

Cost–Benefit Analysis for Biological Control Programs That Targeted Insect Pests of Eucalypts in Urban Landscapes of California

T. D. PAINE,^{1,2} J. G. MILLAR,¹ L. M. HANKS,^{1,3} J. GOULD,^{1,4} Q. WANG,^{1,5} K. DAANE,⁶
D. L. DAHLSTEN,^{6,7} AND E. G. MCPHERSON⁸

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ABSTRACT As well as being planted for wind breaks, landscape trees, and fuel wood, eucalypts are also widely used as urban street trees in California. They now are besieged by exotic insect herbivores of four different feeding guilds. The objective of the current analysis was to determine the return on investment from biological control programs that have targeted these pests. Independent estimates of the total number of eucalypt street trees in California ranged from a high of 476,527 trees (based on tree inventories from 135 California cities) to a low of 190,666 trees (based on 49 tree inventories). Based on a survey of 3,512 trees, the estimated mean value of an individual eucalypt was US\$5,978. Thus, the total value of eucalypt street trees in California ranged from more than US\$1.0 billion to more than US\$2.8 billion. Biological control programs that targeted pests of eucalypts in California have cost US\$2,663,097 in extramural grants and University of California salaries. Consequently, the return derived from protecting the value of this resource through the biological control efforts, per dollar expended, ranged from US\$1,070 for the high estimated number of trees to US\$428 for the lower estimate. The analyses demonstrate both the tremendous value of urban street trees, and the benefits that stem from successful biological control programs aimed at preserving these trees. Economic analyses such as this, which demonstrate the substantial rates of return from successful biological control of invasive pests, may play a key role in developing both grass-roots and governmental support for future urban biological control efforts.

KEY WORDS classical biological control, street tree, urban landscape, natural enemy, Eucalyptus

Eucalypts, including the three closely related genera *Eucalyptus*, *Angophora*, and *Corymbia*, are native to Australia and were first introduced into California in the mid-19th century, planted from seed (e.g., Ingham 1908). The trees were highly valued for their rapid and vigorous growth, tolerance of drought and poor soils, and their horticultural characteristics. Although initially planted for use as railroad ties and mine timbers, they became widely planted for use as wind breaks, fuel wood, shade, and ornamental trees. Because they were initially brought as seed, no insect herbivores were introduced with them, and very few native insects have expanded their host ranges to include eucalypts as host plants (Doughty 2000).

With two exceptions, a seed galling eulophid wasp, *Quadrastichodella nova* Girault (Timberlake 1957), that could have arrived in early shipments of seeds, and the acacia psyllid, *Acizzia uncatoides* (Ferris & Klyver), introduced in 1954 (Ulyshen and Miller 2007) that can occasionally be found colonizing eucalypts, there were no significant pests of eucalypts in California until the latter part of the 20th century. Between 1984 and 2007, however, 16 species of Australian insects, distributed across four different feeding guilds (two species of coleopteran wood borers, three species of coleopteran defoliators, eight species of fluid-feeding psyllids, and three species of hymenopteran gallers), were introduced into California (Table 1; Paine et al. 2010). Two additional species of gall wasps have been introduced into the state since 2008 (Table 1).

The first invasive wood borer of eucalypts introduced into California was *Phoracantha semipunctata* (F.) (Gill 1998). First detected in southern California in 1985, the species quickly spread around the state, killing large numbers of eucalypts (Hanks et al. 1993a). The mortality was so extensive and costs of removal so high that it was reported that entire institutional landscape budgets (e.g., University of California San Diego) could be expended just on removal and replacement of trees killed by the beetle (Paine et al. 1997). The adult beetles are strongly attracted to trees that are damaged or under environmental stress, including drought stress

¹ Department of Entomology, University of California, Riverside, CA.

² Corresponding author, e-mail: timothy.paine@ucr.edu.

³ Present address: Department of Entomology, University of Illinois at Urbana-Champaign, Urbana, IL.

⁴ Present address: United States Department of Agriculture APHIS, Otis, MA.

⁵ Institute of Agriculture and Environment, Massey University, Palmerston North, New Zealand.

⁶ Department of Environmental Science, Policy and Management, University of California, Berkeley, CA.

⁷ Deceased.

⁸ Pacific Southwest Research Station, United States Department of Agriculture Forest Service, Davis, CA.

Table 1. Invasive species feeding on eucalypts in California

Order/family	Species	Year discovered	Biological control agent	Outcome
Coleoptera/Cerambycidae	<i>Phoracantha recurva</i> Newman	1995 ^a	<i>Acetianella longoi</i> Siscaro	Established
	<i>Phoracantha semipunctata</i> (F.)	1984 ^a	<i>Acetianella longoi</i> Siscaro	Complete
Coleoptera/Chrysomelidae	<i>Chrysophtharta m-fuscum</i> (Boheman)	2003 ^b		
	<i>Trachymela sloanei</i> (Blackburn)	1998 ^a	<i>Enoggera reticulata</i> Naumann	Failure
Coleoptera/Curculionidae	<i>Gonipterus scutellatus</i> Gyll.	1994 ^a	<i>Anaphes nitens</i> (Girault)	Complete
Hemiptera/Aphalaridae	<i>Blastopsylla occidentalis</i> Taylor	1983 ^a		
	<i>Cryptoneossa triangula</i> Taylor	1995 ^a	<i>Psyllaephagus perplexus</i> Cockerell	Moderate
	<i>Ctenarytaina eucalypti</i> (Maskell)	1991 ^a	<i>Psyllaephagus pilosus</i> Noyes	Complete
	<i>Ctenarytaina longicauda</i> Taylor	1983 ^a		
	<i>Ctenarytaina spatulata</i> Taylor	1991 ^a		
	<i>Eucalyptolyma maideni</i> Froggatt	2000 ^c	<i>Psyllaephagus parvus</i> Riek	Moderate
	<i>Glycaspis brimblecombei</i> Moore	1998 ^a	<i>Psyllaephagus bliteus</i> Riek	Moderate
Hemiptera/Psyllidae	<i>Acizzia uncatoides</i> (Ferris & Klyver)	1954 ^d		
Hymenoptera/Eulophidae	<i>Aprostocetus</i> Westwood sp.	1995 ^e		
	<i>Epichrysocharis burwelli</i> Schauff	1999 ^f		
	<i>Quadrastichodella nova</i> Girault	1957 ^f		
	<i>Selitrichodes globulus</i> La Salle & Gates	2008 ^g		
	<i>Ophelimus maskelli</i> (Ashmead)	2015 ^h		

^a Gill (1998).
^b von Ellenreider (2003).
^c Garrison and von Ellenreider (2003).
^d Ulyshen and Miller (2007).
^e Schauff and Garrison (2000).
^f Timberlake (1957).
^g La Salle et al. (2009).
^h Burkes et al. (2015).

(Hanks et al. 1996a, 1998a). Females oviposit under exfoliating bark, or in cracks in the bark, and the neonate larvae penetrate the bark to consume the vascular cambium, phloem, and outer layers of xylem tissues, frequently killing the trees. A wide variety of management approaches were investigated, including host plant resistance (Hanks et al. 1999), species susceptibility (Hanks et al. 1993b, 1995b, Paine et al. 2000), cultural practices (Paine et al. 1995, Paine and Millar 2002), and biological control (Hanks et al. 1995a). Introduction and establishment of the encyrtid egg parasitoid *Acetianella longoi* (Siscaro) resulted in complete biological control of *P. semipunctata* throughout the state (Hanks et al. 1995a, 1996).

Unfortunately, a second cerambycid species, the congener *Phoracantha recurva* Newman, was detected in California in 1995 (Hanks et al. 1998b). Although parasitized by *A. longoi*, eggs of *P. recurva* were not preferred by host-seeking wasps and were much less suitable for larval development than those of *P. semipunctata* (Luhring et al. 2000, 2004). In fact, eggs of *P. recurva* proved capable of encapsulating and killing the parasitoid eggs (Reed et al. 2007), which was never observed to occur with eggs of *P. semipunctata*. Consequently, a second strain of *A. longoi* was collected specifically from *P. recurva* eggs in Australia (Wang et al. 2008) and released for biological control of *P. recurva* in California. Parasitized eggs have been recovered from release sites (T.D.P. personal observation), indicating that this strain of parasitoid has established. However, the two wasp strains are indistinguishable by either morphological or molecular techniques, and rarely observed in the field. To date, it has been difficult to fully evaluate the effectiveness of the second strain of *A. longoi* in controlling *P. recurva*.

There have been two efforts to establish biological control of coleopteran folivores. The leaf weevil *Gonipterus scutellatus* Gyll. was discovered in southern California in 1994 (Gill 1998) and caused extensive local defoliation of eucalypts (Hanks et al. 2000). This species has been effectively controlled by the egg parasitoid *Anaphes nitens* (Girault) in many other parts of the world where it has been introduced (Luck 1981). Release of this parasitoid in California quickly resulted in complete biological control (Hanks et al. 2000), reducing weevil populations to very low densities. However, a similar effort directed against another defoliator, the tortoise beetle *Trachymela sloanei* (Blackburn), was not successful. More than 10,000 adults of an egg parasitoid of the tortoise beetle, *Enoggera reticulata* Naumann, were reared and released, but apparently did not establish (Millar et al. 2009). However, this parasitoid was originally recovered from eggs of the congener *T. tincticollis* (Blackburn) rather than from *T. sloanei* itself, which may account for the failure to establish on *T. sloanei*.

Eight species of psyllids that infest eucalypts have been introduced into California from Australia (Paine et al. 2010, 2011b), four of which have been targeted with biological control efforts. The blue gum psyllid, *Ctenarytaina eucalypti* Maskell, causes both distortion of the foliage and defoliation, which was of particular concern to the producers of eucalypt foliage for the floral industry (Dahlsten et al. 1998a,b). Introduction of the encyrtid wasp parasitoid *Psyllaephagus pilosus* Noyes provided complete biological control of that pest in both commercial foliage plantations and urban forest trees (Dahlsten et al. 1998a,b).

The red gum lerp psyllid, *Glycaspis brimblecombei* Moore, produces conical shelters of wax and excrement

called lerps that protect the nymph feeding beneath. High densities of the psyllid caused extensive defoliation of red gums, resulting in widespread mortality of trees across the state (Paine et al. 2000). For example, the affluent community of Rancho Santa Fe in southern California (San Diego, Co.), developed in the early 20th Century in an established eucalypt plantation, was dramatically transformed when approximately half of the trees were killed or removed as a result of long-horned borer and psyllid infestations (Hanks et al. 1996b, T.D.P. personal observation). Similarly, the combined activities of the psyllid and the borers has killed 45% (155 of 345) of the eucalypt trees on the UC Riverside agricultural operations facility. Until the natural enemies that were introduced to control red gum lerp psyllid became established, psyllids on infested trees could only be controlled through insecticide applications (Paine and Hanlon 2010), which jeopardized natural enemies introduced for biological control of other eucalypt herbivores (Paine et al. 2011a). Introduction of the encyrtid wasp *Psyllaephagus bliteus* Riek in 2003 greatly reduced populations of the psyllid (Daane et al. 2005, Dahlsten et al. 2005), except in warmer regions of the state (Daane et al. 2012). In addition, populations of the psyllid with high levels of infection by a bacterial endosymbiont had lower rates of parasitism (Hansen et al. 2007). While tree mortality from psyllid infestation is now very rare, the biological control is incomplete, with continuing defoliation of trees in some areas (Daane et al. 2012).

Biological control has also been moderately successful in controlling the spotted gum psyllid, *Eucalyptolyma maideni* Froggatt, and lemon gum psyllid, *Cryptoneossa triangula* Taylor. A research program was established to control these insects, and parasitoids were collected from Australia (Table 1). A prerelease sampling program was conducted for two years in anticipation of release of parasitoids into the environment. However, just weeks prior to the first release, the parasitoids were discovered at the field monitoring sites, having presumably been accidentally introduced into California via global shipping and commerce. The success of the biological control appears to have been moderated by the presence of an exotic hyperparasitoid (Eatough-Jones et al. 2011).

Several other Australian pests of eucalypts have established in California in recent years, including hymenopterans whose larvae feed within seed, stem, and leaf galls, but they have not yet been the subject of any biological control efforts. There has been a different pattern of introductions of invasive guilds on eucalypts in different parts of the world: California was initially colonized by wood borers and many species of psyllids, whereas Europe was initially colonized by many species of gall wasps (Paine et al. 2011b). However, these hymenopteran insects continue to colonize new areas of the world. For example, the eulophid wasp *Ophelimus maskelli* (Ashmead), first detected in Europe in 2000, was recently discovered in California (Burks et al. 2015). As these introductions continue, they are likely to become the target of classical biological control efforts as damage to trees increases.

There are a number of well-known examples of successful and permanent reduction in pest populations through classical biological control programs (e.g., Clausen et al. 1977). However, the economic return of these programs has rarely been documented (Naranjo et al. 2015), in large part because with successful control, the problem disappears and the focus, and funding support, shift to newly emerging problems. This short attention span does a serious disservice to biological control, because regulatory agencies, growers, and the general public rarely appreciate the magnitude and cost of the damage that a successful project has permanently prevented or eliminated. The complementary studies by Jetter et al. (1997) and Pickett et al. (1996) using tree valuation methods to assess the benefit of biological control of ash whitefly are the only examples of attempts at cost benefit analysis for landscape and street trees. However, these efforts valued change in aesthetic quality of two host tree species caused by a single insect.

There have been a total of eight biological control programs directed against insects feeding on eucalypts (Table 1). However, the benefit accruing from each individual program is impossible to calculate because the herbivore species were often introduced within narrow time periods and interacted on the same host trees. The biological control efforts were often conducted simultaneously rather than sequentially. As has been done with other biological control efforts in landscape trees, it would have been ideal to measure the reduction in damage as a result of establishment of natural enemies for biological control of a single pest species (e.g., Gould et al. 1992). Because the herbivores of eucalypts fed as a community of four guilds causing defoliation, growth deformation, and tree death, it was impossible to assess changes in tree condition attributable to only a single introduced species or a single biological control program. Consequently, it was necessary to determine the entire value of the host resource placed at risk by the entire community rather than partition changes in value due to a single pest species. In addition to extraordinary levels of tree mortality, the cumulative damage to the trees so reduced the perceived value of the tree as a component of the urban forest such that only eucalypts with no significant insect pest problems (8 of the approximately 90 species in the state) were recommended for street tree planting or tree replacement (Hartin and Pittenger 1988, Mahoney et al. 1999). Thus, the objective of the present study was to calculate the total resource value of a critical population of managed eucalypts in California in order to determine the cost–benefit ratio of the biological control programs directed toward their exotic and invasive herbivores. The total cost of the eight classical biological control programs directed against invasive eucalypt herbivores is used to establish the rate of return on the investment in these programs.

Materials and Methods

Biological control programs in California have targeted members of invasive borer, defoliator, and sucking

guilds of herbivores feeding on eucalypts in at least three different genera and many different species groups. Several herbivore species were targeted in each guild. The nature of the damage caused to different species of trees by members of the same guild can be nearly identical. Consequently, rather than attempt to partition out the damage caused by individual species, members of all damaging herbivore guilds are treated as a single community that placed the population of eucalypts at risk of death or replacement with different species.

There is no attempt here to quantify the total number of eucalypts in California. The trees are extensively planted in private, commercial, and recreational landscapes throughout the state. In addition, they also have been planted widely outside of urban areas in farm and ranchlands as windbreaks, shelter woods, plantations, and woodlots. Finally, there are areas where eucalypts have naturalized. For the purposes of this study, the numbers and value of the eucalypt resource are restricted only to municipal street trees. Given the number of eucalypts that can be found across the state growing in different habitats or for other uses, these represent only a small fraction of the value of the eucalypt resource overall, and of the cost savings from the successful biological control programs.

Appraised Value of Eucalypt Street Trees. The tree valuation methods used in this study are similar to those used by Jetter et al. (1997) and Pickett et al. (1996) to determine the return on investment for a biological control program mounted against an invasive pest of urban street trees, the ash whitefly, *Siphoninus phillyreae* (Haliday). Tree valuation was conducted by West Coast Arborists Inc., a large commercial arborist company that contracts tree maintenance services to municipalities across the state. As part of their standard operating procedures, the company uses an industry standard practice to estimate valuations, which is based on the Trunk Formula Method (TFM) developed by the Council of Tree and Landscape Appraisers (2000). Appraisal of a landscape tree using TFM uses the formula: Estimate of Appraised Value = Basic Tree Cost $\times$ species classification number $\times$ condition factor $\times$ location factor. Basic Tree Cost = (Unit Tree Cost $\times$ Appraised Trunk Increase) + installed tree cost. The Unit Tree Cost is equal to the cost of the largest commonly available transplantable size tree of the same or similar species divided by cross sectional area of the trunk. The Appraised Trunk Increase is equal to the trunk area at 1.37 m of the appraised tree minus the trunk area of the replacement tree. The installed cost is equal to the wholesale cost of a replacement tree plus the cost of installation (including labor, equipment, delivery, and any guarantee). For the purposes of the appraisal, the installed tree cost was set by the commercial arborist company at US\$905 for the replacement trees plus US\$900 for installation.

The species classification number (a percentage adjustment) was taken from Western Chapter International Society of Arboriculture standards (Western Chapter International Society of Arboriculture 2004). The species classification number and corresponding

ratings for Condition factor for appraised eucalypts were set at Good (90%) for both. The location factor, a percentage adjustment based on where the tree was planted, the contribution to the site, aesthetics, and function for all of the urban street trees was set uniformly by the appraisers at 80% for Good [(Site = 80% + Placement = 80% + Contribution = 80%) / 3].

The Arbor Access database containing all of the appraised tree values (West Coast Arborists, Anaheim, CA) was queried for the city of Riverside (Riverside Co., CA) and for Orange County Parks (Orange Co., CA). The appraised valuation of all 1,756 eucalypt street trees in Riverside was obtained from the database. Similarly, the mean appraised valuation of the first 1,756 eucalypt trees appearing in the Orange County Parks database was also recorded. The mean value for a single tree then was calculated from the total combined sample of 3,512 trees.

Number of Eucalypt Street Trees. Two independently derived methods were used to estimate the number of eucalypt street trees. The Arbor Access database (West Coast Arborists, Anaheim, CA) was queried for 135 cities in northern, central, and southern California. The number of eucalypt street trees was recorded from each of those cities and a total number of trees determined. The 2013 population of each of the cities was determined from the United States Census Bureau and a total population of the 135 cities was calculated. This total was used to derive a percentage value that reflects the proportion of the state population represented by these cities. However, it was first necessary to eliminate that portion of the state population living in areas where eucalypts are not grown because of environmental conditions. Thus, the populations of 14 counties located in either the northern or eastern mountainous regions of the state were totaled and then subtracted from the total population of the state. The remainder represented the population of California living in areas suitable for eucalypts. The total population of the 135 cities was divided by the modified state total to calculate the proportion of the state population represented by the inventoried cities. The number of eucalypts in those cities was divided by the proportion value to extrapolate to the total number of eucalypt street trees in the state.

The second method is described in detail in McPherson et al. (2015). The authors used tree inventories from 49 communities divided into six different regions (Inland Empire, Inland Valleys, Northern California Coast, Southern California Coast, Interior West, and Southwest Desert) to scale up to state-wide estimates of all street tree species. The total number of eucalypts of all species was extracted from those data.

Total Value of Eucalypt Street Trees. The total value of the eucalypt street tree resource was determined by multiplying the mean appraised value of a eucalypt street tree by the estimated numbers of eucalypt street trees. These values represent a very conservative estimate of the total benefit of the biological control programs because they capture only a fraction of the total number of eucalypts in the state.

Total Cost of Biological Control Efforts. The first biological control effort against exotic pest of eucalypts in California was initiated in 1992 and targeted *P. semipunctata*, and various biocontrol projects targeting different species have continued through 2014. The cost of the biological control programs overall was determined by summing all of the extramural grants awarded to investigators in the University of California in support of the eight research efforts. The grant funds were supplemented by state funds in the form of salaries and benefits of the UC faculty and staff associated with the projects. The salary values were apportioned to the total cost based on the percentage of effort expended on each project. These salary contributions for the 22-yr period were added to the extramural grant awards to calculate the total cost of the biological control programs.

Results

Based on the appraised value of 3,512 eucalypt street trees in the city of Riverside and in Orange County Parks, the mean value of an individual tree was estimated to be US\$5,978 (SD = 3.0). The two methods of estimating eucalypt street tree populations resulted in different numbers. There were 149,666 eucalypts in the street tree inventories of the 135 cities evaluated. The populations of those cities summed to 11,391,644, or 31.4% of the modified total state population of 36,267,125 people. Consequently, the estimated number of eucalypt street trees in California was 476,527 using this method. The method of McPherson et al. (2015) determined the numbers of individual tree species extrapolated from 49 street tree inventories and resulted in a total of 190,666 eucalypt street trees. These two different tree inventory estimates place upper and lower boundaries on the number and value of the street trees.

The total value of eucalypt street trees using the tree estimate from 135 inventories is US\$2,848,678,406, whereas the value based on 49 inventories is US\$1,139,801,348. A total of US\$2,663,097 composed of extramural grants (US\$2,358,247) and University of California salaries committed to the projects (US\$304,850) was expended on the biological control efforts (Table 2). Consequently, the return derived from the biological control efforts for every dollar expended was US\$1,070 for the high number of street trees, or US\$428 for the lower number of trees, that is, between a >400-fold to >1,000-fold return to the citizens of California for every dollar invested in the control programs.

Discussion

Biological control can be a very effective tactic for permanently reducing population densities of a wide range of insect pests. However, despite a number of notable successes, there have also been a significant number of failures (Clausen et al. 1977). These failures may be the result of difficulties in identification, collection, culture, or establishment of effective natural

enemies. It is also entirely possible that no single natural enemy species, or even a number of natural enemies, may provide effective control of an invasive species which has become established in a new region.

The potential benefits of introducing exotic natural enemies also must be carefully weighed against the potential risk of nontarget effects (Stiling 2004). Consequently, many countries have strict permitting processes regarding quarantine procedures, environmental impact assessments, and specificity testing that must be followed to minimize the potential negative environmental effects of introduced natural enemies expanding their host ranges to include native species. Thus, for any biological control program, a substantial investment may be required to elucidate the biology of the natural enemies, conduct thorough specificity testing, and assess the potential effectiveness of the natural enemies under quarantine conditions before any releases into the environment can even be considered. These front-end costs must be incurred without any guarantee of success, and represent a substantial barrier to both initiating and sustaining the required research efforts, because outcomes and outputs may not be realized for several years. That is, given the relatively short time-frame (1–3 yr) and intense competition for most research funding, it may not be possible to generate the critical mass of positive results required to drive subsequent cycles of funding within 1–2 yr.

This is particularly true for biological control in urban environments. The urban clientele is the largest in terms of numbers of potential beneficiaries, but despite the interest of individuals, that clientele is also one of the most diffuse and loosely organized with respect to providing funds in support of specific research programs (Jetter and Paine 2004). The potential benefits that can stem from successful biological control can be substantial, and it is possible to work with a diversity of organizations with vested interests in the success of a program in order to garner the necessary monetary support. However, because there have been so few cost–benefit analyses carried out for biological control programs in general (Naranjo et al. 2015), and in urban environments specifically, sustained support over a multiyear period, at levels required to maintain a program, can be difficult to obtain.

Introduction of the exotic ash whitefly resulted in extensive defoliation of ornamental pear and ash trees in California (Gould et al. 1992). The parasitoid wasp *Encarsia inaron* (Walker) was introduced into California from the Mediterranean region and completely controlled the whitefly, driving whitefly populations well below thresholds at which damage would be noticeable (Pickett et al. 1996). Because the project dealt with a single pest species, Jetter et al. (1997) were able to assess the impact of defoliation by that insect on the host trees. They concluded that there was a return of US\$265 per dollar invested in the control program based on wholesale prices for replacement trees, or US\$337 at retail replacement costs (Jetter et al. 1997). Those cost–benefit ratios are lower than the values calculated for eucalypts, but still clearly

Table 2. Funding for eight eucalypt insect biological control projects

	Extramural grants ^a	UC salaries
<i>Phoracantha semipunctata</i> / <i>Phoracantha recurva</i>	US\$1,657,816	
<i>Trachymela sloanei</i>	US\$116,889	
<i>Gonipterus scutellatus</i>	US\$116,937	
<i>Cryptoneossa triangula</i> / <i>Eucalyptolyma maideni</i>	US\$210,000	
<i>Ctenarytaina eucalypti</i>	US\$50,000	
<i>Glycaspis brimblecombei</i>	US\$206,605	
TDP 1992–2014		US\$184,876
JGM 1992–2006		US\$83,974
DLD		US\$36,000
Totals	US\$2,358,247	US\$304,850

^aFunding agencies are listed in Acknowledgments.

demonstrate the substantial benefit from the successful, permanent control of a single pest herbivore by a natural enemy.

The present study reflects the greater benefit of biological control of eight different insect herbivores from three different feeding guilds. Dahlsten et al. (1998b) successfully achieved biological control of blue gum psyllid in California. The principal beneficiaries of establishment of the parasitoid were commercial producers of *Eucalyptus pulverulenta* Sims, known as silver-leaved mountain gum, which is grown as ornamental foliage for floral displays. The natural enemy permanently suppressed psyllid populations, and eliminated the need for expensive insecticide treatments. The economic analysis conducted for this system focused only on the value of the reduced pesticide treatment costs (Dahlsten et al. 1998a) but nevertheless yielded a benefit: cost ratio of at least 9:1 over 5 yr, and 20:1 over 15 yr. However, that analysis did not factor in the potential benefits to other trees (e.g., street trees) that were also infested by the psyllid, and which benefited directly from the biological control program. The reported costs for that biological control effort are included in the cost calculations in the present analysis, but not the benefits because our analysis focused only on street trees as opposed to trees grown for the floral industry.

The biological control programs against ash whitefly and blue gum psyllid provide different ways of evaluating biological control of insect pests in tree systems. In the case of ash whitefly, the difference in tree quality between infested and uninfested trees was used to assess benefit attributable to the biological control. In the blue gum psyllid example, reduced direct control costs (i.e., pesticide applications) required to manage psyllid populations were used to calculate the benefit of biological control. While each approach is appropriate for the specific insect system, neither is directly applicable for assessing the cumulative benefit of controlling a community of insect herbivores.

The three herbivore guilds represented in the present study cause different types of injury to their host trees and, in some cases, it is impossible to partition out what damage is caused by which insect species. Consequently, the benefit from the biological control is assigned as overall protection of the eucalypt street tree resource. The benefit includes not only the

cumulative assessed valuation for replacement of the street trees, but the valuation method also includes the value of the ecosystem services provided by those street trees. Thus, this estimate is likely to be conservative because the street trees are a subset of the much larger total population of eucalypts in the state.

The results of our analyses clearly demonstrate the highly cost-effective value of successful biological control in urban landscape systems. Although there were differences in the methods used to estimate the total number of urban street trees, the value of the trees exceeded US\$1.0 billion in the lower estimate and exceeded US\$2.8 billion in the higher estimate. The return on research investment in biological control (US\$1,070 per dollar invested for the high number of street trees or US\$430 per dollar invested for the lower number of trees) greatly exceeded the values calculated for the few other biological control programs for California urban trees for which estimates are available. Furthermore, our estimates of total eucalypt value represent only a fraction of the total value of eucalypts in the state because our methods could only reliably capture the value of municipal street trees. Our estimates could not capture the numbers or value of eucalypts planted in other settings, such as windbreaks, institutional and private landscapes, and landscaping along highways. The trees are widely planted throughout the state except in areas with damaging cold winter temperatures in the far northern part of the state, and mountainous areas. Thus, the urban municipal street trees reflect only a fraction of the total population of eucalypts in the state. Consequently, the benefits of the biological control programs are substantially greater than are represented by just street trees. However, it should be noted that even these underestimated values are in the billions of dollars.

The urban landscape has tremendous economic, aesthetic, and ecological value. Plants in the landscape are placed at risk by the continuing invasion of exotic pests and diseases from many different parts of the world. Management of those pests can employ a wide variety of tactics, depending on the particular circumstances. Successful biological control can be a very valuable component of a management system, and in the best cases, may render all other control tactics unnecessary. Although the value of the urban landscape accrues to a very large segment of the national population, those

beneficiaries are, at best, a very loosely organized clientele. Thus, organizing and funding sustained biological control efforts that primarily benefit urban populations has proven to be a substantial challenge, even though there is evidence that those populations are willing to pay more for biological control than other control tactics (Jetter and Paine 2004). Consequently, the most effective argument for developing sustained support for biological control of invasive pests of plants in urban or natural landscapes may be economic rather than ecological. Economic analyses such as the one developed in this study, which unequivocally demonstrate the very substantial rates of return on every dollar invested in successful biological control, provide a compelling argument for supporting future efforts to control invasive pests with their coevolved natural enemies.

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