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- Clout, M. N., and P. A. Williams, eds. 2009. *Invasive Species Management: A Handbook of Techniques*. Oxford: Oxford University Press.
- Genovesi, P. 2007. Limits and potentialities of eradication as a tool for addressing biological invasions (385–400). In W. Nentwig, ed. *Biological Invasions*. Ecological Studies, Vol. 193. Heidelberg: Springer-Verlag.
- McNeely, J. A. 2001. *The Great Reshuffling: Human Dimensions of Invasive Alien Species*. Gland, Switzerland: IUCN.
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# EUCALYPTS

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Over 800 species of eucalypts (*Angophora*, *Corymbia*, and *Eucalyptus*) are native to Australia and a few Pacific islands. These genera include some of the most important solid timber and paper pulp forestry trees in the world. Besides pines, eucalypts are the most commonly and widely cultivated exotic trees. Almost 20 million ha (200,000 km<sup>2</sup>) of eucalyptus plantations exist in tropical, subtropical, and temperate countries. In many countries, eucalypts are the most common and conspicuous nonnative trees. Over 70 species are naturalized (reproduce and maintain their populations) outside their native ranges. However, given the extent of cultivation, eucalypts are markedly less invasive than many other widely cultivated trees and shrubs. Reasons for this relatively low invasiveness are still not completely understood. Conclusions about positive or negative environmental and economic impacts of eucalypts are often anecdotal, highly controversial, and context-dependent.

## TAXONOMY, GROWTH FORMS, REGENERATIVE STRATEGIES, AND HABITATS

Eucalypts (family Myrtaceae, subfamily Leptospermoideae) are currently classified into three genera: *Angophora* (14 species), *Corymbia* (113 species), and *Eucalyptus*

(>740 species). *Angophora* and *Corymbia* are often treated as subgenera of *Eucalyptus*, sensu lato. The genus *Eucalyptus* (sensu stricto) is currently divided into ten subgenera, six of which are monotypic (having only one species). Naturalized eucalypts belong almost exclusively to the two largest subgenera, *Eucalyptus* (*Monocalyptus*, >140 species) and *Symphyomyrtus* (>360 species) (Table 1).

Most eucalypts are trees (10 to >50 m in height), some are “mallees” (multistemmed from ground level, usually <10 m in height), and a few are shrubs. Eucalypts are the tallest nonconiferous trees in the world. Several species (*E. regnans*, *E. grandis*, *E. deglupta*) reach more than 70 m in height. The tallest known specimen of *E. regnans* was 110 m. The tallest known living specimen of this taxon in Tasmania is 99.6 m tall. The maximum age of eucalypt species, estimated from dendrochronological (tree-ring) and radiocarbon measurements, is between 400 and 600 years. Interestingly, in spite of the otherwise enormous range of adaptations among eucalypts, shade-tolerant subcanopy species are not known.

The eucalypt breeding system is one of mixed mating with preferential outcrossing. A reduction in fruit (capsule) production, seed set, and seedling vigor has been demonstrated after self-pollination. However, eucalypts generally do not need any special pollinators. They are pollinated by many species of bees and wasps and, to a lesser extent, by birds, mammals, and wind.

Most eucalypts are well adapted to frequent fires. The most common adaptations are lignotubers and epicormic buds. The lignotuber is a woody swelling at the base of the stem; most eucalypts sprout from lignotubers. The epicormic buds (buds present in the outer bark) allow the sprouting of new branches from stems (after a fire or after a severe winter). Some species are able to sprout from both lignotubers and stems (combination sprouters). Another adaptation to fireprone environments is serotiny (most seeds are kept in fruits and released only after fire). Some successful invaders among eucalypts are obligate seeders, depending completely on seed production (*E. conferruminata*, *E. grandis*). Seeds can be shed in large numbers (up to 4,000 seeds per m<sup>2</sup>). However, eucalypts produce very small seeds, usually 1–3 mm long and less than 2 mg. Some species have seeds even lighter than 0.5 mg (e.g., *E. grandis* and *deglupta*). Eucalypts produce seeds with no obvious endosperm (tissue that surrounds and nourishes the embryo). Therefore, the newly emerged seedlings are sustained by cotyledon photosynthesis, and their roots have to reach suitable substrate very soon.

Eucalypts are the dominant species of the wet coastal and near coastal parts of Australia. However, some species

TABLE 1  
Naturalized Species of *Corymbia* and *Eucalyptus*

|                          |                                               |                                                                                                                                                                                                                                                                                                              |
|--------------------------|-----------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| <b><i>Corymbia</i></b>   |                                               |                                                                                                                                                                                                                                                                                                              |
| <i>calophylla</i>        | C, LS                                         | Australia (Western Australia), Hawaii?, New Zealand?                                                                                                                                                                                                                                                         |
| <i>citriodora</i>        | B, LS                                         | Australia (Victoria, Western Australia), California, Hawaii?, India, South Africa, Zimbabwe                                                                                                                                                                                                                  |
| <i>ficifolia</i>         | C, LS                                         | Hawaii, New Zealand, South Africa                                                                                                                                                                                                                                                                            |
| <i>maculata</i>          | B, LS                                         | Australia (Victoria, Western Australia), South Africa?                                                                                                                                                                                                                                                       |
| <i>torelliana</i>        | B, LS                                         | Australia (Queensland), China, Florida                                                                                                                                                                                                                                                                       |
| <b><i>Eucalyptus</i></b> |                                               |                                                                                                                                                                                                                                                                                                              |
| <i>botryoides</i>        | S, CS                                         | Australia (Norfolk Island, South Australia, Victoria, Western Australia), Hawaii, New Zealand                                                                                                                                                                                                                |
| <i>bridgesiana</i>       | S, LS                                         | Hawaii, South Africa?                                                                                                                                                                                                                                                                                        |
| <i>camaldulensis</i>     | S, CS/SS                                      | Argentina?, Australia (Western Australia) Bangladesh, California, <sup>a,b</sup> Cyprus, France, Greece, Hawaii, <sup>a</sup> India, Israel, Italy, Pakistan, Portugal, Spain, <sup>a,b</sup> South Africa, <sup>a,b</sup> Zimbabwe                                                                          |
| <i>cinerea</i>           | S, LS                                         | Hawaii, New Zealand, South Africa                                                                                                                                                                                                                                                                            |
| <i>cladocalyx</i>        | S, SS                                         | Australia (Victoria, South Australia, Western Australia <sup>b</sup> ), California, Hawaii?, South Africa <sup>a</sup>                                                                                                                                                                                       |
| <i>conferruminata</i>    | S, OS, often confused with <i>E. lehmanii</i> | Australia (Victoria, Western Australia), California, South Africa <sup>a,b</sup>                                                                                                                                                                                                                             |
| <i>crebra</i>            | S, LS                                         | Hawaii, South Africa?                                                                                                                                                                                                                                                                                        |
| <i>deanei</i>            | S, LS                                         | Hawaii, South Africa?                                                                                                                                                                                                                                                                                        |
| <i>degupta</i>           | S, OS                                         | Hawaii, Malaysia?                                                                                                                                                                                                                                                                                            |
| <i>delegatensis</i>      | E, OS                                         | New Zealand, South Africa?                                                                                                                                                                                                                                                                                   |
| <i>elata</i>             | E, LS                                         | New Zealand, South Africa?                                                                                                                                                                                                                                                                                   |
| <i>fastigata</i>         | E, OS                                         | California, New Zealand, South Africa                                                                                                                                                                                                                                                                        |
| <i>globulus</i>          | S, CS, incl. <i>E. maidenii</i>               | Australia (Western Australia), Azores, California, <sup>a,b</sup> Canary Islands, Chile, <sup>a</sup> China, <sup>a</sup> France, Hawaii, <sup>b</sup> India, Italy?, Jamaica, New Zealand, <sup>a,b</sup> Peru, <sup>b</sup> Portugal, <sup>a</sup> Spain, <sup>a</sup> South Africa, <sup>a</sup> Zimbabwe |
| <i>gomphocephala</i>     | S, SS                                         | Australia (Victoria), Cyprus, Hawaii, South Africa, Spain                                                                                                                                                                                                                                                    |
| <i>grandis</i>           | S, OS                                         | Argentina?, California, Florida, New Zealand, Nigeria?, South Africa <sup>a,b</sup>                                                                                                                                                                                                                          |
| <i>gunnii</i>            | S, LS                                         | New Zealand, Portugal, Spain                                                                                                                                                                                                                                                                                 |
| <i>leucosylon</i>        | S, LS                                         | Australia (Victoria), New Zealand?, South Africa                                                                                                                                                                                                                                                             |
| <i>longifolia</i>        | S, LS                                         | Australia (New South Wales), South Africa?                                                                                                                                                                                                                                                                   |
| <i>macarthurii</i>       | S, LS                                         | California, New Zealand, South Africa?                                                                                                                                                                                                                                                                       |
| <i>marginata</i>         | E, LS                                         | Hawaii, South Africa?                                                                                                                                                                                                                                                                                        |
| <i>microcorys</i>        | S, LS                                         | Australia (Western Australia), Hawaii, <sup>a</sup> Sri Lanka, South Africa, Zimbabwe                                                                                                                                                                                                                        |
| <i>muelleriana</i>       | E, LS                                         | Australia (Western Australia), New Zealand?, South Africa?                                                                                                                                                                                                                                                   |
| <i>nitens</i>            | S, SS                                         | New Zealand, South Africa? <sup>a</sup>                                                                                                                                                                                                                                                                      |
| <i>obliqua</i>           | E, LS                                         | New Zealand, South Africa                                                                                                                                                                                                                                                                                    |
| <i>occidentalis</i>      | S, LS                                         | Australia (Victoria), South Africa?                                                                                                                                                                                                                                                                          |
| <i>ovata</i>             | S, LS                                         | California, New Zealand                                                                                                                                                                                                                                                                                      |
| <i>paniculata</i>        | S, LS                                         | Hawaii, <sup>a</sup> South Africa, <sup>a</sup> Zimbabwe                                                                                                                                                                                                                                                     |
| <i>pilularis</i>         | E, OS                                         | Hawaii, <sup>a</sup> New Zealand, South Africa                                                                                                                                                                                                                                                               |
| <i>polyanthemos</i>      | S, LS                                         | Australia (Western Australia), California, South Africa?                                                                                                                                                                                                                                                     |
| <i>pulchella</i>         | E, LS                                         | California, New Zealand                                                                                                                                                                                                                                                                                      |
| <i>regnans</i>           | E, OS                                         | New Zealand, South Africa?                                                                                                                                                                                                                                                                                   |
| <i>resinifera</i>        | S, LS                                         | Hawaii, Mexico?, New Zealand                                                                                                                                                                                                                                                                                 |
| <i>robusta</i>           | S, OS                                         | Brazil?, California, Florida, France, Hawaii, <sup>a</sup> La Réunion Island, Madagascar, <sup>a</sup> Malaysia?, New Zealand, Portugal, South Africa, Spain, Sri Lanka, Zimbabwe <sup>a,b</sup>                                                                                                             |
| <i>rudis</i>             | S, LS                                         | California?, Hawaii                                                                                                                                                                                                                                                                                          |
| <i>saligna</i>           | S, LS                                         | Australia (Western Australia), Florida, Hawaii, <sup>a</sup> New Zealand, South Africa?, Sri Lanka,?, Uganda?                                                                                                                                                                                                |
| <i>salubris</i>          | S, OS                                         | Australia (Queensland), South Africa                                                                                                                                                                                                                                                                         |
| <i>sideroxylon</i>       | S, CS                                         | Botswana?, California, Hawaii, New Zealand, Portugal, South Africa, <sup>a</sup> Spain                                                                                                                                                                                                                       |
| <i>sieberi</i>           | E, SS                                         | New Zealand, South Africa                                                                                                                                                                                                                                                                                    |
| <i>tereticornis</i>      | S, LS                                         | California, Cyprus, Hawaii, India, <sup>a</sup> Mexico (reported as <i>E. resinifera</i> ), New Zealand?, South Africa, Zimbabwe                                                                                                                                                                             |
| <i>viminalis</i>         | S, LS                                         | California, Hawaii, New Zealand, South Africa?                                                                                                                                                                                                                                                               |

NOTE: Naturalized (reproducing and maintaining populations without human help) species of *Corymbia* and *Eucalyptus*. Based on published records, labels on herbarium specimens, information from experienced botanists and foresters, and personal observations. Question marks indicate lack of certainty as to whether the species is already naturalized, or is just a casual resident. Only species reported as naturalized from at least two countries are included. Subgenera: B – *Blakella*, C – *Corymbia*, E – *Eucalyptus* (*Monocalyptus*), S – *Symphyomyrtus*. Regenerative strategies: LS – lignotuber sprouter, SS – stem sprouter, CS – combination sprouter, OS – obligate seeder.

<sup>a</sup> Extensive planting.

<sup>b</sup> Species is classified as invasive in a particular state (spreading spontaneously away from points of introduction).

(*E. rameliana*, *E. pachyphylla*) extend to arid regions with annual precipitation below 350 mm. Within their native range, most eucalypt species grow in tall forests, woodlands, and savannas. Seasonal flooding is essential for successful regeneration of some species (*E. camaldulensis*). Over 20 species of eucalypts can grow on saline soils (e.g., *E. robusta* in swampy estuarine habitats or *E. camaldulensis* in valleys of old river systems). Some small trees or shrubs (e.g., *E. coccifera* or *E. pauciflora* subsp. *niphophila*) are adapted to subalpine areas (900–1,400 m) in Australia.

CULTIVATION

When Australia was settled in the eighteenth century, eucalypts were used for farm buildings, fencing, and firewood. The first eucalypt species to be cultivated from seeds outside its native range was *E. obliqua* in Royal Botanic Gardens at Kew, United Kingdom, in 1774. Other species were soon cultivated in botanical gardens and arboreta

TABLE 2  
Naturalized *Corymbia* and *Eucalyptus* by Regenerative Strategies

| Subgenus             | Number of Species | Regenerative Strategy | Number of Species |
|----------------------|-------------------|-----------------------|-------------------|
| <i>Blakella</i>      | 3                 | Lignotuber sprouters  | 28                |
| <i>Corymbia</i>      | 2                 | Stem sprouters        | 4 (1 invasive)    |
| <i>Eucalyptus</i>    | 10                | Combination sprouters | 4 (2 invasive)    |
| <i>Symphyomyrtus</i> | 30 (6 invasive)   | Obligate seeders      | 9 (3 invasive)    |

NOTE: Numbers of naturalized *Corymbia* and *Eucalyptus* species by subgenera and by regenerative strategy. Only species reported as naturalized in at least two countries are included. Derived from Table 1.

in Europe as botanical curiosities and ornamentals. Once in cultivation, eucalypts appealed to foresters because of their fast growth (even on nutrient-poor soils) and because they yielded a variety of timber and nontimber products. Productivity of properly designed plantations is 20–70 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup>. Today, eucalypts provide saw timber, plywood, fiberboard, pulp for paper, poles, firewood, charcoal, essential oils, honey, and shelter. They are also considered to be suitable trees for biofuel production.

To date, the total area of eucalyptus plantations has been increasing exponentially. The global extent of eucalypt planting outside Australia reached 15.6 million ha in the 1990s—more than four times the global total in the 1970s. In 2008, the total area of eucalyptus plantations was estimated at 19.6 million ha. This is an area larger than the state of Washington, or the nations of Austria and Hungary together. Only one genus of trees is more extensively cultivated than eucalypts: *Pinus* (pines), with a global plantation

area of more than 52 million ha. The most commonly cultivated eucalypt is probably *E. globulus* (Tasmanian blue gum, with 2.3 million ha worldwide in 2008). *Eucalyptus globulus* is the primary source of global eucalyptus oil production, with China being the largest commercial producer. The other three most commonly cultivated eucalypts are *E. camaldulensis* (river red gum), *E. grandis* (flooded gum), and *E. tereticornis* (forest red gum). Current estimates of areas of eucalyptus plantations on individual continents and in Oceania are summarized in Table 3. The American statistic is dominated by Brazil, with over 3.5 million ha of plantations, while in Asia the leader is India, with over 5 million ha, including small cultivations on farms.

Eucalypt planting has accelerated recently in many tropical countries. However, extensive planting in the humid tropics has been inhibited by the incidence of pathogens and insect pests. Only a few species, such as *E. deglupta*, *E. pellita*, and *E. urophylla*, appear to be adapted to hot, humid environments. Eucalypts, because of their rapid growth and capacity for producing biomass, have been recently widely mentioned as feedstock for biofuels (e.g., *E. globulus*, *E. grandis*, *E. robusta*, *E. saligna*, *E. urophylla*). Widespread use for this purpose could substantially increase propagule pressure and increase the probability of local invasions.

ARE EUCALYPTS INVASIVE?

Eucalypts have enjoyed a history of widespread planting similar to that of pines. Given this, and the many species involved (with representatives of most of the major taxonomic and functional groups in the genus), we would expect to find the full range of outcomes: everything from taxa that are highly invasive and cover large areas as invaders to species that fail to recruit any offspring. Indeed, eucalypts, like pines, are prominent species on many national or regional weed lists in many parts of the world. However, they have been orders of magnitude less successful as

TABLE 3  
Areas of Eucalyptus Plantations beyond Their Native Range in 2008

| Million ha |     |                                                          |
|------------|-----|----------------------------------------------------------|
| Asia       | 8.3 | (India: >5.0; China: >2.0; Vietnam: >1.0)                |
| Americas   | 6.4 | (Brazil: >3.6; Chile: >0.3; Argentina: >0.2; Peru: >0.2) |
| Africa     | 2.2 | (South Africa: >0.4; Angola: >0.2; Morocco: >0.2)        |
| Europe     | 1.3 | (Portugal: >0.6; Spain: >0.5; Italy: >0.07)              |
| Oceania    | 0.9 |                                                          |

NOTE: <http://git-forestry-blog.blogspot.com/2008/09/eucalyptus-global-map-2008-cultivated.html> and other sources.



**FIGURE 1** A stand of *Eucalyptus globulus* on Santa Cruz Island, California. Saplings of eucalypts are usually found only close to plantations. (Photograph courtesy of M. Rejmánek.)

invaders than pines and several other widely planted trees, including many fleshy-fruited trees (e.g., *Elaeagnus angustifolia*, *Ligustrum* spp., *Psidium* spp., *Morella* (*Myrica*) *faya*) and legumes (e.g., *Acacia* spp., *Prosopis* spp., *Leucaena leucocephala*). Where eucalypts have invaded, they have very seldom spread considerable distances from planting sites, and their regeneration is frequently sporadic (Fig. 1). Given that many eucalypts produce very large quantities of seeds, and in light of their diverse adaptations for dealing with disturbance (notably fire), their poor (or at best mediocre) performance as invaders is enigmatic. Many other Australian trees, including taxa that evolved under the same conditions as *Eucalyptus*, are much more invasive in other parts of the world (e.g., *Melaleuca quinquenervia*, *Hakea* spp., and many species of *Acacia*). What makes this difference? Are eucalypts inherently less invasive, or are they just a ticking time bomb? There seem to be three major reasons for the limited invasiveness of eucalypts: (1) relatively limited seed dispersal, (2) high mortality of seedlings, and (3) lack of compatible ectomycorrhizal fungi.

**RELATIVELY LIMITED SEED DISPERSAL.** Seeds of planted eucalypts are very small, but they have no adaptations for dispersal (wings or fleshy tissues) that would help them to proceed from local establishment (naturalization) to invasion. The passive release of seeds is undoubtedly aided by wind. However, all rigorous studies of eucalypt seed dispersal and seedling spatial distribution show that in general, seeds are dispersed over quite short distances. This is in agreement with measurements of terminal descent velocities of their seeds. While terminal velocities of seeds of invasive pine species are between 0.7 and 1.5 m s<sup>-1</sup>, and for invasive maples (*Acer*) between 0.9 and 1.2 m s<sup>-1</sup>, terminal velocities of seeds of all tested eucalypt species are between

2.0 and 5.5 m s<sup>-1</sup>. Lower terminal velocity values mean that seeds can be carried by winds for longer distances.

**HIGH MORTALITY OF SEEDLINGS.** As noted above, eucalypts produce very small seeds (usually <2 mg) with no obvious endosperm. Therefore, the newly emerged seedlings are sustained by cotyledon photosynthesis, and their roots have to penetrate into suitable wet substrate very quickly. As a result, eucalypts can successfully regenerate from seeds only on wet, bare soil free of litter. However, seedlings in wet environments frequently die because of damping off caused mainly by parasitic fungi (*Botrytis*, *Colleotrichum*, *Cylindrocladium*, *Fusarium*) and water molds—oomycetes (*Phytophthora*, *Pythium*). Moreover, if there is any dense vegetation around, tiny eucalyptus seedlings are necessarily losers. Therefore, the window of opportunity for eucalyptus seedlings is rather narrow.

**LACK OF COMPATIBLE ECTOMYCORRHIZAL FUNGI.** It seems that the majority, if not all, of ectomycorrhizal fungi (EM) associated with eucalypts outside Australia are Australian species that have spread with their hosts. However, the importance of EM for establishment, growth, and spread of introduced eucalypts is not clear. There has been no example reported from exotic eucalypts that can compare with the dramatic response to mycorrhizal inoculation reported from exotic pine seedlings in Australia or South Africa in the early years of their introduction. With their more finely branched root systems and evolutionary adaptation to low phosphorus soils, eucalypts seem to be less dependent on EM than pines. The lack of EM may be not important for seedlings transplanted from nurseries, but, as some ecologists have suggested, it may be crucial for spontaneous establishment of seedlings away from plantations. However, colonization of eucalypt roots usually does not start with EM, but with ubiquitous nonspecific vesicular-arbuscular endomycorrhizae (AM) (*Gigaspora* spp., *Glomus* spp.). It is possible that AM play a more important role in initial eucalypt seedling establishment than EM.

Finally, we may ask whether some eucalypt species are inherently more invasive than others. Or is it only propagule pressure (the extent of planting) that makes some species more often naturalized, and some of them even somewhat invasive (spreading spontaneously over 100 m from points of introduction)? Tables 1 and 2 show that the majority of species naturalized in at least two countries (30) belong to the subgenus *Symphyomyrtus*. This seems to be just proportional to the size of this subgenus (>360 species). Still, all six species that can be classified as invasive in at least one



**TABLE 4**  
*Eucalyptus* Species with No Conclusive Evidence of Naturalization

| Species             | Subgenus                                  | Regenerative Strategy |
|---------------------|-------------------------------------------|-----------------------|
| <i>acmenoides</i>   | <i>Eucalyptus</i> ( <i>Monocalyptus</i> ) | Lignotuber sprouter   |
| <i>bosistoana</i>   | <i>Symphyomyrtus</i>                      | Lignotuber sprouter   |
| <i>erythrocorys</i> | <i>Eudesmia</i>                           | Lignotuber sprouter   |
| <i>fraxinoides</i>  | <i>Eucalyptus</i> ( <i>Monocalyptus</i> ) | Obligate seeder       |
| <i>jacksonii</i>    | <i>Eucalyptus</i> ( <i>Monocalyptus</i> ) | Lignotuber sprouter   |
| <i>macranda</i>     | <i>Symphyomyrtus</i>                      | Lignotuber sprouter   |
| <i>pauciflora</i>   | <i>Eucalyptus</i> ( <i>Monocalyptus</i> ) | Lignotuber sprouter   |
| <i>preissiana</i>   | <i>Eucalyptus</i> ( <i>Monocalyptus</i> ) | Lignotuber sprouter   |
| <i>pulverulenta</i> | <i>Symphyomyrtus</i>                      | Lignotuber sprouter   |
| <i>punctata</i>     | <i>Symphyomyrtus</i>                      | Lignotuber sprouter   |
| <i>radiata</i>      | <i>Eucalyptus</i> ( <i>Monocalyptus</i> ) | Lignotuber sprouter   |
| <i>smithii</i>      | <i>Symphyomyrtus</i>                      | Lignotuber sprouter   |
| <i>spathulata</i>   | <i>Symphyomyrtus</i>                      | Obligate seeder       |
| <i>torquata</i>     | <i>Symphyomyrtus</i>                      | Lignotuber sprouter?  |

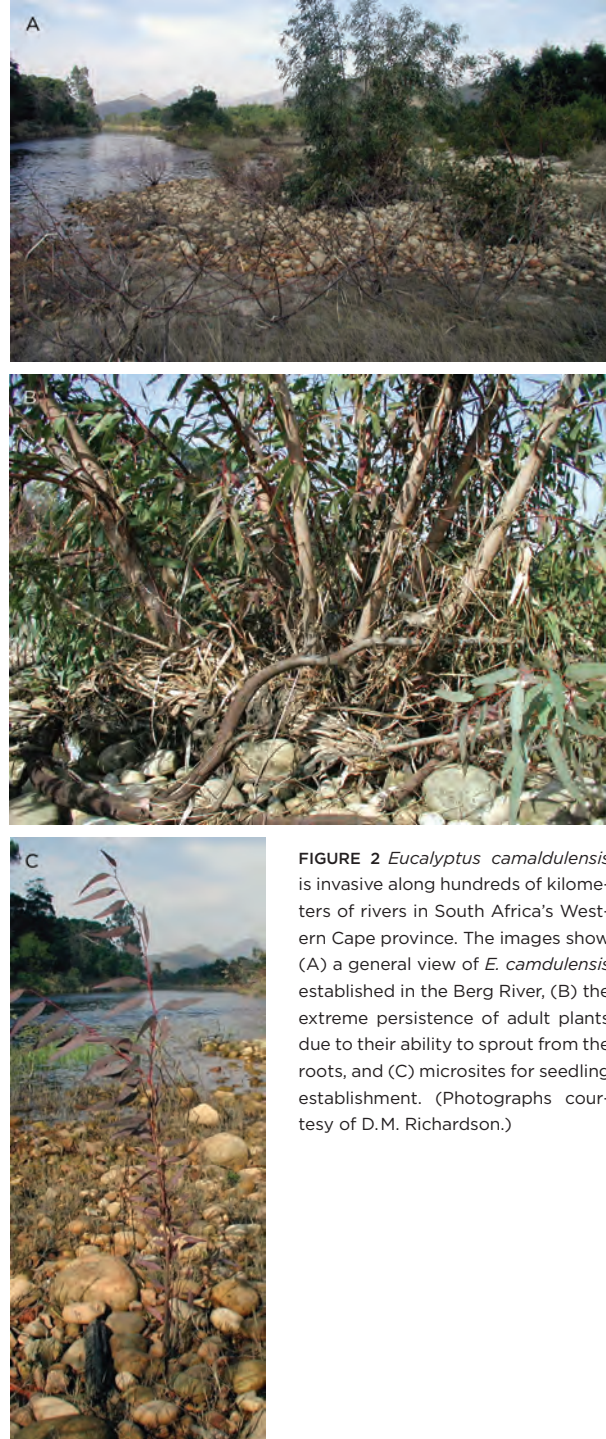
NOTE: Commonly cultivated *Eucalyptus* species with no conclusive evidence of naturalization. Species listed here are relatively commonly cultivated or tested, but the extent of their cultivation is still very limited when compared with many major plantation species listed in the Table 1. Therefore, “no conclusive evidence of naturalization” does not necessarily mean conclusive noninvasiveness.

country belong exclusively to the subgenus *Symphyomyrtus*. There seems also to be a somewhat larger proportion of subgenus *Eucalyptus* species among commonly planted eucalypts with no evidence of naturalization (Table 4). On average, seeds of species in the subgenus *Symphyomyrtus* are smaller (a notable exception, however, is *E. globulus*) than seeds of species in the second largest subgenus—*Eucalyptus* (>140 species). Therefore, terminal velocities of *Symphyomyrtus* seeds should be less, and they could be dispersed somewhat longer distances by wind. Also, none of the species classified as invasive in at least one country is a straight lignotuber sprouter (LS). This could also point to the primary importance of seed dispersal in invasiveness. Nevertheless, the more straightforward explanation is that species classified as invasive have been planted more extensively (see notes in Table 1). Then, however, reasons for their extensive planting may be correlated with their growth and timber characteristics that are associated with particular regenerative strategies.

## ENVIRONMENTAL CONTROVERSIES AND CONTROL METHODS

Considering the amount of planting, eucalypts are relatively noninvasive species. If their potential spread is the only concern, then eucalypts should not be planted near rivers and streams. Temporarily flooded or eroded banks are suitable habitats for spontaneous establishment of their seedlings (Fig. 2). Moreover, their seeds can be dispersed for long distances by running water. However, there are other concerns.

Of all widely used plantation species, eucalypts have attracted by far the most criticism. There are four main concerns: (1) excessive water use and suppression of food crops growing nearby, (2) suppression of ground vegetation (possible allelopathic effects) and resulting soil erosion, (3) increased fire hazard, and (4) generally poor wildlife value. There is some substance to each of these concerns.



**FIGURE 2** *Eucalyptus camaldulensis* is invasive along hundreds of kilometers of rivers in South Africa's Western Cape province. The images show (A) a general view of *E. camdulensis* established in the Berg River, (B) the extreme persistence of adult plants due to their ability to sprout from the roots, and (C) microsites for seedling establishment. (Photographs courtesy of D.M. Richardson.)

Nevertheless, it is important to realize that in many tropical countries, where eucalypts are grown on degraded soils unsuitable for continuing to support native trees (usually abandoned agricultural land), fuel and other products of resprouting eucalypts can greatly reduce the increasing human pressure on the remnants of natural forests. Even here, however, deleterious human practices associated with consecutive cutting cycles may eventually lead to yield decline and forest site degradation on a long-term basis. For long-term site quality and sustainability of biomass production, prolonging the cutting cycles and prohibiting or controlling litter raking appears to be imperative.

Eucalypts may be a major source of both nectar and pollen for honeybees. Because flowering of many eucalypts is abundant and lasts for long periods, some species (particularly *E. camaldulensis* and *E. cladocalyx*) are very valuable for the honey industry. When compared with native vegetation, usually significantly lower species diversity of arthropods, small mammals, and birds is reported from eucalyptus stands. For example, in Angel Island State Park, California, 41 species of birds were observed in native vegetation, but only 30 species in the eucalyptus forest. However, there may be also some other trends: approximately three times more California slender salamanders (*Batrachoseps attenuatus*) were found in eucalyptus vegetation than in native. Even more importantly, in California, eucalypts are major providers of shelter and nectar to the migrating monarch butterfly (*Danaus plexippus*) during winter months.

Allelopathic effects of eucalypts on native species are widely reported. Such reports are mostly based on laboratory bioassays. However, some field trials also point to decline of seed germination and increase of seedling mortality of some native species. If not chemical inhibition, then at least accumulation of dead material on the floor of eucalypt plantations retards regeneration of native species. Mixed-species plantations of eucalypts with native (mainly nitrogen-fixing) species have the potential to increase productivity while maintaining soil fertility and biodiversity.

Tasmanian blue gums (*E. globulus*) were planted in the San Francisco area of California as early as the second half of the nineteenth century. Having been in this landscape for such a long time, many old eucalypts are now treated as trees with “historical value” or as “heritage trees.” Many people feel that eucalypts give California a “unique exotic flavor” lacking in other parts of the United States. This is the reason why removal of eucalypts on Angel Island in the San Francisco Bay (1990–1996) sparked a raging controversy. In a very balanced way, the history of this episode was described by Peter Coates.



**FIGURE 3** It is undeniable that unmanaged stands of some eucalypt species can accumulate highly flammable dead material. To what extent Tasmanian blue gum (*Eucalyptus globulus*) groves contributed to the intensity of the tragic Berkeley–Oakland Hills fire in 1991 remains a subject of bitter discussions. This hazy but dramatic photograph of the 1991 fire was shot by former fire captain Wayne Drager through a plexiglass window, using a disposable camera on a bumpy helicopter flight. (Photograph courtesy of Wayne Drager.)

Because of accumulated litter, dense eucalypt stands are extremely flammable. The situation is exacerbated after winter freezes, when trees drop dead branches and foliage. During the last two weeks of 1990, a mass of frigid arctic air moved into California, and temperatures plunged to record lows along the Pacific Coast. It is very likely that fuel accumulation in unmanaged eucalyptus stands contributed to the intensity of the tragic fire in the Berkeley–Oakland Hills area in October 1991 (Fig. 3).

In arid and semiarid countries, where shortage of water is a big concern, benefits of eucalypt plantations may be outweighed by their negative environmental impacts: namely, their high water consumption. In South Africa, invasive eucalypts have been cleared over large areas as part of a national restoration program called Working for Water. In most areas, standing trees are felled and, where it is practically possible, their timber is harvested. Where recovery of the timber is impractical, felled plants are often stacked and burned. The most challenging management operations involve clearing river banks in large parts of the Western Cape province of dense stands of invasive *E. camaldulensis*. Clearing alone often causes destabilization of the river banks, and research is under way to determine the most effective ways of thinning the invasive stands gradually while simultaneously reintroducing key native plants to stabilize the sites and launch succession toward a sustainable community dominated by native plants.

The fact that eucalypt seeds do not have dormancy, with seed storage in the soil lasting less than a year, makes local



eradication an achievable goal. However, resprouting of cut trees from stumps or lignotubers, which is advantageous in some situations, makes control of eucalypts difficult. Continuously cutting back the regrowth can eventually kill the tree, but this is a labor-intensive and expensive control method. Herbicide applications (triclopyr or glyphosate) to freshly cut stumps can greatly reduce resprouting. Because eucalypts are valued as timber and ornamental trees in many settings, biological control is very unlikely as an option.

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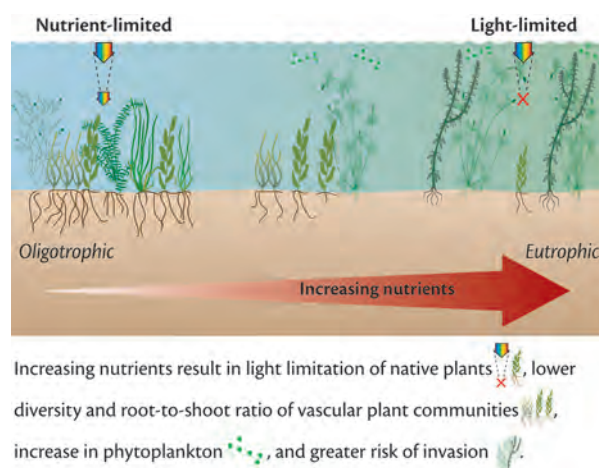
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## EUTROPHICATION, AQUATIC

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Eutrophication is the natural or anthropogenic accumulation of nutrients in soil or water (from Greek *eu* = “well” and *trophe* = “nourished”). Oligotrophic (low-nutrient) waters



**FIGURE 1** The impacts of eutrophication on aquatic ecosystems. (Figure developed by the Integration and Application Network of the University of Maryland Center for Environmental Science.)

contain less than 5–10  $\mu\text{g L}^{-1}$  phosphorus and less than 250–600  $\mu\text{g L}^{-1}$  nitrogen. These nutrient concentrations are at least 2 to 10 times as high in eutrophic waters and can have major effects on biotic communities, including the loss of biodiversity and the invasion of nonnative species (Fig. 1).

### NATURAL AND ANTHROPOGENIC EUTROPHICATION

Eutrophication is a slow natural process. The slow accumulation of nutrients is especially prevalent in depositional environments, such as lakes and wetlands, where nutrients and sediments derived from a watershed are collected in a basin and permanently or temporarily immobilized and stored. For example, estuaries are naturally eutrophic, and hence very productive, because they receive nutrients derived from watersheds and tidal flows. Lakes accumulate sediments and organic matter and over time convert into productive and nutrient-rich shallow lakes and emergent marshes. Other naturally eutrophic systems are areas along the coast where upwelling conveys nutrient-rich water to the surface. As an ecosystem's nutrient status changes over millennial time scales, so does its community structure, with local extinction and colonization of new species working in concert to produce species-rich and productive ecosystems.

However, the process of eutrophication can be greatly accelerated by human activities, such as runoff of excess fertilizer, sewage effluent, and stormwater runoff. In Australia, for example, sites affected by human activity have mean levels of 780  $\mu\text{g L}^{-1}$  N and 95  $\mu\text{g L}^{-1}$  P compared to 300  $\mu\text{g L}^{-1}$  N and 21  $\mu\text{g L}^{-1}$  P at less impacted sites. Because estuaries