

Dual Potential of Allelotoxins for Weed Control and Improved Crop Growth: A Mini-Review

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Abstract: Allelochemicals also known as allelopathins/allelotoxins/phytotoxins are plant secondary metabolites that interfere with growth of neighboring phytodiversity. The release of such chemicals by plants in the naïve introduced range is one of the widely accepted mechanisms of invasion presented as “Novel Weapons Hypothesis”. Recent advances in plant allelopathy suggest the potential of such toxic compounds to replace synthetic pesticides. Literature supports better results of various extracts from invasive plants against different weeds. These chemicals could play effective roles in weed control providing better alternatives to synthetic chemical herbicides, thereby reducing the risk of environmental pollution. Application of allelochemicals at low concentrations at the fields can be a cost-effective and efficient way to inhibit growth of undesired plants and enhance crop productivity. We here, after extensive data research enlisted putative allelotoxins isolated from invader plants and suggest further research on herbicidal and pesticidal activities of these compounds to promote the idea “*weed control through weeds*”. This data presentation supports the novel weapons hypothesis as well as will open doors for strategic research for development of natural agrochemicals.

Keywords: Allelotoxins; Allelochemicals; Allelopathins; Novel Weapons Hypothesis; Hormesis; Sustainable agriculture; Weed control.

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1 Introduction

Some abounding species in introduced range are not as abundant or are rare at home. Plants that attain dominance and become copious in the recipient communities must be ‘performing different’ than in native range. A growing consensus acknowledges that better competition potential (resource completion and/or chemical competition) does help invaders in abounding the naïve range (Hierro et al., 2005; Perkins et al., 2011). In addition, factors including attributes of invader as well as biotic and environmental characters of invaded site are also cited as reasons of successful invasion. “Attributes of the potential invader” represents the intrinsic characteristics of a species that enhance the competitive potential of the invader. An invader impressively produces the competitive effect (i.e., ability to suppress neighbors) as well as shows a robust competitive response (i.e., avoidance of suppression due to neighbors) (Perkins et al., 2011). Several hypotheses have been postulated to justify

invasion mechanism and superabundance of exotics. Observed dejection of species richness in invaded sites, often invoke chemical competition (allelopathy) as a dominant invasion mechanism (Hierro and Callaway, 2003; Hierro et al., 2005).

Practical weed control can be achieved by using allelopathy. Such weed control will neither harm environment nor increase weed management costs. Allelopathic weed control may be applied as a single strategy in certain cropping systems, such as organic farming. Under allelopathic weed control, allelopathic potential of crops is manipulated in such a way that allelochemicals from these crops reduce weed competition (Qasem and Foy, 2001; Arora et al., 2015). The living plants or dead materials express allelopathic activity through allelochemicals exudation. That might be root exudation, leaching from dead or live plant tissues, and volatilization from aboveground plant parts (Weston and Mathesius, 2014; Jabran et al., 2015).

2. Novel weapons for invasion success and Allelotoxins: A potential hypothesis

Allelochemicals/allelotoxins are considered as 'chemical weapons' partly responsible for the impressive inclusion of alien invaders in introduced environments (Ranwala et al., 2014). A number of exotic invasive plants are attributed to have novel chemicals that are more toxic to native and non-adapted native plants, herbivores or soil microbes in the invaded range than in the invader's native range (Callaway and Aschehoug, 2000; Müller-Schärer et al., 2004; Cappuccino and Arnason, 2006;). Such biographical differences in defense biochemistry have been proposed as a mechanism for invasion under the head the "Novel Weapon Hypothesis" contending that the invasive species have a "weapon" or non-trophic, non-resource competitive mechanism of interaction, to which members of its native community are conditioned and hence giving the weapon negligible effect. In the recipient site, in contrast, the community is not conditioned or naive to the weapon, and thus the weapon has a significant negative effect on members of the recipient site (Callaway and Ridenour, 2004; Callaway and Vivanco, 2006).

A large number of allelopathy experiments with exotic species evaluated the phytotoxic activity of the invasive species by means of bioassays in which the germination, seedling growth, and plant biomass are determined under laboratory or greenhouse condition (Cheng and Cheng, 2016; Zhang et al., 2016). *Chrysanthemoide smonilifera* (L.) Norl. spp. Rotundata, *Acroptilon repens* (L.) DC., *Typha angustifolia* L., *Centaurea maculosa* Lam., *Centaurea maculosa* Lam., *Sisymbrium loeselii* L., *Centaurea diffusa* Lam., *Centaurea maculosa* Lam., *Artemisia vulgaris* L., *Solidago canadensis* L., *Centaurea tweediei* Hook. & Arn., are all invasive plants in which allelochemicals are reported for their invasion success (Lorenzo et al., 2013).

2.1 Allelotoxins – The plant chemical weapons: General overview

For over 2,000 years, allelopathy has been widely reported with respect to plant interference involving either direct or indirect and either adverse or beneficial effects of a plant (including microorganisms) on another plant through the chemical(s) release in the environment earliest recorded by Theophrastus, "the father of botany", who wrote about how chickpea "exhausted" the soil and destroyed weeds in 300 B.C. It was 19th century that Hans Molisch (1937), the Austrian plant physiologist, gave it formal name, allelopathy, and is

currently recognized as the father of allelopathy (Li et al., 2010).

Various secondary metabolites produced by various plant part(s) have been considered as potential allelotoxins that may be released into the environment as leachates, exudates, or volatiles (Bais et al., 2003; Weston and Mathesius, 2014; Massalha et al., 2017; Latif et al., 2017). These compounds in addition to effects on other plants, they also have potential in contributing to pest and disease resistance and thus playing an important role in providing the invader a competitive advantage in host range (Weston, L.A. and S.O. Duke. 2003; Kumar et al., 2007; Li et al., 2010).

2.2. Allelotoxins as novel biological weapons: Arguing the phenomenon

A good example of a species validating a novel weapon is the *Homalodis cacoagulata* (Glassy-winged sharpshooter) in the invaded range of Mo'orea and Tahiti. Generalist predators are reported to be lethally intoxicated after preying upon *H. cacoagulata* in the invaded range while generalist predators in the home range are not so badly impacted (Perkins et al., 2011). This weapon can be considered novel due to the contrasting reactions of generalist predators in the native and invaded range. Another interesting favor to the idea was presented by Enge et al., (2012) where they reported that native herbivores in Sweden strongly preferred native algae to an invasive algal species *Bonnemaisonia hamifera* and the reason was proposed presence of 1,1,3,3-tetrabromo-2-heptanone, a secondary metabolite that is not found in native algal species. We interestingly quote the statement that "The exotic species had on average a higher total number of metabolites and more species-unique metabolites compared with their native congeners" by Macel et al., (2014). Here we extensively searched the databases for enlisting allelopathins isolated and characterized through various invasive species in different regions of the world for strong support of our argument (Table 1).

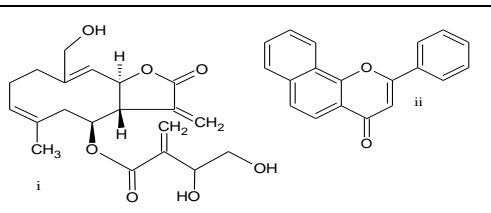
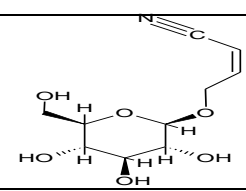
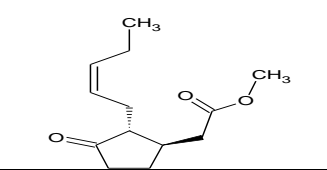
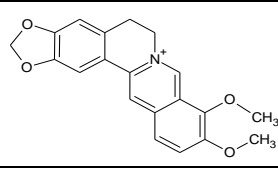

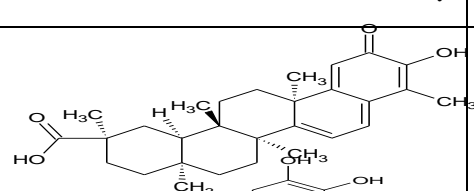
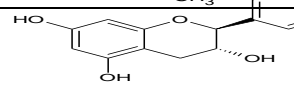
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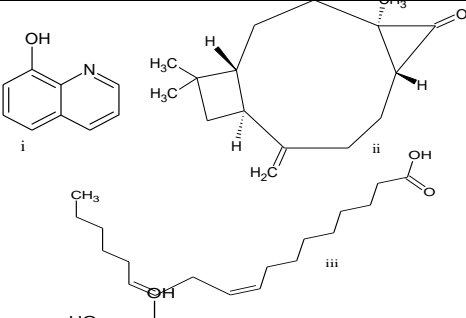
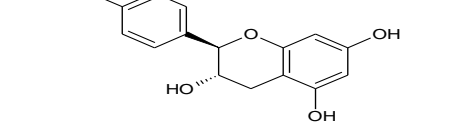
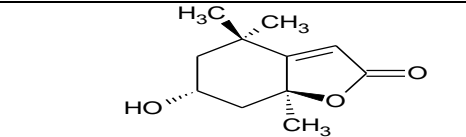
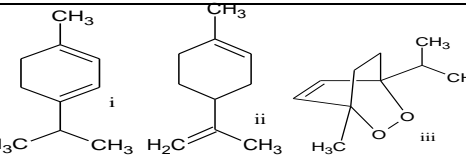
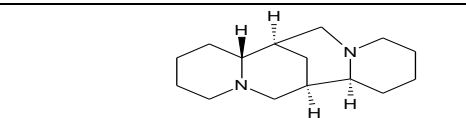
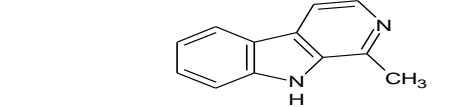
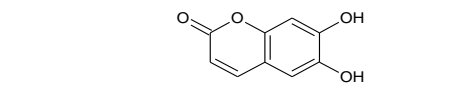
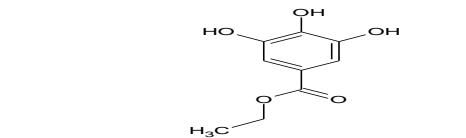
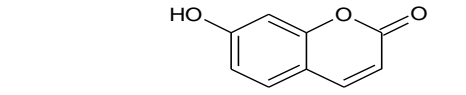
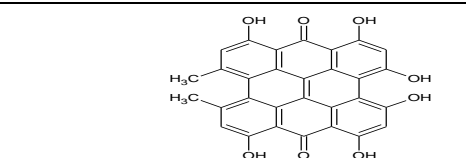
So far, one of the most studied aspects of allelopathy is its role in agriculture for weed management (Jabran et al., 2015; Khaliq et al., 2015). Inhibitory role of allelochemicals is well explored. This role has been directly and indirectly used for weed management (Iqbal and Cheema, 2009; Yazlik, A., and I. Uremis. 2016). A lot of research has been done to explore inhibitory potential of allelopathic crops for weed management. It is substitute of synthetic herbicides as allelochemicals do not have residual or toxic effects (Bhadoria, 2011; Shah et al.,

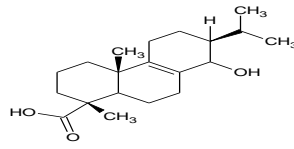
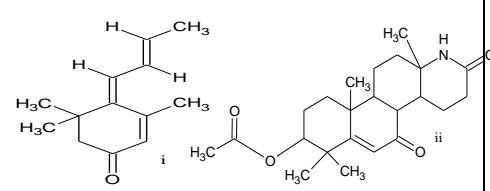
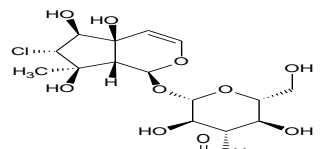
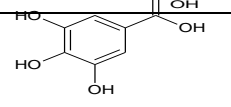
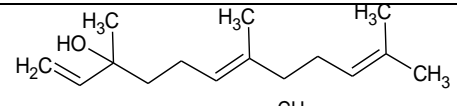
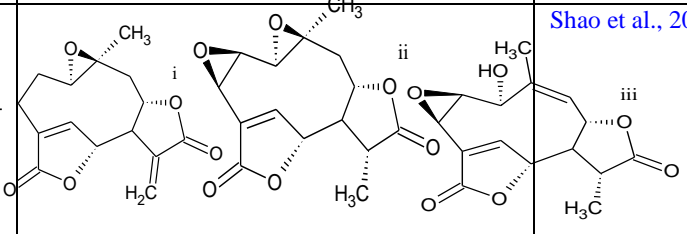
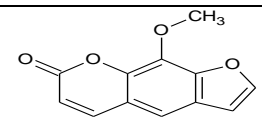
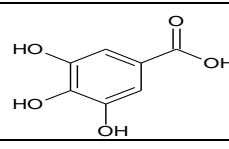
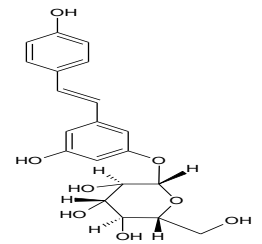
2016). This inhibitory feature is attributed to cessation of important physiological and metabolic processes of plant (Jabran, 2017). On the other hand, allelochemicals promote growth and impart resistance against several abiotic stresses at low concentrations. Few studies have been carried out to investigate

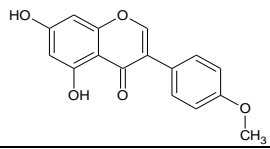
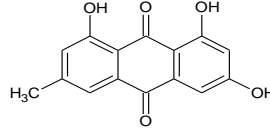
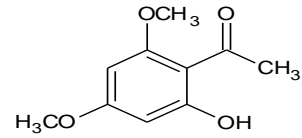
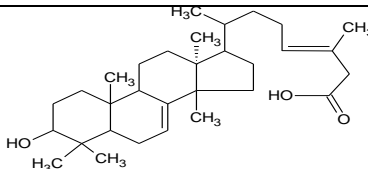
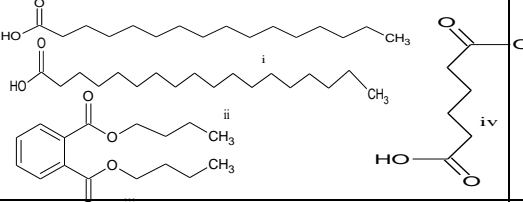
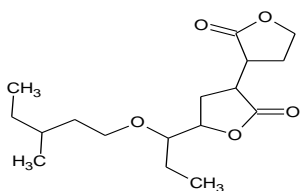
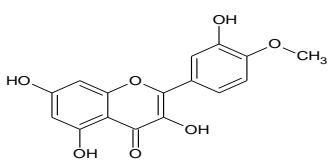
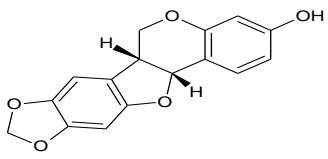
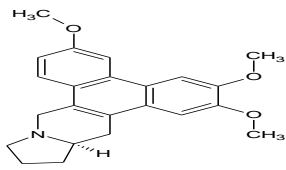
growth promotion by allelochemicals. Allelopathic water extracts application at lower concentrations stimulates germination and growth of different crops that is cost-effective and efficient way to enhance crop productivity (Farooq et al., 2013).

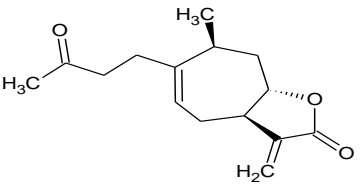
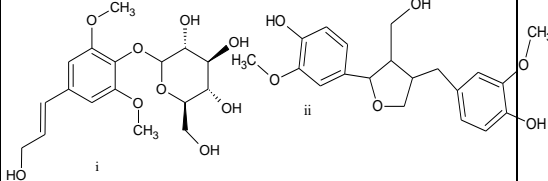
Table 1. Allelochemicals isolated from invasive plants

Plant species	Isolated Allelochemicals	Chemical Structure	Reference
<i>Acroptilon repens</i> (L.) DC.	Cnicin (Sesquiterpene lactone) and 7,8-benzoflavone (Flavone)		Cappuccino and Arnason, 2006; Alford et al., 2007
<i>Alliaria petiolata</i> (Bieb.) Cavara and Grande	Alliarinoside (Glucoside)		Cappuccino and Arnason, 2006; Olsen et al., 2014
<i>Artemisia tridentata</i> ssp. <i>tridentata</i>	Methyl jasmonate (Volatile organic compound)		Preston et al., 2002
<i>Berberist hunbergii</i> DC.	Berberine (Alkaloid)		Cappuccino and Arnason, 2006
<i>Carduus nutans</i> L. and <i>C. acanthoides</i> L.	Aplotaxene (Essential oil)		Silva et al., 2014
<i>Celastrus orbiculatus</i> Thunb.	Celastrol (Terpenoid)		Cappuccino and Arnason, 2006
<i>Centaurea biebersteinii</i> DC.	(-)-Catechin (Flavonoid)		Cappuccino and Arnason, 2006

Plant species	Isolated Allelochemicals	Chemical Structure	Reference
<i>Centaurea diffusa</i> Lam.	8-Hydroxyquinoline (Alkaloid), Caryophyllene oxide (Sesquiterpene), Linoleic acid (Fatty acid)		Callaway and Vivanco, 2006; Quintana et al., 2009
<i>Centaurea maculosa</i> Lam.	(±)-Catechin (Phenol)		Callaway and Vivanco, 2006; Bais et al., 2003; Thorpe et al., 2009
<i>Centro stachys aquatic</i> (R.Br.) Moq.	Loliolide (Terpene)		Bich and Kato-Noguchi, 2009
<i>Chenopodium ambrosioides</i> (L.) Mosyakin & Clemants	α-terpinene (Terpene), limonene (Terpene), ascaridole (Terpene)		Hegazy and Farrag, 2007
<i>Cytisus scoparius</i> (L.) Link	Sparteine (Alkaloid)		Cappuccino and Arnason, 2006
<i>Elaeagnus angustifolia</i> L.	Harman (Amine)		Cappuccino and Arnason, 2006
<i>Euphorbia esula</i> L.	Esulatin (Terpenoid)		Cappuccino and Arnason, 2006
<i>Geranium carolinianum</i> L.	Ethyl gallate (Phenol)		Fujii et al., 2011
<i>Hieracium pilosella</i> L.	Umbelliferone (Coumarin)		Morikawa et al., 2011
<i>Hypericum perforatum</i> L.	Hypericin (Anthraquinone)		Cappuccino and Arnason, 2006

Plant species	Isolated Allelochemicals	Chemical Structure	Reference
<i>Hyptis suaveolens</i> (L.) Poit.	Suaveolic Acid (Terpenoid)		Islam et al., 2014
<i>Imperata cylindrica</i> (L.) P. Beauv.	Tabanone, Hexadecahydro-1-azachrysen-8-yl ester (Alkaloid)		Cardeira et al., 2012; Hagan et al., 2013
<i>Linaria dalmatica</i> (L.) P. Mill.	Linarioside (Glicoside)		Cappuccino and Arnason, 2006
<i>Lythrum salicaria</i> L.	Gallic acid (Phenolic acid)		Cappuccino and Arnason, 2006
<i>Melaleuca quinquenervia</i> (Cav.) Blake	Nerolidol (Sesquiterpene)		Cappuccino and Arnason, 2006
<i>Mikania micrantha</i> H.B.K.	Deoxymikanolide (Sesquiterpenoids), dihydromikanolide (Sesquiterpenes), 2,3-epoxy-1-hydroxy-4,9-germacradiene-12,8:15,6-diolide (Sesquiterpenoid)		Shao et al., 2005
<i>Pastinaca sativa</i> L.	Xanthotoxin (Coumarin)		Cappuccino and Arnason, 2006
<i>Phragmites australis</i>	Gallic acid (Phenolic acid)		Rudrappa et al., 2007
<i>Polygonum cuspidatum</i> Sieb. and Zucc.	Piceid (Glucoside)		Cappuccino and Arnason, 2006

Plant species	Isolated Allelochemicals	Chemical Structure	Reference
<i>Pueraria montana</i> (Lour.) Merr.	Biochanin-A (Isoflavone)		Cappuccino and Arnason, 2006
<i>Rhamnus cathartica</i> L.	Emodin (Resin)		Cappuccino and Arnason, 2006
<i>Sapium sebiferum</i> (L.) Roxb.	Xanthoxylin (Phenol)		Cappuccino and Arnason, 2006
<i>Schinus terebinthifolius</i> Raddi	Schinol (Terpene)		Cappuccino and Arnason, 2006
<i>Spartina alterniflora</i> Loisel.	Hexadecanoic acid (Fatty acid), Octadecanoic acid (Fatty acid), Dibutyl phthalate (Phthalate), Adipic acid (Dicarboxylic acid)		Zheng et al., 2011
<i>Synedrella nodiflora</i> (L.) Gaertn.	3-(5-(1-(3-methylpentyl)oxy)propyl)-tetrahydro-2-oxofuran-3-yl)-dihydrofuran-2(3H)-one (Ketone)		Ghayal et al., 2011
<i>Tamarix ramosissima</i> Ledeb.	Tamarixetin (Flavonol)		Cappuccino and Arnason, 2006
<i>Ulex europaeus</i> L.	Maackiain (Isoflavonoid)		Cappuccino and Arnason, 2006
<i>Vincetoxicum rossicum</i> (Kleopov) Barbar. <i>V. nigrum</i>	Antofine (Alkaloid)		Cappuccino and Arnason, 2006; Gibson et al., 2011

Plant species	Isolated Allelochemicals	Chemical Structure	Reference
<i>Xanthium italicum</i> Moretti	Xanthinosin (Sesquiterpene lactones)		Shao et al., 2012
<i>Cassia uniflora</i> Mill.	Dodecane-4yl-butyrate (Aliphatic ester),	-----	Ghayal et al., 2011
<i>Prosopis juliflora</i> (Sw.) DC.)	Syringin (Glycoside), (-)-Lariciresinol (Lignan)		Nakano et al., 2002

Classical examples of allelopathy for weed control is rice straws left in the fields after harvesting produce that release allelochemicals which suppress growth of neighboring plants. Allelopathy plays role in competitive outcome later in season because allelopathic interactions increase with age and density of rice (Amb and Ahluwalia, 2016). Similarly, Wheat is an important cereals crop extensively studied and used as allelopathic cover crop. It has ability to produce and exude allelochemicals under field conditions which adversely affect weed growth. Numerous chemicals, such as hydroxamic and phenolic acid and short-chain fatty acids, are released from the wheat living plants and decomposing residues which are responsible for wheat allelopathy (Aslam et al., 2017).

Various studies have shown the possibility of using allelochemicals as natural herbicides and growth regulators to promote sustainable agriculture. A large number of allelochemicals have been identified in various weeds. Some allelochemicals from weeds have been extracted, purified and applied as bioherbicides, such asartemisinin and 1,8-cineole from *Artemisia annua* in control of cosmopolitan pest of apples, the codling moth *Cydia pomonella* L. (Durden et al., 2011). Parthenin, hysterin, hymenin, and ambrosin from *Parthenium hysterophorus* in control of *Salvinia molesta*, *Pistia stratiotes*, *Eichhornia crassipes* and *Eragrostis spp.* (Patel, 2011). Studies on weeds are important in order to explore weed species with potential allelotoxin search. These weeds could play effective roles in weed

control instead of synthetic chemical herbicide application, thereby reducing the risk of environmental toxicity due to application of chemical herbicides. Application of allelochemicals at low concentrations to crops can be a cost-effective and efficient way to promote growth and to enhance crop productivity. Allelopathy, thus, can be adopted as a natural alternate of chemical and mechanical options of pest management, crop growth and productivity enhancement. Weed management, insect management, disease management, stress signaling, crop nutrition and growth promotion through physiological regulation, hormonal balance and enzymatic activity has been reported earlier by Farooq et al., 2013.

3. Conclusion and future perspectives

Natural allelotoxins have the potential to be exploited as antibacterial agents, pesticides, fungicides, insecticides and herbicides and/or as leads for new derivatives. Promising results of allelopathy to increase agricultural production decreasing the harmful effects of modern agricultural practices (the indiscriminate use of pesticides) and to maintain soil productivity and a pollution-free environment are ideas to bring under serious consideration. This strategy has potential to become one of strategic sciences to increase agricultural production in sustainable agriculture and to reduce the environmental pollution in modern era.

Investigation is needed to study the growth inhibitory and growth enhancing effects of isolated individual biological weapons. There is a need for the critical examination of the ecological role(s) of the

allelopathy in addition to its effect on plant growth. Field application and testing allelopathy using improved methodologies in the design is requirement of time.

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