Invasion Potential of Chinese Tallowtree 
(*Triadica sebifera*) in California’s Central Valley

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The ecological effects of Chinese tallowtree are well documented in the southeastern United States, yet this known invasive plant continues to be planted extensively in California’s Central Valley, where it has recently naturalized in several locations. Climate modeling suggests that most of California’s lowland riparian habitat is susceptible to invasion by Chinese tallowtree; however, no field tests are available to corroborate this result for California or to identify local environmental constraints that might limit potential habitats. We used observational and experimental methods to evaluate invasion potential of Chinese tallowtree in riparian habitats in California’s Central Valley. High invasion potential, indicated by an intersection of the maxima of dispersal probability, germination, and survivorship of seedlings, occurred at low elevations immediately next to perennial waters. The main factor limiting Chinese tallowtree invasion potential in more elevated habitats appears to be lack of seedling drought tolerance. These findings suggest that California’s riparian habitats are vulnerable to invasion by Chinese tallowtree, especially downstream of current naturalized populations where water or bird dispersal will deposit seeds in environments ideal for germination and growth.

**Nomenclature:** Chinese tallowtree, *Triadica sebifera* (L.) Small.

**Key words:** Invasive plant, *Sapium sebiferum*, germination, seedling survivorship, riparian, Putah Creek.

Chinese tallowtree [*Triadica sebifera* (L.) Small; formerly *Sapium sebiferum* (L.) Roxb.; hereafter, CTT], an ornamental and crop tree native to eastern Asia and known to be invasive elsewhere, has begun to produce naturalizing populations in some riparian systems in California’s Central Valley. Although CTT was originally introduced to the southeastern United States in the late 18th century, it was only much later, after extensive planting for landscaping and seed oil, that escape and colonization of natural areas were widely reported (Bruce et al. 1997; Davis et al. 1946; Howes 1949; Jamieson and McKinney 1938). Such a delay before rapid expansion of an invasive species is often called a lag phase (Crooks and Soule 1999; Sakai et al. 2001). A similar pattern of introduction, followed by lag phase, may now be occurring in California, where CTT became popular as an ornamental only around 1970 (Figure 1).

In the Gulf Coast region, where it occupies wetlands, prairies, woodlands, and forests (Bruce et al. 1995, 1997), CTT enriches the soil (Cameron and Spencer 1989), displaces native plants, and dominates communities, often to the point of monospecificity (Bruce et al. 1997; Jubinsky and Anderson 1996). In this region, CTT may compete with native plants for avian dispersal agents (Renne et al. 2000), and frugivorous birds, particularly yellow-rumped warblers (*Dendroica coronata* L.), may alter migration and distribution patterns in response to CTT fruit availability (Baldwin et al. 2008). Insectivorous birds may also find the quality of woodlands dominated by CTT considerably diminished because of low insect loads (Barrow and Renne 2001). If CTT continues to naturalize and exhibits accelerated spread, similar effects could be expected in California’s Central Valley.

Such invasion should be a concern for land managers in this region because of the conservation value of potentially invaded habitats. Principally because of altered hydrology (Mount 1995) and land conversion (Charbonneau and Kondolf 1993), only 10% of the once extensive riparian habitat remains in the Central Valley (Katibah 1984), and only 3.3% of the Sacramento Valley’s floodplain riparian-forest habitat remains (Hunter et al. 1999). The small amount of remnant habitat, along with a high number of special-status vertebrate species and the high cost of restoring or protecting additional riparian areas, makes these habitats a top conservation priority in California.
Interpretive Summary

This study explores invasion potential of Chinese tallowtree \(\text{Tria}\text{iacta sebifera (L.) Small.}\) in California’s Central Valley. Although a problematic invader in the southeastern United States, Chinese tallowtree is widely planted in California as a landscaping tree. Naturalizing populations of the tree have been discovered in riparian areas along the Sacramento, San Joaquin and American rivers. Because of California’s summer droughts, climate modeling predicts that Chinese tallowtree will be restricted to riparian zones. We performed experimental planting and surveyed a naturalizing population to assess the potential for Chinese tallowtree establishment in Californian riparian systems. Our study found that Chinese tallowtree can colonize areas immediately adjacent to perennial water sources, but will not spread to drier surrounding areas because seedlings cannot survive. More seedlings (80%) planted immediately adjacent to a perennial water source survived the summer drought and grew quickly. Herbivory was not a significant source of mortality.

Adult horticultural Chinese tallowtrees in California’s Central Valley generally produce a large, variable number of seeds annually (39,538 per individual, on average) with high seed viability (95%). Managers of natural areas in California should be aware that Chinese tallowtree is a potential riparian invader that already has a significant presence in many Central Valley watersheds. If events unfold in California waterways as they have in the Southeast, we may expect new populations and increasing ecological effects from this species. Because the seeds are dispersed by birds and flowing water, horticultural individuals near waterways may be sources of invasion. Managers should focus monitoring and removal at streamsides, where naturalizing individuals will be most likely to grow to maturity.

(Brode and Bury 1984; Eng 1984; Hunter et al. 1999). It should, therefore, be of great concern to land managers that CTT may invade these habitats to the potential detriment of many protected species. Transformation of riparian habitats into CTT monocultures, as has commonly occurred in the Southeast, could cause significant effects to species such as the federally threatened valley elderberry

Study Species

Although CTT behaves like a typical r-selected species (Closet-Kopp et al. 2007, Gaines et al. 1974), it also exhibits K-selected characteristics, and this combination contributes to its success in invaded regions. Saplings begin production of medium-sized (95 to 160 mg) seeds at only 3 yr of age. The tree’s waxy, aril-coated seeds are readily dispersed by both birds and water (Bruce et al. 1997; Renne et al. 2002). Vegetative growth of seedlings under optimal moisture conditions can be quite fast because of high specific leaf area (160 to 270 cm²/g) (M. Rejmánek, unpublished data). In contrast to other r-selected woody species, however, CTT is relatively shade tolerant (Jones and McLeod 1990), and its longevity is high (estimated at 80 to 125 yr; Hatch 2007). Combined, CTT’s biological traits give it a Z-score of +7.28 (Jaryan et al. 2007), a value comparable with some highly invasive acacia \((\text{Acacia spp.)}\) and pine species \((\text{Pinus spp.)}\) (where the Z-score is a predictor of invasiveness; Rejmánek and Richardson 1996).

CTT’s tolerance of wide-ranging abiotic and biotic conditions probably contributes to its invasiveness in the southeast United States. In this part of its range, CTT can better withstand elevated soil salinity and temporary flooding than can native vegetation (Conner 1994). Seedlings prefer shade but tolerate a variety of light conditions (Rogers and Siemann 2002). The species grows well both with and without nutrient enrichment (Barrilleaux and Grace 2000; Rogers and Siemann 2002, 2003). CTT has been observed growing in soils with pH ranging from 4.4 to 7.8. in the Himalayas, where it may also be invasive (Jaryan et al. 2007). Although invertebrate herbivory is variable among introduced populations (Siemann et al. 2006), CTT growth and competitive ability is little affected by simulated herbivory (Rogers and Siemann 2003). Additionally, as predicted by the evolution of increased competitive ability hypothesis (Blossey and Notzold 1995), invasive ecotypes of CTT exhibit enhanced relative growth rate, increased nutrient uptake, higher photosynthetic rates, and greater total leaf area relative to native ecotypes, perhaps contributing to observed herbivore tolerance (Zou et al. 2006, 2007, 2008).

Chinese Tallowtree in California. CTT was introduced to California by 1888, probably in the Berkeley area (Butterfield 1964), but it appears (by age of large horticultural individuals) that it was not until the 1970s that the tree was commonly planted throughout California’s Central Valley. Naturalizing populations discovered along the San Joaquin River near Highway 41 (D. Burmester, personal communication), and in Davis (Cal-IPC 2003), Sacramento (Hrusa et al. 2002), Chico, Oroville (CCH 2009), Roseville, and Folsom (R. Robison,
personal communication) are all relatively new and indicate that CTT has at least some potential to spread in California.

Recent climate matching modeling using CLIMEX\(^1\) showed no invasion potential of CTT in California when coarse-scale climatic averages were used (Pattison and Mack 2008). This was largely attributed to California’s long and dry summers, suspected to filter out many exotic plants (Clary et al. 2004). However, when summer precipitation was increased in the model to simulate locally elevated soil moisture, much of California’s riparian habitat (especially in the Central Valley) emerged with climate appropriate for CTT (Pattison and Mack 2008). Field studies using CTT individuals planted at various sites both inside and outside of this model’s predicted range in the eastern United States indicate that projections based on the Pattison and Mack (2008) CLIMEX model are valid for that region (Pattison and Mack 2009). Thus, the findings of Pattison and Mack (2008, 2009) suggest riparian areas in California are at significant risk for invasion but also suggest that habitats lacking perennial water may be unsuitable for CTT.

To explore the extent of potential invasion along the riparian–upland gradient in California and to establish a prediction for local spread, we examined CTT germination and seedling survivorship across a riparian–upland transition at Putah Creek Riparian Reserve in Yolo County, CA. Under the same objective, we surveyed a naturalizing population at North Davis Pond, Yolo County, CA, paying particular attention to location of recruitment and mortality patterns during summer drought. We focus on riparian habitat and adjacent areas where establishment is most probable and conservation concern is high. Together, the experiments conducted at Putah Creek and the North Davis Pond population survey enabled us to discern where, on a local scale and at specific distances from surface water, barriers to invasion are collectively weak enough to permit CTT proliferation without human assistance. Finally, we generate a platform for management recommendations in California’s Central Valley and highlight future research needs.

**Materials and Methods**

**Reproduction.** Reproductive success was measured by estimating seed production for 30 horticultural adults from Davis, Woodland, and West Sacramento, CA, in February 2008 and February 2009. Seed production was estimated by counting numbers of seeds in infructescences and extrapolating for the remainder of each tree.

Viability of 100 CTT seeds collected in winter 2007 from 10 trees in Davis and West Sacramento, CA, was determined by cracking seeds open with pliers and evaluating endosperm texture and color (significantly discolored or soft endosperm was classified as nonviable, and firm, white endosperm was classified as viable). These differences were clearly visible and unambiguous.

**Germination.** CTT seeds from 27 trees were collected from several locations in Davis, CA, in January, 2007, and stored indoors at 25 °C (77 °F) for several weeks in a paper bag. Because dispersal scenario may influence subsequent germination (Baskin and Baskin 1998), we homogenized seeds and randomly subjected them to the most likely dispersal events:

- Bird gut passage (simulated endo-ornithochory): 2-h soak in concentrated $\text{H}_2\text{SO}_4$, followed by thorough washing in distilled water
- Water dispersal (simulated hydrochory): 30-d soak in 19-L (5 gal) bucket outdoors (after Samuels 2004); water changed every 10 d
- Gravity (natural barochory): no treatment; seeds were taken from the top of the litter layer beneath the same trees where all seeds were acquired; seeds were kept separate but subjected to same storage time and conditions
- No dispersal (directly from tree; control): no treatment; seeds taken from the tree were stored at room temperature for 1 mo before out-planting.

![Figure 1. A timeline showing events related to Chinese tallowtree invasion in the southeast United States (above line, filled circles) and in California (below line, empty circles). The two disjunct regions show similarity in invasion progression from first record to naturalization in riparian areas. The broad and problematic distribution of Chinese tallowtree in the southeast United States, where the tree was introduced earlier, may yet manifest in California.](image-url)
Five transects were planted with permeable mesh bags of 20 seeds, each at 2 cm (0.8 in) depth at five equally spaced elevations from 0 m (water’s edge) to 4.57 m (15 ft; high-water mark) in March 2007. Seeds from each treatment and control were buried in separate holes at each planting location and watered only initially with stream water. Seeds were recovered and examined for germination (radical emergence) after 30 d. Ungerminated seeds were dissected and classified as viable or nonviable based on endosperm color and firmness.

We used elevation as a proxy for the changing conditions occurring across a watershed perpendicular to the water’s flow. Plot characteristics were assessed to evaluate seed microenvironmental soil, water, light, and temperature conditions. These factors commonly influence plant establishment and were expected to vary systematically with elevation. Soil samples were obtained at the time of seed recovery in late April 2007 in a span of 30 min in the early afternoon approximately 48 h after light rainfall from 1 to 3 cm below the surface, directly adjacent to locations where seeds had been sown. Samples were stored briefly in sealed plastic bags. Soil water content (SWC) was determined with the formula:

\[
SWC = \frac{((Wet\ mass - Oven-dried\ mass)/Oven-dried\ mass)}{100}\% 
\]

Proportion gravel (PG) was assessed by sifting soil samples through 2-mm sieves and using the formula in Equation 2:

\[
PG = \frac{(Oven-dried\ mass\ of\ particles > 2\ mm)}{Total\ sample\ of\ oven-dried\ mass}\]

Light environment was characterized at each plot by visually estimating the percentage of cover by perennial species in a 5-m radius around plots (annual cover was insignificant in March) and by assessing noontime relative photosynthetically active radiation (PAR) expressed as a proportion of nearby contemporaneous full-sun PAR with a PAR/leaf area index ceptometer. Early afternoon soil temperature was assessed at each plot by burying a thermometer 2 cm deep at a 15° angle between 1:00 P.M. and 1:30 P.M. Conductivity and pH were evaluated at 23 C using a pH/EC/TDS temperature meter. Slope orientation was acquired with a compass and expressed as deviation from north.

Seedling Growth and Mortality. CTT seedlings from the seed lot used in the germination experiment were reared in a greenhouse from April 10, 2007, to April 24, 2007, and randomly assigned and transplanted into the same 25 plots along the five transects used in the germination experiment. Seedlings observed emerging contemporaneously beneath horticultural CTT indicated our transplants were timed appropriately. Eight seedlings were planted at each plot in a two by four arrangement (200 seedlings total). Seedlings were planted 15 cm apart to avoid disturbing vast areas of the reserve and to minimize microenvironmental variation within each plot. Vegetation around each plot was cleared only enough to keep it from touching the transplanted seedlings. A single, cylindrical vertebrate herbivore enclosure, 40 cm in height and 27 cm in diameter, was fashioned from 19-gauge galvanized hardware cloth and placed randomly over half (four) of the seedlings in each plot. To reduce mortality caused by transplant, without substantially altering natural environmental conditions, seedlings were watered only immediately after transplant and 1 wk later. All plants appeared in good health at the end of the first week.

Seedling wilting, height to apical meristem, degree of invertebrate herbivory (percentage of estimated, above-ground biomass removal), suspected vertebrate herbivory (massive, contiguous biomass removal), and mortality were monitored for 163 d, ending when rains returned on October 4, 2007.

Naturalized Population Survey. North Davis Pond is a constructed wetland with perennial or near-perennial water that drains to the Sacramento–San Joaquin River Delta. CTT has been planted extensively in the surrounding parks and suburban landscape. There have been previous attempts to control CTT at this pond to improve habitat for birds (DavisWiki 2009). Dominant woody species on the banks of North Davis Pond included coyote willow (Salix exigua Nutt.), Goodding’s black willow (Salix gooddingii C. Ball), boxelder (Acer negundo L.), and Fremont cottonwood (Populus fremontii S. Wats.). Surveyors inspected the 1,125 m pond perimeter in June, 2007. The height, distance from surface water, visually estimated canopy cover, and reproductive status were noted for all CTT individuals occurring within approximately 15 m of the water’s edge. Islands within the lake were not included in the survey, though they supported many CTT individuals. To estimate seedling survivorship during the harshest period of drought, we marked and followed fifty seedlings (plants < 30 cm in height) selected at regular intervals around the perimeter of North Davis Pond from mid-July until rain returned in October. Initial seedling height, elevation above nearby surface water, visually estimated canopy cover, final height, and survival status were recorded for all tracked individuals.

Statistical Analysis. All data were analyzed with JMP version 5.0.1, SAS institute. Significance was designated at \( P \leq 0.05. \)

Design for the germination study followed a 4 by 5 factorial of treatment × elevation with five replicates at each treatment × elevation combination. Because we were not interested in the effect of transect on germination, transects were treated as blocks in the analysis. Type I split
plot analysis of variance (hereafter, ANOVA) was used to test for effects of treatment and elevation on germination while controlling for variability due to block. The plot (block x elevation) variable was treated as random. Tukey HSD was used in multiple comparisons of least squares means to control for comparisonwise error. No data transformations were necessary because all ANOVA assumptions were met.

To explore the specific microsite characteristics responsible for variation in germination success at different elevations, we ran a multiple linear regression to relate the average germination at each plot (n = 25) to plot microenvironmental characteristics. All assumptions of multiple linear regression were met.

The drought period mortality of 50 CTT individuals followed at North Davis Pond was analyzed in a logistic regression model in which initial seedling height, elevation above water, and visually estimated canopy cover were tested as predictors of seedling death.

**Results and Discussion**

**Reproduction.** Mean seed production for adult horticultural trees was large, but highly variable (39,538 ± SE 9,677 seeds/tree), and positively correlated with tree basal area ($R^2 = 0.68$, $P = 0.001$). Seed viability was 95% for evaluated seeds. Some of our sampled trees carried seed loads well within the range recorded for the invaded Southeast (96,000 ± 12,000 seeds; Renne et al. 2000). Though we sampled only horticultural trees, naturalized trees were observed with similar fruit loads in 2007. The large seed loads and high viability observed in this study, along with the early maturity of CTT observed elsewhere (as early as their third year in Texas and Taiwan; Bruce et al. 1997), collectively indicate that CTT has enormous reproductive potential, at least in the parts of the Central Valley we sampled.

**Dispersal.** Vectored dispersal is known to contribute to invasiveness (Richardson et al. 2000). CTT is dispersed by birds and water in the Southeast (Bruce et al. 1997; Renne et al. 2002) and probably benefits from these same dispersal vectors in California. Although a quantitative examination of dispersal is beyond the scope of this paper, we casually observed consumption of CTT fruits with potential for ornithochory by several bird species (including American robin, European starling, cedar waxwing, northern flicker, Nuttall’s woodpecker, American crow, hermit thrush, and northern mockingbird).

**Germination.** Mean percent germination ranged from 6.1 to 68.3 for all seed treatment–elevation combinations (Figure 2). Germination at the end of one month averaged 38.2% over all plots, well within the range reported for CTT in the invaded Southeast (Samuels 2004). The Type 1 split plot ANOVA ($R^2 = 0.74$) revealed significant effects of block ($P = 0.0429$), elevation ($P = 0.0003$), and seed treatment ($P < 0.0001$) with significant interactions (block x elevation $P = 0.0174$; treatment x elevation $P = 0.0041$). Germination after acid treatment and gravity dispersal was significantly higher than for seeds removed directly from trees (Tukey HSD means separation; $P < 0.05$). Because germination was highest for seeds following acid treatment, as might be expected given germination tests in the Southeast (Renne et al. 2001), bird dispersal could promote CTT spread at Putah Creek. Though we do not know what proportion of seeds will be dispersed by birds in California nor the probability that such dispersal events would bring seeds to suitable sites like Putah Creek, birds have been shown to remove approximately 40% of CTT seed crops in coastal South Carolina (Renne et al. 2000).

Each of the lowest three elevations (0 m, 1.14 m, and 2.28 m) experienced significantly greater germination than the highest elevation (4.57 m) (Tukey HSD means separation; $P < 0.05$). This is consistent with results obtained in Florida where CTT germination peaked within the upper portion of a 1 m elevational gradient adjacent to a lake (Burns and Miller 2004). Notably, 65% of ungerminated seeds across all treatments and elevations were still viable at experiment end, and a larger proportion of seeds would likely have germinated had the experiment run longer.

As it is the environmental factors varying across an elevation gradient, rather than elevation itself, that influences germination, we sought to identify and relate these factors to germination using multiple linear regression. Of the factors examined, a significant negative effect of slope orientation (as deviation from north) ($P = 0.0418$) and significant positive effects of soil temperature ($P = 0.0452$) and conductivity ($P = 0.0393$) (Table 1) on CTT germination were detected. Thus, germination peaked where slopes faced less directly south and afternoon soil temperature was greatest. These results were expected for soil temperature which, when higher and especially when it fluctuates broadly, is known to promote CTT germination (Donahue et al. 2004). South facing slopes might also have promoted germination for this reason, but they did not do so in our study, perhaps because of drier soils. Germination was also highest where salinity was locally elevated, which occurred between the middle and lower elevation plots. Though significant effects of treatment and elevation were detected and some microenvironmental factors were identified as important, noteworthy germination occurred at all elevations and across all treatments and in every plot, indicating that CTT is not germination limited at Putah Creek over the elevation gradient examined.

**Seedling Growth and Mortality.** All 160 seedlings planted at elevation 1.14 m or above died by day 133 of...
the 163-day monitoring period. Out of 40 seedlings planted at the lowest elevation, 32 (80%) survived through the full drought period and were in good health when rains resumed in October (Figure 3). Mean height of surviving plants at experiment end was 21.9 cm, a height almost identical to average heights of seedlings in first-year studies in the invaded Southeast (Bruce et al. 1997). The high survival, healthy appearance, and final height of seedlings at the lowest elevation indicate that this zone is suitable for CTT seedlings.

Herbivory was not a significant factor in plant survival, although 59% (118) of plants experienced some degree (usually very slight) of above-ground invertebrate herbivory. No vertebrate exclosure effect on growth or survival

Table 1. Multiple linear regression of Chinese tallowtree seed germination on plot microenvironmental characteristics, where \( n \) is the number of plots; \( R^2 \) is the coefficient of determination; \( R^2 \) adj. is the adjusted coefficient of determination; \( P \) is the prob > |t|, and Std. \( \beta \) is the standardized partial regression coefficient. *Denotes significance at \( P < 0.05 \).

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was detected. Only one plant experienced the massive, contiguous above-ground removal of biomass indicating potential vertebrate herbivory. Four plants perished due to adjacent burrowing by fossorial rodents. Death of all remaining seedlings at the four higher elevations appeared to be due to drought, as most of these plants looked wilted before death. Although we expected that seedlings farthest from the stream might perish earlier, many seedlings at the second and third elevations above the stream died first. Drought-induced mortality at these elevations was likely boosted by large diameter gravel soils with low water holding capacity and by open canopies providing little shade.

**Naturalized Population Survey.** Our survey at North Davis Pond revealed 629 volunteer CTT individuals within 7 m (perpendicular distance) of the water’s edge, with 75.4% located within 2 m (Figure 4a). Volunteer plant height ranged from 0.5 cm to 550 cm. Most seedlings were small (< 50 cm) (Figure 4b) and likely in their first or second year of growth. Only 7 of the 629 individuals were reproductive, and all of these exceeded 210 cm in height.

Of 50 marked seedlings, 35 survived the drought period until rains resumed in the fall. Survival was unaffected by visually estimated canopy cover (logistic regression, $R^2 = 0.02$, $P = 0.25$), elevation above water ($R^2 = 0.01$, $P = 0.41$), or initial height ($R^2 = 0.02$, $P = 0.33$). On average, surviving seedlings lost 0.17 cm in height because plants experienced some dieback during the drought.

The North Davis Pond survey was qualitatively consistent with conclusions drawn for Putah Creek. All volunteer individuals documented at North Davis Pond were restricted to a 7 m-wide band around the pond’s edge.

Figure 3. Survival profile of Chinese tallowtree seedlings planted at 2 wk of age across five elevations above Putah Creek ($n = 40$ individuals per elevation; error bars omitted for clarity). Seedlings were followed for 163 d (April 24, 2007, to October 4, 2007). Only seedlings immediately adjacent to the stream at elevation 0 cm survived the duration of the experiment.

Figure 4. During a comprehensive perimeter survey of North Davis Pond, 629 volunteer Chinese tallowtree individuals were identified. Most of these individuals were below 50 cm in height and located within 2 m of the water’s edge. (a) Frequency distribution of individual Chinese tallowtree heights. (b) Frequency distribution of individual Chinese tallowtree distances from the pond edge.
Here, however, this pattern could have been caused by (among other hypotheses) drier conditions at higher elevations or extensive hydrochorous dispersal. Many CTT individuals were observed at larger perpendicular distances (> 1 m) from surface water at North Davis Pond than would be expected given the results of the Putah Creek field tests. The survival of these seedlings was probably aided by the denser canopy cover and higher clay and silt content soils at North Davis Pond, which may have lessened drought stress by blocking intense midday sun and increasing plant-available water, respectively.

Riparian Vulnerability to Invasion. Numerous recently naturalized populations demonstrate that riparian areas in the Central Valley are susceptible to CTT invasion. We have shown experimentally that the area immediately adjacent to perennial water in at least one unoccupied site provides highly suitable habitat for CTT germination and initial seedling growth. Because vectored dispersal will deposit seeds in this zone (as may have occurred at North Davis Pond), this area becomes especially vulnerable to invasion by CTT. At coarse spatial scales, susceptible habitat in the Central Valley probably follows the distribution developed by Pattison and Mack (2008) and it is therefore extensive.

However, to the extent that riparian areas in the Central Valley are similar to Putah Creek, invasion may be restricted to perennially moist areas close to surface water (within approximately 7 m perpendicular distance and 2 m vertical distance). It should be with caution and with thoughtful consideration of site-specific conditions that our results for Putah Creek be extended to other riparian systems in the Central Valley. The actual width of the invisible zone in each riparian system will likely vary based on soil characteristics and protective cover, but will probably not extend far into drier habitats.

Recommendations for Management and Future Research. We recommend that managers direct monitoring and removal resources toward the edges of waters where water currents are more likely to deposit seeds and environmental conditions promote germination and seedling survival. The presence of upstream CTT populations (horticultural or otherwise) should be considered when surveying for new populations. Areas of sediment accretion and wrack deposition may be the first areas to exhibit recruitment because this is where seeds will likely be deposited and buried. CTT located in close proximity to perennial water should be a priority for control because these individuals will reproduce in sites proven suitable and can serve as foci for new CTT stands in distant riparian areas. Removal of such nascent populations may be critical for effective control of the species (Moody and Mack 1988; Rejmánek and Pitcairn 2002).

The approximately 40 years since widespread planting began in California (Figure 1) have allowed numerous horticultural individuals to reach reproductive maturity and begin sending large numbers of viable seeds into natural areas, often with the assistance of birds and water. Because propagule pressure is known to enhance the success and speed of invasions (Kolar and Lodge 2001), the proximity of these horticultural individuals should be taken into consideration when searching for CTT. Where possible, landscapers should be encouraged to plant ornamental trees thoroughly tested for invasiveness, preferably with long histories of noninvasiveness in California or similar climates, and not CTT.

Once established, CTT is difficult to locally eradicate. Large individuals resprout after cutting and fire (Bruce et al. 1997). For adult trees, mechanical removal using large machinery is effective but difficult to implement without nontarget effects (Bruce et al. 1997). Intense fires can be an effective control (Grace and Allain 2001), but this is not likely an option in California’s Central Valley where human population is dense and air quality must be considered. Bark and stump herbicide applications are the most effective available control options in the southeast United States (Bogler 2000). Removal efforts should be followed by at least 3 to 5 yr of monitoring and manual removal of new seedlings (Bogler 2000; Bruce et al. 1997). Because seeds can remain viable for at least 7 yr (Cameron et al. 2000), we recommend an additional inspection after 7 yr.

Although the results presented here are in accordance with the model prediction that Californian riparian areas are potential sites of invasion for CTT (Pattison and Mack 2008), more study is needed to evaluate the full extent of this risk. Because our field tests were conducted in a single study site, additional research on the suitability of other riparian systems for CTT such as foothill streams and coastal wetlands would further validate models of potential habitat in California. Examination of abiotic factors such as frost and extreme salinity that are known to limit the extent of potential CTT habitat in the southeast United States (Barrilleaux and Grace 2000; Jubinsky and Anderson 1996) would be useful if conducted in California, because these studies would enable more detailed range predictions. From a management standpoint, demographic studies carried out under various habitat conditions would help prioritize monitoring and removal (Sakai et al. 2001), particularly as CTT invasion in California is still at an early stage.

If incipient invaders can be identified, preventative control efforts will cost substantially less than attempts initiated after species have dispersed widely (Leung et al. 2002; Rejmánek and Pitcairn 2002). Publications geared toward prediction of invasiveness attempt to develop screening methods for new invasives (e.g. Daehler et al. 2004; Jefferson et al. 2004), but field-based assessments of potential invaders are rare. We have provided one such
field study that will help with management, early detection, and rapid response to CTT in California’s Central Valley, but there are many more candidate species for which similar studies could reduce the number of, and effects from, future invasions.

Sources of Materials
1. CLIMEX software, Creative Research Systems, 411 B St., Suite 2, Petaluma, CA 94952.

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