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Impact of pollination on sunflower yield: Is pollen amount or pollen quality what matters?

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ABSTRACT

Local and international information on sunflower pollination indicate that crop yield may be limited by the quality of the pollination service. This work focuses on the response of commercially-grown sunflower hybrids to variations in the amount and quality of the pollen delivered to stigmas, measured in terms of grain set, unit grain weight, grain oil concentration, and oil yield per plant as a way to assess the importance of entomophilous pollination for this crop. Three consecutive experiments including 2–8 experimental treatments each were conducted between 2004 and 2007 in Argentina. The results (a) demonstrate for the first time that the pollen amount and pollen quality that arrive to the stigma have a joint effect on sunflower grain set, (b) suggest that some yield crop components could be sensitive to this joint effect, and (c) remark the probable positive effect of the pollen redistribution across the head. Overall, results underline the importance of pollinators for the crop, and point out to possible mechanisms that explain their beneficial effect.

1. Introduction

Insufficient pollination often limits seed production in plants, sometimes severely (Burd, 1994; Larson and Barret, 2000; Ashman et al., 2004). Pollen limitation occurs when plants produce fewer fruits and/or seeds than they would with adequate pollen receipt. Whereas theory predicts that pollen augmentation should not increase seed production, numerous empirical studies report significant and strong pollen limitation in plants (Knight et al., 2005). Aizen and Harder (2007) consider pollen limitation as the joint effect of quantity and quality limitation, pointing out that quantity limitation probably occurs much less often than has been inferred from pollen-supplementation experiments, and suggesting that an expanded perspective that recognizes the fecundity consequences of pollination with poor-quality pollen would improve the ecological understanding of pollen limitation.

Most of the *Helianthus* (sunflower) wild species are naturally self-incompatible and obligate outcrossers (Heiser et al., 1969; Hurd et al., 1980), therefore the transfer of pollen between plants is necessary for fructification. A sporophytic incompatibility system contribute to the high levels of outcrossing present in wild sunflower, open-pollinated cultivars and some inbred lines (Putt, 1941; Habura, 1957; Free and Simpson, 1964; Fernández-Martínez and Knowles, 1978). In addition the florets of sunflower heads, even when they are perfect, present two mechanisms which are counter to automatic self-pollination: protandry and secondary pollen presentation (Leins and Erbar, 1989; Seiler, 1997). Therefore sunflower requires insect visits to transfer pollen from male phase florets to female phase inside a single head (capitulum).

Breeders have made efforts to develop self-fertile sunflowers, obtaining hybrids which display high levels of auto-compatibility (80–90%) (Fick and Zimmer, 1976; Vranceanu et al., 1988) and that reportedly are free of pollinator dependency. However, experimental work show that sunflower hybrids benefit from the cross pollination that occurs when insects (especially honey bees) are present in the fields (Parker, 1981; Griffiths and Erickson, 1983; Jones, 1988; Virupakshappa et al., 1992; Aslan and Yavuksuz, 2010). Presence of pollinators both increase grain set (Fick, 1979; Robinson, 1980; Krause and Wilson, 1981; Langridge and Goodman, 1981; Freund and Furgala, 1982; Low and Pistillo, 1986; DeGrandi-Hoffman and Watkins, 2000; Singh et al., 2000; DeGrandi-Hoffman and Chambers, 2006; Chambó et al., 2011) and oil concentration in the grain (Furgala et al., 1979; Mahmood and Furgala, 1983; Kleinschmidt, 1986; Calmasur and Ozbek, 1999; Kasina et al., 2007). Research carried out in Argentina generally confirmed these results (Iglesias, 1984; Lorenzatti de Diez, 1986; Ryan and Brugnoni, 1986;

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Table 1
Sunflower materials used as experimental plants and for borders and their self compatibility levels.

Experiment	Year	Experimental plants (*border plants*)
ExpA	2004–2005	Paraíso 30[b] and Contiflor 17[c] (*HA89 line*)
ExpB	2005–2006	Dekasol 4050[a] and a male-sterile line (*Dekasol 4050 and Paraíso 30*)
ExpC	2006–2007	Dekasol 4050[a] (*Dekasol 4050 and Paraíso 30*)

[a] Good.
[b] Very good.
[c] Excellent level of self-compatibility according to staff of Venado Tuerto experimental station, Instituto Nacional de Tecnología Agropecuaria, Argentina (pers. comm. to A. M. Chamer).

Amaro, 1987; González, 1994; but see Astiz et al., 2011; Chamer, 2012).

Perhaps because of the inherent complexity of the factors involved, to date it is unclear whether pollinators enhance sunflower yield by increasing the amount of pollen deposited on the stigmas, by increasing the quality of the deposited pollen, or both. Briefly, the amount of co-specific pollen grains deposited on the stigma depends on (a) the number of pollinator visits received by a floret during a certain period of time (visit rate), and (b) the proportion of sunflower pollen in the pollen loads carried by the pollinators (Dafni et al., 2005). On the other hand, since pollen grains are genetically different both within and between hybrids, pollen quality depends on the proportions of pollen from (a) the same floret, (b) another floret of the same head, and (c) another sunflower plant, which are present in the stigmatic load. Those proportions are expected to vary with the relative abundance of the insect species present in the pollinator assemblage, because more active species will be prone to transport pollen between plants, and the least mobile ones will tend to redistribute pollen within the same sunflower head.

Surprisingly, the size of stigmatic loads in sunflower has apparently never been studied in relation to yield. We are aware of a single record of the size of stigmatic loads in a field-grown sunflower hybrid, in a study unrelated to yield determination (Torretta, 2007). The effect of pollen quality has been only studied in open-pollinated cultivars, which nowadays make up just a little portion of the world's sunflower cultivated area. Free and Simpson (1964) enclosed some sunflower heads singly in muslin bags and other in pairs. Heads enclosed singly with bees had 24% of seed set, but those in pairs with bees had 45%, indicating that although sunflowers are not self-sterile, greater seed production is likely to occur following cross-pollination between florets of different heads than between florets of the same head. Hsieh (1973) obtained 72–83% of seed set from hand cross-pollination vs. 10–35% from hand self-pollination. Low and Pistillo (1986) obtained 58% of seed set from manually cross pollination vs. 22% from excluded but otherwise unmanipulated sunflower heads.

This work will focus on the response of commercially-grown sunflower hybrids to variations in the amount and quality of the pollen delivered to stigmas, measured in terms of grain set, unit grain weight, grain oil concentration, and oil yield per plant as a way to assess the importance of entomophilous pollination for this crop in Argentina. Specifically, we tested the hypothesis that pollen amount and/or pollen quality that arrives to the stigmas influence sunflower yield.

2. Materials and methods

2.1. Crop management and general experimental conditions

Three consecutive experiments were performed at the Facultad de Agronomía, Universidad de Buenos Aires (34°35′S, 58°29′W) during the summers of 2004–2005 (experiment A, hereafter ExpA), 2005–2006 (ExpB), and 2006–2007 (ExpC). Sunflower seeds of three hybrids and a male-sterile line were provided by Advanta Argentina (Balcarce, Argentina) (Table 1). These hybrids differed in their levels of self-compatibility (Table 1). Seeds were sown on 19 November 2004 (ExpA), 25 November 2005 (ExpB), and 8 December 2006 (ExpC) on a silty clay loam soil (typical Argiudol) (ExpA) or in 30 L plastic pots that were placed outdoors and filled with a 3:1 mixture (v:v) of fertilized soil and perlite (ExpB and ExpC). Three seeds were sown in each sowing point (ExpA) or in each pot (ExpB and ExpC), and plant density was later adjusted to 5.1 plants m^{-2}, with a inter-row spacing of 0.7 m. Arrays of 120 (ExpA), 72 (ExpB) and 144 (ExpC) experimental plants were surrounded by two border rows sown at the same date as experimental plants (ExpA) or a week before (ExpB and ExpC, in which border plants would be used as pollen source). In all experiments the crop was protected against weeds, birds, insects and diseases as needed. At V4 stage (Schneiter and Miller, 1981) plants were thinned to one centrally located seedling. Following Rondanini et al. (2003) the plants were watered thrice daily by a drip irrigation system using amounts of water that were periodically adjusted to meet seasonal variations in evaporative demand, and plants were fertilized with a total dressing of 3 g N per plant as $Ca(NO_3)_2$ at 25 days after emergence. Preventive applications of fungicides and insecticides were made periodically. The experiments were laid out in a randomized complete design without sub-sampling, in which homogeneity for every experimental unit (each sunflower head) was assumed.

Environmental conditions prevailing during the experiments are resumed in Table 2. Rainfall varied among experiments (data not shown), but possible differential effects are thought to have been neutralized by the drip irrigation system used. The temperature regime was similar among experimental years, thus crop developmental phases showed only minimal differences between experiments (6 days at the most). Daily incident radiation was also similar among experiments for the E–A and A phases. However, daily incident radiation during the A-PM phase was ca. 15% lower in ExpC as compared to ExpA and ExpB.

Plants were randomly assigned to experimental treatments. Number of treatment levels varied among experiments, and number of replicates per treatment varied also because some plants failed to complete head development (Table 3). All plants were bagged with disposable mob caps before start of anthesis. Mob caps were briefly (<5 min) removed only when a manipulative treatment was scheduled, which always occurred near midday (1200–1600). As heads expanded during the flowering period, mob caps were periodically repositioned to avoid contact with disk florets. Because of mob cap porosity and transparency, possible differences between bagged and unbagged heads in temperature and light availability are not expected to have significantly affected grain set. When anthesis was completed mob caps were replaced by polyester or polyamide cloth bags, which were kept on heads until harvest to prevent damage by birds.

Hand pollination proceeded in two ways. In ExpA, to simulate within-head pollen movement by insects, the target area of the head was gently rubbed with an applicator provided with a 2 × 5 cm velvet band (Fig. 1), causing the redistribution of the locally available pollen (the velvet band was replaced by a fresh one after each