frontiers in Forests and Global Change

ORIGINAL RESEARCH
published: 13 January 2022
doi: 10.3389/ffgc.2021.725582

Long-Term Suppression of Hardwood Regeneration by Chinese Privet (*Ligustrum sinense*)

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Native hardwood regeneration in the southeast United States is hindered by repeat disturbance events and the presence of invasive species. Our study aimed to determine the ability of native species in an unmanaged urban forest fragment to persist following high winds from hurricane Gustav in 2008 and subsequent salvage logging. In 2009, researchers estimated the density and composition of the regeneration and overstory trees as well as percent crown cover of invasive Chinese privet. Percent Chinese privet cover was visibly high, leading them to believe it may be inhibiting native hardwood establishment. Ten years later in 2019, we returned to the plots to take repeat measurements. Forest composition remains the same and privet crown cover remains high. There has been no increase in regenerating individuals, and overstory trees per hectare and basal area remains low. These results confirm that the heavy Chinese privet presence is persistent long term and will require management to promote reproduction of native overstory tree species.

Keywords: disturbance, regeneration, succession, invasive species, hurricanes

OPEN ACCESS

Edited by:
Isabel Cañellas, Centro de Investigación Forestal (INIA), Spain

Reviewed by:
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Mike Walters, Michigan State University, United States

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Specialty section:
This article was submitted to Forest Management, a section of the journal Frontiers in Forests and Global Change

Received: *15 June 2021*
Accepted: *26 October 2021*
Published: *13 January 2022*

Citation:
Turner TN, Dean TJ and Kuehny JS (2022) Long-Term Suppression of Hardwood Regeneration by Chinese Privet (Ligustrum sinense). Front. For. Glob. Change 4:725582. doi: 10.3389/ffgc.2021.725582

INTRODUCTION

Disturbances can facilitate invasion of aggressive, alien species, disrupting the normal regeneration cycle of the forest community. Whether this disruption is permanent or temporary informs managers if patience or intervention is required to replace the lost overstory composition.

There are many forms of disturbance ranging in scale from very large to very small, which affects forest characteristics in different ways and by different degrees. Each landscape level disturbance contains a suite of disturbances; for example, hurricanes include increased precipitation, and storm surge that can result in minor to severe flooding in addition to wind. These can result in tree mortality, altered regeneration patterns, canopy damage, and severe property and infrastructural damage (Dale et al., 2001; Stanturf et al., 2007). Natural regions are often adapted to their common disturbance regime, but human influences are expected to increase disturbance intensity with unprecedented results to ecosystems (Millar and Stephenson, 2015).

The traditional successional pathway following disturbance involves a flow from species with high to low resource requirements as individuals fill in Clements (1916). In this case, seeds of early

colonizing species with high resource requirements often propagate and disperse easily, germinate in high light, and are able to survive dormant for extended periods. This pathway may be hindered by early colonizing, alien, invasive species that instead create undesirable conditions that inhibit the establishment of later colonizing species (Connell and Slatyer Ralph, 1977). For example, early invasion of the alien tree *Acer negundo* L. on a past construction site in southeastern Belarus altered light availability and prevented growth and germination of native grasses and trees (Gusev, 2019). In deforested areas near the Panama Canal, where native plant seed dispersal is reduced, regeneration is additionally hindered by the presence of the invasive grass *Saccharum spontaneum* L. (Hooper et al., 2002, 2005). Increased shade cast by the invasive shrub *Lonicera maackii* (Rupr.) Herder prevents growth of native seedlings in an abandoned forest in Ohio (Gorchov and Trisel, 2003). This alteration of resource availability due to the presence of invasive species creates a new inhibitory pathway of succession that results in a different set of later colonizing and persistent species.

Invasive species are often vigorous and possess qualities also associated with early successional species such as prolific seed dispersal and germination, long seed dormancy, and ability to germinate in spaces with high sun (Connell and Slatyer Ralph, 1977). Swift and early management of the invasive plants is ideal for native regeneration success. In many cases, management practices are delayed for years, and not addressed until the lack of regeneration is severe, and the structure of the forest has noticeably changed (Webster et al., 2006). Management at this stage would benefit from studies that follow the long-term successional pathway of unmanaged forests with dense populations of invasive species.

Large disturbances and invasive species presence differ by region and topography and are quite variable. The southeastern United States commonly experiences hurricanes, which are often accompanied by severe rainfall and flooding with high winds that leave uprooted trees, broken branches, and standing dead, and are followed by fire or insect outbreaks (Foster et al., 1998). In forests, salvage logging attempts to utilize downed and damaged trees while still millable. A side effect of this recovery effort is homogenization of the small-scale variation created by the disturbance, often negating the benefits of disturbance and reducing species diversity (Thom and Seidl, 2016; Thorn et al., 2018). Additionally, the southeastern United States has many invasive plant species of all plant forms from forbs to trees. One woody invasive shrub, Chinese privet (*Ligustrum sinense* Lour.) is particularly problematic in southeastern forests. A decrease in native plant species abundances is apparent where Chinese privet is found growing (Merriam and Feil, 2002; Wilcox and Beck, 2007; Greene and Blossey, 2014), often explained by the dense branching growth form and colony forming growth habit of the shrub (Morris et al., 2002). Additionally, Chinese privet negatively affects songbird and bee populations (Wilcox and Beck, 2007; Ulyshen et al., 2020). Once established, the most successful forms of control involve repeated application of pesticides, which can be very expensive (Hanula et al., 2009; Farmer et al., 2016). The combination of repeat disturbances and the presence of invasive species such as the Chinese privet may severely hinder regeneration of native plants, though whether this is a temporary hindrance to regeneration, or a persistent one, is unknown.

The purpose of this study was to determine the ability of the native species in an unkempt forest to persist and recover following a major disturbance in the presence of a vigorous invasive species. The study was conducted in an unmanaged forest invaded by Chinese privet following severe wind damage and salvage logging. Studies that are able to examine the effects of salvage logging following wind disturbance for the past 5 years are rare (Thorn et al., 2018). In this case, the status of the overstory and abundance of advance regeneration was measured the year following Hurricane Gustav in 2009. The status and abundance of the overstory and natural regeneration were reassessed 10 years hence to answer these questions: (1) has hardwood richness and abundance changed over 10 years; (2) has the presence of Chinese privet affected this change; and (3) is regeneration richness and abundance representative of overstory composition?

MATERIALS AND METHODS

This study was conducted at the Louisiana State University AgCenter Botanic Gardens Forestry Research Area in Baton Rouge, LA, located on the Mississippi River floodplain terrace. The Botanic Gardens were donated to the LSU AgCenter in 1966 by the Burden Family with very specific stipulations. Donor Steele Burden requested that the area north of the property between the United States Interstates 10 and 12, designated for forest research undergo only needed maintenance, remaining as natural as possible. In September 2008, the forest incurred severe wind damage from Hurricane Gustav, followed by salvage logging of downed trees in 2009. Eighty-six percent of the stand is located on Deerford–Verdun complex: a very deep, somewhat poorly drained, fine-silty soils with high concentrations of sodium. The remainder is comprised of Jeanerette: very deep, somewhat poorly drained, fine-silty soil[1]. Prior to the hurricane, the stand was dominated by mature hardwoods in various size and age classes, and the presence of invasive plants such as the Chinese privet and Chinese tallow tree [*Triadica sebifera* (L.) Small] were noted. Forest stands of a terrace site with similar well-developed and well-drained soils are typically able to support a variety of mid- to upland hardwood species such as *Quercus alba* L., *Quercus pagoda* Raf., *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., *Pinus taeda* L., and *Carya* spp. (Hodges, 1997).

In 2009, the density and composition of both the overstory and understory trees in the Forestry Research Area were estimated with systematic, fixed, and variable plot sampling. Natural regeneration was nearly absent indicating that the overstory would not be replaced if lost. Additionally, Chinese privet percent cover was visually estimated at each plot, an invasive shrub that had established within the gaps created by disturbances. Upon initial observations, the percent cover was visibly high, suggesting that the Chinese privet may have been inhibiting establishment of

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native species. This led to the question on whether the inhibition of regeneration was temporary or permanent.

Thirty-six plots totaling 40.5 m^2 were systematically established on a grid at 65.4 m apart. Plot centers were located with a hand-held Garmin GPS using coordinates for the original plot locations within the limits of latitude and longitude up to six decimal places. Once located, plots were recorded and marked with pink flagging tape. Hardwood regeneration richness and abundance within 40.5 m^2 was recorded and separated into size classes: germinants, individuals less than 0.33 m in height, individuals 0.33–1 m in height, individuals greater than 1 m in height and less than 5 cm in diameter at breast height (DBH, 1.37 m), and individuals between 5 and 13 cm DBH. Additionally, the density, size, and species composition of the overstory trees were estimated by horizontal point sampling using a wedge prism with basal area factor 2.30 m^2/ha (Burkhart et al., 2018). Chinese privet crown cover was estimated, with maximum complete cover at 100%. No management actions were taken following the initial measurements.

The measurements were repeated in the spring of 2019. Plot centers were once more located using a Garmin GPS within the limits of latitude and longitude up to six decimal places. The goal was to relocate the original plots, but we found no flagging from the original sampling. Hardwood regeneration richness and abundance was sampled accordingly into the same five categories, and overstory trees were estimated by point sampling using a wedge prism with basal area factor 2.30 m^2/ha. We estimated Chinese privet crown cover visually.

For the data analysis, species were grouped by genus due to low plot counts and mistaken species identification between 2009 and 2019. Statistical analyses were conducted using R: Software (2019). Regeneration data from 2009 and 2019 was compared by size class using independent samples Welsch two-sided *t*-tests, testing the null hypothesis that richness and abundance would remain the same between years. This method was also used to compare Chinese privet percent cover in 2009 and 2019. The overstory basal area and density was calculated and compared in 2009 and 2019. Correlations between overstory basal area per hectare and advance regeneration taller than 1 m plus seedlings and saplings with DBH between 5 and 13 cm were calculated with data collected in 2009 and 2019.

TABLE 1 | Univariate statistics for abundance of overstory trees after hurricane damage and salvage logging in 2009 and 2019 (n = 40).

	Trees per hectare		Basal area (m^2/ha)	
Genus	**2009**	**2019**	**2009**	**2019**
Acer	1.6	0.0	0.1	0.0
Carya	13.3	12.0	0.4	1.4
Celtis	33.7	10.8	1.5	1.3
Diospyros	0.0	8.3	0.0	0.2
Fagus	0.3	4.0	0.1	0.6
Fraxinus	11.7	7.2	0.5	0.3
Ligustrum	11.3	0.0	0.3	0.0
Liquidambar	8.2	9.6	1.1	1.6
Liriodendron	2.9	2.9	0.5	0.9
Magnolia	31.0	8.9	0.9	0.6
Nyssa	2.4	0.0	0.3	0.0
Ostrya	55.9	24.0	1.2	0.5
Platanus	2.0	14.2	0.2	0.6
Populus	0.0	3.2	0.0	0.1
Quercus	26.4	28.6	1.9	4.4
Salix	0.0	5.7	0.0	0.2
Tilia	0.0	6.1	0.0	0.2
Triadica	20.0	5.2	0.7	0.2
Ulmus	25.8	11.7	1.2	1.2
Total	246.6	162.3	10.8	14.4
	(se = 3.46)	(se = 1.73)	(se = 0.13)	(se = 0.23)
	p = 0.14		p = 0.22	

p-values are the probability of a greater value of the t statistic for the null hypothesis that mean values for data collected in 2009 are different from the means for 2019.

TABLE 2 | Mean trees per hectare in 2009 and 2019 for total combined regeneration size classes across all genera.

Size class	**2009**	**2019**
Germinants	38	659
Less than 0.33 m	190	87
0.33–1 m	458	25
Greater than 1 m	183	108
5–13 cm DBH	24	54
Total combined	893	932

RESULTS

In 2009, 20 species (15 genera) were in the overstory, with a total of 246.6 trees/ha and a basal area of 10.8 m^2/ha (**Table 1**). Regeneration was low across all size classes with a total of 893 trees/ha (**Table 2**). Individuals of 16 genera were found in the advance regeneration (all individuals greater than 1 m in height) (**Table 3**). Advance regeneration totaled 272.7 trees/ha. Estimated Chinese privet cover averaged 59.3% across all sites, 27 sites had 50% or greater Chinese privet coverage (**Figure 1**). Aside from the Chinese privet, populations of other woody invasive species were observed in regeneration and in the overstory: paper mulberry [*Broussonetia papyrifera* (L.) L'er. ex Vent.] and Chinese tallow (*Triadica sebifera*), which comprised 38% of the total advance regeneration. The abundance of advance regeneration taller than 1 m combined with that between 3 and 15 cm DBH was independent of overstory basal area per hectare (r = 0.073, p = 0.66).

In 2019, 20 species (16 genera) were found in the overstory with a total of 162.3 trees/ha and basal area of 14.4 m^2/ha (**Table 1**). Regeneration was once again low across all size classes, with a total of 932 trees/ha (**Table 2**). Individuals of 15 genera were found in advance regeneration, totaling 231.6 trees/ha (**Table 3**). Estimated Chinese privet cover averaged 62.3% across all sites (**Figure 1**), with 24 sites estimated to have 50% or greater Chinese privet coverage. The Chinese tallow comprised 27% of the total advance regeneration. There was no significant difference in overstory density between 2009 and 2019 (t = 1.55, df = 18, p = 0.14), nor in basal area (t = 1.28,

TABLE 3 | Sampling statistics for estimates of natural reproduction of total native species and total including alien invasive Triadica sebifera greater than 1-m tall after Hurricane Gustav damage and salvage logging in 2009 and 2019 (n = 18).

	Trees per Hectare	
Genus	**2009**	**2019**
Acer	17.2	3.4
Carya	3.4	0.0
Celtis	12.0	3.4
Crataegus	0.0	3.4
Diospyros	13.7	41.2
Fraxinus	10.3	3.4
Liquidambar	1.7	6.9
Liriodendron	5.1	0.0
Magnolia	3.4	3.4
Ostrya	25.7	32.6
Platanus	15.4	10.3
Populus	1.7	0.0
Prunus	6.9	1.7
Quercus	5.1	25.7
Salix	18.9	3.4
Tilia	0.0	5.1
Ulmus	27.4	25.7
Total Natives	168.1	169.8
Triadica	104.6	61.8
Total	272.7	231.6
	P = 0.52	

p-values are the probability of a greater value of the t statistic for the null hypothesis that mean values for data collected in 2009 are different from the means for 2019.

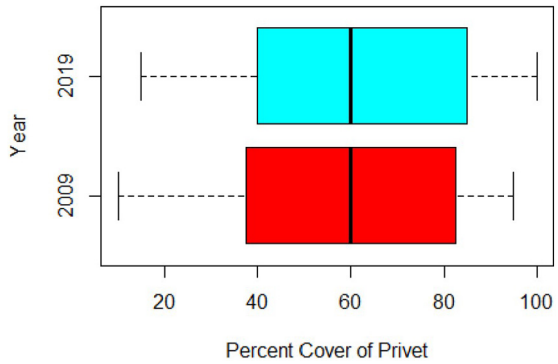

FIGURE 1 | Boxplot of mean estimated percent Chinese privet cover in 2009 and 2019 at the LSU AgCenter Botanic Gardens Forestry Research Area. A Welch Two-Sample T-test reveals there is no significant difference in mean cover between years (α = 0.05, P = 0.4773).

df = 18, p = 0.22) (**Table 1**). *Quercus* spp. are most common in the overstory in both years, with 18% of total basal area in 2009 and 30% in 2019. Chinese privet estimated percent cover remained steady and showed no significant changes between 2009 and 2019 (t = −0.72, df = 36, p = 0.48) (**Figure 1**). Mean regeneration across size classes did not change between 2009 and 2019 (**Table 2**). Advance regeneration was variable between years by genus with no significant change found between years in trees per hectare; however, advance regeneration of genera *Carya*, *Liriodendrons*, and *Populus* were not found in 2019 despite their presence in 2009 and their retention in the overstory (**Table 3**). The two largest categories of advance regeneration again were independent of overstory basal area per hectare (r = 0.013, p = 0.94); however, a trend of Chinese privet coverage inhibiting advance regeneration in these two categories existed (r = −0.29, p = 0.077). No such trend was evident in 2009 (p = 0.96). A strong presence of the alien invasive Chinese tallow was observed for both 2009 and 2019, representing a large proportion of the regeneration within the measurement interval.

DISCUSSION

Following severe wind disturbance and salvage logging in 2009, the overstory was visibly sparse with little natural regeneration, probably a result of the dense presence of the invasive Chinese privet. Natural regeneration was very low across all size classes, compared with the suggested 370 trees per hectare for healthy oak regeneration in bottomland hardwoods (Clatterbuck and Meadows, 1993). Regeneration seemed to reflect the overstory population, with the exception of a few genera in regeneration not found in the overstory (**Tables 1**, **3**). Advance regeneration consisted of a combination of fast-growing, shade-intolerant, pioneer species: *P. occidentalis* and *S. nigra* as well as species that are commonly considered early colonizers but are more tolerant of shaded conditions including *A. negundo*, *A. rubrum*, *O. virginiana*, *U. americana*, *and U. alata* according to Burns and Honkala (1990). The strong presence of early colonizing species is probably linked to the increased light availability from reduced crown cover from storm damage and salvage harvesting. This light availability facilitated the release of Chinese privet already present in the understory.

Ten years later, we found that the overstory density remained sparse. In addition, trees in the advance regeneration categories were fewer with fewer species represented, while no significant increase in Chinese privet cover was found. In Tennessee, Chinese privet that had invaded the redcedar and oak–hickory woodlands of Tennessee was found to outcompete a similar competing native shrub, *Forestiera ligustrina* (Michx.) Poir, by growing taller and maintaining higher leaf areas as crown cover increased (Morris et al., 2002). Likewise, the Chinese privet at our site was able to persist as a competitive presence throughout the understory as its canopy closed, decreasing light availability. In 2009, the overstory density fell well below the suggested stocking goal for healthy bottomland hardwood stands suggested by Goelz and Meadows (1997). Ten years later, the overstory density did not significantly change, but aerial photos show a clear increase in crown coverage (**Figure 2**). In plots where no regeneration nor Chinese privet was found, dense coverage of blackberry *Rubus* spp. was often prominent. *Rubus* spp. are

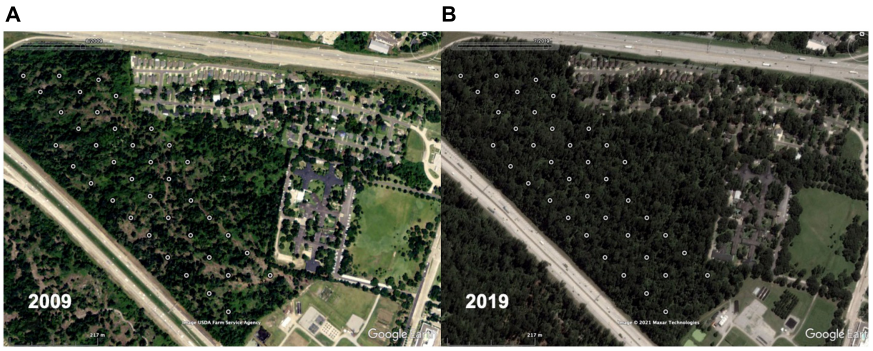

FIGURE 2 | Overhead map of the LSU AgCenter Botanic Gardens Forestry Research Area in 2009 **(A)** and 2019 **(B)**.

commonly found in the understory following harvest and can persist for many years, but generally do not impede regeneration and recede as regeneration overtops it (Donoso and Nyland, 2006). *Rubus* spp. responds quickly to new light availability when already present in the seedbank; however, sapling height is not hindered by its presence, and long-term persistence of *Rubus* spp. only occurs if residual regeneration was inadequate to begin with (Widen et al., 2018). Advance regeneration in 2019 consisted of very shade tolerant species *C. caroliniana* and *D. virginiana* as well as less shade tolerant oak species *Q. michauxii*, *Q. pagoda*, and *Q. nigra* (**Table 3**). On drier sites in Wisconsin, oak seedling survival was increased by removal of tall understory vegetation (Lorimer et al., 1994). Similarly, oak seedlings at this site were likely able to germinate while the canopy was thin and persist to the advanced stage, growing in height with the surrounding vegetation as opposed to hindered beneath it. This agrees with the findings of Collins and Battaglia (2008) that a sparse canopy promotes oak seedling persistence and growth in bottomland hardwoods.

A noticeable presence of the Chinese tallow tree in the advance regeneration was noted both in 2009 and 2019 (**Table 3**). The invasive qualities of this alien include rapid growth rate, successful germination, and growth in both shade and sun, and prolific seeding (Pile et al., 2017). Data collected from the USDA Forestry Inventory and Analysis program reveal that the Chinese tallow has rapidly spread across the southern United States in the last 30 years (Oswalt, 2010). Comparison of the Chinese tallow growing among native species on the coast of South Carolina show that the shrub has a higher initial growth rate than the natives following a disturbance, a problem for coastal and southern areas as its presence is often recorded following hurricane damage (Conner et al., 2014; Pile et al., 2019). The significant presence of the Chinese tallow in regeneration at our site is likely a hindrance to native hardwood growth.

Some management of invasive species presence would be needed to release the advance regeneration present on the site as the regeneration appears to be unable to grow through the Chinese privet. However, the moderate, negative correlation between the larger categories of advance regeneration and Chinese privet coverage suggests that regeneration would respond to suppressing the Chinese privet, previously attempted, though ineffective methods of Chinese privet management include flooding (Brown and Pezeshki, 2000), prescribed fire (Faulkner et al., 1989), and biological defoliation (Zhang et al., 2011). Only the herbicides glyphosate or triclopyr, or a combination of the two, and root trenching effectively manage the shrub (Faulkner et al., 1989; Harrington and Miller, 2005). Triclopyr applied in high concentrations at the base of the plant in January, when seasonal defoliation is greatest, produced the highest mortality on Chinese privet in hardwood stands in Alabama (Enloe et al., 2016). A similar study found that lower concentrations of triclopyr or glyphosate are effective when applied as a cut stump treatment (Enloe et al., 2018). Triclopyr applied with similar methods on bottomland hardwood sites is an adequate herbicide for Chinese tallow as well, though other herbicides such as aminocyclopyrachlor may perform better (Enloe et al., 2015).

Our results show that the Chinese privet remains a persistent hindrance to native regeneration. Where it persists, we found no change in hardwood richness and abundance and no significant increase in the regeneration in the 10 years following the hurricane. This inability of the forest to recover naturally was likely aided by the presence of dense blackberry and the invasive Chinese tallow. Management of these species will be required for native regeneration to increase.

CONCLUSION

Damage from hurricane disturbance disrupts the normal regeneration cycle and often facilitates the invasion of alien invasive species, such as the Chinese privet, which hinders the traditional successional pathway by creating uninhabitable conditions for native species. This study in Baton Rouge, LA, determined the ability of an unmanaged forest to persist and recover following hurricane disturbance in the presence of Chinese privet. Estimations of density and composition of regeneration and overstory taken 10 years apart indicated strongly that Chinese privet crown cover suppressed the natural regeneration of the overstory trees. Additionally, the presence of dense blackberry and invasive Chinese tallow may also had contributed to suppressing natural regeneration. Weak correlation between Chinese privet cover and the larger classes of advance regeneration suggest that management of the invasive

shrub would be successful in improving the growth and reproduction of native trees.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

FUNDING

This research was funded by the Burden Foundation.

ACKNOWLEDGMENTS

We would like to thank the LSU AgCenter Botanic Gardens for allowing data collection on site. Additional support was provided by the McIntire-Stennis project LAB94307. Published with the approval of the director of the Louisiana Agricultural Experiment Station as publication Nbr: 2021-241-36615.

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