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ARTICLE

Vegetation Ecology

Response of invasive shrubs to fire-induced injury in eastern U.S. deciduous forests: Does more injury mean less death?

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Abstract

Invasive shrubs are increasingly altering ecosystem structure and reducing biodiversity in eastern deciduous forests of North America. Among the most aggressive invaders are *Euonymus alatus* (burning bush) and *Ligustrum obtusifolium* (border privet), both were introduced from East Asia in the 19th century. These species form dense thickets and mid-story that displace native flora and disrupt ecological processes. While mechanical and chemical control methods exist, they are often costly, labor-intensive, or environmentally limiting. Prescribed fire is being more widely used as a control method, but the response of these invasive shrubs to burning is not fully understood. This study examines the response of both species to targeted heat injuries to better understand the efficacy of burning as a control method. We applied three burning treatments using a propane torch: basal heating at varying durations (5, 20, and 35 s), crown (foliar) heating, and combinations of each of these treatments. Crown heating alone did not result in any mortality. Longer basal heating durations significantly increased both mortality and sprouting likelihood in both species, although larger stem diameters increased their resilience. The longest (35 s) basal heating caused the greatest mortality, unsurprisingly, but when foliar heating was combined with basal heating, shrubs were actually less likely to die but resprout following treatment. A follow-up assessment, three years post-treatment, showed increased delayed mortality, indicating the importance of long-term monitoring. Findings suggest that long residency times during burning may be necessary to control *E. alatus* and *L. obtusifolium* and that the physiological response to varying types of heat injury from fire is not well understood.

KEYWORDS

delayed mortality, *Euonymous alatus* (burning bush), *Ligustrum obtusifolium* (border privet), prescribed fire, propane torching, resprouting

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INTRODUCTION

Invasive woody plants present a major ecological challenge in eastern deciduous forests of North America by outcompeting native species and altering vegetation structure and composition (Knapp et al., 2023; Webster et al., 2006). Their spread is further facilitated by anthropogenic disturbances such as land use change, fragmentation, and climate change, which create favorable conditions for colonization in disturbed landscapes. Among these problematic invaders, *Euonymus alatus* (Thunb.) (burning bush) and *Ligustrum obtusifolium* (Siebold & Zucc.) (border privet) have emerged as aggressive colonizers across North American landscapes, altering native plant communities and disrupting ecological functions. Both species were introduced to the United States from East Asia in the 19th century mainly for ornamental purposes. *E. alatus* forms dense thickets that suppress understory regeneration through prolific seed dispersal, while *L. obtusifolium* often dominates the midstory, reducing native plant diversity and altering arthropod communities, including pollinators (Coville et al., 2021; Ulyshen et al., 2020).

Effective control of invasive plant species is essential for restoring native plant communities and maintaining ecosystem function (Maynard-Bean & Kaye, 2019). Conventional management approaches, including chemical herbicide application (e.g., Hanula et al., 2009) and mechanical removal (e.g., Maynard-Bean & Kaye, 2019; Ulyshen et al., 2020), remain widely used, but are often limited by costs and labor constraints, or unintended environmental impacts. As a result, targeted thermal treatments, such as prescribed fire and propane torching, have gained attention as potentially more cost-effective and ecologically integrative alternatives (Brancatelli et al., 2024; DiTomaso et al., 2006; Ward & Williams, 2011; Ward et al., 2013). By mimicking natural fire regimes, burning can suppress certain invasive species, reduce seed banks, and promote the regeneration of native vegetation. A recent systematic review found that about 80% of studies evaluating prescribed fire as a tool for managing invasive woody plants reported successful reductions in cover, density, or regeneration of target species (Brancatelli et al., 2024). A study from southern Connecticut showed that directed heating with propane torches effectively reduces invasive Japanese barberry abundance and height, providing a non-chemical alternative for habitat restoration projects in areas where herbicide use is restricted (Ward & Williams, 2011).

Fire-induced responses in woody plants are highly variable and depend on a variety of factors such as fire intensity, frequency, and species-specific traits (DiTomaso et al., 2006; Faulkner et al., 1989). Species with thin bark, shallow roots, or limited belowground carbohydrate reserves tend to exhibit greater post-fire mortality. While fire can significantly increase plant mortality through cambial damage and hydraulic failure (Bova & Dickinson, 2005), many woody shrubs exhibit vigorous post-fire resprouting from basal buds or root crowns allowing them to recover rapidly after being top-killed (Clarke et al., 2013; Lambert et al., 2010). Twidwell et al. (2016) found that high-intensity prescribed burns during drought caused elevated mortality in woody resprouters; many individuals still regenerated via vigorous sprouting. Similarly, some past research observed over 90% resprouting in oak species following frequent burns, despite clear fire-induced top-kill (Peterson & Reich, 2001; Nemens et al., 2018). While single burn events may not be sufficient for long-term control, burning timed with growth vulnerability and follow-up treatments combined with mechanical or chemical treatments can be effective in suppressing resprouting and increasing mortality (Brancatelli et al., 2024; DiTomaso et al., 2006; Faulkner et al., 1989; Richburg et al., 2004; Ward et al., 2013). A two-step approach combining initial top-kill by prescribed fire or mowing with follow-up propane torching or herbicide application has been shown to reduce Japanese barberry cover by over 70% and is effective for long-term control (Ward et al., 2013). In California, two consecutive annual burns effectively controlled shrub encroachment by killing resprouting shrubs (*Baccharis pilularis*) and reducing their cover for longer periods of time (Hopkinson et al., 2020). Season of burning can also affect treatment success: burning woody plants during the growing season, rather than the dormant season, has resulted in higher top-kill and reduced resprouting, making fire timing a critical factor for controlling woody plant abundance in fire-dependent ecosystems (Meunier et al., 2021; Robertson & Hmielowski, 2014).

Despite growing interest in fire-based treatments, relatively few empirical studies have examined fire-induced mortality and resprouting dynamics in invasive woody shrubs of the northeastern United States (Brancatelli et al., 2024). The comparative responses of *E. alatus* and *L. obtusifolium* from targeted heating treatment remain limited. Existing studies typically focus on native species or fire-adapted systems in the southeastern or central United States, limiting their applicability to northern and mid-Atlantic forests. This knowledge gap limits the ability to predict fire outcomes and design tailored prescriptions that effectively control invasive shrubs. To fill this gap, we evaluated fire-induced top-kill, mortality, and resprouting responses in *E. alatus* and *L. obtusifolium* under three targeted heating treatments: foliar crown heating, basal heating, and combined basal and crown heating. We aim

to answer two key research questions: (1) How do *E. alatus* and *L. obtusifolium* respond to foliar and basal heat damage? (2) What treatment combinations maximize mortality while minimizing the need for retreatment? The results will inform the best practices for integrating targeted burning treatments into invasive shrub management strategies in eastern deciduous forests.

METHODS

Study area

The experiment was conducted in a mature, 16-hectare mixed-hardwood stand located within the Arboretum at Penn State University, north of State College, Pennsylvania (latitude 40.8° N, longitude 77.9° W) (Maynard & Kaye, 2021). The site, locally known as Hartley Wood, consists of a diverse overstory primarily composed of native hardwoods such as oaks (*Quercus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.). The soil is classified as Opequon rock-outcrop complex (OxB), characterized by shallow, well-drained soils formed over limestone bedrock, which influences both vegetation structure and fire behavior. The site has long been subject to propagule pressure from nearby ornamental plantings, with historical records indicating the introduction of invasive species since at least the early 20th century. By the mid-2000s, the forest understory was heavily invaded, particularly by *L. obtusifolium*, *E. alatus*, and several invasive honeysuckles (*Lonicera* spp.) (Maynard & Kaye, 2021). These conditions provided an ideal setting for testing the effects of experimental fire treatments on invasive shrub species under varying heating exposure.

Experimental design

Torching experiments were conducted to simulate varying fire-induced injuries and examine patterns of response (sprouting vs. mortality) of *E. alatus* and *L. obtusifolium*. The experiments were conducted at the individual plant level, when shrubs had fully emerged foliage, and in two seasons: fall (December 6–7, 2019) and spring (May 25–27, 2020). A total of 238 shrubs, 119 of each species, were randomly selected for experiments ($n = 7$ for all treatments; Table 1). Individual shrubs were selected for either fall or spring experiments, then assigned to one of three types of heating treatments: foliar crown heating, basal heating, and a combination of crown and basal heatings. Basal heating experiments, including those in combination with crown heating, consisted of three different heating duration treatments (5, 20, or 35 s). Within each treatment season, 7 shrubs of each species were also selected for cut treatments. Finally, seven shrubs from each species were also randomly selected to serve as controls. A numbered aluminum tag was used to mark each shrub for identification. We measured height (in centimeters), basal diameter (in millimeters), and diameter of the largest stem (in millimeters) for each shrub.

TABLE 1 Experimental treatments and replication structure used in the shrub heating study on *Euonymus alatus* (burning bush) and *Ligustrum obtusifolium* (border privet) (sample size: $n = 7$).

Treatment (T)	T × *n*
Fall	
Basal (5, 20, 35 s)	3 × 7
Crown	7
Basal (5, 20, 35 s) + Crown	3 × 7
Cut	7
Spring	
Basal (5, 20, 35 s)	3 × 7
Crown	7
Basal (5, 20, 35 s) + Crown	3 × 7
Cut	7
Control	7
Total (two species)	119 (238)

Note: Fall Experiments: December 6–7, 2019; Spring Experiments: May 25–27, 2020.

Experiments were conducted using controlled and targeted heating. Surface fuels and adjacent vegetation were removed to ensure localized heating and safety. All heating treatments were applied using a Weed Dragon 100,000 BTU Propane Torch kit (model: VT2-23 SVC), which is reported to produce a focused flame with heat up to 1120°C, suitable for precision treatment of woody stems. Fire reflective material (i.e., fire shelter used in wildland fire applications) was used to isolate heating to either foliar or basal locations. Burns were carried out under moderate weather conditions to minimize confounding effects from extreme meteorological variables. During the burn days, December temperatures ranged from 2.9 to 7.1°C with relative humidity between 47.3% and 73.5%. The May burns occurred under warmer and more humid conditions, with temperatures ranging from 17.4 to 24.8°C and relative humidity from 67.2% to 81.7%. Basal heating involved rotating a propane torch, at close proximity (15–20 cm), around the base of each plant for 5, 20, or 35 s, ensuring even heating. Infrared imaging (FLIR Model E95) was captured during burning to determine temperatures at which basal bark was exposed

(Figure 1). The average temperature recorded on the basal bark surface during heating was 500–600°C. Crown heating targeted foliage, whereby the torch was passed over all leaves in close proximity (15–20 cm) for a few seconds to ensure total foliar scorch (i.e., leaf death). Physical contortion and diminishment of foliage were observed during heating, but leaves typically did not ignite. The cut treatment involved removing all stems approximately 5 cm above the ground.

Mortality assessment

The first evaluations were made in July 2020 following the December 2019 and May 2020 burns. Shrubs at this stage were simply marked as "unaffected" (crown foliage was still live) and "looks dead" given the recency of treatments. The second evaluations were conducted in May 2021. This time, shrubs were marked as unaffected, dead, or resprouting. Resprouting refers to basal resprouting but not axillary bud response. The final assessment was conducted in November 2024, and shrubs were marked as dead, unaffected, or resprouting.

DATA ANALYSIS

Out of the 238 total samples, all tags were located during the first assessment, 225 tags were found in the second assessment, and only 116 were recovered in the third assessment. Because the first assessment occurred shortly after the burns, it is less likely to reflect the full impact of fire on shrub mortality. As a result, we used the second assessment data for detailed analysis. We also conducted a comparison of shrub status across all three assessment years using the 116 shrubs that were found among all years. This comparative analysis helps us to understand the time effects on shrub responses. Data analysis was performed using Python software, employing Chi-square tests and multinomial regression.

Chi-square test

We employed Pearson's chi-square test of independence to assess whether shrub responses significantly differed among heating treatments. The chi-square test was used to assess differences among individual treatment effects, providing non-parametric evidence to identify which discrete treatment combinations differed significantly from expected frequencies. Following a significant overall result, we conducted a post hoc analysis using adjusted standardized residuals to identify which specific treatment–shrub response combinations contributed to the observed differences. Standardized residuals (often called Pearson residuals) quantify the deviation of observed frequencies from expected frequencies in standard deviation units. We utilized adjusted standardized residuals, which are normally distributed under the null hypothesis and account for variability in both the row and column totals of the contingency table, providing a more accurate estimate of standard error for each cell (Haberman, 1973). To control for Type I error due to multiple comparisons, we applied a Bonferroni correction. This method adjusts the significance threshold by dividing the original alpha level ($\alpha = 0.05$) by the

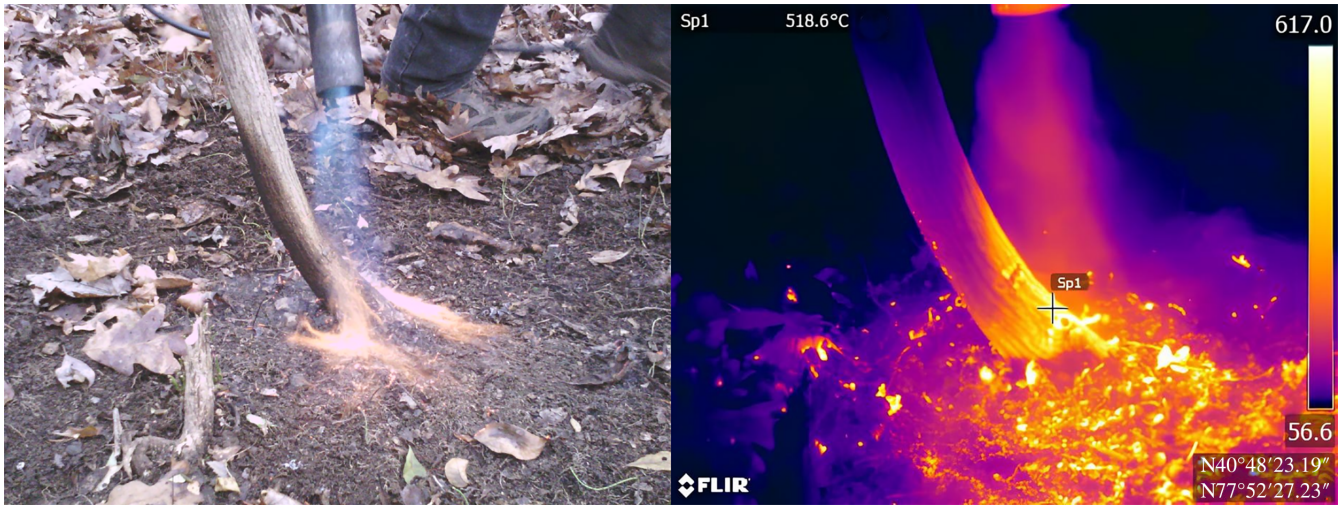


FIGURE 1 Targeted heating experiments using a 10,000 BTU torch. Treatments included basal heating for 5, 20, or 35 s, foliar crown heating (resulting in scorch), and a combination of basal and crown heating (left: visible spectrum; right:thermal infrared image captured with a FLIR camera). Photo credit: Arun Regmi.

number of pairwise comparisons, lowering the chance of false positives. In our analysis, the Bonferroni-adjusted alpha level was calculated as $\alpha_{Bon} = 0.05/21 \approx 0.0024$, and a corresponding critical z value of 3.038 for identifying statistically significant residuals.

Multinomial regression

The multinomial logistic regression was used to model the probability of each shrub response category as a function of continuous predictors and covariates, providing model-based evidence of how heating duration, crown treatment, and stem diameter influenced shrub outcomes. This method was appropriate given the categorical nature of the response variable, which comprised three nominal and mutually exclusive outcome levels: unaffected shrubs (live), dead shrubs (dead), and resprouted shrubs (resprout) (McFadden, 1974). Multinomial regression is well suited for analyzing outcomes that lack an intrinsic order, allowing estimation of relative risk ratios for each response category compared to a reference outcome (McFadden, 1974).

We used two explanatory variables to evaluate how heating treatments influenced shrub responses. The first "duration" was as a continuous variable representing the length of basal heating applied times (0, 5, 20, and 35 s). Treatments with basal heating were assigned to their respective durations (5, 20, or 35 s), while treatments with only crown heating or no heating (controls) were assigned a duration of 0 s. The second variable "crown" was a binary variable indicating whether crown (foliar) heating was applied. Treatments with crown heating (i.e., combined treatments and crown-only treatments) were coded as 1, and those without (i.e., basal heating only or control) were coded as 0. We ran two separate models for each shrub species to account for potential species-specific responses. Observations from the cut-only treatment were excluded from analysis, as these plants did not receive either basal or foliar heating and thus were not relevant to the regression predictors. Of the 105 total samples per species (after excluding 14 cut-only samples), 3 were missing for *E. alatus* and 10 for *L. obtusifolium*, resulting in 102 and 95 observations, respectively, for the final modeling.

RESULTS

Diameter distribution

Samples of *L. obtusifolium* included a higher proportion of small-diameter shrubs compared to *E. alatus*, which had generally larger stem diameters (Figure 2). The mean diameter of the largest stem of *E. alatus* was 28.12 mm, ranging from 6.00 to 55.30 mm (SD = 9.15 mm). In contrast, *L. obtusifolium* had a smaller mean stem diameter of 13.96 mm, ranging from 1.00 to 38.80 mm (SD = 6.25 mm).

Shrub response to treatments

Following heating treatments, 42% of shrubs were found to be unaffected, 38% resprouted after top-kill, and 20% were dead. Overall, *E. alatus* showed greater resistance, with 56% unaffected, 16% mortality, and 28% resprouting, while *L. obtusifolium* experienced higher top-kill (73%) with 24% mortality and a strong resprouting response (49%) (Figure 3).

L. obtusifolium experienced higher mortality than *E. alatus* across all treatments. In both species, the

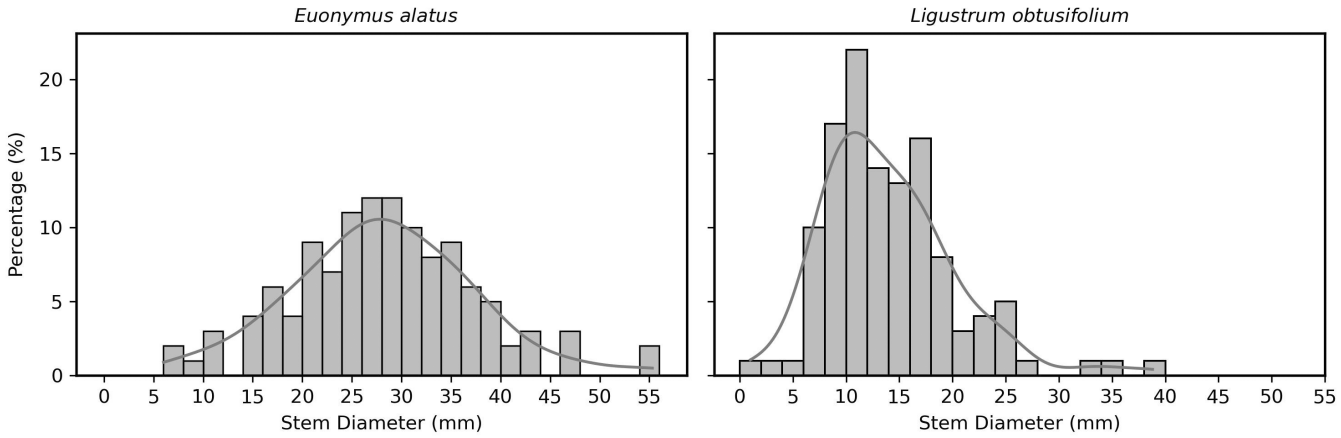


FIGURE 2 Distribution of stem diameters for two invasive shrub species, *Euonymus alatus* (burning bush) and *Ligustrum obtusifolium* (border privet), based on measurements from 119 samples per species.

cut-only treatment led to vigorous resprouting (93%), with minimal mortality (7%). *E. alatus* was unaffected by short-duration heating (5-s), with 100% survival. Adding crown heating (5-s + CR) caused only 7% top-kill, with full resprouting and no mortality. In contrast, *L. obtusifolium* showed greater sensitivity to 5-s basal heating, with 46% top-kill (15% mortality and 31% resprouting). When crown heating was added, mortality increased to 38%, with 31% of shrubs resprouting (Figure 4).

Under the 20-s basal heating, 50% of *E. alatus* were top-killed, with increased mortality (36%) and limited resprouting (14%). In contrast, *L. obtusifolium* experienced substantial top-kill (85%) with relatively lower mortality (31%), but a stronger resprouting response (54%). When crown heating was added (20-s + CR), both species showed increased top-kill and resprouting, but slightly less mortality. *E. alatus* showed 77% top-kill, with reduced mortality (23%) and increased resprouting (54%). *L. obtusifolium* experienced 100% top-kill but only 9% mortality, with a substantial resprouting response (91%) (Figure 4).

Under 35-s basal heating, both species experienced high levels of mortality. *L. obtusifolium* experienced complete top-kill, with 64% mortality and 36% resprouting. *E. alatus* showed greater resistance, with 31% unaffected, 54% mortality, and 15% resprouting. The combined treatment (35-s + CR) reduced mortality in both species (*E. alatus*: 21%; *L. obtusifolium*: 36%), but increased resprouting, particularly in *L. obtusifolium* (64%). The crown-only treatment (CR) resulted in zero mortality for both species, with *L. obtusifolium* showing a higher resprouting rate (31%) than *E. alatus* (14%) (Figure 4).

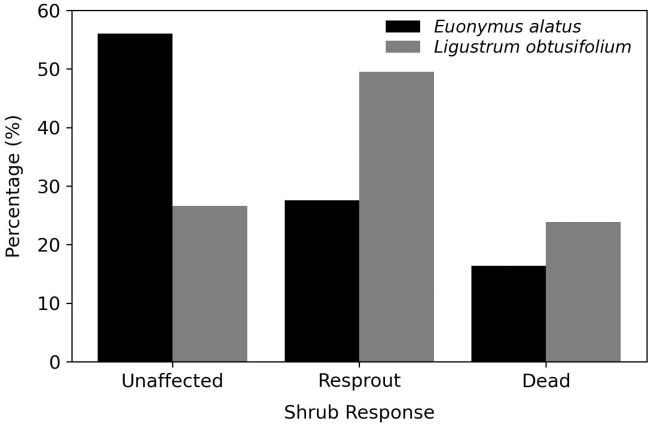


FIGURE 3 Percentage of shrubs in each post-fire response category (unaffected, resprout, dead) for two invasive species: *Euonymus alatus* (burning bush) and *Ligustrum obtusifolium* (border privet).

Results for chi-square test

Shrub responses to heating treatments varied significantly across treatments and between species (Table 2; Figure 5). Shrub responses, categorized as unaffected, dead, or resprout, were significantly associated with heating treatments, indicating that treatment effects were not uniform across species or response types. When limited to a binary comparison of live (combining unaffected and resprouted shrubs) versus dead, treatments still had a strong effect, suggesting differential mortality patterns driven by treatment intensity and type (Table 2).

Post hoc test results

The standardized residual heatmap (Figure 5) reveals distinct species-specific responses to the heating treatments.

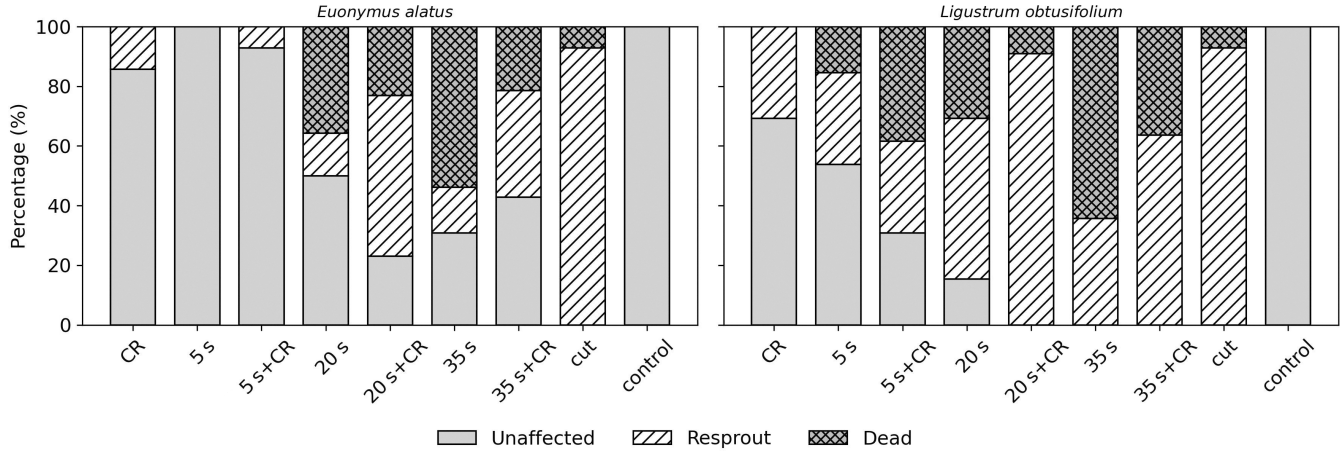


FIGURE 4 Shrub response (unaffected, resprout, dead) of *Euonymus alatus* (burning bush) and *Ligustrum obtusifolium* (border privet) one year following basal heating for 5, 20, or 35 s, crown heating (CR), basal heating (5, 20, or 35 s) + crown heating, as well as a mechanical treatment (cut) and a control group.

For *E. alatus*, the 5-s basal heating led to significantly more unaffected individuals than expected (residual = 3.21), indicating strong tolerance to low-intensity fire. However, under the 35-s basal heating, mortality was significantly higher than expected (3.49), suggesting a threshold beyond which *E. alatus* experiences substantial damage and limited capacity to recover. The combined 20-s basal and crown heating treatment (20-s + CR) resulted in a strong resprouting response (3.31), pointing to moderate regenerative ability under cumulative stress.

In *L. obtusifolium*, the crown-only (CR) treatment yielded a significantly higher number of unaffected shrubs than expected (3.99), indicating the minimal impact of crown heating alone. Consistent with *E. alatus*, the 35-s basal heating resulted in significantly higher-than-expected mortality, reflecting high vulnerability to prolonged heat exposure. The combined treatment (20-s + CR) led to significantly elevated resprouting (3.15), suggesting that while *L. obtusifolium* is more easily top-killed, it can recover vigorously through vegetative regrowth (Figure 5).

TABLE 2 Chi-square tests of treatment effects on survival status (unaffected, resprout, dead; dead vs. live) in *Ligustrum obtusifolium* (border privet) and *Euonymus alatus* (burning bush).

Species	Response category	χ^2	df	*p*
L. obtusifolium	3 (unaffected, resprout, dead)	59.55	14	<0.001
L. obtusifolium	2 (dead vs. live)	21.73	7	0.003
E. alatus	3 (unaffected, resprout, dead)	50.98	14	<0.001
E. alatus	2 (dead vs. live)	25.55	7	0.001

The Bonferroni-adjusted post hoc test confirmed the findings from the standardized residuals analysis, identifying the same significant treatment–response combinations, specifically, elevated mortality under 35-s basal heating for both species, increased resprouting in the cut treatment for *L. obtusifolium* and *E. alatus*, and a higher-than-expected proportion of unaffected shrubs under low-intensity (5-s) heating for *E. alatus*.

Results from multinomial regression

Basal heating duration had a strong positive impact on mortality and resprouting in both species, with longer heating exposure leading to a greater likelihood of both outcomes (Table 3). *L. obtusifolium* showed a more pronounced effect of heating duration relative to *E. alatus*, with higher increases in both mortality and resprouting rates ($\beta = 0.26$ vs. 0.13 for mortality; $\beta = 0.23$ vs. 0.09 for resprouting). Stem diameter was negatively associated with both mortality and resprouting in both species, suggesting that larger stems were more resistant to heat damage and less likely to initiate new growth following top-kill. Surprisingly, the addition of crown heating had no significant impact on shrub mortality, but rather substantially increased the probability of resprouting in both species (Table 3).

Plant response over time (2020–2024)

Using only the 116 shrubs observed in all three assessment years, responses varied notably over time,

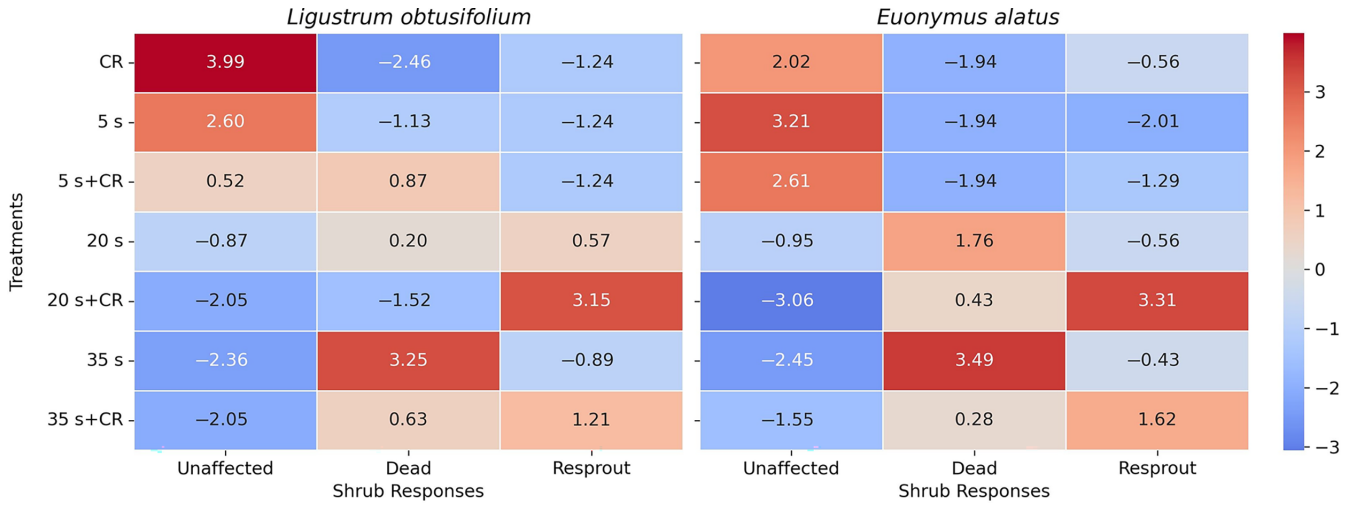


FIGURE 5 Heatmap of adjusted standardized residuals from the chi-square test, showing deviations between observed and expected shrub responses by treatment. Values exceeding the Bonferroni-corrected critical *z* value ($|z| \geq 3.038$) are statistically significant. Positive residuals indicate higher-than-expected frequencies; negative values indicate lower-than-expected frequencies.

indicating delayed mortality effects of the heating treatments. In 2020, approx. 91% of *E. alatus* were found to be live, while 9% showed signs of mortality. In contrast, *L. obtusifolium* exhibited higher initial top-kill, with 65% unaffected and 35% appearing dead, indicating greater initial sensitivity to heating treatments. By 2021, top-kill responses became more evident in *L. obtusifolium* (65%) compared to *E. alatus* (39%). About 17% of *E. alatus* were dead and 22% resprouted, while 37% of *L. obtusifolium* were dead and 29% resprouted.

By 2024, mortality dramatically increased for both species across most treatments, particularly under high-intensity heating (20–35 s and combinations with crown heating), where nearly all shrubs died (Figure 6). Treatments that caused minimal mortality in 2021 (e.g., 5-s and CR) also showed little delayed impact by 2024. *E. alatus* showed a sharp increase in mortality from 17% in 2021 to 52% in 2024, along with a significant decline in resprouting, indicating strong delayed mortality effects and limited post-fire recovery (Figure 7). In contrast, *L. obtusifolium* exhibited a more gradual rise in mortality (37% in 2021 to 44% in 2024) and only a slight decline in resprouting over time, suggesting greater post-fire resilience. These patterns suggest that while some fire-induced mortality occurs immediately, a significant proportion of shrub mortality may occur gradually over time, especially following more intense or combined heating treatment.

DISCUSSION

Our findings demonstrate distinct responses of two invasive shrub species (i.e., *L. obtusifolium* and *E. alatus*) to

TABLE 3 Multinomial logistic regression results showing the effects of heating duration, crown heating, and stem diameter on shrub mortality and resprouting for *Ligustrum obtusifolium* and *Euonymus alatus* (reference level is unaffected shrubs).

	Dead			Resprout		
Variables	**Coefficient**	**SE**	***p***	**Coefficient**	**SE**	***p***
L. obtusifolium ($n = 95$)						
Heating duration (s)	0.260	0.059	**<0.001**	0.235	0.057	**<0.001**
Crown heating[a]	0.735	0.797	0.357	1.518	0.728	**0.037**
Stem diameter (mm)	−0.186	0.076	**0.014**	−0.154	0.069	**0.026**
Constant	−0.639	1.084	0.555	−0.420	1.000	0.674
E. alatus ($n = 102$)						
Heating duration (s)	0.129	0.031	**<0.001**	0.099	0.027	**<0.001**
Crown heating[a]	−0.437	0.679	0.52	1.640	0.743	**0.027**
Stem diameter (mm)	−0.092	0.041	**0.026**	−0.150	0.045	**0.001**
Constant	−1.061	1.240	0.392	0.008	1.192	0.995

Note: Bold indicates singificant variables at 5% alpha level.
[a]Crown heating included basal + crown and crown only treatments.

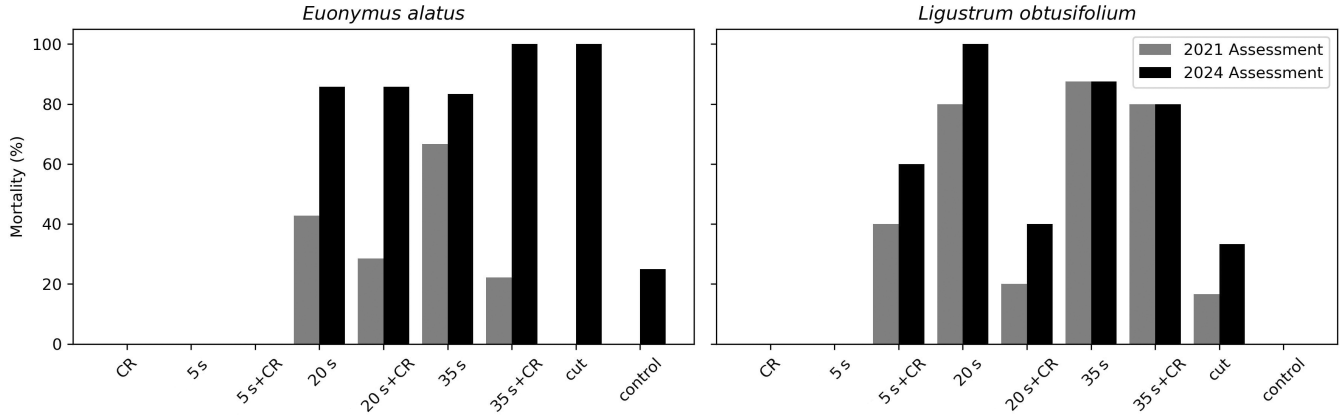


FIGURE 6 Mortality of *Euonymus alatus* (burning bush) and *Ligustrum obtusifolium* (border privet) one year following torching experiments (2021) as well as delayed mortality assessed four years following treatments (2024).

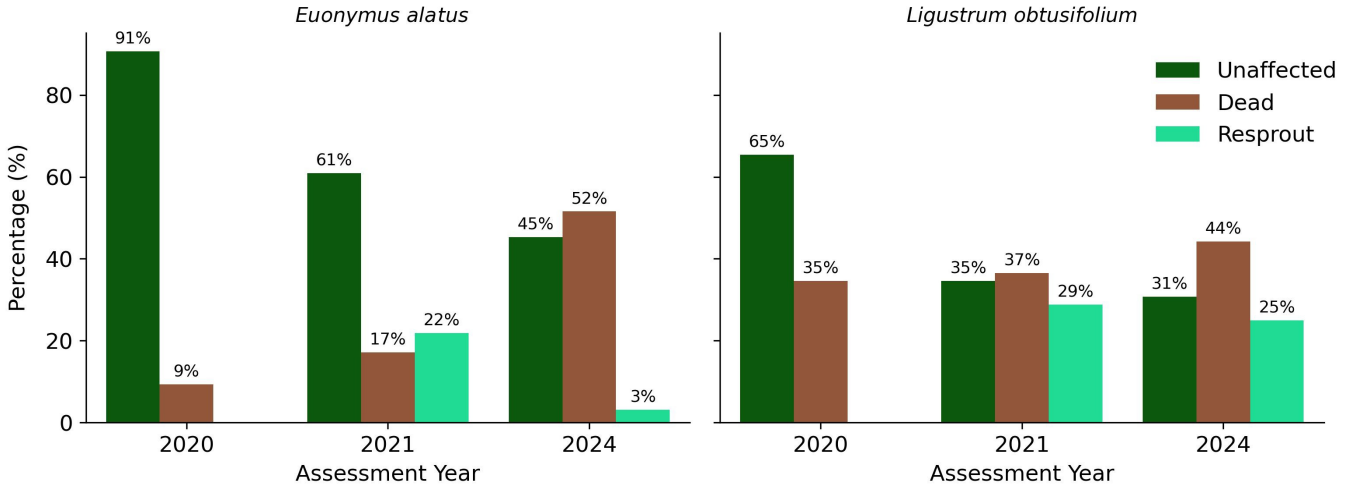


FIGURE 7 Shrub mortality assessments following heating treatments. The first assessment was conducted 1–6 months post-burning (June 2020), the second at one year post-burning (May 2021), and the third at four years post-burning (December 2024). This graph is based on shrubs whose tags were recovered in each of the three assessment years ($n = 116$).

different levels of fire-induced heat damage, revealing species-specific variations in fire tolerance, mortality, and resprouting behavior. *E. alatus* showed a strong resistance to initial fire damage but exhibited limited ability to recover once injured. In contrast, *L. obtusifolium* was more readily damaged by heat but compensated through vigorous post-fire resprouting. These distinct response patterns have important implications for the strategic use of fire as a management tool in controlling invasive woody species.

The findings reveal that heating duration was the most influential factor affecting shrub post-treatment responses in both species. *E. alatus* and *L. obtusifolium* each showed significantly higher mortality with increasing heat exposure time. This is likely because the longer heat exposure causes greater and deeper tissue damage, surpassing the thermal tolerance thresholds of stem and vascular tissues, and ultimately leading to increased post-fire mortality (Bova & Dickinson, 2005; Hood et al., 2018). This finding indicates the importance of fire duration, that is, "residency time," in shaping shrub dynamics in fire-managed systems.

Interestingly, we observed lower mortality when crown heating was combined with basal heating compared to basal heating alone (Figure 4). This pattern reflects potential competing physiological mechanisms between direct tissue damage and auxin-mediated bud activation. Basal heating alone targets vascular tissues in the lower stem and root crown, where extended heat exposure causes phloem and xylem necrosis, disrupting resource transport and increasing mortality (Bova & Dickinson, 2005; Hood et al., 2018; Michaletz & Johnson, 2007). However, apical buds remain intact, maintaining auxin suppression of basal buds. Intact crowns may continue photosynthetic activity, diverting limited post-fire resources to maintain stressed foliage rather than fueling resprouts, which can reduce recovery and increase mortality under severe stress (Bond & Midgley, 2001; Leyser, 2005). When crown heating is added, apical buds are destroyed, eliminating the main source of auxin and breaking the hormonal suppression of basal buds (Bond & Midgley, 2001; Clarke et al., 2013). This dual disturbance not only damages tissues but also may trigger activation of dormant basal meristems, resulting in increased resprouting despite compounded stress at both the crown and base (Clarke et al., 2013; Pausas & Keeley, 2014). This suggests that crown heating triggers a survival prioritization mechanism, where auxin redistribution from damaged apical regions may override localized basal injury signals.

Species responses to fire treatments differed significantly over time, revealing important implications for invasive shrub management. *E. alatus* exhibited a sharp increase in mortality between 2021 and 2024, alongside a substantial decline in resprouting capacity. This suggests that *E. alatus* is highly susceptible to delayed fire-induced mortality, potentially due to cumulative stress or damage to root systems that is demonstrated over time. In contrast, *L. obtusifolium* showed a more gradual increase in mortality and maintained a relatively higher level of resprouting across assessments. This pattern indicates a stronger post-fire resilience in *L. obtusifolium*, which may allow it to persist or recover unless fire treatments are repeated or combined with other control measures. These findings support the potential ecological benefits of fire in the eastern United States, where controlling invasive species is a primary management concern (Regmi et al., 2024).

CONCLUSIONS

Our findings reveal that burning could be a plausible non-chemical method for controlling invasive shrubs; however, response to heat injury depends on both the duration of heating and the specific location where heating was applied. In both *E. alatus* and *L. obtusifolium*, foliar scorch alone had minimal impacts on shrubs, while basal heating resulted in greater mortality. Longer duration of basal heating increased mortality, unsurprisingly; however, combining crown scorch with basal heating actually reduced mortality and resulted in a higher probability of sprouting. This finding indicates that while combined damage may control top growth, it is less effective for the complete removal of these invasive species. *L. obtusifolium* was more sensitive to initial heat, but demonstrated stronger post-fire resilience through vigorous resprouting. *E. alatus* tolerated fire better initially, but was more susceptible to delayed mortality. A better understanding of the physiological mechanisms underlying the response of shrubs to varying heat damage would not only help elucidate how species vary in sensitivity or tolerance to fire but also enable fire managers to more effectively utilize prescribed fire. For instance, increasing the residency time rather than intensity (e.g., by using backing fire) may offer the greatest potential for reducing shrub persistence. Follow-up monitoring, however, is essential, as delayed mortality can occur. Targeted fire application provides a practical, scalable approach to managing invasive shrubs in sensitive ecosystems, especially where chemical use may not be desired.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Regmi & Kreye, 2025) are available from Scholarsphere: https://doi.org/10.26207/qnh8-7v85.

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