PLANT COLONIZATION ON PART
OF THE HOPE LANDSLIDE

by

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Abstract

An investigation into pattern in colonizing vegetation was undertaken on part of the Hope Landslide, British Columbia, which occurred January 9, 1965. The objective of the research was to explain pattern in the vegetation and in so doing, to analyse the relative significance of some of the processes involved in pioneer colonization.

The study area selected was a mud flow: caused by the main rock fall, on which vegetation colonization had been particularly rapid during the 2½ years since the slide. Vegetation was distributed in patches of diverse size, interspersed with many areas of bare substrate. Microtopography was of an irregular hummock and hollow nature. An assortment of substrate types were present.

It was hypothesized that the vegetation pattern was the result of variation in the influence of habitat during the process of colonization. The habitat influence could vary in its potential for the support of colonizing vegetation and in the composition and distribution of the invading seed: including the buried seed.

Microtopography was grouped into 11 classes and substrate into 5 types. These were recorded with the vegetation and species cover along 40, fifty-foot traverses on the mud flow. Non-randomness was demonstrated for vegetation and habitat characteristics by variance : mean ratios. The relationship between habitat characteristics and vegetation was examined by mapping their distributions and then tested by a series of linear correlations. Both vegetation cover and cover of 4 of its component species were found to be positively correlated with one of the substrate types: yellow brown tills.

An attempt was made to trap invading wind blown seed, by locating seed traps on all microtopographic classes. Samples of substrate were taken from soil pits to evaluate their buried viable seed content. Seed traps and substrate samples were kept in a greenhouse for 6 months and all germinations were noted and species identified.

Variation was found in the quantity and compostion of the substrate's buried seed populations. However, inconclusive results from the seed trap germinations, and the lack of mutually exclusive populations in the invading and buried seed sources, made estimations of their relative significance impossible.

It was concluded that the rate and nature of the colonization was dependent on the suitability of the substrate to support vegetation, and the availability of both invading seed from external sources and buried viable seed.

Fig. 2 The Hope Landslide: view from the S.E. January 10. 1965
Mud flow study area in the fore-ground.
British Columbia Government Photograph, Department of Lands and Forests.

To my husband

Acknowledgements

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Chapter 1

Introduction

Plant colonization on surfaces recently exposed as a result of a major landslide, poses several problems when approached from the traditional concepts of primary and secondary succession. Problems are related to the variety of surface materials on which colonization may take place. Primary succession occurs on surfaces which have never previously been occupied by vegetation (Oosting 1956), with all plant input being from external sources. Secondary succession however, occurs on areas which have previously supported vegetation, and much of the colonizing vegetation can be assumed to have its origin in buried viable seed or other plant organs already present at the begining of the succession (Clements 1916). Hence, the sources of plant input on a landslide could be external to the area, or viable material in situ in the landslide debris. In addition, a lack of uniformaty in the habitat conditions may cause variation in the rate of establishment and growth of colonizing vegetation.

Colonization on the mud flow, caused by the 1965 Hope Landslide, was first observed 2½ years after the landslide. Interest was aroused by the uneven distribution of the vegetation on the irregular hummocky micro-topography. Patches of vegetation of variable composition and density were noted, and in addition, a variety of distinctive substrates also distributed in patches could be observed at the surface.

With a landslide of such magnitude, the survival of any standing vegetation was improbable. Therefore, the duration of colonization was known to be short and very few changes in the valley environment or the physical properties of the mud flow habitat would have occurred since the start of colonization.

The pattern of plant cover on some parts of the mud flow indicated great variation in the colonization process. It was decided that the area represented an ideal opportunity to attempt an identification of the sources of plant input and to test some of the possible relationships between colonizing vegetation and habitat, which may have resulted in the observed vegetational pattern.

Vegetation pattern

Research into pattern in vegetation has been restricted mainly to examinations of pattern in the distribution of individual species using the mean square - block size analysis (e.g. Grieg-Smith 1961). Three major types of pattern have been distinguished from this work. Morphological pattern is almost universally observed at a small scale and represents the size of the individual, and a medium scale which occurs when there is an extensive rhizome system. Environmental pattern and sociological pattern are found at a variety of scales (Kershaw 1963). No rigid definition of scale is adhered to in these studies and the distinction between small, medium and large scales made by the authors depends mainly on properties of the species size, dispersal and rhizome spread, or characteristics of the environment.

There are few studies on pattern in pioneer vegetation. Barnes and Stanbury (1951) report that early colonization on china clay residue has a random distribution, followed by vegetative spread resulting in small scale morphological pattern. For colonizing species in heterogeneous environments in Northwest Iceland and South and Central Australia, Anderson (1967) finds that both morphological and environmental pattern are significantly represented. Morphological pattern and sociological pattern defined by Kershaw (1963) as a product of the interaction between species, may be assumed to be of least significance in pioneer colonization on a surface devoid of vegetation. Both would probably increase in significance with time. However, since colonization on the mud flow had occurred for only 2½ years at the time of sampling, explanation of pattern in vegetation was sought in terms of environmental influences.

Origins of flora(1)

Invasion of plant disseminules from external sources is often assumed in colonization studies. On surface materials which have not supported vegetation previously, such as pit heaps (Brierly 1956, Hall 1957) or china clay residue (Barnes and Stanbury 1951), the validity of this assumption cannot be challenged. However, Clements (1916) notes that in secondary succession much of the colonizing vegetation may have its origin in buried viable seed already present at the begining of the succession.

Egler (1954) points out the need for more research into the origin of colonizing vegetation. In particular, he states that the relative significance of the roles played by buried viable seed and seed from other sources requires more study. He presents two models for secondary succession on abandoned fields. The first model, which he terms 'Relay Floristics', is dependent entirely on external invasions, and the second, 'Initial Floristic Composition', on buried viable seed. Both are capable of supporting similar kinds of plant succession although in the case of external invasions a more lengthy time period might be involved. Egler suggests that plant succession is a combination of both processes.

Research into propagule dispersal has generally been treated on the large scale of classical plant geography (e.g. Good 1964). When treated

(1) Throughout this thesis, flora of the mud flow is defined as those plants which are growing on the mud flow

on a more limited scale, studies have been restricted to one or a small number of species: usually trees of economic importance (e.g. Isaac 1930, Hetherington 1965). Very little is known concerning the range and efficiency of seed dispersal for most other species (Webb 1966), or the significance of the process in succession.

The existence of buried seed is well documented and retention of viability over long periods has been reported (e.g. Darlington 1922 and 1931, Porsild, Harrington and Mulligan 1967). Assessments of the density and floristic composition of buried seed populations have been made for a variety of habitats under cultivation (e.g. Brenchley and Warington 1930, Champness and Morris 1948). However, generally a poor correlation between vegetation and the buried seed population has been recorded (e.g. Major and Pyott 1966, Kellman 1970).

Some research has been done on the role played by buried seed in secondary succession (e.g. Numata et al. 1964a, b and c, 1966, 1967). Mueggler (1956) reports a lack of a wind influenced spatial pattern in the distribution of sagebrush recolonization on burned areas. On the basis of seed germinations obtained from soils of the burned areas, he concludes that sagebrush regeneration after fire is the result of growth from seed residual in the soil. Oosting and Humphreys (1940) report that in old field successional series in Durham, N.C. there is a succession of species in the buried seed population as in the surface vegetation. However, seeds from preceeding stages of the vegetation succession are found in the buried seed population, as are seeds of species not yet represented in the vegetation. After investigating a similar succession, Livingston and Allessio (1968) conclude that, on disruption of the forest cover, seed of earlier successional stages often long buried in the soil is present at the site and need not be carried into the disturbed area.

Although the mud flow surface exposed to plant colonization was probably devoid of vegetation, it cannot be assumed that succession would belong wholly to either primary or secondary categories since some of the total debris had supported vegetation prior to the slide. For example, very fine textured peat, typical of a marshy valley situation, was observed. Hence, the source of plant input on the mud flow could be a combination of external sources associated with primary succession, and internal sources suggested for secondary succession.

The problem: an explanation of pattern in colonizing vegetation

Two factors would appear to be critical to the understanding of the vegetation colonization of any newly exposed surface: the first being accessibility of seed to the area, whether this be from a buried source or from an external source, and the second, a process of 'environmental sifting' (Gleason 1939). The environmental sensitivity of many species is well documented. In addition, an element of environmental sifting has been reported to be operative in seed input, from both internal and external sources. For example, Milton (1948) suggests that the duration of viability in buried seeds is affected by soil texture and drainage. Harper, Williams and Sagar (1965) demonstrate that the heterogeneity of the soil surface may determine the chance of a seed finding a suitable crevice for germination.

Pattern in colonizing vegetation on a bare surface may to a large extent be explicable in terms of the above factors: variation in the degree of accessibility to seed, which is dependent on habitat and chance, and variation in the habitat potential in terms of supporting germination and subsequent growth of species.

The research was divided into two major sections. The first was a test for non-random pattern in the distribution of species, vegetation and habitat, which was classified according to substrate and microtopography. The second consisted of an examination of the relationship between vegetational and habitat characteristics on the mud flow. The nature of this relationship was further studied by testing for variation with habitat in the quantity and composition of the buried seed and invading seed from external sources.

Chapter 2

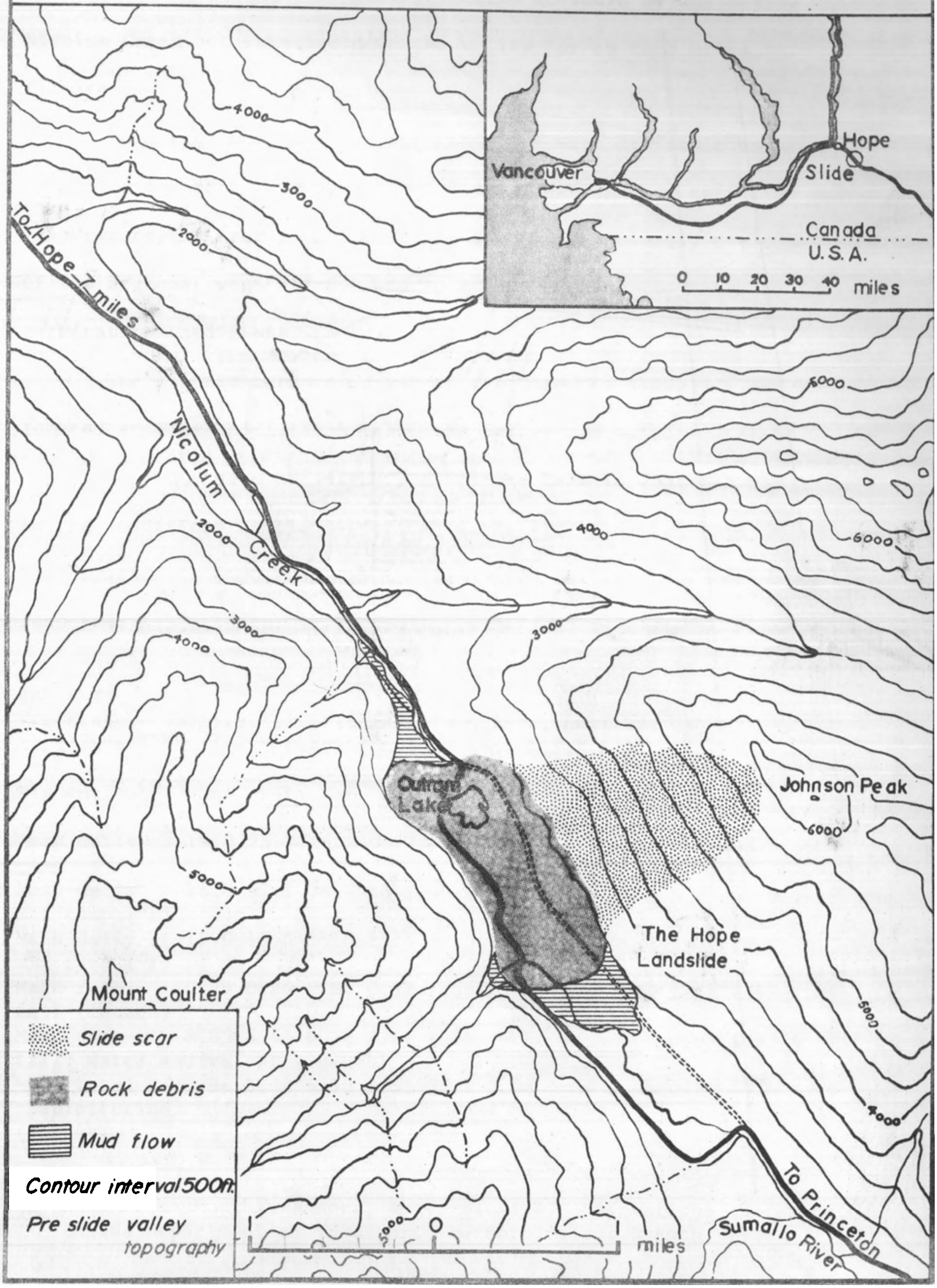
The Hope Landslide

The Hope Landslide is located 12 miles southeast of Hope, British Columbia, on the valley watershed between Nicolum Creek which flows north-west towards Hope and the Sumallo River which flows southeast into Washington. The line of the valley forms the route of the Hope-Princeton highway. (Figs. 1 and 2).

Glaciation has affected the entire Nicolum - Sumallo valley and till is present up to the top of the present slide scar at 5670 feet (Mathews and McTaggart 1969). The vertical interval between the top of Johnson Peak, elevation 6630 feet, to the northeast of the valley and the valley floor is approximately 4300 feet. A previous slide on the same site which occurred at an undetermined post-glacial date, was of comparable dimensions to the 1965 slide. The earlier slide had formed a hummocky valley floor topography of permeable debris, in some areas overlain by a cover of alluvium and swamp, embracing Outram Lake, a shallow irregular body of water approximately 1000 feet square with no surface outlet (ibid.).

The landslide of January 9th, 1965, which involved about 130 million metric tons of rock, is believed to have been triggered by two earthquakes with epicentres within 10 miles of the slide. The rock slide descended to the valley floor, burying much of the debris from the previous slide to a maximun depth of 260 feet. Generally the rock debris did not move far across the valley floor, but a mud flow, generated by the passage of the slide material into Outram Lake and the surrounding area, swept southwesterly against the opposite valley wall to a height of 60 feet above the present valley floor. The majority of the flow was then deflected southeast down the Sumallo River valley and terminated in a tongue shaped

Fig. 1. Location of the Hope Landslide



projection, on average 50 feet in depth (ibid.). A mud flow also occurred to the northwest, where it was restricted in width by the narrow valley of Nicolum Creek but extended down the valley for up to 3 miles.

Climate

Climatic conditions on the landslide were difficult to interpret from existing data. However, some attempt was made to establish approximate temperature and precipitation levels in order to clarify the classification of the regional vegetation, and to act as a guide for later experimental germination conditions.

The closest meteorological stations to the landslide are those located at Hope and Allison Pass, the latter, 20 miles southeast of the landslide. Of these the data from Allison Pass is most closely comparable to the conditions at the landslide (Table 1). The elevation of Allison Pass station is 4400 feet A.S.L. (landslide valley floor approximately 2250 feet A.S.L.), but it is similarly located in a valley floor.

Table I
Temperature and precipitation: Allison Pass, Latitude 49° 08' N, Longitude 120° 50' W, Elevation 4400 feet A.S.L.(1)

Element	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Yr
Mean daily temp. (°F)	19.0	23.7	26.1	34.2	39.4	46.8	54.1	52.5	45.6	38.5	25.3	20.3	35.5
Mean daily max temp. (°F)	26.0	32.1	36.2	43.1	49.4	58.5	67.6	64.9	57.7	47.9	31.8	26.6	45.2
Mean daily min temp. (°F)	12.0	15.4	16.0	25.4	29.5	35.0	40.5	40.2	33.6	29.0	18.7	14.0	25.8
Mean rain-fall (inches)	0.79	0.94	0.81	0.92	1.56	2.05	1.39	2.32	2.62	2.99	1.92	1.18	18.89
Mean snow-fall: water equivalent (inches)	8.05	5.43	4.72	2.61	1.15	-	-	-	0.07	1.27	6.41	7.05	36.76
Mean total precipitation (inches)	8.84	6.38	4.90	3.53	2.71	2.06	1.39	2.32	2.71	4.26	8.61	8.23	55.94

(1) Data from: Monthly Record, Meteorological observations in Canada, Canada Department of Transport, Meteorological Branch, 1966.

With the differences in elevation between Allison Pass and the landslide, temperatures may be expected to be higher at the landslide. Assuming a normal lapse rate of $3.5^{o}F$ per 1,000 feet , or an increase of $7.9^{o}F$, estimates may be made of temperatures at the landslide (Table II).

Table II
Temperature estimates: Hope Landslide, Elevation 2250 feet A.S.L.

Element	January	July	Year
Mean daily temperature (^{o}F)	26.9	62.0	43.4
Mean daily maximum temperature (^{o}F)	33.9	75.5	53.1
Mean daily minimum temperature (^{o}F)	19.9	48.4	33.7

Precipitation is probably between the 62.27 inch mean annual precipitation at Hope and the 55.94 inch mean annual precipitation at Allison Pass, although estimates are difficult to make in such mountain valley situations.

Wind direction, a significant influence in the dispersal of some seeds, can only be inferred from personal observations and records of wind speed and direction taken at Hope meteorological station. No wind directions or speeds are recorded ay Allison Pass.

Between August 21, 1967 and November 3, 1967, during field sampling, winds at mid-day were invariably from the northwest. In the latter half of August and early September, early morning wind conditions were often calm or a light south-easterly, but these changed to north-westerlies during the morning and continued to blow from that direction throughout the remainder of the day. Wind records taken at Hope (Table III) show north-westerlies to be infrequent throughout the year but it can be assumed that all westerlies would be channeled through the northwest-southeast Nicolum-

Sumallo valley as north-westerlies. Mean monthly wind directions for the period 1963 to 1968 (Table III) show that from May to September, winds are predominantly from the west and also that these months have winds of a relatively higher velocity than for the remainder of the year. Thus during the period of greatest seed output, (summer through early fall and during the period between dew evaporation and dusk), winds over the landslide and the mud flow are consistently from the northwest.

Table III
Wind records: Hope, Latitude 49° 23' N, Longitude 121° 26' W, Elevation 152 feet A.S.L. 1963 to 1968 (1)

Month	Speed (mph):Mean No. days				Direction: Mean No. days							
	39+	13-38	1-12	Calm	N	NE	E	SE	S	SW	W	NW
January	0	1	22	8	1	5	8	1	2	2	1	0
February	0	2	19	9	1	4	6	1	3	3	2	0
March	0	2	22	7	1	5	7	1	2	5	2	0
April	0	3	18	7	1	2	3	1	1	8	5	0
May	0	5	20	7	1	1	2	1	3	9	6	1
June	0	6	17	6	1	1	2	1	4	11	5	1
July	0	6	19	7	0	1	1	1	4	12	4	1
August	0	6	18	8	1	1	2	1	4	10	4	0
September	0	3	19	8	1	4	3	1	4	8	1	0
October	0	2	21	9	1	4	6	2	3	5	2	0
November	0	2	21	7	0	5	10	3	1	2	1	0
December	0	1	23	6	2	6	11	1	2	1	1	0

(1) Data from: Monthly Record, Meteorological observations in Canada, Canada Department of Transport, Meteorological Branch, 1966.

Regional vegetation

The lower slopes of the Nicolum-Sumallo valley have been classified as belonging to the 'Coastal Western Hemlock biogeoclimatic zone', a sub-division of the 'Pacific Coastal Mesothermal Forest biogeoclimatic region', whilst the upper slopes belong to the 'Mountain Hemlock zone' of the 'Pacific Coastal Subalpine Forest region' (Krajina 1965). The 'Coastal Western Hemlock zone' is to be found at altitudes of up to 3,000 feet, where annualprecipitation totals 70 - 262 inches, including an annual snowfall of

5 - 295 inches. The landslide probably has a lower annual precipitation than the norm for this zone but temperatures fall within the range of mean annual temperatures of 41^{o} to $49^{o}F$ (January 21^{o} to $41^{o}F$, July 55^{o} to $64^{o}F$). The 'Mountain Hemlock zone' i found at higher elevations: between 3,000 and 6,000 feet which experience lower mean temperatures and a generally greater annual snowfall (ibid.).

Aerial photographs taken prior to 1965 show much of the valley sides covered by hemlock forest with two major exceptions: the first, a series of stone chutes or avalanch paths, mostly on the upper part of the old slide scar, and the second, 5920 acres of forest accidentally burned in 1945, located to the north of the main area affected by the 1965 slide (Anderson, F.W. 1965). The forest adjacent to the lower portions of the recent slide scar and the mud flow consisted of Tsuga heterophylla with Pseudotsuga menziesii, Thuja plicata and Abies amabilis.

The valley floor prior to the slide was marshy with a shallow lake. Marshy areas remain to the northeast of the mud flow, between it and the valley side and also adjacent to the Sumallo River. The remainder of the valley floor was undisturbed by the slide and consists of meadowland used as cattle pasture.

Habitats exposed to pioneer colonization after the slide

The 1965 slide left a variety of habitat types exposed to pioneer colonization, which may be divided into three major categories.

I. The slide scar. This is between 3,000 and 5,000 feet wide and is composed predominantly of massive to slightly schistose greenstone. It is still subject to frequent rock falls and there is no visible colonization by vegetation (Fig. 3)

II. Rock debris in the valley floor. The debris forms an uneven

Fig. 3 The slide scar

Fig. 4 Rock debris in the valley floor

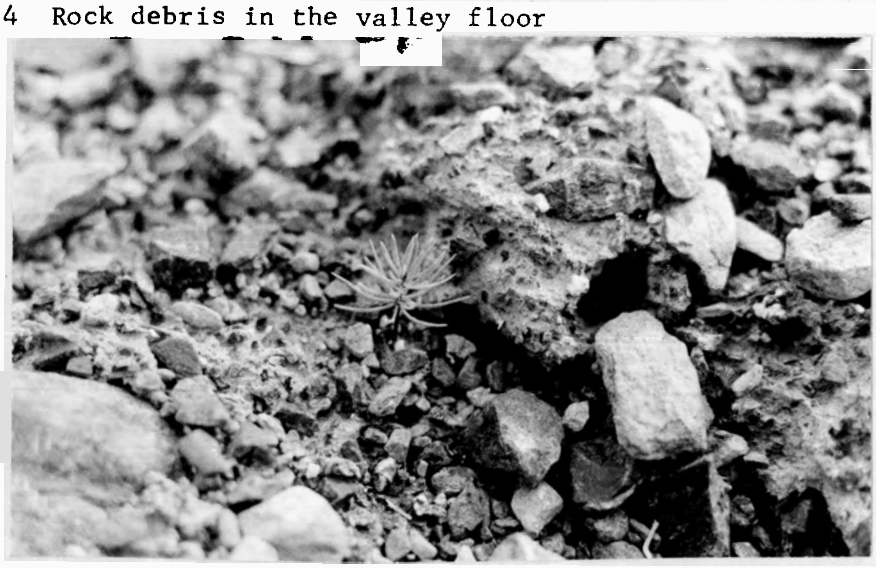


Fig. 5 Douglas fir seedling on the rock debris

topography of an impermeable nature, demonstrated by numerous ephemeral lakes and ponds which have no visible outlet and are consequently accumulating a layer of silt (Fi. 4). Plant growth on this material may be inhibited by a lack of available nutrients, severe dessication in the summer, and flooding or waterlogging in the depressions during the winter. Occasional patches of herbs, grasses, and small shrubs have established, generally on pockets of finer material some of which obviously have a very high orgainic matter content. Scattered tree seedlings are to be found with increasing frequency towards the contacts between the slide material and the forest such as the Pseudotsuga menziesii seedling shown in Fig. 5.

III. The mud flow. On the southeast side of the slide, this habitat has been extensively colonized and is composed of a variety of patchily distributed sediments in irregular hummocks and hollows (Fig. 6). The sediments include gleyed silts, peats, more sandy sediments and very stoney materials. The northwestern mud flow is composed of similar materials but in this case they had been well mixed and consequently formed a more homogeneous habitat. The silts and peats are assumed to have been ejected from the valley floor in the vicinity of Outram Lake by the rock slide. When borings were taken to a depth of 6 feet in the valley floor ½ mile southeast of the mud flow, silts intercalated with thick layers of peat similar in appearance to those on the mud flow were found. The sandy sediments probably originated in the valley-side till deposits and the stoney materials from some of the main rock slide debris.

Fig. 6 Vegetation colonization on the mud flow

Chapter 3

Field sampling, experimental procedure and results

Field sampling techniques were designed to identify types of pattern in vegetation and habitat and to detect any relationships between them. A traverse survey over a large area of the mud flow was undertaken (method adapted from Wilde 1954), with one traverse studied in greater detail. In addition, an experimental study was made of the composition of buried seed and wind blown invading seed.

Sample area

An area 1000 feet by 500 feet, narrowing to 300 feet, was selected on the mud flow and laid out as a grid with intersections at every 100 feet (Figs. 7 and 8). An attempt was made to encompass a sufficiently large portion of the mud flow to allow identification of any overall pattern in the vegetation or habitat, and sampling of all types of substrate, micro-topography, and vegetation. Some areas of the mud flow were avoided when the grid was located because of their association with human activity or atypical physical processes. These areas included:

I. The northern portion of the mud flow where the search for bodies after the slide was concentrated.

II. The southwest portion of the mud flow which was slightly disturbed during the construction of the new highway

III. Perimeters of the mud flow where material was possibly not incorporated into the flow but pushed up in front of the flow(1).

(1) Mathews and McTaggert (1969) infer that this was a relatively insignificant process from the undisturbed snow cover on the valley floor after the slide.

Fig.7. Location of the grid and seed traps

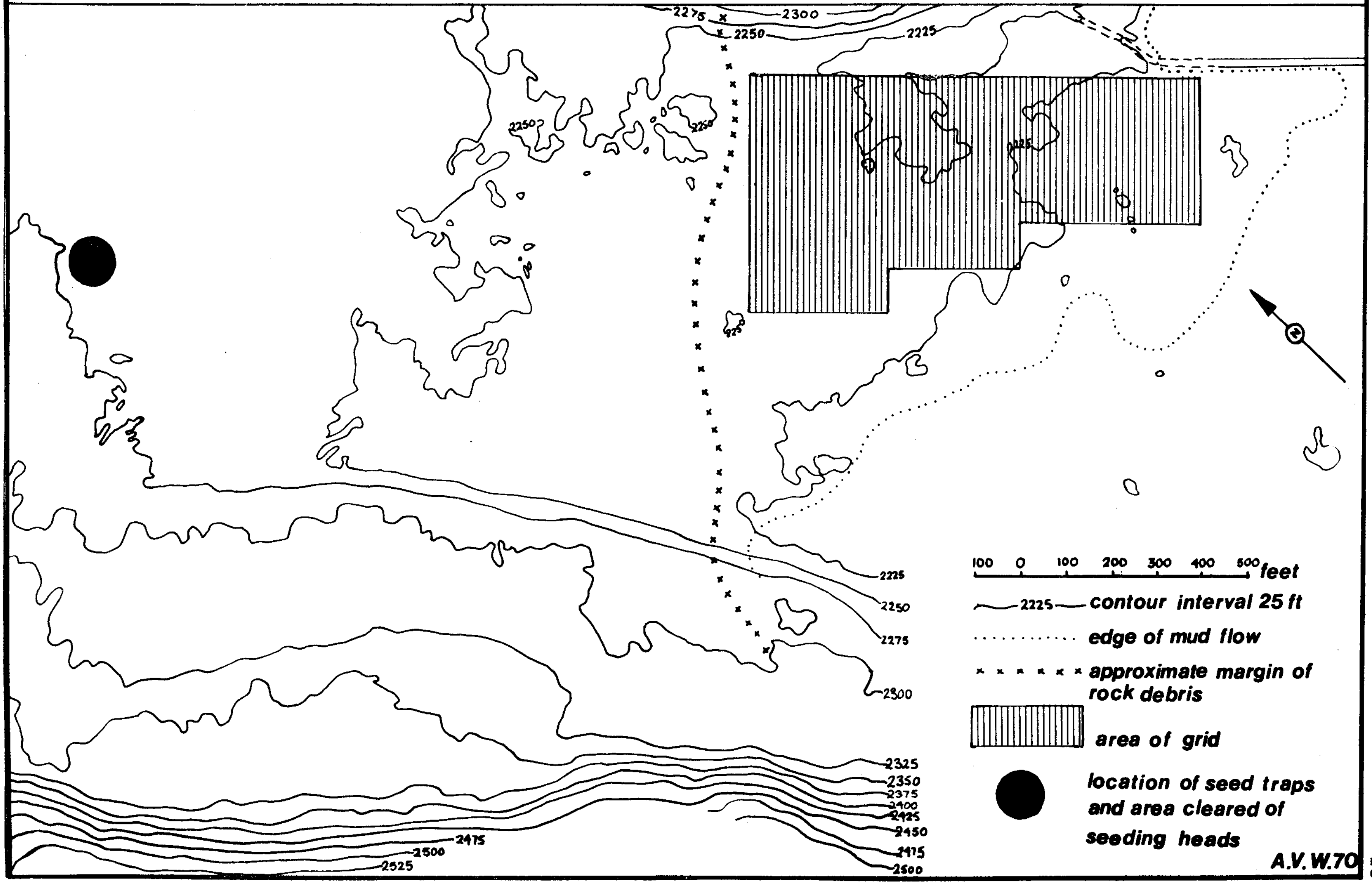
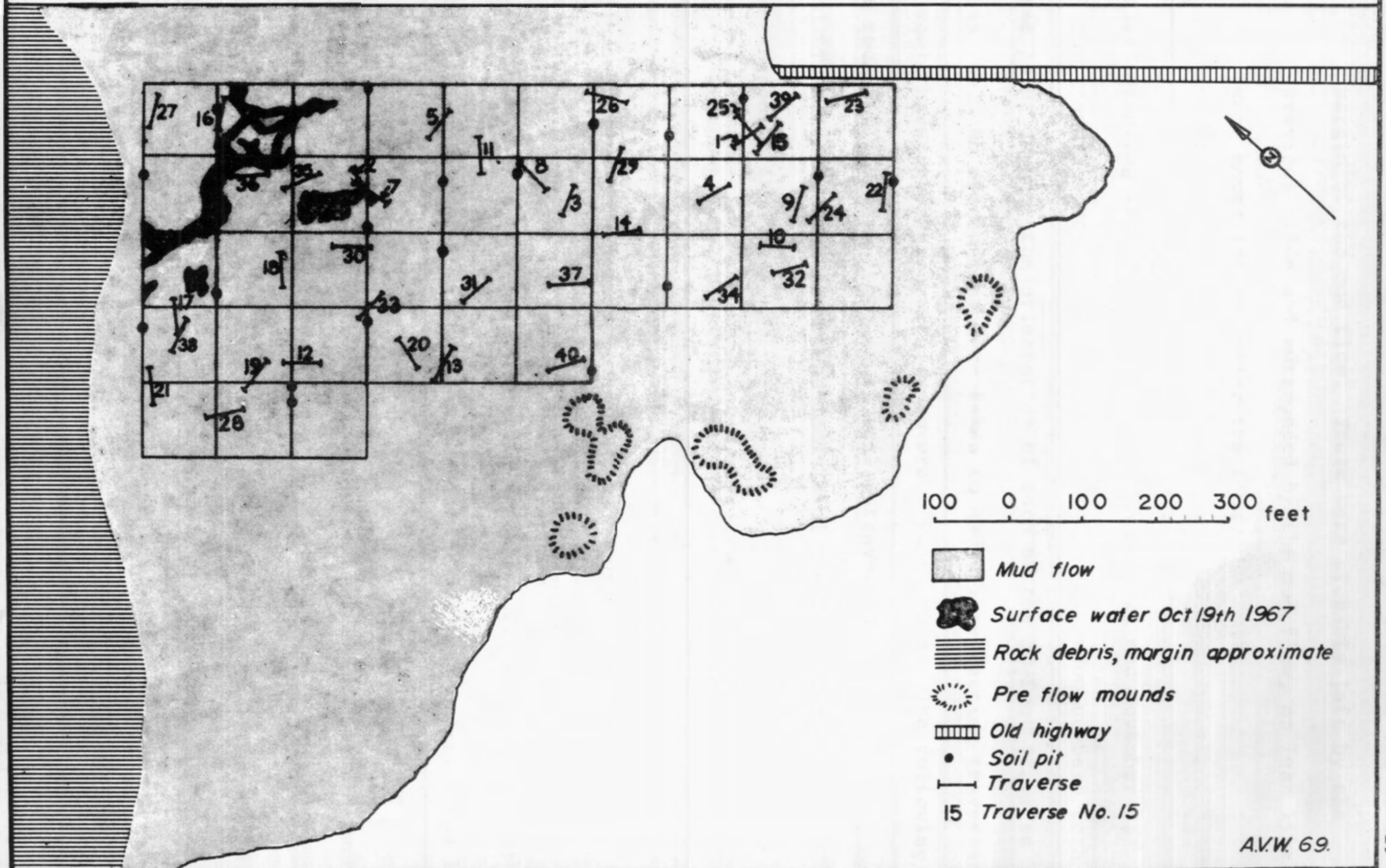


Fig. 8. Location of the grid, traverses and soil pits on the mud flow



IV. Mounds covered by well established vegetation on the southern margin of the mud flow. These were probably left by the previous slide and surrounded by the mud flow, or less likely, were moved intact during the flow.

Traverse survey

Field sampling was carried out between August 22 and November 4, 1967. Forty traverses were located on the grid using random numbers both for a base point and for the orientation of each of the 50-foot traverse lines (Fig. 8). No precautions were taken to avoid intersecting traverses as this would have interfered with the overall randomness. The following data was recorded for each foot length of the traverses:

I. Total vegetation cover and individual species cover, measured in inches.

II. Microtopography, classified according to relative height and aspect. The predominant type of the foot length was noted.

III. Substrate, classified according to colour and texture. The predominant type of the foot length was noted.

I: Vegetation and individual species cover. Cover values were recorded rather than the number of individuals since some of the colonization was by species with underground rhizomes or stolons. For all the cover data, only shoots emerging from an area within 2 inches of the traverse line were included in the sampling. Any portion of the foot length which had a vegetation cover, whether it consisted of one or a number of species, was measured correct to the nearest half inch. The process was repeated for each species occurring in the vegetation of the foot length[1].

(1) Bryophytes were infrequently encountered during the survey but were not included in the study.

II: Microtopography. Microtopography was classed into 11 groups. These were based on height in relation to the nearest hollow, for example, a hummock was classed as high if it were over 3 feet above the nearest hollow, and aspect: north, east, south or west. The groups were as follows:

High hummock, subdivided into: top, north, east, south or west facing slopes

Low hummock, subdivided into: top, north, east, south or west facing slopes

Hollow

Any evidence of waterlogging (Fig. 9) or the existence of surface water was also recorded.

III: Substrate. Substrate was classified in the field into 5 types based on Munsell soil colour charts and texture. The substrate types were as follows:

Grey silts

Organic matter

Grey silts intermingled with organic matter

Yellow brown tills

Stoney material (containing a large proportion of particles over 2 millimetres in diameter: from gravels to boulders)

It was found that the substrate had been subject to much mixing during the slide and the 5 types were to be found on the majority of the traverses (Appendix A). In spite of this mixing process, the patchy substrate distribution was composed of blocks of material with easily recognized margins (Fig. 10). Hence, the classification of the substrates and identification of the predominating substrate over each foot length

Fig. 9 Grey silts showing evidence of previous waterlogging

Fig. 10 Section through substrates showing margins of substrate types
1. Stoney material
2. Grey silts
3. Grey silts intermingled with organic matter
4. Organic matter

Section approximately 2 feet by 1½ feet

was relatively easy.

To demonstrate the reality of the classification, 20 substrate samples were taken from the surface at 5 foot intervals over 100 feet of a randomly selected grid line. Three samples of grey silts, 6 of grey silts intermingled with organic matter, 6 of yellow brown till, and 5 of stoney material were obtained by this method. Four samples of organic matter, which did not occur along the 100 foot line, were obtained on an extension of the line.

The samples were tested in the laboratory for: water content (oven-dry basis), pH (colourmetrically), and carbon content (using the La Motte 'modified dichromate oxidation' method). All particles over 2 millimetres in diameter were removed prior to testing. In addition, texture was determined by decantation (Leeper 1964) for all but the organic matter samples which were greater than 90% carbon. However, as samples were first passed through a 2mm sieve, the main distinguishing characteristic of the stoney material was not included in the textural analysis. Results of the laboratory analysis of substrates are given in Table IV.

All substrate values obtained from the laboratory analysis: pH, water content,carbon content, and percentage by weight of sand, silt, and clay, were tested for significant differences using Snedecor's Variance Ratio Test (Gregory 1963). 'F' ratios and probabilities are shown in Table IV.

Significant differences between the substrates were found in moisture content and percentage carbon, both of which had been observed during field work. All substrate samples were obtained after 2 days of heavy rainfall and water content values indicated that the grey silts, organic matter, and grey silts intermingled with organic matter were most prone to waterlogging: an important habitat characteristic. Dessication, suggested as an

Table IV
Results of the laboratory analysis of substrate samples, showing 'Snedecor's F' values and significance levels for differences between the substrates

Characteristic tested	Substrate type: Grey silts	Organic	Grey silts intermingled with organic matter	Yellow brown tills	Stoney material	F ratio	Significance level
pH	5.6	5.7	5.6	6.2	6.0		
	5.2	5.6	5.4	5.8	5.8	1.98	P>5%
	5.8	5.7	5.4	5.6	5.4		
		5.8	5.2	5.6	5.4		
			5.4	6.0	5.4		
			5.8	5.7			
Water content:	.37	.72	.54	.28	.14		
Grams of water	.39	.56	.54	.29	.12	18.25	1%>P>0.1%
per gram of	.40	1.17	.61	.25	.22		
oven-dry substrate		.67	.41	.20	.16		
			.43	.31	.15		
			.49	.35			
% Carbon	4.3	90	75.8	4.8	2.3		
	4.0	90	82.7	3.7	1.5	182.84	1%>P>0.1%
	6.2	90	83.8	1.5	3.7		
		90	57.7	8.1	2.4		
			72.6	7.2	2.0		
			89.2	6.3			

cont.

Table IV (cont.)

Characteristic tested	Substrate type: Grey silts	Organic matter*	Grey silts intermingled with organic matter	Yellow brown tills	Stoney material	F Ratio	Significance level
Texture analysis *not performed for organic matter							
Sand: particles	17.7		20.8	52.7	44.0		
0.02 - 2.0 mm	34.0		23.7	42.7	44.6	23.56	5%>P>1%
diameter, as %	28.7		23.0	41.5	51.0		
of sand, silt,			25.3	41.6	41.8		
clay and organic			24.3	39.1	56.5		
matter			10.4	39.8			
Silt: particles	65.4		42.0	20.2	34.4		
0.002 - 0.02 mm	57.0		46.8	24.3	26.3	38.78	1%>P>0.1%
diameter, as %	58.2		52.3	27.8	17.7		
of sand, silt			44.1	24.3	31.2		
clay and organic			50.4	26.5	20.3		
matter			48.1	28.6			
Clay: particles	16.9		37.2	27.1	21.6		
less than 0.002	9.0		29.5	33.0	29.1	2.62	P>5%
mm diameter and	13.1		24.7	30.7	31.3		
organic matter as			30.6	34.1	27.0		
% of sand, silt,			25.3	34.4	23.2		
clay and organic			41.5	31.6			
matter							

inhibiting factor in plant growth on the rock debris, would be most severe on the stoney material.

Results of the textural analysis also tended to substantiate field observations. A higher percentage of silt was found in the grey silts and grey silts intermingled with organic matter. Also, the yellow brown tills were found to have a higher percentage of sand.

When compared with a textural triangle based on the Atterberg system of classification (Leeper 1964), grey silts were found to belong between the sandy loams and silts; yellow brown tills to the silty clay loams; and grey silts intermingled with organic matter between the silty clays and silty clay loams. Stoney material was impossible to classify under this system as samples fell within silty loams, silty clay loams and clay loams. However, as mentioned previously, stoney material was identified in the field as containing a large proportion of particles over 2 mm in diameter.

Some degree of variation must be assumed to exist within the classification groups over the entire sampling area. However, the samples taken proved to be significantly different in the characteristics observed in the field, verifying the reality of the classification.

Results of the traverse survey

A summary of the occurrence of vegetation and habitat characteristics is given in Table V. A total of 51 species were recorded on the traverse survey, with frequencies and total cover lengths as summarized in Table VI. Total vegetation cover and habitat characteristics are outlined in Appendix A.

Table V
Summary of vegetation and habitat characteristics recorded on the traverse survey

	Total length of characteristic on traverse survey as % of total traverse length	Mean length for each traverse	Standard deviation for traverse lengths
Hollow	46.7	23.3	6.2
Low hummock side:			
north facing	8.7	4.4	4.7
east facing	8.3	4.2	3.5
south facing	11.9	5.9	5.2
west facing	8.8	4.4	4.4
Low hummock top	12.8	6.4	1.1
High hummock side:			
north facing	0.2	0.1	Recorded on only 1 traverse
east facing	0.8	0.4	1.1
south facing	1.6	0.8	2.2
west facing	1.0	0.5	1.7
High hummock top	1.0	0.5	1.1
Grey silts	25.0	12.5	7.8
Organic matter	7.3	3.6	5.0
Grey silts with organic matter	14.6	7.3	6.2
Yellow brown till	17.9	9.0	6.3
Stoney material	35.3	17.6	10.9
Waterlogged	8.0	4.0	9.9
Vegetation cover	39.1	234.5 (inches)	129.7

Table VI
Species' frequency and cover recorded on the traverse survey

Species (1)	Frequency % (per 2000, one-foot lengths)	Cover (sum of the cover values for the species in all traverses, in inches)
Equisetum arvense L.	37.7	3346
Phleum pratense L.	11.0	806
Epilobium watsonii Barbey.	10.6	478
Agrostis alba L.	7.7	574
Geum macrophyllum Willd.	7.7	717
Ranunculus acris L.	7.5	917
Eriophyllum lanatum (Pursh) Forbes.	6.6	610
Oenothera ?	5.6	445
Rumex acetosella L.	4.7	313
Galium trifidum L.	4.7	244
Poa pratensis L.	3.9	263
Ranunculus repens L.	2.9	274
Cerastium vulgatum L.	2.6	178
Trifolium repens L.	2.4	182
Deschampsia elongata (Hook) Munro.	1.9	117
Juncus ensifolius Wiks.	1.8	78
Trifolium hybridum L.	1.6	126
Cirsium arvense (L.) Scop.	1.5	179
Calamagrostis canadensis (Michx.) Beauv.	1.4	87
Spiraea douglasii Hook. var. *menziesii* (Hook.) Presl.	1.1	77
Carex rostrata Stokes.	0.9	99
Rorippa islandica (Oeder) Borbas.	0.8	55
Montia perfoliata (Donn) Howell.	0.8	54
Agrostis scabra Willd.	0.7	56
Carex mertensii Prescott.	0.6	73
Glyceria pauciflora Presl.	0.6	40
Carex athrostachya Olney.	0.5	36
Rubus parviflorus Nutt.	0.4	37
Sambucus? racemosa L.	0.4	19
Carex diandra Schrank.	0.4	24
Urtica lyallii Wats.	0.3	37
Tolmiea menziesii (Pursh) T. & G.	0.3	24
Montia sibirica (L.) Howell.	0.3	13
Cirsium edule Nutt.	0.2	37
Salix sitchensis Sanson.	0.2	13
Carex bebbii Olney.	0.2	12
Agrostis? palustris Huds.	0.2	7
Aster conspicuus Lindl.	0.2	2
Alopecurus aequalis Sobol.	0.2	20
Aira caryophyllea L.	0.2	8
Rubus leucodermis Dougl.	0.2	8
Anaphalis margaritacea (L.) B. & H.	0.2	5
Rumex crispus L.	0.1	7

Table VI (cont.)

Species	Frequency % (per 2000, one-foot lengths)	Cover (sum of the cover values for the species in all traverses in inches
Rubus spectabilis Pursh.	0.1	6
Myosotis laxa Lehm.	0.1	4
Castilleja miniata Dougl.	0.1	4
Penstemon serrulatus Menz.	0.1	4
Spergularia rubra (L.) Presl.	0.1	4
Veronica americana (Raf) Schw.	0.1	2
Erigeron philadelphicus L.	0.1	2
Prunella vulgaris L. var. lanceolata (Barton) Fern.	0.1	2

(1) Specimens of all species were deposited in the Herbarium of the University of British Columbia.

Detailed study of one traverse

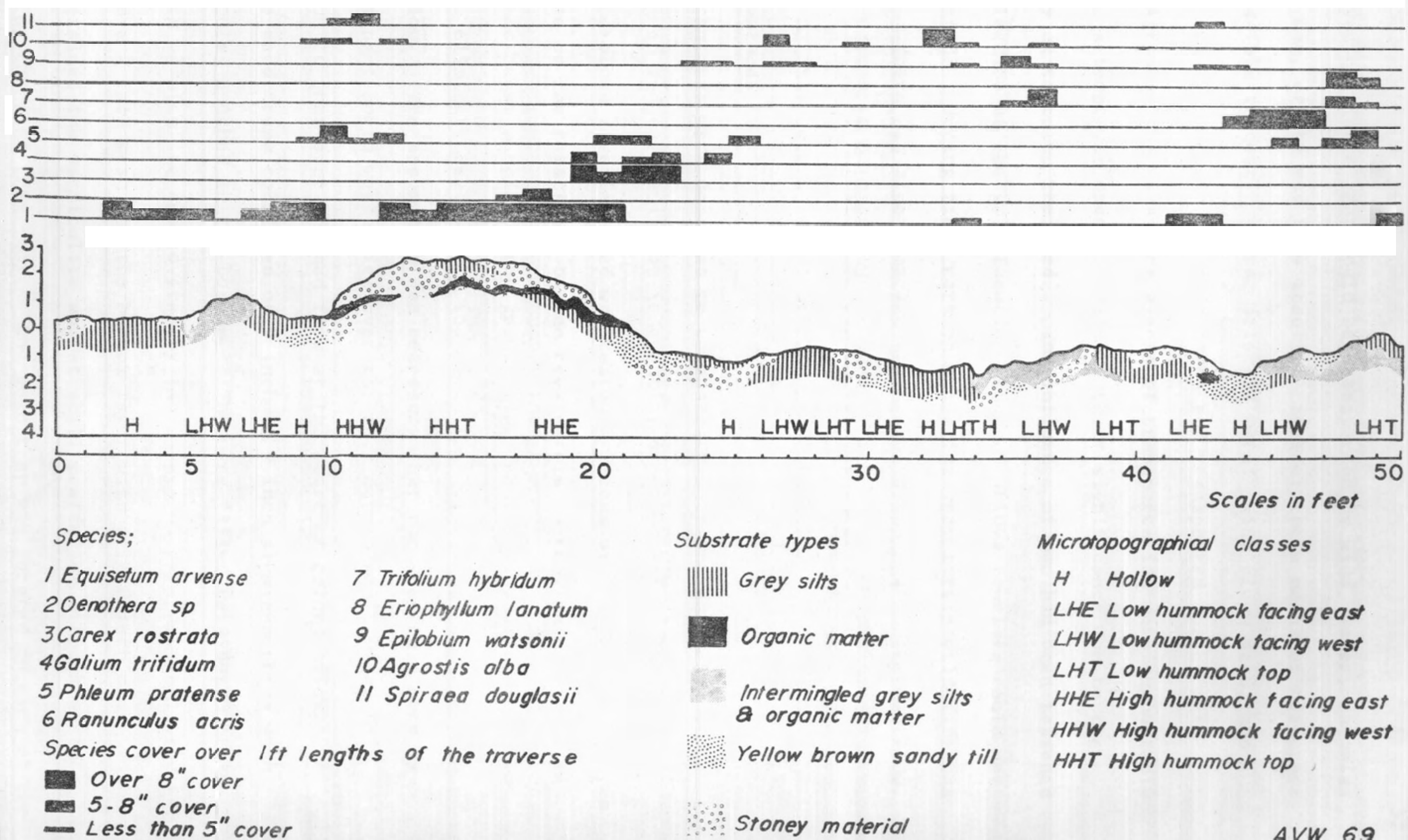
In order to demonstrate the patch distribution of all measured parameters and to slow the relationship between vegetational and habitat characteristics and the recorded data, one traverse was studied in greater detail. Vegetation and species cover, substrate type, and microtopographic class, were recorded in the normal manner for traverse No. 15. In addition, substrates were recorded along a 1 foot trench (Fig. 11) and microtopography was measured by means of a plane table survey.

Species distribution showed both mixed and single stands as well as a range of cover values. All the substrate classes were present in blocks of various size. The traverse was atypical only in the presence of a high hummock in addition to the low hummocks and hollows. No evidence of waterlogging was found on this traverse. Species cover, substrate and microtopography are shown diagrammatically in Fig. 12, and field data is given in Appendix B.

Invading seed

Fig. 11 Trench along traverse No. 15: from the high hummock at 20 feet to the end of the traverse at 50 feet

Fig. 12. Species cover, substrate and microtopography on traverse 15



Invading viable seed could be transported by wind, water, animals: including man, or the mud flow itself. Some of these means of transport were impossible to test. Those selected were: wind blown seed, and viable material buried in the substrates and transported during the slide. Although the remaining agents of transportation were undoubtedly active, no attempt was made to evaluate their significance due to the difficulty of trapping the seed. The influence of man had been lessened by the selection of the grid location, though curious tourists could not be eliminated. During field work on the slide very little wild life was observed. There was also a marked absence of droppings on the mud flow. At the beginning of August there was no running water on the grid area though by October several small streams were observed.

Sampling methods

Techniques were designed to demonstrate both the existence of invading seed and any variation in quantity or composition with habitat.

Wind-blown invading seed was tested by means of 11 seed traps which were placed on the relatively barren rock debris, approximately 1/3 mile from the northwest margin of the grid. The location was selected in an attempt to eliminate seed with a source in the colonizing vegetation on the mud flow. The assumption was necessary that the seed rain born by the predominant north westerlies over the rock debris was similar in composition to that over the mud flow at the start of colonization.

The seed traps consisted of 9 inch by 9 inch aluminum trays with drainage holes punched in the bottom. The were filled to a depth of 1½ inches with vermiculite and covered by two layers of wire netting: the top layer with a ¼ inch mesh and the bottom layer with a 1/10 inch mesh. The netting retained the vermiculite whilst still proffering a rough surface for trapping the seed (Fig. 13). One seed trap was located on each of the microtopographic classes with the aim of indicating the relative effectiveness of the classes in trapping seed (Fig. 14). An attempt was made to avoid contamination from vegetation in the immediate vicinity of the traps by the removal of all flowering or seeding heads within a 50 yard radius of the traps, and repeating this process every week. The seed traps were positioned on August 21, 1967 and removed on November 4, 1967.

Since any seed in the upper layers of the substrate could have already germinated and be included in the colonizing vegetation, sampling of the seed content of the substrates had to be concentrated at a greater depth. Fortunately, in the case of the mud flow, the substrates below the surface were of a similar composition to the surface substrates. Hence, the buried seed content of substrates at depth, would be similar to that at the surface immediately prior to colonization. Exceptions might be due to a normal loss of viability over time, or possibly variation in the moisture content of the substrates with depth, and a consequent loss of viability.

Twenty soil pits, approximately 12 cubic feet in volume, were dug at random locations along the grid lines during September and October, 1967 (Fig. 8 and Fig. 15). On November 3, 1967, 60 samples of substrate were taken from the 18 pits which were free of water. Samples were taken from below 6 inches in depth to avoid contamination from seeds and roots of colonizing vegetation and above the water table on that date. The outer inch of the substrate was also discarded to remove any seeds blown into the pits during September and October. Each sample was selected as being homogeneous with respect to one of the substrate types. The number of samples taken of each substrate type was as follows: grey silts, 12 samples; organic matter, 8 samples; grey silts intermingled with organic

Fig. 13 Seed trap

›s located on low hummock

consists of grey silts,

matter, 11 samples; yellow brown tills, 13 samples; and stoney material, 15 samples. The substrate samples had a surface area of approximately 9.6 square inches and a depth of one inch.

The seed traps and substrate samples were stored at approximately 32^{o}F. for 14 days before removal to a greenhouse, where they were kept at a constant 65^{c}F. and 16 hour day length period for 6 months. The cold treatment and greenhouse conditions were designed to simulate winter and summer conditions on the slide. In addition, germination has been found to be stimulated by cold treatment in many species (Numata and Hayashi 1967).

The seed traps were left intact except for the removal of the surface wire netting. Substrate samples were sprinkled over the surface of 9 inch by 9 inch germination flats, filled to a depth of 2 inches with vermiculite. The average depth of substrate was only .166 inches, and it was believed that all viable material could germinate without further disturbance. Both the seed traps and the germination flats were periodically treated with a mild solution of 10-10-10 commercial fertiliser and kept continually moist. A control was not used.

Results of the invading seed study

A total of 49 germinations were recorded. The numbers of germinations obtained from different substrate types and seed traps placed on the 11 microtopographic classes are given in Table VII.

Table VII
Results of the germination tests

Substrate type or Microtopographic class	Total samples	Total samples with germination	Sample number	Species: number of germinations													Germinations per sample	Total germinations
				*Epilobium watsonii	Athyrium filix-femina	*Geum macrophylum	*Oenothera?	*Rorippa islandica	*Deschampsia elongata	*Montia sibirica	*Agrostis alba	*Cerastium vulgatum	*Phleum pratense	*Carex diandra	Betula occidentalis	Alnus rubra		
Grey silts	12	2	1	-	-	-	-	2	1	-	-	-	-	-	-	-	3	
			2	-	-	-	-	-	-	1	-	-	-	-	-	-	1	4
Organic matter	8	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	
			2	-	-	-	1	-	-	-	-	-	-	-	-	-	1	2
Grey silts with organic matter	11	3	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	
			2	1	-	-	-	-	-	-	-	-	-	-	-	-	1	
			3	2	-	-	-	1	-	-	-	-	-	-	-	-	3	5
Yellow brown tills	13	12	1	-	-	-	-	-	-	-	1	-	-	-	-	-	1	
			2	1	-	-	-	-	-	1	-	-	-	-	-	-	2	
			3	-	2	-	-	-	-	-	-	-	-	-	-	-	2	
			4	-	-	1	-	-	-	-	-	-	-	-	-	-	1	
			5	-	-	-	1	-	-	-	-	-	-	-	-	-	1	
			6	-	4	-	-	-	-	-	-	-	-	-	1	-	5	
			7	-	2	-	-	-	-	-	-	-	-	-	-	-	2	
			8	5	-	-	-	-	1	-	-	1	1	-	-	-	8	
			9	-	1	-	-	-	-	-	-	-	-	-	-	-	1	
			10	-	-	-	-	1	-	-	-	-	-	-	-	-	1	
			11	-	1	-	-	-	-	-	-	-	-	-	-	-	1	
			12	-	3	1	-	-	-	-	1	-	-	-	-	-	5	30
Stoney Material	15	6	1	-	-	1	-	-	-	-	-	-	-	-	-	-	1	
			2	-	-	-	-	-	-	-	1	-	-	-	-	-	1	
			3	-	-	-	-	-	-	-	-	-	-	-	-	1	1	
			4	-	-	-	-	-	-	-	-	-	-	1	-	-	1	
			5	1	-	-	-	-	-	-	-	-	-	-	-	-	1	
			6	1	-	-	-	-	-	-	-	-	-	-	-	-	1	6
Hollow	1	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	1	1
Low hummock north facing	1	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Totals(1)	61	27		14	13	3	3	4	2	2	3	1	1	1	1	1		49

* Species also recorded on the traverse survey

(1) 9 seed traps from microtopographic classes with no germinations not included

Chapter 4

Analysis of results

Test of non-randomness of vegetation and habitat characteristics

Initially non-randomness was tested for all substrates, microtopography, vegetation cover and cover of the 10 most frequent species by variance : mean ratios (Kershaw 1964). A slight modification in the habitat data was made for this and following analyses. High hummock values were included with the low hummock values, since the high hummocks occurred infrequently, and could not be tested statistically with any accuracy. Variance : mean ratios and probabilities are shown in Table VII. Most of the tested parameters demonstrated a high degree of contagion with the exception of hummock tops which were randomly distributed, and hollows which did not demonstrate a highly significant degree of contagion. Thus, a non-random pattern was detected in the vegetation and habitats identified on the mud flow.

Types and causes of pattern on the mud flow

The remainder of the analysis represented an attempt to define the nature and causes of the contagion demonstrated by the variance : mean ratios.

Research into pattern in vegetation at a small scale has mainly been undertaken using mean square : block size analyses. However, the variety of the species indicated that any attempt to analyse patterns by this technique would be a time consuming and possibly unrewarding exercise. Moreover, a smaller sample area would have been necessary if contiguous traverses had been used (Kershaw 1963), and the results would not yield an explanation of any environmental pattern detected without a duplicate analysis of habitat characteristics. Consequently, an analysis of this type was abandoned in favour of map analyses for overall distributional trends, and vegetation : habitat correlations at a more detailed level.

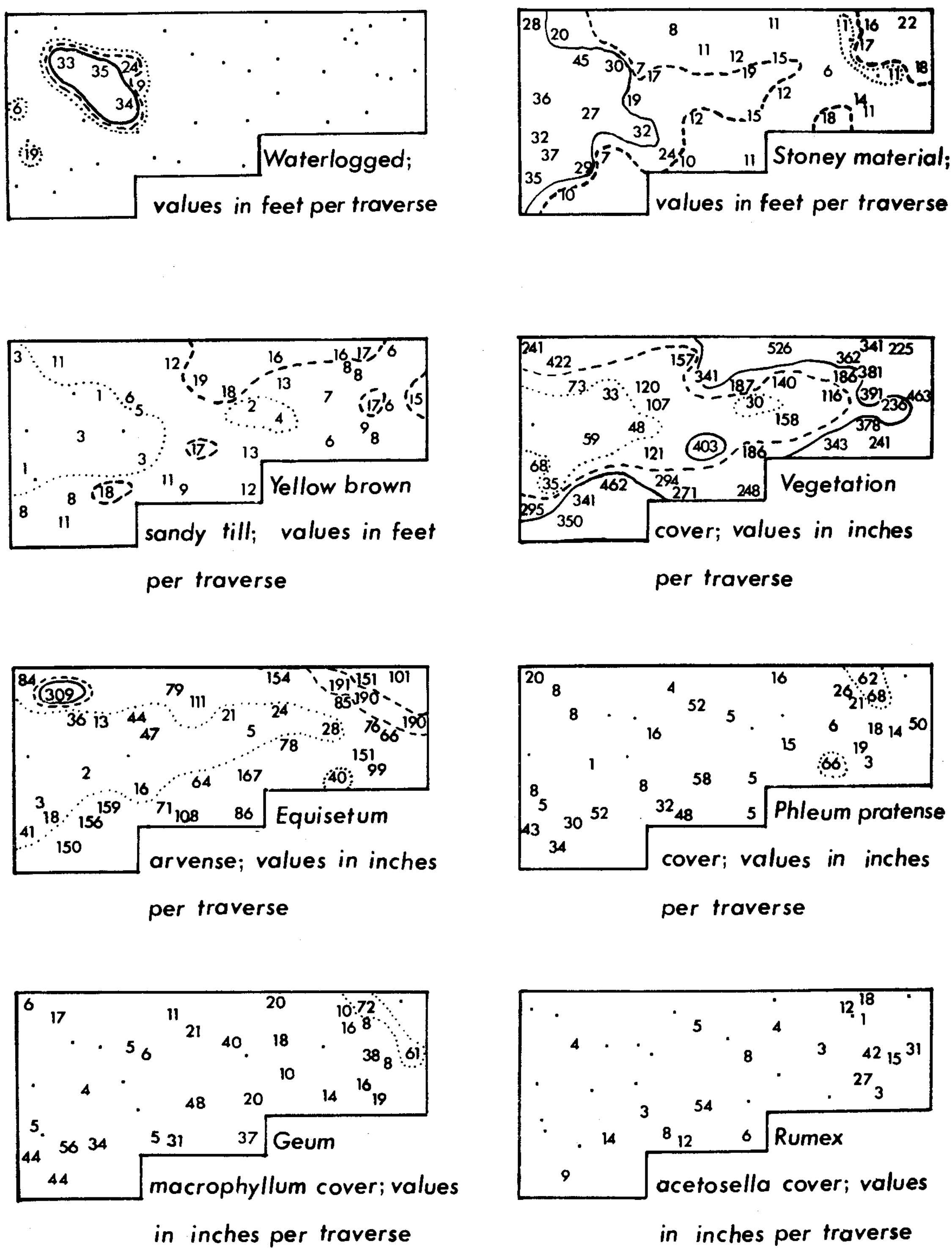
Maps of the three habitat characteristics for which it was possible to distinguish overall pattern (areas showing evidence of waterlogging, stoney material, and yellow brown tills) are shown in Fig. 16.

It would appear that during the slide, superficial material from the valley sides travelled further than more stoney material. The result was a concentration of stoney material in the central and northwestern portions of the mud flow, adjacent to the rock debris, and yellow brown tills on the remaining margins of the mud flow. The role of the grey silts and organic matter during the flow remained unclear since no overall distributions could be detected. Areas showing evidence of waterlogging were only frequent in the northwestern portion of the grid.

The distribution of waterlogged areas demonstrated the most marked degree of contagion when plotted on the grid. A total of 160 feet on 7 traverses located in the northwestern portion of the grid were recorded as showing evidence of waterlogging. When surface water was mapped (October 19, 1967), these areas were found to be either under water or very close to the surface water. Therefore, the areas which were classified as showing evidence of waterlogging during some part of the year were probably seasonally inundated.

On the waterlogged portions of the traverses, a total vegetation cover of only 33 inches was recorded. This represented a mean of less than ¼ inch per foot of the waterlogged areas, compared to a mean cover of approximately 5 inches for all the traverses. This was considered sufficient evidence to assume that establishment of seedlings was poor under these conditions. In addition, fluctuation in the moisture content

Fig 16. Distribution of some habitat and vegetation characteristics on the grid as recorded on the traverse survey



Isolines represent % of traverse covered by habitat or vegetation characteristic

——————— 50%(300 in. or 25 ft.)   - - - - - - - - - 30%(180 in. or 15 ft.)

.... 10%(60 in. or 5 ft.)

A.V.W.70

of soil has been shown to reduce seed viability more than a high but constant moisture content (Steiner 1968). The areas in question were relatively dry below the surface when recorded on the survey. Because of the uncertainty of the margins of the waterlogged areas, and evidence to suggest that seed viability and seedling establishment was poor under these conditions, the 7 traverses on which evidence of waterlogging was recorded were eliminated from all further statistical analysis.

Overall pattern in the vegetation cover appeared to be negatively related to the stoney material and waterlogging, and positively related to the distribution of yellow brown tills, with a very marked decrease in vegetation cover towards the centre and northwestern portions of the grid. The marginal distribution of dense vegetation cover also suggested that distance from the valley side and valley floor vegetation could be a significant factor if colonization were by invading seed. Strong overall pattern was difficult to detect for the 10 species plotted on the grid. Species cover tended to be less dense in the central and northwestern portions of the grid, reflecting the distribution of vegetation cover. Vegetation cover distribution and distributions of the cover of 4 of the species are shown in Fig. 16. The remaining 6 species cover distributions are given in Appendix C.

Relationships between vegetation and species cover and habitat characteristics were tested by means of linear correlation coefficients. These were calculated using the percentage of a traverse covered by a vegetation and habitat variable as data pairs, yielding 33 pairs in each analysis.

These coefficients provide a measure of the co-occurrence of vegetation and habitat variables for the 33 traverses throughout the sample

Table VIII
Variance: mean ratios for 40 traverse values of vegetation and species cover, substrate type, and microtopographic class occurrence

Characteristic tested	Variance : mean ratio	Probability
Grey silts	4.8	P<0.1%
Organic matter	7.0	P<0.1%
Grey silts intermingled with organic matter	5.3	P<0.1%
Yellow brown tills	4.4	P<0.1%
Stoney material	6.8	P<0.1%
Hummocks: north facing	5.3	P<0.1%
Hummocks: east facing	3.7	P<0.1%
Hummocks: south facing	4.4	P<0.1%
Hummocks: west facing	4.5	P<0.1%
Hummocks: top	0.5	P>5%
Hollow	1.7	5%>P>1%
Waterlogged	24.5	P<0.1%
Vegetation	71.7	P<0.1%
Equisetum arvense	34.3	P<0.1%
Phleum pratense	58.6	P<0.1%
Epilobium watsonii	37.2	P<0.1%
Agrostis alba	42.3	P<0.1%
Geum macrophyllum	65.9	P<0.1%
Ranunculus acris	63.8	P<0.1%
Eriophyllum lanatum	28.7	P<0.1%
Oenothera?	52.0	P<0.1%
Rumex acetosella	40.4	P<0.1%
Galium trifidum	26.4	P<0.1%

area. They also serve to verify statistically any correlations in overall distribution trends detected in the map analysis.

The correlation coefficients between total vegetation cover and habitat characteristics are presented in Table IX together with the significance levels of these.

Table IX
Linear correlation coefficients between substrate type occurrence and vegetation cover, and microtopographic class occurrence and vegetation cover

Habitat characteristic	'r' values	Probability
Grey silts	-.090	P>5%
Organic matter	-.072	P>5%
Grey silts intermingled with organic matter	-.005	P>5%
Yellow brown tills	.626	P<0.1%
Stoney material	-.246	P>5%
Hummocks: north facing	-.356	5%>P>1%
Hummocks: east facing	.199	P>5%
Hummocks: south facing	-.054	P>5%
Hummocks: west facing	.232	P>5%
Hummocks: top	-.124	P>5%
Hollow	.088	P>5%

A positive coefficient, significant at the 0.1% level, was obtained between vegetation cover and yellow brown till occurrence, and a negative coefficient, significant at the 5% level, between vegetation cover and the north facing slopes of hummocks. The relationship between the yellow brown tills and vegetation cover, suggested in the map analysis and also evident during field observations, was thus verified statistically. However, the apparent negative overall relationship between the stoney material and vegetation cover (Fig. 16) proved to be insignificant.

Each of the 20 most frequent species were then tested individually for their relationship with substrate types and microtopographic class. Of these, only 4 yielded significant coefficients as shown in Table X.

Table X
Significant linear correlation coefficients obtained between species cover and habitat characteristics

Species	Habitat characteristic	'r' values	Probability
Equisetum arvense	Yellow brown tills	.368	5%>P>1%
Geum macrophyllum	Yellow brown tills	.560	1%>P>0.1%
Rumex acetosella	Yellow brown tills	.597	P<0.1%
Phleum pratense	Yellow brown tills	.350	5%>P>1%

All significant coefficients obtained were for positive relationships between species cover and the occurrence of yellow brown tills. However, the lack of further statistically significant relationships between species and habitat characteristics may be related in part to the low frequencies of most of the species.

The results of the linear correlation analyses indicated that vegetation, as the dependent variable of habitat, demonstrated a cover pattern that corresponded positively to the patchy distribution of yellow brown tills. Less dense cover or bare areas were related therefore to the distribution of the remaining habitat characteristics.

The buried seed and wind blown seed investigations were designed to test for any variation in these populations with habitat characteristics. A comparison of germination values obtained from the substrate types is shown in Table XI.

Table XI
Comparison of germination values obtained from the substrate types

Substrate type	Mean No. of individuals per sample	Mean No. of individuals of species also in mud flow flora	% of substrate samples with germinations	% of substrate samples with germinations of species also in mud flow flora
Grey silts	.33	.33	16.7	16.7
Organic matter	.25	.25	25.0	25.0
Grey silts with organic matter	.45	.45	27.3	27.3
Yellow brown tills	2.31	1.23	92.3	61.5
Stoney material	.40	.33	40.0	33.3

Out of a total of 49 germinations from the substrate samples, 30 individuals comprising 11 species germinated from 12 of the 13 samples of yellow brown tills. Sixteen of the seedlings were species which were also found in the vegetation on the mud flow. This gave a mean of 2.31 individuals per sample of yellow brown till, or a mean of 1.23 individuals of species also found in the mud flow flora. Although there was a great deal of variation in the numbers of germinations obtained from samples of the same substrate type, the results indicated a larger buried seed population in the yellow brown sandy tills than in the other substrates. The population was greater both in terms of total number of germinations and in species also represented in the mud flow flora.

The investigation into wind blown seed gave inconclusive results as to the relative effectiveness of the microtopographic classes in trapping seed. One individual of Epilobium watsonii and Oenothera germinated from seed traps. However, these species also germinated from a variety of substrates and cannot be assumed to have a distribution over the mud flow which has resulted entirely from wind blown invasion. The process of seed invasion was operative therefore but insufficient data existed to relate it to habitat characteristics or pattern in vegetation.

Summary of the analysis of results

Analysis of the data collected on the traverse survey indicated contagion in the distributions of most of the tested parameters, and demonstrated a clear positive relationship between yellow brown tills and cover of total vegetation and four common species. Areas of the mud flow which were seasonally inundated were shown to be negatively related to vegetation cover, due either to poor seedling establishment under these conditions or a low viable seed population. Inconclusive results were obtained concerning the relationship of other habitat characteristics, though a northerly aspect appeared to be negatively related to vegetation cover. Germinations from substrate samples indicated that there was variation in the size and composition of buried seed populations of the substrate types.

Chapter 5

Discussion

Several problems exist which remained untreated during the study and which could complicate the findings discussed in Chapter 4. These problems and the significance of the results obtained on research in plant colonization, are discussed below.

Identification of pattern in vegetation

Grieg-Smith (1964 : 53) states that 'Detection of non-randomness is a starting point for further investigation of factors responsible and not an end in itself'. Research was designed to comply with this concept. Hence, attention was focused on the explanation of the contagious distribution of colonizing vegetation rather than the dimensions of the patches of vegetation.

The study was directed towards an investigation of environmental pattern. At the initiation of the study it was assumed that morphological pattern at a small scale would exist for many species, and that sociological pattern would be relatively unimportant. The latter assumption may have been partially incorrect. Field observations indicated that there were differences in the density and vigour of some species when in competition with others. For example, Equisetum arvense was frequently observed to be growing in dense single stands on a variety of substrates, but when associated with the cover of other species growth was less vigorous. This situation was evident on traverse No. 15 (see Fig. 12 and Appendix B). On the same traverse and others it was noted that a dense cover of Ranunculus acris appeared to inhibit the growth of species. Although sociological pattern resulting from this type of interaction between species would not alter the correlation coefficients between vegetation cover and habitat characteristics, it could create significant differences in the coefficients obtained for the relationships between species cover and habitat characteristics.

Morphological pattern, as stated above, probably existed at a small scale for many species, in particular those with vegetative means of reproduction, e.g. Equisetum arvense, Phleum pratense, Agrostis alba, Eriophyllum lanatum, Trifolium repens. Anderson (1967) also reports the existence of morphological pattern as a result of seed dispersal and subsequent germination. Species with relatively large seeds, such as Geum macrophyllum, were observed to be growing in clumps with many seeds on the surrounding ground. Thus a type of morphological pattern resulting from short range seed dispersal appeared to exist. After initial establishment, it could not be assumed that all morphological spread was dictated by habitat characteristics. Consequently, environmental pattern could be partially obscured by a subsequent morphological spread of species.

However, in spite of the complication of results by the inclusion of other types of pattern, the significant linear correlation coefficients obtained from the traverse data demonstrated that environmental pattern was important on the mud flow.

Invading and buried seed

Vegetation cover was densest towards the northeast, southeast, and southwest margins of the sample area. If the sources of invading seed were the valley-side and floor vegetation, the dense vegetation cover could be accounted for by the normal decrease in seed frequency with distance from the source (e.g. Isaac 1930, Hetherington 1965). More seed would be available therefore in the vicinity of vegetation that was undisturbed by the landslide. Consequently, the location of the seed traps on the rock debris would test the seed rain of adjacent areas only: the northwestern portion of the mud flow which supported little plant colonization.

Very little is known concerning the dispersal and subsequent establishment of species (Webb 1966). Little knowledge of the seed rain was gained from the seed trap germinations other than that two species, with seeds obviously adapted to wind dispersal, were present. However, even if the seed trap experiment had been a greater success, an additional problem exists in the interpretation of such data. Germinations from seed traps would only indicate, with any certainty, the composition of the rain of viable seed at the time of testing and at the sampling site. The seed rain over the rock debris could be locally produced and not applicable to the mud flow. It is therefore not necessarily representative of the seed rain over the mud flow at the start of colonization.

The author is unable to offer suggestions of any practical methods for testing the importance of the seed rain to sites in a state of colonization similar to the mud flow in 1967. Seed disseminating flora on the site could be eliminated as an original source only if sampling had taken place on the mud flow immediately after the slide and before the establishment of colonizing species.

Some similar problems were avoided during the testing for viable seed content of the substrates. Samples were taken at a depth where few seeds could have originated in the mud flow flora, yet the substrates had the same origins as those at the surface. However, several qualifications of the results obtained must be made. Seed viability over long periods has been recorded, but the seeds of some species are relatively short-lived, including the seeds of many trees (Mayer and Poljakoff Mayber 1963).

Therefore germination of some species might have been possible in 1965, whilst seeds of the same species were no longer viable in late 1967. The loss of viability of seeds under certain moisture conditions has previously been mentioned, and although samples were known to be taken from above the water table on November 3, 1967, such a loss of viability could have occurred.

Germination trials were continued for only a 6 month period. Brenchley and Warington (1930) report that germinations continued to be recorded up to the end of the third year after sampling, although the majority of germinations occurred in the first 6 months. Some species have a dormancy period which might prevent their appearance in a limited germination experiment. In addition, species are known to possess differing germination requirements such as temperature range or periodicity, moisture requirements, and oxygen tension (e.g. Cavers and Harper 1966, Harper and Benton 1966, Wareing 1966). Such requirements might be met on the mud flow, but not in the less flexible experimental conditions. Hence, a sample of the total possible germinations was obtained from the substrate samples, but some species might be eliminated due to inherent properties of the seeds, the length of the germination period, and the nature of the germination conditions.

Three of the species which germinated were also found by Kellman (1970) to be included in the viable seed content of forest soil from a Pseudotsuga menziesii - Tsuga heterophylla stand in coastal British Columbia. These were: Alnus rubra, Epilobium watsonii and Anaphalis margaritacea. Others were found in disturbed and undisturbed vegetation close to the mud flow, and will be discussed below.

Finally, a major problem associated with attempts to evaluate the significance of wind blown invading seed and buried seed in colonization, is the lack of mutually exclusive populations in the two sources. For example, Epilobium watsonii and Oenothera? appeared in both seed trap and substrate germinations.

Regional vegetation and the origin of the mud flow flora

Of the 51 species which were recorded in the flora during the traverse survey, 5 have been reported as being characteristic of the 'Coastal Western Hemlock Biogeoclimatic Zone'. Mueller-Dombois (1965) states that Galium trifidum is characteristic of a slope seepage site, and Rubus spectablilis and Geum macrophyllum of alluvial bottom lands in the 'Coastal Douglas-fir and Western Hemlock zone'. Orloci (1965), working on the 'Coastal Western Hemlock Zone' reports Rubus spectabilis to be characteristic of the 'glacial drift land type' and Salix sitchensis, Rubus spectabilis and Equisetum arvense to be found on the 'Squamish Flood-plain land type'. Of these only Geum macrophyllum germinated from the substrate substrate samples. Orloci (ibid.) also mentions Alnus rubra and Athyrium filix-femina as typical of this zone. Both of these species germinated from substrate samples but were not recorded on the traverse survey.

A detailed study of the regional vegetation of the landslide area was not undertaken. However, many of the species recorded on the traverse survey were also observed in the valley-side forest vegetation, for example, Geum macrophyllum, Rubus parviflorus, and Rubus spectabilis. Species observed growing on portions of the valley floor undisturbed by the slide included: Spiraea douglasii and Carex rostrata.

Roadside vegetation, both close to the slide and along the Hope-Princeton highway in both directions included: Equisetum arvense, Epilobium watsonii, Oenothera?, Anaphalis margaritacea, and Eriophyllum lanatum.

Since many weed species have an efficient means of dispersal and great seed longevity (Baker 1965), the majority of these species may have contributed to the mud flow flora either by burial in the substrates or by post-slide invasion. In addition, Gilkey (1957) includes another 5 species recorded on the traverse survey as weeds. These are: Ranunculus repens, Cerastium vulgatum, Cirsium arvense, Rumex crispus, and Prunella vulgaris. Three of the species observed in roadside vegetation or included in the list of weed species also germinated from substrate samples, mostly from yellow brown tills. These were: Epilobium watsonii, Oenothera?, and Cerastium vulgatum.

Equisetum arvense, the most frequent of all the species on the survey, failed to germinate from either the seed traps or the substrate samples. Growth from buried material would be by vegetative reproduction since spores of Equisetum arvense remain viable for only a few days after they are shed, whereas the rhizomes may remain dormant for an indefinite period (Smith 1955). No such material was observed in the substrates at the time of sampling. The sporophyte of Equisetum arvense was observed in the study area during June, but had disappeared by the sampling period. The frequency of Equisetum arvense in all disturbed areas adjacent to the mud flow suggested that it was a common wind dispersed species.

Habitat influence on buried seed and the establishment of colonizing plants

'Environmental sifting' would operate on the buried seed populations, prior to their inclusion in the landslide. Hence, variation in the buried seed content of the substrates may be explained by a consideration of their origins, the effect of differing moisture conditions on seed viability, and a decrease of seed content of soils with depth (Numata et al. 1964).

Grey silts and organic matter substrates originated in the valley-floor deposits. Although no actual depth of these deposits is known, the configuration of the valley would indicate this to be considerable.

Therefore, a low buried seed content would be expected for the majority of these substrates. In addition, the valley was reported to be marshy (Mathews and McTaggart 1969), therefore the seeds would be subject to high soil moisture contents or fluctuations in the moisture contents of the soils, with a consequent possible loss in viability. Yellow brown tills probably originated in the valley-side till deposits. Such deposits are characteristically shallow and well-drained, hence a large buried seed population would be expected. When included in the mud flow, the buried seed populations would continue to be affected by habitat characteristics such as waterlogging.

No evidence was detected to indicate a greater degree of effectiveness in trapping seed for any of the microtopographic classes. Any evaluation of the significance of the process of plant input from external sources must therefore rest on properties of dispersal efficiency known to be possessed by many of the species in both the mud flow flora and the flora of adjacent areas, and the density of the vegetation cover on portions of the mud flow close to vegetation undisturbed by the landslide. However, a further difficulty of evaluating such a distribution lay in the suitablility of the substrates in terms of supporting plant growth.

The clear positive relationship between yellow brown tills and both vegetation cover and cover of 4 species, demonstrated that it was not only the most favourable habitat for the retention of viability of seeds, but also the most favourable habitat for the establishment and growth of species. Hence, the marginal concentration of vegetation could occur even if external invasion were evenly spread over the grid area, since yellow brown tills had a similar concentration. The negative correlation between vegetation cover and north facing hummock slopes possibly indicates that establishment or growth of plants was less successful on colder slopes.

Many hypotheses may be formulated concerning the 'environmental sifting' of colonizing plants, such as dessication being more severe on stoney material thus inhibiting plant growth. However, the analysis of the recorded data did not establish major habitat influences other than the following. Waterlogging appeared to have a negative effect on the establishment and growth of species, and yellow brown tills demonstrated a high degree of suitability for the retention of viability of seeds, and for the establishment and support of colonizing plants.

Chapter 6

Conclusions

Although major problems were encountered in drawing conclusions from the data obtained, some explanation of pattern in the colonizing vegetation emerged.

The majority of the vegetational and habitat characteristics recorded during sampling on the mud flow demonstrated non-randomness in their distributions. Hence, a lack of uniformity in the process of colonization was established.

When these distributions were mapped on plans of the sample area, several distinct overall patterns emerged. Substrates containing a large number of stones were more frequent along the contact of the mud flow with the slide rock debris and in the central portions of the mud flow. Areas subject to seasonal inundation were also concentrated close to the rock debris. A substrate described as a yellow brown till was found to occur mainly on the remaining margins of the mud flow. A similar distribution was found for the densest vegetation cover.

Linear correlation coefficients established a significant positive relationship between the yellow brown tills and vegetation cover. A negative relationship was detected between the waterlogged areas and vegetation cover, and also between north facing slopes of hummocks and vegetation cover. Hence, 'environmental sifting' was of importance during the process of colonization, and environmental pattern existed at both an overall scale and a smaller scale.

Less conclusive results were obtained when the nature of the habitat and vegetation relationships were investigated in terms of buried seed and seed invading from external sources.

Only two germinations were obtained from seed traps designed to test the seed rain over the mud flow. Hence, any conclusions concerning the quantity, composition, or dispersal of wind blown invading seed had to be based on other evidence. The vegetation, surrounding the mud flow but on areas which had not been affected by the landslide, gave some indication of the species which could contribute to the seed rain. In particular, several weed species which occurred both in the mud flow and the roadside floras were postulated as probable external invaders of the mud flow. It was also suggested that a greater volume of wind blown invading seed was available at the edges of the mud flow in contact with undisturbed vegetation. However, the proportion of the vegetation cover which had resulted from wind blown invasions was impossible to estimate due to 'environmental sifting' after invasion, and similarity in the species composition of the wind blown invading seed and buried seed.

Of a total of 49 germinations from substrate samples, 30 were from samples of the yellow brown tills. The significant positive relationship between vegetation cover and yellow brown tills was therefore in part related to the greater availability of seed in these substrates. However, again it was impossible to evaluate the relative significance of the two sources, since many of the seeds with characteristics of longevity were the weed species also noted for an efficient means of dispersal. Hence, buried seed populations were generally composed of both species found in the flora: which in the case of yellow brown tills would be the valley-side forest, and common weed species (e.g. Oosting and Humphreys 1940, Kellman 1970).

As a result of the difficulties outlined above, an evaluation of the relative significance of 'Relay Floristics' and 'Initial Floristic

Composition' could not be made. It appears from the study, that the rate and nature of colonization on any type of surface exposed as a result of earth movement, depends on the suitability of the substrate to support vegetation, and the availability of both invading seed from external sources and germinations from seed of a buried, internal source. As such, each new situation will represent a series of unique events.

It is doubtful whether the time consuming process of extensive investigations into 'Relay Floristics' and 'Initial Floristic Composition' would be justified, except as an aid to some commercial ventures. The regeneration of rangeland after fire, weed populations in arable land, and succession after logging, are examples of problems where a knowledge of the two processes might be of value. In most ecological studies of pioneer colonization however, the relative significance of buried seed and invading seed would appear to be destined to remain an untested though probably important variable in the process of colonization.

Appendix A
Summary of data collected on the traverse survey

Traverse No.	Microtopography: Hollow	Low hummock north	Low hummock east	Low hummock south	Low hummock west	Low hummock top	High hummock north	High hummock east	High hummock south	High hummock west	High hummock top	Evidence of waterlogging	Substrates: Grey silts	Organic matter	Grey silts inter-mingled with organic matter	Yellow brown tills	Stoney material	Vegetation: Vegetation cover
1	8		10	14	15	3							25	10	7	8		186
2	26	12	2	9		1						24	24	3		16	7	120
3	22	10	9	3	1	5							18		11	2	19	30
4	24	3	6	3	7	7							35		2	7	6	116
5	30	5	4	4	2	5							27	1	2	12	8	157
6	34		3		13							6	14				36	
7	24	9		10	4	3						9	18	3	7	5	17	107
8	23	9		8	2	8							7	7	6	18	12	187
9	28	7	3	5	3	4							11	21	1	17		391
10	17		7	5	8	4			6		3		9	4	14	9	14	378
11	26	6		8	6	4							19	1		19	11	341
12	31	4	4		7	4							20		5	18	7	462
13	11		5	9		15			9		1		13	10	8	9	10	271
14	23	6		13		8							5	19	10	4	12	158
15	16		9		11	5		3		1	5		20	1	4	8	17	381
16	22	4	1	17		6							15		4	11	20	422
17	20	18		5	1	6							14	1	2	1	32	68
18	38	4		3		5							4	7	9	3	27	59
19	17		3		3	3		2	8	10	4		9		4	8	29	341
20	22	12	10	5	1								6	1	8	11	24	294
21	27	7	1	7		5	3						5		2	8	35	295
22	30	8		6	5	1							5	1	11	15	18	463
23	23	1	3	5	4	8		4		1	1		5	5	12	6	22	225
24	18	1	5	5	4	7		4		5	1			6	27	6	11	236

Appendix A (cont.)

Traverse No.	Microtopography: Hollow	Low hummock north	Low hummock east	Low hummock south	Low hummock west	Low hummock top	High hummock north	High hummock east	High hummock south	High hummock west	High hummock top	Evidence of waterlogging	Substrates: Grey silts	Organic matter	Grey silts inter-mingled with organic matter	Yellow brown tills	Stoney material	Vegetation: Vegetation cover
25	27	4	8	7	1	3							10	2	21	16	1	362
26	24		10	3	7	6							6		17	16	11	526
27	17	13		7	3	10							13		6	3	28	241
28	25		3	3	8	11							10	9	10	11	10	350
29	17	10	1	9		10			3				7	1	14	13	15	140
30	16		9	10	15							34	8	5	18		19	48
31	32		5		1	7		3		1	1		16	3	2	17	12	403
32	28		5		10	7							16	3	12	8	11	241
33	28		4	2	6	6			4				3		12	3	32	121
34	19		9		12	10							19	7		6	18	343
35	27		9		9	5						35	16		3	1	30	33
36	16	1		25		8						33	5				45	73
37	18	11	4	2	3	8			2	1	1		16	3	3	13	15	186
38	30	2	3	8	1	6						19	7	2	4		37	35
39	25	4		11		8					2		12		5	17	16	341
40	24	3	11	6	3	3							9	10	8	12	11	248
Totals	933	174	166	237	176	255	3	16	32	19	19	160	501	146	291	357	705	9379

Microtopography and substrate values = # feet on the traverse over which the microtopography class or substrate type predominated
Vegetation cover = total vegetation cover for the traverse in inches (maximum possible length 600 inches)

Appendix B
Data recorded on traverse No. 15

Foot # on 50 foot traverse	Vegetation cover in inches	Species cover in inches		Substrate type (1)	Microtopography class (2)
0 - 1	-	-		S	H
1 - 2	-	-		S	H
2 - 3	9	Equisetum arvense	9	G	H
3 - 4	7.5	Equisetum arvense	7.5	G	H
4 - 5	6	Equisetum arvense	6	S	H
5 - 6	5	Equisetum arvense	5	S	LHW
6 - 7	-	-		GO	LHW
7 - 8	5.5	Equisetum arvense	5.5	G	LHE
8 - 9	11	Equisetum arvense	11	G	H
9 - 10	11	Equisetum arvense Phleum pratense Agrostis alba	9 2 3.5	G	H
10 - 11	12	Phleum pratense Agrostis alba Spiraea douglasii	10 3.5 2	O	HHW
11 - 12	12	Phleum pratense Spiraea douglasii	4 8	S	HHW
12 - 13	12	Equisetum arvense Phleum pratense Agrostis alba	11.5 6 2	S	HHW
13 - 14	7.5	Equisetum arvense	7.5	S	HHT
14 - 15	9.5	Equisetum arvense	9.5	G	HHT
15 - 16	10.5	Equisetum arvense	10.5	G	HHT
16 - 17	12	Equisetum arvense Oenothera?	12 2.5	S	HHT
17 - 18	11.5	Equisetum arvense Oenothera?	9 5	S	HHT
18 - 19	10	Equisetum arvense	10	S	HHE

Appendix B (cont.)

Foot # on 50 foot traverse	Vegetation cover in inches	Species cover in inches		Substrate type (1)	Microtopography class (2)
19 - 20	12	*Equisetum arvense*	8.5	S	HHE
		Carex rostrata	10		
		Galium trifidum	6		
20 - 21	12	*Equisetum arvense*	8.5	O	HHE
		Carex rostrata	7		
		Phleum pratense	6		
21 - 22	12	*Carex rostrata*	9	YB	HHE
		Phleum pratense	4.5		
		Galium trifidum	3		
22 - 23	12	*Carex rostrata*	10.5	YB	H
		Galium trifidum	6		
23 - 24	3.5	*Epilobium watsonii*	3.5	G	H
24 - 25	5	*Galium trifidum*	3.5	G	H
		Epilobium watsonii	3		
25 - 26	5.5	*Phleum pratense*	5.5	S	H
26 - 27	7	*Agrostis alba*	6	G	LHW
		Epilobium watsonii	1.5		
27 - 28	1	*Epilobium watsonii*	1	G	LHT
28 - 29	-	-		G	LHT
29 - 30	1.5	*Agrostis alba*	1.5	S	LHT
30 - 31	-	-		S	LHE
31 - 32	-	-		G	LHE
32 - 33	9	*Agrostis alba*	9	G	H
33 - 34	6.5	*Agrostis alba*	3.5	G	LHT
		Equisetum arvense	1.5		
		Epilobium watsonii	1.5		
34 - 35	-	-		GO	H
35 - 36	8	*Epilobium watsonii*	6	GO	LHW
		Trifolium hybridum	2.5		
36 - 37	12	*Trifolium hybridum*	11	GO	LHW
		Agrostis alba	2		
		Epilobium watsonii	0.5		

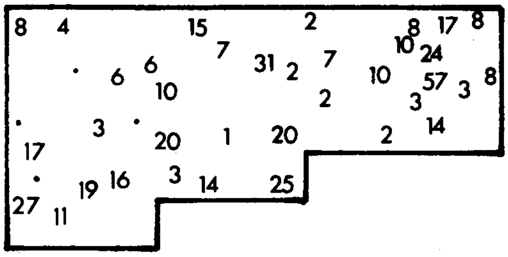
Appendix B (cont.)

Foot # on 50 foot traverse	Vegetation cover in inches	Species cover in inches		Substrate type (1)	Microtopography class (2)
37 - 38	-	-		GO	LHW
38 - 39	-	-		S	LHT
39 - 40	-	-		G	LHT
40 - 41	-	-		S	LHT
41 - 42	6.5	Equisetum arvense	6.5	S	LHE
42 - 43	6	Equisetum arvense	5	S	LHE
		Epilobium watsonii	1.5		
		Spiraea douglasii	2		
43 - 44	6.5	Ranunculus acris	5	YB	H
		Epilobium watsonii	1.5		
44 - 45	8.5	Ranunculus acris	8.5	YB	H
45 - 46	12	Ranunculus acris	12	GO	LHW
		Phleum pratense	5.5		
46 - 47	10	Ranunculus acris	10	GO	LHE
47 - 48	12	Eriophyllum lanatum	10	YB	H
		Trifolium hybridum	5.5		
		Phleum pratense	6		
48 - 49	12	Phleum pratense	9	G	LHW
		Eriophyllum lanatum	6.5		
		Trifolium hybridum	2.5		
49 - 50	7.5	Equisetum arvense	7.5	G	LHT

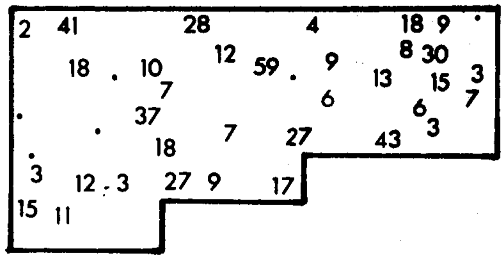
(1) G Grey silts
GO Grey silts intermingled with organic matter
S Stoney material
O Organic matter
YB Yellow brown till

(2) H Hollow
LHE Low hummock east facing
HHW High hummock west facing
HHT High hummock top
LHW Low hummock west facing
LHT Low hummock top
HHE High hummock east facing

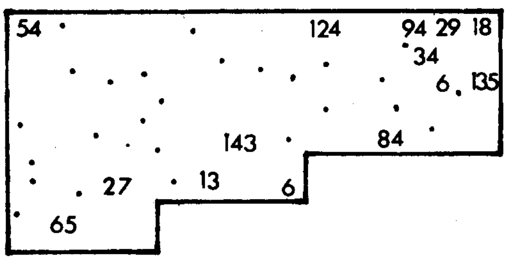
Appendix C Distribution of some species cover values on the grid as recorded on the traverse survey



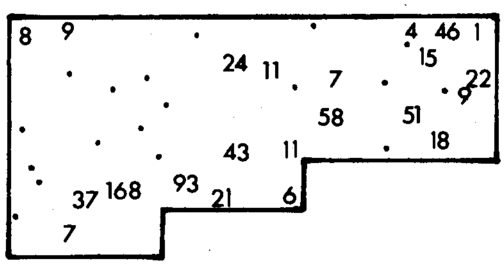
Epilobium watsonii cover; in inches



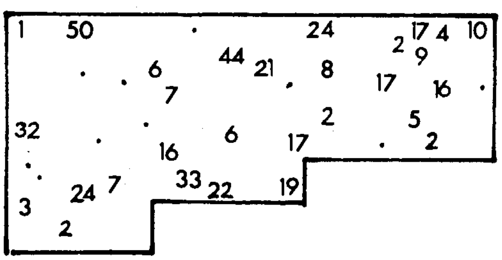
Agrostis alba cover; in inches



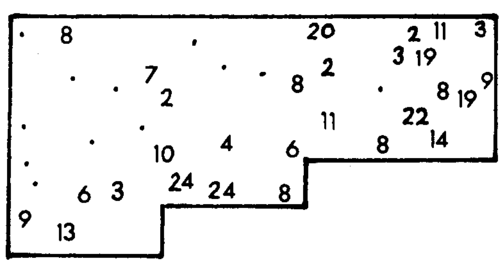
Ranunculus acris cover; in inches



Eriophyllum lanatum cover; in inches



Oenothera? cover: in inches



Galium trifidum cover; in inches

A.V.W.71

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