Seminars in Cell & Developmental Biology xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Seminars in Cell & Developmental Biology

journal homepage: www.elsevier.com/locate/semcdb

Shaping a fruit: Developmental pathways that impact growth patterns

Esther van der Knaap[a,*], Lars Østergaard[b]

[a] Institute of Plant Breeding, Genetics & Genomics, University of Georgia, Athens, GA, 30602, USA
[b] Department of Crop Genetics, John Innes Centre, Norwich Research Park, Norwich, NR4 7UH, United Kingdom

ARTICLE INFO

Article history:
Received 5 July 2017
Received in revised form 20 October 2017
Accepted 26 October 2017
Available online xxx

Keywords:
Tomato
Brassicaceae
Fruit growth
Fruit shape
Fruit size
Hormonal and genetic interactions

ABSTRACT

Angiosperms produce seeds as their progeny enclosed in maternally-derived structures called fruits. Evolutionarily, fruits have contributed enormously to the success of the Angiosperms phylum by providing protection and nutrition to the developing seeds, while ensuring the efficient dispersal upon maturity. Fruits vary massively in both size and shape and certain species have been targeted for domestication due to their nutritional value and delicious taste. Among the vast array of 3D fruit shapes that exist in nature, the mechanism by which growth is oriented and coordinated to generate this diversity of forms is unclear. In this review, we discuss the latest results in identifying components that control fruit morphology and their effect on isotropic and anisotropic growth. Moreover, we will compare the current knowledge on the mechanisms that control fruit growth, size and shape between the domesticated Solanaceae species, tomato and members of the large family of Brassicaceae.

Contents

* Corresponding author.
E-mail address: EsthervanderKnaap@uga.edu (E. van der Knaap).

https://doi.org/10.1016/j.semcdb.2017.10.028
1084-9521/

Please cite this article in press as: E. van der Knaap, L. Østergaard, Shaping a fruit: Developmental pathways that impact growth patterns, Semin Cell Dev Biol (2017), https://doi.org/10.1016/j.semcdb.2017.10.028

1. Introduction

The Angiosperm phylum of flowering plants is the most successful plant phylum comprising >90% of all plants on Earth. They evolved during the Cretaceous Period 100–125 million years ago and their subsequent fast diversification in evolutionary terms remains an enigma and one, which Darwin famously referred to as 'an abominable mystery'. Flowering plants encase their seeds in a fruit or a vessel and from which the phylum name is derived (Greek: Angio = vessel; sperm = seed). Formation of flowers and fruits is indeed considered crucial for their success allowing attraction of pollinators for efficient fertilisation of the ovules and protection and nurturing of the developing seeds. The huge variety of fruit morphologies have led to ingenious ways for efficient seed dispersal. In addition to shape, size also varies significantly among fruits from different or even within species, ranging from the smallest known fruits from *Wolffia angusta* that are no larger than a grain of table salt to the giant pumpkins (*Curcurbita maxima*) that through intensive selection and breeding including highly specialised growth conditions can exceed 1000 kg. The latter case also highlights the result of domestication, a process that Darwin convincingly used to demonstrate evolution by natural selection [1,2]. Domestication of vegetable and fruit crops has often led to dramatic changes in fruit size and created a diversity of fruit shapes within the same species [3–5]. However, in the context of plant development, morphological diversity in crop plants is often underexplored.

Growth and shape of natural structures have been of interest to scientists at least since ancient Greece. From the early days of genetics, it was recognised that features controlling organ size and shape are inherited through generations [6–12]. In tomato, one of the earliest studies into the genetic inheritance of fruit morphology is that of elongated fruit and locule number, traits with a strong genetic inheritance [11,9]. Initially, the locus for elongated and pear-shaped fruit was called *pyriform* (*pr*) [11] but was renamed to *ovate* after *pr* was found to co-segregate with oblong and oval fruit shape [13]. Fruit cell number was the initial term for two related traits, namely *fasciated* (*f* or *fas*) and *locule number* (*lc*) reflecting flat-shaped tomatoes with many carpels as opposed to the wild-type carpel number of two [9,12]. The loci *fas* and *lc* control the same trait, the number of carpel primordia, but with a different degree of severity on the trait [14]. Linkage mapping placed several of the fruit shape loci together with other morphological traits and created one of the first linkage maps in plants [15,16]. In the Brassicaceae, George Harrison Shull crossed the tetraploid *Capsella bursa-pastoris* (heart-shaped fruits) with a natural variant of *C. bursa-pastoris*, named "*heegeri*", which has cylindrical fruits. Shull found a 15:1 segregation in the F_2 generation of heart-to-cylinder [17] leading him to suggest that two genetic loci contribute to the trait. This observation is in agreement with observations reported by the botanist Edmund W. Sinnott two decades later. Sinnott used pumpkin as a model system and his data suggested that it is possible to differentiate between gene activities that regulate shape and those that only affect size [18].

The quantitative nature of fruit weight initially hampered the discovery of genes controlling size traits in crop plants. However, with the advent of molecular genetic linkage maps and improvement in quantitative mapping tools, a large number of loci underlying quantitative traits have been identified including those for fruit and grain size [19–21,3]. This has led to supporting evidence from modern day's developmental genetics and the identification of key factors involved in determining shape and weight in domesticated vegetables and fruits [5,22]. In this review, we provide an overview of the current knowledge in fruit growth with a particular emphasis on examples from fleshy fruits (tomato) and dry dehiscent fruits (Brassicaceae).

2. Shape classifications in tomato and Brassicaceae species

Tomato varieties have traditionally been classified based on fruit morphology into shape categories described by the International Union for the Protection of New Varieties of Plants (UPOV) and the International Plant Genetic Resources Institute [23,24]. A revised tomato classification scheme was developed based on fruit shape analyses that were conducted on a large collection of cultivated accessions that included many heirloom varieties featuring the most diverse fruit shapes [14] (Fig. 1). Independent classification using contour morphometric data from scanned tomato fruit images in conjunction with elliptic Fourier shape modeling and Bayesian classification techniques led to similar results [25]. The latter classification is especially helpful to growers and breeders as it allows also an unbiased evaluation of uniformity of fruit shapes within a certain tomato variety [25]. In fruit and vegetable crops, shape and size uniformity is critical to the industry whereas for molecular geneticists uniformity suggests a strong genetic basis for the trait. Moreover, consumers recognize use type in tomatoes based on their morphology: from the small oval-shaped grape tomato for salads to the blocky and squared Roma tomato for soups and stews to the large and flat beefsteak tomato for slicing. The model plant *Arabidopsis thaliana* belongs to the large Brassicaceae family, which also contains the Brassica genus including important crop plants such as oilseed rape (*B. napus*) and broccoli (*B. oleracea*). Members of the Brassicaceae family exhibit an extraordinary diversity in fruit shape with different basic shape structures such as cylindrical, disc-formed, spherical as well as more complex structures including heart-shaped fruits or fruits that develop outgrowths [26] (Fig. 2). This wide variation among closely related and even within species provides an excellent resource for studying organ-shape formation. In many cases, it is not immediately evident what advantages the different shapes provide for fitness and dispersal. It is also unclear how such variation in form can evolve when coordination of tissue growth and specification is of pivotal importance for timely development and seed release.

3. General developmental principles of the female reproductive structure

Fruits represent the final stage of the life cycle of a plant. Whereas plant growth ensues through axillary shoot development or indeterminate above ground stems, tomato and Brassicaceae fruits classically represent the final growth stage of a terminating floral meristem. Fruits develop from carpels which originate from the fourth and final whorl in the floral meristem. Carpels comprise the female reproductive tissue that produce the female gametophytes. At anthesis, pollen grains land and germinate at the apical stigma and pollen tubes grow through the style and ovary to deliver the male gametophyte and fertilise the ovules. Fertilisation marks the beginning of fruit development and is in most species required for fruits to develop [5,27,28]. In the first phase after fertilisation, fruit growth occurs mainly via cell division, but subsequently enters a second phase of cell expansion, which continues until the fruit has reached its final size [28–32]. There are examples, however, such as avocado, where cells continue to divide throughout fruit development up until ripening [33]. Fruit development is finalized with the ripening and seed dispersal stage. The latter stage as well as fruit set following fertilisation are critical for proper fruit development. Despite the impact of poor fertilisation on shape and size of the affected fruits, this process is not associated with regulating the morphology of the organ in a consistent manner and will therefore not be discussed in this review. The processes of ripening and seed dispersal will also not be discussed because that stage in general does not affect fruit morphology. Readers interested in these

Please cite this article in press as: E. van der Knaap, L. Østergaard, Shaping a fruit: Developmental pathways that impact growth patterns, Semin Cell Dev Biol (2017), https://doi.org/10.1016/j.semcdb.2017.10.028