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Revegetation Dynamics in Early Successional Stages of the Volcano Usu,
Northern Japan, after the 1977-78 Eruptions.

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Abstracts

The vegetation near the summit of the volcano Usu was destroyed by 1-3 m thick layers of volcanic deposits during eruptions in 1977 and 1978. Thereafter, the vegetation gradually recovered and 135 plant species were recognized 6 years after the final eruptions. Of these plants, 95 species had established by vegetative reproduction, 18 species by seed immigration from elsewhere, 5 species by artificial introduction for soil erosion control and 17 species from viable seeds buried in the former topsoil. The summit areas are still covered by thick layers of volcanic ash, however, some areas have been rapidly eroded by rains and snowmelts. Vegetatively reproducing plants such as *Polygonum sachalinense* and *Petasites japonicus* var. *giganteus* contributed more effectively to the early revegetation process than plants with other types of origin.

A permanent quadrat survey for 5 years confirmed the high mortality of seedlings. Since seedling mortality appeared mostly due to the frequent erosions of the volcanic deposits, only ephemeral annuals and well-rooted perennials or woody plants were successful here. The high mortality of seedlings resulted in intensive fluctuation of plant density in all habitats. However, owing to the expansion of perennials, once they became established the plant cover increased from year to year. In particular, *Polygonum sachalinense* and *Petasites japonicus* var. *giganteus* contributed remarkably to the revegetation. Seeds of these plants were frequently provided from their community which were vegetatively propagated on the wall of caldera rim soon after the eruptions. The excavation of those perennial plants demonstrated that they were derived not only from the

seeds but also vegetatively from the old stumps buried in the former topsoil by extending their rhizomes up to the current ground surface.

Analyses of vegetation structure were computed by qualitative and quantitative parameters including species richness, species diversity (H'), evenness (J'), community coefficient (CC), and percentage similarity (PS). Even though species alteration occurred and vegetation cover gradually increased, species richness equilibrated soon after the eruptions. Although H' and J' differed with habitat characteristics such as species composition, nutrient conditions and soil movements, those parameters did not measure recovery rate. CC-value decreased only 40-50% for 5 years, suggesting that species composition did not change much during years in spite of occurring species alteration, but PS rapidly decreased up to 10-20%. A few well-rooted perennial plants were predominant, therefore, PS decline could be derived from dominance-controlled community structure. PS-value detected not only habitat difference, but also recovery rate of the volcanic succession, suggesting that PS is the most effective to evaluate successional pace. The determinants on revegetation pace are such short-term factors as paucity of species compositions, low resource availability, and movements of volcanic deposits.

Key words: buried seed, community coefficient, evenness, immigration, percentage similarity, resource condition, revegetation, soil movement, species composition, species diversity, species richness, tephra, the volcano Usu, vegetative reproduction, volcanic eruption, volcanic succession.

Revegetation dynamics in early successional stages of the volcano Usu,
 northern Japan, after the 1977-78 eruptions
 (1977-78年噴火後有珠山遷移初期植生回復の動態)

和文摘要

火山に代表される一次遷移の決定要因には土壌形成があり、二次遷移にみられる埋土種子や栄養繁殖による回復様式はあまり認められない。一次遷移において植物供給起源・死亡率・回復様式に着目した研究例は少ないが、植生動態を理解する上でこのことは重要である。本研究は火山一次遷移の動態を植生被度・個体数の調査にとどまらず植物供給起源・定着様式・生存死亡要因に着目して調査を行い、植物の適応様式・回復機構を明らかにすることを目的として行った。有珠山は外輪山に囲まれ内部に大有珠（標高727m）・小有珠を有し、その間に火口原と呼ばれる平坦地を持つ火山である。1977-78年噴火時に、噴火以前の森林（ドロノキ・シラカンバ広葉樹林）・牧草地は厚さ1-3mの噴火降灰物の堆積により壊滅状態となった。まず、植生回復における植物供給起源を明らかにするために、山頂部全域で、植生調査・根系調査・種子トラップ調査を行った。次に、地表面のもっとも不安定な火口原に注目し調査を行った。火口原を3つの生息域、ガリー外部(OG)、旧表土の出現したガリー内部(EG)、噴火降灰物に依然覆われたガリー内部(CG)に分け、1984-88年に永久調査区法によって被度・個体数を追跡し、1985年には4月から10月まで成長解析を行った。更に、OGにおいて1983年から個体追跡を行うと共に、根系の発達様式も調査した。環境要因として、土壌侵食量の継年計測、火山灰・旧表土の灼熱損料を測定した。

【結 果】

山頂域で調査期間中に135種を確認し、植生回復は栄養繁殖(95種)・種子散布(18)・人工播種(5)・埋土種子(17)の4つの機構によりなされていることを明らかにした。オオイタドリ・オオブキの栄養繁殖は旺盛であり、外輪山・大有珠では噴火直後から栄養繁殖による回復が認められ、火口原に豊富な種子を供給している。しかし、火口原はいまだに噴火降灰物が厚く堆積し植生回復は極めて遅い。火口原では、土壌侵食により旧表土が表れたガリー内部では、埋土種子起源の植物が顕著であった。

5年間で調査区内には60種が観察され、10種が一年生草本、36種が多年生草本、14種が木本植物であった。一年生植物のほとんどは埋土種子起源であり、木本植物は全てが散布種子由来であった。多年生草本はほとんどが栄養繁殖由来(22種)であるが、場合によっては、埋土種子(6)、人工播種(5)、散布種子(3)によるものであった。オオブキ・オオイタドリでは栄養繁殖および外輪山からの散布種子による回復が顕著であり、3つの生息域で優占している。ヤマハハコ・コウゾリナ・オオウシノケグサ・ドロノキもまた広く生息している。しかし、3つの生息域で植物組成は異なり、一年生植物は旧表土から供給されているためにEGで、散布種子起源である木本植物はOGで優占していた。土壌移動は、1983年にEG; -15cm-+41、CG; -4-+62、OG; -9-+3であり、ガリー内部の方がガリー外部より土壌移動は大きかった。CGではEGと同程度の土壌移動が認められるが埋土種子供給がない結果として総種数は最も少ないものと考えられた。全ての種で個体数は不規則な変動を示し、優占種であるオオブキでさえ比較的地表面の安定したOGにおいて、一調査区当り3から34の間で変動していた。しかし、被度の変動は多くの種で個体数の変動ほど不規則ではなかった。CGの被度は3つの生息域の中で最も早く増大するが、噴火降灰物の厚さがOGよりも薄く土壌移動がEG程大きくはないことに起因しているものと考えられた。即ち、土壌灼熱損料は、噴火降灰物で0.2-1.1%、旧表土では2.5-13.2%を示し、CGでは根系を発達させる大型多年生植物は、根系が旧表土にまで達しており、旧表土中の栄養分を有効に利用でき成長が良好であると考えられる。木本植物は多年生草本より若干遅い成長を示す。人工播種植物の定着は全体的に不良である。シロツメクサは埋土種子起源であるため、生息域はEGに限られているが窒素固定能力を有しており定着は良好である。OGでの結果を基に多年生植物の実生の死亡率を求めると、種間に差はなく80%程度であるが、一度越冬した個体の生存率は高かった。一年生植物のなかでも、スズメノテッポウ・スズメノカタビラ・タチタネツケバナは50%以上の個体が開花結実に至ったが、これらの種は1-3カ月で成体に至ることが可能なグループであった。一年生植物でも、結実に長期間を要するヒメムカシヨモギ・ノボロギクなどは全く結実せずに消滅した。越冬個体が高い生存率を有する原因を明らかにするために根系の発達様式を調査した結果、根系の発達様式は大きく3つに分けられた。タイプA:多数のライゾームを有する型。オオイタドリは地下1-2mにまで根系を発達させている。ほかにオオブキ・イ

タドリ等がこの型に属する。これらの根系は、旧表土に達しているものが多く効率よく旧表土の栄養を利用できる一方、個体によっては噴火以前に旧表土上に定着していた個体が、噴火降灰物を通り抜け栄養繁殖により回復しているものも認められた。タイプB：匍伏型。シロツメクサ・ミヤコグサ・ハイキンボウゲなど良好な匍伏枝を発達させるものであり、マメ科の前2者は窒素固定菌を有している。タイプC：密集したライゾームを有する型。タイプAおよびBに属さないヒメスゲ・シラネワラビなどの多年生草本がタイプCに入る。これらの種の定着は有性繁殖にかなり依存しているが、場合によっては栄養繁殖により定着している。

【考 察 と 結 論】

1. まず、火山植生の決定因子としては植物供給起源の組成・土壤栄養状態・土壤移動強度の3つが主要なものであると結論した。
2. 火山遷移は、コケ期・一年生草本期から始まるといわれているが、これらのステージは有珠山においては認められない。代わって、多年生植物が植生回復に良く寄与している。多年生草本は厚く積もった噴火降灰物上であっても栄養繁殖により十分に回復が可能であることが要因として上げられる。しかし、埋土種子が供給されれば一年生植物期といえるものが認められ、これらは、植物供給起源が植生回復を大きく規定していることを示している。例えば、窒素固定能力を有する多年生植物は貧栄養環境下でしばしば優占することが知られているが、有珠山ではEGのシロツメクサを除くとこれらの植物は定着していない。
3. セントヘレンズ山では、1980年噴火後外来草本の定着が早い。有珠山では外来草本（主として人工散布植物）の定着は不良であるが、散布直後に降雨等により流出したことと窒素固定能を有する種がなかったことが大きな理由だと思われる。
4. 有珠山では実生は豊富に出現するが死亡率は高い。この主要因は土壤移動であり、その結果厳しい環境下では、短い生活間を有する一年生植物、根系を発達させる多年生植物が定着に有利であり今後の植生回復の主体となるものと予測される。

Introduction

Since the first major ecological theory "ecological succession" was arisen (Cowles, 1899; Cooper, 1913; Clements, 1916), mounted studies on plant succession have been conducted (e.g., Gleason, 1917, 1927; Egler, 1954; Odum, 1969; Drury and Nisbet, 1973; Horn, 1974; Connell and Slayter, 1977; Bornkamm, 1981; Tilman, 1988). Although the particular details of plant community succession are unique to each site, there are some general trends that are common to many communities. Firstly, it is a time dependent process with changing vegetation characteristics such as density, cover, species richness, species diversities, and change of species composition (Whittaker, 1975; Bornkamm, 1981). Secondly, it results from modification of the physical and chemical environments by the community and vice versa (Odum, 1971, Tilman, 1982). Thirdly, it culminates in a stabilized ecosystem in which maximum biomass and/or high information content, and symbiotic function between organisms are maintained their communities (Drury and Nisbet, 1974, Odum, 1971). In the present paper, I deal with the former two problems to determine the characteristics of early stages in volcanic succession.

Plant succession is generally categorized into primary succession and secondary succession (Fig. 1) (Odum, 1971; Whittaker, 1975; Tilman, 1982). Primary succession, which occurs following complete destruction of biosystems where the ground surface is covered by rocks and/or inorganic soil (Booth, 1941; Cooper and Rudolph, 1953; Eggler, 1971; Vitousek et al., 1987), is considerably different from secondary succession such as the burned or plowed and abandoned fields (Wright and Bailey, 1982; Walker, 1982; Mallik and Gimingham, 1983; McCune,

	<< Primary succession >>	<< Secondary succession >>
<i>Definition</i>	Development begins on an area that has not been occupied by a community	Development is proceeding in an area from which a community was removed
<i>Field examples</i>	Newly exposed rock, sand surface, and lava flow	Abandoned crop field, and cut-over forest
<i>Source of plants</i>	Immigration only	Buried seeds, vegetative reproduction, and immigration

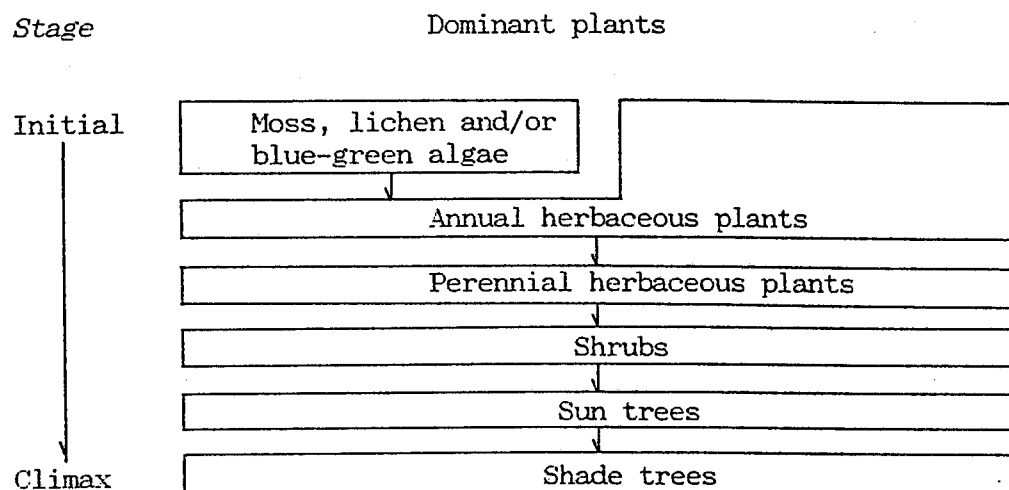


Fig. 1. General concept of plant succession. The definition of primary and secondary succession is referred to Odum (1971).

1988). For instance, the most important process of primary succession is the accumulation of nitrogen in the soil, which is conducted by blue-green algae, mosses, lichens, etc. (Griggs and Ready, 1934; Fosberg, 1959; Tagawa, 1964), while the secondary succession begins with more or less mature soil containing a sizable bank of seeds and vegetative propagules (Tilman, 1982, 1988; Crawley, 1986). Thus, primary succession proceeds very slowly in early stages (Whittaker, 1975; White, 1979; Tilman, 1982).

Regarding origin of plants, primary succession are completely dependent on the seed supply from an external environment, while secondary succession can start with various plant origins such as immigrant seeds, buried seeds and vegetative propagules (Fig. 1). Buried seeds remarkably contribute to secondary succession starting with post-fire forest (Nakagoshi, 1984), cut-over forest (Olmsted and Curtis, 1947; Hill and Stevens, 1981), and abandoned crop field (Harper, et al., 1965; Archibold, 1981). Due to those buried-seed banks containing a large number of annual-plant seeds, the secondary succession usually starts with the dominance of annual plants (Nakagoshi, 1984; Leck, et al., 1989). Annual plants also inhabit in an early stage of primary succession, but the only origin is seed immigration from elsewhere (Odum, 1971; Whittaker, 1975). Hence, I examine those origin of plants to understand the mechanisms underlying the revegetation of volcanoes.

Sites that support primary succession have been provided from the following retreat of glacier (Crocker and Major, 1955; Lawrence, 1958), massive landslides (Flaccus, 1959; Swanston and Swanson, 1976), sand dunes (Olson, 1958), and volcanic eruptions (Griggs, 1933; Tagawa 1964, 1965. del Moral, 1983; Antos and Zobel, 1985a,b, 1986; Wood and

del Moral, 1987, 1988). In most of these studies on primary succession, the changes of species composition, coverage and density of the plants were followed for several years; however, the mortality and the population dynamics within each species were scarcely observed. In such observations, it must be needed to analyse closely the dynamics of revegetation. In the present study, therefore, the revegetation on a recently erupted volcano was followed for 5 years not only by measuring the coverage and the density of plant species but also by examining the survival of each plant individual belonging to various types of life forms.

Although rate of vegetation change is one of the important characteristics of both primary and secondary succession, studies on the rate of succession are relatively scarce. This may be because of difficulty to generalize changes in different vegetation properties (Bornkamm, 1981). To evaluate stability, equitability and complexity in a community, species richness, species diversity and evenness have been applied to various communities (e.g., Peet, 1975; Bazzaz, 1975; Mutoh et al., 1985; Kwiatkowska and Symonides, 1986; McCune, 1988; Tsuyuzaki, 1989a). Percentage similarity and community coefficient are originally used to express inter-community heterogeneity (Sørensen, 1948; Dahl and Hadač, 1941), and those parameters can be used to express the rate of vegetation change during succession with no special modification of the original equations (Bornkamm, 1981). The durations of sequences from the beginning of a succession to the terminal stage (i.e., climax) can be very different (Major, 1974). If we use a chronofunction $v=f(t)$ for the description of vegetation, a stable situation at the end of a succession is indicated by $dv/dt=0$.

It is supposed that the terminal stage reaches when dv/dt is less than 5% (Olson, 1958, Tagawa, 1964, Bornkamm, 1981). Thus, to characterize volcanic succession, I report herein rates of vegetation change on the volcano Usu since the 1977-78 eruptions using popular five parameters including species richness, species diversity, evenness, percentage similarity, and community coefficient, as well as descriptive analyses.

Study Area

The volcano Usu

The volcano Usu, located on the northernmost Japanese island, Hokkaido ($42^{\circ}32'N$, $140^{\circ}50'E$), is composed of two peaks, O-Usu (727 m) and Ko-Usu (552 m) which are enclosed by caldera rim and crater basin (Fig. 2A, Plate A). The summit area of this volcano had been once covered mostly with the forests of *Betula platyphylla* var. *japonica* and *Populus maximowiczii* and partly with artificially-sprayed meadows of *Dactylis glomerata*, *Trifolium repens* and *T. pratense*, and the plant cover was completely deforested by the eruptions in 1977 and 1978, which resulted in a 1 to 3 m thick accumulation of volcanic deposits. Soon after the eruptions, the NW slope of O-Usu and inner wall of caldera rim are covered by a thick layer of volcanic rocks and the crater basin is overlain by volcanic ash with some deeply eroded gullies in which former topsoils is exposed (Fig. 2B, Plate B). In the present paper, the former topsoil means the well-developed soil, which was accumulated prior to the 1977-78 eruptions, covered with thick volcanic deposits. The inner wall of the caldera rim is now inhabited by a community of *P. japonicus* var. *giganteus* and *P.*

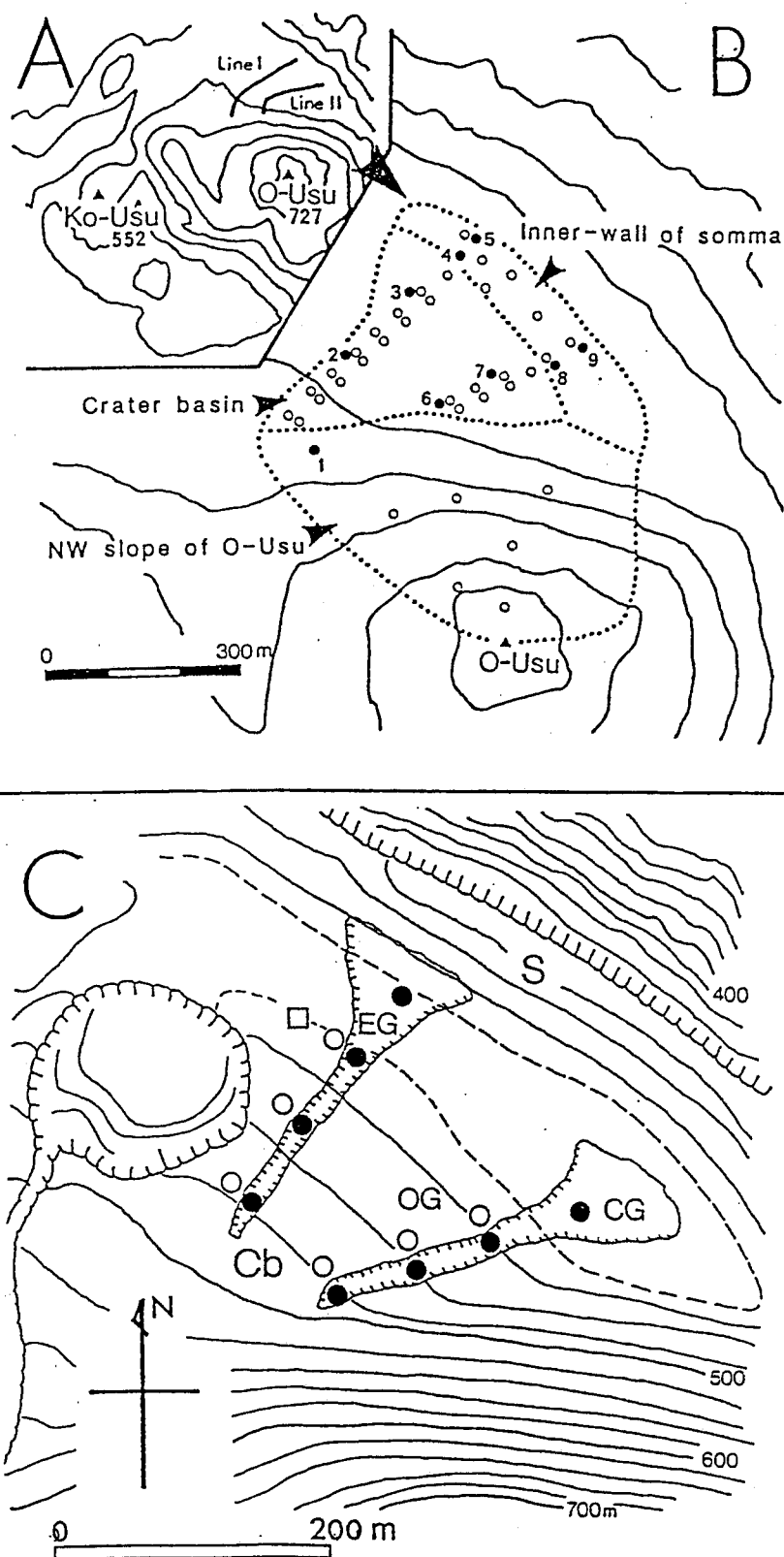


Fig. 2. Study area. A. overall view of the volcano Usu. Closed triangles indicate the summit of the mountains. B. study area of the origin of recovering plants. Locations of seed traps are shown by numerals 1 to 9. Open circles denote quadrats for vegetation description. C. the crater basin surveyed. Cb: crater basin; S: inner-wall of caldera rim. OG, outside the gully; CG, the gully where the former topsoil is still covered by volcanic deposits; EG, the gully where the former topsoil is exposed. Open and closed circles indicate 14 2 m x 5 m quadrats surveyed. Open square shows a 3.2 m x 3.2 m quadrat where the survivorship of plants was examined.

sachalinense which recovered vegetatively soon after the eruptions (Konno, internal report).

Crater basin

On the ground surface, more than 80% of volcanic deposits were composed of ash and pumice whose particle size was mostly less than 16 mm in diameter (Riviere, 1986). In level areas such as the crater basin, however, the ash and pumice layer is still thick and revegetation is very slow, though buried seeds are frequently exposed inside the deep gullies that were formed by erosion at the base of O-Usu (Fig. 2C). The present study was undertaken in the crater basin where many plant species of varied life forms were growing, in spite of high mortality induced mainly by the unstability of the ground surface. Based on geographical nature, the crater basin was divided into three habitats: outside of gully, i.e., hereafter OG, the former-topsoil-exposed gully, i.e., EG, and the former-topsoil-covered gully, i.e., CG (Fig. 2C, Plate C).

Methods

Field survey

Determinations of plant origin

In 1983 and 1984 density and cover of vascular plants were estimated in thirty five 2 m x 5 m quadrats (Fig. 1B). Closely aggregated shoots were regarded as one individual. This fact was confirmed by digging up plants near the quadrats. Species occurring outside the quadrats were also recorded. To confirm seed immigration, seeds immigrating into this surveyed zone were collected

with 9 1 m x 1 m traps set up along two line (Line I and II in Fig. 1, Plate D). Seeds were identified morphologically or by germination tests. The seed-dispersal type of each species was estimated according to Numata and Asano (1969). To confirm viable seeds buried in the former topsoil, the former topsoils collected in 1983 was subjected to the germination test in the greenhouse at room temperature and a 16-hr light period for 3 months until no more seeds germinated. Nomenclature follows Ohwi (1975), Flora of Japan (rev. ed.), Shibundo, Tokyo.

Monitoring of vegetation dynamics

From 1984 to 1988, coverage and density of vascular plants were surveyed within 14 permanently marked 2 m x 5 m quadrats that were located in OG (6 quadrats), in EG (4 quadrats) or in CG (4 quadrats) (Fig. 1C). Additionally, to observe the mortality of annual plants, the growth of each individual within all these quadrats was followed from April to November in 1985. To determine the survival rate of each plant species, all the individuals were mapped from 1983 to 1987 within another quadrat of 3.2 m x 3.2 m outside the gully (Plate E). In 1986 and 1987, the root systems of dominant perennials were observed by digging them up in the crater basin.

Soil analyses

To obtain intensity of soil movement, soil movement was measured on each quadrat, using a transit compass (Tracon LS-25, Ushikata), from 1983 to 1987. Conditions of organic matter in volcanic deposits and former topsoil were estimated by an ignition loss.

Evaluation of recovering pace

Quantitative and qualitative changes of vegetation are described with the help of four parameters, i.e., community coefficient CC (Sørensen, 1948), percentage similarity PS (Dahl and Hadač, 1941), species diversity H' (Shannon and Weaver, 1949), and evenness J' (Pielou, 1975). To evaluate rates of change in revegetation, CC and PS were modified by Bornkamm (1981):

$$CC = 2a/(2a+b+c),$$

where a is the number of species occurring in both the given and the reference year, b the number occurring only in the given year, and c the number of occurring only in the reference year.

$$PS = 2 \sum \min(x_i, y_i) / \sum (x_i + y_i) \times 100,$$

where x_i and y_i are the percentage cover of given species in years x and y . $\min x_i$ or $\min y_i$ is the lower cover value of species occurring in both years.

Results

Origin of recovering plants

Vascular plants summed 135 species in total during 1983 and 1984 (in detail, see Appendix). On the basis of their origin, they were divided into four groups:

*I. Vegetatively recovering species; 95 taxa, arising from buried plants: Particularly the species of *Angelica ursina*, *Aralia cordata*, *Aster ageratoides* var. *ovatus*, *Petasites japonicus* var. *giganteus* and *Polygonum sachalinense* rapidly produced shoots from buried rhizomes, stolons and sprouts, especially on steep slopes such as inner wall of the caldera rim (Konno, int. rep.) where the accumulation of volcanic deposits was not so big as in the crater basin and much of the ash had*

Table 1. Life forms and seed dispersal types of vascular plants observed on the volcano Usu (number of species) during 1983 and 1984. Groups I-IV are described in the text.

	Group				Total
	I	II	III	IV	
Annual	0	3	0	8	11
Perennial	64	8	3	9	84
Woody	31	7	2	0	40
Wind-dispersed					
long distance	7	10	0	0	17
short distance	49	3	4	7	63
Gravity-dispersed	10	1	0	5	16
Self-dispersed	8	2	0	5	15
Animal dispersed	21	2	1	0	24
Total	95	18	5	17	135

Table 2. Occurrence of plant species of groups I-IV in different habitats.

Group	NW slope of O-Usu	Crater basin		Inner-wall of somma
		Gully		
		Inside	Outside	
I	34(81.0%)	27(46.6%)	25(61.0%)	54(81.8%)
II	3(7.1%)	13(22.4%)	11(26.8%)	4(6.1%)
III	3(7.1%)	3(5.2%)	3(7.3%)	5(7.6%)
IV	2(4.8%)	15(25.9%)	2(4.9%)	3(4.5%)
	*	*	*	*
Total	42	58	41	66

* The inter-group differences is significant at $P < 0,05$ (χ^2 -test).

Table 3. Contribution of Groups I-IV to the revegetation at each habitat surveyed. Mean density per 10 m² (above) and mean cover (below) with standard deviation are presented. n: number of quadrats. I to IV, defined in Table 1.

Group	NW slope of O-Usu (n=6)	Crater basin		Inner-wall of somma (n=7)
		Gully		
		Inside (n=12)	Outside (n=10)	
I	- 18.9 $\pm$ 25.9%	20.9 $\pm$ 10.2 2.6 $\pm$ 2.6%	44.3 $\pm$ 19.1 3.7 $\pm$ 2.8%	- 94.2 $\pm$ 5.3%
II	- 0.8 $\pm$ 1.9%	1.8 $\pm$ 3.7 0.2 $\pm$ 0.4%	14.9 $\pm$ 18.2 1.1 $\pm$ 0.7%	0 0%
III	- 1.3 $\pm$ 1.8%	6.9 $\pm$ 10.2 0.8 $\pm$ 0.3%	4.2 $\pm$ 5.4 5.3 $\pm$ 6.3%	0 0%
IV	- 1.0 $\pm$ 1.8% *	12.3 $\pm$ 11.2 2.1 $\pm$ 3.4% NS	0.8 $\pm$ 1.5 0.2 $\pm$ 0.5% *	0 0% *

-: no data. *: the inter-group difference is significant at $P < 0.05$ (χ^2 -test). NS: non-significant.

been washed away by post-eruption rains. Although the other species of this group had not been found by Konno (int. rep.), they were now abundant too, and most of their stalks were observed to reach the former topsoil, suggesting that they were derived from buried vegetative organs. The other species recovered mostly in thinner volcanic layers where the tephra had been eroded. All the species of this group are perennial and some of them were woody species (Table 1). Two of them *P. sachalinense* and *Petasites japonicus* var. *giganteus* frequently produce seeds (Fig. 3).

II. *Immigrant species*; 18 taxa, established from outside the study area, including both herbs and woody species: They did not dominate in any quadrat but were found widespread in the summit area, except on the inner wall of the caldera rim (Table 2) which was already dominated by *P. japonicus* var. *giganteus* and *P. sachalinense*. On the basis of the morphology of the seeds they were assumed to have been transported by winds or animals from external environments (Table 1). Actually some seeds of *Salix* spp. were captured in traps (Fig. 3).

III. *Artificially introduced species*; 5 taxa, for artificial erosion control: those species were introduced by an airplane soon after the eruptions to prevent soil erosion. At present, the former 3 species were dispersing seeds and their seedlings were found especially in OG. However, their total cover was very small (Table 3), indicating that artificial introduction did not to be effective to protect soil erosion.

IV. *Buried-seed species*; 17 taxa, establishing from viable seeds left in the original topsoil, including both annuals and perennials. Their distribution was restricted to the deep eroded gullies of the crater basin (Table 2, Plate F), where the former topsoil became

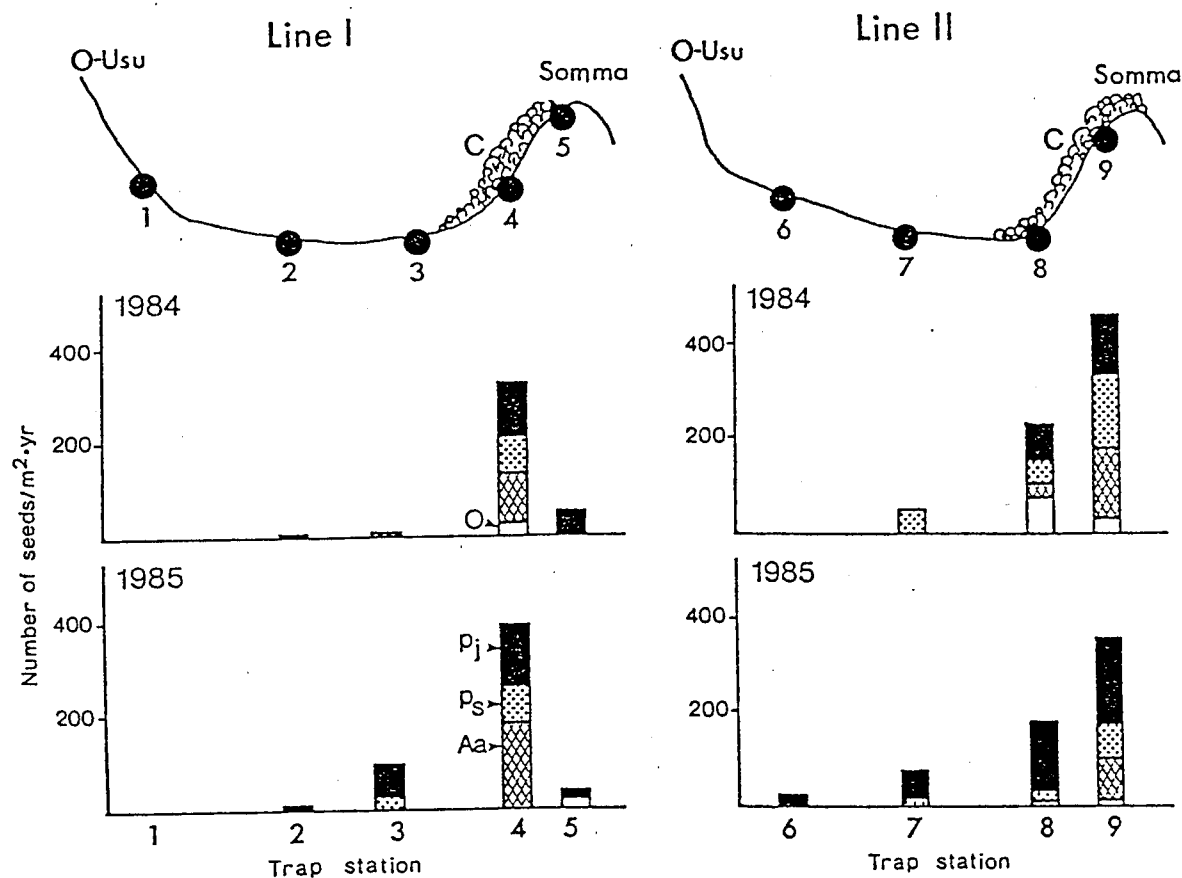


Fig. 3. The number of seeds trapped at each station. Aa: *Aster ageratoides* var. *ovatus*. Pj: *Petasites japonicus* var. *giganteus*. Ps: *Polygonum sachalinense*. O: 'Others' includes *Aralia cordata*, *Aster scaber*, Graminae spp., *Populus maximowiczii* and *Salix* spp. C: community of *Petasites japonicus* var. *giganteus* and *Polygonum sachalinense* which recovered soon after the eruptions (Konno int. rep.).

exposed again. None of these species is known as a long-distance anemochore (Table 1) and a germination test with former topsoil in the greenhouse proved that many seeds a.o. of *A. aequalis* var. *amurensis*, *G. macrophyllum* var. *sachalinense*, *P. annua* and *T. pratensis* were still viable (Tsuyuzaki, 1989b).

Table 3 shows the mean density and the mean cover of the four species groups at each habitat. Group I was predominant in all habitats, especially on the inner wall of the caldera rim where their mean cover was $94.2 \pm 5.3\%$. In contrast, the species of the immigrant group had lower values for both density and cover, suggesting that they established only rarely in the frequently eroded environment. The artificially introduced species did not contribute much either. Although the density of the buried-seed species was as high as 12.3 ± 11.2 per 10 m^2 on the inside of the gully, their cover was only $3.1 \pm 3.4\%$, this must be due to the reason that they had not yet grown as much as the resprouting species of Group I. Plants of Group IV in the gully outside of it had probably developed from the seeds dispersed by adults established in the gully. Thus, vegetatively recovering plants which were perennial herbaceous or woody species, contributed most to the revegetation in the summit area. This is probably because this area is being eroded by rain and these species are more tolerant to frequent disturbance than annual species.

Revegetation dynamics

Out of 60 species observed in the 14 quadrats from 1984 to 1988, 10 were annual, 36 perennial herbs and 14 woody species (Table 4).

Table 4. Yearly fluctuation of densities per 2 x 5 m quadrat (above) and mean percentage cover (below) in each habitat. +: less than 0.1%. .: no individual observed. I: immigrant; BS: buried seed; V: vegetative reproduction; A: artificial introduction. n: number of quadrats surveyed. OG, EG, and CG, described in the text. See also Figs. 4 and 5.

		Gully inside														
		Gully outside (n=6)					With former topsoil exposed (n=4)					Covered with volcanic deposits (n=4)				
Year	LF	1984	1985	1986	1987	1988	1984	1985	1986	1987	1988	1984	1985	1986	1987	1988
Annual																
<i>Paraixeris denticulata</i>	I	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.3 +
<i>Senecio vulgaris</i>	I	.	0.2 +	.	.	.	.	0.5 +	1.8 0.1	2.3 +	0.5 +	.	.	.	.	.
<i>Oenothera biennis</i>	I	.	.	.	.	.	.	.	.	.	0.3 +	.	.	.	.	.
<i>Poa annua</i>	BS	0.3 0.1	0.2 +	.	.	.	0.3 +	5.0 +	1.3 +	.	.	0.2 0.2	.	.	.	.
<i>Alopecurus aequalis</i> var. <i>amurensis</i>	BS	.	.	.	.	.	3.0 +	8.5 0.1	9.5 0.2	2.3 0.1	.	.	.	.	.	.
<i>Erigeron canadensis</i>	BS	.	.	.	0.2 +	.	.	2.8 +	1.8 +	0.3 +	0.3 0.1	.	.	.	.	.
<i>Rorippa islandica</i>	BS	.	.	.	.	.	9.5 0.4	38.3 0.3	3.3 +	4.5 0.2	.	.	.	.	.	.
<i>Polygonum longisetum</i>	BS	.	.	.	.	.	4.8 0.2	15.5 0.1	0.3 +	0.5 +	4.5 +	.	.	.	.	.
<i>Cardamine flexuosa</i> var. <i>fallax</i>	BS	.	.	.	.	.	.	0.5 +	.	.	.	.	.	.	.	0.5 +
<i>Chenopodium album</i> var. <i>centrorubrum</i>	BS	.	.	.	.	.	.	.	.	2.3 0.1	.	.	.	.	.	.
Perennial																
<i>Petasites japonicus</i> var. <i>giganteus</i>	V	3.0 1.1	31.0 3.1	19.5 5.3	34.0 7.6	28.5 8.3	26.8 0.3	10.8 0.7	10.0 1.9	20.8 3.0	18.5 4.2	19.8 2.1	89.8 6.8	33.0 5.1	104.0 8.1	144.5 9.2
<i>Polygonum sachalinense</i>	V	4.3 0.6	20.3 1.5	32.7 4.7	44.5 7.6	9.0 15.5	0.8 +	3.8 0.3	2.3 +	4.0 0.1	1.0 0.1	4.5 1.3	14.3 14.8	31.8 15.0	93.3 20.6	17.5 23.8
<i>Carex oxyandra</i>	V	5.0 0.3	7.3 0.5	9.8 0.5	13.2 0.7	57.5 1.6	.	1.3 0.2	.	.	1.3 0.3	0.3 +	0.3 +	.	1.0 +	10.0 0.7
<i>Polygonum cuspidatum</i>	V	1.0 0.2	0.3 +	0.3 0.3	0.3 0.3	0.7 1.0	.	.	.	.	.	.	.	0.3 0.2	0.3 0.3	0.3 0.8
<i>Agrostis scabra</i>	V	7.7 0.2	0.8 0.2	.	.	0.5 +	.	0.3 +	0.8 0.1	.	1.3 0.3	0.8 0.1	.	.	0.8 +	2.5 0.4
<i>Carex breviculmis</i>	V	0.7 0.1	.	.	.	.	.	.	0.3 +	0.8 0.2	.	.	.	.	.	.
<i>Epilobium montanum</i>	V	0.3 +	1.3 +	0.7 +	0.8 +	0.3 +	1.3 +	3.0 +	0.3 +	0.8 +	0.8 +	.	1.3 +	0.3 +	.	.
<i>Epilobium palustre</i> var. <i>lavandulaefolium</i>	V	0.2 +	.	.	.	0.2 +	.	.	.	.	.	.	.	.	.	1.3 +
<i>Luzula capitata</i>	V	0.3 +	0.3 +	0.2 +	.	.	0.3 0.1	1.0 0.1	1.3 0.2	1.0 0.3	0.8 0.5	0.5 0.1	.	.	.	.
<i>Moehringia lateriflora</i>	V	0.7 +	0.2 +	.	.	.	0.8 +	0.3 +	1.0 +	0.5 +	.	.	.	.	.	.
<i>Eupatrium chinense</i> var. <i>sachalinense</i>	V	0.3 +	.	.	.	.	.	.	.	.	.	0.3 +	.	.	.	.
<i>Aralia cordata</i>	V	.	0.5 +	0.7 +	0.7 0.1	0.7 0.2	0.3 +	.	.	.	.	.	0.5 0.1	0.8 0.1	0.8 0.2	0.3 +
<i>Picris hieracioides</i> var. <i>glabrescens</i>	V	.	0.2 +	0.3 +	0.3 +	0.7 +	0.3 +	0.8 +	0.3 +	0.5 0.2	1.0 0.1	.	.	24.5 +	12.0 0.3	6.3 0.1

continuing.

Table 4. Continued.

Year	LF	Gully inside														
		Gully outside (n=6)					With former topsoil exposed (n=4)					Covered with volcanic deposits (n=4)				
		1984	1985	1986	1987	1988	1984	1985	1986	1987	1988	1984	1985	1986	1987	1988
<i>Juncus fauriensis</i>	V	.	0.7	0.3	0.8	.	.	.	.	.	.	.	.	.	.	.
		.	+	+	+	.	.	.	.	.	.	.	.	.	.	.
<i>Dryopteris austriaca</i>	V	.	.	.	.	0.2	.	.	.	.	.	.	0.5	0.3	0.3	.
		.	.	.	.	+	.	.	.	.	.	.	+	+	+	.
<i>Aster ageratoides</i> var. <i>ovatus</i>	V	.	.	.	.	0.2	.	.	.	.	.	.	0.5	.	.	.
		.	.	.	.	+	.	.	.	.	.	.	+	.	.	.
<i>Taraxacum officinale</i>	V	.	.	.	.	.	0.5	2.3	1.0	1.0	1.5	.	.	0.3	.	.
		.	.	.	.	.	0.2	1.0	0.8	0.9	0.4	.	.	0.1	.	.
<i>Cerastium vulgatum</i> var. <i>hallaisanense</i>	V	.	.	.	.	.	.	1.3	2.0	3.0	13.0	.	0.5	.	1.0	.
		.	.	.	.	.	.	+	+	0.2	0.3	.	+	.	+	.
<i>Plantago asiatica</i>	V	.	.	.	.	.	.	1.3	0.3	0.5	3.0	.	.	.	.	.
		.	.	.	.	.	.	+	+	+	0.1	.	.	.	.	.
<i>Ixeris dentata</i>	V	.	.	.	.	.	.	.	.	.	.	.	3.0	.	.	.
		.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
<i>Spiranthes sinensis</i>	V	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.5
		.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
<i>Sonchus asper</i>	V	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0.5
		.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
<i>Anaphalis margaritacea</i> var. <i>angustior</i>	I	2.2	21.0	15.5	29.3	32.8	0.5	11.0	35.8	31.5	28.8	.	10.0	15.8	40.0	59.3
		0.1	0.2	0.7	1.1	2.5	+	0.2	0.8	4.2	5.0	.	0.3	0.6	1.2	2.5
<i>Equisetum arvense</i>	I	.	.	.	.	.	0.3	1.0	2.8	5.8	10.3	.	.	.	.	.
		.	.	.	.	.	+	+	+	2.3	2.5	.	.	.	.	.
<i>Miscanthus sinensis</i>	I	.	.	.	.	0.2	.	.	.	.	1.5	.	.	.	.	.
		.	.	.	.	+	.	.	.	.	+	.	.	.	.	.
<i>Festuca elatior</i>	A	1.3	2.8	0.2	1.2	1.3	.	0.8	0.5	1.0	3.3	0.5	1.0	0.8	0.5	4.5
		0.1	0.4	+	0.3	0.1	.	0.1	+	0.2	0.3	0.1	0.1	+	+	0.1
<i>Festuca rubra</i>	A	2.5	3.5	3.8	3.7	4.3	0.5	0.3	1.0	4.5	7.0	3.0	1.5	5.5	7.0	6.5
		0.1	0.1	0.2	0.2	0.4	0.1	+	+	0.1	0.3	0.1	0.1	0.1	0.5	1.0
<i>Artemisia montana</i>	A	0.2	.	.	0.2	0.8	.	1.3	13.0	8.8	9.0	7.8	11.0	26.0	7.0	5.5
		+	.	.	+	+	.	+	+	0.2	0.8	0.8	1.1	0.6	0.6	0.9
<i>Agrostis alba</i>	A	.	.	1.3	0.5	0.2	.	0.3	0.3	0.3	0.5	.	.	.	.	0.5
		.	.	0.3	+	+	.	0.1	+	+	0.3	.	.	.	.	+
<i>Lolium perenne</i>	A	.	.	.	.	.	.	.	.	.	0.5	.	.	.	.	.
		.	.	.	.	.	.	.	.	.	0.4	.	.	.	.	.
<i>Trifolium repens</i>	BS	0.8	0.5	1.8	0.8	1.3	2.5	2.8	2.0	4.3	8.3	.	0.5	.	.	.
		0.3	+	+	0.2	0.6	1.0	1.4	6.5	10.4	14.7	.	+	.	.	.
<i>Rumex obtusifolius</i>	BS	.	.	.	.	.	8.0	2.0	4.5	22.8	0.3	0.8	0.8	.	.	.
		.	.	.	.	.	0.6	0.4	0.1	0.4	0.1	+	+	.	.	.
<i>Geum macrophyllum</i> var. <i>sachalinense</i>	BS	.	.	.	.	.	1.3	0.8	.	0.5	0.5	.	.	.	.	.
		.	.	.	.	.	0.2	0.4	.	0.2	0.1	.	.	.	.	.
<i>Ranunculus repens</i>	BS	.	.	.	.	.	0.3	.	1.3	0.8	.	.	.	.	.	.
		.	.	.	.	.	+	.	0.4	0.3	.	.	.	.	.	.
<i>Viola grypoceras</i>	BS	.	.	.	.	.	2.8	2.3	1.5	0.8	0.8	.	.	.	.	.
		.	.	.	.	.	0.1	0.1	+	+	+	.	.	.	.	.
<i>Lotus corniculatus</i> var. <i>japonicus</i>	BS	.	.	.	.	.	.	0.3	1.8	1.0	0.8	.	.	.	.	.
		.	.	.	.	.	.	+	0.2	0.3	0.1	.	.	.	.	.

continuing.

Table 4. Continued.

Year	LF	Gully inside														
		Gully outside (n=6)					With former topsoil exposed (n=4)					Covered with volcanic deposits (n=4)				
1984	1985	1986	1987	1988	1984	1985	1986	1987	1988	1984	1985	1986	1987	1988		
Woody																
<i>Populus maximowiczii</i>	I	3.3 0.2	1.3 0.3	2.7 0.4	3.5 0.9	1.8 1.3	0.3 +	1.8 0.1	2.3 0.3	2.0 0.7	2.0 1.4	1.5 +	1.0 0.1	3.8 0.2	3.5 0.3	5.5 1.4
<i>Salix hultenii</i> var. <i>angustifolia</i>	I	2.0 0.3	2.8 0.3	2.2 0.9	2.2 0.9	1.8 4.3	. .	. .	. .	. .	. .	1.3 0.1	1.8 1.1	2.8 2.0	2.3 2.7	3.0 5.5
<i>Salix integra</i>	I	0.5 0.1	0.7 0.2	0.5 0.2	0.5 0.2	0.7 0.5	. .	0.5 +	0.3 +	0.3 +	0.3 0.1	0.5 0.1	1.0 0.2	0.5 0.1	0.5 0.3	0.5 0.4
<i>Salix sachalinensis</i>	I	0.2 +	7.3 0.1	0.5 0.2	0.3 +	0.8 0.5	. .	0.3 +	0.3 +	0.3 +	0.3 0.8	0.3 +	0.8 0.1	1.3 0.3	1.0 0.3	0.5 0.9
<i>Betula platyphylla</i> var. <i>japonica</i>	I	0.2 0.1	0.3 0.2	0.7 0.6	0.7 0.7	0.8 1.4	. .	0.3 0.2	0.3 +	. .	0.3 0.5	. .	1.0 0.7	1.3 0.9	1.3 1.2	0.5 2.3
<i>Betula maximowicziana</i>	I	0.7 0.1	0.7 0.2	1.0 0.5	1.0 0.5	0.7 0.8	. .	. .	. .	. .	. .	0.5 0.1	0.3 0.1	0.8 0.3	0.5 0.3	1.3 1.4
<i>Betula ermanii</i>	I	0.8 0.1	0.5 0.2	. .	. .	. .	. .	. .	. .	. .	. .	0.5 0.1	. .	. .	. .	. .
<i>Acer mono</i>	I	0.2 +	0.2 +	0.2 +	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .
<i>Larix lepitolepis</i>	I	. .	0.2 +	0.2 +	0.2 +	0.2 +	. .	. .	. .	. .	. .	. .	. .	. .	. .	0.3 0.1
<i>Salix miyabeana</i>	I	. .	. .	0.2 +	0.2 +	0.2 +	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .
<i>Populus sieboldii</i>	I	. .	. .	. .	0.2 +	0.2 +	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .
<i>Prunus sargentii</i>	I	. .	. .	. .	. .	. .	. .	. .	. .	. .	0.3 +	. .	. .	. .	. .	. .
<i>Alnus hirsuta</i>	I	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	0.3 +	. .	. .	. .
<i>Hydrangea paniculata</i>	I	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	. .	9.8 +
Total		58.8 4.1	105.2 7.4	95.2 14.8	139.2 21.4	146.5 40.2	44.5 3.3	122.0 5.8	104.3 11.5	129.8 24.3	121.8 33.6	42.5 4.9	141.3 25.5	149.3 25.5	276.8 36.7	282.5 52.1
Number of species		25	26	23	24	27	21	33	32	31	32	16	22	18	19	25

Most of annuals were of buried seeds, while woody plants all derived from immigrated seeds. Perennials recovered mostly vegetatively (22 species) and occasionally from buried seeds (6), artificially introduced seeds (5) or seeds from off the volcano (3). *Polygonum sachalinense* and *Petasites japonicus* var. *giganteus* seeds were provided from their community, recovered vegetatively on the caldera rim; they were dominant in every habitat. *Anaphalis margaritacea* var. *angustior*, *Picris hieracioides* var. *glabrescens*, *Festuca rubra* and *Populus maximowiczii* were also general at least in the crater basin. However, the total vegetation differed remarkably among the three habitats; thus, annual plants derived from the buried seeds were abundant at EG, while woody plants having immigrated from external environments were dominant at OG. Soil movement ranged from -15 to +41 cm, from -4 to +62 cm, and from -9 to +3 cm in EG, CG, and OG, respectively, in 1983, suggesting that OG was relatively stable and the plants in CG and EG were damaged more by the soil movement. The soil movements gradually decreased and almost ceased in 1986. At OG where the buried seeds were not often provided but erosion occurred as frequently as at EG, the species richness was the lowest every year.

On life form or origin, the density fluctuated variously (Fig. 4), because no species regularly increased its density in any habitats. Even the dominant perennials *Petasites japonicus* var. *giganteus*, which could rapidly develop subterranean shoots, fluctuated from 3 to 34 individuals per quadrat even in the rather stable habitat OG. However, the fluctuation of plant coverage was not so great as that of density. As shown in Fig. 5, total coverage increased annually in every habitat, mostly due to the rapid expansion of such perennial species as *Polygonum sachalinense*, *Petasites japonicus* var.

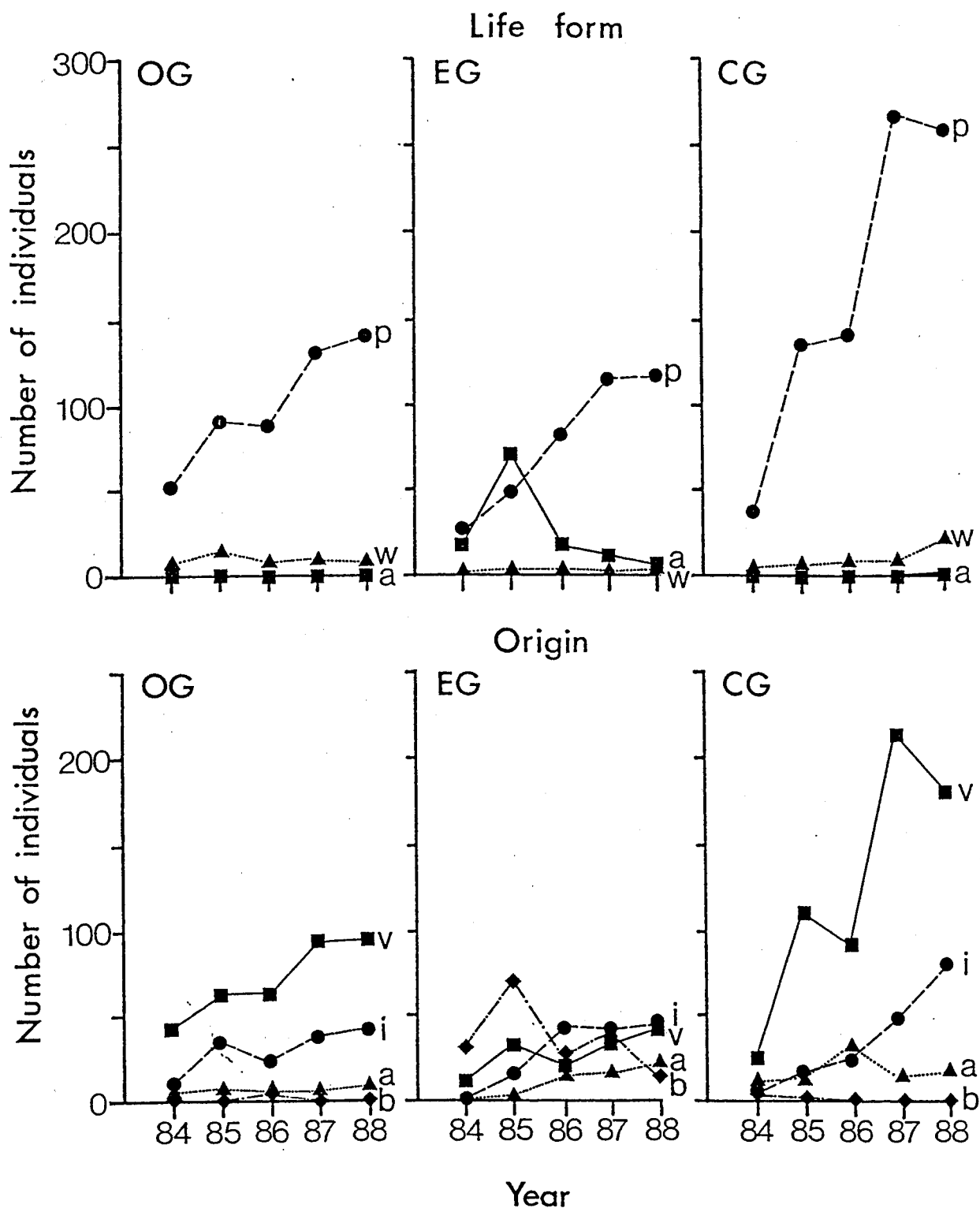


Fig. 4. Yearly fluctuation of density ($/10 \text{ m}^2$) in each habitat. In the figure of life form (upper column), a, p, and w indicate annual plants, perennial herbaceous plants, and woody plants, respectively. In the figure of origin (lower column), v, i, a, and b indicate vegetative reproduction, immigration, artificial introduction, and buried seed, respectively. For OG, CG and EG, see Fig. 2. In detail, see Table 4.

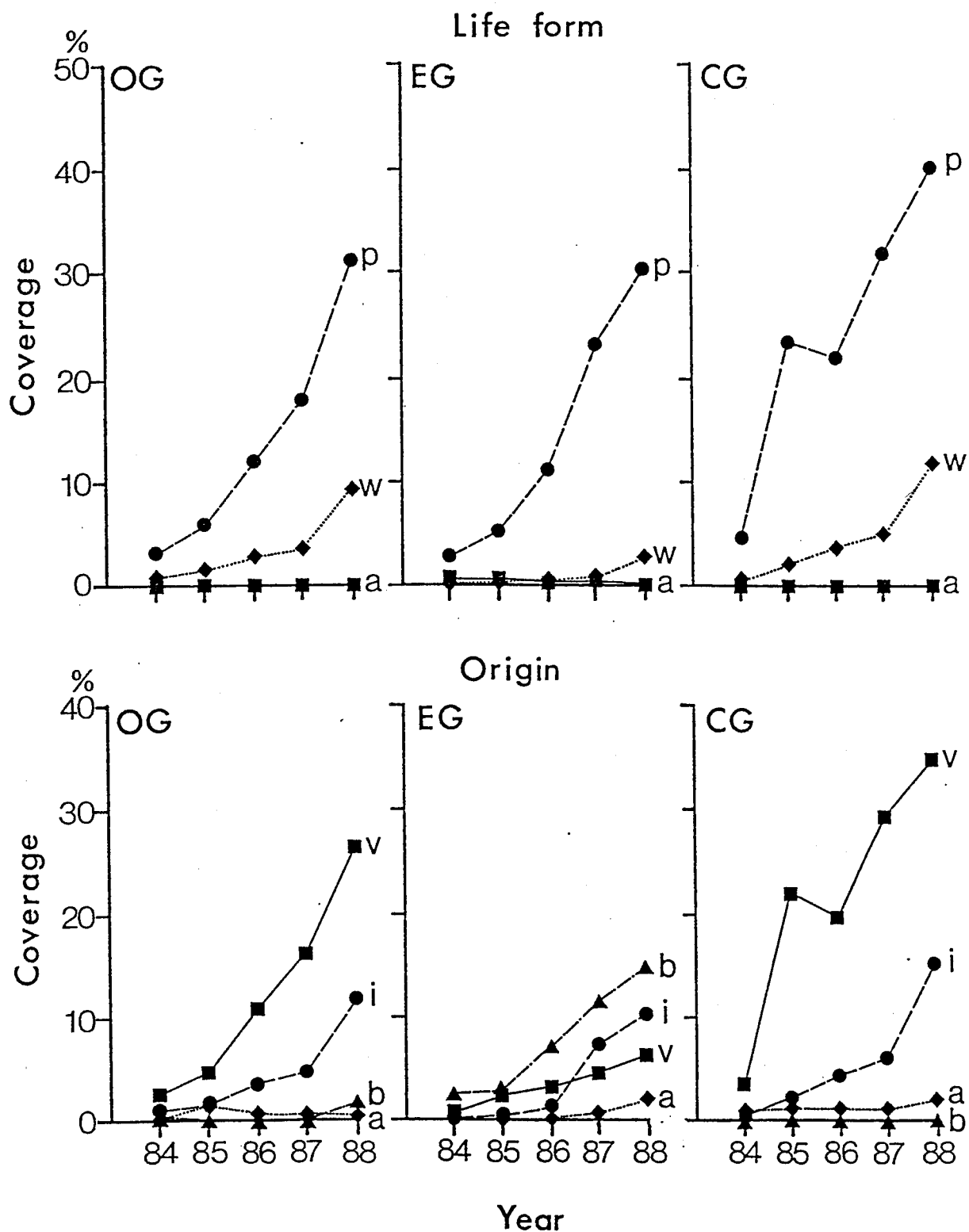


Fig. 5. Yearly fluctuation of coverage in each habitat. Legends are the same as Fig. 4. For OG, CG and EG, see Fig. 2. In detail, see Table 4.

giganteus and *Trifolium repens*. Especially in CG, their cover increased greatly, probably because the layer of volcanic deposits was thinner than in OG and the intensity of soil erosion was lower than in EG. Ignition loss showed 0.2 to 1.1% in the volcanic deposits and 2.5 to 13.2% in the former topsoil, suggesting that the nutrients of the former topsoil was, at least, several times richer than that of the volcanic deposits. In particular, the plants possessing large rhizomes seemed to gain nutrients from the former topsoil more efficiently in CG than in the other habitat. Woody plants such as *Populus maximowiczii*, *Salix hultenii* var. *angustifolia*, *S. integra*, *S. sachalinensis*, *Betula platyphylla* var. *japonica* and *B. maximowicziana* were also expanding gradually in all habitats, but the coverage of annual plants remained very limited. Artificially introduced species contributed rather little to revegetation. Although the density of individuals belonging to the buried-seed group, which included nitrogen-fixing species *Trifolium repens* and *Lotus corniculatus* var. *japonica*, fluctuated in the inside of the gully, their cover increased gradually.

The large fluctuation of density along with the rapid expansion of coverage suggests that mortality is high in young seedlings but relatively low once plants were established. As suggested above, 60 to 80% of seedlings of such perennial species as *Petasites japonicus* var. *giganteus* and *Polygonum sachalinense* died within a year but, once established, many plants survived thereafter (Table 5).

In *Artemisia montana* and *Agrostis scabra* whose seedlings seemed to be fragile, almost no seedlings overwintered to the following year. Twenty-five point nine percent (7/27) of woody plant seedlings

Table 5. Survivorship of perennial and woody plants in a 3.2 m x 3.2 m quadrat from 1983 to 1987. Each numeral is the survival rate of a seedling cohort which occurred in a given year. n: number of seedlings

	n	1983	1984	1985	1987
Perennial					
<i>Petasites japonicus</i>	11	100.0	18.2	9.1	0.0
var. <i>giganteus</i>	16		100.0	25.0	0.0
	15			100.0	20.0
<i>Polygonum sachalinense</i>	5	100.0	20.0	20.0	20.0
	8		100.0	37.5	37.5
	2			100.0	0.0
<i>Artemisia montana</i>	1	100.0	0.0	0.0	0.0
	5		100.0	0.0	0.0
	1			100.0	0.0
<i>Agrostis scabra</i>	1	100.0	0.0	0.0	0.0
	47		100.0	6.4	0.0
	1			100.0	0.0
Others	7	100.0	14.3	0.0	0.0
	9		100.0	33.3	22.2
	2			100.0	0.0
Subtotal					
	25	100.0	16.0	8.0	4.0
	85		100.0	15.3	5.9
	21			100.0	14.3
Woody					
<i>Salix hultenii</i>	12	100.0	16.7	16.7	16.7
var. <i>angustifolia</i>	4			100.0	0.0
<i>Salix sachalinensis</i>	1	100.0	100.0	0.0	0.0
	3			100.0	0.0
<i>Populus maximowiczii</i>	12	100.0	33.3	16.7	16.7
	6		100.0	16.7	16.7
	4			100.0	50.0
Others	2	100.0	0.0	0.0	0.0
	1		100.0	0.0	0.0
Subtotal					
	27	100.0	25.9	14.8	14.8
	7		100.0	14.3	14.3
	11			100.0	18.2
Total					
	52	100.0	21.2	11.5	9.6
	92		100.0	15.2	6.5
	32			100.0	15.6

overwintered and 14.8% (4/27) of them remained alive during the fourth year (Table 5). Even in OG where the soil movement intensity was relatively low, the seedlings showed high mortality rate. Seedling survival of perennials was important for the gully inside to recover vegetation, too, however, mortality of their seedlings was considered to be very high. A half or more annual seedlings matured to fertile plants in *Alopecurus aequalis* var. *amurensis*, *Poa annua* and *Cardamine flexuosa* var. *fallax* which took only 1 to 3 months to grow up to adults; in contrast, no seedling ripened in *Erigeron canadensis* and *Senecio vulgaris* whose growth periods were more than 3 months (Table 6). The maturity rate was intermediate in *Rorippa islandica* and *Polygonum longisetum*, which grew rapidly early in the sterile phase, although their life span was relatively long, 3 to 5 months.

To detect the reason for high survival of overwintered perennial plants, underground organs of well-developed individuals were examined and divided into three types based on morphology (Fig. 6):

Type A: Multicapital rhizomes, which were derived from old crown; *Polygonum sachalinense* developed 1.5 to 2 m deep roots (Plate G). Some of their shoots were attached to the old stumps buried in the former topsoil, suggesting their vegetative recovery from the plants felled by the latest eruption. *Petasites japonicus* var. *giganteus* often elongated large shoots horizontally (Plate H). Although their roots did not reach the former topsoil at present, unlike *Polygonum sachalinense*, their vegetative recovery from the stumps buried in the former topsoil was very likely because some of their subterranean stems were too large to have been derived from the seeds dispersed after the eruption. The vertical roots from the stumps buried in the former topsoil probably disappeared after developing the upper root

Table 6. Fruiting success rates of annual plants in 1985

	Seedling	Fruiting	%
Brassicaceae			
<i>Caldamine flexuosa</i> var. <i>fallax</i>	4	3	75.0%
<i>Rorippa islandica</i>	199	48	24.1%
Poaceae			
<i>Alopecurus aequalis</i> var. <i>amurensis</i>	40	20	50.0%
<i>Poa annua</i>	49	29	59.2%
Polygonaceae			
<i>Polygonum longisetum</i>	64	24	37.5%
Asteraceae			
<i>Erigeron canadensis</i>	15	0	0.0%
<i>Senecio vulgaris</i>	3	0	0.0%
Total	374	124	33.2%

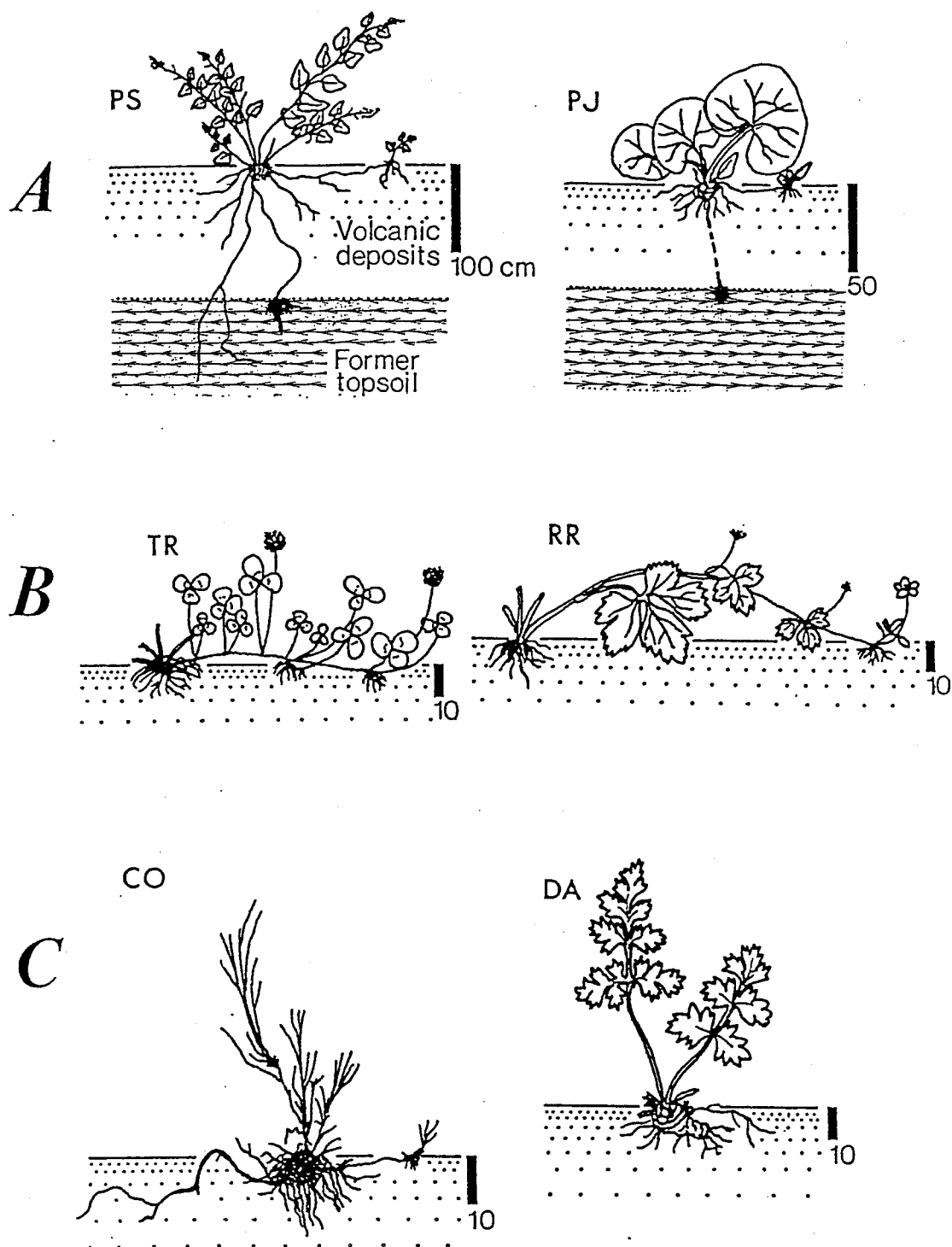


Fig. 6. Root systems of perennial plants. A: Multicapital rhizomes. PS: *Polygonum sachalinense*. PJ: *Petasites japonicus* var. *giganteus*. Of PJ, perished roots were expressed as dotted line. B: Creeping shoots. TR: *Trifolium repens*. RR: *Ranunculus repens*. C: Close-set rhizomes or shoots. CO: *Carex oxyandra*. DA: *Dryopteris austriaca*.

systems very well. *Rumex obtusifolius*, *Polygonum cuspidatum* and *Aralia cordata* also belonged to this type.

Type B: Creeping shoots; Stoloniferous perennial plants such as *Trifolium repens* and *Ranunculus repens* elongated their shoots horizontally and contributed substantially to the enlargement of plant coverage. *Lotus corniculatus* var. *japonicus* and *Potentilla freyniana* also belonged to this type.

Type C: Close-set rhizomes or shoots; Unlike the plants of types A and B which frequently formed stump aggregation, *Carex oxyandra* and *Dryopteris austriaca* were usually isolated from nonspecific individuals. They appeared dependent mainly on sexual reproduction, but vegetative reproduction is also possible because they often elongate rhizomes to produce new shoots several decimeters distant from the mother plants. *Anaphalis margaritacea* var. *angustior*, *Luzula capitata*, *Taraxacum officinale* and *Festuca rubra* also seemed to be of this type.

Recovering pace

From 1984 to 1988, total number of species ranged from 37 to 41 over habitats (Table 7); species composition did not differ much between habitats, indicating that floristic composition did not change much during years. However, at least 5 species, 12% of the total species of each habitat, always disappeared or immigrated in each habitat. The species richness fluctuated slightly during year to year except for the conspicuous increment of it from 1984 to 1985 in EG (Fig. 7), because species disappearance as well as species occurred immigration. To express the recover rate, species richness was

Table 7. Number of species immigrating and disappearing between years.

Habitat	Total number of species observed	Change	Years			
			1984-85	1985-86	1986-87	1987-88
OG	37	Immigration	5	2	3	5
		Disappearance	4	5	2	2
EG	41	Immigration	14	2	2	7
		Disappearance	2	3	3	6
CG	37	Immigration	10	3	3	8
		Disappearance	4	7	2	2

considered inadequate, because changes in floristic composition were not quantified.

Vegetation cover increased annually in every habitat, mostly due to the rapid expansion of well-rooted perennial plants (Type A). Predominance of those plants occurred and interrelated with community structure described below. However, small-sized perennial plants, e.g., *Epilobium montanum*, *E. palustre* var. *lavandifolium*, *Moehringia lateriflora*, *Picris hieracioides* var. *glabrescens*, *Juncus fauriensis* and *Agrostis scabra*, did not establish well; viz. those species repeated immigration and disappearance. Most woody plants were established concomitantly with the perennial herbs, but the rate of their cover increment was slower than that of perennial herbs. Once annual plants disappeared from a habitat, they rarely re-established there. Thus, the succession stage has remained at a perennial-herbaceous stage.

Although diversity, H' , is dependent on both species richness and evenness, the fluctuation of H' was found to be dependent only on evenness, J' (Fig. 7). This probably occurred because species richness, included in H' , was relatively constant; thus, the H' -value was mostly regulated by J' . Both H' and J' were low and/or fluctuated more inside the gully (EG and CG), where the soil movements occurred frequently, suggesting that environmental stress partly determined species diversity and evenness. H' was comparatively stable in OG, although vegetation cover gradually increased. Those parameters determined at least habitat difference, but were insufficient to express recovery pace. In all of those parameters, the species difference between communities is not taken into account, therefore, the sensitivity of community structure change is considered

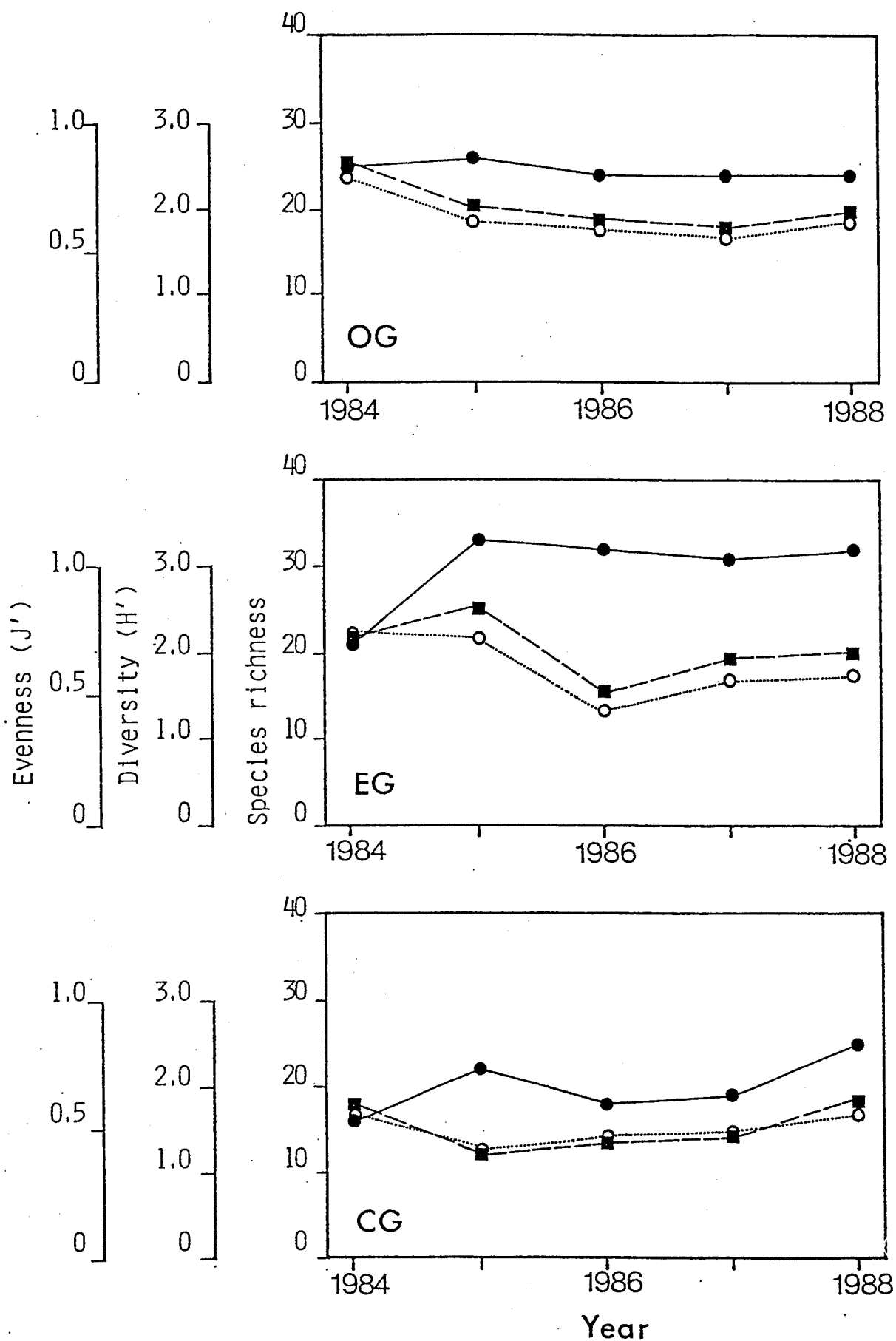


Fig. 7. Yearly fluctuation of species richness (closed circles with full lines), species diversity (closed boxes with interrupted lines), and evenness (open circles with dotted lines) on each habitat. On OG, EG and CG, refer to the text.

to be low. The parameters of succession pace are considered to be required to quantify the degree of species alteration.

CC-value was more than 50% relative to the first year (Fig. 8), being dependent on the stability of species composition and, relative to the preceding year, CC-value in a given year did not change much. These results were derived from the repetition of immigration and disappearance of the small-sized perennial plants (Table 4).

Relative to the first year, the PS decreased over time in the order $CG > EG \geq OG$. Following an initial decrease of PS from 1984 to 1985 in CG, the rate of PS decline slowed. In OG, PS gradually decreased for 5 years. The recovery of EG and OG progressed gradually, probably because soil movement and resource conditions were concerned with those habitat differences: The soil movements inhibited plant establishment more in EG and CG than in OG. Nutrient condition were conspicuously high in EG, where former topsoil was exposed; therefore, vegetation in EG could recover gradually compared with that in CG, where former topsoil was still covered with thick volcanic deposits. To determine whether OG or EG recovered faster was difficult (Plates I and J); however, rate of recover in OG seemed to be slightly faster than that in EG, probably because the effect of soil movement on revegetation was most intense in EG. Succession rate in CG was very slow, because of the paucity of nutrient resources and intense soil erosion. PS explained the change of community structure well.

Discussion

Succession generally starts with dominance of mosses and/or

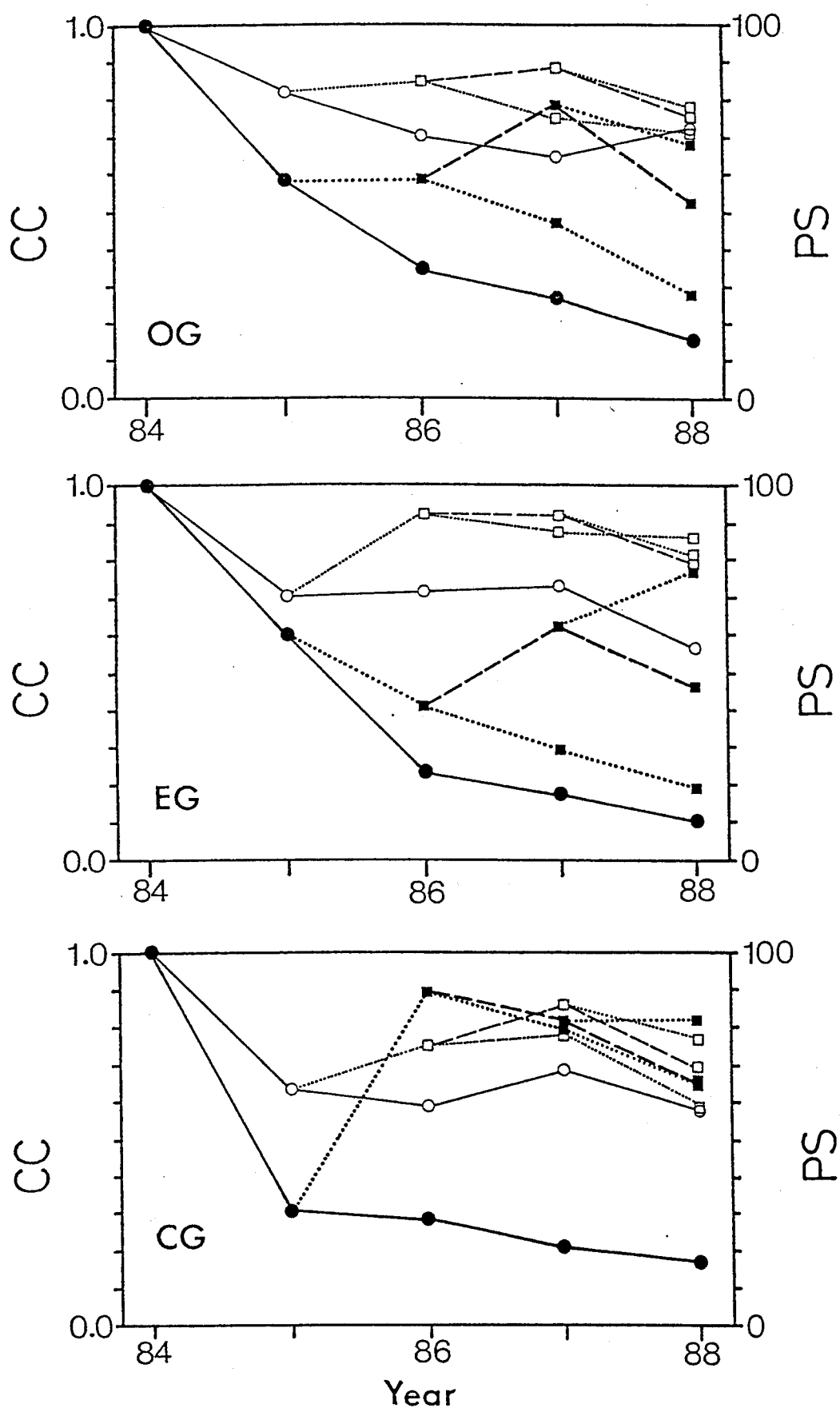


Fig. 8. Indices of similarity in each habitat. CC and PS indicate community coefficient and percentage similarity, respectively. Open and closed circles show the values of CC and PS, respectively, referring to the first year, i.e., 1984. The other symbols the values referring to the preceding year (year-to-year).

lichens after the complete destruction of the previous systems by landslide, ice push, alluvial erosion or volcanic eruption; further revegetation proceeds very slowly up to a climax (Whittaker, 1975; White, 1979; Tilman, 1982, 1988). For instance, soon after the eruptions on Mauna Loa mosses dominated the lava surface (Fosberg, 1959) and the same was reported from Sakurajima (Tagawa, 1964) and the volcanic-ash surface on Katmai (Griggs, 1933). Mosses produce organic matter and promote soil formation and thus they facilitate the establishment of higher plants (Griggs, 1933; Griggs & Ready, 1934). Nevertheless, mosses were rarely observed on the volcano Usu after the latest eruptions (Konno, int. rep.; Riviere, 1982) and soil formation was not initiated by mosses here. Instead of those plants, perennial herbaceous plants have been recently reported to be notably contributed to the volcanic succession (Tezuka, 1961; del Moral 1983; del Moral and Clampitt, 1985; Antos and Zobel, 1985a,b; Wood and del Moral, 1987). In the present study, it is confirmed that such a vegetative recovery of some perennial herbaceous plants is also possible on the volcano Usu in spite of the much thicker volcanic deposits.

In any secondary succession without a moss stage, short-lived plants are usually the pioneers (Whittaker, 1975). In post-fire forests of south-eastern Japan, for instance, the first species would be such annuals as *Crassocephalum crepidioides*, *Erechitites hieracifolia* and *Erigeron sumatrensis* of which seeds had been supplied from the surroundings and from the buried seed bank (Nakagoshi, 1985). The revegetation process on Usu resembles a secondary succession regarding the contribution of annuals derived from buried or immigrated seeds. Contribution of buried seeds on volcanic

revegetation has been mentioned little in the previous studies (del Moral, 1983; Antos and Zobel, 1986; Adams et al., 1987), however, the buried seeds are one of the most important source for revegetation in the volcano Usu (Tsuyuzaki, 1989b). In particular, ca 2,000 seeds per $1/m^2$ were still viable even after 10 years of burial under thick volcanic deposits (Tsuyuzaki, 1989a).

On Mount St. Helens, USA, where a destructive eruption occurred in 1980, most understory herbs were eliminated by 15 cm of tephra (Antos and Zobel, 1985a). Many shrubs and herbs produced vegetative organs and succeeded to recover only one year after having been buried (Antos & Zobel 1985b, 1986). Above the timberline on Mount St. Helens, a few subalpine perennials such as *Juncus parryi* and *Luetkia pectinata* could recover by an active through growth through volcanic deposits, but only if the deposits were not thicker than 8 cm (Del Moral, 1983; Del Moral and Clappitt 1985). Yoshioka (1966) reported on pioneer perennials such as *Mischanthus sinensis*, *Polygonum sachalinense*, *Pteridium aquilinum* and *Sasa kurilensis* on the volcano Koma, but they were not as efficient for revegetation as on Usu because volcanic deposits on Koma were extremely thick in the summit area. Even at a distance of 12 km from Koma, ash accumulations of 1 to 3 m were found. The present study demonstrated that the relatively rapid revegetation on Usu is mostly due to the contribution of rapidly resprouting species especially *Polygonum sachalinense* and *Petasites japonicus* var. *giganteus* which recovered vegetatively on steep slopes where the accumulation of volcanic deposits was not as thick as on flat sites.

Although nitrogen-fixed perennial plants are often inhabited in

nutrient-poor region including volcano by their nitrogen-fixed ability (Vitousek et. al., 1987; Wood and del Moral, 1988), they do not dominate in the volcano Usu except EG. Nitrogen-fixed plants such as *Trifolium repens* and *Lotus corniculatus* var. *japonica* are mostly derived from buried seeds in the volcano Usu, thus, their distribution are too restricted. They may contribute long-term succession, however, their recovery paces are slow until now. On the Pumice Plains of Mount St. Helens, where a destructive eruption occurred in 1980, native plants such as lupines which have ability to fix nitrogen colonized and over 50% of seedlings were exotic (Wood and del Moral, 1988). In contrast with Mount St. Helens, exotic and artificially-introduced plants have never been predominate in the volcano Usu. One reason is that none of artificially-introduced species has nitrogen-fixed ability in the volcano Usu. Likewise, artificial introduction of exotic plants was mostly carried out by an airplane soon after the eruptions, thus, those plants were immediately disappeared by soil erosion.

In the incipient phase of ecological succession on volcano, plant community composition is considerably dependent on the texture of the volcanic deposits. For instance, a *Saccharum spontaneum* grassland, a *Pityrogramma-Nephrolepis* community, a film community of blue-green algae and an *Ipomoea-Canavalia* community were primary established on the scoria, lava flow, ash and pumice and sand bar, respectively, in the Islands of Krakatau (Tagawa et al., 1985). Although the volcanic pumices abundant on the volcano Usu was suitable for the seedling establishment, the mortality of seedlings was very high every year in the present study, resulting in the intensive fluctuation of plant density. This is undoubtedly due to the frequent erosion of the

ground surface, which interferes the development of root systems. This severe natural condition is tolerated mostly by annual plants with short life cycles and some perennial or woody plants possessing developed root systems. In particular, *Polygonum sachalinense* and *Petasites japonicus* var. *giganteus* which have recovered vegetatively on the caldera rim and are providing seeds to the crater basin, are contributive most to the expansion of plant coverage on the volcano Usu.

On the community level, generally, species richness and/or diversity increase throughout early stages of secondary succession (Drury and Nisbet, 1973; Nicholson and Monk, 1974; Bazzaz, 1975; Swaine and Hall, 1983) and primary succession (Tagawa, 1964; Reiners et al., 1971; del Moral and Wood, 1988). On the volcano Usu, species disappearance balanced species immigration on the volcano Usu, and species richness was relatively unchangeable. H' and J' did not increase on the volcano, either. Similar patterns are have been on the other volcanoes: After the catastrophic eruption in 1980 on Mount St. Helens, Washington, USA, species richness and vegetation cover gradually increased over 7 years, but H' was always low (Wood and del Moral, 1987). On Mt. Komagatake, southern Hokkaido, Japan, whose eruption burned and/or buried the most of vegetation in 1929, species richness fluctuated from 20 to 23 and 17 to 25 in the center and at the edge of pumice flow, respectively, from 1935 to 1965 (Yoshioka, 1966).

Three determinants of the rate of vegetation recovery on volcanoes have been proposed:

Firstly, paucity of species composition regulate the low

diversity. Plant sources near the crater basin numbered only 135 species during the surveyed periods and immigrating species could not establish following the two reasons. In secondary succession, CC-value decreased constantly relative to the first year (Bornkamm, 1981). Such decrease was not observed on the volcano Usu, because of the low species richness. Species availability is a key factor of vegetation recovery in volcanic succession (del Moral and Clappitt, 1985; Tsuyuzaki, 1987; Wood and del Moral, 1987).

Secondly, the resource availability, which was considered to be nutrient conditions in soils, restricted to plant growth (Chapin, 1980; Tilman, 1982, 1986). The nutrient content of volcanic deposits, which was very low even 10 years after the eruptions in the volcano Usu, restricted plant growth of all but well-rooted plants.

Thirdly, movements of the volcanic deposits inhibited the plant establishment. Although volcanic pumices abundant on the volcano Usu were suitable for the seedling establishment, frequent erosion of the ground surface, interfered with development of the root system (Tsuyuzaki, 1989). Growth of well-rooted plants predominated community structure (Bornkamm, 1981). Structure was detected well in CG, i.e., similarity of PS to the first year decreased very little after 1985.

Species equitability, or evenness, is regulated primarily by short term factors, i.e., resource levels, and species richness is regulated by long term factors such as community stability and evolutionary time (Nicholson and Monk, 1974). However, species richness during revegetation on the volcano Usu seemed to be regulated by the three rather short term determinants described above. Recovery rate expressed as PS differed among habitats in response to

those 3 short-term determinants.

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References

- Adams, A. B., V. H. Dale, E. P. Smith, and A. R. Kruckeberg. 1987.
Plant survival, growth form and regeneration following the 18 May
1980 eruptions of Mount St. Helens, Washington. Northwest Sci.
61: 160-170.

- Antos, J. A., and D. B. Zobel. 1985a. Recovery of forest understories buried by tephra from Mount St. Helens. *Vegetatio* 64: 103-111.
- , and —. 1985b. Plant form, developmental plasticity, and survival following burial by volcanic tephra. *Can. J. Bot.* 63: 2083-2090.
- , and —. 1986. Seedling establishment in forests affected by tephra from Mount St. Helens. *Amer. J. Bot.* 73: 495-499.
- Archibold, O.W. 1981. Buried viable propagules in native and adjacent agricultural sites in central Saskatchewan. *Can. J. Bot.* 59: 701-706.
- Bazzaz, F.A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* 56: 485-488.
- Booth, W. E. 1941. Algae as pioneers in plant succession and their importance in erosion control. *Ecology* 22: 38-46.
- Bornkamm, R. 1981. Rates of change in vegetation during secondary succession. *Vegetatio* 47: 213-220.
- Chapin, F. S. III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11: 233-260.
- Clements, F.E. 1916. Plant succession. Carnegie Inst. Washington.
- Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Natur.* 111: 1119-1144.
- Cooper, W.S. 1913. The climax forest of Isle Royale, Lake Superior and its development. *Bot. Gaz.* 55: 1-44, 115-140, 189-235.
- Cooper, R., and E. D. Rudolph. 1953. The role of lichens in soil formation and plant succession. *Ecology* 34: 805-807.

- Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Bot. Gaz.* 27: 95-117, 167-202, 281-308, 361-391.
- Crawley, M. J. 1986. The structure of plant communities. In Crawley, M.J. [Ed.], *Plant ecology*, 1-50. Blackwell, Oxford.
- Crocker, R.L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecol.* 43: 427-448.
- Crocker, R. L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *J. Ecol.* 43: 427-448.
- Dahl, E., and E. Hadač., 1941. Strandgesellschaften der Insel Ostoy im Oslofjord. *Nytt Mag. Naturv.* 82: 251-312.
- del Moral, R. 1983. Initial recovery of subalpine vegetation on Mount St. Helens, Washington. *Amer. Midl. Natur.* 109: 72-80.
- , and C. A. Clampitt. 1985. Growth of native plant species on recent volcanic substrates from Mount St. Helens. *Amer. Midl. Natur.* 114: 374-383.
- , and D. M. Wood. 1988. Dynamics of herbaceous vegetation recovery on Mount St. Helens, Washington, USA, after a volcanic eruption. *Vegetatio* 74: 11-27.
- Drury, W.H., and I.C.T. Nisbet. 1973. Succession. *J. Arnold Arboretum* 54: 331-368.
- Eggler, W. A. 1947. Arid southeast Oahu vegetation, Hawaii. *Ecol. Monogr.* 17: 383-435.
- Egler, F.E. 1954. Vegetation science concepts 1. Initial floristic composition, a factor in old-field vegetation development.

- Vegetatio 4: 412-417.
- Flaccus, E. 1959. Revegetation of landslides in the White Mountains of New Hampshire. Ecology 40: 692-703.
- Fosberg, F.R. 1959. Upper limits of vegetation on Mauna Loa, Hawaii. Ecology 40: 144-146.
- Gleason, H.A. 1917. The structure and development of the plant. Bull. Torrey Club 44: 463-481.
- . 1927. Further views on the succession-concept. Ecology 8: 299-326.
- Griggs, R. F. 1933. The colonization of the Katmai ash, a new and inorganic "soil". Amer. J. Bot. 20: 92-113.
- , and D. Ready. 1934. Growth of liverworts from Katmai in nitrogen-free media. Amer. J. Bot. 21: 265-277.
- Harper, J.L., J.T. Williams and G.R. Sagar. 1965. The behaviour of seeds in soil. I. Heterogeneity of soil surfaces and its role in determining the establishment of plant from seed. J. Ecol. 53: 273-286.
- Hill, M.O. and P.A. Stevens. 1981. The density of viable seed in soils of forest plantations in upland Britain. J. Ecol. 69: 693-709.
- Horn, H.S. 1974. The ecology of secondary succession. Ann. Rev. Ecol. Syst. 5: 25-37.
- Kwiatkowska, A.J. and E. Symonides. 1986. Spatial distribution of species diversity indices and their correlation with plot size. Vegetatio 68: 99-102.
- Lawrence, D. B. 1958. Glaciers and vegetation in Southeastern Alaska. Amer. Sci. 46: 89-122.
- Leck, M.A., V.T. Parker and R.L. Simpson. 1989. Ecology of soil

- seed bank. Academic Press., San Diego.
- Major, J. 1974. Differences in duration of successional seres. Handb. Veget. Sci. 8: 195-204.
- Mallik, A. U. and C. H. Gimingham. 1983. Regeneration of heathland plants following burning. Vegetatio 53: 45-58.
- McCune, B. 1988. Ecological diversity in north American pines. Amer. J. Bot. 75: 353-368.
- Morris, W.F., and D.M. Wood. 1989. The role of lupine in succession on Mount St. Helens: Facilitation or inhibition. Ecology 70: 697-703.
- Mutoh, N., M. Kimura, Y. Oshima and H. Iwaki. 1985. Species diversity and primary productivity in *Miscanthus sinensis* grasslands 1. Diversity in relation to stand structure and dominance. Bot. Mag., Tokyo 98: 159-170.
- Nakagoshi, N. 1984. Buried viable seed populations in forest communities on the Hiba Mountains, southwestern Japan. J. Sci. Hiroshima Univ., Ser. B. Div. 2 (Botany) 19: 1-56.
- Nicholson, S.A., and C.D. Monk. 1974. Plant species diversity in old-field succession on the Georgia piedmont. Ecology 55: 1075-1085.
- Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.
- . 1971. Fundamentals of ecology (3rd ed.). Toppan, Tokyo.
- Ohwi, J. 1975. Flora of Japan (rev. ed.). Shibundo, Tokyo.
- Olmsted, N.W. and J.D. Curtis. 1947. Seeds of the forest floor. Ecology 25: 49-52.
- Olson, J. S. 1958. Rates of succession and soil changes on Southern

- Lake, Michigan, sand dunes. Bot. Gaz. 119: 125-170.
- Peet, R.K. 1975. Relative diversity indices. Ecology 56: 496-498.
- Pielou, E. C. 1975. Ecological diversity. John Wiley and Sons, New York.
- Reiners, W.A., I.A. Worley, and D.B. Lawrence. 1971. Plant diversity in a chronosequence at glacier bay, Alaska. Ecology 52: 55-69.
- Riviere, A. 1982. Invasion and recovery of plants after the 1977-78 eruption of Usu Volcano, Hokkaido, Japan. Environ. Sci. Hokkaido 5: 197-209.
- . 1986. Properties of the new volcanic substrate of Mt. Usu with regards to natural revegetation. Environ. Sci. Hokkaido 9: 89-112.
- Shannon, C.E., and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press, Urbana.
- Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. Det Kong. Danske Vidensk. Selsk. Biol. Skr. (Copenhagen) 5: 1-34.
- Swaine, M.D., and J.B. Hall. 1983. Early succession on cleared forest land in Ghana. Journal of Ecology 71: 601-627.
- Swanston, D. N., and F. J. Swanson. 1976. Timber-harvesting, mass erosion, and steep land form geomorphology in the Pacific Northwest. In Coats, D.R. [Ed.], Geomorphology and engineering, 199-221. Dowden, Hutchinson, and Ross Inc., Pennsylvania.
- Tagawa, H. 1964. A study of volcanic vegetation in Sakurajima, southwest Japan I. Dynamics of vegetation. Mem. Fac. Sci. Kyushu Univ. Ser. E. (Biol.). 3: 165-228.

- . 1965. A study of volcanic vegetation in Sakurajima, southwest Japan. II. Distributional pattern and succession. Jap. J. Bot. 19: 127-148.
- , E. Suzuki, T. Partomihardjo, and A. Suriadarma. 1985. Vegetation and succession on the Krakatau Islands, Indonesia. Vegetatio 60: 131-145.
- Tezuka, Y. 1961. Development of vegetation in relation to soil formation in the volcanic island Of Oshima, Izu, Japan. Jap. J. Bot. 17: 371-402.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.
- . 1986. Nitrogen-limited growth in plants from different successional stages. Ecology 67: 555-563.
- . 1988. Plant strategies and the dynamics and structure of plant communities, Princeton University Press, Princeton, New Jersey.
- Tsuyuzaki, S. 1989a. Buried seed populations on the volcano Mt. Usu, northern Japan, ten years after the 1977-78 eruptions. Ecol. Res. 4: 167-173.
- . 1989b. Contribution of buried seeds on the volcano Usu, northern Japan, since the 1977-78 eruptions. Bot. Mag., Tokyo 102: 502-512.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois and, P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238: 802-804.
- Walker, D. 1982. The development of resilience in burned vegetation. In Newman, E.I. [Ed.], The plant community as a working

- mechanism, 27-43. Blackwell, Oxford.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45: 229-299.
- Whittaker, R. H. 1975. *Communities and ecosystems* (2nd ed.). Macmillan, New York.
- Wood, D. M., and R. del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68: 780-790.
- , and —. 1988. Colonizing plants on the Pumice Plains, Mount St. Helens, Washington. *Amer. J. Bot.* 75: 1228-1237.
- Wright, H. A., and A. W. Bailey. 1982. *Fire ecology*. John Wiley, New York.
- Yoshioka, K. 1966. Development and recovery of vegetation since the 1929 eruption of Mt. Komagatake, Hokkaido. *Ecological Review* 16: 271-292.

Appendix. A list of plants collected in the volcano Usu during the year of 1983 and 1984. O, B, and C indicate the location of north-west slope of O-Usu, crater basin, and inner-wall of caldera rim, respectively.

Division Pteridophyta

Family Equisetaceae

1. *Equisetum arvense* Linn. [B]

Family Aspidiaceae

2. *Dryopteris austriaca* (Jacquin) Woytar, ex Schinz et Thellung [O]
3. *D. crassirhizoma* Nakai [O,B]
4. *Matteuccia struthiopteris* (Linn.) Todaro [O,B]

Division Spermatophyta

Subdivision Gymnospermae

Family Pinaceae

5. *Larix leptolepis* (Sieb. et Zucc.) Gordon [B]

Subdivision Angiospermae

Class Dicotyledoneae

Subclass Choripetalae

Family Salicaceae

6. *Populus maximowiczii* Henry [B,C]
7. *Salix hultenii* Floderus var. *angustifolia* Kimura [O,B,C]
8. *S. integra* Thunb. [B,C]
9. *S. sachalinensis* Fr. Schm. [O,B]

Family Betulaceae

10. *Alnus hirsuta* Turcz. [B,C]
11. *A. maximowiczii* Callier [O,B,C]
12. *Betula ermanii* Cham. [O,B]
13. *B. maximowicziana* Regel [O,B]
14. *B. platyphylla* Sukatchev var. *japonica* (Miq.) Hara [B]

Family Ulmaceae

15. *Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai [C]
16. *U. davidiana* Planch. var. *japonica* (Rehd.) Nakai f. *suberosa* (Turcz.) Nakai [C]
17. *U. laciniata* (Trautv.) Mayr [C]

Family Moraceae

18. *Morus bombycis* Koidz. [C]

Family Urticaceae

19. *Boehmeria spicata* (Thunb.) Thunb. [O,C]

Family Polygonaceae

- 20. *Polygonum aviculare* Linn. [B]
- 21. *P. cuspidatum* Sieb. et Zucc. [O,B]
- 22. *P. longisetum* De Bruyn [O,B]
- 23. *P. sachalinense* Fr. Schm. [O,B,C]
- 24. *P. thunbergii* Sieb. et Zucc. [O]
- 25. *Rumex obtusifolius* Linn. [B]

Family Caryophyllaceae

- 26. *Cerastium holosteoides* Fries var. *hallaisanense* (Nakai) Mizushima [B]
- 27. *Moehringia lateriflora* (Linn.) Fenzl [O,B]
- 28. *Stellaria fenzlii* Regel [B]

Family Ranunculaceae

- 29. *Ranunculus repens* Linn. [B]
- 30. *R. quelpaertensis* (Leveille) Nakai [B]

Family Magnoliaceae

- 31. *Magnolia obovata* Thunb. [C]

Family Cruciferae

- 32. *Cardamine flexuosa* With. [O,B,C]
- 33. *C. flexuosa* With. var. *fallax* O.E. Schulz [B,C]
- 34. *Rorippa islandica* (Oeder) Borbas [B]
- 35. *Arabis glabra* (Linn.) Bernh. [C]
- 36. *A. pendula* Linn. [B]
- 37. *A. lyrata* Linn. var. *kamchatica* Fischer [B]
- 38. *A. glauca* H. Boiss. [B]

Family Saxifragaceae

- 39. *Astilbe thunbergii* Miq. var. *congesta* H. Boiss. [O,B]
- 40. *Hydrangea paniculata* Siebold [O,B,C]
- 41. *H. petiolaris* Sieb. et Zucc. [O,C]
- 42. *Schizophragma hydrangeoides* Sieb. et Zucc. [C]

Family Rosaceae

- 43. *Aruncus dioicus* Fern. var. *tenuifolius* Hara [C]
- 44. *Geum japonicum* Thunb. [B]
- 46. *G. macrophyllum* Wild. var. *sachalinense* (Koidz.) Hara [B]
- 47. *Fragaria iinumae* Makino [O,C]
- 48. *F. vesca* Linn. [B]
- 49. *Rosa multiflora* Thunberg [C]
- 50. *Potentilla freyniana* Bornm. [B]
- 51. *Prunus sargentii* Rehder [B]
- 52. *Rubus phoenicolasius* Maxim. [C]
- 53. *Sorbus commixta* Hedl. [C]
- 54. *S. alnifolia* (Sieb. et Zucc.) C. Koch [C]

Family Leguminosae

- 55. *Desmodium oxyphyllum* DC. [C]
- 56. *Lespedeza bicolor* Turcz. [C]
- 57. *Lotus corniculatus* Linn. var. *japonicus* Regel [B]
- 58. *Medicago lupulina* Linn. [B]

59. *Trifolium hybridum* Linn. [B,C]
 60. *T. repens* Linn. [B]

Family Rutaceae

61. *Phellodendron amurense* Rupr. var. *sachalinense* Fr. Schm. [C]

Family Anacardiaceae

62. *Rhus trichocarpa* Miq. [C]
 63. *R. ambigua* Lavallee ex Dippel [C]

Family Celastraceae

64. *Celastrus orbiculatus* Thunb. [C]

Family Aceraceae

65. *Acer mono* Maxim. [B,C]
 66. *A. mono* Maxim. var. *mayrii* (Schwer.) Koidz., ex Nemoto [C]

Family Vitaceae

67. *Vitis coignetiae* Pulliat [C]

Family Tiliaceae

68. *Tilia japonica* (Miq.) Simonkai [C]

Family Actinidiaceae

69. *Actinidia arguta* (Sieb. et Zucc.) Planchon ex Miquel [C]

Family Guttiferae

70. *Hypericum erectum* Thunb. [B]

Family Violaceae

71. *Viola phalacrocarpa* Maxim. [B]
 72. *V. grypceras* A. Gray [B]

Family Elaeagnaceae

73. *Elaeagnus umbellata* Thunb. [C]

Family Onagraceae

74. *Epilobium montanum* Linn. [O,B,C]
 75. *E. cephalostigma* Hausskn. [B]
 76. *E. palustre* Linn. var. *lavandulaefolium* Lecoq et Lamotte [B]
 77. *E. dielsii* Leveille [B]
 78. *Oenothera biennis* Linn. [B,C]

Family Araliaceae

79. *Aralia cordata* Thunb. [O,B,C]
 80. *Kalopanax pictus* (Thunb.) Nakai [C]

Family Umbelliferae

81. *Angelica ursina* (Rupr.) Maxim. [C]
 82. *A. edulis* Miyabe, ex Yabe [C]
 83. *Pleurospermum camtschaticum* Hoffm. [C]
 84. *Torilis japonica* (Houtt.) DC. [C]

Subclass Gamopetalae

Family Oleaceae

85. *Fraxinus lanuginosa* Koidz. [C]

Family Boraginaceae

86. *Myosotis sylvatica* (Ehrh.) Hoffmann [B]
87. *M. palustris* Hill [B]

Family Labitae

88. *Laitae* gen. sp. [O]

Family Scrophulariaceae

89. *Veronica arvensis* Linn. [B]
90. *V. schmidtiana* Regel [O]

Family Plantaginaceae

91. *Plantago asiatica* Linn. [B,C]
92. *P. camtschatica* Cham. [O]

Family Caprifoliaceae

93. *Lonicera morrowii* A. Gray [B]
94. *Sambucus sieboldiana* Blume var. *miquelii* Hara [O]
95. *Viburnum dilatatum* Thunb. [C]
96. *V. opulus* Linn. var. *calvescens* (Rehder) Hara [C]

Family Valerianaceae

97. *Patrinia villosa* (Thunb.) Juss. [C]

Family Compositae

98. *Ambrosia artemisifolia* Linn. var. *elatior* (Linn.) Descourtils [B]
99. *Anaphalis margaritacea* (Linn.) Benth. et Hook. var. *angustior* (Miq.) Nakai [O,B]
100. *Artemisia japonica* Thunb. [C]
101. *A. montana* (Nakai) Pampan. [O,B,C]
102. *Aster ageratoides* Turcz. var. *ovatus* Nakai f. *yezoensis* (Kitam. et Hara) Ohwi [B,C]
103. *A. scaber* Thunb. [C]
104. *A. glehnii* Fr. Schm. [C]
105. *Cacalia hastata* Linn. var. *orientalis* (Kitam.) Ohwi [B,C]
106. *Erigeron canadensis* Linn. [B]
107. *Leibnitzia anandria* (Linn.) Nakai [B]
108. *Eupatorium chinense* Linn. var. *simplicifolium* (Makino) Kitam. [O,C]
109. *E. chinense* Linn. var. *sachalinense* (Fr. Schm.) Kitam. [O,B,C]
110. *Ixeris dentata* (Thunb.) Nakai [B]
111. *Petasites japonicus* var. Maxim. var. *giganteus* (Fr. Schm.) Hort. [O,B,C]
112. *Picris hieracioides* Linn. var. *glabrescens* (Regel) Ohwi [O,B,C]
113. *Senecio cannabifolius* Less. [C]
114. *S. vulgaris* Linn. [B]
115. *Solidago virga-aurea* Linn. var. *leiocarpa* (Benth.) Miq. [C]
116. *Sonchus asper* (Linn.) Hill [B]
117. *Taraxacum officinale* Weber [B,C]
118. *Youngia japonica* (Linn.) DC. [B]
119. *Y. denticulata* (Houtt.) Kitam. [B]

Subclass Monocotyledoneae

Family Gramineae

- 120. *Agrostis scabra* Willd. [O]
- 121. *Alopecurus aequalis* Sobol. var. *amurensis* (Komar.) Ohwi [B]
- 122. *Calamogrostis epigeios* (Linn.) Roth [O,C]
- 123. *C. pseudo-phragmites* (Haller fil.) Koeler [O]
- 124. *Festuca elatior* Linn. [O,B,C]
- 125. *F. rubra* Linn. var. *rubra* Ohwi [O,B,C]
- 126. *Miscanthus sinensis* Anderss. [C]
- 127. *Phleum pratense* Linn. [O]
- 128. *Poa annua* Linn. [B]

Family Cyperaceae

- 129. *Carex breviculmis* R. Br. [O,B]
- 130. *C. longerostrata* C. A. Mey [O]
- 131. *C. lyngbyei* Hornem. [O]
- 132. *C. oxyandra* (Franch. et Savat.) Kudo [O,B]

Family Juncaceae

- 133. *Juncus effusus* Linn. var. *decipiens* Buchen. [B]
- 134. *J. fauriensis* Buchen. [B]
- 135. *Luzula capitata* (Miq.) Miq., ap. Komar. [O,B]

Plate captions.

Photo A. Vegetation of summit area after deforestation by 1977-78 eruptions. Two peaks, O-Usu (left) and Ko-Usu (right), are enclosed by a caldera rim. Crater basin is overlaid between O-Usu and inner-wall of the caldera rim. The 4th eruption constructs a large hole (called 4th crater) in the crater basin. Refer to Fig. 5.

Photo B. Vegetational recovery surveyed in summit area, seeing from the top of O-Usu in 1984. Well-recovered area is inner-wall of caldera rim. In the crater basin, where plant establishment is very sparse, soil movements frequently occurred during the year of 1983 and 1986.

Photo C. A gully where the former topsoil exposed (Line I in Fig. 2), in late-April, 1986.

Photo D. A 1 m x 1 m seed trap used to collect wind-dispersed seeds. See also Figs. 2 and 3. Mesh size of cotton nets to trap seeds is less than 1 mm in diameter. To protect against feeding of seeds by birds and foxes, wire net is set up on the trap.

Photo E. A 3.2 m x 3.2 m quadrat for the estimation of mortality rate during 1983 and 1987. See also Table 5.

Photo F. A colony patch of plants derived from vegetative reproduction (*Petasites japonicus* var. *giganteus* and *Polygonum sachalinense*), artificial introduction (*Festuca rubra*), and buried seeds (*Trifolium repens* and *Rumex obtusifolius*) in the gully where the former topsoil was exposed.

Photo G. Root system of *Polygonum sachalinense*. The maximum root depth is more than 1.5 m. Refer to root system type A in Fig. 6.

Photo H. Root system of *Petasites japonicus* var. *giganteus*. The root usually develops ca 0.5 m in depth. Refer to root system type A in Fig. 6.

Photo I. Vegetation recovery of the gully outside in 1989. Soil movement and micro-topography were measured by level transect and erosion pins as shown in this photo.

Photo J. Vegetation recovery of the gully inside where the former topsoil was exposed in 1989. The brown-colored former topsoil is still covered with ca 1 m volcanic deposits in gully outside, but has been exposed by soil erosion in the gully inside since 1983.

A



B



C



D



E



F



G



H



I



J

