*Article*

# Role of Saponins in Plant Defense against the Diamondback Moth, *Plutella xylostella* (L.)

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**Abstract:** The diamondback moth (DBM), *Plutella xylostella L.* (Lepidoptera: Plutellidae) is very destructive crucifers specialized pest that has resulted in significant crop losses worldwide. The pest is well attracted to glucosinolate-containing crucifers such as; *Barbarea vulgaris* (Brassicaceae), and generally to other plants in the genus *Barbarea*. *B. vulgaris* on their part, build up resistance against DBM and other herbivorous insects using glucosinolates; that are plant secondary metabolites used in plant defense–contained only in plants of the order *Brassicales*. Aside glucosinolates, plants in this genus *Barbarea* (*Brassicaceae*) also contain saponins; which is toxic to insects and act as feeding deterrents for plant herbivores, most importantly, DBM, as it was found to prevent the survival of DBM larvae on the plant. Saponins are plant secondary metabolites have been established in higher concentrations in younger in contrast to older leaves within the same plant. Previous studies have found a relationship between ontogenetical changes in the host plant's saponin content and attraction/resistance to *P. xylostella.* The younger leaves recorded higher concentrations of glucosinolates and saponins, which naturally attracts the plant herbivores. DBM was reported to have evolved mechanisms to avoid the toxicity of the former. The plant-herbivore had adapted glucosinolates for host plant recognition, feeding and oviposition stimulants. Despite the adaptation for oviposition by *P. xylostella* adults, larvae of the insect cannot survive on the same plant. An example is in some varieties of *B. vulgaris*. The triterpenoid saponins which act as feeding deterrents in larvae are responsible for this direct defense mechanism against *P. xylostella.* In the future, trials by plant breeders could aim at transferring this insect resistance to other crops. The previous trials had limited because of lack of knowledge on the biosynthetic pathways and regulatory networks of saponins. Herein, we discussed exclusively; saponins mediated plant defense mechanisms against the DBM.

**Keywords:** brassica; food odour preference; HIPVs; *Plutella xylostella*; trap crop

The capacity of individual plant species to develop novel metabolites has been affirmed in charge of their imperviousness to plant herbivores. Plants have developed surprising diversity of substance protections against plant herbivores in light of bioactive mixtures of low atomic weight. A case of the bioactive mixtures utilized by plants in this regard are the triterpenoid saponins; which encourages plant immunity against a wide range of insect pests, pathogens as well as other herbivores .

Saponins are one of the immeasurable and distinct groups of bio-plant items, and categorize secondary plant metabolites with particular natural properties (Mugford and Osbourn, 2012;Moses *et al.*, 2014). Triterpenoid saponins are mostly found in dicotyledonous species whereas monocots mainly synthesis steroidal saponins. Some leguminous crops such as; pea, sugar beet, soybeans, cowpea, asparagus, capsicum peppers have been reported to contain saponins (De Geyter *et al.*, 2007). For crucifers, just a couple of species from genus - *Barbarea* are identified to create saponin; which are directly related to the plant defense against specialist herbivores, such as the diamondback moth (DBM) (*Plutella xylostella*) (Lepidoptera: Plutellidae) (Khakimov *et al.*, 2015).

About over 200 different structures of saponins had so far been described (Augustin *et al.*, 2012). Likewise, Khakimov *et al.* (2015) reported that blends of different chemical structures are accumulated by saponin producing plants. The biological activity of saponins can be attribute to the amphipathic properties of the constituting molecules; which consist of a hydrophobic triterpene or sterol backbone and a hydrophilic carbohydrate chain. Some saponins have potent biological activities that are influence by other aspects of their structure. Additional gene families who have been reported to be involved in saponin biosynthesis and diversification are methyl and acyltransferases (Thimmappa *et al.*, 2014;Ghosh, 2016). Aside crucifers, saponins occur constitutively in many other plant species as part of their defense system.

The saponin content in plants is dynamic, and it influences various biotic stimuli that are related to pest attack, pathogenic infection, plant mutualistic symbioses with rhizobial bacteria and mycorrhizal fungi. Saponin can also serve as allelopathic agents in competitive interactions between plants (Mugford and Osbourn, 2012).

*P. xylostella* – a typical crucifer specialist; is known worldwide as a severe pest of cruciferous crops such as cabbage (*Brassica oleracea*) and oilseed rape (*B. napus*) (Talekar and Shelton, 1993;Li *et al.*, 2016). Most of the glucosinolates – containing crucifers are all suitable hosts for the plant pest. The attractiveness of *P. xylostella* to these plant species is as a result of the glucosinolates content and its secondary products; such as isothiocyanates (Huang *et al.*, 1994). These compounds have been found to stimulate oviposition by *P. xylostella* adults, as well as, feeding by the larvae (Shinoda *et al.*, 2002). A similar observation has also reported in *Pieris rapae*; another crucifer specialist by Huang *et al.* (1994)**.**

According to the findings of Shinoda *et al.* (2002), the response of DBM larvae is to be suspected that there is a feeding-deterrent in a crucifer - *Barbarea vulgaris*. They recorded an adverse effect of the plant volatile compounds on the specialist pests' larva; as the larvae of the insect pest refuse to feed on the plant. The feeding deterrent was isolated from *B. vulgaris* leaves and was identified through the structure to be a monodesmosidic triterpenoid saponin.

In another related report, a highly feeding deterrent activity to *P. xylostella* larvae were recorded in a chloroform extract of *B. vulgaris* leaves (Serizawa *et al.*, 2001;Newman, 2014). Saponins have been reported from different and unrelated plant families (Khakimov *et al.*, 2015). For Brassicaceae, just a couple of species are known to yield saponins (Nielsen *et al.*, 2010a;Badenes-Perez *et al.*, 2014a). Whereas cereals are insufficient in saponins, aside from a few grasses, like *Panicum virgatum*, *Panicum coloratum* as well as *Avena* spp. (Patamalai *et al.*, 1990;Lee *et al.*, 2001;Osbourn, 2003).

The management of DBM has recorded minimum success as a result of its notorious ability to develop resistance to synthetic insecticides (Talekar and Shelton, 1993). The ability of the pest to adapt plant secondary metabolites for host plant recognition, feeding, and oviposition stimulants has also reported (Ratzka *et al.*, 2002;Renwick *et al.*, 2006;Hopkins *et al.*, 2009). Moreover, inadequate knowledge of the biosynthetic paths and conducting systems of saponins has additionally complicated its application for pest control. However, the prospect of saponins modification as direct plant defense strategies against pests has offered alternative control measure for inclusion in Integrated Pest Management program for DBM.

### Plant defense and evolution

A variety of plants is susceptible to environmental disputes but could not escape. In spite of this evident exposure, the earth's flora has developed to be highly abundant and diverse. It's a reality that not all plants are entirely consume, can be because of top-down control (Hairston *et al.*, 1960), also to bottom-up mechanisms such as the direct defense of plants in response to herbivores (Ehrlich and Raven, 1964). Plants might play a major role in top-down control of herbivores by enrolling natural enemies of their enemies named as an indirect defense (Dicke and Sabelis, 1989). Direct plant defense mechanisms can demand structural adjustments, for example, trichomes, thistles, or silica bodies. Furthermore, auxiliary metabolites potentially built up, that are lethal to herbivores, or attract the natural foes of the herbivores (Renwick, 2002). Disregarding their name, derivative metabolites have a vital impact in the chemical communication between plants and their surroundings. They are of basic significance for the appeal of pollinators (terpenes), protecting the plant as opposed to UV light (flavonoids), pathogens and herbivores (alkaloids, glucosinolates, saponins). The majority of plants comprises a significant range of plant derivatives (Jones *et al.*, 1991). From a developmental point, this range is mystified however even ineffectively understood.

The reciprocal process of adaptation within plants and their insect herbivores was observed by Stahl (1888), and he proposed that the synthetic mixtures may be included. These above thoughts were advanced by Ehrlich and Raven (1964) to deliver a hypothetical background for the compound nature of insect and plant communications. They proposed a well ordered biochemical co-advancement amongst plants and bugs. Unexpectedly, some herbivore species build up a resistance for a biochemical that is dangerous and distasteful to different insect pests. Gradually the biochemical may possibly act as feeding stimulant and attractant for a particular insect, which has changed according to certain conditions and even utilize some biochemicals as a guard, from respective plant. It's useful for the insect pest as the plant constitutes a habitation which is limited for other generalist insect pests that dissuaded by the biochemical (Cornell and Hawkins, 2003;Van der Putten, 2003). As a result, plants require new chemical admixtures to be ensured against the particular group of insects. This procedure may bring about a proportional, well ordered "arms race" inside insect pests and its host plant, driving a wide range of biochemical-barrier mixtures (Iwao and Rausher, 1997) (see **Table**).

**Table. List of chemical defense compounds in plants**

| **Family** | **Genus** | **Plant** | **Reference** | **Secondary metabolite form** |
|---|---|---|---|---|
| *Aceraceae* | *Acer L* | Maples (*Acer velutinum*) | (Glénsk *et al.*, 2009) | Triterpenoid Saponins |
| *Agavaceae* | *Agave* | Sisal (*Agave sisalana*) | (Ribeiro *et al.*, 2013) | Steroidal aglycone |
| *Amaranthaceae* | *Achyranthes* | *Achyranthes bidentata.* | (Mitaine-Offer *et al.*, 2001) | Triterpene saponins; Bidentatoside II and chikusetsusaponin V methyl ester. |
| *Amaranthaceae* | *Chenopodium* | Quinoa (*Chenopodium quinoa*) | (Francis *et al.*, 2002;De Geyter *et al.*, 2007) | Triterpenoid saponins |
| *Amaranthaceae* | *Spinacia* | Spinach (*Spinacia oleracea*) | (Francis, Kerem et al. 2002) | Triterpenoid saponins |
| *Amaranthaceae (Chenopodiaceae )* | *Beta* | Sugar beet (*Beta vulgaris*) | (Massiot *et al.*, 1994;Ridout *et al.*, 1994)( De Geyter, Lambert et al. 2007) | Triterpenoid saponins |
| *Apiaceae* | *Steganotaenia* | *Steganotaenia araliacea* | (Lavaud *et al.*, 1992) | Triterpenoid saponins |
| *Aquifoliaceae* | *Ilex* | American holly (*Ilex opaca* Aiton) | (Potter and Kimmerer, 1989) | |
| *Araliaceae* | *Panax* | Ginseng or red ginseng (*Panax ginseng*) | (Shin *et al.*, 2015)(Luo *et al.*, 2011) | Triterpene Saponins; Ginsenosides, glycosides of triterpenoid aglycones |
| *Asparagaceae* | *Yucca L* | Mojave yucca (*Yucca schidigera*) | (Miyakoshi *et al.*, 2000;Piacente *et al.*, 2005) | Steroidal saponins |
| *Asparagaceae* | *Asparagus* | Asparagus (*Asparagus officinalis*) | (Francis *et al.*, 2002;De Geyter *et al.*, 2007) | Steroidal saponins |
| *Asteraceae* | *Atractylis* | *Atractylis flava* | (Chabani *et al.*, 2016) | Triterpenoid saponins |
| *Brassicacea* | *Barbarea* | Winter cress (*Barbarea vulgaris*) | (Kuzina *et al.*, 2009;Kuzina *et al.*, 2011;Augustin *et al.*, 2012;Khakimov *et* | Triterpenoid saponins; hederagenincellobioside, oleanolic acid cellobioside, epihederagenincellobiosid |

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|---|---|---|---|---|
| | | | *al.*, 2012) | e, and gypsogenincellobioside |
| *Campanulaceae* | *Platycodon* | *Platycodon grandiflorum* | (Ma *et al.*, 2016) | Oleanane-type triterpenoid saponins |
| *Caryophyllaceae* | *Saponaria* | Soapwort (*Saponaria officinalis*) | (Koike *et al.*, 1999;Jia *et al.*, 2002;Hostettmann and Marston, 2005) | Triterpenoid saponins |
| *Columelliaceae* (Formerly; *Loganiaceae*) | *Desfontainia* | Chilean Holly (*Desfontainia spinose*) | (Houghton and Lian, 1986) | Triterpenoids |
| *Combretaceae* | *Combretum* | *Combretum nigricans* | (Simon *et al.*, 2003) | Cytotoxic pentacyclic triterpenes |
| *Compositae* | *Aster* | *Aster auriculatus* | (Wang and Yu, 1998) | Triterpenoid saponins |
| *Compositae* | *Aster* | Tatarinow aster (*Aster tataricus*) | (Dongliang and Yu, 1993) | Triterpene glycoside |
| *Compositae* | *Aster* | *Aster ageratoides* | (Sakai *et al.*, 1999) | Triterpenoid saponins |
| *Compositae* | *Aster* | *Aster batagensis* | (Shao *et al.*, 1994;Shao *et al.*, 1995d;Shao *et al.*, 1995e) | Triterpenoid saponins |
| *Compositae* | *Aster* | *Aster bellidiastrum* | (Schöpke *et al.*, 1995;Schöpke *et al.*, 1997) | Triterpenoid saponins |
| *Compositae* | *Aster* | *Aster lingulatus* | (Shao *et al.*, 1997a;Shao *et al.*, 1997b) | Triterpenoid saponins |
| *Compositae* | *Aster* | *Aster scaber* | (Nagao *et al.*, 1996) | Triterpenoid saponins |
| *Compositae* | *Aster* | *Aster sedifolius* | (Corea *et al.*, 2004) | Oleane-type saponins; Astersedifolioside A, B and C |
| *Compositae* | *Aster* | *Aster yunnamensis* | (Shao *et al.*, 1995a;b;Shao *et al.*, 1995c) | Triterpenoid saponins |
| *Cucurbitaceae* | *Gynostemma* | *Gynostemma pentaphyllum* | **(Hu *et al.*, 2010)** (Shi *et al.*, 2011;Yang *et al.*, 2013) | Gypenosides |

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| *Cucurbitaceae* | *Momordica* | Bitter melon (*Momordica charantia* (L.) | (Keller *et al.*, 2011) | Triterpenoid saponins |
| *Dioscoreae* | *Dioscorea* | Wild yam (*Dioscorea spp; D. villosa, D. zingiberensis*) | (Qin *et al.*, 2009;Waller and Yamasaki, 2013) | Dioscin; a steroidal triterpene saponin. |
| *Fabaceae* | *Glycyrrhiza* | Liquorice or *Glycyrrhizaspp; G. glabra, G.uralensis* | (Xu *et al.*, 1996;Augustin *et al.*, 2011) | Lycyrrhizin; a triterpenoid saponin. |
| *Fabaceae* | *Medicago* | Alfalfa (*Medicago sativa*) | (Massiot *et al.*, 1988;Oleszek *et al.*, 1990;Massiot *et al.*, 1991) | Triterpenoid saponins |
| *Fabaceae* | *Desmodium* | *Desmodium adscendens* | (McManus *et al.*, 1993;Rastogi *et al.*, 2011) | Triterpenoid saponins |
| *Fabaceae* | *Glycine* | Soybeans (*Glycine max*) | (Francis, Kerem et al. 2002, De Geyter, Lambert et al. 2007) (Waller and Yamasaki 2013) (Massiot *et al.*, 1992a) | Triterpenoid saponins; Oleanolic saponins; Soyasapogenol A and B. |
| *Fabaceae* | *Pisum* | Pea (*Pisum sativum L*) | (Francis, Kerem et al. 2002, De Geyter, Lambert et al. 2007) | Triterpenoid saponins; Oleanolic saponins |
| *Fabaceae* | *Phaseolus* | Common beans (*Phaseolus vulgaris*) | (Francis, Kerem et al. 2002, De Geyter, Lambert et al. 2007) | Triterpenoid saponins; Oleanolic saponins |
| *Flacourtiaceae* | *Aphloia* | *Aphloia madagascariensis* | (Dijoux *et al.*, 1993) | Triterpene saponins |
| *Flacourtiaceae* | *Aphloia* | *Aphloia theiformis* | (Gopalsamy *et al.*, 1988) | Triterpene saponins |
| *Hippocastanaceae* | *Aesculus* | Horse chestnut (*Aesculus spp; A. hippocastanum, A. turbinate, A. pavia L)* | (Yoshikawa *et al.*, 1996;Kimura *et al.*, 2006;Zhang *et al.*, 2006;Zhang and Li, 2007;Kimura *et al.*, 2008) | Triterpenoidal saponins; Escins Polyhydroxyoleanene pentacyclic triterpenoid saponins; Aesculiosides |

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| *Lamiaceae* | *Salvia* | *Salvia staminea* | (Topcu *et al.*, 2003) | TriterpenoidSaponin, named *salvistamineol* |
| *Lecythidaceae* | *Petersianthus* | *Petersianthus macrocarpus* | (El Izzi *et al.*, 1992;Massiot *et al.*, 1992b) | Triterpenoid saponins |
| *Lecythidaceae* | *Barringtonia* | *Barringtonia acutangula* | (Pal *et al.*, 1994) | Monodesmosidic glucuronide saponins; Barringtosides A, B and C |
| *Liliaceae* | *Allium* | *Allium aflatunense* | (Kawashima *et al.*, 1991;Mimaki *et al.*, 1999c) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium albanum* | (Ismailov *et al.*, 1976) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium albiflorus* | (Ismaĭlov and Aliev, 1976) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium albopilosum* | (Mimaki *et al.*, 1993) | Steroidal glycosides |
| *Liliaceae* | *Allium* | Elephant garlic (*Allium ampeloprasum*) (also known as Leek) | (MoRITA *et al.*, 1988;MATSUNAGA *et al.*, 1998;Mimaki *et al.*, 1999c) | Steroidal saponins |
| *Liliaceae* | *Allium* | Shallot (*Allium ascalonicum*) | (Fattorusso *et al.*, 2002) | Steroidal saponins |
| *Liliaceae* | *Allium* | Onion (*Allium cepa*) | (Corea *et al.*, 2005;Dini *et al.*, 2005) (Lanzotti *et al.*, 2012;Li *et al.*, 2014) | Steroid saponins; furostanol saponins, ceposide A, ceposide B, and ceposide C |
| *Liliaceae* | *Allium* | *Allium chinense* | (Kuroda *et al.*, 1995;Peng and Yao, 1996;Jiang *et al.*, 1999) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium elburzense* | (Barile *et al.*, 2004) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium erubescens* | (Chincharadze *et al.*, 1979;Kravets *et al.*, 1990) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium fistulosum* | (Do *et al.*, 1992) | Steroidal saponins |

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|---|---|---|---|---|
| *Liliaceae* | *Allium* | *Allium giganteum* | (KELGINBAEV *et al.*, 1976;Kawashima *et al.*, 1991;SAsHiDA *et al.*, 1991;MIMAKI *et al.*, 1994) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium jesdianum* | (Mimaki *et al.*, 1999a) | Steroidal glycosides |
| *Liliaceae* | *Allium* | *Allium karataviense* | (Vollerner *et al.*, 1984;Mimaki *et al.*, 1999b) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium macleanii* | (Inoue *et al.*, 1995) | Steroidal glycosides |
| *Liliaceae* | *Allium* | *Allium macrostemon* | (Peng *et al.*, 1995) | Furostanol glycosides |
| *Liliaceae* | *Allium* | *Allium narcissiflorum* | (Lazur'Evskii *et al.*, 1975;Krokhmalyuk and Kintya, 1976;MIMAKI *et al.*, 1996b) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium nutans* | (Akhov *et al.*, 1999;Akhov *et al.*, 2000) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium ostrowskianum* | (Mimaki *et al.*, 1993) | Steroidal glycosides |
| *Liliaceae* | *Allium* | *Allium porrum* | (Harmatha *et al.*, 1987;Carotenuto *et al.*, 1999;Fattorusso *et al.*, 2000) | Spirostane-type saponin; Spirostanol Saponins. Cytotoxic Saponins. |
| *Liliaceae* | *Allium* | Garlic (*Allium sativum* ) | (MATSUURA *et al.*, 1989;Peng and Yao, 1996;Matsuura, 2001;Lanzotti, 2005) | Steroid saponins |
| *Liliaceae* | *Allium* | *Allium schubertii* | (Kawashima *et al.*, 1993) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium sphaerosephalon* | (Mimaki *et al.*, 1996a) | Furostanol saponin |
| *Liliaceae* | *Allium* | *Allium senescens* | (Inoue *et al.*, 1995) | Steroidal glycosides |

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| *Liliaceae* | *Allium* | *Allium triquetrum* | (Corea *et al*., 2003) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium tuberosum* | (Zou *et al*., 2001;Sang *et al*., 2003) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium turcomanicum* | (Pirtskhalava *et al*., 1979) | Steroidal saponins |
| *Liliaceae* | *Allium* | *Allium vineale* | (Chen and Snyder, 1989) | Molluscicidal saponins |
| *Liliaceae* | *Allium* | *Allium waldstenii* | (Kravets *et al*., 1990) | Steroids of spirostan and furostan series |
| *Loganiaceae* | *Antonia* | *Antonia ovata* | (Magid *et al*., 2010) | Cytotoxic triterpenoid saponins |
| *Myrsinaceae* | *Myrsine* | *Myrsine pellucida* | (Lavaud *et al*., 1994a) | Triterpene saponins |
| *Myrsinaceae* | *Tapeinosperma* | *Tapeinosperma clethroides* | (北川勲 *et al*., 1980;Lavaud *et al*., 1999) | Glucuronide saponins: *Desacyl-jegosaponin, desacylboninsaponin A,* and *sakuraso-saponin* |
| *Nyctaginaceae* | *Pisonia* | *Pisonia umbellifera* | (Lavaud *et al*., 1996a) | Oleanolic acid saponins and Seco-glycopyranosyl moiety. |
| *Phyllanthaceae* | *Glochidion* | *Glochidion eriocarpum* | (Nhiem *et al*., 2012) | Cytotoxic oleane-type triterpene saponins |
| *Phytolaccaceae* | Phytolacca | Pokeweeds (*Phytolacca bogotensis*) | (Montoya *et al*., 2009) | Pentacyclic triterpene saponins |
| *Poaceae* | *Avena* | Oats (*Avena sativa*) | (De Geyter *et al*., 2007) | Steroidal saponins |
| *Quillajaceae* (Formerly grouped as; *Rosaceae*) | *Quillaja* | Soapbark tree (*Quillaja saponaria*) | (Kensil *et al*., 1991;Bankefors *et al*., 2008) | Triterpenic saponins |
| *Ranunculaceae* | *Anemone* | *Anemone flaccida* Fr. Shmidt | (Zhao *et al*., 1990;Zhan *et al*., 2016) | Triterpenoid saponins |
| *Rhamnaceae* | *Ziziphus* | Juá (*Ziziphus joazeiro*) | (Ribeiro *et al*., 2013) | Triterpenicaglycone |

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| *Rosaceae* | *Rosa* | Cherokee Rose (*Rosa laevigata*) | (Yuan *et al.*, 2008) | Triterpene glucosides |
| *Sapindaceae* | *Smelophyllum* | *Smelophyllum capense* | (Lavaud *et al.*, 1994b) | Triterpene saponins |
| *Sapindaceae* | *Filicium* | *Filicium decipiens* | (Lavaud *et al.*, 1998) | Triterpene saponins |
| *Sapindaceae* | *Harpullia* | *Harpullia cupanioides* | (Dimbi *et al.*, 1983;Voutquenne *et al.*, 1998) | Triterpenoïdes |
| *Sapindaceae* | *Sapindus* | Soapberry or Soapnut (*Sapindus mukorossi*) | (Shiau *et al.*, 2009) | |
| *Sapotaceae* | *Tridesmostemon* | *Tridesmostemon claessenssi* | (Massiot *et al.*, 1990) | Tridesmosaponin A and B |
| *Sapotaceae* | *Gambeya* | *Gambeya boukokoensis* | (Wandji *et al.*, 2003) | Gamboukokoensides A and B |
| *Sapotaceae* | *Mimusops* | *Mimusops* spp (*M. elengi, M. hexandra* and *M. manilkara*) | (Lavaud *et al.*, 1996b) | Triterpenoidal saponins |
| *Solanaceae* | *Solanum* | Potato (*Solanum tuberosum*) | (De Geyter *et al.*, 2007) | Steroid saponins |
| *Solanaceae* | *Solanum* | Aubergine (*Solanum melongena*) (otherwise known as Eggplant) | (Francis *et al.*, 2002;De Geyter *et al.*, 2007) | Steroid saponins |
| *Solanaceae* | *Capsicum* | Capsicum peppers (*Capsicum species*) | (De Lucca *et al.*, 2006;De Geyter *et al.*, 2007) | Steroidal saponins; four glucose moieties and three glucose moieties |
| *Symplocaceae* | *Symplocos* | *Symplocos chinensis* | (Li *et al.*, 2003;Fu *et al.*, 2005;Li *et al.*, 2006) | Cytotoxic triterpenoid saponins |
| *Theaceae* | *Camellia* | Tea Plant (*Camellia sinensis*) | (Francis *et al.*, 2002) | Triterpenoid saponins |

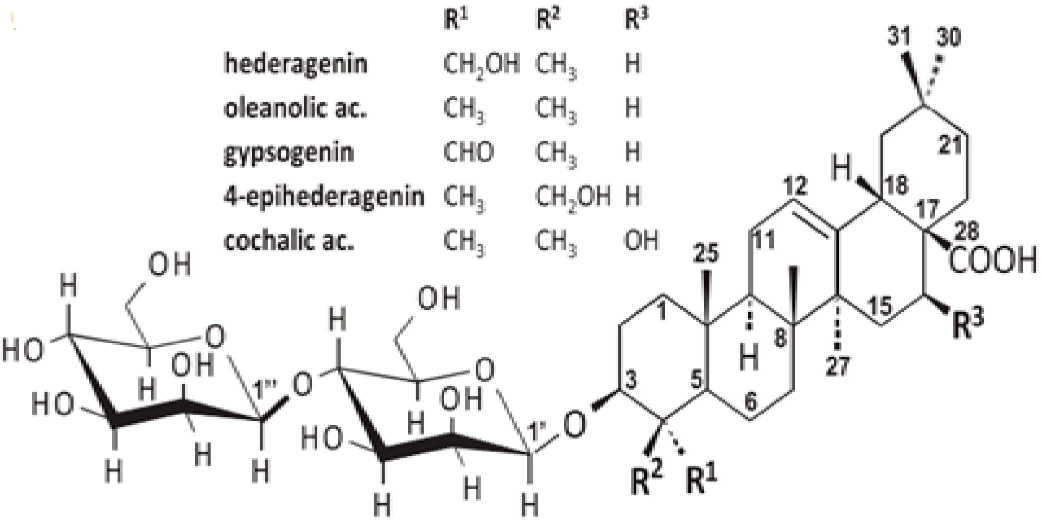
**Chemical variety of secondary metabolites**

A remarkable characteristic for accompanying digestion system is the utmost opportunity of its constituents. Different compounds can alter structurally and quantitatively or may steadily vanish without quick devastating results for development and improvement of the delivering body. Such exceptional characteristics are the premise of biochemical changes, and thus the necessity for modification according to specific pressures applied by an undeniably modifying ecosystem (Hartmann, 1996).

Biochemical diversity is deduced from distinctive change of conventional supporting structures, but such diversity needs serial enzymatic modifications by various product relevancies. Enzyme evolution may start with the substitution, deletion or insertion of a few amino acids, resulting in an alteration of the ratio of goods. The other way by which enzymes may evolve is the inclusion of an inverted portion of the complementary sequence, but those insertions are only viable if they occur in non-essential regions of the DNA and when they do not involve in transcriptional elements (Amtul and Shakoori, 2014). On certain occasions, the gene encoding an enzyme duplicates before mutations take place. In this gene duplication process, one copy supposes a new function while the other copy maintains its original function, called "neofunctionalization" (Pichersky and Gang, 2000;Moore and Purugganan, 2005).

Recently different ecological, evolutionary theories explain the chemical variety of secondary plant compounds. Mainly plants require to be able to compete for the vast range of aboveground and belowground specialist herbivore. Consequently, they may incidentally be in a similar place; and collaborate with phytophagous arthropods, and other microorganisms, like virus, bacteria as welll as fungi (Van der Putten *et al.*, 2001;van Dam *et al.*, 2003;Bezemer and van Dam, 2005). As a result of insect pest's diversity and the co-occurrence scope of bolstering plans, plant requires mixtures of biochemicals for its defence. Thus a wide range of biochemicals may give such protection (Rask *et al.*, 2000). A variety of compounds capacity to produce strong physiological and biochemical effects required to fight different kinds of herbivores. So, a very lethal admixtures may inversely affect many beneficial insects which are factually valuable for plants (pollinators) or evasively (parasitoids) (Poveda *et al.*, 2003;Soler *et al.*, 2007). It happens if the herbivores be a part of an indistinguishable request from the valuable living bodies and jointly the similar physiological features. So the plant should have the capacity to recognize phytophagous insect pests and helpful with comparable characters as well as focus on its defense towards an exact body to maintain a strategic distance from such contrary impact. In this way a substantial diversity of chemicals that would require a high specificity (Fritz and Simms, 1992).

As a result, chemical variety is strongly motivated by the development of phytophagous insect pests. Since development is well on the way to request just a single or a couple of phytophagous insect pests, alternate phytophagous arthropod will remain prevented by the old biochemical. As an outcome, a compound has a capacity to protect, and it might be helpful to extend the biochemical range of a particular plant, in spite of substituting the old synthetic compounds with a recent chemical. Thus, the ethical force of plant and phytophagous insect co-operations involves a distinct and dynamic arrangement of biochemicals.



|  | R$^1$ | R$^2$ | R$^3$ |
|---|---|---|---|
| hederagenin | CH$_2$OH | CH$_3$ | H |
| oleanolic ac. | CH$_3$ | CH$_3$ | H |
| gypsogenin | CHO | CH$_3$ | H |
| 4-epihederagenin | CH$_3$ | CH$_2$OH | H |
| cochalic ac. | CH$_3$ | CH$_3$ | OH |

Recently identified saponins from *B. vulgaris* (Khakimov *et al.*, 2015) (the copyright holder gave permission for the figure's reproduction)

**Balance of costs and benefits by formation of new compounds**

If a gene is changed in an individual plant, the fortune of this gene relies on how it affects the plant’s fitness. A change regarding mutation can be deleterious, neutral or beneficial. If mutations are deleterious, they will quickly diminished, on the other hand, useful ones will soon be changed in the population by natural selection. When the “new” and “old” gene are selectively neutral, polymorphisms can become balanced, and selection keeps segregating alleles for extended periods of time (Mitchell-Olds and Clauss, 2002). Subsequent of the aggregate adjustment of expenses and advantages in the natural ecosystem of the plant portrays the variety among various groups of population and species in amount and kind of protection. Such modification can affect the competitiveness amongst genotypes and as a result the choice for a specific genotype (Simms and Rausher, 1987).

Beside the undeniable advantages clarified in the previous module, large amounts of protection, without an enemy violence, are thought to be expensive (Vrieling *et al.*, 1991;Cipollini, 2002). The defense expenses are mostly visualized regarding to the distribution of minimal assets from different vigor upgrading capacities inside a plant, for example, photosynthesis, development, as well new generation (van der Meijden *et al.*, 1988;Herms and Mattson, 1992). Though, those expenses are not evident, as were assumed for plant biochemicals, especially volatiles along with particular amount of terpenoids by Dicke and Sabelis (1989) and Gershenzon (1994). Some defenses may demand ecological exchanges (Simms and Rausher, 1987) , so when supplies are distributed to protect against a particular phytophagous insect, it can decrease the vigor of the plant when harm triggered by other non-target phytophagous insect increments. Eventually, it is expensive when protection admixtures discourage advantageous living bodies, for example, crop pollinators and expected enemies of the phytophagous insect pests (Strauss *et al.*, 1999).

A diversity of plant defense chemical compounds can act as shields in contrast to insects, involving alkaloids, flavonoids, glucosinolates, and phenolic acids (Rosenthal and Janzen, 1979). Mostly chemical compounds' production is prompted by certain biotic or abiotic factors. Such a schematic arrangement is considered as fight against pathogens and frame insurance economically. Various chemical admixtures involved against insects are the saponins, which have distinctive chemical configurations commonly containing a triterpenoid and steroidal core with a differing quality of glycosylation structures (Hostettmann *et al.*, 1995;Abreu *et al.*, 2012). Saponins are presented in particular 100 various plant categories, even though they mostly are general in species from distinct families or genre, for example, Leguminosae and Liliaceae (Harborne and Baxter, 1996). These are acquired independent from outside signals and lead to the innate immunity, so named as hypo anticipations because they introduced in individual plants.

The negative aspect of cumulating saponins because of primary protection is not just that it has huge measures of vitality, additionally that it make feasible for pathogens to develop moderation. It voided when saponin antecedents cumulate and saponin stuff raises resultantly chemical changes of precursor molecules, which incited by pathogenic contamination (Morrissey and Osbourn, 1999). Perhaps, the saponin substance may build ideally to limited or thorough chemical response of deposited precursors mostly of biochemical compound safety system or because of pathogen given debasement (Szakiel *et al.*, 2011;Sampaio *et al.*, 2016).

About its underlying cause, a vast variety of specialist and generalist insects may be expected to run into them. In the beginning, studies data on the specific activity of saponins against insects was limited to leguminous origins and extracts (Applebaum and Birk, 1979). Hostettmann and Marston (1995) pointed out several high saponin plant parts out of various families, including Aquifoliaceae and Theaceae as well as Leguminosae, are resistant to insects. Recently, a lot of studies showing the structural activity of concentrated or pure saponin fractions against insects has widely elaborated, and influenced insects involves aphids, beetles, caterpillars, and flies (De Geyter *et al.*, 2007;Purkayastha *et al.*, 2016). Nevertheless, the relevant studies of the consequences of various saponins from different origins against insects of different feeding differentiation are still limited.

The behavior of insects change with individual components of host food, some nutrients attract the insects, while others repel. Hence, plants can synthesize some substances that are important for their significant exercises, while the auxiliary metabolites are included during the time spent co-development amongst plants and other living organisms, for example, insects (Alias *et al.*, 2015;Fuenzalida, 2015). *P. xylostella* is a serious pest of cruciferous crops with a cosmopolitan distribution (Furlong *et al.*, 2013). DBM has developed resistance to existing chemical insecticides including the *Bt* toxin (Heckel *et al.*, 1999), making it increasingly difficult to control (Tabashnik *et al.*, 2011).

The capacity of DBM to quickly create imperviousness to insecticides, joined with typically ecological and suitability risks, have fortified enthusiasm for optional controlling systems, for example, trap crops (Shelton and Badenes-Perez, 2006). A trap crop proposed for DBM is wintercress, *Barbarea vulgaris* R. Br. (Brassicaceae) (Badenes-Perez *et al.*, 2004;Lu *et al.*, 2004;Shelton and Nault, 2004;Badenes-Perez *et al.*, 2005). It is a biennial or short-lived perennial plant native to temperate regions worldwide (MacDonald and Cavers, 1991).

### Larval feeding preference and adult oviposition behavior

Larval feeding choice and adult oviposition for younger when contrasted with more seasoned leaves of a specific accommodating plant is a general pattern inside numerous phytophagous insects, particularly in connoisseurs, encompassing *P. xylostella* (Badenes-Perez *et al.*, 2014b). Whenever DBM adults have an option of *B. vulgaris* and different cruciferous crops, despite the fact *P. xylostella* larvae can't continue their lives on a limited range of *B. vulgaris*, as such as plants being much supportive for oviposition of DBM adults (Shinoda *et al.*, 2002;Newman *et al.*, 2016). This non survivorship is thought to be as a result of saponins (Badenes-Perez *et al.*, 2004;2005).

### *P. xylostella* larval survival on cotyledons and true leaves within the same plant

Cotyledons represent to show the capacity of food storage for the improvement of plant, which are the primary photosynthetic network for plant after germination (Boege and Marquis, 2005), cotyledons of brassicaceous plants contain varying contents of glucosinolates (Petersen *et al.*, 2002;Wallace and Eigenbrode, 2002). In *Barbarea* plants, glucosinolates, that might protect the plants against generalist herbivores, were present in cotyledons, but saponins were not, which could defend the plant against specialist herbivores like *P. xylostella.* Similarly, some saponins were not present in cotyledons, indicating that synthesis of saponin-II could be after that of saponin-I (assuming that saponins not translocated from cotyledons to other parts of the plant).

**Saponins presentation in *B. vulgaris* var *arcuata* (Isolation and identification):**

The isolation and identification of a triterpenoid saponin, from the leaves of *B. vulgaris*, which strongly deters feeding of *P. xylostella* larvae and also the first oleane type saponin studied by Shinoda *et al.* (2002). Nielsen *et al.* (2010b)) and Augustin *et al.* (2012) found some other five triterpenoid saponins in *B. vulgaris* namely 3-O-cellobiosyl-hederagenin (hederagenin cellobioside), 3-O-cellobiosyl-oleanoic acid (oleanolic acid), 3-O-cellobiosyl-gypsogenin (gypsogenincellobioside), 3-O-cellobiosylcochalic acid (cochalic acid cellobioside) and 3-O-cellobiosyl-4-epihederagenin (4-epihegragenin cellobioside) Hederagenin cellobioside and oleanolic acid make *B. vulgaris* resistant to *P. xylostella* and are correlated with deterrence of adult females (Kuzina *et al.*, 2009;Augustin *et al.*, 2012;van Mölken *et al.*, 2014). Shinoda *et al.* (2002) discovered that this is not only the first feeding deterrent to *P. xylostella* found in the family Brassicaceae but also the first oleanane-type saponin found in this family. So, advance clarification of the chemical configuration of the saponin may be empowered the development hydrophobic analogs which may characterize as fascinating insecticides and herbicides, which potentially required for ecologically more suitable than present synthetic pesticide and herbicides.

**Biological significance of saponins**

Saponins are depicted as such biochemicals which have extensive spectrum of natural performances. Diverse biological roles have proposed for various saponins, including allelopathic action, anti-carcinogenic, mitigating, cell reinforcement, hemolytic, resistance stimulators, as well as cell layer permeabilizing characteristics, can influence feed consumption, development, proliferation in creatures and cause mortality, development hindrance, limit insects' productiveness and protection against insects and other micro-organisms.

**a) Saponins interference with the feeding behavior**

It has reported that the larvae are not able to attack Brassicaceae species (*B. vulgaris*) due to triterpene (saponin), along with two sugars at the position of C3, which restrain the prosecution of the food uptake (Shinoda *et al.*, 2002). Saponins also showed strong effects against other pathogens like fungi as fungicides and against mollusks as molluscicides, as well as against some bacteria and viruses. In general, it's believed that such biochemicals operate crucially in the plant protection against biotic as well as abiotic factors, as reported from soybean saponins, which had shown detrimental effects against *Tribolium castaneum*, *Bufo viridis* and *Lebistes reticulatus*. Similarly, saponins were also observed to check the cholinesterases as well as the proteolytic drive of other enzymes, like trypsin, chymotrypsin and papain, which leads towards non-specific communication with other protein. Moreover, some studies reported that *Quillaja Saponaria* saponins induce fatality in living insects, and a potent cytotoxic activity on other insects like *Drosophila melanogaster* cells (De Geyter *et al.*, 2012).

b) **Saponins effects on protein digestion**

The toxicity of saponins to various organisms linked to their interaction with biological membranes. Some saponins form complexes with proteins (Potter *et al.*, 1993) and by this action, they apparently inhibit proteinases and affect digestion in insect gut (De Geyter *et al.*, 2012;Amtul and Shakoori, 2014;Soetan *et al.*, 2014). The capability of saponins to penetrate the cell membrane and to induce apoptosis makes saponins cytotoxic to lepidopteran cells (De Geyter *et al.*, 2012).

**c) Enterotoxicity**

Saponins are a group of steroidal or triterpenoid secondary plant metabolites, with divergent biological activities (Tava and Odoardi, 1996;Vincken *et al.*, 2007;Goławska *et al.*, 2012), are responsible for plant defense against antagonists; such as mollusks, pathogens and insects (Dowd *et al.*, 2011;Lee *et al.*, 2016). Moreover, the combination of hydrophilic sugars and hydrophobic sapogenin enable saponins to incorporate into biological membranes. Toxicity of saponins to different organisms seems to be related to their interaction with biological membranes and might be related to their soap-like properties. As a result, detoxification of saponins is probably regarded as enzymatic hydrolysis of the glycosidic bonds, as already produced for fungi (Osbourn, 1996;Osbourn *et al.*, 1998).

A variety of crucifer specialist insects, like as *Pieris brassicae* and *P. rapae* and *P. nemorum* with R-genes, are insusceptible to the defenses of *B. vulgaris*. By finding out the structures of saponins in *B. vulgaris* (Shinoda *et al.*, 2002;Chaieb, 2010) has allowed for investigations into the mechanism by which these in susceptible insects can deal with the potentially toxic saponins. Badenes-Perez *et al.* (2014b) reported that the struggle of *B. vulgaris* to DBM is prompted by two different saponins; I) 3-0-b-cellobiosylhederagenin and II) 3-0-cellobiosyloleanolic acid, which prevent the feeding of DBM. Likewise, it had been reported that the combination of feeding deterrents showed feeding deterrent habituation in insects and the combination of saponins I and II may also be slow down feeding deterrent habituation in *P. xylostella*. Nevertheless, saponins I and II contain similar chemical structures; cross habituation might be easier as compared to compounds with different chemical structures (Akhtar and Isman, 2003a;b;Frisch *et al.*, 2014;Kumar *et al.*, 2015).

Idris and Grafius (1994) and Badenes-Pérez *et al.* (2016) showed that a small percentage of larvae of a *P. xylostella* population collected from the field were able to survive on *B. vulgaris*, even though they did not report the concentration of saponins in these plants. Further research is required to verify in any case being feeding deterrents, saponins I and II, might have a toxic effect on *P. xylostella* larvae. Badenes-Perez *et al.* (2014b) observed that neonates of *P. xylostella* usually try to start feeding on resistant *B. vulgaris*, resulting in feeding signs (Lu *et al.*, 2004).

Dissimilarly to glucosinolates, saponins I and II don't have all the earmarks of being expressed on the leaf covering of *Barbarea* (Badenes-Pérez *et al.*, 2011). Therefore, it is probably that neonates of *P. xylostella* encounter glucosinolates on the leaf surface and start feeding, discontinuing to feed when they get into contact with the saponins in the leaf tissue. Likewise saponins I and II, other saponins have been segregated from P-type *B. vulgaris* var. *arcuata*, which are responsible for resistance of this plant to *P. nemorum* (Nielsen *et al.*, 2010b;Kuzina *et al.*, 2011). Given the similarity in the resistance mechanisms of G-type *B. vulgaris* var. *arcuata* to both *P. nemorum* and *P. xylostella*, these saponins might be required in the resistance of *Barbarea* to *P. xylostella.* Saponins displays higher toxicity, even though the precise mode of action of saponins remains unresolved, its reported by Badenes-Perez *et al.* (2014b) that saponins specifically target pest insects: both the continuous insect cells and the primary midgut cells of *S. littoralis* showed high sensitivity to *Q. saponaria* saponin.

More significantly, the saponins can cause great and quick *in vivo* enterotoxin results on the larvae of *S. littoralis*, and with contents likewise those that can presented in nature. Inedible crops, saponins reported. Therefore, saponins showed substantial evidence for the potency in the control of pest insects, especially insect midgut epithelium as a primary target tissue. So, the insect midgut is an attractive target, as any damaging effect on the midgut epithelial cells will result in starvation, leading towards slow insect mortality. As this component is not the same in midgut cells as the approach of *Bacillus thuringiensis* (*Bt*), it can likewise be of assistance in the management of imperviousness to *Bt*. Furthermore, as aphids are not perceptive to the poisons of *Bt*, all observations propose that saponins may be represent a noteworthy outcomes in developing new, substitute, environmentally favorable aphid control agents amongst integrated pest management.

## Limits of the use of saponins in pest management control

Some saponins have heamolytic and cytotoxic effects due to which the can inhibit the protease activity. Due to this constraint, it's difficult to apply in the field, as they might also toxic the humans. The saponins' function to protect host plant and to discourage phytophagous insects usually is explained according to their performance in the body, such as less food consumption, obstructions as well other poisons (Wittstock and Gershenzon, 2002;Mithöfer and Maffei, 2016). Mostly, the saponins are known as disincentives against insect pests, but their action is obscure yet, however it is identified to interrupt cell sheets (Osbourn, 1996;Sparg *et al.*, 2004).

Moreover, it was assumed with respect to insects that insect resistance, on the base of ecdysteroid receptor complex (EcR), may be due to particular steroidal saponins, which have resemblance with 20-hydroxyecdysone (molting hormone) (Dinan, 2001;Harder *et al.*, 2016). Even though, the saponins' performance was not supported by real resistance reaction to EcR communication, yet rather than loss of cellular unity considerably due to pervasion of the insect cell layer, as described by De Geyter *et al.* (2012). Aside from cellular poisoning quality, saponins additionally exhibited hindrance or antifeedant drive because of herbivores, especially insects. Likewise, other studies have demonstrated that a saponin (aginosid) extracted from leek (*Allium porrum*) caused a noteworthy obstruction in response to two Lepidopteran insect pests, such as *Peridroma saucia* and *Mamestra configurata* (Nawrot *et al.*, 1991) as well aphids (Goławska *et al.*, 2014).

## Conclusions and recommendations

A linkage of glucosinolates and saponins could play a role in the defence of *Barbarea* plants from enthusiast insect pests, adjusted to glucosinolates. Preliminary data on the saponins' performance was constrained to reports of leguminous reserves as well other by-products (Applebaum and Birk, 1979).

Variation in leaf pubescence is common within crucifers (e.g. *B. intermedia*) (Ball, 1993), and therefore not considered a character of taxonomic value. However, it showed that the presence or absence of leaf pubescence in *B. vulgaris* var. *arcuata* seemed to be correlated with many chemical and biological features (Agerbirk *et al.*, 2001;Vermeer *et al.*, 2012;de Jong and Nielsen, 2013), which differed significantly between the two types. It's suggested a greater taxonomic distance between the two types of *B. vulgaris* var. *arcuata,* even though the variability of these characters among presently recognized *Barbarea* taxa was poorly known. Comparative studies of the effects of various saponins of a variety of sources versus insects of various feeding specialization are still limited. The chemical basis of previously reported flea beetle resistance in the G-type of *B. vulgaris* var. *arcuata* is unknown, but resistance is not correlated to glucosinolates or glucosinolate levels (Agerbirk *et al.*, 2001). Resistance may be due to the occurrence of a triterpenoid saponin, which made resistant to *B. vulgaris* against DBM (Shinoda *et al.*, 2002). Development in the interpretation of saponins' biosynthetic system has obstructed due to a distinctive molecular configuration along with the complication of enzymes, related to two major superfamilies, such as I) cytochrome (P450) and II) glycosyltransferase (GT). The greater part of the *Allium* and *Calamus* species consist of saponins, which have crucial role in the health; as such saponins are responsible to decrease the level of garlic cholesterol as well as enhance the anti-fungal function of garlic (Lanzotti *et al.*, 2012;Borah *et al.*, 2016). They display higher toxicity, even though the precise mode of action of saponins remains unresolved, it's reported by Badenes-Perez *et al.* (2014b) that saponins from *Q. saponaria* particularly make approach to *S. littoralis* directly by affecting consistent insect' midgut cells. It might be exemplified significant results in developing new, substitute, environmentally favorable control agents amongst integrated pest management.

Structure–activity studies of saponins as DBM deterrents would, therefore, be useful for the deeper understanding of the components and the systems concerned with insect resistance are appropriate. However, targeted isolation of these insect repellants will elucidate their structures. Hence, the improvement of hydrophobic analogs might be regulated by particular chemical structure of saponins that may be characterized as interesting chemical sprays for a particular range of plants, which are potentially more reasonable natural as compared to the present synthetic herbicide.

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**Author contributions**

All authors contributed to the writing of the' manuscript.

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