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Review

Impact of various factors responsible for fluctuation in plant secondary metabolites

Nidhi Verma, Sudhir Shukla*

Genetics and Plant Breeding, National Botanical Research Institute, Lucknow 226001, India

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ABSTRACT

It is common perception that the content of secondary metabolites in pure lines of advanced generations of pedigree selections or intra- and inter-specific crosses should be stable like other qualitative and quantitative traits, but in fact this is usually not the case. In this review article, we try to give probable explanations on why the content of secondary metabolites fluctuates in subsequent generations of pure lines as well as advanced generations (F_7 onward) of intra- and inter-specific crosses. Genetic, ontogenic, morphogenetic and environmental factors are extremely important in the biosynthesis and accumulation of secondary metabolites. The biosynthesis of PSMs depend upon these various factors, change in only one factor may alter the content of PSMs though other factors remain constant. We here present a detailed view of the possible roles of the various factors in secondary metabolite instability. A good understanding of the mechanisms involved in secondary metabolite synthesis, degradation and accumulation in plants is required for the future formulation of strategies for the genetic improvement of secondary metabolite production in plants.

Contents

* Corresponding author. Fax: +91 522 2205836.
E-mail address: s_shukla31@rediffmail.com (S. Shukla).

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1. Introduction

Plant secondary metabolites (PSMs) or natural products are derived from primary metabolites with diverse physiological activites. These PSMs play a vital role in plants to make a strong interaction of plants with the environment for their survival and fitness which makes these metabolites as essential as primary metabolites (Kliebenstein, 2012). Though secondary metabolites do not have any immediate effect in the survival of plants but have a long term effect (Costa et al., 2012). The plant kingdom produces more than 100,000 secondary metabolites which are limited to certain taxonomic groups. Based on biosynthetic pathway, PSMs are classified into three major groups viz. terpenes (or isoprenoids), phenolic compounds (phenylpropanoids and flavonoids) and nitrogen containing compounds (alkaloids, glucosinolates and cyanogenic glycosides) (Fang et al., 2011).

1.1. Terpenes

Terpenes are synthesized in plants through two different pathways, one occurs in cytoplasm and other in plastids. The mevalonate (MVA) and methylerythritol 4-phosphate (MEP) pathways are involved in terpene synthesis (Fig. 1). The MEP pathway offer precursor for the synthesis of mono- and diterpenes, isoprene, carotenoids, phytohormones, gibberellins, abscisic acid (ABA), phytol, the side chain of plastoquinones, phylloquinones, tocopherols, chlorophylls etc., while MVA pathway provides isopentenyl diphosphate involved in the synthesis of sesquiterpenes, sterols, brassinosteroids, polyphenols and its moiety and is used for prenylated proteins (Pateraki and Kanellis, 2010). The largest group of PSMs also known as terpenoids or isoprenoids, are generally insoluble in water. The biosynthesis of these compounds, acetyl coenzyme-A (acetyl Co-A) is the starting material which also involves fusion of five carbon isoprene units called as isoprenoid. Isopentenyldiphosphate (IPP) is formed as an intermediate in both MVA and MEP pathways, which ultimately leads to the formation of terpenes (IPP) (Taiz and Zeiger, 2006).

Based on five carbon unit (isoprene unit), these terpenes are classified into different groups like monoterpenes (10 carbons or two C_5 units), sesquiterpenes (three C_5 units), diterpenes (four C_5 units), triterpenes (six C_5 units), tetraterpenes (eight C_5 units) and polyterpenoids ($[C_5]_n$). Among them few terpens like gibberellins (diterpenes), sterole (triterpenes), carotenoids (tetraterpenes), and abscisic acid (sesquiterpenes), play an important role in the growth of plants. Additionally, terpenes play a vital role in plant defense as toxic to insects and mammals like pyrethroids found in chrysanthemum act as insecticides. Some plants have volatile terpenes known as essential oils and terpene glycosides called saponins. Saponins are formed through both lipid (steroids or triterpenes) and water soluble elements (sugar) in one molecule, thus, this class of compounds are soap-like. Saponins could be toxic, as it interferes in sterol uptake or disrupt cell membranes after being absorbed in blood (Taiz and Zeiger, 2006).

1.2. Phenolic compounds

The second major group of PSMs belongs to aromatic phenolic compounds which have a phenyl ring bearing one or more acidic hydroxyl group (Achakzai et al., 2009). Phenolic is a group of heterogenous molecules that include more than 10,000 soluble and insoluble (water and organic solvent) compounds (Taiz and Zeiger, 2006). The phenolic compounds are basically formed by malonic and shikimic acid pathways. The malonic acid pathway is highly significant in bacteria and fungi, but is less common in higher plants whereas shikimic acid pathway is very common in bacteria, fungi and plants but not in animals. In shikimic acid pathway, precursors derived from glycolysis and pentose phosphate are converted into different aromatic amino acids in which the most frequent intermediate is phenylalanine (Taiz and Zeiger, 2006). The phenolic compounds have been divided into different groups like lignins, lignans, coumarins, flavonoids, tannins, stibenes, styrylpyrones and arylpyrones (Fang et al., 2011). Simple phenolic compounds are known as phenylpropanoids such as *trans*-cinnamic acid, *p*-coumaric acid and its derivatives. Some phenolic compounds are very complex due to the presence of highly branched polymers of phenylpropanoid groups. Lignin after cellulose, the second most abundant organic substance found in plants, is an example of complex phenolic compound (Taiz and Zeiger, 2006). The phenolics play many physiological roles in plants including reproduction, growth and defense against different biotic or abiotic stresses (Achakzai et al., 2009). They also have allelopathic activity by which they reduce the growth of neighboring plants (Taiz and Zeiger, 2006). Phenolics have antioxident activity due to their redox properties which make them hydrogen donor, reducing agents and singlet oxygen quenchers (Huang et al., 2010; Naghiloo et al., 2012a), thus play considerable role in reducing the risk of cancer in humans (Sharma et al., 2012). They are also linked with several other functions like photosynthesis, protein synthesis, enzyme activity, nutrient uptake etc., in the plants (Sharma et al., 2012). It has been found that phenols can also be used as a stress indicator because they are increased by the exposure of toxic chemicals and stresses in the plants (Siddiqui and Arif-uz-Zama, 2004; Achakzai et al., 2009). Plant phenolics are known as anti-grazing factors because they produce a specific taste and smell in the plants due to which animals, insects and humans do not eat them (Strack, 1997). Major phenolic compound, flavonoids (anthocyanins, flavones, flavonols and isoflavones) have crucial role in plant growth and defense mechanism against microbes and insects (Taiz and Zeiger, 2006). Some flavonoids like anthocyanins act in the development of color of petals to attract the pollinators (De Sousa et al., 2007; Khatiwora et al., 2010).

1.3. Nitrogen containing compounds

The third important category of secondary metabolites includes nitrogen-containing compounds such as alkaloids, glucosinolates and cyanogenic glycosides. Alkaloids are low molecular weight compounds and have more than 12,000 nitrogen containing compounds in their family (Facchini, 2001). The alkaloids are synthesized from few amino acids like lysine, tyrosine and tryptophan etc. (Taiz and Zeiger, 2006). Alkaloids can be further classified into different groups like terpenoid indole alkaloids (TIAs), benzylisoquinoline alkaloids (BIAs), purine alkaloids, tropane alkaloids (TPAs) and nicotine etc. TIAs include more than 3000 compounds such as antineoplastic agents (vinblastine and camptothecin), antimalarial drug (quinine) and strychnine (a rat poison), are primarily synthesized from tryptophan. Some TIAs play a role in plant protection against pests and pathogens (Facchini, 2001). The plant species *Catharanthus roseus* and *Rauvolfia serpentina* are the source of some medicinally important TIAs like vinblastine for cancer and ajmaline for heart disorders. The biosynthesis of BIAs, another group of alkaloids, starts from condensation of tyrosine, an amino acid. This group of alkaloids contain approximately 2500 compounds of pharmacological properties like morphine (analgesic), codeine (cough suppressant), papaverine (muscle relaxant), sanguinarine and berberine (antimicrobial agent) etc. These alkaloids are mainly found in menispermaceae, berberidaceae, ranunculaceae and papaveraceae plant families. TPAs include hyoscyamine and scopolamine, which are derived from *Hyoscyamus*, *Atropa* and *Datura* plant species. Calystegines (glucosidase inhibitor), a widely distributed tropane alkaloid is found in Solanaceae and Convolvulaceae plant family. Nicotine is derived from ornithine and it