


Review

Relationship of Melatonin and Salicylic Acid in Biotic/Abiotic Plant Stress Responses

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Abstract: Melatonin (*N*-acetyl-5-methoxytryptamine) was discovered in plants in 1995, while salicylic acid was the name given to the active ingredient of willow in 1838. From a physiological point of view, these two molecules present in plants have never been compared, even though they have a great number of similarities, as we shall see in this work. Both molecules have biosynthesis pathways that share a common precursor and both play a relevant role in the physiology of plants, especially in aspects related to biotic and abiotic stress. They have also been described as biostimulants of photosynthetic processes and productivity enhancers in agricultural crops. We review the coincident aspects of both molecules, and propose an action model, by which the relationship between these molecules and other agents and plant hormones can be studied.

Keywords: antioxidant; nitric oxide (NO); phyto-melatonin; plant hormones; plant stress; Reactive oxygen species (ROS); salicylic acid

1. Melatonin and Salicylic Acid in Plants

Melatonin (*N*-acetyl-5-methoxytryptamine) is a pleiotropic molecule with a wide range of cellular and physiological actions in living organisms, including animals and plants. It was discovered in animals (cow) by Lerner and colleagues in 1958 and in 1959 in humans [1,2]. Then, in 1995, two papers simultaneously demonstrated the presence of melatonin in plants, and it is now accepted that melatonin is present in all higher plants [3,4], where it is sometimes referred to as phyto-melatonin [5,6]. Chemically, melatonin is an indoleamine derivative of the amino acid tryptophan, and its biosynthetic melatonin pathways from tryptophan have been extensively studied in both animals and plants (Figure 1). Tryptophan is converted into 5-hydroxytryptophan in animals, whereas in plants tryptophan is mainly transformed into tryptamine. These last two compounds are converted into serotonin (5-hydroxytryptamine), which is finally converted into melatonin (*N*-acetyl-5-methoxytryptamine) through the compounds *N*-acetylserotonin or 5-methoxytryptamine (see Figure 1). All the enzymes involved in melatonin biosynthesis have been described and characterized in many species of animals and plants [7].

The name salicylic acid (SA) (*ortho*-hydroxybenzoic acid) was given to the active ingredient of willow (*Salix* sp.) bark by Raffaele Piria in 1838. The first commercial production of synthetic SA began in Germany in 1874. Aspirin, a trade name for acetylsalicylic acid, was introduced by the Bayer Company in 1898 and it rapidly replaced the use of SA as it produced less gastrointestinal irritation but had similar medicinal properties [8]. Salicylic acid is a phenolic compound. The shikimic acid pathway takes part in the biosynthesis of most plant phenolic compounds. The most common pathway in plants for SA synthesis is the phenylalanine pathway (Figure 1). However, SA biosynthesis may also be carried out by the isochlorogenic acid pathway. The hydroxylation of benzoic acid catalyzed by the enzyme benzoic acid 2-hydroxylase synthesizes SA. Benzoic acid is synthesized by *trans*-cinnamic

acid (produced from phenylalanine by the action of enzyme phenylalanine ammonia lyase), either via β -oxidation of fatty acids or via a non-oxidative pathway in which *trans*-cinnamic acid is hydroxylated to form *ortho*-coumaric acid followed by oxidation of the side chain (Figure 1) [9–12].

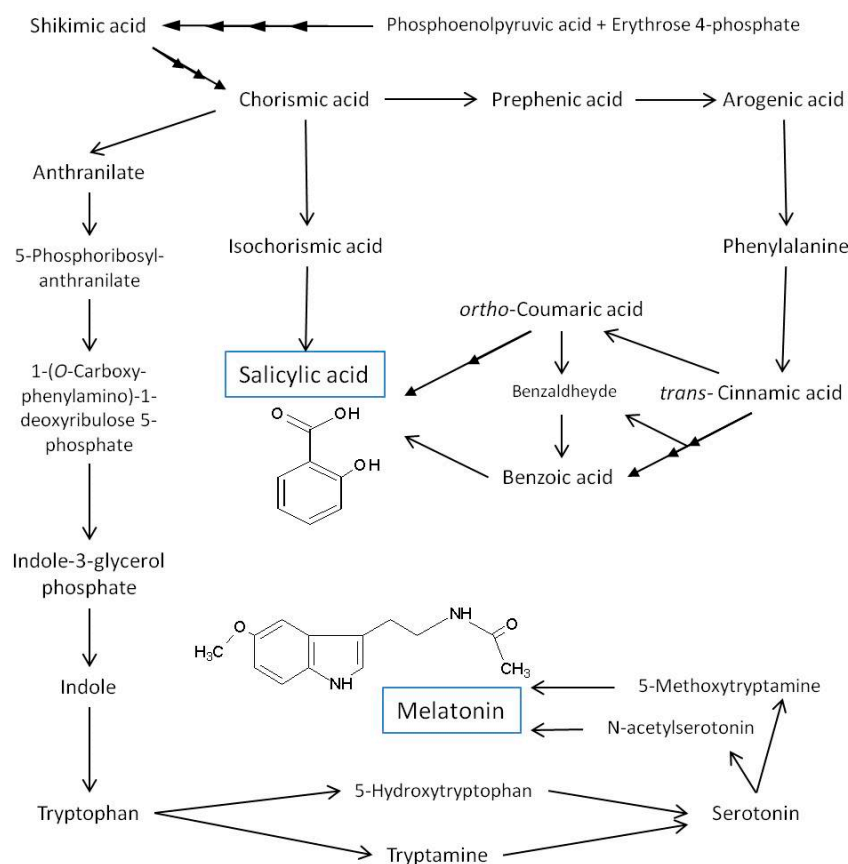


Figure 1. Biosynthetic routes of salicylic acid and melatonin in plants.

Melatonin and SA biosynthesis pathways share a final common precursor—chorismic acid—which is generated from shikimic acid (a condensation product of phosphoenolpyruvic acid from glycolysis and erythrose 4-phosphate from the pentose phosphate pathway (Figure 1). Chorismic acid is the precursor of the synthesis of three aromatic amino acids—phenylalanine, tryptophan and tyrosine. Melatonin is synthesized from tryptophan through the anthranilate/indole pathway and SA from phenylalanine, in addition to the direct isochorismic acid route (Figure 1).

With respect to catabolism, melatonin is usually hydroxylated in different positions of the indole ring, with 2-hydroxymelatonin being the major catabolite [13]. In the case of SA, several conjugates have been described, such as methyl salicylic acid, salicyloyl-L-aspartic acid, salicylic acid 2-O- β -glucoside and salicyloyl-glucose ester [9].

2. Common Effects of Melatonin and SA in Abiotic Plant Stress

Melatonin has been considered a multiregulatory molecule in higher plants because of the wide and diverse range of cellular and physiological actions attributed to it. In 2004, the action of melatonin as a growth promoter was demonstrated in etiolated *Lupinus albus* [14]. Also, melatonin is able to induce root primordials from pericycle cells, generating new adventitious and lateral roots [15]. A significant role of melatonin against abiotic stress was also postulated, using a cold-induced apoptosis model in carrot cells [16]. Thus, melatonin has been attributed with the capacity to regulate cellular and plant growth; promote seed germination and rooting; optimize photosynthetic efficiency and water/CO₂ foliar exchange; regulate the internal biological clock and flowering and

ripening/senescence processes; and finally, to act as an endogenous biostimulator against abiotic or biotic stressors [17,18].

Many physiological functions have also been assigned to SA. In 1989, Carswell and colleagues reported that acetyl SA can promote colony formation in maize protoplasts, suggesting a role in the regulation of the cell cycle [19]. The first indication of a physiological effect on the part of SA was the discovery of its role in flowering induction and bud formation in tobacco cell cultures [20]. The pioneering works of Malamy et al. (1990) on the effect of SA in Tobacco Mosaic Virus [21] and of Métraux et al. (1990) on the role of SA as signaling in systemic acquired resistance (SAR) [22] clearly demonstrated the implications of SA in plant pathogen responses. Also, SA influences seed germination, seedling establishment, cell growth, respiration, stomatal closure, senescence-associated gene expression, basal thermotolerance, nodulation in legumes, and fruit yield, among others [8,9,23,24]. In both cases (melatonin and SA), the role in some of these processes may be indirect because they modulate the synthesis and/or signaling of other plant hormones [25,26] (see below). Table 1 presents a list of the physiological effects in which both molecules (melatonin and SA) seem to play a relevant role. As can be seen, there are many coincidences between both molecules, but undoubtedly the aspects that have aroused most interest are those related to their actions in improving resistance to stress situations.

Table 1. Common physiological effects described for melatonin and SA in plants.

	Physiological Effect
Vegetative development	Seed germination Plant growth Photosynthesis Mineral nutrition Crop yield Carbohydrate metabolism Nitrate metabolism Antioxidant network Senescence Plant pathogen response
Reproductive development	Flowering Seed formation
Abiotic stress Water stress: drought, flooding Salinity Metals UV, extreme light Temperature stress: cold, heat Biotic stressors Fungi Bacteria	Greater Resistance

Tables 2 and 3 show some representative examples in which the protective roles of melatonin and SA against different abiotic stresses have been studied. As can be seen, many aspects show close similarities between both molecules. In general, both are involved in responses to abiotic stress situations, including a marked improvement in the water status in drought situations, enhanced biosynthesis of photosynthetically active pigments as well as of the photosynthetic rate, an increase in metabolites and antioxidant enzymes to balance the redox status, osmotic adjustment to reduce of membrane injury under stress conditions, and in some cases, growth promotion and enhanced productivity and yield [8,17,18,27–30].

Table 2. Effects of melatonin in abiotic stress responses.

Abiotic Stress	Plant Species	Melatonin Treatment (μM)	Effects Observed	Reference
Cold	<i>Arabidopsis</i>	10–30	↑ fresh weight, shoot height and primary roots, survival	[31,32]
Cold	Cucumber	50–500	↑ GSH pool, ↓ ROS burst	[33]
Cold	<i>Rhodiola crenulata</i>	0.1	↑ cryopreservation of callus	[34]
Cold	American elm	0.1–0.5	↑ regrowth frozen shoots	[35]
Cold	Watermelon	150	↑ photosynthesis, ↓ cold-related microRNA	[36]
Cold	Wheat	1 mM	↑ redox balance, Chls, osmorregulation, ↓ ROS burst	[37]
Cold	Cabbage	10–1000	↑ anthocyanins, proline, redox balance, ↓ ROS burst	[38]
Cold, salt, drought	Bermudagrass	20–100	↑ fresh weight, osmorregulation, ↓ ROS burst, cell damage	[39,40]
Cold, salt, drought	<i>Arabidopsis</i>	50	↑ sucrose, survival rate	[41]
Cold, drought	Barley	1 mM	↑ photosynthesis efficiency, ABA, water content, ↓ ROS burst	[42]
Heat	<i>Phacelia</i>	0.3–90	↑ germination	[43]
Heat	<i>Arabidopsis</i>	5–20	↑ thermotolerance	[44]
Heat	Tomato	10	↑ thermotolerance and cell protection	[45]
Metal-Cu	Pea	5	↑ plant survival	[46]
Metal-Cu	Red cabbage	1–100	↑ fresh weight, germination, ↓ membrane peroxidation	[47]
Metal-Cd	Tomato	25–500	↑ Cd tolerance, phytochelatin, ATPase activity	[48]
Metal-Pb	Tobacco	0.2	↑ cell culture growth, ↓ mortality cells, ROS burst	[49]
Oxidative	<i>Arabidopsis</i>	5–10	↑ plant survival, autophagy, ↓ oxidized proteins	[50]
Oxidative	<i>Pisum sativum</i>	50–200	↑ photosynthesis efficiency, pigments, water content, ↓ ROS burst	[51]
Salinity	<i>Malus</i>	0.1	↑ shoot height, leaf number, chlorophylls, ↓ electrolyte leakage	[52]
Salinity	<i>Malus</i>	0.1	↑ shoot height, K^+ channels, K^+ level, ↓ ROS burst	[53]
Salinity	Citrus	1	↑ osmorregulation, Chls, ↓ ROS burst, membrane peroxidation	[54]
Salinity	Sunflower	15	↑ root and hypocotyl growth, antioxidant potential	[55]
Salinity	Cucumber	1	↑ germination, GA_4 , ↓ ROS burst, membrane peroxidation, ABA	[56]
Salinity	<i>Vicia faba</i>	100–500	↑ plant height, RWC, photosynthetic pigments, osmolites, phenolic	[57]
Salinity	Tomato	50–150	↑ photosynthesis, PSII efficiency, D1 protein turnover, ↓ ROS burst	[58]
Alkalinity	Tomato	0.25–1	↑ seedling growth, photosynthesis, ion homeostasis, ↓ ROS burst	[59]
Salinity, drought	Soybean	50–100	↑ seedling growth, leaf size, biomass, seed yield	[60]
Drought	Cucumber	100	↑ germination, root growth	[61]
Drought	Grape	0.05–0.2	↑ seedling growth, osmorregulation, photosynthesis, ↓ ROS burst	[62]
Drought	<i>Malus</i>	100	↑ water status, Chls, photosynthesis efficiency, ↓ ROS burst	[63]
Leaf-senescence	Barley	0.01–1	↓ senescence, ↑ Chls	[64]
Leaf-senescence	<i>Malus</i>	10 mM	↓ senescence, ROS burst, ↑ Chls, photosynthesis efficiency	[65,66]
Leaf-senescence	<i>Arabidopsis</i>	20–125	↓ senescence, ROS burst, ↑ Chls, photosynthesis efficiency	[67]
Leaf-senescence	Rice	10–20	↓ senescence, ROS burst, cell death, ↑ Chls	[68]
Leaf-senescence	Perennial ryegrass	20–100	↓ senescence, ROS burst, ↑ Chls, photosynthesis efficiency	[69]

↑, Increased content or increased action. ↓ Decreased content or decreased action.

Table 3. Effects of SA in abiotic stress responses.

Abiotic Stress	Plant Species	SA Treatment (μM)	Effects Observed	Reference
Cold	<i>Hordeum vulgare</i>	100	↑ antioxidative enzymes, ice nucleation activity	[70]
Cold	<i>Musa acuminata</i>	500	↑ chloroplast and mitochondria ultrastructure	[71]
Cold	<i>Lycopersicon esculentum</i>	100	↑ resistance, antioxidative enzymes, PR proteins	[72]
Cold	<i>Prunus persica</i>	1 mM	↑ antioxidative enzymes, antioxidant metabolites, firmness	[73]
Heat	<i>Triticum aestivum</i>	500	↑ proline content, water potential, gas exchange, glutamyl kinase activity	[74]
Heat	<i>Arabidopsis thaliana</i>	10	↑ survival, thermotolerance, ↓ oxidative damage	[75]
Metal-Cd	<i>Brassica juncea</i>	1 mM	↑ mineral nutrients	[76]
Metal-Cd	<i>Cucumis melo</i>	100	↑ photosynthesis efficiency, water use efficiency	[77]
Metal-Cd	<i>Glycine max</i>	120 mM	↑ Chls, photosynthesis efficiency, antioxidative enzymes, GSH	[78]
Metal-Cd	<i>Ricinus communis</i>	500	↓ gas exchange, Chls	[79]
Salinity	<i>Glycine max</i>	500	↑ antioxidative enzymes, ascorbate	[80]
Salinity	<i>Vigna radiata</i>	500	↑ photosynthesis efficiency, plant dry mass, glycinebetaine	[81]
Salinity	<i>Torreya grandis</i>	500	↑ photosynthesis efficiency, net CO ₂ assimilation rates, Chls	[82]
Drought	<i>Zea mays</i>	1	↑ net dry weight, water potential, leaf rolling	[83]
Drought	<i>Simarouba glauca</i>	50	↑ polyphenols, alkaloids	[84]
Drought	<i>Triticum aestivum</i>	1 mM	↑ moisture content, dry mass, Rubisco, SOD, Chls	[85]
UV-B	<i>Poa pratensis</i>	150 mg/m ²	α-tocopherol, SOD, CAT, anthocyanins	[86]

↑, Increased content or increased action. ↓, Decreased content or decreased action.

3. Melatonin and SA in Biotic Stress (Plant Pathogen Response)

Tables 4 and 5 provide a list of the papers related to the positive effect of melatonin and SA on plant pathogen responses. In the first paper, related to melatonin and fungus plant-pathogen infection, melatonin-treated apple trees using root irrigation improved the resistance of *Malus prunifolia* against the fungus *Diplocarpon mali* (Marssonina apple blotch). At 20 days, the treated trees showed a lower number of damaged leaves, higher chlorophyll content, a more efficient Photosystem II, and less defoliation than infected untreated trees. In general, melatonin helped plants with resistance to fungal infection, reducing lesions, inhibiting pathogen expansion, and generally alleviating disease damage [87]. Also, in some in vitro assays, different concentrations of melatonin showed growth inhibition activities against plant fungal pathogens such as *Alternaria* spp., *Botrytis* spp., and *Fusarium* spp. The same occurred in plant-pathogen attacks by *Penicillium* spp. in non-sterilized *Lupinus albus* seeds [17]. Table 4 shows five papers that used the *Arabidopsis/Pseudomonas syringae* as a model of plant-bacterial pathogen interaction. Melatonin induced pathogen-related genes in *Arabidopsis* (also in tobacco plants), which is in accordance with the possible role of this methoxyindole as a defence signalling molecule against pathogens in plants. In a recent and significant paper, Zhang et al. (2017) demonstrated that melatonin attenuates severe potato late blight caused by *Phytophthora infestans*. Melatonin induced plant innate immunity against fungal infection, inhibiting mycelial growth and changing expression of many genes associated with stress and virulence [88]. In sum, melatonin up-regulates pathogenesis-related, SA and ethylene-dependent genes, an effect that was suppressed in mutants defective in SA and ethylene signalling. Also, melatonin increased nitric oxide (NO) and SA-related genes, accompanied by reduced susceptibility to the pathogen, leading to an increase in both melatonin and NO. *SNAT* knockout mutants not only exhibited reduced levels of melatonin, but also lower levels of SA, along with a greater susceptibility to the pathogen [89]. No studies on plant viruses and melatonin have been published to date. Nevertheless, in animals, melatonin is a good therapeutic alternative for fighting bacterial, viral and parasitic infections [90]. Also, during sepsis, melatonin has been reported to block the overproduction of pro-inflammatory cytokines and increase interleukin-10 levels. With respect to viral infection, Venezuelan equine encephalomyelitis (VEE) is an important human and equine disease caused by the VEE virus. Reactive oxygen species (ROS) have been implicated in the dissemination of the responsible virus, and its deleterious effects may be diminished by melatonin treatment. The administration of melatonin significantly decreased the virus level in the blood and brain compared with the levels seen in infected control mice [90].

Table 4. Effects of melatonin in biotic stress responses.

Plant Species	Biotic Stressor	Melatonin Treatment (μ M)	Effects Observed	Reference
<i>Malus prunifolia</i>	<i>Diplocarpon mali</i>	50–500	↑ Resistance to fungal infection ↓ Leaf lesions, cell death ↓ Pathogen expansion	[87]
<i>Arabidopsis</i> and tobacco	<i>Pseudomonas syringae</i> DC3000	10	↑ Defence related genes ↑ Resistance (10-fold vs. mock)	[91]
<i>Arabidopsis</i>	<i>Pseudomonas syringae</i> DC3000	SE of SNAT	↓ Melatonin (50%), SA ↓ Defence related genes ↓ Resistance to infection	[89]
<i>Arabidopsis</i>	<i>Pseudomonas syringae</i> DC3000	20	↑ NO and melatonin ↑ Defence related genes ↑ Resistance	[92]
<i>Arabidopsis</i> and tobacco	<i>Pseudomonas syringae</i> DC3000	1	↑ MAP kinases cascade	[93]
<i>Arabidopsis</i>	<i>Pseudomonas syringae</i> DC3000	50	↑ CBF/DREB1 (stress factors) ↑ CCA1 (internal clock factors) ↑ Defence related genes	[41,94]
<i>Lupinus albus</i>	<i>Penicillium</i> spp.	20–70	↑ Resistance to fungal infection	[17]
Rice	<i>Xanthomonas oryzae</i> , <i>XooMagnaporthe oryzae</i> , blast fungus	–	Changes in melatonin biosynthesis enzymes transcripts	[95]
<i>Solanum tuberosum</i>	<i>Phytophthora infestans</i>	10 mM	↑ Resistance to fungal infection ↑ fungicide effects, ↓ virulence	[88]
<i>Manihot esculenta</i>	<i>Xanthomonas axonopodis</i>		MeRAV1/2 (AP2/ERF) upregulate 7 melatonin biosynthesis genes	[96]

↑, Increased content or increased action. ↓, Decreased content or decreased action.

With respect to SA, the exogenous application of SA at non-toxic concentrations to susceptible fruits and vegetables could enhance resistance to pathogens and help control post-harvest decay [97]. SA effectively reduced fungal decay in a concentration-dependent manner, as can be seen in the examples of Table 5. In the case of SA, some studies indicate that it inhibits viral replication [98–100].

Table 5. Effects of SA in biotic stress responses.

Plant Species	Biotic Stressor	SA Treatment (mM)	Effects Observed	Reference
<i>Fragaria ananassa</i>	<i>Botrytis cinerea</i>	1–2	↓ ethylene, fungal disease, ↑ fruit quality	[101]
<i>Lycopersicon esculentum</i>	<i>Botrytis cinerea</i>	5	↓ ethylene, lycopene, fungal disease, ↑ fruit quality	[97]
<i>Mangifera indica</i>	<i>Collectotrichum gloeosporioides</i>	2	↑ colour, firmness, ↓ disease severity	[102]
<i>Malus domestica</i>	<i>Penicillium expansum</i>	0.07–0.7	↑ efficacy of antagonist <i>C. laurentii</i>	[103]
<i>Prunus avium</i>	<i>Penicillium expansum</i>	2	↑ antioxidative enzymes, chitinase, glucanase, fungal resistance	[104]
<i>Pyrusbretschneideri</i>	<i>Penicillium expansum</i>	2.5	↑ antioxidative enzymes, PAL, chitinase, glucanase, ↓ disease severity	[105]

↑, Increased content or increased action. ↓, Decreased content or decreased action.

4. Melatonin, SA and ROS/RNS Network

A relevant role for NO in melatonin responses is proposed, mainly for auxin-like and plant immune responses. NO and other radical nitrogen species (RNS) and ROS are key signals that increase under abiotic/biotic stress [8,106]. Generally, RNS and ROS signals tend to act in a coordinated way. NO levels are self-regulated and also regulate the ROS network through NO-dependent, post-translational modifications [107]. NO modulates several functions through protein modifications by nitration, S-nitrosylation and the ligation of NO to transition metals, but also through the modification of lipids (nitro-fatty acids) and DNA (8-nitroguanine) [108–112]. Moreover, NO triggers a set of responses to alleviate stress and cellular damage, which includes transient metabolic reprogramming in both primary and secondary metabolic pathways [107].

Abiotic and biotic stress induce an increase in endogenous melatonin through the upregulation of melatonin biosynthetic genes [96,113]. Melatonin also increases NO levels through the upregulation of nitrate reductase (which usually reduces nitrate to nitrite, but can also reduce nitrite to NO using NADPH as a cofactor). Also melatonin induces the NO synthase-like pathway, in iron

deficiency-induced NO in rice [114]. Thus, melatonin can also act as an NO and ROS scavenger, and curiously, in an NO feedback mechanism, NO induces melatonin biosynthesis [113].

Although some data point to the possibility that melatonin might act as an upstream signal, the complexity of the melatonin–NO interaction makes it difficult to elucidate whether melatonin is upstream or downstream of NO. Also, H_2O_2 (an important signal molecule in stress situations), seems to be decisive in the upregulation of melatonin biosynthesis enzymes, taking as a response an increase in melatonin levels in stressed plants. In short, mitogen-activated protein kinase (MAPK) signalling, SA, NO, and H_2O_2 , as well as their cross-talk, are required for melatonin-mediated innate immunity in *Arabidopsis*. Also, melatonin and NO change the expression of several transcription factors and hormone signalling elements, which determines the overall anti-stress response. Also, some plant hormones such as IAA, CKs and ABA can stimulate NO production [25,26].

This complex relationship between ROS, NO and melatonin is pictured in Figure 2. In the case of abiotic stress, no model including the signalling cascade for melatonin and SA has been proposed to date. Fleta-Soriano et al. (2017) studied the role of melatonin in plant response to drought stress and recovery in maize plants [115]. Furthermore, in that study, the endogenous contents of melatonin positively correlated with those of stress-related phytohormones, particularly with those of SA, although exogenous application of melatonin did not alter the contents of any phytohormone.

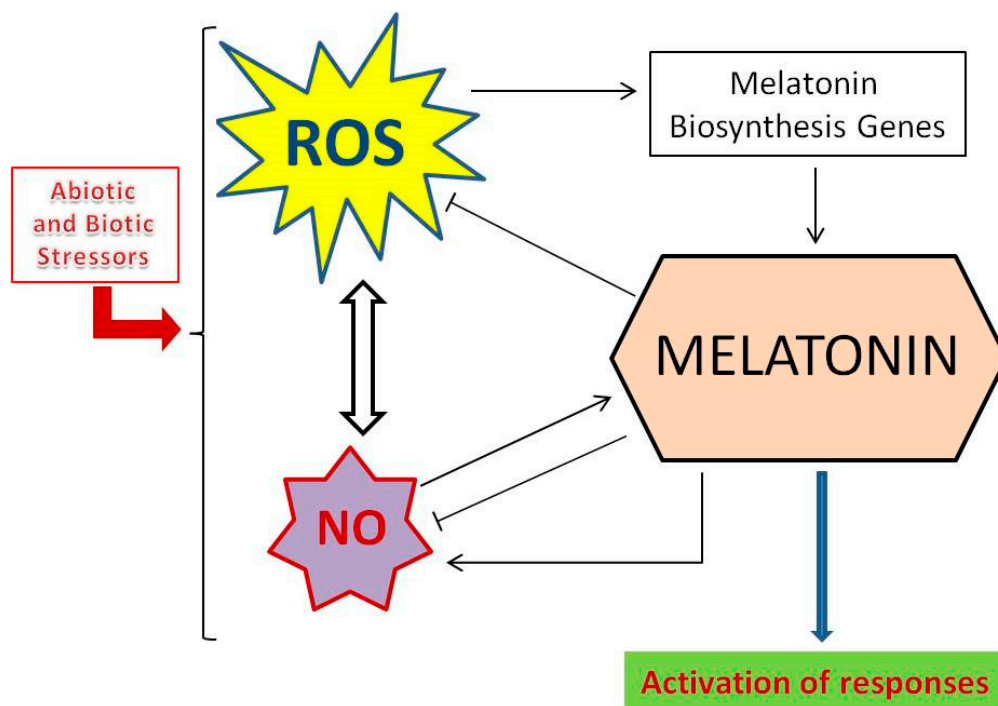


Figure 2. Effect of abiotic/biotic stressors on the antioxidant network ROS/NO/melatonin.

A model of melatonin/SA/NO/ROS action in biotic stress responses (pathogen resistance) has been proposed [9,25] (Figure 3). Pathogen attack increases NO, SA and melatonin levels through ROS. In the well-known model of *Arabidopsis/Pseudomonas syringae* DC3000 (avrRpt2), plant–pathogen interactions revealed that the mitogen-activated protein kinase cascade (MAPKKK3) and OXI1 (oxidative signal-inducible1) kinases are responsible for triggering melatonin-induced defence signalling pathways [93,116]. The key enzyme in SA biosynthesis—isorchismate synthase-1 (ICS-1)—was upregulated by melatonin, increasing SA levels and triggering a pathogen-induced response. Also, melatonin and NO were able to induce jasmonic acid (JA) biosynthesis and increase several sugar and glycerol levels, all of which activate pathogen-related gene expression. The melatonin-induction of ethylene biosynthesis, through ACC synthase (ACS6), collaborates in the

induction of pathogenesis-related genes (PR), whereby ethylene insensitive (EIN), enhanced disease susceptibility 1 (EDS1), phytoalexin deficient 4 (PAD4) and NPR1 factors are key signalling components in the plant SA- and ethylene-mediated defence responses [17,41,91,92,96,116–119]. More recently, it has been demonstrated that *MeRAV1* and *MeRAV2* factors (apetala2/ethylene response factor, AP2/ERF) are essential for plant disease resistance against bacterial blight in cassava through the upstream of transcription factors of melatonin biosynthesis genes [96].

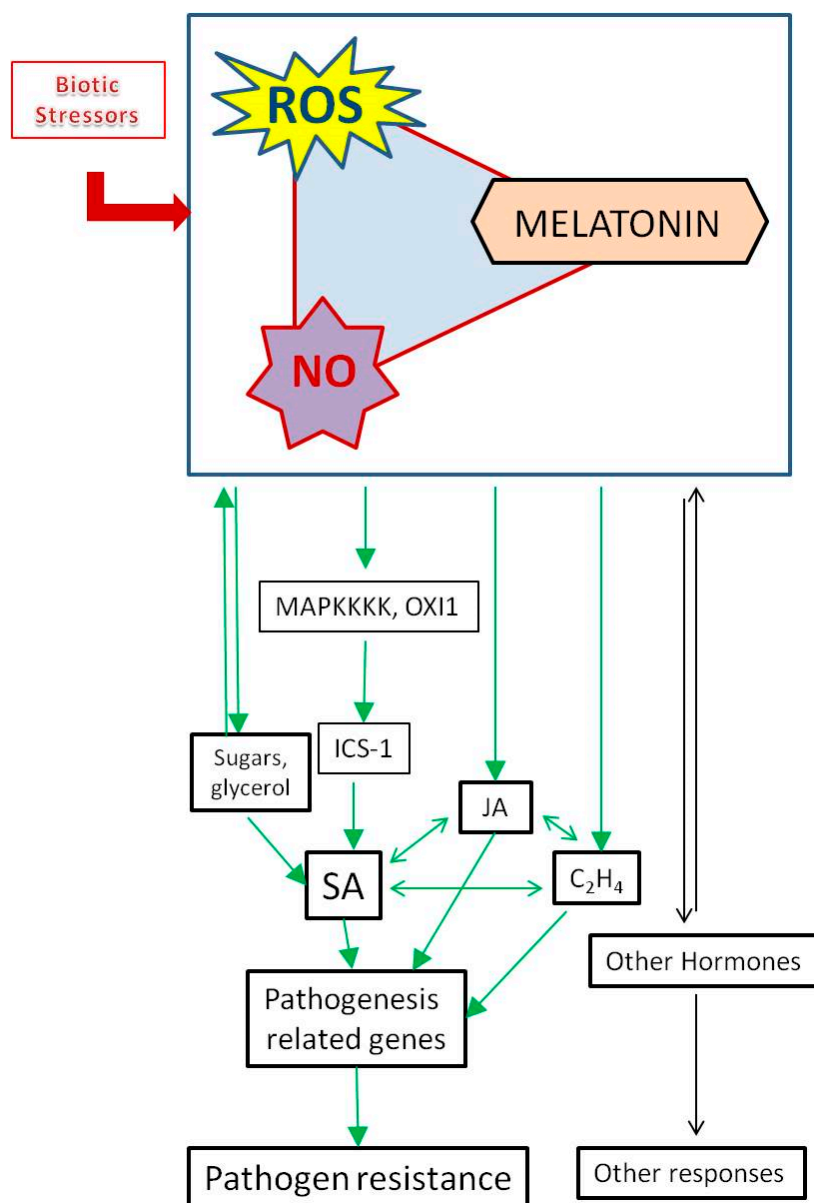


Figure 3. Model of ROS/NO/melatonin action on biotic stress responses (pathogen resistance).

5. Future Perspectives for Melatonin and SA in Agronomic Applications

Both molecules are of great interest as modulating agents of anti-stress responses in plants. Also, both have the capacity to directly or indirectly interact with ROS and RNS. Knowledge of the possible relationships with other hormones in aspects related to pathogen resistance and the response to abiotic stresses is of great relevance. The possibility of “sensitizing” plants to abiotic agents through priming or other methods might be of interest in order to increase the resistance of crops. SA- or melatonin-induced activation to reduce damage caused by water deficits (drought), while maintaining

the proper metabolism in the face of this stress situation is clearly an essential objective for increasing plant/crop development and yield. Obtaining transgenic plants that overexpressed SA and melatonin biosynthesis genes could be another interesting approach, both for research *per se* and for application in crops, provided that the limitations to the use of transgenic plants are not transgressed. In both cases, the over-accumulation of SA and melatonin in plant tissues increase the resistance response against stressors. Figure 4 shows a schematic model in which both molecules studied in this paper present agonist behaviour to reduce or moderate the harm caused by stressors with the final aim of improving plant development and crop yield.

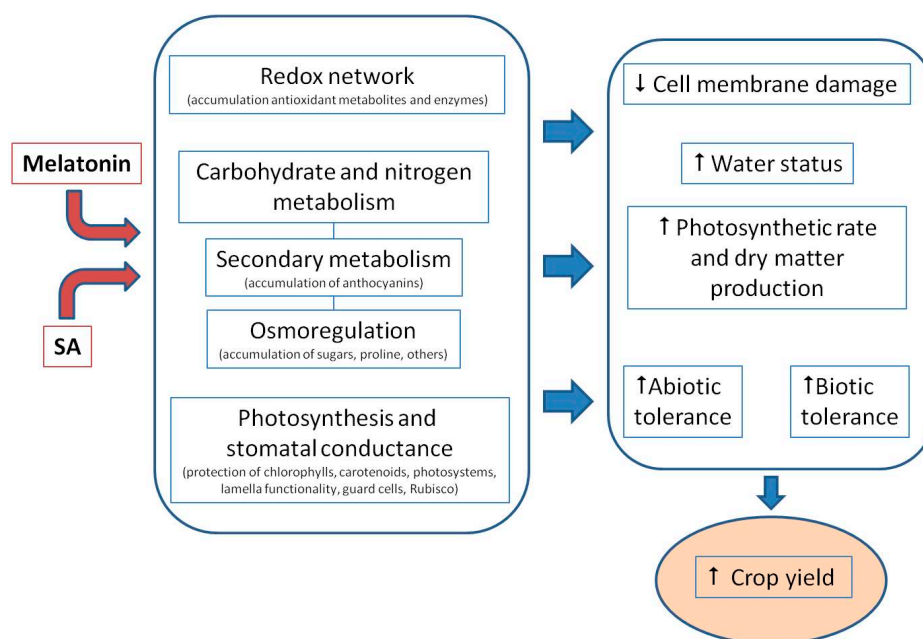


Figure 4. Melatonin/SA model of biostimulating activity in plants to enhance resistance to stress situations and increase crop yield.

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