Review

The Biology of Australian Weeds 20. Mimosa pigra L.

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Name

The genus Mimosa (Mimosaceae) contains 400-450 species which are mostly native to central and south America (Lewis and Elias 1981). Mimosa pigra was first identified by Linnaeus (1759a), who also named a separate species, M. asperata, on the basis of its different leaf morphology. M. pigra was described as having an erect prickle between the pinnae and M. asperata as having prickles in opposite pairs between the pinnae (Linnaeus 1759b). Both leaf forms can occur on the same plant, however. Bentham (1875), in revising the tribe Mimoseae, therefore united the two species under M. asperata. The plant was subsequently renamed M. pigra.

The common name in Australia is mimosa or giant sensitive plant. Note however that mimosa bush is a common name for Acacia famesiana in Queensland. Furthermore, M. invisa, a weed in Queensland but not elsewhere in Australia, is there known as giant sensitive plant, whilst M. pigra is called giant sensitive tree (Anon. 1984). The latter name seems hard to justify. We suggest that the following nomenclature is appropriate: common sensitive plant (M. pudica); creeping sensitive plant (M. invisa; after B. Napompeth, pers. comm.); and giant sensitive plant (M. pigra).

Description and Account of Variation

Description

The following description of Mimosa pigra var. pigra (Figure 1) was compiled from Hutchinson and Dalziel (1958), Brenan (1959), and Lonsdale and Segura (1987).

M. pigra is a leguminous shrub, up to 6 m tall in moist, open sites in the tropics. Stems armed with broad-based prickles up to 7 mm long. Leaves bipinnate and sensitive to touch, through movements of the pinnules, pinna rhachises and petiole. Petiole 0.3 - 1.5 cm long; rhachis 3.5 - 12 (- 18) cm long, with a straight, more or less erect or forwardpointing slender prickle at the junction of each of the 6 - 14 (- 16) pairs of pinnae, and sometimes with stouter spreading or deflexed prickles between the pairs. Leaflets 20 - 42 pairs per pinna, linear-oblong, 3 - 8 (- 12.5) mm long, 0.5 - 1.25 (- 2) mm wide; venation nearly parallel with midrib, margins often setulose. Flowers mauve or pink, borne in tight, subglobose pedunculate heads 1 cm in diameter, each head containing c. 100 flowers, produced 1 - 2 (- 3) together in upper axils. Calyx minute, laciniate, 0.75 - 1 mm long. Corolla about 2.25 - 3 mm long. Stamens 8. Pods in clusters of about 7 (1 - 27), brown, densely bristly all over, 3 - 8 cm long, 0.9 - 1.4 cm wide, breaking transversely into about 21 (14 - 26) partially dehiscent segments, each containing a seed, the

pod sutures persisting as an empty frame. Ripe seeds light brown to brown or olive green, oblong, 2.2 -2.6 mm wide and 4 - 6 mm long, weighing 0.011 g (range 0.006 -0.017 g). The whole process from flower bud to ripe seed takes about 5 weeks. The basic chromosome number in the genus is n=13(Goldblatt 1981), but the number for M. pigra is not known.

Distinguishing characters

In Australia, the plant may be confused with Leucaena leucocephala, Aeschynomene spp., Sesbania spp. and juveniles of Acacia pachyphloia, but is distinguished readily from all of them by its sensitive leaves. Neptunia dimorphantha, a native sensitive plant, resembles a seedling of M. pigra, but lacks the prominent prickles on the stem and leaf rhachis. M. pudica may be distinguished from M. pigra by its leaves, which have only 1 - 2 pairs of pinnae, in contrast to the 6 - 14 pairs on M. pigra leaves.

Intraspecific variation

There are two varieties, var. pigra and var. berlandieri Gray, of which only the former has spread around the world. They differ slightly in pod morphology, var. berlandieri having little pubescence on the pods (Turner 1959), whereas those of var. pigra are densely pubescent. In Australia, M. pigra seems invariant, on the basis of isozyme analysis (J.J. Burdon, pers. comm.), so it seems that all Australian plants may have come from a single introduction.

History

M. pigra has apparently been misidentified, firstly as M. rubricaulis by Holtze (1892) and later as M. acanthocarpa by Goode (1926), as discussed by Miller and Lonsdale (1987). It was probably introduced to Australia at the Darwin Botanic Gardens in the 20 years prior to 1891, either accidentally in seed samples, or intentionally, as a curiosity, because of its sensitive leaves (Miller and Lonsdale 1987). It lingered in the Darwin region causing an occasional nuisance (Swarbrick 1983, Miller and Lonsdale 1987) and was noticed upstream from Adelaide River Township (Figure 2) in 1952. By 1968, it had spread downstream on the Adelaide River to the Marrakai Crossing, and, by 1975, had reached the Arnhem Highway bridge (Miller et al. 1981, Figure 2). The population subsequently increased dramatically until, by 1981, much of the Adelaide River floodplain was covered by practically monospecific stands (Figure 3).

Geographical Distribution

Australia

At present, the distribution of M. pigra stretches in an arc across 450 km of the Northern Territory, from the Moyle River in

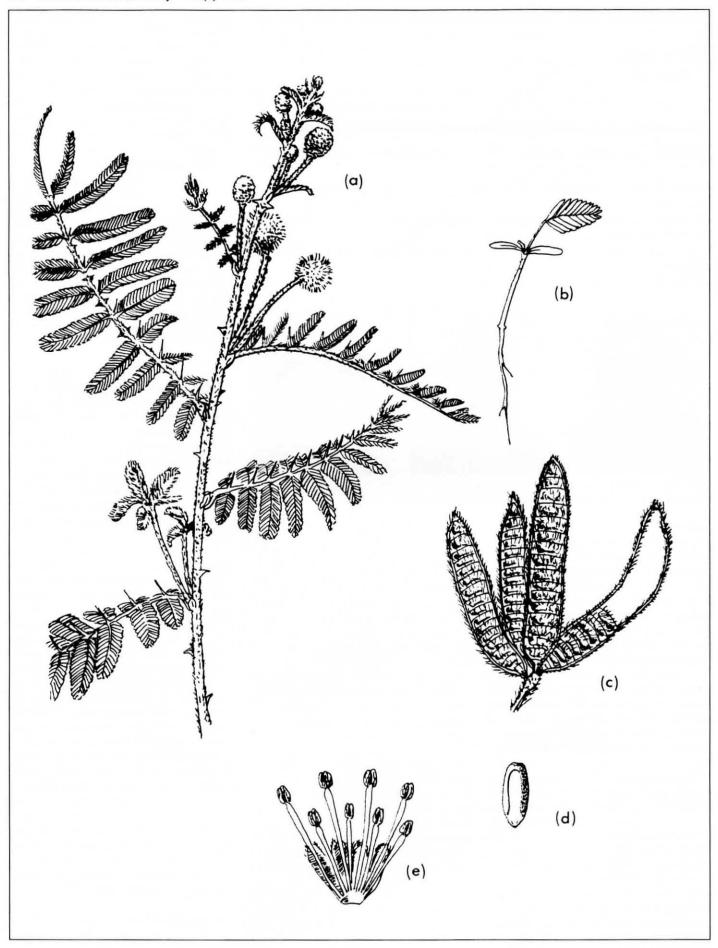


Figure 1. *Mimosa pigra* (a) part of flowering stem, (b) seedling, (c) pods, (d) seed, and (e) flower, opened out (a, d and e after Brenan 1959).

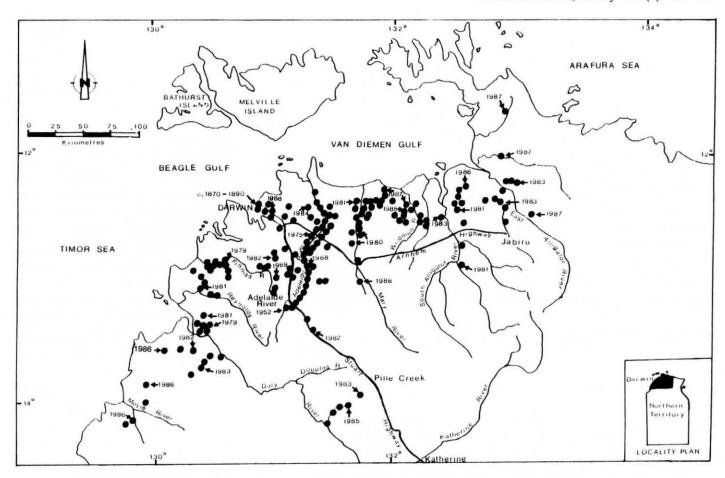


Figure 2. Distribution of Mimosa pigra in the Northern Territory in April 1988, showing the year of first report at selected locations, from Miller (1988b).

the west to Arnhemland in the east (Pitt and Miller 1988, Figure 2, Figure 4). The major infestation is still that on the Adelaide River, but there are large areas in the Daly, Finniss, Mary and East Alligator River systems.

Outside Australia

M. pigra originated in tropical America and is now widespread throughout the tropics (Figure 5). Bentham (1875) noted that it was found widely by early explorers in tropical Africa and the Mascarene islands, yet was unlikely to represent a relict of some primitive flora as it had not diverged into specifically African varieties, and was present in precisely the form that was most common in America. He concluded that the plant must have been carried over to Africa independently of humans. We know that the seeds are capable of floating in their pod segments, but it seems unlikely that they could have travelled across the Atlantic in this way since they are supported not by natural buoyancy but by surface tension. It is possible that the seeds were dispersed by birds, but they are not notably adapted to this and there is no evidence that birds consume the seeds in the native range. The early widespread distribution in Africa remains an enigma.

Questions also surround its distribution in the Indo-Pacific region. Ridley (1930) described the movement of M. pudica around the Pacific as early as the 16th century by Jesuit missionaries interested in its sensitivity, via their settlements in Manila, and the same maybe be true of M. pigra, since there is a record of the plant in the Philippines (Robert 1982). Given that two early records for M. pigra come from botanic gardens in Australia (Miller and Lonsdale 1987) and Indonesia (K.L.S. Harley pers. comm.) it is also possible that botanists were partly responsible for its spread.

The earliest records for various countries outside its native range are: Egypt 1829, India 1867 or before, New Guinea 1960, Singapore 1965, and Sumatra 1975 (C.R. Dunlop, pers. comm.); Thailand 1947 (Wara-Aswapati 1983); Java 1844 (Hasskarl 1844); Uganda 1862, Tanzania 1929, and Kenya 1945 (Brenan 1959); Nigeria 1822, Senegal 1824, Sierra Leone 1891, French Guinea c. 1898, and Ghana c. 1925 (Hutchinson and Dalziel 1958).

Habitat

Climatic Requirements

M. pigra favours a wet-dry tropical climate (Figure 6). Except around dams and watercourses, M. pigra would probably not be a major problem in regions with less than 750 mm annual rainfall (Miller 1983). Because of plant competition, it seems unlikely to succeed in tropical rain forest areas which generally are found where rainfall is greater

than about 2250 mm, although clear-felling would probably allow the plant to flourish. The best indication as to how far M. pigra may spread into the subtropics comes from its north American range. The plant occurs in Florida as far north as Gainesville (Latitude 29°; W.T. Haller, pers. comm. to K.L.S. Harley), but is not as tall or aggressive there as it is elsewhere in its introduced range. This is perhaps because the climate in the region, though warm enough to allow it to persist, has cool winters, with freezing temperatures on average once in every four years (W.T. Haller, pers. comm. to K.L.S. Harley). Miller (1983) has made the conservative prediction that M. pigra would be a problem in tropical Australia in areas with >750 mm annual rainfall, which gives the potential distribution shown in Figure 4.

Substratum

M. pigra does not appear to grow preferentially in any one soil type, but is most commonly found in moist situations such as floodplains and river banks in soils ranging from heavy black cracking clays through sandy clays to coarse siliceous river sand. Seed production (Lonsdale et al. 1988) and the plant's life expectancy (see "Population Dynamics" below) are greater on the black cracking clays of the lower Adelaide River floodplain than on the sandy clays of the upper Adelaide River. Seed longevity, by contrast, was found to be greater on sandy clays (Lonsdale *et al.* 1988), although this now appears to vary between sites (W.M. Lonsdale, unpublished results).

Communities

M. pigra in northern Australia invades sedgeland and grassland communities on open floodplains, particularly in areas where feral buffalo (Bubalus bubalis) or fires have removed the vegetation. It forms dense, practically monospecific tall shrubland in which the ground flora is sparse to non-existent. Similarly, it invades the paperbark (Melaleuca) swamp forests fringing the floodplains, where it forms a dense understorey, and shades out native tree seedlings (Braithwaite et al. 1989). In addition, it can invade billabongs, leaving only small remnants of open water at the centre of the billabong.

Growth and Development

Morphology

Mature plants have a large number of branches growing from the base, with a skirt of fibrous adventitious roots forming in seasonally inundated sites. A large central taproot penetrates 1 - 2 m into the soil, together with a lateral root system that extends up to 3.5 m from the stem (Robert, 1982) at a depth of about 5 cm (J.L. Pitt and W.M. Lonsdale, unpublished results).

Plant size is negatively dependent on density (Lonsdale and Segura 1987). This relationship differs between Australia and the native range, however. At a given density, plants tend to be smaller in the native range than in Australia, presumably a result of the activities of natural enemies (see later; Lonsdale and Segura 1987).

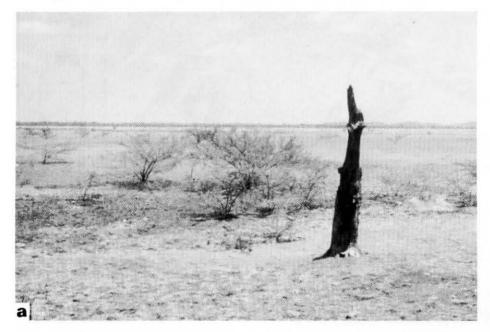




Figure 3. Transformation of the floodplains of the Adelaide River by *Mimosa pigra* between (a) 1978 and (b) 1981. Note the tree stump in both pictures.

The cotyledons are small and foliar. The first leaf is pinnate and sensitive, with subsequent leaves being bipinnate. Prickles on stems and leaves (from about the six-leaf stage) are presumably to repel browsers, but are not effective for all species e.g. elephants in Nigeria (Geerling 1973).

Perennation

In seasonally moist sites, mature plants survive the dry season, which may last from May to December in the Northern Territory savanna zone, by steadily losing leaves (Lonsdale 1988) until, by around August, 40 - 50% have fallen (Miller 1988b). In permanently moist sites such as river banks, or when watered, growth and flowering can continue more or less all year round (Wanichanantakul and Chinawong 1979), although the proportion of buds reaching anthesis may be very low during the dry season (Wara-Aswapati 1983). Indeed, Lonsdale (1988) found that, over several seasons, the proportion of all initiated flower buds that produced seeds was in the range 2.1 - 4.5%.

A large proportion of the *M. pigra* population, however, lies dormant in the soil as the seed bank. Mature plants in dense stands are at densities in the order of 1 - 3 m⁻², whilst seed densities in the soil at some sites in northern Australia can average over 12 000 m⁻² (Figure 7; Lonsdale *et al.* 1988).

Physiological data

Transpiration rates have been measured by the cut shoot method at Chiangmai in Thailand (Niyomyati and Wara-Aswapati 1985). The average transpiration rate for 1 m long shoots was 131 g d-1, almost all of which was through the leaves. The rate of loss of water varied seasonally and ranged from 240 g d-1 (per g fresh weight of leaf tissue) in November (early in the dry season) to 480 g d-1 in April (late in the dry season). The values are inversely related to the relative humidity of those months.

Growth rates of seedlings measured over five weeks of growth in a shade house, at a midday photon flux density of about 200 μmol m⁻² s⁻¹, were around 0.8 g g⁻¹ week⁻¹ (Lonsdale and Abrecht, 1989). In the field, there is a strong seasonality in growth rate, as well as a decline with age (Miller 1988b; Figure 8). Growth rates of seedlings reached a maximum value of 2.4 g g-1 month-1 (0.6 g g-1 week-1), whilst plants in their second wet season averaged 0.6 g g-1 month (0.15 g g-1 week-1), and negative relative growth rates occurred in the dry season (Miller 1988b), as large quantities of biomass (7.6 t ha-1) are lost as litter (Lonsdale 1988). Rates of height growth have been measured in a shade house at up to 1.08 cm d-1 (recalculated from Wanichanantakul and Chinawong 1979) in the first 90 d or so after germination. In the field, Miller (1988b) measured maximum rates of height growth at 40 cm month-1 (1.33

cm day-1) in seedlings and at 33 cm month-1 (1.1 cm day-1) in plants more than 12 months

The compound leaf of many species in the genus Mimosa is sensitive to a variety of stimuli: electrical, mechanical, chemical, thermal, wounding and light (Simons 1981). Motor organs termed pulvini perform these movements; they are bulbous regions at the base of the petioles, pinna rhachises and pinnules (in the case of M. pigra), which contain motor cells with numerous vacuoles and loose fibrillar walls. Extensor cells take up potassium ions and swell during leaf opening, while flexor cells take up potassium during closure, the movement of potassium ions into each cell type being driven by an efflux of hydrogen ions (Hart 1988, p. 85). Thus, both closure and opening are active events. The mechanism by which touch induces closure (seismonasty) is not completely understood (Simons 1981), although it appears that touch elicits action potentials that are rapidly conducted to the pulvini. Sleep movements (nyctinasty) also occur in this species and are driven by an endogenous rhythm whose timing is regularly reset by phytochrome (Hart 1988, p. 85).

Phenology

With the exception of plants growing in permanently moist conditions, the wet season, generally between December and April in northern Australia, is the main period of growth. Depending on the rather unpredictable rainfall (Taylor and Tulloch 1985), new leafy shoots appear in December and a dense canopy develops by January. The main flowering period is from February to April, but flower production may begin as early as December, or as late as February, and continues for as long as water is available (Lonsdale 1988). Maturation of flower buds takes 7 - 9 days from bud formation. Production of mature seed pods takes a further 25 or more days (Wanichanantakul and Chinawong 1979), the first seeds falling generally by no later than March, and the peak seed fall occurring between April and June (Lonsdale 1988).

Mycorrhizae and nodules

Mycorrhizae have not been found in M. pigra. Associations do however exist with only a narrow range of strains of Rhizobium (Date and Halliday 1980); for example, the plant was unable to form nodules with strains from Leucaena leucocephala and Sesbania erubescens (R.A. Date pers. comm.). Large pink root nodules have been detected on M. pigra in Thailand (Lumyong and Petpichittakul 1982) and in Mexico, where the plant is native (W.M. Lonsdale, pers. obs.). Small crotalarioid nodules occur on some plants in Australia and are an effective nitrogen source for M. pigra (R. A. Date, pers. comm.). It is not known whether these

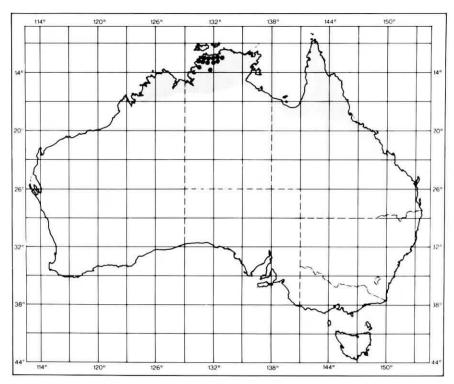


Figure 4. Distribution of Mimosa pigra in Australia, based on Miller (1988b), with the potential distribution (stippled) suggested by Miller (1983).

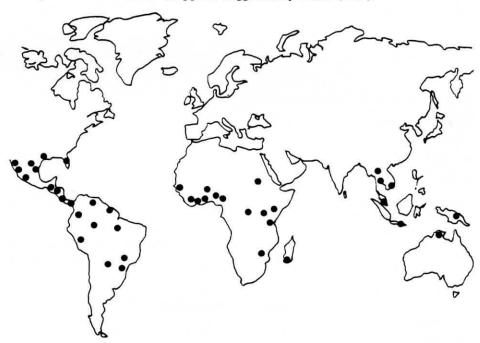


Figure 5. Global distribution of Mimosa pigra.

are native or introduced strains of Rhizobium. However, their rarity and small size suggests they may not be a significant source of nitrogen for M. pigra populations as a whole.

Reproduction

Floral biology

Under ideal conditions, plants can begin flowering 6 - 8 months after germination. In its native range, the plant is bee-pollinated

(Janzen 1983), and occasional visits by native bees have been observed in northern Australia. We are not yet certain that the flowers are self-compatible, but given the prolific seed production in isolated plants 10 km or more from the nearest conspecific stand, it seems likely that they are. Indeed, the apparent shortage of pollen vectors suggests that the majority of seed production is by autogamy. It is possible that wind pollination is occurring, given that the smallest pollen units in the angiosperms, at 6 μ , are found in

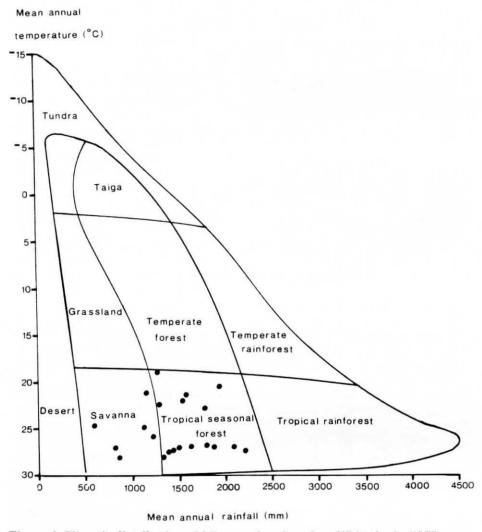


Figure 6. Climatic distribution of *Mimosa pigra*, based on Whittaker's (1975) climate classification.

this genus (Elias 1981). The critical experiment of bagging flowers has proved impossible to do so far, as the presence of bags induces abscission of flower buds.

A form of vivipary has been observed under wet conditions, seeds will germinate in the pod while still on the branch (Miller 1988b).

Seed Production and Dispersal

In northern Australia, the average number of seeds per pod is 21.0, with 7.1 pods per infructescence (Lonsdale and Segura 1987). Because most M. pigra infestations in the region are monospecific stands with a closed canopy and varying densities of plants, it is not very instructive to speak of seed production per plant. Rather, it is preferable to speak in terms of production per unit area of canopy. This has been measured at 9103 m⁻² per year in a typical mature stand on black cracking clay in Australia (Lonsdale 1988), and proved invariant over two years and along a gradient of soil moisture (Lonsdale 1988) and stand density. As a rule of thumb, taking a typical stand density to be about 1 m⁻² (Lonsdale and Segura 1987), this estimate would give a typical annual production of about 9000 seeds per plant. Growing individually in a shade house, plants can produce seeds at a mean monthly rate of 8000 seeds per plant (Wanichanantakul and Chinawong 1979).

The seed pods are covered with bristles that facilitate floating by surface tension and thus the rapid spread of the weed through river systems.

Physiology of seeds and germination

M. pigra is hard-seeded - that is, moisture leaves the new seed gradually, probably through the hilum, which acts as a one-way valve so that the moisture content of the seed eventually equilibrates with the lowest humidity it encounters (cf. Harper, 1977, p. 77). Once the process of desiccation is completed, germination depends on breaking down the physical barrier to moisture formed by the impermeable seed coat. There is no requirement for freezing, nor any sensitivity to light, for germination to occur.

Seeds can remain viable for more than five years in the laboratory (Wara-Aswapati 1983). Under field conditions in Australia, loss of viable seeds from the seed bank is broadly exponential in pattern (Lonsdale et

al. 1988). The half-life varies from 9.4 weeks at the surface of black cracking clay to 99.0 weeks at 10 cm depth in light sandy clay. Nevertheless, because there is such a huge population of seeds in the soil at any one time, and because the rate of loss is much slower for the small proportion of seeds that are deep in the soil, it is likely that control measures for new seedlings would have to be maintained for many years after the eradication of mature plants (Lonsdale et al. 1988). Indeed, observations suggest that seeds can last for at least 23 years in sandy soils (S.E. Pickering, pers. comm.).

Losses from the seed bank have been found experimentally to result from the dramatic diurnal heating and cooling of soils in the region, with daily extremes from 67.0°C down to 19.9°C in September (W.M. Lonsdale, unpublished results). This loss is probably not a direct killing effect of high temperatures, since temperatures of 70°C in the laboratory had no effect on viability (W.M. Lonsdale, unpublished results). Rather, it appears that the fluctuations break the seed coat and allow the seed to imbibe. Indeed, Dillon and Forcella (1985) found that temperature fluctuations of just 20°C enhanced germination in the laboratory.

Seeds have a U-shaped pleurogram or fracture, clearly visible in dried seeds, which is of uncertain significance. Germination is phaneroepigeal with foliar cotyledons (cf. Duke and Polhill 1981). Percentage germination is highest in seeds sown at 1 cm in the soil, and declines to zero as sowing depth increases to 10 cm (Shibayama et al. 1983). The vast majority of seeds are within 10 cm of the surface (Lonsdale et al. 1988).

Large numbers of seeds (c. 1500 m⁻²; Lonsdale and Abrecht, in press) germinate beneath the canopy upon release, as they land on the moist bare soil left by the receding floodwaters in May and June. Their survival during the dry season is poor (Lonsdale and Abrecht, in press), depending largely on the availability of soil moisture (Figure. 9). Additional germination occurs at the start of the wet season, and a flush of germination often follows a fire (Shibayama and Pornsuksawang 1983).

Vegetative reproduction

M. pigra does not naturally reproduce vegetatively, although reproduction from cut stems, left on the ground, has been observed in Mexico (J.D. Gillett, pers. comm.).

Hybrids

There are no known hybrids of M. pigra.

Population Dynamics

The rate of population increase has been measured from aerial photographs of a black soil floodplain of the Adelaide River, and, assuming constant density, one can estimate a value for r of 0.64 per year (W.M. Lonsdale, unpublished results). At a similar floodplain site near Oenpelli Arnhemland, an infestation which covered about 200 ha in 1984 had expanded to about 5500 ha of dense stand by 1989, thereby giving an estimate of r at 0.66 per year. If one includes the 2000 ha of scattered plants also in the area as being equivalent to 500 ha of dense stand, the estimate of r becomes 0.68 per year. As a rule of thumb, these estimates equate to a doubling time of about one year.

The longevity of plants varies on different soil types. For plants of height >20 cm, tagged in August 1982, the half-life was 28 months on black cracking clay, whilst on lighter sandy clay it was 22 months. For a larger sample of tagged plants, ranging in height from 20 cm to over 5 m, the mean subsequent duration was 21.4 months on the heavier soil (n = 147), and significantly less at 13.3 months on the lighter soil (n = 160; P =0.007; W.M. Lonsdale, unpublished results). This is presumably a consequence of the greater moisture-holding capacity of the heavier soil. Note that these figures are not intended to indicate the maximum lifespan, biased as they are by the high death rate amongst smaller plants. Miller (1988b), for example, found deaths of plants reaching maturity to occur from about five years of age. Furthermore, plants in mature stands are constantly dying and being replaced by seedling recruitment, and we know of stands which have persisted in this way for at least 15 years.

As seedlings, the plant is susceptible to competition from grasses (Miller 1988b), and the success of M. pigra in Australia was probably facilitated by the overgrazing of floodplains by massive herds of feral water buffalo in the mid to late 1970s. Once M. pigra has formed a typical dense stand (Figure 3b), the photosynthetically active photon flux density at ground level is generally as low as about 5% of the incident value in the growing season, falling in some places down to 1% (W.M. Lonsdale, unpublished results). Herbaceous vegetation and tree seedlings, consequently, cannot persist. The plant thus forms monospecific thickets many hectares across.

Importance

Detrimental

The dense thickets, by competing with pastures, hindering mustering, and preventing access, pose a threat to pastoral industries, particularly the buffalo industry, in Australia (Miller et al. 1981). They also restrict access to waterways for fishermen and others.

The plant also poses an enormous problem for conservation. In Australia, a largely intact natural landscape is being completely altered (Braithwaite et al. 1989). Some 450 km2 of floodplain and swamp forest have

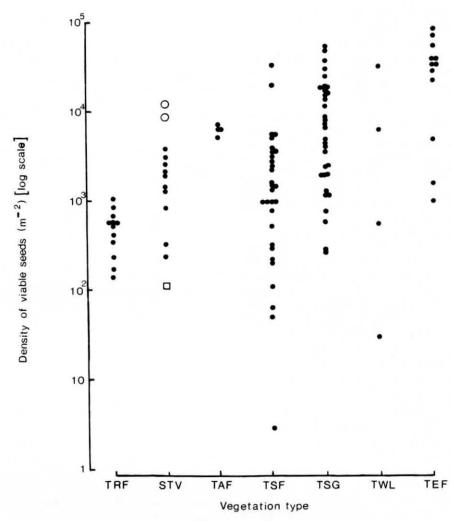


Figure 7. Seed bank sizes in some of the world's temperate and tropical vegetation types, from various sources, including figures for alien (○) and native (□) populations of Mimosa pigra The vegetation types are: TRF, tropical rain forest; STV, secondary tropical vegetation; TAF, tropical agricultural fields; TSF, temperate and subtropical forests; TSG, temperate and subtropical grassland and shrubland; TWL, temperate wetlands; and TEF, temperate agricultural fields. (From Lonsdale et al. 1988).

been covered by dense monospecific stands of M. pigra which have little understorey except for seedlings and suckers of M. pigra. Braithwaite et al. (1989) found that M. pigra thickets had fewer birds and lizards, less herbaceous vegetation, and fewer tree seedlings than the native vegetation. Furthermore, it is also probable that the magpie goose (Anseranas semipalmata), which once had a range extending as far south as New South Wales, but now depends on the wetlands of northern Australia for its survival, is endangered by the spread of this weed, since it needs dense stands of native sedges for nesting and food. Conversely, the rare marsupial mouse Sminthopsis virginiae has become more abundant as a result of M. pigra. It probably shelters from predators in the dense thickets, venturing out into native vegetation at night to feed (Braithwaite and Lonsdale 1987).

Lastly, Kakadu National Park in northern Australia had two hundred and thirty thousand visitors in 1988. Many of these visitors

would have come to see the abundant birdlife of the wetlands, which cover about 20% of the area of the park. These wetlands, and, by extension, the economically important tourist industry, are gravely threatened by M. pigra.

Mimosine, an amino acid toxic to higher animals, has been isolated from M. pigra at levels of about 0.2% of leaf dry weight (B. Lowry, pers. comm.). The standard assay for mimosine may fail to detect it at this concentration (R. Megarrity, pers. comm.), and this could explain the absence of mimosine reported by Vearasilp et al. (1981). It is doubtful whether the foliage would be toxic at this level of mimosine; for example, Niemsup and Siri (1983) in Thailand reported that buffalo fed on rice straw plus M. pigra foliage lost less weight than those fed on rice straw only, the usual cultural practice.

In Thailand, M. pigra is considered to be a serious weed, particularly in irrigation systems. It is also a safety hazard along roads and interferes with access to electric power

lines (Robert 1982, Napompeth 1983, Harley et al. 1985, Thamasara 1985). Robert (1982) argued that, in Thailand, the greatest costs of M. pigra were sediment accumulation in irrigation systems and reservoirs, and that, for controlling the weed with herbicides, the benefit-cost ratio using a 15% discount rate would be 433 for irrigation canals and 32 for reservoirs. Direct agricultural losses to M. pigra were discounted in Robert's analysis. However, infestations grow in fallow rice paddies, making reclamation more expensive, 75% of the cost of preparation of infested land being for the control of M. pigra (B. Napompeth, pers. comm.). Niyomyati and Wara-Aswapati (1985) attempted to calculate the loss of water caused for the agriculture of the Chiangmai Valley in Thailand by transpiration from the large infestations of M. pigra in the region. However, such calculations should be approached with caution: most of the M. pigra populations in Thailand grow in standing water, and it may be that the reduction in evaporation from the shade cast by the weed (which was not taken into account by the authors), would more than counterbalance any loss through transpiration.

Beneficial

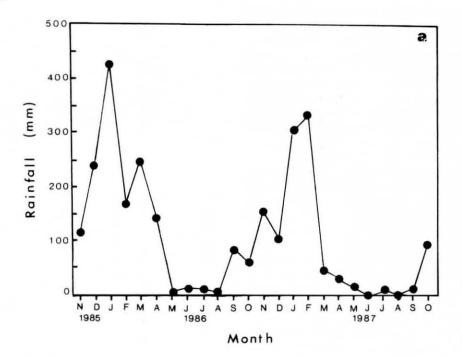
M. pigra was introduced to Thailand in 1947 (Wara-Aswapati 1983) as a green manure and cover crop. It was also believed that, being prickly, the plant would restrict access by livestock to ditch banks and the edges of reservoirs, and thus control erosion (Napompeth 1983). Although now generally regarded in Thailand as a very serious weed, it is used as a source of firewood and bean poles (Robert 1982). Farmers in the Chiangmai region have developed a machete with a notch cut in the end which allows them to push over the prickly stems (Kittipong 1987).

The foliage can be used as a substitute for Leucaena leucocephala in animal feed, having a crude protein content of 20 - 23% (Vearasilp, Phuagphong and Ruengpaibul 1981, Vearasilp, Potikanond and Rajja-Apai 1981).

Samples of fibreboard have been made from the wood in Thailand but were found to absorb an unacceptable amount of moisture for commercial use. Additional chemical treatment to prevent this is too expensive (Robert 1982).

Legislation

In Australia, M. pigra has been declared a "noxious weed" or given similar status under various weed or quarantine Acts. In 1966 it was declared as a Class A noxious weed (to be eradicated) throughout the Northern Territory under the Noxious Weeds Ordinance (now an Act). In 1978 it was changed from a Class A to a Class B noxious weed (spread to be controlled) within 100 m of the banks of the Adelaide and Margaret Rivers,



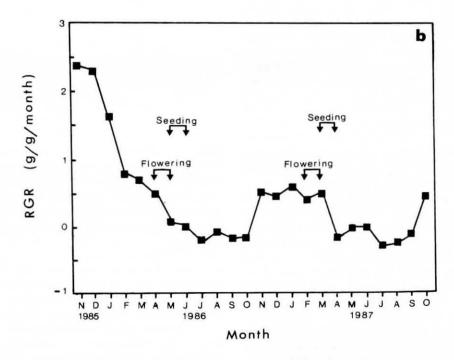


Figure 8. Changes in the relative growth rate of *Mimosa pigra* with season and age. (a) Monthly rainfall at Adelaide River Post Office, and (b) relative growth rates measured over the same periods, on the upper Adelaide River (from Miller 1988b).

but remained as a Class A weed elsewhere (Miller et al. 1981). Currently it is declared as a Class A noxious weed in areas south of 14°S latitude (Katherine) and a Class B noxious weed in areas north of 14°S latitude (Miller 1988a). In Western Australia M. pigra was declared in 1979 as a category P1 plant (not to be introduced) north of 26°S latitude, under the Agriculture and Related Resources Protection Act (K.R. Dean, pers. comm.). In Queensland it is declared under

the Rural Lands Protection Act (1985-88) as a P1 and P2 plant, meaning that its introduction into Queensland is prohibited, and, if found, must be destroyed (N.D. Herron, pers. comm.). *M. pigra* is also subject to Australian quarantine control, being a prohibited import under the Commonwealth Quarantine Act (Anon. 1981).

In Thailand *M. pigra* was declared a noxious weed in 1983 under the Plant Quarantine Act (Thamasara 1985), in an attempt to

Table 1.Herbicides tested in the Northern Territory for control of *Mimosa pigra*, 1965-1989.

Herbicide			Method of Application			
	Foliar		Soil	Basal	Cut	Stem
	Ground	Air		bark	stump	injection
Atrazine						
Clopyralid	•	*				
Dicamba		*	•	•		
Dicamba + MCPA		•				
Ethidimuron						
Fluroxypyr	•	*				
Fosamine	•					
Glyphosate	•					•
Hexazinone Liquid	•		•		•	•
Hexazinone granules						
and grid balls			•			
Imazapyr	•					
Karbutilate			•			
Metsulfuron methyl	•					
Picloram + 2,4-D	•					
Picloram + 2,4,5-T				•	*	
2,4,5-T	•					
Tebuthiuron			*			
Triclopyr	•			•	•	*
Triclopyr + picloram	•	*		•		•

prevent its establishment in uninfested or lightly infested areas (Harley et al. 1985). Under this Act eradication of existing infestations is required in all provinces except eight northern provinces which are heavily infested (B. Napompeth, pers. comm.). In Malaysia it was gazetted as a noxious weed under the Dangerous Pests and Noxious Plants (Import and Export) Regulations (Chan et al. 1981). In the United States it was included in the federal noxious weed list in 1984 (White 1984), control being undertaken in central Florida (Westbrooks and Eplee 1987).

Response to Herbicides

Miller et al. (1981) recognized that biological control would be the most cost-effective and long-term control method for M. pigra. However, other control methods are needed to contain the weed while the biological control research is progressing; to eradicate isolated infestations; to enable the use of land for more intensive agricultural development than may be achieved by biological control agents; and to develop large scale control methods in the event of failure of biological control (Miller 1988b).

M. pigra is susceptible to a number of herbicides. They have been tested in central America, Australia, Thailand and Malaysia (Nieto and Agundis 1960, Chaves et al. 1974, Davis and Simagrai 1979, Kittipong 1980, 1983; Miller et al. 1981, 1983; Premasthira and Shibayama 1983, Suwunnamek 1983a, 1983b; Harley et al. 1985, Ng and Abbas 1986, Shibayama and Kittipong 1986, Miller 1988b). The herbicides tested in Australia in the period 1965 to 1989 are listed in Table 1.

From 1965, when control work began in the Northern Territory, the herbicides used were 400 g L^{-1} 2,4,5-T mixed with either water (0.33% v/v) or diesel (2.2% v/v), 800 g L^{-1} 2,4,5-T (1.1% v/v) as a foliar spray or 100 g L^{-1} picloram + 400 g L^{-1} 2,4,5-T mixed with diesel (2.0 - 2.2% v/v) as a foliar or basal bark spray (Miller *et al.* 1981, Miller 1988b). In 1980, glyphosate as a high volume foliar spray at a product dilution of 1% was recommended for use in town areas (Miller and Pickering 1980; Miller *et al.* 1981).

In 1982 soil treatment with spots of the residual herbicide, hexazinone (4 mL of concentrated liquid product per plant or 4 mL m⁻² in a grid pattern) was recommended for application to new, isolated infestations (Miller and Pickering 1983).

Harley et al. (1985) listed the herbicides recommended for use in different situations in Australia and Thailand. In addition to those already mentioned, the recommendations for the Northern Territory included dicamba as the dimethylamine salt (200 g/L) at a product rate of 6 - 7 L ha-1, when aerially applied, or 1% v/v as a spot spray in town areas, pastoral areas, roadsides and water reservoirs; and ethidimuron (700 g kg1) at 0.5% w/v or 7.5 kg ha⁻¹ for residual control of small isolated infestations in pastoral areas. In Thailand, the following herbicides were recommended: bromacil (800 g kg-1) at a product rate of 12.5 kg ha-1, or bromacil + diuron (800 g kg⁻¹) at a rate of 18.75-25 kg ha-1, on dam walls and in non-agricultural areas; fosamine ammonium (480 g L-1) at a rate of 0.75 - 1.25% v/v as a foliar spray beside canals, roadsides and in water reservoirs; dicamba (480 g L-1) at 0.5-1.5% v/v

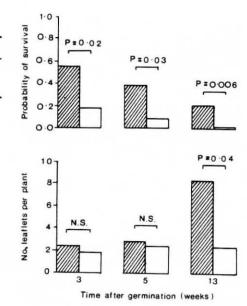


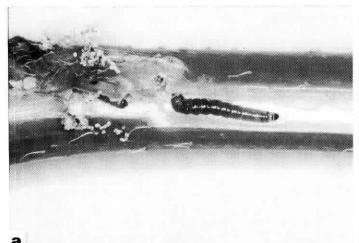
Figure 9. (a) Probabilities of survival and (b) numbers of leaflets per plant for *Mimosa pigra* seedlings in the field during the dry season when water was manipulated (from Lonsdale and Abrecht 1989). Differences between treatments were tested against Student's testatistic. Watered ((()), Unwatered (())).

(spot spray) or 9.4 - 12.5 L ha⁻¹ as a foliar spray along roadsides and canals if the water depth is > 1 m and in non-agricultural areas; and glyphosate at 0.75 - 1.25% v/v (spot spray) or 6.25 - 12.5 L ha⁻¹ as a foliar spray beside canals, roadsides, in reservoirs and in agricultural areas before cropping or after harvest.

The response of M. pigra to dicamba as a foliar applied herbicide varies with the season. Application in the wet season gives a more rapid defoliation and better kill than during the dry season. This is probably because of the effect of environment on both the plant and the herbicide (Miller 1988b). In one experiment mean temperatures during application were similar (32.5°C in the wet season and 32.4°C in the dry season) but there was a large difference in relative humidity (75.5% and 39.4% respectively). The average monthly rainfall and total rainfall over the three months prior to herbicide application was considerably higher in the wet season than in the dry season resulting in large differences in soil moisture content. Dicamba is volatile unless the relative humidity is high (Behrens and Lueschen 1979).

Miller (1988b) concluded that the poorer response of *M. pigra* to dicamba in the dry season was because of greater loss of herbicide by evaporation in the air or after deposition on the leaf surface, poor absorption of the herbicide, a lower receptive leaf area, and reduced rate of transport and deposition of dicamba at its sites of physiological action.

For aerial spraying of herbicides, it is pos-



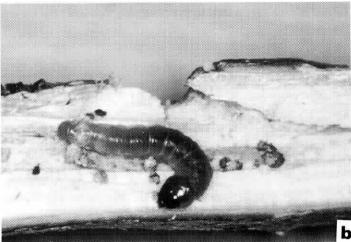


Figure 10. Larvae of the stem boring moths (a) Neurostrota gunniella and (b) Carmenta mimosa, imported from Mexico and released in Australia for biological control of Mimosa pigra.

sible that some of the detrimental effects under hot and dry conditions can be reduced by application in the early morning, when the air is still, when relative humidity is higher and when inversion conditions result in maximum spray deposition (Miller 1988b).

Recent research has evaluated other herbicides suitable for foliar application, basal bark, cut stump, stem injection and soil application. Fluroxypyr (300 g L-1) at 450-600 g a.i. ha-1 and metsulfuron methyl (600 g kg-1) at 35-45 g a.i. ha-1 are recommended as aerially applied foliar sprays (I.L. Miller and J.L. Pitt, unpublished results). However, there is considerable regrowth from seeds if non-residual herbicides are used. The response of M. pigra to the residual, root-absorbed, pelleted herbicide, tebuthiuron, varies between land systems and soil type. Recommended rates of application for the black clays of the seasonally flooded sub-coastal plain are 1.0 to 1.5 kg a.i. ha-1 or 1.5 to 2.0 kg ha-1 for a faster kill and possibly a higher level of long-term control of seedlings (Miller 1988b). Soil-applied karbutilate granules (100 g kg-1) give a 100% kill at 2.5 kg a.i. ha-1 (I.L. Miller and J.L. Pitt, unpublished results).

M. pigra is susceptible to cut stump applications of glyphosate, hexazinone, imazapyr, triclopyr, triclopyr + picloram, triclopyr + picloram + 2,4-D and dicamba (Thamasara et al. 1985., I.L. Miller and J.L. Pitt, unpublished results). Susceptibility is, however, also affected by the season of application. In the dry season, more regrowth occurred, the plant response was slower, and more concentrated solutions of the herbicide were required for effective kills than in the wet season. Dicamba is the most cost-effective herbicide for cut-stump application, a 1.8% solution being effective in the wet season and a 10% solution being effective in the dry season. A 12.5% solution of hexazinone was also highly effective in both seasons.

By basal bark application, M. pigra is susceptible to triclopyr, triclopyr + picloram, dicamba and 2,4,5-T + picloram mixed in diesel. Preliminary work has shown that basal bark applications of herbicides mixed in water are also effective (Harley et al. 1985). Aqueous solutions of triclopyr as the butoxyethanol ester + picloram as the tri-isopropanolamine salt and dicamba diamine killed M. pigra after application to the lower bark in the wet season. Only triclopyr + picloram was effective in the dry season (I.L. Miller and J.L. Pitt, unpublished results).

The response of M. pigra to stem injection of herbicides is slower than by basal bark application, and many of the herbicides tested (Table 1) were ineffective. Only concentrated hexazinone liquid (25% product) and concentrated dicamba (20% product) gave high levels of kill in both the wet and dry seasons (I.L. Miller and J.L. Pitt unpublished results).

Response to Other Human Manipula-

Because there is little grassy understorey in thickets of M. pigra, it is difficult to destroy infestations with fire. However, by applying fuel such as gelled gasoline from aircraft, the stands can be completely burnt (I.L. Miller and W.M. Lonsdale, unpublished results). Follow-up control must then be carried out, because although seeds on the soil surface are destroyed, germination of seeds from the seed bank, within 5 cm of the soil surface, is enhanced (Miller 1988b, I.L. Miller and W.M. Lonsdale, unpublished results). A fire of lower intensity occurring in June was found to give an overall kill of only 10%, although greater mortality occurred amongst young plants and those already stressed by herbicides (Miller 1988b).

Miller (1988b) has argued that, by using herbicides to open the canopy and allow herbaceous vegetation to regrow, fire can then be employed to clear infested areas, with subsequent sowing of competitive pasture species to suppress regeneration from seed. Biological control agents too may promote fires in the same way as herbicides.

Responses to Natural Enemies

In general, the plant seems low in palatability to higher animals. In Costa Rica, part of the native range, captive peccaries (Tayassu pecari), whitetailed deer (Odocoileus virginianus) and tapir (Tapirus bairdii) will reject the foliage on the basis of odour, whilst cattle and horses will not browse it even when food is scarce (Janzen 1973). Cattle and water buffalo will occasionally browse young shoots in Australia, and seedlings have been found germinating from dung (Miller and Lonsdale 1987), but usually ungulates have little impact on the plants in the region. By contrast, in Yankari Game Reserve in Nigeria, it is a useful source of dryseason browse for elephant and small ungulates (Geerling 1973). Bronze-wing pigeons (Phaps chalcoptera) have been observed eating the fallen seeds in Australia (C. On, pers. comm.). Wilson (1989) showed experimentally that seeds beneath the canopy in Australia were removed predominantly by vertebrates, while those on the open flood plain were mostly removed by ants. He concluded, however, that post-dispersal seed predation was unlikely to inhibit the spread or maintenance of the weed.

Currently there is a collaborative biological control program involving CSIRO, Northern Territory Department of Primary Industry and Fisheries, the Australian Centre for International Agricultural Research and the National Biological Control Research Center in Thailand. The program includes exploration for biological control agents in the native range of mimosa, testing the host specificity of selected agents in quarantine in Brisbane, mass rearing, release and monitoring of biological control agents in the Northern Territory and Thailand. Since 1984, the main focus of the exploration has been Mexico, although there were earlier searches for biological control agents in Brazil during 1980-81, with brief visits to Mexico, southern USA, and Venezuela (Harley et al. 1985). Surveys have also been made in Honduras (Habeck and Passoa 1983) and Costa Rica (K.L.S. Harley, pers. comm.).

M. pigra in its native range is attacked by more than 200 species of insect herbivores and several fungal pathogens (K.L.S. Harley and J.D. Gillett, unpublished results). Most insects are in the orders Coleoptera or Lepidoptera, and collectively they attack flowers, seeds, stems and leaves. In Australia, Wilson and Flanagan (in press) collected 114 species of insects from mimosa, most being polyphagous, ectophagous and native or naturalized to Australia, and most being active mainly in the wet season (Flanagan and Wilson in press). There were fewer species of Coleoptera and more Hemiptera collected in Australia than in Mexico. They concluded that insects released in Australia for biological control of mimosa would find a largely unexploited food source. In Mexico, less than 5% of insects on mimosa are known to be host specific. Five species have been released in Australia and four in Thailand following rigorous host specificity testing.

The first insects introduced to Australia for biological control of mimosa were the seed-feeding beetles, Acanthoscelides quadridentatus and A. puniceus (Fam. Bruchidae) from Mexico. They were released in Australia in 1983 and in Thailand in 1984 (Kassulke et al., in press). Adults oviposit on mature seed pods and larvae tunnel through the wall of the pod and into the seed, thereby rendering it non-viable. Pupation occurs within the seed pod and the average duration of the life-cycle for each species is about 40 days (Kassulke et al., in press). Unfortunately these species have not yet attained high population densities in Australia or Thailand and have had no significant impact on seed production.

The leaf- and bark-feeding beetle, Chlamisus sp. (Fam. Chrysomelidae), from Brazil, was released in Australia and Thailand in 1985 and 1986, respectively. This beetle has had no impact on the growth of M. pigra and the population density is so low that it is now difficult to find in the field, although it does persist.

Two stem-boring moths, Neurostrota gunniella (Fam. Gracillariidae; Figure 10a) and Carmenta mimosa (Fam. Sesiidae; Figure 10b) were released in Australia in 1989. N. gunniella established readily. The young larvae mine leaf pinnules, and older larvae tunnel in the stems, causing them to die. The life-cycle takes from 28 to 40 days at 25°C (Davis et al., in press). C. mimosa complements the action of N. gunniella by tunnelling in stems of larger diameter. Eggs are usually placed at a plant node and newly emerged larvae enter the young stems, and may later exit to graze and girdle the stem, thereby causing death of the stem above the feeding site. Older larvae tunnel in stems, causing death of the branch, and sometimes move down the stems to cause severe damage to roots. The life-cycle takes about 112 days (I.W. Forno et al., unpublished results). Important insects yet to be tested for their host specificities are the seed- and flower-feeding weevils, Apion spp., Chalcodermus serripes, Sibinia fastigiata, S. ochreosa, S. pervana and S. seminicola. These are currently being studied in Mexico and quarantine approval has been given to import them into Australia for further testing.

Two fungal pathogens, Phloeosporella sp. (Coelomycetes) and a rust Diabole cubensis (Uredenales), severely debilitate M. pigra in Mexico. Phloeosporella sp. attacks leaves, branches, main stems and seed pods, causing leaf fall and cankers on the stems which lead to ring-barking and die-back (H. Evans, pers. comm.). D. cubensis causes chlorosis to stems and leaves, resulting in premature leaf fall. Both fungi are attacked by hyperparasitic fungi in their native range, and it seems likely that their effects on M. pigra would be even more damaging when introduced into Australia without their natural enemies. The CAB International Institute of Biological Control is studying the life-cycles and host specificities of these fungi in Mexico and Britain.

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Errata

Some errors occured in the paper by H. Haas Vol. 4(1) 38-44.

- Page 38: Table 1. 1st Column; Pulses '1' should read '13'.
- Table 2. '1000 kg/ha' should read '100 kg/ha'.
- Page 39: Top of column 1; Kg/ha N 1970/71 should read '145'.
- Page 40: Table 5 ends with the words '(no herbicides).' and not the sentence commencing 'Since May...'.
- Column 3, point 4): The phrase 'by the Toxicological Board of the Ministry of Agriculture' should be omited.
- Page 41: Table 7. MCPA '85' should read '185'.

In the paper by Kon and Blacklow Vol 4(2) 51-60 the species name *Bromus rigidus* was misspelt in the title.

The editor apologises for these errors.