

Potential Invasiveness for *Eucalyptus* Species in Florida

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To assess the potential invasiveness of common eucalyptus species planted for pulpwood, mulch wood or bioenergy crops, field surveys of eucalyptus seedling recruitment were conducted in north and central Florida locations within seed bearing eucalyptus stands and in the proximate plant communities where seed dispersal may occur. Plant communities included non-grazed pasture, intensively site-prepared forestland, abandoned forest road and upland mixed pine- hardwood forest. No eucalyptus seedlings were found in any of the 310 1-m² survey plots across the two locations. Second, seed addition studies were conducted to determine the relative potential for seedling emergence and survival among *Eucalyptus amplifolia*, *E. camaldulensis* and *E. grandis* added into plots at two seed densities, under disturbed and nondisturbed conditions, in the understory of the eucalyptus stands and in each of the aforementioned proximate plant communities. Overall, the probability of emergence of added seed was very low ($P = 0.0$ to 0.0032), and seed density effects were not significant. Emergence was significantly greater in disturbed conditions compared to nondisturbed conditions for seedlings originating from natural seed rain from the eucalyptus canopy in central Florida. The amount of time that seedlings survived was greater for *E. camaldulensis* compared to the other species but no seedlings survived more than 13 wk. These data indicate that under specific favorable conditions, eucalyptus seedlings may establish within or proximate to planted stands, but the overall level of invasiveness demonstrated by *E. amplifolia* and *E. grandis* is low for north or central Florida. The demonstrated role of disturbance in facilitating eucalyptus seedling recruitment suggests that a stable perennial plant community (native grasses) should be established instead of bare soil buffer zones to mitigate spread.

Nomenclature: Cabbage gum (*Eucalyptus amplifolia* Naudin); yellow mallee (*Eucalyptus incrassata* Labill.); river red gum (*Eucalyptus camaldulensis* Dehnh.); rose gum [*Eucalyptus grandis* W. Hill ex Maiden].

Key words: Disturbance, establishment, experimental assessment, propagule pressure, survival, weed risk assessment.

Members of the diverse *Eucalyptus* genus (family Myrtaceae) are native to Australia and over 70 species are naturalized elsewhere (Rejmánek and Richardson 2011). These forestry species are widely planted for pulpwood, mulch wood, energy wood, and windbreaks. After their introduction to many countries, at least seven species have been identified as invasive (Richardson and Rejmánek 2011). Contributing to the extensive propagation of eucalyptus is their perennial growth form, prolific seed production, low incidence of disease, pest resistance, drought tolerance, and their ability to rapidly accumulate biomass and grow in soils of relatively low fertility (Booth 2012). Some eucalypts also have undesirable economic and ecological impacts including increased fire intensity (Pagni

1992), reduction of natural river flows (Le Maitre et al. 2002), and alteration of the native faunal composition and density (Sax 2002). Several eucalyptus species, including *E. camaldulensis* Dehnh., *E. grandis* W. Hill ex Maiden, and *E. amplifolia* Naudin, are being planted in the southeastern United States for pulpwood, mulch wood or as bioenergy feedstock (Rockwood 2012). Because of their history of invasiveness elsewhere and their suite of ecologically advantageous traits, potential invasiveness in the southeastern United States is a concern.

Prevention, which can be described as avoidance through appropriate risk assessments and quarantine enforcement (McCormick and Howard 2013), is often considered the most cost-effective approach for dealing with biological invasions (Leung et al. 2002). Two recent studies assessed the invasion risk of eucalyptus in the southeastern United States using observational approaches. Callaham et al. (2013) conducted surveys in the vicinity of 19 eucalyptus stands in Florida and South Carolina to determine the risk of seedling establishment. They observed limited spread of

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Management Implications

Because of its potential for fast growth and high fiber yields, eucalyptus plantations are being established in the southeastern US Coastal Plain as a source of pulpwood, mulch wood and possibly biofuel. Two quantitative study approaches used within seed bearing *Eucalyptus amplifolia* stands and their proximate native and modified plant communities in north and central Florida found low invasive potential overall. Surveys at the two locations found no eucalyptus recruitment, suggesting limited success for seedling establishment. The subsequent study evaluated the invasive potential of three commercially important eucalyptus species by adding seed at two densities to disturbed (forest litter or vegetation removed to expose mineral soil) and nondisturbed sites. The combined research findings demonstrated that eucalyptus seedling establishment and survival were generally low at the northern and central Florida locations, although greater numbers of seedlings were observed in disturbed conditions, within the eucalyptus stands and for *E. camaldulensis* as compared to *E. grandis* or *E. amplifolia*. Seed addition at 500 or 1000 expected germinants per m² did result in seedling establishment, but no seedlings survived more than 13 wk. Whereas these results do not support previous weed risk assessment conclusions of high invasion risk for *E. camaldulensis*, they suggest that caution is warranted regarding the cultivation of *E. camaldulensis*, especially concerning practices that might increase soil disturbance near eucalyptus stands. The demonstrated role of disturbance in facilitating eucalyptus seedling recruitment suggests that perennial native plant communities should be established instead of bare soil buffer zones. Future research is needed for south Florida where subtropical temperatures favor eucalyptus growth and where commercial plantations are becoming more common.

eucalyptus into unmanaged habitats south of 27° N, but suggested that further evaluations should be done before *Eucalyptus* species are adopted for widespread planting. Gordon et al. (2011, 2012) applied the Australian Weed Risk Assessment (WRA), a widely used literature-based tool, to evaluate the risk posed by 38 of the most commercially important *Eucalyptus* species. The WRA uses 49 “yes” or “no” questions about a species’ current weed status in other parts of the world, climate and environmental preferences, and biological attributes, to conclude if a species has high risk, low risk or requires further evaluation (Pheloung et al. 1999). Gordon et al (2012) determined that 15 *Eucalyptus* species have low risk of invasion in the United States, 14 have high risk and 9 require further information. When the WRA was modified to assess the invasion risk of three species specifically in Florida, Gordon et al (2011) concluded that *Eucalyptus grandis* and *E. camaldulensis* posed high invasion risk and that further information was required for *E. amplifolia*.

While the WRA offers a useful starting point, more quantitative tests are needed to evaluate the many species and taxa of biofuel crops that are being proposed for introduction (Barney and DiTomaso 2008; Chimera et al 2010; Davis et al 2010; Hulme 2011). Invasion risk is

shaped not only by species life history traits but also by stochastic processes and local interactions with the biotic and abiotic features of ecosystems in the new range that can greatly affect the population’s performance (Hulme 2011; Minton and Mack 2010). These complex processes and relationships are often nonlinear and affected by temporal lag effects and positive feedbacks (Hulme 2011). Therefore, it is difficult to predict invasions based solely on qualitative information using literature-based tools like the WRA.

Experiments are needed to understand invasion risk relative to complex ecological processes and to resolve differing conclusions from observational and literature based work. Experiments to evaluate invasion risk should take into account both the traits of introduced species and the environmental context (Ewel et al 1999; Flory et al. 2012; Parker and Kareiva 1996). Additionally, consideration needs to be given to the effects of propagule pressure and site disturbance on seedling emergence and survival. Disturbance such as vegetation removal is possibly an important driver of invasion (Elton 1958) and has been suggested to be a prerequisite for eucalyptus establishment (Wevill and Read 2010). High propagule pressure has also been observed as one of the mechanisms responsible for tipping the balance to invasion (Lockwood et al. 2005) and it is thought to be an especially important factor for eucalyptus population performance (Gordon 2012; Rejmánek and Richardson 2011). Eucalyptus propagule pressure can potentially be very high considering that seed rain from mature eucalyptus can be up to 4,000 seeds m⁻² (Rejmánek and Richardson 2011). Experimental evaluation of invasion risk was needed to understand invasion risk relative to the interacting effects of propagule pressure, species’ traits, and environmental conditions; and to resolve unclear conclusions from previous work.

The objective of this study was to evaluate the potential invasiveness of three eucalyptus species being considered for large-scale planting in Florida through two approaches. First, site surveys were conducted to determine the abundance and height distribution of eucalyptus seedling recruitment within seed bearing stands and in the proximate plant communities where nseed dispersal may occur. Plant communities included upland mixed pine-hardwood forest, non-grazed pasture, intensively site-prepared forest land and abandoned forest road. Second, seed addition studies were conducted to determine the relative potential for seedling emergence and survival among *E. amplifolia*, *E. camaldulensis* and *E. grandis* sown at two seed densities under disturbed and nondisturbed conditions in the understory of reproductively mature eucalyptus stands and in each of the aforementioned proximate plant communities.

Materials and Methods

Study Areas and Surveys. Separate studies were conducted in the proximity of mature *E. amplifolia* stands at two

Table 1. Vegetation community characteristics at two Florida study locations.

Study location	Vegetation community	Soil series ^a	Canopy cover ^b
			%
Gainesville	<i>E. amplifolia</i> seed orchard	Blitchton sand	74.9 ± 1.9
Gainesville	Abandoned forest road	Lochloosa fine sand	64.0 ± 4.3
Gainesville	Upland mixed forest	Blitchton sand	98.3 ± 0.2
Quincy	<i>E. amplifolia</i> progeny test	Dothan-Furquay complex	90.4 ± 0.7
Quincy	Intensively prepared forestland	Dothan Furquay complex	0.0 ± 0.0
Quincy	Non-grazed pasture	Dothan Furquay complex	0.0 ± 0.0

^a USDA 2012. Web Soil Survey. <http://websoilsurvey.nrcs.usda.gov/app/HomePage.htm>. Accessed: January 10, 2014.

^b Means and standard errors for canopy cover measured over the center of each treatment plot.

locations in Florida during the spring and summer of 2012. Both stands were planted with seedlings or rooted cuttings 1 m (3.3 ft) apart on rows 3 m apart, but were thinned to relatively wide spacing between trees providing some direct sunlight in the understory (Table 1), potentially fostering seedling establishment (Booth 2013).

The study in central Florida (Gainesville) was located within and proximate to a *E. amplifolia* seed orchard on the University of Florida campus (29°37'36" N, 82°21'32" W) at approximately 23 m elevation. About half of the trees were planted in 1992 and half in 1995 using seedlings or rooted cuttings placed 1 m apart on rows 3 m apart. The stand was 0.4 ha (1.0 ac) with a triangular shape (104 m by 80 m by 76 m). At the time of the study the mean stand basal area was 25.7 m² ha⁻¹ and the mean height of dominant trees was 34.7 m. There had not been any vegetation management in the 2 yr prior to initiating this study, so the stand contained many other species including silk tree (*Albizia julibrissin* Durazz.), sweetgum (*Liquidambar styraciflua* L.), water oak (*Quercus nigra* L.), earleaf greenbrier (*Smilax auriculata* Walter), and grape (*Vitis* sp.). The stand is adjacent to an abandoned forest road that supported Carolina dichondra (*Dichondra carolinensis* Michx.), blackberry (*Rubus* sp.), water oak seedlings and earleaf greenbrier. The *E. amplifolia* stand is also adjacent to upland mixed pine-hardwood forest with an overstory canopy comprised of loblolly pine (*Pinus taeda* L.), live oak (*Quercus virginiana* Mill.) and American elm (*Ulmus americana* L.). Virginia creeper (*Parthenocissus quinquefolia* L.) and eastern poison ivy [*Toxicodendron radicans* (L.) Kuntze] were common in the understory of the upland mixed forest. The Gainesville location has a temperate climate with highest temperatures in July (mean 27 C or 80.6 F), lowest temperatures in January (mean 13 C), a mean extreme minimum temperature of -6.7 to -3.9 C, and 125 cm (49 in) mean annual precipitation (NOAA 2002).

The study in north Florida (Quincy) was located within and proximate to a 150 m by 60 m 0.9 ha *E. amplifolia* progeny test planted with container seedling stock in 1999

at the North Florida Research and Education Center, south of Quincy (30°32'32" N, 84°35'25" W) at approximately 73 m elevation. At the time of the study the mean stand basal area was 24.1 m² ha⁻¹ and the mean height of dominant trees was 23.8 m. The stand also contained Chinese privet (*Ligustrum sinense* Lour.), common persimmon (*Diospyros virginiana* L.), eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall) and blackberry. This stand is adjacent to non-grazed pasture comprised of vaseygrass (*Paspalum urvillei* Steud.) and field paspalum (*Paspalum laeve* Michx.). The stand is also adjacent to intensively site prepared forestland that previously supported a 13-yr-old eastern cottonwood clone test, harvested in January 2012, and was prepared for planting eucalyptus in March 2012 by the rake/pile/burn/disk method (Lowery and Gjerstad 1991). The plant community on the intensively prepared forestland contained a diverse array of species including dogfennel [*Eupatorium capillifolium* (Lam.) Small], redstar (*Ipomoea coccinea* L.), tievine (*Ipomoea cordatotriloba* Dennst.), common yellow oxalis (*Oxalis stricta* L.), purple passionflower (*Passiflora incarnata* L.), pink purslane (*Portulaca pilosa* L.) and sicklepod (*Senna obtusifolia* L.). The Quincy location has highest temperatures in July (mean 27 C), lowest temperatures in January (mean 10 C), a mean extreme minimum temperature of -9.4 to -6.7 C, and 143 cm mean annual precipitation (NOAA 2002).

In May 2012, line transect sampling was used to identify natural recruitment of *E. amplifolia* seedlings from the mature eucalyptus trees. At each study location, 1 m² plots (72 Gainesville, 238 Quincy) were evaluated using a sampling frame placed every 10 m on line transects established 20 m apart across the narrow dimension of the stand and 60 m into the proximate plant communities. Eucalyptus seeds are typically dispersed by wind within an estimated radius equal to twice the canopy or tree height (Cremer 1966, 1977), and 60 m is approximately twice the canopy height of these stands. At Gainesville there were 10 transects with 25 sample points within the eucalyptus stand, 22 within the abandoned forest road and 25 sample

points in upland mixed pine-hardwood forest. At Quincy there were 14 transects with 56 sample points within the eucalyptus stand, 134 sample points within non-grazed pasture and 48 sample points within intensively site-prepared forestland.

Germination Testing. Seeds were collected from wild trees in Australia between 1999 and 2008 and stored frozen by the University of Florida Seed Foundation prior to our use. Germination capacity of *Eucalyptus* species is highly variable, ranging from 11% to 98% (USDA 2008). Prior to initiating the seed addition experiment, the expected germination rates of *E. amplifolia*, *E. camaldulensis* and *E. grandis* seed stocks were determined in order to calculate the amount of seed needed to give equal numbers expected seedling establishment in seed addition experiment plots. The germination rate for each species was determined by measuring the mean number of germinating seeds per g. The use of weight-specific germination rates was preferable because eucalyptus seeds are small (1 to 3 mm (0.04–0.12 in) long and weigh less than 0.5 mg to 2.0 mg (1.8×10^{-5} oz to 7.1×10^{-5} oz) [Rejmánek and Richardson 2011]) and are intermixed with inert chaff from their woody seed capsules, making it difficult to count individual seeds accurately. Germination was evaluated in a seed incubator under conditions that corresponded to mean minimum (20.1 C) and maximum (32.5 C) temperature (NOAA 2002) and 14 h photoperiod for June in north-central Florida (NMOC 2012). Light was provided with the higher temperature for 14 h, followed by the lower temperature without light for 10 h. While some alpine *Eucalyptus* species require cold-moist stratification (Boland 1986), the species used in this study are not known to require any dormancy breaking procedures. Eight 0.05 g (1.8×10^{-6} oz) samples of each seedlot were tested for each species. All materials that were exposed to seeds during preparation of the samples were autoclaved to reduce the likelihood of microbial growth. Samples were placed in 9 cm glass Petri dishes containing two thicknesses of filter paper as a substrate. Three ml (0.1 oz) of sterile distilled water was applied to the filter paper using a glass pipette. Seeds were dispersed evenly over the filter paper, and the Petri dishes were sealed with paraffin film to prevent samples from desiccating. A germination count was made after 5 d and every 2 d thereafter. During each count, normal and abnormal germinated seeds were counted separately and removed from the dish. A normal eucalyptus seedling had a healthy radicle, hypocotyl and cotyledons. The recommended test duration for *E. grandis* is 14 d, and while there were no specific recommendations for the test duration for *E. amplifolia* and *E. camaldulensis*, 10 to 21 d is generally suitable for most species (Boland 1986). The final count was made at 14 d and the total number of normal germinated seeds in each sample was used to

calculate the mean number of germinating seeds per g. The germination rates for *E. grandis*, *E. amplifolia*, and *E. camaldulensis* were 655 seeds g^{-1} (SD 174), 92 seeds g^{-1} (SD 29), and 388 seeds g^{-1} (SD 113), respectively, with differences among species means using Fisher's Protected LSD test.

Experimental Design of Seed Addition Studies. The potential for eucalyptus seedling establishment and survival in common native or modified vegetation communities was evaluated through a seed addition approach similar to da Silva et al. (2011). Sampling plots were established within the understory of the *E. amplifolia* stand and in two proximate communities at both study locations, resulting in 63 plots at each location. At the Gainesville location, proximate communities included an upland mixed pine-hardwood forest and an abandoned forest road. At the Quincy location, proximate communities included a nongrazed pasture and an intensively prepared site for eucalyptus planting, as described above. In each vegetation community, seeds of *E. amplifolia*, *E. camaldulensis* and *E. grandis* were placed on separate nested paired plots to examine the effects of disturbance and seeding density for each species. Adjacent 0.75 m^2 -paired plots were randomly left nondisturbed or were disturbed through removal of the vegetation layer and soil scarification with a rake. In the center of each of the paired plots, two nested 0.25 m by 0.25 m paired subplots were randomly assigned to addition of amounts of seed expected to result in either 500 or 1,000 germinated seedlings m^{-2} (equivalent to 31 or 62 expected seedlings per subplot). These levels were chosen to reflect the hypothesized intermediate and maximum levels that occur naturally based on estimates of actual seed rain in the literature (Virtue and Melland 2003). The 0.625 m^2 nonseeded areas outside of the smaller nested paired seeded subplots within the disturbed or nondisturbed treatments were used to observe eucalyptus seedling establishment from mature trees. Randomly distributed paired plots were replicated eight times in each vegetation community type for *E. amplifolia* and *E. grandis*, and only five times for *E. camaldulensis*, because of a shortage of seed. Seeds were added on June 7, 2012 in Quincy and on June 8, 2012 in Gainesville, following 2.0 cm and 13.1 cm of rain (tropical storm event) in the previous 24 h at each location, respectively (IFAS 2012).

Seedlings were counted at 2, 4, 6, 8, 11, 14, 17, 21, and 25 wk after seeds were added into plots to determine emergence and survival of eucalyptus seedlings. Newly emerged seedlings at each counting date were marked with uniquely colored toothpicks to distinguish them from new seedlings in subsequent counts. Surviving seedlings of each emergence date group were counted at each census so that the approximate length of time that seedlings survived could be determined.

Statistical Analyses. *Germination Rates and Field Emergence.* Seed incubator mean germination rates for the three *Eucalyptus* species were compared using Fisher's Protected LSD test. The low level of emergence observed in field studies allowed for three statistical models that were of interest.

1. The cumulative eucalyptus seedling emergence count was compared for seeded and nonseeded areas of plots located within the eucalyptus stands at the two study locations in order to determine if there was a difference in emergence because of adding seed compared to the base levels of seed rain. Emergence was analyzed using a generalized linear model with a Poisson distribution. The natural log of subplot area was used as an offset (McCullagh and Nelder 1989) to account for different seeded and nonseeded subplot size.
2. In order to determine if treatment effects were significant, cumulative eucalyptus seedling emergence counts, expressed as the proportion of seedlings that emerged relative to the expected 93 total seedlings in paired subplots, were used as a response variable. Emergence data from both locations were analyzed together in a generalized linear model with a binomial distribution and a logit link function using PROC GLIMMIX (SAS v. 9.3, SAS Institute, Cary, NC). Community, species, disturbance, disturbance by species, and species by community were considered fixed effects. Emergence data were pooled across high and low density seeded subplots because seedling counts were too low to evaluate the effect of seeding density in each subplot, and seeding density effects were not significant. The random effect of plot within each community was removed from the model because it was a source of nonconvergence. Insignificant interactions were also removed.
3. The cumulative eucalyptus seedling emergence counts, summed across nonseeded areas of the 21 disturbance treatment plots (total 13.1 m²) within the two eucalyptus stands, served as an additional response variable. This variable reflected seedling emergence caused by natural recruitment. A generalized linear model (PROC GLIMMIX) was used to analyze the fixed effect of disturbance. Counts were summed across plots within a community because variation across plots could not be estimated because of the absence of observed emergence in some plots.

Survival. The duration of survival for each of the eucalyptus seedlings observed was determined based on when each seedling was first observed and when it was last observed. The middle value of this range was assigned to each seedling to approximate survival time. Pearson's chi-squared tests (PROC FREQ) (SAS v. 9.3, SAS Institute, Cary, NC) were used to analyze the significance of species,

disturbance and vegetation community for ranges of survival time (< 1 mo, 1 to 2 mo, > 2 mo). Survival data were pooled for the Gainesville and Quincy locations because survival time did not differ by location. Analyses of survival time for the three species were performed using the number of observed seedlings in both seed addition subplots and in the surrounding whole plots, to account for the possibility of movement of the added seed. The significance level for all tests was $\alpha = 0.05$.

Results and Discussion

Study Area Surveys. The 1-m² survey plots in the eucalyptus stands and proximate plant communities included various types of ground cover: grasses, vines, forbs, shrubs, trees, bare mineral soil and leaf litter. No eucalyptus seedlings were found in any of the 72 plots at the Gainesville study location or in the 238 plots at the Quincy location. Flowering in *E. amplifolia* occurs relatively late compared to other species, typically not flowering abundantly until approximately age 8 yr (personal communication, Donald Rockwood, Professor Emeritus, University of Florida). Eucalyptus was planted at the Gainesville location in 1992 and 1995, so trees had been producing seed for 12 to 9 yr at the time of the study. The Quincy site was planted in 1999 and trees had likely been producing seed for 5 yr prior to the survey. The lack of natural eucalyptus recruitment observed in these surveys is consistent with results of a similar study that found natural recruitment of eucalyptus seedlings adjacent to only 4 of 16 surveyed eucalyptus stands in Florida (Callahan et al. 2013). Similar surveys in Brazil found recruitment within eucalyptus stands, but not in adjacent pine communities (Emer and Fonseca 2010).

Main Effect of Seeding. In the Gainesville study, seedling emergence in seed addition subplots was not significantly different ($P = 0.947$) than the level of emergence resulting from natural seed rain. In contrast, at Quincy emergence was significantly greater ($P = 0.017$) in seeded areas compared to the surrounding nonseeded areas, that were used as an experimental control to quantify seed rain. The older stand in Gainesville may have produced more seed, diminishing the effect of seed addition. The disparity in the significance of seeding at the two sites may also be related to heavy rainfall in Gainesville, which could have spread seed from the subplots into the surrounding nonseeded area. A tropical storm event in Gainesville caused 13.3 cm of rainfall in the week following seeding treatments, whereas only 1.8 cm of rainfall occurred in Quincy as the result of this system. Although the effect of seed removal by insects was not examined in this study, previous studies suggest that it should be considered as a possible factor contributing to differences in seeding emergence at

Table 2. Probability of emergence and predicted seedlings per hectare for added *Eucalyptus* seed of three species in various community types at two study locations in Florida, as predicted by a generalized linear model.

Location	Vegetation community	<i>Eucalyptus</i> species	Probability of seedling emergence	Predicted seedlings ha ⁻¹
Gainesville	Eucalyptus stand	<i>E. amplifolia</i>	3.02×10^{-11}	0.00
		<i>E. camaldulensis</i>	3.24×10^{-03}	24,068.40
		<i>E. grandis</i>	1.27×10^{-03}	9,426.48
	Forest road	<i>E. amplifolia</i>	4.46×10^{-06}	33.20
		<i>E. camaldulensis</i>	1.29×10^{-03}	9,597.60
		<i>E. grandis</i>	6.34×10^{-04}	4,716.96
	Upland mixed forest	<i>E. amplifolia</i>	3.02×10^{-11}	0.00
		<i>E. camaldulensis</i>	2.59×10^{-09}	0.02
		<i>E. grandis</i>	3.66×10^{-09}	0.03
Quincy	Eucalyptus stand	<i>E. amplifolia</i>	4.46×10^{-06}	33.20
		<i>E. camaldulensis</i>	1.94×10^{-03}	14,411.28
		<i>E. grandis</i>	3.66×10^{-09}	0.03
	Non-grazed pasture	<i>E. amplifolia</i>	3.02×10^{-11}	0.00
		<i>E. camaldulensis</i>	2.59×10^{-09}	0.02
		<i>E. grandis</i>	3.66×10^{-09}	0.03
	Intensively prepared forestland	<i>E. amplifolia</i>	3.02×10^{-11}	0.00
		<i>E. camaldulensis</i>	2.59×10^{-09}	0.02
		<i>E. grandis</i>	3.66×10^{-09}	0.03

the two locations. Wellington and Noble (1985) found that in stands of *Eucalyptus incrassata* Labill. in Australia, which had natural seed rain up to 10^{-6} seed ha⁻¹ yr⁻¹, 65 to 100% of seeds were harvested rapidly by ants, although seed harvesting activity was spatially and temporally variable.

Treatment Effects on Emergence of Added Seed.

Differences in the probability of emergence for disturbance treatment, *Eucalyptus* species, vegetation community type, and interactions between and among these factors were not significant. The predicted probabilities of eucalyptus seedling emergence in seed addition subplots varied by up to eight orders of magnitude for different treatment combinations, but were very low overall ($P = 0.0$ to 0.0032) (Table 2). These predicted levels of seedling emergence became meaningful when propagule pressure was considered on a per hectare basis (e.g., 500 germinated seeds m⁻² is equivalent to 5×10^6 germinants ha⁻¹). Predicted emergence was generally higher within disturbed (7.61 seedlings ha⁻¹) than in nondisturbed areas (0.06 seedlings ha⁻¹). The highest level of emergence for the three tested *Eucalyptus* species was predicted for *E. camaldulensis* (17 seedlings ha⁻¹). The Gainesville eucalyptus stand had the highest predicted emergence (37 seedlings ha⁻¹) among the various vegetation communities studied. Correspondingly, the vegetation community by species combination that yielded the highest predicted seedling emergence was *E. camaldulensis* in the Gainesville

eucalyptus stand ($24,068$ seedlings ha⁻¹) (Table 2). Da Silva et al. (2011) reported similar low levels of eucalyptus emergence in seed addition studies in Brazilian plant communities. When approximately 10,000 total seeds were added across forty 1 m² plots, only 111 total seedlings were observed at five periodic censuses. In their study, new seedlings were not distinguished from survivors in previous counts, so assuming some level of seedling mortality during the 1-yr census, the number of emerged eucalyptus seedlings would be higher than the total number at periodic assessments. They observed the greatest mean number of eucalyptus seedlings (37) in disturbed plots within the eucalyptus stand at 15 d from sowing. At 180 d from sowing only one seedling survived across all of their seed addition treatments and no seedlings were observed at 270 or 360 d from sowing, supporting their conclusion of low invasive potential.

Disturbance and Emergence from Natural Seed Rain.

The effect of disturbance on emergence of eucalyptus seedlings in nonseeded areas, which are assumed to originate from natural seed rain, was significant ($P = 0.0005$) in the Gainesville eucalyptus stand. The generalized linear model predicted greater emergence for the disturbed condition ($18,004$, 95% confidence interval $9,403$ to $35,846$ seedlings ha⁻¹) compared to the nondisturbed condition ($3,317$, 95% confidence interval $1,232$ to $8,931$ seedlings ha⁻¹). In Quincy, the effect of disturbance was not significant ($P = 0.097$). It is likely that

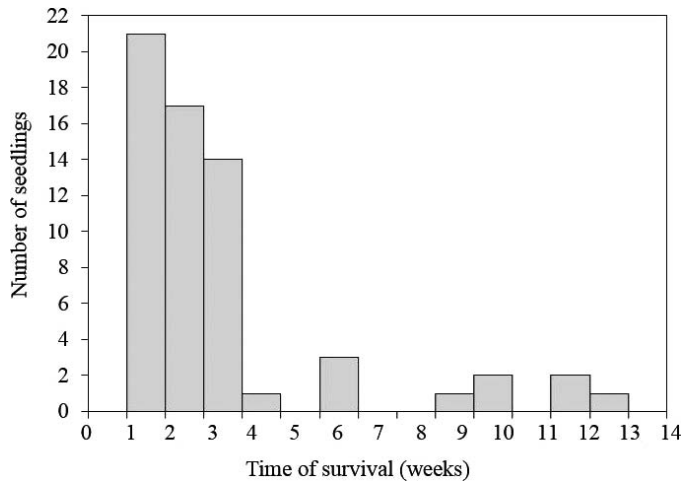


Figure 1. Duration of *Eucalyptus* seedling survival across three *Eucalyptus* species (*E. amplifolia*, *E. camaldulensis*, *E. grandis*) and two study locations in Florida. No seedlings survived more than 13 wk.

the sample size of only three seedlings in nonseeded areas in Quincy was inadequate to detect differences in emergence because of disturbance. This trend of greater emergence in disturbed areas was expected considering that disturbance improved germination of *Eucalyptus* seedlings in other studies (da Silva et al. 2011). This result also supports the hypothesis of Wevill and Read (2010) that rare disturbances such as fire or flooding which suppress competition are necessary for eucalyptus to establish because eucalyptus seedlings are sustained by cotyledon photosynthesis and must establish roots quickly in a suitable environment (Rejmánek and Richardson 2011).

Seedling Survival. Of the 62 seedlings that emerged, 54 seedlings (86%) survived less than 1 mo, and none survived for more than 13 wk (Figure 1). Pearson's chi-squared tests found that vegetation community and disturbance did not significantly affect the amount of time that seedlings survived. Species emerged as a significant factor affecting the amount of time that seedlings survived ($\chi^2 = 9.72$, 4 df, $n = 62$, $P = 0.045$). While all three species had a similar number of seedlings that survived for up to 2 mo, only seedlings in plots seeded with *E. camaldulensis* survived for more than 2 mo (Figure 2). Similar to these results, Emer and Fonseca (2010) also found that eucalyptus seedlings that were transplanted into various native and modified communities were short lived, surviving only 2.7 to 9.3 mo. The significantly greater time of survival that was detected for *E. camaldulensis*, in combination with the highest predicted emergence observed in the seed addition studies, may indicate that *E. camaldulensis* does have a relatively greater ability to establish than the other species tested. These results may support previous research that suggested *E. camaldulensis* has high potential for invasiveness.

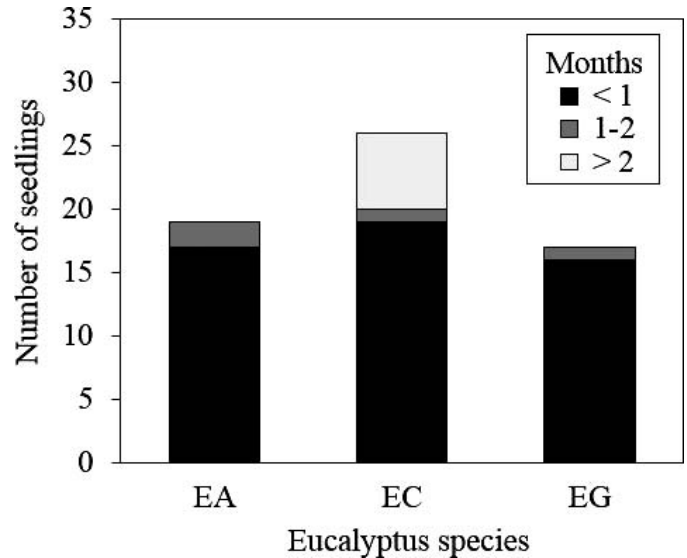


Figure 2. Duration of seedling survival for *E. amplifolia* (EA), *E. camaldulensis* (EC) and *E. grandis* (EG) seedlings across two study locations in Florida. No seedlings survived more than 13 wk.

Gordon et al. (2012) determined that *E. camaldulensis* has a Weed Risk Assessment (WRA) score of 18, representing a high invasion risk level and tying with Tasmanian blue gum (*Eucalyptus globulus* Labill.) as the eucalyptus species with the highest score out of the 38 species evaluated. Additionally, Rejmánek and Richardson (2011) reported that *E. camaldulensis* is the most widespread eucalyptus species and has naturalized in 16 regions globally. However, the failure of *E. camaldulensis* seedlings to survive beyond 13 wk also provides support contrary to the high invasion risk level predicated by the Weed Risk Assessment (Gordon 2012). Our mixed findings regarding *E. camaldulensis* invasiveness suggest that it may be appropriate to recommend that *E. camaldulensis* growers implement invasion risk management practices as a precautionary measure.

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