Mowing inhibits the invasion of the alien species Solidago altissima and is an effective management strategy

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Abstract

Biological invasions of exotic plant species affect nutrient cycling, soil characteristics, ecosystem stability, and Biodiversity. Therefore, management measures to protect the ecosystem and native species against invasive species are becoming more important. The tall goldenrod, *Solidago altissima* L., is an invasive alien plant with currently limited distribution on the Jeju island, while successfully invaded areas with similar climates in China and Japan. Therefore, it has a high possibility of invasion and may have an adverse effect on the ecosystem of Jeju Island. The aim of this study was to develop an environmentally friendly management strategy to control *S. altissima* with understanding of the major factor that makes difference of invasion success between Japan and Jeju island. Plant communities are monitored and allelopathic effects of *S. altissima* are tested.. Furthermore, the effectiveness of mowing at varying frequencies and timing for the control of *S. altissima* were applied. *S. altissima* already dominates several plant communities on Jeju Island, harms the plant community via allelopathy, and reduces biodiversity. However, our study shows that mowing is an effective method to control *S. altissima* populations. Mowing inhibits early invasion of *S. altissima* and also reduces dominance and reproductive features of *S.* altissima where invasion has already processed. Therefore, mowing should be adopted for the management of *S. altissima* invasion. Mowing is an environmentally friendly management method for the control of *S. altissima* and could be applied to other invasive species.

Introduction

Globalization and increased trading activities have led to the increased spread of exotic plants (Hulme 2009). Some introduced exotic plants are more competitive than indigenous species, invading and rapidly expanding in the new habitat. These invasive plants could inhibit the establishment and growth of native plants, consequently altering the plant community structure and reducing biodiversity by the extinction of native species, in serious cases (Bellard et al. 2016). Therefore, the invasion of exotic plant species affects ecosystem properties, including nutrient cycling (Aguilera et al. 2010), soil characteristics (Castro-Díez et al. 2019), hydrology (Boyce et al. 2012), and fire regimes (Underwood et al. 2019). This could threaten ecosystem stability and cause economic losses (Pejchar, Mooney 2009). Accordingly, governments have developed control measures to protect against invasive species.

Jeju Island, the largest island of South Korea, has a unique ecosystem due to its isolation from the mainland, the Korean peninsula (Kim 2009). The island was designated as a Biosphere Reserve by the United Nations Educational, Scientific and Cultural Organization (UNESCO) in 2002, owing to its unique ecosystem and biodiversity. However, the invasion of alien species jeopardizes its biodiversity (Ryu et al. 2017). The tall goldenrod, *Solidago altissima* L., is an invasive alien plant with the potential to harm biodiversity on the island, although its distribution on the island is currently limited (Ryu et al. 2017).

S. altissima originated in North America and successfully invaded Korea, Japan, China and Europe (Nakagawa, Enomoto 1975; Takafuji et al. 2020; Weber 2000). It was introduced to the Korean peninsula before 1974 for honey production (Information of Korean Alien Species, t.ly/SpgY) and is currently distributed in southwestern areas of the Korean peninsula (Kil, Kim 2014). It is a tall perennial grass with a height of 100–250 cm and grows in dense colonies. It has allelopathic effects and develops overwintering rhizomes underground (Meyer, Schmid 1999). Although aboveground shoots disappear in the winter, rhizome connections persist for up to 5–6 years. Therefore, it dominates invaded areas and excludes native herbaceous species, indicating that it may have an adverse effect on the ecosystem of Jeju Island.

The aim of this study was to develop an environmentally friendly management strategy to control *S. altissima*. We compared plant communities dominated by *S. altissima* and invaded but not yet dominated by the species. We also tested the allelopathic effects of *S. altissima* to evaluate its competitive advantage over other species. Furthermore, we investigated the effectiveness of mowing at varying frequencies and timing as well as the application of Eco200, an eco-friendly herbicide, for the control of *S. altissima*.

Materials And Methods

Site description

We investigated the current *S. altissima* distribution around Jeju National University and found several populations that were big enough to set multiple quadrats. We selected *S. altissima* populations with adjacent uninvaded (not dominant) areas to compare vegetation. The geographic coordinates of the sites are listed in Table S1. Sites 1–7 were dominated by *S. altissima* with adjacent uninvaded areas; these sites were used for biodiversity and management studies. Sites 8–10 were in an early stage of invasion and thus had several small patches of *S. altissima.* Effects of mowing and herbicide use on the invasion of early patches of *S. altissima* were studied at these sites. The average annual temperature and precipitation at the center of the research sites were 16.6°C and 1769.5 mm in 2018 and 20.4°C and 1841.1 mm in 2019 (Korean Meteorological Administration 2019).

Comparison of vegetation between *S. altissima*-dominant areas and uninvaded areas

Vegetation was investigated in areas dominated by *S. altissima* or by native species (*S. altissima* uninvaded) in sites 1–7 in July 2018. Ten quadrats were monitored in each area, for 70 total quadrats. A phytosociological method was used to investigate the vegetation (Braun-Blanquet 1964). Plants were identified based on ‘Colored Flora of Korea’ by Lee (2003)). Importance values for herbaceous vegetation were calculated according to Cottam, Curtis (1956)) as follows Brower et al. (1998)):

Importance Value =(Relative frequency + relative coverage)/2

Management of *S. altissima*-dominated communities by repeated mowing and eco-friendly herbicide use

Large quadrats (300 m^2) were established in the areas dominated by *S. altissima* at sites 1–7. Ten small quadrats (2 × 2 m, with a 50 cm buffer zone on all sides) were established within large quadrats at each site. Fig. S1 shows an example of the quadrat arrangement. Quadrats were randomly assigned to two sets of control (untreated), Mowing 1 (mowed once in July), Mowing 2 (mowed twice in May and September), Mowing 3 (mowed three times in May, July, and September), or Eco 200 treatments; thus there were 14 replicates for each treatment. For Eco 200 treatments, 30% of *S. altissima* shoots were cut near the ground, and the cut surface was covered by Eco 200 block, as instructed by the manufacturer (Eco Industry Inc., Pyeongtaek, Korea). Eco 200 is a small, round clay-type block that contains aglycones, an eco-friendly herbicide. Eco 200 was applied three times, in May, July, and September.

Shoots of *S. altissima* within small quadrats (2 × 2 m) were counted in March 2018, before the experiment. Shoots of *S. altissima* in each treatment group were then counted in April 2019. The vegetation and coverage of *S. altissima* in the control or treated quadrats were also investigated in July 2018 (before the experiment) and 2019 (after 1 year of the experiment), following the method described in section 2.2. We measured the height of *S. altissima* shoots to determine the effects of repetitive mowing on plant growth. The height of *S. altissima* was measured in July 2018 and April 2019 in the first-year experiments, and in May, July, and September 2019 in the second-year experiments. Each measurement was performed before the mowing application.

The aboveground biomass of *S. altissima* was measured in September 2019 before the last mowing. We harvested and weighed *S. altissima* shoots in a small 40 × 40 cm quadrat inside the experimental quadrat. Leaves on five randomly selected individuals were also counted.

The effect of mowing frequency on the biomass of rhizomes of *S. altissima* was also evaluated. In June and July 2020, after digging a 40 × 40 cm wide area to a depth of 15 cm, rhizomes of *S. altissima* inside the experimental quadrat were harvested. Soil was cleaned from the harvested rhizomes and the biomass was weighed.

Finally, the effect of mowing on the reproductive characteristics of *S. altissima* was determined by estimating flowering rates in October 2019. Five individuals were randomly chosen in the quadrats of each treatment for the detection of flowers.

Effects of mowing frequency and eco-friendly herbicides on the early establishment of *S. altissima* invasion

The effects of mowing and eco-friendly herbicide use on the establishment of early patches of *S. altissima* were evaluated at three sites (sites 8–10). Shoots were counted in the quadrat in March 2018. A size marker was placed in patches of *S. altissima*, and photos were obtained vertically from the top. The *S. altissima* patch area was calculated using ImageJ (Song 2019). *S. altissima* plants were assigned to control, Mowing 3, removal of 20% of shoots followed by Eco 200 treatment, and removal of 100% of shoots followed by Eco 200 treatment (two replicates for each site, therefore, six replicates for each treatment) to evaluate whether management at an early stage would prevent the invasion of *S. altissima*. Shoots of *S. altissima* were counted, and photos were obtained following the method described above in

March 2019 to measure areas of *S. altissima*. The effects of treatments on reproductive characteristics of *S. altissima* patches were evaluated following the method described above.

Allelopathic effect of *S. altissima*

The allelopathic effect of *S. altissima* was evaluated. Fresh leaves and roots (1:1 ratio) of *S. altissima* were washed with clean water and placed in a triturating juicer. The extract of *S. altissima* was filtered with filter paper (Whatman No. 2). The filtered extract was then diluted with distilled water to obtain 0%, 20%, and 50% *S. altissima* extract (Kim et al. 2005). *Lactuca sativa* L. and *Oenothera biennis* L. were used in the germination test. Ten seeds were evenly dispersed in each Petri dish. Then, 5 ml of the diluted extract was applied to the seeds. The Petri dishes were maintained in a growth chamber (HB-301L; Hanbaek Scientific Co., Bucheon, Korea) at 25°C and 80% humidity with 12 h of daylight. The germination of seeds and the growth of seedlings were checked every 3 days. The position of each Petri dish was randomly changed every 3 days.

Microbial community comparison between Korea and Japan

Soil sampling

In May 2016, soil samples were collected from *S. altissima* dominant sites of Jeju and Shiga prefecture, Japan. The sampling site of Shiga was near Center for Ecological Research, Kyoto University (135° 95' 69", 34° 97' 12").

All samples were collected at sites were *S. altissima* is dominant with more than 80% coverage and population size over 10 m^2.

DNA extraction, PCR, and NGS sequencing

Before genomic DNA (gDNA) isolation for each plant, the root section was washed twice by vortexing with phosphate-buffered saline (PBS, pH 7.0). The gDNA from treated-root samples was extracted using a Power Soil DNA kit (Qiagen). To analyze microbial community structure, we conducted PCR amplification using a dual-indexed primer set specific for the V4 region of 16S rRNA gene of bacteria, as described previously (Kang et al. 2019). The size for the PCR products was separated and confirmed by agarose gel electrophoresis, and purified using PCR Clean-up kit (LaboPass, South Korea). For experimental-technical replication, all gDNAs were amplified in duplicates. For massive sequencing (NGS), the pooled amplicons were sequenced using an Illumina MiSeq platform at Macrogen Inc. (Seoul, South Korea) according to the manufacturer’s instructions.

Sequence processing and statistical analysis

In total, we analyzed 20 samples based on the Mothur (v 1.45.0) pipeline (Schloss et al. 2009). Briefly, to improve the sequencing quality, raw reads were removed based on its size (less than 300 bp) and non-matched to Silva reference database supplied by Mothur webpage (https://mothur.org/wiki/silva_reference_files/). Chimeric sequences were removed by using uchime

(Edgar et al. 2011). Bacterial amplicon sequence reads were classified against reference Silva database (release 138.1). Before diversity analysis, all samples were randomly subsampled to 20,000 reads per sample to account for differences in the number of reads across samples. Operational taxonomic unit (OTU) calculated at distance 0.03. Diversity indices (e.g. Shannon, Simpson, Chao 1, and good's coverage) were estimated using the Mothur package.

Statistical analysis

All experimental results are presented as averages ± standard error. Details of replicates are listed in the descriptions of relevant figures or tables. Data were analyzed by ANOVA; for factors with $p < 0.05$, post hoc Tukey's honest significant difference (HSD) tests were used. All statistical analyses were performed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA).

Results

Comparison of vegetation between *S. altissima*-dominant areas and uninvaded areas

In the area dominated by *S. altissima*, we detected 44 and 37 plant species in 2018 and 2019, respectively (Table S3). Plants belonging to Asteraceae were most frequent, followed by Gramineae and Rosaceae. In the area dominated by native species, we found 53 plant species in 2018 (Table S4). Asteraceae was most frequent, followed by Gramineae and Fabaceae. All species detected in the areas dominated by *S. altissima* or native species in 2018 and 2019 are listed in Table S2.

The average relative coverage of *S. altissima* was 83.2% in *S. altissima*-dominant sites, compared with 5.6% at sites dominated by native species (Fig. 1a). The average number of total species per quadrat differed significantly between *S. altissima*-dominated and or native species-dominated areas (i.e., 4.8 and 7.8, respectively) (Fig. 1b). The average number of native species also differed significantly between *S. altissima*-dominated and or native species-dominated areas (i.e., 3.1 and 4.9, respectively).

In the area dominated by *S. altissima*, the importance value was highest for *S. altissima* (0.409), followed by *Pueraria lobata* (0.141) and *Artemisia princeps* (0.087) in July 2018 (Table S3). In the area dominated by native species, *Glycine soja* (0.166), *P. lobata* (0.158), and *Erigeron canadensis* (0.154) had the high importance values. The importance value for *S. altissima* was 0.104, ranking 6th in July 2018 (Table S4).

Management of *S. altissima*-dominated community by repeated mowing and eco-friendly herbicide application

The coverages of *S. altissima* did not differ significantly between 2018 and 2019, regardless of the treatment applied to quadrats (Fig. S2). The quadrats that were mowed three times in 2018 had a lower *S. altissima* coverage in 2019 than in 2018; however, the variance was high and the difference was not statistically significant. Therefore, mowing treatment for 1 year did not affect the coverage of *S. altissima*, regardless of mowing frequency.

The importance value for *S. altissima* changed significantly after mowing treatment for 1 year. The importance value for *S. altissima* was 0.409 in 2018 and decreased to 0.321 in 2019. Consistent results were obtained at all sites subjected to mowing (Table S5).

In July 2018, 2 months after the first treatment (mowing or Eco200), the height of *S. altissima* in the mowing group was significantly different from that of the control group, with no difference in the height of *S. altissima* between the Eco 200 treatment and control group (Table S6). After 1 year of mowing or Eco 200 treatment, in April 2019, the height of the dead shoots differed significantly between the control group and the Mowing 1, Mowing 2, and Mowing 3 groups (Table 1). In particular, the average heights in the Mowing 2 and Mowing 3 groups were one-tenth that of the control group (Table 1). However, the height of the dead shoots in the Eco 200 group was not significantly different from that in the control group, and was larger than those in the mowing treatment groups.

Table 1
Heights of dead shoots of *S. altissima* after 1 year of treatment in April 2019

Site	Control	Mowing 1	Mowing 2	Mowing 3	Eco 200
Site 1	162.8 ± 6.62^{a}	85.7 ± 5.52^{b}	29.5 ± 2.74^{c}	21.3 ± 2.09^{c}	77.9 ± 8.94^{b}
Site 2	213.2 ± 12.08^{a}	87.1 ± 7.33^{c}	38.4 ± 2.17^{d}	29.0 ± 2.01^{d}	144.8 ± 9.57^{b}
Site 3	163.4 ± 7.31^{a}	66.3 ± 4.55^{c}	40.7 ± 2.57^{d}	33.4 ± 2.11^{d}	143.4 ± 7.13^{b}
Site 4	191.6 ± 3.84^{a}	160.8 ± 7.90^{b}	59.2 ± 1.66^{d}	81.9 ± 6.50^{c}	166.9 ± 12.33^{b}
Site 5	181.7 ± 4.76^{a}	114.7 ± 2.90^{b}	89.5 ± 10.23^{c}	46.6 ± 5.12^{d}	183.8 ± 9.00^{a}
Site 6	174.8 ± 4.34^{a}	82.9 ± 4.49^{c}	39.7 ± 2.51^{d}	31.6 ± 2.47^{d}	153.3 ± 3.12^{b}
Site 7	165.5 ± 4.79^{a}	91.2 ± 6.02^{b}	64.7 ± 3.24^{c}	44.0 ± 3.67^{d}	153.8 ± 7.25^{a}

Mowing 1: mowed once in July; Mowing 2: mowed twice in May and September; Mowing 3: mowed three times in May, July, and September; Eco 200: 30% of shoots in the quadrats were cut near the ground, and the cut surfaces were covered with the Eco 200 block. Data are presented as means ± standard errors of 20 replicates. Means within a column followed by different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey's test). Units: cm.

We continued the experiment to determine the effects of mowing on the growth of *S. altissima* in 2019. We measured the height of shoots of *S. altissima* in May, July, and September, before each mowing treatment. The height of the shoot already differed between the control and Mowing 2 or Mowing 3 groups in May 2019, before mowing (Table 2). Height did not differ between the Mowing 1 and control groups. In July, heights in the Mowing 2 and Mowing 3 groups were significantly different from that in the control group, with no difference between the Mowing 1 and control groups (Table S7). In September, heights in all treatment groups were significantly different from that in the control group (Table 3).

Table 2
Heights of *S. altissima* before mowing treatment in May 2019

Site	Control	Mowing 1	Mowing 2	Mowing 3
Site 1	101.0 ± 3.2^{a}	101.0 ± 3.0^{a}	81.1 ± 2.6^{b}	64.9 ± 3.1^{c}
Site 2	116.5 ± 4.7^{a}	111.8 ± 4.7^{a}	82.9 ± 4.1^{b}	72.5 ± 6.6^{b}
Site 4	89.1 ± 2.2^{a}	74.8 ± 2.2^{b}	49.5 ± 3.1^{d}	59.8 ± 1.6^{c}
Site 5	93.5 ± 2.5^{a}	99.5 ± 2.3^{a}	78.0 ± 2.0^{b}	77.1 ± 2.0^{b}
Site 6	125.3 ± 5.2^{a}	117.0 ± 3.0^{a}	86.5 ± 3.0^{c}	105.0 ± 3.4^{b}
Site 7	123.3 ± 3.3^{a}	119.3 ± 2.9^{ab}	111.3 ± 2.8^{bc}	110.3 ± 3.1^{c}
Site 8	96.0 ± 4.0^{a}	94.5 ± 4.1^{ab}	84.5 ± 3.3^{bc}	81.0 ± 3.1^{c}

Mowing 1: mowed once in July; Mowing 2: mowed twice in May and September; Mowing 3: mowed three times in May, July, and September. Data are presented as means ± standard errors of 10 replicates. Means within a column followed by different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey’s test). Units: cm.

Table 3
Heights of *S. altissima* before mowing in September 2019

Site	Control	Mowing 1	Mowing 2	Mowing 3
Site 1	168.0 ± 3.27^{a}	64.0 ± 3.32^{c}	100.5 ± 9.14^{b}	67.5 ± 3.1^{c}
Site 2	192.0 ± 11.3^{a}	79.0 ± 4.07^{c}	111.0 ± 6.9^{b}	73.0 ± 7.61^{c}
Site 3	159.0 ± 4.99^{a}	123.0 ± 7.12^{b}	84.5 ± 5.89^{c}	47.0 ± 2.71^{d}
Site 4	190.0 ± 2.98^{a}	102.0 ± 3.89^{b}	112.5 ± 8.07^{b}	62.0 ± 5.33^{c}
Site 5	217.0 ± 10.23^{a}	87.5 ± 4.9^{c}	137.0 ± 4.96^{b}	62.5 ± 3.1^{d}
Site 6	177.5 ± 6.76^{a}	97.5 ± 5.44^{c}	120.5 ± 4.97^{b}	60.0 ± 2.58^{d}
Site 7	143.5 ± 12.2^{a}	81.0 ± 2.77^{b}	138.5 ± 3.5^{a}	62.0 ± 4.67^{b}

Mowing 1: mowed once in July; Mowing 2: mowed twice in May and September; Mowing 3: mowed three times in May, July, and September. Data are presented as means ± standard errors of 10 replicates. Means within a column followed by different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey’s test). Units: cm.

The number of shoots of *S. altissima* did not differ significantly between groups in March 2018 before the experiment started (Fig. 2). After 1 year of mowing or Eco 200 treatment, the number of shoots of *S. altissima* was significantly lower in the Mowing 3 group than in the control group in April 2019 (Fig. 2).

Mowing 1, Mowing 2, and Eco 200 treatments did not reduce the number of shoots compared with the number observed in the control group.

The number of leaves was lower in mowing treatment groups than in the control group (Table S8). Mowing 3 (mowed twice before harvesting) had the fewest leaves between the control and treatment groups. The aboveground biomass of *S. altissima* was also significantly lower in the mowing treatment groups than in the control group. However, there were no significant differences between mowing treatments (Fig. 3).

The biomass of rhizomes was significantly affected by mowing treatment and by the frequency of mowing after 2 years (Fig. 4). Plants subjected to mowing once a year had 933.6 g/m^2 rhizomes, similar to the rhizome content of control plants (987.7 g/m^2). However, plants that were mowed two or three times had 732.0 g/m^2 or 535.3 g/m^2 rhizomes, respectively, which were significantly lower than the estimate for control plants.

Effects of mowing frequency on reproductive characteristics

We found that flowering rates of *S. altissima* were affected by mowing. All individuals in the Mowing 1 group had flowers, significantly higher than the flowering rate of the control group (93 ± 7%). However, the flowering rates in the Mowing 2 (0%) and Mowing 3 groups (20%) were significantly lower than that in the control group in Fall 2019 (Fig. 5).

Effects of mowing frequency and eco-friendly herbicide application on the early establishment of *S. altissima* invasion

Although there were no statistically significant differences between the control and treatment groups due to high variances, patches of *S. altissima* showed the greatest expansion in the control group, followed by the 20% Eco 200 and 100% Eco 200 groups (Table 4). In particular, 100% mowing and Eco 200 treatment decreased the patch area of *S. altissima*.

Table 4
Change in areas occupied by *S. altissima* in patch-type communities from March 2018 to March 2019

Control	Mowing 3	Eco 20%	Eco 100%
205.2 ± 107.3	24.7 ± 44.0	104.5 ± 85.2	-31.7 ± 13.0

Mowing 3: mowed three times in May, July, and September; Eco 20%: 20% of shoots were mowed and treated with Eco 200; Eco 100%: 100% of shoots were mowed and treated with Eco 200. Data are presented as means ± standard errors of six replicates.

The flowering rate decreased with the frequency of mowing in the patches (sites 8–10) of *S. altissima* (Fig. S3). All individuals flowered in the control quadrats. However, the flowering rate in the Mowing 3 group was 75%, which was significantly lower than that in the control group. The Eco 20% and Eco 100% patches had no flowering individuals (Fig. S4).

Allelopathic effect of *S. altissima*

S. altissima extract adversely affected the germination rates of *Lactuca sativa* L. and *Oenothera biennis* L. (Table S9). For *L. sativa*, the germination rate was 32.9% at 3 days and increased to 44.3% at 6 days in the control group. For *O. biennis*, the germination rate was 45.7% at 6 days and increased to 65.7% at 12 days in the control group. However, when treated with the extract of *S. altissima*, the germination of seeds of both plants was delayed or did not occur. *L. sativa* seeds did not germinate until 9 days after treatment with a 20% dilution of the *S. altissima* extract and did not germinate at all when treated with a 50% dilution of the *S. altissima* extract. The seeds of *O. biennis* showed similar responses to *S. altissima* extract, although small numbers of seeds germinated, even when treated with 50% *S. altissima* extract (Table S9). The growth of roots of both plants was also significantly reduced by treatment with the *S. altissima* extract (Table S10). *L. sativa* seedlings showed root elongation of only 0.8 mm 12 days after treatment with a 20% dilution of *S. altissima* extract. The roots of *O. biennis* seedlings did not grow when treated with *S. altissima* extract, regardless of the concentration.

Discussion

Although its current distribution is limited on Jeju Island, the tall goldenrod *S. altissima* L. is an invasive alien plant with the potential to harm biodiversity on the island. Areas dominated by *S. altissima* have fewer total plant species and fewer native species compared with corresponding estimates for areas dominated by native species (Fig. 1b). In the dominated area, the average importance value for *S. altissima* (0.409) was much higher than that for *Glycine soja* (0.166), the dominant species in native species-dominated areas. The area dominated by *S. altissima* was mostly covered by *S. altissima*, and other species occupied very small areas (Fig. 1a). *Pueraria lobata* ranked second in areas dominated by *S. altissima* because this species is well-adapted to disturbed habitats, with similar properties to those of *S. altissima*, such as a perennial habit, strong rhizomes, and fast growth (Follak 2011). These results revealed the strong invasiveness of *S. altissima* and its adverse effects on other species and biodiversity. Therefore, controlling *S. altissima* is very important to maintain the unique ecosystem of Jeju Island.

The extract of *S. altissima* strongly inhibits the germination and growth of *L. sativa* and *O. biennis* (Table S9 and S10). These two plant species have soft seed coats and thus have the potential to be affected by allelopathic chemicals. The roots of *S. altissima* release cis-dehydromatricaria ester (DME), which has allelopathic effects on several plant species (Ito et al. 1998; Kobayashi et al. 1980). Furthermore, *S. altissima* responds to competition with surrounding plant species, inducing the production of allelopathic chemicals (Uesugi et al. 2019). Therefore, the allelopathic property of *S. altissima* might contribute to its successful invasion of disturbed habitats and the suppression of native plant species on Jeju Island.

We evaluated the effects of mowing and Eco 200 (eco-friendly herbicide) for the development of an environmentally friendly method for controlling *S. altissima*. Our focus on mowing was based on simple monitoring by the corresponding author during research in Shiga prefecture, Japan, where *S. altissima* is a highly dominant alien species (Prefecture 2019; Sakata et al. 2018; Sugino, Ashida 1977; Takafuji et al.

2020). However, in Jeju Island, Korea, although *S. altissima* invasion occurred > 20 years ago (Yang 2003), its distribution is very limited compared with that in Shiga, despite similar climate and land use patterns. Mowing could explain this difference between the two regions (Song et al. 2018). In Jeju, monitoring in 2015–17 confirmed that *S. altissima*-dominated areas were not subjected to mowing. However, most green spaces in Jeju are managed by mowing by the local government, and those areas did not undergo *S. altissima* invasion. However, *S. altissima*-dominant areas in Shiga were not subjected to mowing in 2013. This was confirmed by the corresponding author during a visit to Shiga in 2016, where there was no sign of mowing in *S. altissima*-dominant areas, while managed (mowed) urban green spaces had much less *S. altissima* invasion. More broadly, *S. altissima* invasion was more successful in Japan than in Korea. It is already widely distributed along roadsides, riversides, and railways in the mid-west of Honshu and Northern Kyushu (Nakagawa, Enomoto 1975) and expanded to all areas of Japan. However, the distribution of *S. altissima* in Korea was restricted to the southern areas, including only 35.5% of research sites in 2020 (Park et al. 2020). Owing to the differences in invasion histories, it is meaningless to directly compare distributions in Korea and Japan. Furthermore, the lower average winter temperature in mainland Korea than in Japan may explain the difference. However, in similar environments, the abundance of *S. altissima* is much higher in Japan than in Korea. Frequent mowing might favor species that are resilient to mowing, such as *E. annuus*, and prevent the establishment of *S. altissima* in Korea. The frequent use of mowing to manage green spaces in Korea (Song et al. 2018) could explain the difference between the two countries. Also microbial community analysis results did show some differences between Korea (Jeju) and Japan (Shiga), but the difference is not the major factor of *S. altissima* invasion and dominance differences between two regions (Fig. S5 and S6 for further discussion).

Mowing is very effective for the control of *S. altissima*, although the timing and frequency are crucial for successful control. Mowing affected the growth and reproduction of *S. altissima* in various ways. Mowing reduced the height, number of shoots, and number of leaves of *S. altissima*, thus decreasing the importance value for the species (0.409 in 2018, 0.321 in 2019). Previous studies have reported similar effects of mowing on *S. altissima* in Europe (Weber 2000); however, our results provide the first evidence for the effects of mowing in Asia.

Frequent mowing is more effective than infrequent mowing to control the growth of *S. altissima*. The height of shoots was clearly influenced by the frequency of mowing. Plants were shorter under more frequent mowing (Mowing 3) than under less frequent mowing (Mowing 1 and 2) and no mowing (control) in September 2019 (Table 3). Similar trends were found for other vegetative characteristics. In particular, rhizome weights were significantly lower under more frequent mowing (Fig. 4). Repeated mowing depletes the conserved resources in the rhizomes of *S. altissima* to compensate for the loss of aboveground biomass. Stoll et al. (1998) reported similar effects of frequent mowing on the below-ground biomass of *S. altissima*. Because a reduction of biomass inhibits exotic plant invasion (Wilson, Clark 2001), a reduction of rhizome biomass by repetitive mowing is a promising strategy for the control of *S. altissima*. Considering the key importance of rhizomes for the persistence of *S. altissima* in invaded habitats, frequent mowing could reduce the growth of *S. altissima*, resulting in low plant heights and biomass in subsequent years. Indeed, the Mowing 3 treatment suppressed the growth of *S. altissima* and decreased the importance value for the species in the plant community.

The timing of mowing strongly affected the reproductive characteristics of *S. altissima*. When *S. altissima* was mowed in September, during its flowering season (Mowing 2 and Mowing 3), flowering rates were significantly reduced compared with those in the control group (Fig. 5). However, when *S. altissima* was mowed 2 months before the flowering season (Mowing 1), flowering rates were not different from those in the control group. Although *S. altissima* propagates from rhizomes, seeds are essential for long-distance dispersal. Therefore, preventing seed setting by mowing in the flowering season is an effective method to prevent the expansion of *S. altissima*.

However, mowing has the potential to increase exotic species invasion. Some exotic species take advantage of open spaces resulting from mowing. For example, *Alternanthera philoxeroides* and *Erigeron annuus* successfully invade mowed sites and expand their habitats (Jia et al. 2009; Song et al. 2018). Mowing is thought to be the main cause of the successful invasion of *E. annuus* in Korea (Song et al. 2018). Continuous mowing might select for individuals with better reproductive ability and defense traits against herbivores (Chavana et al. 2021). Therefore, increased invasion of target species or expansions of other non-native plant species can occur when mowing is applied without vegetation monitoring and consideration of the ecology of plant species in the community. When *S. altissima* dominates an area, virtually no other species can grow; accordingly, mowing can be carried out without any negative effects on native species. However, in the early stage of invasion, selective mowing aimed at only the target species and considering the growth status of the plant (Song et al. 2018), should be planned and conducted. Our results indicating that mowing prevents alien species invasion were contrary to those of a previous study (Song et al. 2018) showing that mowing induces the invasion of alien species. These contradictory findings could be explained by a difference in resilience between *S. altissima* and *Erigeron annuus*. While mowing once increased the aboveground biomass and flower weight of *E. annuus*, *S. altissima* did not show similar responses. This can be explained by differences in plant height and growing season. As the height of *E. annuus* is < 1 meter, and flowering starts in late May, the effects of mowing activities after June are quite restricted. However, for heights of > 2 meters and a flowering period in October, mowing in any season would have an effect. As mowing activity usually happens after the rainy season (late June to mid-July) in Korea (Song et al. 2018), the effects of mowing would be particularly significant to *S. altissima*. Furthermore, on Jeju Island, mowing for the management of weeds is sometimes applied three times per year in public places (Song 2016), making the establishment of *S. altissima* populations difficult.

Although the eco-friendly herbicide Eco 200 was not effective for the control of *S. altissima* in areas already dominated by *S. altissima*, it was effective to control patches of *S. altissima* (Table 4). Mowing 3 suppressed the expansion of *S. altissima* patches; however, the addition of Eco 200 reduced the size of *S. altissima* patches. This approach requires less effort for the control of invasive plants at an early stage (Naylor 2000). Furthermore, Eco 200 treatment with mowing is very effective in preventing the flowering of *S. altissima* in patch communities (Fig. S5). Although mowing alone reduced the flowering rate of *S.*

altissima, 75% of individuals still flowered. Eco 200 treatment reduced the flowering rate of *S. altissima* to 0%. Therefore, the treatment of *S. altissima* patches with mowing and Eco 200 could be a cost-effective way to control the species overall. The effectiveness of Eco 200 was limited to *S. altissima* patches not in the dominant population; this can be explained by the weak rhizome development in *S. altissima* patches. However, the eco-friendly herbicide is expensive (around 0.5 US dollars per clay-type block), and the long-term effects on the soil and other plants are still unknown. Alternatively, mowing was a strong inhibitor of *S. altissima* invasion and reduced the rate of increase of *S. altissima* patches (Table 4) as well as the flowering rate.

Conclusion

Our results show that *S. altissima* already dominates several plant communities on Jeju Island, harms the plant community via allelopathy, and reduces biodiversity. Therefore, management of such invasion is required. In this study, Mowing treatments clearly show that mowing is an effective method to control *S. altissima* populations. Therefore, mowing should be adopted for the management *S. altissima* invasion. Mowing inhibits early invasion of *S. altissima* and also reduces dominance and reproductive features of *S. altissima* where invasion has already processed. Also, the combined treatment of Mowing and Eco 200 treatment are very effective for the control of *S. altissima* patches. Mowing timming and numbers should be decided by vegetation status. Thus, regular vegetation monitoring can contribute to the development of an effective control strategy to suppress *S. altissima* in the early stage of invasion. Jeju Island also is threatened by invasive plants other than *S. altissima*. Our results for the environmentally friendly control of *S. altissima* could be applied to other invasive species.

Declarations

Author contributions

HR : Investigation, Data curation, Writing - original draft; **ML** : Investigation, Data curation; **MK** : Investigation; **US**: Conceptualization, Methodology, Investigation, Writing - review & editing

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Data availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Competing Interest

The authors declare no competing interests.

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Figures

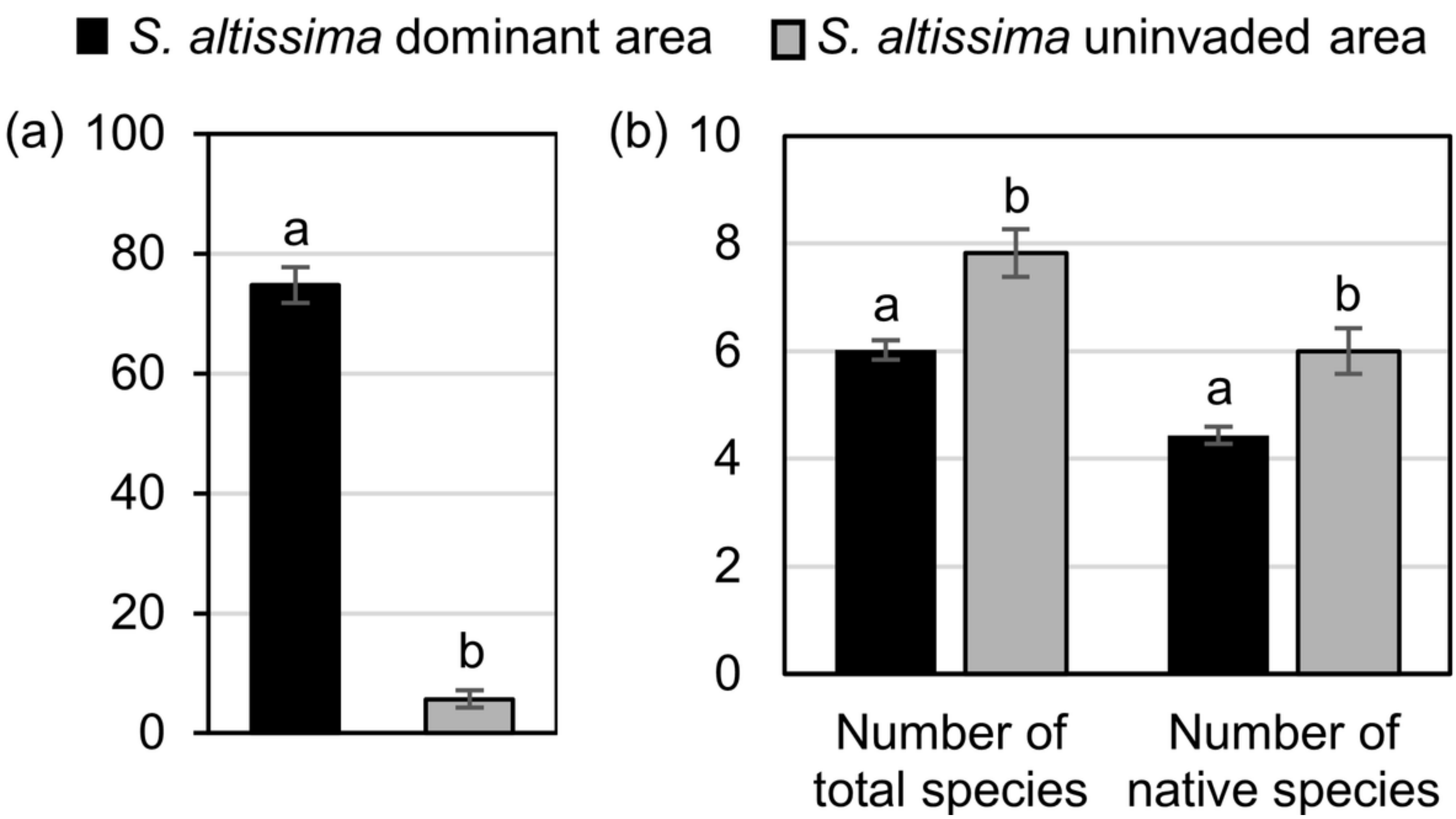

Figure 1

(a) Coverage of *S. altissima* and (b) the average number of species per quadrat in the *S. altissima*-dominant areas or uninvaded areas.

Data are presented as means ± standard errors of 14 replicates. Bars with different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey’s test).

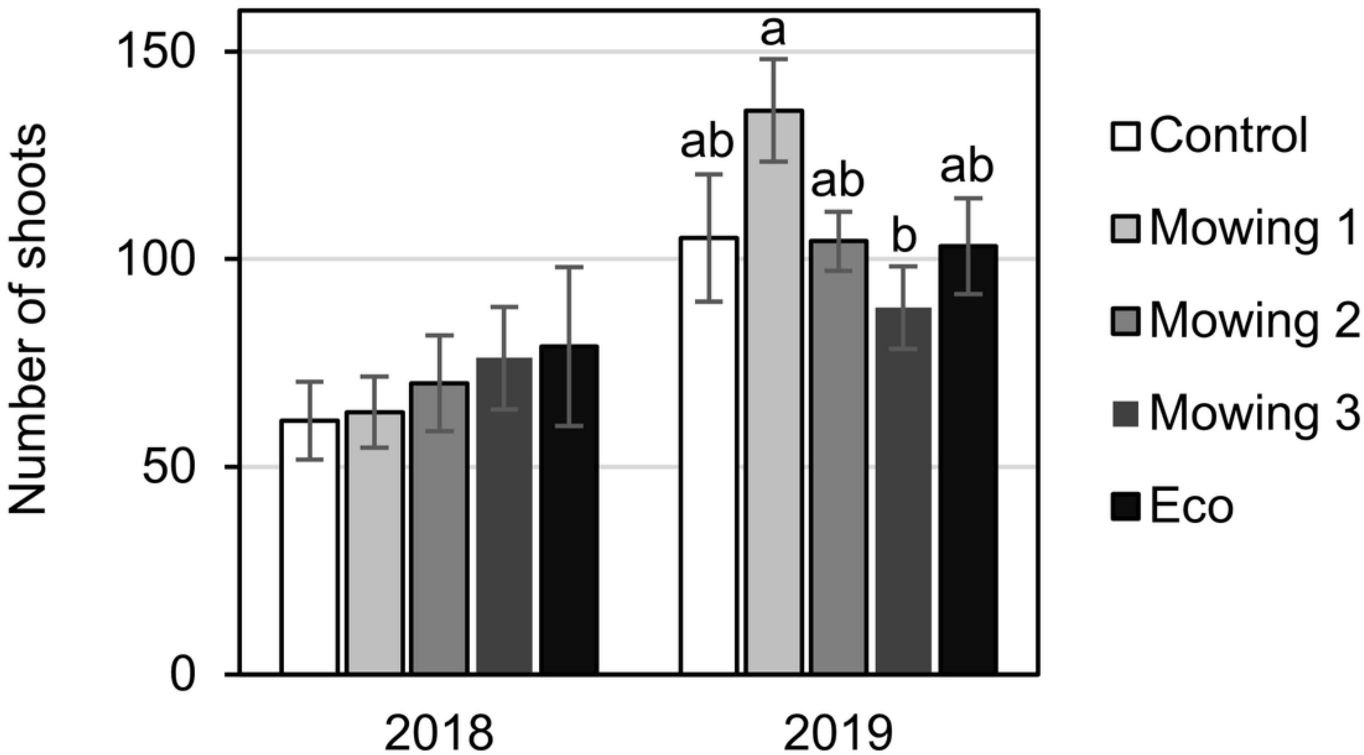

Figure 2

Number of shoots of *S. altissima* in March 2018 and April 2019.

Mowing 1: mowed once in July; Mowing 2: mowed twice in May and September; Mowing 3: mowed three times in May, July, and September; Eco 200: 30% of shoots in the quadrats were cut near the ground, and the cut surfaces were covered with Eco 200 block. Data are presented as means ± standard errors of 14 replicates. Bars with different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey’s test).

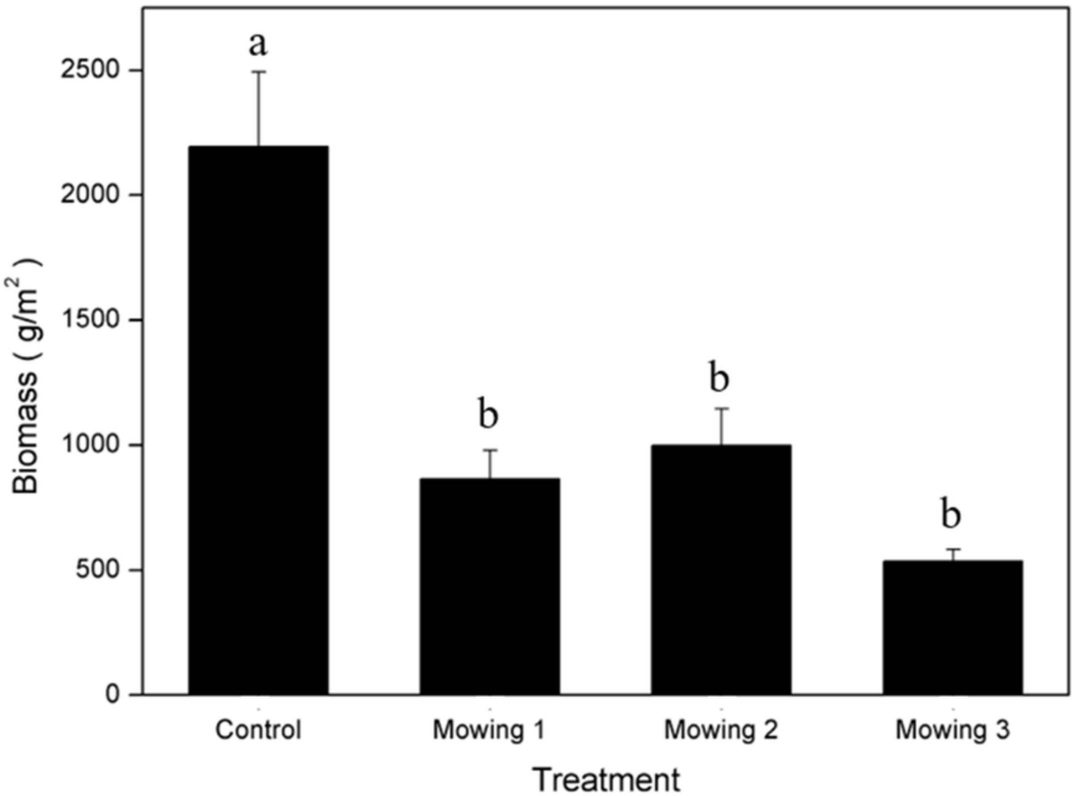

Figure 3

Aboveground biomass of *S. altissima* in September 2019.

Mowing 1: mowed once in July; Mowing 2: mowed twice in May and September; Mowing 3: mowed three times in May, July, and September. Data are presented as means ± standard errors of 14 replicates. Bars with different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey’s test).

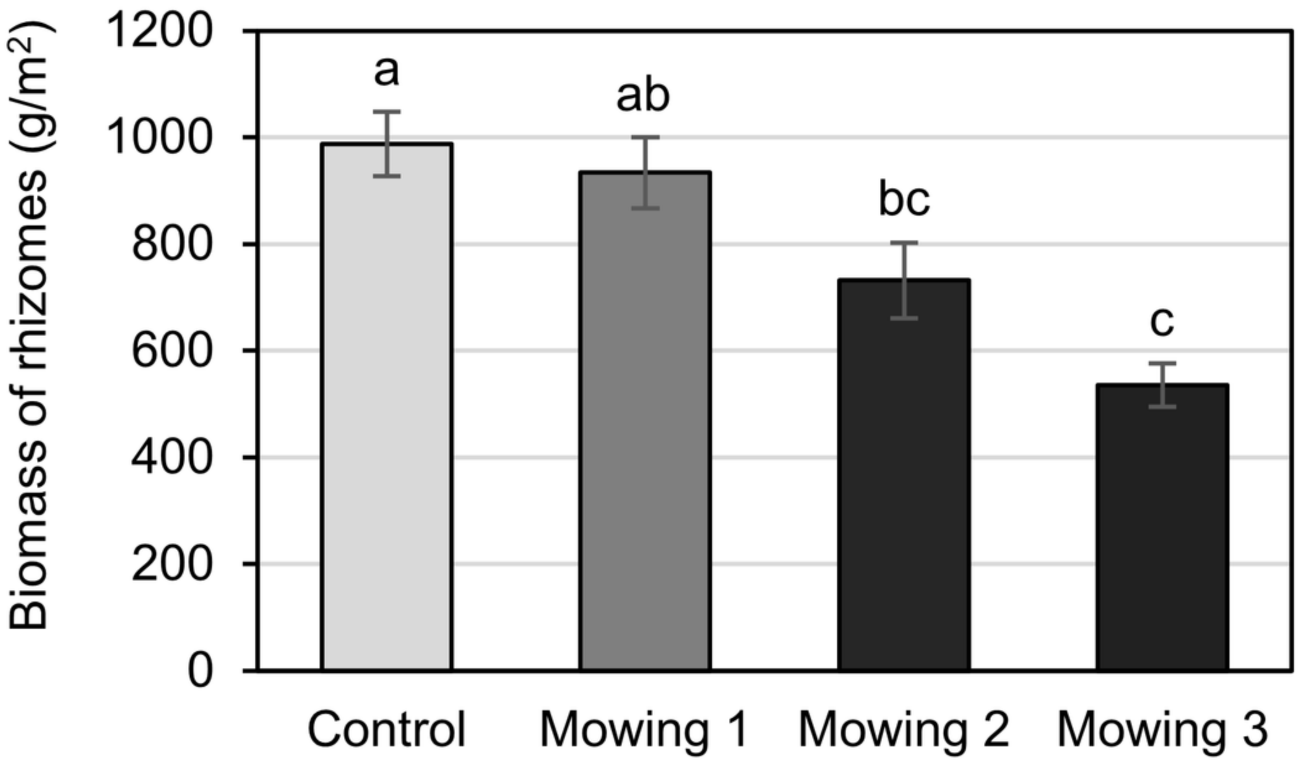

Figure 4

Biomass of rhizomes of *S. altissima* in September 2019.

Mowing 1: mowed once in July; Mowing 2: mowed twice in May and September; Mowing 3: mowed three times in May, July, and September. Data are presented as means ± standard errors of 14–16 replicates. Bars with the different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey's test).

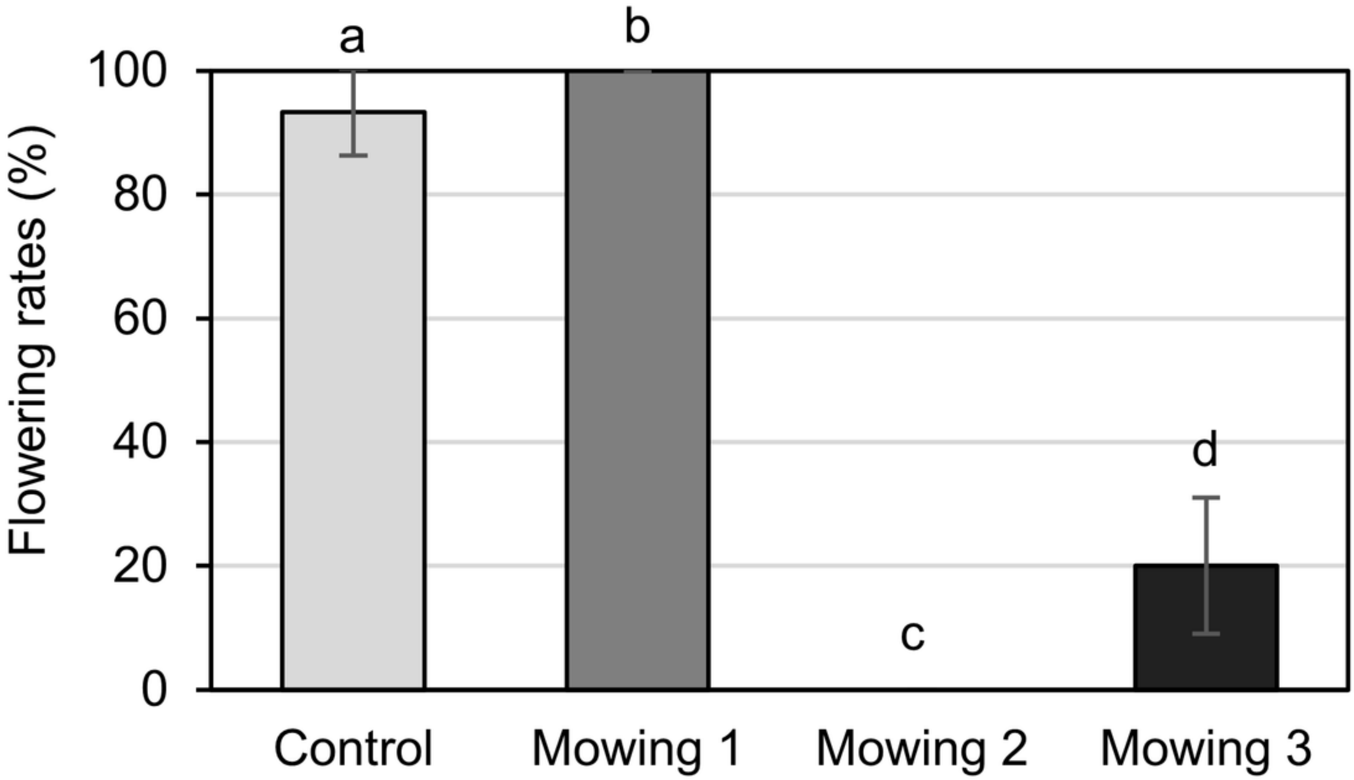

Figure 5

Effects of control practices on flowering rates of *S. altissima* in October 2019.

Control: mowed once in July; Mowing 2: mowed twice in May and September; Mowing 3: mowed three times in May, July, and September. Data are presented as means ± standard errors of 14 replicates. Bars with different letters are significantly different at $p < 0.05$ (ANOVA with post hoc Tukey's test).

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