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Inter-male Pollen Competition, Pollination Success & Seed Set, Offspring Fitness and Ploidy Configuration in Plantain and Banana (*Musa spp*) Crosses

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ABSTRACT: Four tetraploid plantain hybrids were used as female or maternal/ seed parents (TMPx 1658-4, TMPx 2796-5, TMPx 7152-2 and TMPx 5511-2). One diploid plantain hybrid (TMP2x 2829-62), and 2 diploid banana hybrids (TMB2x 15101-2 and SH 3362) were used as male or paternal/ pollen parents. Sets of females were hand pollinated with pollen from the males as follows: single hit was pollen from TMP2x 2829-62; double hit was equal mixture of pollen from TMP2x 2829-62 + TMB2x 15101-2; and triple hit was equal mixture of pollen from all 3 males TMP2x 2829-62 + TMB2x 15101-2 + SH 3362. There were 30 crosses for each pollination type replicated 3 times in 2 polycross blocks. There were significant differences ($P > 0.05$) in pollination success and seed set among the different pollination types. Pollination success was highest with the single hit and declined significantly by (47%) in the double hit and (71%) in the triple hit compared to the single hit. Seed set declined significantly by 50.4% from single hit to double hit and further declined by 89.4% from single hit to triple hit. The single hit produced significantly higher numbers of TMPx 7152-2 seeds than from other maternal parents, whereas the double and triple hits produced significantly more seeds from TMPx 1658-4 than from other maternal /seed parents. Triple hit produced higher germination rate and seedlings with significantly higher seedling vigour. Double and triple hits produced all triploid offspring whereas the single hit produced triploid and tetraploid offspring in a 2:1 ratio.

KEY WORDS: Multiple paternities, Pollen sources, Pollination intensity, Pollination type, Seedling vigour, Single hit, Double hit, Triple hit.

I.INTRODUCTION

This experiment investigated the effects of crosses with one source of pollen (single hit), two sources of pollen (double hit) and three sources of pollen (triple hit) on inter-male pollen competition, pollination success and seed set, offspring fitness and ploidy configuration in plantain and banana.

II. SIGNIFICANCE OF THE STUDY

This experiment was conducted to assess the effect of pollen competition and multiple paternities on pollination success in the form of resulting seed set, the ploidy configuration of resultant offspring and effect on offspring fitness of plantain and banana (*Musa* spp) crosses.

III. LITERATURE SURVEY

Cross-breeding in *Musa* relies on the fertilization of female-fertile parents by pollen of male parents to generate hybrid seed. Diploid parents produce more pollen than polyploid cultivars or hybrids [1], which suggests the need for using the former as male parents. Pollination is the act of transferring pollen grains from the male anther of a flower to the female stigma of the same or another flower. It is therefore possible that in nature, pollen from several males could be transferred by vectors (insects, animals, wind, and water) on to the same female stigma thereby ensuring pollination by

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Vol. 7, Issue 1 , January 2020

pollen from more than a single male. This condition, called polyandry, a condition in which a female flower or plant is pollinated and fertilized by pollen from more than one male in any single breeding season is probably ubiquitous in plants except those that habitually self-fertilize, or that disperse their pollen in pollen packages, such as polyads or pollinia [2]. Thus pollen from several males either immediately after each other or at increasing intervals could pollinate a single female stigma as long as that stigma is receptive [3]. It seems therefore that the frequent multiple paternities observed within open-pollinated species should not really come as a surprise and is probably for the maintenance of genetic variability. Multiple paternities have been found in insect pollinated hermaphrodite species, in dioecious species [4] and in those pollinated by birds [5] and by bats [6]. It has also been reported in flowers with few ovules [7], [8] and many ovules or seeds [4], [9]; in self-incompatible [4], [6], [8] and self-compatible species as well as in plants with complex inflorescence [10] versus solitary flowers [11]. The result of course is that pollen from different males will be in competition to fertilize the ovule and produce seeds. The desire of every living organism, including plants, is to create offspring for the next generation so that the species can continue in perpetuity. One of the ways that plants can produce offspring is by making seeds. Seeds contain the genetic information to produce a new plant. The number and relative abundance of males contributing to a seed crop has been reported to influence reproductive performance, including seed production, fruit maturation, and the vigour of resulting offspring [12], [13]. It was reported [14] that fruits produced by multiple pollinator visits had greater seed numbers (206 vs. 147) than fruits produced by a single pollinator visit. Another study found that individual seeds were heavier in fruits where pollen from a single male sired most seeds than in fruits where pollen from two males had a more even paternity share [15]. In a more recent study of experimental evolution, lines crossed with either one or two pollen donors (monogamous, M, or polyandrous, P, lines) at early floral stages in mixed-mating *Collinsia heterophylla* (Plantaginaceae), P showed enhanced pollen competitive ability and reduced maternal seed set compared to M, in accordance with sexually antagonistic evolution of pollen [16]. In most animal-pollinated species, even in the absence of competitors, only 1% of pollen is exported to conspecifics i.e. belonging to the same species [17]. This low efficiency follows from factors at several levels including limited pollen pick-up by pollinators [18], passive loss during transport [19], removal of pollen from the pollinator's body by active grooming or preening [20], moving of the pollen to corbiculae or scopae of bees [21] and pollen deposition on flowers of the same plant (a form of pollen discounting; [22]. Even this partial list suggests that pollen might have little prospect of reaching stigmas of other conspecifics, but when we add competition for pollination and fertilization, and the selective responses of the female stigmas to the presence of pollen from several males, the opportunities for loss could even multiply.

The movements of pollinators within and between species alone can greatly influence these factors, and even add new possibilities. It has been stated [14] that the progeny produced by multiple pollinator visits were more vigorous than those produced by single visits with respect to five measures of vegetative growth. Their data demonstrated that conditions for pollen competition exist in nature and support the prediction that pollen competition enhances offspring vigour. Low pollen loads on stigmas may impact on the quality of the offspring produced by reducing pollen competition. Competition among pollen grains in their race down the pistil to fertilize ovules allows the sorting of males according to their associated vigour and competitiveness. Given that at least 60% of a plant's genome is expressed during pollen-tube growth and elongation [23], it is possible that the offspring resulting from an intense pollen-tube competition might be of better quality than those produced in the absence of pollen competition, especially if the high competitive ability of successful pollen grains is translated into growth advantages in the progeny they father [24]. Plants enjoying high pollination intensity and thus high seed set might thus produce smaller seeds than those whose seed set is pollen-limited, and vice versa. Indeed, pollen-limited flowers have been reported to produce larger seeds [25], likely because resources are shared between fewer embryos than would be the case for fully seeded fruits [26]. There has been substantial work directed either towards understanding the importance of pollination intensity on seed set in natural and experimental plant populations [27]. [28], and on how competition among pollen grains might affect offspring fitness [29], [30]. Furthermore, pollination and reproduction are only components of fitness, and subsequent events such as dispersal and germination of seeds, emergence of seedlings, and growth of seedlings to sexual maturity may enhance or reduce effects at the pollination stage [31], [32].

Selection for pollen traits that enhance pollen competition and mating success have now been well demonstrated in the post pollination stage. These traits include pollen size [33], pollen provisioning [34] and pollen-tube growth rate [35], [36], providing clear functional links between pollen traits and male reproductive success. Some workers [37] have suggested that pollen of rival males is constantly covered or displaced by pollen of competitors. Several authors [2], [38], [39], [40] have reported that many flowering plants are often sired by pollen from three to six donors and

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Vol. 7, Issue 1 , January 2020

therefore the number of pollen donors in a mixture should closely match male diversity within the focal population. This therefore means preparing realistic mixtures of pollen when conducting such studies. Few studies have explored the dynamics of pollen competition between more than two plants. Fewer still have investigated the phenomenon of pollen competition in *Musa* species. No doubt the possibility of measuring pollination success and seed production, in addition to providing a glimpse into performance and vigour of resulting offspring early in the life cycle from multiple paternities in *Musa* should throw up valuable information. To the best of our knowledge we are not aware of any pollination study that has investigated this yet in *Musa spp* in any context.

IV. METHODOLOGY

This study was carried out at the International Institute of Tropical Agriculture (IITA) High Rainfall Station, Onne (4°51'N, 7° 03'E, 10m above sea level), in Rivers State, south-eastern Nigeria. The rainfall pattern is monomodal, distributed over a 10month period from February through December, with an annual average of 2400mm. Relative humidity remains high all year round with mean values of 78% in February, increasing to 89% in the months of July and September. The mean annual minimum and maximum temperatures are 25^0C and 27^0C, respectively, while solar radiation / sunshine lasts an average of 4hours daily [41]. The soil is derived from coastal sediments of the Niger Delta, freely drained and acidic (pH 4.3), and made up of mainly Kaolinite. Onne soils are also high in phosphorus 60mg kg^{-1}, manganese 0.2mmol kg^{-1}, but low in nitrogen [42], [43].

Experimental Materials

Four tetraploid plantain hybrids were used as female or maternal/ seed parents (TMPx 1658-4, TMPx 2796-5, TMPx 7152-2 and TMPx 5511-2). One diploid plantain (TMP2x 2829-62) hybrid, and 2 diploid bananas (TMB2x 15101-2 and SH 3362) hybrids were used as male or paternal/ pollen parents and planted in 2 *Musa* polycross blocks as described in [44].

Treatment Applications and Experimental Design

Pollen Competition, Pollination Success and Seed Set

To assess inter-male pollen competition in the polycross scheme, targeted hand pollination was carried out on selected plants in the 2 polycross blocks. The inflorescence of the four tetraploid females and three diploid males were protected by transparent plastic bags before anthesis of either of the flowers. At anthesis pollen from the anthers of the male diploid hybrids was dusted on the stigmas of the female tetraploids. This was done between 0700 and 1030 hours. For the single male parent pollination (single hit), using pollen from a single male (TMP2x 2829-62 – chosen for its early flowering and shortest time to fruit filling), anthers of the male were brushed uniformly over the entire stigmatic surfaces of each of the females after which the inflorescence of the females were again bagged to avoid possibility of further pollination from other sources by vectors. An equal mix of pollen from two males (double hit) TMP2x 2829-62 + TMB2x 15101-2 (SH 3362 is an introduction from Honduras and is very late flowering relative to the others) was brushed against the entire stigmatic surfaces of another set of the four females after which the inflorescence of the females were again bagged. This served as double male pollination. Finally, an equal mix of pollen from all three males (triple hit) that is (TMP2x 2829-2 + TMB2x 15101-2 + SH 3362) was brushed against the entire stigmatic surfaces of the third set of females after which the inflorescence of the females were again bagged. This served as the triple male pollination. Thus there were 30 crosses each for the single, double and triple hits totalling 120 crosses. Each of these treatments was replicated 3 times within each of the 2 polycross blocks (see description of polycross blocks in [44]. At maturity the fruit bunches of the maternal/ seed parents were harvested, ripened, and the seeds extracted, washed and air-dried. Well-formed hard seeds were collected from each maternal /seed parent and the total number of seeds produced counted.

Offspring Performance and Fitness

An equal number of seeds (15 seeds each) from each of the pollination types (single, double and triple hits) were planted in three replications in the nursery and the nature and vigour of offspring /seedlings produced from each pollination style (single, double and triple hits) were observed to ascertain level of fitness of offspring from each

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Vol. 7, Issue 1 , January 2020

category. Percentage germination of seedlings was calculated, while seedling height and seedling dry weight on the 42nd day post-emergence were recorded for the purpose of determining seedling vigour according to [45] as below:
i) Vigour Index-I = Standard germination (%) × Average seedling length (cm)
ii) Vigour Index-II = Standard germination (%) × Average seedling dry weight (g)
For dry weight determination, the seedlings were taken and dried in an air oven at 100°C temperature for 48 hours.

Ploidy Configuration

Flow cytometry was carried out on the seedlings using cigar leaf as described in [44] in order to obtain the ploidy configuration and the relative frequency of offspring from each of these pollination types.

Data collection and analysis

All data collected were subjected to analysis of variance (ANOVA) in a randomized complete block (RCB) design using the GLM procedure of Statistical Analyses Software (SAS) version 9.1 and any effects found to be significant were tested at a significance level of 5% while treatment means were compared using LSD also at 5% significance level.

V. EXPERIMENTAL RESULTS

Inter-male Pollen Competition, Pollination Success and Seed Set

Significant differences ($P > 0.05$) in pollination success and seed set were observed among the different pollination types (Table 1). Pollination success was highest with the single hit and declined significantly with increasing sources of pollen in the double hit (47%) and triple hit (71%) compared to the single hit (Table 1). When pollen source was increased from two (double hit) to three (triple hit) pollination success again declined significantly by 44% indicating intense inter-male pollen competition to fertilize the ovules as pollen source increased. The highest number of seeds was obtained from the single hit compared to the double and triple hit pollination types. Seed set declined significantly by 50.4% when pollen source was increased from single source (single hit) to two (double hit) and further declined by 89.4% when it was increased from single source (single hit) to three (triple hit). Compared to seed set in the double hit, triple hit resulted in a 78.6% decline in seed set. The implication is that seed set was higher when all the pollen was from a single male parent indicating perhaps that intra-male pollen competition when pollen is from a single source may be less intense and that there was no inter-male pollen competition. In contrast, the lower seed yield in the double hit and triple hit may be indicative of increasing intensity of inter-male pollen competition as the sources of pollen increased. Similar findings of reduced seed set had been reported [16] with multiple pollen sources and [37] had suggested that pollen of rival males is constantly covered or displaced by pollen of competitors thereby limiting actual pollen that reaches the ovules. However, although inter-male pollen competition may be detrimental to seed yield, it may result in improved seed germination and seedling survival rate.

Table 1. Pollination success and seed set obtained from seed parents pollinated with pollen from a single male parent (single hit) or equal mixture of pollen from two male parents (double hit) or equal mixture of pollen from all three male parents (triple hit) at the International Institute of Tropical Agriculture (IITA) High Rainfall Station, Onne, Rivers State, Nigeria

Pollination Types	Pollination success (% crosses with seeds)	Overall Seed Set of maternal parents
Single hit	15.4±0.03	554±0.02
Double hit	8.1±0.06	275±0.06
Triple hit	4.5±0.11	59±0.07
$LSD_{0.05}$	0.20	31.11

The number of seeds produced by each of the maternal/ seed parents from the pollination types - single, double and triple hits is shown in Fig. 1. The pollination types resulted in significantly different (*P* > 0.05) numbers of seeds from the four maternal /seed parents. For example, the single hit produced significantly higher numbers of TMPx 7152-2 seeds (4.6 times more) than from the other maternal parents, whereas from TMPx 1658-4 the triple hit produced

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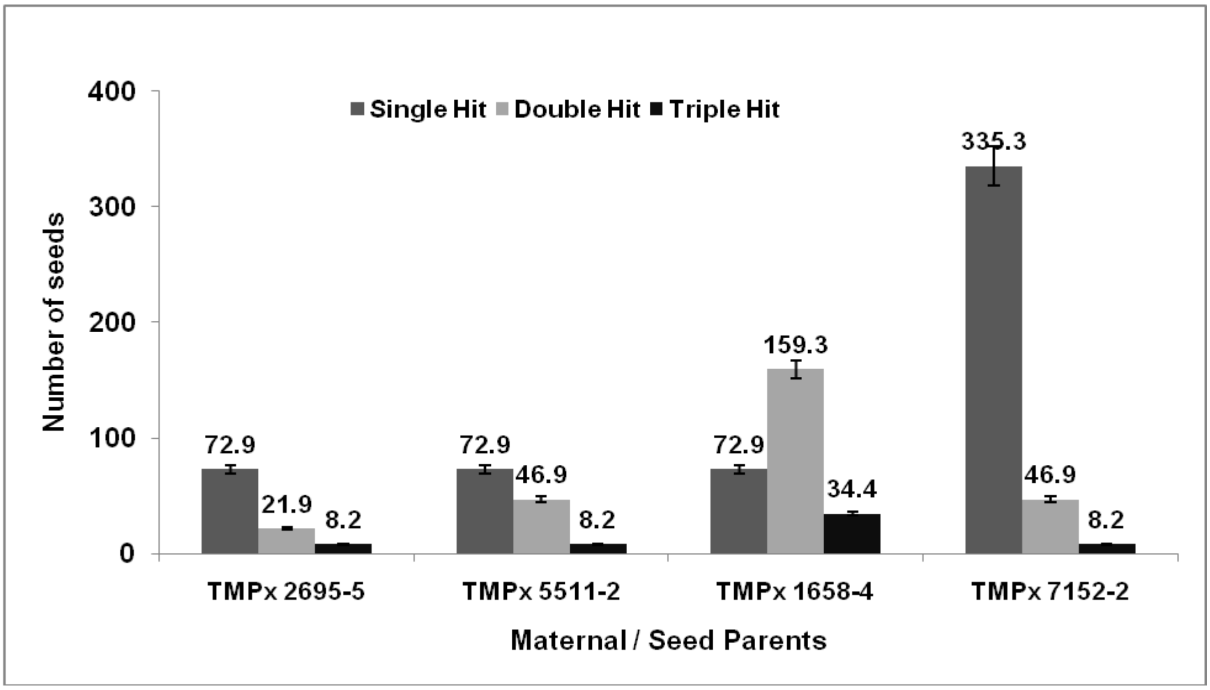
Vol. 7, Issue 1 , January 2020

significantly higher (4.2 times more) seeds than from the other maternal /seed parents. The situation was however different with the double hit which produced a more varied complement of seeds from the maternal seed parents with the significantly highest number of seeds from TMPx 1658-4 (7.3 times more than from TMPx 2796-5) and (3.4 times more from TMPx 5511-2 and TMPx 7152-2). Because of these differences inter-male pollen competition might have considerable consequences for *Musa* hybrid population dynamics under open pollination when sources of pollen increase [46]. Further studies are needed to determine the exact cause or causes of this phenomenon whether it has to do with the preferences, nature, compatibility, or receptivity of the stigmas of these females to the different pollen sources and or to the increasing number of pollen sources.



Fig, 1. Number of *Musa* seeds produced by the four maternal /seed parents from single hit (pollen from a single male parent), double hit (equal mixture of pollen from 2 male parents) and triple hit (equal mixture of pollen from all 3 male parents).

Offspring Fitness

Although pollen competition may be detrimental to seed yield, it may improve seed germination and seedling vigour or survival rate. Seeds with high vigour grow at a faster rate compared to seeds having poor vigour potential. Vigorous seeds metabolize their food reserves rapidly, germinate, and establish in the field. Therefore, any method used to determine the quickness of growth of the seedling will give an indication of seed vigour level [47]. In this study, *Musa* seeds from the triple hit had significantly higher percentage germination (3 times higher) than the single hit and double hit pollination types (Table 2). There was no significant difference between germination percentage of the seeds from the single and double hits. Seedlings obtained from the triple hit were significantly taller and had higher dry weights than those from the single and double hits. However, there was no significant difference between height of seedlings and dry weight of seedlings from the single and double hits. This would seem to indicate a higher level of seed vigour and growth advantage arising not from two pollen sources but from multiple pollen sources as reported by [24]. The triple hit cross also had a higher number of emerging seedlings than either the single or double hit crosses. In zucchini squash, seedlings from high pollen competition had higher germination rates [48]. Other authors [29], [30] had also declared that competition among pollen grains might affect offspring fitness. This study also showed that with respect to both seedling vigour indices (Table 2), seedlings of the triple hit pollination type had significantly higher seedling vigour (about 4 times higher) than seedlings from the single and double hits.

ISSN: 2350-0328
International Journal of Advanced Research in Science, Engineering and Technology
Vol. 7, Issue 1 , January 2020

Table 2. Fitness of *Musa* offspring: Percentage germination and seedling vigour indices arising from single, double and triple hit pollination types at the International Institute of Tropical Agriculture (IITA) High rainfall station, Onne, Rivers State, Nigeria

Pollination Types	Percentage germination of seeds	Seedling height (cm)	Seedling Vigour Index I	Seedling dry weight (g)	Seedling Vigour Index II
Single hit	12.3±0.11	56.5±0.57	694.95	1,393.2±0.16	17,133.9
Double hit	11.4±0.30	61.7±0.13	703.38	1,445.8±0.10	16,482.12
Triple hit	36.8±0.38	76.9±0.27	2,829.92	1,682.3±0.06	57,124.64
$LSD_{0.05}$	1.486	11.161		145.802	

±S.D.

Ploidy Configuration of Offspring

Flow cytometry analysis of the hybrids obtained from the experiment on inter-male competition showed only two ploidy levels (Fig. 2). Hybrids from single pollen source (single hit) gave both 3x and 4x hybrids in a ratio of 2:1. This suggests the production of 2n gametes. However, hybrids from equal mixtures of pollen from the two males (double hit), and all three male parents (triple hit), were all 3x (Fig. 2). This suggests that meiosis was regular in the female and male parents.

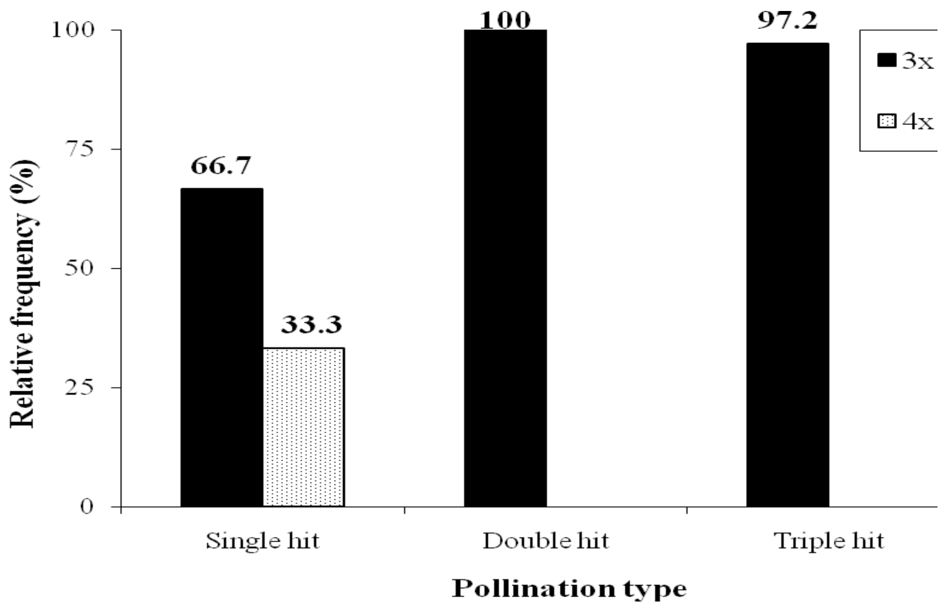


Fig. 2. Ploidy configuration of *Musa* offspring from inter-male pollen competition (single hit, double hit and triple hit) pollination types from 4x-2x crosses

VI. CONCLUSION AND FUTURE WORK

This study found that pollination success and seed set declined significantly with when maternal /seed parents were pollinated with different sources of pollen from the single hit (one pollen source) to the double hit (two sources of pollen) and the triple hit (three sources of pollen) as a result of inter-male pollen competition. The single, double and triple hit pollination types produced significantly dissimilar proportions of seeds in some of the maternal /seed parents. Offspring from the triple hit had higher germination percentage and seed and seedling vigour than those from the single

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International Journal of Advanced Research in Science, Engineering and Technology
Vol. 7, Issue 1 , January 2020

and double hits. Double and triple hits produced all triploid offspring while the single hit produced triploid and tetraploid offspring in a 2:1 ratio.

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