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Novel Classification Forms for Xenia

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***Abstract*. The xenia effect refers to the phenomenon whereby the pollen genotype directly affects seed and fruit development during the period from fertilization to seed germination, which leads to different characteristics in phenotypic traits. The xenia effect can create differences in the endosperm and embryo formed after double fertilization and can also alter various fruit parameters, such as the fruit-ripening period; the fruit shape, size, and color; the flavor quality, such as sugars and acids; as well as the nutrient quality, such as anthocyanins. The xenia effect manifests in various ways, playing an important role in increasing the yield of fruit trees, improving fruit appearance and internal quality, as well as in directional breeding. Compared with other pomology research areas, our understanding of the xenia effect is still in its infancy. Currently, xenia is classified into two types: xenia and metaxenia. In the former, the direct effects of the pollen genotype are exhibited in the syngamous parts of the ovules; that is, the embryo and endosperm only. In the latter, the effects of the pollen genotype are demonstrated in structures other than the embryo and endosperm; that is, in tissues derived wholly from the mother plant material, in seed parts such as the nucellus and testa, as well as in the carpels and accessory tissues. However, the current classification has various shortcomings. In the present study, we propose a novel classification based on whether the appearance of xenia results from the tissue formed by double fertilization. Three xenia types are proposed: double-fertilization xenia, non–double-fertilization xenia, and combined xenia. The new classification has great theoretical and practical significance for future studies on the xenia effect and its mechanisms and also provides a more effective, broader application of xenia in improving the yield and quality of fruit trees.**

As early as 1868, Darwin devoted six pages to describe "the direct or immediate action of the male element on the mother form" in his book *The Variation* (Liu, 2008); a phenomenon that now we call xenia. Xenia refers to the direct effect of the pollen genotype on the development and characteristics of the seed and fruit in the period that spans fertilization to seed germination. During this period, xenia causes phenotypic variations in the seed and fruit that reflect the traits of the pollinizer parent; however, these traits are not inherited by the progeny. When the female and male reproductive cells combine, the pollen genotype can directly affect the maternal tissue outside the embryo and endosperm, such as the seedcoat and pericarp, and cause differences in the traits, color, and quality of the hybridized fruit and seed (Denney, 1992; Pozzi et al., 2019; Shi et al., 2008). Studies have shown that xenia is widely present in fruit trees. Not only does it affect the formation of the endosperm and embryo following double fertilization, but also causes differences in seed shape and size. It can also alter the fruit-ripening period (Mizrahi et al., 2004) (Fig. 1), fruit shape and size (Zhang et al., 2016b) (Fig. 2), color of the pericarp, fruit flavor, and the contents of certain substances (Kumar and Das, 1996; Zhou et al., 2011). Thus, studying the xenia effect has great significance in fruit production, of which fruit and seed are the main targets for harvest. It can also provide a theoretical reference for the pollination configuration of the cultivar, increased yield, improvements in internal and external fruit qualities, as well as in the genetics, physiology, and breeding science of fruit trees (Denney, 1992; Liu, 2008; Shi et al., 2008). Currently, many pomologists and horticulturists have realized the practical and theoretical importance of xenia; however, although the available studies have focused on the observation and classification of xenia, this classification is far from comprehensive.

As fruits and seeds are the targets of human consumption, the impact of xenia on phenotypic traits has been classified into two types: xenia and metaxenia (Denney, 1992; Liu, 2008; Shi et al., 2008). In xenia, the pollen genotype directly affects the seeds formed after fertilization in the female parent in the current year and causes differences in seed shape, size, and color. Metaxenia is the phenomenon whereby the pollen genotype directly affects the fruit shape, maturation period, size, color, flavor, and content of substances in the current year and results in variations in these traits (Denney, 1992; Shi et al., 2008; Zhou et al., 2011). In the late 19th century and early 20th century, the definition of these two terminologies was one of the most discussed topics among scholars. In fact, the differentiation and definition of these two types of xenia, particularly relating to which kind of xenia the difference in the pericarp belongs to, still puzzles researchers today (Kahriman et al., 2017; Suaib and Suleman, 2018). Although xenia research in fruit trees has made great progress in recent years, we propose that the current classification of xenia and metaxenia is limited and hinders the progression of further xenia research. For example, the classification of xenia in *Carya cathayensis* Sarg., or Chinese hickory, is perplexing. Based on the currently accepted definitions of xenia, the xenia in *C. cathayensis* should be classified as xenia because the pollen genotype directly affects the seeds formed after fertilization in the female parent in the current year and causes differences in seed quality, oil content, and crude protein content (Wang et al., 2010). However, recent research has demonstrated that enhancing the photosynthetic capacity of the exocarp is the primary contributor to the differences in fruit enlargement in apomixis (Huang et al., 2019). It thus seems more reasonable to classify this as metaxenia based on the fundamental cause of the differences in the fruit.

In pomegranate, the pollen genotype not only significantly affects the fruit shape, length and diameter, fruit color, and fruit peel thickness, but also alters the seed weight, length and diameter, hardness, and toughness (Gharaghani et al., 2017), and thus cannot be classified into either type of xenia. These examples demonstrate that the current classification of xenia and metaxenia cannot reflect whether the tissue formed by xenia obtained paternal information through double fertilization. It also does not indicate the fundamental cause of the xenia. Thus, to facilitate the development of xenia research, it is necessary that the physiological processes of the formation of the organs and

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tissues that exhibit xenia are explored, focusing on whether the appearance of xenia resulted from tissue formed by double fertilization. Based on this, the present study offers a revised classification of xenia as three types: double-fertilization xenia, non–double-fertilization xenia, and combined xenia. This novel xenia classification could offer great theoretical and practical significance in future research on xenia and its mechanisms, as well as a more effective, broader utilization of xenia to increase the yield and quality of fruit trees.

Double-Fertilization Xenia

Double-fertilization xenia refers to the phenomenon whereby the pollen genotype transfers information from the male parent via the double-fertilized tissue (embryo or endosperm) in the period from fertilization to seed germination, causing differences in the embryo, endosperm, and seedcoat, as well as in the fruit-ripening period, fruit shape, size, pericarp color, fruit flavor, and nutrient content. As Table 1 shows, double-fertilization xenia has been reported many times in Chinese chestnut (*Castanea mollissima* Blume), the seeds of which are mainly used for human consumption (Wang and Peng, 2015). The pollen genotype was found to affect the gene expression level of pyruvate phosphate dikinase in the leaves of *C. mollissima* and enhance its photosynthetic rate (Liang et al., 2016b), thereby causing a xenia effect in fruit size (Chen and Shi, 2009; Liang et al., 2016a; Lu et al., 2004), fruit shape, and single-fruit weight (Yang et al., 2018), and quantitative traits such as the content of starch and soluble sugar (Wang and Peng, 2015; Zhang et al., 2016a), fats, proteins, amylose, and vitamin C (Wang and Peng, 2015; Zhang et al., 2016b). In peony, cross-pollination increased the number of seeds per fruit, seed volume, and seed and kernel weight (Xie et al., 2017) and upregulated the expression of 10 genes related to fatty acid and triglyceride biosynthesis during seed development (Xie et al., 2019), leading to an increased content of three unsaturated fatty acids: oleic acid, linoleic acid, and α-linolenic acid (Xie et al., 2017).

When common corn is pollinated with high-oil corn, the development and growth of the embryo in the corn is promoted, and the weight of the embryo is significantly increased (Dong, 2007). In addition, when inducer lines with anthocyanin markers, such as R1-Navajo, which in combination with other dominant genes in the anthocyanin synthesis pathway causes deep pigmentation of the endosperm tissue in the crown region of the kernel and purple pigmentation in the embryo tissue, are crossed (as the male parent) with the source germplasm (as the female parent) lacking anthocyanin color markers, all the resulting hybrid kernels are expected to express the Navajo phenotype in the endosperm and embryo (Prasanna et al., 2012) (Fig. 3). Furthermore, the content of

Fig. 1. A branch of *Hylocereus polyrhizus* bearing two fruits at different stages of ripening (Mizrahi et al., 2004). The red, ripe fruit originated from pollination with the pollen of *Hylocereus undatus* clones, whereas the green, unripe fruit resulted from pollination with *Selenicereus grandiflorus* pollen. This photograph was taken 34 d after pollination.

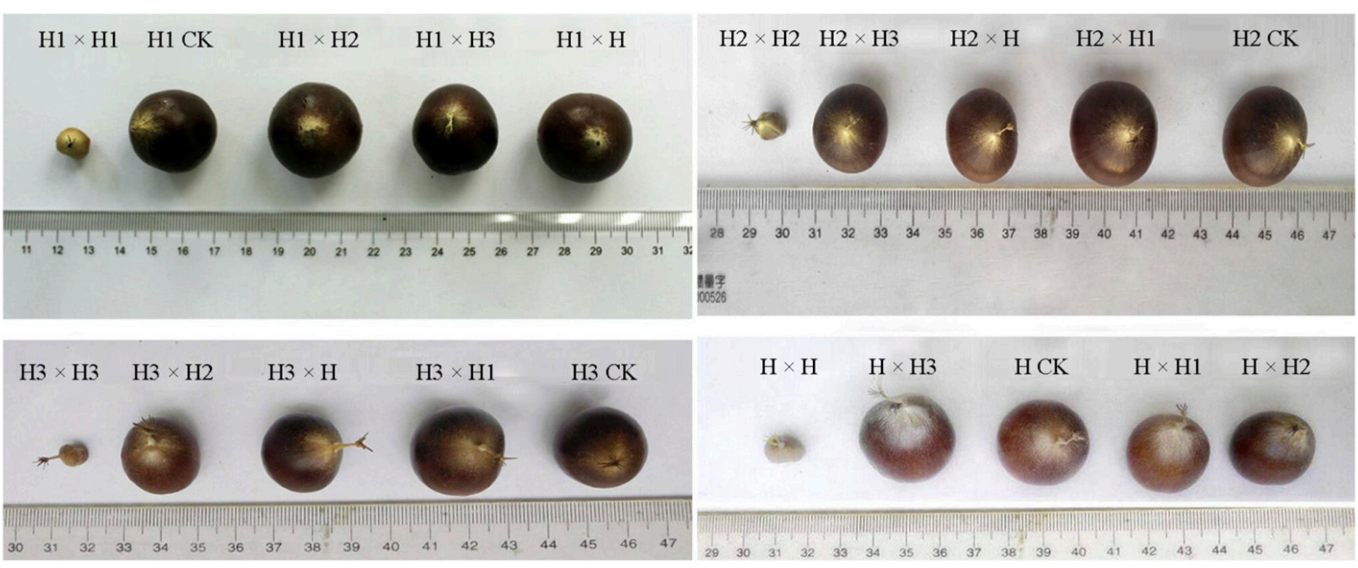

Fig. 2. Comparisons of the fruit sizes and colors for different pollination combinations (Zhang et al., 2016b). H1 = Huali 1; H2 = Huali 2; H3 = Huali 3; H = Huangzhen; CK = natural pollination. Huali 1 and Huali 2 pollinated by Huangzhen resulted in lighter-skinned fruits compared with the fruits resulting from natural pollination for these two varieties, whereas Huangzhen pollinated by Huali 2 and Huali 3 resulted in a darker-skinned fruit. These results were consistent with the color of the pollen donors. In contrast, Huali 3 pollinated by Huali 2 resulted in a lighter-skinned fruit than the skin color of the pollen donor.

Table 1. Phenotypic characteristics of double-fertilization xenia in some plants.

No.	Species	Phenotypic characteristics of xenia	Reference
1	Chestnut (*Castanea mollissima* BL.)	Soluble sugar content, starch content	Wang and Peng (2015)
2	Chestnut (*C. mollissima* BL.)	Fruit size, starch content, pyruvate phosphate dikinase, photosynthesis	Liang et al. (2016b)
3	Chestnut (*C. mollissima* BL.)	Fruit size	Chen and Shi (2009)
4	Chestnut (*C. mollissima* BL.)	Fruit size, number of nuts in cupula	Liang et al. (2016a)
5	Chestnut (*C. mollissima* BL.)	Fruit shape, single-fruit weight	Yang et al. (2018)
6	Chestnut (*C. mollissima* BL.)	Fruit size, average weight of nut	Lu et al. (2004)
7	Henry chestnut (*Castanea henryi* RW.)	Soluble sugars, fats, proteins, amylose, vitamin C	Zhang et al. (2016a)
8	Henry chestnut (*C. henryi* RW.)	Soluble sugars content, fats, proteins, amylose, vitamin C	Zhang et al. (2016b)
9	Tree peony (*Paeonia* section *Moutan* DC.)	Number of seeds per fruit, seed volume, seed and kernel weights, linoleic acid concentration, oleic acid concentration, oil extraction ratio, fatty acid composition	Xie et al. (2017)
10	Tree peony (*Paeonia* section *Moutan* DC.)	Fatty acid and triacylglycerol biosynthetic pathway genes	Xie et al. (2019)
11	Maize (*Zea mays* L.)	Embryo development and growth, embryo weight	Dong (2007)
12	Maize (*Z. mays* L.)	Total unsaturated fatty acids	Chen and Dong (2017)
13	Maize (*Z. mays* L.)	Color of endosperm and embryo	Prasanna et al. (2012)
14	Almonds (*Amygdalus communis* L.)	Amygdalin content	Sánchez-Pérez et al. (2012)
15	Almonds (*A. communis* L.)	Fatty acid composition	Alizadeh-Salte et al. (2018)
16	Almonds (*A. communis* L.)	Oleic acid, fatty acid composition, tocopherol concentrations, linoleic acid ratio	Kodad et al. (2009)
17	Clementine (*Citrus*)	Fruit yield, fresh weight, number of seeds per fruit	Papadakis et al. (2009)
18	Mandarins (*Citrus*)	Single-fruit weight, soluble solids and total acid content, number of seeds per fruit	Yildiz and Kaplankıran (2017)
19	Ponkan (*Citrus*)	Total soluble solids, total sugars, polyphenolic and antioxidant capacities, titratable acidity, carotenoid content, total polyphenolic content, free radical-scavenging	Wang et al. (2018)
20	Pummelo (*Citrus*)	Contents of indole-3-acetic acid (IAA), gibberellic acid $(GA)_{1+3}$, and cytokinins (CTKs)	Nie and Liu (2002)
21	Pummelo (*Citrus*)	*Cis*- and *trans*-linalool oxides contents, cytochrome P450 78A7 gene, fruit aroma quality, linalool oxide synthase gene	Zhang et al. (2019a)

oleic acid in the kernels increased significantly, while the content of stearic acid, linoleic acid, and linolenic acid decreased. At maturity, the kernels from the hybridized generation contained higher amounts of total unsaturated fatty acids than the kernels from the selfed common corn (Chen and Dong, 2017).

In *Citrus*, cross-pollination increased the number of seeds per fruit (Papadakis et al., 2009; Yildiz and Kaplankıran, 2017) and the contents of indole-3-acetic acid (IAA), gibberellic acid $(GA)_{1+3}$, and cytokinins (CTKs) (Nie and Liu, 2002), thereby causing a xenia effect in quantitative traits such as the content of soluble solids, total acid, total sugars, titratable acidity, antioxidants, carotenoids, and total polyphenolics (Wang et al., 2018; Yildiz and Kaplankıran, 2017). Furthermore, cross-pollination upregulated the expression of the cytochrome P450 78A7 gene and linalool oxide synthase gene, which are associated with fruit aroma quality, leading to increased contents of *cis*- and *trans*-linalool oxides (Zhang et al., 2019a). In addition, the pollen genotype in almond could regulate the amount of amygdalin transported from the embryo to the seedcoat, thereby affecting the taste (Sánchez-Pérez et al., 2012). It could also control the amount of unsaturated fatty acids, including oleic acid and linoleic acid (Alizadeh-Salte et al., 2018) and tocopherol concentrations (Kodad et al., 2009) in the almond kernels.

Non–Double-Fertilization Xenia

Non–double-fertilization xenia refers to the phenomenon whereby the pollen genotype transfers information from the male parent through non-double, or single, fertilization pathways during the period from fertilization to seed germination, which then causes differences in the embryo, endosperm, and seedcoat, as well as fruit-ripening period, fruit shape, size, pericarp color, flavor, and nutrient content. As indicated in Table 2, the pollen genotype in red bayberry could regulate the activity of sucrose phosphate synthase and sucrose synthase, significantly affecting the fruit color, quality, size, hardness, content of soluble solids, total sugars, vitamin C, and titratable acids (Qi et al., 2017). When *C. cathayensis* was pollinated with the pollen from *Carya illinoinensis* (Wangenh.) K. Koch, or pecan nut, the pericarp of *C. cathayensis* became green (Fig. 4), and the genes related to photosynthetic pathways, including chlorophyll synthesis, light harvest, and carbon fixation, were upregulated (Huang et al., 2019; Xu et al., 2017). The exocarp of the fruit exhibited an enhanced photosynthetic rate, resulting in increased fruit biomass, fruit length, fruit diameter, shell thickness, shell weight, nut weight, and dry weight (Wang et al., 2010; Xu et al., 2017).

In kiwifruit, cross-pollination caused a xenia effect in fruit mass, fruit shape, transverse diameter, longitudinal diameter, and flesh firmness (Qi et al., 2007), and increased the contents of quantitative traits, including soluble solids, total sugar, total acid, titratable acid, vitamin C, total polyphenols, total flavonoids, chlorophyll, and carotenoids (Seyrek et al., 2017; Xiao et al., 2013). In apple, cross-pollination caused a xenia effect in the fruit stalk, fruit lenticel, flesh cell interspace, flesh cell size (Li et al., 2016), fruit longitudinal diameter, fruit transverse diameter, fruit shape index (Yu et al., 2017), and single-fruit weight (Zhang et al., 2019b), and increased quantitative traits such as fruit hardness and the content of anthocyanins, soluble sugar, soluble solids, acidity, vitamin C, total phenolics, total flavonoids, volatiles, and other characteristic compounds (Wang et al., 2016; Yu et al., 2017; Zhang et al., 2018, 2019b).

In addition, the pollen genotype in pear results in a xenia effect in external appearance, such as fruit size, fruit shape index, and lenticels on fruit skins (Lee et al., 2017; Stern et al., 2018), as well as in quantitative traits such as single-fruit weight, fruit firmness, soluble solid content, titratable acidity, vitamin C (Liu et al., 2016; Mansur et al., 2019; Sha et al., 2006), sugar, amino acids, fatty acid content, lignin synthesis, and stone cells (Li et al., 2018). In blueberry, cross-pollination causes a xenia effect in fruit-ripening time, fruit size, and single-fruit weight (Ehlenfeldt and Kramer, 2012; Miller et al., 2011; Taber and Olmstead, 2016), resulting in a xenia effect in the external

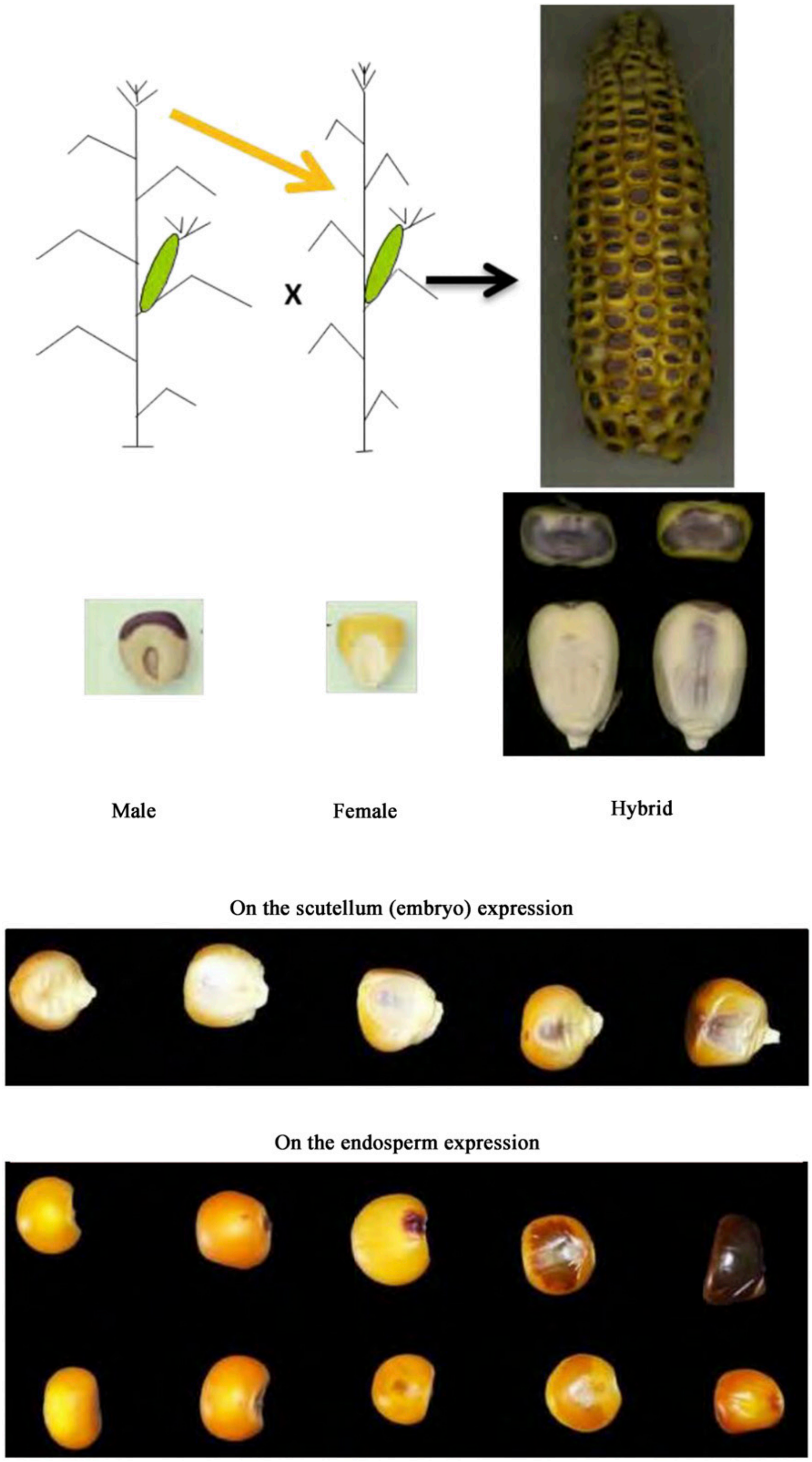

Fig. 3. As reported by Prasanna et al. (2012), when inducer lines with anthocyanin markers, such as R1-Navajo, which in combination with other dominant genes in the anthocyanin synthesis pathway causes deep pigmentation of the endosperm tissue in the crown region of the kernel and purple pigmentation in the embryo tissue, are crossed (as the male parent) with the source germplasm (as the female parent) lacking the anthocyanin color markers, all the resulting hybrid kernels are expected to express the Navajo phenotype in the endosperm and in the embryo.

appearance, such as in the pedicel and sepal, as well as fruit depression, altered fruit shape, and fruit stem separation. This xenia also has an impact on the nutritional quality, such as the soluble solid content, anthocyanin content, and total acid content (Yang et al., 2015; Yang et al., 2017). Cross-pollination causes a xenia effect in single-fruit weight as well as in the contents of soluble solids, titratable acid, total sugar, and vitamin C in plum (Zhang et al., 2017); in fruit size, soluble solid content, and firmness in peach (Shen et al., 2011); and in fruit size, single-fruit weight, and polysaccharide content in wolfberry (He et al., 2013).

Combined Xenia

Combined xenia refers to the phenomenon whereby the pollen genotype transfers information from the male parent via the double-fertilized tissue (embryo or endosperm) and non–double-fertilized tissue during the period from fertilization to seed germination, causing differences in the embryo, endosperm, seedcoat, fruit maturation period, fruit shape, size, pericarp color, fruit flavor, and nutrient content. As indicated in Table 3, the pollen genotype in tomato not only influences the pilose on the tomato fruit, but also affects the seed size (Piotto et al., 2013) (Fig. 5). In macadamia, the pollen genotype significantly influences the timing of embryo and endosperm development, kernel mass, timing of the hardening of the husk, shell mass, pericarp mass (Herbert et al., 2019a, 2019b), nut setting, nut apical papilla size, stalk length and thickness, nut transverse diameter, nut shape index, kernel rate, amino acid composition, aspartic acid content, oleic acid content, linoleic acid content, and total sugar content (He et al., 2016).

The pollen genotype not only significantly affects the fruit shape and length, single-fruit weight and diameter, fruit peel color (Fig. 6), fruit peel thickness, soluble solid contents, and lignin contents of pomegranate, but also significantly affects the aril color (Fig. 6), seed weight, seed length and diameter, seed hardness, seed toughness, and 1000-seed weight (Gharaghani et al., 2017; Xue et al., 2016). Similar results have also been reported in grape, namely that the pollen genotype directly affects the berries and seeds formed after fertilization in the female parent in the current year and causes differences in berry set, berry weight, berry length and width, as well as the number of seeds per berry, viable seed rate, seed size, 100-seed weight, and seed width, height, and thickness (Sabir, 2011, 2015). In litchi, cross-pollination causes a xenia effect in fruit size, fruit shape index, fruit weight, flesh recovery, skin thickness, total soluble solid contents, total sugars, vitamin C, total acid, the sugar-acid ratio, flesh texture and flavor, fruit cracking incidence, maturation date, and seed traits (Liu et al., 2011), as well as the contents of anthocyanins and chlorophyll in the peel (Qiu et al., 2006).

Discussion

The effect of xenia is of great agronomic importance for the production of fruits and seeds, having applications in plant breeding and in increasing grain yield or the size and quality of fruit (Pozzi et al., 2019). Although the practical importance of xenia has been

Table 2. Phenotypic characteristics of the non–double-fertilization xenia in some plants.

No.	Species	Phenotypic characteristics of xenia	Reference
1	Red bayberry (*Myrica rubra*)	Soluble solids, total soluble sugars, titratable acids	Qi et al. (2017)
2	Hickory (*Carya cathayensis*)	Chlorophyll synthesis, light capture, and carbon assimilation	Huang et al. (2019)
3	Hickory (*C. cathayensis*)	Fruit size, exocarp color, photosynthetic rate	Xu et al. (2017)
4	Hickory (*C. cathayensis*)	Exocarp color, fruit shape, single-fruit weight, fruit length, fruit diameter, fruit shape index, shell thickness, shell weight, and nut weight	Wang et al. (2010)
5	Kiwifruit (*Actinidia chinensis* Planch)	Fruit mass, soluble solids content, transverse diameter, longitudinal diameter, fruit shape index, flesh firmness, fruit shape	Qi et al. (2007)
6	Kiwifruit (*A. chinensis* Planch)	Fruit shape, single-fruit weight, soluble solids content, total sugar content, total acid content, vitamin C content	Xiao et al. (2013)
7	Kiwifruit (*Actinidia eriantha* Vines)	Dry matter, total sugar, titratable acid, vitamin C, total polyphenol, total flavonoid, chlorophyll and carotenoid contents	Seyrek et al. (2017)
8	Apple (*Malus domestica* L.)	Fruit stalk, fruit lenticel, flesh cell interspace, flesh cell size	Li et al. (2016)
9	Apple (*M. domestica* L.)	Single-fruit weight, fruit shape index, hardness, anthocyanin, soluble sugar content, soluble solids	Zhang et al. (2018)
10	Apple (*M. domestica* L.)	Volatile and characteristic compounds	Wang et al. (2016)
11	Xinjiang wild apple (*Malus sieversii* L.)	Fruit longitudinal diameter, fruit transverse diameter, shape index, acidity, soluble solid content, fruit stalk length	Yu et al. (2017)
12	Apple (*M. domestica* L.)	Single-fruit weight, fruit firmness, vitamin C content, sugar-acid ratio, total phenolics and total flavonoids, valuable phenolic compounds	Zhang et al. (2019a)
13	Jingbaili pear (*Pyus ussuriensis*)	Fruit setting, fruit weight, soluble solids content, titratable acidity	Sha et al. (2006)
14	Dangshan Su pear (*Pyrus bretschneideri*)	Sugar, amino acid, and fatty acid content, lignin synthesis, stone cell	Li et al. (2018)
15	Korla Fragrant pear (*Pyrus*)	Single-fruit weight, fruit firmness, fruit shape index, sugar-acid ratio, content of soluble solids and vitamin C	Mansur et al. (2019)
16	Qing Xiang pear (*Pyrus*)	Single-fruit weight, hardness, soluble solids content, soluble sugar content, vitamin C content	Liu et al. (2016)
17	'Niitaka' pears (*Pyrus pyrifolia* Nakai)	Fruit size, external appearance, fruit shape index, lenticels on fruit skins	Lee et al. (2017)
18	European pears (*Pyrus communis*)	Fruit size	Stern et al. (2018)
19	Blueberry (*Vaccinium* spp.)	Single-fruit weight, fruit size	Miller et al. (2011)
20	Blueberry (*Vaccinium* spp.)	Fruit size, fruit-ripening time	Ehlenfeldt and Kramer (2012)
21	Blueberry (*Vaccinium* spp.)	Single-fruit weight, fruit size, fruit-ripening time	Taber and Olmstead (2016)
22	Blueberry (*Vaccinium* spp.)	Single-fruit weight, soluble solid content	Yang et al. (2015)
23	Blueberry (*Vaccinium* spp.)	Single-fruit weight, longitudinal diameter, fruit diameter, fruit shape index, fruit depression, pedicel, sepal, fruit shape and fruit stem separation, soluble solid content, anthocyanins content, total acid content	Yang et al. (2017)
24	European plum (*Prunus domestica* L.)	Single-fruit weight, soluble solids contents, titratable acids contents, total sugar content, vitamin C content	Zhang et al. (2017)
25	Jinhua DaBai peach (*Amygdalus persica* L.)	Fruit size, soluble solid content and firmness	Shen et al. (2011)
26	Wolfberry (*Lycium barbarum* L.)	Fruit size, single-fruit weight, polysaccharide content	He et al. (2013)

Fig. 4. Xu et al. (2017) reported on the changes in the shape of hickory fruits pollinated with two different pollens following pollination. The hickory fruits cross-pollinated (CP) by pecan pollen were significant larger and greener than those self-pollinated (SP) by hickory pollen.

realized by many agronomists and horticulturists, its mechanism remains poorly understood, and there has been very little focus on the physiological and molecular mechanisms of xenia (Liu, 2008). In previous studies on xenia, researchers initially primarily focused on the xenia phenomenon of the edible portion of the fruit. For instance, in *C. mollissima* (Wang and Peng, 2015) and *C. cathayensis* (Wang et al., 2010), studies were mainly concerned with the seed portion and were less concerned with the fruit portion. In contrast, in pear (Stern et al., 2018) and apple (Wang et al., 2017), studies were mainly concerned with the fruit portion rather than the seed portion. Thus, the classification of xenia into two types, namely xenia and metaxenia (Denney, 1992; Liu, 2008; Shi et al., 2008), was based only on the xenia exhibited in the edible portion. However, this classification is highly limited, as studies focused on the xenia of the edible seed part neglected the xenia of the fruit part, and vice versa. This led us to speculate that there was no xenia in the fruits of *C. cathayensis* and that the formation of xenia in *C. cathayensis* was due to differences in the seed following double fertilization. In addition, recent research suggests that enhanced photosynthesis in *C. cathayensis* plays an important role in the xenia of the pollen (Huang et al., 2019).

The xenia in *Citrus*, including clementine, mandarins, ponkan, and pummelo, could be classified as metaxenia according to the edible portion. However, previous studies have shown that cross-pollination increases the number of seeds per fruit in *Citrus* (Papadakis

Table 3. Phenotypic characteristics of the combined xenia in some plants.

No.	Species	Phenotypic characteristics of xenia	Reference
1	Tomato (*Solanum lycopersicum*)	Fruit size, pilosity, seed weight	Piotto et al. (2013)
2	Macadamia (*Macadamia ternifolia* F. Muell.)	Nut and kernel size, kernel mass, kernel recovery	Herbert et al. (2019a)
3	Macadamia (*M. ternifolia* F. Muell.)	Nut mass, kernel mass, and kernel recovery	Herbert et al. (2019b)
4	Macadamia (*M. ternifolia* F. Muell.)	Nut setting, nut apical papilla size, stalk length and thickness, nut transverse diameter, nut shape index, kernel rate, amino acid composition, aspartic acid content, oleic acid content, linoleic acid content and total sugar content	He et al. (2016)
5	Pomegranate (*Punica granatum* L.)	Fruit shape, length, diameter, color, fruit peel thickness. Seed weight, length, diameter, hardness, toughness	Gharaghani et al. (2017)
6	Pomegranate (*P. granatum* L.)	Fruit shape index, single-fruit weight, soluble solids contents, lignin contents, number of seeds, edible rate. Aril juice yield, seed hardness, 1000-seed weight.	Xue et al. (2016)
7	Grape 'Narince' (*Vitis vinifera* L.)	Berry set, berry and seed sizes, seed number per berry, percentage of viable seeds	Sabir (2015)
8	Grape 'Italia' (V. *vinifera* L.)	Berry setting, seed number per berry, viable seed rate, seed sizes, 100-seed weight, seed width, height, and thickness	Sabir (2011)
9	Litchi 'Dongliu No. 1' (*Litchi chinensis* Sonn.)	Fruit size, fruit shape index, flesh recovery, skin thickness, soluble solids contents, total sugars, vitamin C and total acid, sugar-acid ratio, flesh texture and flavor, fruit cracking incidence, maturation date, seed traits	Liu et al. (2011)
10	Litchi 'Guiwei' (*L. chinensis* Sonn.)	Fruit longitudinal diameter, fruit shape index, fruit weight, flesh recover rate, total soluble solids, contents of sugars, acid and vitamin C in juice, contents of anthocyanins and chlorophyll in peel	Qiu et al. (2006)

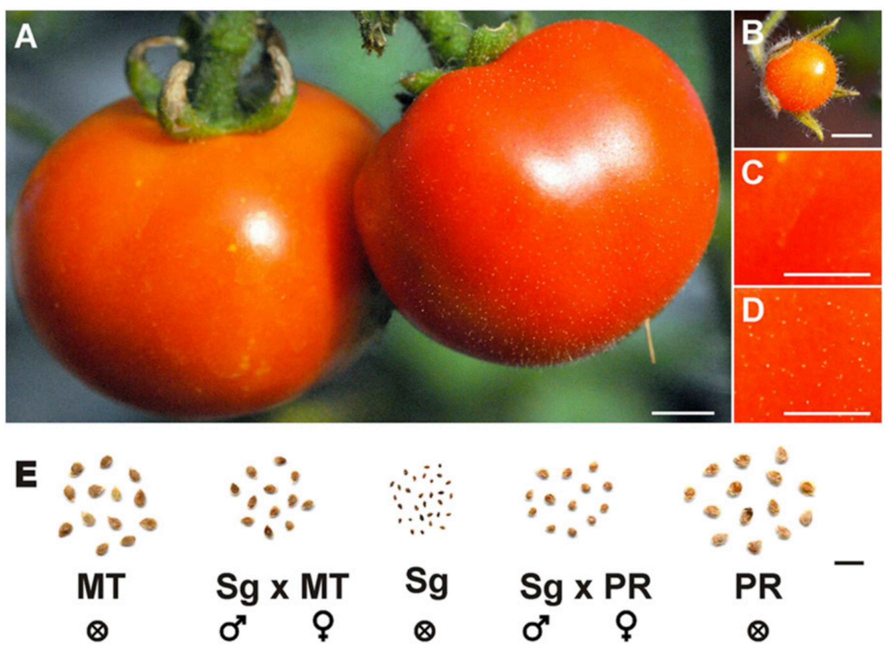

Fig. 5. Piotto et al. (2013) reported the effect of *Solanum galapagense* (Sg) pollen on the trichome density of cultivar Micro-Tom (MT) and on the seed weight of both cultivar MT and cultivar Pusa Ruby (PR). (**A**) Increase in trichome number in the fruits of cultivar MT pollinated by *S. galapagense* (left) compared with fruits from the same plant obtained by selfing (right); (**B**) fruit of *S. galapagense* showing a high trichome density; (**C**) epidermis of the selfed MT fruit showing low trichome density; (**D**) epidermis of the MT fruit after pollination by *S. galapagense*; (**E**) reduction in the seed size of cultivar MT and cultivar PR following pollination by *S. galapagense* (Sg × MT and Sg × PR). MT, Sg, and PR are selfed seeds. Bar = 5 mm.

et al., 2009; Yildiz and Kaplankıran, 2017) as well as the contents of IAA, GA_{1+3}, and CTKs (Nie and Liu, 2002), thereby causing a xenia effect in nutrient quality traits (Wang et al., 2018; Yildiz and Kaplankıran, 2017). These results suggested that the xenia was due to the differences in the seed following double fertilization. Furthermore, in tomato (Piotto et al., 2013), macadamia (Herbert et al., 2019a, 2019b), pomegranate (Gharaghani et al., 2017; Xue et al., 2016), grape (Sabir, 2011, 2015), and litchi (Liu et al., 2011; Qiu et al., 2006), xenia has been detected in both the seeds and fruit and thus cannot be classified into either xenia or metaxenia. The preceding research on the formation mechanisms of xenia suggests that a new xenia classification is required.

Achievements in molecular and cell biology over the past century have provided new approaches for studying the mechanisms of xenia. MicroRNA (miRNA) molecules are key regulators of posttranscriptional eukaryotic genes, which are ubiquitous in plants (Chen et al., 2018a), highly specific, and involved in the regulation of a series of biological processes (Chen et al., 2018b; Voinnet, 2009). MiRNA molecules are capable of transferring and transporting between different cells and organisms in plants (Liu, 2008) and causing phenotypic changes in developmental tissues (Kim et al., 2001; Piotto et al., 2013). Interestingly, Engel et al. (2003) discovered that the miRNA molecules in the sperm of maize plants could move between various organs under normal or nutrient-limiting conditions (Thieme et al., 2015) and could be released and transmitted into the cellular microenvironment, resulting in more efficient signal transmission than that of hormones (Kim et al., 2001). Moreover, miRNA molecules can regulate pollen fertility and fertilization capacity in a dosage-dependent manner (Akagi et al., 2014), as well as affect the fruit development, fruit size, fruit coloring, and fruit maturation period of horticultural plants (Chen et al., 2018a). Thus, it was speculated that miRNA from pollen might be transferred and expressed to the non–double-fertilized maternal tissue through intercellular transmission, thus demonstrating xenia (Kim et al., 2001).

However, the manner in which the miRNA molecules enter the fruit is unclear. Pollen is the primary cause of xenia, as its function is to produce sperm and transport it into the embryo sac for double fertilization. Differences in the seed number and contents of endogenous hormones and polyamines of the style and pulp, or in the transfer and expression of genetic information from different genotypes of pollen, can be the result of differences in vitalities of the pollen, endogenous hormones and polyamines of the pollen of different varieties, and pollination compatibilities between different varieties, which may lead to xenia. A core aspect of studying the formation mechanisms of xenia involves clarifying how the paternal

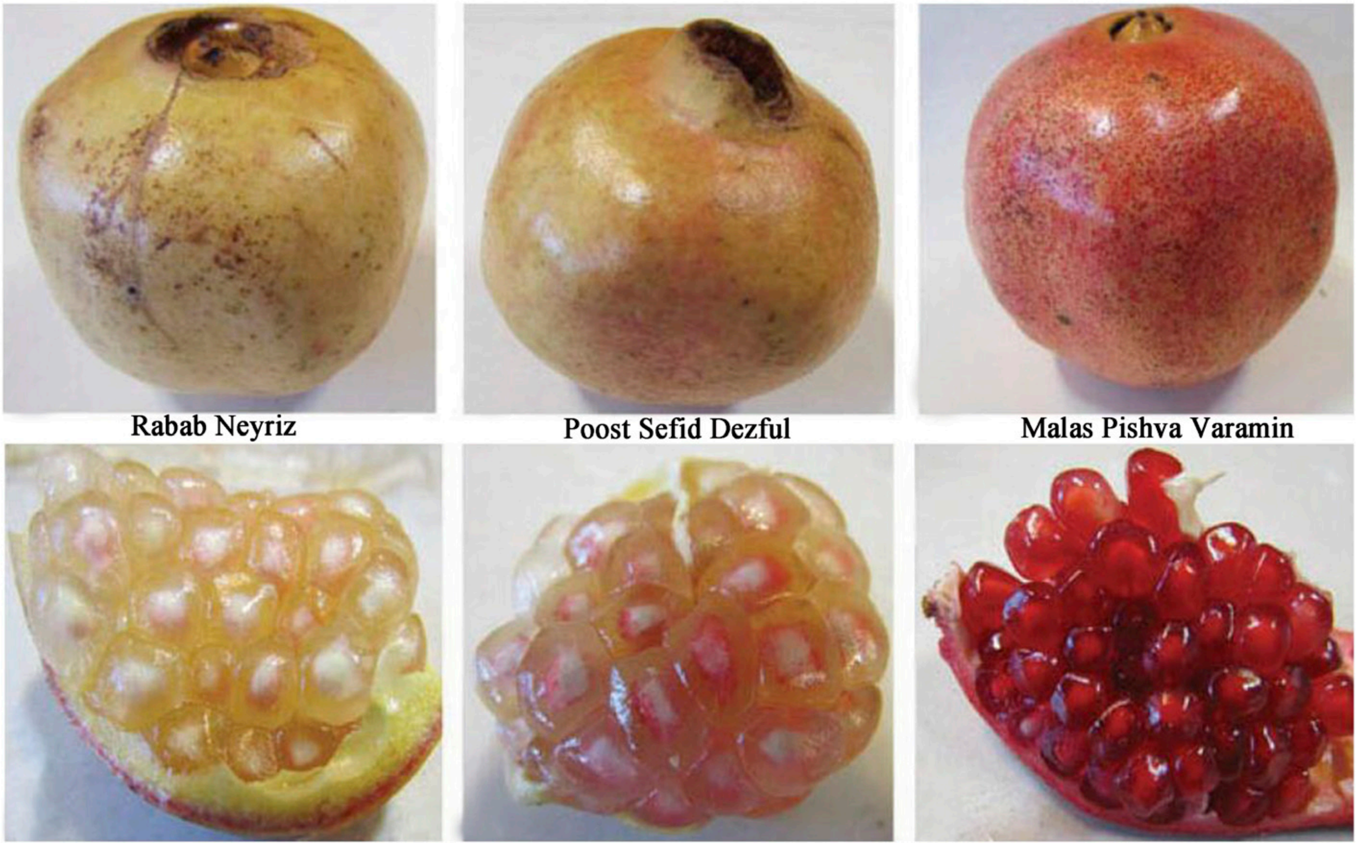

Fig. 6. Gharaghani et al. (2017) reported the effects of pollen sources from 'Rabab Neyriz', 'Poost Sefid Dezful', and 'Malas Pishva Varamin' on the peel color and aril color of 'Malas Yazdi' pomegranate. Fruit peel and aril color were affected by pollen source, and 'Malas Pishva Varamin' as the pollinizer produced fruits with greater redness than those of the other pollen sources.

information carried by the pollen can cause transcriptional expression and regulate the appearance of xenia during fruit growth and development. Although previous studies have explored the molecular mechanisms of xenia formation, they have been restricted by the existing classification, as studies focused on the xenia of the edible seed part cannot reflect whether the tissue formed by xenia obtained paternal information through double fertilization. As available studies on xenia mechanisms have been limited by the current research paradigm, three xenia types, including double-fertilization xenia, non–double-fertilization xenia, and combined xenia, were proposed in the present study. This new classification method, which addresses whether the appearance of xenia originated from the tissue formed by double fertilization, not only solves the inadequacies of the current classification but also provides a new approach for research into the formation mechanisms of xenia.

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