

Article Addendum

Bud development and hydraulics

An innovative way to forecast shoot architecture

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The distal zone of one-year-old apple (*Malus domestica*) shoots was studied on five cultivars for bud size and composition (number of appendages) and hydraulic conductance before bud burst. Our hypothesis was that bud development was related to hydraulic conductance of the sap pathway to the bud independent of an acrotonic (proximal vs. distal) effect.

Bud size and composition, and hydraulic conductance, were highly variable for all cultivars. A positive correlation was demonstrated between both the number of cataphylls and green-leaf primordia and hydraulic conductance. Cultivar and bud size affected the intercept of these relationships more than the slope suggesting similar scaling between these variables but different hydraulic efficiencies. A great proportion of small buds were also characterized by null values of hydraulic conductance.

Our study suggests that hydraulically mediated competitions exist between adjacent buds within a same branching zone prefiguring the variability of lateral types in the following growing season. It is hypothesized that this developmental patterning is driven by hydraulic characteristics of the whole-metamer, including the subtending leaf, during bud development.

In perennials, a growth unit, defined as the portion of an axis developed during an uninterrupted period of growth, may result from two developmental processes whether it stems from the terminal meristem, which built the previous growth unit or from an axillary meristem. These processes are referred to as apical growth and branching, respectively.¹ In both cases the new growth unit may originate from a bud comprising a preformed shoot elaborated during a period of rest related to either external factors such as low temperature and drought or within-plant competitions. The bud is composed of external cataphylls and internal green-leaf primordia. In the case of a terminal bud, the number of appendages and the type of lateral

(vegetative, floral) it will become is partially determined by the length or number of nodes of the supporting growth unit.²⁻⁴ However, the determinism of the number of appendages composing the axillary bud remains unknown. In recent papers we explored the possibility that hydraulics is highly related to the axillary bud development.

Hydraulics to Complement the Architectural Approach of Axillary Bud Development

The classical concept of acrotony describes the higher potential of development of axillary buds in distal positions along the parent shoot compared to axillary buds in proximal positions.^{5,6} Cochard et al.⁷ in *Fagus* confirmed that paralleling this acrotonic gradient there is an increase in the hydraulic conductance of the xylem sap pathway to the bud (K_{LAT}) prior to bud burst. Two recent works in a range of apple (*Malus domestica*) cultivars with contrasted shoot architectures suggest that this relationship is localized, i.e., at the level of each individual bud. First, Han et al.,⁸ evidenced a reduction of K_{LAT} in the lower face of arched apple shoots where there is a higher proportion of aborted buds compared to the upper face. Second, Lauri et al.,⁹ showed that, in the distal zone of shoots usually characterized by a high proportion of vegetative and floral axillary branches mixed with latent buds and aborted laterals, there is a positive correlation between both the number of cataphylls and green-leaf primordia, and K_{LAT} (Fig. 1). Moreover, cultivar and bud size affect the intercept of these relationships more than the slope suggesting similar scaling between these variables but different hydraulic efficiencies. Indeed, whatever K_{LAT} values the numbers of cataphylls and leaf primordia are higher in certain cultivars compared to others and higher for large buds compared to small and medium-sized buds. A great proportion of small buds are also characterized by null values of K_{LAT} .

The Xylem Pathway has an Important Role in Transporting Nutrients to the Developing Bud

All together, these studies clearly showed that bud development, i.e., external size and content potentially forecasting the latent, vegetative or floral pattern of growth at bud burst, is linked to the xylem pathway entering into the bud. These results bring more support to previous conclusions that the xylem is able in itself to supply water, mineral nutrients and sugars to the bud before the new phloem becomes functional.¹⁰ Therefore, the phloem does not

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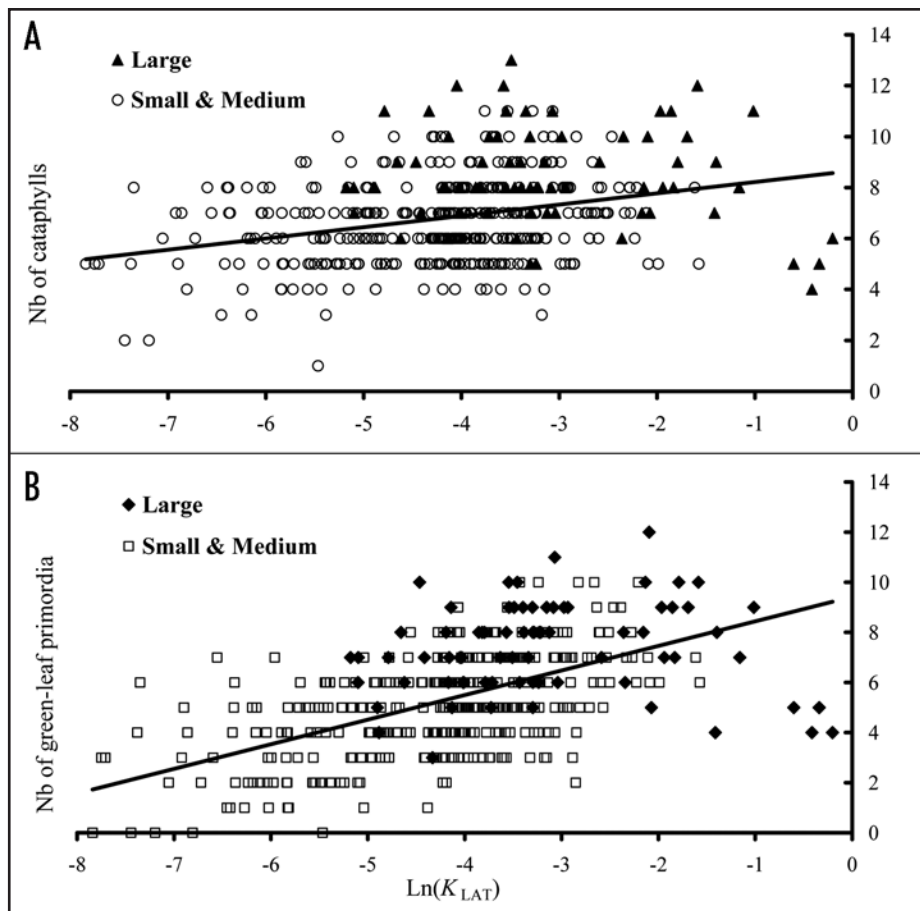


Figure 1. Relationships between $\ln(K_{LAT})$ of the xylem-vascular system connected to the bud and the number of (A) cataphylls, and (B) green-leaf primordia of this bud, for buds of five apple (*Malus domestica*) cultivars. For each appendage category, buds are split into two external size categories: “small and medium” and “large”. Regression lines are computed for cataphylls in (A) ($\text{Nb of cataphylls} = 0.443 \times \ln(K_{LAT}) + 8.662$, $R^2 = 0.09$, $n = 432$) and for green-leaf primordia in (B) ($\text{Nb of green-leaf primordia} = 0.981 \times \ln(K_{LAT}) + 9.425$, $R^2 = 0.31$, $n = 432$). Reproduced from *New Phytologist*, Lauri et al.⁹

appear to be the only pathway for transport of nutrients as usually stated (reviewed in ref. 11). Our results also suggest that hydraulically mediated competitions exist between adjacent buds within a same branching zone prefiguring the variability of lateral types (latent and aborted buds, vegetative and floral laterals) in the following growing season. It is hypothesized that this developmental patterning is dynamically related to the hydraulic characteristics of the whole-metamer, including the subtending leaf, during bud development. To relate axillary bud organogenesis and hydraulics the year of parent shoot growth in relation to metamer development will contribute to the understanding of the building of shoot architecture.

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