Reviews

The Biology of Australian Weeds 32. *Cabomba caroliniana* Gray

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Name

Cabomba is an aboriginal American word for aquatic plant. The specific name *caroliniana* indicates that Gray's material was collected in south-eastern USA. The plant is called cabomba or fanwort in Australia and Carolina watershield, Washington grass and fish grass in the USA (Chittenden 1951, Mabberley 1987, Parsons and Cuthbertson 1992).

Description

It is now generally agreed that *Cabomba* and the related genus *Brasenia* constitute a separate family, the Cabombaceae (Ørgaard 1991). The Cabombaceae is characterized by submerged rhizomatous stems, floating, long-stalked, peltate leaves or submersed short-stalked, dissected leaves, long-stalked hypogynous flowers with three sepals and three petals, that are usually emergent and abundant perisperm in the seeds (Figures 1 and 2) (Osborn *et al.* 1991).

There has been some confusion over the species constituting the genus *Cabomba*. Eleven species have been described: *C. aquatica* Aublet, *C. australis* Spegazzini, *C. caroliniana* A. Gray, C. *furcata* Schultes & Schultes f., *C. haynesii* Wiersma, *C. palaeformis* Fassett, *C. piauhyensis* Gardner, *C. pubescens* Ule, *C. pulcherrima* (Harper) Fassett, *C. schwartzii* Rataj and *C. warmingii* Caspary. Five species are currently recognised: *C. aquatica* Aublet, *C. caroliniana* A. Gray, *C. furcata* Schultes & Schultes f., *C. haynesii* Wiersma and *C. palaeformis* Fassett (Ørgaard 1991). Only one species, *Cabomba caroliniana*, is known to be naturalized in Australia. The current definition of this species includes the previously separate species *C. australis* and *C. pulcherrima*, and several natural and horticultural varieties (Ørgaard 1991). Three types of cabomba (*C. caroliniana* var. *caroliniana*, *C. caroliniana* var. *multipartita* and *C. caroliniana* var. *pulcherrima*) from eight sites in Florida assessed for genetic diversity were found to be genetically indistinguishable. The differences were ecophenotypic rather than genotypic (Wain *et al.* 1983, 1985). Ecophenotypic plasticity is well known in aquatic plants (Sculthorpe 1967). Godfrey and Wooten (1981) and Martin and Wain (1991) report that cabomba with high levels of purple pigment grows in very warm waters but that plants from cooler waters have little purple pigment and are green. Conversely, Leslie (1985) reports aquarists as saying that the purple colour develops in response to cold water conditions, whilst Ørgaard (1991) suggests shoot colour is strongly influenced by light conditions; shoots becoming reddish brown in bright light. Colour is the only morphological trait that distinguishes *C. caroliniana* var. *pulcherrima* (Wain *et al.* 1983). Because of the ecophenotypic plasticity, differentiation of *Cabomba* species is best done on the basis of seed characteristics such as size, shape and surface structure (Ørgaard 1991). On the basis of flower colour, three varieties of cabomba are now distinguished (Ørgaard 1991): *C. caroliniana* var. *caroliniana*, *C. caroliniana* var. *pulcherrima* and *C. caroliniana* var. *flavida* with, respectively, white, purple and yellow flowers. The cultivars *rosifolia*, *multipartita*, *paucipartita* and 'Silbergrune' (= 'Trifolia') are traded by aquarists but all appear to be clones of *C. caroliniana* (Chittenden 1951, Rataj and Horeman 1977, Wain *et al.* 1988, Martin and Wain 1991, Ørgaard 1991).

Unless otherwise specified, in this paper the term 'cabomba' refers to *C. caroliniana* as defined by Ørgaard (1991) and its horticultural varieties.

Because of the confusion surrounding the identity of cabomba in Australia a detailed description is given here, based on Raciborski (1894, in Sculthorpe 1967), Fassett (1953), Sanders (1979), Schneider and Jeter (1982), Moseley *et al.* (1984), Ito (1986) and Ørgaard (1991).

In the seedling the first few pairs of leaves are lanceolate and devoid of laminae. These are succeeded by transitional leaves until the submerged adult leaf form appears.

Plants are strictly aquatic and completely submerged except for flowers and occasional floating leaves. Stems may be up to 10 m long. They are slightly compressed, 2–4 mm in diameter and increase

Figure 1. *Cabomba caroliniana* showing the mass of submerged leaves, small floating leaves and solitary flowers (image provided by the Information Office of the University of Florida, IFAS, Center for Aquatic Plants, Gainesville).

in width acropetally in the internodal region. Scattered short, white or reddish-brown hairs are present. The 'rhizomes' are erect, stout stems which have become prostrate and partially buried; they are not true rhizomes. They have opposite buds and sometimes small leaves. Some rhizomes are runners (horizontal) and possess upturned, erect heads. New rhizomes and floating shoots arise as axillary branches to these shoots. Rhizomes are fragile and break and decay quickly. Adventitious roots occur on the rhizomes at 45 degrees dextral and sinistral to the leaves and branches.

Shoots are grass green to olive green, sometimes reddish brown, often coated with mucilage and more or less pubescent. When present, the floating leaves are alternate, with the blades peltately attached to the petioles (Figure 2) and they have a firm texture. Floating leaves are peltate, entire, green to olive green, narrowly elliptic or ovate (trullate or sagittate), 5–20 mm in length and 1–3 mm wide. They are borne on the flowering branches. Submerged leaves are petiolate, opposite or less commonly in whorls of three, and divided. The divisions are linear but the terminal divisions are slightly spathulate. The semicircular leaves may be divided dichotomously and trichotomously several times (Figure 2) to give a great number of terminal divisions: from 3–20 on the lower stem to 150–200 for larger apical leaves. The leaflet margin is serrulate to denticulate, the teeth being barely visible. The teeth are really 3-celled trichomes that secrete a gelatinous mucus which covers the entire plant. The venation of the submerged leaves corresponds to the leaf division. Erect and flowering shoots have proximately decussate phyllotaxy which changes near the surface of the water to 1/3 with a flower at nearly every node.

Flowers are solitary and raised above the water surface (Figure 2) attached to a long axillary stalk and are 6–15 mm in diameter and 6–12 mm long; milk-white, pale yellow or purplish. The flower is hermaphroditic and generally trimerous but di- and tetramerous flowers are found. Sepals three, elliptic to obovate, 5–12 × 2–7 mm, pale yellow to milk white, if whitish then often purplish tinged on margins and veins, base often greenish yellow on the

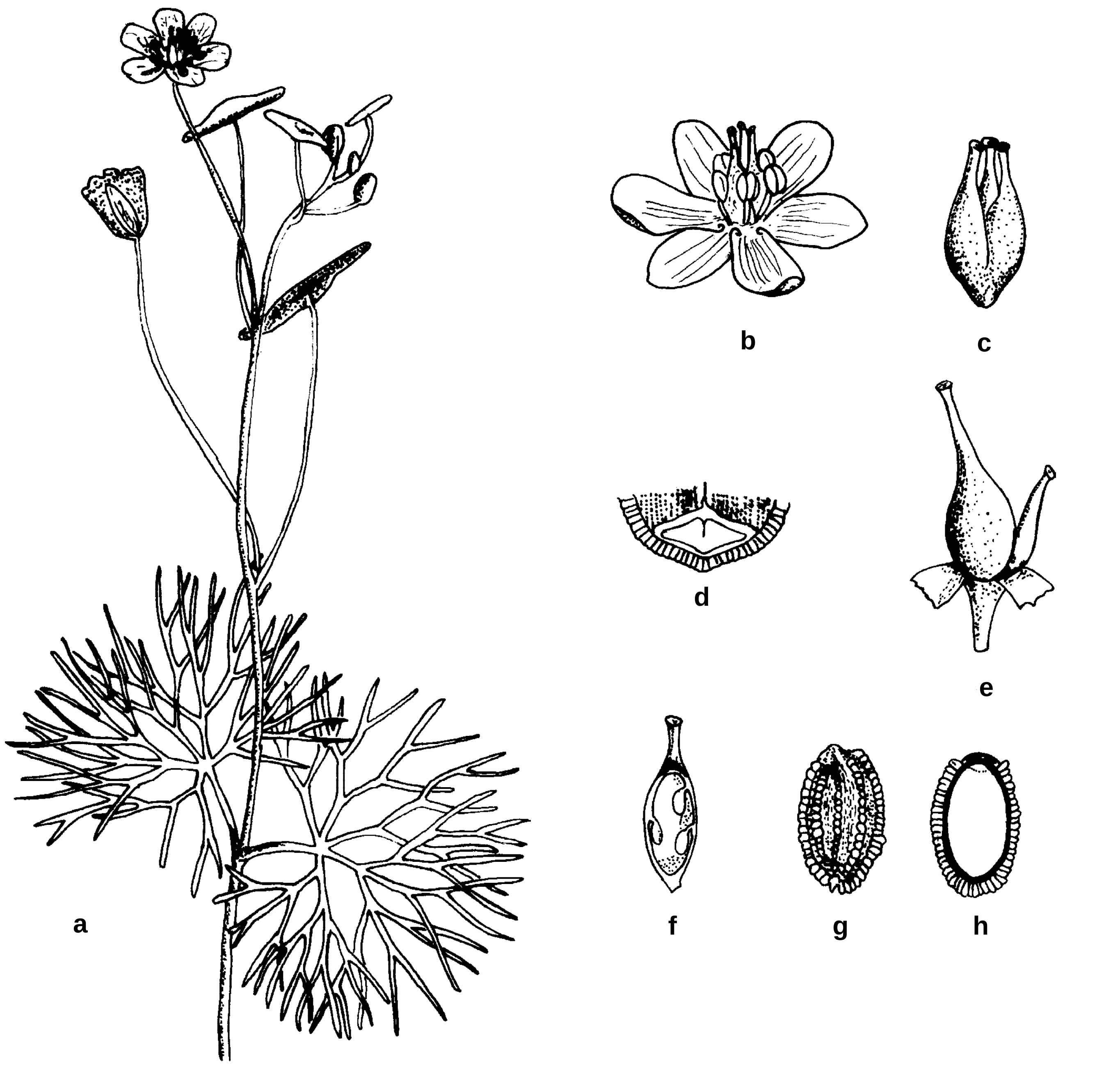

Figure 2. ***Cabomba caroliniana*** **(Redrawn after Watson and Dallwitz 1995 onwards) (a) submerged leaves, floating leaves and flower, (b) flower, (c) pistil, (d) base of seed showing embryo enclosed by albumen, (e) fruit, (f) vertical section of carpel showing ovule attachment, (g) seed showing sculpturing and (h) L.S. seed.**

abaxial face. The three petals alternate with the sepals and are slightly fused together at the base and are obovate to elliptic, 4–12 × 2–5 mm, pale yellow to white, purple tinged or bright purple, with apex obtuse or emarginate. The petal base is extended into two equal semicircular lobes curved more or less inwards towards the middle of the petal and partially covering the claw (Figure 2); the lobes with two more or less conspicuous yellow, elliptic, separate patches which function as nectaries; claw a deep yellow at the base, becoming paler apically. Stamens (3–)6 usually in one whorl. If six are present they are inserted on radii between petals and sepals. If three, they are antepetalous. Carpels (2–)3(–4), antepetalous when four, divergent at maturity and with 1–5 anatropous, pendulous ovules (Figure 2) and stigma clavate. Two ovules are attached at the dorsal side and one at the ventral side. Seeds (Figure 2) ovate to ellipsoid-oblong, 1.5–3.0 × 1.0–1.5 mm long, verrucate, the cristate-costate outer testal layer composed of irregularly digitate cells uniformly and densely perforated with simple pits with four longitudinal rows of tubercles formed by the radial elongation of digitate cells. Seeds covered with elongate processes and coated in a gelatinous slime. Pollen grains 60–90 µm in polar axis, prolate (boat shaped to oblong), elliptic, monosulcate, supratectal sculpturing striate; monads at maturity. Fruit (Figure 2) green when fresh, carried below the water surface, apocarpous with 1–4 dark brown carpels.

Chromosome number: $2n$=39, c.78, c.104; the basic number proposed by Ørgaard (1991) is x=13 (not x=12 as previously proposed; counts of $2n$=24 are probably miscounts) so specimens of cabomba are apparently triploid, hexaploid or octoploid. The ploidy of Australian cabomba has not been reported.

Seeds have not been reported from cabomba in Australia, so current identification must be largely based on vegetative characters.

History

Cabomba is of relatively recent introduction into Australia; the earliest record is from 1967 (Garraty *et al.* 1996) but it was not considered naturalized in Australia by Sainty and Jacobs (1981) and was first added to the New South Wales flora in 1986 (Jacobs and Lapinuro 1986). A longstanding assumption has been that naturalized populations are due to aquarists dumping unwanted plants into local waterways, but more commonly, areas have been deliberately planted to allow wild cultivation for the aquarium trade.

Cabomba was introduced into Australia from the USA as an aquarium plant. The earliest Australian herbarium record is in 1967 from cultivated material at Oyster Bay, New South Wales. In Queensland, cabomba was first noticed as a pest in 1989 when, as a result of an aquarium escape, it was infesting the swamp that fed Leslie Creek (Atherton Tablelands) although it had been present since 1986. It overgrew the fish breeding ponds at 'Quinkin Ponds' and by the end of the year it had infested the length of the creek and had spread into at least one arm of Lake Tinaroo, into which the creek flows. By 1991 further infestations were reported from Avondale Creek, north of Cairns and a drainage channel at Goondi, near Innisfail. In southern Queensland, concern about its weed potential developed when it was first observed in Six Mile Creek, the original impoundment for Lake MacDonald (Noosa shire), in April 1992 (Anderson and Garraty 1994) although non-weedy outbreaks were observed in the Caboolture River in 1991.

As a result of the infestation in Leslie Creek, its spread into Lake Tinaroo and the possible infestation of associated irrigation systems, cabomba was declared as P2 (to be eradicated) in Atherton and Eacham shires in May 1990 and the declaration extended in July 1992 to the Johnstone and Mulgrave shires.

To date *C. caroliniana* var. *caroliniana* is the only taxon to have naturalized in Australia, although pink cabomba (*C. furcata*, previously *C. piauhyensis*) and green cabomba (*C. caroliniana* var. *caroliniana*, previously *C. australis*) are regularly traded by aquarists.

Figure 3. The known distribution of cabomba in Australia.

Distribution

Cabomba has a curious and disjunct distribution in that it is considered to be native to the south-eastern USA and southern Brazil, Paraguay, Uruguay, and north-eastern Argentina (Ørgaard 1991). This distribution and that of other members of the genus suggest it could be naturalized in the USA and originally be a native of South America.

Because of its extensive use in the aquarium trade, cabomba has been introduced to Malaysia, India, Japan and New Guinea (Ørgaard 1991). In Japan cabomba is considered a noxious weed (Oki 1992). Cabomba is sold as an aquarium plant, but is not yet naturalized in the ASEAN region (Malaysia, Singapore, Philippines, Indonesia, Thailand, Brunei) where it has the potential to cause serious problems in aquatic ecosystems. It is considered imperative that strict quarantine regulations are enforced against cabomba in the ASEAN region (Revilla *et al.* 1991).

The known distribution of naturalized cabomba in Australia is shown in Figure 3. Infestations are currently restricted to the Northern Territory, north-east Queensland (Atherton Tableland and coastal districts) and the south-eastern Queensland, central and northern New South Wales coasts, with a single inland record from the Griffith area. In Victoria, cabomba is largely restricted to South Gippsland but it is considered a potential threat to permanent, freshwater, aquatic vegetation throughout the state. Currently it is rare or localized although some populations are quite large (Carr *et al.* 1992).

The potential distribution of cabomba in Australia is difficult to establish as there is no good model available for predicting the distribution of a fully aquatic weed.

However, two approaches have been taken. Firstly, CLIMEX (Skarratt *et al.* 1995) has been used to model the weed's potential distribution based on temperature tolerance, since temperature is a major determinant of distribution in aquatic plants (Sculthorpe 1967). Secondly, GARP (Stockwell 1996a,b), a rule-based model that deduces from a species' current Australian distribution environmental rules which determine its distribution has been used. Rules for cabomba were based on average air temperatures and their ranges, average rainfall and rainfall variation, soil type and soil nutrients. Clearly, with a weed such as cabomba which is in its initial invasive stages, all environments in which it can occur may not be represented in its current distribution and this limits the usefulness of this second approach. However, in Australia, cabomba is currently distributed across a wide climatic zone (Figure 3) which may mitigate against this problem.

Figure 4. The distribution of *Cabomba caroliniana* in Australia predicted using CLIMEX (EI=Ecoclimatic Index; EI=10, potential for a permanent population extremely low; EI=100, this potential extremely high).

Figure 5. The distribution of *Cabomba caroliniana* in Australia predicted using GARP.

The CLIMEX model was developed by matching the USA distribution of cabomba. The final model predicted the distribution of cabomba in the south-eastern USA but also predicted the presence of the weed along the west coast. This probably indicates that the distribution in the USA is not determined solely by temperature. Interestingly, subsequent to the development of this model, the first records of cabomba in this region (Washington and Oregon) were found (Anon. 1995). The model predicted the recorded occurrence of cabomba in South America (Ørgaard 1991) but also a more extensive distribution, suggesting again that temperature is not the sole factor determining the distribution of this species. The model suggests that much of coastal Australia, except for the north-west, is excellent habitat for cabomba, and the optimal area for growth of the weed is coastal Queensland (Figure 4).

GARP predicted a much more restricted distribution of cabomba in Australia (Figure 5) than CLIMEX, and indicated the distribution would be centred on southern coastal Queensland and New South Wales.

CLIMEX probably overestimates the potential distribution of cabomba whilst GARP probably underestimates its potential distribution. Both models make predictions of the distribution irrespective of whether there is a suitable water body for the weed to inhabit. Nonetheless, the results from both models suggest that the southern coastal strip of Queensland is suitable, if not optimal, habitat for cabomba.

Habitat

Cabomba is found in ponds, ditches, small shallow lakes and slow flowing streams in coastal vegetation of swamp forest and bog, and inland in areas of savanna (Ørgaard 1991). It can grow in water up to 10 m deep but most commonly the plants grow rooted in shallow water (up to 3 m) (Tarver *et al.* 1978, Sanders 1979, Schneider and Jeter 1982, Hanlon 1990).

Ørgaard (1991) suggests that cabomba species are adapted to habitats subjected to significant annual water level fluctuations through having the ability to grow rapidly to keep pace with increases in water depth during the wet season. If so they would be pre-adapted to conditions found in many Australian aquatic systems. Like most fully aquatic plants, cabomba is sensitive to the drying out of its habitat. In experiments conducted in aquaria, only 6.7% of cabomba seedlings survived a 30 day drawdown of the water level in which the hydrosoil remained unsaturated, and growth of survivors started within 14 days of refilling aquaria. If the hydrosoil was saturated, 53% of seedlings survived and regrowth was evident after seven days (Sanders 1979). These observations support Ørgaard's suggestions.

Climatic requirements
Cabomba likes a warm-temperate, humid climate, with rain throughout the year and an annual temperature of 15–18°C (Ørgaard 1991). Although it can withstand temperatures of less than 0°C, its preferred temperature range is 13–27°C (Leslie 1985).

pH
Cabomba is reported from acid and alkaline waters (Ørgaard 1991), but the optimum pH for growth is 4–6 and growth inhibition occurs at pH 7–8. Above pH 8 the stem becomes defoliated and growth is inhibited (Riemer 1965, Gregory and Sanders 1974, Tarver and Sanders 1977). Consequently cabomba grows best in acidic waters (such as those around the Florida panhandle) (Hanlon 1990). This is perhaps accounted for by nutrients being more available in acidic waters (Gregory and Sanders 1974, Sanders 1979).

Nutrients
In Japan cabomba grows well in nutrient rich water. The ranges (mg L^{-1}) of habitat variables in which it occurs in Japan are: COD 3.2–8.23, inorganic-N 0.68–1.76, and organic-N 0.06–0.25 (Oki 1992). Cabomba also grows optimally at very low calcium ion concentrations (4 ppm); higher levels of calcium inhibit growth (Riemer 1965).

Turbidity
The response of cabomba to water turbidity has been investigated in aquaria (Gregory and Sanders 1974, Sanders 1979). Growth was measured at low (30–45 Jackson turbidity units) medium (70–110 JTU) and high (300–2350 JTU) turbidities. Growth at medium turbidities was greatest, followed by growth at high turbidities. Moderate turbidity (70–110 JTU) enhanced stem length growth compared to non-turbid (0–10 JTU) conditions and it is postulated that this is due to an auxin effect, producing longer cells at moderate turbidity levels. Moderate to high turbidities (300–350 JTU) enhanced adventitious root development. Decreased underwater light intensity generally leads to growth limitation in submerged aquatic plants, so this result is somewhat counter-intuitive. In these experiments turbidity was maintained by stirring the hydrosoil. This could have led to an increased release of nutrients to the water, hence increased availability to the plant, as the shoots and stem are the main sites of nutrient uptake (Sanders 1979). Nevertheless, cabomba appears to be able to grow well in turbid conditions, and since Australian freshwaters are generally turbid and turbid water caused by inflows usually helps to control aquatic weed problems, this characteristic of the weed is of concern.

Light
In contrast to the above findings, in cultivation, cabomba is demanding of light and water quality and sensitive to competition and water motion (Ørgaard 1991), although Anderson and Garraty (1994) state that as an indoor water plant it tolerates poor lighting.

Substratum
In Queensland cabomba appears to prefer silty substrata into which it does not root deeply. Where it occurs on hard or stony substrata the plant's vigour is reduced (Garraty *et al.* 1996).

Plant associations
In south-east Queensland cabomba coexists with (but tends to dominate) submerged native species including *Hydrilla verticillata* (L.f.) Royle, *Nymphoides indica* (L.) Kuntze, *Eleocharis sphacelata* R. Br., *Hygrophila salicifolia* (Vahl) Nees, *Polygonum* spp., *Najas tenuifolia* R. Br., *Potamogeton javanicus* Hassk., *Utricularia* spp., *Vallisneria spiralis* L. and the exotic *Nymphaea capensis* Thunb. (Anderson and Garraty 1994). Cabomba grows in association with *Lepironia* sp. and salvinia (*Salvinia molesta* D.S. Mitchell) in the Glenbrook Lagoon in New South Wales.

In the eastern USA cabomba coexists with other native aquatic herbs including *Nymphaea odorata* Aiton, *Nuphar lutea* (L.) Sibth. and Smith, *Myriophyllum* spp. including *M. aquaticum* (Vell.) Verdc. and *Brasenia schreberi* J.F. Gmelin (Guerra 1974, Schneider and Jeter 1982). The latter authors report that it is extremely persistent, forms dense stands and under good growing conditions can crowd out other previously established native species.

Growth and development

Morphology
The general morphology of the plant is shown in Figures 1 and 2 and has been described by Ørgaard (1991). One to 10 adventitious roots can form spontaneously at the nodes of erect, vegetative and free floating shoots, without the need for contact with a substratum. In Queensland, 3–40 strong, flexible stems, 2–6 mm thick, arise from a single root mass. Some horizontal stems may become buried and fragment to give rise to new erect shoots on separate plants (Garraty *et al.* 1996). Adventitious roots are thin, white and unbranched. Older, embedded roots are numerous, long, very slender, branched and purple when fresh, drying to dark brown to black.

Perennation
Cabomba is an aquatic perennial (Tarver and Sanders 1977), growing from short rhizomes with fibrous roots (Hellquist and Crow 1984, in Madsen 1996).

Physiology
Cabomba is not cyanogenic; it contains alkaloids, but saponins/sapogenins are absent (Watson and Dallwitz 1995).

Phenology
Little is known of the life cycle of cabomba in Queensland. In north Queensland it grows and flowers continuously throughout the year, and in south-east Queensland buoyant stems up to 6 m long are produced in summer with a growth rate of up to 5 cm per day (P. Bell personal communication 1995). In July and August these stems lose buoyancy, lie across the surface of the hydrosoil and fragment. When growth recommences, fragments reroot and initiate new plants (G. Diatloff personal communication). These observations are similar to those of Riemer and Ilnicki (1968). In mild winters, this die back may not occur (T. Anderson personal communication).

The following description refers to the life cycle of cabomba in the USA. Towards the end of the growing season, stems become denuded and brittle and hard. Terminal stems especially tend to break free and these remain green and leafy until spring. Some terminal buds remain attached to the substratum, even under ice. Growth starts around April (Riemer and Ilnicki 1968). Even defoliated stem fragments buried in mud under ice may regrow (Ørgaard 1991).

Most of the material supplied to the aquarium trade originally came from the San Marcos River in Texas. Here the plant is perennial and flowers throughout the year, and although the number of flowers drops drastically during November–February, isolated flowers can still be found. Floating leaves are produced during the flowering period (Schneider and Jeter 1982) and fruits appear shortly after the first flowers have emerged (Riemer and Ilnicki 1968). Fruit take about a month to mature (Schneider and Jeter 1982).

In the southern USA peak seed production is during May–October, but occurs from April to December (Sanders 1979). In Louisiana cabomba flowers from May to December, with peaks in May and September (Sanders and Mangrum 1973). In New Jersey, it begins flowering in late June/early July and maximum flowering occurs in late July and continues through August. A few flowers continue to emerge until the first frosts (Riemer and Ilnicki 1968). Fruit set is often abundant throughout most of the year, but most seed is produced between May and October (Hanlon 1990).

Mycorrhiza
There are no records of mycorrhizal associations with cabomba.

Reproduction

Floral biology
This account of the floral biology of cabomba is based on Tarver and Sanders (1977), Sanders (1979), Schneider and Jeter (1981, 1982), Ørgaard (1991) and Osborn *et al.* (1991).

Pollen fertility is low in cabomba (45–95%) compared to the rest of the genus and is related to the high level of polyploidy. Flowers contain relatively few, large pollen grains and have low pollen-ovule ratios (560 ± 123 [95% confidence limits] grains per flower, pollen-ovule ratio 62 ± 14). These features are characteristic of entomophily (insect pollination). Flowers undergo dianthesis over two consecutive days, during which flowers are structurally and functionally pistillate on the first day and staminate on the second. Flowers open in the morning around 10 a.m. and close in the afternoon at around 4 p.m. On closing, flowers submerge. When open they are raised 1–4 cm above the water surface due to elongation of the peduncle. This occurs some two hours before anthesis. Consequently, during the morning, second day flowers stand slightly higher than first day flowers.

Flowers are protogynous on the first day, stamens are short filamented and indehiscent, and the longer pollen receptive stigmas arch out over the nectaries. The filaments elongate on the second day so that the anthers are level with the stigmas, but they point out towards the nectaries. The anthers undergo extrorse dehiscence on the second day some two to three hours after the flower is fully open, but by then the stigmatic papillae are flaccid (suggesting loss of stigmatic receptivity) and the carpels re-oriented inwards. Initially the pollen is a sticky mass, but it dries and become powdery. Flowers waterlogged by rain do not release pollen. If skies are overcast, anther dehiscence may be delayed by a few hours and stigmatal sensitivity extended.

The perianth persists until the seeds are released. Seeds are contained in long pistils and vary from one to three per pistil depending on time of year (1 in May, 2–3 in September). Fruit are mature by 2–4 weeks. Pistils containing mature seed separate from the pedicel and fall to the bottom. The fruit wall decomposes and the seeds are released and lie on the hydrosoil surface. Eventually, seeds sink into the substratum and are here protected from desiccation. It is speculated that seeds have the capability of remaining viable after long periods of desiccation or dormancy (Madsen 1996).

Schneider and Jeter (1982) claim that autogamy and apomixis do not occur and protogyny is absolute (stigmas only receptive on the first day and never on the second day) but Ørgaard (1991) observed fruit setting without either hand pollination or detected insect pollination, so that some degree of autogamy seems possible. Similarly, Sanders' (1979) observations suggest that cabomba is only facultatively entomophilous. Wind or rain would be sufficient to displace pollen onto the stigmas. Certainly though, self-pollination appears to be a rare event (Hanlon 1990). Tarver and Sanders (1977) found water, wind and hand pollination failed to produce seed but that insect pollination was successful. Forty per cent of flowers which had been visited by insects produced mature seed after about one month. Twenty per cent of flowers visited on the first day produced seed and 60% of flowers visited on the second day produced seed, so pollination is due to insects and cross-pollination is the rule. Principal pollinators were *Enallagma* and *Anax* (Odonata), *Halictus* and *Apis* (Tarver and Sanders 1977) but Odonata probably are accidental pollinators as they are not nectar or pollen feeders. The major pollinators observed by Schneider and Jeter (1982) were small ephydrid flies.

Cabomba flowers are visited by numerous insects, particularly small flies. On the first day whilst a fly is taking nectar, a stigma is in close proximity to its back or head. On the second day the anther is in this position. Flies were seen to carry pollen. The changes in morphology during flower development ensure that pollen is transferred from the two-day-old flowers to the stigma of one-day-old flowers. After anthesis the flower is pulled beneath the water surface, either by an acute bend in the peduncle, by coiling of the peduncle or loss of turgor pressure in the peduncle. Only fertilized flowers (swollen carpels – evident one week after pollination) were pulled underwater by the peduncle. Flowers, not dehisced on the second day or wet by rain, are pulled underwater but become water logged and do not release pollen. Abscission of the fertilized flower is prevented by auxins released by the ovary and transported down the peduncle. The coiling of the peduncle may also be due to auxins. The coiling is thought to protect carpels from being broken from the peduncle by fish and severe wave action.

Seed production and dispersal
After fertilization, the perianth encloses the fruits and within a few days the anthocarp becomes submerged due to recurvation of the pedicel (Ørgaard 1991). Fruit (pistils) break away from the plant and fall to the bottom, decompose and leave the seed at the hydrosoil surface (Sanders 1979). The perianth persists until the seeds are released 14–30 days after anthesis. The seed is green when fresh with a scattered dark pigmentation and slowly turns brown with age. It is globose to ovoid-oblong with slightly flattened ends (Ørgaard 1991). Seed anatomy is similar to that of the nymphaceous genera: there is abundant perisperm, little endosperm, a haustorial tube and a small dicotyledonous embryo (Schneider and Jeter 1981).

Schneider and Jeter (1982) indicate that submerged as well as emergent flowers are produced in the San Marcos River, but pollen release does not occur in these flowers and seeds are not produced.

Seeds have not been recorded from Australian plants although two herbarium specimens from south-east Queensland possess fruit. Since potential pollinators are plentiful, cabomba in Queensland may be sterile.

Ørgaard (1991) suggested that as for most water plants, seed dispersal is effected by water birds, and this could be important in ensuring dispersal between lakes or river systems. Sanders (1979) states that the floating pistil helps disperse the seed. However, cabomba's range extension in the USA is generally considered to be due to the discarding of unwanted plants by aquarists (Hanlon 1990, Madsen 1996).

Physiology of seeds and germination
In the colder, north-western part of cabomba's USA distribution, fruit setting is often sparse (Ørgaard 1991) and in New Jersey, sexual reproduction is negligible or non-existent as Riemer and Ilnicki (1968) found no seedlings, no seeds germinated and no seeds were found with embryos.

In Louisiana seed is produced but viability is low and only about 25% of seeds germinate naturally (Sanders 1979). About 5% of seeds germinate immediately and do not require a period of after-ripening. In experiments to assess the importance of different environmental conditions on germination, only 1.8% germination occurred. Seeds generally germinate 5–10 weeks after fertilization (Tarver and Sanders 1977) but seed can remain viable for more than two years. Factors believed to be important in affecting germination are red light, temperature and high carbon dioxide levels (Sanders 1979). The embryo remains viable for up to eight hours if allowed to desiccate. Seed set in cabomba is reduced compared to that of congeners. This could be explained by reduced pollen fertility and / or reduced stigmatic receptivity; both associated with high ploidy. Climate and the environment may also affect seed set in this species (Schneider and Jeter 1982).

Vegetative reproduction

Cabomba grows and disperses mainly from fragmentation (Sanders 1979, Hanlon 1990). Any detached shoot with at least one pair of expanded leaves is capable of growing into a mature plant. Larger sections than this can root at the nodes. A motorboat passing through a cabomba bed can produce hundreds of disseminules and in many situations this is probably the major dispersive and infestive mechanism (Sanders 1979).

As Riemer and Ilnicki (1968) note, vegetative reproduction is very important in many aquatic plants. For example, *Ceratophyllum demersum* L. often does not reproduce sexually because conditions are too cold, but reproduces entirely by axillary buds on plant fragments from the previous year. Nevertheless, the species is abundant and often dominant in freshwaters where it does not sexually reproduce.

Hybrids

Reproduction in cabomba is largely asexual and hybrids have not been recorded. However, since *C. haynesii* is possibly a hybrid between *C. palaeformis* and *C. furcata* (Ørgaard 1991), hybrids involving cabomba could conceivably occur.

Population dynamics

Cabomba is capable of rapid spread once it has been introduced into a suitable water body. It was first reported from Lake MacDonald (south-eastern Queensland) in April 1992, and by 1995 had invaded almost the whole of the lake's extensive littoral zone, where it had replaced much of the submerged native vegetation (Anderson *et al.* 1996). Although under suitable environmental conditions cabomba is extremely persistent and competitive and can exclude well established native species (Riemer and Ilnicki 1968), it can itself be out-competed by such weeds as *Egeria* (=*Anacharis*) *densa* Planch. (Sanders and Mangrum 1973). Extracts of cabomba have allelopathic effects at medium and high concentrations and since allelopathy plays a role in determining the distribution of higher plants (Rice 1979), this could be a mechanism whereby cabomba can oust native species (Elakovich and Wooten 1989).

Importance

Detrimental

Cabomba is still in its early invasive stages in Australia and the actual extent of the infestation is not known. Currently it appears to be having little impact but until a survey has established its detailed distribution, its true importance cannot be known. Meanwhile, its potential impact can be judged by reference to its impact overseas.

Cabomba has the potential to cause blockages in the Panama Canal (Hearne 1966). However, most information on cabomba is from the USA. It is a problem throughout the Gulf states, particularly in Louisiana (Tarver and Sanders 1977). In Florida, although the plant is extending its range (Sanders 1979) and increasing in abundance, it is not yet regarded as a nuisance plant (Hanlon 1990, Martin and Wain 1991). It is, however, one of the 19 plant species that cannot be transported, imported, cultivated, collected or sold in Florida (Clugston 1990).

Heavy infestations can raise water levels causing overflows and seepage losses. Oxygen depletion can occur when massive dieback and consequent decomposition occurs (Gracia 1966). Dense stands can interfere with recreational, agricultural and aesthetic functions of lakes and reservoirs (Riemer and Ilnicki 1968). In the USA commercial fishing camps have been forced to close or have had their income severely reduced (Sanders 1979).

Figure 6. Cabomba showing the long thick stems which could easily entangle divers or swimmers and impede boating and water flow.

Similar losses are unlikely to occur in Australia since natural lakes are relatively few and impoundments are not as intensively utilized. Nevertheless, the potential exists for economic losses from damage to amenity values. Even threats to human health and safety may ensue as water skiers or swimmers could easily become entangled by the weed's long thick stems (Figure 6) and drown.

In Queensland, cabomba infestations may deleteriously affect water quality (Anderson *et al.* 1996, Garraty *et al.* 1996) through increasing water colour, with a subsequent estimated increase in the treatment costs for potable water of $A50 per ML. There is also a suggestion (T. Anderson personal communication) that in southern Queensland the sudden release of manganese caused by the dieback and decomposition of large amounts of cabomba in the winter months could affect the manganese cycle and cause a reduction in water quality. Further research is required into these situations. If present in water storages, heavy infestations, because of the large volume of plant material, could cause water loss from overflow or seepage. Owing to these problems and the ability of cabomba to grow rapidly, cabomba has the potential to become a major weed in water storages.

Irrigation canals could provide an ideal habitat in which cabomba could grow and where it could impede water flow, cause overflows and blockages. Although it is difficult to assess the economic loss this might cause, the nuisance value could be high.

Anderson and Garraty (1994) have assessed the impact of cabomba on native aquatic plants and water quality in Lake MacDonald, Queensland. In summer the mean standing crop of cabomba was 1.02 kg m^{-2}, a seven fold increase from early spring levels. Other species were found only at very low standing crops in infested areas, compared to their abundance in uninfested areas. These results suggest that a primary concern with cabomba in Australia should lie with its potential as an environmental weed. Its ability to replace native aquatic plants, with the likely displacement of native fish and invertebrate populations, together with the ability to infest large areas of water, suggest that native aquatic life would be considerably endangered if cabomba was allowed to establish throughout the country.

Control costs are currently minimal as very little control has been attempted and most of this has been associated with experimental trials. In Queensland so far,

$A250–300 000 has been spent in trying to control cabomba in the Ewen Maddock Dam (R. Rainbird personal communication) and estimated costs for mechanical control in Lake MacDonald are $A125 000 for the harvester and $A20 000 per annum for harvesting costs (K. Garraty personal communication). The cost of treating a volume of 20 000 m^3 of water (100 × 100 × 2 m) with the 2,4-D n-butyl ester / diatomaceous earth mixture (see below) would be approximately $A3000. Clearly, on cost grounds alone, it is unlikely large scale infestations would be chemically treated.

Beneficial

Where naturalized, cabomba provides the usual benefits that aquatic plants generally have in aquatic systems: it oxygenates the water, protects against bank and bed erosion and removes nutrients from the water. It can also provide cover for young fish and a habitat for invertebrates, as well as being a source of food for wild life, including water fowl (Oki 1992). However, whilst it does provide fish habitat in the USA, it has no wildlife value (Martin and Wain 1991). In regions where it is invasive, it is not clear whether native fish and invertebrates utilize it readily as a habitat. Research is needed to clarify the situation in Australia.

Like many aquatic weeds, cabomba effectively removes plant nutrients (phosphorus and nitrogen) from water. Anderson *et al.* (1996) showed cabomba reduced dissolved nitrogen by 25% and dissolved phosphorus by 44% in Lake MacDonald. Harvesting and removal of cabomba may therefore be a way of limiting eutrophication in some waters.

Cabomba is a widely grown and commercially important aquarium and outdoor aquatic plant in many countries. Its finely dissected submerged leaves are attractive (particularly in the purple form) and it is used as an aquarium oxygenator (Chittenden 1951, Mabberley 1987). Cabomba grows well in shallow, well lit and eutrophic freshwater, flowering prettily at the surface and rapidly forming large colonies.

Legislation

Cabomba is proclaimed as a prohibited or restricted plant only in Queensland, where all *Cabomba* species are declared plants under the provisions of the Rural Lands Protection Act (1985). The genus is declared as category P3 for the whole state: where found, the numbers or distribution of the plant should be reduced. It is illegal to sell or keep the plant throughout the state.

Although cabomba is not declared, proclaimed or restricted in any other state, the modelling results suggest that this would be appropriate. Sainty and Jacobs (1994) also note that all species of cabomba are sold as aquarium plants. They are therefore likely to escape into suitable freshwater habitats in countries to which they are introduced. Due to their similarity with *C. caroliniana* and the ease of vegetative propagation, it is possible that those species not already commercially available in Australia will become so, and that species other than cabomba will become naturalized.

Weed management

Herbicides

Whilst it has been reported that cabomba is susceptible to a variety of commonly used herbicides (endothall, 2,4-D, 2,3,5-T, silvex, diquat, dichlorprop), their effects are erratic (Hiltibran 1974, 1977), retreatment is often necessary and managers consider cabomba difficult to control (Leslie 1985, Madsen 1996).

Results of trials with 2,4-D are inconsistent (Hiltibran 1974), but a granulated formulation of 2,4-D as the butoxyethanol ester has been useful as a treatment for water weeds, including cabomba, in potable water supplies in Texas (Guerra 1974).

Symmetrical triazines (e.g. simazine) are well known as effective aquatic herbicides. The growth of cabomba has been reduced by treatment with the triazine terbutryn. However terbutryn can stimulate growth at low dosages (Riemer and Trout 1980).

The potassium salt formulation of endothol-silvex controls cabomba, particularly with the addition of surfactant (X-77®), and has a low toxicity to fish and mammals (Lapham 1966). The granular formulation is recommended for the margins of deep water areas.

Endothall acid can be used to control cabomba if formulated as the potassium salt as in Aquathol K®, or the more toxic alkylamine salt as in Hydrothol 191®. For many years Hydrothol 191 has been used to control cabomba in Florida at application rates of 0.5–1.5 ppm without causing fish kills or obvious adverse environmental effects. Endothall acid breaks down rapidly and completely. It does not leave residues, accumulate in the hydrosoil or food chain, or move significantly from the treatment site. Emergent plants need not be affected and it is not toxic to fish. Not more than 10% of the water body should be treated at any one time with rates exceeding 1.0 ppm. A weighted hose should be used to apply the liquid herbicide as close to the bottom as possible, or preferably, the granular formulation should be used (Moore 1991).

Endothall is not registered in Australia except as a defoliant for crops and as a post-emergence herbicide for *Poa annua* L. (winter grass) in turf.

Sonar® (fluridone) is an effective herbicide for cabomba (Tarver 1985). It gives long term control, is easy to apply and is selective, as many plants are not susceptible (Tarver 1985, 1987). It is not volatile, is unaffected by pH (4–14), has an average half-life of 20 days and is decomposed by ultra-violet light into non-herbicidal, non-toxic products. It is not deactivated by adsorption onto suspended organics or clay particles, hence it is effective in turbid waters. It acts by interrupting carotenoid synthesis and since carotenoids seem to protect chlorophyll from photo-degradation by UV light, affected plants show symptoms of bleaching (chlorosis). Fluridone is a systemic herbicide and plants will absorb it via the leaves and shoots and the roots. Control normally takes 30–90 days and this slow action helps prevent oxygen depletion of the water due to massive decomposition of dead vegetation. Control is best achieved during periods of active growth. To control cabomba in Florida, but to avoid damage to other susceptible plants such as lilies, a very early spring application (January–March) is used. Toxicity to fish occurs at about 7.6–22 ppm and to invertebrates at circa 1.4–4.4 ppm (the normal application rate concentration is around 0.1 ppm). The US Environmental Protection Authority has concluded that Sonar® does not pose a risk as a chronic or acute toxicant in aquatic systems. Only the slow release formulation (release occurring over 7–14 days) is approved for rivers by the US EPA and control is poor if it is applied during rapid flow conditions. In still waters a spreader / sinking agent is recommended (Tarver 1987). When used in northern Queensland on Lesley Creek in an experimental field application, cabomba control was ineffective, perhaps due to the application being into moving water. Sonar is not commercially available in Australia.

In south-east Queensland before 1992, no attempt had been made to control or eradicate cabomba infestations because it had appeared non-invasive and there were no suitable herbicides registered for use. With the advent of the weed in two water storages, it was realised effective control methods were required. As a result an effective and relatively cheap chemical control for cabomba has been devised (Diatloff and Anderson 1995). 2,4-D n-butyl ester plus diatomaceous earth is mixed at 1 part to 20 parts of water and injected 2 m below the water surface through a series of weighted nozzles to achieve a final concentration of 10 ppm clay / 2,4-D active ingredient. This method of application allows the mixture to spread sideways to provide a blanket cover of the area being treated and completely cover the plant, which takes up the herbicide through its leaves and stems. It is important that the approximate depth of the area being treated is known so that the volume of water to be treated can be estimated to allow the correct application rate. In trials in the Ewen Maddock Dam this method provided effective control of cabomba within a matter of days and 2,4-D is now registered in Queensland for use against cabomba.

Fluridone was also assessed as a herbicide for cabomba in these trials but gave almost no control. The reasons for this clearly require more research, but fluridone is totally water soluble and in the trials it appeared to dissipate completely throughout the water body before any control could be effected. This may also explain why previous attempts at control using 2,4-D have given erratic results. A water soluble form may have been used. In contrast 2,4-D ester is emulsifiable, not water soluble and is adsorbed onto the diatomaceous earth, so it does not disperse very far. This enables quite precise control in applying the herbicide and localization of the area being treated. The 2,4-D is quite selective in its action: other species present during the trials were not affected except for water lilies, which quickly re-colonized from adjacent areas (Diatloff and Anderson 1995).

With careful application and attendance to ensuring the required concentration of active ingredient is met, it may also be feasible to use this method to control cabomba in slowly flowing streams and it should certainly be applicable to still water canals. In the case of infestations in irrigation canals, problems with using 2,4-D could arise as many crops are susceptible to the herbicide. However, if the canal can be bypassed, isolating the infestation, and its use withheld for a period, control work can be carried out. Before bringing the canal back on line, bioassays can be performed using very sensitive test plants to ensure no subsequent damage to crops when the canal is brought back online. Since the half-life of 2,4-D in most aquatic systems is quite short, canals may only need to be off-line for relatively short periods.

The use of 2,4-D in potable water supplies may cause some concerns. However, when properly used, it is non-persistent in the environment at harmful levels and does not accumulate in food chains (Gangstad 1986). If used away from the take-off points, or if the reservoir can be taken off-line for a while, with close monitoring, its use for the control of cabomba may be acceptable.

Drawdown

Laboratory experiments have shown that drawdown, with subsequent drying of the hydrosoil, may be an effective management tool. In the field, extreme temperatures accompanying the drying out are likely to render drawdown even more effective. If drawdown is used as a management technique, water removal should be complete (Sanders 1979).

For several years drawdown has been used as a management tool for aquatic weeds in Louisiana and is considered the only economic method (Manning and Sanders 1975). Drawdowns of 1.5–2.5 m have given 90% control of many weeds, including cabomba, but unfortunately have enhanced the spread of water hyacinth and alligator weed. Tarver and Sanders (1977) showed that consecutive autumn-winter drawdowns yielded a 99% reduction of cabomba in Black Lake, Louisiana but cabomba re-established after the lake refilled, due to the germination of seedlings. In Louisiana a complete winter drawdown is the best way to manage cabomba, although results are dependent on weather conditions during drawdown (Manning and Sanders 1975).

In the USA the use of drawdown has been controversial, owing to the economic losses ensuing from the temporary deprivation of fishing rights, boating facilities and hunting. Since the effective use of drawdown depends on the weather during the drawdown period, these losses may not be balanced by effective weed control, so proper timing is essential. During drawdown, cabomba fragments capable of growth may get carried or washed into the shallow remaining areas, and become rooted. These areas then act as refuges for the weed, resulting in rapid reinfestation (Sanders 1979).

In Australia, economic losses from drawdown are not the same as in the USA, as water bodies are not so intensively used for recreational purposes. However, water, particularly potable water, is a scarce resource in Australia and drawdown may not be acceptable for this reason. If it is an acceptable treatment, drawdown is the best available option for cabomba control, particularly in potable water supplies. Generally the thick silt in which cabomba becomes rooted takes a long time to dry, so in the wet tropics where much of the current Queensland infestation is found, drawdown would be best carried out in winter. If drawdown is used, it may require supplementary treatments to guarantee weed control. Diuron can be sprayed on the exposed root bases to enhance and speed control and it is registered in Queensland for use in this type of situation. Alternatively 2,4-D n-butyl ester can be used.

In Queensland, two drawdowns (of 4 and 7 m respectively) have been used to control cabomba in the Ewen Maddock Dam. The first gave incomplete control due to heavy rains partially refilling the dam. The second drawdown was more successful as the dam was dry for 4–5 months and most plants were killed. With partial refilling, two small reinfestations were noticed which were brought under control by hand pulling plants.

Other treatments

Mechanical control methods can be very effective for aquatic weeds and are the most popular control method in Japan, but only temporary control is provided and this is expensive (Oki 1992). In the USA mechanical techniques have proven ineffective (Madsen 1996). McComas (1994) provides a comprehensive survey of mechanical control methods, many of which could be used against cabomba. Cabomba does not root deeply and can easily be lifted out by the roots, although in deeper water this operation has to be carried out by divers. A suction dredge has been devised for use in the Ewen Maddock Dam (P. Bell, R. Rainbird personal communication) and a mechanical harvester has been used for control of cabomba in Lake MacDonald (Garraty *et al.* 1996). The mechanical harvester used in Lake MacDonald effectively halved the cabomba standing crop (from 48.7 to 25.9 t ha^{-1}) but in three weeks cabomba had grown back to pre-cut levels (51.9 t ha^{-1}).

Cabomba grows well in nutrient rich waters and is an efficient utilizer of dissolved phosphate. In these situations harvesting of cabomba may lead to an increase in water quality due to a reduction in dissolved phosphate and nitrate in the water (Anderson *et al.* 1996, Garraty *et al.* 1996). The removed material may be used for composting, but if the amounts removed are quite small, this may not be a financial proposition, nor may it be necessary as cabomba placed on the bank decomposes in 3–4 weeks.

A problem with using mechanical controls against cabomba is that the plant easily fragments and these fragments can float away and recolonize the treated area or invade adjacent non-weedy areas. As a consequence, mechanical harvesting is not suitable for small or new infestations, but may be the only acceptable method for large infestations in potable water supplies. Fragmentation is minimized by using a suction dredge and, additionally, the whole plant is removed, including the root ball.

For infestations in small creeks and irrigation canals, control through shading may be viable, although cabomba does appear to grow well at low light intensities. Adequate bankside vegetation can provide sufficient shade to stop submerged aquatic plants from growing (Dawson 1989). If the weed beds are localized, a temporary covering of the affected area by black shading fabric can effectively control the plants (Dawson 1989). This option may be particularly suitable for infested irrigation canals, although weed fragments must be contained to avoid infestation away from the treated area.

Natural enemies

Chinese grass carp (white amur, *Ctenopharyngodon idella* (Val.)) is an effective biological control agent for cabomba. It has been used in Arkansas, apparently with no adverse effects on fish and waterfowl populations. It is very effective, as the fish can ingest several times its own body weight per day of submerged vegetation. In Arkansas, fish stocked at 22 fish ha^{-1} gave complete cabomba control in less than five years. In a Florida lake, control was achieved in two years by a residual population of 84 kg ha^{-1} (17 fish) and the only changes attributable to grass carp were an increase in nitrate-nitrite, presumably due to the decomposition of faecal plant material from the fish. Native fish populations did change, but with no discernible pattern in relation to carp populations (Beach *et al.* 1978).

In South Carolina, sterile (triploid) grass carp are being used to control *Hydrilla* and *Elodea* (de Kozlowski 1991). Sterility is ensured through fish being checked by three different facilities. Carp with a minimum length of 25 cm are stocked at a rate of 60 per vegetated hectare.

Whilst grass carp appear to be an effective biological control agent for aquatic weeds such as cabomba and their effect on native ecosystems can be reduced by using sterile triploids, their release into Australian waters is not likely to be acceptable due to their general herbivorous habit, their pest potential, and infestations of cabomba being insufficient to warrant consideration of carp as a control agent.

Invertebrate herbivores of cabomba are poorly known; the larva of the moth *Paraponyx diminutalis* Snellen attacks cabomba (Buckingham and Bennett 1989) but also attacks a wide range of other aquatic plants and is probably unsuitable as a biological control agent. Adults of the larval leaf-mining fly *Hydrellia balciunasi* Bock have been recorded from cabomba in Queensland (Balciunas and Burrows 1996). The polyphagous snail *Marisa cornuarietis* (L.) was reported as feeding on an unidentified cabomba species in laboratory tests in Puerto Rico by Ferguson and Butler (1966).

Revilla *et al.* (1991) reported the presence of the free-living nematodes *Dorylaimus* spp., *Rhabditis* spp. and *Mononchus* spp. on aquarium collections of cabomba from Malaysia, but these genera are commonly found on aquatic plants.

Management strategies

There are two major problems constraining action in relation to cabomba. Firstly, new infestations are difficult to detect since inspections for this type of weed are not regularly made and, as a fully submerged aquatic plant, it is not easy to see until the affected area is quite large. Secondly, it grows very quickly and is highly invasive. Unless early control is initiated, the weed quickly establishes throughout the system and eradication is a hopeless task.

The first constraint could be met through the development of an adequate and easily used detection system for submerged aquatic weeds. The SAVEWS system for the hydro-acoustic detection and mapping of submerged water plants being developed by the Tennessee Valley Authority and the US Army Corps of Engineers (Sabol and Melton 1995) is worthy of consideration for the easy detection of cabomba infestations in impoundments. Integrating the regular use of such a monitoring system into the routine management of reservoirs and impoundments would go a long way to meeting the second constraint through enabling early control efforts.

Control practices need to be integrated into the general management of the impoundment, canal or river. Since cabomba is likely to be able to establish in farm dams, landholders also need to be aware of this potential and integrate checks for the weed into their general property management plan.

The control practices used must be tailored to the particular type of water body being treated. In a potable water supply, very regular mechanical harvesting may be the only viable method. If an impoundment can be taken off-line, then a suitably timed drawdown and a chemical treatment of the root mass may be an available option. If drawdown is not an available option, the infestation may be thinned by an initial chemical treatment and the remaining plants removed by hand. If impoundments flow, or could overflow, into catchment headwaters, containment plans must be put into place which will stop cabomba washing into the river system.

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