Saponins and their role in biological processes in plants

Ahmad Faizal · Danny Geelen

Abstract Saponins are steroid and triterpenoid glycosides that display diverse biological activities. The wide-spread occurrence in plants as well as the potential for pharmaceutical application has led to saponin extraction and identification in numerous species. Although these efforts are important to extend our knowledge of naturally occurring saponin structures, recent attention has been given to the biosynthesis and distribution in plants. In this review, we present recent advances on saponin production and distribution and highlight studies showing effects on the growth and development.

Keywords Plant defense · Plant development · Saponin biosynthesis · Steroidal saponin · Triterpenoid saponin

Introduction

Saponins are structurally complex amphiphatic glycosides of steroids and triterpenoids that are widely produced by plants (Sparg et al. 2004; Vincken et al. 2007) and also by certain marine organisms, such as starfish and sea cucumbers (Tang et al. 2009; Van Dyck et al. 2010). Their name is derived from Latin *sapo* meaning soap, because they have surfactant properties forming stable soap-like foam upon shaking in aqueous solution. Chemically, the term saponin defines a group of high molecular weight glycosides that consist of a glycan moiety linked to an aglycon which is also called genin or sapogenin (Hostettmann and Marston 2005). The chemical structure of sapogenin defines the classification of saponins as triterpenoid saponins (30 carbon atoms) (Fig. 1a) which occur mainly in the class of Magnoliopsida and steroidal saponins (27 carbon atoms with a 6-ring spirostane or a 5-ring furostane skeleton), which are almost exclusively present in the class of Liliopsida (Sparg et al. 2004) (Fig. 1b). According to the carbon skeleton of the aglycon, saponins are sometimes further classified into 12 main classes, namely the: dammaranes, tirucallanes, lupanes, hopanes, oleananes, 23-nor oleananes, taraxasteranes, ursanes, cycloartanes, lanostanes, cucurbitanes, and steroids (Vincken et al. 2007). Moreover, saponins are often present as complex mixtures and their composition may vary depending on the genetic background, the tissue type, the age and the physiological state of the plant and environmental factors (Szakiel et al. 2011a).

Saponins as secondary metabolites are different from the components of primary metabolism due to the fact that they are non-essential for basic metabolic

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processes in the plant. Plants synthesize diverse secondary metabolites that have been clearly demonstrated to play a role in the adaptation of plants to their environment. The production of these secondary molecules may be part of the response to external factors including various biotic and abiotic stimuli. Alternatively, they contribute to the innate immunity as phytoprotectants including phytoanticipins which are constitutively produced and inducible phytoalexins (Dixon 2001).
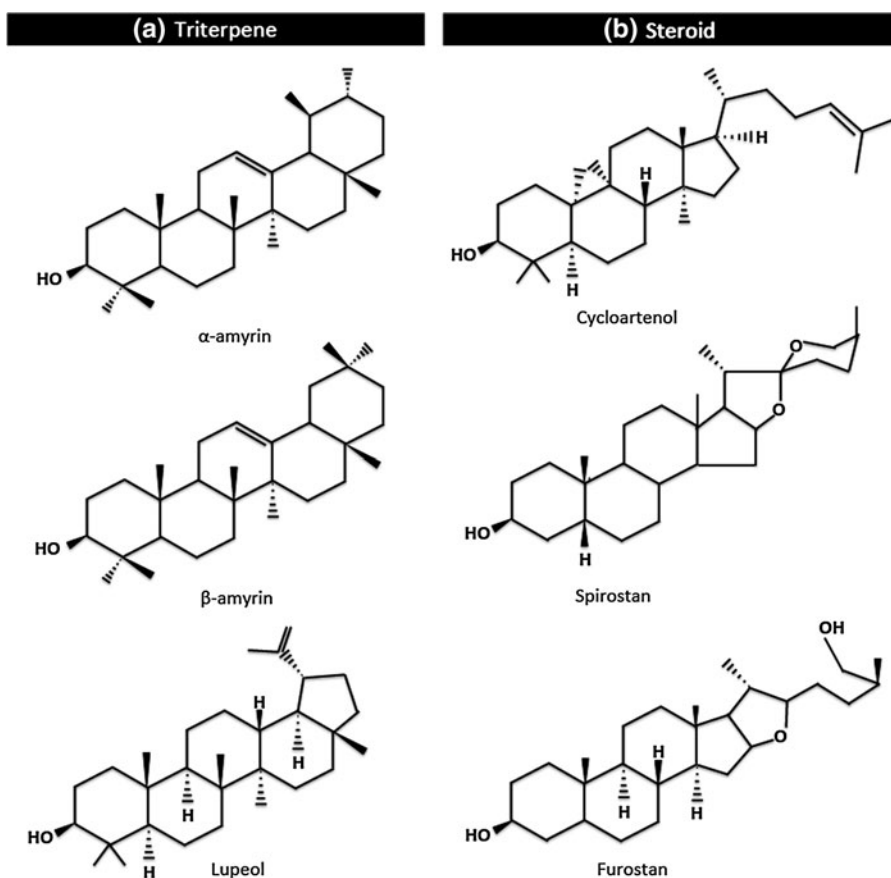
Saponins have also been studied for their wide range of properties, including beneficial and detrimental effects on human health, pesticidal, insecticidal, molluscicidal and fungicidal activity, bitterness and sweetness and other industrial applications such as foaming and surface active agents (Sun et al. 2009; Takahashi et al. 2010; Dawid and Hofmann 2012; Diab et al. 2012; De Geyter et al. 2012a; Chen et al. 2013; Kumar et al. 2013). The pharmacological activities have been reviewed extensively (Lacaille-Dubois and Wagner 2000; Francis et al. 2002; Sparg et al. 2004;

Hostettmann and Marston 2005; Park et al. 2005; Augustin et al. 2011; Osbourn et al. 2011). Here we present a review of saponin production and distribution in plants and their possible roles in biological processes including developmental regulation.

Biosynthesis of saponins

Saponin backbones are synthesized via the isoprenoid pathway through a largely unidentified number of sequential and/or parallel enzymatic steps. Squalene (30-carbon intermediate), which is a precursor for both triterpenoid and steroidal saponins is produced from the mevalonate and non-mevalonate [2-*C*-methyl-D-erythritol 4-phosphate (MEP)] pathways through a series of enzymatic reactions involving geranyl diphosphate synthase (GPS), farnesyl diphosphate synthase (FPS) and squalene synthase (Misawa 2011). Subsequently, squalene is transformed into 2,3-oxidosqualene by squalene epoxidase. The

Fig. 1 The common classes of triterpene (**a**) and steroid (**b**) sapogenin

cyclization of 2,3-oxidosqualene by oxidosqualene cyclases (OSCs) leads to production of tetracyclic sterols through the activity of cycloartenol synthase (CS). Furthermore, steroidal saponins are thought to derive from intermediates in phytosterol pathway downstream of cycloartenol formation. However, the steps at which steroidal saponins and phytosterol biosynthesis diverge have not been elucidated, although cholesterol has been suggested as a candidate precursor of steroidal saponins (Phillips et al. 2006; Vincken et al. 2007). Triterpene saponin biosynthesis branches off the phytosterol pathway by alternative cyclization of 2,3-oxidosqualene through the activity of enzymes such as β-amyrin synthase (βAS), α-amyrin synthase (αAS), lupeol synthase (LuS) and dammarenediol synthase (DDS) (Haralampidis et al. 2002; Vincken et al. 2007).

The occurrence of saponins in plant

Saponin producing plants are found in various geographical regions and climatic zones around the world. These include annual and biennial herbs, grasses, perennial evergreen, shrubs, trees, and wild and cultivated species. Table 1 provides a list of saponin research in the last 4 years (2008–2012) across many different plant families. Although the list is not complete, it does give a good overview of the plant species and families which have been the focus of saponin research in recent years. Of the approximately 100 species listed, about half of these have been investigated for biological activities. Furthermore, a number of species listed were selected based on previous ethnobotanical studies on related species either from the same genus or family. One example is the genus *Maesa* from the family Primulaceae. They were investigated because they contain maesasaponins of which some were reported to have anti-cancer and lack haemolytic activity, which is commonly activity for most saponins. The substitution at position C-22 is an essential structural feature that influences haemolytic activity (Sindambiwe et al. 1998). These favorable biological properties prompted further research to investigate other species within the same genus (Leonard et al. 2003; Maes et al. 2004; Germonprez et al. 2005; Foubert et al. 2009).

Sparg et al. (2004) reported that steroidal saponins are almost exclusively found in the class of Liliopsida

or monocotyledonous angiosperms. This is confirmed by the presence of steroidal saponin in Agavaceae, Asparagaceae, Dioscoreaceae, Liliaceae, Poaceae, Smilacaceae, and Taccaceae. The exception, however, found in Scrophulariaceae and Solanaceae, two plant families from class of Magnoliopsida or dicotyledoneus angiosperms in which all the species studied contained steroidal saponin. The diversification of triterpenoid and steroidal saponins may have come from a species-specific independent evolution but it is currently not clear to what extent the biosynthesis genes for triterpene and steroid sapogenins are conserved. This diversity of both triterpenoid and steroidal saponins biosynthesis will be an important issue to be addressed in the future when more biosynthesis genes of different species have been identified.

The distribution and localization of saponin in plants

Saponin production has been found to vary in individual organs and tissues. Many plant species store saponins in the roots, where these molecules may act as antimicrobial phytoprotectants. For example, The major saponin from *Avena* spp., avenacin A-1, is localized in the epidermal cell layer of oat root tips and also in the lateral root initials, representing a chemical barrier to invading soil-borne microbes that attack plant tissues (Morrissey and Osbourn, 1999; Papadopoulou et al. 1999; Haralampidis et al. 2002).

Different distribution of saponins was found in the root of other species. The distribution of saikosaponins from *Bupleurum falcatum* root has been reported in the outer phloem layer which possesses many secretory canals, especially in the parenchyma cells located around pericycle but not in the mucilaginous exudates within the secretory canals (Tani et al. 1986). In *Panax ginseng*, ginsenosides were found located outside the root cambium, particularly in the periderm and outer cortex outside the phloem (Kubo et al. 1980; Tani et al. 1981). The study of histochemical localization of saponins indicated that saponins reacts with vanillin-acetic acid glacial-perchloric acid solution to produce color from pale red to purplish red (Du and Liu 1992; Tan et al. 2008). Based on this technique, histochemical studies of *Bupleurum chinense* organs showed that in the root primary structures, saponins were mainly distributed in the pericycle and primary phloem.

Table 1 A list of plant species from which saponins have been isolated in 4 recent years (2008–2012)

Family	Species	Saponin type	References
Class of Magnoliopsida			
Amaranthaceae	*Achyranthes fauriei*	Triterpenoid	Ando et al. (2008)
	Alternanthera philoxeroides	Triterpenoid	Fang et al. (2009)
	Celosia cristata	Triterpenoid	Wang et al. (2010)
Araliaceae	*Aralia elata*	Triterpenoid	Lee et al. (2009a)
	Cussonia arborea	Triterpenoid	Kougan et al. (2009)
	Hydrocotyle bonariensis	Triterpenoid	Tabopda et al. (2012)
	Hydrocotyle sibthorpioides	Triterpenoid	Huang et al. (2008)
	Meryta denhamii	Triterpenoid	Cioffi et al. (2008)
Apiaceae	*Eryngium yuccifolium*	Triterpenoid	Zhang et al. (2008)
	Physospermum verticillatum	Triterpenoid	Tundis et al. (2009)
Aquifoliaceae	*Ilex kudingcha*	Triterpenoid	Zuo et al. (2012)
	Ilex pubescens	Triterpenoid	Wang et al. (2008a)
Asteraceae	*Aster sedifolius*	Triterpenoid	Cammareri et al. (2008)
	Lactuca scariola	Triterpenoid	Yadava and Jharbade (2008)
	Silphium radula	Triterpenoid	Calabria et al. (2008)
Balsaminaceae	*Impatiens siculifer*	Triterpenoid	Li et al. (2009)
Bignoniaceae	*Incarvillea delavayi*	Triterpenoid	Ge et al. (2009)
Brassicaceae	*Barbarea vulgaris*	Triterpenoid	Nielsen et al. (2010)
Caesalpiniaceae	*Cassia angustifolia*	Triterpenoid	Khan and Srivastava (2009)
Campanulaceae	*Codonopsis lanceolata*	Triterpenoid	Shirota et al. (2008)
Caprifoliaceae	*Lonicera macranthoides*	Triterpenoid	Chen et al. (2009)
Caryophyllaceae	*Dianthus superbus*	Triterpenoid	Chen et al. (2010b)
	Dianthus versicolor	Triterpenoid	Ma et al. (2009)
	Gypsophila altissima	Triterpenoid	Chen et al. (2010a)
	Gypsophila pacifica	Triterpenoid	Nie et al. (2010)
	Gypsophila pilulifera	Triterpenoid	Arslan et al. (2012)
	Silene viscidula	Triterpenoid	Xu et al. (2012)
	Psammosilene tunicoides	Triterpenoid	Deng et al. (2009)
Chenopodiaceae	*Salicornia herbacea*	Triterpenoid	Kim et al. (2012)
Chrysobalanaceae	*Licania arianeae*	Triterpenoid	de Carvalho et al. (2008)
Combretaceae	*Terminalia ivorensis*	Triterpenoid	Ponou et al. (2010)
	Terminalia tropophylla	Triterpenoid	Cao et al. (2010)
Convovulaceae	*Ipomoea batatas*	Triterpenoid	Dini et al. (2009)
Euphorbiaceae	*Glochidion eriocarpum*	Triterpenoid	Kiem et al. (2009)
Fabaceae	*Abrus precatorius*	Triterpenoid	Xiao et al. (2012)
	Albizia inundata	Triterpenoid	Zhang et al. (2011)
	Caragana microphylla	Triterpenoid	Jin et al. (2011)
	Gleditisia sinensis	Triterpenoid	Gao et al. (2008b)
	Medicago Arabica	Triterpenoid	Tava et al. (2009)
	Pueraria lobata	Triterpenoid	Niiho et al. (2010)
	Pueraria thomsonii	Triterpenoid	Niiho et al. (2010)
Iridaceae	*Crocus sativus*	Triterpenoid	Rubio-Moraga et al. (2011)
Lecythidaceae	*Stauntonia chinensis*	Triterpenoid	Gao et al. (2008a)
Loganiaceae	*Antonia ovata*	Triterpenoid	Magid et al. (2010)

Table 1 continued

Family	Species	Saponin type	References
Mimosaceae	*Cylicodiscus gabunensis*	Triterpenoid	Tene et al. (2011)
	Tetrapleura tetraptera	Triterpenoid	Note et al. (2009)
Myrsinaceae	*Ardisia gigantifolia*	Triterpenoid	Wen et al. (2008)
	Ardisia kivuensis	Triterpenoid	Ndontsa et al. (2012)
	Ardisia pusilla	Triterpenoid	Tian et al. (2009)
Phytolaccaceae	*Phytolacca americana*	Triterpenoid	Wang et al. (2008b)
	Phytolacca bogotensis	Triterpenoid	Montoya et al. (2009)
Polygalaceae	*Polygala crotalarioides*	Triterpenoid	Hua et al. (2010)
	Polygala tenuifolia	Triterpenoid	Li et al. (2008)
	Securidaca longepedunculata	Triterpenoid	Mitaine-Offer et al. (2010)
Primulaceae	*Androsace umbellata*	Triterpenoid	Wang et al. (2008c)
	Maesa ambigua	Triterpenoid	Foubert et al. (2009)
	Maesa argentea	Triterpenoid	Foubert et al. (2009)
	Maesa brevipaniculata	Triterpenoid	Foubert et al. (2009)
	Maesa perlarius	Triterpenoid	Foubert et al. (2009)
Ranunculaceae	*Actaea racemosa*	Triterpenoid	Cicek et al. (2010)
	Anemone raddeana	Triterpenoid	Lu et al. (2009)
	Clematis chinensis	Triterpenoid	Liu et al. (2009)
	Clematis parviloba	Triterpenoid	Yan et al. (2009)
	Nigella glandulifera	Triterpenoid	Xin et al. (2009)
	Pulsatilla turczaninovii	Triterpenoid	Xu et al. (2012)
Rhamnaceae	*Ampelozizyphus amazonicus*	Triterpenoid	Diniz et al. (2009)
Rosaceae	*Potentilla anserine*	Triterpenoid	Zhao et al. (2008)
	Sanguisorba officinalis	Triterpenoid	Zhang et al. (2012b)
Rubiaceae	*Fadogia ancylantha*	Triterpenoid	Mencherini et al. (2010)
	Gardenia jasminoides	Triterpenoid	Wang et al. (2012)
Sapindaceae	*Blighia sapida*	Triterpenoid	Mazzola et al. (2011)
	Xanthoceras sorbifolia	Triterpenoid	Chan et al. (2008)
	Xerospermum noronhianum	Triterpenoid	Jean et al. (2009)
Sapotaceae	*Achras sapota*	Triterpenoid	Ahmed et al. (2008)
	Diploknema butyracea	Triterpenoid	Saha et al. (2010)
	Sideroxylon foetidissimum	Triterpenoid	Sanchez-Medina et al. (2009)
Scrophulariaceae	*Digitalis ciliata*	Steroidal	Gvazava and Kikoladze (2010)
Solanaceae	*Cestrum diurnum*	Steroidal	Fouad et al. (2008)
	Solanum lycocarpum	Steroidal	Nakamura et al. (2008)
Symplocaceae	*Symplocos lancifolia*	Triterpenoid	Acebey-Castellon et al. (2011)
Class of Liliopsida			
Agavaceae	*Agave utahensis*	Steroidal	Yokosuka and Mimaki (2009)
	Dracaena mannii	Steroidal	Tapondjou et al. (2008)
	Yucca desmettiana	Steroidal	Diab et al. (2012)
Asparagaceae	*Asparagus filicinus*	Steroidal	Wu et al. (2010)
Dioscoreacea	*Dioscorea nipponica*	Steroidal	Zhang et al. (2012a)

Table 1 continued

Family	Species	Saponin type	References
Liliaceae	*Anemarrhena asphodeloides*	Steroidal	Lee et al. (2010)
	Chamaelirium luteum	Steroidal	Challinor et al. (2011)
	Chlorophytum borivilianum	Steroidal	Acharya et al. (2008)
	Chlorophytum nimonii	Steroidal	Lakshmi et al. (2009)
	Chlorophytum orchidastrum	Steroidal	Acharya et al. (2010)
	Paris delavayi	Steroidal	Zhang et al. (2009)
	Trillium erectum	Steroidal	Hayes et al. (2009)
	Tupistra chinensis	Steroidal	Liu et al. (2012)
	Ypsilandra thibetica	Steroidal	Xie et al. (2009)
Poaceae	*Panicum virgatum*	Steroidal	Lee et al. (2009b)
Smilacaceae	*Smilax excelsa*	Steroidal	Ivanova et al. (2009)
Taccaceae	*Tacca integrifolia*	Steroidal	Shwe et al. (2010)

Earlier report can be found in Sparg et al. (2004) and Dinda et al. (2010)

However, in mature roots, they were mainly distributed in vascular cambium and secondary phloem. In addition, they were also found to accumulate in mature fruit (Tan et al. 2008). The relationship between structural features of various organs and saponin accumulation was also studied in the important Chinese traditional medicinal plant *Achyrantus bidentata* (Li and Hu 2009). Here, leaves are an active synthesis site rather than for storage. This is supported by the disappearance of saponins from leaves when they withered. *A. bidentata* saponins mainly accumulate in the primary root as well as in cambium cells and in the phloem cells of tertiary vascular bundles. In addition, the presence of saponin-related substances in stem vascular bundles indicated that the stems function as transport organ (Li and Hu 2009). Hence, saponins are commonly found in the outer cell layers and particularly in the epidermis to be effective as a first barrier against microbial attack. In addition, saponins accumulate in phloem as a transitory phase during transport from the shoot to the root (Henry et al. 1991; Li and Hu 2009) or as an intrinsic component to combat insects or root-knot nematodes that feed on phloem sap (Dorhout et al. 1993). Furthermore, the phloem also represents a metabolically active site for biosynthesis of sterol and saponins as reported in *Panax ginseng* (Han et al. 2010).

Triterpene saponin in *Polygala tenufolia* accumulates in roots, stems and leaves (Teng et al. 2009). In the roots, saponin accumulated mainly in phelloderm,

secondary phloem, and rarely in xylem ray and xylem parenchyma cells. In stems, saponin was distributed in the cortex, less in the epidermis and secondary phloem. In leaves, saponin was mainly present in the palisade tissue and less in the epidermis and spongy tissue (Teng et al. 2009). This result indicated that saponin was mainly located in the parenchyma cells of the vegetative organ as similarly reported in the distribution of ginsenosides from *Gynostemma pentaphyllum* (Liu et al. 2005).

The accumulation of oligofurostanosides (steroidal saponins) has been reported in *Dioscorea caucasica* leaves. A histochemical study showed that this type of saponin accumulated in the leaf epidermis receptacle cells. These cells are generally for storage of specific metabolites. On the other hand, oligofurostanosides have not been detected in the mesophyll tissues of the leaf where they are synthesized, which provides evidence for active transport from the mesophyll cells to the receptacle cells located in the epidermal layer (Gurielidze et al. 2004).

The quantification of triterpene saponins in aerial and subterranean organs of barrel medic (*Medicago truncatula*) revealed that roots contained the highest amount of saponin followed by leaf and seed, respectively. However, differential accumulation of specific triterpene saponins was reported. Medicagenic acid conjugates (Fig. 2a) were highly accumulated in leaf and seed, whereas soyasapogenol (Fig. 2b) was found to be higher in the root (Huhman et al. 2005).

Medicagenic acid conjugates in aerial parts have been correlated with biological activity as plant defense against herbivory (Agrell et al. 2003) and the accumulation of soyasapogenol in roots as plant–microbe signaling (Oleszek and Stochmal 2002; Confalonieri et al. 2009) and allelopathic interactions (Waller et al. 1993; Khanh et al. 2005; Tava and Avato 2006). Hence, the differential distribution of specific saponins is most likely the result of spatially controlled biosynthesis and active transport.
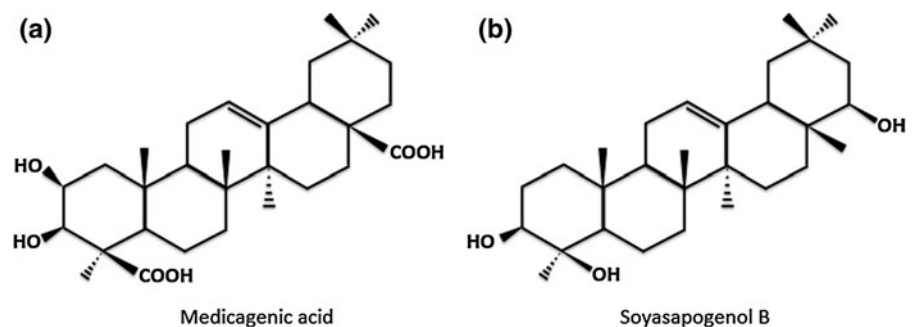
In addition to the intracellular accumulation of saponins, plants may also adopt alternative strategies to make use of the saponins they produce. A recent study has shown that pentacyclic β-amyrin synthesized through ectopic expression of the triterpenoid synthase AtLUP4 in Arabidopsis leaves, accumulates in the intracuticular wax layer (Buschhaus and Jetter 2011). Pentacyclic β-amyrin, naturally absent from Arabidopsis, is removed from the epidermal synthesis site via export into the cuticle with the help of an unknown transporter (Buschhaus and Jetter 2012). The transporter is likely a non-specific steroid or lipid transporter that exhibits a broad substrate spectrum including triterpenoid compounds. Indeed, cutin and wax exporters ABCG11 and ABCG12/CER5 (Bird et al. 2007) share homology with sterol ABCG transporter (Tarr et al. 2009), and are potential candidate triterpenoid transporters. The secretion of triterpenoid saponins suggest that they not only function as indigestive against chewing or sucking insects but potentially also as insect deterrent as was recently shown in an artificial feeding assay with *Quillaja saponaria* saponins pathogen attack, but they may also help to maintain flexibility in the cuticle and avoid cuticular cracks.

Saponins in plant defense

For many secondary metabolites, synthesis is stimulated upon challenge by biotic or abiotic stresses. Although this is a strategy to combat pathogens and build protection in a cost-effective way, some saponins are produced independent from external signals and contribute to the innate immunity. These saponins are referred to as phytoanticipins as they are present in unchallenged plants. The downside of accumulating saponins as a first defense is not only that it consumes substantial amounts of energy, but also that it allows pathogens to develop tolerance. This is avoided when saponin precursors accumulate and saponin content increases as the result of chemical modifications of precursor molecules, which are stimulated upon pathogen infection (Morrissey and Osbourn 1999). For instance, the saponin content may rise due to partial or complete hydrolysis of stored precursors as part of plant defense mechanism or by pathogen controlled degradation (Szakiel et al. 2011b).

Oat has become a model to study saponin biosynthesis as part of the interaction with fungi and bacteria (Osbourn 1996; Osbourn et al. 2003; Mugford et al. 2009). Two types of saponins are constitutively produced, triterpene avenacins and steroidal avenacosides, which are present in roots and leaves, respectively. Avenacins are available in an active glycoslyated form and accumulate in epidermal cells of the root tip. Avenacins have potent antifungal activity and confer resistance to a broad range of soil-borne pathogens (Osbourn 1996). In addition, they are also released into the soil rhizosphere at biologically active concentrations by an unknown mechanism (Papadopoulou et al. 1999; Haralampidis et al. 2002).

Fig. 2 Medicagenic acid **a** found to be higher in shoot, while soyasapogenol B **b** found to be accumulated in root of *M. truncatula*
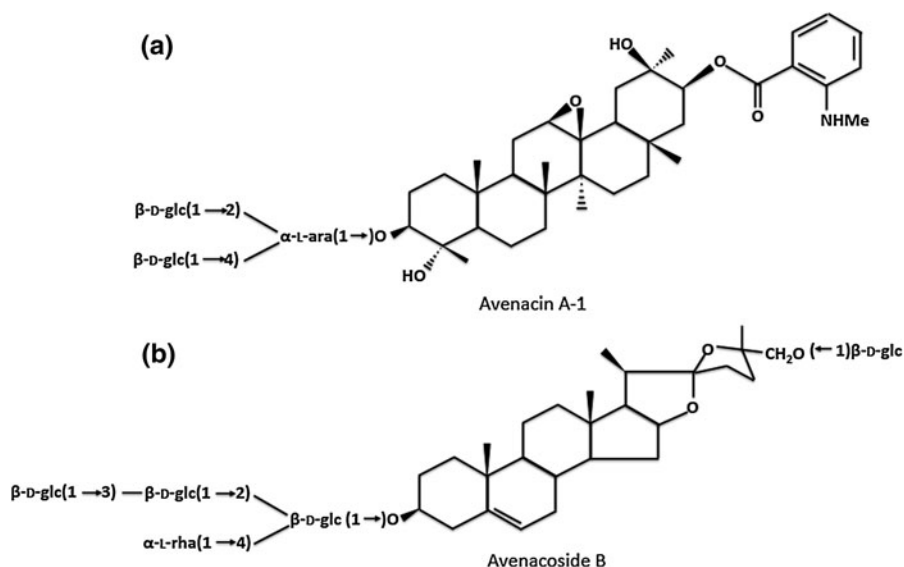
The active avenacin A-1 (Fig. 3a) is stored in the vacuole and represents the major UV fluorescent compound allowing its detection in a fluorescence microscope (Papadopoulou et al. 1999). The increased disease susceptibility of oat variants lacking avenacins supports the importance of saponin in pathogen resistance as phytoprotectants. Furthermore, accumulation of avenacin biosynthesis pathway intermediates in oat roots resulted in callose accumulation, a well known defense mechanism which suggests that accumulation of intermediates also trigger other defense mechanisms (Mylona et al. 2008).

In contrast to avenacins, steroidal avenacosides (Fig. 3b) are known to be stored in plant vacuole as an inactive bidesmosidic form. They are activated when pathogenic fungi damage the plant tissue and disrupt membranes allowing the plant enzyme β-glucosidase to hydrolyse the D-glucose unit forming toxic monodesmosides (Morant et al. 2008; Augustin et al. 2011). The active form of avenacosides disrupts the plasma membrane of fungi by forming membrane pores, which cause fungal cell death. This deleterious effect is associated with the formation of a complex between saponin and ergosterol, the major membrane sterol in fungi. (Weete 1989; Bonanomi et al. 2009). As ergosterol is not present in plants, these complexes do not form and phytotoxicity is avoided in plant cells.

Another role of saponins in plants is to protect them against herbivores and/or insects. Plants frequently endure attack by life-threatening organisms including herbivores and insects. The role of saponins in plant protection against herbivores is mostly based on their action as deterrents, toxins and digestibility inhibitors (Wittstock and Gershenzon 2002; Massad 2012; Mithofer and Boland 2012). The exact mode of saponins as deterrents or toxins is not known, but it is mostly associated with their capacity to disrupt cell membranes. For instance, the lysis of hematocytes and a number of other cell types is a standard cytotoxicity test for saponins (Osbourn 1996; Sparg et al. 2004). In insects, it was hypothesized that steroidal saponins may exert an antagonistic/competitive activity on the ecdysteroid receptor complex (EcR) based on their similarities to the insect moulting hormone 20-hydroxyecdysone (Dinan et al. 2001). However, De Geyter et al. (2012a) showed using both triterpenoid and steroidal saponins on insect cells that the action of saponins was not based on true antagonistic interaction with EcR signaling, but rather because of loss of cellular integrity presumably because of permeation of the insect cell membrane. In addition to cellular toxicity, saponins also showed deterrent or antifeedant activity against insects. It has been reported that a steroidal saponin, aginosid isolated from *Allium porrum* showed strong deterrent effects against two lepidopterans, the variegated cutworm (*Peridroma saucia*), and the bertha armyworm (*Mamestra configurata*) (Nawrot et al. 1991).

Fig. 3 Two different type of saponins produced by oat

Similarly, both deterrent and toxic effects were reported for triterpene saponins against aphids. Spraying faba bean leaves with *Q. saponaria* saponins at sublethal concentrations confirmed that aphids are more sensitive to the taste effect than to their toxicity (De Geyter et al. 2012b).

Constitutive metabolites can be produced in larger amounts after infection. In this circumstance, their status may refer to phytoalexin, although it would depend on whether or not the constitutive concentrations were sufficient for plant protection (Dixon 2001). The inducibility of saponin biosynthesis has in most cases been analyzed using in vitro cultures. For example, the exposure of plant cell cultures of *P. ginseng, Glycyrrhiza glabra, M. truncatula* to methyl jasmonate or other elicitors showed that squalene synthase, squalene epoxidase and β-amyrin synthase are rapidly induced (Hu et al. 2003; Hayashi et al. 2004; Suzuki et al. 2005; Lambert et al. 2011). However, the possible role of saponins as phytoalexin in intact plants is still unclear.

Phytotoxicity of saponins

The toxicity of saponins is not restricted to pathogens or other attacking organisms, but also plants may display sensitivity. For example *M. sativa* saponins applied to wheat seedlings lead to a significant reduction in growth although that germination seems not affected (Oleszek 1993). Waller et al. (1999) reported that soyasaponin I isolated from mungbean (*Vigna radiata*) showed phytotoxic effect on shoot elongation and root growth of *Lactuca sativa*. Additional investigations showed that medicagenic acid inhibits plant growth when applied at high concentration (Guenzi et al. 1964; Waller 1989; Waller et al. 1993; Li et al. 2005). Furthermore, by comparing different structure of saponins from *Medicago* species, it was shown that monodesmoside saponins are in general more active than the related bidesmosides (Tava and Avato 2006). It was hypothesized that a possible mechanism of saponins phytotoxicity may be related to the water absorption at the lipid bilayer interface (Scognamiglio et al. 2012).

Saponins have also been shown to affect cellulose synthesis (Ohana et al. (1998a). Using tobacco cell suspension culture, it was shown that glycosylated triterpene saponins (GTS) isolated from *Pisum*

sativum inhibited β-1,4-glucan synthesis. This action involved plant diguanylate cyclase (dgc) as a target of GTS in the cellulose synthesis apparatus (Ohana et al. 1998b). The elucidation of the complete chemical structure of the saponin (Fig. 4) has enabled the synthesis hydrophobic analogs that may represent novel herbicides, which are potential for ecologically better acceptable than current synthetic herbicides.

In conclusion, phytotoxicty of secondary metabolites such as saponins may play an important role in the framework of agricultural ecosystem. The release of toxic saponins into soil can be exploited not only for sustainable cropping systems in crop rotation, but also for weed management systems.

Saponin role in plant development

Physiological effects associated with plant growth regulation have been reported for saponins. The study on germination process of fenugreek seeds (*Trigonella foenum-graecum*) showed that the diffusible saponin substances located both in the endosperm and perisperm inhibited the production of α-galactosidase activity needed to germinate (Zambou et al. 1993). In addition, a spirostanol saponin from *Yucca* induced callose synthesis in carrot cells (Messiaen et al. 1995).

A γ-pyronyl triterpenoid saponin termed chromosaponin 1 (CSI) (Fig. 5) was isolated from pea and

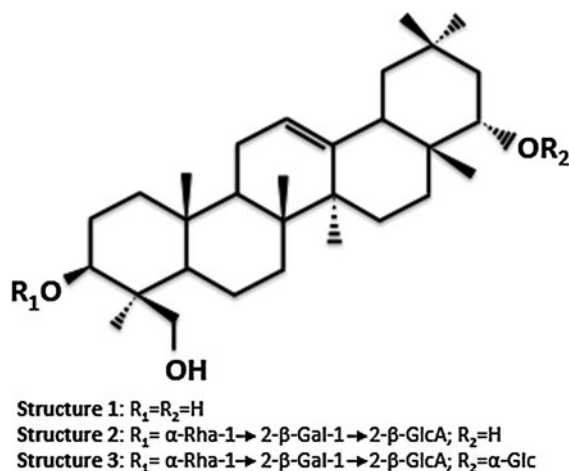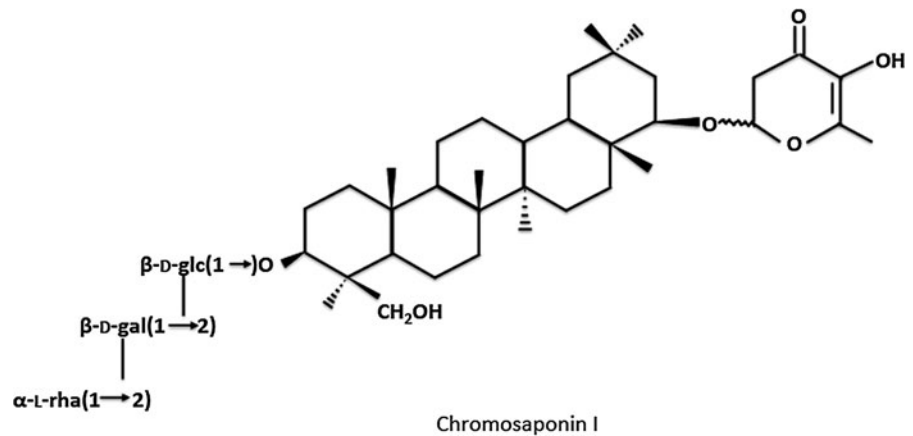Structure 1: R₁=R₂=H
Structure 2: R₁= α-Rha-1➛ 2-β-Gal-1➛2-β-GlcA; R₂=H
Structure 3: R₁= α-Rha-1➛ 2-β-Gal-1➛2-β-GlcA; R₂=α-Glc

Fig. 4 Structure of purified GTS isolated from *P. sativum*

Fig. 5 The chemical structure of chromosaponin I (CSI)

Chromosaponin I

other leguminous plants. CSI is a conjugate of soya-saponin I and γ-pyrone, and was reported to stimulate the growth of lettuce roots (*Lactuca sativa* L. ev. Grand Rapids). The stimulation effect was confirmed by a similar test with Trolox (6-hydroxy-2,5,7,8-tetra-methylchroman-2-carboxylic acid), another amphipathic reductant. In contrast, no root regulation effects were observed using hydrophilic reductants including ascorbate, NADPH, NADH and glutathione (Tsurumi and Tsujino 1995). Therefore, the root growth stimulatory activity was suggested to result from amphipatic reducing activity of CSI.

The influence of CSI on root growth was further investigated in Arabidopsis (Rahman et al. 2001). CSI specifically interacts with the AUX1 protein in regulating the gravitropic response of Arabidopsis roots. Application of 60 μM CSI disrupted the vertically oriented elongation of wild type roots grown in agar plates but oriented the elongation of agravitropic mutant *aux1-7* roots toward gravity. In *aux1-7* roots, CSI stimulated the uptake of IAA and induced gravitropic bending. The correlation between auxin uptake and gravitropic bending suggests that CSI may regulate gravitropic response by inhibiting or stimulating the uptake of endogenous auxin in root cells (Rahman et al. 2001). Furthermore, the growth rate of Arabidopsis roots was accelerated when the seedlings were treated with 300 μM CSI. The length of mature epidermal cells was increased by 2–3 folds and the number of epidermal cells was also increased by twofold (Rahman and Tsurumi 2002). This result indicated that saponin affects cell elongation, which previously has been reported to inhibit ethylene signaling (Rahman et al. 2000).

Genetic analysis of avenacin A-1 *saponin-deficient* (*sad*) mutants, the major avenacin produced by oats showed their expression is tightly regulated and is restricted to the epidermal cell layer of root tips (Mylona et al. 2008). Mutants defective for *Sad1*, the gene for the first committed enzyme in the pathway, show normal root morphology. Thus, saponins are not required for root development. However, mutations at the two loci, *Sad3* and *Sad4* resulted in stunted root growth, membrane trafficking defects in the root epidermis, and root hair deficiency. *sad3* and *sad4* - mutants are both affected in their ability to glucosylate avenacins and accumulate the same intermediate, monodeglucosyl avenacin A-1. These mutants have epidermis-specific membrane trafficking defects that are suppressed by mutations at *Sad1*, indicating that accumulation of monodeglucosyl avenacin A-1 is the cause rather than a consequence of the observed root defects. This result suggested that *Sad3* and/or *Sad4* - may be required specifically for triterpene glycosylation. Alternatively, they may have functions in root growth and development that indirectly affect the glycosylation process.

Soyasapogenol B, a triterpene saponin which is present in most legume species was reported to stimulate germination of barley seeds (*Hordeum vulgare*) (Macias et al. 1997). In addition, Soyasapogenol B isolated from common vetch (*Vicia sativa*) showed a stimulatory activity on broomrape (*Orobanche minor*) seed germination, but did not stimulate any other *Orobanche* species (Evidente et al. 2011). It showed high stimulatory activity on *O. minor* seed germination when tested at 10^{-3}–10^{-4} M. At 10^{-5} M, no stimulatory activity was observed, suggesting poor

specificity. Nevertheless, this stimulatory activity could be important for weed germination control strategies, as an alternative to strigolactones which are unstable in water (Akiyama et al. 2010).

Takagi et al. introduced two different RNAi cassettes driven by seed-specific promoter to target β-amyrin synthase expression in *Glycine max* (Takagi et al. 2011). This experiment resulted in a sufficient reduction of saponin content of soybean seeds. Such saponin deficiency, however, did not appear to affect the growth of plants under greenhouse conditions, suggesting that seed saponins are not required for normal growth and development in soybean (Takagi et al. 2011).

Root nodulation

Expression and biochemical studies have suggested a possible involvement of β-amyrin and derived saponins in the regulation of root nodulation. Indeed, overexpression of *AsOXA1*, a β-amyrin synthase from *Aster sedifolius* in *M. truncatula* caused in a subset of lines enhanced root nodulation (Confalonieri et al. 2009). The improvement of nodulation is, however, presumably indirect as these plants did not exhibit significant differences in saponin content in roots or in growth and biomass performance compared with the control plants. Similarly reported by Hayashi et al. (2004) who examined the expression pattern of β-amyrin synthase in different tissues of *Glycyrrhiza glabra*, found high levels of β-amyrin synthase mRNA and triterpene saponins in root nodules. Interestingly, by analyzing pea root nodules, Hernandez and Cooke (1996) were able to detect β-amyrin in peribacteroid membranes and the microsomal fraction of nodule cells, which mostly corresponded to plant cell endoplasmic reticulum vesicles. Further investigation showed that the host plant synthesized β-amyrin, but this compound was not detected in free-living bacteria or in the plasma membrane of roots.

Lupeol, another type of the triterpene aglycon, has been reported to influence nodule formation in *Lotus japonicus* by down-regulating the expression of early nodulin gene *ENOD40*. A clear decrease in *ENOD40* expression was observed in plants treated with lupeol when compared with untreated plants. The effect was very rapid after the addition of lupeol at 10 min and was even more pronounced at 6 and 12 h post-inoculation with nodule bacterium *Mesorhizobium loti*. Further investigation showed that lupeol has no direct effect on *Mesorhizobium loti*. In addition, the silencing of lupeol synthase (LuS) gene resulted in a phenotype that was similar to that observed for plant overexpressing *ENOD40* (Delis et al. 2011). Thus, in the absence of lupeol, the expression of *ENOD40* is elevated leading to a more rapid nodulation phenotype. As it has been previously reported, *ENOD40* leads to accelerated nodulation in *Medicago* as a consequence of extensive cortical cell division and increased initiation of primordia (Charon et al. 1999). However, this effect appears to be specific lupeol as application of another triterpene, β-amyrin has no effect on *ENOD40* expression (Delis et al. 2011). So far, it is not known whether lupeol act by modifying enzymes or other compounds required for nodulation.

Concluding remarks

The wide spread occurrence of plant saponins underwrites the importance of this group of secondary metabolites in the plant kingdom. While most studies support a role for saponins as phytoprotectants, a role for saponins in the regulation of plant growth and development remains one of the possible functions that warrant further investigation.

The biosynthetic pathway of saponin is still not fully unraveled although major progress has been made for oat and other saponin producing plants. Furthermore, the diversity of both triterpenoid and steroidal saponins has led to increasing interest of these compounds in recent years. It also offers the opportunity for further research on phytochemistry and biological activity of saponins. Accordingly, much effort has been put into elucidation of possible roles of saponins in plants, as well as their prospect application for industry. In the next years additional efforts should focus on the tissue specificity of saponin production as well as more detailed analysis of the cellular localization and storage of saponins. These studies will provide further insight into the functions of saponins in plants and promote the exploration of plant-derived natural products in the future.

References

Acebey-Castellon IL, Voutquenne-Nazabadioko L, Huong DTM, Roseau N, Bouthagane N, Muhammad D, Debar ELM, Gangloff SC, Litaudon M, Sevenet T, Nguyen VH, Lavaud C (2011) Triterpenoid saponins from *Symplocos lancifolia*. J Nat Prod 74:163–168

Acharya D, Mitaine-Offer AC, Kaushik N, Miyamoto T, Paululat T, Lacaille-Dubois MA (2008) Furostane-type steroidal saponins from the roots of *Chlorophytum borivilianum*. Helv Chim Acta 91:2262–2269

Acharya D, Mitaine-Offer AC, Kaushik N, Miyamoto T, Paululat T, Mirjolet JF, Duchamp O, Lacaiile-Dubois MA (2010) Steroidal saponins from *Chlorophytum orchidastrum*. J Nat Prod 73:7–11

Agrell J, Oleszek W, Stochmal A, Olsen M, Anderson P (2003) Herbivore-induced responses in alfalfa (*Medicago sativa*). J Chem Ecol 29:303–320

Ahmed R, Rashid F, Ahmed VU, Mohammad FV, Noorwala M, Bibi N, Kazmi SU (2008) Saponins from the seeds of *Achras sapota*. J Asian Nat Prod Res 10:7–16

Akiyama K, Ogasawara S, Ito S, Hayashi H (2010) Structural requirements of strigolactones for hyphal branching in AM fungi. Plant Cell Physiol 51:1104–1117

Ando H, Fukumura M, Hori Y, Hirai Y, Toriizuka K, Kuchino Y, Ida Y (2008) Two new glucuronide saponins, Achyranthosides G and H, from *Achyranthes fauriei* root. J Nat Med 62:57–62

Arslan I, Celik A, Chol JH (2012) A cytotoxic triterpenoid saponin from under-ground parts of *Gypsophila pilulifera* Boiss. & Heldr. Fitoterapia 83:699–703

Augustin JM, Kuzina V, Andersen SB, Bak S (2011) Molecular activities, biosynthesis and evolution of triterpenoid saponins. Phytochemistry 72:435–457

Bird D, Beisson F, Brigham A, Shin J, Greer S, Jetter R, Kunst L, Wu XW, Yephremov A, Samuels L (2007) Characterization of Arabidopsis ABCG11/WBC11, an ATP binding cassette (ABC) transporter that is required for cuticular lipid secretion. Plant J 52:485–498

Bonanomi G, Vinale F, Scala F (2009) The role of natural products in plant-microbe interactions. In: Osbourn AE, Lanzotti V (eds) Plant-derived natural products. Springer, USA, pp 301–320

Buschhaus C, Jetter R (2011) Composition differences between epicuticular and intracuticular wax substructures: how do plants seal their epidermal surfaces? J Exp Bot 62:841–853

Buschhaus C, Jetter R (2012) Composition and physiological function of the wax layers coating Arabidopsis leaves: β-amyrin negatively affects the intracuticular water barrier. Plant Physiol 160:1120–1129

Calabria LM, Piacente S, Kapusta I, Dharmawardhane SF, Segarra FM, Pessiki PJ, Mabry TJ (2008) Triterpene saponins from *Silphium radula*. Phytochemistry 69:961–972

Cammareri M, Consiglio MF, Pecchia P, Corea G, Lanzotti V, Ibeas JI, Tava A, Conicella C (2008) Molecular characterization of beta-amyrin synthase from *Aster sedifolius* L. and triterpenoid saponin analysis. Plant Sci 175:255–261

Cao S, Brodie PJ, Callmander M, Randrianaivo R, Rakotobe E, Rasamison VE, Kingston DGI (2010) Saponins and a lignan derivative of *Terminalia tropophylla* from the Madagascar Dry Forest. Phytochemistry 71:95–99

Challinor VL, Stuthe JMU, Bernhardt PV, Lehmann RP, Kitching W, De Voss JJ (2011) Structure and absolute configuration of helosides A and B, new saponins from *Chamaelirium luteum*. J Nat Prod 74:1557–1560

Chan PK, Zhao M, Che CT, Mak E (2008) Cytotoxic acylated triterpene saponins from the husks of *Xanthoceras sorbifolia*. J Nat Prod 71:1247–1250

Charon C, Sousa C, Crespi M, Kondorosi A (1999) Alteration of enod40 expression modifies *Medicago truncatula* root nodule development induced by *Sinorhizobium meliloti*. Plant Cell 11:1953–1965

Chen Y, Feng X, Wang M, Jia XD, Zhao YY, Dong YF (2009) Triterpene glycosides from *Lonicera*. II. Isolation and structural determination of glycosides from flower buds of *Lonicera macranthoides*. Chem Nat Compd 45:514–518

Chen Q, Luo JG, Kong LY (2010a) Triterpenoid saponins from *Gypsophila altissima* L. Chem Pharm Bull 58:412–414

Chen X, Luo JG, Kong LY (2010b) Two new triterpenoid saponins from *Dianthus superbus* L. J Asian Nat Prod Res 12:458–463

Chen J, Zhang S, Yang X (2013) Control of brown rot on nectarines by tea polyphenol combined with tea saponin. Crop Prot 45:29–35

Cicek SS, Schwaiger S, Ellmerer EP, Stuppner H (2010) Development of a fast and convenient method for the isolation of triterpene saponins from *Actaea racemosa* by high-speed countercurrent chromatography coupled with evaporative light scattering detection. Planta Med 76:467–473

Cioffi G, Dal Piaz F, Vassallo A, Venturella F, De Caprariis P, De Simone F, De Tommasi N (2008) Antiproliferative oleanane saponins from *Meryta denhamii*. J Nat Prod 71:1000–1004

Confalonieri M, Cammareri M, Biazzi E, Pecchia P, Fevereiro MPS, Balestrazzi A, Tava A, Conicella C (2009) Enhanced triterpene saponin biosynthesis and root nodulation in transgenic barrel medic (*Medicago truncatula* Gaertn.) expressing a novel beta-amyrin synthase (*AsOXA1*) gene. Plant Biotechnol J 7:172–182

Dawid C, Hofmann T (2012) Structural and sensory characterization of bitter tasting steroidal saponins from asparagus spears (*Asparagus officinalis* L.). J Agric Food Chem 60:11889–11900

de Carvalho MG, Candido LFD, da Costa PM, do Nascimento IA, Braz-Filho R (2008) Triterpenes acids and saponins isolated from *Licania arianeae* Prance (Chrysobalanaceae). J Nat Med 62:360–361

De Geyter E, Smagghe G, Rahbe Y, Geelen D (2012a) Triterpene saponins of *Quillaja saponaria* show strong aphicidal and deterrent activity against the pea aphid *Acyrthosiphon pisum*. Pest Manag Sci 68:164–169

De Geyter E, Swevers L, Soin T, Geelen D, Smagghe G (2012b) Saponins do not affect the ecdysteroid receptor complex but cause membrane permeation in insect culture cell lines. J Insect Physiol 58:18–23

Delis C, Krokida A, Georgiou S, Peña-Rodríguez LM, Kavroulakis N, Ioannou E, Roussis V, Osbourn AE, Papadopoulou KK (2011) Role of lupeol synthase in *Lotus japonicus* nodule formation. New Phytol 189:335–346

Deng X-T, Liu X-X, Zhu D, Wang Q (2009) A new triterpenoid saponin from *Psammosilene tunicoides*. Chinese J Nat Med 7:101–104

Diab Y, Ioannou E, Emam A, Vagias C, Roussis V (2012) Desmettianosides A and B, bisdesmosidic furostanol saponins with molluscicidal activity from *Yucca desmettiana*. Steroids 77:686–690

Dinan L, Bourne PC, Meng Y, Sarker SD, Tolentino RB, Whiting P (2001) Assessment of natural products in the Drosophila melanogaster B-II cell bioassay for ecdysteroid agonist and antagonist activities. Cell Mol Life Sci 58:321–342

Dinda B, Debnath S, Mohanta BC, Harigaya Y (2010) Naturally occurring triterpenoid saponins. Chem Biodivers 7:2327–2580

Dini I, Tenore GC, Dini A (2009) Saponins in *Ipomoea batatas* tubers: isolation, characterization, quantification and antioxidant properties. Food Chem 113:411–419

Diniz LRL, Santana PC, Ribeiro APAF, Portella VG, Pacheco LF, Meyer NB, Cesar IC, Cosenza GP, Brandao MDL, Vieira MAR (2009) Effect of triterpene saponins from roots of *Ampelozizyphus amazonicus* Ducke on diuresis in rats. J Ethnopharmacol 123:275–279

Dixon RA (2001) Natural products and plant disease resistance. Nature 411:843–847

Dorhout R, Gommers FJ, Kolloffel C (1993) Phloem transport of carboxyfluorescein through tomato roots infected with *Meloidogyne incognita*. Physiol Mol Plant P 43:1–10

Du X, Liu M (1992) Studies of histochemistry of saikosaponins. China J Chin Mater Med 17:261–263

Evidente A, Cimmino A, Fernandez-Aparicio M, Rubiales D, Andolfi A, Melck D (2011) Soyasapogenol B and trans-22-dehydrocampesterol from common vetch (*Vicia sativa* L.) root exudates stimulate broomrape seed germination. Pest Manag Sci 67:1015–1022

Fang JB, Yao Z, Chen JC, Liu YW, Takaishi Y, Duan HQ (2009) Cytotoxic triterpene saponins from *Alternanthera philoxeroides*. J Asian Nat Prod Res 11:261–266

Fouad MA, Mohamed KM, Kamel MS, Matsunami K, Otsuka H (2008) Cesdiurins I-III, steroidal saponins from *Cestrum diurnum* L. J Nat Med 62:168–173

Foubert K, Vermeersch M, Theunis M, Apers S, Cos P, Claeys M, Luc VP, Pieters L, Maes L (2009) LC-MS Analysis of 13, 28-Epoxy-oleanane saponins in *Maesa* spp. extracts with antileishmanial activity. Phytochem Anal 20:159–167

Francis G, Kerem Z, Makkar HPS, Becker K (2002) The biological action of saponins in animal systems: a review. Brit J Nutr 88:587–605

Gao H, Wang Z, Yang L, Yu Y, Yao ZH, Wang NL, Zhou GX, Ye WC, Yao XS (2008a) Five new bidesmoside triterpenoid saponins from *Stauntonia chinensis*. Magn Reson Chem 46:630–637

Gao ZZ, Xia YF, Yao XJ, Dai Y, Wang Q (2008b) A new triterpenoid saponin from *Gleditisia sinensis* and structure-activity relationships of inhibitory effects on lipopolysaccharide-induced nitric oxide production. Nat Prod Res 22:320–332

Ge X, Lin DC, Zhang WD, Zhang XR (2009) Triterpenoid saponins and monoterpenoid glycosides from *Incarvillea delavayi*. J Asian Nat Prod Res 11:838–844

Germonprez N, Maes L, Van Puyvelde L, Van Tri M, Tuan DA, De Kimpe N (2005) In vitro and in vivo anti-leishmanial activity of triterpenoid saponins isolated from *Maesa balansae* and some chemical derivatives. J Med Chem 48:32–37

Guenzi WD, Kehr WR, McCalla TM (1964) Water-soluble phytotoxic substances in alfalfa forage: variation with variety, cutting, year, and stage of growth. Agron J 56:499–500

Gurielidze K, Gogoberidze M, Dadeshidze I, Vardosanidze M, Djaoshvilo M, Loinkatsi N (2004) Tissue and subcellular localization of oligofurostanosides and their specific degrading beta-glucosidase in *Dioscorea caucasica* Lipsky. Phytochemistry 65:555–559

Gvazava LN, Kikoladze VS (2010) Furostane-type steroidal saponin from *Digitalis ciliata*. Chem Nat Compd 46:246–249

Han JY, In JG, Kwon YS, Choi YE (2010) Regulation of ginsenoside and phytosterol biosynthesis by RNA interferences of squalene epoxidase gene in *Panax ginseng*. Phytochemistry 71:36–46

Haralampidis K, Trojanowska M, Osbourn AE (2002) Biosynthesis of triterpenoid saponin in plants. Adv Biochem Eng Biot 75:31–49

Hayashi H, Huang P, Takada S, Obinata M, Inoue K, Shibuya M, Ebizuka Y (2004) Differential expression of three oxidosqualene cyclase mRNAs in *Glycyrrhiza glabra*. Biol Pharm Bull 27:1086–1092

Hayes PY, Lehmann R, Penman K, Kitching W, De Voss JJ (2009) Steroidal saponins from the roots of *Trillium erectum* (Beth root). Phytochemistry 70:105–113

Henry M, Rochd M, Bennini B (1991) Biosynthesis and accumulation of saponins in *Gypsophila paniculata*. Phytochemistry 30:1819–1821

Hernandez LE, Cooke DT (1996) Lipid composition of symbiosomes from pea root nodules. Phytochemistry 42:341–346

Hostettmann K, Marston A (2005) Saponins. Cambridge University Press, Cambridge

Hu XY, Neill S, Cai WM, Tang ZC (2003) Hydrogen peroxide and jasmonic acid mediate oligogalacturonic acid-induced saponin accumulation in suspension-cultured cells of Panax ginseng. Physiol Plantarum 118:414–421

Hua Y, Chen CX, Zhou J (2010) Two new triterpenoid saponins from *Polygala crotalarioides*. Chin Chem Lett 21:1107–1110

Huang HC, Liaw CC, Zhang LJ, Ho HU, Kuo LMY, Shen YC, Kuo YH (2008) Triterpenoidal saponins from *Hydrocotyle sibthorpioides*. Phytochemistry 69:1597–1603

Huhman DV, Berhow MA, Sumner LW (2005) Quantification of saponins in aerial and subterranean tissues of *Medicago truncatula*. J Agr Food Chem 53:1914–1920

Ivanova A, Mikhova B, Klaiber I, Dinchev D, Kostova I (2009) Steroidal saponins from *Smilax excelsa* rhizomes. Nat Prod Res 23:916–924

Jean TP, Shaari K, Paetz C, Ismail IS, Abas F, Lajis NH, Ahmad VU (2009) Bidesmosidic oleanane saponins from *Xerospermum noronhianum*. Helv Chim Acta 92:1973–1982

Jin GL, Zheng CJ, Xin WB, Mao ZJ, Sun PX, Zeng ZX, Qin LP (2011) Triterpenoid saponins from the seeds of *Caragana microphylla*. Arch Pharm Res 34:869–873

Khan NA, Srivastava A (2009) Antifungal activity of bioactive triterpenoid saponin from the seeds of *Cassia angustifolia*. Nat Prod Res 23:1128–1133

Khanh TD, Chung MI, Xuan TD, Tawata S (2005) The exploitation of crop allelopathy in sustainable agricultural production. J Agron Crop Sci 191:172–184

Kiem PV, Thua VK, Yen PH, Nhiem NX, Tung NH, Cuong NX, Minh CV, Huong HT, Hyun JH, Kang HK, Kim YH (2009) New triterpenoid saponins from *Glochidion eriocarpum* and their cytotoxic activity. Chem Pharm Bull 57:102–105

Kim YA, Kong CS, Lee JI, Kim H, Park HY, Lee HS, Lee C, Seo Y (2012) Evaluation of novel antioxidant triterpenoid saponins from the halophyte *Salicornia herbacea*. Bioorg Med Chem Lett 22:4318–4322

Kougan GB, Miyamoto T, Mirjolet JF, Duchamp O, Sondengam BL, Lacaille-Dubois MA (2009) Arboreasides A-E, triterpene saponins from the bark of *Cussonia arborea*. J Nat Prod 72:1081–1086

Kubo M, Tani T, Katsuki T, Ishizaki K, Arichi S (1980) Histochemistry.1. Ginsenosides in ginseng (Panax ginseng C A Meyer, root). J Nat Prod 43:278–284

Kumar S, Verma AK, Das M, Jain SK, Dwivedi PD (2013) Clinical complications of kidney bean (*Phaseolus vulgarisss* L.) consumption. Nutrition 29:821–827

Lacaille-Dubois MA, Wagner H (2000) Bioactive saponins from plants: an update. In: Rahman Au (ed) Studies in natural products chemistry, part B, vol 21. Elsevier, Amsterdam, pp 633–687

Lakshmi V, Kumar R, Pandey K, Joshi BS, Roy R, Madhusudanan KP, Tiwari P, Srivastava AK (2009) Structure and activities of a steroidal saponin from *Chlorophytum nimonii* (Grah) Dalz. Nat Prod Res 23:963–972

Lambert E, Faizal A, Geelen D (2011) Modulation of triterpene saponin production: in vitro cultures, elicitation, and metabolic engineering. Appl Biochem Biotechnol 164:220–237

Lee J, Ha Y, Jeong C, Kim Y, Park Y (2009a) Isolation and tandem mass fragmentations of an anti-inflammatory compound from *Aralia elata*. Arch Pharm Res 32:831–840

Lee ST, Mitchell RB, Wang ZR, Heiss C, Gardner DR, Azadi P (2009b) Isolation, characterization, and quantification of steroidal saponins in switchgrass (*Panicum virgatum* L.). J Agr Food Chem 57:2599–2604

Lee B, Jung K, Kim DH (2010) Timosaponin AIII, a saponin isolated from *Anemarrhena asphodeloides*, ameliorates learning and memory deficits in mice. Pharmacol Biochem Be 94:496

Leonard S, Capote R, Germonprez N, Van Puyvelde L, De Kimpe N, Vermeersch H, Rosier J, Maes L, Roets E, Hoogmartens J (2003) Liquid chromatographic method for analysis of saponins in *Maesa balansae* extract active against leishmaniasis. J Chromatography A 1012:39–46

Li J, Hu Z (2009) Accumulation and dynamic trends of triterpenoid saponin in vegetative organs of *Achyranthus bidentata*. J Integr Plant Biol 51:122–129

Li YZ, Liang WJ, Zhang XK, Liu FM, Zhu XH (2005) Allelopathic activity of root saponins of alfalfa on wheat, corn and barnyard grass. Allelopathy J 15:119–123

Li CJ, Yang JZ, Yu SS, Chen NH, Xue W, Hu JF, Zhang DM (2008) Triterpenoid Saponins with neuroprotective effects from the roots of *Polygala tenuifolia*. Planta Med 74:133–141

Li W, Bi XY, Wang K, Li DX, Satou T, Koike K (2009) Triterpenoid saponins from *Impatiens siculifer*. Phytochemistry 70:816–821

Liu SB, Lin R, Hu ZH (2005) Histochemical localization of ginsenosides in *Gynostemma pentaphyllum* and the content changes of total gypenosides. Acta Biol Exp Sin 38:54–60

Liu LF, Ma XL, Wang YX, Li FW, Li YM, Wan ZQ, Tang QL (2009) Triterpenoid saponins from the roots of *Clematis chinensis* Osbeck. J Asian Nat Prod Res 11:389–396

Liu CX, Guo ZY, Xue YH, Cheng J, Huang NY, Zhou Y, Cheng F, Zou K (2012) Five new furostanol saponins from the rhizomes of *Tupistra chinensis*. Fitoterapia 83:323–328

Lu JC, Xu BB, Gao S, Fan L, Zhang HF, Liu RX, Kodama H (2009) Structure elucidation of two triterpenoid saponins from rhizome of *Anemone raddeana* Regel. Fitoterapia 80:345–348

Ma L, Gu YC, Luo JG, Wang JS, Huang XF, Kong LY (2009) Triterpenoid saponins from *Dianthus versicolor*. J Nat Prod 72:640–644

Macias FA, Simonet AM, Galindo JCG (1997) Bioactive steroids and triterpenes from *Melilotus messanensis* and their allelopathic potential. J Chem Ecol 23:1781–1803

Maes L, Germonprez N, Quirijnen L, Van Puyvelde L, Cos P, Berghe DV (2004) Comparative activities of the triterpene saponin maesabalide III and liposomal amphotericin B (AmBisome) against *Leishmania donovani* in hamsters. Antimicrob Agents Ch 48:2056–2060

Magid AA, Bobichon H, Borie N, Lalun N, Long C, Moretti C, Lavaud C (2010) Cytotoxic triterpenoid saponins from the stem bark of *Antonia ovata*. Phytochemistry 71:429–434

Massad TJ (2012) Interactions in tropical reforestation—how plant defence and polycultures can reduce growth-limiting herbivory. Appl Veg Sci 15:338–348

Mazzola EP, Parkinson A, Kennelly EJ, Coxon B, Einbond LS, Freedberg DI (2011) Utility of coupled-HSQC experiments in the intact structural elucidation of three complex saponins from *Blighia sapida*. Carbohyd Res 346:759–768

Mencherini T, Picerno P, Del Gaudio P, Festa M, Capasso A, Aquino R (2010) Saponins and polyphenols from *Fadogia ancylantha* (Makoni tea). J Nat Prod 73:247–251

Messiaen J, Nérinckx F, Van Cutsem P (1995) Callose synthesis in spirostanol treated carrot cells is not triggered by cytosolic calcium, cytosolic pH or membrane potential changes. Plant Cell Physiol 36:1213–1220

Misawa N (2011) Pathway engineering for functional isoprenoids. Curr Opin Biotech 22:627–633

Mitaine-Offer AC, Penez N, Miyamoto T, Delaude C, Mirjolet JF, Duchamp O, Lacaille-Dubois MA (2010) Acylated triterpene saponins from the roots of *Securidaca longepedunculata*. Phytochemistry 71:90–94

Mithofer A, Boland W (2012) Plant defense agaist herbivores: chemical aspects. Annu Rev Plant Biol 63:25.20–25.21

Montoya G, Arango GJ, Unger M, Holzgrabe U (2009) O-Glycoside sequence of pentacyclic triterpene saponins from *Phytolacca bogotensis* using HPLC-ESI/Multi-stage tandem mass spectrometry. Phytochem Anal 20:465–474

Morant AV, Jorgensen K, Jorgensen C, Paquette SM, Sanchez-Perez R, Moller BL, Bak S (2008) beta-glucosidases as detonators of plant chemical defense. Phytochemistry 69:1795–1813

Morrissey JP, Osbourn AE (1999) Fungal resistance to plant antibiotics as a mechanism of pathogenesis. Microbiol Mol Biol Rev 63:708–724

Mugford ST, Qi XQ, Bakht S, Hill L, Wegel E, Hughes RK, Papadopoulou K, Melton R, Philo M, Sainsbury F, Lomonossoff GP, Roy AD, Goss RJM, Osbourn A (2009) A serine carboxypeptidase-like acyltransferase is required for synthesis of antimicrobial compounds and disease resistance in oats. Plant Cell 21:2473–2484

Mylona P, Owatworakit A, Papadopoulou K, Jenner H, Qin B, Findlay K, Hill L, Qi X, Bakht S, Melton R, Osbourn A (2008) Sad3 and Sad4 are required for saponin biosynthesis and root development in oat. Plant Cell 20:201–212

Nakamura S, Hongo M, Sugimoto S, Matsuda H, Yoshikawa M (2008) Steroidal saponins and pseudoalkaloid oligoglycoside from Brazilian natural medicine, "fruta do lobo" (fruit of Solanum lycocarpum). Phytochemistry 69:1565–1572

Nawrot J, Koul O, Isman MB, Harmatha J (1991) Naturally occurring antifeedants: effects on 2 polyphagous lepidopterans. J Appl Entomol 112:194–201

Ndontsa BL, Tchinda A, Teponno RB, Mpetga JS, Frederich M, Tane P (2012) Ardisikivuoside, a New Triterpenoid Saponin from Ardisia kivuensis (Myrsinaceae). Nat Prod Commun 7:515–516

Nie W, Luo JG, Kong LY (2010) New triterpenoid saponins from the roots of Gypsophila pacifica Kom. Carbohyd Res 345:68–73

Nielsen NJ, Nielsen J, Staerk D (2010) New resistance-correlated saponins from the insect-resistant crucifer Barbarea vulgaris. J Agr Food Chem 58:5509–5514

Niiho Y, Nakajima Y, Yamazaki T, Okamoto M, Tsuchihashi R, Kodera M, Kinjo J, Nohara T (2010) Simultaneous analysis of isoflavones and saponins in Pueraria flowers using HPLC coupled to an evaporative light scattering detector and isolation of a new isoflavone diglucoside. J Nat Med 64:313–320

Note OP, Mitaine-Offer AC, Miyamoto T, Paululat T, Pegnyemb DE, Lacaille-Dubois MA (2009) Tetrapterosides A and B, two new oleanane-type saponins from Tetrapleura tetraptera. Magn Reson Chem 47:277–282

Ohana P, Delmer DP, Carlson RW, Glushka J, Azadi P, Bacic T, Benziman M (1998a) Identification of a novel triterpenoid saponin from Pisum sativum as a specific inhibitor of the diguanylate cyclase of Acetobacter xylinum. Plant Cell Physiol 39:144–152

Ohana P, Delmer DP, Volman G, Benziman M (1998b) Glycosylated triterpenoid saponin: a specific inhibitor of diguanylate cyclase from Acetobacter xylinum. Biological activity and distribution. Plant Cell Physiol 39:153–159

Oleszek W (1993) Allelopathic potentials of alfalfa (Medicago sativa) saponins: their relation to antifungal and hemolytic activities. J Chem Ecol 19:1063–1074

Oleszek W, Stochmal A (2002) Triterpene saponins and flavonoids in the seeds of Trifolium species. Phytochemistry 61:165–170

Osbourn A (1996) Saponins and plant defence—a soap story. Trends Plant Sci 1:4–9

Osbourn AE, Qi X, Townsend B, Qin B (2003) Dissecting plant secondary metabolism—constitutive chemical defences in cereals. New Phytol 159:101–108

Osbourn A, Goss RJM, Field RA (2011) The saponins—polar isoprenoids with important and diverse biological activities. Nat Prod Rep 28:1261–1268

Papadopoulou K, Melton RE, Leggett M, Daniels MJ, Osbourn AE (1999) Compromised disease resistance in saponin-deficient plants. Proc Natl Acad Sci USA 96:12923–12928

Park J, Rhee D, Lee Y (2005) Biological activities and chemistry of saponins from Panax ginseng C. A. Meyer. Phytochem Rev 4:159–175

Phillips DR, Rasbery JM, Bartel B, Matsuda SPT (2006) Biosynthetic diversity in plant triterpene cyclization. Curr Opin Plant Biol 9:305–314

Ponou BK, Teponno RB, Ricciutelli M, Quassinti L, Bramucci M, Lupidi G, Barboni L, Tapondjou LA (2010) Dimeric antioxidant and cytotoxic triterpenoid saponins from Terminalia ivorensis A Chev. Phytochemistry 71:2108–2115

Rahman A, Tsurumi S (2002) The unique auxin influx modulator chromosaponin I: a physiological overview. Plant Tissue Cult 12:181–194

Rahman A, Tsurumi S, Amakawa T, Soga K, Hoson T, Goto N, Kamisaka S (2000) Involvement of ethylene and gibberellin signalings in chromosaponin I-induced cell division and cell elongation in the roots of Arabidopsis seedlings. Plant Cell Physiol 41:1–9

Rahman A, Ahamed A, Amakawa T, Goto N, Tsurumi S (2001) Chromosaponin I specifically interacts with AUX1 protein in regulating the gravitropic response of Arabidopsis roots. Plant Physiol 125:990–1000

Rubio-Moraga A, Gerwig GJ, Castro-Diaz N, Jimeno ML, Escribano J, Fernandez JA, Kamerling JP (2011) Triterpenoid saponins from corms of Crocus sativus: localization, extraction and characterization. Ind Crop Prod 34:1401–1409

Saha S, Walia S, Kumar J, Dhingra S, Parmar BS (2010) Screening for feeding deterrent and insect growth regulatory activity of triterpenic saponins from Diploknema butyracea and Sapindus mukorossi. J Agric Food Chem 58:434–440

Sanchez-Medina A, Stevenson PC, Habtemariam S, Pena-Rodriguez LM, Corcoran O, Mallet AI, Veitch NC (2009) Triterpenoid saponins from a cytotoxic root extract of Sideroxylon foetidissimum subsp gaumeri. Phytochemistry 70:765–772

Scognamiglio M, D'Abrosca B, Fiumano V, Chambery A, Severino V, Tsafantakis N, Pacifico S, Esposito A, Fiorentino A (2012) Oleanane saponins from Bellis sylvestris Cyr. and evaluation of their phytotoxicity on Aegilops geniculata Roth. Phytochemistry 84:125–134

Shirota O, Nagamatsu K, Sekita S, Komoto N, Kuroyanagi M, Ichikawa M, Ohta S, Ushijima M (2008) Preparative separation of the saponin lancemaside A from Codonopsis lanceolata by centrifugal partition chromatography. Phytochem Anal 19:403–410

Shwe HH, Aye M, Sein MM, Htay KT, Kreitmeier P, Gertsch J, Reiser O, Heilmann J (2010) Cytotoxic steroidal saponins from the rhizomes of Tacca integrifolia. Chem Biodivers 7:610–622

Sindambiwe JB, Calomme M, Geerts S, Pieters L, Vlietinck AJ, Vanden Berghe DA (1998) Evaluation of biological activities of triterpenoid saponins from Maesa lanceolata. J Nat Prod 61:585–590

Sparg SG, Light ME, van Staden J (2004) Biological activities and distribution of plant saponins. J Ethnopharmacol 94:219–243

Sun H-X, Xie Y, Ye Y-P (2009) Advances in saponin-based adjuvants. Vaccine 27:1787–1796

Suzuki H, Reddy MSS, Naoumkina M, Aziz N, May GD, Huhman DV, Sumner LW, Blount JW, Mendes P, Dixon RA (2005) Methyl jasmonate and yeast elicitor induce differential transcriptional and metabolic re-programming in cell suspension cultures of the model legume Medicago truncatula. Planta 220:696–707

Szakiel A, Paczkowski C, Henry M (2011a) Influence of environmental abiotic factors on the content of saponins in plants. Phytochem Rev 10:471–491

Szakiel A, Pączkowski C, Henry M (2011b) Influence of environmental biotic factors on the content of saponins in plants. Phytochem Rev 10:493–502

Tabopda TK, Mitaine-Offer AC, Miyamoto T, Tanaka C, Mirjolet JF, Duchamp O, Ngadjui BT, Lacaille-Dubois MA (2012) Triterpenoid saponins from Hydrocotyle bonariensis Lam. Phytochemistry 73:142–147

Takagi K, Nishizawa K, Hirose A, Kita A, Ishimoto M (2011) Manipulation of saponin biosynthesis by RNA interference-mediated silencing of beta-amyrin synthase gene expression in soybean. Plant Cell Rep 30:1835–1846

Takahashi S, Hori K, Hokari M, Gotoh T, Sugiyama T (2010) Inhibition of human renin activity by saponins. Biomed Res 31:155–159

Tan LL, Cai X, Hu ZH, Ni XL (2008) Localization and dynamic change of saikosaponin in root of Bupleurum chinense. J Integr Plant Biol 50:951–957

Tang HF, Cheng G, Wu J, Chen XL, Zhang SY, Wen AD, Lin HW (2009) Cytotoxic asterosaponins capable of promoting polymerization of tubulin from the starfish Culcita novaeguineae. J Nat Prod 72:284–289

Tani T, Kubo M, Katsuki T, Higashino M, Hayashi T, Arichi S (1981) Histochemistry.2. Ginsenosides in ginseng (Panax ginseng, root). J Nat Prod 44:401–407

Tani T, Katsuki T, Kubo M, Arichi S (1986) Histochemistry.9. Distribution of saikosaponins in Bupleurum falcatum root. J Chromatogr A 360:407–416

Tapondjou LA, Ponou KB, Teponno RB, Mbiantcha M, Djoukeng JD, Nguelefack TB, Watcho P, Cadenas AG, Park HJ (2008) In vivo anti-inflammatory effect of a new steroidal saponin, mannioside A, and its derivatives isolated from Dracaena mannii. Arch Pharm Res 31:653–658

Tarr PT, Tarling EJ, Bojanic DD, Edwards PA, Baldan A (2009) Emerging new paradigms for ABCG transporters. Biochim Biophys Acta 1791:584–593

Tava A, Avato P (2006) Chemical and biological activity of triterpene saponins from Medicago species. Nat Prod Commun 1:1159–1180

Tava A, Mella M, Avato P, Biazzi E, Pecetti L, Bialy Z, Jurzysta M (2009) New triterpenic saponins from the aerial parts of Medicago arabica (L.) Huds. J Agr Food Chem 57:2826–2835

Tene M, Chabert P, Note O, Kenla TJN, Tane P, Lobstein A (2011) Triterpenoid saponins from Cylicodiscus gabunensis. Phytochem Lett 4:89–92

Teng HM, Fang MF, Cai X, Hu ZH (2009) Localization and dynamic change of saponin in vegetative organs of Polygala tenuifolia. J Integr Plant Biol 51:529–536

Tian Y, Tang HF, Qiu F, Wang XJ, Chen XL, Wen AD (2009) Triterpenoid Saponins from Ardisia pusilla and their Cytotoxic Activity. Planta Med 75:70–75

Tsurumi S, Tsujino Y (1995) Chromosaponin I stimulates the growth of lettuce roots. Physiol Plantarum 93:785–789

Tundis R, Bonesi M, Deguin B, Loizzo MR, Menichini F, Conforti F, Tillequin F, Menichini F (2009) Cytotoxic activity and inhibitory effect on nitric oxide production of triterpene saponins from the roots of Physospermum verticillatum (Waldst & Kit) (Apiaceae). Bioorgan Med Chem 17:4542–4547

Van Dyck S, Gerbaux P, Flammang P (2010) Qualitative and quantitative saponin contents in five sea cucumbers from the Indian Ocean. Mar Drugs 8:173–189

Vincken JP, Heng L, de Groot A, Gruppen H (2007) Saponins, classification and occurrence in the plant kingdom. Phytochemistry 68:275–297

Waller GR (1989) Biochemical frontiers of allelopathy. Biol Plantarum 31:418–447

Waller GR, Jurzysta M, Thorne RLZ (1993) Allelopathic activity of root saponins from alfalfa (Medicago sativa L) on weeds and wheat. Bot Bull Acad Sinica 34:1–11

Waller GR, Yang CF, Chen LF, Su CH, Liou RM, Wu SC, Young CC, Lee MR, Lee JS, Cheng CS, Chou CH, Kim D (1999) Saponins produced during the life cycle of mung-beans and their role as allelochemicals. Advances in plant glycosides, chemistry and biology 6:105–130

Wang JR, Zhou H, Jiang ZH, Liu L (2008a) Two new triterpene saponins from the anti-inflammatory saponin fraction of Ilex pubescens root. Chem Biodivers 5:1369–1376

Wang LY, Bai LT, Nagasawa T, Hasegawa T, Yang XY, Sakai JI, Bai YH, Kataoka T, Oka S, Hirose K, Tomida A, Tsuruo T, Ando M (2008b) Bioactive triterpene saponins from the roots of Phytolacca americana. J Nat Prod 71:35–40

Wang Y, Zhang DM, Ye WC, Yin ZQ, Fung KP, Zhao SX, Yao XS (2008c) Triterpenoid saponins from Androsace umbellata and their anti-proliferative activities in human hepatoma cells. Planta Med 74:1280–1284

Wang Y, Lou ZY, Wu QB, Guo ML (2010) A novel hepato-protective saponin from Celosia cristata L. Fitoterapia 81:1246–1252

Wang J, Lu J, Lv C, Xu T, Jia L (2012) Three new triterpenoid saponins from root of Gardenia jasminoides Ellis. Fitoterapia 83:1396–1401

Weete JD (1989) Structure and function of sterols in fungi. Adv Lipid Res 23:115–167

Wen P, Zhang XM, Yang Z, Wang NL, Yao XS (2008) Four new triterpenoid saponins from Ardisia gigantifolia Stapf. and their cytotoxic activity. J Asian Nat Prod Res 10:873–880

Wittstock U, Gershenzon J (2002) Constitutive plant toxins and their role in defense against herbivores and pathogens. Curr Opin Plant Biol 5:300–307

Wu JJ, Cheng KW, Zuo XF, Wang MF, Li P, Zhang LY, Wang H, Ye WC (2010) Steroidal saponins and ecdysterone from Asparagus filicinus and their cytotoxic activities. Steroids 75:734–739

Xiao ZH, Wang FZ, Sun AJ, Li CR, Huang CG, Zhang S (2012) A new triterpenoid saponin from *Abrus precatorius* Linn. Molecules 17:295–302

Xie BB, Liu HY, Ni W, Chen CX (2009) Ypsilandrosides C-G, five new spirostanol saponins from *Ypsilandra thibetica*. Steroids 74:950–955

Xin XL, Yang Y, Zhong J, Aisa HA, Wang HQ (2009) Preparative isolation and purification of isobenzofuranone derivatives and saponins from seeds of *Nigella glandulifera* Freyn by high-speed counter-current chromatography combined with gel filtration. J Chromatogr A 1216:4258–4262

Xu W, Fang J, Zhu Z, Wu J, Li Y (2012) A new triterpenoid saponin from the roots of *Silene viscidula*. Nat Prod Res 26:2002–2007

Xu HJ, Shi XW, Ji X, Du YF, Zhu H, Zhang LT (2012) A rapid method for simultaneous determination of triterpenoid saponins in *Pulsatilla turczaninovii* using microwave-assisted extraction and high performance liquid chromatography–tandem mass spectrometry. Food Chem 135:251–258

Yadava RN, Jharbade J (2008) New antibacterial triterpenoid saponin from *Lactuca scariola*. Fitoterapia 79:245–249

Yan LH, Xu LZ, Lin J, Yang SL, Feng YL (2009) Triterpenoid saponins from the stems of *Clematis parviloba*. J Asian Nat Prod Res 11:332–338

Yokosuka A, Mimaki Y (2009) Steroidal saponins from the whole plants of *Agave utahensis* and their cytotoxic activity. Phytochemistry 70:807–815

Zambou K, Spyropoulos CG, Chinou I, Kontos F (1993) Saponin-like substances inhibit alpha-galactosidase production in the endosperm of fenugreek seeds—a possible regulatory role in endosperm galactomannan degradation. Planta 189:207–212

Zhang ZZ, Li SY, Ownby S, Wang P, Yuan W, Zhang WL, Beasley RS (2008) Phenolic compounds and rare polyhydroxylated triterpenoid saponins from *Eryngium yuccifolium*. Phytochemistry 69:2070–2080

Zhang T, Liu H, Liu XT, Chen XQ, Wang Q (2009) Steroidal saponins from the rhizomes of *Paris delavayi*. Steroids 74:809–813

Zhang HP, Samadi AK, Rao KV, Cohen MS, Timmermann BN (2011) Cytotoxic oleanane-type saponins from *Albizia inundata*. J Nat Prod 74:477–482

Zhang L-J, Yu H-S, Kang L-P, Feng B, Quan B, Song X-B, Ma B-P, Kang T-G (2012a) Two new steroidal saponins from the biotransformation product of the rhizomes of *Dioscorea nipponica*. J Asian Nat Prod Res 7:640–646

Zhang PY, Qin SH, Zhao HX, Wang FL, Guo HJ, Bai H (2012b) A new triterpenoid saponin from *Sanguisorba officinalis*. J Asian Nat Prod Res 14:607–611

Zhao YL, Cai GM, Hong X, Shan LM, Xiao XH (2008) Anti-hepatitis B virus activities of triterpenoid saponin compound from *Potentilla anserine* L. Phytomedicine 15:253–258

Zuo WJ, Dai HF, Zeng YB, Wang H, Chen HQ, Wang JH (2012) Two new triterpenoid saponins from the leaves of *Ilex kudingcha*. J Asian Nat Prod Res 14:308–313