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Review

"Carbon gain vs. water saving, growth vs. defence": Two dilemmas with soluble phenolics as a joker

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ABSTRACT

Despite that phenolics are considered as a major weapon against herbivores and pathogens, the primal reason for their evolution may have been the imperative necessity for their UV-absorbing and antioxidant properties in order for plants to compensate for the adverse terrestrial conditions. In dry climates the choice concerning the first dilemma (carbon gain vs. water saving) needs the appropriate structural and metabolic modulations, which protect against stresses such as high UV and visible radiation or drought, but reduce photosynthesis and increase oxidative pressure. Thus, when water saving is chosen, priority is given to protection (including phenolic synthesis), instead of carbon gain and hence growth. At the global level, the different choices by the individual species are expressed by an interspecific negative relationship between total phenolics and photosynthesis. On the other hand, the accumulation of phenolics in water saving plants offers additional defensive functions because these multifunctional compounds can also act as pro-oxidant, antifeeding or toxic factors. Therefore phenolics, as biochemical jokers, can give the answer to both dilemmas: water saving involves high concentrations of phenolics which also offer high level of defence.

Contents

1. Phenolics act as multifunctional secondary metabolites

It has been proposed that resource allocation to secondary metabolism is antagonistic to that of primary metabolism. In other words plants have to cope with the dilemma of

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Table 1
Tissue localization, spectral, chemical and bioactivity properties of major classes of phenolic compounds related to their protective and defensive roles in plants.

Phenolic class	Tissue localization	λ_{max} (nm)	ε in λ_{max} ($\times 10^4\ M^{-1}\ cm^{-1}$)[a]	Prooxidant activity[b]	ROS scavenging capacity[c]	Toxicity to herbivores and pathogens[d]
Hydroxybenzoates and hydroxycinnamates	Cuticle, epidermis, mesophyll	227–332 (UV-C, UV-B, UV-A)	1.8–1.9	215–469	2.03 ± 0.67	Low to medium
Flavonol aglycones Flavonol glycosides	Superficial structures Epidermis, mesophyll	250–390 (UV-C, UV-B, UV-A)	1.5–2.1	469–1841	2.92 ± 1.39 1.97 ± 0.72	High Low to medium
Flavone aglycones Flavone glycosides	Superficial structures Epidermis, mesophyll	250–350 (UV-C, UV-B, UV-A)	0.8–2.1	69–1745	1.66 ± 0.38 1.27 ± 0.67	High Low to medium
Flavanonols	Superficial structures	290–340 (UV-B, UV-A)	No data	–	1.65 ± 0.36	No data
Flavanone aglycones Flavanone glycosides	Superficial structures Epidermis, mesophyll	225–330 (UV-B, UV-A)	1.8–2.3	44–430	1.58 ± 0.20 0.94 ± 0.20	High Low to medium
Catechins	Mainly mesophyll	270–280 (UV-C, UV-B)	ca. 0.4	–	3.68 ± 1.20	High
Tannins	Mainly mesophyll	Depending on structure	Depending on structure	Depending on structure	High[e]	High
Anthocyanins	Epidermis, mesophyll	267–275 (UV-C, UV-B), 475–545 (Vis)	Low to medium in UV depending on acylation		2.89 ± 1.45 2.55 ± 0.63	Low[f]

[a] Data from [71,72].
[b] Measured as the cooxidation rate of ascorbate ($k \times 10^3\ min^{-1}$); data from [36]
[c] Measured as Trolox equivalent antioxidant capacity; the concentration of Trolox with the equivalent antioxidant capacity of a 1 mM concentration of the experimental substance. Data from [45,64,73]. Values are means ± SD.
[d] Data from [5]
[e] Trolox equivalents of 2.6 or considerably higher have been reported depending on structure and degree of polymerization [74].
[f] Anthocyanins display low toxicity but possess other indirect defensive roles through colouration.

investing the photosynthetic products between the conflicting demands of growth (including maintenance cost) and defence [1]. However, in many cases, resource allocation to secondary metabolism is not seriously compromised by leaf or shoot growth [2], and usually reflects the need of protection of primary metabolic processes against the side effects of abiotic stress factors. A coordinated regulation of primary and secondary metabolism frequently leads to parallel and not reciprocal changes of the corresponding metabolites [3]. Thus, in many cases, resource allocation to secondary metabolism is not exclusively determined by the demands of defence against biotic stresses, but also by the protection needs against abiotic ones. This may be a result of the multifunctionality of almost all classes of secondary metabolites. Among them, phenolics are considered as fulfilling the wider array of functions.

Phenolics are the most commonly studied compounds because of their universal presence in high concentrations (requiring significant resources) and their significant roles in plant cells and tissues [4,5]. The term "phenolic" is used to define carbon-based metabolites that possess one (simple phenols) or more (polyphenols) hydroxyl substituents bonded onto an aromatic ring. These compounds are considered to be among the most important chemical weapons against a diverse array of herbivores ([1] and the literature therein). However, this highly diverse group of secondary metabolites fulfils multiple functions: (a) as constitutive bioactive compounds, they take part in the defence against herbivores or pathogens. Phenolics may also be synthesized de novo during in situ defence responses which include the accumulation of phytoalexins or during hypersensitive response, a systemic plant reaction against pathogens. Induced synthesis of phenolics is not examined in this review. Notably, the constitutive accumulation of phenolics is related to the growth vs. defence dilemma. Effective defence requires considerable amounts of carbon skeletons and energy for the synthesis of secondary metabolites (among which phenolics predominate). Therefore, effective defence usually retards the investment of carbon and energy in growth processes. For this reason, highly defended plants usually show low growth rates [1], (b) as absorbing filters, they reduce the penetration of UV and visible radiation into sensitive targets [6], (c) as antioxidants, they reduce the damage caused by reactive oxygen species (ROS) [7,8], (d) as regulators of soil processes they control the recycling and thus the availability of nutrients for plants and soil microbes [9] and (e) as signal molecules they play a significant role in the interactions between plants and other organisms [10], as well as in morphogenesis [11]. It should be also noted that function (e) requires the presence of phenolics in considerably lower concentrations than each of the other functions.

Phenolics are a group of compounds with numerous separate chemical structures. Thus, two questions should be addressed: (i) Is the multifunctionality of phenolic compounds a result of the different chemical properties of each individual subclass or could the majority of phenolic compounds be involved in more than one (or even in all) of the above different functions? And (ii) Is there a hierarchy among these functions that could affect plant survival? Concerning the first question, data from Table 1 show that all phenolic subclasses show similar spectral and biochemical properties, differing much less that an order of magnitude between different structures. Concerning their in vivo protective role, our data show that total phenolics, but also the condensed tannins subpool, are similarly correlated with photosynthetic capacity. This indicates that at least one phenolic subpool shows similar protective behaviour to that of the total pool (see Fig. 1, Table 1 and Section 2). Concerning the second question, the antioxidant and UV protective function of phenolics probably has priority over defence against biotic stress factors (see Sections 3 and 5), but both their protective and defensive roles may occur in parallel (see Section 6).

2. Tissue localization and function of phenolics

The diverse group of phenolics is subdivided at the molecular level into many sub-groups, such as simple phenols, lignans, coumarins, flavonoids, tannins, quinones, etc., based on the construction of the carbon skeleton, the kind of substituent and the degree of polymerization [4]. Moreover the solubility and the toxicity of each molecule depend on glycosylation, whereas their antioxidant properties depend on the number of hydroxyl