Soil and Vegetation Characteristics Associated with the Invasion of *Humulus japonicus* in Riparian Zones

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Abstract

Riparian zones are frequently exposed to floods and artificial disturbances, promoting the invasion of aggressive native plant species. *Humulus japonicus* is particularly dominant in Korean riparian areas, where its vining habit enables it to overgrow surrounding vegetation. Despite being designated as an ecosystem-threatening species by the Ministry of Environment, ecological insights into its invasive success remain limited. We compared soil and vegetation characteristics between sites invaded and uninvaded by *H. japonicus* to identify habitat preferences. Additionally, we assessed sex ratios and seed banks, which are critical for the maintenance of dioecious annual plant populations like *H. japonicus*. Uninvaded sites had significantly higher coverage of perennial plants, and the coverage of *H. japonicus* was negatively correlated with that of perennial plants across invaded sites. In contrast, the coverage of annual and biennial species was positively associated with the presence of *H. japonicus*. Among soil characteristics identified by canonical correspondence analysis as explanatory variables for species composition, soil water content was higher in uninvaded sites than in invaded sites. These results suggest that the establishment of *H. japonicus* is associated with the structure of riparian vegetation and soil water content, although the causal relationships among those remain unclear. No viable *H. japonicus* seeds were found in uninvaded soils, and only a small number were detected in invaded sites, indicating that seed dispersal from upstream may play a critical role in maintaining population size. The biotic and abiotic factors identified in this study warrant further investigation to clarify their causal roles in the invasion of *H. japonicus* through manipulative experiments.

Keywords *Humulus japonicus, abundance of perennial plant, soil water content, riparian zone*

Introduction

Riparian zones are transitional areas between terrestrial and aquatic ecosystems, providing important habitats for diverse organisms [1]. They are highly dynamic in space and time, showing strong heterogeneity due to hydrological and structural disturbances [2, 3]. Such disturbances often promote the success of invasive weeds [4]. However, ecological studies on their role in riparian plant invasions remain limited. *Humulus japonicus* Siebold & Zucc. is an annual dioecious vine native to East Asia and widely distributed in Korea [5]. In riparian zones, it forms dense cover along riverbanks and levee slopes [6, 7], climbing over or smothering plants such as *Phragmites australis* and *Miscanthus sacchariflorus* [8, 9]. Its spread reduces native plant diversity and can trigger pollen allergies, leading to its designation as an ecosystem-disturbing species by the Ministry of Environment. However, ecological information on this species remains scarce. We compared invaded and uninvaded sites to identify environmental factors that enhance or limit its invasiveness. Additionally, considering its annual dioecious life history, we examined the seed bank and sex ratio of populations. Therefore, we would like to answer the following questions:

(1) Are there differences in soil and vegetation characteristics between *H. japonicus*-invaded and uninvaded sites?
(2) Are there correlations between *H. japonicus* coverage and soil and vegetation characteristics?
(3) Do seed bank quantity and sex ratio correlate with the dominance of *H. japonicus*?

Materials and Methods

1. Experimental Species



Figure 1. The experimental plant species is *Humulus japonicus*. *H. japonicus* is an annual, dioecious, herbaceous invasive vine native to East Asia and widely naturalized across South Korea. Images adapted from National Institute of Biological Resources.

2. Study sites and field survey

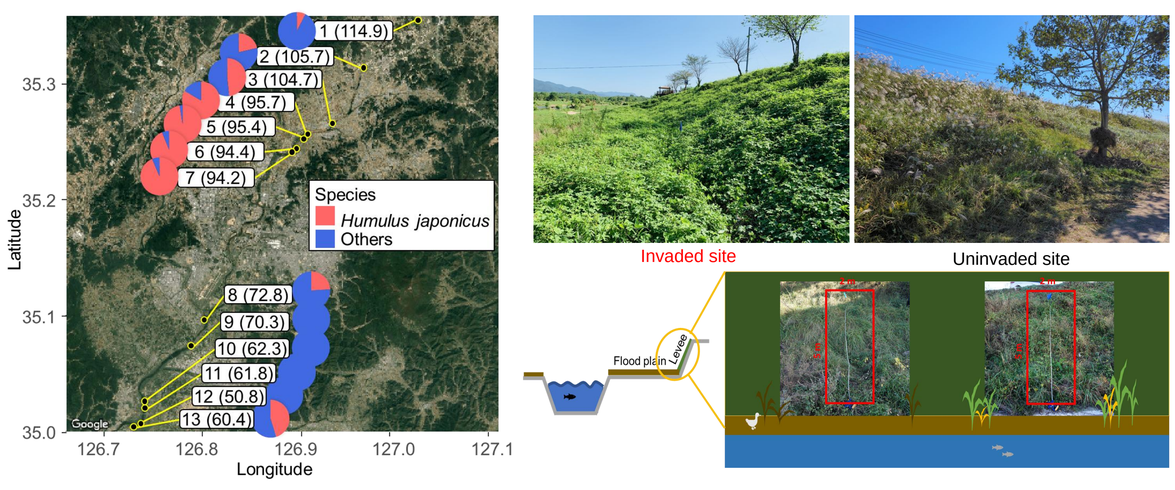


Figure 2. Location of the study sites along the Yeongsan-gang River. Accumulated distance from the estuary (km) for each site is indicated within parenthesis. Relative abundance of *Humulus japonicus* for each site is also given. For the field survey, two 2 × 5 m^2 quadrats were established at each site.

3. Collected data

- Biotic environmental factors: coverage of plants and bare ground area for each site, Shannon-Weiner species diversity index (H')
- Abiotic environmental factors: soil pH, available phosphate, total phosphorus, nitrogen, ammonium nitrogen, nitrate nitrogen, exchangeable potassium, organic matter, moisture, and hardness
- Sex determination and seed bank

4. Statistical analysis

- All statistical analyses were performed using R 4.2.1 (R Foundation for Statistical Computing, Vienna, Austria)
- Analysis of variance (ANOVA), Pearson's chi-squared test, and chi-square goodness-of-fit test against the 1:1 sex ratio ('*car*' package), Canonical correspondence analysis ('*vegan*' package), Spearman's rank correlation ('*corrplot*' package)

Results and Discussion

◆ High soil water content and perennial coverage in uninvaded sites

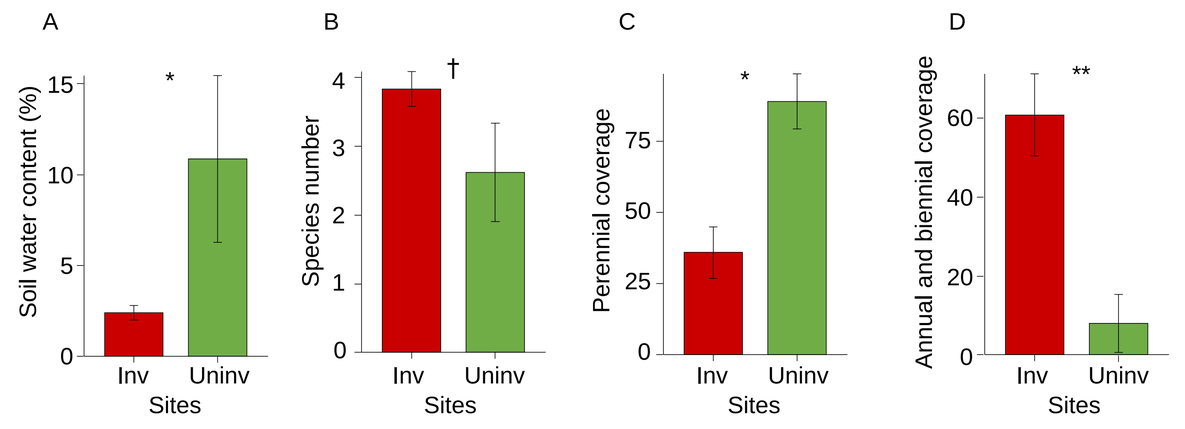


Figure 5. Differences in soil and vegetative characteristics between *Humulus japonicus*-invaded and uninvaded sites. (A) Soil water content, (B) number of plant species, (C) annual and biennial plant coverage and (D) perennial plant coverage are presented. Statistical significances from analysis of variance are given. † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$. Inv, invaded sites; Uninv, uninvaded sites.

The co-occurrence of rapidly spreading annuals and *H. japonicus* in disturbed areas suggests its ability to establish and expand quickly, whereas perennial plant communities may restrict its establishment.

◆ Invaded and uninvaded sites showed different plant compositions and soil characteristics

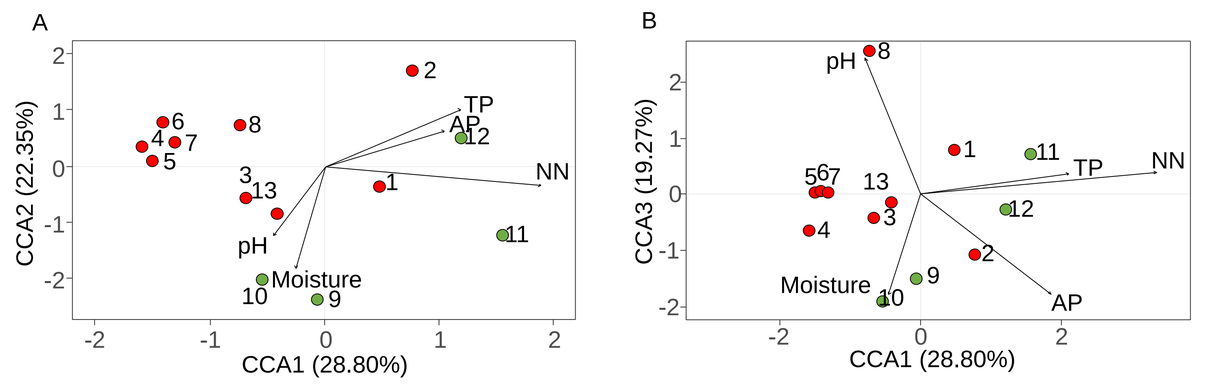


Figure 6. Canonical-correspondence analysis (CCA) and correlation analyses showing the relationships between environmental and vegetation factors to *Humulus japonicus* invasion. (A) CCA results depicting relationships between plant species composition and soil characteristics (CCA axes 1 and 2). (B) CCA results for axes 1 and 3. Red dots indicate *H. japonicus*-invaded sites, and green dots indicate uninvaded sites. OM, organic matter; AP, available phosphorus; TP, total phosphorus; AN, ammonium nitrogen.

Most soil properties did not differ between invaded and uninvaded sites, likely due to homogenization by the 2020 flood. In contrast, variation in soil moisture suggests that *H. japonicus* may be vulnerable to excessive water availability.

◆ Positive correlation between *H. japonicus* and annual and biennial coverage

Only a few viable seeds of *H. japonicus* were found in soil cores from invaded sites, whereas no viable seeds were detected in uninvaded sites. Populations of *H. japonicus* exhibited a male-biased sex ratio, and significant differences in sex ratios were observed among invaded sites ($P < 0.05$).

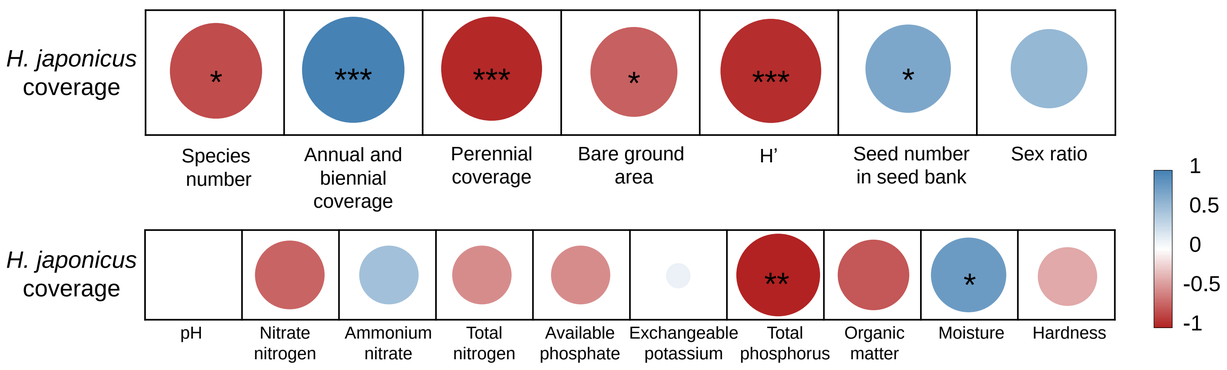


Figure 7. Results of correlation analyses between the coverage of *Humulus japonicus* and soil and vegetation characteristics for *Humulus japonicus*-invaded sites. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Conclusion

We conducted a comparative study between invaded and uninvaded sites of *Humulus japonicus*, an ecologically problematic invasive vine. The main differences between the two site types were not soil nutrients but soil moisture and the cover of perennial plants. In addition, *H. japonicus* populations exhibited a male-biased sex ratio and a shallow soil seed bank. Our findings suggest that further research is needed to clarify the interactive effects of soil moisture and interspecific competition on invasion success. This study represents the first ecological comparison of invaded and uninvaded sites of *H. japonicus* designated as an ecosystem-disturbing species and provides essential baseline information for developing effective management strategies that incorporate its ecological traits.

Acknowledgement

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