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Resource competition modulates the seed number–fruit size relationship in a genotype-dependent manner: A modeling approach in grape and tomato

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ABSTRACT

Fruit size is a key criterion of the external quality of the fruit and may affect consumer acceptance. We used a model to analyze the effects of seed number on fruit size in two fleshy fruits, grape and tomato, of different genotypes, grown in different carbohydrate availability conditions. The two-parameter model described within-fruit resource competition and accurately represented the commonly observed decrease in fresh weight per seed with increasing seed number, regardless of the species, genotype or carbohydrate level considered. However, carbohydrate levels strongly modified the correlation between seed number and fresh weight per fruit, resulting in an increase, no change, or a decrease in individual fruit weight with increasing seed number per fruit. In grape, lowering carbohydrate levels decreased the parameter reflecting the potential fresh weight of one-seeded fruit under a given resource availability, whereas the response to carbohydrate level was genotype-dependent in tomato and more strongly reflected the level of competition for resources. The values obtained for this parameter suggested that there was an undercompensating competition for resources in domesticated grape and tomato genotypes. Finally, colocalizations of quantitative trait loci for fruit fresh weight and model parameters indicated that plant susceptibility to competition might determine fruit fresh weight.

1. Introduction

Fleshy fruits (such as tomato and grape) and their processed products (e.g. wine or raisins from grapes) are essential components of a healthy human diet. The fleshy pulp of such fruits also functions as an attractant and reward for frugivores, which facilitate the dispersal of the seeds of fleshy fruits in nature. Fruit quality may determine consumer preference in humans, but it also affects the attractiveness of the fruit to seed dispersers and, consequently, the fitness of the plant (Fleming and Estrada, 1993). For example, fruit quality in tomatoes for consumption in the fresh state is determined by a set of attributes describing both external (size, color, firmness) and internal (flavor, aroma, texture) properties (Causse et al., 2010). In particular, fruit size is an important criterion of fruit external quality affecting consumer acceptance. Moreover, fruit size may also affect the chemical composition of the fruit, which is the major determinant of fruit sensory characteristics. In grape, small berries are generally of higher quality for juice composition, wine composition and are, thus, associated with higher wine sensory scores (Walker et al., 2005). A similar negative relationship between fruit size and organoleptic quality has also been reported for tomatoes, for which smaller fruits are considered tastier than larger fruits (Ibarbia and Lambeth, 1971). An understanding of the mechanisms regulating fruit size is therefore of both scientific and agronomic interest.

Many physiological processes are involved in fruit growth (water and carbon fluxes, DNA endoreduplication, cell division and expansion) (Bertin et al., 2003; Guichard et al., 2005; Tsukaya, 2008), but seed number is known to play a key role in determining fruit size (Cawthon and Morris, 1982; Walker et al., 2005) through the production of hormones (Coombe, 1960; Rylski, 1979). In several species of fleshy fruits, higher seed number appears to be associated with larger fruit size (Almekinders et al., 1995; Bertin et al., 1998; Ollat et al., 2002). Moreover, fruit size is strongly

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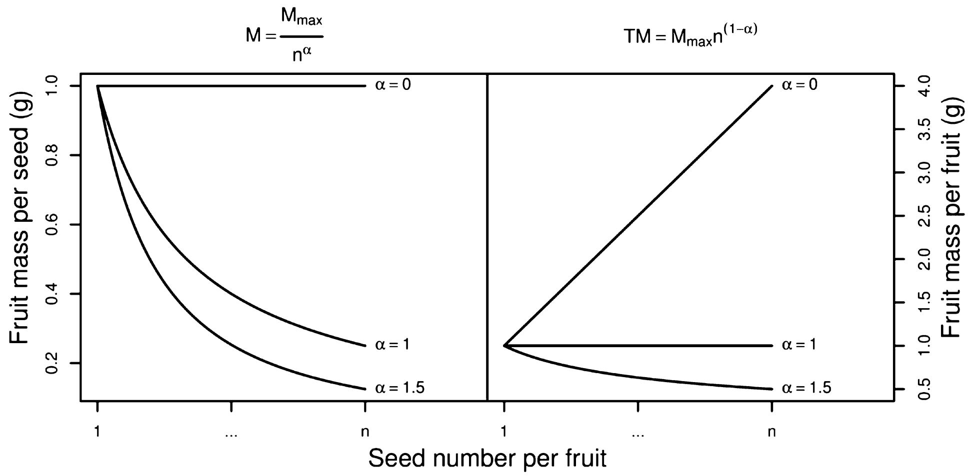

Fig. 1. Presentation of the model, with different α values corresponding to undercompensating competition ($0 < \alpha < 1$), exact compensating competition ($\alpha = 1$), and overcompensating competition ($\alpha > 1$).

influenced by environmental conditions (e.g. water stress, nutrient availability, light, temperature) (Guichard et al., 2005; Ho and Adams, 1995). In particular, changes in the carbon supply due to a disturbance of the sink–source ratio of the plant affects fruit size in several species, including peach (Morandi et al., 2008), tomato (Heuvelink, 1997), apple (Link, 2000), and grape (Kliewer, 1970; Ollat and Gaudillere, 1998). In these species, greater carbon supply is associated with higher fruit fresh weight. Furthermore, the fruits within an inflorescence vary with their position in the inflorescence, with basal fruits generally larger than distal fruits (Bertin et al., 1998; Tarter and Keuter, 2005). The underlying reasons for this position effect are unclear but may relate to (1) direct effects of inflorescence architecture; (2) competition for resources, assuming that basal fruits benefit from having priority access to carbohydrate fluxes; or (3) a combination of these two possibilities. However, the effects of interaction between seed number, carbohydrate level and fruit position on fruit size have been less studied.

The genes or quantitative trait loci (QTL) underlying the relationship between seed number and fruit size are unknown. Linkage has been detected between QTL and traits contributing to the determination of fruit size and seed number in tomato (Causse et al., 2004; Foolad, 2007; Grandillo et al., 1999; Prudent et al., 2009) and grape (Cabezas et al., 2006; Mejia et al., 2007). However, only a few QTL for seed number and fruit size are colocalized, suggesting that the genetic link between fruit size and seed number may be masked by competition for resources within or between fruits. We therefore evaluated the impact of changes in carbon supply on the relationship between fruit size and seed number. We also used a modeling approach to dissect complex traits (e.g. fruit size) into simpler traits with biologically meaningful model parameters. The combination of model parameters with genetic information has already facilitated the identification of loci governing the genetic variability of traits such as sugar concentration (Prudent et al., 2011) and leaf growth (Chenu et al., 2009). Mathematical models may thus be useful tools for determining the genetic determinism underlying the relationship between seed number and fruit size.

We used a modeling approach (i) to determine the genetic potential of genotypes in terms of seed number and fruit weight, and (ii) to quantify the level of competition for resources between fruits. We first checked whether the same model of competition for resources could be applied to both tomato and grape. We then investigated the extent to which changes in carbon supply affected the potential fresh weight per seed and the level of competition for resources between seeds in several genotypes/cultivars. Finally, we investigated the colocalization of QTL for seed size, seed number and model parameters, to investigate the genetic determinism of these traits.

2. Materials and methods

2.1. Model description

The model used here was developed from the universal allometry rules described by Enquist (Enquist, 2002), and adapted by Lescourret and Génard (2003) for the theory of competition for resources. This model describes competition between the individuals of a population, at various levels of organization (from fruit to inflorescence, plant and, finally, to plant population). According to this theory, the mass of each individual within the population decreases as the number of individuals increases within the population, because of competition for resources. The initial three-parameter model was simplified to a model with two parameters, which better fitted our datasets:

$$M = \frac{M_{\max}}{n^{\alpha}} \qquad \text{TM} = M_{\max} n^{(1-\alpha)} \tag{1}$$

where TM is the total mass of the population, n is the number of individuals in the population, M is the mass of an individual in the population, $M_{\max}$ is a parameter reflecting the potential weight that an individual can reach in the absence of intrapopulation competition for resources under a given external resource availability (namely, the weight when there is only one individual in the population, or more specifically in our context, the fruit weight of fruits with one seed under a given carbon supply level) and α is a parameter reflecting the level of competition between the individuals of the population, determining the shape of the relationship (Fig. 1). In this study, we focused on a single level of organization: the tomato fruit or grape berry, the "population" of which consists of seeds and their associated flesh weight. Thus, TM is the fruit mass, n is the number of seeds per fruit, and M is the fruit fresh weight per seed. The model was coded in R software. By using different values of α, this model can be made to simulate three types of competition, as defined by Begon et al. (1996): (1) undercompensating competition, in which the population mass increases with the number of individuals within the population. This situation is simulated by using α values of between 0 and 1; (2) exact compensating competition, in which population mass remains constant as the number of individuals increases. This situation applies at an α value of 1; (3) overcompensating competition, in which the population mass