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DIVERSITY, REPRODUCTION, AND POTENTIAL FOR INVASIVENESS OF *EUCALYPTUS* IN CALIFORNIA

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ABSTRACT

In the 150 years since their introduction to the state, species in the genus *Eucalyptus* have become the most common non-native trees in California. A clearer understanding of the ability of different species to reproduce in the state is important for how we monitor the ecological impact of these abundant non-native trees and for predicting possible future invasions. Here we present current data on the diversity of *Eucalyptus* in California, which species are spontaneously reproducing, or have the potential to do so, where they can be found, how they can be identified, and our analysis, based on herbarium and field observations, of the potential ecological impacts of various species in the locations where they have been introduced. We also present a new dichotomous identification key, and botanical drawings of all naturalized species. We discuss the degree to which factors such as life history traits, commonness of planting, and native range influence reproductive behaviors of different species.

Key Words: Australia, California, *Eucalyptus*, invasive, key, naturalization, weed.

The genus *Eucalyptus* L'Hér. (Myrtaceae) includes some of the most important solid timber and paper pulp forestry trees in the world (Doughty and Places 2000). They have also become the most abundant, ecologically successful, and controversial exotic trees in California. Species in the genus were first imported into the state as early as the mid 1850s, to be grown initially as horticultural oddities for the nursery trade, then later as a promising fiber source and possible savior of a forecasted timber drought (Butterfield 1935; Santos 2006). By 1880, a number of species, but primarily *E. globulus* Labill. (Fig. 1A), were being extensively planted for lumber, pilings and posts, fuel wood, medicinal products, tannin, oil, windbreaks, and as street and park trees (Groenendaal 1983). As the California forestry and fuel economy evolved many of the thousands of hectares of *Eucalyptus* plantations remained uncut, and parts of the state are now bearing the ecological legacy of this vast unharvested crop.

Since the time of its initial introduction into California, the genus was promoted by various agents including private landholders, commercial firms, and state and federal agencies. The planting craze that took place around the turn of the last century, the enthusiasm of certain individuals in high-profile state public office, and biomass fuel experimentation by the U.S. Department of Energy and the California Department of Forestry following the 1973 Arab oil embargo have all significantly helped propagate the genus in the state. The prevalence of eucalypts in California is more the result of large scale intentional plantings than it is the result of extensive naturalization. Needless to say, these species, mostly *E. globulus*, have become controversial in the regions where they are now conspicuous features of the landscape. There are many popular articles containing the most emotive writing, much of which is based loosely at best on scientific observation, regarding the various impacts of eucalypts on California's landscapes and wildlife. They are admired as erosion control, wildlife habitat, and aesthetically valuable landscape and heritage trees or demonized as America's largest, most fire prone, most dangerous, bird killing, weeds (Bulman 1988; Williams 2002).

The genus, which contains more than 700 species, according to the most recent formal classification (Brooker 2000), is almost entirely endemic to the Australian continent with a small number of species occurring natively in the southern Philippines, New Guinea and parts of Indonesia (Williams and Woinarski 1997). Eucalypts exhibit a great range of adaptation to different moisture conditions (Boland and Hall 1984), and they rival other large tree genera (i.e., *Ficus*, *Pinus*, *Quercus*) in having great diversity in mature tree size. Species range from small multistemmed shrubs (mallees), to some of the tallest and largest forest trees on earth. In fact, the putative tallest angiosperm in North and South America is a 75.05 m (246.2 ft) *E. globulus* off the coast of California, on Santa Cruz Island (Steve Sillette personal communication, Humboldt State University).

A great number of species, representing the gamut of diversity in the genus, have been introduced into cultivation in California over the last 150 yr. The correct identification of *Eucalyptus* species in cultivation is often difficult,

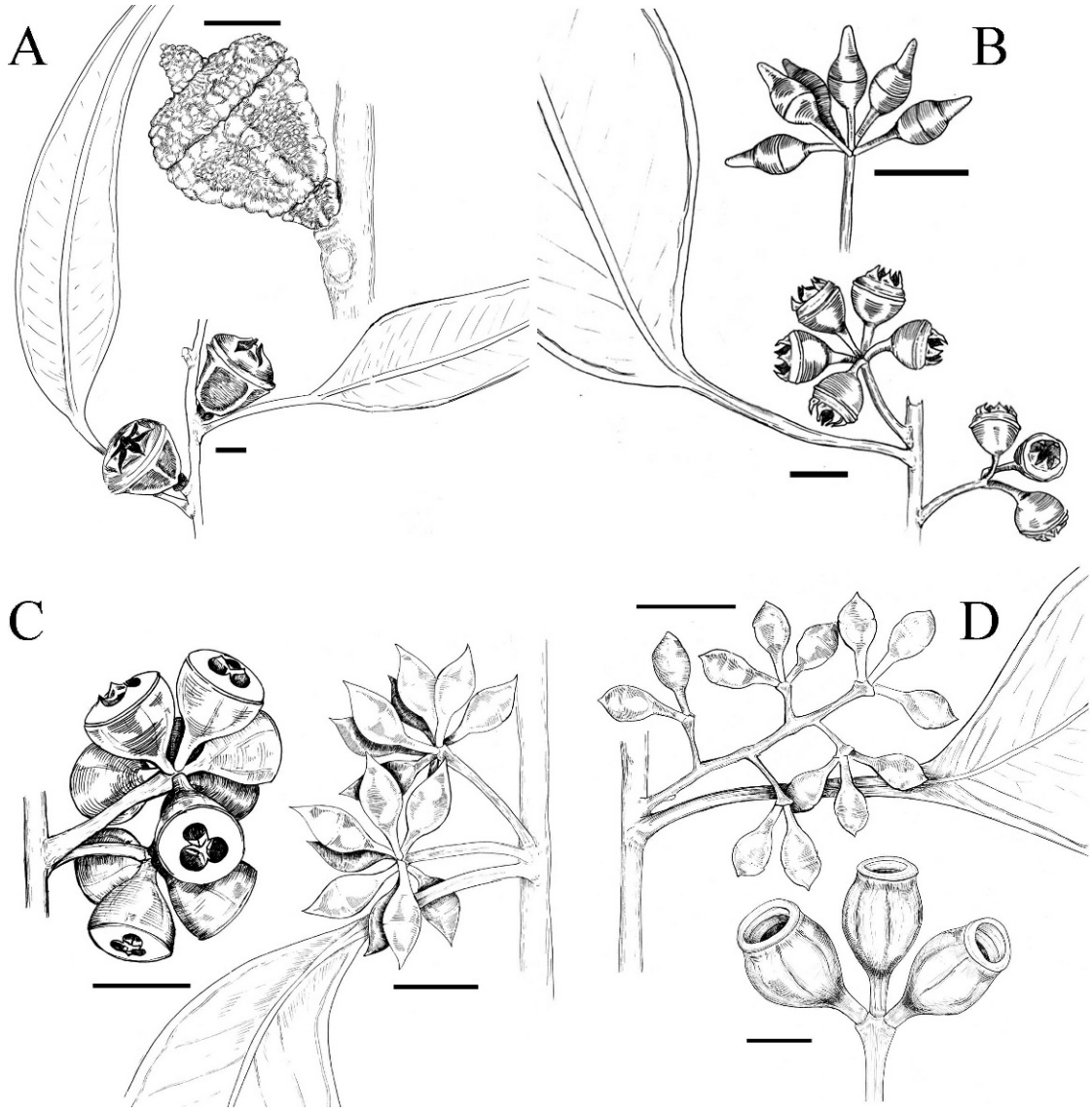

FIG. 1. Illustrations of fruits and buds of: A. *Eucalyptus globulus* subsp. *globulus* (*Howell 32582*, CAS). B. *Eucalyptus camaldulensis* (*Sanders 21982*, CAS). C. *Eucalyptus fastigata* (*Ritter 345*, OBI). D. *Eucalyptus citriodora* (*Eastwood s.n.*, CAS 45201). All size bars = 1 cm.

but is essential for studying the potential of different species to become invasive. The bark, leaves, and reproductive structures are greatly varied and at times all need to be examined for accurate identification (Pryor 1976; Brooker and Kleinig 1996). Many species retain the dead bark year after year, giving rise to a trunk covered in a hard, weathered, outer layer (e.g., *E. sideroxylon* A. Cunn. ex Woolls), while others annually decorticate, resulting in a completely smooth trunk (e.g., *E. citriodora* Hook. = *Corymbia citriodora* (Hook.) K. D. Hill & L. A. S. Johnson). Eucalypts are definitively heterophyllous, with juvenile leaves that differ from adult leaves in phyllotaxis, shape, petiolation, and glaucousness (Jacobs 1955). Juvenile leaves are commonly sessile, decussate, glaucous, oriented horizontally, discolorous (dorsiventral) and often cordate, orbicular, or ovate in shape, whereas adult leaves tend to be petiolate, alternate, glabrous, pendulous, lanceolate, and concolorous (isobilateral) (Coppen 2002).

As in most genera, the defining aspects of *Eucalyptus* are in the reproductive structures. The flowers of only a small number of species develop singly in leaf axils (e.g., *E. globulus*), while more commonly they develop in 3-, 7-, 9-, 11-, etc. flowered umbels (intact inflorescences always

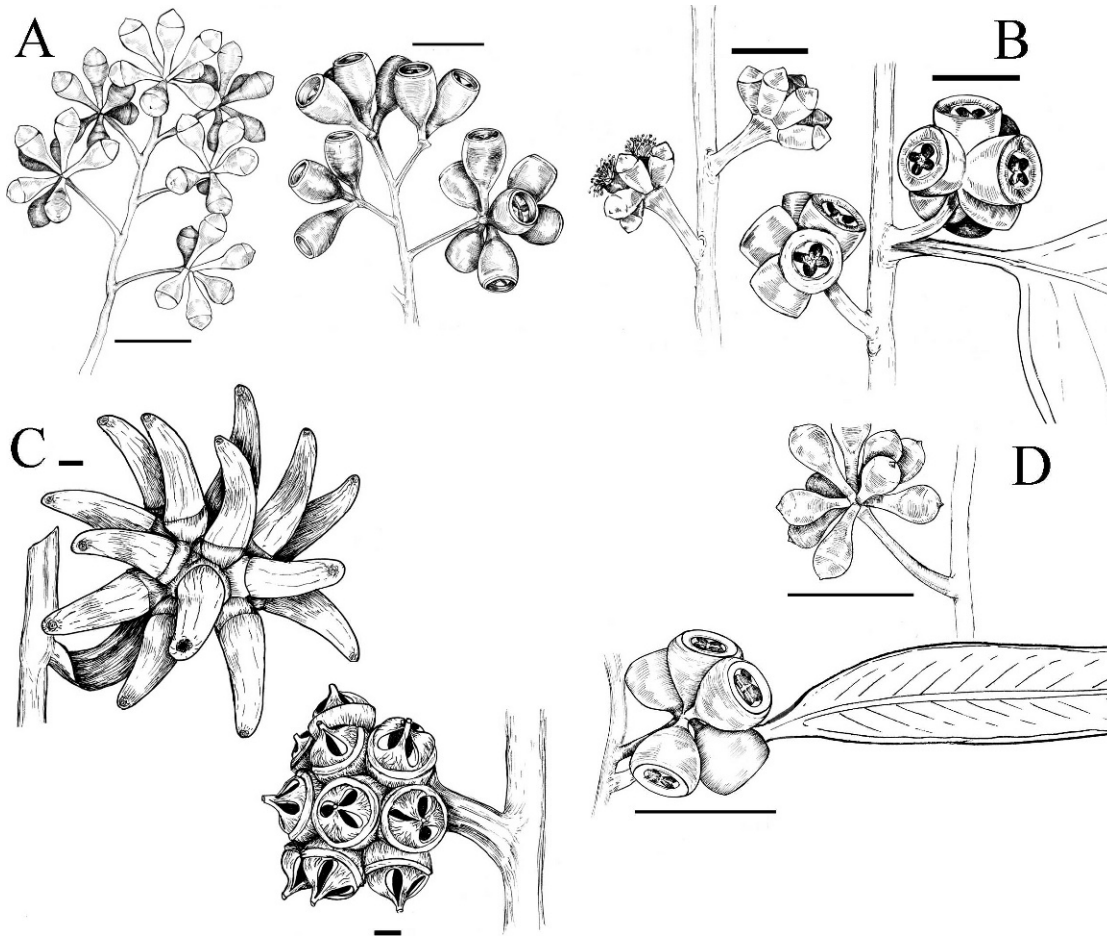

FIG. 2. Illustrations of fruits and buds of: A. *Eucalyptus polyanthemos* (*Twisselmann 18559*, CAS). B. *Eucalyptus kitsoniana* (*Ritter 263*, OBI). C. *Eucalyptus conferruminata* (*McClintock s.n.*, CAS 994288). D. *Eucalyptus pulchella* (*Kawahara 800*, CAS). All size bars = 1 cm.

have odd numbers of flowers) or heads. Individual umbels may develop singly or paired in leaf axils (e.g., *E. camaldulensis* Dehnh., Fig. 1B and *E. fastigata* H. Deane & Maiden, Fig. 1C) or in branched axillary or terminal panicles (e.g., *E. citriodora*, Fig. 1D and *E. polyanthemos* Schauer, Fig. 2A). Individual flowers, which are often small, white, and inconspicuous in the tree crown, have either one or two bud caps (opercula) derived from the fused petals and/or sepals. In a number of species (mostly subgenus *Symphyomyrtus* (Schauer) Brooker) the outer bud cap, derived from united sepals, sheds early in the development of the flower, leaving a diagnostic ring-like scar around the middle of the inner bud cap. The inner bud cap is shed at anthesis, exposing numerous spreading stamens. The inferior ovary is sunken in and fused to the hypanthium (invaginated pedicle) wall. After fertilization, when the stamens and the style fall from the flower, the ovary develops into a woody capsule with valves dehiscing at the top, allowing tiny, wind-dispersed seeds to be shed (Slee et al. 2006).

There have been a number of past treatments of cultivated and naturalized eucalypts in California. In Eric Walther's 1928 key to the species grown in California, he included 99 distinct species, known to be growing in the state at the time (not necessarily naturalized however), and made mention of over 100 others (Walther 1928). Three species, *E. polyanthemos*, *E. globulus*, and *E. tereticornis* Sm., were treated in Munz's 1959 flora of California, and a number of other commonly planted species including *E. sideroxylon*, *E. viminalis* Labill., and *E. camaldulensis* have been listed as naturalized in the floras of various regions and counties (Howell 1958; Munz and Keck 1959; Howell 1970; Beauchamp 1986; Thomas 1991; Smith and Wheeler 1992; Junak et al. 1995; Moe et al. 1995; Matthews 1997; Best et al. 2000). The two most commonly planted

eucalypts in California, *E. globulus* and *E. camaldulensis*, are treated in the California Invasive Plant Inventory Database (California Invasive Plant Council 2006–2009) with invasive ratings of moderate and limited respectively. In the most recently published state flora, The Jepson Manual: Higher Plants of California, nine species were included as naturalized (McClintock 1993). Since this 1993 volume, new observations of eucalypt naturalization have been made and those discoveries are reported here.

In order to further elucidate the status of the genus in California, we have generated a database of all, or nearly all, past and current collections of *Eucalyptus* in the state's many arboreta, botanical gardens, experimental forestry sites, and other public and private plantings. We report here our results and interpretations from many hours of field observations, herbarium study, and plant collection throughout the state. We present current data on the diversity of *Eucalyptus* in California, which species are spontaneously reproducing, or have the potential to do so, where they can be found, how they can be identified, and our analysis of the potential ecological impacts of the various species where they have been introduced. When monitoring new plant invasions and potential invasions, correct species identification is paramount. For this reason we have included a new key to species, notes on identifying morphological characters, and approximate distributions of naturalized species in California. It is our hope that this paper can act as a guide to the most commonly found naturalized eucalypts for field botanists, land managers, landscape architects, horticulturalists and silviculturalists, as well as anyone wishing to learn more about the genus in our state.

Methods

From 2003 to 2008, the authors visited and studied the *Eucalyptus* collections in herbaria throughout the state including, the University of California and Jepson Herbarium (UC, JEPS), the California Academy of Sciences (CAS), the Chico State Herbarium (CHSC), the U.C. Riverside Herbarium (UCR), the San Diego Natural History Museum (SD), the Hoover Herbarium of California Polytechnic State University, San Luis Obispo (OBI), the Cheadle Center for Biodiversity and Ecological Restoration (UCSB), and the Santa Barbara Botanical Garden Herbarium (SBBG). In addition, field observations and collections of *Eucalyptus* were made from stands and small plantings of multiple species in 31 of California's 58 counties, including all coastal counties with the exception of Del Norte County. Morphological data and planted ranges for the species notes and key were based on field observations of living specimens and construction of the key was accomplished by conventional means.

For all sites observed, the level of reproduction was gauged based on the number, if any, of spontaneously occurring new individual trees (from seed, not stump sprouting). In order to determine naturalization the number of young trees (those that were clearly not planted) in the area of adult trees were counted, distances from original introduction sites were approximated, sapling juvenile leaves were visually inspected for proper identification, and saplings were pulled up, with the root included, for herbarium vouchers. Species were considered naturalized if new propagules met the criteria defined by Richardson et al. 2000 (species establishes new self-perpetuating populations, undergoes dispersal, and becomes incorporated into resident flora). Where it was relevant, sapling age was determined by main stem growth ring analysis by cutting the main trunk and counting the growth rings in the cross section. We also noted any observations made on herbarium vouchers of collections being made from apparently reproducing or clearly reproducing stands.

We also visited living *Eucalyptus* collections at many of California's botanical gardens, arboreta, publics parks, university campuses, and private collections including the Huntington Botanical Gardens (San Marino), the University of California Botanical Garden (Berkeley), the Stanford University campus (Palo Alto), Golden Gate Park and Strybing Arboretum (San Francisco), Balboa Park (San Diego), the Los Angeles County Arboretum (Arcadia), U.C. Davis Arboretum (Davis), U.C. Riverside Botanical Garden (Riverside), Fullerton Arboretum (Fullerton), Vasona Lake *Eucalyptus* Grove (Los Gatos), Quail Botanical Garden (Encinitas), the Ruth Bancroft Garden (Walnut Creek), U.C. Santa Barbara campus (Goleta), Palomar College Arboretum (San Marcos), Orpet and Franceschi Parks (Santa Barbara), Cal Poly campus (San Luis Obispo), and the U.C. Santa Cruz Arboretum (Santa Cruz). Records for all accessioned *Eucalyptus* were compiled from the above collections as well as any published records of species planted at some time in the past in California. A database of species names and locations was created based on any species designated in published records, identified in living collections, or in visited herbaria. The classification system for *Eucalyptus* followed in this paper is found in Brooker 2000.

Results

After thorough examination of herbaria, living collections, and introduction records, we found evidence for the introduction, or attempted

introduction, of 374 distinct species of *Eucalyptus* to California beginning in 1853. Of these 374 taxa, we were able to confirm that as of December 2008, 202 species are represented by one or more mature living trees in the state. Forty eight attempted introductions are apparently now no longer extant in California. We were not able to locate or confirm the existence, or non-existence, of the remaining 124 species. Of the 202 extant species in California, only 38 are widely planted (represented by 10 or more trees in 15 or more different locations), and more than 150 are represented by fewer than 5 mature individuals (approximately 20 of these being represented by a single surviving mature specimen). Six of the seven subgenera (as recognized by Brooker in 2000) are represented in California.

Most of the *Eucalyptus* diversity in California can be found in only a few collections. The U.C. Santa Cruz Arboretum, the Los Angeles County Arboretum, and the Huntington Botanical Garden each have more than 75 extant species and records of having attempted many more. Other collections at the U.C. Davis Arboretum, the Stanford campus, the Cal Poly campus in San Luis Obispo, and the U.C. Berkeley Botanical Garden have 25 or more different extant species. There are many other collections in California with fewer than 25 species.

In the horticultural collections and forestry plantations in California we found evidence of regular and widespread spontaneous reproduction from seed of 18 of the 202 extant species (Table 1). Nine of these 18 species were included in the treatment of naturalized *Eucalyptus* in the 1993 edition of the Jepson Manual (McClintock 1993). Contrary to this treatment, we could find no evidence for the naturalization, or spontaneous reproduction of *E. pulverulenta* Sims, the very commonly planted species used for stem cuttings by the cut flower industry. We observed nine previously unrecorded occurrences of eucalypt naturalization. Seven of these nine newly observed naturalized species were found in the Max Watson Grove at the Arboretum at U.C. Santa Cruz (36°58′49.11″N, 122°3′29.17″W), where approximately 80 different species were planted in 1964. In this grove we observed extensive reproduction, with trees ranging in age from 1 to 30 yr (based on main stem growth ring analysis), of both commonly planted species such as *E. camaldulensis* (Fig. 1B) and species rare in California such as *E. kitsoniana* Maiden (Fig. 2B).

One interesting case of recently recognized eucalypt naturalization in Southwestern California is that of *E. conferruminata* D. J. Carr & S. G. M.Carr (Fig. 2C). This species has been sold and planted widely in California, under the misapplied name *E. lehmannii* (Schauer) Benth., for more than half a century for use primarily as a dense screen along roadways, houses, and agricultural fields. We have not found *E. lehmannii*, as recognized by Carr and Carr (1980), growing in California (Carr and Carr 1980). *Eucalyptus lehmannii* has a bud cap 9–15 times as long as wide, a thin peduncle that is 5–9 cm long, and a palpably round apical bud, where the closely related and very commonly grown *E. conferruminata* has a bud cap that is 4–4.5 times as long as wide, a thick, strap-like peduncle that is 2–4 cm long, and an apical bud that is palpably trigonous when rolled between the fingers. *Eucalyptus lehmannii* is also capable of regeneration after fire by sprouting from an underground lignotuber, where *E. conferruminata* is an obligate seeder (Nicolle 2006). The first observation of reproduction of *E. conferruminata* was made in San Diego County in 2006 (Jon Rebman personal communication, San Diego Natural History Museum). We have confirmed collections of spontaneously reproducing *E. conferruminata* from San Diego County (*Rebman 163346*, OBI, 33°7′15.49″N, 117°16′20.04″W), Santa Barbara County (*Ritter & Yost 379*, OBI, 34°26′0.76″N, 119°52′19.55″W), and San Luis Obispo County (*Ritter & Yost 380*, OBI, 35°14′21.39″N, 120°38′26.12″W). Reproduction was moderate in the areas described above, with fewer than 50 seedlings at each site. Collections have also been made from an area where reproduction was extensive, with hundreds of new plants regenerating from seed, in Gaviota, Santa Barbara County (*Ritter & Yost 381*,

TABLE 1. COMMON *EUCALYPTUS* SPECIES IN CALIFORNIA. A. Taxa naturalized in California. B. Commonly planted taxa that would be expected to reproduce if planted more frequently, based on taxonomic similarity to reproducing species and reports from other areas with similar climates. C. Commonly planted *Eucalyptus* species for which there is no evidence of reproduction.

Naturalized (A)	Expected naturalization (B)	No evidence of naturalization (C)
E. camaldulensis	*E. amygdalina*	*E. calophylla*
E. citriodora	*E. blakelyi*	*E. cornuta*
E. cladocalyx	*E. botryoides*	*E. erythrocorys*
E. conferruminata	*E. dalrympleana*	*E. ficifolia*
E. fastigata	*E. dives*	*E. leucoxylon*
E. globulus	*E. gunnii*	*E. macranda*
E. grandis	*E. maculata*	*E. melliodora*
E. kitsoniana	*E. neglecta*	*E. nicholii*
E. macarthurii	*E. nicholii*	*E. pauciflora*
E. mannifera	*E. paniculata*	*E. preissiana*
E. ovata	*E. radiata*	*E. pulverulenta*
E. parvula	*E. regnans*	*E. punctata*
E. polyanthemos	*E. resinifera*	*E. rudis*
E. pulchella	*E. rubida*	*E. spathulata*
E. robusta	*E. rudis*	*E. torquata*
E. sideroxylon	*E. saligna*	*E. diversicolor*
E. tereticornis		*E. megacornuta*
E. viminalis		

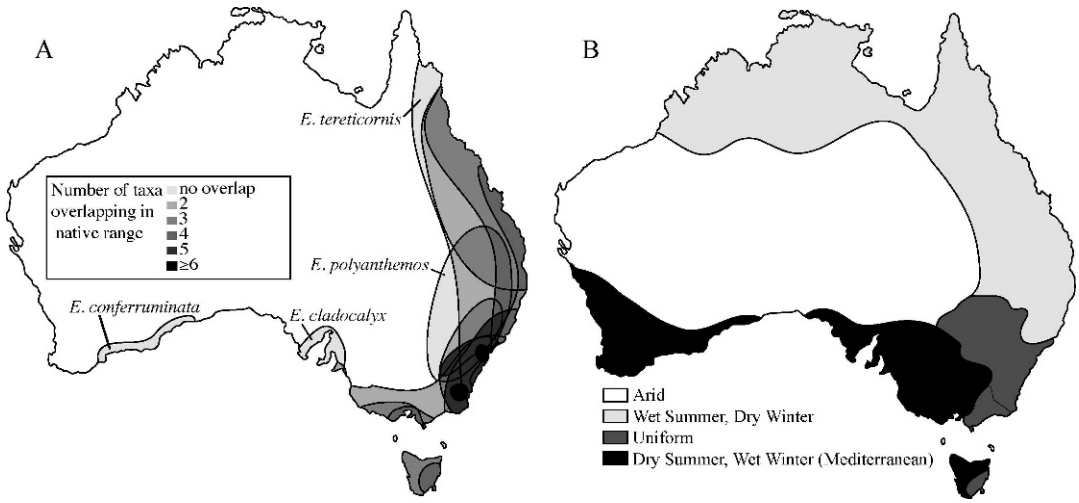

FIG. 3. Native ranges and seasonal rainfall patterns of *Eucalyptus* reproducing in California. A. The approximate native ranges of the 18 taxa spontaneously reproducing in California. Only species which have a portion of their range not overlapping with other species are labeled. The *E. camaldulensis* native range (throughout Australia except for the southwest) is excluded from the figure. B. The seasonal rainfall patterns within the native ranges of reproducing taxa. Based on Williams (1997) page 94.

34°28′24.92″N, 120°12′48.86″W). This reproduction began in earnest after the 2004 Gaviota fire, which burned to the sea through an area densely planted with *E. conferruminata*. In areas where *E. conferruminata* reproduction is taking place, all observed saplings were less than 10 yr old, based on main stem growth ring analysis.

DISCUSSION

The over 200 species of *Eucalyptus* living in California represent a unique example of a significant and purposeful introduction of a genus of trees into cultivation outside their native range. *Eucalyptus* species are not only the most prevalent non-native trees in California; there is no other genus of introduced trees represented by more species in the state (McMinn and Maino 1935). This diversity of *Eucalyptus* represents an opportunity to observe the process of naturalization, or lack of naturalization, in different and closely related species. It became apparent during the course of this study that different eucalypts are spontaneously reproducing at different rates, sometimes regardless of how frequently they are planted. In some groves, such as the Max Watson Grove at the Arboretum at U.C. Santa Cruz, where over 70 different mature species remain, we observed copious reproduction from seed of some species and could find no evidence of reproduction of other species, planted just a short distance away.

The degree of spontaneous reproduction in different species may correlate with the taxonomic subgenus and section to which they belong, and therefore future invasions could possibly be predicted for closely related yet uncommonly planted species (Table 1). Of the eighteen taxa that have become naturalized in the state, all but 3 are in the subgenus *Symphyomyrtus* (Pryor and Johnson 1971). The exceptions are *E. fastigata* (Fig. 1C) and *E. pulchella* Desf. (Fig. 2D), both in the subgenus *Eucalyptus* (*Monocalyptus* of Pryor and Johnson 1971), and *E. citriodora* in the subgenus *Corymbia* (see species notes for a brief discussion of the recent elevation of the subgenus *Corymbia* to the genus level). Within the subgenus *Symphyomyrtus*, 7 of the 18 naturalized taxa are in the large section *Maidenaria* L. D. Pryor & L. A. S. Johnson ex Brooker, which has a total of 80 taxa. It is possible that other species in this section, if planted more commonly, would be predicted to naturalize more readily in California than species in other sections (Table 1). In a contrasting situation, *Symphyomyrtus* sections *Dumaria* (23 taxa) and *Bisectae* (50 taxa), which are represented by over 50 living taxa in California, have only one species (*E. conferruminata*) that is apparently naturalized.

Eucalyptus, although almost entirely endemic to Australia, has a broad native range ($\sim 1.6 \times 10^7$ km^2) including species that have evolved in myriad climate types, including temperate rainforests, deserts, humid subtropical coastal areas, and Mediterranean climate regions. The 18 taxa naturalized in California are native primarily to southeast and east Australia, with the exception of *E. conferruminata* and *E. cladocalyx* F. Muell., which have coastal distributions in southern West Australia and southern South Australia (Fig. 3A). *Eucalyptus camaldulensis* has a widespread but largely inland distribution (occurring

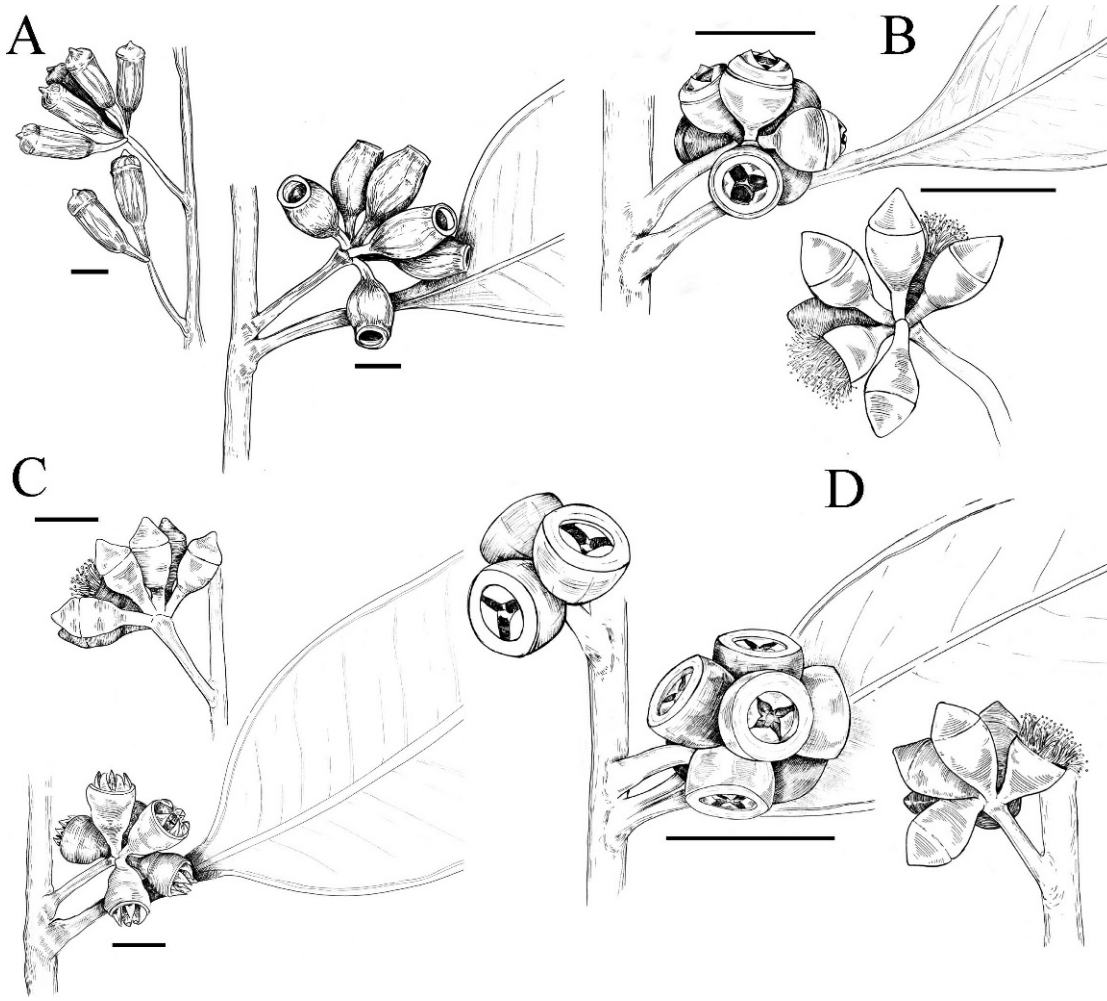

FIG. 4. Illustrations of fruits and buds of: A. *Eucalyptus cladocalyx* (*R. Philbrick B65-44*, CAS). B. *Eucalyptus mannifera* (*Ritter 226*, OBI). C. *Eucalyptus grandis* (*Broder 1472*, CAS). D. *Eucalyptus parvula* (*McClintock s.n.*, CAS 474279). All size bars = 1 cm.

in every mainland Australian state) and is usually found near permanent or seasonal watercourses. It is interesting to note that most of the naturalized taxa in California are native to areas with different seasonal rainfall patterns than those found in Mediterranean climate areas of cismontane California. Eastern Australia, and parts of southeastern Australia, have either uniform year-round or summer maximum precipitation (Fig. 3B).

Of the 18 naturalized taxa, only *E. conferruminata* and *E. cladocalyx* (Fig. 4A) have native ranges that fall entirely in winter maximum rainfall Mediterranean type climate areas of Australia. At present, there are 74 taxa alive in California with a native range entirely in Mediterranean areas of southern and southwestern Australia. Of these 74, 13 are planted widely (represented by 10 or more trees in 15 or more different locations). There is no evidence of spontaneous reproduction from seed or naturalization of any of these species, with the exception of *E. conferruminata* and *E. cladocalyx*.

It is noteworthy that some eucalypt species reproduce frequently in California while others, which are closely related, planted as frequently and in the same locations, do not apparently reproduce. Two examples of this phenomenon are *E. camaldulensis* and its closest relative *E. rudis* Endl., and *E. sideroxylon* and two of its closest relatives *E. leucoxylon* F.Muell. and *E. melliodora* A. Cunn. ex Schauer. *Eucalyptus camaldulensis* is widely naturalized in central and southern California. Its closest relative, *E. rudis*, which is endemic to southwestern West Australia, is commonly planted in California,

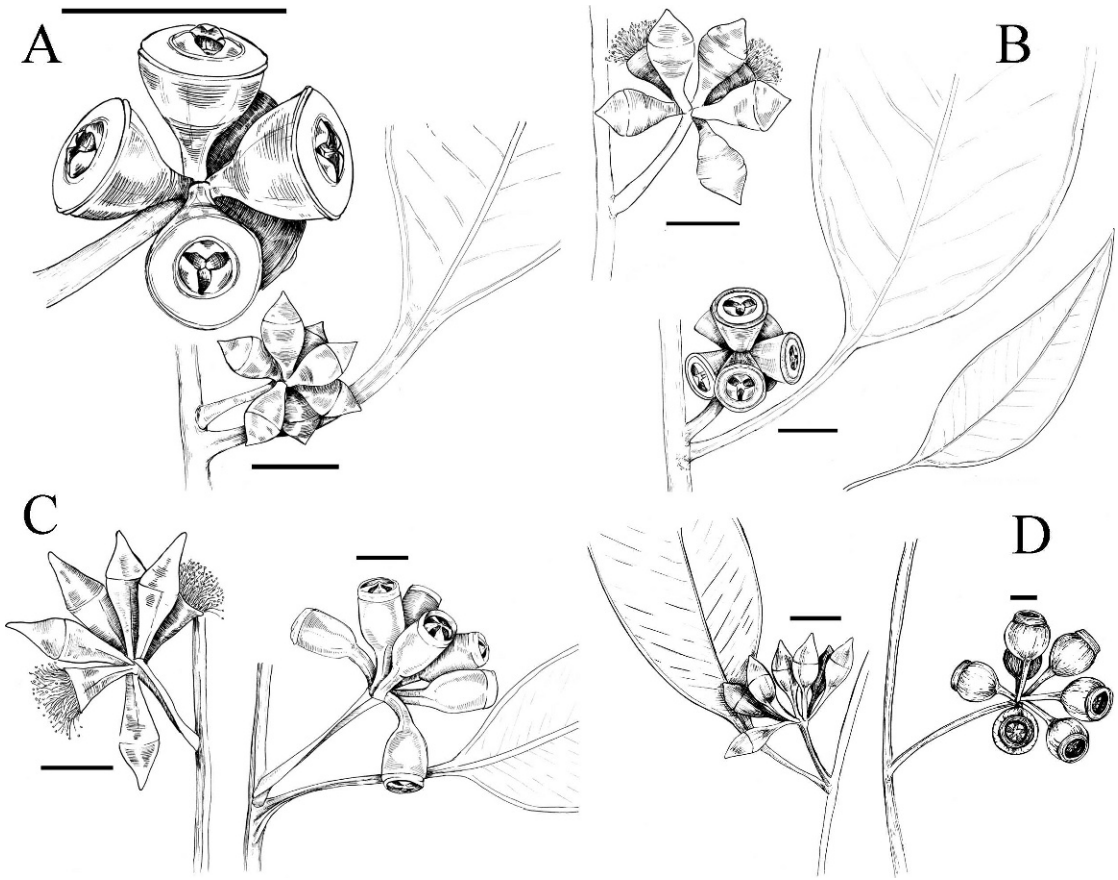

FIG. 5. Illustrations of fruits and buds of: A. *Eucalyptus macarthurii* (*Ritter 232*, OBI). B. *Eucalyptus ovata* (*Huber 1203*, CAS). C. *Eucalyptus robusta* (*Pollard s.n.*, CAS 556588). D. *Eucalyptus sideroxylon* (*McClintock s.n.*, CAS 863986). All size bars = 1 cm.

especially along roadways in the central western and southern parts of the state, yet there is no evidence of even occasional reproduction from seed of this species. Similarly, *E. leucoxylon* and *E. melliodora*, both horticulturally important species that are planted frequently throughout the state, apparently do not reproduce, whereas *E. sideroxylon* saplings can be found in many areas where this species is grown. Conversely, *E. nicholii* Maiden & Blakely, which is planted very commonly throughout the state, apparently rarely or never reproduces although its close relatives *E. mannifera* (Fig 4B), *E. macarthurii*, and *E. parvula* do so extensively. Why this disparity in reproduction of closely related species exists in California is a question requiring further study. The native ranges of the closely related species, mycorrhizal fungal associations (especially during seed germination), soil types, and a number of other factors that might affect germination and recruitment of new trees could all play a role in explaining this observed variation in reproduction.

We observed widespread reproduction of a number of species in the Max Watson Grove at the Arboretum at U.C. Santa Cruz, such as *E. fastigata* (Fig. 1C), *E. grandis* W. Hill ex Maiden (Fig. 4C), *E. kitsoniana* (Fig. 2B), *E. parvula* L. A. S. Johnson & K. D. Hill (Fig. 4D), and *E. macarthurii* H. Deane & Maiden (Fig. 5A), which are not planted frequently elsewhere in California. *Eucalyptus kitsoniana*, *E. parvula*, and *E. macarthurii* are rarely grown elsewhere outside Australia (Jacobs 1981) and are very uncommon in California. It is tempting to speculate that if other fast growing timber species such as *E. fastigata* and *E. grandis* were planted widely in California, instead of *E. globulus*, then there could be as much or more reproduction and expansion of these plantations. Had *E. diversicolor* F. Muell., a fine timber species from Southwest Australia that apparently does not reproduce where it is grown in California, been promoted instead of *E. globulus*, would there be no issue with expanding groves? Not surprisingly, a correlation exists between the commonness of

which a species is planted in California and the number of observations (and possibly the actual degree) of spontaneous reproduction and naturalization.

The recently recognized and locally extensive reproduction of *E. conferruminata* (Fig. 2C) in parts of California is an interesting case of possible naturalization after a long period of latency. There have been a number of observations made of non-native species that only become invasive after a long lag time subsequent to their initial introduction (Ellstrand and Schierenbeck 2000). This species, which is planted commonly along a number of roads, highways, and freeways in western Central and Southern California (and has been for over 50 yr), is considered a serious threat to wildlands in the Mediterranean climate Cape Province of South Africa where it has been planted as a sand-binder and windbreak. *Eucalyptus conferruminata* is listed as a Category 1 plant as defined in the South African Conservation of Agricultural Resources Act 43 (1983) (its planting, propagation, and importation is prohibited) in the Western Cape, due to the fact that it forms thickets in areas of coastal fynbos (Richardson et al. 1996; Henderson 2001; Le Maitre et al. 2002; Forsyth et al. 2004). Why after being planted so commonly in California for more than 50 yr is this species now just beginning to become naturalized? *Eucalyptus conferruminata*, which reproduces in the wild only after fire, may only become naturalized after repeated fires in cultivated areas (Nicolle et al. 2008). Another possibility is that a different genotype of this species was introduced into South Africa; a genotype that does not require fire for profuse reproduction. Genetic fingerprinting or chloroplast haplotype analysis would be useful in elucidating any genetic component to these vastly different levels of naturalization of the same species in similar Mediterranean climates (McKinnon et al. 2001; Freeman et al. 2001).

Guide To Using The Key

This key includes the 18 species known to the authors to spontaneously reproduce in California. There are many commonly planted species for which there is no evidence of any reproduction (see above) and these have been omitted from the key. However, the user of the key is encouraged to use the species notes (Appendix 1) as there are lists of non-reproducing species that are closely related to those found in the key.

Key To *Eucalyptus* Species Spontaneously Reproducing In California

1. Inflorescences of terminal or axillary panicles of umbels
   2. Leaves lanceolate, lemon-scented; bark smooth . . . . . *E. citriodora*
   2′ Leaves ovate, elliptic, or orbicular, not lemon-scented; bark variable (often rough [subsp. *vestita* L. A. S. Johnson & K. D. Hill], or occasionally smooth, [subsp. *polyanthemos* L. A. S. Johnson & K. D. Hill]) . . . . . *E. polyanthemos*

1′ Inflorescences of unbranched umbels or heads borne in leaf axils or flowers borne singly in leaf axils
   3. Flowers borne singly in leaf axils, ± sessile; fruit > 1.5 cm wide . . . . . *E. globulus*
   3′ Flowers in 3-to 15 flowered axillary umbels or heads; fruit ≤1 cm wide
      4. Leaves lighter abaxially (discolorous)
         5. Bark rough, persistent on trunk and large branches, thick, fibrous; fruit valve tips remaining fused after dehiscence . . . . . *E. robusta*
         5′ Bark smooth, shedding from trunk and large branches, occasionally rough up to ~1 m on trunk; fruit valve tips distinct after dehiscence
            6. Fruit prominently ribbed, barrel-shaped; valves of mature fruit not exserted (sunken inside hypanthium) . . . . . *E. cladocalyx*
            6′ Fruit smooth, obconical; valves of mature fruit exserted and incurved . . . . . *E. grandis*
      4′ Leaves same color on both sides (concolorous)
         7. Bark rough, persistent on trunk and large branches, brown to black
            8. Bark deeply furrowed, hard, black; outer stamens without anthers (staminodes); filaments red or white . . . . . *E. sideroxylon*
            8′ Bark fibrous, brown; stamens all fertile; filaments always white
               9. Umbels often paired in leaf axils; bud cap scar absent . . . . . *E. fastigata*
               9′ Umbels always singe in leaf axils; bud cap scar present . . . . . *E. macarthurii*
         7′ Bark smooth, shedding from trunk and large branches, sometimes rough up to ~2 M on trunk, gray, white, or tan
            10. Flowers and fruit fused at the base into a dense, spherical head, >3 cm in diameter . . . . . *E. conferruminata*
            10′ Flowers and fruits free at the base
               11. Inflorescences mostly 3-flowered umbels . . . . . *E. viminalis*
               11′ Inflorescences 5-to 15-flowered umbels or heads
                  12. Valves of mature fruit not exserted (sunken below level of hypanthium rim)
                     13. Flowers and fruit stalked; leaves linear, generally ≤0.5 cm wide; bud cap scar absent . . . . . *E. pulchella*
                     13′ Flowers and fruit sessile; leaves lanceolate, elliptic, or ovate, generally ≥1 cm wide; bud cap scar present

14. Mature crown retaining large numbers of opposite, sessile, juvenile leaves; adult leaves ± 1 cm wide . . . . . *E. parvula*
14′ Mature crown with only alternate, stalked, adult leaves; adult leaves > 2 cm wide . . . . . *E. kitsoniana*

12′ Valves of mature fruit level with or exserted beyond rim of hypanthium
15. Bark smooth to ground level, powdery to the touch, mottled, shedding in plates; leaves narrow-lanceolate, dull bluish green . . . . . *E. mannifera*
15′ Bark often rough up to ~1m on trunk, not powdery to the touch, shedding in short strips; leaves lanceolate to broad-lanceolate, glossy green
16. Fruit obconic; valves slightly exserted or occasionally level with hypanthium rim; bud cap conic . . . . . *E. ovata*
16′ Fruit cup-shaped; valves strongly exserted; bud cap horn-shaped, beaked, or occasionally conic
17. Bud cap beaked, +- equal to hypanthium length; seeds yellow . . . . . *E. camaldulensis*
17′ Bud cap horn-shaped to conic, not beaked, +- two times hypanthium length; seeds dark brown . . . . . *E. tereticornis*

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APPENDIX 1

NOTES ON 18 NATURALIZED SPECIES

Each note depicts herbarium vouchers that are representative of each taxon, characters that are particularly helpful in identifying each species, and a list of closely related species that are commonly cultivated in California. These characters may not be included in the key and characters common to many species have been omitted.

Eucalyptus camaldulensis Dehnh. (Fig. 1B). *Sanders 21982* (CAS 997534); *Ertter 11231* (UC 1619995). Leaves often infested with lerp psyllids; bud cap beaked; seeds yellow; most widespread *Eucalyptus* in Australia, second most commonly planted species in California. Related species: *E. rudis*.

Eucalyptus citriodora Hook. = *Corymbia citriodora* (Hook.) K. D. Hill & L. A. S. Johnson (Fig. 1D). *Eastwood s.n.* April 16, 1916 (CAS 45201); *Hunt s.n.* May 1907 (UC 132066). Bark smooth throughout; trees are often self pruning; leaves lemon-scented. Very commonly grown in coastal California. In Brooker's 2000 treatment of eucalypts he included *Angophora* and *Corymbia* as subgenera of *Eucalyptus* whereas other concurrent and more recent work has supported the status of *Angophora* and *Corymbia* as separate genera (Ladiges et al. 1995; Brooker 2000; Udovicic and Ladiges 2000; Steane et al. 2002). There are only two widely planted species in California, *E. citriodora* Hook. = *C. citriodora* (Hook.) K. D. Hill & L. A. S. Johnson (Lemon-scented Gum) and *E. ficifolia* F. Muell. = *C. ficifolia* (F. Muell.) K. D. Hill & L. A. S. Johnson (Red-flowering Gum), whose names are affected by this taxonomic revision, and only the former is naturalized to any degree. Although we recognize the validity of the latter work, for the purpose of simplicity in treating a smaller group of naturalized species, we have used the genus name *Eucalyptus* in the broad sense (*sensu* Brooker 2000). Related species: *E. maculata*.

Eucalyptus cladocalyx F. Muell. (Fig. 4A). *Philbrick B65-44* (CAS 907112); *Barber 100(330)* (JEPS 41016). Bark mottled, cream and orange; leaves distinctly discolorous; buds on leafless shoots; fruit barrel-shaped, longitudinally ribbed. Very commonly planted in western Santa Barbara Co., Orange Co., and San Diego Co. Related species: Not closely related to any other species.

Eucalyptus conferruminata D. J. Carr & S. G. M. Carr (Fig. 2C). *McClintock s.n.* May 1989 (CAS 994288); *Ingham s. n.* (UC 1552464). Bark smooth, gray; peduncles flattened, erect to down-curved; inflo-

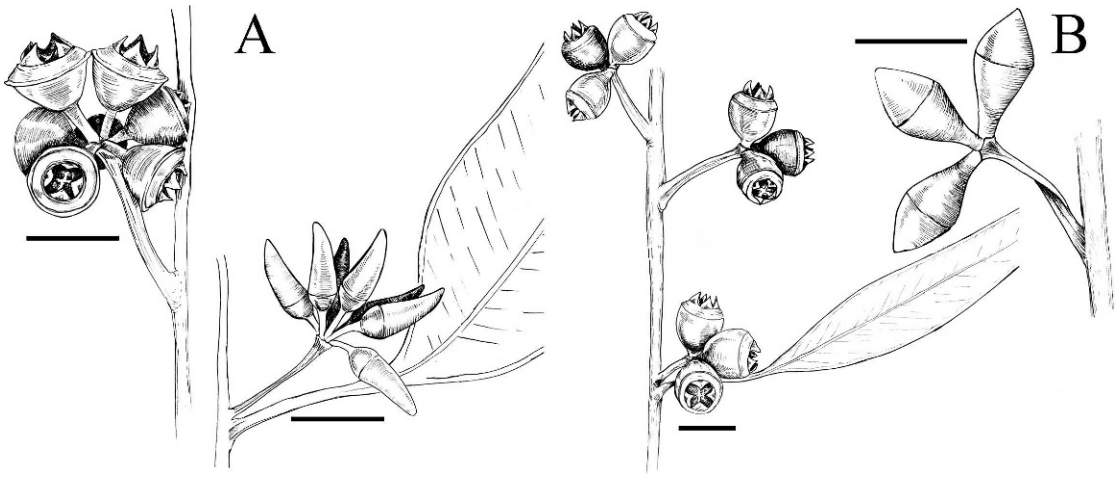

FIG. 6. Illustrations of fruits and buds of: A. *Eucalyptus tereticornis* (*Boyd s.n.*, CAS 931360). B. *Eucalyptus viminalis* (*Keil 25866*, OBI). All size bars = 1 cm.

rescence head-like; bud cap stoutly horn-shaped; stamens greenish-yellow; fruits fused. Commonly planted as a screen along roadsides in San Francisco Bay Area, San Luis Obispo Co., and Santa Barbara Co. Related species: *E. lehmannii*, *E. megacornuta*, *E. cornuta*.

Eucalyptus fastigata H. Deane & Maiden (Fig. 1C). *Ritter 345* (OBI 67945). Bark rough, brown, fibrous, stringy on trunk and large branches, smooth above; inflorescences axillary, usually paired; buds 11–15 per umbel; bud cap scar absent. Rarely planted in California, extensive reproduction at U.C. Santa Cruz Arboretum. Related species: *E. regnans*.

Eucalyptus globulus Labill subsp. *globulus*. (Fig. 1A). *Howell 32582* (CAS 515534); *Ertter 17840* (UC 1789210). Adult leaves dark green, falcate; buds square, warty, glaucous, sessile, single in leaf axils. Most commonly grown species in the state; extensive reproduction throughout coastal California. Found less frequently south of Santa Barbara County. Very commonly naturalized in Monterey and Santa Cruz counties. Other less commonly planted subspecies (*E. g.* subsp. *maidenii* F. Muell. [with 7 buds per umbel] and *E. g*. subsp. *bicostata* (Maiden) Blakely & Simmonds [with 3 buds per umbel]) also spontaneously reproduce where they are planted. Related species: *E. nitens*, *E. cypellocarpa*.

Eucalyptus grandis W. Hill ex Maiden (Fig. 4C). *Broder 1472* (CAS 602795); *Yost & Ritter 202* (OBI 68038). Bark powdery, pale gray, rough to 1 m above ground then smooth above; leaves discolorous, glossy; bud cap beaked; fruit valves exerted and incurved. Planted occasionally in California, extensive reproduction at U.C. Santa Cruz Arboretum. Related species: *E. saligna*.

Eucalyptus kitsoniana Maiden (Fig. 2B). *Ritter 263* (OBI 68004). Bark smooth throughout, copper colored; buds and fruit sessile. Rarely planted in California; extensive reproduction at U.C. Santa Cruz Arboretum. Related species: *E. neglecta*.

Eucalyptus macarthurii H. Deane & Maiden (Fig. 5A). *Ritter 232* (OBI 68092); *Walter s.n.* April 1912 (UC 170413). Bark rough, brown, fibrous to small branches; leaves narrowly lanceolate; buds sessile to subsessile; fruit obconic; fruit valves at capsule rim level. Rarely planted in California; extensive reproduction at U.C. Santa Cruz Arboretum. Related species: *E. nicholii*.

Eucalyptus mannifera Mudie (Fig. 4B). *Ritter 226* (OBI 65677); *Sanders s.n.* March 1986 (UC 1608078). Bark smooth, mottled, powdery; buds ovoid 2–5 mm wide; bud cap scar present; fruit valves generally 3 per capsule, exerted above capsule rim. Planted occasionally in coastal California. Related species: *E. nicholii*.

Eucalyptus ovata Labill. (Fig. 5B). *Huber 1203* (CAS 597552); *Bolmore s.n.* May 1900 (JEPS 41030). Bark smooth throughout, occasionally rough on lower trunk and large branches; leaves often lacking visible oil glands; fruit obconic. Occasionally planted in California; extensive reproduction at U.C. Santa Cruz Arboretum. Related species: *E. brookeriana*, *E. camphora*.

Eucalyptus parvula L. A. S. Johnson & K. D. Hill (Fig. 4D). *McClintock s.n.* November 1967, (CAS 474279); *Yost & Ritter 255* (OBI 68012). Bark smooth throughout; leaves often opposite and sessile (juvenile) in mature crown, elliptical to ovate; buds and fruit sessile. Rarely planted in California; extensive reproduction at U.C. Santa Cruz Arboretum. Related species: *E. nicholii*.

Eucalyptus polyanthemos Schauer (Fig. 2A). *Twisselmann 18559* (CAS 55013); *Barber s.n. February 1894* (JEPS 1896). Leaves bluish-gray, ovate, elliptic, or orbicular; inflorescences terminal panicles; staminodes present. Very common landscaping tree throughout western California. Reproduces occasionally. Related species: *E. leucoxylon*, *E. melliodora*.

Eucalyptus pulchella Desf. (Fig. 2D). *Kawahara 800* (CAS 485858); *Keil 24454* (OBI 53723). Bark gray, completely smooth or occasionally rough to 1 m above ground level; leaves linear, peppermint scented; inflorescences axillary, buds 9 to >15 per umbel; bud cap scar absent. Rarely planted in California, extensive reproduction in Joaquin Miller Park, Alameda Co. (37°48′49.40″N, 122°10′57.43″W). Related species: *E. amygdalina*, *E. dives*, *E. radiata*.

Eucalyptus robusta Sm. (Fig. 5C). *Pollard s.n.* March 1970 (CAS 556588); *Sanders 13849* (UC 1792828). Bark

thick, fibrous, spongy, reddish brown, easily torn from trunk; leaves discolorous, glossy; fruit valves remain joined at tip after dehiscence. Occasional landscaping plant throughout western California. Reproduces occasionally. Related species: *E. botryoides*, *E. resinifera*.

Eucalyptus sideroxylon A. Cunn. ex Woolls (Fig. 5D). *McClintock s.n.* August 1989 (CAS 863986); *Gross 387* (UC 1870241). Bark rough, hard, gray-black; buds 7 per umbel; staminodes present. Very common landscaping plant throughout western California. Reproduces occasionally. Related species: *E. leucoxylon*, *E. melliodora*.

Eucalyptus tereticornis Sm. (Fig. 6A). *Boyd s.n.* February 1981 (CAS 931360); *Ertter 17604* (UC 1789216). Similar in appearance to *E. camaldulensis*; bud cap horned not beaked; seeds dark brown not yellow. Grown commonly in California. Occasionally form hybrids with *E. camaldulensis* in California. Related species: *E. blakelyi*, *E. dealbata*, *E. dwyeri*.

Eucalyptus viminalis Labill. (Fig. 6B). *Keil 25866* (OBI 542293); *Ertter 10146* (UC 1607671). Bark gray, rough to 1 m above ground level then smooth above, shed in long ribbons; buds 3 per umbel; fruit cup-shaped; fruit valves exerted beyond capsule rim. Very common landscaping plant throughout western California. Extensively naturalized in parts of San Francisco Bay Area; reproduces regularly elsewhere in the state. Related species: *E. dalrympleana*, *E. rubida*.