

REVIEW PAPER

Lantana invasion: An overview

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We review the key features of *Lantana* (*Lantana camara* L.), an invasive plant species considered to be among the world's 10 worst weeds. *Lantana* occurs in diverse habitats and on a variety of soil types, and its spread is encouraged by animal activities and by human disturbances, such as cultivation, road construction, and changes in fire regimes. *Lantana* is morphologically distinct in the different regions of its invasive range compared to those regions in its native range. The biological attributes contributing to the success of *Lantana* as an invader species include: fitness homeostasis, phenotypic plasticity, dispersal benefits from destructive foraging activities, widespread geographic range, vegetative reproduction, fire tolerance, better competitive ability compared to native flora, and allelopathy. Mechanical, chemical and biological options for the eradication and control of *Lantana* are available. It is emphasized that ecosystem-level consequences of *Lantana* invasion, particularly on the biodiversity of native flora, are little understood and studies are needed to fulfill this knowledge gap.

Keywords: biological attributes, geographic spread, invasive species, *Lantana*, management.

INTRODUCTION

Invasion of exotic species is among the most important global-scale problems experienced by natural ecosystems. Although biological invasion is a natural process, the recent enhanced rate of invasions is clearly a human-caused phenomenon and constitutes one of the most important effects that humans have exerted on the planet. Disturbance, whether regular or episodic, is a natural feature of dynamic ecosystems (Sousa 1984; Gurevitch & Padilla 2004) but it also facilitates the invasion process. As a result of the rapid modification of natural habitats, the pace of invasion has particularly accelerated during the past century (Schei 1996). Extinction of species related to invasion is an outcome of human activities. Invasive species are the second largest threat to global biodiversity after habitat destruction and the number one cause of species extinction in most island states (Schei 1996). In the past, many of the irretrievable losses of native biodiversity due to biological invasion have gone unre-

corded but, today, there is an increasing realization of the ecological costs of this process. Over 40% of the plants listed as threatened and endangered species in the United States of America are at risk from invasive species (Wilcove *et al.* 1998).

Alien plants are widespread throughout the world, in agriculture, forest and natural areas. Alien species usually have much greater potential for invasion than the indigenous plants as they might be more effective competitors and experience relatively little pressure from natural predators compared to those which have evolved in their native land. The majority of invaders pose threats to the invading ecosystem by virtue of their aggressive qualities, which can include superior growth by effectively competing for resources, efficient dispersal, and rapid establishment. These invaders come in many shapes and sizes. They may be trees, shrubs, small herbaceous plants, or aquatic species, but they have in common the ability to spread and reproduce rapidly; thus, overcoming biological, physical, and environmental thresholds. Some of the invaders arrive by accident but the majority of introductions have been intentional, through a number of sources. Batianoff and Butler (2003) have rated *Lantana* among the highest ranked invasive species in Queensland, Australia. Also, it is among the world's 100 worst invasive alien species, as recognized by the Invasive

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Species Specialist Group (IUCN 2001). Although *Lantana* is regarded as one of the principle invasive species, limited comprehensive studies on its biology and ecology are available. Therefore, a review of the key features of this invasive plant species is long overdue. We review the key features of *Lantana* which make this species a successful invader.

HABITAT

Lantana is a member of the family Verbenaceae and is a pantropical weed affecting pastures and native forests in >60 countries worldwide (Parsons & Cuthbertson 2001). It occurs in diverse habitats and on a variety of soil types. The plant generally grows best in open, unshaded situations, such as degraded land, pasture, edges of tropical and subtropical forests, warm temperate forests, beachfronts, and forests recovering from fire or logging. It also invades forest plantations and riparian zones.

In its native range in tropical America, *Lantana* generally occurs in small clumps ≤ 1 m in diameter (Palmer & Pullen 1995). In its naturalized range, it often forms dense monospecific thickets, 1–4 m high and ≈ 1 –4 m in diameter (Swarbrick *et al.* 1998), although some varieties climb trees and reach heights of 8–15 m (Swarbrick *et al.* 1998).

In India, *Lantana* was first introduced in the early nineteenth century as an ornamental plant but now it is growing densely throughout India (Thakur *et al.* 1992). In Australia, the plant was first reported in 1841 and by 1897, it was recognized as one of the most troublesome weeds (Van Oosterhout *et al.* 2004). It is now spreading to form impenetrable thickets on the edges of forest and covers $\approx 4 \times 10^6$ ha across Australia (Van Oosterhout *et al.* 2004). Globally, it infests millions of hectares of grazing land and is of serious concern in 14 major crops including coffee, tea, rice, cotton, and sugarcane.

Disturbed areas, such as roadsides, railway tracks, and canals, are also favorable for the species (Munir 1996). It does not appear to have an upper temperature or rainfall limit and is often found in tropical areas receiving 3000 mm of rainfall year⁻¹. *Lantana* seldom occurs where temperatures frequently fall $< 5^\circ\text{C}$ (Cilliers 1983). *Lantana* cannot survive under dense and intact canopies of taller native forest species and it is susceptible to frosts, low temperature, and saline soils. This plant tends to rot in boggy or hydromorphic soils and is sensitive to aridity (Van Oosterhout *et al.* 2004).

REPRODUCTIVE BIOLOGY

The plant usually flowers as early as the first growing season after its establishment and, in most places, flowers all the year round if adequate moisture and light are available (Gujral & Vasudevan 1983; Duggin & Gentle 1998). In cooler or drier regions, flowering occurs only in the warmer or wetter months (Winder 1980; Swarbrick *et al.* 1998). Inflorescences are produced in pairs in leaf axils. Wide variations in flower color, size, and shape have been reported (Van Oosterhout *et al.* 2004), with flowers opening as yellow and changing to pink, white or red depending on the variety. In some forms, a yellow ring is present around the opening of the corollary tube (Sinha & Sharma 1984). A visual clue to pollinating insects is provided by the yellow coloration of the flowers and color change in the flower might be stimulated after pollination (Mohan Ram & Mathur 1984). *Lantana* is a major source of nectar for many species of butterflies and moths, which enhance the pollination success of the species. Differences in corolla length, inflorescence diameter, and number of flowers inflorescence⁻¹ attract some butterfly species to visit *Lantana* more frequently than others. According to this view, different varieties of *Lantana* might have different species of pollinators and, thus, little cross-pollination would occur between species or varieties of *Lantana* both in the naturalized (Dronamraju 1958) and native ranges (Schemske 1976). Thrips play a more important role in the pollination of *Lantana* than lepidoptera or butterflies, as thrips are present year-round (Sinha & Sharma 1984; Mathur & Mohan Ram 1986). Honeybees, sunbirds (India), and humming birds (Brazil) are believed to play a minor role in pollination (Winder 1980). Goulson and Derwent (2004) advocated that fruit-set is limited by pollinator abundance. They found that substantial populations of *Lantana* in Australia appear to be pollinated by honeybees, with a significant positive correlation between *Lantana* seed-set and honeybee presence. Individual *Lantana* flowers are capable of self-pollination, but need insects for rapid and higher pollination.

Pollination in *Lantana* results in 85% fruit-set, with an Australian study showing that each inflorescence bears about eight fruits (Barrows 1976); whereas, in India, ≈ 25 –28 fruits are produced (Sharma G., 2003, personal observation), showing intraspecific variation (Thorp 2000). The fruit is a round, fleshy, drupe, ≈ 0.5 cm wide, initially green, but turning purple then blue-black. Each drupe contains 1–2 seeds that are ≈ 0.1 –0.2 cm long. *Lantana* seeds germinate at any time of the year with sufficient soil moisture, light, and temperature (Gentle & Duggin 1997; Duggin & Gentle 1998; Parsons &

Cuthbertson 2001). The germination rate of *Lantana* is low (4–45%) due to seed dormancy, low seed viability and/or meiotic instability (Graaff 1986; Duggin & Gentle 1998; Sahu & Panda 1998). These low germination rates are offset by the extremely low rates of seedling mortality experienced in the field (Sahu & Panda 1998).

PLOIDY LEVEL

In Australia, most naturalized varieties are tetraploid ($n = 44$), but several varieties are triploid ($n = 33$), one is diploid ($n = 22$), and one is pentaploid ($n = 55$) (Everist 1981). The ploidy levels of *Lantana* in India are similar to those in Australia, with the exception that no weedy variety has been found to be diploid in India (Sinha & Sharma 1984). However, apart from correlative evidence to suggest that pentaploid forms are better adapted than other forms to high altitude conditions in India (Ojha & Dayal 1992), there is little evidence to suggest that different ploidy levels have distinguishing traits or are of ecological significance in the invasion potential of the species. It is now widely recognized that *Lantana* is morphologically distinct in different regions of its naturalized range compared to *Lantana* in its native range (Smith & Smith 1982).

DISPERSAL OF PROPAGULES

Seeds are widely dispersed, predominantly through migration by birds (Swarbrick *et al.* 1998), but also by kangaroos, bearded dragons, sheep, goats, cattle, foxes, jackals, monkeys and, possibly, rodents (Wells & Stirton 1988). The construction of nests by broken *Lantana* twigs also leads to its spread. Bird species feed on *Lantana* fruits and, in some locations, seed dispersal has been facilitated by the introduction of exotic bird species. By feeding on exotic species, such as *Lantana*, birds might increase the density and distribution of the species at the expense of native vegetation and might displace other bird species (Loyn & French 1991).

ESTABLISHMENT

As *Lantana* flowers year-round, it can produce numerous seeds. Activities that increase light intensity and soil temperature stimulate the germination of the deposited seeds (Gentle & Duggin 1997; Duggin & Gentle 1998). The removal of fleshy pulp from the seed results in increased germination (Parson & Cuthbertson 2001). Germination is reduced in low light conditions, such as the understory of intact forest. Broken *Lantana* stems and root parts can remain viable for a considerable amount of

time and can regrow from the base of the stem and form a rooted horizontal stem when in contact with moist soil (Day *et al.* 2003).

Lantana grows as individual clumps or as dense thickets, crowding out more desirable species. This can be attributed to its competitive ability and to allelopathy exhibited by the plant. Some perennial plant species, including *Lantana*, are likely to release and add allelochemicals to the soil over more than one season (Malik 1998), which is probably the reason to invade or dominate an ecosystem (Gentle & Duggin 1997).

There are several regions where *Lantana* is currently limited by the presence of intact forest, which restricts its growth (Duggin & Gentle 1998). However, logging aggravates invasion by opening the canopy, allowing *Lantana* to spread or become thicker (Binggeli 1999). In India, where there are still large areas of native forests, *Lantana* is currently restricted to small, isolated infestations, but it has the potential to spread widely following further clearing of forest for timber or agriculture. In disturbed native forests, it has become the dominant understory species, disrupting succession and decreasing biodiversity.

BIOLOGICAL ATTRIBUTES AS KEY FACTORS FOR INVASION

Lantana possesses a number of attributes in its life cycle that characterize it as an invader (Fig. 1). There is still uncertainty as to which attributes make some species more invasive or what makes some ecosystems more invadable than others. (Drake *et al.* 1989; Lodge 1993). However, it is always desirable to develop the capability of predicting the invasiveness of an alien plant on the basis of a small number of biological characteristics. Based on the available information, the biological attributes conferring invasiveness for *Lantana* can be summarized in seven ways.

Fitness homeostasis and phenotypic plasticity

The ability of an individual or population to maintain relatively constant fitness over a range of environments is known as homeostatic fitness. Phenotypic plasticity is the ability of a genotype to modify its growth and development in response to changes in the environment (Dorken & Barrett 2004). Accordingly, plastic responses in vegetative structure are thought to promote survival and propagation of an exotic species in the new heterogeneous environment (Santamaria 2002). Values such as mean “relative physiological performance” or mean

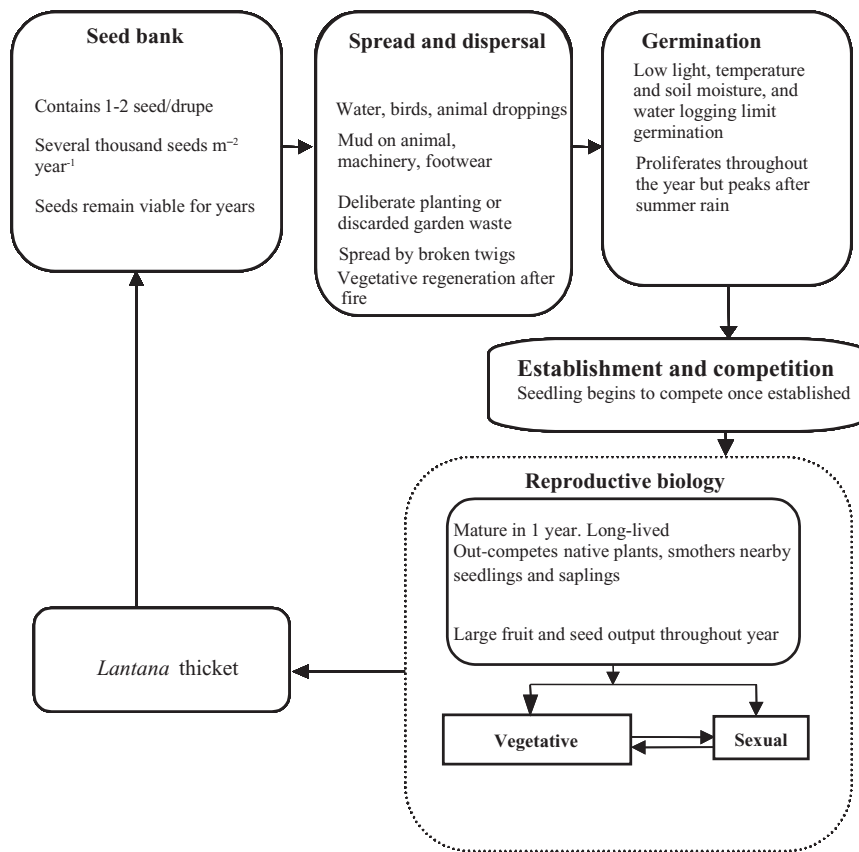


Fig. 1. Attributes of *Lantana* related to its invasive potential.

“relative ecological performance” across environmental gradients can be used as an alternative for population fitness homeostasis (Austin *et al.* 1985). Artificial defoliation of *Lantana* during spring compared to defoliation in autumn produced more stems and resulted in a greater allocation of biomass to reproductive structures. This suggests that the species compensates for defoliation, exhibiting its invasive potential (Broughton 2003).

Interaction with animals

The success of *Lantana* may be attributed to the presence of a range of pollinators, accounting for the high percentage of fruit-set. Once formed in high numbers, the seeds of *Lantana* are dispersed efficiently through the participation of a variety of animal dispersal agents that feed on its fruit. The process of invasion is further improved by nutrient additions, with animal droppings, canopy removal, and soil disturbance creating a good seed bed. Duggin and Gentle (1998) and Gentle and Duggin (1997) demonstrated that physical soil disturbance associated with cattle grazing might also increase resource availability due to the removal of competitive biomass. *Lantana* itself benefits from the destructive foraging activities of vertebrates, such as pigs, cattle, goats,

horses, sheep, and deer, through enhanced vegetative propagation (Thaman 1974; Fensham *et al.* 1994).

Geographical range

Lantana has a widespread distribution (35°N–35°S) beyond its native range, becoming naturalized in ≈60 countries (Day *et al.* 2003). The distribution of *Lantana* spp., using the CLIMAX model (Day *et al.* 2003) and Myers biodiversity hot spots (Myers *et al.* 2000), shows substantial overlap with each other, which could indicate a severe threat for the ecosystems in hot-spot areas. *Lantana* covers an altitudinal range of up to 2000 m in the Pulnis hills in southern India, but Mathews (1972) could not determine the genotypic and the phenotypic differences in the individuals occurring at different altitudes. The distribution of *Lantana* is still expanding, with many countries and islands that were listed in 1974 as not having *Lantana* (e.g. Galapagos Islands, Solomon Islands, Palau, Saipan, Tinian, Yap, and Futuna Island; Thaman 1974) being infested with *Lantana* more recently (Waterhouse & Norris 1987). The density of *Lantana* infestations within its native range is also increasing, which has been recognized as an additional threat to ecosystems.

Vegetative reproduction

Once established, the rapid vegetative growth of *Lantana* facilitates the formation of large, impenetrable clumps (Van Oosterhout *et al.* 2004) and high seed production. The more common means of vegetative spread is through layering, where horizontal stems produce roots when they come in contact with soil (Swarbrick *et al.* 1998); in addition, suckering also can occur. Prostrate stems can root at the nodes if covered by moist soil, fallen leaves or other debris. In Australia, it is commonly well-spread by landholders dumping vegetative material in bushland (Day *et al.* 2003). *Lantana* stems or leaves could develop roots and grow into plants and eventually flower.

Fire tolerance

Although *Lantana* burns readily during hot, dry conditions, even when green (Gujral & Vasudevan 1983), moderate and low intensity fires can promote the persistence and spread of *Lantana* thickets, rather than reducing them. Moreover, the removal of competing neighborhood plant species and increases in soil nutrients following burning can increase its germination (Gentle & Duggin 1997; Duggin & Gentle 1998). Under conditions of increased soil fertility (Duggin & Gentle 1998), its re-establishment is encouraged following mechanical or chemical control of mature plants.

Competitive ability

Under conditions of high light, soil moisture, and soil nutrients, the mortality rate of mature *Lantana* plants in its naturalized range is very low (Sahu & Panda 1998). *Lantana* infestations are very persistent and, in forest communities, have the potential to block succession and displace native species, resulting in a reduction in biodiversity (Loyn & French 1991; Duggin & Gentle 1998).

At some sites, *Lantana* infestations have been so persistent that they impede the regeneration of rainforest (Lamb 1991). *Lantana* is a very effective competitor with native colonizers (Duggin & Gentle 1998) and is capable of interrupting the regeneration processes of other indigenous species by decreasing germination, reducing early growth rates, and increasing mortality. This results in marked changes in the structural and floristic composition of natural communities. Therefore, as the density of *Lantana* in forests increases, species richness decreases (Fensham *et al.* 1994). *Lantana* does not invade intact forests, but is found on its margins (Humphries & Stanton 1992).

Allelopathy

The allelopathic effect of *Lantana* is well-documented and results in severe reductions in seedling recruitment of nearly all species under its cover (Anonymous 1962). No growth or only stunted growth have been observed for other species growing close to *Lantana* due to allelopathic effects, as shown by the fern *Cyclosorus dentatus* Forsk. (Pteridophyta), milkweed vine (*Morrenia odorata* Lindl.; Asclepiadaceae), rye (*Lolium multiflorum* Lam.; Poaceae) and many crops, such as wheat, corn, and soybean (Achhireddy & Singh 1984; Achhireddy *et al.* 1985).

As many as 14 phenolic compounds are present in *Lantana* that can reduce the seed germination and growth of young plants (Jain *et al.* 1989). A series of aromatic alkaloids and phenolics can be extracted from the various plant parts of *Lantana* (Khan *et al.* 2003). Allelochemicals promote or inhibit the crop growth based on their concentration (Ambika *et al.* 2003), and the concentration increases from root, stem to leaf (Chaudhary & Bhansali 2002), making the leaf toxic to grazing animals (Ambika *et al.* 2003).

HYPOTHESES APPLICABLE TO THE INVASION SUCCESS OF LANTANA

Based on the analysis of the traits of invasive species, a number of hypotheses are proposed as a mechanism conferring invasiveness to a plant. Fluctuating Resource Hypothesis (FRH; Davis *et al.* 2000: 529) states that a "plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources". This could happen subsequent to disturbance in a habitat. Meanwhile, the Presence of Empty Niche hypothesis (PEN; Mack *et al.* 2000) asserts that a species-poor habitat is more susceptible to invasion than a species-rich one, as new niche opportunities are created following the disturbance. The Enemy Release Hypothesis (ERH; Keane & Crawley 2002) suggests that invaders perform better in their introduced range than in their native range because they lose their enemies (often, but not always, parasites) during the process of colonization. The evolution of Increased Competitive Ability (EICA; Muller-Scharer *et al.* 2004) hypotheses is based on the fact that exotics, when liberated from their native specialized enemies, can allocate resources, otherwise used for costly traits that helped them resist those enemies, in the development of traits that provide greater competitive advantage. Whereas, Allelopathic Advantage Against Resident Species (AARS) or Novel Weapon hypotheses (NW) (Callaway & Ridenour 2004) suggest that invasive

Invasion process Supporting theories for successful invasion

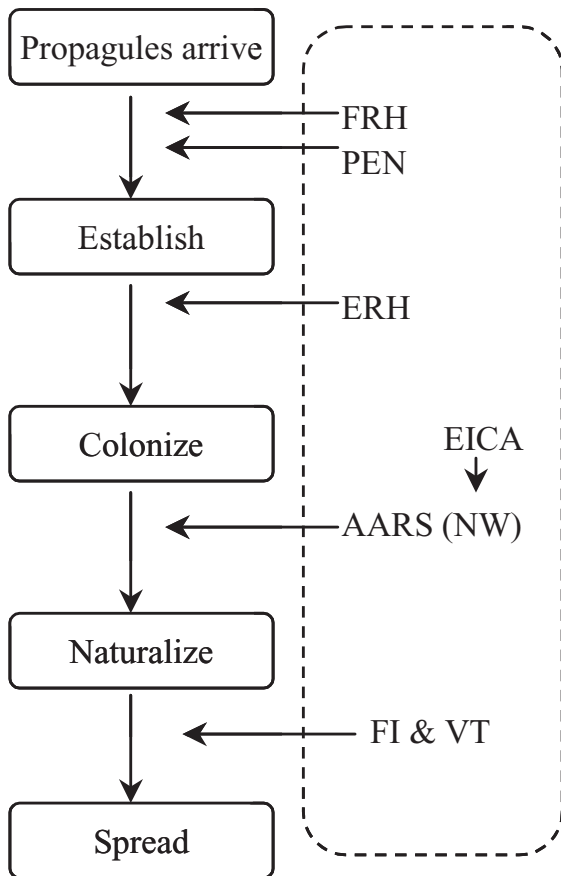


Fig. 2. The stages of *Lantana* invasion with different theories applicable for the transition from one to the other stage. AARS, Allelopathic Advantage Against Resident Species; EICA, Evolution of Increased Competitive Ability; ERH, Enemy Release Hypothesis; FI, Faunal Interaction; FRH, Fluctuating Resource Hypothesis; NW, Novel Weapon; PEN, Presence of Empty Niche; VT, Vegetative Traits. The theories box shows that different mechanisms may operate during the invasion process.

plants possess novel biochemical weapons that function as unusually powerful allelopathic agents or as mediators of new plant–soil microbial interactions. Once the plant gets naturalized, it can spread through interaction with the faunal diversity (FI) of the region and through the possession of its vegetative traits (VT) (Sharma *et al.* 2005).

Figure 2 suggests that no single theory is responsible for the success of *Lantana* invasion as different theories operate at different stages of the invasion process. For

example, after the arrival of the propagules, FRH and PEN play a role in *Lantana*'s establishment. Once it gets established, ERH helps in colonization. Subsequently, EICA, through developed AARS (NW), gives a supportive advantage to naturalize, and FI and VT encourage *Lantana*'s spread. Therefore, trait analysis of *Lantana* indicates that the invasiveness of this species is explained only when a set of hypotheses is applied.

MANAGEMENT OPTIONS

Shading by intact canopies is an effective barrier against *Lantana* invasion and is the most appropriate strategy for managing invasion (Duggin & Gentle 1998). Apart from managing and manipulating ecosystems, manual and mechanical removal, along with chemical and biological control options, also are well-explored for the control of *Lantana*. All these control strategies, however, have associated drawbacks. Manual removal is a labor-intensive and low-efficiency technique. Mechanical control is inefficient in dealing with very extensive invasions and is also difficult in undulating, rocky terrain. Chemical control involves the use of inorganic/organic herbicides. A serious disadvantage is the high cost of most of the chemical control programs. Safety to other plant species and the environment is of vital importance when using herbicides to control invasive species. Feasible and unfeasible control agents are outlined in Table 1.

The biological control of *Lantana* started in 1902. Since then, 41 agents have been released in ≈50 countries (Julien & Griffiths 1998). However, no biocontrol agent has satisfactorily controlled the spread or reduced the density of *Lantana* to date. In India, the biocontrol agent, *Teleonemia scrupulosa* Stal., released for *Lantana* control, failed as the control agent could not cope with the vigorous regrowth of *Lantana* at the onset of the monsoon rains, or the control agent itself suffered heavy mortality during the winter months (Sharma 1988). According to Mathur and Mohan Ram (1986), the introduction of biocontrol agents to reduce thrip populations is an attempt to decrease pollination and seed production. Furthermore, Goulson and Derwent (2004) argued that the cost-effective control of *Lantana* could be achieved by managing honeybees.

One of the best ways to minimize the impact of *Lantana* on the ecosystem is to exploit its biomass so that its presence can be reduced significantly while giving economic benefits. *Lantana* extracts have wide-spectrum biocidal potential that can be used commercially. *Lantana* biomass also can be exploited to increase the nutrient status of the soil (Sharma *et al.* 2003) and for biogas production

Table 1. Comparison of *Lantana* control techniques and their feasibility (based on Day *et al.* 2003)

Control technique	Feasible	Unfeasible
Biological control	If effective biocontrol agents are available but not already present	If biocontrol agents affect other species deemed to be important
Mechanical control	If area is easily accessible by machinery without significant damage and action of the machine will not damage the land further	Close to rivers, undulating landscapes and terrain
Manual removal	If labor is cheap and easily available, area to be cleared is limited and this technique is used after fire or mechanical removal	When the cost of labor exceeds the land value
Fire regime	If area to be covered is extensive and there is little risk of the fire spreading	Fire should not be used as a control technique unless follow-up chemical or manual treatments are used
Chemical control	If area is limited and of high value, used as follow-up treatment, early stages of infestation or on the edge of the species range	When the cost exceeds the land value

(Saini *et al.* 2003). *Lantana* stems are being used in India for making baskets, trashcans, flower pots, fruit plates, laying the roofs of huts in villages, weaved hedges, and for making sitting furniture.

FUTURE PROSPECTS

Ecological interest in biological invasion has been driven both by practical problems and by increasing ecological understanding of the organisms dispersing and colonizing new environments (Drake *et al.* 1989; Vitousek *et al.* 1997). Although the impacts of exotic plant invasion on community structures and ecosystem processes are well-appreciated, the pathways or mechanisms that underlie these impacts are poorly understood.

Lantana is considered to be a weed of international significance because of its widespread distribution and substantial impact on agriculture, forestry, and biodiversity. There is a scarcity of knowledge on the extent of *Lantana* invasion and its impacts. The consequences of *Lantana* invasion at the ecosystem level are little understood and there is an urgent need for studies on biological invasion. Increased public awareness about the effects of invasive species on the ecosystem, leading to environmental change and degradation, is of widespread concern for developing sustainable land-use systems. Predicting *Lantana* invasion at this stage is complicated, but economic and ecological outcomes, either good or bad, will soon be important concerns for all members of society.

A nation-specific strategy to identify and catalog invasive species, such as *Lantana*, must be developed in consultation with the representatives from local and State Gov-

ernment conservation agencies and community groups (non-governmental organizations engaged in environmental conservation). A national strategy must include the component of *Lantana* impact minimization through the development of best-practise guidelines, an increase in community awareness about its deleterious effects on ecosystems, spread prevention, and management coordination.

As species invasion is an international problem, cooperation from other countries and agencies is needed for the successful implementation of management and action plans. Particularly, the involvement of neighboring countries is essential in order to check the transboundary movement of invasive species and to develop a common strategy to control invasive species, such as *Lantana*.

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