

Ecological constrains on ovule development in Mediterranean orchids

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Ovule development represents an important component of female reproductive investment in flowering plants. In orchids, ovule development and subsequent ovary enlargement is triggered by a signal produced by pollen arrival on the stigma (Zhang and O'Neill, 1993). This peculiarity, unique among angiosperms, is likely to confer an important resource allocation advantage in orchids as they typically produce thousands of ovules. Interestingly, the stage of ovule development before pollination has been found variable in different orchid groups ranging from ovule primordial to immature ovules (Tsai *et al.*, 2008). However, so far, it is not clear whether this variation is driven by a phylogenetic or an ecological constrain.

We investigated stages of ovule development at anthesis in the Mediterranean orchid genera *Anacamptis*, *Dactylorhiza*, *Himantoglossum*, *Ophrys*, and *Orchis*, all belonging to the monophyletic Orchidinae and characterized by different flowering times and pollination strategies (rewarding vs. deceptive).

We found that ovule development ranges from ovule primordial (with archesporial cells) to immature ovules (at first meiotic division with developed inner and outer ovule teguments). These results sharply contrast with what found in tropical orchids, as *Phalenopsis*, where ovule development is still at primordial stage even one month after pollination.

Variation in ovule development stages between closely related species was found depending on flowering time and pollination strategy. In one species pair, *Himantoglossum robertianum* and *H. hircinum*, a clear correspondence between flowering time and ovule development was observed. Indeed, at anthesis, in the early blooming *H. robertianum*, ovules are at the primordial stage, whilst in the late blooming *H. hircinum* inner and outer teguments are already developed. Likely *H. robertianum*, blooming in January, might benefit from a longer amount of time to complete ovule development before the annual summer drought. In another species pair, with contrasting pollination strategies, the rewarding *Anacamptis coriophora* and the deceptive *A. morio*, both flowering at the same time, we found that the rewarding species has developed ovule and teguments while *A. morio* ovules are still developing. Likely, *A. morio* may reduce the cost of advanced ovule development being exposed to the high risk of fruiting failure due to the low levels of pollination typical of deceptive species (Tremblay *et al.*, 2005).

Overall these results strongly suggest that, in the Mediterranean habitat, orchid ovule developmental stage is modulated by ecological factors, as flowering time or pollination strategy, and can be selected for optimizing the female reproductive investment.

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