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Interpreting the ontogenetic delay of shoot development in Mediterranean pines: adaptive trait or phylogenetic constraint?

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Juvenile developmental rates are relevant life history traits in plants. Pines show an especially marked vegetative (heteroblastic) phase change during early developmental stages, shifting from a shoot with primary needles and free growth to a shoot with secondary needles and cyclic preformed growth. In previous works we have confirmed - within the subgenus *Pinus* - a marked divergence in heteroblastic phase change between Mediterranean (Subsect. *Pinaster*) and Eurasian pines (Subsect. *Pinus*) that share neighbouring habitats along the Mediterranean Basin. A high genetic variation between populations and high additive variance within populations has been shown in Maritime pine (*Pinus pinaster*). These facts, together with a significant relationship between the heteroblastic stage of the plants and their field survivorship in some species, as well as marked morpho-physiological differences between primary and secondary needles suggest a relevant adaptive value of the timing of heteroblastic change, at least in some Mediterranean pines.

However, we still do not know to which extent interspecific differences in this trait might be due to a phylogenetic constraint or to relatively recent adaptation. On the other hand, the fact that one of the species with a more exaggerated ontogenetic delay, the Canary Islands pine (*Pinus canariensis*), has also the rare ability of resprouting in adult stage, could suggest that both traits are evolutionarily linked. To test these hypotheses, we performed a nursery common garden experiment with 30 species covering all subsections of subgenus *Pinus* (*Dyploxylon*) and a smaller sample of subgenus *Strobus* (*Haploxylon*). We used the ratio of secondary needle dry mass to total foliar dry mass, reflecting the degree of heteroblastic change, as a quantitative ontogenetic index.

Results confirmed the rarity of ontogenetic delay in the genus: within subsection *Pinaster*, *Pinus canariensis*, *P. halepensis*, *P. pinea* and *P. roxburghii* (the Himalaya's chir pine) shared this character, but not their close relatives *Pinus pinaster* and *P. brutia*. No other species of subgenus *Pinus* showed such a marked delay. The apparent delay in some *Haploxylon* pines (*P. cembroides* and *P. lambertiana*) cannot be separated from their extremely low growth rates. On the other hand, with the exception of the Canary Islands pine, all sprouter species assayed (*P. merkusii P. rigida*. *P. oocarpa* and *P. leyophylla*) showed normal or fast heteroblastic development rates, which seems to discard an evolutionary correlation between resprouting ability and delayed shoot ontogeny in pines.

We discuss the relevancy of these findings (i.e. patterns of trait evolution) in the light of new ongoing research on Mediterranean pines molecular phylogeny of DNA sequence data and the correlations with other life history traits of the species (i.e. patterns of correlated evolution).

Keywords: Correlated evolution, Heteroblasty, Ontogeny, Phylogeny, Resprouting