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Original Research Article

The response of the invasive princess tree (*Paulownia tomentosa*) to wildland fire and other disturbances in an Appalachian hardwood forest

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ABSTRACT

This study examined the response of princess tree (*Paulownia tomentosa*) to different disturbances and its potential to spread throughout its current range in the U.S. The study was established in Shawnee State Forest in southern Ohio, USA, which has historically experienced disturbances from mining, logging, ice storms and wildfire. Plots were established for vegetation sampling where fire had occurred with and without princess tree present, and where no fire had occurred with and without princess tree present. To determine the influence of disturbance types on the density of princess tree, redundancy analysis (RDA) was used. High stem density of princess tree seedlings occurred in areas that experienced high fire intensities and herbicide treatment. Seedlings on southwest slopes increased in abundance as the time from the last logging activity increases. Princess tree saplings were present in greater densities in areas that experienced medium fire intensities and the highest ice storm damage. Sapling density is greatest as ground cover and vegetation height increases and slope decreases. Princess trees reach maximum stem density on northeast slopes in areas not impacted by the 2009 fire. All disturbances considered, including wildfire, have created conditions conducive to princess tree growth and expansion into forest areas.

1. Introduction

The invasion of nonnative plant species into ecosystems is a major threat to global biodiversity and ecosystem degradation (Pysek and Richardson, 2010; Early et al., 2016). The number of these invasions have significantly increased worldwide over the past two centuries and continues to grow (Seebens et al., 2017). While no country is immune to invasion of nonnative plants, the volume and pattern of invasions have been linked to global trade networks (Chapman et al., 2017). Accordingly, there continues to be an influx of nonnative species to the U.S., many of which have become invasive (Allendorf and Lundquist, 2003) and are significant threats to forests and native species (Keeley, 2006; Moser et al., 2009). Many of these introductions are the result of the horticultural trade (Lehan et al., 2013). Most managers faced with control of nonnative plant species are lacking in sustainable environmental and economic plans of approach, as solutions prove to be costly in terms of funds, labor, collaboration efforts, and time (Larson et al.,

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2011). However, nonnative plant species change the dynamics of native ecosystems in numerous ways, making sound management crucial.

Nonnative species can greatly alter the fire regime of an ecosystem. Exotic plants can increase the fuel-bed flammability, making fires more frequent; increasing the likelihood of crown fires by changing the structure of a forest; and promoting fire spread by increasing rates of plant tissue decomposition or adding more flammable chemical compounds via plant tissues (Brooks et al., 2004; Mandle et al., 2011). Princess tree (*Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud.), an invasive species introduced into the U.S. from China as an ornamental and landscape tree during the mid 1800s, has very brittle branches and large leaves which likely add to the amount of coarse woody debris and leaf litter buildup on a forest floor (Hu, 1961). As fuel density, type, and arrangement are integral parts of a fire regime, princess tree, and other nonnative plants, may alter the intensity, frequency, and periodicity of fire regimes by changing the fuel characteristics of a habitat (Brooks et al., 2004). After years of fire suppression, there is an increase in use of prescribed burns and manipulation of fire severity to return ecosystems to their historical regime (Keeley, 2006). However, the use of prescribed fire and manipulation of fire severity leaves cleared gaps that are susceptible to exotic plant invasions by species that were not present in the historical landscape (Brooks et al., 2004; Keeley, 2006). Additionally, many invasive species benefit from fire by subsequently sprouting, adding to their spread in introduced habitats (Keeley, 2006; Mandle et al., 2011).

The silvical characteristics of princess tree make it a likely species to escape cultivation (Hu, 1961; Tang et al., 1980; Beckjord and McIntosh, 1983; Rebbeck, 2012). This likelihood of escaping cultivation, plus the capacity to exist on dry infertile sites make this species a prime candidate to invade and occupy disturbed sites (Tang et al., 1980; Donald, 1990; Essl, 2007). Princess tree has the capability of invading post-fire sites, particularly where fire severity was high (Black et al., 2018). When princess tree invades post-fire sites, it can alter the native plant community in terms of composition and structure (Lovenshimer and Madritch, 2017). Since escaping cultivation in the U.S., the tree is mostly found in recently disturbed areas, such as after a wildfire, hurricane, or anthropogenic activity – logging, building of roads and utility corridors, and mining (Tang et al., 1980; Williams, 1993; Langdon and Johnson, 1994; Kuppinger et al., 2010).

Understanding the relationship between princess tree and disturbances is critical in creating effective management plans for the future control of this woody invasive species. The objective of this study was to determine which of the many disturbances that have occurred at Shawnee State Forest in southern Ohio are contributing to the expansion of princess tree throughout the region, and if the nonnative species can establish after both large and small-scale disturbances. It is hypothesized that more severe large-scale disturbances would promote greater princess tree colonization of an area as compared to less severe small scale or no disturbances.

2. Materials and methods

2.1. Study area description

The study was conducted at Shawnee State Forest (38.704°N, 83.092°W), located in the unglaciated hills of the Allegheny Plateau in southern Ohio. Shawnee State Forest occupies over 25,000 ha, is characterized by highly dissected topography composed of narrow ridges, steep hillsides, and valleys, and is comprised of oak (*Quercus* spp.) and other hardwood species (Table 1).

Throughout Shawnee's history many disturbances have influenced the forest. The entire region has been exposed to farming, logging and mining for many decades. In 2003, an ice storm caused severe tree damage, resulting in large amounts of down woody debris on the forest floor. In April, 2009, a large wildfire consumed approximately 1200 ha, where many areas of the forest experienced moderate to high fire intensities. Because of the wildfire severity and the extent of the damage to trees, a timber regeneration harvest (clearcut) of the areas that experienced moderate to high fire intensities was performed in the fall of 2009.

Since nonnative invasive species have been an issue in Shawnee State Forest, the Ohio Department of Natural Resources Division of Forestry (ODNRDF) applied triclopyr and imazapyr herbicides in October – December 2009, to targeted invasive species of princess tree and tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle). For stems with diameter-at-breast height (dbh) less than 0.5 cm triclopyr

Table 1
The distribution of the major forest tree species by topographic position in the Shawnee State Forest, southern Ohio.

Ridges		Mid Slopes	
Scientific name	Common name	Scientific name	Common name
Carya glabra	Pignut hickory	*Acer rubrum*	Red maple
Cary tomentosa	Mockernut hickory	*Acer saccharum*	Sugar maple
Pinus echinata	Shortleaf pine	*Carya ovata*	Shagbark hickory
Quercus alba	White oak	*Liriodendron tulipifera*	Yellow-poplar
Quercus marilandica	Blackjack oak	*Nyssa sylvatica*	Blackgum
Quercus montana	Chestnut oak	*Quercus alba*	White oak
Quercus velutina	Black oak	*Quercus rubra*	Northern red oak
Sassafras albidum	Sassafras	*Quercus velutina*	Black oak
	Bottomland		
	Scientific name	**Common name**	
	Fagus grandifolia	American beech	
	Platanus occidentalis	American sycamore	
	Prunus serotina	Black cherry	

was applied using a cut and spray method; for stems between 0.5 and 1.6 cm dbh triclopyr was applied via basal bark spray; and large trees over 1.6 cm dbh had stems injected with imazapyr. In the spring and fall of 2010, follow-up herbicide treatments were applied to princess tree using the previous methods.

2.2. Vegetation sampling

For this study, vegetation was sampled at Shawnee State Forest in late June – September 2011 (Fig. 1). A ground survey of the entire accessible 1200 ha impacted by the fire was initially conducted to map the locations of princess tree; some areas were not accessible because of current logging or the highly dissected topography. Clumps of princess trees (20–30 m^2 area) and individual stems that were at least 30 m from the next nearest princess tree stem were mapped as one point. The same procedure was conducted in the area surrounding and adjacent to the fire perimeter, extending approximately 2 km outward from the fire boundary. Within this larger area of mapped princess trees, we randomly selected 61 of these points and a sample plot was established at each point with the point serving as the plot center. This resulted in 28 plots in the burned area (FP – fire with princess tree present) and 33 plots outside the burned area (NFP – no fire with princess tree present). The minimum possible density of princess trees within a plot was one stem. Each of the 61 plots had a matched plot (FNP – Fire, No Princess tree and NFNP – No Fire, No Princess tree) where princess tree was absent but had similar slope steepness, aspect, elevation, and soil type. Matched paired-plots were established within 75 m of each other with the exception of five plots where princess tree was too abundant and the topography too dissected. For these five, its matched plot was established elsewhere in Shawnee where princess tree was absent, but with similar topography. All plots were within approximately 100 m of a logging road or dozer line.

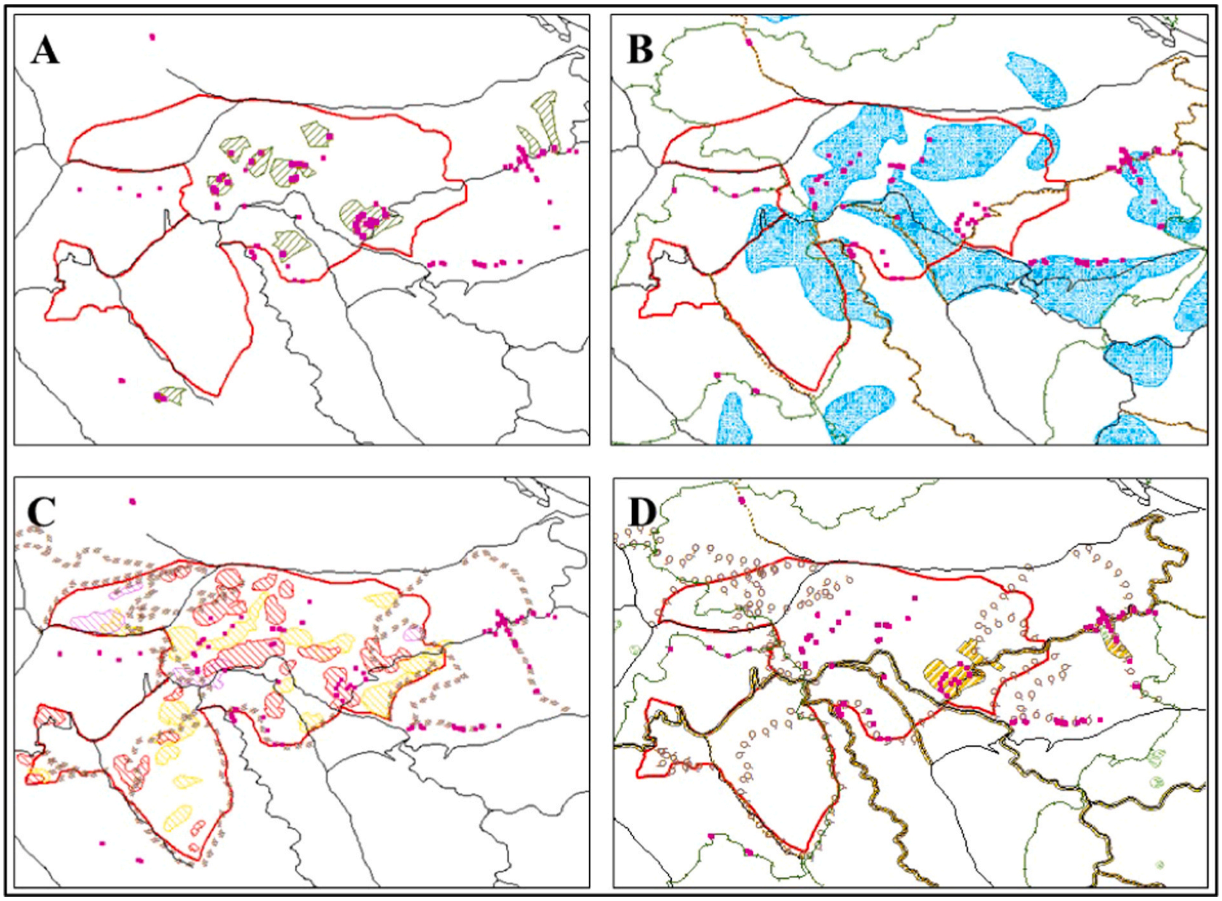

Fig. 1. Maps showing location of study plots (pink squares) in relation to the different disturbances in Shawnee State Forest, Ohio. The perimeter of the 1200 ha wildfire is indicated by the red line and access road are indicated by the black lines. Map A displays the areas that were logged from 2005 to 2011 with the green-hashed areas. Map B displays in the blue-shaded areas where 33–100% canopy occurred from the 2003 ice storm. Hiking trails (green) and bridle trails (brown) are also shown. Map C displays the locations of the fire intensity levels: red shaded areas = high intensity, purple shaded areas = moderate-high intensities, yellow shaded areas = moderate intensities. All other areas within the fire perimeter are considered low intensity. Dozer lines are indicated by the brown-hashed areas. Map D displays the areas (yellow hashed areas) targeted by herbicide treatments. Mapped areas of princess tree not targeted with herbicide are shown by the green hashed areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Each of the 122 sample plots was 10 × 4 m in size. Percent slope, aspect (transformed using the method of Beers et al. (1966)), elevation, latitude and longitude (using a Garmin GPS 76 hand-held GPS unit, accuracy 15 m), and canopy closure (using a densiometer) were collected for each plot. Soil type (soil series) was determined from the latitude and longitude using the U.S. Department of Agriculture Web Soil Survey. Within each plot, total percent cover of vegetation for the entire plot and average vegetation height were estimated. Princess tree stems were excluded from vegetation cover and average vegetation height measurements as they were measured separately. Total percent cover of the understory vegetation layer was defined as the percent of the plot covered by forbs, grasses, herbs, vines, and woody shrubs less than 1 m in height. Average height of the understory vegetation layer was determined by first randomly locating four quadrats within each plot. The maximum height of the vegetation was measured in the center of each quadrat with the use of a telescoping height pole and the average of these four measurements were recorded as the average vegetation height for that plot. Stem counts of all identified herbaceous species and woody species were collected within the entire 10 × 4 m plot; plants were identified to the species level whenever possible. For the plots with princess tree present (FP and NFP), a circular area with a 15 m radius extending from the 10 × 4 m plot center was created; all princess tree stems within this area were counted, their height and dbh (diameter-at-breast-height, 1.4 m) were recorded, and whether the tree had seeded based on any opened persistent capsules. Each princess tree stem, in multiples or clumps, was counted and recorded separately, not dependent on origin (root or trunk sprout).

2.3. *Princess tree density statistical analysis*

To determine the influence of disturbance types on the density of princess tree, redundancy analysis (RDA) was used with CANOCO software Version 4.56 (Biometris-Plant Research International, Wageningen, The Netherlands). RDA is a direct linear ordination method that redefines the sample units as linear combinations of the explanatory variables; thus, samples are distributed in the space defined by the explanatory matrix (Leps and Smilauer, 2003; McCune and Grace, 2002). The significant axes represent actual variation in the species data, as opposed to noise, and allow identification of the most influential environmental variables sampled (ter Braak and Smilauer, 2002). RDA was chosen after conducting detrended canonical correspondence analysis (DCA), which suggested a short gradient length, indicating more homogenous species data which are better fit by a linear than unimodal model (Leps and Smilauer, 2003).

The environmental matrix factors consisted of the following continuous variables: slope, transformed aspect (Beers et al., 1966), elevation, percent ground cover of understory vegetation, average height of understory vegetation, canopy closure, and the amount of time (years) since the last logging activity in the area in which a plot occurred based on available data from ODNRDF during the period of 2005–2011. The following categorical variables were used: soil series (Berks channery silt loam or Shelocta-Brownsville association), fire intensity (outside the fire boundary, low intensity, moderate to moderate-high intensity, and high), herbicide application (binary), and ice damage resulting in overstory mortality (binary). Ice damage mortality was determined by examining crown condition (broken branches) and by use of an ODNRDF map of Shawnee State Forest displaying where 33–100% canopy mortality occurred from the 2003 ice storm. Fire intensity categorization used was that defined by ODNRDF (Table 2). Princess tree stems were divided into three size categories of seedlings ($<$ 1.4 m height), saplings ($\geq$ 1.4 m height, $\leq$ 3.0 cm dbh) and trees ($>$ 3 cm dbh), and density was defined as the number of princess tree stems per hectare.

Analysis of Variance was conducted on the stem density by size category to determine if differences existed in densities between the burned and unburned areas. Duncan's Multiple Range Test (DMRT) was used to determine what means differed, if any, at the 0.05 alpha level. Pearson Correlation Analysis (PCA) was performed on disturbance, physiographic, and environmental variables to determine if any correlation existed among these variables that could affect the presence of princess tree.

3. Results

Results of the RDA show a significant relationship between the princess tree stem density and the environmental variables (Monte Carlo Test, $P = 0.002$). Together, the first two canonical axes explained 48.5% of the variation. The first canonical axis was also statistically significant by itself (Monte Carlo Test, $P = 0.002$), explaining 36.7% of the variation in the stem density data. The most important environmental variables contributing to the first and second axes were canopy closure, ground cover, and average understory vegetation height based on axis coordinates (Table 3).

In Fig. 2 the arrows representing the different size classes of princess tree stems point in the direction of the greatest rate of increase of abundance. Quantitative environmental variables are represented by vectors, with lengths relating to a variable's importance to the ordination. The direction of an environmental variable vector indicates its correlation with each of the canonical axes; vectors can be considered to pass backwards through the origin as well. Nominal environmental variables are represented by their centroid. The

Table 2
Fire intensity definition used to classify post-fire conditions at Shawnee State Forest by the Ohio Department of Natural Resources, Division of Forestry (ODNRDF) after the 2009 wildfire.

Fire intensity	Description
High intensity	A stand experiencing or expected to experience $\geq$ 95% canopy mortality within one growing season
Moderate-high intensity	A stand experiencing or expected to experience 75–94% canopy mortality within one growing season
Moderate intensity	A stand experiencing or expected to experience 50–74% canopy mortality within one growing season
Low intensity	A stand experiencing or expected to experience $<$ 50% canopy mortality within one growing season

Table 3
Redundancy analysis of princess tree (*Paulownia tomentosa*) stems density showing correlations of species ordination axes with environmental variables.

Environmental variable	Axis 1	Axis 2
Canopy Closure	0.71	-0.13
No Fire	0.53	-0.05
Ground Cover	-0.51	-0.26
High Fire Intensity	-0.40	0.06
Aspect	0.38	-0.08
Slope	0.36	0.21
Last Logging (years)	-0.28	0.03
Low Fire Intensity	-0.19	0.08
Herbicide Application	-0.19	0.18
No Herbicide Application	0.19	-0.18
Medium Fire Intensity	-0.18	-0.14
Average Understory Vegetation Height	-0.14	-0.42
Shelocta Brownsville Assoc.	-0.10	0.09
Berks channery silt loam	0.10	-0.09
Ice Damage to Overstory	-0.08	-0.35
No Ice Damage to Overstory	0.08	0.35
Elevation	0.01	-0.06

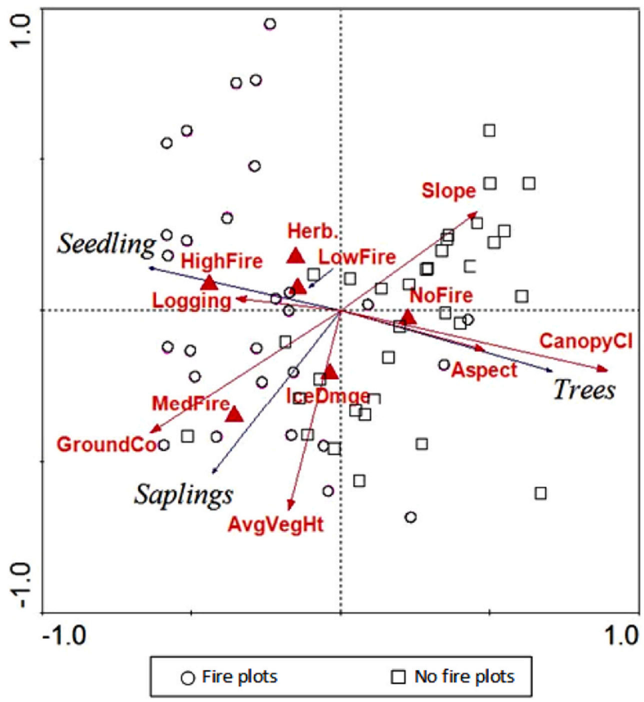

Fig. 2. Redundancy analysis tri-plot of princess tree (*Paulownia tomentosa*) stem density by stem size class (seedlings, saplings, and trees) and environmental variables. Seedling, saplings and trees vectors are stems per hectare. HighFire = high fire intensity, LowFire = low fire intensity, MedFire = moderate fire intensity, NoFire = outside the burn area, Logging = years since last logging activity, IceDmge = 2003 canopy ice damage, Herb = herbicide application, GroundCo = percent ground cover, AvgVegHt = average understory vegetation height, CanopyCl = canopy closure.

environmental variables elevation and soil type (Berks channery silt loam and Shelocta Brownsville association), and no herbicide application and no ice damage, are not included in Fig. 2 because of the proximity of their value to the origin, indicating little importance to the ordination.

Sample plots impacted by the 2009 fire are generally restricted to the left of the ordination and have experienced other disturbances, such as logging and targeted herbicide application, as well as ice storm damage to certain plots. These areas have more gradual slopes facing southwest. There is more understory vegetation, measured by percent ground cover and average vegetation height (Fig. 2). These plots also had more open canopies, with an average canopy closure of 21% (range 0–90%).

Sample plots not impacted by the 2009 fire are generally restricted to the right of the ordination. Most plots have not been impacted by recent large disturbances, though some still displayed residual damage from the 2003 ice storm. The plots were on steep slopes facing northeast and have more canopy closure (Fig. 2). The canopy closure on these sample plots averaged 81%, with a range of 16–100%.

Sapling density was greatest as understory vegetation cover and vegetation height increases and slope decreases (Fig. 2). Seedlings on southwest slopes show trends of increasing abundance as the time from the last logging activity increases. Princess tree saplings grew in greater density in areas that experienced medium fire intensities compared to other fire intensities and where ice storm damage appeared to be highest. Tree size stems of princess tree attained maximum stem density on northeasterly slopes not impacted by the 2009 fire.

Princess tree saplings were able to establish at high densities in areas where high amounts of ground cover and tall vegetation occurred, regardless of whether the area had experienced fire or not. Princess tree saplings were significantly taller than the understory vegetation in both burned and unburned areas (Fig. 3). Princess tree saplings were significantly taller in unburned areas compared to burned areas. Understory vegetation were of similar height in both burned and unburned areas.

Analysis of Variance and testing of means (DMRT) revealed that significant differences existed in the number of princess tree stems per hectare by stem size class between burned and unburned areas, and within burned and unburned areas (Fig. 4). Seedling and sapling densities were significantly higher in areas that experienced the 2009 wildfire compared to the unburned areas. Conversely, there were significantly more tree-sized princess tree stems in unburned areas compared to areas burned by the 2009 wildfire. The significantly greater number of seedlings and saplings in the burned areas suggests that fire played a role in the recruitment of new stems to the area with the majority not attaining tree size at the time of sampling. A significantly higher number of tree size stems in the unburned areas suggests that princess tree regeneration had established earlier as a result of previous disturbances and have been present long enough to attain tree size.

The number of princess tree stems per hectare were further evaluated by disturbance effect using Pearson Correlation Coefficients (PCC) (Table 4). Fire intensity was treated as an ordinal variable (0–4; no fire – high fire intensity) and the other disturbances as dichotomous variables (0 = disturbance did not occur; 1 = disturbance occurred). Only fire intensity and logging displayed significantly ($p < 0.05$) moderate correlations to seedling and tree stem numbers per hectare. Fire intensity had a moderate positive correlation with princess tree seedlings per hectare (0.3838, $p = 0.0023$), indicating that areas that experienced higher fire intensity produced more princess tree seedlings per hectare. On the other hand, the tree size stems per hectare displayed a moderate negative correlation with fire intensity (− 0.4062, $p = 0.0012$), indicating that more numbers of tree size princess tree stems per hectare occurred in areas where fire intensity was lower. Sapling size princess tree stems displayed a weak correlation with fire intensity.

The occurrence of past logging had a moderate positive correlation with princess tree seedlings (0.3678, $p = 0.0036$) indicating

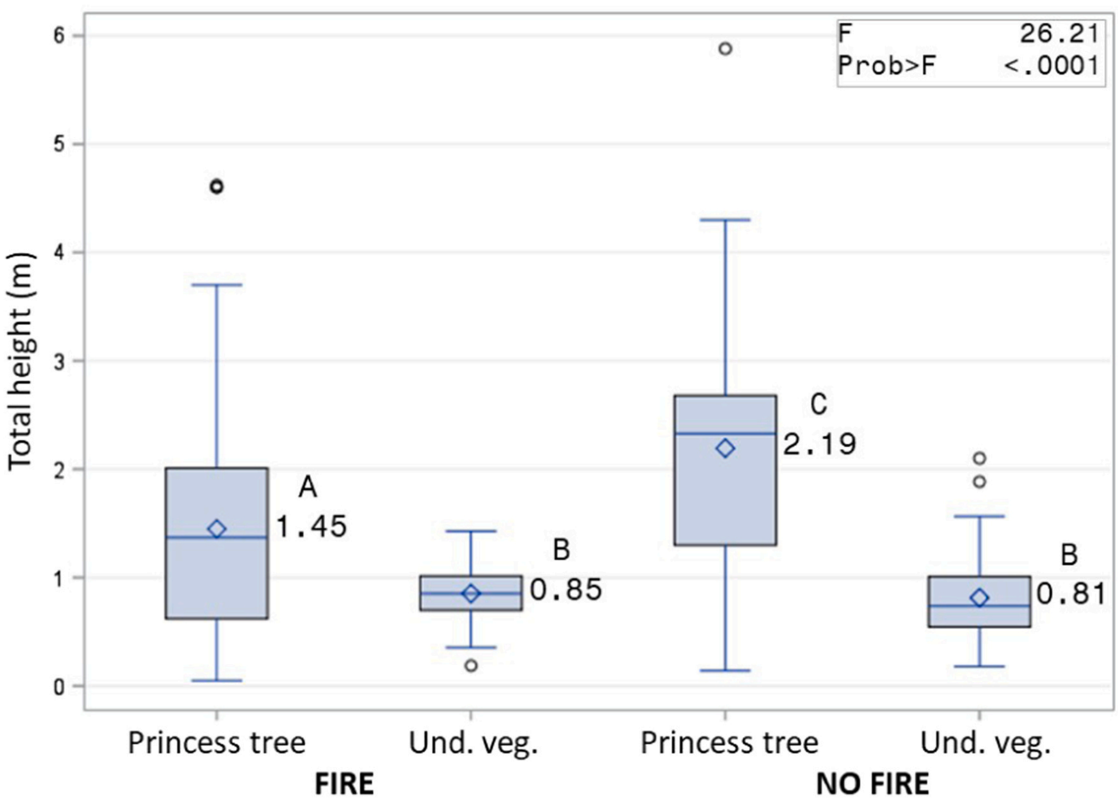

Fig. 3. Height comparison of sapling-sized (0–3 cm dbh) princess trees (*Paulownia tomentosa*) with understory vegetation (Und. veg.). The mean total height value is displayed and means with different letters are significantly different ($p < 0.05$).

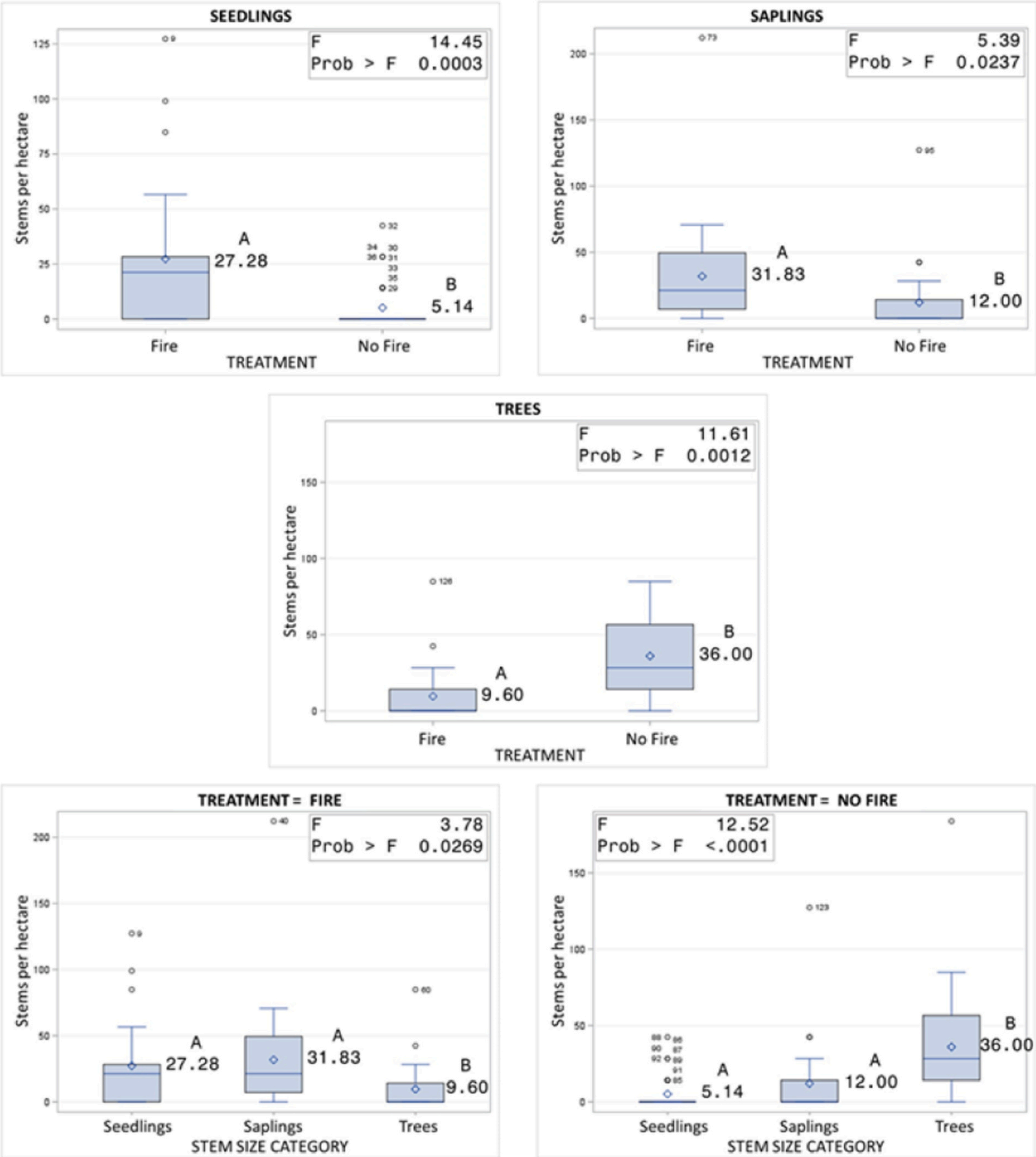

Fig. 4. Box plots of princess tree (*Paulownia tomentosa*) stems by stem size class (seedlings = < 1.4 m ht., saplings = 0–3 cm dbh, trees > 3 cm dbh) between burned and unburned areas, and between size classes within burned and unburned areas. Stem size class mean is displayed and means with same letters are not significantly different ($p < 0.05$).

seedling numbers were more likely to occur in areas that had experienced logging in the past. Logging had a moderate negative correlation with tree size stems per hectare ($-$ 0.3072, $p = 0.0160$) indicating that tree size princess tree stems were less likely to occur in areas that had experienced past logging activities. Sapling-sized stems displayed weak correlation with past logging activity.

We wanted to see if any relationship existed between the physiography of the study area and the disturbance type, and between the disturbance type and the resulting vegetation features that could influence the occurrence of princess tree. PCC was performed on disturbance type with environmental variables of interest (Table 5), and it was discovered that disturbance type was not associated with any physiographic features of concern (slope, aspect, elevation, soil type). However, disturbance type had an effect on vegetative

Table 4
The Pearson Correlation Coefficients (PCC) and the corresponding p-value relating princess tree (*Paulownia tomentosa*) stem numbers per hectare by size category with disturbance type.

		Disturbance type			
Size category	Statistic	Fire intensity	Ice damage	Herbicide	Logging
Seedlings	PCC	0.3838	0.0116	0.1899	0.3678
(< 1.4 m ht.)	p-value	0.0023	0.9291	0.1427	0.0036
Saplings	PCC	0.1456	0.1461	-0.1006	0.1638
(0–3 cm dbh)	p-value	0.2629	0.2613	0.4405	0.2071
Trees	PCC	-0.4062	0.0291	-0.1880	-0.3072
(> 3 cm dbh)	p-value	0.0012	0.8239	0.1469	0.0160

features (ground cover, understory vegetation height, canopy cover) which can affect princess tree stems.

Fire intensity had a moderate positive correlation (0.3705, $p = 0.0033$) with ground cover and a strong negative correlation (− 0.7828, $p < 0.0001$) with canopy cover (Table 5), suggesting that fire intensity played a role in altering the forest canopy structure. Areas that experienced canopy damage during the 2003 ice storm displayed a moderate negative correlation (− 0.2758, $p = 0.0314$) with canopy cover and areas that has been logged in the past displayed a strong negative (− 0.5640, $p < 0.0001$) correlation with canopy cover. Areas that had been treated with herbicides revealed a moderate positive correlation (0.3913, $p = 0.0018$) with understory vegetation height.

None of the measured physiographic features of the study area displayed any significant correlations with the number of princess tree stem numbers per hectare. However, some vegetative features displayed significant correlations with the number of princess tree stems per hectare (Table 6). Canopy cover was significantly correlated with seedling and tree-sized princess tree stems per hectare, displaying a negative correlation (− 0.6027, $p < 0.0001$) with seedlings per hectare and a positive correlation (0.4988, $p < 0.0001$) with trees per hectare. Sapling-sized stems per hectare displayed a weak negative correlation with canopy cover. This would indicate that seedlings are more abundant in areas with less forest canopy and tree-sized stems are more abundant where there is more dense forest canopies.

The only other vegetation feature that displayed a significant relationship with numbers of princess tree stems was the amount of vegetative ground cover, which displayed a significant negative correlation (− 0.3260, $p = 0.0104$) with tree-sized stems per hectare. This suggests that as the number of tree-sized stems per hectare increases the amount of vegetative cover decreases.

4. Discussion

Our study area has experienced many types of disturbances over the previous decade at the time of sampling, including a widespread wildfire in the spring of 2009, pre and post-fire logging, an ice storm in 2003, and targeted herbicide application to princess tree and other invasive species. Sampling for this study occurred 2 years after the wildfire, 8 years after the ice storm, 1–2 years after targeted herbicide treatments, and 1–7 years after logging activity.

These disturbances resulted in alterations of the forest structure, particularly the forest canopy. Areas that had experienced fire, logging, and ice storm damage created more open canopies. Areas that experienced higher fire intensities resulted in more open canopies and higher amounts of ground cover. Areas that experienced targeted herbicide treatment of invasive species resulted in greater understory vegetation height. It is these disturbances, and their effects on the receiving environment that determines the success or failure of invasive plant species (Bugnot et al., 2016). Princess tree, a very shade intolerant species requiring abundant sunlight and bare mineral soil for optimal germination and establishment is an invasive pioneering species that is able to take

Table 5
The Pearson Correlation Coefficients (PCC) and the corresponding p-value relating environmental variables with disturbance type.

Environmental		Disturbance type			
Variable	Statistic	Fire intensity	Ice damage	Herbicide	Logging
Slope	PCC	-0.1100	-0.1166	0.0162	-0.0557
	p-value	0.3989	0.3707	0.9016	0.6699
Aspect	PCC	0.1343	-0.1176	0.1512	0.1341
	p-value	0.3021	0.1128	0.2447	0.3028
Elevation	PCC	0.0489	-0.1714	-0.1608	0.2402
	p-value	0.7083	0.1865	0.2157	0.0622
Soil	PCC	-0.0166	0.0515	0.1310	-0.0927
	p-value	0.8989	0.6934	0.3142	0.4775
Ground cover	PCC	0.3705	0.0281	0.2243	0.1161
	p-value	0.0033	0.8296	0.0823	0.3731
Vegetation height	PCC	-0.0501	-0.0138	0.3913	-0.2077
	p-value	0.7016	0.9161	0.0018	0.1083
Canopy cover	PCC	-0.7828	-0.2758	0.0812	-0.5640
	p-value	< .0001	0.0314	0.5339	< .0001

Table 6
The Pearson Correlation Coefficients (PCC) and the corresponding p-value relating vegetation variables with princess tree (*Paulownia tomentosa*) stems per hectare by stem size class.

Size category	Statistic	Vegetation variables		
		Ground cover	Vegetation height	Canopy Cover
Seedlings	PCC	0.2270	-0.0258	-0.6027
(< 1.4 m ht.)	p-value	0.0785	0.8437	< .0001
Saplings	PCC	0.2004	0.1177	-0.1322
(0–3 cm dbh)	p-value	0.1215	0.3661	0.3100
Trees	PCC	-0.3260	-0.0630	0.4988
(> 3 cm dbh)	p-value	0.0104	0.6295	< .0001

advantage of such conditions (Hu, 1961; Longbrake, 2001; Rebbeck, 2012).

The high density of princess tree seedlings and saplings in areas of the forest is likely a result of the 2009 fire and post-fire logging. These open areas have allowed princess tree to establish as a seedling, and its rapid growth enabled it to remain above native vegetation, reaching sapling-size (Hu, 1961; Beckjord and McIntosh, 1983). Studies have recorded princess tree juvenile stems growing about 1 m per year and sprouts more than 5 m, and can root sprout after fire, with enough leaf area to successfully shade out any vegetation undergrowth (Beckjord and McIntosh, 1983). While we did not record stem origin (seed vs. sprout), it is likely the many sapling stems originated as sprouts following the fire as princess tree has a very high sprouting ability (Rebbeck, 2012). Additionally, if princess tree seedlings were growing in response to pre-fire disturbances in the area, they likely did not survive the fire of 2009. Princess tree is not considered to be fire resistant – branches are brittle with thin bark, making it likely stems were killed by fire (Hu, 1961; Innes, 2009).

The seed source for the high density of princess tree seedlings found after the fire is not certain. Germination could be from seeds stored within the soil, as princess tree produces a large seed bank (Young and Young, 1992; Hyatt and Casper, 2000). Rebbeck (2012) reports that princess tree seed banks remain viable for only 2–3 years. Hyatt and Casper (2000) found princess tree seed mortality exceeded 70% over a two year period, and only two individuals germinated from this seed source. The low viability of the species' seed

Fig. 5. A mature princess tree (*Paulownia tomentosa*) inside the study area but outside the 2009 wildfire area producing multiple seed capsules as a potential seed source for disturbed areas.

bank indicates this is probably not a significant source for new germination (Hyatt and Casper, 2000).

It is more likely the seed source for the high density of princess tree seedlings that was observed in 2011 are mature princess tree stems that survived the 2009 fire or mature princess tree stems outside the burn area (Fig. 5). It would not be uncommon for mature princess trees to seed-in post-fire areas (Lovenshimer and Madritch, 2017). A single seed capsule may contain upwards of 2000 seeds (Hu, 1959) that can be dispersed 3 km from the parent tree (Langdon and Johnson, 1994; Kuppinger, 2008). Field investigations have commonly discovered princess tree seedlings 4 km from the parent plant (Hu, 1961; Langdon and Johnson, 1994). Thus, it is possible that the parent source for seedlings within the burn is a mature princess tree some distance away, especially considering the clumped distribution of sample plots with the species present. It is likely that the canopy reduction or removal that resulted from the wildfire created conditions for princess tree establishment because seedling establishment is positively correlated with fire intensity and subsequent canopy removal (Black et al., 2018).

We also observed many princess tree sprouts as a result of the ineffective herbicide application (based on visible hack marks). The two methods employed, stem injection and basal bark spray, are known to result in stump and root sprouts after main stems of princess tree are deadened (Miller, 2003). Multiple sprouts could thus be contributing to the high density of princess tree seedlings found. The root sprouts, however, may also be a result of the 2009 fire. Although no princess tree stems were aged, it still cannot be determined if the high density of seedlings is a result of the wildfire or the herbicide application, as both occurred in the same year. It is likely that root sprouts from both disturbances led to the high density of seedlings; but the 2009 fire seems to be the greater contributor, as this was the more influential factor in the RDA model.

Outside the burn area, it is probable that the 2003 ice storm created forest canopy openings that favored princess tree colonization. While we could not confirm this, canopy openings within the forest were positively correlated with the areas damaged by the ice storm. The canopy gaps can allow seeds from distant trees to invade the open floor (Boerner et al., 1988). The mature princess trees that were already established within the forest are a possible seed source for colonization of the ice-damaged areas which, eight years later, and are now dense with sapling-sized stems.

Princess tree saplings grew in greater density in areas that experienced medium fire intensities compared to other fire intensities and where ice storm damage appeared to be highest. These also were areas where taller understory vegetation and more ground cover existed. Some studies have shown that princess tree has the ability to successfully outgrow other vegetation in certain circumstances, indicating that native vegetation regrowth is not necessarily an impediment to the species' survival (Beckjord and McIntosh, 1983). In our study we found that princess tree saplings were significantly taller than the understory vegetation, and saplings were significantly taller in burned areas than unburned areas, probably the result of more open canopies. In the unburned areas it is likely that the severe crown damage from the 2003 ice storm played a significant role. Whether these saplings in the burn areas originated from seed or sprout we do not know. If seedlings germinated immediately in post-fire conditions, it is possible with its rapid growth rate that princess tree was able to establish as saplings before surrounding vegetation outcompeted it (Kuppinger et al., 2010).

We do not know what the tree-size stem density of princess tree was prior to the 2009 fire in the study area. We found significantly higher densities of princess trees, both juvenile and seed-bearing, in areas not impacted by the 2009 fire. There is a notable absence of any large disturbance outside of the burn area in recent years, further evidenced by the high amount of canopy closure. Although no empirical data was collected on the size and frequency of the canopy gaps in the stands, field observations revealed princess trees growing in overstory openings. Any tree size stems that did occur in the burned areas prior to the fire probably did not survive or were top-killed and produced sprouts which subsequently became seedling and sapling-sized trees.

5. Conclusions

The distribution of invasive plant species across the globe continues to evolve and spread. Understanding the pathways and mechanisms that enables a species to become invasive in different ecosystems is critical to their future management and preservation of biodiversity. This study provides further insight into the spread and establishment mechanisms of princess tree- an invasive species in the U.S. and other locations around the world.

The significantly greater number of seedlings and saplings in the burned areas suggests that fire played a major role in the recruitment of new stems to the area with the majority not attaining tree size at the time of sampling. A significantly higher number of tree-size stems in the unburned areas suggests that princess tree regeneration had established earlier as a result of previous disturbances and have been present long enough to attain tree size.

Across the study area there have been multiple disturbances in the past decade – ice storm damage, a large wildfire, logging, and herbicide treatments – that are interacting to influence the structure and composition of the forested landscape. All of these disturbances have created conditions conducive to princess tree growth, verifying that this exotic species takes advantage of disturbances to become established. The primary driver that appears to perpetuate princess tree post-disturbance is the extent and size of canopy openings. Studies have found that fire as a disturbance promotes the invasion and establishment of princess tree (Lovenshimer and Madritch, 2017, Black et al., 2018), and this study corroborates those findings.

However, we also found princess tree growing in small canopy gaps within the forest, often as the result of a single tree fall. It remains to be seen if princess tree populations will persist in these areas as the small canopy gaps continue to close and no new disturbances occur. Only returning to the study area years later will determine if princess tree has regenerated in the mature closed stands or has been replaced by native woody species, and if density of the species has decreased in the areas impacted by the 2009 wildfire. Long term research is necessary to determine if princess tree can persist after colonizing a recently disturbed area, or if it is dependent upon continual disturbances for a self-sustaining population. Similarly, more work is needed to determine if princess tree can expand its range in introduced habitats without the aid of disturbances, a key stage of an invasion by any species (Allendorf and

Lundquist, 2003).

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Angela Chongpinitchai: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft. **Roger A. Williams**: Methodology, Validation, Formal analysis, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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