



# Indole is an essential molecule for plant interactions with herbivores and pollinators

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## Abstract

Indole is a well-characterized molecule that is used as a building block for a multitude of natural compounds. It can be utilized directly as a free indole or it can serve as a substrate for indole-derived metabolites. Besides serving as a substrate for the essential amino acid tryptophan, it is also involved in a variety of plant functions. One of the most important processes in which involving indole is the chemical interaction between plants and insects. These insects are classified into two groups: i) herbivores, which feed on plant tissue (e.g. caterpillars) or consume nutrients from the phloem (e.g. aphids), and ii) pollinators, which feed on plant nectar and pollen and serve as vectors for transferring male gametes between flowers. The nature of indole and indole-derived metabolite usage may differ based on the type of interactions. While indole is a volatile compound emitted to the plant's surrounding, functioning as a remote signal, indole-derived metabolites are mainly non-volatile and mostly function as deterrents that harm herbivores by "direct contact". In this review, we discuss the major role of indole in determining plant fitness by attracting pollinators and repelling herbivores.

## Indole biosynthesis and catabolism

Indole is an aromatic heterocyclic organic compound, consisting of a six-membered benzene ring fused to a five-membered nitrogen-containing pyrrole ring [1]. In plants, indole is produced via the shikimate pathway, resulting in tryptophan (Trp) biosynthesis (**Figure 1**). The biosynthesis of Trp is catalyzed by the two enzymatic steps: Trp synthase-alpha subunit, which converts indole-3-glycerol into indole, and channels it directly to the Trp synthase-beta subunit for further conver-

sion into Trp (existing as a  $\alpha_2\beta_2$  tetramer complex; [2]). During Trp biosynthesis, indole-3-glycerol phosphate is produced and directed into different pathways leading to the biosynthesis of both volatile and non-volatile compounds (**Figure 2**). The indole molecule is embedded in many biological systems including the neurotransmitter serotonin, the hormone melatonin, or scent compounds in human's sweat and flowers [1,3]. In plants, this molecule plays a role in many functions, ranging from Trp production to the coloring of yellow petals (terpenoid indole alkaloid), and the biosynthesis of defense and scent metabolites



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[4-7]. Indole is also known as a substrate for the phytohormone auxin (indole-3-acetic acid), which is fundamental in regulating many aspects of plant growth and development [8,9]. Auxin can be synthesized through the Trp-dependent auxin biosynthetic pathway or the Trp-independent pathway as recently reported [5,10]. In monocots that produce non-volatile defense metabolites such as benzoxazinoids, free indole can be produced by the indole-3-glycerol phosphate lyase enzyme, named *Bx1* [11-13]. In addition, indole is probably catalyzed by the enzyme indole-synthase (*INS*) in *Arabidopsis thaliana* and indole-3-glycerol phosphate lyase (*IGL*) in maize (*Zea mays*; [6,14,15]). In relation to plant-insect chemical interactions, indole serves as a precursor for deterrence metabolites that are involved in plant defense against herbivores (e.g. benzoxazinoids, gramine, glucosinolates, and serotonin); in addition indole is emitted as a scent (to attract pollinators or predators) or as an aerial priming agent to non-attacked plant tissues. Because indole is involved in a wide range of plant functions, it is considered to be a major factor in determining plant fitness.

### Indole is a fundamental compound in pollinators' attraction by scent signals

Floral signals are an important component of plant-pollinator interactions, and are composed of two major traits: visual (e.g. color and shape) and olfactory scents volatile compounds; [16]. Although visual cues are important in attracting pollinators, they often elicit fewer specific responses than odors [17-19]. One major scent compound that plays a role in these interactions is indole. It is the most prolific nitrogen-containing volatile found in the petals of flowering plants and it is biosynthesized and emitted from the flowers of over 30 distinct plant families [20]. In some plant species, indole accumulation and/or emission is restricted to floral tissues, which highlights its role in scent formation [21]. In several classes of insects, such as the grey-backed mining bee (*Andrena vaga*), hummingbird moth (*Hyles lineata*) and the housefly (*Musca domestica*), indole was reported to elicit substantial antennal responses, indicating that these species can detect and react to this signal when foraging and subsequently during pollination [22,23].

Indole is occasionally a constituent of floral scent bouquets in nocturnal, moth-pollinated plants [24,25]. For example, in a reproduction isolation experiment, Bischoff *et al.* (2014) showed that indole contributed to the promotion of hawkmoth visits to *Ipomopsis* flowers [26]. The author's showed that, overall, hawkmoths preferred to visit *I. tenuituba*, which is light-pink and naturally emitting indole, regardless of the artificial addition of the metabolite. In the case of *I. aggregate*, which has red petals and does not emit indole, the hawkmoth visitation rate was increased when indole was added. Indole is also involved in the attraction of insects to the flowers of "sapromyophilous" plants, which mimic carrion and dung odors to attract flies for pollination services. These plants typically do not produce nectar and rely heavily on sensory cues to ensure pollination [27]. Flowers of such plants (e.g. *Periploca laevigata*, *Stemona species* and *Satyrium pumilum*) usually emit a blend of sweet and putrid volatiles that are associated with both ovipositional/mating sites and potential food sources [23,28,29]. Indole, being present in animal waste (Cosse and Baker, 1996) and carrions, is regarded as a signal leading the insects to the aforementioned, sites as well as to the flowers of dung and carrion-mimicking plants [22,25].

### Indole is emitted as a signal for herbivore damage

In response to mechanical and herbivore damage, plants release a specific blend of volatile compounds. These volatiles can affect herbivores in different manners by: i) attracting natural enemies that feed on herbivores (i.e., predators and parasitic wasps) to locate their prey or host [31], ii) signalling to other herbivores that the plant has initiated the production of deterrent compounds; iii) signalling that herbivores are already present on the plant and its nutritional value is reduced, therefore helping to reduce additional herbivore damage [32], and iv) function as an aerial priming agent to non-attacked neighboring plants, which will allow them to induce their defense mechanisms in preparation for future attacks [33]. An example of aerial priming was recently reported by Erb *et al.* (2015). This research revealed that herbivore-infested maize leaves emit indole to enhance the induction of defensive mechanisms in systemic leaves and neighboring maize plants in a species-specific manner. Indole emission increased the biosynthesis of mono and homo-terpenes in the systemic leaves of attacked plants as well as the production of the stress phytohormones, such as jasmonic acid conjugate and abscisic acid in neighboring plants [33].

### Indole serves as a precursor for toxic metabolites against herbivores

In plants, Trp and its substrate indole, serve as precursors for various classes of toxic, deterrent metabolites that play a defensive role against insects and pathogen by interfering with their life cycle [2,34,35], as depicted in **Figure 3**. These classes of metabolites differ between monocots and dicots and among the plant species in each group. In monocots, for example, the two millet species, foxtail millet (*Setaria italica*) and Japanese barnyard millet (*Echinochloa esculenta*), as well as rice plants (*Oryza sativa*) accumulate serotonin in response to pathogen or herbivore infestations [37,38]. For example, rice leaves were fed on by rice striped stem borer (*Chilo suppressalis*) larvae for either 24 h or 48 h which induced of four Trp-derived metabolites including serotonin, tryptamine, feruloyl tryptamine (*Fer-Try*) and *p*-coumaroylserotonin [38]. High concentrations of tryptamine in *Catharanthus roseus* plants have also been shown to express anti-oviposition activity toward whiteflies (*Bemisia tabaci*; [39]) and anti-feeding activities in tobacco and poplar toward *Malacosoma disstria* and *Manduca sexta* caterpillars [40]. Other monocots such as maize, wheat (*Triticum genus*), rye (*Secale cereale*), and wild barley (*Hordeum genus*) produce benzoxazinoids [11,41-43] while the cultivated barley species (*Hordeum vulgare*) produces gramine, an indolic defense compound, against aphids and pathogens [44,45]. Benzoxazinoids were shown to cause negative effects against a wide range of pests, including insects (aphids and caterpillars), bacteria, fungi and nematodes [13,46-48,50-52]. The mode of action of these specialized metabolites is to deter insects by antibiosis properties caused by inhibition the digestive proteases responsible for detoxification and pest salivation and therefore, to affect the insect's fitness [53]. For example, feeding experiments of cereal aphids on an artificial diet containing benzoxazinoid conjugates showed increased aphid mortality which supports a toxic function for these metabolites [48,52].

Dicot plants that belong to the Brassicaceae family, produce one or more indole glucosinolates which are among the most widely distributed glucosinolates in nature [54]. Glucosinolates remain compartmentalized and come in contact with the pest only upon tissue damage, followed by myrosinases

( $\beta$ -thioglucoside glucohydrolase) activity and release of defensive hydrolysis products including isothiocyanates, nitriles, and epithionitriles which are toxic compounds [55,56]. The glucosinolates levels increase and their composition can change in response to herbivory and pathogen attack in several Brassicaceae species [57,58]. For example, a defensive role for indole glucosinolates was observed in the case of the *A. thaliana atr1D* mutant plant, which over produces indole glucosinolates. This in turn confers resistance to Brassicaceae-generalist herbivore, *Myzus persicae* aphids. Conversely, the *Arabidopsis cyp79B2/cyp79B3* double mutant, which possess low levels of indole glucosinolates, responded to *M. persicae* more rapidly [59,60]. Interestingly, the *cyp79B2/cyp79B3* double mutant was tested for Brassicaceae-specialist herbivores, *Pieris rapae*, oviposition and received fewer *P. rapae* eggs than the wild-type [61]. It was suggested that the role of indole glucosinolates and their breakdown products in plant-herbivore interactions, remains complex due to their differential influence on generalist and specialist herbivores [62].

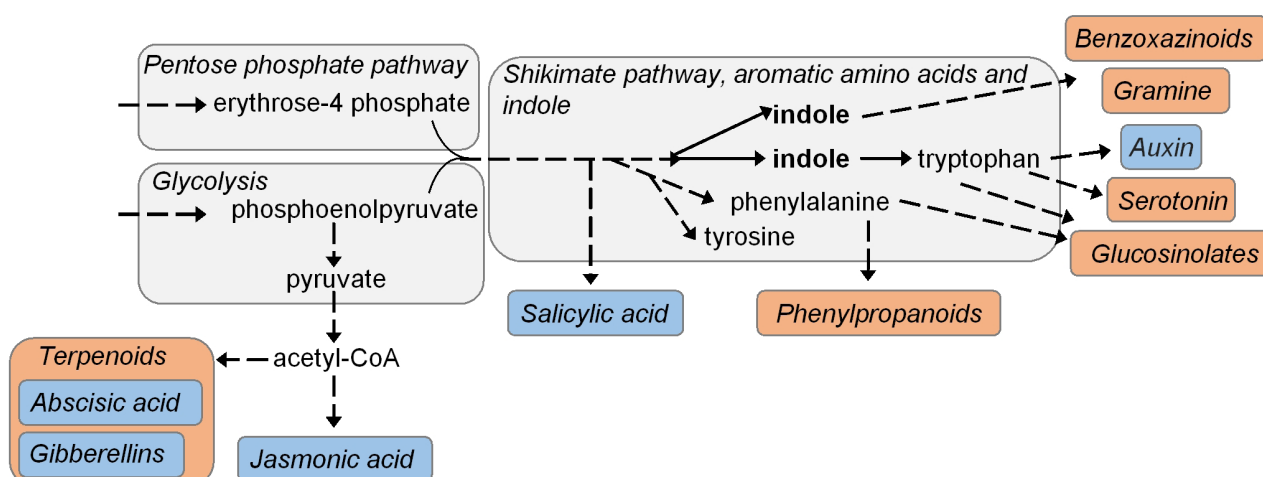
## Perspective

Indole is an essential metabolite that often determines the outcome of plant and insect interaction. On the one hand, indole is involved in positive plant-insect interactions by serving as part of the volatile signals emitted by plants to attract their pollinators. On the other hand, indole is involved in negative plant-insect interaction by serving as a substrate for several classes of specialized metabolites that are function in repelling herbivores. Therefore, we suggest that further study the biosynthesis and catabolism of indole under insect infestations should be further studied. Additionally, it would be prudent to explore the indole flux during visits of co-occurring insects from different guilds at different plant developmental stages.

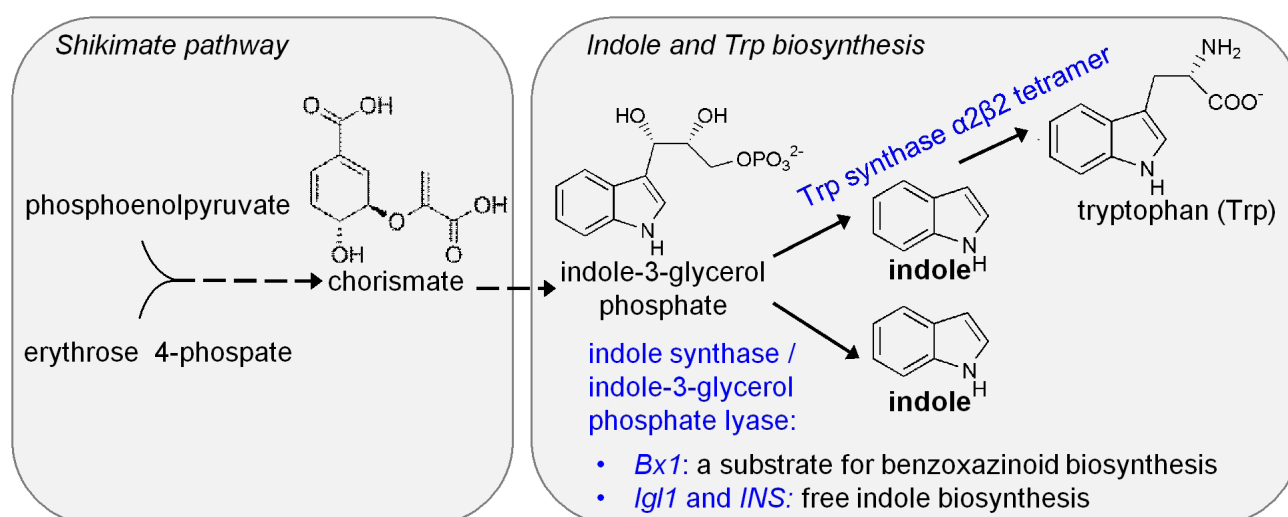
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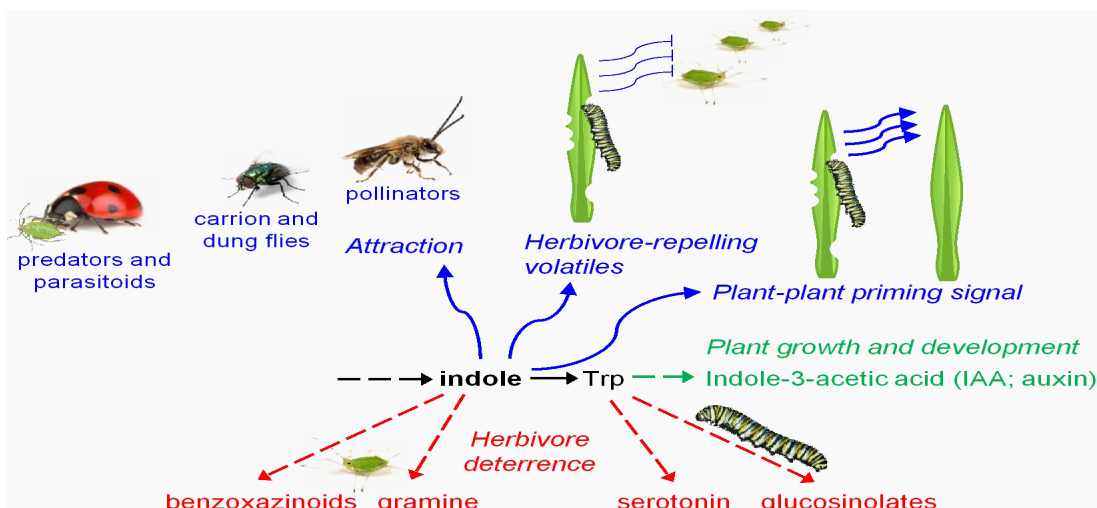
## Figures



**Figure 1:** An overview of indole biosynthesis (grey box), several major classes of specialized metabolites (orange box) and phytohormones biosynthesis (blue box).



**Figure 2:** Schematic representation of indole and Trp biosynthesis. In blue are the enzymatic reactions.



**Figure 3:** A summary of the major functions of indole and indole-derived metabolites. In blue are the functions of indole and indole-derived volatile metabolites, in red are the classes of non-volatile deterrent metabolites; in green are the indication of the roles of indole and Trp in plant growth and development.

## References

- Wu Y.J. Heterocyclic Scaffolds II: Reactions and Applications of Indoles. In G. Gribble, ed (Berlin). 2010; 1-29.
- Tzin V, Galili G. New Insights into the shikimate and aromatic amino acids biosynthesis pathways in plants. *Mol. Plant* 3. 2010; 3: 956-972.
- Gribble G.W. Introduction. In *Indole Ring Synthesis: From Natural Products to Drug Discovery*. 2016; 1-38.
- Warskulat A, Tatsis EC, Dudek B, et al. Unprecedented Utilization of Pelargonidin and Indole for the Biosynthesis of Plant Indole Alkaloids. *Chembiochem*. 2016; 17: 318-327.
- Mano Y, Nemoto K. The pathway of auxin biosynthesis in plants. *J Exp Bot*. 2012; 63: 2853-2872.
- Zhang R, Wang B, Ouyang J, et al. Arabidopsis indole synthase, a homolog of tryptophan synthase alpha, is an enzyme involved in the Trp-independent indole-containing metabolite biosynthesis. *J Integr Plant Biol*. 2008; 50: 1070-1077.
- Van Der Fits L, Memelink J. Primary and Secondary Metabolism ORCA3, a Jasmonate-Responsive Transcriptional Regulator of Plant ORCA3, a Jasmonate-Responsive Transcriptional Regulator of Plant Primary and Secondary Metabolism. 2000; 295: 295-297
- Wang R, Estelle M. Diversity and specificity: auxin perception and signaling through the TIR1/AFB pathway. *Curr Opin Plant Biol*. 2014; 21: 51-58.
- Teale WD, Paponov IA, Palme K. Auxin in action: signalling, transport and the control of plant growth and development. *Nat Rev Mol Cell Biol*. 2006; 7: 847.
- Wang B, Chu J, Yu T, et al. Tryptophan-independent auxin biosynthesis contributes to early embryogenesis in *Arabidopsis*. *Proc Natl Acad Sci*. 2015; 112: 4821-4826.
- Frey M, Schullehner K, Dick R, et al. Benzoxazinoid biosynthesis, a model for evolution of secondary metabolic pathways in plants. *Phytochemistry* 2009; 70: 1645-1651.
- Nomura T, Ishihara A, Iwamura H, et al. Molecular characterization of benzoxazinone-deficient mutation in diploid wheat. *Phytochemistry*. 2007; 68: 1008.
- Handrick, V. et al. Biosynthesis of 8-O-methylated benzoxazinoid defense compounds in maize. 2016; 28: 1682-700.
- Frey M, Stettner C, Pare PW, et al. An herbivore elicitor activates the gene for indole emission in maize. *Proc Natl Acad Sci. USA*. 2000; 97: 14801.
- Jin Z, Kim JH, Park SU, et al. Cloning and characterization of indole synthase (INS) and a putative tryptophan synthase  $\alpha$ -subunit (TSA) genes from *Polygonum tinctorium*. *Plant Cell Rep*. 2016; 35: 2449-2459.
- Cna'ani A, Spitzer-Rimon B, Ravid J, et al. Two showy traits, scent emission and pigmentation, are finely coregulated by the MYB transcription factor PH4 in petunia flowers. *New Phytol*. 2015; 208: 708-714.
- Dudareva N, Negre F, Nagegowda DA, et al. Plant Volatiles: Recent Advances and Future Perspectives. *CRC. Crit Rev Plant Sci*. 2006; 25: 417-440.
- Burger H, Dötterl S, Ayasse M. Host-plant finding and recognition by visual and olfactory floral cues in an oligolectic bee. *Funct Ecol*. 2010; 24: 1234-1240.
- Kunze J, Gumbert A. The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. *Behav Ecol*. 2001; 12: 447-456.
- Knudsen JT, Eriksson R, Gershenzon J. Diversity and Distribution of Floral Scent. *Bot Rev*. 2006; 72: 1-120.
- Jürgens A, Webber AC, Gottsberger G. Floral scent compounds of Amazonian Annonaceae species pollinated by small beetles and thrips. *Phytochemistry*. 2000; 55: 551-558.
- Dotterl S, Füssel U, Jürgens A, et al. 1,4-Dimethoxybenzene, a floral scent compound in willows that attracts an oligolectic bee. *J Chem Ecol*. 2005; 31: 2993-2998.
- Zito P, Dotterl S, Sajevo M. Floral Volatiles in a Sapromyophilous Plant and Their Importance in Attracting House Fly Pollinators. *J Chem Ecol*. 2015; 41: 340-349.
- Levin RA, Raguso RA, McDade LA. Fragrance chemistry and pollinator affinities in Nyctaginaceae. *Phytochemistry*. 2001; 58: 429-440.
- Raguso RA, Levin RA, Foose SE, et al. Fragrance chemistry, nocturnal rhythms and pollination "syndromes" in *Nicotiana*. *Phytochemistry*. 2003; 63: 265-284.
- Bischoff M, Jürgens A, Campbell DR. Floral scent in natural hybrids of *Ipomopsis* (Polemoniaceae) and their parental species. *Ann Bot*. 2014; 113: 533-544.
- Johnson SD, Jürgens A. Convergent evolution of carrion and faecal scent mimicry in fly-pollinated angiosperm flowers and a stinkhorn fungus. *South African J Bot*. 2010; 76: 796-807.



28. Van Der Niet T, Hansen DM, Johnson SD. Carrion mimicry in a South African orchid: Flowers attract a narrow subset of the fly assemblage on animal carcasses. *Ann Bot.* 2011; 107: 981-992.
29. Chen G, Gong WC, Ge J, et al. Variation in floral characters, particularly floral scent, in sapromyophilous *Stemona* species. *J Integr Plant Biol.* 2017; 59: 825-839.
30. Cosse AA, Baker TC. House Flies and Pig Manure Volatiles : Wind Tunnel Behavioral Studies and Electrophysiological Evaluations &TM House Flies and Pig Manure Volatiles : Electrophysiological Evaluations . *J Agric Entomol I.* 1996; 13: 301-317.
31. Dicke M, Sabelis MW, Takabayashi J, et al. Plant strategies of manipulating predator-prey interactions through allelochemicals: Prospects for application in pest control. *J Chem Ecol.* 1990; 16: 3091-3118.
32. Bernasconi ML, Turlings TCJ, Ambrosetti L, et al. Herbivore-induced emissions of maize volatiles repel the corn leaf aphid, *Rhopalosiphum maidis*. *Entomol Exp Appl.* 1998; 87: 133-142.
33. Erb M, Veyrat N, Robert CAM, et al. Indole is an essential herbivore-induced volatile priming signal in maize. *Nat Commun.* 2015; 6: 6273.
34. Kokubo Y, Nishizaka M, Ube N, et al. Distribution of the tryptophan pathway-derived defensive secondary metabolites gramine and benzoxazinones in Poaceae. *Biosci Biotechnol Biochem.* 2016; 8451: 1-10.
35. Balmer D, Flors V, Glauser G, et al. Metabolomics of cereals under biotic stress: current knowledge and techniques. *Front Plant Sci.* 2013; 4: 82
36. Lookadoo SE, Pollard AJ. Chemical contents of stinging trichomes of *Cnidoscolus texanus*. *J Chem Ecol.* 1991; 17: 1909-1916.
37. Ishihara A, Hashimoto Y, Tanaka C, et al. The tryptophan pathway is involved in the defense responses of rice against pathogenic infection via serotonin production. *Plant J.* 2008b; 54: 481-495.
38. Ishihara A, Hashimoto Y, Miyagawa H, et al. Induction of serotonin accumulation by feeding of rice striped stem borer in rice leaves. *Plant Signal Behav.* 2008a; 3: 714-716.
39. Thomas JC, Adams DG, Nessler CL, et al. Tryptophan Decarboxylase, Tryptamine, and Reproduction of the Whitefly. *Plant Physiol.* 1995; 109: 717-720.
40. Gill RIS, Ellis BE, Isman MB. Tryptamine-induced resistance in tryptophan decarboxylase transgenic poplar and tobacco plants against their specific herbivores. *J Chem Ecol.* 2003; 29: 779-793.
41. Grun S, Frey M, Gierl A. Evolution of the indole alkaloid biosynthesis in the genus *Hordeum*: distribution of gramine and DIBOA and isolation of the benzoxazinoid biosynthesis genes from *Hordeum lechleri*. *Phytochemistry.* 2005; 66: 1264.
42. Ishihara A, Kumeda R, Hayashi N, et al. Induced accumulation of tyramine, serotonin, and related amines in response to *Bipolaris sorokiniana* infection in barley. *Biosci Biotechnol Biochem.* 2017;81: 1090-1098.
43. Adhikari KB, Tanwir F, Gregersen PL, et al. Benzoxazinoids: Cereal phytochemicals with putative therapeutic and health-protecting properties. *Mol Nutr Food Res.* 2015; 1324-1338.
44. Sepulveda BA, Corcuera LJ. Effect of gramine on the susceptibility of barley leaves to *Pseudomonas syringae*. *Phytochemistry.* 1990. 29: 465-467.
45. Velozo JA, Alvarez RI, Wächter GA, et al. Increase in gramine content in barley infested by the aphid *Schizaphis graminum* R. *Phytochemistry.* 1999; 52: 1059-1061.
46. Niemeyer H. Hydroxamic acids derived from 2-hydroxy-2H-1,4-benzoxazin-3(4H)-one: key defense chemicals of cereals. *J Agric Food Chem.* 2009; 57: 1677-1696.
47. Makowska B, Bakera B, Rakoczy-Trojanowska M. The genetic background of benzoxazinoid biosynthesis in cereals. *Acta Physiol Plant.* 2015; 37: 176.
48. Elek H, Smart L, Martin J, et al. The potential of hydroxamic acids in tetraploid and hexaploid wheat varieties as resistance factors against the bird-cherry oat aphid, *Rhopalosiphum padi*. *Ann Appl Biol.* 2013; 162: 100-109.
49. Thackray DJ, Wratten SD, Edwards PJ, et al. Resistance to the aphids *Sitobion avenae* and *Rhopalosiphum padi* in Gramineae in relation to hydroxamic acid levels. *Ann Appl Biol.* 1990; 116: 573-582.
50. Tzin V, Lindsay PL, Christensen SA, et al. Genetic mapping shows intraspecific variation and transgressive segregation for caterpillar-induced aphid resistance in maize. *Mol Ecol.* 2015; 24: 5739-5750.
51. Tzin V, Hojo Y, Strickler SR, et al. Rapid defense responses in maize leaves induced by *Spodoptera exigua* caterpillar feeding. *J Exp Bot.* 2017; 68: 4709-4723.
52. Feng R, Houseman JG, Downe AER, et al. Effects of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and 6-methoxybenzoxazinone (MBOA) on the detoxification processes in the larval midgut of the European corn borer. *Pest Biochem Physiol.* 1992; 44: 147.
53. Meihls LN, Handrick V, Glauser G, et al. Natural variation in maize aphid resistance is associated with 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one glucoside methyltransferase activity. *Plant Cell.* 2013; 25: 1-16.
54. Agerbirk N, De Vos M, Kim JH, et al. Indole glucosinolate breakdown and its biological effects. *Phytochem Rev.* 2008; 8: 101.
55. Francis F, Lognay G, Wathelet JP, et al. Effects of Allelochemicals from First (*Brassicaceae*) and Second (*Myzus persicae* and *Brevicoryne brassicae*) Trophic Levels on *Adalia bipunctata*. *J Chem Ecol.* 2001; 27:243-256.
56. Kliebenstein DJ, Kroymann J, Brown P, et al. Genetic Control of Natural Variation in *Arabidopsis* Glucosinolate Accumulation. *Plant Physiol.* 2001; 126: 811 LP-825LP.
57. Doughty KJ, Porter AJR, Morton AM, et al. Variation in the glucosinolate content of oilseed rape (*Brassica napus* L.) leaves. *Ann Appl Biol.* 1991; 118: 469-477.
58. Mewis I, Appel HM, Hom A, et al. Major Signaling Pathways Modulate *Arabidopsis* Glucosinolate Accumulation and Response to Both Phloem-Feeding and Chewing Insects. *Plant Physiol.* 2005; 138: 1149 LP-1162 LP.
59. Kim JH, Lee BW, Schroeder FC, et al. Identification of indole glucosinolate breakdown products with antifeedant effects on *Myzus persicae* (green peach aphid). *Plant J.* 2008; 54: 1015-1026.
60. Kim JH, Jander G. *Myzus persicae* (green peach aphid) feeding on *Arabidopsis* induces the formation of a deterrent indole glucosinolate. *Plant J.* 2007; 49: 1008-1019.
61. de Vos M, Kriksunov KL, Jander G. Indole-3-Acetonitrile Production from Indole Glucosinolates Deters Oviposition by *Pieris rapae*. *Plant Physiol.* 2008; 146: 916-926.
62. Robin AHK, Hossain MR, Park, JI, et al. Glucosinolate Profiles in Cabbage Genotypes Influence the Preferential Feeding of Diamondback Moth (*Plutella xylostella*). *Front Plant Sci.* 2017; 8: 1244.
63. Leek H, Smart L, Martin J, et al. The potential of hydroxamic acids in tetraploid and hexaploid wheat varieties as resistance factors against the bird-cherry oat aphid, *Rhopalosiphum padi*. *Ann Appl Biol.* 2013; 162: 100-109.
64. Maag D, Kohler A, Robert CAM, et al. Highly localised and persistent induction of *Bx1*-dependent herbivore resistance factors in maize. *Plant J.* 2016; 1-16.