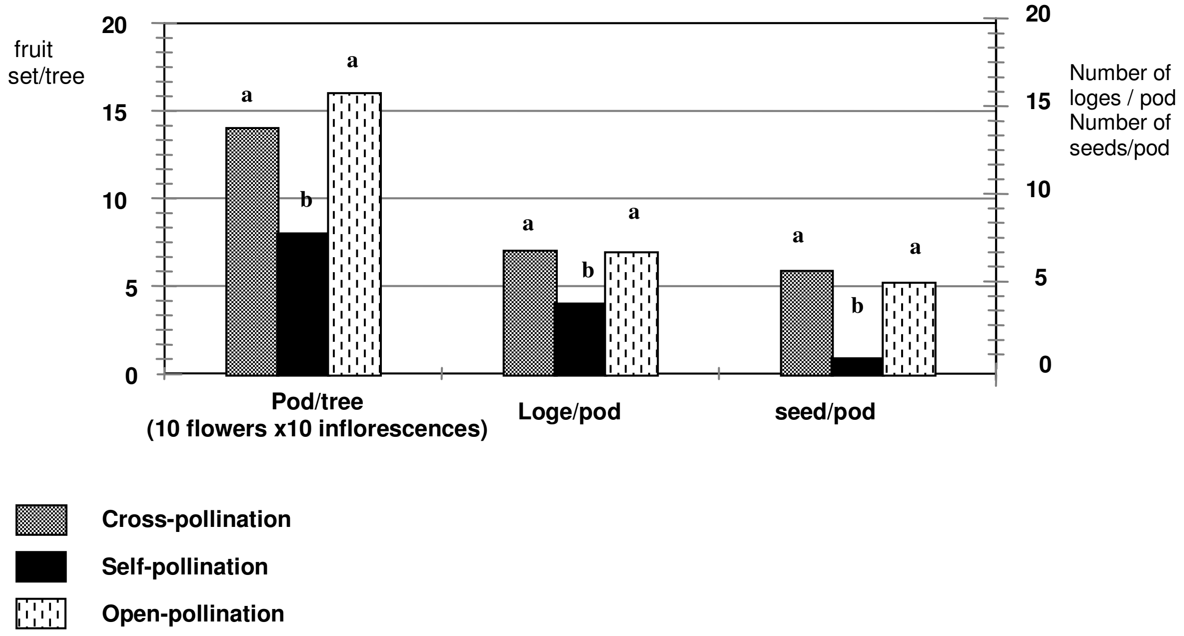

Figure 3. Mean of fruit number per tree, loges number per fruit and seeds number per pod for 3 pollination modes (cross, self and open).

cross pollination and open pollination and the other hand self pollination. In Figures 3a and 3c, there are differences between self pollination and the others (hand cross pollination and open pollination).

DISCUSSION

The absence of pollen tubes on flowers at C stage is a sign of absence for geitonogamy in *T. indica*. The low pollen germination and the slow growing of pollen tube as well as the difficulty for fertilization of ovules observed in self-pollination for *T. indica* is due to pre-zygotic self incompatibility; but it is only partial. It appears initially on the stigmate then on the style and thereafter within the ovary. This incompatibility is more emphasized when the pollen tubes reach the ovules where they were sometimes rejected by the ovules. Hossaert (1988), in his study on *Lathyrus sylvestris* highlighted a total self-incompatibility whereas Diallo (1995) reported that *Genista scorpius* is partially self-incompatibility. Many biologists pointed out that the pre-zygotic self-incompatibility is due to gametic nature. Thus Shivanna and Owens (1987) reported that in some crop, this phenomenon is controlled by multiple alleles on a locus. Seavey and Bawa (1986) described self-incompatibility as a delayed mechanism of self-incompatibility.

Results revealed that *T. indica* is a species in which cross-pollination and self-pollination coexist together. However the species is likely cross-pollination. At fruiting stage, it was observed that abortions of post-zygotic, are more important in self-pollination, this revealed losses of offspring formation due to consanguinity. However, the number of fertilized ovules and the fruit formed in self pollination system indicate that the non compatibility post zygotic was partial. Whatever the pollination system, seed's abortion are not only related to self-incompatibility. They would be probably a result of whole factors among which one can quote the limitation of the resources which imposes a sorting by the female. Hossaert (1988) showed that in the event of limited resources allocation pollen tubes resulting from cross-pollinisation (genetically higher) are favoured. Similar studies carried out on other leguminous plant species by Bawa and Buckley (1989) and Hossaert (1988) showed that only a small part of flowers produced can give fruits in a very small number of ovules which could be developed out into seeds.

The partial self-incompatibility thus observed expressed the strategy adopted by certain cross pollinated species to survive under extreme hard conditions. Somehow it is better to produce connected offsprings, in the hope that some will survive in the medium rather than to be disappeared without perpetuating its genes. Larsen (1982) reported that self-incompatibility is like a flexible system; while self-fertilization seems to be a phenomenon to mitigate the insufficiency of pollinators or absence of efficient pollinators.

In order to limit consanguineous' individual within the population, species have a strategy of control on the stigmate, style or within the ovary or ovule level. *T. indica* is a cross-pollinated species preferentially which is only partially self-incompatible. After a self-pollination phase, a whole process tends to limit seed' formation. Those appear at stigmate level or on the style and in the ovary by a low presence of pollen tubes or their withdraw by ovules, which is observed by a formation of an elbow on the level of pollen tube.

In this study we show that open pollination and cross pollination give better quantitative seed than self pollination. A high rate of seed abortion is observed what ever the pollination system; which is clearly higher in self-pollination system. Results revealed that there is a post-zygotic self-incompatibility and others factors which were not related to pollination system intervened in seed development after the fertilization of ovules. Many factors are responsible for the often low proportion of mature fruits produced relative to the number of flowers initiated in angiosperms. Number of seeds per fruit can also be limited by quantity and/or quality of pollen (Bierzychudek, 1981; Young and Young, 1992), by the availability of resources (Stephenson, 1981; Willson and Burley, 1983; Burd, 1994), or by predation on developing seeds (English-loeb and Karban, 1992; Gomez, 1993). In addition to these proximate factors, patterns in fruit set (e.g., the large numbers of flowers relative to fruits in many hermaphroditic plants) may reflect evolutionary strategies driven by sexual selection (Lloyd, 1979; Bawa, 1980; Givnish, 1980; Bawa and Beach, 1981; Webb, 1981; Casper and Charnov, 1982) or by predator satiation e.g. among-year variation in mast-fruiting systems (Gautier-Hion, 1990).

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