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Insight into strigolactone hormone functions in plant parasitic weeds: a regulatory perspective

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The strigolactones (SLs) are plants hormones that have multiple functions in architecture and development. The roles of SLs in shoot branching and stem secondary growth of autotrophic plants are established. SL is also involved in the interaction between root parasitic plants and their host plants. SLs are exudates by the root of the host plant in search of a fungal partner for symbiotic association, while parasitic plants utilize this facility to detect the host root. The first formed tubercle of *Philapanhche*, whose germinations are driven by host-derived SLs, exudates parasitic derived SLs (PSLs) and could encourages germination of the adjacent parasitic seeds, resulting in parasite cluster formation. The existence of aboveground spikes in clusters suggests an intriguing approach for increasing parasite population by amplifying PSLs, which result in massive parasitic seed germination. PSLs probably have a role in the increased branching of Broomrapes opposing the host plant, resulting in the parasites' clustered appearance aboveground. This review highlights the distinct roles of SLs and PSLs, and their potential role in host-parasitic interaction.

Keywords: Auxin, Broomrape, Carotenoid cleavage dioxygenase (CCDs) Cyanohydrins, Cytokinin, Haustoria, Host-parasitic interaction, Karrikin, *Orobanche*, *Philapanhche*, Phloem Root parasite, *Striga*, Xylem

Introduction

The parasitic weeds like *Cuscuta*, *Aeginetia*, *Orobanche*, *Phelipanche*, *Alectra* and *Striga*, generally belong to the Convolvulaceae, Orobanchaceae, and Scrophulariaceae family of flowering plants. The genus *Striga*, *Orobanche* and *Phelipanche* include more than 40 species causing the problem to agriculturally grown dicot corps, respectively including a member of Brassicaceae, Solanaceae, Compositae, etc.[1,2]. Striga and Orobanche species are affecting the African and Mediterranean-Asian regions, respectively. Parasitic weeds use a variety of techniques to attack their hosts in order to survive. They evolve special organs like haustoria to robe the nutrition from the host plant[3]. The degree of dependency is differing from species to species. In combination with other biotic stresses, parasitic weeds, which constitute approximately 4000 species from more than 20 higher plant families, cause a massive loss in yield and productivity in staple and other food crops[1]. Infestation with parasitic weed reduces the host's photosynthetic process.

Parasitic plant seeds develop hundreds of microscopic seeds that are dormant for many years in the agricultural field, and each year it is increasing in presence of a suitable host[3]. They show a complex life cycle and remain underground for a long time and emerge only during inflorescence. Parasitic plants have a special organ called haustoria, which when in contact with the host plant's xylem and phloem deprives the host plant of assimilatory obtained nutritional material and diverts the majority of it to itself[1,4]. The germination of their seed is stimulated by certain compounds called strigolactones (SLs) exudates by the host strigolactones (HSLs) and parasitic weed evolved detection system to host by several signal transduction mechanisms[5,6]. The germination of parasitic seeds should occur at the appropriate period, which coincides with the growth of the host plant. SLs are a prominent class of

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phytohormones with distinct stereo specificities and structures[7]. HSLs are exudates in very little quantities by the root of the host plant in search of Mycorrhizal hyphae for the symbiotic association. The parasitic attack is proportional to HSLs exudation by the host plants[8]. The study has shown that SLs are derived from carotenoids[9]. The production of plant secondary metabolites is affected as a result of viral infection[10]. Ibdah *et al.*[11] also suggests that the CMV virus decreases carotenoid production by suppressing *phytoene desaturase* (*PDS*) expression and leads to a reduction in *Phelipanche* infection in tobacco host roots. During phosphate starvation, the host plant induces the exudation of HSLs and this property is conserved in the plant kingdom[12]. It increases the probability of symbiont association with the fungal partner and also raises the risk of parasitic attack especially *Striga* and *Orobanche*. On the other hand, increased fertilizer minimizes the chance of *Striga* attack and increases HSL development[13]. Broomrape developed a distinctive preconditioning strategy followed by Strigolactone detection to minimize seedling emergence failure and compensate for such challenges[1].

During the time course of evolution, parasitic plants removed their function of autotrophic nature but retain some important genes. It is interesting to find the *carotenoid cleavage dioxygenases* (*CCDs*) gene in the transcriptome of *Orobanche/Phelipanche* (http://ppgp.huck.psu.edu/). The induced expression of *CCD7* and *CCD8* was observed during the tubercle development in *Phelipanche* and *Striga*[14,15]. The transient knockdown of Phelipanche *CCDs 7-8* and mannitol transporter leads to resistant development in the host plant[14,16]. The present review discusses the brief about host-derived SLs and the possible function of parasitic derives (PSLs).

Strigolactones: an insight

SLs are a family of signaling molecules produced in all embryophytes including dicots, monocots, charales, and at least one moss[17]. The presence of SLs biosynthesis genes in lower plants like green algae, Bryophytes, and parasitic angiosperm have also been reported[14,15]. These are terpenoid lactones that help to survive better in stress. More than 25 SLs have been characterized, which are produced in different quantities by plants[18]. Accumulating evidence suggests that SLs suppress shoot branching while accelerating root branching for improved plant survival[6,19]. Kohlen *et al.*[12] who studied biosynthesis of SLs, observed that it is enhanced during phosphate starvation, and also revealed that root-derived SLs are transported to the shoot and regulate branching. Few putative SLs -like compounds were also detected in the sap of xylem in *Arabidopsis thaliana*, one of which was not detected in root exudates. Different new SLs in plant root exudate like pyranolactone in maize have been discovered[20]. SLs contain a labile ether bond that is easily hydrolyzed in the rhizosphere[19]. The concentrations of these compounds are more near the root than in other rhizospheric regions[19].

SLs consist of four ring molecules having an ABC-ring system connected via an enol ether bridge to a butenolide D-ring[21]. Different substitutions are found on the A and B rings[22]. The activity of SLs differs with changes in molecular structure. The half-life of SLs varies greatly depending on pH and also degraded quickly in water[22]. SLs are perceived in very low quantities and are very sensitive[22]. The precursor for the formation of SLs is (+)-5-deoxystrigol[23]. Similar to SLs, a compound called Karrikins is found in smokes. Karrikin is a class of butenolide molecules that regulates seed germination via a light-dependent way and shows active site similarity to SLs[24]. Another molecule called Cyanohydrins is also found in wildfire smoke-induced seed germination similar to SLs[25]. Similar to SLs, Karrikins also signal through common F-box protein[25]. The analogs like Methyl phenlactonoates and repressors of SLs signaling have also been discovered[26]. SLs analog, Triazole Ureas bind to SLs receptor and antagonize SLs responses while SMXL6/SMXL7/SMXL8 work as a key repressor in SLs signaling pathways[27]. Contalactone and debranones, mimic the SLs and act similar to artificial SLs GR24[28].

Strigolactone biosynthesis pathway

A large family of non-heme iron-dependent carotenoid cleavage dioxygenase (CCDs) enzymes is involved in SLs formation by oxidative cleavage in the carotenoids pathway[23,29]. CCDs 7 and 8 are supposed to be directly involved in SLs production[30]. SLs are mainly formed in roots but lower parts of the shoot are also suggested as the site of SLs biosynthesis[31]. About, two CCDs, viz, CCD7 and CCD8, and a class-III cytochrome P450 monooxygenase are involved in SLs production[30,32]. CCDs catalyse the process by selective cleavage of carotenoids, which are found across the plant kingdom and are thought to have diverged several million ago in CCD7 and CCD8[33]. Because of their monooxygenase or dioxygenase activity, CCDs are also known as carotenoid cleavage oxygenases (CCOs), and the names CCO and CCD are sometimes used indiscriminately[33]. First CCD was discovered in *Zea mays* (maize) as Vp14 (90-cis-epoxycarotenoid dioxygenase 1 (NCED1)) in 1990, which is now identified in various microorganisms, plants and mammals[33,34]. Mostly, five CCDs as 1, 4, 7, 8, and NCEDs are found in all plants, however, 9 CCDs have been identified in Arabidopsis. Generally, CCDs are structurally conserved (Reviwed by Harrison and Bugg, (2014)[33]. Compounds like abamine and nordihydroguaiar etic acid (NDGA) work as inhibitors of CCDs in the *in-vitro* condition[35]. CCD7 and CCD8 cleave the 9-cis-b-carotene to produce the SL precursor carlactone[23]. Studies indicate that strigolactones are derived from carotenoids, via two conserved carotenoid cleavage enzymes (CCDs) coded by CCD7 and CCD8. The gene responsible for coding CCD7 protein are *MAX3, RMS5*, and *HTD1/D17*, while *MAX4, RMS1, D10*, and *DAD1* are responsible for CCD8 protein [23,36,37]. In the first step of SLs biosynthesis, D27 (SL biosynthesis gene, *DWARF27*) converts all-trans β-carotene to 9-cis-β-carotene[38]. Further 9-cis-β-carotene is converted to β-apo-10'-carotenal by CCD7 followed by the formation of carlactone by CCD8 mediated reaction[30]. Later the carlactone was transported to the cytosol and converted to SLs with the help of the MAX enzyme, which is probably a cytoplasmic cytochrome P450 enzyme[32,38]. Mutation in the CCDs and other enzymes leads to a reduction in SLs formation (Reviewed by Koltai[39]), suggesting the CCDs are playing important role in these pathways. Another enzyme, the Lateral Branching Oxidoreductase enzyme is involved in the production of Arabidopsis SLs biosynthesis at the final stages[40]. Its synthesis is also regulated by several factors and regulators like zaxinone[41]. The stability of SLs depends on several factors like the pH of the solvent and nucleophiles presence[42].

Transportation, exudation, and perception of SLs

SLs are transported through xylem sap probably via an ATP-binding cassette (ABC) transporter PDR1 in the case of Petunia[12]. In *Petunia axillaris*, SLs transporter pleiotropic drug resistance 1 (PaPDR1) is required for mycorrhizal association and lateral bud outgrowth inhibition and identified their co-expression interaction with strigolactone biosynthetic gene DAD1 (CCD8)[43]. The loss of *PDR1* gene showing the characteristic of SLs impaired functions by reducing symbiotic interactions, and increasing branching patterns[44]. SLs exudations are exceeded during phosphate starvation via the ABC transporter *PhPDR1*, which induce during phosphate starvation[44]. SLs mediated response requires F-Box leucine-rich repeat protein encoded by MAX2/RMS4/D3 and possibly also an α/β-hydrolase[15, 33, 45]. In petunia, DAD2 encoded α/β-hydrolase, hydrolyses GR24, and binds to the MAX2 proteins leading to the signalling of SCF-mediated pathway and phenotypic responses of plants[46]. About 11 SLs receptors have been characterized by *Striga hermonthica*[47]. Bioinformatical and other analyses have also shown that DAD2, DWARF14 may also work as SLs receptors[46,48]. DWARF14 (D14) is an α/β Hydrolase protein that can inhibit tillering of rice. Its degradation is SLs dependent, and it is also considered one of the SLs receptor. During perception of SLs pathway receptor DWARF14 hydrolyzed SLs and bind to the fragmented hormone product[49].

SLs in root development

Studies have shown that in addition to auxin, SLs modulate and regulate root development[50] (Fig. 1). SLs and their metabolism-related gene have been discovered across the plant kingdom. In liverworts and charales, SLs help in the elongation of rhizoids. It is also reported, SLs control developmental and ecophysiological processes in moss[51]. SLs increase meristem of root and root hair elongation and regulate

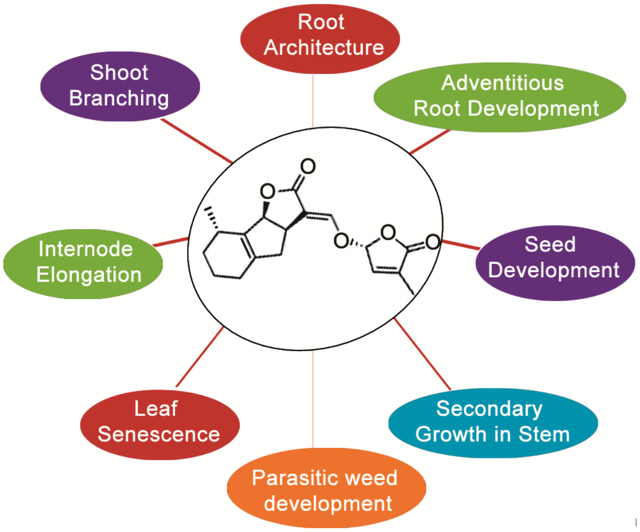

Fig. 1 — Multifunctional of Strigolactones in plant growth and development

lateral-root formation depending upon phosphate availability[52,53]. By changing root architecture, plants try to overcome phosphate starvation. SLs inhibit lateral-root formation under phosphate availability but induce lateral root formation under phosphate deficiency, suggesting SLs play signification role in regulation of root development in stress conditions[52,53]. Accumulating studies show the same above said functions in pea and tomato[52,53,54]. Application of exogenous SLs reduces adventitious root formation in a MAX2/RMS4-dependent way[53]. SLs are necessary for increasing Arabidopsis seedling's root-hair in phosphate deficiency[55]. SLs possibly reduce the cambial activity required for adventitious root initiation[51]. Experiments on wild-type rice plants and strigolactone biosynthesis mutant line indicate that SLs might regulate adventitious root development differently in monocots and dicots. SLs affect the efflux of auxin by PIN auxin-efflux carriers, consequently it helps in regulating the growth of lateral roots[45]. Auxin is also an important factor regulating the root architecture. Experiment and analysis of SLs and auxin signalling mutants showed that SLs work upstream of an auxin signalling pathway[21,55]. In lateral root formation, SLs and cytokinin work similarly and influence the distribution of auxin[21]. SLs and Cytokinin suppress the adventitious rooting via independent and different pathways[54]. SLs also help in root hair elongation. Exogenous GR24 treatment in Arabidopsis SLs (*max3* and *max4*) mutants increases root hair size similar to wild type, showing the importance of SLs in root architecture[51]. Along with the change in root phenotype, SLs are also involved in other root characteristics like root nodule formation[51]. Exogenous application of synthetic SLs GR24 induces the formation of the nodule in *Medicago sativa*[56], while the opposite results were also demonstrated by Foo *et al.*[36] proving the interesting role of SLs in nodule formation. SLs stimulate the activity of root apical meristem and also work antagonistically to the auxin[57].

SLs in shoot development

SLs also inhibit the shoot branching to increase the survival chance of host plants by more focusing on root development during phosphate starvation. The parasitic plants utilize this capability to detect the host root. Similar to the auxin and cytokinin, strigolactone, regulate shoot branching and are important in determining the fates of axillary buds, but the exact way of their interaction is still unknown[21,58]. Studies of grafting and classical techniques have shown that SLs are transmissible and can move toward the shoot region[21,32] and can be detected in the xylem sap[12]. SLs are supposed to transport and exudate through root by *PDR1* gene and *PDR1* mutant shows heavy branching[44]. Auxin synthesized in the shoot apex moves basipetal and indirectly inhibits the outgrowth of axillary buds, while cytokinin travels acropetally and induced outgrowth of axillary buds on the other hand SLs are produced from the root and transferred to the shoot, where they suppress the formation of lateral buds. Thus, auxin, cytokinin, and SLs work together for controlling axillary bud growth. Auxin inhibits indirectly the growth of axillary but cytokinin and SLs act directly on the axillary bud[57]. Cytokinin-mediated induction of axillary bud is antagonized by the SLs[57]. Removing of apical auxin forming source leads to suppression of *MAX3* and *MAX4* expression causes a decrease in SLs biosynthesis and opposite leads to induction of cytokinin biosynthetic genes *PsIPT1* and *PsIPT2*[57]. SLs seem to give feedback on cytokinin production by inhibiting *PsIPT1* expression[57,59].

SLs in senescence

Senescence is a critical phase in the relocalization of carbon and nitrogen resources, as well as during biotic/abiotic stress and stage factor induction[60]. A recent study found that SLs substantially increased leaf senescence in dark settings[60]. Notably, SLs alone are unable to induce the senescences. However, it is reported that the SLs mediated induction of senescence in leaves via increasing ethylene activity[60]. Thus, ethylene and strigolactone production in the leaf regulates dark-induced senescence. SLs also help with resource distribution by compensating for nutrient deficiencies during plant growth[61,62]. Further expression of SLs biosynthesis gene *MAX3* and *MAX4* induces in ethylene treated and dark incubated leaf[60]. Recently, the role of SLs in drought-induced stomatal opening has been studied, and it has been demonstrated that miR156 regulates the SLs function in stomatal behaviour during water stress[63].

PSLs in broomrapes: perspective and functional importanceHSLs are exuded by host roots to the rhizosphere, and they are involved in the establishment of interaction with parasitic weeds and mycorrhizal fungi, and rhizobium[64]. HSLs function is conserved in the plant kingdom and helps in symbiotic colonization by fungi, controlling rhizoid elongation, parasitic attack, suppression of shoot axillary buds, induction of stem secondary growth and inhibit to formation adventitious-root, plant length determination, length of root-hair and promotion of primary-root meristem[52-54,65-67]. Further, suppression of lateral-root formations are a few examples of SLs works in plants but the detailed function of PSLs in parasitic plants is still unknown. Although there is no report of direct detection of PSLs in parasitic plants, the finding of SLs biosynthesis-related genes and changing of their expression during the life cycle of parasitic plants showed their presence in parasitic plants like *Phelipanche* and *Striga*[14,15,68]. The EST database of the parasitic genome project is also showing the expression of *CCD7* and *CCD8* in the life cycle of parasitic weeds (http://ppgp.huck.psu.edu/). Further, knockdown expressions of parasitic *CCD7* and *CCD8* lead to a reduction in parasitic attachment, dyeing of parasitic tubercle, and resistant development in the host plant[14]. These results showed that PSLs might involve playing important role in host parasitic interaction, tubercle development, branching of parasitic inflorescence, etc. By boosting the concentration of PSLs generated by pre-established tubercles, PSLs are probably implicated in the induction of germination of neighbouring parasite seeds. As the host-derived SLs are very fewer quantities and they are just near the root. The growth of tubercle in clustered form and emergence of inflorescence in clustered form might be indicating the possible function of PSLs. The study of agricultural filed infested with the Broomrapes of different crops also suggest the same conclusion.

Broomrapes growing in clustered form observed in brinjal, carrot, and mustered filed in North India are also showing the clustered pattern of inflorescence emergence (Fig. 2). The underground clustered development of the tubercle might be showing the aboveground clustered development of parasitic inflorescence. Further, another function of parasitic SLs is predicted that it might be involved in the branching of parasitic stems. As in autotrophic plants, SLs suppress the shoot branching, in the case of Broomrape, it might be showing the opposite function. SLs are also involved in the secondary

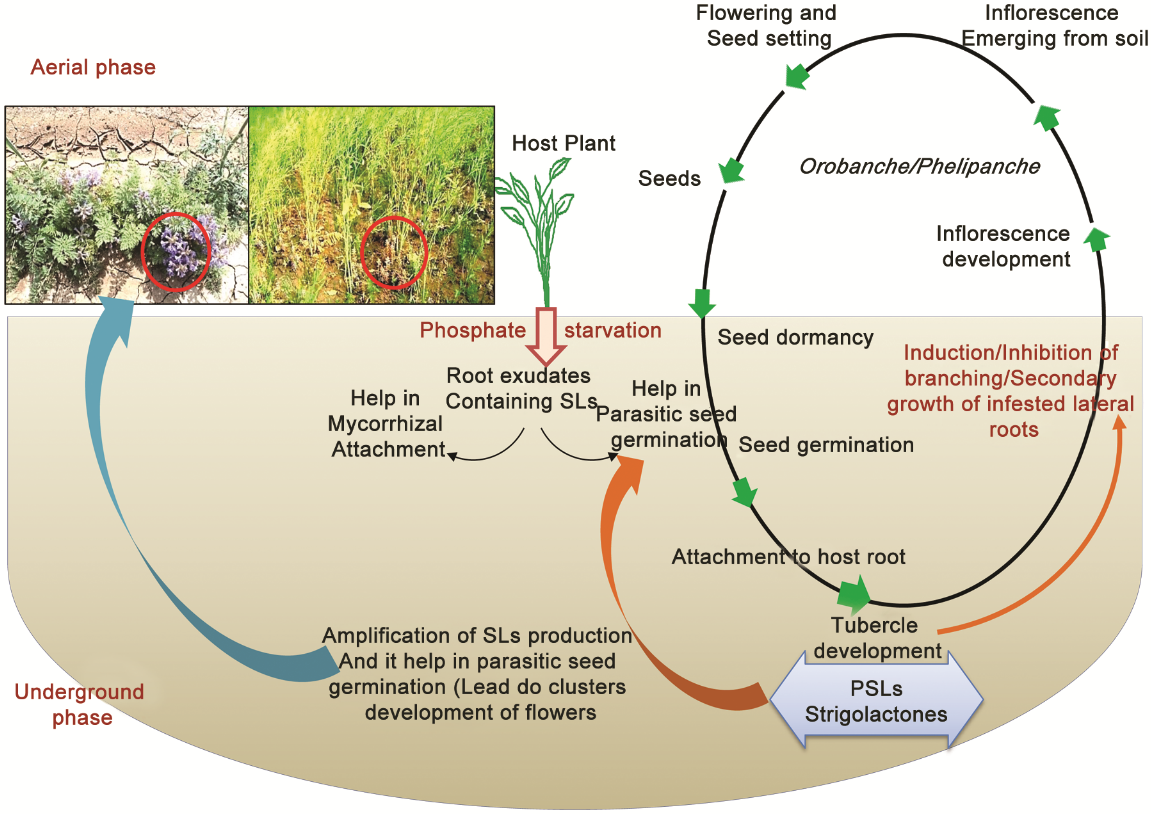

Fig. 2 — Function of parasitic plant-derived strigolactones (PSLs) in host and parasitic plant interaction**.** [It shows the emergence of *Phelipanche* inflorescence on carrot plants and mustard plants. Red ring showing the emergence of inflorescence in clustered form, Soucre: Dr. S S Punia-CCS HAU, HISAR, Department of Agronomy, India provided Orobanche infested field pictures]

growth of plants[64,69]. The lateral roots of the host plant infested with the tubercle of Broomrapes show much thicker and more secondary growth than the non-infested lateral roots. The initial finding showed the transverse section of infested lateral roots is stronger having more xylem regions than non-infested lateral roots. So it might be possible that the parasitic derived SLs are inducing the secondary growth of the host lateral root and thus it causes more strength to infested root. It could be also helpful in enhancement in the robbing of nutrients from autotrophic host plants.

Conclusively, the PSLs help in the production of more seeds by increasing the number of branches, help in attaching the host root by strengthening the infested root, and finally amplifying the PSLs in the rhizospheric region for more germination of relative parasitic seeds. Thus, PSLs are supposed to be very important for the parasitic itself similar to the autotrophic plant-derived SLls. It was also observed that the tubercles grown near the host plants are generally in cluster form and are in decreasing order of their size and age. Inflorescences are grown aboveground and also can be seen in patches form. We assume that the first formed tubercles produce Strigolactones, which stimulates germination and breaks preconditioning to neighbouring parasite seeds, resulting in tubercle cluster growth (Fig. 2). Relative expression profiling of *CCD7* and *CCD8* in different parasitic weeds will give the complete scenario regarding the probable function of these genes in parasitic weeds. There are different species of *Orobanche* and *Phelipanche* they are branched and unbranched like *O. cernua* is unbranched species. Particularly, the *CCD7* and *CCD8* help in branching/unbranching patterns different than of autotrophic angiosperm, which enhances the number of flowers and also the seed production. Further, the role of SLs and their mediators in crop improvement programs have also been discussed by several authors in changing the shoot, root architecture, and tillering[70]. Like partial loss-one of SL biosynthesis gene, high tillering and dwarf 1/dwarf17 (*HTD1/D17*), encoding (*CCD7*), increase the number of the tiller and improves rice productivity[71].

Conclusion

In light of parasitic weed's harmful nature, comprehensive molecular and physiological knowledge of these weeds is important for addressing these issues. Accumulating studies describe the function of strigolactones (SLs) in host plant and emphasis their role in the parasitic and host interactions, as well as the role of parasitic derived SLs (PSLs) in the development of the weeds. PSLs might involve playing important role in host parasitic interaction, tubercle development, branching of parasitic inflorescence, etc. It is interesting to examine how host strigolactones (HSLS) and PSLs coordinate throughout the plant and surrounding weed growth and development.

Conflicts of interest

Authors declare no competing interests.

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