彩色马铃薯色素相关基因座的种类、功能与染色体定位

赵昶灵，李孙文*，张维明

（云南农业大学 农学与生物技术学院，昆明 650201）

摘 要：综述了与彩色马铃薯色素产生与分布相关基因座的观念起源、种类、功能和染色体定位。与彩色马铃薯色素相关基因座的观念起源于试图解释四倍体和二倍体马铃薯块茎和其他部位颜色呈现遗传行为的两个遗传模式。与彩色马铃薯色素相关的13个基因座可划分为4类，第1、第2和第3类分别与马铃薯花色苷的合成、酰化和分布有关，第4类与马铃薯类胡萝卜素的产生相关。基因座 *I*，*P*，*R* 和 *Y* 分别编码一个 MYB 结构域转录因子、类黄酮3′，5′-羟化酶、二氢黄酮醇4-还原酶和β-胡萝卜素羟化酶。基因座之间复杂多样的互作综合决定了彩色马铃薯色素特别是花色苷的产生与分布。基因座 *D* 和 *R* 定位在马铃薯的2号染色体上，*E*，*F*，*I* 和 *PSC* 在10号染色体上，*P* 在11号染色体上，*Y* 在3号染色体上。可为彩色马铃薯颜色呈现的遗传机理探索提供参考。

关键词：彩色马铃薯；色素；基因座；种类；功能；染色体定位

GLC Number：Q343.1 **Document Code**：A **Article ID**：1000-3142(2010)03-0377-09

Category, functions and chromosomal locations of the gene loci related to colored potato pigments

ZHAO Chang-Ling, LI Sun-Wen*, ZHANG Wei-Ming

(*College of Agricultural Sciences and Biotechnology, Yunnan Agricultural University*, Kunming 650201, China)

Abstract: This paper summarized the idea origin, category, functions and chromosomal locations of the gene loci involved in the production and distribution of the pigments in colored potatoes. The idea of the gene loci related to the pigments in colored potatoes originated from the two genetic models which attempted to explain the inheritant behaviors of the colorations of the stem tubers and other parts of tetraploid and diploid potatoes. The overall thirteen gene loci related to the pigments in colored potatoes could be classified into four kinds. The first, second and third kinds were related to the synthesis, acylation and distribution of the potato anthocyanins respectively, and the fourth kind was related to the production of the potato carotenoids. Locus *I*, *P*, *R* and *Y* encoded a MYB-domain transcription factor, flavonoid 3′,5′-hydroxylase, dihydroflavonol 4-reductase and β-carotene hydroxylase respectively. Various and complicated interactions among the gene loci synthetically determined the production and distribution of the pigments, especially the anthocyanins, in colored potatoes. Locus *D* and *R* were located on Chromosome 2 of potato, *E*, *F*, *I* and *PSC* on Chromosome 10, *P* on Chromosome 11, and *Y* on Chromosome 3. This paper could provide a reference for the exploration on the genetic mechanism of the colorations of colored potatoes.

Key words: colored potato; genetic locus; category; function; chromosomal location

Received date:: 2008-08-04 **Accepted date**:: 2009-04-19

Foundation item: Supported by grants from the Provincial Department of Science and Technology of Yunnan(2006C0030Q); the Startup Fund for Doctor of Yunnan Agricultural University(A2002096)

Biography: ZHAO Chang-Ling(1969-), Male, Born in Dujiangyan City of Sichuan Province, Doctor of Science, Full Professor, working in Plant physiology, Phytochemistry, Bioinformatics and Plant biochemistry and molecular biology, (E-mail)zhaoplumblossom7@163.com.

* Author for correspondence, E-mail: swl68@yahoo.cn

Generally, the skins and/or fleshes of the stem tubers of potato(*Solanum tuberosum*)are white, yellow or saffron yellow. Worldwide, the potato cultivars in which the skins and/or fleshes of the stem tubers are red, purple, blue or orange are intuitively denominated colored potatoes (Brown*et al.*, 2003; Brown, 2004; Jansen & Flamme, 2006).

The coloration patterns of the skins and fleshes of the stem tubers of colored potatoes are changeable and fascinating. Not all of the colors of the skins are consistent with those of the fleshes(Groza *et al.*, 2004). Colored skins do not mean the fleshes are definitely colored. However, if the fleshes are colored, the skins are usually colored, e. g. the red or purple fleshes are often accompanied by the red or purple skins respectively(Brown *et al.*, 2003), and red or blue colored fleshes have identically colored skins(Brown *et al.*, 2003; de Jong *et al.*, 2003a). Furthermore, the tuber skins of colored potatoes are uniformly colored, but the colorations of the fleshes are diverse, i. e. the fleshes may range from partial pigmentation to complete pigmentation (Brown *et al.*, 2003), resulting in the colorful arcs, rings or radiating stars in the fleshes. Cases in point are the potato cultivars native to the Andes of South America and the local potato cultivar 'Zhuanxinwu' planted in Baoshan Town of Xuanwei City in Yunnan Province of China(Brown *et al.*, 2003; Zhao *et al.*, 2007).

Various pigmentations of colored potatoes result basically from the accumulation of anthocyanins in the specific parts of the stem tubers. It has been proved that the skin and flesh colors of the stem tubers of potatoes are mainly determined by two different classes of pigment, i. e. carotenoids and anthocyanins(Lewis *et al.*, 1998). Carotenoids lead to the white, yellow or saffron yellow of the skins and/or fleshes(Lewis *et al.*, 1998; Brown *et al.*, 1993, 2003; Morris *et al.*, 2004). Anthocyanins lead to the red, purple or blue of the skins and/or fleshes, fundamentally producing colored potatoes(Hung *et al.*, 1997; Fossen *et al.* 2003). In the stem tubers of colored potatoes, anthocyanins always accumulate principally in the periderms and peripheral cortexes(Howard *et al.*, 1970; Burton *et al.*, 1989). In fact, anthocyanins may produce anywhere in the plants of colored potatoes, e. g., in stem tubers, flowers, sprouts or stems(Jung *et al.*, 2005), and they also result in the red, purple or blue of the upground parts of the potatoes(Harborne, 1960; Hung *et al.*, 1997; Lewis *et al.*, 1998; Brown *et al.*, 2003).

This summary delt with the idea origin, category, functions and chromosomal locations of the gene loci involved in the production and distribution of the pigments, i. e. anthocyanins and carotenoids, in colored potatoes, attempting to provide a reference for the further molecular biological studies on the pigments, especially the anthocyanins, of colored potatoes.

1 Establishment of the idea of the gene loci involved in the production and distribution of colored potato pigments

The idea of the gene loci involved in the production and distribution of the pigments in colored potatoes was established primarily on the two classic genetic models which tried to explain the inheritant behaviors of the colorations of the stem tubers and other parts of tetraploid and diploid potato plants.

The first genetic model was originally raised by Salaman(1910) to elucidate the color inheritance of the stem tuber of tetraploid European potato varieties. In this model, the purple, red and white of the tuber were postulated to be controlled by three independent gene loci, i. e. D, R and P. The red of the tuber skin results from the complementary action of the dominant D and R, and, together with P, D and R make the skin purple (Salaman, 1910). Afterwards, Locus E was proposed to be related to the accumulation of the anthocyanins in the tuber epidermis and bud eye, R was believed to express in the tuber cortex(Salaman, 1926; Lunden, 1937).

The second genetic model was raised by Dodds & Long(1955, 1956) to elucidate the color inheritance of the stem tuber of diploid cultivated potato cultivars. In this model, Locus P, R/R^{pw}, E, I and F were introduced to explain the various accumulations of the anthocyanins in different parts of the potato plants.

However, in the 1990s, the above two models were united to a great extent since they were compared each other by Howard(1970) and de Jong(1991). Although, for the diploid and tetraploid potato cultivars, the number and functions of the genes involved in the production and distribution of the anthocyanins were tremendously different, the genes coding the similar traits in these cultivars were thought to belong to the same(de Jong, 1991; van Eck *et al.*, 1994). van Eck *et al.* (1994) further evaluated the two genetic models in detail and proposed to unify some of the gene locus names properly. R/R^{pw} and *PSC* were revoked. R/R^{pw} was replaced by *D*. *R*, *E*, *I* and *PSC* were thought to be actually a same locus on Chromesome 10 of potato, and involved in the tuber skin coloration(van Eck *et al.*, 1994).

2 Category and functional characteristics of the gene loci involved in the production and distribution of colored potato pigments

2.1 Coloration-related functions of the gene loci

There are 13 gene loci related to colored potato pigments, i. e. anthocyanins and carotenoids, in all, and they can be devided into 4 kinds(Table 1—3).

Table 1　Functions of the gene loci involved in the synthesis and acylation of the anthocyanidins and the production of the carotenoids in colored potatoes

	Gene locus				
	Locus involved in the synthesis of anthocyanidins			Locus involved in the acylation of anthocyanins	Locus involved in the production of carotenoids
	D	*P*	*R*	*Ac*	*Y*
Function	Required for the synthesis of red anthocyanins in each part of the plant	Encoding the basic factors required for the production of blue/purple petunins in any tissue of the plant and controling the formation of methylic delphinin	Encoding a basic factor required for the production of red pelargonins in any tissue of the plant and controling the production of acylated pelargonin in tuber and the cyanin in flower	Controlling the acylation of the anthocyanins	Required for the accumulation of yellow carotenoids in tuber flesh
Literature	Swaminathan & Howard (1953); Harborne (1960); Lunden (1974); van Eck *et al.* (1993, 1994)	Dodds & Long (1955, 1956); Harborne (1960); Lunden (1974); van Eck *et al.* (1993, 1994); de Jong *et al.* (2004a); Jung *et al.* (2005)	Dodds & Long (1955, 1956); Harborne (1960); Lunden (1960); van Eck *et al.* (1993, 1994); de Jong *et al.* (2003b, 2004a)	Dodds & Long (1955); Harborne (1960)	Bonierbale *et al.* (1988); de Jong *et al.* (2004a)

2.1.1 The gene loci related to the synthesis of colored potato anthocyanidins　These loci, including *D*, *P* and *R*, decide the kind of anthocyanidins synthesized, leading to the specific coloration of the stem tuber or other parts of the potato plants(Table 1). *D* is the dominant gene deciding the synthesis of red anthocyanins in each part of the potato plants. Genetype *dd* leads to the pink tubers and seedlings, and white flowers(Dodds & Long, 1955, 1956). *P* is the dominant gene deciding the synthesis of purple anthocyanins in each part of potato plants, especially in the embryonal axes and bud tips(Lunden, 1937). Moreover, *P* controls the appearance of the blue pigments in diploid potatoes(Dodds & Long, 1955, 1956). Dominant *R* regulates not the color of the tuber skin, but that of the outer layers of the tuber cortex(Lunden, 1937).

2.1.2 The gene locus related to the acylation of colored potato anthocyanins　The locus in point is *Ac*(Table 1). It controls the acylation of the anthocyanins, actually deciding the existent states of anthocyanins in the specific parts of potatoes. Swaminathan & Howard (1953) found diploid potatoes display both acylated and non- acylated anthocyanins while only acylated forms are present in the tetraploid potatoes. Harborne(1960) and Rodriguez-Saona *et al.* (1998) discovered the pigments resulting in colored potatoes are varied types of acylated anthocyanidin glycosides. Brown *et al.* (2003) testified red-fleshed potatoes contain predominantly acylated glycosides of pelargonidin while the purple-fleshed potatoes contain predominantly acylated glyco-

sides of petunidin and peonidin. In addition, *Ac* also controls the linkage of glucose residue at the C5 of the anthocyanidins, and the methylation of the delphinidin or cyanidin derivates(Harborne, 1960).

2.1.3 The gene loci related to the distribution of colored potato anthocyanins These loci decide whether the anthocyanins appear in the specific parts of tuber and leaf or in the flowers and stems(Table 2,3).

Table 2 Functions of the gene loci deciding the anthocyanins appear in the specific parts of the tuber in colored potatoes

	Gene locus				
	B	*E*	*I*	*Pf*	*PSC*
Function	Controlling the distribution of the anthocyanins in tuber	Participating in the pigmentations of the epidermis and bud eyes of tuber	Controlling the distribution of the anthocyanins and being required for the tissue-specific expression of red/ purple anthocyanins in tuber skin	Controlling the appearance of anthocyanins in the interior tissues of tuber beyond the periderm and deciding the distribution of the anthocyanins in the tubers of diploid potatoes	Controlling the purple skin color in diploid potatoes
Literature	Dodds & Long (1955)	Lunden (1960)	Dodds & Long (1955, 1956); Harborne (1960); van Eck *et al.* (1993,1994); de Jong *et al.* (2004a)	Harborne (1960); de Jong (1987, 1991); van Eck *et al.* (1994)	Gebhardt *et al.* (1989)

Table 3 Functions of the gene loci deciding the anthocyanins appear in the flower and the specific parts of the leaf in colored potatoes

	Gene locus		
	Locus deciding the anthocyanins appear in flower	Locus deciding the anthocyanins appear in the specific parts of leaf	
	F	Pd	Pv
Function	Controling the distribution of the anthocyanins and related to the specific expression of the anthocyanins in flower	Controlling the production of the anthocyanins on leaf back	Controlling the production of the anthocyanins on the abdominal part of leaf
Literature	Dodds & Long (1955); Lunden (1974); van Eck *et al.* (1993)	Kessel & Rowe (1974); Garg *et al.* (1981)	Kessel & Rowe (1974); Garg *et al.* (1981)

(1)The gene loci deciding the anthocyanins appear in the specific parts of tuber are *B*, *E*, *I*, *Pf* and *PSC* (Table 2). *B* and *I* were first raised by Dodds & Long (1955)to control the distribution of the anthocyanins in the tuber. *E* was initially used by Lunden(1960)to explain the phenotype of the skin color. It participates in the pigmentations of epidermis and bud eyes. *I* is required for the tissue-specific expression of anthocyanins in tuber skin(Dodds & Long, 1956), which is proved by de Jong(1991) and de Jong *et al.* (2004a). It controls whether the anthocyanins appear in the skin and flesh (Harborne, 1960). Genotype *ii* causes the absence of the tuber pigmentation(Dodds & Long, 1956). *Pf* was originally proposed by Harborne (1960) to control the presentation of anthocyanins in the interior tissues of the tuber beyond the periderm. It decides the distribution of the anthocyanins in the tubers of diploid potatoes, and controls the flesh color(de Jong *et al.*, 1987). *PSC* was introduced by Gebhardt *et al.* (1989)to control the purple skin color in diploid potatoes.

(2)The genetic locus deciding the anthocyanins appear in the flowers is *F*(Table 3). Like *B* and *I*, *F* were first raised by Dodds & Long(1955, 1956)to control the distribution of the anthocyanins. Lunden (1937, 1974) thought *F* is related to the specific expression of the anthocyanins in the flower, and it is involved in the contrast between self-coloured flowers and flecked ones.

(3)The gene loci deciding the anthocyanins appear in the specific parts of the leaf are *Pd* and *Pv*(Table 3). *Pd* and *Pv* were formally put forward by Kessel & Rowe(1974)and Garg *et al.* (1981). They are both the single dominant genes which respectively control the production of the anthocyanins on the back and the abdominal part of leaf. Koopmans *et al.* (1951) ever thought *Pv* is recessive, but Kessel & Rowe(1974)and Garg *et al.* (1981)thought *Pv* is dominant.

(4)The genetic locus related to the production of colored potato carotenoids: The locus in point is *Y*(Table 1). It is required for the accumulation of yellow carotenoids in the tuber fleshes(de Jong *et al.*, 2004a).

2.2 Enzyme or protein factors encoded by the specified gene loci

For the gene loci related to colored potato pigments, only *I*, *P*, *R* and *Y* have been definitely proved to encode specific enzymes or protein factors, i. e. *I* encodes a transcription factor(TF), *P*, *R* and *Y* encode an enzyme respectively(Table 4).

(1) *I* encodes a MYB-domain *TF*, i. e. anthocyanins 2(AN2)of *Petunia* spp. (de Jong *et al.*, 2003a, b, 2004a, b; Jung *et al.*, 2005) (Table 4). AN2 is a R2R3-type MYB factor, and is involved in the activation of anthocyanin coloration. MYB proteins contain a conserved DNA-binding domain (the MYB domain) with 1-3 imperfect repeats(R1-R3) which define their binding specificity to the target gene promoters(Martin & Paz-Ares, 1997). R2R3-type proteins form the largest class of MYB factors in plants, and among them are the factors involved in the activation of anthocyanin pigmentation in various plants(Elomaa *et al.*, 2003). As the homologous gene of *C1* of *Maize*(*Zea mays*)and the third regulator of the anthocyanin pathway in *Petunia* spp., *AN2* acts in concert with *AN1* and *AN11* to activate the promoter of dihydroflavonol 4-reductase gene(*DFR*) in the petal limbs (Quattrocchio *et al.*, 1998; Quattrocchio *et al.*, 1999). It can interact with either of two distinct basic helix- loop-helix(bHLH) factors, JAF13 or *AN1*, and functions upstream of AN1 but not of *JAF13*(Elomaa *et al.*, 2003).

Table 4　Enzymes or protein factors encoded by the specified gene loci involved in the pigment synthesis in colored potatoes

Genetic locus	Enzyme or protein factor encoded	Literature
I	MYB-domain transcription factor (AN2)	de Jong *et al.* (2003a, 2003b, 2004a, 2004b); Jung *et al.* (2005)
P	flavonoid 3′,5′—hydroxylase (F3′,5′H)	de Jong *et al.* (2003a, 2003b, 2004a, 2004b); Jung *et al.* (2005)
R	dihydroflavonol 4-reductase (DFR)	de Jong *et al.* (2003a, 2003b, 2004a, 2004b); Jung *et al.* (2005)
Y	beta-carotene hydroxylase (BCH)	de Jong *et al.* (2004b)

(2)*P* encodes flavonoid 3′,5′-hydroxylase(F3′,5′H)(de Jong *et al.*, 2003a, b, 2004a; Jung *et al.*, 2005) (Table 4). *F3′,5′H* has been regarded as the "blue gene" in higher plants(Okinaka *et al.*, 2003). In plant organs or tissues whose colors are determined by anthocyanins, the hydroxylation pattern of the B-ring of dihydrokaempferol(DHK)is the most important step to decide the organ color(Stafford, 1990). If the B-ring of DHK is hydroxylated at the 3′ position due to the catalyzing of flavonoid 3′-hydroxylase(F3′H), DHK will be transferred to dihydroquercetin(DHQ), leading to the production of the cyanins which are responsible for the red color. If the B-ring of DHK is hydroxylated at both the 3′ and 5′ positions due to the catalyzing of F3′,5′H, DHK will be transferred to dihydromyricetin (DHM), leading to the production of the delphinins which are responsible for the blue/ violet color(Lewis, 1996; Brugliera *et al.*, 1999).

(3)*R* encodes dihydroflavonol 4-reductase(DFR) (de Jong *et al.*, 2003, b, 2004a, b; Jung *et al.*, 2005)(Table 4). DFR catalyzes the reduction of DHK into leucopelargonidin, ultimately producing pelargonidins(Lewis, 1996; de Jong *et al.*, 2004a). So, *R* is necessary for the production of red pelargonins in any tissue of all red potatoes(de Jong, 1991; Lewis, 1996). Overexpression of a DNA encoding DFR in sense orientation has been proved to result in a 4-fold increase in petunidin and pelargonidin derivatives in the tubers(Stobiecki *et al.*, 2003).

(4)*Y* encodes β-carotene hydroxylase(BCH)(de Jong *et al.*, 2004b)(Table 4). BCH catalyses the conversion of β-carotene into β-cryptoxanthin, and further into zeaxanthin(Sun *et al.*, 1996; Hirschberg, 2001; Tian & DellaPenna, 2001), contributing to the synthesis of yellow carotenoids in the tuber flesh. It is found that silencing of BCH can increase the total carotenoid and β-carotene levels in the tubers(Diretto *et al.*, 2007).

2.3 Interactions among the gene loci

2.3.1 Interactions among *D* or *P* and *E*, *F*, *R* *D* or *P* is complementary with *E*, *F* and *R*which determine the colors of the flower and tuber skin(Lunden, 1937; van

Eck *et al.*, 1994).

(1) *P*, *R* and *D* control the purple, red and white of the tuber skins of tetraploid potatoes respectively, the appearance of red pigments in the tuber is due to the complementary effect between the dominant *D* and dominant *R*, and, if *D* and *R* interact simultaneously with *P*, the tuber skin will be purple(Salaman, 1910). The combination of *R* with *D* or *P* can deepen the skin color, namely make the skin black (Lunden, 1937), producing red or blue/purple tuber skin (van Eck *et al.*, 1994). Genotype *D-R-* makes the skin red (Swaminathan & Howard, 1953), and D-*P*-*R*- result in an intensely colored tuber cortex with a black skin (Lunden, 1937; van Eck *et al.*, 1994). The almost white tuber skin phenotype of ddppR- is difficult to distinguish from white-skinned *D-rr* or *P-rr* genotypes (Lunden, 1937). In the absence of *P*, *D* controls the red of the tubers, flowers and buds (Dodds & Long, 1955, 1956). Genotype *dd* procuces pink tubers, pink sprouts and white flowers (Dodds & Long, 1955). Harborne (1960) thought *P* and *R* all determine the kind of the anthocyanins. However, the epistatic interactions among *D*, *P* and *R* are not elucidated completely. *P* is epistatic to *R* (Dodds & Long, 1955). In tubers, *P* is also epistatic to *D*, but in flowers, *P* is incompletely epistatic to *D* (Dodds & Long, 1955, 1956). Lunden (1974) thought, for the flower colors in diploid potatoes, *P* is epistatic to *D*. However, van Eck *et al.* (1993) believed *D* is epistatic to *P*.

(2) In the absence of dominant *E*, *F* and *R*, the presence of a dominant *D* can be reflected by the weak brownish-red of the sprout tips, stems, flower stalks and calyx (Lunden, 1937).

(3) When *E* is dominant, it regulates the presence of red or purple hue in tuber epidermis in combination with *D* or *P*, respectively (van Eck *et al.*, 1994). Genotype *ppddE-* produces the slender reddish color of the tuber, with stronger pigmentation in the bud eyes and at the sprout bases (Lunden, 1937; van Eck *et al.*, 1994).

(4) *D*、*F* and *P* are unlinked, they control the inheritance of the flower colors in diploid potatoes, and *F* is regulated by D and *P* (Lunden, 1974). Genotype *D-ppF-* provides redish purple flowers, *ddP-F-* light blue flowers, *D-P-F-* blueish purple flowers and *ddppF-* or——ff white flowers (Lunden, 1937). Genotype *DDff* produces anthocyanins throughout the plant, *DDF-* and *DDff* leads to white flowers (van Eck *et al.*, 1994).

(5) *F-R-* leads to self-coloured flowers, *ff R-* leads to flecked flowers which are white flowers with some pigmentation due to leaky alleles of ff (van Eck *et al.*, 1994).

2.3.2 Interactions among *I*, *P*, *R* and *Y* *I*, *R* and *P* are the three classical loci which are involved in the the coloration of the tuber skin in diploid potatoes (Dodds & Long, 1955, 1956). The diploid I, R and P mimic functionally and are likely allelic to the tetraploid *D*, *R* and *P*, respectively, which was originally described by Salaman (1910). Genotype *iippR-* offer red sprouts with white tuber skin (Dodds & Long, 1955). de Jong (1991) further summarized the variations of the red, purple and white tubers in diploid and tetraploid potatoes are all controlled by the unlinked *R*, *P* and *I*. Tubers with genotype *I-PpRr* or *IiP-rr* have purple skin while those with genotype *I-ppR-* are red. Potatoes lacking a functional allele at *I* produce white tubers, irrespective of the alleles present at *R* and *P*. On the other hand, just because the stem tubers of colored potatoes contain carotenoids as well as anthocyanins (Lewis *et al.*, 1998; Brown *et al.*, 1993, 2003; Brown, 2004), de Jong *et al.* (2004b) believed the variations of the tuber coloration is synthetically controlled by four independent and unlinked loci, i. e. *R*, *P*, *I* and *Y*.

2.3.3 Interactions among *D*, *P* and *I* *I* is epistatic to *D* and *P* (Harborne, 1960). It epistatically controls the presence and absence of the pigmentation of the tuber skin and flesh even when *D* and *P* are present (de Jong *et al.*, 2004b; Jung *et al.*, 2005). In the absence of a dominant *D*, dominant *I* can lead to the pink of tuber skin (van Eck *et al.*, 1994). Genotype *DDiiP-* offer purple sprouts with white tuber skin (Dodds & Long, 1955).

2.3.4 Interactions among *D*, *P* and *Ac* Generally, *D*, *P* and *Ac* collectively control the production of the anthocyanins (Harborne, 1960).

2.3.5 Interactions among *B*, *F* and *I* *B*, *F* and *I* are tightly linked, they all control the distribution of the pigments in potato plants (Dodds & Long, 1955).

2.3.6 Interaction between *Pf* and *I* *Pf* is linked to *I*

(Harborne, 1960; de Jong, 1987). For the anthocyanin distribution in the tuber of diploid potatoes, *Pf* controls the flesh color(de Jong, 1987).

2.3.7 Interaction between *Pd* and *Pv* *Pd* and *Pv* are both dominant genes. They are linked, and the distance between them is 40 mapping units(Kessel & Rowe, 1974; Garg *et al.*, 1981).

3 Chromosomal locations of the gene loci involved in the production and distribution of colored potato pigments

Along with the development of Amplified Fragments Length Polymorphism(AFLP) technology and the establishment of the genetic map of potato(Bonierbale *et al.*, 1988; Gebhardt *et al.*, 1989), Locus *D*, *E*, *F*, *I*, *P*, *PSC*, *R* and *Y* have been detected to locate on the specific chromosome of potato, and *E*, *F*, *I* and *PSC* all conformably locate on Chromosome 10(Table 5).

Table 5 Chromosomal locations of the gene loci involved in the production and distribution of colored potato pigments

Gene locus	Chromosomal location	Literature
D	2	van Eck *et al.* (1993, 1994)
E	10	van Eck *et al.* (1994)
F	10	van Eck *et al.* (1993)
I	10	van Eck *et al.* (1993, 1994)
P	11	van Eck *et al.* (1993, 1994)
PSC	10	Gebhardt *et al.* (1989)
R	2	van Eck *et al.* (1993)
Y	3	Bonierbale *et al.* (1988)

4 Discussion

In recent years, colored potato anthocyanins have displayed a broad applying perspective in modern society. On one hand, as natural colorants, the anthocyanins not only endue the tubers with various and peculiar coloration patterns but also are regarded as the good alternatives to synthetic dyes(Francis, 1989; Opheim & Andersen, 1992; Bridle & Timberlake 1997; Brown *et al.*, 2003; Brown, 2004). On the other hand, the anthocyanins have been proved to be provided with multiple pharmacological activities, such as antioxidant (Brown, 2004, 2005; Lachman & Hamouz, 2005; Reyes *et al.*, 2005), antivirus(Hayashi *et al.*, 2003) and anticancer(Hayashi *et al.*, 2006; Reddivari *et al.*, 2007). Therefore, increasing the anthocyanin content has been one of the important targets in the breeding practice of potatoes(Brown *et al.*, 2003; Brown, 2005).

A full understanding of the gene loci involved in the production and distribution of the pigments, especially the anthocyanins, of colored potatoes will not only provide a profound level to explore the mechanism by which the anthocyanins synthesize and accumulate *in vivo* but also underlie the work to create the potato cultivars with new genotypes. The previous work that the coloration phenotypes of the stem tuber and other parts of potatoes were due to the extence of the particular gene loci is necessary and elementary, but it is superficial and insufficient. The elucidation of the chromosomal locations of the gene loci and the enzymes and ptotein factors encoded by the loci is the further and critical step to explain the color-forming of potatoes. Later researches on the sequence structures and expression properties of the genes should be the cogent basis to create the new genotypes of potatoes with high functional and commercial values for the food, nutraceutical, cosmetic and medicinal industries.

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