

PITS CONSERVE SPECIES DIVERSITY IN AN OVERGRAZED GRASSLAND

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(Received 20th March 2006; accepted 15th May 2007)

Abstract. Decrease in species diversity by overgrazing is one of the crucial indicators for ecosystem deterioration. Sika deer (*Cervus nippon* Temminck) has grazed various plants on Nakajima Island, Hokkaido, Japan, for a few decades, due to low food availability. We examined if diverse microtopography supported high species diversity by conserving specific plants on the grassland of the island where overgrazing by deer occurred. Based on TWINSpan analysis, three plant community types were classified: grasslands represented by short seed plants, ferns, and unpalatable forbs. Grasslands dominated by short and/or unpalatable seed plants established on the flat ground, while fern species except *Equisetum arvense* did not establish there. Soil hardness was higher on short-plant grasslands than on unpalatable-forb grasslands, suggesting that palatability on plants was related to plant community differentiation on the flat ground. Of 10 fern species recorded, 9 species established mostly in deep pits. Pit depth was more important than pit area to maintain high fern diversity. Those results indicated that diverse microtopography, i.e., pit development, supports fern diversity, because of the multiplier effects of predator avoidance and preferable sites for fern establishment. Diverse and/or specific microtopography must be a prerequisite to conserve rare species and high diversity in such disturbed areas.

Keywords: *fern diversity, grassland, microtopography, overgrazing by deer, palatability, pit depth*

Introduction

Grazing by mammals, including deer, greatly affects plant species composition in relation to species attributes, such as palatability and morphological traits, and *vice versa* [8, 23]. Particularly, deer are over-populated on the world-natural heritages assigned by UNESCO in Japan, and modify the ecosystems [30]. Overgrazing by deer has been conspicuous for a few decades in a grassland on Nakajima (or Nakanoshima) Island, Hokkaido, northern Japan, because grassland often shows higher productivity than forest under story [15]. Palatable plants decline greatly in the grassland on Nakajima Island after the explosion of deer density, and then deer tend to eat whatever food is available when food availability is low, e.g., in winter [24]. Palatability is related to taxa and/or life-forms, for example, livestock-grazed sites have a higher proportion of prostrate species, early flowering, cryptophytes (plant whose growth buds survive seasons with adverse conditions below ground), etc. than ungrazed sites in grasslands, Central Spain [17, 20]. Totally, moose has negative effects on vascular plants but has few effects on mosses [5].

Diverse microtopography supports high species diversity and/or rare species in disturbed ecosystems by changing micro-environments [21, 28, 29]. Microsites may provide safe sites for plant establishment by escaping from grazing pressures. We

suspect that plants can escape from grazing by two ways: unpalatable habits and the utilization of microtopography. Furthermore, when plants can escape from grazing by using microtopography, the characteristics of microtopography, such as shape and size, influence grazing pressures [1]. We evaluate: (1) Palatability is related to plant community differentiation, in particular, unpalatable plants still remained on overgrazed areas. (2) Specific species establish in distinct microhabitats by avoiding grazing. (3) What microhabitat characteristics regulate species diversity? To demonstrate those, we examined how the effects of deer overgrazing modified plant community structure with reference to plant taxa, i.e., seed plants vs ferns, and microtopography, i.e., flat vs pit.

Study area and methods

Nakajima Island (497 ha, summit = 455 m a.l.s.) is enclosed by a caldera lake, Lake Toya. Volcanic upheaval formed this island 40,000-50,000 BP. On this island, three major vegetation types are recognized: deciduous forest represented by *Acer mono* and *Tilia japonica*, needle-leaved plantation, and grassland [15]. The snow period is from December to April and the maximum snow depth is ca 50 cm on February in usual years.

On the island, a male adult sika deer (*Cervus nippon* Tamminck) was introduced in 1957, an 1-year-old female was introduced in 1958, and a pregnant was introduced in 1965. All deer on this island in the present is considered to be originated from the three individuals. The population became over-populated, i.e., 31.5/km², in 1980, and then palatable plants, such as *Angelica ursina*, *Polygonum sachalinense*, *Cacalia hastata* var. *orientalis* and *Miscanthus sinensis*, were fed and their abundance declined [11], while unpalatable plants, e.g., *Pachysandra terminalis*, *Cynanchum caudatum*, and *Senecio cannabifolius*, became dominant in areas where palatable plants decreased in cover. Deer density was 57.5/km² in maximum recorded in 1983, and then crashed in the spring of 1984 due to starvation, and then sika deer began feeding on fallen leaves and unpalatable plants [24].

The vegetation surveys were conducted in the late June of 1996 on the grassland where depressions had been established. When the survey was conducted, the whole ground surface on the grassland was completely modified by deer grazing and thus we could not establish ungrazed plots. Of the depressions, pits that had perpendicular side-wall were developed conspicuously (*Figure 1*). These pits seemed to be developed by ancient volcanic activities, i.e., depression holes and fumaroles. A few conical depressions were also observed. To investigate the topographical effects on plant community patterns, we measured long/short axes and depth of depressions. Surface area is calculated as oval shape. Since the surface area of depressions averaged 0.78 m², 27 1 m × 1m quadrates were additionally set up on the flat ground, i.e., elevation difference was zero. Hereafter, we call depressions and quadrates 'plot' for the convenient sake. Cover on each taxa was recorded in each plot. Nomenclature follows [18] for seed plants, [16] for ferns, and [7] for mosses. Litter thickness was measured by a ruler, and the soil hardness was measured by a hardness tester (Type A-0858, Yamaoka System, Tokyo) on each plot. On the measurement of litter thickness and soil hardness, five points were measured and the averaged value was used for each plot. On four pits selected, soil temperature, soil moisture and photon flux density (PFD) were measured at 0, 10, 20 and 40 cm deep in the summer of 2005. The ranges of pit-section diameter and depth were, respectively, from 22 cm to 130 cm and from 40 cm to 110

cm. Air temperature and PFD at 20 cm above the ground surface were also measured. In each depth, the measurements were conducted three times. Soil temperature was measured by inserting the sensor of a portable thermometer (Digimult Model D611, Takara Thermsitor Instruments Co., Ltd, Yokohama) into soil. Soil moisture was measured by time-domain reflectance (TDR), using a portable water content meter (Hydrosense, Campbell Scientific, Inc., Logan, Utah). The unit of water content is volumetric (%). Photon flux density (PFD) was measured by two sensors (Quantum LA-190SA, LI-COR Inc., Lincoln, Nebraska). One sensor was used for control and another is for the reference. For the reference, PFD was measured adjacent to the side-wall of pit. Then, PFD was expressed as relative PFD by $(\text{PDF at the target})/(\text{PDF at control}) \times 100$. The relationship between relative PFD and distance from the ground surface was examined by a logarithmic regression [31].

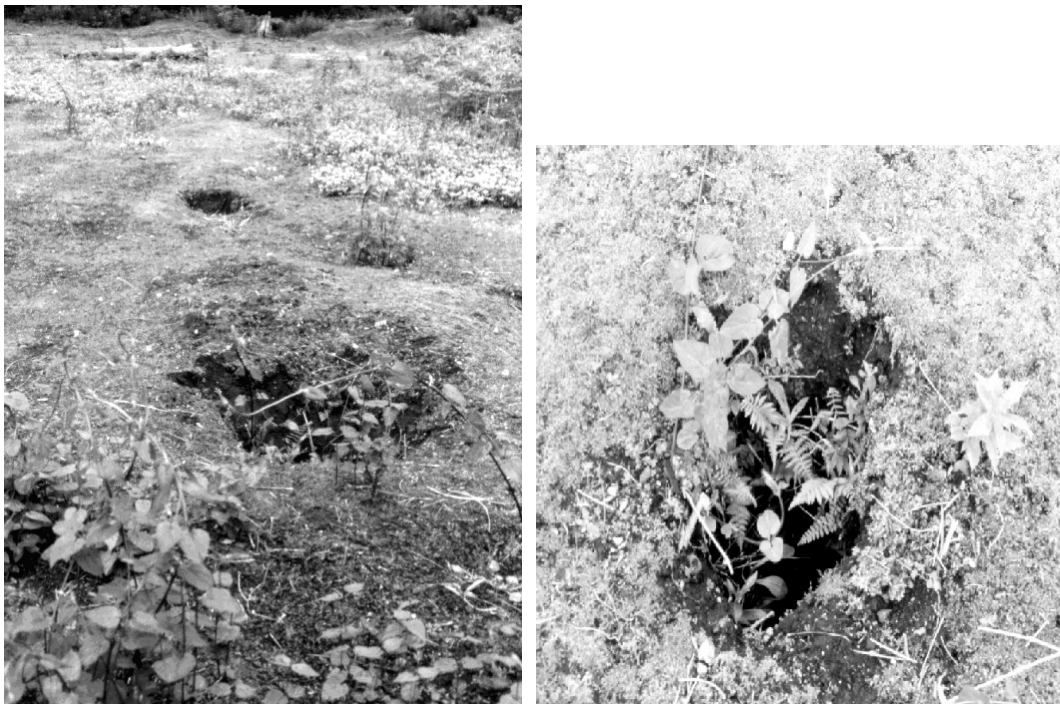


Figure 1. *Vegetation patterns in the surveyed area.*

A: Three surveyed pits are shown by enclosed circles. B: Close-up of a pit. The arrow indicates the establishment of fern.

Three taxa were used in the present study: moss, fern, and seed plants. Plant community types were extracted by TWINSpan cluster analysis [9]. Detrended correspondence analysis (DCA) was performed to inspect the establishment patterns of species and plots [10]. On TWINSpan and DCA, species that were recorded in two or more plots were used after square-root transformation. Species richness may not be appropriate for the comparison of community diversity, because plot size varied. Therefore, not only species richness but also Shannon-Wiener's species diversity (H') was calculated on each plot based on cover values [31]. H' is more robust against sample size effects than species richness [13]. The multiple comparisons were conducted by Scheffe's tests when ANOVA had the significant difference at $P < 0.05$.

To confirm the significant characteristics of pits on fern diversity, zero-inflated Poisson regression was applied by using number of fern species as dependent variable and depth and area as independent variables [14]. On the regression, 1 m × 1 m quadrates established on the flat were not used, because the area did not represent the area of concave part. We examined three models, fern richness explained by pit depth, by area, and by depth and area as follows.

$$P(Y = 0|x, z) = 1 - p(x) + p(x)\exp(-\lambda(z)), \quad (\text{Eq. 1})$$

$$P(Y = r|x, z) = p(x) \frac{\exp(-\lambda(z))\lambda(z)^r}{r!}, \text{ where } r > 0 \text{ (integer)}. \quad (\text{Eq. 2})$$

Here $p(x)$ is the probability of observing at least one fern species in a plot, $\lambda(z)$ is the truncated Poisson distribution of the number of observed fern species. Based on Akaike's Information Criteria, we selected the best model [22].

Results

Plant community patterns

In total, 47 seed plants, 10 ferns and 4 mosses were recorded. The most frequent seed plant taxa were *Sagina japonica* and *Cynanchum caudatum*, both of which frequencies were > 80% (Table 1). Based on TWINSpan cluster analysis, three plant community types (hereafter, groups A, B and C) are recognized (Figure 2). Groups A and B are separated from group C by the dominance of a moss, *Polytrichum juniperium*, and by low cover and frequency of *Senecio cannabifolius* and *Pachysandra terminalis* (Table 1). *S. cannabifolius* is a tall forb, and *P. terminalis* is a stoloniferous shrub-like forb. Both of them are unpalatable for deer. Group A was separated from group B by the dominance of *Sagina japonica*. Group B did not have any representative species for community type, but if pressed *S. japonica* and *Cynanchum caudatum* established most frequently with low cover. Furthermore, group B and was characterized by the establishment of ferns, represented by *Athyrium vidalii*, *Matteuccia struthiopteris*, and *Dryopteris austriaca*. The other ferns were *Equisetum arvense*, *Aachnioides standihii*, *Dennstaedtia wilfordii*, *Lunathyrium pycnosorum*, *Adiantum pedatum*, *Cyrtomium fortunei* var. *clivicola*, and *Matteuccia orientalis*. Four moss species were recorded from 90% of the plots examined. The common mosses were *Ceratodon purpureus*, *Polytrichum juniperium*, *Myuroclada maximoviczii*, and *Marchantia polymorpha*. Although a few other minor mosses were also established infrequently with low cover, the identification of those minor moss species was difficult in the field. Therefore, the minor moss species were recorded together with any common moss species.

Total plant cover per plot averaged 35% for all the plots (Table 1), but differed greatly between the three community types. Group C showed the highest total cover, i.e., 65%, but group B showed only 5%. Ferns established less in groups A and C, while they established frequently in group B with < 1% in averaged cover. Averaged moss cover was < 10% in any plant community groups, although mosses established in 90% of plots.

Table 1. The leading species of seed plants and ferns based on TWINSpan cluster group. Mean coverage is shown with percentage frequency in parentheses. +: less than 1%. -: no individuals observed. Mean plot depth, litter thickness and soil hardness are shown with standard error. The same letters indicate non-significantly different at $P < 0.01$ (Scheffe's test). Pseudospecies grouped by TWINSpan are boldface.

Cluster group code	A	B	C	Total
Number of plots	27	36	31	94
Depth (cm)	11 ± 12 ^a	80 ± 7 ^b	11 ± 3 ^a	37 ± 4
Litter thickness (cm)	2.5 ± 0.4 ^a	5.0 ± 0.7 ^a	3.1 ± 0.4 ^a	2.8 ± 0.3
Soil hardness (kg/cm ²)	3.4 ± 0.3 ^a	2.3 ± 0.2 ^b	1.8 ± 0.3 ^b	2.5 ± 0.3
Seed plant				
<i>Sagina japonica</i>	23.5 (100)	0.1 (72)	3.3 (87)	7.9 (85)
<i>Cynanchum caudatum</i>	4.3 (78)	0.2 (72)	5.3 (94)	3.2 (81)
<i>Veronica arvensis</i> *	0.1 (67)	+ (67)	0.2 (90)	0.1 (74)
<i>Oxalis corniculata</i>	0.7 (81)	0.1 (61)	0.9 (71)	0.5 (70)
<i>Taraxacum officinale</i> *	1.3 (85)	+ (39)	1.7 (77)	1.0 (65)
<i>Poa annua</i>	1.8 (93)	0.1 (56)	0.8 (56)	0.8 (66)
<i>Erigeron annuus</i> *	0.1 (56)	0.1 (61)	0.1 (29)	0.1 (49)
<i>Pachysandra terminalis</i>	-	0.7 (11)	29.0 (74)	9.8 (29)
<i>Senecio cannabifolius</i>	-	0.1 (11)	17.8 (58)	5.9 (21)
Fern				
<i>Athyrium vidalii</i>	+ (4)	0.1 (39)	-	+ (16)
<i>Matteuccia struthiopteris</i>	-	0.2 (33)	-	+ (13)
<i>Dryopteris austriaca</i>	-	0.1 (33)	-	+ (13)
Total cover				
Seed plant	34.1 (100) ^a	2.3 (100) ^b	61.2 (100) ^c	30.9 (100)
Fern	+ (7) ^a	0.6 (61) ^b	+ (3) ^a	0.2 (27)
Moss	7.3 (96) ^a	1.9 (92) ^a	3.9 (84) ^a	4.1 (90)
All	41.4 (100) ^a	4.8 (100) ^b	65.1 (100) ^c	35.2 (100)

* naturalized plants.

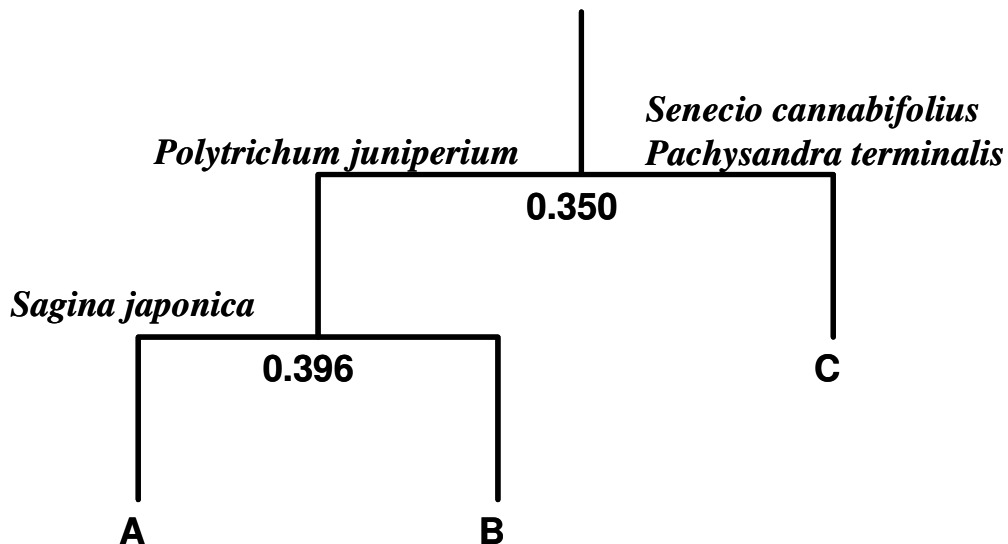


Figure 2. Plant communities determined by TWINSpan. Eigenvalues and indicator species for each division are shown.

Biodiversity

Species richness (total number of species per plot) did not differ significantly among the three groups, and species diversity was also not different (Table 2). Seed plant richness and diversity were not different among the groups, as well as total species richness and diversity, because major species composition was from seed plants. In contrast, fern species richness and diversity were significantly higher in group B than in groups A and C.

Because one or less fern species established in depressions less than 50 cm deep, fern diversity was zero there (Table 2). Therefore, fern species richness and diversity were clearly higher in pits with > 50 m deep (Figure 3). Zero-inflated Poisson regression detected that the model only using pit depth was best to explain fern species richness, indicating that pit depth is more important than pit area to conserve fern diversity. The equations, $p(x)$ and $\lambda(z)$ are:

$$\log(\lambda(z)) = a + b \cdot (\text{depth}) = 4.665 - 0.101 \cdot (\text{depth}) \quad (\text{Eq. 3})$$

$$\text{logit}(p(x)) = \log(p(x)/(1 - p(x))) = c + d \cdot (\text{depth}) = 0.341 + 0.004 \cdot (\text{depth}) \quad (\text{Eq. 4})$$

Here, a , b , c and d are respective coefficients. The coefficients a and b were not significant and c and d were significant at $P < 0.05$. Those implied that the depth is positively related to presence/absence of ferns, although fern species richness is not explained by Poisson distribution.

Table 2. Comparison of species richness and diversity between cluster groups determined by TWINSpan in relation to total species, seed plant, and fern. Each value shows mean with standard error. The same letters indicate non-significantly different at $P < 0.01$ (Scheffe's test).

Cluster group code	A	B	C	Total
All				
Species richness	8.6 ± 0.3 ^a	10.3 ± 0.7 ^a	9.4 ± 0.4 ^a	9.5 ± 1.0
Species diversity	1.14 ± 0.09 ^a	1.41 ± 0.12 ^a	1.08 ± 0.08 ^a	1.22 ± 0.13
Seed plant				
Species richness	7.1 ± 0.2 ^a	6.8 ± 0.5 ^a	8.2 ± 0.3 ^a	7.3 ± 0.8
Species diversity	0.98 ± 0.09 ^a	1.23 ± 0.09 ^a	0.91 ± 0.07 ^a	1.05 ± 0.11
Fern				
Species richness	0.1 ± 0.1 ^a	1.7 ± 0.3 ^b	0.0 ± 0.0 ^a	0.7 ± 0.1
Species diversity	0.00 ± 0.00 ^a	0.39 ± 0.09 ^b	0.00 ± 0.00 ^a	0.15 ± 0.02

Environmental characteristics and plant communities

Soil moisture was highest 40 cm below the ground surface of pits, i.e., 33% ± 2 (s.e.) at 0 cm deep, 34% ± 4 at 10 cm, 32% ± 3 at 20 cm, and 42% ± 2 at 40 cm. Air temperature ranged between 18.7°C and 22.2°C, and averaged 20.2°C ± 0.6. Soil temperature at 0 cm in depth was slightly higher than air temperature, i.e., 20.9°C ± 0.4, probably because of direct solar radiation. Then, soil temperature decreased to 19.7°C ± 0.5 at 10 cm in depth, and 19.2°C ± 0.5 at 20 cm. At 40 cm in depth, soil temperature was lowest, i.e., 17.6 ± 0.6. RPFd was 69% ± 7 at 20 cm above the ground surface, and was 7% ± 5 on the deepest locations, i.e., 40 cm in depth. As expected, RPFd

decreased logarithmically with increasing pit depth: $RPF = 43 \cdot \log(\text{pit depth}) - 164$ ($r^2 = 0.974$, significant at $P < 0.01$). In summary, pits of which depth was more than 40 cm support high soil moisture and low temperature, and avoided direct solar radiation.

Group B established significantly deeper plots than groups A and C (Table 1), while the depths of plots were not different between groups A and C (Table 1). Groups A and B established on shallower sites, i.e., elevation difference in plot less than 50 cm, and the depths of plots in group C ranged from 20 cm to 205 cm (Figure 3). The establishment sites for ferns were restricted in these pits, in particular, of which depth was more than 50 cm (Figure 4). A fern recorded from groups A and C was *Equisetum arvense*, a micorphyllous fern that established only on shallow pits even in group B, while macrophyllous ferns were restricted to establish in deep depressions, i.e., more than ca 50 cm in depth. Those implied that the establishment sites for ferns were restricted to pits, while groups A and C were not differentiated by topography.

Litter thickness did not differ between the three groups. Soil hardness on group A differed from that on groups B and C. In particular, soil was the hardest in group A and was the softest in group C, suggesting that trampling and/or its related factors were related to the differentiation between groups A and C.

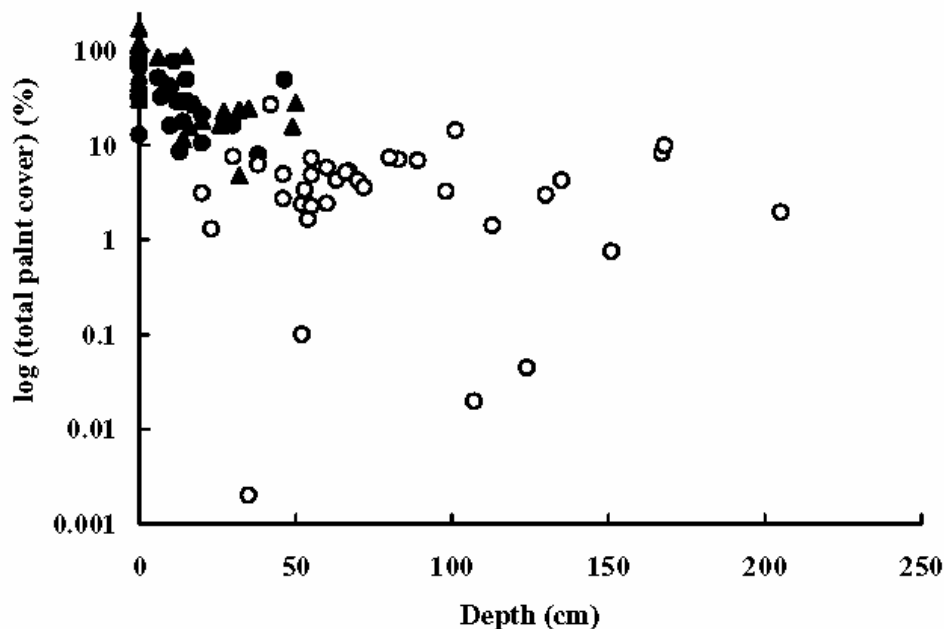


Figure 3. Relationship between plot depth and total plant cover. Closed circles, open circles and closed triangles indicate TWINSpan cluster groups, A, B and C, respectively.

Detrended correspondence analysis

Detrended correspondence analysis (DCA) showed that ferns tended to aggregate the scores on the first two axes (Figure 5), i.e., the ferns showed the lowest scores on axes I and II. Four seed plants, *Hydrangea petiolaris*, *Aruncus dioicus* var. *tenuifolius*, *Galium spurium* var. *echinospermon* and *Gnaphalium uliginosum* were also clustered with ferns. Those implied that those seed plants as well as ferns restricted to establish in deep pits. In total, the scores of the three plant community groups were ordered as: $C > A > B$

along axis I, and $A > C > B$ along axis II. The species scores on the three unpalatable plants, i.e., *Cynanchum caudatum*, *Senecio cannabinifolius*, and *Pachysandra terminalis*, showed higher scores on axis I, indicating that group C was supported by unpalatable plants. Plots in group A showed higher scores on axis II. On the species scores of axis II, the highest scores on seed plants were obtained by *Zoysia japonica*, *Mazus japonicus*, and *Erigeron canadensis*. A moss, *Ceratodon purpureus*, also showed high score on axis II. *Z. japonica*, *M. japonicus* and *C. purpureus* are innately short. *E. canadensis* became short in the grazed area, suggesting that grazing and trampling modified plant community structures via the alteration of plant morphological traits. Those also suggested that plants in group B avoided grazing effects.

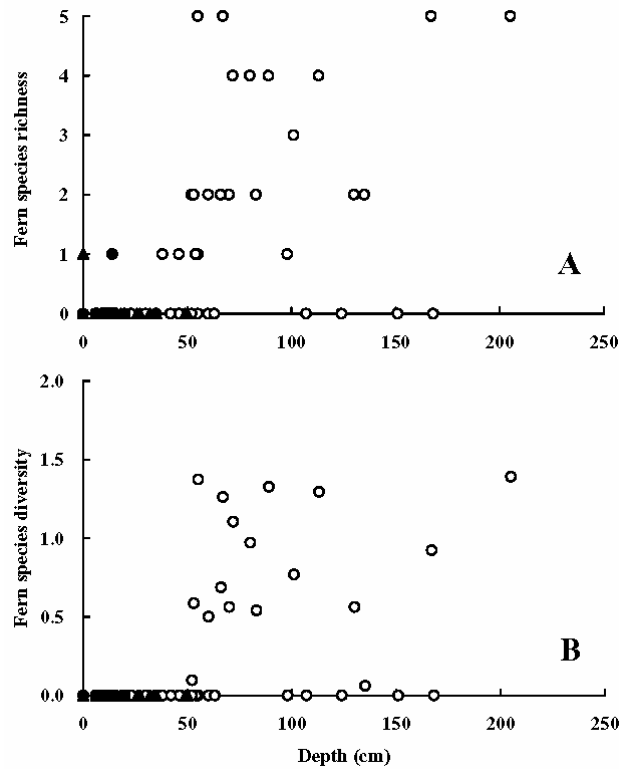


Figure 4. Relationships between plot depth and fern species richness (A) and between plot depth and fern species diversity (B). Symbols, same as in Fig. 3.

Discussion

Species composition in pits was characterized by the presence of ferns. In particular, pits with more than 50-cm deep support most ferns. The size of treefall pits does not affect species richness in a tropical rainforest, Puerto Rico, but affects the establishment of specific species [28]. In the present study, pit depth influences fern diversity more than pit area. Spatial heterogeneity, including microtopography and its related environmental factors such as light and soil moisture, is one of the determinants on plant community structures [1, 25]. Pit conserved fern species diversity on Nakajima Island, by the avoidance from deer feeding. Pothole develops more variable plant

community than barren areas on Mount St. Helens, USA, although the plant community patterns are not well-documented by surface area of pothole and the properties of the volcanic deposits [6]. While, the pits on Nakajima Island support fern diversity, because the pit depth is related to light intensity and soil moisture and is important for the specific (macrophyllous) fern establishment. Those mutual advantages for ferns could support fern diversity in the pits.

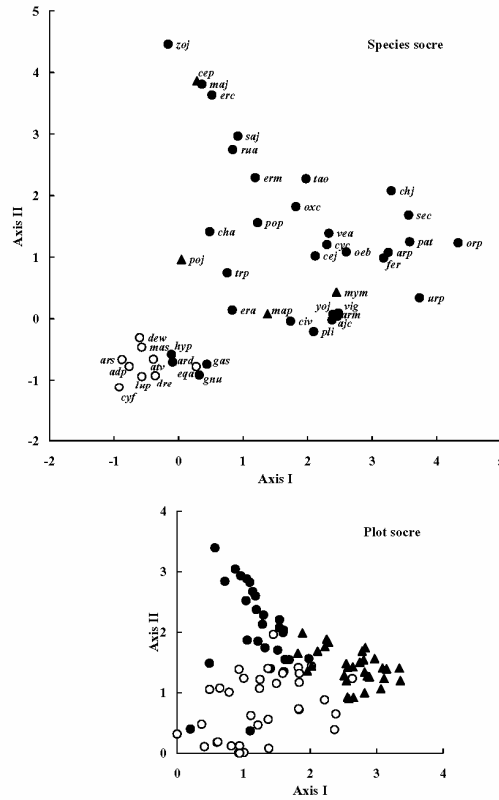


Figure 5. Species (A) and plot (B) scores on detrended correspondence analysis. Species with frequencies more than 1 were used.

A: Seed plants (closed circles); saj = *Sagina japonica*, vea = *Veronica arvensis*, oxc = *Oxalis corniculata*, cyc = *Cynachum caudatum*, erm = *Eragrostis multicaulis*, tao = *Taraxacum officinale*, era = *Erigeron annuus*, yuj = *Youngia japonica*, pat = *Pachysandra terminalis*, sec = *Senecio cannabifolius*, pop = *Poa pratense*, oeb = *Oenothera biennis*, hyp = *Hydrangea petiolaris*, rua = *Rumex acetosella*, arp = *Arisaema peninsulae*, vig = *Viola grypoceras*, gas = *Galium spurium* var. *echinospermon*, zoj = *Zoysia japonica*, pli = *Plectranthus inflexus*, trp = *Trifolium pratense*, civ = *Cirsium vulgare*, erc = *Erigeron canadensis*, cej = *Cercidiphyllum japonicum*, arm = *Artemisia montana*, orp = *Oreorchis patens*, maj = *Mazus japonicus*, chj = *Cloranthus japonicus*, gnu = *Gnaphalium uliginosum*, ajc = *Ajuga ciliata* var. *villosior*, urp = *Urtica platyphylla*, fer = *Festuca rubra*, cha = *Chenopodium album*, ard = *Aruncus dioicus* var. *tenuifolius*. Ferns (open circles); atv = *Athyrium vidalii*, mas = *Matteuccia struthiopteris*, dra = *Dryopteris austriaca*, eqa = *Equisetum arvense*, Ars = *Arachniodes standichii*, dew = *Dennstaedtia wilfordii*, lup = *Lunathyrium pycnosorum*, adp = *Adiantum pedatum*. Mosses (closed triangles); mym = *Myuroclada maximoviczii*, map = *Marchantia polymorpha*, poj = *Polytrichum juniperinum*, cep = *Ceratodon purpureus*. B: Closed circles, open circles and closed triangles show scores on TWINSpan cluster groups A, B and C, respectively.

Plant communities were differentiated by the presence/absence of palatable plants on the flat ground. A few plant species persist and dominate on heavily-grazed areas where palatable plant species decline [8]. On the flats, i.e., in groups A and C, *Pachysandra terminalis* and *Senecio cannabifolius*, both of which were unpalatable plants for deer [12, 24], were dominant in group C, while these two species were not common in group A. *Cynanchum caudatum* that was also unpalatable for deer was common in groups A and C. Soil hardness was lower in group C than in group A, suggesting that differences in environmental factors were also related to the intensities of grazing and trampling. Those results indicated that the intensities of trampling and/or feeding were lower in group C where unpalatable plants were dominant. Therefore, plant communities differentiated with the gradient of grazing intensities. The grazing of red deer influence productive grasslands more than unproductive ones on the Isle of Rum in Scotland [27], and tall plants decrease richness and height even by weak deer browsing on a riparian deciduous forest in central Japan [17]. Livestock grazing increases prostrate life form and clonal reproduction in Dehesa grasslands, due to trampling (Peco et al. 2005), but increases short-lived plants in south-western Pyrennees [3]. The mortality of tussock grass declines by grazing [19]. Short plants were common on the flats, as well as mosses. Mosses were widespread in the grassland on Nakajima Island, because mosses are not greatly damaged by cervids (Crete et al. 2001). Plant taxa and/or life forms are related to the palatability of deer, i.e., the short morphological form, including mosses, and therefore feeding by deer affected differences in species composition between groups A and C.

Food habits of sika deer varies greatly between regions in the Japanese Archipelago [2], i.e., deer eat whatever they can eat when food resources are limited. For example, reindeer eat goose droppings when food resources become low [26]. Even though white-tailed deer is one of the most common herbivores, it behaves as a carnivore when food resources are deficient [4]. We emphasize that diverse microtopography supports higher landscape-level species richness and diversity by the establishment of various taxa, even though overgrazing eliminates various plants.

Acknowledgements We thank T. Sato and K. Takita for their help on plant identification, and Akasaka M for field assistance. The voucher specimens of ferns have kept in Hokkaido University Museum. M. Nakajima gave us great peace of mind when we were working. This work is partly supported by the grants from the Ministry of Education, Culture, and Science of Japan.

REFERENCES

- [1] Alados C.L., Pueyo Y., Navas D., Cabezudo B., Gonzalez A. and Freeman D.C. (2005): Fractal analysis of plant spatial patterns: a monitoring tool for vegetation transition shifts. – *Biodiversity and Conservation* 14: 1453-1468.
- [2] Campos-Arceiz A. and Takatsuki S. (2005): Food habits of sika deer in the Shiranuka Hills, eastern Hokkaido: a northern example from the north-south variations in food habits in sika deer. – *Ecological Research* 20: 129-133.
- [3] Canals R.M. and Sebastia M.T. (2000): Analyzing mechanisms regulating diversity in rangelands through comparative studies: a case in the southwestern Pyrennees. – *Biodiversity and Conservation* 9: 965-984.
- [4] Case D.J., McCullough D.R. (1987): White-tailed deer forage on alewives. – *Journal of Mammalogy* 68: 195-197.

- [5] Crete M., Ouellet J.-P., Lesage L. (2001): Comparative effects on plants of caribou/reindeer, moose and white-tailed deer herbivory. – *Arctic* 54: 407-417.
- [6] del Moral R. (1999): Plant succession on pumice at Mount St. Helens, Washington. – *American Midland Naturalist* 141: 101-114
- [7] Hattori S., Iwatsuki Z., Mizutani M. (1972): Coloured illustrations of Bryophytes of Japan. – Hoikusha Publishing Co., Ltd., Osaka, Japan. Pp. 405. (in Japanese)
- [8] Hendricks H.H., Bond W.J., Midgley J.J., Novellie P.A. (2005): Plant species richness and composition a long livestock grazing intensity gradients in a Namaqualand (South Africa) protected area. – *Plant Ecology* 176: 19-33.
- [9] Hill M.O. (1979): TWINSPLAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. – Department of Ecology and Systematics, Cornell University, Ithaca.
- [10] Hill M.O., Gauch H.G. (1980): Detrended correspondence analysis: an improved ordination technique. – *Vegetatio* 42: 47-58.
- [11] Kaji K., Koizumi T., Ohtaishi, N. (1988): Effects of resource limitation on the physical and reproductive condition of sika deer on Nakanoshima Island, Hokkaido. – *Acta Theriologica* 33: 187-208.
- [12] Kaji K., Yajima T., Igarashi T. (1991): Forage selection by introduced deer on Nakanoshima Island and its effect on the forest vegetation. – Proceedings of the International Symposium on Wildlife Conservation, INTECOL 1990. pp. 52-55.
- [13] Lponce M., Theunis L., Delabie J.H.C., Roisin Y. (2004): Scale dependence of diversity measures in a leaf-litter ant assemblage. – *Ecography* 27: 253-267.
- [14] Martin T.G., Brendan B.A., Wintle A., Rhodes J.R., Kuhnert P.M., Field S.A., Low-Choy S.J., Tyre A.J., Possingham H.P. (2005): Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. – *Ecology Letters* 8: 1235-1246.
- [15] Miyaki M., Kaji K. (2004): Summer forage biomass and the importance of litterfall for a high-density sika deer population. – *Ecological Research* 19: 405-409.
- [16] Nakaike T. (1982): New flora of Japan. Pteridophyta. – Shibundo Co., Ltd. Publishers, Tokyo. pp. 808.
- [17] Nomiya H., Suzuki W., Kanazashi T., Shibata M., Tanaka H., Nakashizuka T. (2002): The response of forest floor vegetation and tree regeneration to deer exclusion and disturbance in a riparian deciduous forest, central Japan. – *Plant Ecology* 164: 263-276.
- [18] Ohwi J. (1983): New flora of Japan (2nd edn). Phanerogams. – Shibundo Co., Ltd. Publishers, Tokyo. pp. 1716.
- [19] Oliva G., Collantes M., Humano G. (2005): Demography of grazed tussock grass populations in Patagonia. – *Rangeland Ecology and Management* 58: 466-473.
- [20] Peco B, de Pablos I., Traba J., Levassor C. (2005): The effect of grazing abandonment on species composition and functional traits: the case of Dehesa grasslands. – *Basic and Applied Ecology* 6: 175-183.
- [21] Perelman S.B., Burkart S.E., Leon R.J.C. (2003): The role of a native tussock grass (*Paspalum quadrifarium* Lam.) in structuring plant communities in the Flooding Pampa grasslands, Argentina. – *Biodiversity and Conservation* 12: 225-238.
- [22] R Development Core Team (2005): R: A language and environment for statistical computing. – R Foundation for Stat. Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- [23] Stockton S.A., Allombert S., Gaston A.J., Martin J.-L. (2005): A natural experiment on the effects of high deer densities on the native flora of coastal temperate rain forests. – *Biological Conservation* 126: 118-128.
- [24] Takahashi H., Kaji K. (2001): Fallen leaves and unpalatable plants as alternative foods for sika deer under food limitation. – *Ecological Research* 16: 257-262.
- [25] Tsuyuzaki S., Haraguchi A., Kanda F. (2004): Effects of scale-dependent factors on herbaceous vegetation in a wetland, northern Japan. – *Ecological Research* 19: 349-355.

- [26] van der Wal, R., Loonen M.J.J.E. (1998): Goose droppings as food for reindeer. – *Canadian Journal of Zoology* 76: 1117-1122.
- [27] Virtanen R., Edwards G.R., Crawley M.J. (2002): Red deer management and vegetation on the Isle of Rum. – *Journal of Applied Ecology* 39: 572-583.
- [28] Walker L.R. (2000): Seedling and sapling dynamics of treefall pits in Puerto Rico. – *Biogropica* 32: 262-275.
- [29] Werner K.J., Zedler J.B. (2002): How sedge meadow soils, microtopography, and vegetation respond to sedimentation. – *Wetlands* 22: 451-466.
- [30] Yumoto, T., Matsuda, H. (2006):. Deer devour world heritages: The ecology of deer and forest. – Bun-ich Co. Ltd., Tokoyo (in Japanese)
- [31] Zar J.M. (1999): *Biostatistical Analysis*, 4th ed. – Prentice-Hall, Englewood Cliffs.