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Canonical correspondence analysis of early volcanic succession on Mt Usu, Japan

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Canonical correspondence analysis (CCA) was applied to explore revegetation patterns during early succession on Mt Usu. Vegetation was buried by deposits of ash and pumice from 1 to 3 m in depth from the 1977–78 eruptions. Three habitats were selected: tephra, tephra in gully and original surface. Plant density and plant cover data were analyzed separately. Environmental factors consisted of five quantitative variables (organic matter, elevation, distance from colonizing source, erosion and deposition of volcanic deposits) and three nominal variables (habitat types: tephra, tephra in gully and original surface). Canonical correspondence analysis showed that the original surface played a special role in vegetation development because the old topsoil supplied both nutrients and seed-bank species. The CCA also suggested that the environmental factors that influence plant density and cover differ. Distance from colonizing source affected plant density while erosion affected cover. Using CCA, factors could be distinguished that influenced seedling establishment from vegetation expansion and vegetation recovery dynamics could also be more clearly interpreted.

Key words: buried topsoil; canonical correspondence analysis (CCA); erosion; succession; Mt Usu.

INTRODUCTION

Canonical correspondence analysis (CCA) was developed by ter Braak (1986, 1987a). This approach simplifies the analysis of species–environment relationships in a way analogous to linear regression (Hill 1991). Canonical correspondence analysis differs from indirect methods such as principal component analysis and (detrended) correspondence analysis in that it incorporates linear correlations and regressions between distributional data and environmental factors. CCA is a direct ordination method with axes that result from the joint variation of the environmental and species data. CCA is effective only if an appropriate set of environmental data has been collected for the samples in the analysis (Kent & Coker 1992).

Disturbance and physical stress strongly control vegetation patterns on harsh environments such as volcanoes (White 1979; Tsuyuzaki 1991; del Moral 1993; del Moral & Bliss 1993). Environmental factors such as substrate instability, nutrient deficiency, and distance from plant sources interact in complex ways such that the factors that influence succession are complex (Walker & Chapin 1987). The objective in this paper was to determine whether CCA effectively evaluates these environmental variables and can help to explain the influence of environmental variables on vegetation development patterns.

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STUDY AREA

Mt Usu is one of the most active volcances in Japan (42°32′N, 140°50′E). It includes two peaks, O-Usu (727 m) and Ko-Usu (609 m), which are enclosed by a caldera rim and a crater basin. Before the 1977–78 eruptions, the vegetation near the summit consisted of broad-leaved deciduous forests dominated by *Populus maximowiczii* and *Betula platyphylla* var. *japonica*, and a human-created grassland dominated by introduced *Dactylis glomerata* and *Trifolium repens* (Tsuyuzaki 1987).

The 1977–78 eruption destroyed aboveground vegetation and deposited from 1 to 3 m of pumice and ash (tephra). Owing to substantial erosion of these deposits, many gullies were created within the crater basin. Soon after the eruptions, perennial herbs such as *Polygonum sachalinense* and *Petasites japonicus* var. *giganteus* sprouted from the inner wall of the caldera rim. These herbs were able to recover vegetatively due to the rapid erosion of volcanic deposits and exposure of pre-eruption soils (Tsuyuzaki 1987). On the crater basin surface, continued instability prevented revegetation for several years (Tsuyuzaki 1991). Revegetation of the crater basin has resulted from long-distance seed dispersal from less impacted habitats, recovery of buried vegetative parts, species introduced by humans for soil erosion control, and germination of seeds buried in the original topsoil that was exposed by erosion (Tsuyuzaki 1987).

METHODS

In 1984, density and per cent cover of each vascular plant species were recorded in twenty-two 2 m × 5 m quadrats. Closely aggregated perennial shoots were regarded as a single individual. Excavations confirmed that these assumptions were true in most cases (Tsuyuzaki 1987). The plots were located on tephra (T) outside gullies (10 quadrats), in gullies (G) with a partially eroded tephra surface (four quadrats), or in gullies that were eroded to the original surface (OS; eight quadrats). Distance from the caldera rim and elevational difference between plots were determined for each plot using a transit compass and measuring tapes. Surface ground movements, that is, erosion and deposition of volcanic deposits, were measured by the changes of relative height of each plot surface from spring to fall 1984 using a transit compass. Surface organic matter was estimated by loss on ignition at 800°C for 8 h.

Environment–species and environment–plot relationships were investigated by canonical correspondence analysis (CCA) using CANOCO (ter Braak 1987a). Species matrices were composed either of per cent cover or of density. The results of CCA are based simultaneously on species abundance and the values of environmental variables. Canonical correspondence analysis differs from correspondence analysis (CA) in that the ordination axes are constrained to optimize their linear relationships to a set of environmental variables. The nature of the relationships can be shown in the ordination diagram by vectors with lengths proportional to their importance and directions showing their correlations with each axis. Species and samples are plotted in the ordination diagram so that major relationships can be directly observed. Nominal environmental variables (habitat categories in this study) are indicated at the centroid of the sample scores belonging to the class. Statistical validity of resulting environmental axes can be evaluated by an unrestricted Monte Carlo permutation test (ter Braak 1987a, 1988).

Relationships between density and cover results were explored using Spearman's rank correlation test (Zar 1984).

RESULTS

Environment

Table 1 shows environmental variables used and the range of their values in each habitat type. The distance from the caldera rim varies from 50 m to 400 m above the plots and elevation varies by 46 m. The floor of the crater basin is unstable. Measured soil movements varied from a loss of 10 cm to a redeposition of 62 cm. Organic matter is the only available surrogate for soil nutrients, which are very low. New tephra surfaces had little organic matter,

Table 1. Environmental variables used

Variable	Habitat*	Minimum–maximum
Distance from caldera rim (m)	T	100.0–400.0
	G	50.0–200.0
	OS	50.0–400.0
Relative elevation difference (m)	T	0.0– 46.0
	G	0.0– 35.0
	OS	0.0– 45.0
Organic matter† (%)	T	0.2– 1.1
	G	0.2– 0.5
	OS	2.5– 13.2
Deposit of tephra (cm)‡	T	0.0– 9.0
	G	0.0– 62.0
	OS	0.0– 41.0
Erosion of tephra (cm)‡	T	0.0– 9.0
	G	0.0– 4.0
	OS	0.0– 10.0

*Three variables, tephra (T), gully (G), and old surface (OS), are nominal.
†Evaluated by loss on ignition of volcanic soils.
‡Movements of volcanic deposits are classified into two categories.

while the exposed old surface had higher levels. The three habitats have unique, but overlapping environmental characteristics (Tsuyuzaki 1989b). The relative importance of these environmental factors was not readily apparent, so CCA was applied.

Vegetation

There were 40 vascular plants (T, 29 species; G, 16 species; OS, 25 species) in the plots surveyed. These species broadly overlapped the three habitats (Table 2). Total cover ranged from 0.8 to 21.4%, and density per plot from 15 to 143. *Petasites japonicus* var. *giganteus* occurred in all plots and *Polygonum sachalinense* was also common. No other species had a frequency of over 50%. Although *Rumex obtusifolius, Trifolium repens, Rorippa islandica, Viola grypoceras, Ranunculus repens, Polygonum longisetum* and *Poa annua* established in habitat OS with high densities, their cover was limited. In contrast, woody species such as *Populus maximowiczii, Betula ermanii, B. maximowicziana* and *Salix sachalinensis* established well in both tephra (habitats T and G), but were rare in newly exposed soil (habitat OS).

Canonical correspondence analysis

Density analysis

Table 3 summarizes the result of CCA for the first two axes using both density and cover of plants.

Table 2. Mean percentage cover (left) and density/10 m^2 (right) of dominant species, used in CCA ordination. Abbreviations used for CCA ordination are also shown.

Species	Abbreviation	Percentage cover/density			
		Tephra (n = 10)	Gully (n = 4)	Old surface (n = 8)	Total (n = 22)
Petasites japonicus var. *giganteus*	PJ	1.4/18.8 (10)	2.1/19.8 (4)	0.4/6.6 (8)	1.1/14.5 (22)
Polygonum sachalinense	PS	1.0/7.7 (9)	1.3/4.5 (4)	0.2/2.3 (6)	0.8/5.1 (19)
Festuca rubra	FR	0.2/2.2 (5)	0.1/3.0 (2)	0.2/1.4 (4)	0.2/2.0 (11)
Salix hultenii var. *angustifolia*	SH	0.4/2.6 (9)	0.1/1.3 (2)	—	0.2/1.4 (11)
Rumex obtusifolius	RO	0.0/0.2 (1)	0.0/0.8 (1)	1.2/4.9 (8)	0.5/2.0 (10)
Populus maximowiczii	PM	0.1/2.2 (5)	0.0/1.5 (3)	0.0/0.1 (1)	0.1/1.3 (9)
Festuca elatior	FE	0.2/2.0 (5)	0.1/0.5 (1)	0.5/3.1 (2)	0.3/2.1 (8)
Anaphalis margaritaceae var. *angustior*	AN	0.1/7.4 (5)	—	0.1/0.4 (2)	0.3/3.5 (7)
Betula ermanii	BE	0.1/0.8 (5)	0.1/0.5 (2)	—	0.1/0.5 (7)
Trifolium repens	TR	0.2/0.5 (1)	—	2.0/1.6 (5)	0.8/0.8 (6)
Rorippa islandica	RI	—	—	0.4/6.6 (6)	0.2/2.4 (6)
Moehringia lateriflora	ML	0.1/2.1 (3)	—	0.1/0.9 (3)	0.1/1.3 (6)
Epilobium montanum	EM	0.0/0.9 (2)	—	0.1/0.8 (4)	0.0/0.7 (6)
Polygonum cuspidatum	PC	1.1/1.1 (4)	—	0.3/0.3 (1)	0.1/0.6 (5)
Luzula capitata	LC	0.3/0.3 (2)	0.1/0.5 (1)	0.1/0.4 (2)	0.1/0.4 (5)
Carex oxyandra	CO	0.5/7.1 (3)	—	—	0.2/3.3 (4)
Agrostis scabra	AS	0.1/4.6 (3)	0.1/0.8 (1)	—	0.1/2.2 (4)
Viola grypoceras	VG	—	—	0.4/2.5 (4)	0.0/0.9 (4)
Betula maximowizciana	BM	0.1/0.5(3)	0.1/0.5 (1)	—	0.0/0.3 (4)
Picris hieracioides var. *glabrescens*	PH	0.0/0.2 (2)	—	0.1/0.3 (2)	0.0/0.2 (4)
Salix sachalinensis	SS	0.1/0.4 (3)	0.0/0.3 (1)	—	0.0/0.2 (4)
Artemisia montana	AR	0.0/0.1 (1)	0.8/7.8 (2)	—	0.1/1.5 (3)
Ranunculus repens	RR	—	—	0.3/1.8 (3)	0.1/0.6 (3)
Polygonum longisetum	PL	—	—	0.1/2.4 (3)	0.0/0.9 (3)
Poa annua	PA	0.0/0.3 (2)	—	0.0/0.1 (1)	0.0/0.2 (3)

Frequency values are shown in parentheses.
No plants were observed in the dashed areas.
The other species abbreviations used in Figs 1 and 3 are: AA, *Alopecurus aequalis* var. *amurensis;* BP, *Betula platyphylla* var. *japonica*; CA, *Carex breviculumis*; CH, *Cerastium holosteoides*; CV, *Cerastium vulgatum*; EH, *Epilobium fastigiatoramosum*; EP, *Epilobium palustre*; GS, *Geum macrophyllum* var. *sachalinense*; SI, *Salix integra*; TO, *Taraxacum officinale*.

With respect to density, 14.8% of the species variation is explained by axis I, which has a 0.97 correlation between species and environmental factors. This axis accounts for 34.6% of the explained species–environment relationships. The second axis shows a 0.90 species–environment correlation and explains 9.2% of the species variation and 21.5% of the species–environment relationships.

Of the available environmental variables, old topsoil was strongly correlated to axis I in the density analysis. Organic matter and tephra were also related to this axis. The second axis is less distinct, as weaker predictors dominate. Distance from the rim, gully and elevation are associated with axis II. Compared to unconstrained Monte Carlo permutation tests on both axes, these results are significant at $P<0.02$.

Canonical correspondence analysis of the density data produced two species groups on the first axis (Fig. 1). All species with high scores on this axis were those establishing on old soil, for example, *Trifolium repens, Rorippa islandica* and *Poa annua.* Along the second CCA axis, woody plants *Populus maximowiczii, Salix integra, Betula maximowicziana,* and *B. ermanii* and perennial herbs such as *Petasites japonicus* var. *giganteus* and *Artemisia montana,* showed relatively high scores on the second axis. *Cerastium vulgatum, Ranunculus repens* and *Festuca elatior* had low scores on axis II.

Plots were clearly classified by CCA into two groups along the first axis (Fig. 2). Plots on old soil were separated from the tephra and gully plots. Along the second axis, the plots in the gully with tephra were separated from those on tephra and exposed soil.

Cover analysis

Eigenvalues, species–environment correlations, and percentage variances of the cover analysis were slightly higher than those of density (Table 3). The environmental factors related to axis I were the same as with the density analysis. Old topsoil was strongly correlated to axis I. Organic matter and tephra were also significant. However, factors correlated to axis II differed from those of the density analysis. Erosion was the sole factor with a high correlation to the second axis. These results are significant at $P<0.01$ (unconstrained Monte Carlo permutation tests on both axes).

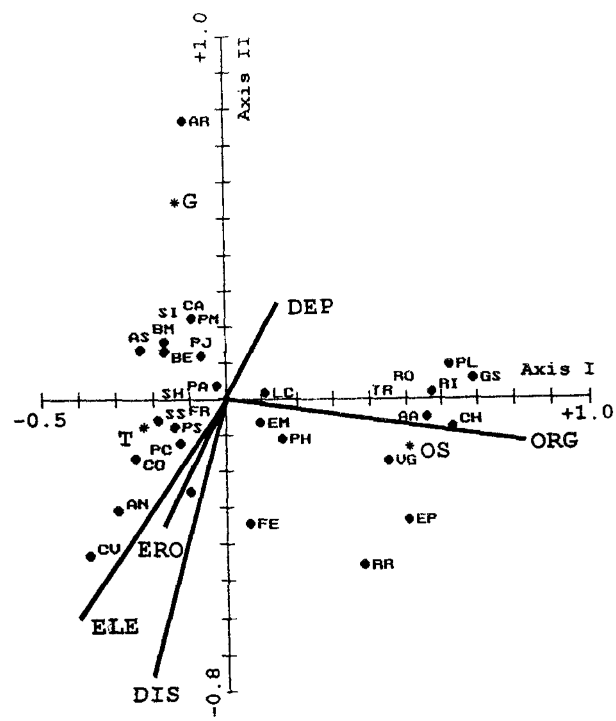

Fig. 1. CCA ordination diagram showing species scores evaluated by plant densities. Environmental variables: DIS = distance from caldera rim; ELE = relative elevation difference; ORG = organic matter; DEP = deposit of tephra; ERO = erosion of tephra; T = tephra outside gully; OS = old-soil-exposed gully; G = tephra inside gully. Centroid of the scores of nominal environmental variables are shown by asterisks. Species codes are shown in Table 2. The abbreviations of species without dots indicate that the scores are hidden under the abbreviation letters.

When cover values were used for CCA ordination, the species were again divided into two groups along axis I (Fig. 3) in a way similar to the density analysis. *Ranunculus repens* showed a high value on the second axis, while *Epilobium palustre* scored lowly.

Along the first axis, CCA using cover produced two groups, plots with old soil and those without (Fig. 4), similar to the CCA using density. However, habitat differentiation between tephra and gully was unclear in this case, since all tephra surfaces were similar in both dimensions.

Density and cover

To compare the differences between CCA evaluated by density and by cover, Spearman's rank correlation test was used on species with more than six occurrences. In all cases, correlation coefficients were

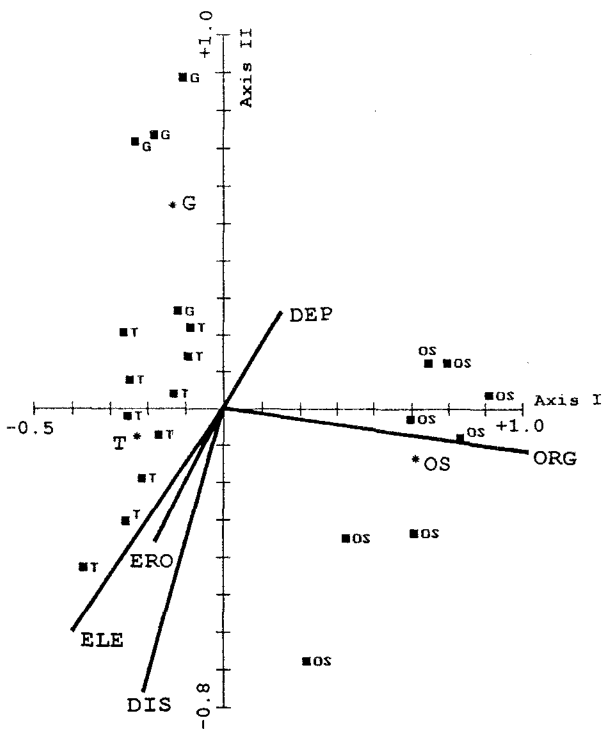

Fig. 2. CCA ordination diagram showing plot scores evaluated by plant densities. Notations as in Fig. 1.

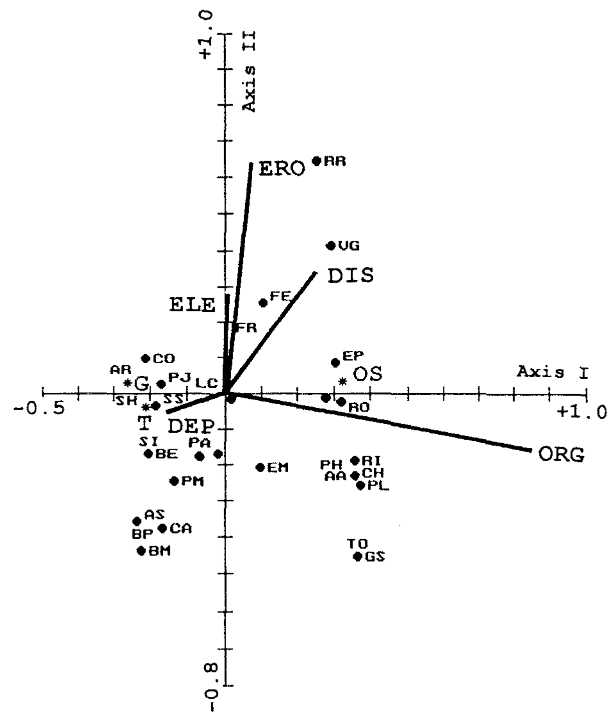

Fig. 3. CCA ordination diagram showing species scores evaluated by percentage cover. Refer to Fig. 1 for codes.

Table 3. Eigenvalues and intra-set correlations of standardized environmental variables with the first two CCA axes

Parameter type	Density		Cover	
Axis	I	II	I	II
Eigenvalue	0.587	0.365	0.697	0.355
Species–environment correlations	0.970	0.899	0.986	0.937
Percentage variance				
Of species data	14.8 (14.8)	9.2 (24.0)	16.7 (16.7)	8.6 (25.3)
Of species–environment relation	34.6 (34.6)	21.5 (56.1)	39.6 (39.6)	20.2 (59.8)
Intra-set correlations				
Distance from caldera rim	− 0.202	− 0.684 (1)	+ 0.253	+ 0.328 (2)
Elevation difference	− 0.392	− 0.540 (3)	+ 0.007	+ 0.266 (3)
Organic matter	+ 0.802 (2)	− 0.109	+ 0.840 (2)	− 0.151
Deposition of tephra	+ 0.142	+ 0.237	− 0.154	− 0.053
Erosion of tephra	− 0.174	− 0.322	+ 0.070	+ 0.598 (1)
Tephra	− 0.723 (3)	− 0.225	− 0.654 (3)	− 0.123
Gully	− 0.159	+ 0.596 (2)	− 0.419	+ 0.042
Old surface	+ 0.915 (1)	− 0.222	+ 0.973 (1)	+ 0.092

On the inter-set correlation, the first three leading variables are shown in parentheses.
Cumulative percentage variances are shown in parentheses.

positive. Except for *Populus maximowiczii*, which showed a highly significant correlation between density and cover ($r^2 = 0.723$, $P<0.01$), the species showed non-significant or weakly significant relationships (range: $r^2 = 0.013$ to 0.498) between cover and density value ordinations. These results

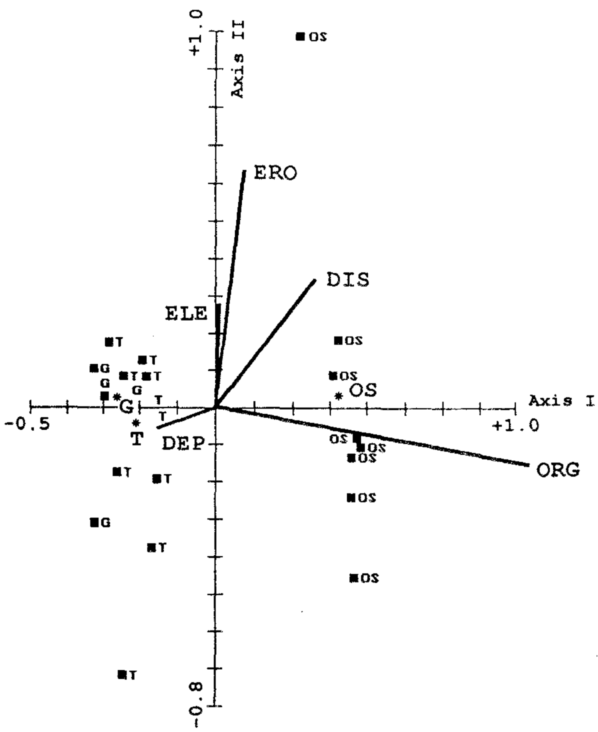

Fig. 4. CCA ordination diagram showing plot scores evaluated by percentage cover. Refer to Fig. 1 for codes.

suggest that those two parameters are related to environmental variables in somewhat different ways.

DISCUSSION

Tsuyuzaki (1991) suggested that the three major determinants of vegetation recovery on Mt Usu are: low species richness in the plant sources, low nutrient content of the tephra, and surface instability. Canonical correspondence analysis helps to elucidate the mechanism that controls this vegetation development.

Exposed surfaces contain more organic matter and a seed bank (Tsuyuzaki 1989a). Exposed surface habitats can recover rapidly and do not require invasion by seeds. This pattern is similar to that described by del Moral and Wood (1988, 1993b) on a scoured ridge on Mount St Helens. All species that show high scores on axis I are seed bank species that are conspicuous on old surfaces (Tsuyuzaki 1989a, 1991). Corresponding to this species-ordination pattern, plots on old soil were distinct from those on both tephra surfaces. Axis I is related strongly to old surfaces and to organic matter because organic matter is virtually absent in tephra (Tsuyuzaki 1989b). Canonical correspondence analysis using both density and cover shows that the weight of the nominal parameter OS is higher than that of organic matter. This implies that this nominal variable includes more information than just organic matter, or that it is less variable.

The second CCA axis in the density analysis is related to distance from the caldera rim. The number of seeds captured by seed traps decreased with distance from the caldera rim (Tsuyuzaki 1987). Therefore, the distance from the caldera rim is a surrogate for dispersal distance. Species producing long-distance, wind-dispersed seeds, such as the Salicaceae, Betulaceae and Asteraceae, show relatively high scores on the second CCA axis obtained with density, while most species with low scores on the second axis are gravity-dispersed. On Mount St Helens, many wind-dispersed seeds were captured by seed traps (Dale 1989; del Moral & Wood 1993a). The pace of revegetation and/or seedling densities decrease with increasing distance from plant sources (Halpern & Harmon 1983; Wood & Morris 1990; del Moral & Wood 1993b). On Mt Usu, there are two sources of colonists. Survivors in less-impacted habitats surrounding the crater basin serve as sources of wind-dispersed seeds. Seed banks in old soil contain species with a variety of dispersal types. A large number of seeds were swept down by erosion from upper to lower elevations (Tsuyuzaki 1989a), therefore, elevation also affected seedling establishment patterns.

Seedling mortality was over 70% in 1985 on tephra where the ground surface movements were moderate (Tsuyuzaki 1989b), suggesting that seedling mortality was higher inside gullies where the severe surface movements occurred. Physical amelioration must occur on new surfaces before seedlings can successfully colonize (del Moral & Clampitt 1985; del Moral & Wood 1988; del Moral 1993). On Mt Usu, erosion enhanced the amelioration process (Kadomura *et al.* 1983). Therefore, habitat differences mediated by usually destructive processes strongly influence vegetation development patterns.

Surviving underground organs provide an important mechanism for rapid recovery in the crater basin (Tsuyuzaki 1989b). The rapid increase of below- and aboveground biomass of residual plants resulted in rapid recovery (Tsuyuzaki 1987; del Moral & Wood 1988). Therefore, the second axis on CCA ordination evaluated by cover is primarily related to erosion of volcanic deposits.

Vegetation development patterns were detected using CCA ordination as follows. The seed bank strongly influenced succession patterns on Mt Usu. Succession on exposed surfaces is a secondary succession derived from the seed bank (Tsuyuzaki 1987). On tephra, both inside gullies and on uneroded surfaces, there were few, if any, survivors, and seed dispersal from outside the caldera was required to start primary succession. On these sites, distance from the rim has controlled density and secondary soil movements have controlled cover development.

So far, indirect ordination methods such as principal component analysis and detrended correspondence analysis have been widely applied to understand vegetation establishment patterns. However, these methods distort relationships among samples (e.g. horseshoe, arch, compression and hump effects), and require subsequent procedures to extract significant environmental factors (ter Braak 1987a; Kent & Coker 1992). These distortions are greatly decreased with CCA, and significant environmental factors are directly identified (ter Braak 1987b). Canonical correspondence analysis has clarified details of revegetation on Mt Usu and revealed how different aspects of community structure respond to different determining factors. Where patterns are less well understood, CCA should be of considerable value in understanding the details of species–environmental relationships.

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