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Additional site for pollen germination in carrot

In angiosperms, pollination – either self or by various agents – mediates the transfer of pollen grains from the anther to the stigma, the site where pollen grains land; the compatible among these hydrate and subsequently germinate to produce pollen tubes that facilitate fertilization of the egg. However, in a few species, besides germinating on the surface of the stigma, pollen grains have been observed occasionally to germinate at other sites also, including the anther[1], intra-floral parts[2], ovary wall[3] and nectary[4]. In plants of *Daucus carota* L. ssp. *sativus*, the cultivated carrot, we observed pollen grains germinating at a hitherto unreported site, i.e. the stylopodium, the bulbous base of style, capping the epigynous ovary. Presence of the stylopodium is a characteristic feature of the family Apiaceae. It harbours a nectary. The observation is important as it puts on record one more site within the flower that has the potential of receiving the pollen grains and providing the necessary environment for them to germinate and produce pollen tubes. More significant is the observation that the pollen tubes formed at this site reach the ovules, leading to the formation of fruit.

D. carota, a biennial umbellifer, is represented by two subspecies, namely *sativus* and *carota*, in Jammu and Kashmir. The former is cultivated for its swollen napiform root and the latter grows wild. The wild forms were studied and collected from natural populations inhabiting Kud and Batote area. Plants of the cultivated form were grown in the Botanical Garden of the University of Jammu through seeds procured from the market. Both subspecies are andromonoecious and protandrous, exhibiting strong dichogamy[5].

Anthesis follows a sequential and centripetal order both at the level of umbellet and umbel. The stamens and petals are curved inwards in a bud and thereafter spread out as the flower opens gradually. As the anthers curve out, they dehisce and the process takes 2–3 days. There comes a time during anthesis when the anther is positioned in such a way that the self-pollen can easily fall on the stylopodium (Figure 1 *a*). Thus, some of the self-pollen invariably land on the stylopodium. Once the anthers have emptied their contents, the female phase begins. By the time the stigma becomes receptive, the pollen grains of the self-flower and every other flower in the same umbel are mostly dispersed, and the stylopodium is loaded with pollen grains belonging to the self-flower. Thus the stigma has the chance to receive cross-pollen only, whereas the stylopodium that is already loaded with self-pollen can be contaminated by cross-pollen also if an insect visits the flower.

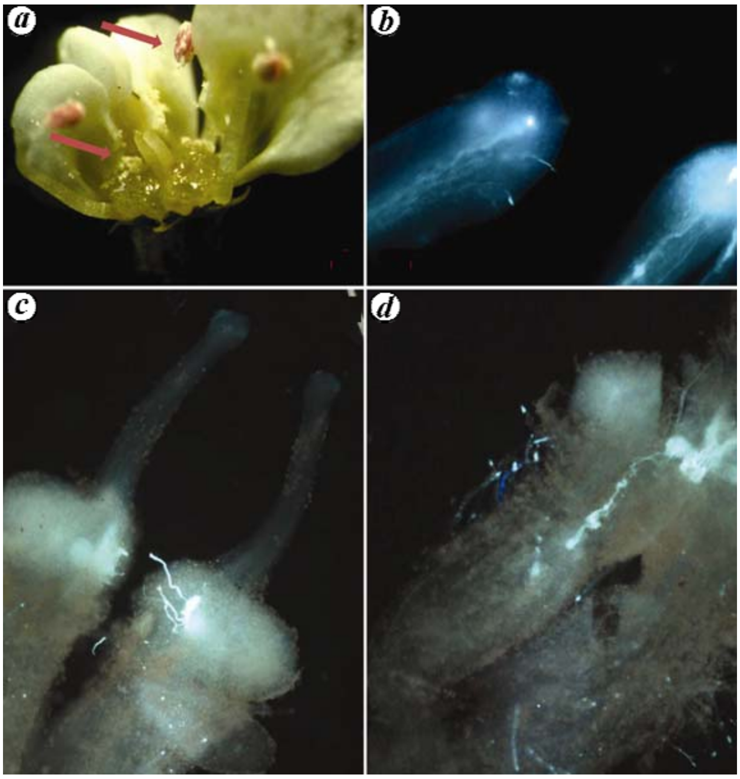

Figure 1. ***a***, A flower of *Daucus carota* ssp. *sativus* in male phase showing self-pollen on the stylopodium. ***b***, Pollen grains germinating on the surface of the stigma. ***c***, Pollen grains germinating on the surface of the stylopodium only, with no pollen load on the stigmatic surface. ***d***, A gynoecium with only one ovule being fertilized when pollen grains germinate on the surface of the stylopodium.

In order to analyse pollen germination as it occurs in nature, 60 flowers of ssp. *sativus* in the female phase were randomly picked up in nature and fixed in 70% alcohol. These were later scanned using the decolourized aniline blue fluorescence method[6]. No pollen load was found on nine gynoecia, either on the stigma or the stylopodium. In six gynoecia, the pollen–pistil interaction pathway was conventional where pollen grains were seen germinating on the stigma (Figure 1 *b*). However, in the remaining 45 gynoecia, pollen germination was recorded exclusively on the surface of the stylopodium (Figure 1 *c*). Pollen tubes were seen emerging from the pollen grains and entering the ovary (Figure 1 *d*). However, these were being attracted to only one of the ovules; the other remaining unfertilized.

To confirm whether the pollen grains on the stylopodium affect seed set, stigmatic pollination was experimentally inhibited. The stigmas of 22–36 flowers per umbellet ($n = 4$) were clipped off during the male phase to check if fruit formation occurs. In another set of experiments, the stigmas of 30–40 flowers per umbellet ($n = 4$) were sealed with glue (Camlin Krafty glue) during the male phase for the same purpose. Three weeks later, fruit formation was noticed. On pooling the data of the two experiments, an average of $32.87\% \pm 6.45$ ($n = 8$) fruit set was observed per umbellet. While in the control (i.e. on open pollination), an average of $73.44\% \pm 6.34$ fruit was set. Though the difference between the fruit set in open-pollinated umbellets and in experimental umbellets is quite vivid, it nevertheless indicates that pollen germination on the stylopodium does lead to fruit formation in *D. carota* ssp. *sativus*.

Following these observations, 40 gynoecia of wild carrot (*D. carota* ssp. *carota*) were also scanned using the fluorescence technique. However, no such observation was recorded in the carpels of wild carrot. These followed the conventional pollen–pistil interaction pathway.

The adaptive significance of having an additional site for pollen germination in cultivated carrot is being worked out. There are two possibilities: (i) If the pollen grains germinating on the stylopodium are self only, then the advantage this accrues to the plant is the ability to practice self- and cross-pollination simultaneously. The progeny structure will depend upon the comparative rate of growth of self-pollen tubes through the stylopodium and cross-pollen tubes through the stigma, their ability to affect fertilization and the amount of consequent inbreeding depression in the progeny. (ii) If the pollen grains germinating on the stylopodium are both self and cross, extra stigmatic germination is then a supplementary mechanism that ensures availability of pollen tubes for fertilization of the ovules in the absence of pollen load on the stigma.

Extra stigmatic pollen germination has been reported in species of phylogenetically diverse families like Callitrichaceae, Fabaceae, Brassicaceae, Papaveraceae and now Apiaceae, which suggests that the phenomenon is not infrequent. It raises a plethora of questions, most important amongst these being the adaptive significance of the process that challenges the screening of pollen grains by the stigma.

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