The Biology of Australian Weeds
25. *Lantana camara* L.

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Name

Lantana camara was known by at least five polynomial descriptive names, starting with *Lantana*, *Viburnum* and *Periclymenum*, before Linnaeus gave it its binomial name in 1753. He retained *Lantana* (origin obscure) and described a number of species including *camara* (a West Indian name) and *aculeata* (prickly), a species now included within the *L. camara* complex (*L. camara sensu lato*). Linnaeus' *L. camara* was non-prickly whilst his *L. aculeata* was prickly; both were described from European garden material (Schauer 1851).

Lantana has become the common name for the most abundant and complex species within the genus. It contains several hundred wild and cultivated forms.

Description

Lantana is a brittle, much branched, thicket-forming shrub, normally 2–4 m tall but capable of becoming a liane up to 15 m tall if given support (Figure 1).

The arching, scrambling or prostrate stems are initially 4-angled but become cylindrical and up to 15 cm thick with age. Young stems are hairy and in the weedy forms carry sharp recurved prickles along the angles, whilst those of the non-weedy forms are rounder, more slender and without prickles.

The opposite pairs of ovate leaves occur on 1–3 cm long petioles. Each leaf is 3–10 cm long and 2–6 cm wide, with a bluntly pointed, rounded or heart-shaped base, finely toothed margin and bluntly pointed tip. The leaves are rough and finely hairy on both surfaces and strongly veined below, and have a strong characteristic smell when crushed. The upper epidermis carries very few stomata. Both the stomata and the trichomes from both surfaces of leaves have been related to taxonomy (Raghavan and Arora 1960, Shah and Mathew 1982).

Inflorescences develop in the axils of young leaves. They are compact, flat to dome-shaped and 2–3 cm across and each is supported by a finely hairy 2–8 cm long peduncle with a club-shaped tip. Each inflorescence contains 20–40 sessile flowers, each subtended by a stiff deciduous bract. The flower buds are angular and tightly packed, and open from the outside of the inflorescence towards the centre. Each flower has a 9–12 mm long tube and four unequal rounded petals 4–8 mm across. Newly opened flowers normally have yellow throats, and the petals vary from white to cream, yellow, pink, orange, red or purple. After pollination flowers darken, lose the yellow centre and fall, except in non-weedy forms which mostly fail to set seed and retain their flowers longer. Pollen grains are almost globular, tricolpate and 30–35 µm across and are finely textured (d'Almeida and Roland-Heydacker 1985).

Figure 1. Lantana (*Lantana camara* L.) (Line drawing by Dr. G. Scott).

In weedy forms about half of the flowers usually produce a single-seeded fleshy spherical fruit 5–7 mm in diameter, at first hard and green but ripening to purple or black and then consisting of a thin skin containing a purple pulp around the stony, pear-shaped, 3–4 mm diameter seed. The non-weedy forms set very few fruits. Each seed contains one or sometimes two embryos, and in the latter case both may germinate.

The root system typically consists of a short tap root with laterals, which divide repeatedly to form a root mat. Lantana does not sucker from damaged or broken roots, but will regrow vigorously from the base of the stem and more slowly from rooted horizontal stems in contact with moist soil.

Variation within the species

Lantana is an aggregate species, derived through horticultural and natural hybridization, selection and somatic mutation from a number of similar and probably closely related (though spatially separated) tropical American species. This has resulted in many hundreds of forms, which are also referred to as cultivars and varieties (Howard 1969). The forms vary in ploidy, bush shape, flower colour, prickliness, response to the environment and natural enemies, and chemical composition, including toxicity to animals. At least 29 forms have become naturalized in eastern Australia (Smith and Smith 1982) and probably others in the Northern Territory and Western Australia. A number of non-weedy forms are sold by nurseries. Smith and Smith (1982) considered that 19 forms were sufficiently common in eastern Australia to be economically important as either weeds or poisonous plants.

The basic chromosome number of *Lantana* is 11, with 12 being the basic number for the rest of the genus (Raghavan and Arora 1960). Diploid, triploid, tetraploid, pentaploid and hexaploid forms of lantana have been reported in South Africa (Stirton 1977, Spies and Stirton 1982, Spies 1984), and triploid, tetraploid and pentaploid lantanas in India (Sen and Sahni 1955). Raghavan and Arora (1962) showed that Indian diploids were small, stunted and very rare and that the weedy forms were mostly tetraploids with some triploids. Koshoo and Mahal (1967) claimed that the breeding system combines sexual, semisexual and asexual (apomictic) systems, and Stirton (1977) stated that polyploidy has developed through both auto- and allopolyploidy.

Most of the weedy forms of lantana in South Africa and India and probably Australia appear to be tetraploids, whilst most of the non-weedy ornamental forms appear to be triploids.

After growing many weedy forms of lantana together in South Africa to study their cytology and the morphology of their inflorescences, bracts and flowers, Spies (1984) concluded that 'plants on different ploidy levels are morphologically similar'. A similar study of Indian plants by Natarajan and Ahuja (1957) showed that non-prickly forms occurred at 2n, 3n and 4n levels, flower colour varied within all ploidy levels, and all ploidy levels contained forms with both nil and good seed set.

Tandon and Bali (1955) compared diploid and triploid forms and found that the latter was more vigorous, had larger and darker leaves, produced more and larger flowers and, unlike the diploid, was largely sterile. Raghavan and Arora (1960) found no correlations between flower colour or lower leaf epidermal patterns and five levels of ploidy.

Swarbrick (unpublished) compared the morphology of seven weedy forms from Smith's collection at the CSIRO in Brisbane (now destroyed) and six ornamental forms from commercial nurseries under uniform conditions in south-eastern Queensland. He studied bush volume, average length of the third internode from the shoot tip, average length of fourth node leaves, average number of prickles per 5 cm of angle on the third internode and average number of flowers and fruits per inflorescence. Analysis of results showed that the weedy forms were all very similar and were characterized by larger bushes, longer internodes and leaf blades, prickly stems and high levels of fruit production, whereas most of the ornamental forms produced smaller bushes, had shorter internodes and leaves, lacked prickles, and while producing similar numbers of flowers, set very few fruit. The ornamental form 'Drap d'or' occupied an anomalous position since it showed the large bush size, long internodes and large leaves of the weedy group but the lack of prickles and low seed production of the ornamental group, suggesting significant differences in its derivation from both other ornamental and weedy forms.

History

Lantana was probably first introduced into Europe about 1640 from Brazil (Howard 1969), where both prickly and non-prickly taxa are considered to be native, common and widespread (Schauer 1851). Introductions continued throughout the 17th, 18th and 19th centuries (Swarbrick 1985) resulting in an aggregate species of mixed parentage (Howard 1969, Stirton 1977). Lantana became a favourite hothouse plant in Europe in the late 19th century, with 397 new varietal names being added to nurserymen's catalogues between 1850 and 1900 (Howard 1969). Many of these forms would have been distributed to the colonies, including Australia.

The first Australian record of lantana was in 1841 at the old Botanic Gardens in Adelaide (Bailey 1841), and was followed by many others. The plant was quickly spread northwards along the coast, with the first Australian collections of apparently naturalized lantanas from the Brisbane River in 1861 and near Sydney in 1862 (Swarbrick 1985). By 1897 lantana was described as being 'a huge rambling shrub and a most troublesome weed which has spread to an alarming extent, and forms impenetrable thickets on the banks of streams, deserted farms and the edges of scrubs' in the Brisbane area and as being 'equally abundant about Port Jackson' (Bailey 1897). Lantana appears to have been grown in Western Australia by 1875 (Swarbrick 1985) but may have only spread to the Northern Territory during or since the Second World War (I.L. Miller personal communication). Further expansion into previously unoccupied areas is probably still occurring, often assisted by land clearing or other human disturbance (Humphries and Stanton 1992).

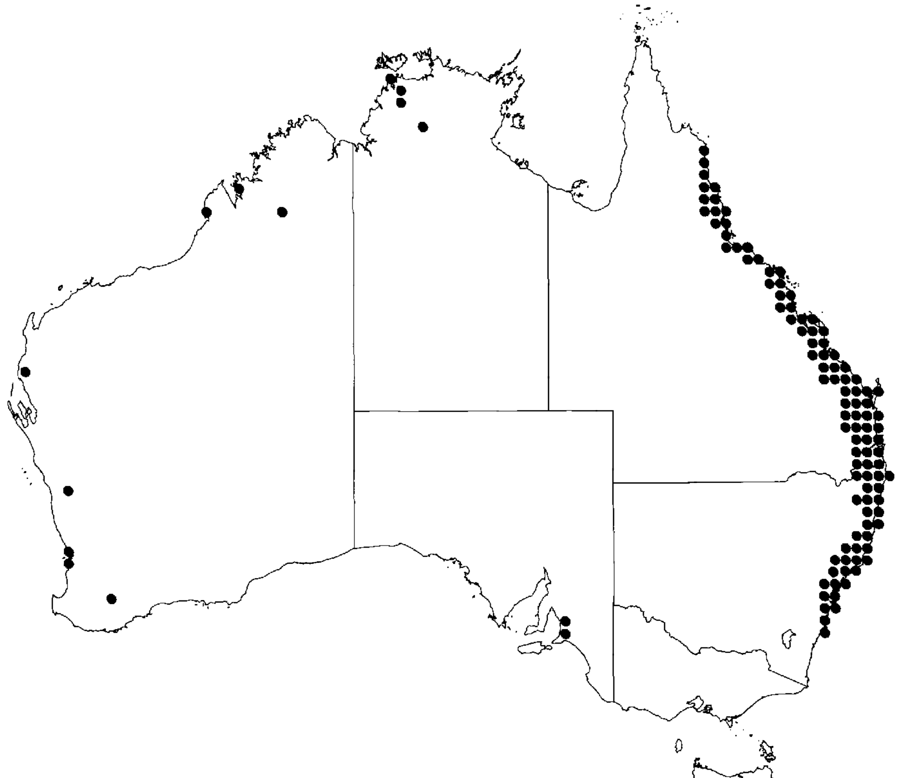

Figure 2. The Australian distribution of lantana (Parsons and Cuthbertson 1992, with permission).

Geographical distribution

Australia

Lantana is widely distributed throughout coastal and subcoastal areas from Ulladulla in New South Wales to Cape Melville in Queensland, with very scattered infestations in the Northern Territory, Western and South Australia (Figure 2). It is also present as a weed on both Lord Howe and Norfolk Islands (Swarbrick 1985).

Outside Australia

Lantana is widely grown as an ornamental shrub throughout the tropics, subtropics and warm temperate zones. It is established as a weed throughout the tropics and subtropics, from southern USA and the Mediterranean in the north to South Africa and the northern tip of New Zealand in the south (Figure 3).

Habitat

Climatic requirements

Lantana grows well over a wide range of warm temperate, subtropical and tropical climates (Gujral and Vasudevan 1983). It does not grow at temperatures below 5°C and the shoots are sensitive to frost (Thaman 1974, Winder 1980). Thaman also reported that lantana grows equally well on the drier leeward and moister windward sides of high islands across the Pacific. In south-eastern Queensland it is similarly found in moist coastal areas that naturally support rainforest and drier eastern slopes of the Dividing Range which support open eucalypt woodland, but ceases to the west of the Dividing Range where both drought and frost occur. The upper temperature limit for lantana growth is not known. Lantana grows

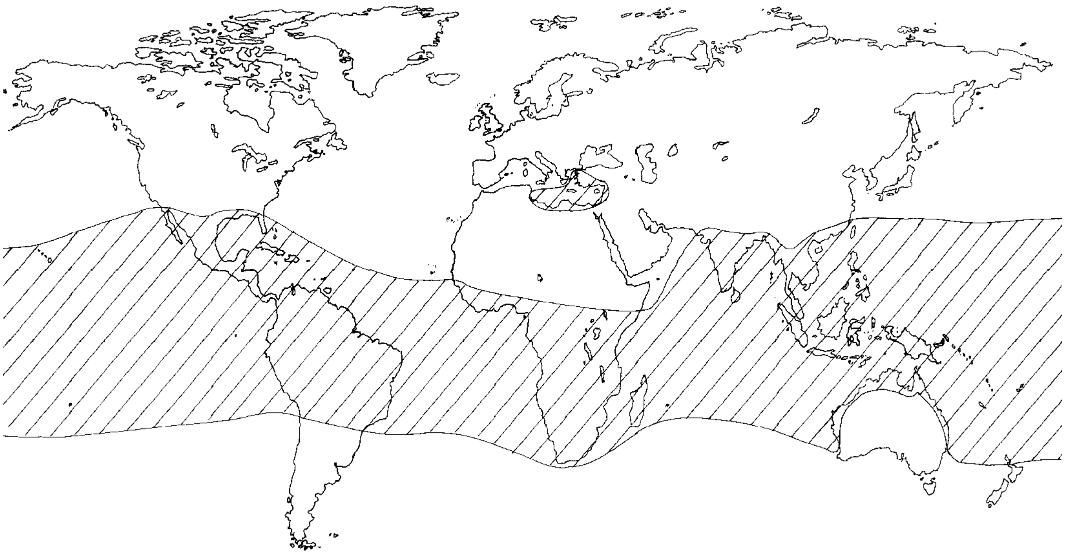

Figure 3. The world distribution of lantana as a weed in suitable terrestrial habitats. (Redrawn from Holm *et al.* 1977, Stirton, 1977 and other sources).

from 'within a few yards of the beach' (Thaman 1974) to 1000 m on the Great Dividing Range (M.J. Russell personal communication).

Lantana grows best under conditions of constant rainfall or where soil moisture is available throughout the year. Humphries and Stanton (1992) reported that in northern Queensland it is mostly confined to areas receiving more than 1250 mm per year and in the wet tropical areas its vigour and density decline with decreasing rainfall. They noted that in the subtropics it is rarely found west of the 750 mm isohyet. Bartholomew and Armstrong (1978) suggested the 650 mm isohyet as its western limit in south-eastern Queensland. Low temperatures and dry soil independently limit the growth of lantana. Most susceptible areas are probably already infested, although further advances are likely around their fringes and perhaps along river systems in the Gulf of Carpentaria, the Northern Territory and Western Australia.

Substrata

Lantana grows best on rich organic soils developed under rainforests, although it is also reported to tolerate poor soils and almost pure sands (Winder 1980). Its roots tend to rot in waterlogged soils (Thaman 1974), and it does not become established in sandy soils which dry out to depth during the dry season unless there is a local source of soil moisture. Lantana grows on well drained clay soils and on volcanic soils derived from basalts (Humphries and Stanton 1992), a situation parallelled by its vigorous growth on high volcanic islands in Polynesia (Florence *et al.* 1983). In the wet tropics of northern Queensland lantana is mostly confined to the deeper, moister and better drained metamorphic and granitic soils, not occurring where soils are shallow and severely drained (Humphries and Stanton 1992).

Lantana has a very low tolerance of soil salinity, which induces chlorosis (Thaman 1974) and is severely damaged or killed by 7.5 mg boron per litre in sand culture (Francois and Clark 1979). Winder (1980) noted that lantana is very rare on hard, phosphate deficient soils of open eucalypt forests. Lamb (1988) has shown that lantana increases the levels of organic matter and nitrate nitrogen in the soils below well established clumps. The leaf litter and soil from beneath such clumps is sometimes collected for use in gardens, where 'lantana mulch' is considered a desirable material for boosting plant growth.

Plant communities

Parsons and Cuthbertson (1992) reported that lantana 'occurs as a weed along roadsides, creek banks, fence lines, and waste places and is a common component of weedy pastures (and) park lands… and may become the dominant understorey in open forests and tropical tree plantations.' It readily invades open and semi-open plant communities such as road verges, grasslands and woodlands, and proliferates under lightly shaded conditions such as mature hoop pine plantations and the early stages of commercial exotic pine plantations. It also forms monospecific stands along road sides and fence lines and in open grasslands.

Lantana initially invades woodlands as isolated plants under perching and roosting trees, from which foci it rapidly invades the rest of the area (Lamb 1988). Humphries and Stanton (1992) reported lantana as a 'serious invader of open forest communities' in northern Queensland, as it is for similar situations elsewhere throughout its global range (e.g. Marr 1962, Gujral and Vasudevan 1983). Eucalypt seedlings generally fail to establish under lantana (Driscoll and Quinlan 1985), probably because of their light requirement during germination. Grasses and most herbs are shaded out by dense lantana thickets, leaving bare ground when the lantana is physically or chemically removed (Swarbrick unpublished). Lamb (1988) has shown that within ten years of invasion the nature of eucalypt woodland changes significantly and possibly irreversibly from dominance by native trees to dominance by the exotic shrub.

Humphries and Stanton (1992) noted that lantana is unable to invade tropical rain forest in northern Queensland and only persists along edges and where the canopy is broken, a similar situation to that found in dry vine scrubs in south-eastern Queensland (Swarbrick unpublished). Many rainforest species germinate and develop under lantana, eventually growing through it and shading it out. Broadleaf privet (*Ligustrum lucidum*) also behaves in this way around Toowoomba (Swarbrick unpublished). Following initial disturbance lantana may, however, form a stable community in such areas and resist rainforest re-establishment for several decades (Lamb 1991). Stocker and Mott (1981) showed that lantana may slow down or even block grass invasion of disturbed rainforest and that it can protect rainforest margins from damage by low intensity fires at least early in the dry season.

In south-east Queensland lantana invades and dominates native woodland that has been cleared to increase its grazing capacity (Collins 1976). Clearing increases sunlight at ground level and decreases interspecific plant competition. Whilst this initially increases growth of native pasture species it also allows invasion by lantana, with which the native grasses are unable to compete.

Many authors note that lantana is less common in undisturbed native communities than in those that have been disturbed by cultivation, grazing, road works etc. in which it often dominates the secondary succession.

Animal associations

The seeds of lantana are primarily distributed by fruit-eating birds and mammals, and the plant provides shelter and food for many species of animals and small birds. Whilst providing nectar for pollinating insects (see under Pollination below) it is toxic to many grazing animals (see under Detrimental importance below).

Many species of native and exotic birds have been recorded feeding on lantana fruits in Australia (Liddy 1985, Loyn and French 1991). R.J.S. Beeton (personal communication) argues that lantana is generally beneficial to wildlife in south-eastern Queensland, providing feeding sites for seed-, leaf- and litter-feeding insects and shelter for small birds and mammals. Both Driscoll and Quinlan (1985) and Alcova (1987) surveyed birds and small mammals along lantana-infested and lantana-free transects in tall woodland in Brisbane. Dense lantana altered the incidence of some birds and animals, but the results were neither clearcut nor repeatable. No differences were found in the species of ground litter fauna between lantana-infested and lantana-free tall open woodland and open forest in Brisbane by Traby (1986), although lantana-free areas generally had significantly higher numbers of springtails and mites.

Exotic birds such as Indian mynahs are responsible for spreading lantana in Hawaii and New Caledonia and are significant intra- and inter-island distributors of its seeds (Thaman 1974). Indian mynahs are now spreading throughout parts of Australia in which lantana is already established. In South Africa lantana seeds are spread by birds, rodents and monkeys (Wells and Stirton 1981), and in India the fruits are eaten by cattle, sheep, goats, foxes and jackals and the seed dispersed by many species of birds including sparrows, parrots and crows (Bisht and Bhatnagar 1979). The spread of lantana in New Caledonia is assisted by the soil disturbance caused by exotic ungulates including deer, cattle, horses and goats (Thaman 1974).

Growth and development

Morphology

Lantana is very plastic in its responses to light intensity and support. Seedling densities vary from less than one to several per square metre. At densities of less than 1 m^{-2} seedlings commonly branch near the base to produce rounded young plants, whilst at higher densities competition for light results in more upright plants. Over a number of years some plants dominate and shade out the rest, with each dominant plant eventually occupying several square metres. Adjacent plants interlock and grow through and over each other, producing an impenetrable thicket several metres high with a canopy of active shoots. New shoots constantly arise from the base of large healthy plants, whilst older shaded stems lose vigour and die. Seedlings germinating under such clumps usually fail to establish. Prostrate stems root at the nodes if they become covered by moist fallen leaves and debris, sometimes developing into vigorous connected daughter plants. The presence of a low branched tree or other support allows lantana to scramble upwards to a height of 10–15 m, in which case the lower stems lose their branches and assume a flexible liane-like form.

Established lantana bushes regrow vigorously from dormant basal buds after shoot removal and flower within a few months under favourable conditions.

Perennation

Lantana is a perennial shrub, constantly renewed at the base and long lived under favourable conditions. Plants tend to die only under stressful conditions including intense or prolonged drought or shading by taller evergreen mesophytic plants.

Phenology

Parsons and Cuthbertson (1992) reported that lantana seedlings germinate throughout the year provided sufficient moisture is present, with a peak after the first summer rains. Initial growth is slow until the root system is established, after which it increases as the season advances. They reported that the first flowers are produced in the field during the second summer, although flowers can be produced six months after germination in the greenhouse (Hannan-Jones unpublished).

Lantana exhibits rapid shoot growth under favourable conditions of soil and air humidity, temperature and light, resulting in year-round shoot production. It also achieves marked drought tolerance under temporarily dry conditions through defoliation.

Lantana flowers whenever soil moisture is available and air humidity and temperature are high, resulting in almost continuous flowering and fruit set along the Queensland and New South Wales coasts. A distinct flush of flowers a few weeks after soaking rains is more common towards the drier inland margins of its Australian distribution, usually followed by significant fruit set.

Reproduction

Floral biology

Parsons and Cuthbertson (1992) reported that under good conditions lantana plants flower from early summer until March or April of the year after germination and every summer thereafter from September or October until March or April. Many authors (e.g. Auld 1969) have shown, however, that lantana can flower throughout the year under moist, warm and well lit conditions.

Freshly opened flowers produce nectar (Kugler 1980), which attracts many species of insect pollinators. Both self and cross pollination are brought about through visits of large insects such as butterflies, moths and various kinds of bees (Dronamraju 1958, Schemske 1976, Kugler 1980) and by the movements of smaller insects such as thrips within individual flowers (Mohan Ram and Mathur 1984, Mathur and Mohan Ram 1986). Thrips were only found in yellow (newly-opened) flowers by Mathur and Mohan Ram (1978), entering through the throat and pushing past the anthers to feed on the stigmatic exudate. Thrips eat, carry and deposit pollen grains as they move about within the flower, and carry pollen grains on their legs and abdomens as they seek out other yellow-throated flowers within the same inflorescence.

Ramachandra Rao (1920) described pollination of lantana by butterflies in India and Kugler (1980) pollination by bumble, honey and other types of bees as well as by butterflies and moths in Crete. Activities included probing the flower tube by the insect's proboscis, the unconscious gathering of pollen grains onto the proboscis from the anthers halfway up the petal tube, and their transfer to the next flower visited. Mathur and Mohan Ram (1986) showed that butterflies seek nectar in both newly opened (unpollinated) and in older (pollinated) flowers, but that they spend more time probing newly opened flowers.

After pollination, lantana flowers lose their yellow centres and usually darken in colour. Mathur and Mohan Ram (1978) and Mohan Ram and Mathur (1984) analysed this colour change, in which the yellow carotenoids of the newly opened flower are masked by red anthocyanins. The yellow carotenoids remain dominant in unpollinated flowers.

Seed development

A considerable literature exists on the cytology and seed development of lantana.

Padmanabhan described the development of the endosperm in lantana in 1959 and Koshoo and Mahal (1967) investigated the cytology of lantana seeds, studying pollen viability and seed production in diploids, triploids, tetraploids and pentaploids. All ploidy levels exhibited some level of pollen viability and produced seed from open pollination. These authors suggested that the seeds resulted from normal sexual union in the diploids and from either facultative or obligate apomixis at other ploidy levels, and concluded that lantana's 'reproductive versatility' is based on 'a complicated mixture of sexual, semisexual and totally apomictic biotypes'. Each biotype or form was thought to be the basis for the evolution of new forms, leading to the 'intricate reticulation of taxonomic differences' within the aggregate species.

Stirton's 1977 review of the literature on lantana threw doubt on Koshoo and Mahal's 1967 suggestion that apomixis plays some part in seed production since this finding was not supported by any other author. Spies and Stirton (1982a) examined embryo sac development in 20 South African forms of lantana, specifically looking for evidence of apomixis but failing to find any. Ovules from diploid, triploid and tetraploid forms all contained normal sexual embryos, but no normal embryo sacs were found in either pentaploid or hexaploid forms. Forty two and a half per cent of ovules contained two sexual embryo sacs, suggesting the possibility of two embryos developing to maturity within such seeds.

Spies and Stirton (1982b) concluded from further studies of the cytology of South African lantanas that there are large genomic differences between forms at the same ploidy levels, indicating either the hybridization of different cultivars before their introduction into South Africa or a high rate of post introduction evolution within the species, or possibly both. Differences in chromosomal behaviour between the South African and Indian forms indicate the introduction of different groups within the complex into the different countries, and it would be safe to assume that the Australian lantanas will be different again.

Seed production and dispersal

The average percentage fruit set in a number of open pollinated weedy lantanas was 36.7–48% in inflorescences averaging 32.6 flowers each (Auld 1969, Mathur and Mohan Ram 1986, Swarbrick unpublished). Since there are normally two inflorescences per node during active growth, the total number of fruits produced by a lantana plant under good growing conditions is several thousand per square metre per year. In the Philippines Cadigal (personal communication) recorded an average of 24 fruits per inflorescence, 511 inflorescences per plant, and 12 264 fruits per plant.

Lantana seeds may either be transported away from the plant or fall beneath the parent plant. Most fruits are thought to be dispersed by birds, often locally but also to distances of up to 1 km or more. The seeds resist digestion during passage through the vector, and initial infestations from bird-dispersed seeds are most commonly seen under fences, trees and other obvious perches.

Physiology of seeds and germination

Whilst investigating the effects of the lantana seed fly *Ophiomyia lantanae* on the germination of lantana seeds from Natal, Graaff (1986) recorded a very low germination rate even in uninfested fruit. Of 1200 seeds examined only 48% had fully formed embryos. Breaking the dormancy (possibly caused by the woody seed coat) by 180 days of dry storage increased germination from 29 to 47% after 85 days. The lantana seed fly also affected the germination percentage of infested fruits (see under Response to natural enemies below).

The influence of the fruit pulp as an inhibitor for lantana seeds does not appear to have been specifically tested. Hiet (1944, 1946) reported significant increases in the germination of dry-stored lantana seeds after removal of the pulp. Hannan-Jones (unpublished) observed that 44% of seeds collected from the faeces of handled wild birds germinated, compared with 10% for seeds from the same bushes which retained their pulp and 46% for similar but cleaned seeds. It appears that the pulp around lantana seeds serves not only to attract seed vectors but also to delay or even inhibit the germination of seed falling under the parent bush.

Vegetative reproduction

Parsons and Cuthbertson (1992) reported that new lantana stems may arise from lateral roots in early spring and that the size of lantana clumps increases by suckering. The growth of stems from lantana roots has not been observed by any of us despite close association with lantana and careful observation over many years. Lantana bushes often have prostrate stems with adventitious roots which, when covered with moist litter root, send up vigorous shoots from the nodes. These shoots may be confused with root suckers.

After cutting back lantana regrows vigorously from dormant buds at the bases of the stems. It can also be propagated by stem tip or hardwood stem cuttings placed in moist rooting media or by hardwood cuttings planted directly into moist soil.

Hybrids

The lantana complex is itself of hybrid origin (e.g. Howard 1969), and hybridizes freely within itself (e.g. Howard 1970, Spies 1984) to produce fertile hybrid swarms morphologically similar to the parent plants. Members of the lantana complex can also hybridize back to the original species from which the modern complex arose. Sanders (1987) has shown that a weedy tetraploid *L. camara* crosses with the diploid Floridan *L. depressa* to produce a triploid resembling the naturally occurring Bahaman *L. ovatifolia*, and that such hybrids form a morphological continuum between the parental taxa.

Importance

Detrimental

Pastures. The main economic damage caused by lantana is through decreased productivity of pasture land. Lantana readily invades uncultivated pastures, and unless controlled spreads to exclude useful native grasses and fodders. The plant is unpalatable and scarcely eaten, and the trampling and deposition of dung by large hoofed animals are instrumental in the germination and establishment of new seedlings.

Lantana contains a number of chemicals toxic to animals, especially the triterpene lantadenes A and B (Everist 1981). Whilst ungulates are primarily affected, there have been some cases of human poisoning. All forms of lantana are thought to be toxic, although the toxicity varies considerably between forms (Seawright 1965). Lantana poisoning occurs most frequently in cattle and less often in sheep, probably because few sheep are kept in areas prone to lantana invasion. Although photosensitization is the commonest symptom of lantana poisoning in sheep, acute damage is mainly to the liver and chronic damage to the liver, kidneys and gut (Seawright and Hrdlicka 1977).

Nearly 4 million ha of pasture are thought to be infested with lantana in Australia (Parsons and Cuthbertson 1992), mostly in coastal and subcoastal Queensland and New South Wales. Annual losses due to lantana in pastures are estimated to be A$7.7m, comprising 1500 cattle deaths (A$0.5m), 4.5% reduced performance (A$2.0m), 7.3% loss of pasture (A$3.0m) and A$2.2m in control costs (Culvenor 1985).

Similar problems exist in other tropical and subtropical countries, e.g. in India (Singh *et al.* 1970) and Hawaii (Waterhouse and Norris 1987). Annual losses due to lantana in the Solomon Islands are estimated to be A$70 000 and in Fiji to be A$800 000 (Anon. 1993a).

Natural ecosystems. Lantana is a serious invader of disturbed ecosystems conserved for their natural and semi-natural attributes throughout its Australian and overseas distribution. It is among the most widespread and obvious of the exotic species in the Wet Tropics World Heritage Area of northern Queensland (Humphries and Stanton 1992), where it invades disturbed rainforest. Whilst lantana persists along roadsides, creeks and other open situations it is shaded out by the dense canopy as rainforest becomes re-established. Lamb (1981), on the other hand, has noted the persistence of lantana for over 30 years after deliberate rainforest disturbance in south-eastern Queensland. Lantana may play an important role in the marginal fire ecology of rainforests, depending on local topography, wind and moisture content of the vegetation and admixture of other fuels such as exotic grasses (Humphries and

Stanton 1992). Under different conditions lantana may either increase or decrease the fuel load along the rainforest margin.

Lantana is mainly an invader of open (in Australia especially eucalypt) woodland (Lamb 1988, Humphries and Stanton 1992). It commonly forms dense monospecific stands several metres tall which exclude native herbs, shrubs and tree and climber seedlings, greatly reducing the area's conservation value, making it impenetrable to people, and greatly increasing the fire hazard under dry conditions. Infested woodland near Brisbane had significantly fewer shrubs, saplings and trees in the smaller size classes in areas of dense lantana than in adjacent and otherwise similar lantana free areas (Alcova 1987) (Table 1).

Table 1. Mean density of shrubs, saplings and trees per hectare in three lantana free and lantana infested areas of woodland near Brisbane (Alcova 1987).

	Mean density per hectare in each size class (diameter 1m above ground)				
	<6 cm	6–15 cm	16–30 cm	31–60 cm	>61 cm
Lantana free	1248	436	173	85	14
Lantana infested	379	182	108	74	19

Dry lantana burns readily even when green (Gujral and Vasudevan 1983), and unless drought stressed the plant recovers quickly after fire from basal dormant buds. Together with its smothering nature this gives lantana a distinct advantage in moist coastal and subcoastal woodlands. Lamb (1988) showed that during the first ten years after invasion lantana altered the whole balance of eucalypt woodland. The amount of wood and twig litter fall decreased as the native trees lost vigour, whilst the amount of lantana litter fall sharply increased. The amount of nutrient in the litter decreased, suggesting that more was taken up by the lantana with less available to the native species. The concentration of nitrate nitrogen in the soil and litter increased to the advantage of the lantana and other exotic weeds. Lamb concluded that 'the processes by which the community maintains itself ... are at risk, and the longer the process continues the more unpredictable the result will be.' Regeneration of native plant communities after clearing dense lantana may be slow where few viable native plant propagules are left in the soil. For the first year or more such areas tend to be dominated by ephemerals including cobbler's pegs (*Bidens pilosa*), after which exotic and native grasses begin to dominate and shrub and tree seedlings appear (Swarbrick unpublished).

Lantana is an aggressive invader of natural ecosystems in many other countries, for example, the Galapagos Islands (Washington 1985), many Pacific islands (Thaman 1974) and South Africa (Stirton 1978).

Forestry. Lantana is a serious weed of commercial hoop pine plantations in coastal south-eastern Queensland, competing with tree seedlings for light, interfering with access throughout the life of the plantation, and increasing both management and harvesting costs and fire hazard. The cost of lantana control in these plantations exceeded A$0.9m in 1976/1977 (Master 1985) but has since dropped to about A$0.5m (Wells 1984). Lantana control accounts for about 30% of the establishment and 25–50% of the harvesting costs of this crop (Wells 1984a). Lantana is not a problem in established exotic pine plantations which shade it out, but in 1966/1967 the Forestry Commission of New South Wales spent about A$5500 attempting to establish biological control in indigenous forests within the state (Baur 1967). Lantana is also a serious weed of forestry in India (Ghosh 1980), ousting valuable timber species, inhibiting natural regeneration of forest trees, causing problems during the establishment of plantations, creating a serious fire hazard and poisoning grazing stock.

Tropical Plantations. Lantana is a major weed of coconuts throughout the tropics, thriving in the moist disturbed soils and high light conditions, significantly reducing yields and interfering with management and harvest (Thaman 1974, Waterhouse and Norris 1987). Annual production losses of 1–3% occur in coconut plantations in Vanuatu, Solomon Islands and Fiji, worth A$230 000, A$390 000 and A$500 000 respectively (Anon. 1993a).

Transport and industry. Lantana is one of the eight most troublesome weeds affecting railway land in New South Wales, because of its size and the rapidity of its spread (Mahoney 1967). It is also a problem along disturbed power line easements throughout south-eastern and coastal Queensland.

Allelopathy. Like most other plants, lantana can be shown to produce chemicals which inhibit the germination and growth of other plants in the laboratory. The allelopathic effect of lantana against agronomic crops such as wheat and soybeans and annual weeds (Mersie and Singh 1987) is probably of little importance, but Singh and Achhireddy (1987) have shown that lantana is also allelopathic to citrus, a crop in which it is a major weed in Florida. Achhireddy and Singh (1984) showed that lantana is allelopathic to the perennial weed *Morrenia odorata* in Floridan citrus orchards. Lantana may also be allelopathic to many endemic Australian plants, giving it an advantage in competition with them once established (Swarbrick, unpublished). Wadhawani and Bhardwaja (1981) observed that lantana inhibits the germination of spores of the fern *Cyclosorus dentatus* in India. Both Achhireddy *et al.* (1985) and Singh *et al.* (1989) have attempted to isolate the allelopathic chemicals within lantana.

Host for other pests. In India lantana has been shown to be a symptomless host for the sandalwood spike disease caused by *Chlorogenus santali* and a primary host for the dodder *Cuscuta reflexa* from which it spreads to more useful plant species (Nayar and Srimathi 1968, Prasad 1966). Waterhouse and Norris (1987) reported that lantana provides cover for rats, wild pigs and other vermin in Fiji and provides a favourable microclimate for tsetse fly in East Africa.

Beneficial

Ornamental. Both the weedy and nonweedy forms of lantana are grown extensively as garden ornamental shrubs in the areas in which it is a weed and elsewhere. The non-prickly, non-fruiting triploid forms make better ornamentals than the prickly fruiting forms, since they are shorter and denser in habit and their flowers persist much longer due to failure of fertilization.

Essential oils and insecticides. The mixed essential oils in lantana flowers and leaves can be fractionated to provide oils useful for perfumery and possibly beneficial drugs (Ahmad *et al.* 1962, Peyron *et al.* 1971), but do not seem to have been commercialized as yet. The ability of lantana and its extracts to control other organisms suggests that it may be used as a biocide. Dried and powdered lantana protects stored potatoes against potato tuber moth in south-east Asia (Anon. 1988), whilst lantana extract can protect ripe tomato fruits against the combination of a fruit fly and an associated fruit rotting fungus (Sinha and Saxena 1987). On the other hand Ahmed and Agnihotri (1977) have shown that lantana leaf extracts failed to inhibit a range of test fungi.

Stockfeed. Lantana seeds are at times so abundant in India that they can be

Table 2. Herbicides reported for the control of lantana.

Herbicide	Method of application Foliar Ground	 Aerial	 Soil	 Basal bark	 Cut Stump	 Stem injection
2,4-D + 2,4,5-T	10,23,24,25	20				
2,4-D	Q,N,3,4,9,10,12, 16,18,19,23,25	2		Q,N,2	Q,N,13	
2,4,5-T	11,23			Q	11	Q
Amitrole	4					
Bromacil			14			
Buthidazole			2			
Dicamba		20				
Dicamba + MCPA	9,17,18,19					
Dicamba + 2,4,5-T					11	
Dichlorprop	Q,N,2,3,6,9, 16,17,18,19	2		Q,2	Q	
Ethidimuron	22					
Fenoprop	22	20				
Fluroxypyr	Q,2,27					
Fosamine	4,9,12,16,17,18,26					
Glyphosate	Q,N,SA,2,7,9,11,12, 17,18,19,22,26,29	2			8,11	
Hexazinone			2			
Imazapyr	SA,7,11,19				SA,7,8,11	
Metsulfuron methyl	Q,2,8,9,19 18,21,27					
Paraquat	24	20				
Paraquat + diquat		20				
Picloram	SA,7,10,12	2	2		SA,7,13	
Picloram + 2,4-D	Q,N,9,12,17,18,19	20			13	
Picloram + 2,4,5-T	10,11				11	
Picloram + triclopyr	Q,N,8,9,18,19				SA,7,8	
Tebuthiuron		Q,N	SA,2,7,14			
Triclopyr	Q,11,26	Q		Q	Q,N,11,13	

Q Registered for use on lantana in Queensland, Australia (Source: Infopest)
N Registered for use on lantana in New South Wales, Australia (Source: Peskem)
SA Registered for use on lantana in South Africa (Source: Erasmus 1991)

1 Abell 1973
2 Armstrong *et al.* 1987
3 Batholomew and Armstrong 1978
4 Campion 1978
5 Chang *et al.* 1982
6 Diatloff and Percy 1973
7 Erasmus 1991
8 Erasmus 1992
9 Fenton 1987
10 Ghosh 1980
11 Graaff 1986
12 Killilea 1983a
13 Killilea 1983b
14 Killilea 1983c
15 Love 1989
16 Master 1985
17 McMillan and Strachan 1984
18 McMillan and Strachan 1989
19 McMillan 1989a
20 Motooka *et al.* 1967b
21 Motooka *et al.* 1991
22 Phillips and Tucker 1976
23 Sinha 1976
24 Soni 1980
25 Tam 1947
26 Toth and Smith 1984
27 Vitelli and van Haaren 1988
28 Vitelli and Dorney 1991
29 Wells 1984a

harvested and used for stockfeed (Lall *et al.* 1983a and 1983b).

Legislation

Lantana was a declared noxious weed throughout much of New South Wales for many years, but was removed from the noxious weeds lists in the 1980s since it was uneconomic to control in most situations. Parsons and Cuthbertson (1992) reported that it is still a declared plant in certain shires and municipalities in New South Wales and is a Classes B and C weed throughout the Northern Territory outside town areas.

Although all forms of lantana are declared noxious weeds in Natal, attempts have recently been made to allow the sale of the largely sterile triploid forms. Spies and du Plessis (1987) have reacted against this attempt by showing that even the triploid forms are capable of producing fertile pollen and occasional viable seeds and can hybridize with other forms of the plant.

Response to herbicides

Many chemical control trials have been conducted against the various forms of lantana in Australia, South Africa, Zimbabwe, India, Taiwan and the USA (Table 2). The comparative efficacy of various herbicides and factors affecting their efficacy are discussed below.

Effect of herbicide type

The most effective herbicide groups are the phenoxy acid (2,4-D, 2,4,5-T, dichlorprop and MCPA), benzoic acid based (dicamba), and pyridine based (fluroxypyr, picloram, clopyralid and triclopyr) groups. Inhibitors of acetolactate synthetase such as the sulfonylureas (metsulfuron methyl) and imidazolinones (imazapyr) and inhibitors of EPSP synthetase in the shikimic acid pathway such as glyphosate also show good activity. Inhibitors of photosynthesis such as the triazine, uracil, urea and bipyridyl groups of herbicides have little effect on lantana, possibly due to its ability to drop leaves and refoliate rapidly.

The order of decreasing effectiveness on red flowered lantana in northern New South Wales was glyphosate, picloram/ triclopyr, 2,4-D + picloram, dichlorprop, fosamine, dicamba + MCPA, metsulfuron methyl and 2,4-D (Fenton 1987). Trials over three years with 'Helidon White' indicated the following order of decreasing effectiveness at the rates used: fluroxypyr, glyphosate, dichlorprop and metsulfuron methyl (Hannan-Jones unpublished). Fluroxypyr controlled 'Common Pink' more effectively than metsulfuron methyl (Vitelli 1991, Armstrong *et al.* 1987), whilst at the rates used fosamine was equally or more effective than the recommended rates for 2,4-D amine or dichlorprop (Master 1985). Toth (1984) demonstrated that glyphosate was more effective than fosamine, whilst Armstrong *et al.* (1987) showed glyphosate to be more effective than dichlorprop as a low volume foliar spray with a sprinkler sprayer, particularly when applied in a wet autumn and under shade.

Soil applied picloram granules, tebuthiuron, hexazinone and buthidazole all failed to control lantana in south-eastern Queensland with or without prior burning (Armstrong *et al.* 1987). In Hawaii, however, hexazinone has been shown to be as effective as tebuthiuron in some situations (Motooka *et al.* 1991). Tebuthiuron was more effective in November than in May in Zimbabwe (possibly due to a lack of rainfall after application), whilst soil applied bromacil was ineffective (Killilea 1983c).

Effect of application method and addition of surfactants

The response of lantana to a given herbicide can be influenced by its method of application and by the addition of surfactants.

High volume foliar application of fluroxypyr was a more effective method than low volume gas gun, sprinkler sprayer or aerial application (Love 1989). However, fosamine was more effective when applied by low volume gas gun than by high volume overall spraying (Toth and Smith 1984).

Herbicide screening by the Queensland Department of Lands on 'Helidon White' (Armstrong *et al.* 1987) indicated that 2,4-D was more effective than dichlorprop when applied as a basal bark treatment whereas the reverse was true when comparing their high volume foliar efficacy. In Hawaii, triclopyr was ineffective as a foliar application, but was effective when applied as a basal application in diesel oil, which suggested that there was some impediment to triclopyr uptake in foliar treatments (Motooka *et al.* 1991).

Aerial application of 2,4-D, glyphosate, dichlorprop and picloram has given unsatisfactory control of lantana, whereas ground application has been shown to be quite effective (Armstrong *et al.* 1987).

The addition of a surfactant to fluroxypyr gave better control of one undescribed form in northern Queensland (Love 1989), but there appeared to be no significant differences in effect between various surfactants used with metsulfuron methyl in Hawaii (Motooka *et al.* 1991).

Effect of season and climate

Control of lantana with herbicides shows a distinct seasonal response for glyphosate, fluroxypyr, dichlorprop and metsulfuron methyl for the 'Helidon White' form in south-eastern Queensland (Hannan-Jones unpublished, Figure 4). This effect has been shown for these and other herbicides at other locations and for other lantana forms (Killilea 1983b, Wells 1984b, Fenton 1987, Vitelli and Van Haaren 1988). For growth regulating hormones, such as 2,4-D, dichlorprop, fluroxypyr and picloram, which are most effective between December and April, this effect is closely connected to the growth activity of the plant and possibly with increased translocation of the applied herbicides within the plant. In the case of fosamine, the effect is associated with the onset of leaf senescence and a possible basipetal translocation of fosamine into the wood of the plant and acropetal translocation into the next year's buds (Campion 1978).

In north-eastern Australia autumn is a time of reducing rainfall, and both Fenton (1987) and Vitelli and Van Haaren (1988) have noted that the poorer results in autumn correspond with water stress and reduced foliage cover, whilst Killilea (1983b) has related this effect to the onset of cooler weather. Trials in south-eastern Queensland have shown correlations between temperature and rainfall and plant mortality due to foliar applied fluroxypyr, with plant mortality decreasing after a period with average minimum temperature below 15°C and more than 30 mm of rain being required in the preceding six weeks for a significant response from foliar applied fluroxypyr (Hannan-Jones unpublished).

Low rainfall before cut stump treatment has reduced the effectiveness of many herbicides in Zimbabwe (Killilea 1983a). In Australia good results have been obtained under wet summer conditions by Fenton (1987) and the best results for fosamine have coincided with the main autumn flowering period (Campion 1978).

Effect of plant form

The great variability within the lantana complex may well be responsible for its variable response to similar herbicide treatments (Graaff 1986). Some reports indicate that 2,4-D is effective for lantana control (Abell 1973), while others state that it is ineffective (Tam 1947).

Various forms of lantana throughout Queensland have shown quite different responses to 2,4-D amine as a high volume overall spray, in that pink and white flowered forms both died within four months, but red forms recovered, normal regrowth appearing within six weeks of treatment even though there were no significant differences in either leaf wettability or spray retention (Diatloff and Haseler 1965). In Northern New South Wales McMillan (1989a) has shown that red-flowered lantanas are more

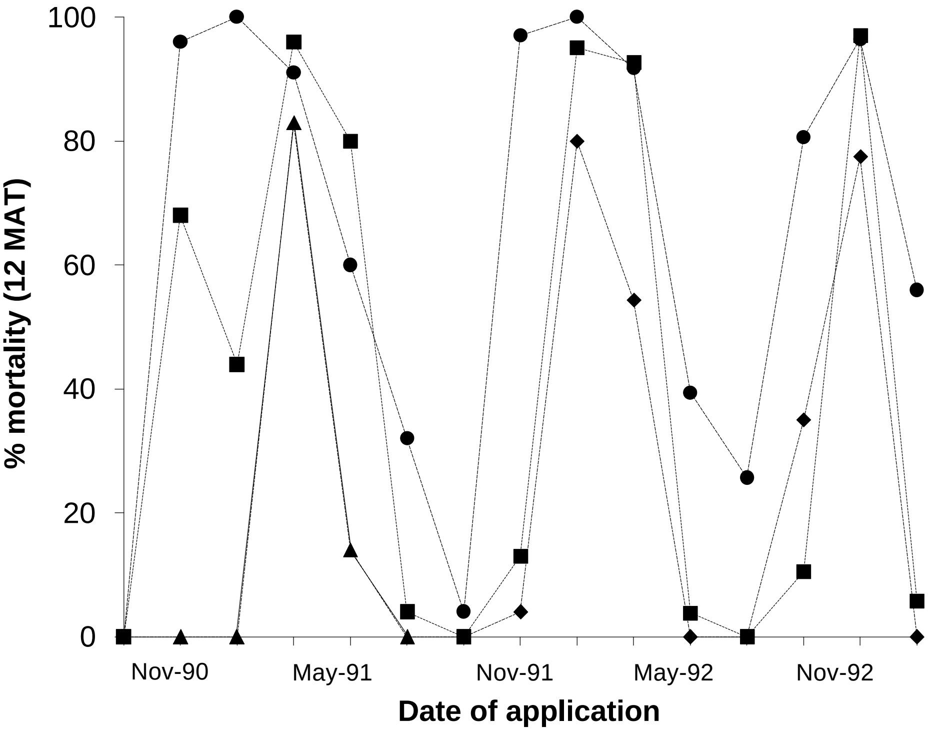

Figure 4. Seasonal response of *L. camara* to selected foliar applied herbicides (Hannan-Jones, unpublished).
-●- Fluroxypyr, -■- Glyphosate, -▲- Metsulfuron methyl, -◆- Dichlorprop.

difficult to control with herbicides than ‘Common Pink’. Only 2,4-D and fluroxypyr have exhibited variable effects on lantanas of different flower forms in northern Queensland (Vitelli and Dorney 1991).

In Mauritius the pink flowered form has been shown to be easily killed by MCPA or 2,4-D, whereas even under the most favourable conditions the lethal dosage for the orange flowered form is three times as great (Birch 1961).

Effect of plant size

In Queensland it has been observed that glyphosate gives decreasing control of lantana with increasing plant size depending on the method of application (Wells 1984b), whilst fosamine is decreasingly effective as plant height exceeds 2 m, perhaps due to a ‘shading effect of plant size on foliage coverage or ... larger plants [having] a physiological characteristic that made them less susceptible to fosamine’ (Master 1985). Similarly Killilea (1983b) noted that smaller plants were more easily killed than larger bushes by overall spraying with a number of herbicides and that plants with thinner stems were more susceptible to cut stump treatment. The volume of applied herbicide required to control lantana has been shown to be proportional to the volume of the plant rather than the leaf surface area (McMillan 1992), which may explain some of the size effects described by earlier workers.

Response to fire, physical control and competition

Although the use of fire to control of lantana in pasture is widely recommended (e.g. Goodchild 1951, Saint-Smith 1964, Bartholomew and Armstrong 1978), very little experimental work has been published on its use and effects. Fire is generally insufficient by itself for lantana control, and additional treatments including sowing competitive pasture species, controlled grazing and follow-up burns and chemical treatments are usually required. Little information is available on the seasonality of burning, the effect of meteorological conditions at the time of the burn or the occurrence of rain after burning, the quality and type of fuel, whether a ground or crown fire is preferable, or time of reintroduction of stock after the fire.

Several authors have reported the effects of mechanical clearance of lantana in pastures (e.g. Goodchild 1951, Saint-Smith 1964, Bartholomew and Armstrong 1978). All have shown that cultivation gives very effective control of lantana but that effective pasture establishment and management are essential and that some follow-up control is generally required.

In south-east Queensland several trials are being conducted into the direct sowing of competitive fodder plants such as such as glycine (*Neonotonia wightii*) and leucaena (*Leucaena leucocephala*) into lantana thickets (in the belief that grazing stock attempting to graze will trample down the lantana) and into the replacement of lantana with native trees (M. Roberts personal communication, J.C. Galletly personal communication). Degraded rainforest clearings in northern New South Wales choked with lantana are also being regenerated by planting and tending selected rainforest pioneer, secondary and tertiary species until a canopy is formed and the lantana is reduced by a lack of light (R. Hynes personal communication).

The Queensland Forest Service has successfully used a combined harvester and mulcher to clear lantana and other woody regrowth from between rows of hoop pine (*Araucaria cunninghamii*) plantations to allow access to the trees for trimming and felling, but the machine is unsuitable for rough or hilly terrain (P. Lees personal communication).

In India the establishment of fodder trees such as *Grewia optiva*, *Bauhinia variegata* and *Populus* spp. after clearing lantana has shown some success in preventing the return of lantana. The fast spreading vine *Pueraria thunbergiana* is also a promising replacement for lantana (Sharma 1988). In Zambia, Anderson (1963) investigated the clearing of lantana from amongst thick natural bush using a combination of trimming and specially designed one- or three-man operated levers to grub out individual lantana bushes. All but the longest lateral roots can be completely removed, but soil disturbance causes a flush of lantana and other weed seedlings.

Response to natural enemies

Surveys of the phytophagous insect fauna of *Lantana camara* and closely related species have yielded 544 species in North and Central America (Palmer and Pullen in press) and 345 species in Brazil (Winder and Harley 1983). Most are probably polyphagous and thus unsuitable as biological control agents.

Lantana was the first weed against which biological control was attempted. Koebele in 1902 collected 23 insect species in Mexico and shipped them to Hawaii, where eight were eventually established (Perkins and Swezey 1924). Julian (1992) lists 32 insect species that have been deliberately released in 25 countries. Since then the leaf-feeding chrysomelid beetle *Charidotis pygmaea* and oecophorid moth *Ectaga garcia* have been released in Queensland (Willson 1993) and the leaf-mining chrysomelid beetles *Uroplata girardi* and *Octotoma scabripennis* and leaf sap sucking bug *Teleonemia scrupulosa* have been released in the Solomon Islands (Anon. 1993b) (Table 3).

The exploration for and primary host specificity testing of these insects has been carried out by the Hawaiian Department of Agriculture, the Commonwealth Scientific and Industrial Research Organization and the Queensland Department of Lands, Australia. The distribution of biocontrol agents to many African and Pacific Island countries has been carried out by the International Institute of Biological Control using species already imported into other countries, and the South African Plant Protection Research Institute has imported and released biocontrol agents in South Africa since 1961 (Cilliers and Neser 1991).

Despite this massive effort lantana remains one of the world’s worst weeds (Holm *et al.* 1977) and thus its biological control can be considered to have been unsuccessful, even though levels of control ranging from minor to significant have been achieved in some countries. The main reasons for this overall lack of success can be attributed to the extreme variability of the plant coupled with its ability to colonize diverse habitats. Introduced insects may show preferences for one or more of the many forms of lantana or may fail to thrive in some of the environments in which the weed can survive.

The insect species used as biological control agents have been collected from several species of *Lantana.* These include *L. tiliaefolia* and *L. glutinosa* in Brazil (Winder and Harley 1983) (both now considered to be subspecies of *L. urticifolia,* Palmer and Pullen in press), and *L. camara, L. urticifolia, L. urticoides* and *L. hirsuta* in Mexico, USA and Central America (one or more of which belong to the *camara* section of the genus, Palmer and Pullen in press). Most agents have been collected from Mexico, with the only successful agent from Brazil being *U. girardi* (Table 3).

The successful establishment rate of control agents has ranged from zero with *Alagoasa parana, Autoplusia illustrata* and *Teleonemia elata* to over 95% with *U. girardi*, *Epinotia lantana* and *T. scrupulosa,* whilst their effectiveness has ranged from established but having no discernible control through minor and partial to significant control (Julien 1992) (Table 3).

Studies of the effect of introduced insects on lantana have been limited to the four species most widely established, *Ophiomyia lantanae*, *Teleonemia scrupulosa*, *Uroplata girardi* and *Octotoma scabripennis.*

The agromyzid fly *Ophiomyia lantanae* was one of the original insects found on lantana by Koebele and is now established in nine of the 11 countries in which it has been released. It oviposits in green

Table 3. Insect species released as biological control agents of *Lantana camara,* their establishment and effectiveness.

Species	Country of origin of agent	Lantana host[A]	No. of countries		Effectiveness rating[B]
			released	established	
Root Feeders					
Coleoptera					
Parevander xanthomelas	Mexico	C	1	0	–
Stem Feeders					
Coleoptera					
Aerenicopsis championi	Mexico	C,H,U	1	0	–
Plagiohammus spinipennis	Mexico	H	5*	2*	1–3
Lepidoptera					
Hepialus sp.	Mexico	–	1	0	–
Diptera					
Eutreta xanthochaeta	Mexico	C,U	3*	1	1
Leaf Feeders					
Hemiptera					
Leptobyrsa decora	Peru and Colombia	–	9*	2*	1–2
Teleonemia elata	Brazil	T,G	5*	0	–
Teleonemia harleyi	Trinidad	–	1*	1*	1
Teleonemia prolixa	Brazil	T,G	1*	0	–
Teleonemia scrupulosa	Mexico	C,H,U,Uc	21*	20*	1–3
Coleoptera					
Alagoasa parana	Brazil	T,G	2*	0	–
Charidotis pygmaea	Brazil	T	1*	0	–
Octotoma championi	Costa Rica	C,H,U	3*	1*	1
Octotoma plicatula	Mexico	–	1	0	1–4
Octotoma scabripennis	Mexico	C,U	9*	6*	2
Uroplata fulvopustulata	Mexico, Costa Rica, Panama	C,U	3*	1*	–
Uroplata girardi	Brazil	T,G	21*	19*	1–4
Uroplata lantanae	Brazil	T	2*	0	–
Lepidoptera					
Autoplusia illustrata	Colombia	2*	0	–	
Cremastobombycia lantanella	Mexico	C,H,U,Uc	1	1	2
Diastema tigris	Panama, Trinidad	U	10*	1	1
Ectaga garcia	Brazil	T	18	0	–
Hypena strigata	Kenya, Zimbabwe	–	6*	6*	1–2
Neogalea esula	California	C,U,Uc	4*	2*	1–2
Pseudopyrausta acutangulalis	Mexico	C,U,Uc	3	0	–
Salbia haemorrhoidalis	Florida, USA, Cuba	C	12*	7*	1–3
Diptera					
Calcomyza lantanae	Trinidad	C	2*	2*	2–3
Flower Feeders					
Lepidoptera					
Epinotia lantana	Mexico	C,H	4*	4*	1–3
Lantanophaga pusillidactyla	Mexico	C,H	4	3*	1–3
Thecla bazochii	Mexico	C,H	3*	2	1
Thecla sp.	Mexico	C	2	1	1
Seed/Fruit Feeders					
Coleoptera					
Apion sp. *A*	Mexico	T	1	0	–
Apion sp. *B*	Mexico	–	1	0	–
Diptera					
Ophiomyia lantanae	Mexico	–	11*	9*	–

[A] Insects found on the following species: C=*L. camara*, H=*L. hirsuta*, U=*L. urticifolia*, Uc=*L. urticoides*, T=*L. tiliaefolia*, G=*L. glutinosa*.

[B] Effectiveness rating: 1 = established, 2 = minor control, 3 = partial control, 4 = significant control.

* Released and / or established in Australia.

fruits, where larvae feed on the fleshy pulp and may enter the seed and feed on the embryo (Thakur *et al.* 1992). Larvae pupate either in the fruit or peduncle (Cilliers and Neser 1991), and both Wilson (1960) and Thakur *et al.* (1992) have shown that they make the berries less attractive to birds, slowing down the rate of spread of lantana. Indian studies by Thakur *et al.* (1992) showed that the insect has little effect on germination, which in both infested and non infested seed was less that 15%. In South Africa seed germination at some sites was significantly reduced by the fly, contributing to lantana control (Graaff 1987).

The tingid bug *T. scrupulosa* is established in 20 countries. It oviposits in stems, petioles and peduncles, most often where adults have flowers on which to feed (Currie and Fyfe 1939). The nymphs feed in groups (generally on the undersides of leaves) and the adults on leaves, flowers and occasionally young stems. Oviposition and feeding cause chlorosis, distortion and leaf abscission, heavy attack resulting in complete defoliation and systemic dieback of the plant (Harley and Kassulke 1971). The bug prefers low rainfall areas, and populations peak during autumn and early winter before drought and frost defoliate plants, causing insect numbers to fall rapidly. Harley *et al.* (1979) suggest that population levels may be influenced by changes in the physiology of the plant. Randomized exclusion trials by Harley *et al.* (1979) showed that a red flowered form was the preferred host, with 'Common Pink' being the least preferred, whilst in South Africa Cilliers (1987) has noted that *T. scrupulosa* has also shown a preference for certain forms of lantana. Heavy attack by the bug in Queensland helps to reduce the aggressiveness of some forms of lantana, and although it is common throughout lantana areas of South Africa it seldom reaches highly damaging population levels.

U. girardi and *O. scabripennis* are leaf-mining hispine beetles. *O. scabripennis* is established in six countries and *U. girardi* in 19. The eggs are laid singly into the upper surface of leaves and covered with an exudate from the insect's collaterial glands (Harley 1969a). The larvae tunnel into the leaf, feeding on the mesophyll and leaving both upper and lower epidermis undamaged whilst forming feeding galleries radiating from a central chamber before pupating in the leaf. The resultant mines of *O. scabripennis* are much less tortuous that those of *U. girardi*. After emergence the adults feed on the upper leaf surface. The effect of these two beetles on lantana has been studied by Cilliers (1987), who showed that in association with *T. scrupulosa* they destroy 25% of the annual leaf production of lantana in Natal.

O. scabripennis prefers cooler inland areas whereas *U. girardi* does well in hot wet areas. In Queensland these insects can cause defoliation of lantana over the summer–autumn months, markedly reducing its vigour, competitiveness and flowering. This defoliation allows grasses to grow through the lantana plants, which are further damaged if grazed by cattle. A cold climate strain of *U. girardi* has been established in inland areas of South Africa (Cilliers and Neser 1991), and after its release in the Solomon Islands in 1993 *U. girardi* successfully controlled the 'Hawaiian Pink' form on an island in the Russell Islands group (Anon. 1993b).

While *T. scrupulosa, U. girardi* and *O. scabripennis* have been effective in attacking leaves and tips of lantana, none of the agents released to date have successfully attacked the roots. The root boring cerambycid beetle *Parevander xanthomelas* was released in Hawaii in small numbers in 1902 but failed to establish. This beetle has now been approved for introduction into Australia for host specificity testing in quarantine.

The stem boring cerambycid beetle *Aerenicopsis championi* was described by Mann (1954) as an insect of great potential, but failed to establish in Hawaii despite large numbers being released (Fullaway 1958). It has been host tested in Australia and is expected to be released in Queensland in 1994. Eggs are laid in leaf petioles and the larvae on hatching feed down through the petioles into the tips and then down the stems for distances of up to 1.2 m. As the larvae feed, the stems are hollowed out and killed.

Another stem boring cerambycid *Plagiohammus spinipennis* has been released in five countries, but has only become established in Hawaii where it is exerting some control in high rainfall areas. The eggs are inserted into the stems usually within 600 mm of the plant base. The larvae girdle the stems and tunnel into the xylem tissue. Multiple infestations of stems result in them being killed or weakened so severely that they are readily broken, reducing tall plants to mutilated stumps (Harley 1969b). Although established in low numbers at one site in Australia (Taylor 1989), *P. spinipennis* has failed due to the plant forming callus tissue at the oviposition site, destroying the eggs and neonate larvae before they enter the xylem tissue (Willson 1974). It appears that the success of *P. spinipennis* in Hawaii was due to the condition of the stems that were very soft and spongy near to the ground (K.L.S. Harley personal communication). A similar condition prevailed in Mexico where Koebele described the lantana stems as usually very soft and knotty near the ground as a result of a fungal disease (Perkins and Swezey 1924).

A stem sap sucking membracid bug, *Aconophora compressa*, is currently undergoing host specificity tests in Queensland and is expected to be released within 12 months. This insect causes considerable dieback of lantana stems in Mexico (Willson and Palmer 1992).

Other insect species under investigation by Queensland Department of Lands are the leaf-mining gracillarid moth *Cremastobombycia lantanella* and the leaf-sucking mirid bug *Adfalconia intermedia*.

Four fungal pathogens have been found in Brazil. These are the rusts *Prospodium tuberculatum* and *Puccinia lantanae*, a hyphomycete *Mycovellosiella lantanae* and *Ceratobasidium* sp., a web blight. Field assessments indicate that *P. tuberculatum* and *M. lantanae* are both damaging and host specific in cool climates. *P. lantanae* and *Ceratobasidium* sp. are similarly damaging in tropical areas. Laboratory and greenhouse studies have commenced to determine their biology and immediate host range (Tomley and Evans 1992).

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