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Does paternal sterility impact on progeny germination and survivorship, case study in strawberries

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ABSTRACT

Studies on the parental role on progeny performance have mostly focused on the maternal parent, while less attention was given to the paternal parent. This study investigated the impact of paternal pollen sterility (ranging from 3.1 – to 77.2%) on F_1 seed germination and progeny survivorship in *Fragaria* (strawberry, Rosaceae) using controlled crosses. In crosses within *F. vesca* ssp. *vesca* the paternal pollen sterility was not correlated with F_1 seed germination ($N = 14$, $p > 0.074$) and progeny survivorship (N = 14, *p* > 0. 0.710). Paternal sterility in crosses between *F. vesca* ssp. *vesca* and *F. vesca* ssp. *monophylla* did not affect on F_1 seed germination ($N = 7$, $p > 0.295$) and progeny survivorship ($N = 6$, $p > 0.812$). Similarly, no correlation was found between father pollen sterility and F_1 seed germination ($N = 6$, $p > 0.924$) and progeny survivorship ($N = 6$, $p > 0.215$) in crosses between *F. vesca* ssp. *americana* and *F. vesca* ssp. *vesca*. Furthermore, crossing different maternal plants by pollen of the same paternal plant in all three cross types produced progeny with variable levels of F_1 seed germination and survivorship. These results indicate the crucial role of maternal plant on progeny performance and support the general idea of the importance of maternal rather than paternal parent on progeny performance.

Key words: maternal impact, paternal impact, progeny performance, reproductive fitness, parental impact, *Fragaria*, strawberry

IZVLEČEK

ALI MOŠKA STERILNOST VPLIVA NA KALITEV IN PREŽIVETJE POTOMCEV? PRIMER RAZISKAVE NA JAGODNJAKIH (*Fragaria*)

Raziskave vloge staršev na uspevanje potomcev so pri rastlinah pogosto osredotočene na ženskega straša, manj pozornosti je posvečeno vlogi moškega starša. Ta raziskava je preučevala vpliv moške sterilnosti peloda (v razponu od 3,1 do 77,2 %) na kalitev in preživetje F1 potomcev jagodnjaka (*Fragaria,* Rosaceae) po kontroliranih križanjih. Po križanju gozdnega jagodnjaka (*F. vesca* L. ssp. *vesca*) moška sterilnost peloda ni korelirala s kalitvijo F1 semen ($N = 14$, $p > 0.074$) in preživetjem potomcev (N = 14, *p* > 0. 0.710). Enako moška sterilnost po križanjih med taksonoma *F. vesca* ssp. *vesca* in *F. vesca* ssp. *monophylla* ni imela vpliva na kalitev F1 semen ($N = 7$, $p > 0.295$) in preživetje potomcev ($N = 6$, $p > 0.812$). Podobno ni bila ugotovljena korelacija med moško pelodno sterilnostjo in kalitvijo F1 semen ($N = 6$, $p > 0.924$) ter preživetjem potomcev ($N = 6$, $p > 0.215$) po križanjih med taksonomoma *F. vesca* ssp. *americana* in *F. vesca* ssp. *vesca*. Še več, po križanjih različnih materinskih rastlin s pelodom iste očetovske rastline je imelo po vseh treh vrstah križanj potomstvo spremenljivo kalivost F1 semen in spremenljivo preživetje. Ti rezultati kažejo na odločilno vlogo materinskega starša na uspevanje potomcev in podpirajo splošno idejo o ključni, večji vlogi materinske rastline primerjalno z očetovsko.

Ključne besede: materinski vpliv, očetovski vpliv, uspevanje potomcev, reproduktivni potencial, starševski vpliv, *Fragaria*, jagodnjak

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1 INTRODUCTION

The variations in F_1 phenotype are thought to be affected mainly by maternal parents, although the parental genotype and environment do also affect of progeny performance (Roach and Wulff, 1987). The maternal effects on progeny performance are carried out via the different mechanisms including through cytoplasmic genetic, since organelles such as plastids and mitochondria can be directly transferred from the maternal plant to the offspring (Raghavan, 2005). The maternal parent can also affect on progeny via the endosperm because the endosperm contains more doses of maternal than paternal genes, and also contains enzymes and the nutrients resources important for germination and developing of the embryo (Bernasconi, 2003). In addition, the other maternal effects on offspring are caused by the structural or physiological effects of maternal tissues e.g. integuments of the ovule and the wall of the ovary surrounding the developing embryo and endosperm. These structures which form the seed coat, fruit, and accessory seed structures determine seed dormancy, dispersal, and germination (Raghavan, 2005). The impact of maternal parent on the progeny is different from the equal chromosomal contribution by both paternal and maternal parents (Roach and Wulff, 1987).

The level of progeny performance e.g. F_1 seed germination, survivorship and fertility are crucial in the natural selection in plants and therefore, in speciation (Niklas, 1997). In addition, based on "biological species concept" assessing the components of reproductive fitness in F_1 progeny in plants is important for understanding species delimitation and patterns of speciation (Kay, 2006), and has been used to delimit species boundaries in several plant congeneric species e.g. *Coreopsis* (Archibald et al., 2005), *Glycine*, *Silene*, *Streptanthus* (Moyle et al., 2004) and *Zigiber* (Kay, 2006).

There have been wide studies on the impact of maternal parent on the variations of the F_1 progeny performance in plants (e.g. Lloyd, 1980; Bernasconi 2003; Obeso, 2004; Halpern 2005; Raghavan, 2005; Gehring and Delph, 2006; Bayer et al., 2009; Holland et al., 2009; Diggle et al., 2010). These studies indicated that the levels of offspring performance in plants are mainly controlled by maternal parent, while the impact of paternal parent on the progeny performance has been less investigated (Holland et al., 2009). Therefore, it is important to understand the effects of pollen donor diversity on progeny performance in plants (Leishman et al., 2000; Westoby et al., 2002; Beaulieu et al., 2007).

In the current study the impact of paternal pollen sterility on F_1 seed germinations and progeny survivorship was investigated through controlled cross pollination in diploid species of *Fragaria* L. (strawberry, Rosaceae). The genus *Fragaria* is a perennial herb and comprises of about 22 species some of which have several subspecies (Staudt 1989, 2009).

2 MATERIALS AND METHODS

2.1 Species study

Several genotypes of each of the following diploid taxa within *Fragaria vesca* were used in the study. 27 controlled cross-pollinations were made among *F. vesca* ssp. *vesca*, *F. vesca* ssp. *vesca* var. *alba*, *F. vesca* ssp. *vesca* f. *monophylla*, and *F. vesca* ssp. *americana* using different genotypes (Table 1). 14 intra-subspecific crosses were made within *F. vesca* ssp. *vesca* by including *F. vesca* ssp. *vesca* var. *alba*. 6 crosses were carried out between *F. vesca* ssp. *vesca* and *F. vesca* ssp. *vesca* f. *monophylla*, and 6 crosses were performed at inter-subspecific level between *F. vesca* ssp. *vesca* and *F. vesca* ssp. *americana*.

2.2 Controlled crosses

In making controlled crosses, the floral buds on seed parents were emasculated approximately 3-4 days before anthesis by removing the stamens, and then the stigmas were pollinated by directly rubbing the anthers from the paternal parent. The cross-pollinated flowers were covered by a double-layer of fibre fleece to avoid uncontrolled open-pollination and desiccation. The cross-pollination was repeated within 3-4 days to ensure the pollination. After 3 weeks, the originating berries were collected and the seeds (achenes) were separated from the berries. The seeds were treated by absolute sulphuric acid for 2 minutes for removing dormancy, and then were germinated in growth cabinets under 16/8 h light/dark regime at 16 °C on peat for a week. The levels of F_1 seed germination was calculated on the basis of the percentage of germinated seeds to the total number of seeds sown. The seedlings were transferred to the glasshouse. The level of F_1 progeny survivorship was obtained from the percentage of the progeny survived to the total seedlings by the end of the year.

To select the pollen donor plants with variable levels of pollen sterility, a large number of plants were examined, and subsequently, several plants with a wide range of pollen sterility (3.1 to 77.2%) were select for conducting crossing experiments. The levels of pollen sterility of pollen parents were measured on the basis of proportion of the unstained pollen using 0.05% cotton blue in lactophenol by randomly studying a minimum of 500 pollen grains under light microscope. The pattern of nutrients and water supplies for all plants under study were kept consistent to eliminate the impact of resource variations on the progeny performance.

2.3 Statistical analyses

Relationship of the paternal parent pollen sterility with F_1 seed germination and progeny survivorship were tested on the basis of Pearson Rank Correlation test (SPSS, ver. 11.2). Kruskal-Wallis Test (SPSS, ver. 11.2) was used to test the significance level of pollen sterility variation in each cross type.

Table 1: Plant materials used in this study.

Species	Source & determination	Geographical distribution
F. vesca ssp. *vesca* L.	Royal Botanic Garden, Kew, UK	Europe (England, UK)
F. vesca ssp. *vesca* var. *alba* L.	NCGR*/197.000 PI 551572	Europe
F. vesca ssp. *vesca* L.	NCGR/478.000 PI 551826	Europe
F. vesca ssp. *vesca* var. *alba* L.	NCGR/198.000 PI 551573	Europe
F. vesca ssp. *vesca* L.	University of Joensuu, Finland	Europe (Finland)
F. vesca ssp. *vesca* L.	Poyntzfieldherbs, Nursery, Inverness, UK	Europe (Scotland, UK)
F. vesca ssp. *vesca* f. *monophylla*	NCGR/612.000 PI 551909	Europe
F. vesca ssp. *americana* (Porter) Staudt	NCGR/554.001 PI 551881	USA, East

*National Clonal Germplasm Repository, Corvallis, Oregon, USA.

3 RESULTS AND DISCUSSION

The variations in the levels of the paternal parent pollen sterility and F_1 seed germination and progeny survivorship originating from controlled cross-pollinations in *Fragaria* are shown in Table 2. In intra-subspecific crosses within *F. vesca* ssp. *vesca* paternal parent with significant variation in pollen sterility (ranging from 3.1 to 77.2%; N =14, $df = 5$, $p < 0.023$, Kruskal-Wallis Test) produced great variation in F_1 seed germination (ranging from 38.5 to 100%) and progeny survivorship (60-100%). However, pollen parent sterility was not correlated with F_1 seed germination (N =14, $p > 0.074$) and progeny survivorship (N =14, $p > 0.710$; Figure 1, A).

Reciprocal crosses between *F. vesca* ssp. *vesca* and *F. vesca* ssp. *vesca* f. *monophylla* using pollen donors with dramatic male sterility variation ranging from 6.8 to 77.2 (N =7, $df = 5$, $p < 0.05$, Kruskal-Wallis Test) resulted in highly variable levels of F_1 seed germination and progeny survivorship (5.9 - 87.5% and 85.7 - 96.6%, respectively). However, there was no correlation between pollen parent sterility and F_1 seed germination (N = 7, $p > 0.295$) and progeny survivorship (N = 6, $p > 0.812$, Figure 1, B).

Although crossing several plants of *F. vesca* ssp. *americana* by pollen of *F. vesca* ssp. *vesca* with highly variable pollen sterility (3.1 to 77.2%) though not significant (N = 6, $df = 5$, $p > 0.082$, Kruskal-Wallis Test) gave rise to large variations in F_1 seed germination (48.3 – 92.4%) and progeny survivorship (42.9 - 100%). There was no correlation between father pollen sterility with seed germination (N = 6, $p > 0.924$) and progeny survivorship (N = 6, $p > 0.215$; Figure 1, C).

Within each cross type, crossing different maternal plants by pollen of the same paternal plant produced progeny of variable levels of performance. For example, within *F. vesca* ssp. *vesca* crossing three different individual plants by pollen of a single pollen donor with 3.1% sterility produced progeny with 38.5 to 54.5% F_1 seed germination and 60 to 100% progeny survivorship.

The results of the current investigation showed that the pollen parent sterility does not affect on F_1 seed germination and progeny survivorship in *Fragaria*. These data are consistent with the general view that the levels of progeny performance in plants are mostly influenced by maternal parent (Lloyd, 1980; Obeso, 2004; Gehring and Delph, 2006). In addition, the results of the current study do agree with previous reports from other taxa e.g. *Hydrophyllum appendiculatum* (Wolfe, 1995), *Lesquerella fendleri* (Mitchell, 1997) and *Mirabilis jalapa* (Niesenbaum, 1999; Davis, 2004), and *Pachycereus schottii* (Holland et al., 2009), which have shown that pollen donor diversity did not affect on seed and fruit set nor on later components of life history. In contrast, the pollen donor diversity in *Rhamnus alpinus* has been reported to affect on different reproductive components of F_1 progeny e.g. embryo size (Nakamura and Stanton, 1989), seed size, germination rate, seedling vigor and survivorship (Banuelos and Obeso, 2003), and the embryos developments (Diggle et al., 2010).

Contrary to above-mentioned reports, several other studies indicated the impact of both maternal and paternal parent on the progeny performance. For instance, in *Raphanus sativus* seed growth rate (Diggle et al., 2010), and embryo/seed development rate (Marshall and Diggle, 2001) were shown to be affected by both maternal and paternal parents. This simultaneous impact of both paternal and maternal on progeny performance indicates genotypic interactions (Marshall et al. 2000). While the impact of paternal plant on progeny performance depends on the identity of the pollen-receiving individual and also on interaction between recipient and donor plants (Bernasconi, 2003).

Table 2: Variations in the levels of paternal pollen sterility and originating F_1 seed germination and progeny survivorship in controlled cross-pollinations in *Fragaria*.

Controlled crosses (Seed parent X pollen parent)	%Paternal sterility	No. seeds sown	No. seeds germinated	% F_1Seed germination	No.F_1seedlings	No. F_1 plants survived	% F_1progeny survivorship
F. vesca ssp. *vesca* X *F. vesca* ssp. *vesca*	3.1	13	5	38.5	9	9	100.0
	3.1	11	5	45.5	5	3	60.0
	3.1	11	6	54.5	5	5	100.0
	17.06	20	14	70.0	14	13	92.9
	17.06	11	9	81.8	6	5	83.3
	18.14	22	16	72.7	16	13	81.3
	18.14	17	13	76.5	14	12	85.7
	21.6	22	18	81.8	16	15	93.8
	21.6	24	21	87.5	21	16	76.2
	21.6	14	14	100	13	10	76.9
	34.63	36	29	80.6	35	34	97.1
	34.63	55	49	89.1	49	38	77.6
	77.2	24	16	66.7	18	16	88.9
	77.2	35	35	100	29	29	100.0
F. vesca ssp. *monophylla* X *F. vesca* ssp. *vesca*	6.8	60	49	81.7	49	46	93.9
	6.8	24	21	87.5	21	18	85.7
	6.8	21	15	71.4	15	13	86.7
F. vesca ssp. *vesca* X *F. vesca* ssp. *monophylla*	34.6	67	42	62.7	42	40	95.2
	34.6	33	25	75.8	29	28	96.6
	77.2	101	6	5.9	25	24	96
	77.2	35	29	82.9	ND	ND	ND
F. vesca ssp. *vesca* X *F. vesca* ssp. *americana*	3.1	58	28	48.3	41	41	100.0
	3.1	20	16	80.0	16	11	68.8
	18.14	85	71	83.5	71	66	93.0
	18.14	66	61	92.4	61	59	96.7
	77.2	41	28	68.3	28	12	42.9
	77.2	52	41	78.8	28	23	82.1

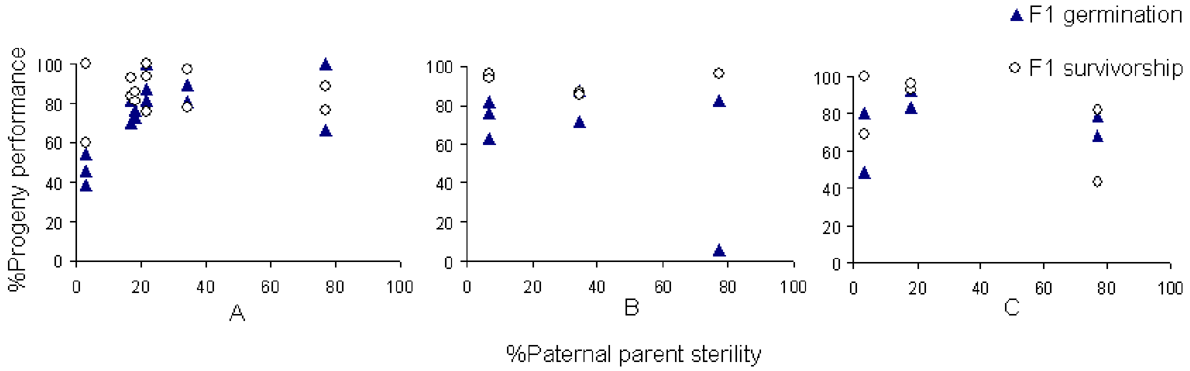

Figure 1. Lack of correlation between paternal pollen sterility and progeny performance in controlled crosses in *Fragaria*. A) Intra-subspecific crosses within *F. vesca* ssp. *vesca*, B) *F. vesca* ssp. *vesca* and *F. vesca* ssp. *vesca* f. *monophylla*, C) Inter-subspecific crosses between *F. vesca* ssp. *vesca* and *F. vesca* ssp. *americana*.

4 CONCLUSION

The results of the current study obtained from *Fragaria* along side those data reported from other plant taxa indicate that patterns of parental impact on offspring performance and reproductive fitness appear to be very diverse. Understanding the pattern of parental plants on the progeny performance could be used in improving the crop quantities and qualitative.

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