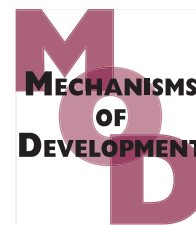


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Evolutionary, genetic, environmental and hormonal-induced plasticity in the fate of organs arising from axillary meristems in *Passiflora* spp.

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ABSTRACT

Tendrils can be found in different plant species. In legumes such as pea, tendrils are modified leaves produced by the vegetative meristem but in the grape vine, a same meristem is used to either form a tendril or an inflorescence. *Passiflora* species originated in ecosystems in which there is dense vegetation and competition for light. Thus climbing on other plants in order to reach regions with higher light using tendrils is an adaptive advantage. In *Passiflora* species, after a juvenile phase, every leaf has a subtending vegetative meristem, and a separate meristem that forms both flowers and a tendril. Thus, flowers are formed once a tendril is formed yet whether or not this flower will reach bloom depends on the environment. For example, in *Passiflora edulis* flowers do not develop under shaded conditions, so that tendrils are needed to bring the plant to positions where flowers can develop. This separate meristem generally forms a single tendril in different *Passiflora* species yet the number and position of flowers formed from the same meristem diverges among species. Here we display the variation among species as well as variation within a single species, *P. edulis*. We also show that the number of flowers within a specific genotype can be modulated by applying Cytokinins. Finally, this separate meristem is capable of transforming into a leaf-producing meristem under specific environmental conditions. Thus, behind what appears to be a species-specific rigid program regarding the fate of this meristem, our study helps to reveal a plasticity normally restrained by genetic, hormonal and environmental constraints.

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1. Introduction

The *Passiflora* genus (Passifloraceae) is represented by almost 600 species organized in 4 subgenera (Muschner et al., 2003; Hansen et al., 2006). Most of these species are found

in tropical regions and, among them, there is *Passiflora edulis*, the edible passion fruit. Two of *Passiflora* subgenera are species-rich: subgenus *Passiflora* with 236 species and subgenus *Decaloba* with 214 species. On the other hand, the subgenera *Astrophaea* and *Deidamiodes* have 57 and 13 species,

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respectively (Ulmer and MacDougal, 2004). Among *Passiflora* species there is a great diversity of floral shapes and floral organ innovations such as the corona filaments, and the androgynophore, which reflects the adaptive plasticity driven by different pollination syndromes (Ulmer and MacDougal, 2004; Aizza and Dornelas, 2011).

Most of *Passiflora* species show a clear juvenile stage, especially within the subgenus *Passiflora*. In *P. edulis* juvenile leaves are lanceolate while non-juvenile leaves are tri-lobed (Fig. 1A). As the transition leaves become more complex, a meristem capable of making both a tendril and a flower is formed in their axils (Nave et al., 2010). This meristem is present in axils of all non-juvenile leaves except for the first 2–3 leaves of every axillary shoot. Under environmental conditions in which flowers develop, they appear side-by-side with tendrils (Ulmer and MacDougal, 2004; Nave et al., 2010). *Passiflora* species originated in ecosystems in which there is dense vegetation and competition for light. Thus climbing on other plants in order to reach regions with higher light using tendrils is an adaptive advantage.

Tendrils can be found in different plant taxa. In legumes such as pea, tendrils are modified leaves produced by the vegetative meristem but in grape vine tendrils are formed by the axillary meristems, which can originate either a tendril or an inflorescence (Gourlay et al., 2000; Calonje et al., 2004). In the genus *Passiflora*, on the other hand, the same meristem produces a tendril and one or more flowers (Akamine and Girolami, 1959; Krosnick and Freudenstein, 2005; Nave et al., 2010).

Here we show that flowers and tendrils share a common ontogenetical program and modifications/variations in this program by evolutionary, genetic and environmental mechanisms shape the plasticity in the fate of organs arising from axillary meristems in the genus *Passiflora*. As this developmental plasticity in one particular species (e.g. *P. edulis*) might be modulated by environmental clues (such as hormone concentration, photoperiod, and temperature) and is enclosed within the range of variability already existing among *Passiflora* species, we postulate that this plasticity might be under natural selection pressure.

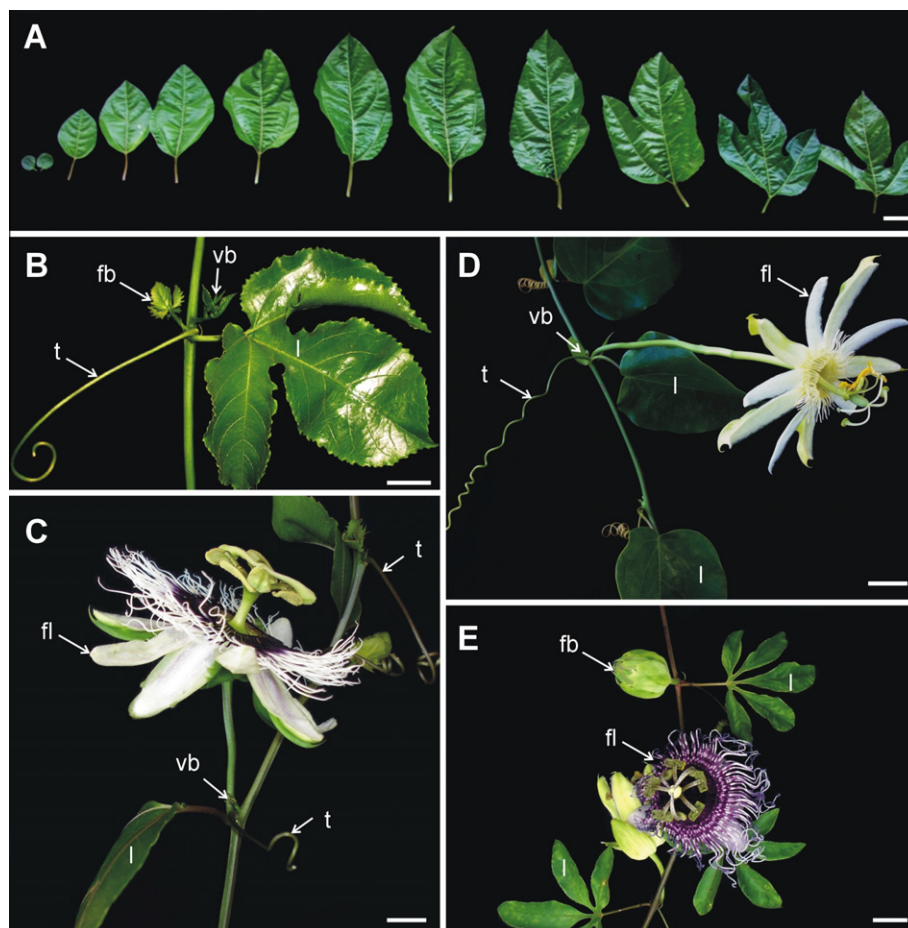


Fig. 1 – (A) Transition from cotyledons to juvenile leaves to non-juvenile leaves (from left to right) in *Passiflora edulis* Sims. **(B–D)** Reproductive branches of different species of *Passiflora*. Species from subgenus *Passiflora*, show a single flower and a tendril per node. **(B)** Node of *Passiflora edulis* Sims. **(C)** Branch of *P. edulis*. **(D)** Branch of *Passiflora galbana* Mast. **(E)** Branch of *Passiflora cincinnata* Mast. fb: flower bud; fl: flower; l: leaf; t: tendril; vb: vegetative bud (corresponds to an accessory axillary bud). Bars: 2 cm.

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