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## **Hierarchical Developmental Timeline Warping: a generic method to design realistic plant architecture models**

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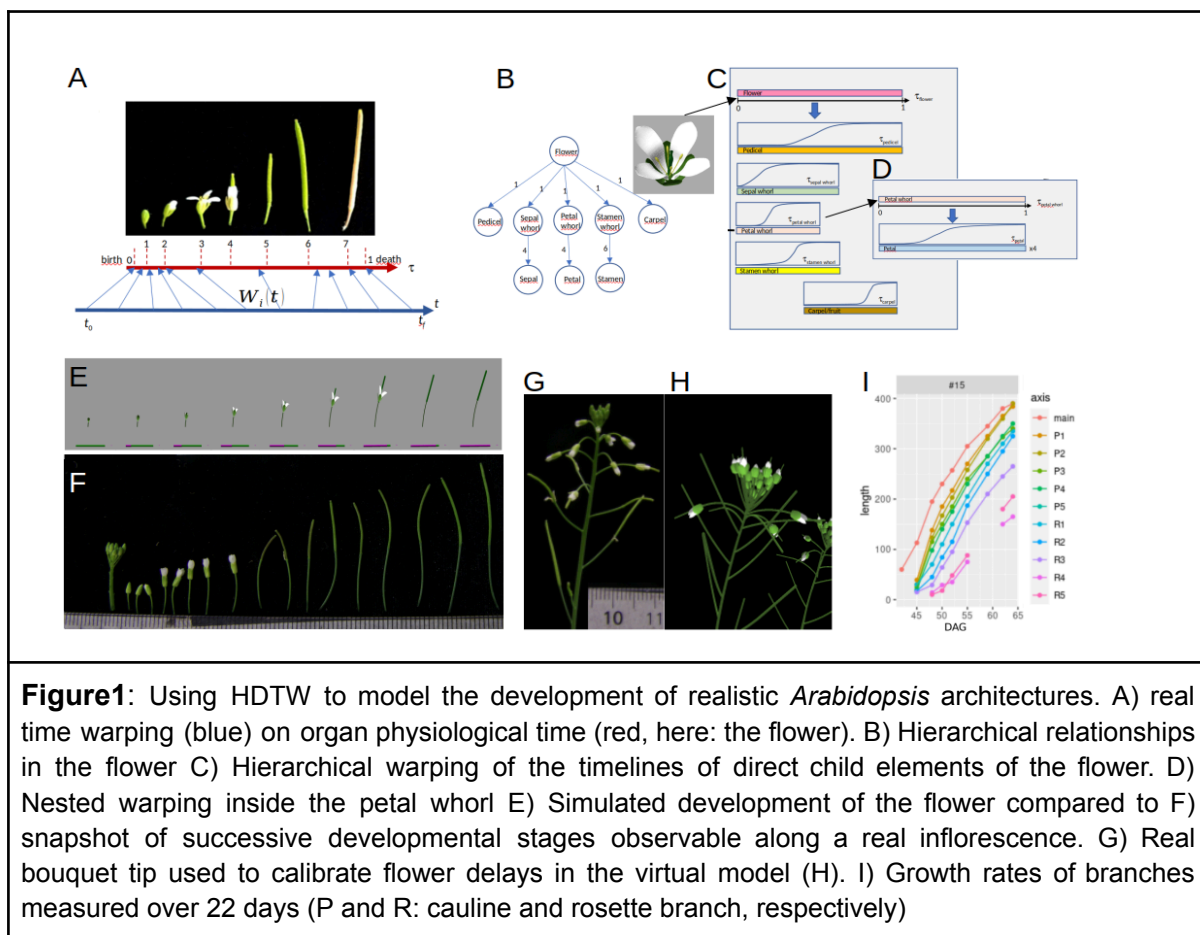
Virtual models of plant architecture are needed for diverse applications in developmental biology, agronomy, botany or computer graphics. They can be used for hypothesis testing, data annotation and augmentation associated with deep-learning training or for producing photorealistic rendering of plants. To match the increasing needs of these applications in precision and realism, virtual plants with increasing realistic details are required. However, the design of such detailed models remains a complex task and new techniques are required to ease this process.

L-systems (Prusinkiewicz 1990) is now a standard procedural approach to model plant architecture development. Their use has been eased by efficient modeling environments (Prusinkiewicz 2018, Boudon 2012) and over years, these systems have incorporated solutions to better capture plant growth dynamics, such as positional information to describe gradients of characters along plant axes (Prusinkiewicz 2001) or multiscale descriptions of plant architectures (Ferraro 2002, Boudon 2012). However, one aspect is still partially lacking: a conceptual strategy to naturally orchestrate in time the growth of different plant parts.

A first step in this direction was proposed in (Prusinkiewicz 2018) where all the parameters controlling the various aspects of organ state or growth are described by functions of a normalized time between 0 and 1. This normalized time is then mapped on either the absolute time of the simulation, or the organ age (i.e. a relative time), using a timeline that stretches each parameter normalized time onto absolute/relative time. Thanks to a timeline editor, the variation in time of the different functions is graphically controlled and the different parameter timelines are adjusted to absolute or relative time. Illustrating the flexibility of this timeline-based strategy, (Cieslak 2021) showed very realistic virtual plant architectures reconstructed by visual and interactive calibration on 2D photographs of real plants.

In this approach, however, all plant parameters are controlled at a unique level of organization, making it difficult to handle the complexity of a possibly important number of control parameters and to design modular components. To tackle these issues, we developed a complementary timeline-based approach, where the hierarchy of plant parts is described by a corresponding hierarchy of developmental timelines. For each simple or composed organ, a reference (normalized) timeline is defined. Different stages of development of the organ are associated with different time-points of this reference timeline between 0 and 1 (Fig 1A). These stages are characteristic morphological steps, which can be easily and reproducibly defined across different individuals, genotypes, or even species, but do not occur at identical time points. In composed organs, the timelines of the component organs are therefore mapped onto that of the parent organ using user-defined warping functions, reflecting genetic or environmental regulations. At the plant level, this builds a hierarchy of timelines warped onto each other in a nested manner (Fig 1B,C,D). At the top level of the hierarchy, the timeline is itself warped onto the real chronological time (Fig 1A). Hence, the developments of all organs are synchronized with each other as well as with the absolute timeline. To model different genotypes or growth conditions, the component

models can be tuned independently (e.g. changing their size or shape) while their synchronization with the parent organ is adapted using timeline warping functions. We tested our HDTW strategy in order to reproduce realistic virtual architectures of the model plant *Arabidopsis thaliana*. For this, we grew real plants in standard indoor conditions and manually collected various quantitative information on the plant at different scales, focusing on the relative and absolute developmental dynamics of many plant parts and organs. Depending on the trait, hierarchical timelines were either calibrated by measuring the same plants over days (Fig. 1I), or from snapshot pictures, taking advantage of the repetition of the same developmental sequences along the plant axis (Fig. 1F,G). Models constructed with this strategy can reproduce precisely plant architectural dynamics at different scales (Fig. 1E,H).



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