SUBALPINE BUNCHGRASS MEADOW
INTERSPECIFIC ASSOCIATION ANALYSIS AS
RELATED TO ECOSYSTEM DYNAMICS

by

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INTRODUCTION

Analysis of interspecific association is a method of studying

spatial patterns of populations of organisms at one moment in time.

Combining results from stands of different ages could reveal how popu-

lations vary with time, but few studies of interspecific association

make reference to such population dynamics (Pielou 1969, p. 79). It

is useful to visualize interspecific associations as descriptions of

stages in community succession, and to cautiously use the association

analyses and a posteriori reasoning, to help understand the dynamics

of an ecosystem.

Phytosociological pattern is much influenced by the competitive

relations of species as controlled by the environment. Pattern can be

coactive (distribution determined by species interaction in competi-

tion) and vectorial (distribution determined by external forces, such

as light, temperature, humidity gradients, changes of state in certain

directions, winds, etc.) (Hutchinson 1953).

Co-occurring species may display non-independent pattern if

affected by the same environmental factors (e.g., soil, topography)

or if they have favorable or unfavorable interspecific effects (e.g.,

mutualism, parasitism, allelopathy). Positive interspecific association

may occur when one species of a co-occurring pair of species benefi-

cially affects the other, either directly or by altering the micro-

environment, or when both species have similar tolerance for an environ-

mental factor. Conversely, negative association may occur when one

species disadvantageously affects the other or has a dissimilar habitat

requirement. The factors specifically causing the pattern are not
necessarily revealed by statistically testing interspecific associa-
tion.

Interspecific association analyses have been mentioned as
direct techniques for classifying communities and ecosystems, but are
limited to the extent that they only determine co-occurrence of species
in a particular vegetation type. But interspecific association analy-
ses might have application to ecosystem differentiation and descrip-
tion in a more abstract way. The task of understanding the many eco-
systems in the world is massive, so any principles revealed by inter-
specific association studies which make the effort simpler and more
reliable would be of general benefit to ecology. For instance, if
particular interspecific associations are reflections of successional
stages, or if their type (positive or negative) or frequency is in
general correlated with habitat rigor, this would lead to a more com-
plete understanding of ecosystems.

One might wish to better understand the extent that physical
environment affects interspecific associations within a community. An
environmentally-severe, uniform habitat could cause essentially random
plant occurrence without distinct associations and with frequent coexis-
tence of related species that have extremely similar requirements
(Savile 1960), or conversely association could increase if subordinate
plants cluster around a nucleus of dominants which provides favorable
micro-habitat. For example, harsh habitat conditions observed in the
subalpine meadow studied here might override biological inter-effects
between species and thus greatly influence what associations could occur.

This basic principle is expandable, applying to interspecific association differences between ecosystems. Perhaps one could find correlation between biomes and their type or frequency of interspecific associations, i.e., one might predict the interspecific associations expected in an alpine or subalpine situation as contrasted with a deciduous or tropical forest.

Similarly, would it be possible to predict the interspecific associations relating to successional status of a single ecosystem? Are particular interspecific associations more commonly found in seral stages than at climax? There may be different factors causing such associations as succession proceeds, and these varying factors may be reflected in the types and strengths of associations. Does the statement of Whittaker (1965) hold true, i.e., does a plant community evolve toward dissociation (in the sense of scattering of distributional centers in habitat-space)? Ecosystems undergoing succession might produce predictable patterns of interspecific associations.

Comparing variation in the interspecific associations of a particular species between different ecosystems would also provide information on the autecology of that species. If species A were positively associated with species B in one ecosystem, and negatively associated with that same species in another ecosystem, valuable ecological information would be gained not only about the two ecosystems, but also about the autecology of the two species.

In a survey of the literature I found no studies specifically utilizing inter-ecosystem comparison of interspecific associations as a general method of investigating ecosystem dynamics or species

autecology. Interspecific association analysis has been used as a
method of comparing grazed vs. ungrazed grassland (Cook and Hurst 1962).

Combining analyses of interspecific association with succes-
sional studies may help indicate what specifically causes associations
to occur in an ecosystem. On a seral site undergoing rapid succession
one might expect associations to commonly arise as a result of differ-
ential seedling survival when new species enter the area. Those dissem-
inules germinating in favorable micro-habitats would survive. Therefore
patterns of vegetation would reflect habitat heterogeneity. Conversely,
a site nearer climax would not be encountering a great influx of new
species or a great shift in species dominance.

Usual plant ecological application of interspecific association
analyses is to neglect statistically non-significant associations and
to explain significant associations by inductive reasoning (Hurlbert
1969). Plotless analyses such as mutually nearest neighbor and compar-
ison with distances from random points (Goodall 1965) were not considered
mathematically rigorous in this population of few distinct individuals.
Analyses based on abundance data, $\sqrt{x^2/n}$ (Williams and Lambert 1960),
$\sin (\sqrt{x^2/n} \times 90°)$ (Vries 1954), covariance analysis (Kershaw 1961), and
R_ξ (Morisita 1959), were likewise inadequate because they can be
strongly influenced by interspecific competition, the species' frequen-
cies, and within-quadrat heterogeneity (Hurlbert 1969) and may have
limited applicability to interspecific association analysis per se.

Several attempts have been made to develop a quantitative coef-
ficient as a measure of interspecific association based on presence-
absence data. These were reviewed by Cole (1949) who stipulated that

desirable properties of such an association coefficient are (Pielou 1969):

1. It should be zero when the observed frequencies are equal to those expected on the null hypothesis of independence; that is when $\underline{a}$ = Expected $\underline{a}$ where $\underline{a}$ = number of quadrats having co-occurrence of the two species.

2. It should be +1 (or -1) when $\underline{a}$ - Expected $\underline{a}$ has its maximum possible positive (or negative) value compatible with the observed marginal totals of a 2 x 2 contingency table.

3. The coefficient should vary linearly with $\underline{a}$.

The most commonly used analysis is probably the C_7 coefficient of interspecific association (Cole 1949), based on presence-absence data, which measures the degree to which the co-occurrence of two species is more frequent or less frequent than is expected on the basis of chance. An algorithm as prescribed by Cole was used in this study for the calculation of this coefficient and the determination of statistical significance of association.

Pielou (1969) stated that C_7 makes no distinction between complete and absolute association. If species B had a higher frequency than species A, complete positive association would result if A was never found in the absence of B, though there would necessarily be some quadrats in which B was found without A. Absolute positive association requires that neither species may occur without the other.

Since a large number of comparisons is made, a few results may correspond to a low probability by chance alone. No importance can therefore be attached to isolated cases of apparent association

(Greig-Smith 1957), particularly in those cases involving species with very low frequencies.

This study compared C_7 values with interplant distance data measured from surrounding subordinates to the nearest individual of the dominant species as a qualitative measure of C_7's efficiency. Statistical testing of departures from expected distances in a similar vegetation type was done by Scott (1961) but was not feasible in this study due to statistical problems caused by non-random pattern of the dominant (Goodall 1965).

STUDY AREA

The study plot was in the Yakima Park meadows on a 26°, south-facing slope on Sourdough Ridge 1 km northeast of Sunrise Ranger Station, Mount Rainier National Park, Washington, at an elevation of 2100 m. Sourdough Ridge is a surface exposure of the intrusive Tatoosh Pluton dating from early Miocene or late Pliocene (Fiske, Hopson, and Waters 1963). The study area was on a pumice substrate originating primarily from the 4395 m Mount Rainier volcano (12.5 km to the southwest) over 2000 years ago (Crandell 1969). Less than 150 years ago a relatively small ash and pumice eruption blanketed part of the nearby area, but may not have reached Yakima Park. No evidence of this ash or pumice is present on the study area (D. R. Mullineaux, personal communication).

There has been no readily discernible soil development. Surface texture (determined by the Bouyoucos hydrometer method of Johnson (1966) is a loose sandy loam (58% sand, 32% silt, 10% clay). Numerous

larger fragments of pumice and gravel ranging from 2 mm to ca 3 cm in diameter comprise about 20% of the soil by weight. Kuramoto and Bliss (1970) said subalpine soil development may be slow due to steepness and exposure of the slope, the short growing season, and coarseness of the material. This slope probably clears of snow in May or early June of most years due to its aspect and wind and therefore may be subject to considerable frost action.

Long-term climatic data have not been collected for the area. It is relatively dry compared to many neighboring areas on the west-slope of the Cascade Mountain crest, due to a "rain-shadow" effect from Mount Rainier. Climatic data have been recorded at Paradise Ranger Station (1661 m) on the south slope of Mount Rainier and are summarized here as a rough approximation of the climate at Yakima Park, which would in general be drier, warmer, more sunny and have less annual snowfall and less summer rain than at Paradise.

The mean growing season at Paradise is 150 days. Mean annual precipitation is 269.2 cm with mean monthly precipitation for June, July, August, and September of 11.94, 4.29, 6.65, and 17.43 cm, respectively. Mean annual temperature is 3.7° C with long-term mean monthly temperatures for June, July, August, and September of 7.8°, 11.8°, 11.7°, and 9.0° C, respectively (Singer 1971). Precipitations for June, July, August, and September of 1971 were 13.36, 4.24, 2.11, and 16.46 cm, respectively, and mean monthly temperatures were 4.5°, 12.8°, 13.5°, and 6.2° C, respectively (U.S. Dept. of Commerce 1970, 1971). Mean annual snowfall is 14.78 m (Singer 1971). Snowfall of 25.60 m the winter preceding this study (U.S. Dept. of Commerce 1970, 1971) was a record for official recording stations.

The study was done on a subalpine meadow near timberline in the parkland subzone of the _Tsuga mertensiana_ vegetation zone (Franklin and Dyrness 1969, Franklin and Bishop 1969). A subalpine meadow is an herb- or shrub-dominated community in the forest-tundra ecotone where trees do not, at present, dominate (Löve 1970, Franklin et al. 1971). The meadow is dominated by _Festuca viridula_ tussocks and is interspersed with _Abies lasiocarpa_-dominated groups of krummholz-like shrubs and trees (see photo in Franklin and Mitchell 1967, p. 10). The upper end of the study was downslope about 2 m from a shrub-group.

A well-used hiking trail is 30 m downslope from the plot, but has not resulted in noticeable human disturbance to the area. The vegetation showed no apparent change due to grazing by native herbivores during the study time. Soil mounds of the northern pocket gopher (_Thomomys talpoides shawi_ Taylor) were occasionally found and at times partially buried the herbaceous vegetation. A female Columbian black-tail deer (_Odocoileus hemionus columbianus_) was seen in the area but was not observed grazing on the study plot.

The presence of charcoal in plots used by Franklin and Mitchell (1967) several hundred meters downslope indicates that fire may have affected this study area. Kuramoto and Bliss (1970) emphasized the importance of fire in causing subalpine meadows. The current invasion of trees into the subalpine meadows of Mount Rainier has been studied by Franklin and Mitchell (1967) and Franklin et al. (1971), and they concluded that fire has had little to do with the creation and mainten-ance of the subalpine meadows at Yakima Park. They noted almost no recent invasion of trees.

FIELD METHODS

Six north-south oriented 25 m x 1 m belt transects were layed out side-by-side to form a contiguous plot of 150 m^2. The plot was subjectively placed on an area of essentially uniform vegetation-type, slope, and substrate and did not include or directly border shrub-groups or obvious frost hummocks.

A m^2 (inside dimension) square frame of welded electrical conduit divided into sections of 4 dm^2 by string was used for mapping. Basal coverage of all vascular plants was hand-plotted ($\pm$ 2 cm) at a scale of 1:5 on 1-cm-interval graph paper (20 x 20 cm). Strongly clumped or spreading species (Erigeron peregrinus, Arenaria rubella, Phlox diffusa) and the tussock-forming Festuca viridula were mapped by clump basal boundary. Discrete individuals of these and other rhizomatous or spreading species (Arnica parryi, Achillea millefolium, Anemone occidentalis, Polygonum newberryi, Penstemon procerus, Ligusticum grayi, Sitanion hystrix, and Trisetum spicatum) are virtually impossible to discern without digging.

Field work was done between 16 July and 19 August, 1971. Attempts at use of vertical, black-and-white 35 mm photographs of m^2 quadrats from a tripod were unfruitful due to alignment difficulties and problems distinguishing plants on the photos.

Voucher specimens are deposited in the Herbarium of Kansas State University, Manhattan, Kansas. Nomenclature follows that of Hitchcock, et al. (1955-1969).

DATA ANALYSIS AND RESULTS

Interspecific association analyses were based on presence-absence data in dm^2 quadrats from which Cole's C_7 coefficients were calculated. The strongly rhizomatous or clumped herbaceous vegetation-type presents several problems to the interspecific association investigator. Plotless analyses and analyses based on abundance were not considered feasible in this vegetation where distinguishing individuals was difficult, clumps lacked discrete boundaries, and clumps of different species overlapped.

Quadrat size must be carefully chosen when evaluating association from frequency data. Quadrats must be large enough to theoretically allow all species to occur as pairs, yet not so large as to include all of the abundant species and therefore spuriously suggest positive association. Not more than one plant may grow within a quadrat which is too small. Nonvalid negative associations will appear in quadrats too small and a preponderance of positive associations will appear in quadrats too large.

Data were collected for the 190 species-pair combinations (20 different species) for 15,000 contiguous dm^2 quadrats and arranged in 2 x 2 contingency tables as follows

<div align="center">

Species B
</div>

		Present	Absent	
	Present	a	b	a + b
Species A	Absent	c	d	c + d
		a + c	b + d	n = a + b + c + d

Individuals were considered present in all quadrats in which they discretely occurred or into which bases overlapped.

In statistical analyses those _Festuca_ or _Erigeron_ clumps < 2.5 cm in longest dimension were classed separately from the larger clumps on the assumption that the small plants would have little ecological effect in comparison to the larger clumps.

C_7 coefficients were calculated and the 2 x 2 tables tested with Chi-square on an IBM 360/50 computer at the Kansas State University Computing Center following the algorithms as prescribed by Cole (1949). C_7 ranges from -1.00 when two species have perfect negative association to +1.00 when two species have perfect positive association.

Algorithm:

If $ad \geq bc$ then

$$C_7 = \frac{ad - bc}{(a+b)(b+d)}$$

$$S \text{ (standard error)} = \left(\frac{(a+c)(c+d)}{n(a+b)(b+d)}\right)^{\frac{1}{2}}$$

OR, if $ad < bc$ and $a \leq d$ then

$$C_7 = \frac{ad - bc}{(a+b)(a+c)}$$

$$S = \left(\frac{(b+d)(c+d)}{n(a+b)(a+c)}\right)^{\frac{1}{2}}$$

OR, if $ad < bc$ and $a > d$ then

$$C_7 = \frac{ad - bc}{(b+d)(c+d)}$$

$$S = \left(\frac{(a+b)\,(a+c)}{n\,(b+d)\,(c+d)}\right)^{\frac{1}{2}}$$

For all conditions

$$\chi^2 = \left(\frac{c_7}{S}\right)^2$$

It has been suggested that species with low frequency (less than ca. 30%), or major vs. minor species, should not be tested with Cole's c_7 coefficient (Vasilevich 1961, Cook and Hurst 1962). Festuca viridula tussocks showed the highest frequency (20%) of all species in this study at a dm^2 quadrat size. The results of this study were in most cases considered valid reflections of true ecological relationships qualitatively observed in the field prior to data collation. Statistical rigor would of course increase with increasing species frequencies, but the objective of obtaining ecological information is still achieved with lower frequency data. Species' frequencies are shown in Table 1.

Quadrat size could have been enlarged to obtain higher frequencies, but much information on species interactions would be lost. No correlation between frequency of a species and its number of positive associations was found (correlation coefficient with alpha = 0.05), suggesting that confidence can still be placed in the results. The observed vegetation pattern was such that a larger quadrat might mask true negative associations and show ecologically less meaningful positive associations.

The c_7 values given in Table 2 show 74 significant positive and 16 significant negative associations (Chi-square with alpha =

THIS BOOK CONTAINS NUMEROUS PAGES WITH DIAGRAMS THAT ARE CROOKED COMPARED TO THE REST OF THE INFORMATION ON THE PAGE.

THIS IS AS RECEIVED FROM CUSTOMER.

TABLE 1. Species frequency in dm^2 quadrats (n = 15,000)

Species Name	Frequency (%)
Achillea millefolium L.	4.4
Agoseris glauca var. *dasycephala* (T. & G.) Jeps.	5.8
Anemone occidentalis Wats.	< 1.0
Arenaria rubella (Wahlenb.) J.E. Smith	3.3
Arnica parryi var. *parryi* Gray	< 1.0
Aster ledophyllus var. *ledophyllus* Gray	< 1.0
Carex sp.	< 1.0
Erigeron peregrinus ssp. *callianthemus* var. *angustifolius* (Pursh) Greene	
-clump	6.7
-individual	5.2
Eriogonum pyrolaefolium Hook.ex A. Murr.	4.9
Festuca viridula Vasey	
-tussock	19.9
-individual	2.1
Ligusticum grayi Coult. & Rose	5.3
Lupinus latifolius var. *subalpinus* (Piper & Robins.) C.P. Smith	< 1.0
Penstemon procerus Dougl. ex. R. Graph. var. *tolmiei* (Hook.) Cronq.	5.6
Phlox diffusa Benth.	11.1
Poa sp.	< 1.0
Polygonum newberryi Small	12.4
Sitanion hystrix (Nutt.) J.G. Smith var. *hystrix*	< 1.0
Trisetum spicatum (L.) Richter	< 1.0

TABLE 2. C_7 coefficients of interspecific association (upper right) and their standard deviations (lower left). Statistically significant coefficients (Chi-square; alpha of 0.05) are underlined.

	Achillea	Agoseris	Anemone	Arenaria	Arnica	Aster	Carex	Erigeron clump	Erigeron indiv.	Eriogonum	Festuca tussock	Festuca indiv.	Ligusticum	Lupinus	Penstemon	Phlox	Poa	Polygonum	Sitanion	Trisetum
Achillea		-0.21	-1.00	0.11	0.04	-1.00	-1.00	0.15	0.09	-0.47	0.65	0.05	0.11	-0.17	0.11	0.07	0.00	-0.57	-1.00	0.13
Agoseris	0.15		-1.00	-0.17	-0.25	-0.15	-1.00	-0.21	-0.14	0.02	0.20	0.01	0.03	-0.06	-0.11	0.07	0.08	0.04	0.05	-0.16
Anemone	1.41	1.22		-1.00	-1.00	-1.00	-1.00	0.03	0.04	-1.00	-0.54	-1.00	-1.00	-1.00	-1.00	0.08	0.09	-1.00	-1.00	-1.00
Arenaria	0.01	0.18	-1.00		0.00	-1.00	-1.00	0.19	0.12	-0.80	0.67	0.09	0.11	0.04	0.18	0.18	-1.00	-0.60	-1.00	0.08
Arnica	0.02	0.27	1.62	0.02		-1.00	-1.00	0.10	-0.01	0.03	0.16	0.01	-0.36	-1.00	0.01	0.02	-1.00	0.01	-1.00	-1.00
Aster	2.09	0.11	3.41	2.41	5.07		-1.00	-1.00	-1.00	0.02	0.00	-1.00	0.37	-1.00	-1.00	-1.00	-1.00	0.09	-1.00	-1.00
Carex	0.81	0.70	16.51	0.03	1.97	9.52		0.03	0.39	0.01	0.32	0.07	0.17	0.03	0.07	0.25	-1.00	-0.75	-1.00	0.02
Erigeron clump	0.01	0.12	6.42	0.01	0.03	1.67	0.05		0.11	-0.66	0.69	0.22	0.13	0.10	0.13	0.06	0.46	-0.65	-1.00	0.13
Erigeron indiv.	0.01	0.14	0.08	0.01	0.39	1.90	0.04	0.01		-0.64	0.64	0.15	0.14	0.19	0.12	0.10	0.28	-0.56	0.16	0.08
Eriogonum	0.17	0.01	0.07	0.01	0.02	1.96	0.04	0.01	0.13		-0.37	-0.16	-0.44	-0.63	-0.64	-0.06	-1.00	0.02	-1.00	-0.68
Festuca tussock	0.02	0.02	1.32	0.19	0.05	0.22	0.04	0.04	0.15	0.07		0.20	0.45	0.74	0.51	0.26	0.32	-0.28	0.75	0.67
Festuca indiv.	0.01	0.02	0.60	0.02	0.01	3.06	0.09	0.01	0.01	0.25	0.03		0.05	0.05	0.14	0.17	0.07	-0.24	-1.00	0.06
Ligusticum	0.01	0.01	2.07	0.01	0.59	0.11	0.03	0.01	0.01	0.15	0.02	0.01		0.12	0.06	0.05	0.14	-0.67	-1.00	0.03
Lupinus	0.63	0.54	1.27	0.01	1.55	7.37	0.04	0.01	0.01	0.59	0.07	0.02	0.03		0.11	0.03	-1.00	-0.85	-1.00	-1.00
Penstemon	0.01	0.14	4.97	0.01	0.02	1.84	0.04	0.01	0.01	0.15	0.02	0.01	0.01	0.11		0.11	0.09	-0.62	-1.00	0.09
Phlox	0.01	0.01	1.24	0.02	0.03	1.27	0.06	0.01	0.01	0.10	0.01	0.02	0.01	0.05	0.01		0.08	-0.13	-1.00	0.12
Poa	0.05	0.05	0.11	1.15	2.41	11.57	0.06	0.01	0.05	0.94	0.11	0.03	0.05	3.51	0.05	0.05		-1.00	-1.00	-1.00
Polygonum	0.10	0.01	0.81	0.12	0.03	0.17	0.47	0.08	0.09	0.01	0.04	0.15	0.09	0.36	0.09	0.06	0.57		-1.00	-0.18
Sitanion	1.48	0.08	11.67	1.70	3.58	17.31	6.73	1.18	0.07	1.39	0.16	2.17	0.08	5.21	1.30	0.11	8.25	0.95		-1.00
Trisetum	0.07	0.50	4.60	0.02	1.41	6.83	0.01	0.09	0.03	0.55	0.06	0.02	0.03	2.06	0.03	0.04	3.26	0.34	4.83	

0.05; 1 df). These are schematically expressed in Figures 1 and 2 to show all species and their respective associations.

Festuca tussocks have frequency more than twice that of most other species, the greatest number of positive associations, and are involved in all associations with $C_7 > 0.50$. Comparisons of all C_7 values involving Festuca tussocks were made with interplant distance measurements from a subordinate individual to its nearest tussock neighbor to uncover major ambiguities in C_7 results due to low frequencies. The nearest neighbor method applied in tussock grassland by Scott (1961) used an F-test to determine significance of deviation of measurements from expected distances in a random population. This test assumes random pattern of tussock plants, so a test of randomness was made.

If the plant individuals occur independently and at random in the available quadrats, one expects to find that the number of individuals per quadrat is a Poisson variate (Pielou 1969, p. 81). A Poisson series with observed mean density of 4.32 Festuca tussocks per m^2 was calculated and the observed numbers of quadrats containing 0, 1, 2,...., 12 tussocks compared with random expectation by Chi-square (Greig-Smith 1957) (Fig. 3).

The observed Chi-square of 98.0 is much greater than expected (alpha = 0.01; 10 df) and thus indicates non-random tussock pattern. The frequencies in interplant distance classes were therefore compared with the respective C_7 value for each species associated with Festuca tussocks but not statistically tested for divergence from expected interplant distances in a random population.
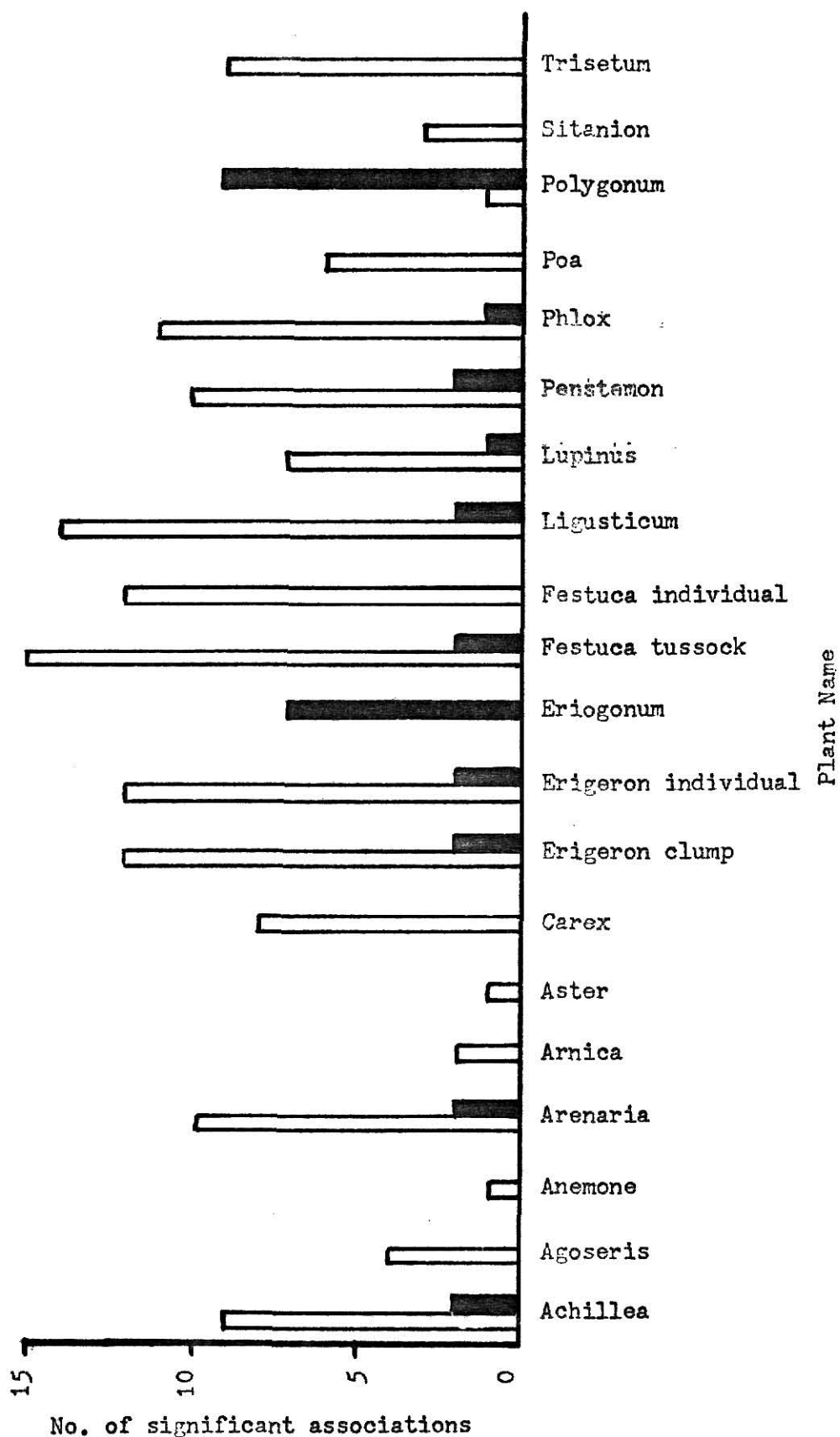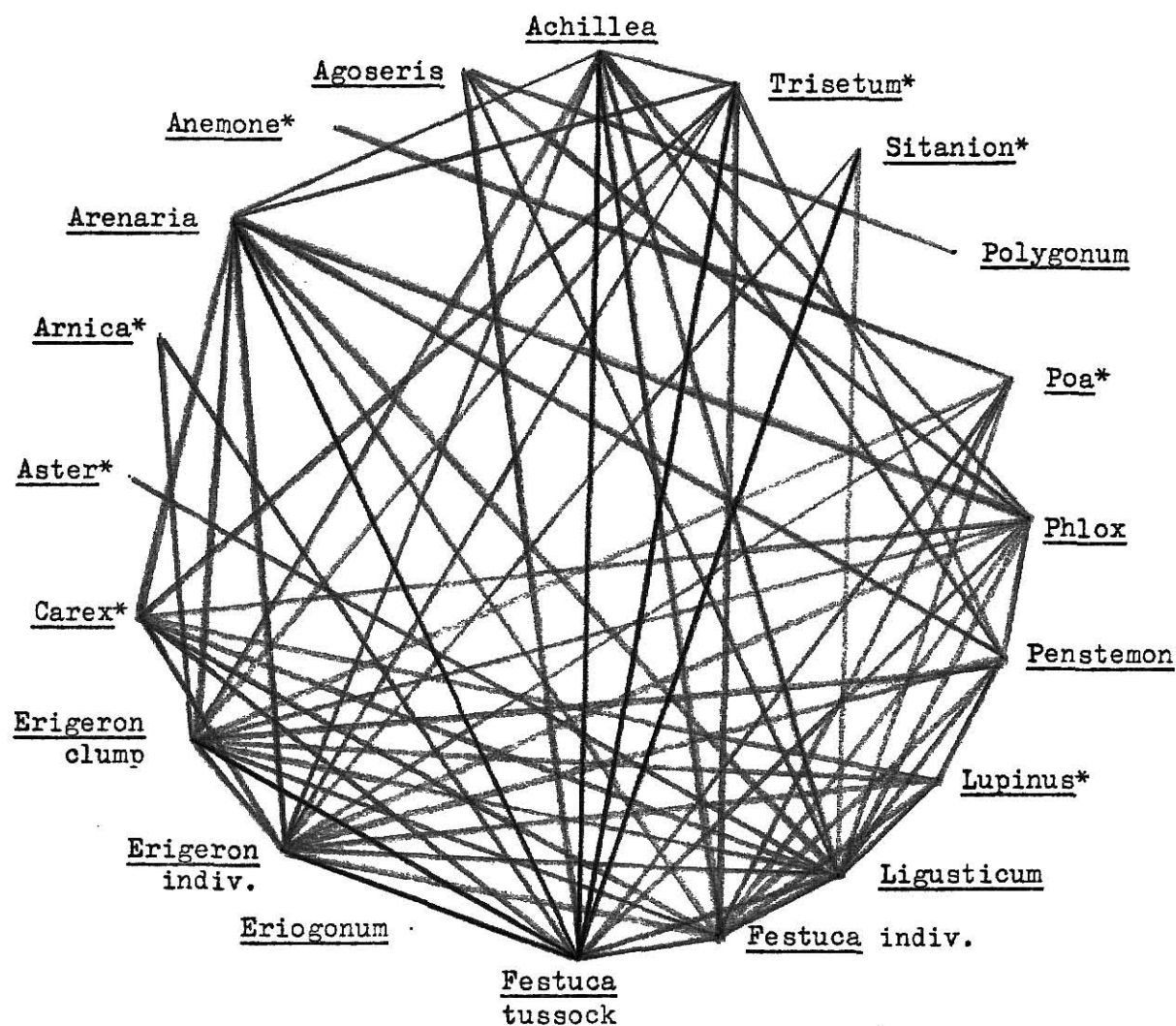
16

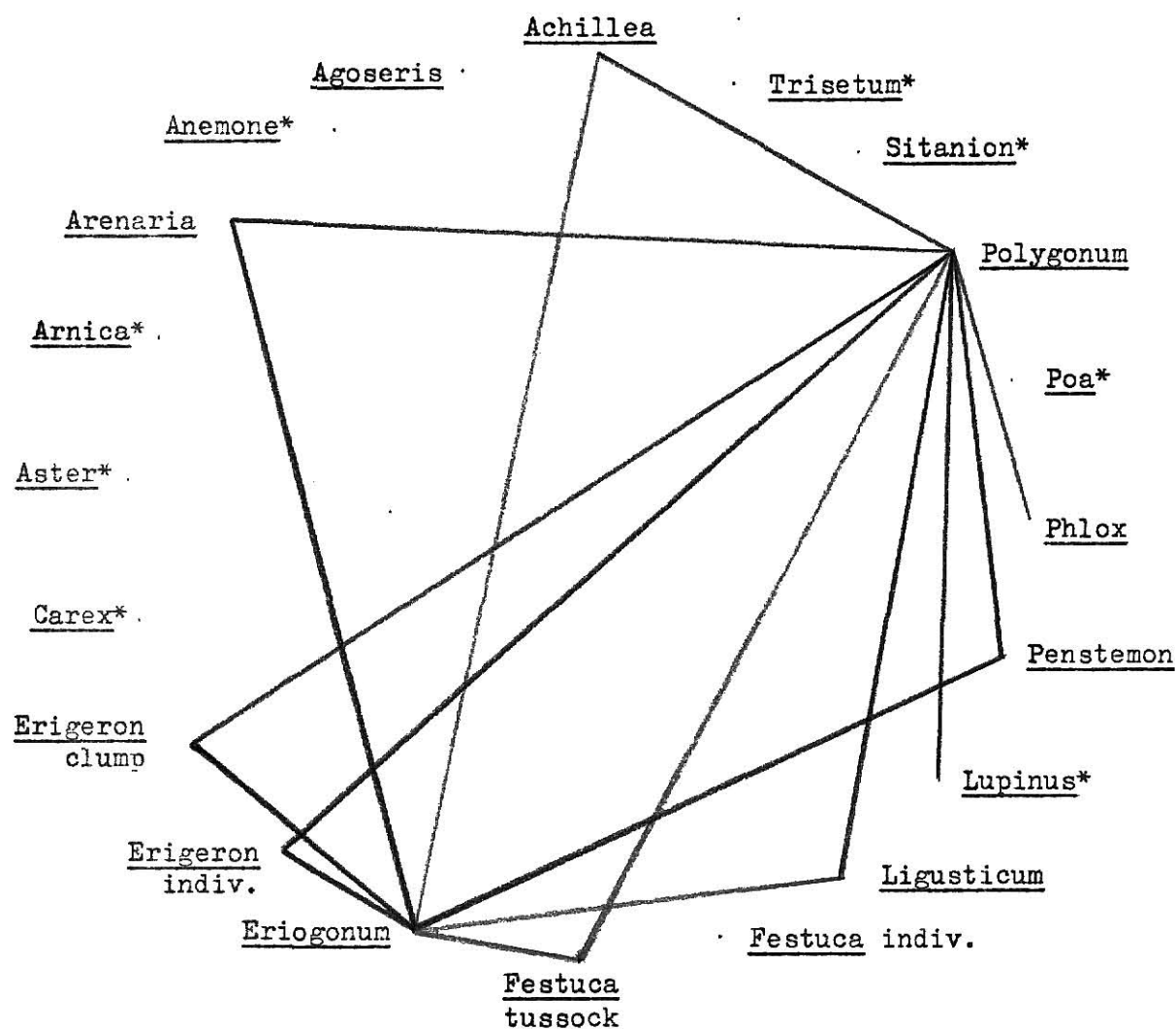*Fig. 1.* Number of significant positive (open bar) and negative (solid bar) interspecific associations involving each species.

Symbols: * = frequency less than 1% at dm^2 quadrat-size
          ━ = C$_7$ less than 0.50 (slight positive association)
          ▬ = C$_7$ greater than 0.50 (strong positive association)

Fig. 2. Significant interspecific associations as determined by Cole's C$_7$ coefficient.

Symbols: * = frequency less than 1% at dm^2 quadrat-size
           ➡ = C_7 greater than -0.50 (slight negative association)
           ➡ = C_7 less than -0.50 (strong negative association)

Fig. 2.   continued

Number of Plants Per Quadrat

No. of quadrats
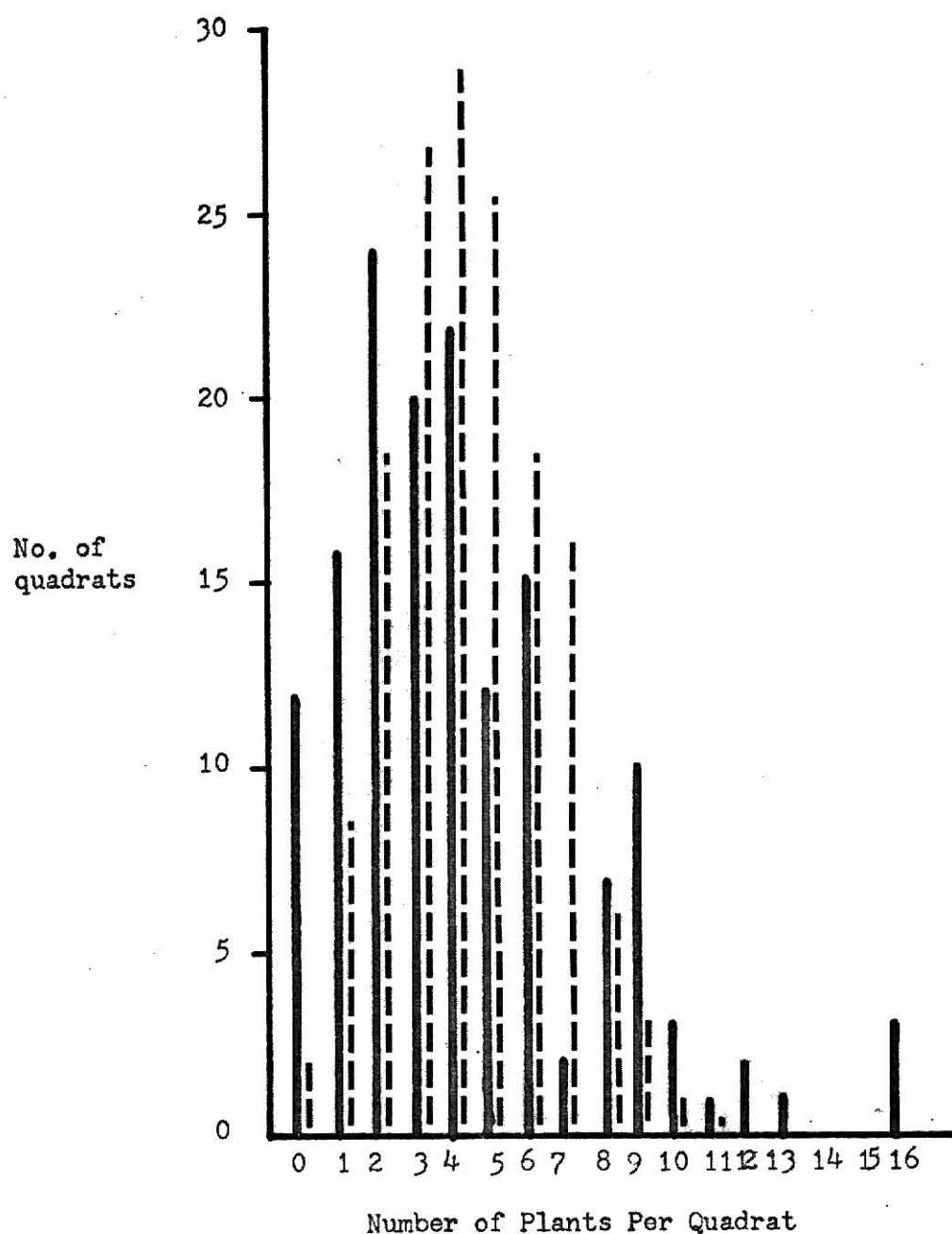
* Solid bars: observed. Open bars: Poisson series.
Total number of m^2 quadrats = 150. Mean density = 4.32 tussocks/m^2.
χ^2_{obs} = 98.0 $\chi^2_{.01}$ (11 df) = 24.7

Fig. 3. The distribution of the expected number of Festuca tussocks per m^2 if they were randomly distributed (from Poisson series and observed numbers*

Interplant distance measurements were partitioned into classes by distance from the tussock margin (0.0--1.9 cm, 2.0--3.9 cm, 4.0--5.9 cm, ..., 38.0--39.9 cm, 40.0--49.9 cm, 50.0--59.9 cm, >60.0 cm). Penstemon, Phlox, Erigeron, and Arenaria patches commonly overlap Festuca tussocks, so percents of overlap were used as distance classes (10-50%, and > 50%) in these species to show degree of co-occurrence. No apparent large-scale ambiguities exist (Fig. 4, Appendix Table 1), except in cases of very low frequency (e.g., Lupinus) where interplant distances and C_7 values poorly reflect one another. Aster, with n = 2, is not shown in Fig. 4.

Apparent positive association is noticeable for Penstemon, with no individuals more than 18 cm, and Arenaria, with no individuals more than 24 cm from the nearest tussock. Overall, the distance distributions for those species with frequencies <1.0% seem to closely reflect the respective C_7 values.

The distance data were partitioned into classes by direction from nearest tussock (NW, NE, SE, SW). The One-Way Analysis of Variance (ANOVA) and Least Significant Difference were used to test for differences in mean distance to the tussock among directions for each species. Percent-overlap measures were recorded as 0 distance for these tests. Calculations were done by the IBM 360/50 using a KSU Stat Lab Statistical Program. Five of the 17 species tested (Achillea, Arenaria, Arnica, Eriogonum, and Polygonum) showed a significant ANOVA (alpha = 0.05), but only two of these had equal variances among directions according to Bartlett's Test for Homogeneity of Variances (Fryer 1966). One must assume equal population variances before testing with ANOVA, so the

21
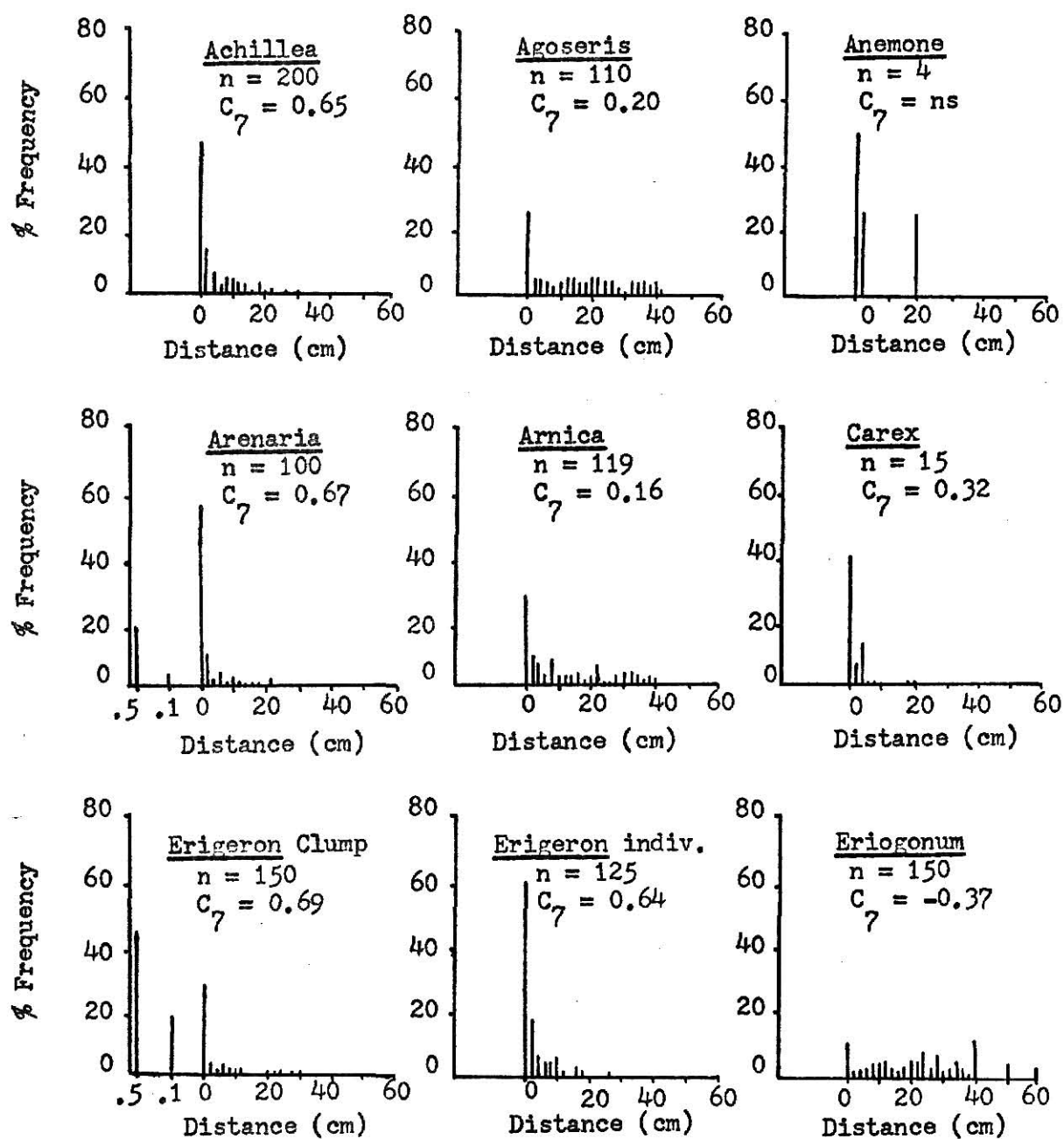
Fig. 4. Distribution of distances* of subordinate
species from nearest Festuca tussock
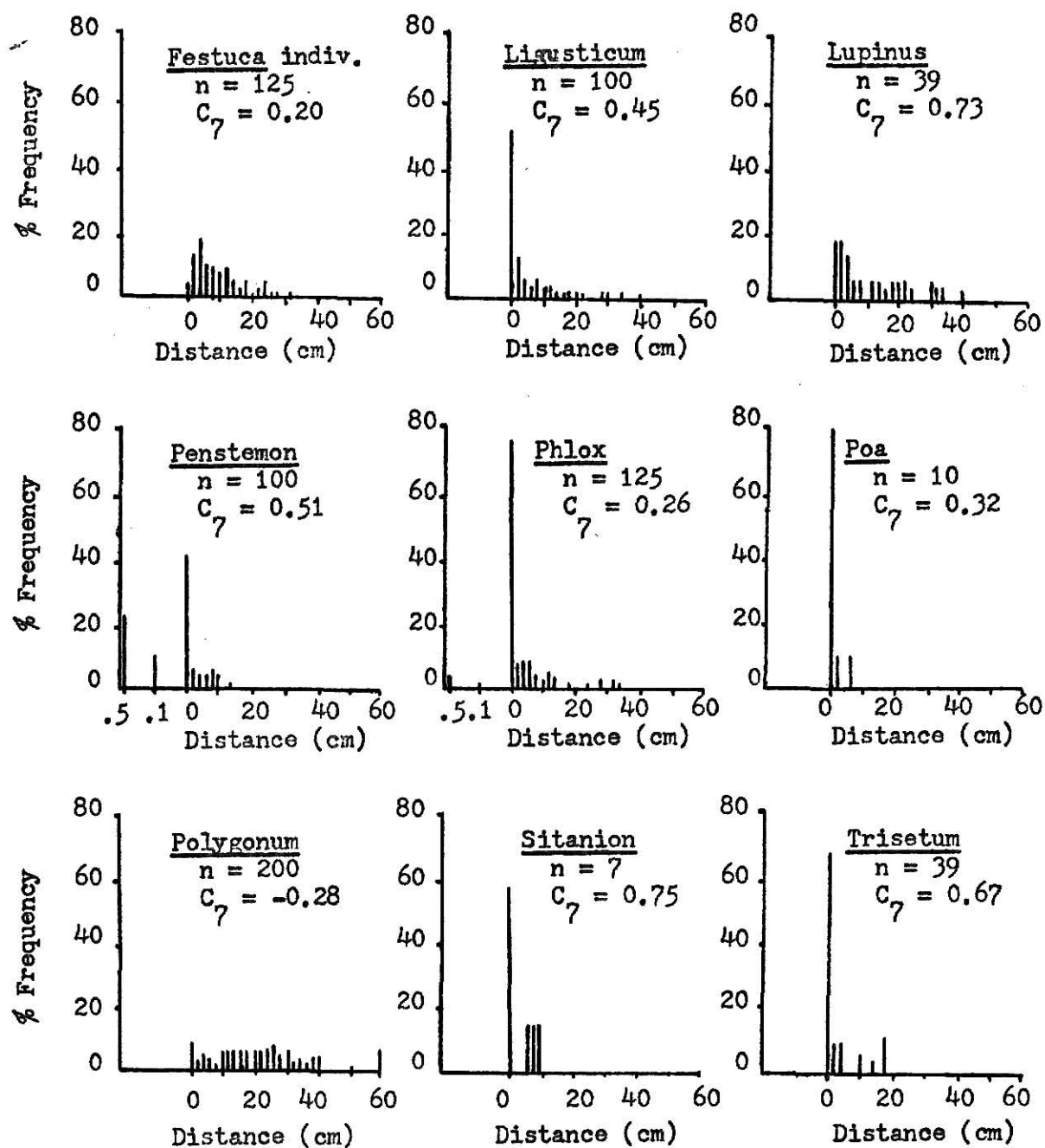
Fig. 4. (continued)

*   Distance classes:

        .5 =   50% of clump boundary overlapping the
              Festuca tussock

        .1 = 10 - 50% of clump boundary overlapping
              the _Festuca_ tussock

0 - 38 = classes of distance to nearest tussock
              partitioned into 2 cm intervals

      44 = 40 - 48 cm distance

      54 = 50 - 58 cm distance

      64 = 60 - 68 cm distance

Fig. 4.   (continued)

significant results of only two tests (Arnica and Eriogonum) are considered statistically valid (Appendix Table 2).

The tests show that Arnica grows closer to Festuca tussocks in the NE quarter than in the NW or SE quarters but is not significantly different from SW, and Eriogonum grows closer to Festuca tussocks in the NE quarter than in all other directions. The significant result for Eriogonum may be a chance, because significance was lost when the few measurements over 40 cm were truncated. No test was made with the Erigeron clumps data because their large size and irregular shape made specific direction classes meaningless.

Distance data by direction were grouped for an investigation of slope influences (above = NE + NW; below = SE + SW). Species positively associated with Festuca tussocks were investigated for the number of plants within 12 cm above or below the nearest tussock. The two species negatively associated with Festuca tussocks were similarly tested using all distances. Statistical significance was determined with Chi-square tests (Table 3). Erigeron clumps and Polygonum occur mostly above, and Arenaria and Phlox occur mostly below Festuca tussocks.

DISCUSSION

Analyses showed significant positive associations between Festuca tussocks and 15 species: Achillea, Agoseris, Arenaria, Arnica, Carex, Erigeron clumps, Erigeron individuals, Festuca individuals, Ligusticum, Lupinus, Penstemon, Phlox, Poa, Sitanion, and Trisetum. In contrast, Eriogonum and Polygonum were found to be negatively

TABLE 3. <u>Number of plants within 12 cm above (north of) or below (south of) nearest Festuca tussock</u>

Species	<u>No</u>. above	<u>No</u>. below	Chi-square Significance
Achillea	85	77	ns
Agoseris	27	21	ns
Anemone	4	0	ns
Arenaria	24	55	**
Arnica	27	41	ns
Aster	2	0	ns
Carex	7	5	ns
Erigeron clump	82	35	**
Erigeron indiv.	64	56	ns
Eriogonum*	77	73	ns
Festuca indiv.	42	39	ns
Ligusticum	56	39	ns
Lupinus	14	9	ns
Penstemon	47	52	ns
Phlox	38	71	**
Poa	4	6	ns
Polygonum*	120	80	**
Sitanion	5	2	ns
Trisetum	19	15	ns

associated with _Festuca_ tussocks and most of its subordinate associates. _Anemone_ and _Aster_ showed no association with _Festuca_ tussocks. Positive associations existed among many subordinates associated with Festuca tussocks, but deciding if this was a direct interspecific reaction or was due to mutual association with _Festuca_ would be most difficult.

To extract meaning from the associations found one can view the interspecific associations as occurring in a point-of-time in the continuum of community succession. Presumably the first perennial plant to colonize the study site would be _Polygonum_, commonly found on disturbed trailsides and the most common species on a trail near the study site virtually un-used for the past 10 years. Occurring with _Polygonum_ would be _Eriogonum_, a common plant on nearby disturbed sites. The slope steepness, causing soil surface instability, and its south aspect make the micro-environment very severe (e.g., by increasing frost action and summer temperatures). One can assume that species which are positively associated with _Festuca_ tussocks are less tolerant than _Polygonum_ and _Eriogonum_ of such conditions.

Festuca was found on the inside part of the un-used trail in small, gently sloping ditches. _Festuca_ might occur there due to trapping of disseminules, decreased moisture runoff, and collection of organic debris which would increase soil fertility. The uphill side of exposed rocks, soil stabilized by _Polygonum_ and _Eriogonum_, animal tracks, and mounds made by the northern pocket gopher forming small flattened areas and depressions are possible sites in an open meadow where _Festuca_ may establish.

When a _Festuca_ plant becomes a large clump it changes the micro-climate. Shading and insulation will limit temperature extremes and reduce evaporation rates from the soil surface. Snows will be trapped in the grass clump and will melt more slowly than in the interspace between clumps.

Kuramoto and Bliss (1970) found that in soils of the dry grass-forb communities of the Olympic Mountains (a vegetation type similar to the community studied here) an A_1 horizon occurs only in patches and mostly in association with clumps of _Festuca idahoensis_. The fibrous root system apparently stabilizes this coarse soil so that a poorly developed A_1 can be maintained. Changes in leaching, pH, nutrient supply, and other physical and chemical factors of this modified soil environment would interact to modify the micro-habitat (Kershaw 1963). The _Festuca_ clumps therefore can be expected to alter the substrate so that it is more favorable for the _Festuca_-associated subordinates.

Festuca tussocks would serve as an efficient trap for plant disseminules, and the more mesic micro-habitat found within the tussocks would be more favorable for the survival of these disseminules.

The protection from grazing afforded plants growing near the base and within _Festuca_ tussocks was mentioned by Scott (1961) in a New Zealand grassland extensively grazed by sheep. This would seem to be an unimportant feature of the tussocks in the present study, however. Cattle grazing permits were issued for only three summers during and after World War I in Mount Rainier National Park (Franklin et al. 1971). As mentioned earlier, little effect of grazing by native herbivores could be found.

It seems that the favorable effects of the altered micro-
habitat within or near a _Festuca_ tussock would allow seedlings to sur-
vive and therefore be the prime cause for positive associations. The
reasons favoring the co-occurrence of species must necessarily be
overriding the negative effects of competition. Whittaker (1965)
assumed that although vascular plant species are competitors for light,
water, and nutrients, they must be partial competitors with some dif-
ferences in requirements to make possible their mutual occurrence in
communities and their distributional overlap. It is possible that two
species which display positive association _in situ_ might actually nega-
tively affect one another and therefore segregate when grown in a two-
species culture.

What could be said about the similarity of the subordinant
species in habitat requirements? Since large areas of ground between
Festuca tussocks contain only a small number of species, it is reason-
able to conclude that those species negatively associated with _Festuca_
tussocks (_Eriogonum_ and _Polygonum_) resemble each other in being intoler-
ant of _Festuca_ tussocks or their associates. This shows that _Eriogonum_
and _Polygonum_ are forced into an association which might be detectable
using a larger quadrat-size. This association would correspond to the
"secondary contagion" mentioned by Ashby (1948) caused by overlap in
tolerance ranges or mutual intolerance of other positively associated
species groups.

Milthorpe (1961) believed that in ungrazed perennial grasses
the development of tussock habit, accumulation of dead leaves which
shade new tillers and encourage microbial activity, and the local deple-
tion of soil fertility and decreased root activity would lead to the

decline of the plant. Succession would occur as the decline in vigor
of the older parts of a grass tussock provided a new site for invasion
of other species. A common within-clump pattern in this study was a
"shelf" of soil covered with subordinants interspersed with or parti-
ally surrounded by fragments of a Festuca tussock, presumably one which
had begun to deteriorate. The overall species composition of the site
might not have changed, but species A might have invaded an area for-
merly occupied by B, whereas the reverse might have occurred on another
site nearby. Cyclical regeneration as suggested by Watt (1947) has
also been discussed as a possible cause of vegetation patterns by
Kershaw (1963) and Greig-Smith (1952). However, no obvious example of
cyclical regeneration involving Festuca was found.

Association between a Festuca tussock and its associates has
thus far been explained primarily in terms of micro-environment.
Kershaw (1963) emphasized that phytosociological patterns are not only
a reflection of micro-environment but also of intrinsic properties of
the plants themselves. Therefore pattern could also be a product of
species-species interaction and individual-individual interaction,
which may or may not be directly modified by the micro-environment.
Vasilevich (1961) stated that the more uniform the habitat, the more
intereffect between species will be important in determining patterns.
He cited Bray (1956) who said that within the confines of a discrete
plant society an association between species by occurrence depends
mainly upon their intereffect. The point at which species intereffect
is no longer expressed in altered habitat is unclear. The presence of
a given species may depend upon previous conditioning of the habitat

by _Festuca_ and this is, in a sense, interaction between species (Cole 1949). There is a possibility of direct interspecies effects such as allelopathy, but it is suggested that vegetation patterns in this study are primarily a result of habitat alteration by other species.

With such a contrast of micro-habitats around _Festuca_ tussocks vs. the interspaces between tussocks it would be logical to attribute interspecific associations, at least at the scale (quadrat size) investigated here, to be due primarily to the altered habitat. Yet it is entirely possible that another level of association would develop between subordinant species-pairs within the _Festuca_ tussock association-unit due to direct interspecific effects. The complexity of such associations might make them virtually undiscernable by the techniques used here.

An indication of this complexity is found when investigating directional association of subordinant species around the _Festuca_ tussocks, such as in _Arnica_ and _Eriogonum_, which grow closer to tussocks on the northeast side. _Erigeron_ clumps and _Polygonum_ more often occurred above the nearest tussock than below, and _Arenaria_ and _Phlox_ were more common below the nearest tussock. _Arnica_ was slightly positively associated and _Eriogonum_ slightly negatively associated with _Festuca_ tussocks. Closer proximity in the northeast quarter may be due to physically altered micro-environment (e.g., shading in the afternoon) or absence of allelopathic toxins leaching downhill from _Festuca_ or one of its associates. An intensive micro-habitat study is needed to make the results more autecologically interpretable.

The occurrence of _Erigeron_ clumps, positively associated with _Festuca_ tussocks, on the uphill side of the tussocks may be due to the

causes mentioned above regarding _Arnica_ and _Eriogonum_ or to trapping of disseminules. Other causes for associations above tussocks may be factors of the interspace between tussocks. Slope above a tussock is generally less-steep than below due to substrate-holding by the plant. Seedlings of _Erigeron_ may more easily establish on the gentle slope and consequently display positive association with the _Festuca_.

Significant reduction in _Polygonum_ below tussocks suggests an allelopathic cause. Its negative association with tussocks was shown earlier; this dissociation may therefore be due to a combination of steepness of the below-tussock slope, competitive incompatibility, and allelopathy. The distinction of the latter two processes is difficult realizing that allelopathic substances may limit nutrient availability and therefore affect competition (Risser 1969).

A detailed investigation of patterns within or near a tussock would presumably find small-scale associations caused by direct species-species or individual-individual interaction. Extended development of the _Festuca_ community might result in a more dense bunchgrass vegetation type with reduced density of _Eriogonum_ and _Polygonum_ in the interspaces between tussocks. Subordinate species would then find increased area suitable for survival and growth.

Application of the interspecific associations found was limited by lack of autecological information. Attempting to explain the causes and implications of interspecific associations in a plant community is perplexing when little is known about the species' autecology. There-fore, one value of this study is a more complete basis for seeing what macroscopic relationships do exist in this subalpine vegetation type and suggesting further studies.

Relations of early colonizers (<u>Eriogonum</u> and <u>Polygonum</u>) with later invaders (primarily <u>Festuca</u>) are also needed points of study. Steep trails, essentially unplanned, exist in the Yakima Park meadows which have become deep scars on the mountainside because of previously inadequate management and heavy-hiker use. Revegetating the denuded areas is difficult due to low percentages of seedling survival. The ecological roles of the various species as herein hypothesized are worth consideration when planning trail restoration projects on ecologically comparable sites.

It is hazardous to extrapolate the basic findings of this study into broad synecological generalizations. One cannot safely generalize about many ecosystems having investigated only one. Important also is the fact that only one successional stage was studied. However, this study indicates some trends that may be plausible explanations for synecological events observed elsewhere. The generation of valid hypotheses was an objective of this study.

Observing succession from the original colonization by <u>Eriogonum</u> and <u>Polygonum</u> moving to the present condition of clusters of <u>Festuca</u> tussocks and its associates interspersed with <u>Eriogonum</u> and <u>Polygonum</u> suggests that interspecific associations are more common now than would be found in the earlier stages of succession. But will this trend continue?

One might hypothesize that this process is happening in other ecosystems under similar, uniformly harsh environmental conditions. Early colonizers establish a pattern which is a function primarily of disseminule dispersal and interspecies competition. Over time the habitat will develop heterogeneity as a result of these colonizers

and other factors as previously discussed. New species will invade and intensify this heterogeneity, promoting associations between invader species due to differential seedling survival. If a habitat becomes more homogeneous as succession proceeds the interspecific associations caused by habitat differences would disappear and give way to either a state of dissociation or to associations resulting from biological intereffects.

If this generality were found to hold true in ecosystems similar to this subalpine meadow, would it also apply to extremely different ecosystems as well? The dynamics of a more "favorable" ecosystem might follow a totally different set of developmental patterns.

The utility of inter-ecosystem comparisons might more effectively apply to comparison within a physiognomic category, e.g., bunch-grass communities. One could also hypothesize that the dynamics found here were a function of substrate conditions or the subalpine situation.

Information derived from the present study could be valuable in understanding species autecology. Do the same or related species of subordinate plants commonly associated with Festuca tussocks have similar associations in other ecosystems? Is the presence of Festuca in a seral community correlated with the invasion of other species whose seedlings could survive in the altered micro-habitat? Is the directional association or slope effect displayed by a species, e.g., Arenaria, characteristic to that species throughout its range, or only under specific environmental conditions?

Future investigation of the synecological and autecological utility of interspecific association studies should focus on variability

between ecosystems, succession, and variation of associations of par-
ticular species between ecosystems.

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APPENDIX TABLE 1. Total numbers of subordinates occurring in 2-cm interval distance classes from nearest Festuca tussock

Distance* (cm)	Achillea	Agoseris	Anemone	Arenaria	Arnica	Aster	Carex	Erigeron (clump)	Erigeron (indiv.)	Eriogonum	Festuca (indiv.)	Ligusticum	Lupinus	Penstemon	Phlox	Poa	Polygonum	Sitanion	Trisetum
>50%				18				66						23	3				
10-50%				2				25						10	1				
0	98	28	0	56	33	0	6	41	75	15	4	52	7	41	76	8	15	4	26
2	28	4	2	10	11	0	1	5	21	3	17	13	7	6	7	1	6	0	3
4	15	5	1	2	8	0	2	1	8	3	23	7	5	4	8	0	8	0	3
6	7	4	0	3	4	1	1	3	5	4	14	4	2	4	8	1	6	1	0
8	11	3	0	1	9	0	1	2	5	6	13	6	2	6	4		4	1	0
10	11	4	0	2	3	1	1	1	6	6	10	3	0	5	2		11	1	2
12	8	6	0	1	4		0	1	1	7	13	3	2	0	4		10		0
14	7	5	0	0	3		0	0	0	5	8	2	2	1	3		13		1
16	2	4	0	1	5		0	0	2	3	4	1	1		0		10		0
18	6	5	0	1	2	1	0	0	1	4	6	2	2		1		11		4
20	2	5	1	1	3	1		1	0	8	1	1	2		0		11		
22	3	6		2	7			1	0	8	3	1	2		0		11		
24	0	4			1			1	0	12	6	0	1		1		12		
26	1	4			1			0	1	5	1	0	0		0		13		
28	0	2			4			1		10	1	1	0		2		8		
30	1	1			5			1		3	0	1	2		0		11		
32		5			5					5	1	0	0		2		4		
34		1			3					8		1	1		1		6		
36		4			2					4		0	0				4		
38		3			4					4		0	0				5		
40-48		4			2					17		1	1				8		
50-58		2								6							1		
60-68										4							12		

APPENDIX TABLE 2. <u>Total numbers of subordinates occurring within each quarter from the nearest Festuca tussock</u>

Species	Direction				
	<u>NE</u>	<u>SE</u>	<u>SW</u>	<u>NW</u>	<u>n</u>
<u>Achillea</u>	38	22	59	73	198
<u>Agoseris</u>	25	27	29	29	110
<u>Anemone</u>	2	0	0	2	4
<u>Arenaria</u>	9	22	46	18	95
<u>Arnica</u>	20	41	26	32	119
<u>Aster</u>	1	0	0	1	2
<u>Carex</u>	6	6	1	2	15
<u>Erigeron</u> indiv.	39	23	33	30	125
<u>Eriogonum</u>	40	33	40	37	150
<u>Festuca</u> indiv.	28	27	34	36	125
<u>Ligusticum</u>	24	29	13	34	100
<u>Lupinus</u>	17	6	7	9	39
<u>Penstemon</u>	27	29	24	20	100
<u>Phlox</u>	28	48	32	17	125
<u>Poa</u>	2	3	3	2	10
<u>Polygonum</u>	53	45	35	67	200
<u>Sitanion</u>	2	0	2	3	7
<u>Trisetum</u>	6	8	10	15	39

SUBALPINE BUNCHGRASS MEADOW
INTERSPECIFIC ASSOCIATION ANALYSIS AS
RELATED TO ECOSYSTEM DYNAMICS

by

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Interspecific associations among 20 vascular plant species in a sloping, seral subalpine meadow at Mount Rainier, Washington, were investigated.

Interspecific association analysis helps in the understanding of differences among ecosystems and successional stages within ecosystems. Interspecific associations caused by habitat heterogeneity and interspecies effects may reflect the overall ecological process and successional status of an ecosystem. The type (positive or negative) and frequency of interspecific associations may also reflect habitat severity.

Basal coverage of all plants was mapped with an accuracy of $\pm$ 2 cm on a contiguous area of 150 m^2. Using presence-absence data in 1 dm^2 quadrats, tests of 190 species pairs were made with Cole's C_7 coefficient of interspecific association resulting in 74 significant positive and 16 significant negative associations. Eight subordinate species are strongly positively associated with the dominant Festuca tussocks and the strength of association in some cases is a function of slope and direction from nearest tussock. Probable causes for positive associations with Festuca tussocks are increased slope stability, improved soil fertility, trapping of disseminules, and more mesic microclimate. Polygonum newberryi and Eriogonum pyrolaefolium occur mostly in the interspace away from the Festuca tussocks. These species are colonizers on bare soil and are probably being replaced by Festuca and its associates. Their inability to persist may be due to competition, altered micro-habitat, and allelopathy. It is noteworthy that the pioneer species have strong negative association coefficients with Festuca clumps.