



Signals that stop the rot: Regulation of secondary metabolite defences in cereals



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ABSTRACT

Plants accumulate a vast arsenal of chemically diverse secondary metabolites for defence against pathogens. This review will focus on the signal transduction and regulation of defence secondary metabolite production in five food security cereal crops: maize, rice, wheat, sorghum and oats. Recent research advances in this field have revealed novel processes and chemistry in these monocots that make this a rich field for future research.

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1. The role of secondary metabolites in defence in cereal crops

Cereal crops such as maize (*Zea mays*), wheat (*Triticum aestivum*), oat (*Avena sativa*), rice (*Oryza sativa*) and sorghum (*Sorghum bicolor*) are consumed throughout the world and are crucial components of the world's calorific intake. In 2013, cereal production exceeded approximately 55 million tonnes in Africa alone (www.fao.org/worldfoodsituation/csdb/en/) – with maize the main produce followed by wheat and rice (statistics.amis-outlook.org/data/index.html). Viruses, bacteria, fungi, and herbivores are biotic

stressors that threaten crop yields and economic stability. Therefore, it is crucial that plant defence mechanisms are understood in order to develop sustainable crop enhancement programs. Plants are sessile organisms that lack circulating cells, such as macrophages in mammals, whose purpose is to recognise non-self molecules and elicit an immune response. Instead, each plant cell acts autonomously and is programmed to recognise and respond to pathogens [1]. The mechanisms by which plants defend themselves include the production of secondary metabolites with antimicrobial properties and these responses are controlled by signal transduction pathways [2].

Early researchers in the field coined the terms “phytoanticipins” and “phytoalexins” for antimicrobial compounds involved in constitutive and *de novo* defence in crop plants, respectively [3]. Phytoanticipins are compounds produced constitutively in cereals and are involved in above and below ground protection [4–6]. They are preformed and stored as inactive, conjugated molecules in the vacuole [6,7]. When a plant is challenged by a pathogen, these molecules are activated and rapidly released in order to fight off the invader [7–9]. They are especially relevant during infection by necrotrophic pathogens, which rely on tissue injury and host cell

Abbreviations: PRRs, pattern-recognition receptors; PAMPs, pathogen-associated molecular patterns; PTI, PAMP-triggered immunity; ROS, reactive oxygen species; VIGS, virus induced gene silencing; SAR, systemic acquired resistance; JA, jasmonic acid; Et, ethylene; SA, salicylic acid; BX, benzoxazinoids; CPS, copalyl diphosphate synthase; ABA, abscisic acid; BTH, benzothiadiazole derivative; PAL, phenylalanine ammonia lyase; AMF, arbuscular mycorrhizal fungus; VOC, volatile organic compounds; y1, yellow seed1.

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death for effective infection [7]. Benzoxazinoids (BXs) are the predominant phytoanticipin in the major Poaceae crop plants, maize and wheat, but are absent from oat, rice and sorghum [10–13]. Interestingly, unlike Poaceae crop plants, where BXs are limited to seedlings or young plants, dicot plants accumulate BXs during all developmental stages in both above and below-ground parts [14]. BXs are associated with maize resistance to both fungal diseases (i.e. northern and southern corn leaf blight and corn smut), and insect pests (i.e. the European corn borer and the maize plant louse) [15–18].

An array of phytoalexins are produced in cereal crop plants in response to pathogens and belong to several chemically diverse classes of compounds, including, but not limited to, flavonoids, terpenoids and saponins [19–22]. Flavonoid phytoalexins, such as avenanthramides in oat [23], 3-deoxyanthocyanidins in sorghum [24] and sakuranetin in rice [25] are phenolic metabolites that originate from phenylalanine [26]. Plants rely on these phenols for growth and reproduction, pigmentation and as defensive molecules against pathogens [26]. Terpenoid phytoalexins in rice (oryzalexins, phytocassanes and momilactones) [25] as well as maize (kauralexins and zealexins) [27,28] are synthesised via the isoprenoid pathway. Saponins are glycosylated triterpenoids, protective molecules that are absent in all cereals except the genus *Avena* and likewise synthesised via the isoprenoid pathway using the precursor mevalonate [23,29,30]. Dicotyledonous plants, such as *Arabidopsis thaliana*, tobacco and cotton, also produce terpenoid phytoalexins [20,31]. More discussions about phytoalexin production in the model dicot, *A. thaliana* are extensively reviewed by Ahuja, Kissen and Bones (2012) [20]. The biosynthesis of monoterpene terpenoids is catalysed by a large class of enzymes termed terpene synthases (TPS), and these enzymes have been credited with the diversity of terpenoids [32–34]. Terpenoids function as plant hormones, vitamins, pigments and, critically, in plant–pathogen interactions [22].

Many secondary metabolites exhibit anti-microbial properties, as illustrated in sorghum, which produces 3-deoxyanthocyanidins, red-coloured flavonoid phytoalexins at the site of *Colletotrichum sublineolum* colonisation [24,35,36]. A combination of these red/orange-coloured compounds, known as apigeninidin and luteolinidin, are synthesised in the cytoplasm of epidermal sorghum cells in response to *C. sublineolum* [24,37]. The compounds accumulate in inclusion bodies which enable their translocation to the infected area, where they undergo structural modifications and release their content, killing both the pathogen as well as the plant cells [38].

The definitions of phytoalexins and phytoanticipins are based on the mode of regulation and synthesis of the compound and not necessarily by the chemical structure, which makes the terminology imprecise since the same compound can act as both a phytoalexin and a phytoanticipin depending on the host plant or even the organ of the host plant [7,39]. As an example, sakuranetin, a flavonoid compound, acts as a phytoalexin in rice, where it accumulates in response to rice blast and bacterial blight disease [40–44]. However, in blackcurrants, sakuranetin is constitutively present in the leaves, and is therefore also defined as a phytoanticipin [45]. Likewise, momilactone A, a diterpenoid compound in rice, is constitutively present in rice seed husks and roots, but induced in rice leaves upon infection with rice blast [41].

In this review, we firstly describe the diversity of defensive secondary metabolites (primarily phytoalexins and phytoanticipins) in the economically-important cereal crops rice, maize, wheat, sorghum and oat. We furthermore discuss how signalling pathways influence accumulation of antimicrobial secondary metabolites, and conclude with a “future perspectives” section in which on-going research questions are identified.

2. Pathogen recognition, signal transduction and defence secondary metabolite synthesis

2.1. Pathogen recognition events that lead to secondary metabolite production

Plants boast a sophisticated, organ- and cell-specific surveillance system, which recognises pathogens and responds by triggering the innate immunity signal transduction pathway [2,46]. Essentially, the plant cell surface contains pattern-recognition receptors (PRRs) that identify pathogen-associated molecular patterns (PAMPs) [46]. PAMPs are conserved molecules, either secreted or surface-exposed, that are characteristic of pathogens. Examples of PAMPs recognised by plants include bacterial flagellin, fungal β -glucans and chitin [2,46]. Once PAMPs are perceived by a plant cell, a process termed PAMP-triggered immunity (PTI) is initiated [1]. This process involves a complex local and systemic intracellular signalling cascade promulgated through gene expression changes involving WRKY and TGA transcription factors [1]. In the interaction between cereals and fungi, β -glucan and chitin are representative fungal PAMPs and are polysaccharides that crosslink to form a scaffold within fungal cell walls [47]. There are several reports that β -glucan and chitin elicit a plant immune response in cereals leading to production of secondary metabolites [47–51]. Chitin fragments, such as N-acetylchito oligosaccharides, were shown to be a potent elicitor of momilactone accumulation in rice suspension cells, which leads to growth inhibition of fungi such as *Magnaporthe grisea* (responsible for rice blast fungus) [50]. Chitosan, a derivative of chitin, elicits both sakuranetin and momilactone production in rice seedlings [51]. An example of a PRR is OsCEBiP, a plasma membrane glycoprotein that acts as a receptor for chitin elicitors and has a demonstrated role in disease resistance of rice against *M. grisea* [49]. Upon chitin elicitor binding, OsCEBiP forms a complex with OsCERK1, a receptor kinase that is responsible for triggering downstream signalling (Fig. 1A) [52,53]. Phytoalexin production after chitin induction was lower in an *OsCEBiP* gene-specific knockdown line than the wild-type [53]. This observation was later replicated in an *OsCERK1* knock-down line [52]. Furthermore, expression of defence-related genes was suppressed, including a key gene required for the biosynthesis of diterpenoid phytoalexins [52]. Similarly, β -glucan was shown to elicit production of momilactones as well as small amounts of oryzalexins in rice suspension cells [47]. Upon exposure to β -glucan from *Colletotrichum graminicola* (responsible for anthracnose), the expression of putative phytoalexin biosynthetic genes in maize were up-regulated by more than 150-fold [54]. Interestingly, the same study showed that *C. graminicola* ostensibly attempts to evade maize PAMP-elicited defence responses by down-regulating its β -glucan production during the biotrophic growth phase to establish a compatible interaction [54]. Another study in maize demonstrated phytoalexin accumulation after wounded stems were treated with a pectinase elicitor derived from *Rhizopus microsporus* [27]. Pectin is a component of plant cell walls and a target for fungal pectinolytic enzymes during pathogen attack [55]. Likewise, momilactone accumulation was shown to be accelerated by the over expression of selenium-binding protein homologue gene (*OsSBP*), a receptor for the fungal elicitor, cerebroside from *M. grisea*, which triggered resistance to *M. grisea* and *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) (the causal organism of bacterial blight disease) [56]. Thus, PAMPs – and PRR recognition of PAMPs – set in motion PTI-specific signalling pathways that lead to accumulation of antimicrobial secondary metabolites.

Plant-derived molecules have also been shown to act as elicitors and provoke an immune response [57–60]. ZmPep1 is a peptide encoded by the maize gene *ZmPROPEP1*, whose expression is

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