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RESEARCH PAPER

Response of riparian vegetation to the removal of the invasive forb, *Solidago gigantea*, and its litter layer

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In order to explore the methods of recovering native grasses into exotic vegetation, the response of riparian vegetation to the removal of the above-ground shoots and/or litter of *Solidago gigantea* in a flood plain in Hokkaido, northern Japan, was investigated. The four treatments were: the removal of the above-ground shoots of *S. gigantea* (A); the removal of the litter of *S. gigantea* (L); the removal of both the above-ground shoots and litter of *S. gigantea* (AL); and a control (C). The vegetation cover and *S. gigantea* cover decreased in the A and AL treatments and increased in the L and C treatments. The understory plant cover increased in the A and AL treatments, but did not change in the L and C treatments. The increases in the understory cover in the A and AL treatments were associated with increases in *Phalaris arundinacea*. The seedling emergence of *P. arundinacea* was promoted by AL. In a greenhouse, the *S. gigantea* litter tended to decrease the seed germination of *P. arundinacea*. The AL treatment also increased the abundance of the other exotic plant, *Solidago altissima*. The continuous removal of the above-ground shoots and litter of *S. gigantea* long term is effective for promoting the recovery and emergence of native riparian grassland vegetation. However, this method also promotes the recovery of other exotics.

Keywords: litter accumulation, removal experiments, resource competition, restoration of native vegetation, *Solidago gigantea*.

Invasive plants often cause a reduction in native plants and alterations in the soil nutrient dynamics in disturbed ecosystems (Kohli *et al*. 2009; Nigatu *et al*. 2010; Saito & Okubo 2011). In order to restore native ecosystems, the development of vegetation management methods to reduce the abundance of invaders and to increase that of natives is needed urgently.

Solidago gigantea Aiton is one of the conspicuous invasive forbs in the northern hemisphere (Weber & Jakobs 2005) and often predominates in disturbed habitats, such as *Phalaris arundinacea* grassland and *Phragmites australis* grassland, both of which occur by the river side and lake shore (Namikawa *et al*. 1995; Güsewell *et al*. 2005). In the riparian habitats of Japan, the area dominated by *S. gigantea* (579 ha) was the fifth-largest among those dominated by invasive plant species, as of 1999 (Miyawaki & Washitani 2004). An invasion by *S. gigantea* often causes a reduction in the native plant species in disturbed areas (Weber & Jakobs 2005). The thick litter layer of *Solidago canadensis*, closely related to *S. gigantea*, also reduces the species richness, plant density, and seedling establishment in old fields (Carson & Peterson 1990). In addition, an invasion by *S. gigantea* in grassland vegetation will accelerate the litter decomposition due to the differences in litter traits between invasive forbs and native grasses (Scharfy *et al*. 2011) and also will alter the soil nutrient dynamics (Chapuis-Lardy *et al*. 2006; Koutika *et al*. 2007; Scharfy *et al*. 2009). The replacement of *S. gigantea* vegetation by vegetation that is dominated by native grasses, such as *P. arundinacea* and *P. australis*, is

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required in order to restore not only the native vegetation, but also the ecosystem's properties. However, research about the management of *S. gigantea* and the restoration of the invaded vegetation is limited.

The removal of the above-ground shoots of invasive plants is used frequently for eradicating the invaders and/or restoring the native vegetation (Myers & Bazely 2003; Radosevich *et al.* 2007). The removal of invasive plants often increases the abundance and species richness of the native plants by reducing the competitive interference (D'Antonio *et al.* 1998; Jäger & Kowarik 2010). The removal of the thick litter layer also often promotes the emergence and establishment of plants (Carson & Peterson 1990; Ruprecht *et al.* 2010). In a coastal Californian meadow, forb species were suppressed by both competition from exotic annual grasses and direct interference by their litter (Coleman & Levine 2007). Therefore, removing both the invasive plants and their litter should be conducted in order to promote the establishment of native vegetation. However, the removal of invasive plants frequently facilitates the establishment and expansion of not only natives, but also exotics (Hulme & Bremner 2006; Reid *et al.* 2009), and the facilitated exotics can threaten the natives again (e.g. Larson & Larson 2010). Therefore, the responses of both native and invasive plants to removal should be investigated in order to evaluate the effects of removal on vegetation recovery.

The effects of the removal of the above-ground shoots and/or litter layer of *S. gigantea* on the invaded vegetation were compared in order to explore the methods of restoring the native grasslands. First, *S. gigantea* vegetation and its neighboring *P. arundinacea* vegetation in a flood plain of Hokkaido, northern Japan, were investigated in order to describe the native grassland vegetation that is assumed to be the restoration goal. Second, the response of the riparian vegetation to the removal of the above-ground shoots and/or litter layer of *S. gigantea* was investigated. Third, the effects of the *S. gigantea* litter on the seed germination of the dominant native species, *P. arundinacea*, were examined in a greenhouse because the litter was expected to inhibit the emergence and establishment of the seedlings. If large individuals of *P. arundinacea*, with vigorous clonal reproductive ability by rhizomes, are not in the *S. gigantea* vegetation, the seedling emergence and establishment of *P. arundinacea* are prerequisites in promoting the regeneration.

MATERIALS AND METHODS

Experimental design

The study was conducted on a flood plain along the lower reach of the Ishikari River in Ishikari City, Hokkaido, northern Japan. The mean temperature and annual precipitation were 7.9C° and 957.0 mm, respectively (1990–2009; Japan Meteorological Agency 2010). The soil is characterized by homogenous fine soil containing grey spots, indicating that the soil is submerged and moist (Niiyama 1987).

In order to describe the characteristics of the native grassland vegetation and the *S. gigantea* vegetation, a vegetation survey was conducted on the *S. gigantea* vegetation (number of plots = 13) and the neighboring *P. arundinacea* vegetation (n = 11) in the flood plain by using 1 m × 1 m quadrats on June 10 2011. The cover of each species (%) was visually estimated and the litter depth (cm) was measured with a ruler. The distance between the *S. gigantea* vegetation and the *P. arundinacea* vegetation was <4 m in each plot. As the distance from the river channel was not different between the two vegetation types (~140 m), the abiotic environments, such as the flooding frequency and soil water content, were considered to be similar between them.

The removal experiments were carried out in the *S. gigantea* vegetation. The litter layer was composed mostly of dead *S. gigantea* stems. In late June 2008, five 4 m × 4 m plots were set up in the vegetation. The plots were divided into four subplots (1 m × 1 m quadrats with 0.5 m buffer zones) that were randomly assigned to one of the four treatments. The four treatments were: (i) the removal of the above-ground shoots (leaves and stems) of *S. gigantea* (A); (ii) the removal of the litter of *S. gigantea* (L); (iii) the removal of the above-ground shoots and litter of *S. gigantea* (AL); and (iv) a control (C). The above-ground shoots of *S. gigantea* were clipped out at ground level by using pruning shears and the litter was removed by hand and shears. In late July 2008, the removal of the above-ground shoots of *S. gigantea* was carried out again because the *S. gigantea* cover had regrown. On June 19 2008, vegetation surveys were conducted in 1 m × 1 m quadrats to clarify the characteristics of the vegetation before the treatments. The cover of each species was visually estimated. The maximum height of each species also was measured. On August 14 2009, the vegetation was surveyed in order to evaluate the effects of the treatments on the characteristics of the vegetation. The nomenclature refers to Osada (1989) for the native grasses, Ohwi and Kitagawa (1983) for the other natives, and Shimizu (2003) for the exotics. In late July and late September 2008, the seedlings (except those of *S. gigantea*) were counted and marked with metal flags. On August 14 2009, the survival of the seedlings that were marked in the previous year was checked.

In order to examine the influences of the *S. gigantea* litter on the seed germination of the dominant native, *P. arundinacea*, seed germination experiments were conducted in a greenhouse at the Center of Advanced Science and Technology, Hokkaido University, Sapporo, Japan. On August 21 2008, the seeds of *P. arundinacea* were collected from riparian vegetation near the studied *S. gigantea* vegetation. The seeds were stored in paper bags under room temperature until they were used. The *S. gigantea* litter, mainly composed of dead stems, was collected from the *S. gigantea* vegetation in late fall in 2008. Thirty-four transparent plastic trays with a 16 cm × 16 cm surface area and 5 cm depth were filled with vermiculite. One-half of the trays was covered by *S. gigantea* litter with a 5–7 cm depth. The other half of the trays that was not covered by litter was used as a control. In each tray, 50 *P. arundinacea* seeds were sown on the vermiculite surface on December 13 2008. The level of seedling emergence was counted for 61 days until no more germination occurred. In order to clarify the effects of the *S. gigantea* litter on light intensity, temperature and light data-loggers (HOBO, UA-002–64; Onset Computer Corporation, Bourne, MA, USA) were established on the center of the vermiculite surface in two trays that were covered by the litter and two control trays during the experimental period.

Statistical analyses

The cumulative cover of the plants, excluding *S. gigantea*, was used as the understory plant cover. Differences in the vegetation characteristics (i.e. vegetation cover, *S. gigantea* cover, understory plant cover, cover of each common plant species, maximum height of the understory plants, maximum height of *S. gigantea*, and species richness) between 2008 and 2009 were obtained by subtracting the values of 2008 from those of 2009. The changes in the vegetation characteristics from 2008 to 2009 were used as the response variables in order to evaluate the effects of the treatments on the riparian vegetation. A generalized linear model (GLM) with Gaussian error distribution was applied in order to compare the differences in the response variables between the treatment types. To clarify the combinations of treatment types that best explain the response variables, the relationships between the response variables and the treatment types were examined by model selection by Akaike's information criteria (AIC) (Burnham & Anderson 2002). All the possible groupings of treatment types were used to construct the 15 GLMs and the best model of them was selected by AIC. In order to represent the specific groupings, various expressions were introduced; for example, (A + L)(AL + C), which means that the response variables in A and L are different from those in AL and C, but that they are not different between A and L and between AL and C. Differences in the number of emerged seedlings in 2008 between the treatment types were analyzed by GLM with Poisson error distribution. The 15 possible models were constructed and the best model of them was selected by AIC.

In the greenhouse experiment, the number of emerged seedlings was compared between the trays covered by litter and the control trays by GLM with Poisson error distribution. Two models were constructed. Model I assumed that the number of seedlings differs between the tray types. Model II assumed that the number of seedlings is not different between them (i.e. the null model). The best model was determined by AIC. All the analyses were carried out using the statistical program, R 2.10.1 (R Development Core Team 2009).

RESULTS

Characteristics of the *Solidago gigantea* vegetation and the *Phalaris arundinacea* vegetation

Twenty-two species were recorded in the studied plots in June 2011. Of them, six species were exotic. The cover of the native herbs, such as *P. arundinacea*, *Artemisia montana*, and *Petasites japonicus* var. *giganteus*, was low in the *S. gigantea* vegetation, while the exotics, *Rudbeckia laciniata* and *Festuca arundinacea*, were abundant in the *P. arundinacea* vegetation (Table 1). The litter depth tended to be higher in the *S. gigantea* vegetation than in the *P. arundinacea* vegetation.

Removal experiment

Thirteen species were recorded in the *S. gigantea* vegetation (Table 2). Six species were native and seven species were exotic. Before the experiment was conducted, the vegetation was predominated by *S. gigantea*. *Phalaris arundinacea*, *P. australis*, and *Carex dispalata* were the common natives in the vegetation and *Vicia villosa* subsp. *varia* and *Solidago altissima* were the common exotics.

The vegetation cover and *S. gigantea* cover were low in the A and AL treatments, but they increased in the L and C treatments (Fig. 1). The understory plant cover increased in the A and AL treatments, but did not change in the L and C treatments. (A + AL)(L + C) was selected as the best model of the GLMs for explaining the changes from 2008 to 2009. The increases in the understory plant cover of the A and AL treatments were associated with increases in *P. arundinacea* (Fig. 2 and Table 2). The cover of the native grass, *P. australis*, increased in the A treatment, but the increase was slight (Fig. 2). The cover of the native sedge, *C. dispalata*, was not affected by the experiments (Fig. 2). These results

Table 1. Means and standard deviations for the cover of plant species with >5% frequencies in *Solidago gigantea* vegetation and the neighboring *Phalaris arundinacea* vegetation

Species	*Phalaris arundinacea* Vegetation	*Solidago gigantea* Vegetation
Solidago gigantea†	21.3 ± 27.0	93.8 ± 6.0
Phalaris arundinacea	71.8 ± 28.2	3.1 ± 3.9
Artemisia montana	12.5 ± 8.5	2.1 ± 2.4
Phragmites australis	0.9 ± 0.9	2.0 ± 1.6
Poa pratensis†	0.5 ± 0.8	1.6 ± 2.0
Rudbeckia laciniata†	2.4 ± 4.0	0.6 ± 2.2
Solidago altissima†	0.2 ± 0.6	1.5 ± 2.9
Miscanthus sacchariflorus	–	0.7 ± 1.4
Cirsium kamtschaticum	1.2 ± 2.7	0.2 ± 0.4
Vicia villosa subsp. *varia*†	1.3 ± 4.2	1.5 ± 4.1
Equisetum arvense	0.1 ± 0.3	0.1 ± 0.3
Petasites japonicus var. *giganteus*	6.4 ± 14.3	–
Festuca arundinacea†	3.6 ± 9.2	–
Carex dispalata	–	1.1 ± 3.3
Calystegia japonica	–	0.2 ± 0.6
Vegetation cover (%)	94.9 ± 5.7	96.1 ± 4.0
Litter depth (cm)	7.1 ± 2.2	9.2 ± 2.0

† Exotic species.

indicated that the removal of the above-ground shoots of *S. gigantea* reduced the cover of *S. gigantea* and increased that of the native grass, *P. arundinacea*. The cover of the exotic forb, *S. altissima*, increased in the AL treatment and (A + L + C)(AL) was selected as the fittest model (Fig. 2 and Table 2), indicating that the cover of *S. altissima* increased when both the above-ground shoots and the litter of *S. gigantea* were removed. The removal experiments did not affect the cover of the exotic legume, *V. villosa* subsp. *varia* (Fig. 2). The fittest model for explaining the effects of removal on species richness was the null model (Fig. 1). This showed that the species richness was not affected by the removal experiments. The maximum height of the understory plants, mainly composed of *P. arundinacea* or *P. australis*, in the L and AL treatments increased compared with that in the A and C treatments (Fig. 1), showing that the removal of the litter layer facilitated the height growth of the understory plants. The maximum height of *S. gigantea* was not different between the treatments (Fig. 1). All the emerged seedlings were of *P. arundinacea*. The highest density of seedlings was observed in the AL treatment (Fig. 1). A few seedlings emerged in the A and L treatments, but no seedling emerged in the C treatment. (A + L)(AL)(C) was selected by AIC for explaining the differences in seedling density between the treatment types, showing that the seedling density was highest in the AL treatment, was intermediate in the A and L treatments, and was lowest in the C treatment. All the emerged seedlings died until August 2009, probably because of the shading by the recovered large plants, including *S. gigantea*. No seedling of the understory plants emerged in 2009.

Seed germination experiment in the greenhouse

The level of seed germination of *P. arundinacea* was higher in the control trays (mean ± standard deviation; 0.94 ± 1.09 seeds per tray) than in the trays that were covered by litter (0.35 ± 0.61 seeds per tray), although the number of germinated seeds was extremely low in the greenhouse, probably related to seed dormancy. The AIC of model I (75.2) was lower than that of the null model (77.9), showing that the number of germinated seeds was different between the litter-covered and bare surfaces. The litter of *S. gigantea* might decrease the seed germination. In addition, there is a possibility that the experiments in this study underestimated the effect of the litter because the litter's thickness on the trays was shallower than that in the *S. gigantea* vegetation (Table 1). The mean, minimum, and maximum light intensity were 130, 0 and 40,000 lx under the litter and 3100, 0, and 69,000 lx in the control. The light intensity at the vermiculite surface was lower under the litter. The mean, minimum, and maximum temperature on the vermiculite surface was 13.6, 8.6, and 24.5°C in the litter-covered trays and 13.5, 8.6, and 24.6°C in the control trays. The temperature on the vermiculite surface was not affected by the litter.

DISCUSSION

The cover of the native grass, *P. arundinacea*, increased in the A and AL treatments. The removal of invasive plant canopies often increases the abundance or growth of plants due to the reduction in light competition (Coleman & Levine 2007; Siemens & Blossey 2007). Disruption of the *S. canadensis* canopy by disturbances improves the levels of light and soil moisture and increases the understory plant cover (Armesto & Pickett 1985). The rhizome density of *S. altissima* is decreased by mowing due to the reduced production of new rhizomes (Meyer & Schmid 1999). Therefore, the below-ground competition between *S. gigantea* and *P. arundinacea* might be weakened because of a reduction in *S. gigantea* rhizome production by the removal of the above-ground shoots. The removal of *S. gigantea* shoots could promote

Table 2. Means and standard deviations for the cover of plant species in 1 m × 1 m plots in each experiment

Species	Pre-experiment	A	L	AL	C
	Number of plots				
	20	5	5	5	5
Solidago gigantea†	93.3 ± 7.0	46.0 ± 19.8	98.0 ± 2.7	46.0 ± 20.7	95.0 ± 6.1
Phalaris arundinacea	9.8 ± 7.7	41.0 ± 20.1	9.2 ± 6.5	37.0 ± 23.9	11.0 ± 8.4
Phragmites australis	1.9 ± 2.1	4.4 ± 1.7	1.8 ± 1.9	1.2 ± 1.3	2.2 ± 1.6
Carex dispalata	3.3 ± 4.8	0.6 ± 1.3	5.8 ± 4.7	6.2 ± 5.2	1.2 ± 1.6
Vicia villosa subsp. *varia*†	3.5 ± 4.9	5.2 ± 6.9	3.8 ± 4.8	7.8 ± 7.5	1.2 ± 2.2
Solidago altissima†	0.3 ± 0.8	4.0 ± 6.3	0.6 ± 0.9	12.0 ± 26.8	0.8 ± 1.3
Rudbeckia laciniata†	–	0.6 ± 1.3	–	–	–
Miscanthus sacchariflorus	0.9 ± 3.4	–	2.0 ± 2.7	2.0 ± 3.1	0.6 ± 1.3
Rumex obtusifolius†	0.2 ± 0.9	–	0.2 ± 0.4	0.2 ± 0.4	–
Equisetum arvense	0.0 ± 0.1	–	–	–	–
Poa pratensis†	0.0 ± 0.1	–	–	0.2 ± 0.4	–
Polygonum sachalinense	–	–	–	–	4.0 ± 8.9
Trifolium repens†	0.0 ± 0.0	–	–	–	–
Vegetation cover (%)	96.9 ± 4.1	87.0 ± 7.6	100.0 ± 0.0	89.0 ± 8.9	100.0 ± 0.0
Understory cover (%)‡	19.8 ± 11.1	55.8 ± 17.6	23.4 ± 15.9	66.6 ± 25.1	21.0 ± 11.2
Maximum height of understory plants (cm)	134.3 ± 24.1	161.3 ± 21.8	184.0 ± 12.9	179.0 ± 21.9	176.0 ± 16.7
Maximum height of *S. gigantea* (cm)	109.3 ± 11.9	165.0 ± 28.6	174.0 ± 11.4	170.0 ± 33.9	177.0 ± 14.8
Species richness	4.0 ± 1.1	4.6 ± 0.5	5.2 ± 1.6	5.0 ± 1.2	4.4 ± 1.5

† Exotic species; ‡ understory cover is the cumulative cover of plants, excluding *S. gigantea*. A, removal of the above-ground shoots of *S. gigantea*; AL, removal of the above-ground shoots and litter of *S. gigantea*; C, control; L, removal of the litter of *S. gigantea*.

the growth and expansion of *P. arundinacea* by releasing above-ground and below-ground interference from *S. gigantea*.

The maximum height of the understory plants, mainly *P. arundinacea* or *P. australis*, increased in the treatments that removed the litter of *S. gigantea* (i.e. L and AL). This litter is likely to impede the initial growth of native grasses in early spring because thick litter layers often become a mechanical barrier for the sprouting of understory plants (Facelli & Pickett 1991a). The removal of the *S. gigantea* litter might assist the development of native grassland by facilitating the initial growth of native grasses.

The greenhouse experiment suggested the possibility that the *S. gigantea* litter decreases the seed germination of *P. arundinacea*, although the seed germination rate was extremely low in the greenhouse. In addition, the *S. gigantea* litter lowered the light intensity on the ground surface. The light intensity decreases with increases in *Solidago* litter (Facelli & Pickett 1991b). The seed of *P. arundinacea* does not germinate in the dark (Lindig-Cisneros & Zedler 2001). The thick litter in *S. gigantea* vegetation might inhibit the seed germination of *P. arundinacea* because of the low light availability on the ground surface. In the removal experiments, the highest density of seedlings was observed in the AL treatment, while a few seedlings emerged in the A and L treatments. Invasive plants often hamper the emergence and establishment of other plants by both their canopy and litter (Foster & Gross 1998; Craine & Orians 2004; Coleman & Levine 2007). *Solidago gigantea* will suppress the seed germination and seedling emergence of *P. arundinacea* by interference from both its canopy and litter. All the emerged seedlings died 1 year after the experiments, suggesting that the litter removal did not promote the seedlings' establishment. The removal of the above-ground shoots and litter layer effectively promotes the seedling emergence of *P. arundinacea*, but it is not suitable for seedling establishment. As the causes of death of the emerged seedlings were considered to be mainly the shading by the recovered large plants, including *S. gigantea*, the above-ground shoots and litter layer need to be continuously removed to facilitate the seedlings' establishment.

The removal of an invasive plant often facilitates the establishment and growth of other exotic plants (Reid

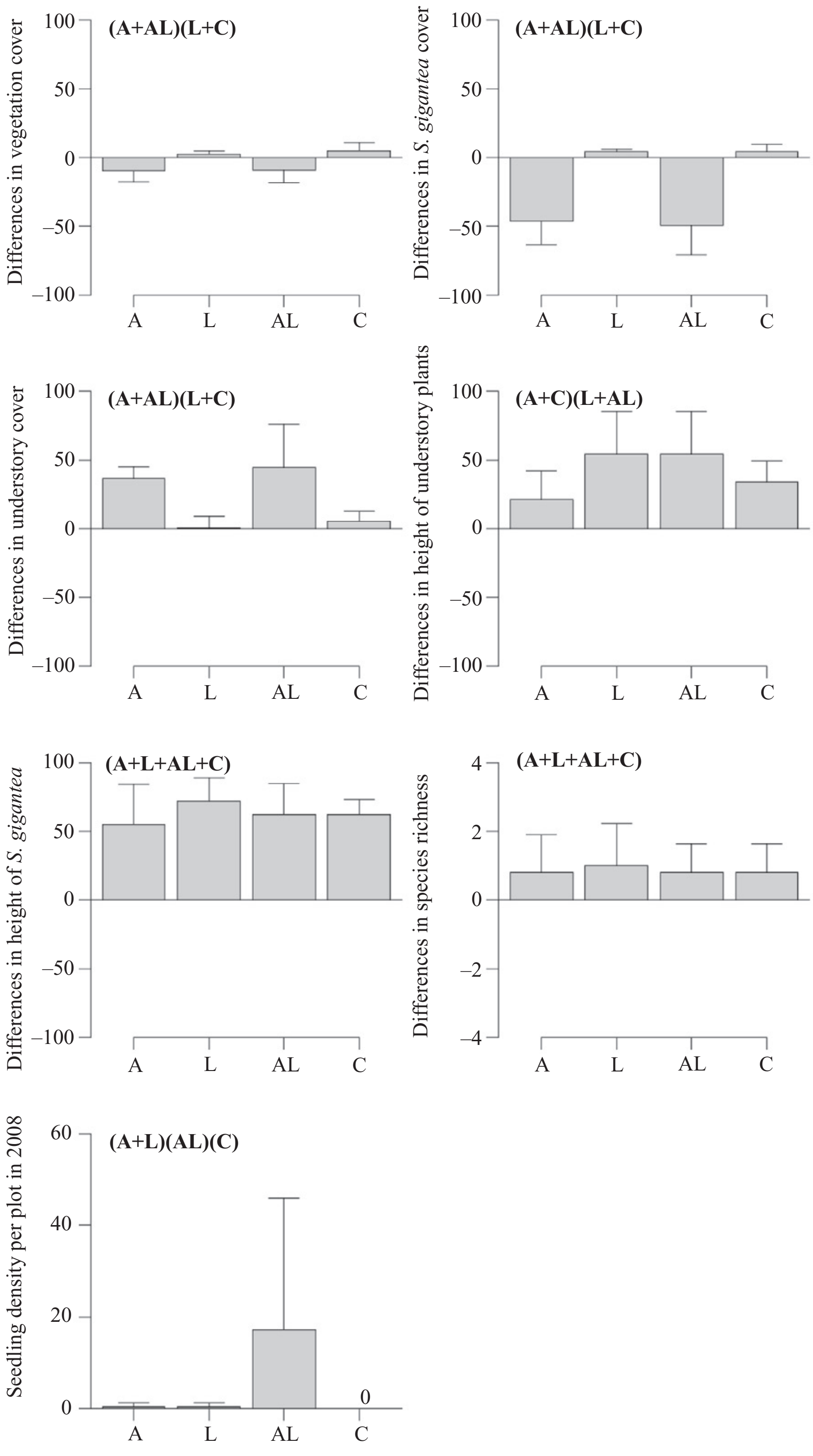

Fig. 1. Response of vegetation characteristics to each removal treatment. The means and standard deviations are shown. The differences in vegetation characteristics between 2008 and 2009 were obtained by subtracting the values of 2008 from those of 2009. The bold letters show the fittest generalized linear model with the smallest Akaike's information criteria that explains the response variables best. A, removal of the above-ground shoots of *Solidago gigantea*; AL, removal of the above-ground shoots and litter of *S. gigantea*; C, control; L, removal of the litter of *S. gigantea*.

et al. 2009). The removal of the above-ground shoots and litter of *S. gigantea* facilitated the recovery of both the natives and the exotic forb, *S. altissima*, the latter being observed in the *S. gigantea* vegetation. These results indicated that *S. gigantea* suppresses *S. altissima* by interference from its canopy and litter accumulation and that the removal of the suppression by the shoots and litter promotes the growth of *S. altissima*. As *S. altissima* negatively

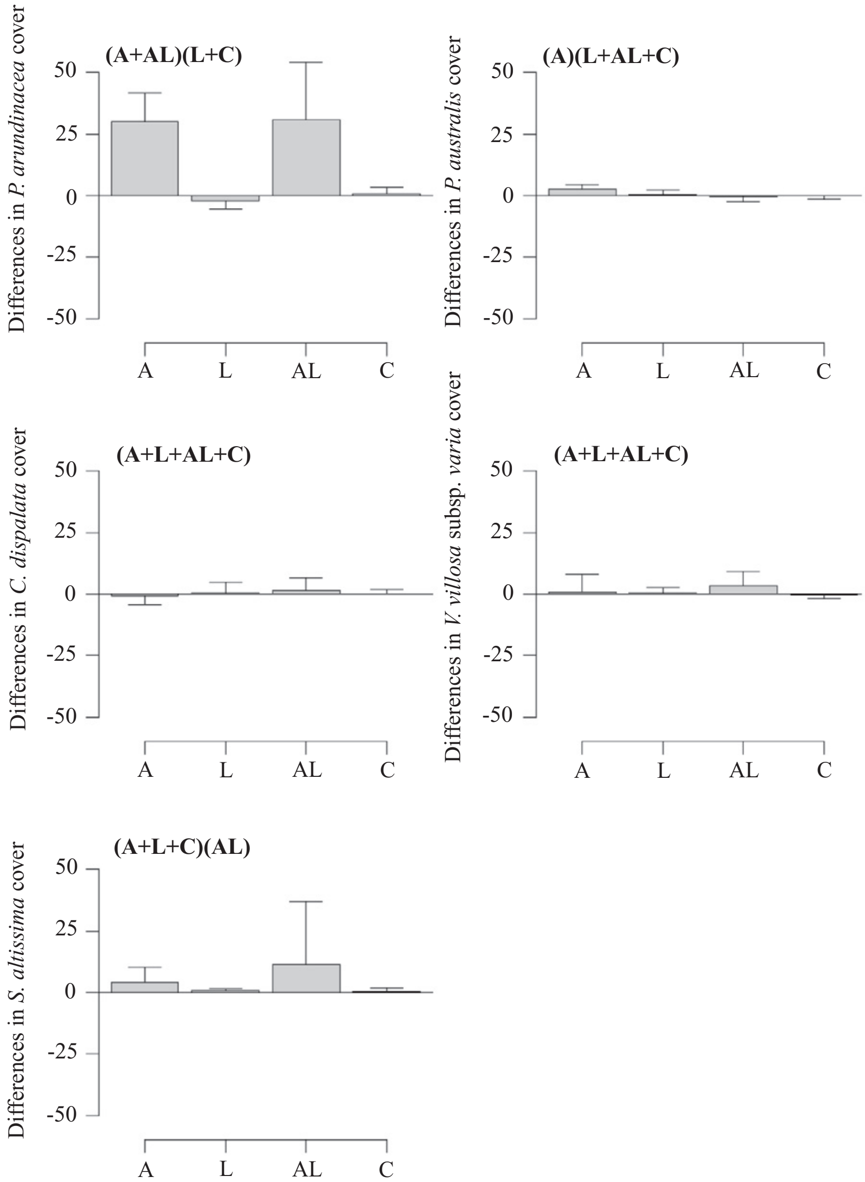

Fig. 2. Response of the common understory plant species to each treatment. The means and standard deviations are shown. The differences in plant cover between 2008 and 2009 were obtained by subtracting the cover of 2008 from that of 2009. The bold letters show the fittest generalized linear model with the smallest Akaike's information criteria that explains the response variables best. A, removal of the above-ground shoots of *Solidago gigantea*; AL, removal of the above-ground shoots and litter of *S. gigantea*; C, control; L, removal of the litter of *S. gigantea*.

affects the native plants (Kobayashi *et al*. 1980), the compensatory increases in *S. altissima* might impact the native plants, such as *P. arundinacea*. The removal of not only *S. gigantea*, but also the other exotics, should be conducted in order to promote more effectively the native vegetation's recovery.

This study showed that the removal of the above-ground shoots and litter of *S. gigantea* is an effective tool for promoting the emergence and recovery of native grassland vegetation if exotics, such as *S. altissima*, are not present in the *S. gigantea* vegetation. Not only the above-ground shoots of *S. gigantea*, but also its litter layer, should be removed when the replacement of *S. gigantea* vegetation by native grassland is needed. However, the cover of *S. gigantea* reached 40% 1 year after the removal of the above-ground shoots in this study. As *S. gigantea* has a high regeneration ability from the rhizome fragments (Weber 2011), *S. gigantea* could regrow rapidly following the removal experiments. The rapid recovery of *S. gigantea* again negatively influences native plants. The continuous removal of the *S. gigantea* canopy and its litter long term is required in order to reduce *S. gigantea* and to facilitate the establishment of native grassland vegetation. In addition, the development of management tools to inhibit more effectively the abundance of *S. gigantea* is needed.

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REFERENCES

Armesto J.J. and Pickett S.T.A. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology* **66**, 230–240.

Burnham K.P. and Anderson D.R. 2002. *Model Selection and Multiple Inference*, 2nd edn. Springer, New York.

Carson W.P. and Peterson C.J. 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. *Oecologia* **85**, 8–13.

Chapuis-Lardy L., Vanderhoeven S., Dassonville N., Koutika L.S. and Meerts P. 2006. Effect of the exotic invasive plant *Solidago gigantea* on soil phosphorus status. *Biol. Fertil. Soils* **42**, 481–489.

Coleman H.M. and Levine J.M. 2007. Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. *Biol. Invasions* **9**, 65–71.

Craine S.I. and Orians C.M. 2004. Pitch pine (*Pinus rigida* Mill.) invasion of Cape Cod pond shores alters abiotic environment and inhibits indigenous herbaceous species. *Biol. Conserv.* **116**, 181–189.

D'Antonio C.M., Hughes R.F., Mack M., Hitchcock D. and Vitousek P.M. 1998. The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. *J. Veg. Sci.* **9**, 699–712.

Facelli J.M. and Pickett S.T.A. 1991a. Plant litter: its dynamics and effects on plant community structure. *Bot. Rev.* **57**, 1–32.

Facelli J.M. and Pickett S.T.A. 1991b. Plant litter: light interception and effects on an old-field plant community. *Ecology* **72**, 1024–1031.

Foster B.L. and Gross K.L. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology* **79**, 2593–2602.

Güsewell S., Zuberbühler N. and Clerc C. 2005. Distribution and functional traits of *Solidago gigantea* in a Swiss lakeshore wetland. *Bot. Helv.* **115**, 63–75.

Hulme P.E. and Bremner E.T. 2006. Assessing the impacts of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *J. Appl. Ecol.* **43**, 43–50.

Jäger H. and Kowarik I. 2010. Resilience of native plant community following manual control of invasive *Cinchona pubescens* in Galápagos. *Restor. Ecol.* **18**, 103–112.

Japan Meteorological Agency 2010. [*Climate Statistics*.] [Cited 4 October 2010.] Available from URL: http://www.data.jma.go.jp/obd/stats/etrn/index.php (in Japanese).

Kobayashi A., Morimoto S., Shibata Y., Yamashita K. and Numata M. 1980. C_{10}-polyacetylenes as allelopathic substances in dominants in early stages of secondary succession. *J. Chem. Ecol.* **6**, 119–131.

Kohli R.K., Jose S., Singh H.P. and Batish D.R. 2009. *Invasive Plants and Forest Ecosystems*. CRC Press, Boca Raton, FL.

Koutika L.S., Vanderhoeven S., Chapuis-Lardy L., Dassonville N. and Meerts P. 2007. Assessment of changes in soil organic matter after invasion by exotic plant species. *Biol. Fertil. Soils* **44**, 331–341.

Larson D.L. and Larson J.L. 2010. Control of one invasive plant species allows exotic grasses to become dominant in northern Great Plains grasslands. *Biol. Conserv.* **143**, 1901–1910.

Lindig-Cisneros R. and Zedler J. 2001. Effect of light on seed germination in *Phalaris arundinacea* L. (reed canary grass). *Plant Ecol.* **155**, 75–78.

Meyer A.H. and Schmid B. 1999. Experimental demography of rhizome populations of establishing clones of *Solidago altissima*. *J. Ecol.* **87**, 42–54.

Miyawaki S. and Washitani I. 2004. Invasive alien plant species in riparian areas of Japan: the contribution of agricultural weeds, revegetation species and aquacultural species. *Glob. Environ. Res.* **8**, 89–101.

Myers J.H. and Bazely D.R. 2003. *Ecology and Control of Introduced Plants*. Cambridge University Press, Cambridge.

Namikawa K., Wang X. and Saito M. 1995. [Vegetation in the floodplain of the Barato River, central Hokkaido, Japan.] *J. Hokkaido Univ. Educ. Sect. II B* **45**, 7–16 (in Japanese with English abstract).

Nigatu L., Hassen A., Sharma J. and Adkins S.W. 2010. Impact of *Parthenium hysterophorus* on grazing land communities in north-eastern Ethiopia. *Weed Biol. Manag.* **10**, 143–152.

Niiyama K. 1987. [Distribution of salicaceous species and soil texture of habitats along the Ishikari River.] *Jpn. J. Ecol.* **37**, 163–174 (in Japanese with English abstract).

Ohwi J. and Kitagawa M. 1983. [*New Flora of Japan*.] Shibundo, Tokyo (in Japanese).

Osada T. 1989. [*Illustrated Grasses of Japan*.] Heibonsha, Tokyo (in Japanese).

R Development Core Team 2009. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Comuputing, Vienna.

Radosevich S.R., Holt J.S. and Ghersa C.M. 2007. *Ecology of Weeds and Invasive Plants*, 3rd edn. John Wiley & Sons, Hoboken, NJ.

Reid A.M., Morin L., Downey P.O., French K. and Virtue J.G. 2009. Does invasive plant management aid the restoration of natural ecosystems? *Biol. Conserv.* **142**, 2342–2349.

Ruprecht E., Enyedi M.Z., Eckstein R.L. and Donath T.W. 2010. Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation. *Biol. Conserv.* **143**, 449–456.

Saito T.I. and Okubo K. 2011. The relationship between alien herb *Coreopsis lanceolata* and soil texture types on gravelly floodplain vegetation in central Japan. *Veg. Sci.* **28**, 39–47.

Scharfy D., Eggenschwiler H., Olde Venterink H., Edwards P.J. and Güsewell S. 2009. The invasive alien plant species *Solidago gigantea* alters ecosystem properties across habitats with differing fertility. *J. Veg. Sci.* **20**, 1072–1085.

Scharfy D., Funk A., Olde Venterink H. and Güsewell S. 2011. Invasive forbs differ functionally from native graminoids, but are similar to native forbs. *New Phytol.* **189**, 818–828.

Shimizu T. 2003. [*Naturalized Plants of Japan*.] Heibonsha, Tokyo (in Japanese).

Siemens T.J. and Blossey B. 2007. An evaluation of mechanisms preventing growth and survival of two native species in invasive Bohemian knotweed (*Fallopia* × *bohemica*, Polygonaceae). *Am. J. Bot.* **94**, 776–783.

Weber E. 2011. Strong regeneration ability from rhizome fragments in two invasive clonal plants (*Solidago canadensis* and *S. gigantea*). *Biol. Invasions* **13**, 2947–2955.

Weber E. and Jakobs G. 2005. Biological flora of central Europe: *Solidago gigantea* Aiton. *Flora* **200**, 109–118.