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Morphophysiological Investigations in Some Dominant Alien Invasive Weeds

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1. Introduction

Allelopathy generally refers to any direct or indirect, harmful or beneficial effect of one plant on other plants, animals including microorganisms, through the production of chemical compounds that are released into the environment (Rice 1984). These donor plants affect the germination, growth and development of the recipient plant species (Einhellig 1987). The science of allelopathy has a very crucial role in maintaining the phytodiversity / biodiversity of a particular region. In fact, the phenomenon of biodiversity is the reflection of allelopathic interactions in that area. The losses in phytodiversity which are taking place at an alarming rate throughout the world is mainly ascribed to introduction of invasive / alien species which substitute the native ones. Invaded plant species and their success as well as secret have always threatened the world's biodiversity.

"The invasive plants are also known as alien, exotic or introduced ones, which are new to a specific area, become dominant, replacing / substituting the native plant species". These wide-spreading, non-indigenous species adversely affect the habitats they are invading in. The most important aspect of the alien plant is their rapid growth, establishment over new and large areas. Introduced species often find no natural enemies in their new habitat and therefore spread easily and quickly, especially in open disturbed areas. Invasive plants reproduce fast, either vegetatively or by seed. Their phenomenal growth allows them to overwhelm and displace existing vegetation and form dense Monothickets.

1.1 Ecological impacts of invasive plants on the environment

The general ecological impacts of invasive plants on natives and their surrounding environment are given in nutshell:-

- Competition with (and/or replacement of) native plants along with rare and endangered once.
- Loss of habitat and food sources of native insects, birds, wildlife and plants including microorganisms.
- Disruption of native plant-animal associations
- Elimination of native plant communities
- Prevention of establishment of native plants
- Acute competition for space, water, sunlight and nutrients due to its reduction
- Change of the soil structure and chemistry

- Morphophysiological interactions with native flora and fauna through release of allelochemicals / ecochemicals

1.2 Scope of allelopathy

At present it is well established that allelopathic phenomenon exist in different ecosystems including forest ecosystem and it can be exploited for increasing the productivity of crops as well as forest plant species in sustainable manner. According to Reigosa et al. (1999), allelopathy can affect distribution pattern of plants and biodiversity. They further explained that in a climax forest, germination and growth of understorey species must cope with allelochemicals released by the dominant trees. Those trees could release different chemicals, producing differences in the species composition. Similarly, Carballeira and Reigosa (1999) also indicated that monocultures (pure stands) allow the accumulation of particular allelochemicals affecting species composition. The occurrence of some weeds growing better than others within a monoculture could be a result of accumulation of allelochemicals. The allelopathic effects can affect small-scale vegetation patterns, by strengthening the associations between plants or not allowing them to grow in their vicinity. The research in allelopathy has increased greatly from 1960 onwards (Putnam 1985).

Inderjit *et al.* (2005a, b) has discussed in detail the challenges, achievements and opportunities in allelopathy research. They further highlighted that the novel research findings of allelopathy relevant to enzymes and genes involved in production of putative allelochemicals, allelochemical persistence in the rhizosphere, the molecular target sites of allelochemicals in sensitive plant species and the influence of allelochemicals upon other organisms will lead to enhanced utilization of natural products for pest management or as pharmaceuticals and nutraceuticals. The research and development in allelopathy is of extreme urgency for improvement of agriculture, forestry and global environment (Reigosa and Pedrol, 2002), because it deals majorly with invasive and native plant species.

2. Allelobiogenesis - concept and mechanism

Allelobiogenesis is nothing but the stress created by allelopathic effects of donor plants on recipient plants. In other words it is biotic stress and at the same time it is abiotic stress also. Allelobiogenesis is a typical stress combination of biotic and abiotic factors. Plant - plant, plant - animal and plant - micro-organism interactions can be considered as biotic stress.

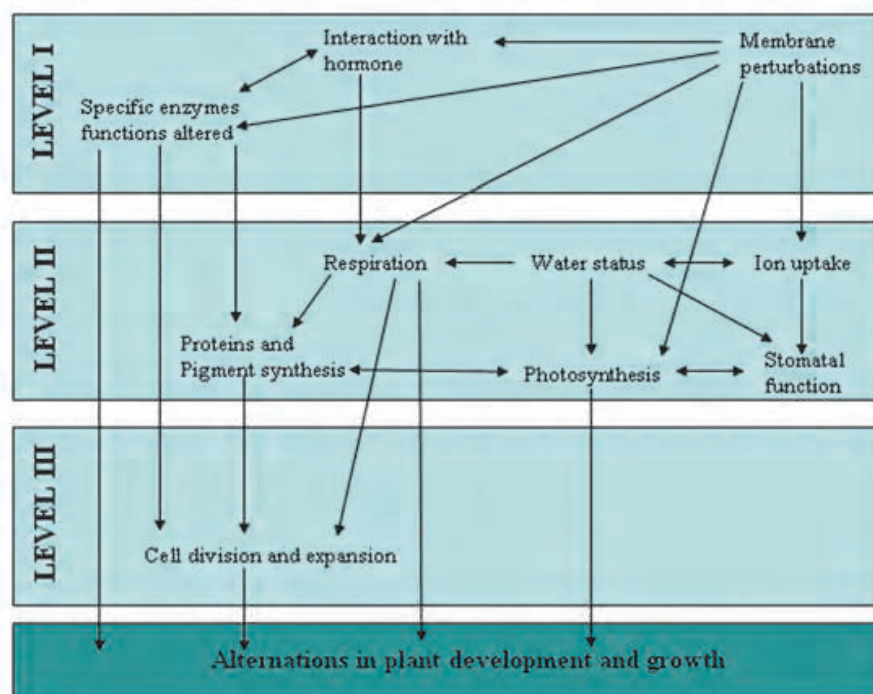
The influence / stress of one plant on the other plant is mainly through the phytochemicals / ecochemicals / allelochemicals released by these donor plants. Hence the stress is obviously of abiotic nature. These allelochemicals are mainly secondary metabolites like alkaloids, glycosides, tannins, flavonoids, phenols etc. and the stress created by such allelochemicals is abiotic stress. The stress created by such allelopathic interaction or allelochemicals is allelobiogenesis. A weed exhausting nutrients from the soil voraciously and producing nutrient stress on associated crop as it shows dominance on associated crop by its faster growth and encroachment over crop species is biotic allelobiogenesis, e.g. *Parthenium* the invasive weed growing in association with *Sorghum*.

The exotic weed *Parthenium* is releasing large no. of allelochemicals through root exudation, leaching and volatilization in the surroundings and these allelochemicals cause very adverse effects on seed germination and growth and all the metabolic processes such as photosynthesis, respiration, absorption of water and minerals. This stress can be well explained as "abiotic allelobiogenesis".

Weeds have many ill / negative characters, which cannot be neglected at all. Many of the weeds cause damages to agroecosystems and also disturb/ reduce natural phytodiversity. Weeds cause great harm to the crops in various ways as they cause 30 - 40% yield losses, increase the expenditure of various cultural practices, reduce the efficiency of agricultural implements. Perennial weeds reduce quality of fertile lands, cause obstacles for water flowing in canals. Weeds reduce crop yield and its quality as they compete with crops for resources like soil, water, nutrients and light. Weeds are alternative hosts for many pests and pathogens. Many weeds like *Prosopis*, *Calotropis* etc. reduce the germination capacity of crops' seeds due to the phytotoxins/ allelochemicals/ ecochemicals, many a times which are the secondary metabolites, secreted by them in the soil.

Aquatic weeds like *Eichhornia* and different types of algae produce toxins, which are harmful to aquatic flora and fauna. Weeds harbour organisms like mosquitoes, which cause or transmit diseases. Some weeds are poisonous to humans and produce pollens, which cause allergies. These studies will be more helpful, if emphasis on interactions among the plants is highly focused by the researchers. Studies on allelopathic potential and the biochemical characterization of native and invasive weeds has become the top priority to get rid of the ill effects of native and invasive weeds.

Mechanism of action and physiological effects of allelochemicals at different levels



Source : Einhellig (1986)

Diagram 1. Mechanism of action and physiological effects

2.1 Allelopathic interactions between plants

Allelopathic interactions are primarily based on the synthesis and release of secondary metabolites by higher plants that initiate a wide array of biochemical reactions, which induce several biological changes, however, many of these are yet to be understood. In

nature, many plant species grow together and interact with each other by inhibiting or stimulating the growth and development through allelopathic interactions. In any ecosystem, the dominant plants growing within it are exhibited in the form of pure stands or monothickets. Such ecosystems always show the zones of inhibition around them (Nilsen 2002, Chase and Leibold 2003). The ecosystems infested by dominant weeds show drastic alterations in their structure and function.

All the weed species, which are the part of dynamic ecosystems, originate in natural environment and become hurdle to the crops (Aldrich 1984). These weeds have some diagnostic features, such as short seed dormancy period, high rate of seed germination, rapid seedling growth, high reproductive ability, life cycle of a short span, very high environmental plasticity, self-compatibility, effective and efficient methods of dispersal of propagules, production of different types of novel ecochemicals or allelochemicals and tolerance to biotic and abiotic stresses (Baker 1965), which enable them to grow and survive in varied habitats and inhospitable ecological conditions.

As a result of this these weeds are becoming dominant throughout the world (Colautti and MacIsaac 2004, Lee and Klasing 2004, Jeschke and Strayer, 2005). As stated by Li et al. (2009), the invasion of exotic weeds is mainly due to their easier establishment and faster growth under diverse environmental conditions. Lonsdale (1999) claimed that the propagules' pressure, adaptive characters and susceptible environment favour the invasibility to which Carlton (2001) called biological invasion.

2.2 Plant invasions and encroachments

The whole biosphere is facing the problem of invasion of different weed species, hence studies on plant invasions and allelopathy will help in understanding the mechanism of invasions, and consequences of them on global biodiversity and ecosystem functioning. These invasions pose many ecological, economic and social problems. A team approach to solve these complicated problems is necessary.

According to MacDougall and Turkington (2005), the alien species highly out compete the native species or escape from adverse environmental conditions and dominate the community. According to vacant niche hypothesis (Elton 1958) the empty places such as barren lands, roadsides, open grounds etc. are generally invaded by such weeds. There are different hypotheses explaining the invasion mechanisms (Inderjit et al. 2005a, b). The diversity of these weeds is governed by population, ecosystem dynamics, disturbances, nutrient supply and climatic factors. The biotic restrictions on them, force to skip from their previous habitat and start surviving in new habitats, helping in the process of invasion. The enemy release hypothesis advocated by Mack et al. (2000) also supports the above view. If the invader is resistant enough and tolerant to herbivory, then its competitive ability increases and it becomes very aggressive due to production of some defensive chemicals (Carpenter and Cappuccino 2005).

The disturbances by some plant species, grazing pressure, fluctuation in resource availability (Davis et al. 2000), soil moisture, available light (Meekins and Mc Carthy 2001), phenotypic plasticity and hybridization (Daehler 2003) results in to successful invasion. The novel weapon hypothesis (Callaway and Ridenour 2004), biotic resistance hypothesis (Maron and Vilà 2001), and the genetic shift hypothesis (DeWalt et al. 2004) also explain the mechanism of invasion. To understand the distribution of invasive weeds and their associates in a natural community, the eco-distribution mapping is of paramount importance.

Biological species invasions alter ecological systems in a multitude of ways. Worldwide an estimated 80% of endangered species could suffer losses due to competition with or predation by invasive species.

3. Compilation of updated work

To have the information about the previous work done on allelopathy in general, its role in different fields of agriculture and botany, different types of interactions such as weed – weed, weed – crop, the impact of leachates, extracts and residues on recipient plants, allelochemicals existing in different donor plants, their chemical structures, mode of release of these ecochemicals in the environment, their accumulation, mechanism of action, their effect on seed germination, seedling growth, mineral nutrition, microbial activity in the soil etc. a review of literature is given in nutshell.

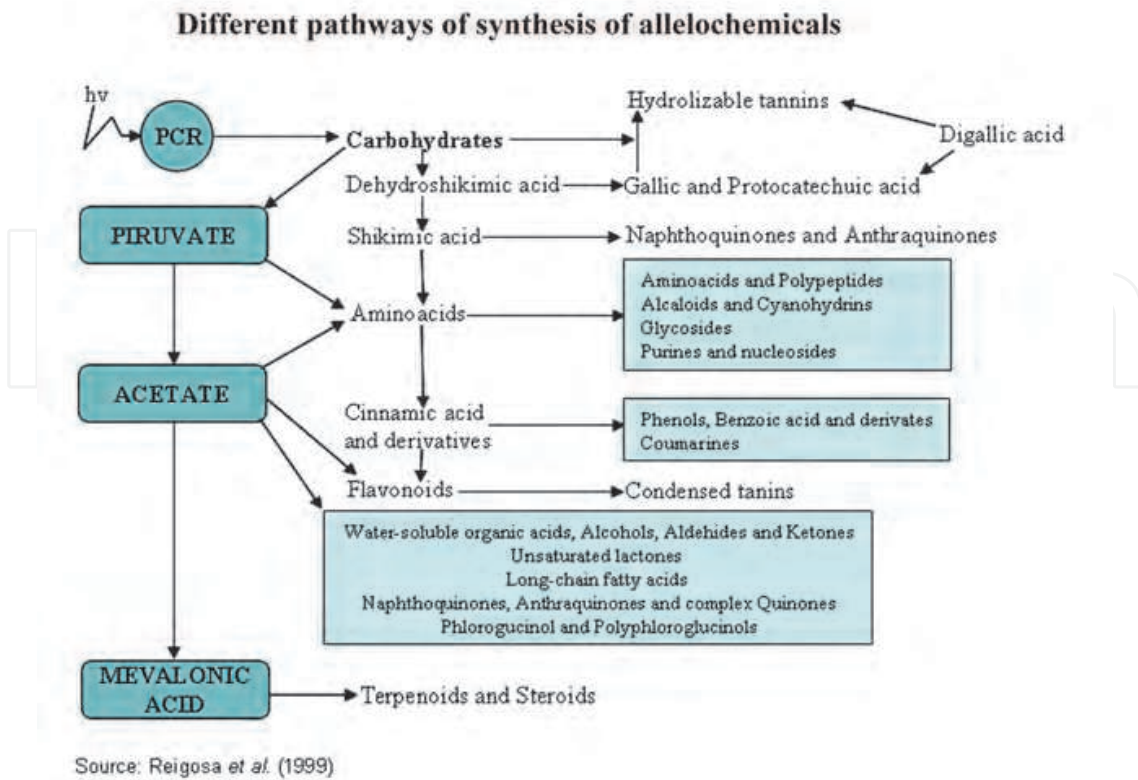
Studies on allelopathy were made thousands of years before the term was coined by Molisch (1937). The term allelopathy is derived from two Latin words *Allelon* means each other and *pathos* means to suffer. He, for the first time studied the effect of numerous plant species and their plant parts viz.- roots, shoots, leaves, flowers, fruits, leachates, extracts and residues on seed germination, seedling growth and maturity of crops. Later on many scientists at different corners of the world, contributed to this field by carrying out the research on various aspects of allelopathy. At present the research on allelopathy is being carried out in more than 85 countries. In India, the research in this field took a great speed after 1950.

Vilai-Santisopasri (2003) studied the allelopathic effects of *Eupatorium adenophorum* Spreng. on growth of some crops and weeds. Hierro and Callaway (2003) had investigated in detail the invasion of exotic plants and their role in allelopathy. Many workers like Rice (1979), Gill and Sandhu (1996), Pawar and Chavan (1999), Chou (1999), Wang et al. (2001), Cheema et al. (2002) had great contribution in allelopathy through their basic research. Recently, many researchers like Narwal et al. (2003a, b), Podolska et al. (2003), Navaz et al. (2003), Batish et al. (2002), Singh and Singh (2003) and Azania et al. (2003) have introduced multidisciplinary approach in allelopathy.

According to Fujii et al. (2002) allelopathy now refers to any process involving secondary metabolites produced by plants, microorganisms, viruses and fungi, that influence the growth and development of agricultural and biological systems. The allelopathy workers like Bhatt and Chauhan (2000), Singh and NarsingRao (2003) and Leather and Einhellig (2005) also claimed that secondary metabolites produced by donor plants, when released into environment, play a key role in ecology and physiology of recipient plants. They further advocated that the released allelochemicals as well as the phytochemicals present in the leachates / extracts have stimulatory or inhibitory influence on seed germination, seedling growth and yield of recipient plants.

The allelopathic impact of invasive weeds on seed germination, seedling growth, growth parameters like plant height, number of leaves per plant, leaf area, yield contributing parameters like number of flowers and fruits per plant, weight of fruit and grains etc in different crops had been studied in detail by Rice (1979), Patil and Hegde (1988), Devi et al. (1997), Kulvinder et al. (1999), Bhalerao et al. (2000a, b), Wang et al. (2001), Kong and Hu (2001), Lin et al. (2002), Bhalerao (2003), Jadhav (2006), Hase (2008) and Vaidya (2009). Presently the allelopathy research work is mainly focused on identification of allelochemicals, their mode of action and ecological significance.

According to many researchers allelopathy now refers to any process involving secondary metabolites produced by plants, microorganisms, viruses and fungi that influence the



Induction of biosynthesis of allelochemicals.

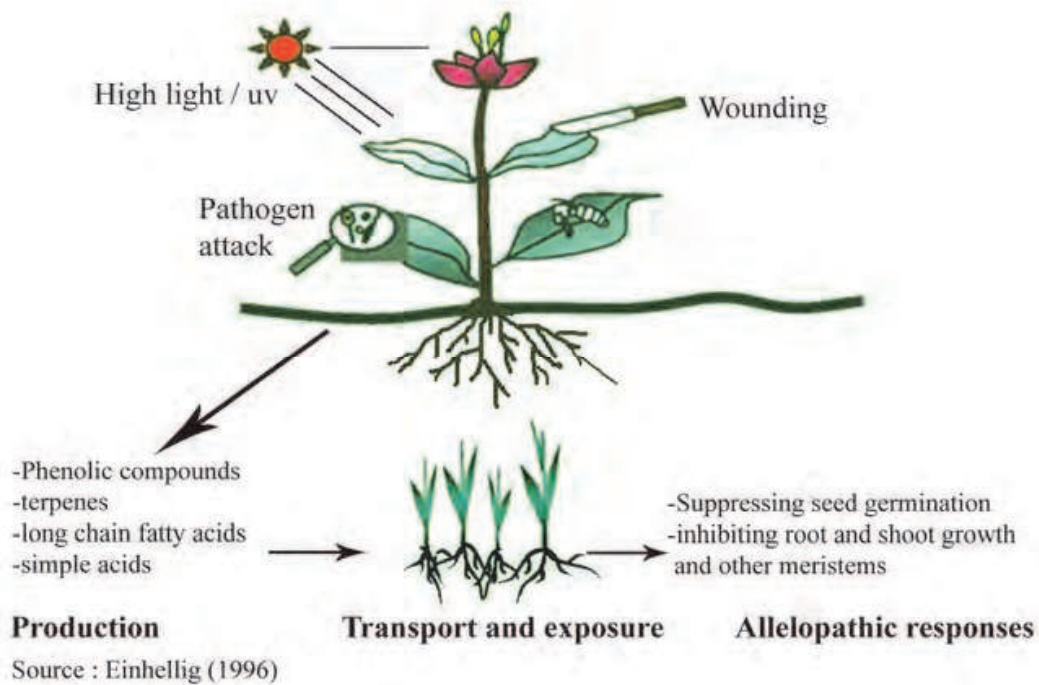


Diagram 2. Different pathways of synthesis of allelochemicals

growth and development of agricultural and biological systems. The allelopathy workers also claimed that secondary metabolites produced by donor plants, when released into environment, play a key role in ecology and physiology of recipient plants. They further advocated that the released allelochemicals as well as the phytochemicals present in the leachates / extracts/ residues have stimulatory or inhibitory influence on seed germination, seedling growth and yield of recipient plants.

Today this subject has come into lime-light because of its multidisciplinary nature, which covers agriculture, biological sciences, biochemistry, physiology, biotechnology and even genetic engineering.

3.1 Invasion success of weeds

The light has been thrown on the success of invasive alien weeds outside their native boundary and probable causes of this. The biological processes and specific characteristics of invasive weeds are important factors in their introduction, spread, and establishment that threatens the ecosystems, habitats, or species with economic/ environmental harm. Therefore the detailed investigations on the ecological, physiological and molecular aspects of invasive weeds' allelopathy should be conducted in order to understand community structure and declining phytodiversity.

3.2 Allelochemicals in invasive and native weed species

Isolation, identification and characterization of allelochemicals present in roots, stems, leaves, flowers, fruits, seeds, bark, residues, litter, dried leaves (trash) and their leachates, extracts and residues have a pivotal role in allelopathy research, without which any predictions, possibilities, hypothesis and explanations are not possible. Asteraceae plants with their leachates, extracts and residues of different plant parts are well known for their allelopathic activity because of their allelochemicals like phenolic acids and terpenoids (Chon et al. 2003).

Many researchers like Ghayal et al. (2007a, b, c) and Li et al. (2009) have given prime importance for identification of allelochemicals, ecochemicals, novel bioactive compounds which are the secondary metabolites existing in their leachates, extracts and residues. They have characterized diverse groups of allelochemicals like terpenoids, flavonoids, phenolic compounds and essential oils existing in the invasive and native weeds.

4. About the study area

The big campus of University of Pune established in 1949, at Ganeshkhind occupies an area of 164.8 hectares, which is situated about seven km north-west of Pune city proper and lies between 18°34' North latitude and 73°53' East longitude at an elevation of about 1880 m. At present 1/4th area is occupied by roads, buildings and gardens.

Ganeshkhind stands on pediment surface of amygdaloidal basalt. These rocks are traversed by many veins and veinlets of silica and chalcedony. The poor soil of study area is reddish brown on higher grounds and deeper dark brown (black cotton soil) on flat areas. The soils are alkaline and are of pedocal type (Varadpande 1972). The average rainfall, climate and other environmental conditions of the campus are more or less similar to that of Pune city. The rainfall is restricted to couple of months in monsoon and the maximum annual rainfall is 31.78cm. The temperature during hot season goes up to 40 – 42°C but normally it is cool as compared to Pune city.

4.1 Weed floristic of study area

The phytosociological studies were conducted at all the four selected sites in Pune University campus. The different plant species were recorded with respect to their distribution, frequency, density and abundance. All four study sites (I to IV) showed the vegetation composition of various types of herbs, shrubs, trees, climbers and twinnings.

The results on phytosociological studies at site I reported in Table 1 (a) indicated that this site was having highest weed diversity. The most abundant weeds at this site with maximum frequencies were *Cassia uniflora* (93.33%), *Achyranthes* (90.00%), *Synedrella nodiflora* (90.00%) and *Oplismenus* (83.33%). These were followed by *Acalypha*, *Bidens*, *Boerhaavia* and *Euphorbia geniculata*, all these were at par having frequency (80.00%). *Alternanthera tenella* was also showing better population with frequency 76.67%. Remaining native plants like *Cynotis* and *Calotropis* and invasive plants have shown less frequency, density and abundance.

The results of site II recorded Table 1(b) revealed that at this site, 43 different weed genera were recorded including about 19 genera of invasive weeds. The most abundant weeds with maximum frequencies were *Synedrella nodiflora* (96.67%), *Cassia uniflora* (93.33%), and *Cassia absus* (86.67%). These were succeeded by *Acalypha*, *Bidens* and *Euphorbia geniculata* which were at par having frequency (83.33%). Remaining plants showed discrete occurrence. At sites I and II *Cassia uniflora* was showing very thick population density, as these sites were exposed to sunlight for longer period.

The results on phytosociological studies of site III reported in Table 1 (c) illustrated that at this site, only 24 genera were reported including about 12 genera of invasive weeds. The plants recorded at this site in order of highest frequency were *Synedrella nodiflora* (93.33%), *Cassia uniflora* (80.00%) and *Rauwolfia* (73.33%). As opposite to sites I and II, at site III, there was complete dominance of *Synedrella nodiflora* only, which was virtually forming monothickets / pure stands. *Synedrella nodiflora* being shade lover was showing luxuriant growth and very high dominance at this site. The shady conditions along with high soil moisture favoured the luxuriant growth of *Synedrella nodiflora* and *Rauwolfia*.

The results listed in Table 1 (d) regarding phytosociological studies carried out at site IV revealed that, there were about 32 genera of weed species including 14 genera of invasive weeds. The weeds with highest frequency were *Cassia uniflora* (96.67%), *Synedrella nodiflora* (93.33%) and *Euphorbia geniculata* (76.67%), which were followed by *Acalypha*, *Achyranthes* and *Alternanthera*. At this site there was highest human interference as compared to the remaining three sites. The fast growing invasive weed *Lantana camara* showed successful invasion only at this site with frequency 63.33%.

No.	Dominant species	Associated species	Nature of association
1	<i>Cassia uniflora</i>	<i>Achyranthes aspera</i>	Very common
2	<i>Cassia uniflora</i>	<i>Blainvillea acmella</i>	Occasional
3	<i>Acalypha ciliata</i>	<i>Cassia uniflora</i>	Rare
4	<i>Alternanthera tenella</i>	<i>Cassia uniflora</i>	Common
5	<i>Synedrella nodiflora</i>	<i>Cassia uniflora</i>	Common
6	<i>Oplismenus compositus</i>	---	Very common
7	<i>Euphorbia geniculata</i>	<i>Cassia uniflora</i>	Common

Table 1. (a) Weed-weed interactions at site I in Pune university campus

No.	Dominant species	Associated species	Nature of association
1	<i>Bidens pilosa</i>	<i>Cassia uniflora</i>	Very common
2	<i>Cassia uniflora</i>	<i>Achyranthes aspera</i>	Very common
3	<i>Triumfetta rhomboidea</i>	<i>Cassia obtusifolia</i>	Common
4	<i>Alternanthera tenella</i>	<i>Boerhaavia erecta</i>	Common
5	<i>Cassia absus</i>	<i>Achyranthes aspera</i>	Common
6	<i>Cassia uniflora</i>	<i>Synedrella nodiflora</i>	Occasional
7	<i>Cassia uniflora</i>	<i>Parthenium hysterophorus</i>	Rare

Table 1. (b) Weed-weed interactions at site II in Pune university campus

No.	Dominant species	Associated species	Nature of association
1	<i>Synedrella nodiflora</i>	<i>Cassia uniflora</i>	Very common
2	<i>Synedrella nodiflora</i>	<i>Achyranthes aspera</i>	Common
3	<i>Cassia uniflora</i>	<i>Tithonia tagetiflora</i>	Common
4	<i>Cassia uniflora</i>	<i>Achyranthes aspera</i>	Common
5	<i>Rauwolfia tetraphylla</i>	<i>Euphorbia geniculata</i>	Common

Table 1. (c) Weed-weed interactions at site III in Pune university campus

No.	Dominant species	Associated species	Nature of association
1	<i>Cassia uniflora</i>	<i>Achyranthes aspera</i>	Common
2	<i>Cassia uniflora</i>	<i>Alternanthera tenella</i>	Common
3	<i>Lantana camara</i>	<i>Cassia uniflora</i>	Occasional
4	<i>Acalypha ciliata</i>	<i>Cassia uniflora</i>	Common

Table 1. (d) Weed-weed interactions at site IV in Pune university campus

Mishra et al. (1997), Chapin et al. (2000), Kumar et al. (2004), Jadhav (2006), Saswade (2007) and Thakur and Khare (2009) have also carried out the phytosociological studies on various invasive and native weeds. The phytosociological studies on *Potentilla recta* and other species, the invasive, noxious weed from Eurasia were carried out by Werner and Soule (1976). Zouhar (2003), Endress and Parks (2004) had also conducted phytosociological studies on these invasive weeds from U.S. The dominance of *Cassia uniflora* and *Synedrella* in the study area may be attributed to their aggressive nature, allelopathic potential, adaptations in morphological and reproductive features along with specific type of physiological, biochemical and enzymological mechanisms allowing their faster growth and tolerance to biotic and abiotic stress conditions.

4.2 Invasion components

Along with the two dominant weed species like *Cassia uniflora* and *Synedrella nodiflora* at all the four sites, the major co-occurring species recorded were *Acalypha ciliata*, *Boerhaavia erecta*, *Cassia obtusifolia*, *Lagasca mollis*, *Peristrophe bicalyculata*, *Parthenium hysterophorus* and *Triumfetta rhomboidea*. The fact worth to mention was establishment of

monothickets (Bhakat et al. 2006) of *Cassia uniflora* at sites I, II and IV and that of *Synedrella* at site III.

The results of GPS mapping of weeds in Pune University campus strongly support the phytosociological observations recorded through quadrat studies. The GPS mapping had given the exact latitude, longitude and altitude of each plant species. More than 200 waypoints were recorded to confirm the dominance of selected weed species like *Cassia uniflora*, *Synedrella nodiflora*, *Alternanthera tenella*, *Bidens pilosa*, *Blainvillea acmella*, *Acalypha ciliata*, *Euphorbia geniculata*, *Triumfetta rhomboidea*, *Cassia obtusifolia* etc. It has also indicated the dominance of *Cassia uniflora* and *Synedrella nodiflora* at all the four selected sites. These selected weeds were located at 18°55' north latitude and 73°82' east longitude and an altitude of 568.63m and 571.48m respectively.

The Millenium Ecosystem Assessment (2005) have claimed that invasive species are the most important drivers of ecosystem change, which can very well alter the vegetational set up of a particular area. Such phytosociological studies on various weeds occurring in crop ecosystems have been carried out by researchers like Bartariya et al. (2005) and Seal et al. (2009) have also reported the dominance of invasive weeds in different ecosystems.

4.3 Secrets of invasion / encroachment and aggressiveness

The invasive weeds can exploit many niches left available and keep changing the phytodiversity of these niches or ecosystems. Unless the phytosociological studies of such areas are carried out, it is difficult to know the extent of encroachment over natives and invasion by the invasive plants. Phytosociology will help to understand the growth characteristics, dominance, distribution and adaptations which enable these plants to sustain the changes in the environment. These studies help to determine the distribution, prevalence, competing ability, behaviour and survival of weeds (Rao, 2000). The results recorded in Tables 1(a, b, c and d) clearly showed the higher dominance of *Cassia uniflora* and *Synedrella nodiflora*, at different sites in the university campus amongst the co-occurring species. These two invasive weed species have caused the reduction in the native phytodiversity of Pune University campus. As suggested by Rizvi and Rizvi (1992), allelopathic interactions of these weeds might be playing a crucial role in existing vegetation pattern of Pune University campus.

The dominance of *Cassia uniflora* and *Synedrella* in the study area may be attributed to their aggressive nature, allelopathic potential, adaptations in morphological and reproductive features along with specific type of physiological, biochemical and enzymological mechanisms allowing their faster growth and tolerance to biotic and abiotic stress conditions.

Plants are chemically well defended in their environments, because their exposure to any stress leads to the qualitative and quantitative changes in the plant biochemicals and enzymes as a part of defense mechanism. These defensive chemicals are nothing but allelochemicals only, which act as feeding deterrents or alter the physiology and development of the attacking organisms (Pathipati UshaRani 2008). Even the different organic compounds often have role in ecological development which mediates interactions between the donor plants and the recipient organisms. The defensive allelochemicals and organic compounds have crucial role in the weed-weed associations formed in the campus of Pune University. The allelopathic potential of invasive weeds like *Cassia* and *Synedrella* can be ascribed to the above mentioned factors.

Allelochemicals always affect many aspects of plants' ecology e.g. distribution, growth, succession, structure of communities, dominance, diversity and productivity (Takeuchi et al. 2001). The population of *Cassia uniflora* had always shown its shifting nature, i.e. area with monothickets during first year will show very less population next year on the same spot. It may be due to the resource exhaust, autotoxicity and heavy accumulation of allelochemicals making the area inhospitable for its own growth. However, it requires further confirmation and experimentation in details.

4.4 Morphological specifications of invasive and native weeds

An attempt was made to study the morphological and reproductive features of invasive and native weeds from Pune university campus (Table 2). The maximum plant height was recorded for *Cassia uniflora*, (104.66cm), which was followed by *Triumfetta* (103.66cm) and *Achyranthes* (96.33cm).

The root length indicates easy and proper establishment of the plants. The maximum root length was recorded for *Alternanthera* followed by *Rauwolfia* and *Achyranthes*.

The highest number of branches per plant was observed in *Achyranthes* and followed by *Triumfetta*, while the weed species like *Acalypha* and *Oplismenus* were without any branch. The number of branches in remaining weeds was next to the above weed species.

Cassia obtusifolia had maximum third leaf area and it was followed by *Rauwolfia* and *Triumfetta*. The third leaf area in remaining weeds was very less as compared to them.

The results on fresh biomass per plant indicated that *Cassia obtusifolia* was having highest biomass and *Triumfetta* was next to it. The weight of fresh biomass in the remaining weeds was comparatively very less.

The dry biomass per plant showed wide variations ranging from 0.89g to 17.43g. The *Cassia* species e.g. *C. obtusifolia* and *C. uniflora* were having highest dry biomass 17.43g and 12.4g per plant respectively.

The highest fresh biomass per m² area was recorded in *Triumfetta*, *Cassia uniflora* and *Blainvillea*. The remaining weeds recorded comparatively less biomass per m² area in the campus of Pune University.

Many research workers like Sen (1977), Weaver and McWilliams (1980), Wilson (1988) had given due importance to morphological studies of native and invasive weeds. Ehrenfeld (2003) proposed that the invasive plants share many physical characteristics and tend to alter habitats. They have very high productivity and above ground biomass. They grow earlier in the season and show faster growth rate than native species. All such features might be applicable to *Cassia* and *Synedrella*, because of which they are dominant in the campus, showing luxuriant growth.

Unless we know the morphological features of weeds, the attempts for their effective management are difficult. With this view, Sutherland (2004) has described all the morphological details of different terrestrial and aquatic weeds of India. Similarly Monaco et al. (2002) had also investigated the various morphological characteristics of different weeds from USA. The life cycle of a plant can be understood well by its morphological structures, developmental processes and whole plant activities that occur during each phase of its life cycle. He further stated that selected phenotypes dominate their neighbours, because the timing of their life history optimizes their relative fitness and minimizes mortality. Same explanation may be true for the dominance of different invasive weeds including *Cassia* and *Synedrella* over the natives of Pune University campus.

*Weed spp.	Plt. Ht. cm.	Root length cm.	No. of Branches/plt.	No. of leaves / plt.	III Leaf area cm ²	Fresh biomass / plt. g	Dry biomass / plt. g	Fresh biomass / m ² g
Cul	104.66 a ± 4.18	17.66 c ± 0.70	7 d ± 0.28	18 e ± 0.4	20.41 d ± 0.81	36.3 d ± 1.45	12.4 ± 0.49	2316.2 b ± 92.64
Snl	63.66 e ± 3.18	17 c ± 0.85	8 c ± 0.4	31a ± 1.5	14.9 e ± 0.74	15.68 g ± 0.78	4.1 ± 0.20	282.42 f ± 14.12
Alt	91 b ± 6.37	22.66 a ± 1.58	9 b ± 0.63	28 b ± 1.96	12.8 ef ± 0.89	21.5 f ± 1.50	8.3 ± 0.58	356.84 e ± 24.98
Eug	73.66 c ± 2.20	13.3 d ± 0.39	3 h ± 0.09	10 g ± 0.3	18.41 d ± 0.55	19.06 f ± 0.57	4.6 ± 0.13	114.36 g ± 3.43
Bod	46.33 g ± 2.77	8.16 g ± 0.48	4 g ± 0.24	15 f ± 0.9	11.8 fg ± 0.70	31.13 e ± 1.86	10.7 ± 0.64	108.39 g ± 6.50
Ach	96.33 b ± 5.77	20 b ± 1.2	11 a ± 0.66	24 d ± 1.44	12.2 fg ± 0.73	34.72 d ± 2.08	10.2 ± 0.61	347.2 e ± 20.83
Bln	66 de ± 2.64	5.5 h ± 0.22	6.33 e ± 0.25	7.33 h ± 0.29	13 ef ± 0.52	12.33 hi ± 0.49	1.43 ± 0.05	579.51 c ± 23.18
Aca	49.66 f ± 3.47	4.5 hi ± 0.31	0 i ± 0	26 c ± 1.82	10.5 g ± 0.73	9.33 i ± 0.65	1.75 ± 0.12	171.67 g ± 12.01
Tum	103.66 a ± 3.10	9.66 f ± 0.28	11 a ± 0.33	25 cd ± 0.75	33.66 c ± 1.00	88.33 b ± 2.64	3.1 ± 0.09	2473.24 a ± 74.19
Cab	52.26 fg ± 2.61	11.4 e ± 0.57	8.33 c ± 0.41	7.33 h ± 0.36	18.5 d ± 0.92	11.66 hi ± 0.58	3.02 ± 0.15	139.92 g ± 6.99
Cfl	71.83 cd ± 2.15	13.16 d ± 0.39	6.66 de ± 0.19	14.66 f ± 0.43	45 a ± 1.35	91.66 a ± 2.74	17.43 ± 0.52	366.64 e ± 10.99
Bdn	55.23 f ± 3.31	7.96 g ± 0.47	8.33 c ± 0.49	9.66 g ± 0.57	33.1 c ± 1.98	12.9 gh ± 0.77	2.35 ± 0.14	472.14 d ± 28.32
Raw	63 e ± 4.41	20.76 b ± 1.45	5.33 f ± 0.37	20.33 e ± 1.42	42.66 b ± 2.98	56.66 c ± 3.96	9.5 ± 0.66	396.62 e ± 27.76
Opl	23.12 h ± 0.92	3.2.i ± 0.12	0 i ± 0	10 g ± 0.4	3.5 h ± 0.14	5.35 j ± 0.21	0.89 ± 0.03	112.35 g ± 4.49
p=	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Data are the pooled means of three estimates each over two years ± standard deviation. 'p-value' denotes the significance of difference between the means by one way ANOVA statistics. a The values followed by different letters differ significantly by Duncan's multiple range test at p=0.05.

* **Cul:** *Cassia uniflora* Mill.non Spreng; **Snl:** *Synedrella nodiflora*(L) Gaertn; **Alt:** *Alternanthera tenella* Colla; **Eug:** *Euphorbia geniculata* Orteg.; **Ach:** *Achyranthes aspera* L.; **Bod:** *Boerhaavia erecta* L.; **Bln:** *Blainvillea acmella* L.; **Aca:** *Acalypha ciliata* Forsk.; **Tum:** *Triumfetta rhomboidea* Jacq.; **Cab:** *Cassia absus* L.; **Cfl:** *Cassia obtusifolia* L.; **Bdn:** *Bidens biternata* Lour.; **Raw:** *Rauwolfia tetraphylla* L.; **Opl:** *Oplismenus compositus* P.Beauv.

Table 2. Morphological features of invasive and native weeds

4.5 Reproductive capabilities of invasive and native weeds

The invasive and native weeds showed considerable variations in reproductive characters (Table 3 a). The type of inflorescence in majority of the weeds studied was mostly head,

spike or cyme. Only in *Euphorbia*, it was cyathium, and in *Oplismenus* it was panicle. In almost all the weeds the inflorescence was axillary, but only in *Achyranthes* and *Cassia absus*, it was terminal.

For the number of inflorescences per plant *Triumfetta*, was at first rank, which was followed sequentially by *Alternanthera*, *Synedrella* and *Cassia uniflora*. The weed species like *Blainvillea*, *Acalypha* and *Achyranthes* were at medium position, while the least number was noted in *Oplismenus*.

The number of flowers, florets and flowerbuds per inflorescence was also a diagnostic feature for all the weeds. *Acalypha* was having highest number of male and female flowers together, whilst *Achyranthes* was following it (Table 3a). *Oplismenus* was in third position and it was followed by *Synedrella*. Remaining weeds had very few numbers of flowers/ florets/ flowerbuds and the lowest number of flowers was in *Triumfetta*.

The number of fruits per inflorescence is very important reproductive character which was in the order of -

Snl > Ach > Bdn > Alt > Tum > Bln > Aca > Cul > Cfl > Cab > Opl > Eug > Raw (Table 3b).

The number of seeds per plant was not showing the same order as that of number of fruits (Table 3b). This was due to the number of seeds per fruit, which is again a specific and variable character for a particular plant. The descending sequence for number of seeds per plant was:

Cfl > Snl > Ach > Cul > Aca > Bdn > Tum > Cab > Alt > Bod > Bln > Eug > Opl > Raw.

Weed species	Type of Inflorescence	No. of Inflo. / plant	No. of flowers, florets or floral buds per inflo.
Cul	Axillary raceme/ subsessile pairs, Crowded upwards	38.0 d ± 1.52	8.0 fgh ± 0.32
Snl	Axillary heads	60.0 c ± 3.00	21.0 cd ± 1.05
Alt	Axillary clusters	75.0 b ± 5.25	9.0 fgh ± 0.63
Eug	Cyathium	9.0 i ± 0.27	8.0 fgh ± 0.24
Bod	Umbels in terminal corymbose panicles	30.0 e ± 1.8	13.0 efg ± 0.78
Ach	Terminal spikes	21.0 g ± 1.26	36.0 b ± 2.16
Bln	Heads in erect terminal cymes	25.33 f ± 1.01	13.0 efg ± 0.52
Aca	Androgynous spikes	23.0 fg ± 1.61	178.3 a ± 12.48
Tum	Dense terminal and leaf opposed cymes	90.0 a ± 2.7	4.0 h ± 0.12
Cab	Terminal raceme	8.66 i ± 0.43	14.0 ef ± 0.7
Cfl	Axillary subsessile pairs of flowers	9.33 i ± 0.27	14.33 ef ± 0.42
Bdn	Corymbose paniced heads	15.66 h ± 0.93	16.66 de ± 0.99
Raw	Umbelliform cyme	9.66 i ± 0.67	7.33 gh ± 0.51
Opl	Panicle	2.0 j ± 0.08	24.0 c ± 0.96
p=		<0.001	<0.001

Table 3. (a) Reproductive features of invasive and native weeds

The results on reproductive capacity of invasive and native weeds revealed that the highest reproductive capacity was recorded in *Cassia obtusifolia*, which was followed by *Synedrella*. While *Achyranthes* and *Cassia uniflora* were on the third rank. The least reproductive capacity was reported in *Boerhaavia* (Table 3b).

Weed species	No. of fruits / inflo.	No. of fruits / plant	No. of seeds / fruit	No. of seeds / plant	Reproductive Capacity
Cul	9	2736 f ± 109.44	8	21888 d ± 875.52	18604 c ± 744.16
Snl	21	26460 a ± 1323	1	26460 b ± 1323	23814 b ± 1190.7
Alt	9	6075 d ± 425.25	1	6075 gh ± 425.25	3037.5 fg ± 212.62
Eug	8	576 h ± 17.28	3	1728 k ± 51.84	691.2 h ± 20.73
Bod	13	5070 e ± 304.2	1	5070 hi ± 304.2	2028 g ± 121.68
Ach	32	24192 b ± 1451.52	1	24192 c ± 1451.52	19353.6 c ± 1161.21
Bln	13	4280.77 e ± 171.23	1	4280.77 ij ± 171.23	2996.539 fg ± 119.86
Aca	1	4100.9 e ± 287.063	3	12302.7 e ± 861.18	6679.89 e ± 467.59
Tum	12	4320 e ± 129.6	2	8640 f ± 259.2	3247.72 f ± 97.43
Cab	14	1697.36 g ± 84.86	4	6789.44 g ± 339.472	3394.72 f ± 169.73
Cfl	14	1915.91 fg ± 57.47	32	62266.9 a ± 1868.007	28020.11 a ± 840.60
Bdn	37	9653.14 c ± 579.18	1	9653.14 f ± 579.18	8205.05 d ± 492.30
Raw	7	495.65 h ± 34.6955	2	991.309 k ± 69.39	7183.4 e ± 502.83
Opl	24	1152 gh ± 46.08	1	1152 k ± 46.08	6220.8 e ± 248.83
p=		<0.001		<0.001	<0.001

Table 3. (b) Reproductive features of invasive and native weeds

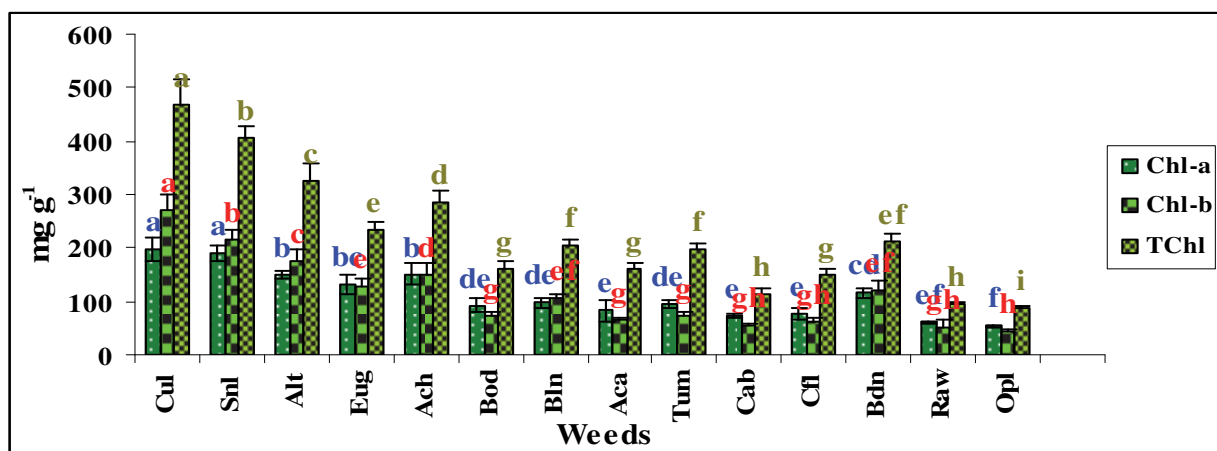


Fig. 1. Photosynthetic pigments in the invasive and native weeds

The role of reproductive capacity of weeds from arid zones was carried out by Sen (1981). Many researchers like Khanh et al. (2009) had studied the reproductive biology of Russian thistle, barnyardgrass, *Solidago canadensis* and *Bidens pilosa* respectively. Some have investigated the allelopathic potential of reproductive organs (flowers and fruits) of *Lantana camara* and explained their role in successful invasion, encroachment and dominance of it.

The role of reproductive capacity of weeds from arid zones was carried out by Sen (1981) and Kanchan and Jayachandra (1977) for *Parthenium hysterophorus*. The seed output and other propagules was studied by Stevens (1957) for different weed species. Many researchers like Young (1991), Norris (1992), Huang Hua et al. (2007) and Khanh et al. (2009) had studied the reproductive biology of Russian thistle, barnyardgrass, *Solidago canadensis* and *Bidens pilosa* respectively. Hu and Wang (2001) studied the reproduction of two weedy vines. Qiaoying Zhang et al. (2009) had investigated the allelopathic potential of reproductive organs (flowers and fruits) of *Lantana camara* and explained their role in successful invasion, encroachment and dominance of it.

The reproductive characters are the probable indicators of plants' invasiveness and aggressiveness in the ecosystem. Not only this, but they are also the factors deciding their density and abundance. Dekker (2005) had also opined similarly indicating the role of reproductive features in plant invasion. Bhan et al. (1976) also emphasized on the role of reproductive behavior of *Phalaris minor* in its dominance and invasion. In the present study also, the comparison made on the basis of morphological and reproductive characters between invasive and native weeds revealed that the selected invasive weeds were superior in all the above-mentioned features, reflecting on their dominance over natives in the campus of Pune University. Friedman and Waller (1983) also stated that the seeds of plants act as allelopathic agents, releasing the different types of allelochemicals in their surrounding environment and which help to establish their dominance.

4.6 Light harvesting components in invasive and native weeds

The results shown in Figure 1 revealed that amongst invasive weeds *Cassia uniflora* and *Synedrella* had higher chlorophyll a, b and total chlorophyll contents, followed by *Alternanthera*. Amongst invasive weeds *Bidens* and *Blainvillea* are at par for chlorophyll contents. Amongst the natives *Triumfetta* was following *Achyranthes* for photosynthetic pigments. Remaining invasive and native weeds were at intermediate state for the contents of photosynthetic pigments. Whilst, *Oplismenus* and *Rauwolfia* had shown the lowest chlorophyll contents. The invasive weeds like *Cassia uniflora*, *Synedrella* and *Alternanthera* had shown maximum amount of chlorophyll a, chlorophyll b and total chlorophylls.

The results recorded on photosynthetic pigments in different invasive and native weeds were corroborating with that of photosynthetic rate and other gas exchange parameters (Table 4 and Figure 1). Ghayal et al. (2009) have quantified the photosynthetic pigments in different invasive, native, aquatic as well as terrestrial weeds. Pawar (2004), Jadhav (2006), Castillo et al. (2007), Vaidya (2009) have quantified the photosynthetic pigments in different invasive, native, aquatic as well as terrestrial weeds. Wang et al. (2004) also recorded significant contents of chlorophylls and better photosynthetic rate in *Eupatorium*. Bhalerao (2003) had made similar observations regarding photosynthetic pigments in fern species like *Tectaria* and *Pteridium* from Mahabaleshwar area.

Photosynthetic pigments are the master molecules in carbon assimilation process, which govern photosynthetic efficiency. Sampietro et al. (2007) explained that the growth, development, dominance and allelopathic potential of any plant species mostly depend on its physiological, biochemical and enzymological characteristics. The growth, development, dominance and allelopathic potential of any plant species mostly depend on its physiological, biochemical and enzymological characteristics. The allelochemicals in it are also important along with above aspects. The amount of photosynthetic pigments usually correlates with photosynthetic rate, which is directly or indirectly reflected into

accumulation of reserved food materials like starch and dry matter accumulation rate and dry biomass. Considering this the dominance of *Cassia*, *Synedrella* and other native weeds can be correlated with higher amount of chlorophyll contents, enhanced photosynthetic rate and increased accumulation of reserved food materials.

4.7 Carbon assimilation rate of invasive and native weeds

The selected invasive weeds like *Cassia*, *Synedrella* and *Alternanthera* had shown the highest photosynthetic rate, stomatal conductance and transpiration rate as compared to native weeds such as *Achyranthes* and *Boerhaavia* (Table 4). Amongst the natives *Achyranthes* was superior in all above mentioned parameters over other weeds like *Triumfetta*, *Boerhaavia*, *Cassia absus* and *Rauwolfia*.

The third leaf area was maximum in *Cassia obtusifolia*, which was followed by *Rauwolfia* and *Triumfetta*. There was no significant difference in water use efficiency (WUE) amongst the investigated invasive and native weeds. On the basis of dry matter accumulation rate (DMAR) *Cassia uniflora* was topmost, which was followed by *Synedrella* and *Alternanthera*. Similarly the results for dry weight per plant (Table 4) indicated highest values for *Cassia obtusifolia* followed by *Cassia uniflora* and *Boerhaavia*.

According to McDowell (2002) the success of invasion and dominance of invasive weeds in any ecosystem over co-occurring species can be ascribed to their superiority in physiological attributes like photosynthetic rate, stomatal conductance, third leaf area and DMAR, but all such parameters mostly remained unexplained and unexplored. Understanding of such factors may give valuable insight to resolve the problem of invasion. Photosynthesis is the key catabolic process in the life cycle of any plant, which synthesizes various types of photo-assimilates and reflects into overall productivity and metabolic status of that plant. The secondary metabolites acting as allelochemicals are mainly derived from carbohydrates synthesis during photosynthesis.

Research workers like Durand and Goldstein (2001) and Ewe and Sternberg (2003) have also recorded the significant difference in photosynthetic rate, stomatal conductance, transpiration rate and total leaf area for the various invasive weeds and claimed that these weeds were highly dominant over the associated natives because of their superiority in above parameters.

According to Pattison et al. (1998) successful invasive species should have elite morphological and physiological traits, which increase their photon capturing ability and light utilization efficiency. But unfortunately this type of invagination has remained obscure due to paucity of experimental work, except few reports on light capturing mechanism, photon-saturated photosynthetic rate, specific leaf area (SLA) investigated in some invasive weeds by Ewe and Sternberg (2003). According to Durand and Goldstein (2001) invasiveness of alien species is dependent on photosynthetic efficiency. They further claimed that invasive species have a higher ability to capture solar radiations at the minimum cost of energy (ATP), diverting more resources for their growth, development, reproduction and yield. Coupled with the above distinctive features of photosynthesis, the invasive weeds have very high abiotic stress tolerance capacity, which enables them to survive and reproduce successfully, under extremely harsh environmental conditions like drought.

The water use efficiency (WUE) is always positively co-related with the rate of photosynthesis, however in present studies it has not shown any significant differences,

amongst the invasive and native weed species investigated. Funk and Vitousek (2007) have reported the positive co-relation with leaf traits and WUE in some weeds. Blicher et al. (2003) had also reported higher water use efficiency in the invasive weed *Centaurea maculosa* over three native grasses.

Weed Sps.	Photosynthetic rate $\mu\text{mol cm}^{-2} \text{sec}^{-1}$	Stomatal conductance $\text{mmol cm}^{-2} \text{sec}^{-1}$	III leaf area cm^2	Transp. rate $\text{mmol cm}^{-2} \text{sec}^{-1}$	WUE $\mu\text{molm mol}^{-1}$	DMAR / m^2 / day	Dry weight / plant g
Cul	29.55 a \pm 4.84	0.353a \pm 0.064	20.41 d \pm 0.82	1.181 a \pm 0.21	25.02 \pm 1.00	19.16 a \pm 0.77	12.40 b \pm 0.50
Snl	29.122 ab \pm 6.15	0.351ab \pm 0.038	14.90e \pm 0.75	1.152 ab \pm 0.242	25.28 \pm 1.26	5.90b \pm 0.30	4.10g \pm 0.21
Alt	27.3ab \pm 0.43	0.34a \pm 0.072	12.80ef \pm 0.90	1.053 abc \pm 0.13	25.93 \pm 1.81	4.18c \pm 0.29	8.30f \pm 0.58
Eug	27.137 ab \pm 3.06	0.318a \pm 0.027	18.41d \pm 0.55	1.048 bcd \pm 0.033	25.89 \pm 0.78	2.66d \pm 0.08	4.60g \pm 0.14
Ach	27.237 ab \pm 2.01	0.324a \pm 0.027	12.20fg \pm 0.73	1.052 abc \pm 0.095	25.88 \pm 1.55	2.58d \pm 0.15	10.20d \pm 0.61
Bod	22.1 bc \pm 3.79	0.256bc \pm 0.041	11.80fg \pm 0.71	0.874 cde \pm 0.16	25.29 \pm 1.52	2.62d \pm 0.16	10.70cd \pm 0.64
Bln	23.308 bc \pm 8.59	0.272bc \pm 0.10	13.00ef \pm 0.52	0.968 cd \pm 0.28	24.08 \pm 0.96	0.46gh \pm 0.02	1.43jk \pm 0.06
Aca	21.833 bc \pm 0.45	0.253bcd \pm 0.006	10.50g \pm 0.73	0.845 cde \pm 0.020	25.84 \pm 1.81	0.85fg \pm 0.06	1.75ij \pm 0.12
Tum	22.483bc \pm 5.01	0.266bc \pm 0.058	33.66c \pm 1.01	0.889 cde \pm 0.19	25.29 \pm 0.76	1.46e \pm 0.04	11.35c \pm 0.34
Cab	19.5c \pm 0.7	0.178de \pm 0.014	18.83d \pm 0.94	0.731 def \pm 0.038	26.68 \pm 1.33	0.26h \pm 0.01	3.02h \pm 0.15
Cfl	21.533bc \pm 0.51	0.21cde \pm 0.018	45.00a \pm 1.35	0.832 cde \pm 0.032	25.88 \pm 0.78	0.58gh \pm 0.02	17.43a \pm 0.52
Bdn	26.542ab \pm 3.88	0.309a \pm 0.044	33.10c \pm 1.99	1.016 bcd \pm 0.15	26.12 \pm 1.57	1.09ef \pm 0.07	2.35hi \pm 0.14
Raw	17.867c \pm 1.53	0.143e \pm 0.033	42.66b \pm 2.99	0.702 ef \pm 0.0603	25.45 \pm 1.78	0.32h \pm 0.02	9.50e \pm 0.66
Opl	15.283d \pm 1.38	0.125e \pm 0.015	3.50h \pm 0.14	0.592 f \pm 0.047	25.82 \pm 1.03	0.16h \pm 0.01	0.98k \pm 0.04
	<0.001	<0.001	<0.001	<0.001	0.81	<0.001	<0.001

DMAR – Dry Matter Accumulation Rate

Data are the pooled means of three estimates each over two years \pm standard deviation. 'p-value' denotes the significance of difference between the means by one way ANOVA statistics. a The values followed by different letters differ significantly by Duncan's multiple range test at $p=0.05$.

* **Cul:** *Cassia uniflora* Mill.non Spreng; **Snl:** *Synedrella nodiflora*(L) Gaertn; **Alt:** *Alternanthera tenella* Colla; **Eug:** *Euphorbia geniculata* Orteg.; **Ach:** *Achyranthes aspera* L.; **Bod:** *Boerhaavia erecta* L.; **Bln:** *Blainvillea acmella* L.; **Aca:** *Acalypha ciliata* Forsk.; **Tum:** *Triumfetta rhomboidea* Jacq.; **Cab:** *Cassia absus* L.; **Cfl:** *Cassia obtusifolia* L.; **Bdn:** *Bidens biternata* Lour.; **Raw:** *Rauwolfia tetraphylla* L.; **Opl:** *Oplismenus compositus* P.Beauv.

Table 4. Photosynthetic parameters of invasive and native weeds

Photosynthesis is the unique process that governs the plant productivity and biomass production. Hence the increased photosynthetic rate in invasive weeds might be able to increase biomass as the rate of dry matter accumulation rate resulting into higher biomass production. All these factors might be responsible for the higher dominance of selected invasive weeds in the study area. The invasive weeds studied in the present investigation like *Cassia uniflora*, *Synedrella* and *Alternanthera* had shown higher rate of photosynthesis, stomatal conductance, transpiration and dry matter accumulation rate over other invasive and native weeds, which might be the basic reason for the success of invasion and dominance in the campus of University of Pune (M.S.)

4.8 Biochemical nature invasive and native weeds

The results recorded on organic constituents like total sugars and starch indicated that *Cassia uniflora* had highest contents, which was followed by *Synedrella*, *Alternanthera* and *Bidens*. The remaining invasive and native weed species were on par for the contents of total sugars and starch, while *Cassia absus*, *Rauwolfia* and *Oplismenus* were at par but lower than the above mentioned weeds for starch and total sugars (Figure 2).

The invasive weeds like *Cassia uniflora* had shown highest contents of proteins and free amino acids, which was followed by *Synedrella* and *Alternanthera*. While *Bidens*, *Blainvillea* and *Euphorbia* were at par. The native weed *Achyranthes* had maximum contents of proteins and free amino acids, followed by *Triumfetta* and *Boerhaavia*. While remaining weed species had comparatively very less contents of proteins and free amino acids (Figure 3).

The dominant invasive and native weeds were having comparatively higher contents of reducing and total sugars, starch, proteins etc. They further explained that the superiority in organic constituents was contributing for the luxuriant growth and allelopathic potential. The chemicals released from damaged roots, root exudates and leaf leachates such as amino acids and carbohydrates may not directly act as allelopathic agents, but they can modify the activities of allelochemicals. The maximum contents of organic constituents like total sugars and starch have also indicated the better photosynthetic efficiency of these weeds over co-existing ones. The contents of primary metabolites like sugars, carbohydrates, amino acids, proteins etc. in plants also have allelopathic potential. The higher contents of all above organic constituents in *Cassia* and *Synedrella* might be responsible for their allelopathic potential.

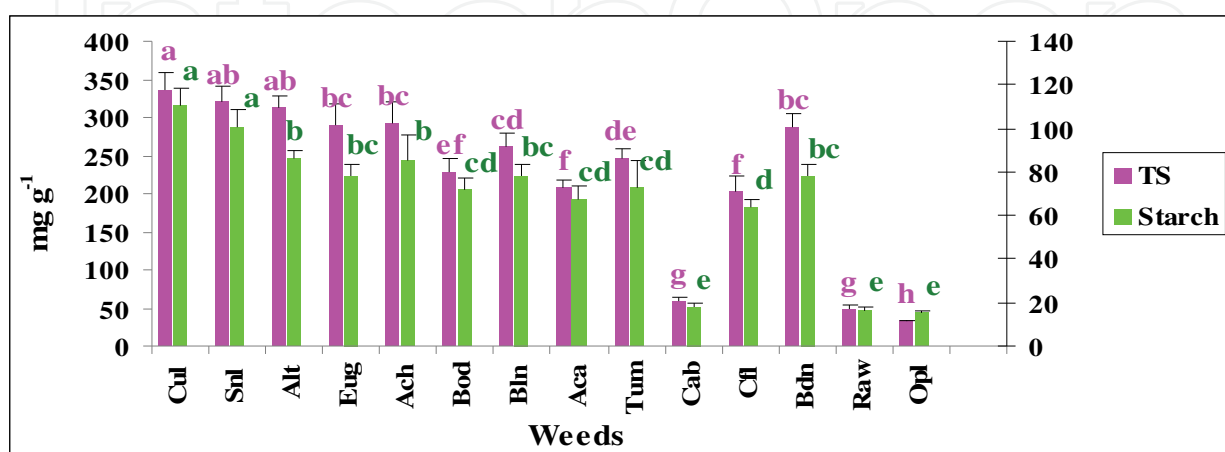
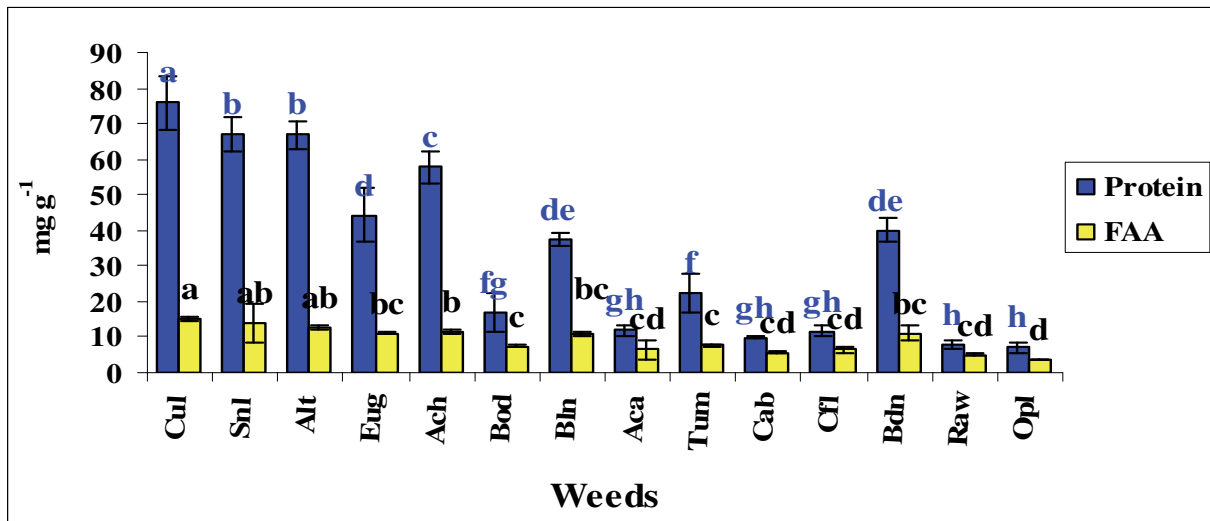


Fig. 2. Total sugars and starch contents in the invasive and native weeds



#Data columns are the pooled means of three replicates over two years with standard deviation as error bars. a Different letters at the data points denote significant difference by Duncan's multiple range test at $p < 0.05$.

Fig. 3. Protein and free amino acid contents in the invasive and native weeds

According to Blum (1996, 1997) and Inderjit and Nilsen (2003), allelopathic action can be explained by investigating the organic compounds in plants, because they may have additive effect or joint action on various biosynthetic pathways of primary and secondary metabolites. The contents of various organic constituents existing in plants may indicate their allelopathic potential, luxuriant growth and aggressive nature. Similar explanations may be applicable for the luxuriant growth and aggressive nature, faster encroachment and dominance of *Cassia* and *Synedrella* at all the four selected sites in Pune University campus, as both the weeds were highly superior in photosynthetic pigments, different photosynthetic parameters and organic constituents like sugar, starch, proteins and free amino acids.

4.9 ROS scavenging mechanism of invasive and native weeds

As it is well documented that invasive and native weeds have stress tolerant abilities and sustenance to withstand harsh ecological conditions due to the presence of osmolytes, antioxidants and ROS scavenging enzymes, an attempt was made for analysis of these parameters.

The results recorded in Table 5 on various antioxidants/ osmolytes/ compatible solutes like proline, glycine betaine and phenolics revealed that *Cassia uniflora* was having highest contents. It followed by *Synedrella* and *Alternanthera*. However the results on glycine betaine were not significant and for phenolics all the three weed species were at par.

The analysis of MDA content (lipid peroxidation) revealed that *Cassia uniflora* had lowest value, which was followed by *Synedrella* and *Alternanthera*. While *Achyranthes* was lowest amongst the native weeds.

The results on MSI showed that the index was highest in *Cassia uniflora* which was followed by *Synedrella* and *Alternanthera*.

The results reported in Table 5 on the relative water content of invasive and native weeds showed that here also *Cassia uniflora* was topmost, succeeded by *Synedrella* and *Alternanthera*.

Weed species	Proline m moles/g DW	Glycine Betaine mg/g	Phenols mg/g	Lipid Peroxidation T bars	MSI	RWC %
Cul	38.28 a ± 4.68	0.42 a ± 0.01	8.43 a ± 2.75	0.03 d ± 1E-04	75.64 a ± 5.67	64.8 a ± 5.83
Snl	34.48 b ± 2.63	0.37 a ± 0.01	8.22 a ± 0.61	0.03 cd ± 0.002	70.11ab ± 9.93	49.5 b ± 12.63
Alt	25.57 c ± 1.02	0.33 a ± 0.21	8.19 a ± 0.53	0.04 d ± 1E-04	65.63 bc ± 2.45	41.57 c ± 5.56
Eug	11.82 de ± 0.35	0.30 a ± 0.18	6.59 abc ± 1.36	0.04 cd ± 0.061	60.76 cd ± 4.55	27.9 de ± 3.90
Ach	12.44 d ± 0.74	0.334 a ± 0.023	7.36 ab ± 0.47	0.05 bcd ± 0.002	61.13 cd ± 3.97	36.1 cd ± 5.05
Bod	6.54 gh ± 0.32	0.27 a ± 0.01	4.59 bcd ± 1.38	0.05 bcd ± 0.03	48.44 f ± 2.99	17.6 fg ± 1.40
Bln	9.264ef ± 2.87	0.303 a ± 0.009	6.17 abc ± 2.85	0.08 bcd ± 0.08	57.36 de ± 3.15	23.4 efg ± 3.51
Aca	6.27 h ± 0.43	0.26 a ± 0.19	4.06 d ± 0.38	0.101 bcd ± 0.003	47.53 f ± 4.51	15.34 gh ± 2.14
Tum	8.37 efg ± 0.58	0.28 a ± 0.01	4.75 cd ± 0.26	0.1 bcd± 0.005	50.45 ef ± 3.095	19.65 efg ± 1.37
Cab	12.41 d ± 0.21	0.24 ab ± 0.017	5.82 bcd ± 1.75	0.103 bcd ± 0.004	45.53 f ± 1.15	15.69 gh ± 0.62
Cfl	20.84 c ± 0.29	0.26 a ± 0.18	6.66 abc ± 0.27	0.13 bc ± 0.008	47.38 f ± 3.554	18.83 ef ± 2.61
Bdn	9.486 def ± 0.379	0.305 a ± 0.015	6.34 abc ± 2.74	0.13 bc ± 0.15	57.94 de ± 4.34	25.9 ef ± 3.88
Raw	15.24 cd ± 0.31	0.059 b ± 0.002	5.69 bcd ± 0.202	0.17 b ± 0.007	38.66 g ± 2.51	15.52 gh ± 0.071
Opl	7.54 fgh ± 0.22	0.054 b ± 0.003	4.41 cd ± 0.61	0.36 a ± 0.02	34.57 g ± 2.593	12.01 h ± 0.261
	<0.001	0.024	<0.001	<0.001	<0.001	<0.001

Data are the pooled means of three estimates each over two years ± standard deviation. 'p-value' denotes the significance of difference between the means by one way ANOVA statistics. ^a The values followed by different letters differ significantly by Duncan's multiple range test at p=0.05.

* **Cul:** *Cassia uniflora* Mill.non Spreng ; **Snl:** *Synedrella nodiflora*(L) Gaertn; **Alt:** *Alternanthera tenella* Colla; **Eug:** *Euphorbia geniculata* Orteg.; **Ach:** *Achyranthes aspera* L.; **Bod:** *Boerhaavia erecta* L.; **Bln:** *Blainvillea acmella* L.; **Aca:** *Acalypha ciliata* Forsk.; **Tum:** *Triumfetta rhomboidea* Jacq.; **Cab:** *Cassia absus* L.; **Cfl:** *Cassia obtusifolia* L.; **Bdn:** *Bidens biternata* Lour.; **Raw:** *Rauwolfia tetraphylla* L.; **Opl:** *Oplismenus compositus* P.Beauv.

Table 5. Osmolytes and antioxidants in invasive and native weeds

The alien species like *Cassia uniflora*, *Synedrella* and *Alternanthera* have higher contents of different types of antioxidants as compared to the co-occurring invasive and native weeds at the selected sites of Pune University campus (Table 5). Along with this lower values of lipid peroxidation and higher MSI and RWC might be offering them additional mechanisms for abiotic stress tolerance. As a result of this the selected invasive weeds might have succeeded to invade and encroach over the native plants of Pune University campus even during the harsh environmental conditions.

The enhancement in various antioxidants was reported by many allelopathy workers like Tambussi et al. (2000), Horling et al. (2003), Guha et al. (2004), Yang and Lu (2005) in different types of invasive plants growing in terrestrial and boreal forest communities of North America. The role(s) of different antioxidants and osmolytes existing in the invasive and native weeds of forest and cropland ecosystems are very much important. They have explained that the antioxidants were helpful for these weeds to become dominant over co-occurring plant species.

The free radicals are constantly generated under stress conditions which are quenched by an efficient antioxidant network in the plant body. The complex network of such adaptive mechanisms at physiological and molecular levels cause changes in the synthesis and accumulation of various osmolytes, antioxidants and antioxidant enzymes, which provide stress tolerance to the plants (Bagul et al. 2005, Bhattacharya et al. 2009).

Proline is a major organic osmolyte accumulating in a variety of plant species in response to biotic and abiotic stresses, though its actual role in plant osmo-tolerance remains controversial. It is also thought to help in stabilization of sub-cellular structures (e.g. membranes and proteins), and to scavenge free radicals under stress conditions. Proline is known to occur widely in higher plants and normally accumulates in large quantities in response to environmental stresses (Kavi Kishore et al. 2005).

The rapid breakdown of proline upon relief of stress may provide sufficient reducing agents that support mitochondrial oxidative phosphorylation and generation of ATP for recovery from stress and repairing of stress induced damages (Zhu 2002). In response to drought or salinity stress in plants proline also helps for cytoplasmic osmotic adjustment. Accumulation of proline under stress in many plant species has been correlated with stress tolerance, and its concentration has been shown to be generally higher in stress - tolerant than in stress - sensitive plants (Ashraf and Harris 2004, Ashraf and Foolad 2007). Comparatively higher amount of proline accumulation in *Cassia* and *Synedrella* might be functioning as mentioned above providing stress tolerance to these weeds, as a result of which both the weeds were able to survive throughout the year and producing large no. of seeds even under unfavourable stress conditions. These outnumbering seeds of both the invasive weeds when germinate during favourable season, naturally establish the monothickets or pure stands which caused substitution of many natives resulting into loss of phytodiversity of Pune University campus.

Malondialdehyde (MDA) is a product of lipid peroxidation by a thiobarbituric acid reaction. During drought conditions high activities of antioxidant enzymes are associated with lower concentration of MDA, being linked to drought tolerance (Gao et al. 2008). Like proline lowest values of MDA in *Cassia* and *Synedrella* can be linked with drought tolerance and better survival in extremely adverse environmental conditions.

One of the most common responses in plants to abiotic stresses is overproduction of different types of compatible organic solutes (Serraj and Sinclair 2002), which protect the plants from stress injuries by cellular osmotic adjustment, detoxification of ROS, protection of membrane integrity and stabilization of enzymes/ proteins. The antioxidants also protect cellular components from dehydration injury. These solutes include proline, sucrose, polyols, trehalose and quaternary ammonium compounds (QACs) such as glycine-betaine, alanine-betaine, proline-betaine, choline *O*-sulfate, hydroxyproline-betaine and pipercolate-betaine (Rhodes and Hanson 1993).

Amongst the many quaternary ammonium compounds known in plants, glycine betaine occurs most abundantly in response to dehydration stress (Venkatesan and Chellappan 1998, Mansour 2000). GB is abundant mainly in chloroplast where it plays a vital role in adjustment and protection of thylakoid membrane, thereby maintaining photosynthetic efficiency. The results of present investigation on antioxidants indicated more accumulation of GB in *Cassia* and *Synedrella* as compared to the native weeds at selected sites of Pune University campus. Along with high proline and low MDA, GB might also be contributing for stress tolerance and thereby maintaining the photosynthetic efficiency of both the dominant invasive weeds as suggested by Genard et al. (1991).

RWC has special significance in physiological activities of plants. The results of the present investigation indicated that *Cassia* and *Synedrella* had significantly higher RWC as compared to other invasive and native weeds. It may be the additional physiological adaptation for drought tolerance along with above mentioned antioxidants.

Likewise MSI decides the extent of membrane perturbations in structure and dysfunctioning in the cellular activities during the stress conditions. The membrane stability index (MSI) is very important parameter that gives idea about the stress tolerance ability of invasive and native weeds. The MSI of weeds under investigations agree with this. Increase in allelochemicals in these weeds might also be helping the weeds to get more stress tolerance. Membranes are barriers isolating aqueous compartments of the cells and the membrane proteins participate in signal reception and in transport of specific solutes giving them stability and thereby afford stress tolerance to the plants (Ramadevi et al. 1997). The higher values of MSI in both the invasive weeds recorded in the present investigation may be having similar role as mentioned above, because of which these weeds are tolerating extreme environmental conditions, survive comfortably and invade successfully in the new habitats. On the contrary the native weeds are not able to tolerate the stress conditions and hence make the place for highly tolerant invasive weeds. This results in to loss of native phytodiversity in that particular ecosystem.

4.10 Antioxidant enzymes in invasive and native weeds

The activities of antioxidant enzymes like PPO (Polyphenol oxidase), POX (Peroxidase) and SOD (Superoxide dismutase) (Figure 4, 5), were stimulated in *Cassia uniflora* followed by *Synedrella* and *Alternanthera*. The remaining invasive and native weeds followed the above mentioned weed species. The difference in stimulation of these enzymes might be due to the difference in stress tolerance ability of these weeds. More accumulation of antioxidants and stimulated activities of antioxidant enzymes might be becoming helpful for stress tolerance to these weeds. The results of the present investigations are in agreement with the findings of Bhalerao (2003), Jadhav (2006), Vaidya (2009) and Ghayal et al. (2009). They have also reported comparatively higher stimulation of antioxidant enzymes like PPO, POX and SOD in some invasive as well as native weeds of forest, aquatic and terrestrial ecosystems. They further concluded that more accumulation of antioxidants and stimulated activities of antioxidant enzymes were helpful for stress tolerance to these weeds.

Antioxidative enzymes, such as superoxide dismutase (SOD), peroxidases (POD) and polyphenol oxidase (PPO), are the most important components in the ROS scavenging system. SOD dismutates O_2^- to H_2O_2 , POD and PPO subsequently scavenge the H_2O_2 . The activities of antioxidant enzymes are usually stimulated on exposure to oxidative stress, for protecting the plants, because these enzymes scavenge the reactive oxygen species (Tanaka 1994). The invasive and native weeds studied in the present investigation had shown very

high stimulation in the activities of above mentioned enzymes in response to stress conditions, which might be responsible for survival of these weeds in extreme ecological conditions existing in the campus of Pune University. Ping Lu et al. (2007) supported the above view.

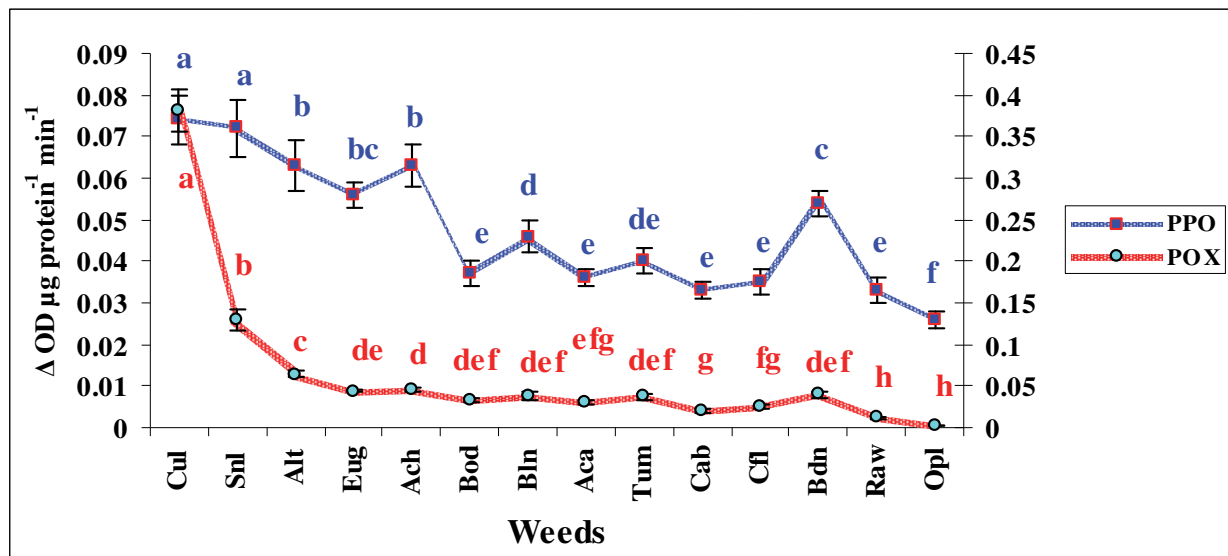
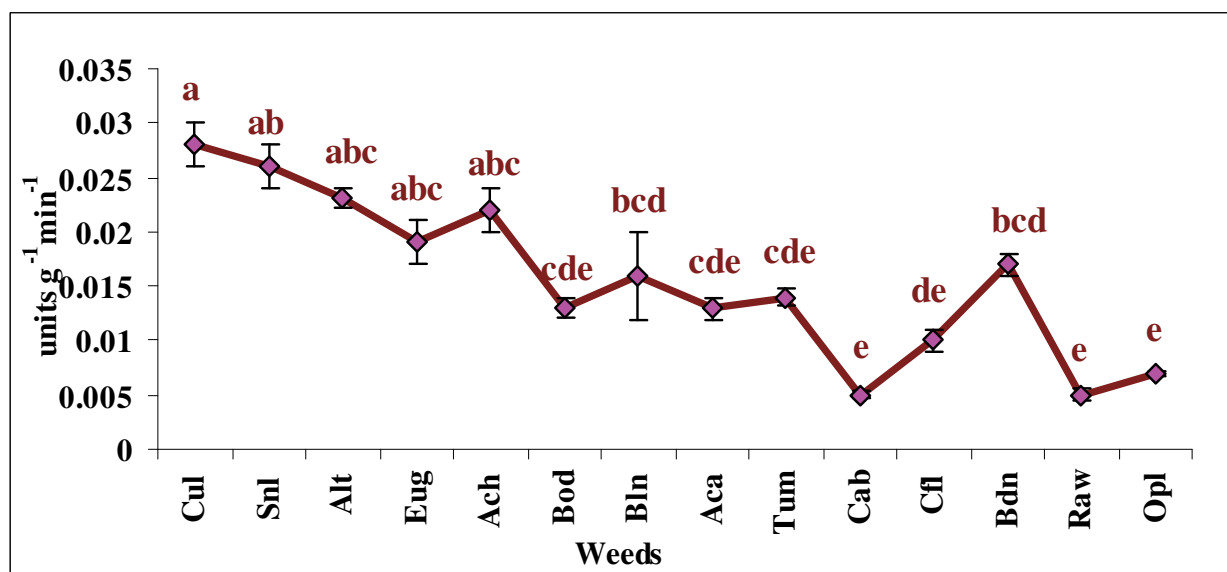


Fig. 4. Activity of polyphenol oxidase and peroxidase in the invasive and native weeds



#Data points are the pooled means of three replicates over two years with standard deviation as error bars. a Different letters at the data points denote significant difference by Duncan's multiple range test at $p < 0.05$.

Fig. 5. Activity of superoxide dismutase in the invasive and native weeds

5. Allelobiogenesis of invasive weeds

To understand the allelopathic nature of any plant, extraction, identification and characterization of allelochemicals in its roots, stems and leaves has predominant role. In fact, all the interpretations in allelopathy are mostly based on such investigations. However, collection, isolation and complete identification, characterization and quantification of allelochemicals is difficult and a challenge to the allelopathy scientists. The allelochemicals like terpenes, steroids, flavonoids, alkaloids etc. have major impact on physiology of recipient plants, right from gene to organism level e.g. the monoterpenes which are the main constituents of the essential oils from many higher plants, interfere with basic biological processes like DNA replication, respiration, enzyme activities, seed germination and plant growth. These monoterpenes have allelopathic action. Triterpenes from many different weeds like *Cassia*, *Lantana*, *Mikania* are known for their allelopathic responses and great ecological significance with respect to invasion Ghayal et al. (2007a).

The allelochemicals like terpenoids, steroids, phenols and bitter essential oils present in roots, stems and leaves of *Cassia* and *Synedrella* might be released in to their environment, through various processes in the form of extracts, leachates, root exudates and even residues of all above plant parts which in due course of time become allelopathic to associated invasive and native weeds as a result of which they were suppressed slowly and substituted by *Cassia* and *Synedrella*. This phenomenon was observed at all the four sites of Pune University campus.

5.1 GC-MS study

The phytosociological dominance of *Cassia uniflora* and *Synedrella nodiflora* at the four selected sites in Pune University campus recorded previously and the inhibitory weed-weed interaction between these invasive weeds and co-occurring native weeds can be attributed to the different types of allelochemicals existing in them which are detected with GC-MS. The allelopathic potential exhibited by both the weeds might be due to different types of allelochemicals existing in them.

The distribution, quantity and type of allelochemicals depends on various factors such as age of the plant, growing season, vegetative or reproductive phase, environmental conditions and habitat. The allelopathic influence of extracts, leachates or residues of such plants is due to the different types of allelochemicals such as salts, esters, fatty acids, alkaloids, glycosides, terpenoids, flavonoids and steroids present in them. Their solubility in different solvents and mechanism of actions of such allelochemicals mostly depend on their chemical nature. These allelochemicals might be exuded, excreted or released from the plants. The chemical nature of such allelopathic compounds governs the process of invasion, dominance, distribution and encroachment over co-occurring species in any ecosystem.

Many researchers have isolated more than ten thousand low molecular weight secondary metabolites from higher plants and fungi. These compounds or their analogs are new sources of allelochemicals. Drager (2002), Mashhadi and Rodosevich (2003), Bhalerao (2003), Haig (2004), Elzaawely et al. (2005), and Alonso-Amelot (2006) had detected different types of allelochemicals from various weeds and fern species with GC-MS technique and studied their allelopathic activity. Ru Bai et al. (2009) also reported many allelopathic compounds by GC-MS in root exudates of *Malus prunifolia*. Qiaoying Zhang et al. (2009) detected allelopathic potential of flowers and fruits of *Lantana camara* which was ascribed to the allelochemicals by GC-MS. Seal et al. (2009) had also identified different allelochemicals

in weed species like Shepherd's purse (*Capsella bursa-pastoris*) by GC-MS and studied its phytotoxicity.

5.2 IR, NMR, and MASS spectra studies

The dominance, negative weed-weed interaction, encroachment over native weeds as well as successful invasion of *Cassia uniflora* and *Synedrella* recorded at all the four selected sites in the campus of Pune University can be attributed to the existence of different types of allelochemicals in the leaves of both the weeds such as 2(4H)-Benzofuranone,5,6,7,7a-tetrahydro-4,4,7a-trimethyl (Dihydroactinidiolide), 2-pentadecanone, Isobutyl phthalate, 4,4,8-trimethyltricyclo [6.3.1.0(1,5)]dodecane-2,9-diol, Hexadecanoic acid, Phytol, Dioctyl phthalate, Neophytidiene, Caryophyllene oxide and Di-isooctyl phthalate. The presence of above allelochemicals in both the invasive weeds was well documented by Ghayal et al. (2007). The presence of allelochemicals such as Dodecane-4-yl butyrate in *Cassia* leaves and 3-(5-(1-(3-methylpentyloxy) propyl)-tetrahydro-2-oxofuran-3-yl)-dihydrofuran-2(3H)-one in *Synedrella* leaves were detected for the first time in the present investigation.

Many allelopathy researchers such as An et al. (2000), Orr et al. (2005) and Santos et al. (2007) separated, identified and quantified the allelochemicals from different weeds and tested their phytotoxicity. Yang et al. (2006) also have separated and identified allelochemicals by NMR in *Ageratina adenophora* and studied their allelopathic activity on rice seedlings. Isolation and bioactivity of withaferin A from *Withania somnifera* roots was done by Kannan and Kulandaivelu (2007). Leicach et al. (2007, 2009) have used different methods of chromatography and spectroscopy for alkaloid separation and identification from different plants and elaborately discussed the importance of extraction, separation and identification of allelochemicals from different plants having allelopathic activity. Ma et al. (2009) and Li et al. (2009) have attempted the isolation and identification of allelochemicals by NMR and Mass in invasive plants *Ipomoea cairica* and *Polygonatum odoratum* respectively. The results of the present investigation are in conformity with the above findings. These allelochemicals usually had greater adverse impact on the physiological as well as biochemical processes, enzymological activities, nutrient uptake and assimilation, reproductive abilities, growth and development of recipient plant species. The changes induced by allelochemicals at molecular level are also expressed in phenotypes. The antimicrobial activity in leaf leachates and extracts of *Cassia* and *Synedrella* might be due to the presence of allelochemicals such as terpenoids, steroids, flavonoids, pungent and bitter essential oils and various types of phenols present in them.

6. Conclusions

The present investigations attempted on phytosociology, physiology, biochemistry and enzymology of selected weeds, phytochemicals and allelochemicals existing in them, their allelopathic potential tested through seed germination bioassays, seedling growth and physiological, biochemical and enzymological changes including treated seedlings of test-crops due to leachates of selected invasive weeds, clearly revealed that the basis for all such events was allelopathic nature of *Cassia* and *Synedrella*.

The weed - crop interactions at molecular, cellular and whole plant level were also attempted with special emphasis, as these weeds in future are likely to invade agroecosystems and croplands. At present slowly they are spreading from wastelands to agricultural lands and competing with the crops of interest and cause significant yield loss.

The studies on impact of leachates, extracts and even residues of *Cassia* and *Synedrella* revealed that higher concentrations had severe and very dreadful influence on physiology, biochemistry and enzymology of test crops and such negative changes were also manifested on growth and yield attributes of crops interacting with weeds.

These investigations have also thrown a light on successful invasion of both the weeds in the campus of Pune University, their dominance, aggressiveness and encroachment over native and even other invasive weeds. The ecological and morphological superiority enabled them to do so very efficiently and effectively. The exclusive dominant nature of selected invasive weeds and their allelopathic potential resulted into the loss of native phytodiversity, which is the major threat of such invasion to any ecosystem. Such investigations may become the basis for exploring environmental and ecological degradations in nature.

7. Future research

The need for research and development in allelopathy for the improvement of agriculture, forestry and different types of ecosystems, community structures and functioning is of extreme urgency, because the understanding of allelopathy has major role(s) in the interactions between invasive/ exotic and native weeds, weeds-crops, crops-crops etc. These studies are of utmost importance in agriculture, forestry and environmental degradation. Many of these weeds cause damages to agroecosystems and disturb natural phytodiversity. Their dominance, luxuriant growth, persistence throughout the year, tolerance to biotic and abiotic stress conditions and allelopathic potential might be the probable factors of successful invasion in new habitats.

The use of naturally produced huge weed biomass for weedicidal, cytotoxic, larvicidal, insecticidal and antimicrobial activity is gaining ground in sustainable agriculture. With this view many research workers have reported the antimicrobial activity in different plant parts and extracts, leachates or residues of large number of plant species available in plenty.

The richness of bioactive compounds, secondary metabolites and variety of allelochemicals present in these weeds and other co-dominant weeds can give enticement to screen their cytotoxic, genotoxic, larvicidal, antimicrobial activities etc. The results of such experiments could be positive, if the analyses of their bioactive compounds, antioxidants and antioxidant enzymes is given due importance. The studies on genomics and proteomics of different weeds, having biotic and abiotic stress tolerance can be exploited with the aid of biotechnological tools, to have such type of agronomic traits in various crops. Only the coupling of all the aspects of studies can give an applied touch to the entire field of allelopathy.

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Changing environmental condition and global population demands understanding the plant responses to hostile environment. Significant progress has been made over the past few decades through amalgamation of molecular breeding with non-conventional breeding. Understanding the cellular and molecular mechanisms to stress tolerance has received considerable scientific scrutiny because of the uniqueness of such processes to plant biology, and also its importance in the campaign “Freedom From Hunger”. The main intention of this publication is to provide a state-of-the-art and up-to-date knowledge of recent developments in understanding of plant responses to major abiotic stresses, limitations and the current status of crop improvement. A better insight will help in taking a multidisciplinary approach to address the issues affecting plant development and performance under adverse conditions. I trust this book will act as a platform to excel in the field of stress biology.

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