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Integrating architecture and physiological perspectives in fruit development

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Highlights: Architectural properties of a fruit, such as its shape, vascular patterns, and skin morphology, play a significant role in determining the distributions of water, carbohydrates, and nutrients inside the fruit. Understanding the impact of these properties on fruit quality is difficult, because they develop over time and are highly dependent on both genetic and environmental controls. We developed a 3D fruit model that can be used to investigate effects of the principle architectural properties on fruit quality.

Keywords: Fruit quality, water and carbon transport, fruit vasculature, skin microcracking, *Prunus persica*

INTRODUCTION

Fruit size, shape, composition and texture are all major qualities that determine consumer preference. Understanding the factors that regulate the development of these qualities is challenging, because they result from the interplay between physical and physiological processes that are under the control of both genetic and environmental factors. In the last 15 years, fruit quality has been largely investigated by using process-based models that treat the fruit as one large, homogeneous compartment, neglecting the fruit's internal structure (Bertin et al., 2006).

The architectural properties of a fruit, such as its size, shape, internal structure (number of carpels) and pattern of vasculature, however, can be remarkably diverse among varieties (Rodriquez et al., 2011). Since water and carbon are delivered to fruit tissues through a complex vasculature system, these architectural properties may have a significant impact on the distribution of water and carbon inside the fruit. For example, vascular patterns may account for the preferential supply of metabolites to specific tissues, and for causing physiological disorders such as blossom-end-rot (apical tissue necrosis) and shrivelling of the fruit's skin. Also, there is a positive relationship between the distribution of sugars inside the fruit and the morphology of its skin. Water loss due to transpiration depends on both the pattern and density of cuticular cracks (Gibert et al., 2007, 2010) and the microclimate surrounding the fruit (Li et al., 2001), which increases the soluble solids content (sugar level) inside the fruit.

The aim of this work was to investigate effects of fruit architectural properties on fruit quality by means of a 3D functional-structural fruit model that integrates architectural and physiological perspectives in fruit quality development, under the control of the environment. Existing 3D fruit models focus on the external shape of the fruit and treat its interior as homogeneous, without differentiation into tissue types (Saudreau et al., 2007, Mebatsion et al., 2011). Additionally, these fruit models do not consider the vascular tissue that supplies the fruit with resources and how the supply and other physiological processes affect fruit growth. In the following, we describe our generic 3D fruit model, which accounts for fruit shape, tissue compartmentalization, and vascular patterns, and use it to investigate the impact of fruit structure on sugar composition and distribution within a nectarine fruit.

RESULTS AND DICUSSION

We present a generic 3D fruit model that integrates architectural features and physiological processes of fruit development, with effects of the environment. For the fruit architecture, the geometry of the various fruit tissues is represented using 3D geometric shapes and the topological connections between them. For the physiological processes, we consider only those that are involved in the balance of water and carbon flows between the fruit, plant, and environment, as these drive fruit growth. In addition, we consider how this balance is modulated by exogenous factors like the availability of resources from the plant and the environmental conditions, such as temperature and humidity, and by endogenous factors that control the transport and accumulation of water and carbon to various fruit tissues via the xylem vessels and phloem sieve tubes. The challenge is to represent the different fruit architectures as seen in nature, and to integrate the physiological processes that modulate fruit quality development.

A generic 3D model of fruit development

To construct a generic functional-structural fruit model, we developed a modelling pipeline in the OpenAlea platform (Pradal et al., 2009) that involves three steps: (a) creating a 3D volumetric mesh representation of the internal and external fruit structure, (b) generating a complex network of vasculature that is embedded within this mesh, and (c) integrating aspects of the fruit's function, such as water and carbon transport, with the fruit's structure. The model describes the late phase of fruit development when fruit growth is mostly due to cell expansion, once cell division has stopped.

Most methods for generating 3D fruit geometry represent the external shape of the fruit using equation-based techniques (Saudreau et al., 2007), or using reconstructions from images (Mebastion et al., 2011), and assume the fruit has a homogeneous internal structure. For that reason, in a previous work (Cieslak et al. 2012), we developed a procedure for generating a 3D volumetric representation of fruit architecture, including the external shape and internal structure. To generate the geometry of the large tissues, such as the pericarp, the reconstruction algorithm uses Delaunay refinement that produces high quality tetrahedral meshes from 3D image data (Alliez et al., 2011), where each tetrahedron is labelled according to the part of the fruit tissue it represents. To generate the geometry of the vascular tissue, we used an algorithmic approach based on the assumption that vascular bundles are competing for space within the fruit, which was originally proposed for synthesizing leaf venation patterns (Runions et al., 2005). Figure 1 shows architectural models of nectarine and peach fruit that were constructed using this procedure.

Based on this procedure, we made a generic model of fruit development by incorporating a model of water and carbon transport, which includes the flow of water and carbon in the fruit's vasculature. This was achieved by extending a previously developed process-based model of fruit growth (Fishman and Génard, 1998) with features of recently developed phloem-xylem transport models that can handle branched architectures (Lacointe and Minchin, 2007). In this approach, the tetrahedral elements of the mesh are treated as compartments that represent a collection of cells within the fruit, and the model captures the aggregated response of those cells to changes in water and carbon content. The transport of water and carbon through the vasculature is based on the hypothesis of osmotically driven bulk flow, where a hydrostatic pressure gradient (due to differences in local sugar concentrations) drives the flow of water and carbon between regions of sugar loading and unloading. In our model, we assume loading of sugar occurs outside of the fruit's vasculature so that sugar concentration in the pedicel is taken as input, whereas unloading may occur at any point inside the fruit that is linked by vasculature.

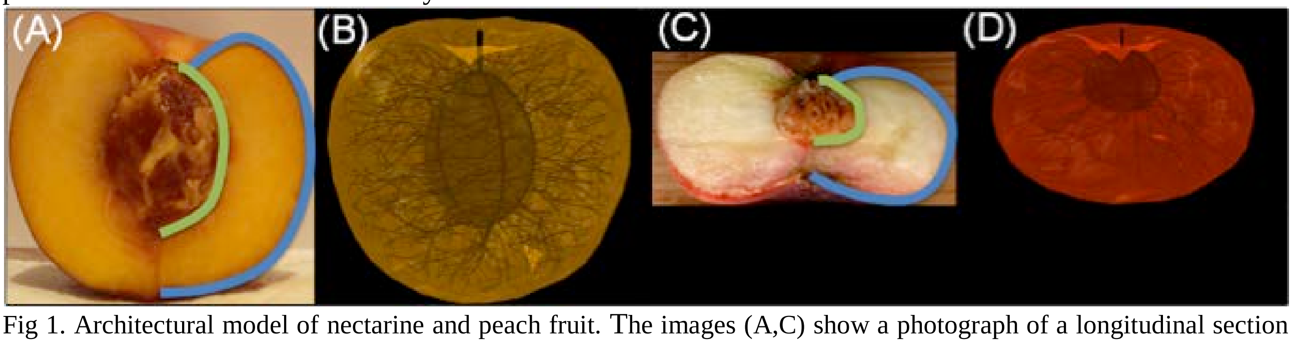

Fig 1. Architectural model of nectarine and peach fruit. The images (A,C) show a photograph of a longitudinal section of a nectarine and peach fruit, respectively, that were used to generate 3D volumetric meshes (B,D). The user-defined blue and green lines highlight the exocarp and endocarp, respectively, which are used to define two polyhedral surfaces (one for the stone and another for the fruit's surface) that serve as input into the mesh generation procedure. The green-line defines the main ventral and dorsal vascular bundles on the endocarp, whereas the branching secondary bundles are generated algorithmically according to the competition for space (Runions et al., 2005).

Application to modelling sugar distribution inside nectarine fruit

In nectarine fruit (*Prunus persica*), the spatial pattern of cuticular cracks on the fruit skin varies between the polar regions (stylar and peduncle ends) and equatorial regions (Gibert et al., 2007). This pattern changes the rate of water loss due to transpiration on different parts of the skin (Gibert et al., 2010), which may have an effect on the sugar concentrations inside the fruit. To analyse how such a pattern can cause a heterogeneous distribution of sugar inside a nectarine fruit, we used our functional-structural fruit model to perform simulations on the basis of our own experiments and on the work of Gibert et al. (2007, 2010).

The percentage of microcracks on 32 regions (four transversal and eight longitudinal sections) of the fruit's skin has been measured by image analysis using a similar procedure as Gibert et al. (2007). For each of the 32 regions, the sugar content (degrees Brix) in the internal and external section of the fruit's mesocarp (for a total of 64 measurements) was assessed. A linear relationship was found between the percentage of microcracks and sugar content (degrees Brix) for both the external and internal regions of the fruit (Fig. 2A,B). A 3D visualization of the results shows a gradient of sugar concentration from the fruit interior towards the fruit surface (Fig. 3A).

We then created a functional-structural nectarine model using our modelling pipeline (Fig. 1B) and used it to simulate nectarine growth from 60 to 140 days after full bloom (dafb), because the heterogeneity in sugar distribution arises over time as the microcracks appear during the last 20 days of growth. During this time, the increase in fresh weight may be as much as 125 g (Gibert et al., 2007). The initial fresh mass was set to 25 g (Gibert et al., 2007) whereas the values of input variables (including temperature and humidity) and parameters were taken from a model of peach fruit growth (Fishman and Génard, 1998). However, the stomatal, cuticular, and crack components of conductance were modelled according to equations and parameters developed by Gibert et al., (2010). The percentages of cuticular cracks on the 32 regions of the fruit surface were taken from our own experiments, but the total cuticular crack surface area per fruit surface area was modelled as a function of the fruit fresh weight (g) according to data from Gibert et al., (2007).

At the end of the simulation (140 dafb), the sugar concentrations of the 64 exterior and interior regions of the fruit were compared with sugar content (degrees Brix) data from our own measurements. In qualitative agreement, the model output showed a direct linear relationship between sugar content and the percentage of microcracks (Fig. 2C,D). A 3D visualization of the model output also shows a gradient of sugar concentration from the interior to the exterior of the fruit (Fig. 3B). Furthermore, simulations with no microcracking (not shown) resulted in a decrease in sugar content for the whole fruit, which is in agreement with the observed outcome of covering fruit with clear plastic film (Li et al., 2001). Although the parameter values have not yet been fitted to data, these results show that our model is capable of simulating the observed effects of architectural features, like skin microcracking, on the quality of the fruit.

CONCLUSIONS

We integrated architectural and physiological perspective in fruit development to construct an integrative computational model of fruit. The result was a dynamic system that gives us the ability to model fruit growth driven by resource availability and exogenous factors like temperature and humidity. With this type of functional-structural model, it is possible to investigate the important architectural features that affect fruit quality. We demonstrated this by examining the role of skin microcracking on determining the distribution of sugar content in nectarine fruit. This model will lead to more work on quantifying the effects of architectural features on fruit quality, such as examining effects of asymmetric vascular structure on nutrient distribution in tomato fruit.

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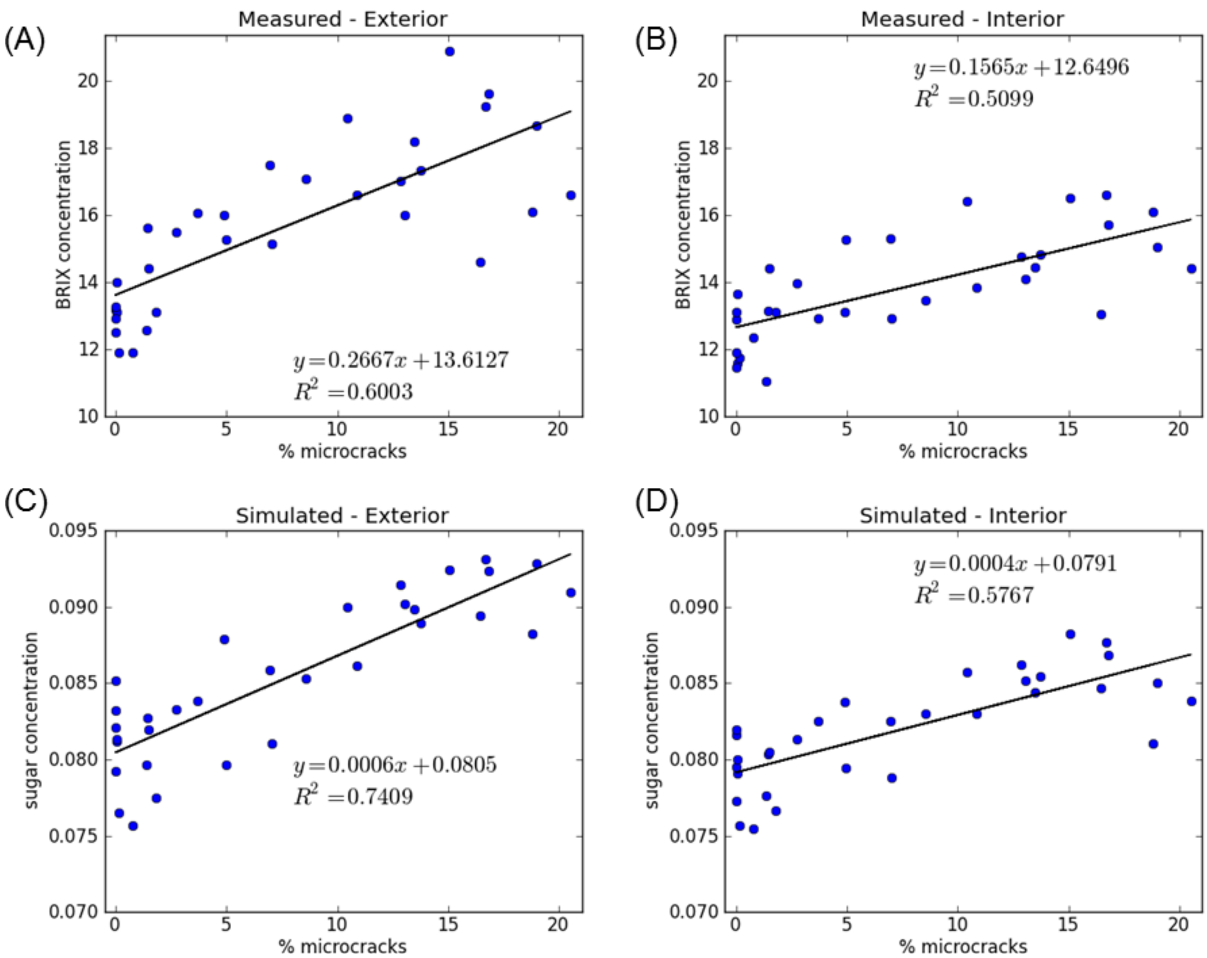

Fig. 2. Sugar content in nectarine fruit as a function of the percentage of microcracks at 140 dafb. The two graphs on the top show the results of measurements on the percentage of microcracks and sugar content (degrees Brix) in the exterior region (A) and interior region (B) of a nectarine fruit. The two graphs on the bottom show the simulations results of sugar content (g soluble sugars / g FW) in the exterior region (C) and interior region (D) obtained by modelling increased surface conductance due to microcracks.

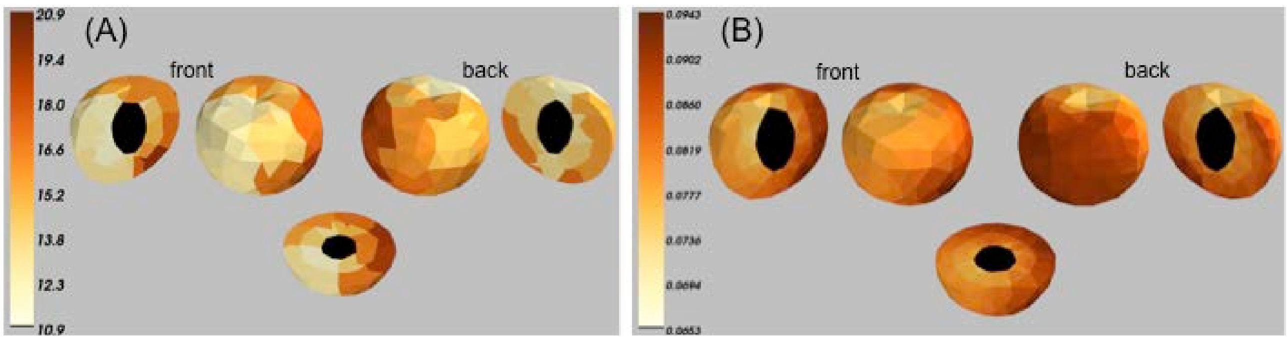

Fig. 3. A 3D visualization of sugar content in a nectarine fruit at 140 dafb. Each tetrahedron is coloured according to measured sugar content in degrees Brix (A), or to the model output in g soluble sugars / g FW (B). The visualization shows the whole fruit from the front and back, with corresponding longitudinal sections, and a transversal section. Dark brown indicates high sugar content while light yellow indicates low sugar content. The tetrahedra representing the stone are coloured black, as the sugar content is assumed not to change.