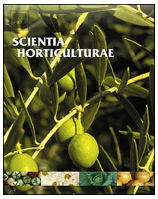
Scientia Horticulturae 235 (2018) 391–396

Contents lists available at ScienceDirect

Scientia Horticulturae

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



Heredities on fruit color and pigment content between green and purple fruits in tomato

Fangman Li[a,b,1], Xietian Song[a,b,1], Lang Wu[a,b], Haixu Chen[a,b], Yan Liang[a,b,*], Yan Zhang[a,b,*]

[a] College of Horticulture, Northwest A&F University, Yangling, Shaanxi, PR China
[b] State Key Laboratory of Crop Stress Biology in Arid Region, Northwest A&F University, Yangling, Shaanxi, PR China

ARTICLE INFO

Keywords:
Fruit color heredity
Green fruit
Multigenerational joint analysis
Pigment content heredity
Purple fruit
Tomato

ABSTRACT

Fruit color and pigment content are two important traits that largely determine the quality of tomato fruits. In this study, six genetic populations, namely, P_1, P_2, F_1, BC_1, BC_2 and F_2, were generated using tomato plants with green and purple fruits as female and male parents, respectively. The genetic developments of fruit color and pigment content were investigated through multigenerational joint analysis of quantitative traits. Results demonstrated that the optimal genetic model of fruit color between green and purple fruits was MX1-AD-ADI. The major gene heritabilities of shade values in BC_1, BC_2 and F_2 generations were 88%, 63% and 82%, and their polygene heritabilities were 9%, 11% and 14%, respectively. The heredity of lycopene content conformed to MX2-ADI-AD model. The heritabilities of major genes in BC_1, BC_2 and F_2 were 67%, 78% and 97%, while those of polygenes were 21%, 0% and 0%, respectively. The genetic model of chlorophyll was MX1-AD-ADI. The heritabilities of major genes in BC_1, BC_2 and F_2 were 62%, 77% and 62%, respectively, and those of polygenes were all 0%. The inheritance of carotene was in accordance with MX2-ADI-ADI model. The heritabilities of major genes in BC_1, BC_2 and F_2 were 80%, 47% and 57%, while those of polygenes were 0.01%, 0.02% and 14%, respectively. This study provides valuable information for fruit quality improvement in tomato breeding.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is an important vegetable crop, widely consumed across the globe due to its rich nutrient content, special taste and diverse edible methods. Fruit color is a key determinant of fruit quality that largely affects the initial quality assessment by the consumers (Stommel et al., 2005; Breksa et al., 2015). Tomato fruit color is mainly related to pigment contents, such as chlorophyll, carotene, lycopene and anthocyanin, and their relative proportions (Saengnil and Kaewlublae, 1997; Zhao et al., 2012; Borghesi et al., 2016). For example, the chlorophyll content is relatively high in the green fruits, while the red and orange fruits are characterized by high lycopene and carotene contents, respectively. Therefore, the genetic development of fruit color and pigment content in tomato is an interesting research area to improve fruit quality and satisfy the demands of consumers with different preferences.

Regarding the heredity of tomato fruit color, the yellow fruit color trait is controlled by recessive alleles (do Rêgo et al., 1999), whereas the black fruits of cherry tomato exhibit recessive inheritance controlled by two pairs of interactive major genes (Lin et al., 2013). However, the genes that control fruit peel and flesh color in purple and red tomato fruits show independent inheritances (Ruan, 2013). Transparent fruit peel is recessive relative to yellow peel, while purple flesh is recessive relative to pink flesh. In accordance with the law of free segregation and independent assortment, the hybridization of purple and yellow fruits produces fruits with pink flesh color in F_1 generation and fruits with four flesh colors, such as pink, purple, yellow and green, in F_2 generation, respectively. Besides, purple flesh is dominant relative to green flesh (Ruan, 2013). This finding suggests that purple flesh is controlled by two co-dominant genes. Therefore, different inheritances occur among various colors of tomato. However, genetic studies on green tomatoes have rarely been carried out.

Furthermore, most of the studies on the genetic development of pigment contents in the fruits are focused on lycopene, chlorophyll and carotene. In tomato, the heredity of lycopene content has been reported to conform to the mixed inheritance model of major gene + polygene, but the inheritance models of various tomato varieties differ in terms of the number of major gene pairs, additive effect, dominant effect, epistatic effect and heritability (Zhang et al., 2000; Li et al., 2006). Vasanthi et al. (2005) inferred that chlorophyll content in the leaf of

---

[*] Corresponding authors at: College of Horticulture, Northwest A&F University, Yangling, Shaanxi, PR China.
E-mail addresses: liangyan@nwsuaf.edu.cn (Y. Liang), zhangyan2014@nwsuaf.edu.cn (Y. Zhang).

[1] These authors contribute equally to the manuscript.

https://doi.org/10.1016/j.scienta.2018.03.030
Received 14 September 2017; Received in revised form 12 March 2018; Accepted 13 March 2018

groundnut (*Arachis hypogaea*) might be a quasi-quantitative trait. Likewise, chlorophyll *a in maize (Zea mays)* is controlled by two major genes with additive effects, and the heritability is 56.3% (Irfan et al., 2014). By comparison, chlorophyll *b* is regulated by the two pairs of co-dominant major genes plus additive polygenes. The heritabilities of major genes and polygenes are 1.12% and 93.26%, respectively. Chlorophyll *a* plus b are controlled by the two pairs of additive-epistasis major genes and additive polygenes, and their respective heritabilities are 56.2% and 5.2%. In cassav*a (Manihot esculenta*), some major genes are responsible for most of the variations of total carotenoids in roots, however, their effect is modified by few minor genes and at least by one single dominant gene that may inhibit carotenoid accumulation in roots (Yacenia et al., 2013). Nevertheless, the genetic development of chlorophyll and carotene contents in tomato fruits has seldom been examined.

Tomato fruit color is used as a qualitative as well as quantitative character determining the fruit quality (do Rêgo et al., 1999; Causse et al., 2003; Lin et al., 2013). For quantitative inheritance, fruit color is often distinguished through visual observation combined with colorimeter, but this strategy is disadvantageous because of poor accuracy caused by the excessive wide color range of human eyes. In addition, each examined sample yields three indexes, namely, *L* (lightness of color), *a* (degree of red and green) and *b* (degree of orange and blue), which impedes accurate color expression and causes an overlap among the ranges of *L*, *a* and *b* in fruit color classification, leading to decreased accuracy of analysis to some extent.

The quantitative traits of plants can be described by the major gene plus polygene mixed inheritance model (Gai and Wang et al., 1998; Zhang et al., 2000; Zhang and Gai, 2009). In this model, the quantitative traits can be controlled by multiple pairs of genes that have diverse effects, in which, the major genes that can be detected show great effect, while the polygenes that are difficult to be discovered under the experimental conditions display weak effect. Heritability, the ratio of the genetic variance (variance from the mean effect of the genes) to the phenotypic variance in a genetic group for a quantitative trait, represents the genetic ability of variation and also serves as an indicator of the similarity between parent and offspring (Wray and Visscher, 2008). The heritabilities can be divided into two types, major gene heritability and polygene heritability, in the major gene plus polygene mixed genetic model.

In this study, we used tomato plants with green and purple fruits as parents and constructed genetic groups with six generations through an incomplete diallel cross. To increase the accuracy and reliability of our results, the shade value, which is transformed from *L*, *a* and *b* values with the following equation: $2000 \times a/L \times (a^2 + b^2)^{0.5}$ (Richardson and Hobson, 1987), was used to explore the genetic development of fruit color. The genetic developments of lycopene, chlorophyll and carotene contents in tomato fruits were also analyzed. Thus, this paper aimed to provide new insights into the basic theories of the heredities of tomato fruit color and pigment content, and to establish a solid basis for the breeding of high-quality tomato varieties.

2. Materials and methods

2.1. Plant materials

In this study, two different tomato varieties, ‘Lv Ying’ (green fruit, P_1) and ‘Zi Ying’ (purple fruit, P_2) were used as parent materials (Fig. 1). Then the six generations of genetic groups, namely, P_1, P_2, F_1 (reciprocal crosses), BC_1, BC_2 and F_2, were constructed. They were simultaneously planted in the same greenhouse in the experimental field of Northwest A&F University. The numbers of plants of P_1, P_2, F_1, BC_1, BC_2 and F_2 were 20, 20, 30, 50, 50 and 150, respectively. In the full-ripening stage, 10 fruits in the second inflorescence were harvested to analyze fruit colors and pigment contents.

2.2. Detection of fruit color

The color of fruit surface was examined using the CHROMAMET-ECR-400 full-automatic colorimeter (KONICA MINOLTA, Tokyo, Japan) at three points chosen uniformly along the equatorial plane of fruit to obtain *L*, *a* and *b* values (*L* value, lightness of measured color: 0 is black, and 100 is white; *a* value, degree of red and green in measured color: $a > 0$ is reddish, while $a < 0$ is greenish; *b* value: degree of orange and blue in measured color: $b > 0$ presents orange, and $b < 0$ presents blue).

Moreover, 10 fruits from each plant and the mean values of *L*, *a* and *b* were determined to calculate the shade value with the following equation: $2000 \times a/L \times (a^2 + b^2)^{0.5}$ (Richardson and Hobson, 1987). The shade value mainly reflects the color of fruit surface.

2.3. Measurement of pigment contents

For each plant, 10 fruits with consistent maturity were selected from the second inflorescence and preprocessed at 4 °C for 12 h. Then, they were ground into a homogenate in a dark or low-lit room. Two homogenate samples (2.7–2.9 g) were collected and placed in two 10 mL centrifuge tubes. One tube was added with 80% acetone, shaken evenly, and sonicated for 30 min to extract chlorophyll and carotene. Subsequently, the extracting solution was transferred into a 25 mL brown volumetric flask and dissolved with 80% acetone to obtain a constant volume (Khalyfa et al., 1992; Chang et al., 1998). Furthermore, another tube was processed with absolute methanol, added with petroleum ether containing 2% dichloromethane, and subjected to ultrasonic wave for 30 min to extract lycopene. Chlorophyll, carotene and lycopene were quantified by spectrophotometric method as described previously (Ruan, 2013). All measurements were repeated with three biological replicates.

2.4. Statistical analysis

The data were examined through multigenerational joint analysis for major gene plus polygene mixed inheritance model (Gai and Wang et al., 1998; Zhang et al., 2000; Zhang and Gai, 2009), and the quantitative traits of plants were subjected to segregation analysis using SEA software package (Cao et al., 2013). Then, the optimal genetic model was chosen from 24 models, including one pair of major genes model, two pairs of major genes model, polygene model, one pair of major genes + polygene model and two pairs of major genes + polygene model, according to the minimization principle of Akaike’s information criterion (AIC) and model compatibility test containing homogeneity examination U_1^2, U_2^2, U_3^2, Smirnov test (${}_nW^2$) and Kolmogorov test (D_n). The corresponding genetic parameters were then estimated. The frequency distributions of shade value and pigment content were assessed with SPSS 23.0.

3. Results

3.1. Heredity of fruit color between green and purple fruits based on shade value

We firstly performed the hybridization of green fruit × purple fruit and then constructed the six generations of genetic groups. The fruit colors in each genetic group were measured by colorimeter, and shade values were generated. Further, we explored the heredity of fruit color based on the shade value. As shown in Table 1, the shade values of F_1 fruits from reciprocal crosses ($P_1 \times P_2$ and $P_2 \times P_1$) had no significant difference, indicating that the heredity of fruit color in this cross combination was controlled by nuclear genes. Moreover, the frequency distributions of shade values in F_2, BC_1 and BC_2 generations were analyzed using SPSS (Fig. 2). We found that the frequency distribution of shade values in F_2 generation yielded two peaks around −2,500 and