



Controlling noxious weeds in urban riparian wetlands: non-selective mowing increases *Sicyos angulatus* invasion while controlling *Humulus scandens*

Minwoo Oh¹ · Chaeho Byun² · Minki Hong¹ · Yoonjeong Heo³ · Jaesang Chung⁴ · Hojeong Kang⁵ · Eun Ju Lee³

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Abstract

Invasive plant species pose major challenges to riparian wetland management. We conducted a pilot-scale field experiment over a single growing season to assess how non-selective mowing and subsequent sowing affected two noxious vines, *Sicyos angulatus* and *Humulus scandens*, in an urban riparian wetland in the Republic of Korea. Mowing paradoxically increased invasion by *S. angulatus* but decreased invasion by *H. scandens*, while sowing after mowing had no additional effect. This differential response indicates that non-selective mowing can shift invasion pressure rather than reduce it, emphasizing the need for species-specific, phenology-based mechanical management rather than uniform disturbance regimes. Mowing temporarily increased species richness and diversity, but the effect diminished over time, and community composition shifted toward species with heavier seeds and lower specific leaf area. Our results highlight that non-selective mowing for invasive species management should be applied with caution, as it can produce species-specific and even contradictory effects.

Keywords Biotic resistance · Functional traits · Invasive species management · Multi-species invasion · Riparian wetland management

Introduction

Invasive alien plants pose serious ecological and management challenges because they can alter community composition (Xu et al. 2022), nutrient cycling (Raheem et al. 2024), and hydrological processes (van Oorschot et al. 2017), thereby reducing native biodiversity and ecosystem functioning. Riparian wetlands are particularly vulnerable to invasion due to frequent anthropogenic (Ehrenfeld 2008; Park et al. 2019) and hydrological disturbances (Magee and Kentula 2005; Wang et al. 2022), and the high connectivity of propagule dispersal along waterways (Schmiedel and Tackenberg 2013; Hoppenreijns et al. 2025).

Most previous control studies have focused on single-species invasions (Brandt et al. 2023), testing mechanical (Ramula 2020), chemical (Hinkson et al. 2024), or biotic resistance-based (Byun and Lee 2018) strategies in isolation. However, in real-world riparian ecosystems, multiple invasive species often co-occur, and management actions targeting one species may inadvertently promote another. Such

Minwoo Oh and Chaeho Byun contributed equally to this work as co-first authors.

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✉ Eun Ju Lee
ejlee@snu.ac.kr

¹ National Institute of Ecology, Seoecheon 33657, Republic of Korea

² Department of Biological Sciences, Gyeongbuk National University, Andong 36729, Republic of Korea

³ School of Biological Sciences, Seoul National University, Seoul 08826, Republic of Korea

⁴ Department of Agriculture, Forestry and Bioresources, Seoul National University, Seoul 08826, Republic of Korea

⁵ School of Civil and Environmental Engineering, Yonsei University, Seoul 03722, Republic of Korea

contradictory outcomes remain poorly understood, representing a key knowledge gap in invasion ecology. Although the biotic resistance theory predicts that increased resident plant biomass or diversity suppresses invaders (Byun et al. 2018, 2023), its applicability under multi-invader interactions has rarely been tested under field conditions.

In this study, we investigated whether non-selective mowing (with and without sowing native and crop species) could reduce the dominance of two co-occurring noxious vines, *Humulus scandens* (Lour.) Merr. (native but noxious) and *Sicyos angulatus* L. (invasive), in riparian wetlands. Although these two species co-occur, they differ markedly in phenological and functional traits (e.g., germination timing, reproductive phenology, and seed characteristics), which are likely to underlie differential responses to identical management interventions.

It should be noted that this study was not designed as a restoration trial, but rather as an ecological field experiment aimed at understanding species-specific responses to multi-species management interventions in invaded riparian wetlands.

Previous studies have shown that non-selective mowing can reduce invasive plant biomass, but its effectiveness strongly depends on species-specific traits, such as phenological timing (Milakovic et al. 2014; Zhang and Shea 2019). In addition, previous greenhouse experiments have shown that seed sowing can suppress biomass accumulation of *S. angulatus* through increased competitive pressure (Byun et al. 2020). However, in particular, differences in post-disturbance regeneration strategies among invasive species can lead to contrasting responses to the same management intervention (Anfang et al. 2020).

Based on these previous findings, we expected that non-selective mowing and subsequent seed sowing would differentially affect the two target vine species according to their life-history traits and regeneration strategies. Specifically, we hypothesized that (1) non-selective mowing and seed sowing would reduce the aboveground biomass of both target species, (2) the combined treatment (mowing+sowing) would enhance suppression relative to either treatment alone—potentially through increased competition from other plants, and (3) both species would respond with differing magnitudes, reflecting their phenological and functional divergence. By explicitly comparing two target species with contrasting life-history strategies within a unified experimental framework, this study provides new insights into the mechanistic basis of biotic resistance and the potential for unintended outcomes in multi-species invasion management.

Materials and methods

Study site description

The study was conducted in a riparian wetland along the Han River (37°34'25.09"N, 126°51'49.03"E) in Sangam-dong, Mapo-gu, Seoul, the Republic of Korea. The site was chosen based on prior-year observations indicating dominance by *S. angulatus* and *H. scandens* (plant coverage > 70%). The site experiences a temperate monsoon climate, with a mean annual temperature of 13.5 °C and mean annual precipitation of approximately 1,273 mm, concentrated from June to September (30-year average, 1991–2020; Korea Meteorological Administration 2023). The wetland is situated within a Han River riparian wetland park managed as part of an urban waterfront park system. Dominant resident vegetation includes *H. scandens*, *S. angulatus*, *Calystegia hederacea* Wall., *Galium spurium* L., *Phragmites australis* (Cav.) Trin. ex Steud., *Chenopodium album* L., *Mentha canadensis* L., and *Vicia sativa* L., which are typical of urban riparian communities in the region. The site is representative of urban riparian wetlands along the Han River, where regular mowing and vegetation maintenance are commonly conducted for flood control in nearby managed park areas. However, the experimental plots were established in an unmanaged section adjacent to the riverbank, where public access is restricted and no mowing or vegetation maintenance occurs. This unmanaged condition allowed us to observe vegetation responses without direct human disturbance.

Target species

Humulus scandens is a fast-growing annual vine native to East Asia (Ohwi 1965; Zhou and Bartholomew 2003). It was first introduced to Europe and North America as an ornamental plant, where it became naturalized and even an invasive species (Small 1978; Tutin et al. 1993; Meyers-Rice 1999; Balogh and Dancza 2008). It grows in floodplains and is mainly distributed along riversides (Balogh and Dancza 2008). The ecological traits of *H. scandens* include a dense canopy, vines, and a high growth rate, which facilitate its ability to outcompete other native species in invaded areas, where it threatens native biodiversity. It can also cause pollen allergies with potentially harmful effects on human health (Park et al. 1999). It is regarded as a native species in the Republic of Korea, but it is a controlled species under the management of the Ministry of the Environment. Its seedlings emerge between March and April (Song et al. 2010), grow maximally in July, and stop growing toward the end of August. This species also exhibits weak seed dormancy and a high germination rate (Schulz and Clark 2022). *Sicyos angulatus* is another annual vine and an invasive alien

species in the Republic of Korea. It was introduced prior to 1989 and was used as a rootstock plant for grafting cucumber (Lee et al. 1991). While it usually prefers wet habitats, it is a generalist plant species that occurs even in forests (Jung et al. 2017). The flowering season is from June to September (Bang 2014). It is native to North America but is now found in Europe, Australia, the Caribbean region, and Northeast Asia. It is usually found along riverbanks and roadsides (Kil et al. 2005), and its seeds are dispersed by rivers (Uchida et al. 2012). Like *H. scandens*, it is also a vine, but employs a different mechanism to climb over other plants. *H. scandens* uses stiff downward-pointing hairs along its stem to climb on other plants, whereas *S. angulatus* uses tendrils with 3 to 4 branches coiled in two opposite directions, the tension of which contributes to strong but flexible climbing behavior (Gerbode et al. 2012). It covers vegetation and reduces the light received by understory vegetation by one-fifth (Kil et al. 2005). It continuously germinates during the growth season, has a high fruit set (98%), produces a large number of seeds per plant (150–200), and shows rapid seedling growth from the seed bank (Kil et al. 2005) after it is removed. Additionally, it blooms at the end of July, soon after seedlings are found at the end of May; this short life cycle makes it even more difficult to prevent, control, and eliminate (Kil et al. 2005). It also possesses strong combinational dormancy (both physical and physiological), which contributes to its persistence in the soil seed bank (Qu et al. 2012).

Experimental design and data sampling

A randomized complete block design was used in this study. The invaded area was divided into three blocks, each containing three treatment plots (control, mowing, and mowing+sowing) with four replicates per block, resulting in 36 plots in total. All treatments were conducted in 3 m × 3 m square plots in June 2019. Within each 3 m × 3 m plot, a 1 m × 1 m subplot located near the center was designated as the sampling unit for aboveground biomass harvest, to minimize edge effects and ensure consistent sampling among plots. This hierarchical structure (block → plot → subplot) is illustrated in Fig. S1 to clarify the experimental layout and the smallest unit of replication.

A hand-operated, butane-powered mowing machine (Mitsubishi TL231, equipped with a dual nylon-line cutter) was used to remove the vegetation of all species, including that of both resident species and the two target noxious species in each plot. After mowing, all aboveground vegetation and surface litter were removed to reduce potential soil legacy effects (Schuster et al. 2018), while belowground root materials were left undisturbed. Six species were sown following the removal of vegetation, including *Zea mays*

(crop), *Secale cereale* (crop), *Trifolium repens* (cover crop), *Pennisetum alopecuroides* (native), *Lespedeza cuneata* (native), and *Lespedeza bicolor* (native). These species were chosen based on previous results of 1:1 competition greenhouse studies investigating the invasive species *Ambrosia trifida* L. and *S. angulatus* (Byun and Lee 2018; Byun et al. 2020b).

The seed mixture used in this field experiment was composed of six representative species selected from the broader pool of species used in the previous greenhouse experiments (Byun et al. 2020b). Building upon the insights gained from those controlled experiments, this study aimed to examine species-specific responses to multi-species management interventions under realistic field conditions where multiple invaders co-occur, rather than to evaluate restoration success. Thus, the mixture served as an ecological tool for simulating competitive pressure under realistic riparian conditions, not as a restoration treatment.

The six species used for sowing were selected to represent a gradient of competitive strategies and ecological relevance to riparian restoration. The first two species, *Z. mays* and *S. cereale*, are annual herbaceous plants included as short-lived benchmark crops, representing highly competitive (Byun et al. 2020b) but non-persistent species used as reference standards for evaluating biotic resistance to invasive vines. These species are not naturalized in Korea (Kang et al. 2020) and show limited long-term adaptation to riparian conditions, which makes them suitable for short-term competitive testing while posing minimal risk of establishment. All crop individuals were removed before seed set to prevent unintended propagation.

The third species, *T. repens*, is a perennial herbaceous legume included as a cover crop species, widely used in restoration and erosion control practices (Ogle and St. John 2008). Although non-native, it was introduced to Korea before 1911 and has long been naturalized throughout the country (Jung et al. 2017). It is commonly used as a forage and ground-cover plant and frequently occurs along riparian and semi-wetland habitats (Huh 2017). While it can locally dominate riparian wetlands, it has not been classified as an ecosystem-disturbing or invasive alien species under the Ministry of Environment, the Republic of Korea. This regulatory status reflects that current ecological risk assessments consider its competitive impact to be limited and its overall ecological risk to be low in managed environments.

The remaining three native species—*P. alopecuroides* (perennial herbaceous grass), *L. cuneata* (woody legume), and *L. bicolor* (woody legume)—are ecologically suited to riparian habitats. *P. alopecuroides* and *L. bicolor* occur in riparian wetlands and tolerate periodic inundation (Lee et al. 2025); *P. alopecuroides* has been shown to form persistent communities on urban stream levee slopes following

restoration (Yang 2014). *L. bicolor* has also been applied in riparian restoration projects in Northeast China (Yu et al. 2014) and *L. cuneata* is known to successfully colonize riparian wetlands in the United States (DeBerry and Hunter 2024). In Korea, all three native species have been identified as potential candidates for revegetation of riverbank slopes (Cho et al. 2012). Furthermore, regular ecosystem monitoring by the Hangang River Basin Environmental Office (2023) has confirmed that *T. repens*, *P. alopecuroides*, *L. cuneata*, and *L. bicolor* co-occur with *S. angulatus* and *H. scandens* in riparian wetlands of the Han River. Therefore, the native species used in this study can be considered ecologically appropriate for riparian and levee restoration contexts in the study region.

Thus, the combination of native, cover, and benchmark crop species provides an ecologically rational framework for evaluating competitive and functional responses under mowing disturbance. In restoration contexts, the use of non-native but non-invasive species can also be justified when native species alone cannot provide sufficient competitive resistance against invasive plants or when introducing additional functional diversity may facilitate subsequent recovery processes (Schuster et al. 2018).

The seed density was 1,200 viable seeds per plot per species (7,200 viable seeds per plot for a total of six species, i.e., 800 viable seeds per square meter). This density was selected based on practical restoration experience representing typical restoration seeding rates used in similar field settings, and its adequacy was later supported by a greenhouse competition experiment with *S. angulatus* showing biomass suppression at comparable densities (Byun et al. 2020b). We recognize that this rate may not be optimal for achieving maximal biotic resistance, but consider it ecologically reasonable and operationally feasible for field implementation. The number of viable seeds (i.e., pure live seeds) was predetermined by germination tests conducted on representative samples (100 seeds $\times$ 3 replicates per species) following the protocol described in previous studies (Byun 2022, 2023a, b; Byun et al. 2022).

Plant cover (%) was surveyed for all plant species within each plot to calculate diversity indices. Plant cover was visually estimated by ocular observation as the proportion of ground area occupied by each species when viewed vertically from above, following the definition of “species cover” (Fehmi 2010). The surveys were conducted two to three weeks after the treatments (late June) and repeated in July and October of the same year to capture seasonal changes in vegetation structure.

These three surveys were conducted to capture the temporal dynamics of vegetation responses to the treatments. The first survey (late June, approximately 2–3 weeks after treatment) focused on the initial recruitment of the sown

seed mixture and early regeneration of the target species. The second survey (July) aimed to record additional seedling recruitment and establishment, as sequential recruitment events are common in disturbed riparian wetlands. The third survey (October) was performed immediately before harvest to assess the final vegetation structure and biodiversity, reflecting the cumulative outcomes of the treatments over the growing season.

Additionally, the densities of newly germinated *S. angulatus* seedlings were determined to assess their early recruitment response after the treatments. In contrast, *H. scandens* seedlings were not recorded because no new seedling emergence was observed after treatment; instead, we observed clear vegetative resprouting from basal stem nodes that survived mowing. *H. scandens* primarily regenerates vegetatively from these basal nodes, and its seed germination mostly occurs in early spring (March–April) before June (Song et al. 2010), which explains the absence of seedling emergence during our survey period. Meanwhile, *S. angulatus* germinates continuously throughout the growing season and rapidly recruits from the soil seed bank after canopy removal (Kil et al. 2005). The seedling survey thus reflected the initial recruitment response of *S. angulatus* from the existing soil seed bank after vegetation removal.

Although the pre-treatment soil seed bank was not directly quantified, the randomized complete block design (RCBD) minimized the influence of potential spatial heterogeneity such as seed density, soil moisture, nutrients, light availability, or microtopography. Because treatments were randomly assigned within each block, such unmeasured variability was orthogonalized to treatment effects, allowing valid comparisons of vegetation recovery even without explicit seed bank data. Additionally, four replicates per control and treatment level within each block were established to account for fine-scale heterogeneity typical of riparian wetlands.

The aboveground biomass was harvested in October 2019, when both *S. angulatus* and *H. scandens* had reached their maximum vegetative growth but before visible senescence. This period corresponded to the fruiting stage for *S. angulatus*, which flowers from June to September and begins senescence with temperature decline in late October (Bang 2014; Kil et al. 2005). The timing, therefore, represented the end of the growing phase and the peak of standing biomass. The aboveground biomass was collected within a 1 m $\times$ 1 m subplot per 3 m $\times$ 3 m plot, located near the center to minimize edge effects from surrounding vegetation. A smaller subplot was used instead of harvesting the entire plot due to practical limitations in handling and dry oven capacity, while ensuring representative sampling of each treatment. Harvested biomass was divided into that of *S. angulatus*, *H. scandens*, and other plants, dried at 80 °C for 48 h, and

weighed. Reproductive structures (fruits and seeds) were not separately collected, as the focus of this study was on vegetative biomass and competitive interactions.

This experiment was conducted over a single growing season (June–October 2019) as a pilot-scale field trial designed to capture short-term vegetation responses to mowing and sowing. Consequently, the findings represent short-term ecological patterns and may not fully reflect long-term successional or interannual dynamics.

Statistical analysis

We analyzed treatment effects on vegetation responses using a series of Analysis of Variance (ANOVA) and Analysis of Covariance (ANCOVA) models within a randomized complete block design (RCBD). Blocks were treated as fixed factors because they were deliberately established within a single study site rather than randomly sampled from a broader region (Dixon 2016; Frey et al. 2024). In balanced RCBDs without block $\times$ treatment interactions, fixed- and random-effect modeling of blocks yield identical treatment estimates (Ganju 2000; Dean et al. 2017). However, when the number of block levels is small ($n=3$), random-effect modeling can produce unstable parameter estimates (Bolker et al. 2009; Harrison 2015). Therefore, treating blocks as fixed effects was both statistically sound and experimentally appropriate in this study.

The aboveground biomasses of all harvested plants, including *S. angulatus* and *H. scandens*, were initially analyzed with block effects included in the model. However, because the block effect was not significant and its removal improved model fit, the final analysis was conducted using one-way ANOVA with treatment as a fixed factor.

To separate treatment effects from competition effects of other plants, we then fitted a two-way ANCOVA model to the aboveground biomass of *S. angulatus*, using the biomass of all other plants as a covariate and treatment and blocks as fixed factors. The model was specified as:

$$AGB_{ij} = \mu + \tau_i + \beta AGB_{others, ij} + \gamma_j + \epsilon_{ij}$$

where AGB_{ij} is aboveground biomass of target species specific to treatment i and block j ; μ is the grand mean; τ_i is the fixed effect of treatment i ; β is the regression coefficient for the covariate (biomass of other plants); $AGB_{others, ij}$ is the aboveground biomass of all plants other than the target species in treatment i and block j ; γ_j is the fixed effect of block j ; ϵ_{ij} is the residual error term in each experimental unit (combination of block and treatment).

The aboveground biomass of other plants was included as a covariate to account for the simultaneous competitive influence on *S. angulatus* aboveground biomass, rather than

as a mediating variable. In contrast, seedling density of *S. angulatus* was excluded because it is strongly influenced by treatment (i.e., mowing), and including it would partition the total treatment effect into indirect components, thereby obscuring causal inference.

To further disentangle these relationships, we analyzed the seedling density of *S. angulatus* separately to assess its independent response to treatments and its potential influence on subsequent biomass production. Seedling density measured a few weeks after treatment was compared across treatments and blocks using two-way ANOVA. To complement this analysis and test whether early recruitment of *S. angulatus* seedlings contributed to its later dominance, we performed correlation and partial correlation analyses between seedling density and harvest biomass. These analyses directly evaluated the linkage between early regeneration and end-of-season biomass accumulation, clarifying the causal chain between mowing-induced seedling emergence and subsequent dominance of *S. angulatus*.

The effects of treatments on the aboveground biomass of *H. scandens* were also analyzed using the same method as for *S. angulatus*, except that seedling density was not examined because no new seedlings emerged after treatment.

The species richness, Shannon's diversity index ($H' = -\sum p_i \ln p_i$), and Simpson's diversity index ($1 - D = 1 - \sum p_i^2$) over time at each level of the treatment were assessed using a two-way ANOVA with treatment and block as fixed factors. Here, p_i denotes the proportional abundance of the i th species, and relative cover was used as a measure of species abundance. Coverage data were selected because vegetation surveys were conducted repeatedly during the growing season to capture temporal changes in community diversity, whereas biomass measurements require destructive sampling and thus cannot be performed multiple times within the same plots. While coverage effectively reflects spatial dominance, it may overestimate the contribution of climbing species with extensive canopy spread relative to their actual biomass.

For all ANOVA and ANCOVA models, when the treatment factor was significant, pairwise comparisons among treatment levels were conducted using Tukey's honestly significant difference (HSD) test implemented in the *emmeans* package (version 1.5.4; Lenth 2021) to control for family-wise Type I error and to obtain treatment-level adjusted means (i.e., model-based means accounting for covariates and the block factor) for post hoc comparisons and visualization of group differences. The relative importance of explanatory variables was calculated by averaging sequential sums of squares over all possible orderings of variables (Lindeman et al. 1980) using the *relaimpo* package (version 2.2.3; Grömping 2006).

The functional trait shift of the community by treatment was determined by community weighted mean (CWM) trait values. As for the functional traits, dry seed mass, plant height vegetative, specific leaf area (SLA), and leaf dry matter content (LDMC) of all species that appeared in the plots were collected from the TRY database (Kattge et al. 2020). The collected trait values were averaged by reference first, and the median was calculated among different references. Missing values were imputed by means of genus trait values wherever possible (Table S1). The CWM trait matrix (plot $\times$ CWM trait) was calculated by matrix multiplication of the relative percent cover matrix (plot $\times$ species) and the trait matrix (species $\times$ trait).

Because *S. angulatus* lacked reliable LDMC data even after genus-level imputation, and CWM SLA and LDMC were highly correlated (Pearson $r=0.63$), only SLA was retained in the final analysis. Principal component analysis (PCA) was performed on the standardized CWM trait matrix, and the results were visualized using a biplot. To assess the robustness of excluding LDMC, we conducted sensitivity analyses confirming that the overall ordination structure and interpretation remained consistent even when LDMC (which had a higher imputation frequency) was included (see Fig. S2 and Supplementary Methods for detailed sensitivity analyses).

Although species-level trait data were primarily obtained from the TRY database (Kattge et al. 2020), not all species

occurring in the plots had complete records for all traits. To minimize data loss, missing values were imputed using genus-level means when species-level data were unavailable. This approach follows common practice in community trait-based analyses, as genus-level averages generally capture phylogenetically conserved trait patterns while maintaining reasonable comparability among taxa. However, we acknowledge that this imputation introduces additional uncertainty, particularly for traits that are more variable within genera (e.g., SLA). Consequently, the functional trait analysis should be interpreted as representing general patterns of community-level trait shifts rather than precise species-specific trait values.

All the analyses and graphics were performed in R 4.3.0 (R Core Team 2023).

Results

The effect of mowing and sowing seed mixtures on the biomass of *S. angulatus* and *H. scandens*

The total aboveground biomasses among three levels of treatment (control, mowing, and mowing+sowing) were compared (Fig. 1a). The total aboveground biomasses of all harvested plants (mean $\pm$ SE) were not significantly different between the treatments (control: 383.0 ± 28.2 g DW

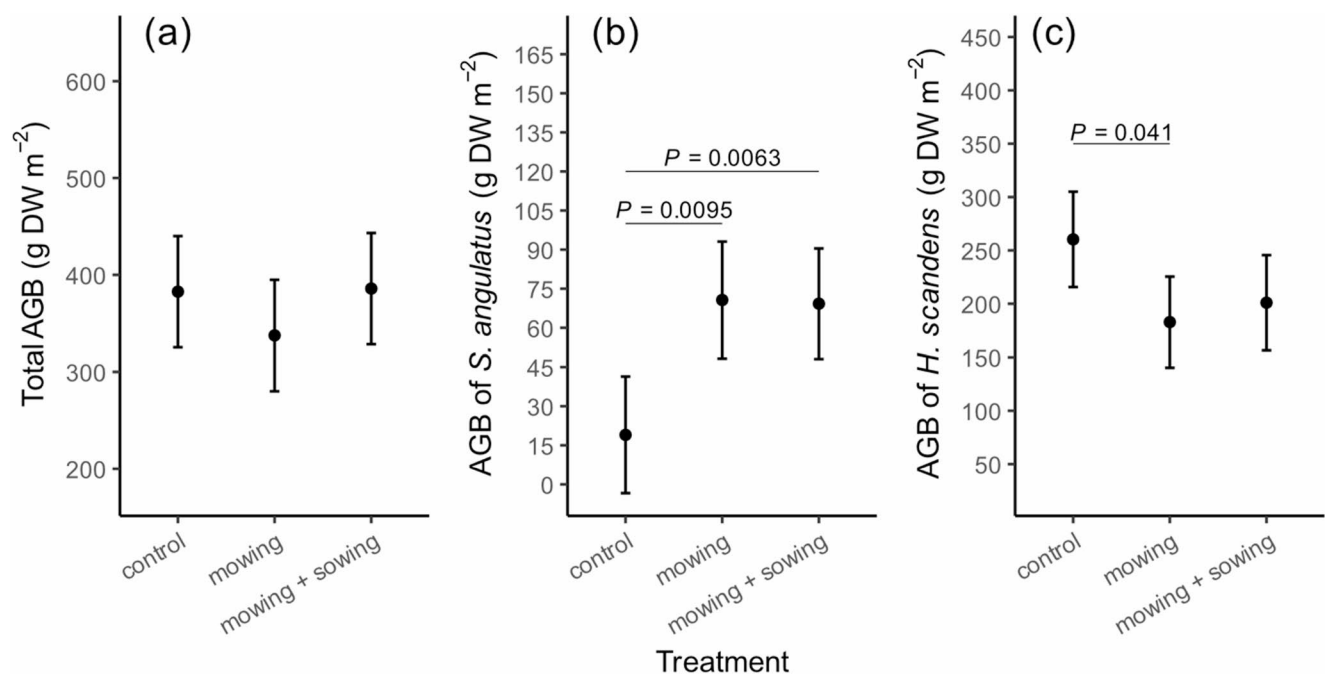


Fig. 1 Aboveground biomass (AGB) of (a) all harvested plants, (b) *Sicyos angulatus*, and (c) *Humulus scandens*. Filled circles indicate adjusted means with 95% confidence intervals. Pairs with significant differences are connected by horizontal solid lines, with adjusted *P*-values indicated above them. In panel (a), *P*-values are derived from

Tukey's HSD post hoc comparisons following a one-way ANOVA. In panels (b) and (c), *P*-values are derived from Tukey's HSD post hoc comparisons following two-way ANCOVA. AGB, aboveground biomass (g DW m⁻²); DW, dry weight

m^{-2} , mowing: $337.0 \pm 28.2 \text{ g DW m}^{-2}$, mowing+sowing: $386.0 \pm 28.2 \text{ g DW m}^{-2}$; $F_{2,33} = 0.917$, $P = 0.409$).

The aboveground biomasses of *S. angulatus* and *H. scandens* were then analyzed separately while accounting for block effects and the aboveground biomasses of all the other plants (Table S2; Fig. 1b–c). Importantly, these species showed opposite responses to mowing.

The aboveground biomass of *S. angulatus* (mean $\pm$ SE) was $19.0 \pm 11.0 \text{ g DW m}^{-2}$ in the control plots, $70.7 \pm 11.0 \text{ g DW m}^{-2}$ in the mowing plots, and $69.2 \pm 10.4 \text{ g DW m}^{-2}$ in the mowing+sowing plots (Fig. 1b). On average, *S. angulatus* biomass increased by 272% (mean difference = 51.7 g DW m^{-2} , $t(30) = 3.17$, $P = 0.0095$; Tukey's HSD) in the mowing plots and by 264% (mean difference = 50.2 g DW m^{-2} , $t(30) = 3.33$, $P = 0.0063$; Tukey's HSD) in the mowing+sowing plots compared with the control, both representing statistically significant and large standardized effects (Cohen's $d = 1.16$ and 1.22 , respectively).

Conversely, the aboveground biomass of *H. scandens* (mean $\pm$ SE) was $260 \pm 21.9 \text{ g DW m}^{-2}$ in the control plots, $183.0 \pm 20.9 \text{ g DW m}^{-2}$ in the mowing plots, and $201.0 \pm 21.8 \text{ g DW m}^{-2}$ in the mowing+sowing plots (Fig. 1c). On average, *H. scandens* biomass was reduced

by 29.8% (mean difference = 77.5 g DW m^{-2} , $t(30) = 2.56$, $P = 0.041$; Tukey's HSD) in the mowing plots and by 22.8% (mean difference = 59.4 g DW m^{-2} , $t(30) = 1.84$, $P = 0.174$; Tukey's HSD) in the mowing+sowing plots compared with the control. The reduction in the mowing plots was statistically significant ($P = 0.041$), whereas the reduction in the mowing+sowing plots was not ($P = 0.174$), although both standardized effects were large (Cohen's $d = 0.93$ and 0.67 , respectively).

Together, these results indicate that mowing promoted the recruitment and dominance of *S. angulatus* while suppressing the regrowth potential of *H. scandens*.

The block effects were significant for both *S. angulatus* and *H. scandens* (Table S2), indicating that site-level environmental heterogeneity (e.g., soil moisture or microtopography) contributed to variation in biomass among blocks. However, because the randomized complete block design orthogonalized treatment assignment within blocks, these block effects do not confound the treatment effects. The biomass of other plants was a significant covariate only for *H. scandens*, showing a negative association between *H. scandens* biomass and the surrounding plant community. No significant interaction was found between treatment and block, or between treatment and the biomass of other plants.

Seedling density of *S. angulatus*

To explore the cause of the increased biomass of *S. angulatus* in the mowing and mowing+sowing plots, we compared the seedling density of *S. angulatus* after a few weeks of treatment (Fig. 2). The seedling density of *S. angulatus* (mean $\pm$ SE) was $1.36 \pm 0.89 \text{ individuals m}^{-2}$ in the control plots, $4.86 \pm 0.89 \text{ individuals m}^{-2}$ in the mowing plots, and $7.72 \pm 0.89 \text{ individuals m}^{-2}$ in the mowing+sowing plots.

On average, seedling density of *S. angulatus* increased by 257% (mean difference = $3.5 \text{ individuals m}^{-2}$, $t(31) = 2.77$, $P = 0.025$; Tukey's HSD) in the mowing plots and by 467% (mean difference = $6.4 \text{ individuals m}^{-2}$, $t(31) = 5.04$, $P = 0.000056$; Tukey's HSD) in the mowing+sowing plots compared with the control, both representing statistically significant and large standardized effects (Cohen's $d = 0.996$ and 1.81 , respectively).

Between the mowing and mowing+sowing plots, seedling density showed a considerable but non-significant increase (mean difference = $2.9 \text{ individuals m}^{-2}$, $t(31) = 2.27$, $P = 0.076$; Tukey's HSD; Cohen's $d = 0.814$), with relatively large variability among replicates. This indicates that sowing additional species did not hinder *S. angulatus* recruitment during the early post-disturbance phase, and that the observed variation was largely driven by stochastic differences in seed bank germination following mowing.

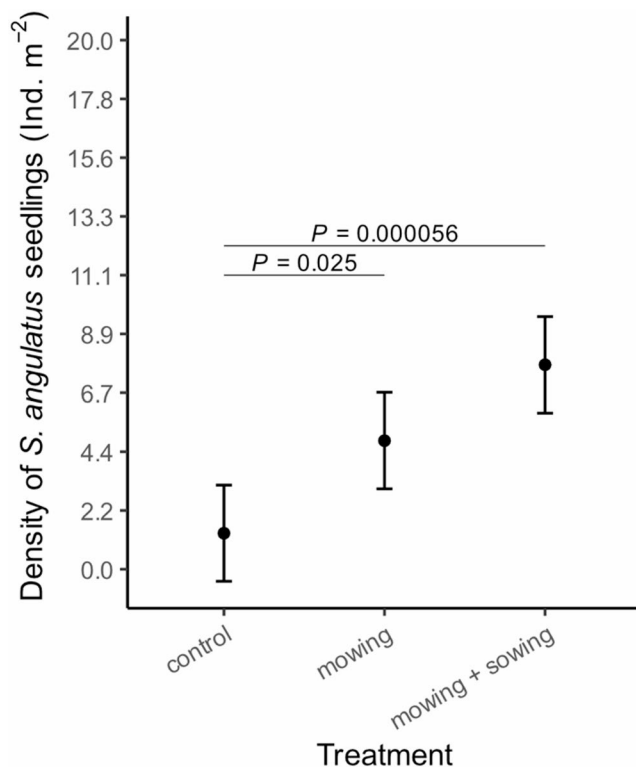


Fig. 2 Density of the seedlings of *Sicyos angulatus* a few weeks after each treatment. Filled circles indicate adjusted means with 95% confidence intervals. Pairs with significant differences are connected by horizontal solid lines, with adjusted P -values indicated above them. The P -values are derived from Tukey's HSD post hoc comparisons following two-way ANOVA. Ind., Individual

To further examine whether the surge in seedling density was associated with the subsequent increase in biomass, we analyzed the relationship between early-summer seedling density and final biomass of *S. angulatus*. The early-summer seedling density of *S. angulatus* was positively associated with its harvest biomass (Pearson $r=0.598$, $P<0.001$), and this relationship remained significant even after controlling for treatment and block effects (partial $r=0.407$, $P=0.014$), indicating that the association was not solely driven by treatment-level differences. These results support a recruitment-driven recovery pathway consistent with the species' continuous germination and persistent seed bank, suggesting that mowing-induced seedling proliferation directly contributed to the later increase in *S. angulatus* biomass.

Changes in biodiversity after mowing or mowing and sowing seed mixtures

In June, treatment significantly affected species richness ($F_{2,31} = 19.35$, $P<0.001$) (Fig. 3; Table S3). Species richness (mean $\pm$ SE) was highest in the mowing+sowing plots (11.1 ± 0.5), intermediate in control plots (9.8 ± 0.5), and lowest in the mowing plots (6.8 ± 0.5). Tukey's HSD tests (Table S4) showed that mowing significantly reduced species richness compared with the control (mean difference=3.0, $t(31)=4.20$, $P<0.001$) and with the mowing+sowing treatment (mean difference=4.33, $t(31)=6.07$, $P<0.001$).

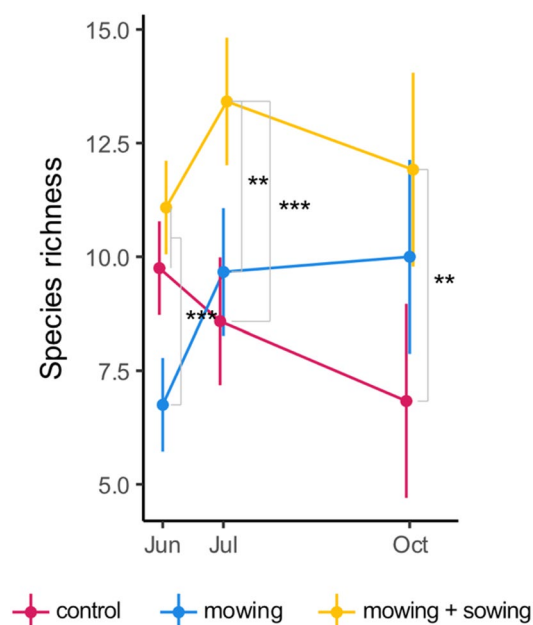


Fig. 3 Changes in species richness over time following each treatment. Filled circles indicate adjusted means with 95% confidence intervals. Pairs with significant differences are connected by vertical solid grey lines, with significance symbols indicated above them (* $P<0.05$, ** $P<0.01$, *** $P<0.001$). P -values are derived from Tukey's HSD post hoc comparisons following two-way ANOVA

In July, treatment still significantly affected species richness ($F_{2,31} = 13.59$, $P<0.001$) (Table S3). Species richness (mean $\pm$ SE) was 8.6 ± 0.7 for the control, 9.7 ± 0.7 for mowing, and 13.4 ± 0.7 for mowing+sowing plots. According to Tukey's HSD tests (Table S4), richness in the mowing+sowing plots was significantly higher than in both the control and mowing plots ($P\leq0.01$), indicating rapid recovery of diversity after sowing.

In October, treatment significantly affected species richness ($F_{2,31} = 6.03$, $P=0.006$) (Table S3). Species richness (mean $\pm$ SE) was 6.8 ± 1.0 for the control, 10.0 ± 1.0 for mowing, and 11.9 ± 1.0 for mowing+sowing plots. According to Tukey's HSD tests (Table S4), richness in the mowing+sowing plots was significantly higher than in the control plots ($P=0.0047$), indicating rapid recovery of diversity after sowing.

These results indicate that biodiversity initially declined following mowing but recovered rapidly by mid-season, whereas sowing caused a transient increase that diminished by autumn. The Shannon and Simpson diversity indices showed trends similar to species richness (Table S3-4; Fig. S3) and are therefore presented in the Supplementary Information.

The effect of mowing and sowing seed mixtures on CWM traits

PCA of CWM traits revealed clear shifts in community functional composition among treatments (Fig. 4). The first two principal components explained 92.3% of total variance (PC1=60.25%, PC2=32.06%). Plots from the mowing and mowing+sowing treatments were separated from the control plots mainly along PC2, reflecting trait syndromes associated with disturbance. In the mowing and mowing+sowing plots, SLA was smaller than in the control plots, but dry seed mass was higher. The virtual plot of *S. angulatus* is located above the mowing and mowing+sowing plots, in which the dry seed mass and SLA were high. On the other hand, the virtual plot of *H. scandens* is near the centroid of the control plots, in which dry seed mass was small to moderate, and SLA was relatively high.

Discussion

Differential effects of mowing on the biomasses of *S. angulatus* and *H. scandens*

Using the biomass of two noxious vines over one growing season, we found that the responses of the targeted species to mowing and mowing+sowing differed dramatically and in opposite directions. Total biomass remained unchanged

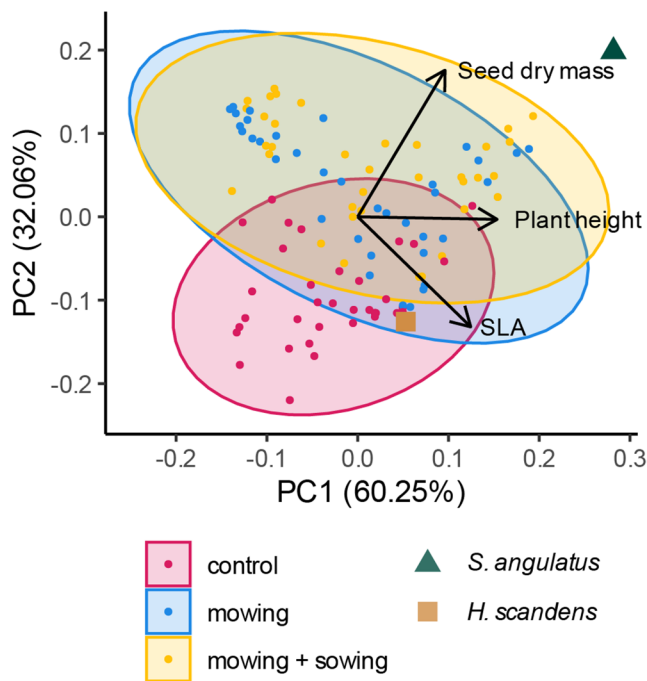


Fig. 4 Principal component analysis (PCA) biplot showing differences in community-weighted mean (CWM) traits among treatments. Each filled circle represents a plot surveyed in June, July, and October 2019. Ellipses indicate one standard deviation ($\approx 66\%$ confidence region) for each treatment group under a multivariate normal assumption. Loading vectors of dry seed mass, plant height, and SLA are overlaid. The filled triangle and square represent virtual plots composed solely of *S. angulatus* and *H. scandens*, respectively

after mowing or mowing+sowing. This pattern suggests that light and nutrient limitations within plots may have constrained overall productivity to a similar upper limit across treatments. However, community structure was largely affected. This presents a critical management challenge: the same treatment that reduces one invasive species (*H. scandens*) actually promotes the other (*S. angulatus*). The decrease in the biomass of *H. scandens* was attributed to limited regeneration from mowed shoots and depletion of its seed bank by June. On the other hand, the increase in biomass of *S. angulatus* was linked to an increase in the number of its seedlings after mowing or mowing+sowing, likely triggered by increased light availability following canopy removal.

These results support previous field findings on *S. angulatus* (Byun et al. 2025), which showed that sowing after mowing did not significantly enhance invasion suppression compared to mowing alone. The limited effectiveness of the seed mixture in our study likely reflects its low diversity and the use of species not fully adapted to the riparian environment.

It is important to note that the seed mixture in this study was not designed as a restoration treatment but as an experimental tool to simulate competitive pressure under realistic

riparian conditions. This field experiment builds upon previous greenhouse studies (Byun et al. 2020b, 2022) that tested the competitive suppression of *S. angulatus* under controlled conditions using a broader seed mixture. In the present study, we refined the experimental design by selecting a representative subset of six species from that mixture—two woody, two annual herbaceous, and two perennial herbaceous species—to capture distinct growth forms relevant to riparian vegetation. Furthermore, we extended the scope of the experiment by including an additional target species, *H. scandens*, thereby enabling a comparative evaluation of multi-species management responses among co-occurring invaders in a field setting.

The biomass of other plants was negatively correlated with the biomass of the two noxious vines, indicating that seed sowing of other plant species negatively affected the growth of the invasive species. However, the negative association was stronger for *H. scandens* than for *S. angulatus*, suggesting that *H. scandens* was more sensitive to interspecific competition. This pattern is consistent with its lower regrowth capacity after mowing, as *H. scandens* appeared to rely primarily on basal stem resprouting rather than recruitment from a persistent seed bank. However, since the soil seed bank was not directly quantified, this interpretation should be viewed as a plausible explanation rather than a confirmed mechanism. Additionally, block effects were notable, suggesting spatial heterogeneity in the abundance of the target species at the study site, which necessitated the use of blocking to accurately test treatment effects.

These results suggest that mowing changed the dominant plant species from *H. scandens* to *S. angulatus*. For managers, this means that the timing of mowing relative to species phenology is critical: early-season mowing (before *S. angulatus* germination) might be more effective, while late-season mowing (after *H. scandens* seed set) could prevent its regeneration.

A limitation of this study is that the reproductive output (e.g., seed yield) of *S. angulatus* was not quantified separately from vegetative biomass. Since reproductive capacity is a critical indicator of population persistence and invasion success, future studies should incorporate direct measurements of fruit and seed production across the full phenological cycle to assess the long-term effects of mowing on reproductive dynamics.

Promotion of *S. angulatus* germination by mowing

The seedling density of *S. angulatus* increased after mowing and mowing+sowing, which led to an increase in its aboveground biomass. The physical disturbance caused by mowing and canopy removal often triggers the germination of seed banks (D'Antonio and Meyerson 2002; Anfang et al.

2020); thus, although no additional post-germination control was implemented in this study, multiple rounds (Kettenring and Adams 2011) of effective mechanical control (e.g., hand-pulling or selective cutting of newly emerged seedlings) (Byun and Singh 2025) are recommended to prevent re-establishment and ensure the success of revegetation efforts. The combinational dormancy (physical and physiological) of *S. angulatus* seeds, previously documented by Qu et al. (2012), may contribute to the maintenance of a persistent seed bank reservoir. This dormancy likely allowed *S. angulatus* to persist and subsequently germinate soon after mowing in June.

Similar patterns have been reported for other invasive species. For instance, forestry mowing increased light availability and subsequently promoted the regeneration of the invasive shrub *Rhamnus cathartica* L. by enhancing seedling survival and growth (Anfang et al. 2020).

Mantoani and Osborne (2022) likewise observed that mechanical removal of *Gunnera tinctoria* (Molina) Mirb. led to an increase in seedling number; however, they also found that the regrowth of a native species and an extreme weather event, to which *G. tinctoria* was more vulnerable than the native species, helped to control its growth. In contrast to that study, our field experiment showed that sowing native and crop seeds was not sufficient to suppress reinvasion or enhance community recovery in the short term.

The emergence of *H. scandens* is predicted to start in the first week of April and to reach its maximum emergence rate within only 3–4 days in Seoul (Song et al. 2010). Because of this rapid and concentrated germination, *H. scandens* predominates in early spring and likely depletes most of its seed bank by June, resulting in reduced resilience to mowing after the germination period compared with *S. angulatus*.

A key limitation is the lack of direct seed bank data. Although RCBD minimized background heterogeneity, we cannot fully separate the roles of pre-existing seed reserves from species' inherent regeneration strategies. Future work should quantify seed density and viability before and after mowing to partition these mechanisms and to forecast post-treatment regeneration—an essential step for adaptive restoration planning.

Temporary increase in biodiversity after mowing or mowing and sowing seeds

Biodiversity was initially increased by mowing, which reduced the dominance of *H. scandens* and temporarily opened space for other species to establish. This short-term increase in diversity is consistent with the intermediate disturbance hypothesis (Catford et al. 2012), as the mowing intensity represented a moderate disturbance—strong enough to reduce competitive exclusion by the dominant

vine, but not so severe as to eliminate most resident species. However, this effect was transient, as diversity converged among treatments by the end of the growing season, reflecting the short-term nature of our single-season experiment.

Sicyos angulatus rapidly recovered after seedling emergence, and it dominated the communities and restricted or even reduced biodiversity after mowing and mowing + sowing. Thus, the initial increase in biodiversity conferred by seed sowing in the mowed plots did not persist throughout the experimental period. However, mowing or mowing + sowing increased functional diversity, which was indirectly shown by the size of the ellipses in the PCA biplot (Fig. 4). Increased functional diversity can enhance biotic resistance by promoting complementary resource use and niche occupation among resident species (Byun et al. 2020a; Li et al. 2022; Mazzochini et al. 2023). However, in our study, this effect appeared transient, suggesting that maintaining functional diversity may require repeated management interventions.

The shift in CWM traits after mowing or mowing and sowing seed mixtures

In our experiment, a single mowing event temporarily constrained the dominance of *H. scandens* and altered successional trajectories, leading to a distinct post-disturbance community composition compared with the control plots. The observed shift toward species with higher seed mass and lower SLA indicates a functional trade-off consistent with the leaf–height–seed (LHS) framework (Westoby 1998), reflecting a transition toward more stress-tolerant and disturbance-resilient strategies. In this regard, *S. angulatus* was more opportunistic, which was reflected in its increased germination rate, higher seed mass, and higher SLA, which might have contributed to its survival in the mowed plots.

Large-seeded species have an advantage in seedling emergence (Moles and Westoby 2006). Seed mass contributes to a longer persistence of the seed bank; therefore, mowing all plants up to ground level might shift the CWM seed mass to a larger one. Additionally, it is possible that small-seeded plants are more readily removed by single mowing because they generally have a high germination percentage and germinate rapidly in early spring. On the other hand, *S. angulatus* has a high seed mass and combinational dormancy (both physical and physiological) (Qu et al. 2012), which may confer continuous germination over many months and high resistance to disturbance.

CWM SLA in control plots exceeded that in mowing and mowing + sowing plots, a trend that is seemingly at odds with the LHS scheme (Westoby 1998), which posits that plants with a high SLA are typically more prevalent in ruderal environments. This unexpected deviation from the

predictions of the LHS scheme is probably because a single mowing is not a frequent disturbance in a ruderal environment. Recurrent mowing has been reported to increase CWM SLA (faster growth), indicating acquisitive strategies by plant species (Bouchet et al. 2017).

It should be noted that a portion of the trait data used in this study was supplemented from external databases, and some missing values were imputed using genus-level means. Although this approach is common in trait-based community analyses and preserves overall ecological patterns, it inevitably introduces some uncertainty in the precision of species-level trait estimates. Therefore, interpretations of the functional trait results should be viewed as reflecting general community-level shifts rather than exact trait values of individual species.

Management implications

Non-selective mowing is widely used by local governments and land managers in riparian weed management due to its simplicity and cost-effectiveness. However, our experimental results indicate that its outcomes can vary substantially depending on the regeneration strategies of co-occurring species. In our study, mowing conducted after the seedling recruitment period effectively reduced *H. scandens* biomass but concurrently facilitated the dominance of *S. angulatus*. These contrasting species-specific responses highlight that non-selective mowing, although commonly implemented in practice, may inadvertently shift rather than resolve invasion problems when applied without consideration of target species' life-history traits and phenological timing.

To improve management practicality and compliance with Korean environmental regulations—which prohibit herbicide use in natural areas—manual and selective mechanical removal methods should be prioritized. Both hand-pulling and selective cutting were shown to be effective mechanical control methods in previous field trials (Byun and Singh 2025). Among these, hand-pulling is practical for small or accessible infestations, whereas selective cutting using weed mowers is recommended for larger areas where manual removal is impractical. Future cost-effectiveness analyses comparing labor requirements, fuel use, and long-term suppression efficiency are needed to optimize these approaches for operational use.

For *H. scandens*, hand-pulling after the end of the germination period (March–April) may reduce seedling emergence, as observed in our field experiment, where no new seedling emergence was detected and vegetative regrowth was limited to basal stem nodes that survived mowing. Although the underlying cause cannot be confirmed because the soil seed bank was not quantified, this pattern

is consistent with the species' early germination phenology and weak seed dormancy.

Although mowing during the vegetative period (June) effectively reduced aboveground biomass in our experiment, incorporating an additional late-season mowing before flowering or full seed maturation could further limit seed production and, consequently, population growth rate. This inference is supported by previous studies on other invasive species: mowing before flowering markedly reduced reproductive success in *Ambrosia artemisiifolia* L. (Milakovic et al. 2014; Lommen et al. 2018), while combining early and late mowing most effectively decreased population growth and spatial spread in *Carduus nutans* L. (Zhang and Shea 2019).

For *S. angulatus*, repeated early-season hand-pulling (May–June) targeting newly germinated seedlings is likely most effective, given its strong seed bank persistence and continuous germination, as also reflected in our results showing a strong positive correlation between seedling density and final biomass. In addition, late-season cutting before flowering or full seed maturation may further reduce seed input and prevent reinforcement of the soil seed bank, thereby enhancing long-term control effectiveness.

We recommend seed bank assessment and multi-year management cycles to address persistent seed reserves and predict secondary invasions. Mowing also shifted community composition toward species with higher seed mass, suggesting that functional traits related to disturbance tolerance should be considered when designing control strategies. Evaluating the ratio of invasive to native seeds in the seed bank may help anticipate the consequences of mowing on community biomass recovery.

Study limitations

This study was limited to a single riparian site under relatively stable hydrological conditions, restricting the spatial generalizability of our findings. Because hydrological regimes are key drivers of riparian vegetation dynamics, future multi-site experiments across diverse floodplain settings and hydrological gradients are needed to validate the robustness of these management outcomes.

Additionally, our single-season observation limits inference on long-term dynamics. While the inclusion of non-native crop species in the seed mixture was justified for short-term competitive testing and minimizing establishment risk, such species are not expected to persist under natural riparian conditions. Monitoring over multiple years and testing native-only seed mixtures adapted to local riparian environments would yield more ecologically grounded and restoration-relevant recommendations.

Furthermore, temporal fluctuations such as flood pulses, groundwater variation, or prolonged inundation can strongly influence species regeneration and post-disturbance succession, and should be explicitly incorporated into future experimental designs.

Conclusion

We examined the effects of non-selective mowing, with and without seed sowing, on two invasive vines, *S. angulatus* and *H. scandens*, in an urban riparian wetland in Seoul, the Republic of Korea, over one growing season. The results revealed a management paradox: mowing suppressed *H. scandens* but facilitated *S. angulatus*. Mowing initially increased biodiversity by reducing *H. scandens* dominance, but this effect was short-lived. These contrasting responses indicate that non-selective mowing can inadvertently favor one invader while suppressing another, thereby shifting rather than solving invasion problems.

The effectiveness of mechanical control depends strongly on species traits, phenological timing, and seed bank dynamics. Our findings emphasize that even well-intentioned interventions can produce unintended outcomes when multiple invasive species with different life-history strategies coexist. However, these results should be interpreted cautiously, as the experiment was conducted over a single growing season at one site. Thus, they provide a pilot-scale understanding rather than definitive management guidance. Therefore, management planning should integrate ecological traits, field conditions, and seed bank composition to ensure sustainable and context-specific invasive plant control.

Future studies should extend observations over multiple sites and years, empirically test the effects of mowing timing based on species phenology and life-history traits to validate the management recommendations proposed in this study, and rely exclusively on native or locally adapted species to develop ecologically sustainable and operationally practical management strategies for riparian wetlands.

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Author contributions Minwoo Oh, Eun Ju Lee, Chaeho Byun, and Hojeong Kang contributed to the study conception and design. Material preparation and data collection were performed by Minwoo Oh, Minki Hong, Yoonjeong Heo, Jaesang Chung, and Chaeho Byun. The data were analyzed by Minwoo Oh. The first draft of the manuscript

was written by Minwoo Oh and Chaeho Byun, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets and code generated during the current study are available from Figshare: <https://doi.org/10.6084/m9.figshare.26360746.v1>.

Declarations

Competing interests The authors declare no competing interests.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT Pro and Claude AI to improve the readability and language of the manuscript, but not to generate any content. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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