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Review

Pathway and genes for the biosynthesis and action of abscisic acid incarnation flowers

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The pathway and genes for the biosynthesis and action of abscisic acid (ABA) have been elucidated in great detail using major model plants and crops, such as Arabidopsis, maize, rice and tomato, tobacco and so on, as experimental materials. However, a few studies have been done with minor crops and ornamentals. ABA plays a causal role in the induction of ethylene biosynthesis in carnation flowers. In this review, therefore, it was aimed (1) to reconstitute the pathway for ABA biosynthesis and action in carnation with ABA-related genes, which were recently identified from its flower tissues, and (2) to cross-check the identities of the identified genes with genes deposited in a carnation data base (Carnation DB), which was recently released to the public. A total of eleven identified ABA-related genes were allocated in their right steps, reconstituting the pathway for ABA biosynthesis and action. Furthermore, the cross-check of the genes in the reconstituted pathway with those in the Carnation DB could specify the function of five genes, which had remained un-annotated in the Carnation DB. This review suggested that the pathway for ABA biosynthesis and action, the same as that in major model plants and crops, is functioning in carnation, and implied that this is the case in other minor crops and ornamentals.

Key words: ABA biosynthesis and action, ABA-related genes, Carnation DB, carnation flowers, carnation genome data base, ethylene biosynthesis.

INTRODUCTION

Abscisic acid (ABA) is a plant hormone nearly ubiquitous in higher plants, and acts in the control of a wide range of essential processes of plant growth and development as well as plant adaptation to environmental stresses. The best known functions, for example, are those in the maintenance of seed dormancy and stomatal closure in response to drought stress (Arteca, 1996; Buchanan et al., 2000; Srivastava, 2001). ABA plays a causal role in the induction of ethylene biosynthesis in carnation flowers (Onoue et al., 2000; Nomura et al., 2013).

Recent genetic and biochemical studies using major model plants and crops, such as Arabidopsis, maize, rice and tomato, tobacco and so on, as experimental materials have revealed the pathway for ABA biosynthesis and action in great detail. Also, almost all the major genes for the enzymes involved in the pathway have been identified (Finkelstein, 2013; Nambara and Marion-Poll, 2005; Xiong and Zhu, 2003). However, a few studies have been done and much remains to be dissolved with minor crops and ornamentals, which have horticultural importance.

In this review, therefore, it was aimed to reconstitute the pathway for ABA biosynthesis and action in carnation with ABA-related genes, which were recently identified from its flower tissues (Nomura et al., 2013), and to cross-check the identities of the identified genes with genes deposited in a carnation data base (Carnation DB), which was recently released to the public.

Involvement of Abscisic Acid in Ethylene Production in Carnation Flowers

Ethylene is a primary plant hormone involved in the senescence of cut carnation flowers (Abeles et al., 1992; Borochov

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and Woodson, 1989; Reid and Wu, 1992; Satoh, 2011). In carnation flowers undergoing natural senescence, ethylene is first produced from the gynoecium and induces autocatalytic ethylene production in petals (Shibuya et al., 2000; ten Have and Woltering, 1997). Eventually, ethylene produced in the petals accelerates in-rolling of the petals resulting in wilting of the flowers (Manning, 1985; Peiser, 1986; Woodson et al., 1992); therefore, the gynoecium plays a causal role in controlling petal senescence.

In carnation flowers, ethylene is synthesized through the following pathway, the same as that in other plants: L-methionine → S-adenosyl-L-methionine → 1-aminocyclopropane-1-carboxylate (ACC) → ethylene. ACC synthase (ACS) and ACC oxidase (ACO) catalyze the last two reactions. So far, three genes encoding ACC synthase (DcACS1, DcACS2, and DcACS3: Dc came from Dianthus caryophyllus) (Henskens et al., 1994; Jones and Woodson, 1999)and a gene encoding ACC oxidase (DcACO1) (Park et al., 1992)have been identified from carnation. These genes are expressed in a tissue-specific manner in senescing carnation flowers;DcACO1 and DcACS1 are expressed in both the gynoecium and petals of carnation flowers undergoing senescence, whereas DcACS2 and DcACS3 are expressed in the gynoecium but not as much as DcACS1 (Henskens et al., 1994; Jones and Woodson, 1999; Park et al., 1992; ten Have and Woltering, 1997). Nukui et al. (2004) investigated the expression of the genes in flowers of 'White Candle' carnation, whose flowers produce little ethylene and have a longer vase-life, and suggested that DcACS1 expression plays a regulatory role in the ethylene production in the gynoecium of this cultivar. Therefore, DcACS1 and DcACO1 are considered as the key genes for ethylene biosynthesis in the gynoecium and petals of senescing carnation flowers.

Ethylene production is induced by pollination in the carnation gynoecium (Jones and Woodson, 1997; Nichols, 1977).

However, many carnation cultivars do not have another sand cannot be pollinated by their own pollen. They nonetheless show an increase in ethylene production in the gynoecium, probably due to factors other than pollination.

Previous studies revealed that (1) exogenously-applied abscisic acid (ABA) accelerated the senescence of cut carnation flowers through the stimulation of ethylene biosynthesis (Mayak and Dilley, 1976a, b; Nowak and Veen, 1982; Ronen and Mayak, 1981), (2) ABA content increased transiently in the gynoecium of cut carnation flowers after harvest, reaching a maximum content before the surge in ethylene production in the flowers (Nowak and Veen, 1982; Onoue et al., 2000), and (3) ABA action was expressed in the gynoecia but not in the petals (Shibuya et al., 2000). These results suggested that ABA is a crucial factor in the induction of ethylene biosynthesis in carnation flowers.

Recently, Nomura et al. (2013) investigated further the Role of ABA in triggering ethylene production in the gynoecium of senescing carnation flowers by examining changes in ABA content and expression of genes for ABA biosynthesis and action. Ultimately they showed that the expression of both DcNCED1a and DcNCED1b, which are involved in ABA biosynthesis, and DcPYR1, an ABA receptor gene, are associated with the induction of DcACS1 and DcACO1expression, leading to ethylene biosynthesis.

Pathway and Genes for Aba Biosynthesis and Action Incarnation Flowers

Nomura et al. (2013) identified a total of eleven genes involved in ABA biosynthesis, catabolism and action and reconstituted the ABA-related pathway in carnation flowers (Figure 1). In carnation flowers, as in other plants, ABA is thought to be synthesized through the carotenoid (C40) pathway. In this pathway, zeaxanthin epoxidase (ZEP) converts zeaxanthin to all-trans-violaxanthin via antheraxanthin by two epoxidation reactions. One gene corresponding to ZEP (Marin et al., 1996), DcZEP1, was identified from carnation. All-trans-violaxanthin is then converted to two 9-cis-epoxycarotenoids, 9-cis-violaxanthin and 9'-cis-neoxanthin. Two 9-cis-epoxycarotenoids are cleaved by 9-cis-epoxycarotenoid dioxygenase (NCED) to form a C15 precursor, xanthoxin. Four genes corresponding to NCED(Burbidge et al., 1999; Iuchi et al., 2001; Tan et al., 1997; Wang et al., 2011)were identified from carnation, and they were grouped into two distinct genes, each consisting of two isoforms, i.e., DcNCED1a and -b and DcNCED2a and -b. The reaction catalyzed by NCED has been recognized as the rate-determining step in ABA biosynthesis in plants (Burbidge et al., 1999; Iuchi et al., 2001; Tan et al., 1997; Wang et al., 2011). This was true in ABA biosynthesis in carnation flower tissues (Nomura et al., 2013).

ABA can be catabolized by the hydroxylation at C-8'producing 8'-hydroxy ABA, which is then spontaneously isomerized to form phaseic acid (Cutler and Krochko, 1999). The hydroxylation is mediated by ABA 8'-hydroxylases (Cytochrome P450 CYP707A enzymes) (Kushiro et al., 2004; Zhu et al., 2011). One gene (DcCYP707A1) was identified from carnation as a corresponding gene of CYP707A genes in other plants.

In the ABA signal transduction pathway, the core components are ABA receptor (PYLs: PYR/PYL/RCAR) (Ma et al., 2009; Melcher et al., 2009), negative regulators (PP2Cs: type 2C protein phosphatases), and positive regulators (SnRK2s: subfamily 2 of SNF1-related kinases). In this pathway, PYLs (ABA receptors) bind ABA to form a complex (Ma et al., 2009; Melcher et al., 2009; Nishimura et al., 2009; Park et al., 2009), then the complex inhibits PP2C from dephosphorylating SnRK2 (Fujii et al., 2009; Melcher et al., 2009; Yoshida et al., 2006). Then, SnRK2 is activated and phosphorylates downstream effectors, thus switching on ABA-responsive

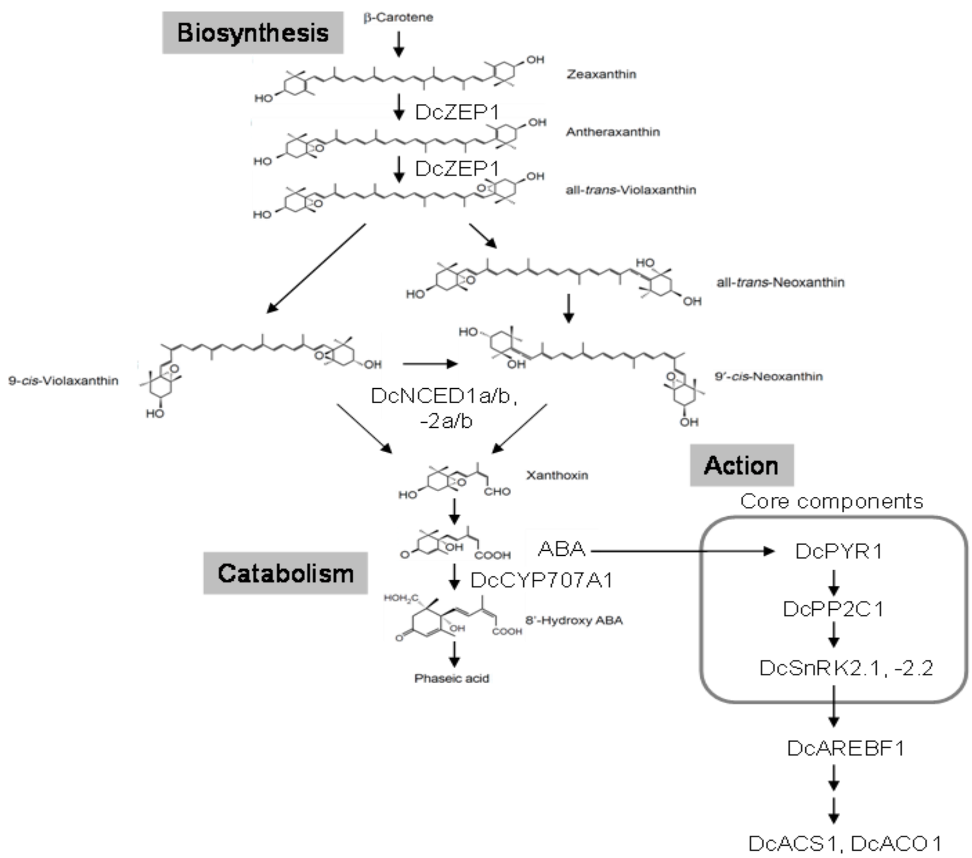

Figure 1.Pathway for ABA biosynthesis, catabolism, and action in carnation flowers.
DcZEP1, zeaxanthin epoxidase; DcNCED1a/b, -2a/b, 9-cis-epoxycarotenoid dioxygenase; DcCYP707A1, ABA 8'-hydroxylase; DcPYR1, ABA receptor; DcPP2C1, type 2C protein phosphatase; DcSnRK2.1, -2.2, subfamily 2 of SNF1-related kinase; DcAREBF1, ABA responsive element binding factor; DcACS1, 1-aminocyclopropane-1-carboxylate (ACC) synthase; DcACO1, ACC oxidase.

genes such as AREBFs (ABA responsive element binding factor) (Furihata et al., 2006; Kobayashi et al., 2005). As to carnation genes corresponding to the genes involved in these reactions, Nomura et al. (2013) identified one gene (DcPYR1) corresponding to PYR, one gene (DcPP2C1) corresponding toPP2C, and two genes (DcSnRK2.1 and -2.2) corresponding toSnRK2 and one gene (DcAREBF1) corresponding to AREBF (Figure 1). The ABA-related genes identified from carnation flower tissues covered nearly all the genes involved in ABA biosynthesis, catabolism and action, reconstituting those pathways (Figure 1).

Nomura et al. (2013) revealed that the expression of DcPYR1 gene played a primary role in the ABA signal transduction in carnation flower tissues.

Cross-Check of Aba-Related Genes Identified from Carnation Flowers with Genes Deposited in a Carnation Genome Database (Carnation Db).

After the study of Nomura et al. (2013) was published, a carnation genome data base, Carnation DB, was released to the public from Kazusa DNA Research Institute (Yagi et al., 2014; http://carnation.kazusa.or.jp/). We became interested in knowing whether or not all the genes described above are included in the Carnation DB.

To see whether the ABA-related genes identified from carnation flowers (Nomura et al., 2013) have corresponding genes in the Carnation DB, we conducted ‘Keyword Search’ (http://carnation.kazusa.or.jp/), in which names of translates (enzymes or protein factors), symbols and abbreviations of respective genes were used as queries. For details, ‘9-cis-epoxy-carotenoid dioxygenase’ and ‘NCED’ were used as queries for DcNCED1a/b, -2a/b; ‘zeaxanthin epoxidase’ and ‘ZEP’ for DcZEP1; ‘ABA 8'-hydroxylase’ and ‘CYP707A’ for DcCYP707A1: ‘abscisic acid receptor’, ‘regulatory components of ABA receptor’, ‘PYL’, ‘PYR’ and ‘RCAR’ for DcPYR1; ‘protein phosphatase 2C’ and ‘PP2C’ for DcPP2C1;‘ subfamily 2 of SNF1-related protein kinase’ and ‘SnRK2’ for DcSnRK2.1, -2.2; ‘ABA-responsive element binding protein’ and ‘AREB’ for DcAREBF1. The results of the ‘Keyword Search’ were presented by genes

Table 1. Matching of the ABA-related genes cloned form carnation flowers with genes in the Carnation DB*

Cloned ABA-related genes		Genes in the Carnation DB			
Genes	DDBJ acc. no.	With annotation		Without annotation	
DcNCED1a	AB750605	*Dca17005.1* (100%)		–	
DcNCED1b	AB750606	*Dca17005.1* (98%)	(3)**	–	(0)
DcNCED2a	AB750607	*Dca29385.1* (100%)		–	
DcNCED2b	AB750608	*Dca29385.1* (99%)	(3)	–	(0)
DcZEP1	AB750609	*Dca60413.1* (99%)	(1)	–	(0)
DcCYP707A1	AB750610	–	(2)	*Dca6114.1* (99%)	(2)
DcPYR1	AB750611	–	(2)	*Dca26583.1* (98%)	(7)
DcPP2C1	AB750612	–	(23)	*Dca7747.1* (100%)	(68)
DcSnRK2.1	AB750613	–		*Dca21457.1* (99%)	
DcSnRK2.2	AB750614	–	(0)	*Dca17590.1* (100%)	(1331) ***
DcAREBF1	AB750615	*Dca52171.1* (99%)	(2)	–	(0)

* Carnation DB was on July 30, 2014.

**Figures in parentheses show the number of genes which were hit by 'Keyword Search' using the names of translates (enzymes or protein factors), symbols and abbreviations of respective genes as queries (keywords).

*** 'Protein kinase' was used as a query (keyword).

with the highest identity (98 to 100 % identity depending on respective genes) and total numbers of genes, which were hitin the respective search.

The number of genes which were found in the Carnation DB by 'Keyword Search' with the queries (keywords) specific to each of previously-identified genes differed from one (DcZEP1) to 1331 (DcSnRK2). All the eleven identified genes had corresponding genes in the Carnation DB with 98 to 100% identity in the deduced amino-acid sequence. Four identified genes showed 100% identity, five identified genes showed 99% identity, and two identified genes showed 98% identity (Table 1).

Nomura et al. (2013) obtained two isoforms each of DcNCED1, DcNCED1a and DcNCED1b, and of DcNCED2, DcNCED2a and DcNCED2b. However, there was only one gene each, Dca17005.1 and Dca29385.1 in the Carnation DB. This difference might have been caused by the difference in the carnation cultivars used, i.e., genes for ABA-related events were identified using 'Light Pink Barbara' (Nomura et al., 2013) and the Carnation DB was constructed using 'Francesco' cultivar (Yagi et al., 2014). Also, this discrepancy might have been produced by putting two very similar genes (isoforms) into one gene in the process of constructing the Carnation DB. DcPYR1 had 98% identity with Dca26583.1, and this slight difference in identity might also have been due to the cultivar difference between the gene cloning and the data base construction. Six of the genes found in the Carnation DB were already annotated, whereas the remaining five genes were not. The present findings suggest their physiological functions; Dca6114.1 for DcCYP707A1, Dca26583.1 for DcPYR1, Dca7747.1 for DcPP2C1, Dca21457.1 for DcSnRK2.1, and Dca17590.1 for DcSnRK2.2 (Table 1). The present findings suggested the mutual dependability between the previously identified ABA-related genes (Nomura et al., 2013) and the Carnation DB (Yagi et al., 2014) and added physiological functions to five un-annotated genes in the Carnation DB.

In conclusion, the present review could reconstitute the pathway for ABA biosynthesis, catabolism and action in carnation plants, using eleven ABA-related genes which were recently identified from carnation flower tissues. Furthermore, the cross-check of identified ABA-related genes with genes deposited in the Carnation DB identified five un-annotated genes in Carnation DB as DcCYP707A1, DcPYR1, DCPP2C1, DcSnRK 2.1 and DcSnRK2.2. The present results suggested that the pathway for ABA biosynthesis and action, the same as that in major model plants and crops, is functioning in carnation plants, and implied that this is the case in other miner clops and ornamentals.

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