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Review

Evolution and current status of research in phenolic compounds

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Abstract

Phenolic compounds are ubiquitous in plants which collectively synthesize several thousand different chemical structures characterized by hydroxylated aromatic ring(s).

These compounds play several important functions in plants. They represent a striking example of metabolic plasticity enabling plants to adapt to changing biotic and abiotic environments and provide to plant products colour, taste, technological properties and putative health promoting benefits.

Phenolic compounds represent the most studied phytochemicals and have been widely exploited as model systems in different areas of plant research. Initial studies in the field concerned the analytical characterization of a wide range of structures and of relevant enzymes with PAL being one of the most studied plant enzymes. This research is still active due to the complexity of the structures and the biosynthetic pathways As an example, the nature and functions of enzymes involved in lignin synthesis have been revisited several times, even in recent years.

More recently, molecular biology and genomics have provided additional understanding of the mechanisms underlying the synthesis of these compounds with special emphasis on the regulation of gene expression by environmental factors. The extensive characterization of genes encoding the different enzymatic steps of flavonoid synthesis and cytochrome P450 genes have been among the most recent advances in this area.

Metabolic engineering of lignins and flavonoids has been deeply investigated. Significant positive results have been obtained in both areas but the negative European opinion towards genetically modified organisms has considerably hampered potential applications. From a more basic point of view, global approaches (such as transcript and metabolite profiling) have investigated the repercussions of these engineered modulations of specific phenolics synthesis on other branches of plant metabolism. These studies have revealed a substantial and sometimes unexpected network of regulatory interactions.

In the present time, the societal demand and an increasing interest for practical applications has stimulated a wide range of biological and epidemiological studies aiming at characterizing the health promoting properties of specific phenolic compounds with antioxidant activities towards cancer, cardiovascular and neurodegenerative diseases or for use in antiaging or cosmetic products.

Increased emphasis on sustainable development should stimulate innovative investigations on phenolic synthesis for improving plant biomass and for a better control of plant and animal health.

Keywords: Phenolic compounds; Phenylpropanoids; Lignins; Flavonoids; Biosynthetic pathways; Multigene families; Transcription factors; Cytochrome P450 genes; Metabolic engineering; Antioxidant activities; Health promoting properties

Abbreviations: AFLP, Amplified fragment length polymorphism; cDNA, complementary desoxyribonucleic acid; CYP, cytochrome P450; 4CL, 4-hydroxycinnamoyl-coA ligase; C3H, *p*-coumarate 3-hydroxylase; C4H, cinnamate 4-hydroxylase; CAD, cinnamyl-alcohol dehydrogenase; CCoAOMT, caffeoyl-CoA *O*-methyltransferase; CCR, cinnamoyl-CoA reductase, COMT I, caffeic/5-hydroxyferulic acid *O*-methyltransferase; F5H, ferulate 5-hydroxylase; HCT, hydroxycinnamoyltransferase; PAL, Phe ammonia-lyase; SAD, sinapyl-alcohol dehydrogenase.

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1. Introduction

How could we imagine plant species without polyphenols? They have been a feature of plants since early colonisation of the land. These so called secondary metabolites are indeed crucial for many important functional aspects of plant life. These include structural roles in different supporting or protective tissues, involvement in defence strategies, and signalling properties particularly in the interactions between plants and their environment.

Collectively, higher plants synthesize several thousand known different phenolic compounds and the number of these fully characterized is continually increasing. Leaves of vascular plants contain esters, amides and glycosides of hydroxycinnamic acids, glycosylated flavonoids especially flavonols and proanthocyanidins and their relatives. Lignin, suberin and pollen sporopollenin are examples of phenolic containing polymers. Some soluble phenolics are widely distributed e.g. chlorogenic acid but the distribution of many other structures is restricted to specific genera or families making them convenient biomarkers for taxonomic studies. Their common feature is the presence of a hydroxy-substituted benzene ring within their structure.

Different physicochemical methods have, since the beginning of the 20th century, permitted the characterization of a plethora of complex structures and at the present time the technical advances both in chromatographic techniques and in identification tools particularly the diverse forms of mass-spectrometry allow us to meet the challenges of separation and characterization of compounds of increasing complexity, of high molecular weight, low stability and low abundance (Whiting, 2001).

The biosynthetic routes of phenolic metabolism derive from primary metabolism and there is increasing evidence that duplications of essential genes of primary metabolism have been an important basis for gene recruitment in secondary metabolism. In the course of evolution, these duplicated genes have acquired new functions and have been optimized and diversified for their roles in new pathways (Dixon and Steele, 1999; Lehfeldt et al., 2000). The phenylpropanoid pathway leading to lignins involves a common set of biochemical reactions in vascular plants already present 400 million of years ago with the emergence of erect vascular land plants. The biosynthesis of other phenolic compounds including flavonoids for use as sunscreens was also a likely early event in land plant evolution. From an evolutionary point of view these metabolic backbones have been progressively enriched to provide specific adaptations to different plant families and the remarkable biochemical diversity we can observe.

It is particularly important to note that phenolics have wide impacts on human activities in the agroindustrial and food sectors exerting either positive or negative influences on the processes or on the quality of the products and these characteristics have motivated specific research programmes.

Beyond a continuous flow of information related to the characterization of new structures several phases may be schematically delineated in phenolic research during the last 50 years:

1 The characterization of the enzymatic steps leading to the common precursors of the phenylpropanoid pathway and to specific branches of phenolic metabolism.
2 The use of molecular biology to probe the changes in gene expression associated with the plasticity of phenolic metabolism.
3 The emergence of functional genomics, providing a more accurate picture of the diversity of the genes/enzymes involved in phenolic metabolism.
4 The exploitation of genetic engineering for optimizing the phenolic profiles of plants (particularly lignin and flavonoid patterns).
5 The explosion of epidemiological studies supporting the protective role of food polyphenols in human health.

It is not possible due to space limitations to cover all these different topics in depth, which have been in some cases treated in recent reviews, including in this journal (see for example the issue related to Tannins and related