Vegetational Relationships With Air Mass Frequencies: Boreal Forest and Tundra

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ABSTRACT. Recent studies have demonstrated a striking correspondence between air mass frequencies and the position of the North American forest border. Analysis by principal component techniques demonstrates that relative abundance of certain species in a number of kinds of plant communities found in central northern Canada is strongly correlated with the frequencies of given air mass types. The conclusion is reached that distribution and frequency of occurrence of at least a number of species found in the plant communities of that region are markedly influenced by climate. In addition, the result can be interpreted as evidence supporting the continuum theory of species distribution in vegetation of the region.

RÉSUMÉ. *Rapports entre la végétation et les fréquences des masses d'air, pour la forêt boréale et la toundra.* De récentes études ont démontré une correspondance frappante entre les fréquences des masses d'air et la position de la limite de la forêt en Amérique du Nord. Une analyse démontre que l'abondance relative de certaines espèces dans un bon nombre de sortes de communautés végétales que l'on retrouve dans le centre du Canada nordique est fortement liée aux fréquences de types donnés de masses d'air. On en arrive à la conclusion que la distribution et la fréquence d'au moins un certain nombre d'espèces présentes dans les communautés végétales de cette région sont fortement influencées par le climat. De plus, on peut interpréter ce résultat comme une preuve à l'appui de la théorie du continuum de distribution des espèces de la végétation de la région.

РЕЗЮМЕ. *Зависимость распределения растительности в северных лесах и тундре от повторяемости воздушных масс различных типов.* Исследования, проведенные за последнее время, выявили четкую зависимость расположения границы северо-американских лесов от особенностей в годовом ходе повторяемости воздушных масс различных типов. Делается заключение, что распределение определенных видов растительности в исследованном районе тесно связано с климатом.

INTRODUCTION

Whoever first made the observation that each of the various species of plants grows in certain characteristic habitats is surely lost in the obscurity of the distant past. Since the days of Humboldt (1807), Schimper (1903), and Warming (1909) as well as many other early workers, the literature on the relationships of plants to climate has become voluminous. Until recently, however, detailed studies of plant-climate relationships were hampered by the absence of adequate techniques for the sampling and statistical description of vegetational communities as well as by lack of meteorological data from remote areas where vegetational communities exist in natural undisturbed condition.

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Recent studies conducted by the author and others (Larsen 1965, 1967, 1971, and mss. in prep.; Bryson 1966) have demonstrated a striking correspondence between a climatic parameter (air mass frequencies) and the position of the North American forest border. In such studies, there is an assumption made that the isopleth under consideration delineates an ecotonal region where one or more parameters of the environmental complex exceed the tolerance limits of the trees. In all studies of these relationships, the advantage of working with the forest border is obvious. It can be visualized, mapped, and geographical position determined with a fair degree of accuracy. But the fact that here, in the forest-tundra ecotone, large numbers of shrub and herbaceous species also show changes in abundance along environmental gradients has seldom if ever been taken into account. It is the purpose of this paper to show that changes in the abundance of some of these other species in the vegetation are as striking as the more visible changes that occur in the arboreal stratum.

There are, as a result of demonstrable correlation between frequencies of

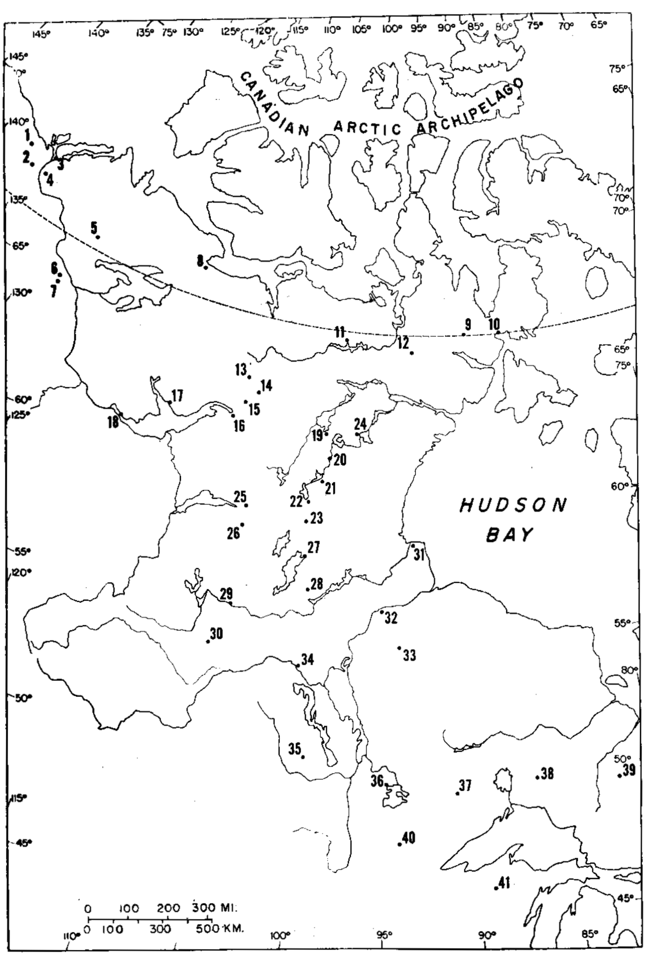

FIG. 1. Study areas in which sampling of vegetational communities was conducted. 1) Trout Lake (N.W.T.); 2) Canoe Lake; 3) Reindeer Station; 4) Inuvik; 5) Colville Lake; 6) Florence Lake; 7) Carcajou Lake; 8) Coppermine; 9) Curtis Lake; 10) Repulse Bay; 11) Pelly Lake; 12) Snow Bunting Lake; 13) Aylmer Lake; 14) Clinton-Colden Lake; 15) Artillery Lake; 16) Fort Reliance; 17) Yellowknife; 18) Fort Providence; 19) Dubawnt Lake; 20) Dimma Lake (Kazan River); 21) Ennadai Lake; 22) Kasba Lake; 23) Kasmere Lake; 24) Yathkyed Lake; 25) Black Lake; 26) Wapata Lake; 27) Brochet; 28) Lynn (Zed) Lake; 29) Otter Lake; 30) Waskesiu Lake; 31) Churchill; 32) Ilford; 33) God's Lake; 34) Rocky Lake; 35) Clear Lake; 36) West Hawk Lake; 37) Raven Lake; 38) Klotz Lake; 39) Remi Lake; 40) Bagley (Pike Bay); 41) Trout Lake.

species and frequencies of prevailing air mass types, some implications lending support to the continuum concept of vegetation (Curtis 1959; McIntosh 1967). There is also the possibility for some practical application in using vegetational composition as a climatic indicator for regions lacking detailed climatic records. Since a number of the species showing high correlations with air mass frequencies are among the dominant species in some of the plant communities of some areas, the utility of this interesting practical application of the continuum concept becomes apparent.

This paper reports an analysis of relative abundance of certain species in a number of kinds of plant communities found in central northern Canada. Their frequency values show correlations with air mass frequencies which are sufficiently high to warrant the conclusion that distribution and frequency of occurrence in plant communities are a response to the distribution of climatic conditions.

THE STUDY

The study was conducted from 1958 to 1969 (and is being continued), with data obtained so far from more than 40 sites mostly in the area to the north of the southern limit of boreal forest (Fig. 1). At each of the study sites, plant communities to be sampled were selected on the basis that they fell into one of the following 7 general categories: black spruce forest, white spruce and/or balsam fir (mixed wood) forest, jack pine forest, aspen forest, rock field (fellfield) tundra, tussock muskeg tundra, and low meadow tundra.

In each instance, the basis for selection of a stand for sampling was initially visual, employing aerial photographs (coverage available from the Canadian National Air Photo Library) and then inspection on the ground. This initial visual selection had as its basis the criterion that stands appear homogenous over at least a large enough area to enclose a transect. In all but a few instances, the stands were a great deal larger than this; in most areas, one or more of these communities occupied a relatively large proportion of the total landscape. In the case of the forest communities, the trees and saplings were sampled by the point quarter method (Cottam and Curtis 1956) and for a stand to be included in the analysis the data obtained had to establish clearly that the indicated dominant species (black spruce, white spruce and/or balsam fir, etc., see above) possessed an important value (Curtis 1959) greater than that of all other tree species in the sample combined. Tundra sampling sites were selected by the same visual means. Topographic position was the main criterion for selection in the case of the tundra communities: rock fields occupy hill summit areas, tussock muskeg occupies intermediate slopes and has a layer of peat and plant detritus overlying the upper horizon of inorganic soil material, and the low meadows are lowlands usually inundated at least in spring and early summer by an inch or two of water. Frequency tabulations (Greig-Smith 1964) of the forest understory communities and the tundra communities were obtained using quadrats 1 sq. m. in shape and size, arranged equidistant (usually 30 paces apart) along a compass line. Details of the sampling method and more complete descriptions of the communities of the northern forest and tundra are given in a previous paper (Larsen 1965).

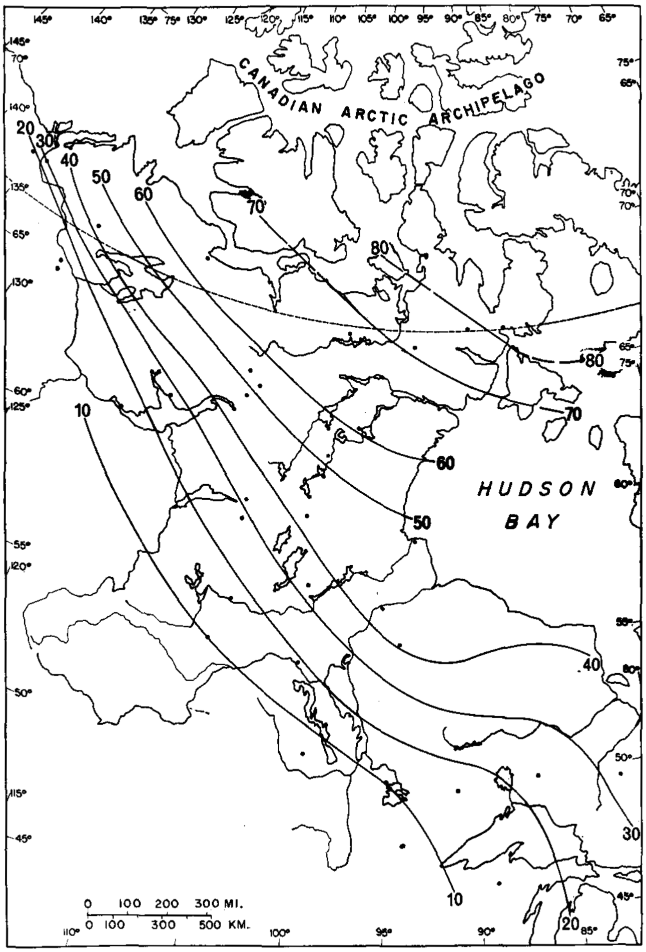

FIG. 2. Air mass frequency: Arctic (see Bryson 1966).

During each summer of field work, as many study sites were visited as could be arranged. The earlier years of the study were spent largely in the forested areas, the later years in the tundra and forest-tundra ecotone. At each study site, transects were run through stands of as many of the communities indicated above as were available. Replication was achieved by running transects through as many different stands of each of the communities as were available or as time allowed.

The data collected afford an opportunity to study variations in frequency of each species in each community over the geographical range of the survey and to correlate these frequency data with environmental parameters. The number of different study areas (Fig. 1) in which the various communities were sampled (as far as this paper is concerned) is as follows: black spruce 25, white spruce 12, jack pine 12, aspen 10, rock field 14, tussock muskeg 9, low meadow 7.

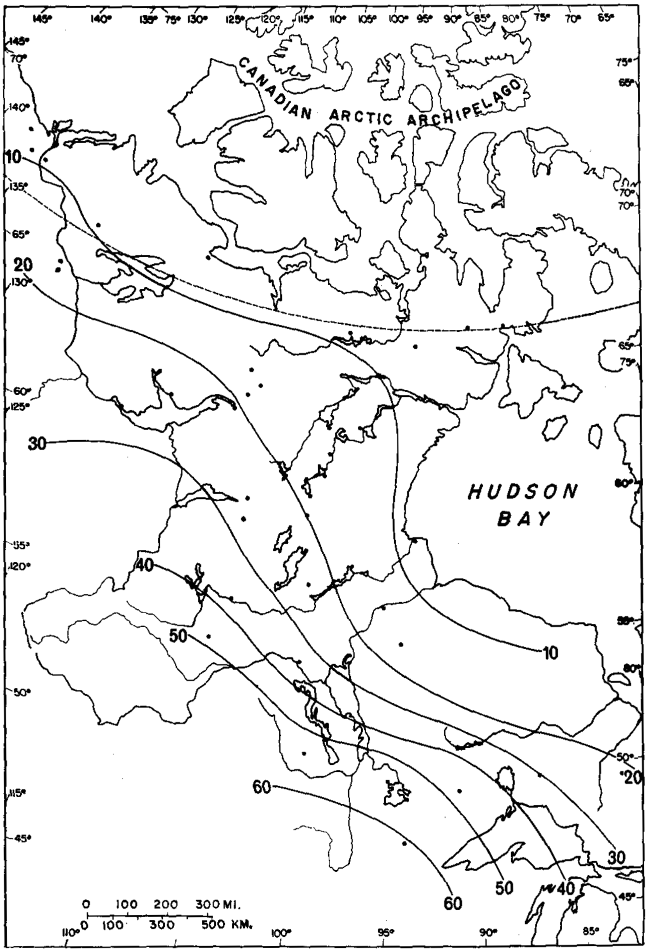

FIG. 3. Air mass frequency: Pacific (See Bryson 1966).

ANALYSIS

For the principal component analysis, a matrix was constructed using the data from each community separately (7 matrices in all). Species were arrayed on one axis, study areas on the other. Values in the matrix represented the average frequency value in the designated community of each species occurring at more than one study area and with a value of 15 or more in at least one of them. Number of species in each analysis was as follows: black spruce 104, white spruce 109, aspen 64, jack pine 67, rock field 62, tussock muskeg 72, low meadow 55.

With this matrix it becomes possible to employ principal component analysis to extract from the data those species which behave similarly in respect to average frequency values from one study area to another. Additionally, since frequency of air mass types at each study area is available (Bryson 1966), frequencies of occurrence for the plant species can be correlated with air mass frequencies. In the initial analysis, frequencies of the 4 air mass types employed (arctic air, Pacific air, Alaska-Yukon air, and southern air (see Figs. 2 to 5), were included

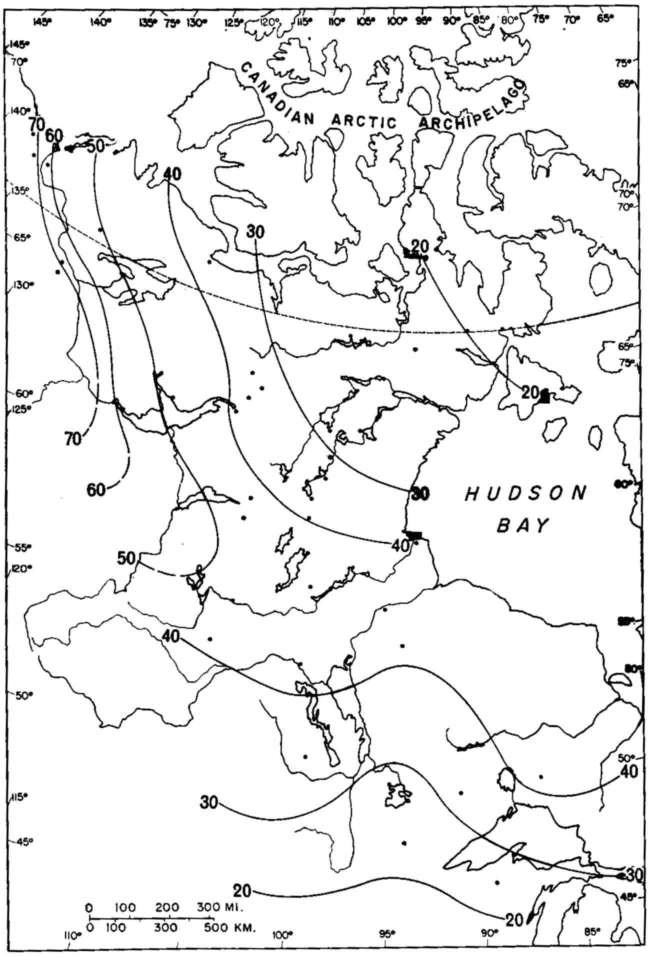

FIG. 4. Air mass frequency: Alaska-Yukon (see Bryson 1966).

in the matrix of vegetational values and accorded the same weight as the plant species frequencies. The computer printout thus provided correlation coefficients for individual species — air mass relationships as well as groupings of both species and air masses in the components. Principal component analysis was conducted on the 7 data matrices. Rather pronounced relationships were revealed between air mass frequencies and the frequencies of a number of species occurring in the communities.

RESULTS

Loadings of species and air mass frequency types ranged in value from −.20 to +.23. Values greater than ±.10 were considered of sufficient magnitude to warrant inclusion in initial tabulations; further selection was then made on the basis that the species to be included in the tabulation (Tables 1 and 2) should have a correlation of ±.50 or more with an air mass type.

TABLE 1. Species of greatest importance in the various communities.

	Correlations Arctic	Pacific	Alaska	Southern	Loading	% VE
BLACK SPRUCE COMMUNITY						
Species with high +r with arctic air masses						
Empetrum nigrum	.69	-.55	-.03	-.46	.16	.49
Rubus chamaemorus	.73	-.59	.00	-.51	.14	.37
Vaccinium uliginosum	.56	-.55	.17	-.42	.16	.47
Vaccinium vitis-idaea	.65	-.65	.29	-.74	.17	.51
Species with high +r with Alaska air masses						
Andromeda polifolia	.06	-.31	.50	-.28	.11	.23
Picea mariana (seedlings)	.39	-.66	.59	-.55	.13	.30
Species with high +r with southern air masses						
Cornus stolonifera	-.26	.36	-.35	.53	-.10	.18
Galium triflorum	-.44	.54	-.40	.61	-.12	.29
Species with high +r with Pacific air masses						
Galium triflorum	-.44	.54	-.40	.61	-.12	.29
Rubus pubescens	-.50	.51	-.20	.41	-.17	.52
WHITE SPRUCE COMMUNITY						
Species with high +r correlations with Pacific air masses						
Aster ciliolatus	-.51	.65	-.24	.42	.10	.30
Cornus canadensis	-.38	.48	-.22	.26	.10	.30
Cornus stolonifera	-.52	.62	-.23	.54	.11	.32
Corylus cornuta	-.51	.64	-.25	.46	.10	.32
Equisetum arvense	-.37	.55	-.32	.38	.10	.31
Fragaria virginiana	-.54	.66	-.19	.36	.10	.28
Galium boreale	-.55	.65	-.18	.36	.10	.28
Lathyrus ochroleucus	-.66	.85	-.27	.27	.11	.34
Maianthemum canadense	-.54	.66	-.34	.84	.14	.56
Mertensia paniculata	-.57	.69	-.26	.57	.12	.43
Petasites palmatus	-.67	.88	-.30	.25	.12	.39
Rubus idaeus	-.47	.64	-.27	.37	.10	.26
Species with high +r with southern air masses						
Aralia nudicaulis	-.36	-.26	-.20	.78	.17	.38
Galium triflorum	-.30	.35	-.25	.85	.11	.37
Maianthemum canadense	-.54	.66	-.34	.84	.14	.56
Rubus pubescens	-.10	.12	-.26	.67	.10	.27
Species with high +r with arctic air masses						
Betula glandulosa	.67	-.49	-.19	-.34	-.11	.37
Empetrum nigrum	.76	-.62	-.08	-.42	-.14	.59
Ledum decumbens	.56	-.45	-.07	.28	-.12	.42
Ledum groenlandicum	.51	-.58	.30	-.44	-.16	.69
Salix glauca	.63	-.61	.15	-.38	-.15	.56
Vaccinium uliginosum	.65	-.57	.00	-.34	-.15	.60
Vaccinium vitis-idaea	.65	-.65	.13	-.62	-.13	.49
Species with high +r with Alaska air masses						
Arctous alpina	.25	-.55	.67	-.33	-.15	.69
Carex scirpoidea	.12	-.44	.72	-.19	-.13	.51
Carex vaginata	.26	-.49	.53	-.27	-.15	.63
Dryas integrifolia	.34	-.53	.50	-.29	-.15	.61
Equisetum scirpoides	.03	-.45	.78	-.38	-.12	.44
Eriophorum spissum	.06	-.40	.74	-.17	-.12	.43
Larix laricina (seedlings)	.01	-.42	.77	-.37	-.10	.31
Saussurea angustifolia	.11	-.43	.71	-.19	-.13	.45
JACK PINE COMMUNITY						
Species with high +r with Alaska and arctic air masses						
Vaccinium vitis-idaea	.51	-.61	.68	-.84	.20	.58
Species with high +r with Pacific air masses						
Maianthemum canadense	-.72	.84	-.73	.65	-.19	.55
Species with high +r with southern air masses						
Alnus rugosa	-.37	.48	-.58	.63	-.13	.25
Aster ciliolatus	-.26	.38	-.54	.63	-.17	.43
Cornus canadensis	-.47	.48	-.43	.62	-.18	.48
Diervilla lonicera	-.35	.56	-.81	.79	-.17	.43
Gaultheria procumbens	-.25	.43	-.65	.66	-.11	.17
Lycopodium obscurum	-.38	.60	-.84	.81	-.19	.55
Maianthemum canadense	-.72	.84	-.73	.65	-.19	.55
Oryzopsis asperifolia	-.31	.50	-.75	.74	-.14	.29
Trientalis borealis	-.37	.56	-.77	.77	-.15	.35

	Correlations				Loading	% VE
	Arctic	*Pacific*	*Alaska*	*Southern*		
ASPEN COMMUNITY						
Species with high +r with Alaska air masses						
Epilobium angustifolium	.09	−.29	.69	−.86	.11	.19
Linnaea borealis	.19	−.40	.75	−.86	.11	.19
Species with high +r with southern air masses						
Petasites palmatus	−.16	−.03	.43	−.51	.17	.48
Pyrola asarifolia	−.28	.04	.51	−.68	.12	.25
Species with high +r with Pacific and southern air masses						
Oryzopsis asperifolia	−.44	.67	−.85	.71	−.10	.17
ROCK FIELD COMMUNITY						
Species with high +r values with arctic air masses						
Cassiope tetragona	.61	−.84	−.29		.22	.79
Dryas integrifolia	.67	−.58	−.46		.18	.53
Polygonum viviparum	.59	−.66	−.35		.17	.49
Salix arctica	.69	−.56	−.50		.21	.69
Species with high +r values with Pacific air masses						
Arctous alpina	−.68	.56	.49		−.19	.57
Betula glandulosa	−.82	.45	.68		−.18	.53
Carex glacialis	−.34	.64	.09		−.16	.43
Empetrum nigrum	−.49	.83	.17		−.21	.70
Ledum decumbens	−.47	.68	.21		−.18	.54
Loiseleuria procumbens	−.46	.60	.24		−.15	.36
Rhododendron lapponicum	−.20	.55	−.01		−.13	.27
Vaccinium uliginosum	−.48	.58	.27		−.18	.50
Vaccinium vitis-idaea	−.50	.86	.16		−.20	.67
TUSSOCK MUSKEG COMMUNITY						
Species with high +r with arctic air masses						
Arctagrostis latifolia	.58	−.14	−.41		.17	.74
Carex aquatilis (stans)	.56	−.09	−.41		.16	.66
Carex atrofusca	.60	−.31	−.36		.19	.95
Carex scirpoidea	.55	−.40	−.30		.18	.81
Eriophorum anqustifolium	.60	−.26	.37		.17	.77
Luzula confusa	.54	−.12	−.38		.12	.37
Poa arctica	.53	−.43	−.27		.19	.89
Polygonum viviparum	.53	.06	−.43		.13	.41
Pyrola secunda	.58	−.06	−.44		.13	.43
Salix arctica	.59	−.34	−.35		.19	.97
Salix glauca	.51	−.42	−.26		.18	.85
Salix reticulata	.59	−.35	−.35		.19	.96
Saussurea angustifolia	.55	−.43	−.28		.19	.93
Stellaria longipes	.59	−.31	−.36		.19	.95
Species with high +r with Pacific air masses						
Cassiope tetragona	.27	−.64	.00		.18	.80
Dryas integrifolia	.00	−.58	.19		.14	.50
Hierochloe alpina	.23	−.56	.00		.17	.77
Lupinus arcticus	.28	−.66	−.32		.18	.82
Species with high +r with Pacific air masses						
Ledum decumbens	.17	.68	−.32		−.13	.42
Rubus chamaemorus	.25	.82	−.47		−.12	.39
Vaccinium vitis-idaea	−.38	.45	.14		−.17	.76
LOW MEADOW COMMUNITIES						
Species with high +r values with arctic air masses						
Arctous alpina	.65	−.93	.13		−.19	.97
Calamagrostis canadensis	.65	−.91	.09		−.19	.93
Carex aquatilis (stans)	.49	−.88	.35		−.19	.92
Carex atrofusca	.51	−.56	−.14		−.13	.46
Carex vaginata	.56	−.62	−.13		−.15	.55
Dryas integrifolia	.67	−.95	.13		−.20	.99
Eriophorum angustifolium	.61	−.90	.16		−.17	.76
Pedicularis sudetica	.76	−.99	.03		−.20	.95
Polygonum viviparum	.71	−.87	−.05		−.19	.89

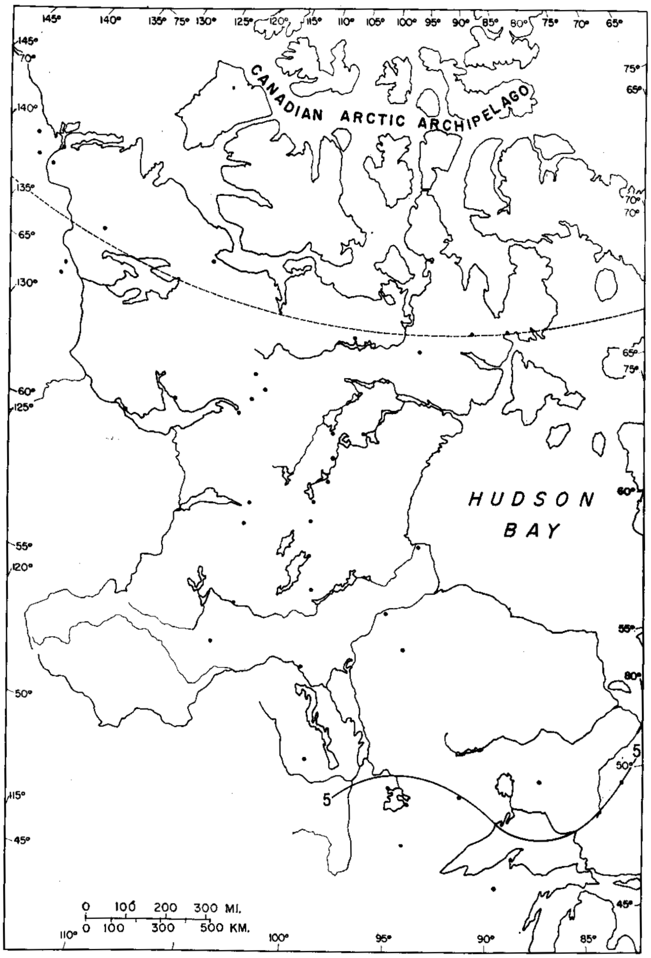

FIG. 5 Air mass frequency: Southern (see Bryson 1966).

TABLE 2. Species in low meadow communities of greatest importance in the second eigenvector. Designations identical to presentation in Table 1.

	Correlations				Loading	% VE
	Arctic	*Pacific*	*Alaska*	*Southern*		
LOW MEADOW COMMUNITY						
Species with high +r values with arctic air masses						
Betula glandulosa	.55	−.13	−.80		.12	.15
Species with high +r values with Alaska air masses						
Andromeda polifolia	−.74	.55	.55		−.21	.43
Carex physocarpa	−.55	.18	.74		−.13	.16
Scirpus caespitosus	−.71	.42	.68		−.21	.42
Vaccinium uliginosum	.00	−.44	.59		−.44	.19
Species with high +r values with Alaska air masses						
Betula glandulosa	.55	−.13	−.80		.12	.15
Carex chordorrhiza	.08	.38	−.67		.13	.15
Hierchloe alpina	.41	−.09	−.61		.30	.85
Luzula confusa	.41	−.09	−.61		.30	.85
Poa arctica	.44	−.11	−.63		.30	.85
Potentilla palustris	.37	.05	−.73		.29	.81
Salix planifolia	.45	−.12	−.64		.29	.81

(Loading of arctic air in eigenvector 2 is .19; of Alaska air is −.22).

The high degree of correlation between species and air mass types can be demonstrated initially by the loading values of the air mass types in the first component. In the analysis, these loadings reveal the degree to which the frequency values of the air mass types may be considered to correspond to the frequency values of the species grouped in the first component (see Table 3).

It is apparent that loadings of air mass types attain values nearly as high as the highest in the analysis. There is strong indication that species grouped into the first eigenvector demonstrably are responding to an environmental factor at least closely related to air mass frequencies.

TABLE 3. Loading values of air mass types.

Community	*Arctic*	*Pacific*	*Alas.-Yukon*	*Southern*
Black spruce	.17	−.16	.04	−.12
White spruce	−.11	.15	−.09	.11
Aspen	.01	−.06	.14	−.13
Jack pine	.18	−.21	.20	−.21
Rock field	.18	−.20	−.11	.00
Tussock muskeg	.10	−.09	−.05	.00
Low meadow	−.13	.19	−.02	.00

Another measure of the degree to which these species correlate with air mass frequencies is the eigenvector coefficient; this is a measure of the importance at each study site of the species with high loading values in the eigenvector. In other words, species in the first component of the black spruce community, for example, become of increasing importance in the community northward. Thus, the eigenvector coefficients for study sites northward will be numerically larger than those southward; they will correlate positively with arctic air mass frequency values which also increase northward (see Table 4).

TABLE 4. Correlations between the eigenvector coefficients (for the first eigenvector) and the air mass frequencies.

	Correlation Coefficient			
Community	*Arctic*	*Pacific*	*Alas.-Yukon*	*Southern*
Black spruce	.73	−.68	.15	−.53
White spruce	−.60	.79	−.50	.61
Aspen	.02	−.24	.58	−.53
Jack pine	.69	−.80	.76	−.79
Rock field	.80	−.81	−.44	.00
Tussock muskeg	.50	−.44	−.25	.00
Low meadow	−.68	.95	−.11	.00

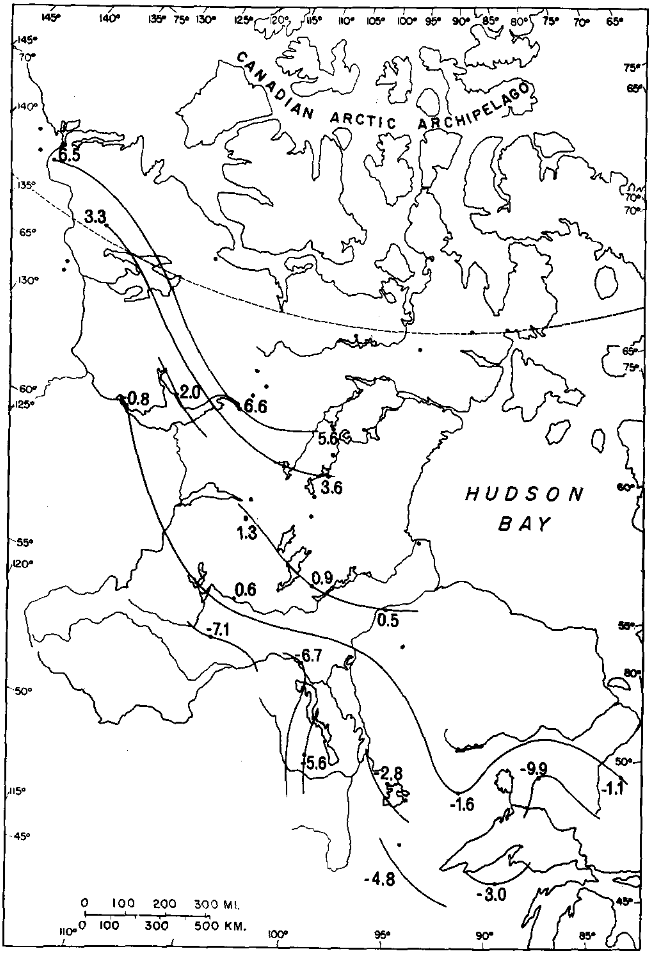

FIG. 6. Isopleths of eigenvector coefficients for the black spruce community. Eigenvector coefficients indicate the importance of the species group comprising the first factor (component) at each of the study sites. This group of species increases in importance northward and therefore possesses frequencies that are positively correlated with the frequency of arctic air masses.

It is thus apparent that species with high values in the first component are correlated, in the case of black spruce for example, to a high degree with arctic air (positively), Pacific air (negatively), and southern air (negatively), with a small positive correlation with air of Alaska-Yukon origin. The obverse is true in the case of white spruce. Species in the other communities also show high correlations (positive or negative) with two or more of the air mass types.

Species with loading values of at least ±.10, and with correlation coefficients with at least one air mass type of ±.50 are listed in Table I. The geographical relationships of eigenvector coefficients of the black spruce community are shown in Fig. 6; the species of significance in the first component are those attaining greatest importance in the black spruce stands of the northern forest border ecotone.

It should be indicated that inclusion of air mass data in the matrix containing largely species frequency data will have a certain influence upon the analytical result which would not be present were these data not included. Since the air mass data represent a very minor proportion of the total matrix, however, and since no additional weighting is given them in the computations, this effect is of minor consequence and for all practical purposes negligible. It is mentioned here only to indicate that the author is aware of the resulting slight bias.

SPECIES BEHAVIOUR

It is probably of some considerable significance that all species in the black spruce community possessing high positive correlations with arctic air also show similarly high correlations with this air mass type as part of the white spruce community, where again they possess the highest loadings of all the species. The loadings in the white spruce community, however, are negative and a larger group of species, these highly correlated with Pacific air, possess positive loadings (although individually they are of lesser value). These species are weakly correlated with Pacific air in the black spruce communities, but here in the white spruce communities they show a high average correlation with Pacific air. Another group shows a high correlation with air of southern origin.

Species in the aspen community show little correlation with either arctic or Pacific air, but a significant group is positively correlated with Alaska-Yukon air and negatively with southern air. There are few species in the jack pine community that are positively correlated with arctic or Alaska-Yukon air but a group of 9 species is correlated positively with southern and Pacific air.

The 3 tundra communities also possess species groups demonstrating high correlations with air mass types and in each community the largest group showing this characteristic is the one correlated with the frequency of arctic air masses. It is of interest that several of the species are found in more than 1 community type and that 2 are found in all 3. Only in the rock field community is there a complement of species correlated highly with other than arctic air; this group is correlated with Pacific air. These species obviously become more frequent in the rock field community as the forest border is approached.

In each instance where a number of species of a given community are shown to be correlated with an air mass type, it is apparent that they will also be correlated with one another in their frequency values. The average of inter-correlations among the species of the groups listed are as follows: black spruce community, average of inter-correlations among species highly correlated with arctic air is .61; black spruce, Alaska-Yukon air, .76; white spruce, arctic, .75; white spruce, Pacific, .80; white spruce, Alaska-Yukon, .74; jack pine, southern, .57; rock field, arctic air, .41; rock field, Pacific air, .38; tussock muskeg, arctic air, .76; low meadow, arctic air, .85. It is evident that the rock field community is the most variable in respect to inter-species correlations.

Since the frequencies of the air mass types are inversely correlated with one another, it is to be expected that species which are positively correlated with one air mass type will be negatively correlated with another — or with other — type(s). It can also be noted that, for example, species correlated positively with arctic air are also correlated positively with Alaska-Yukon air and that species correlated with Pacific air are often also correlated with southern air. Thus one

TABLE 5. Correlation between eigenvector coefficients and distance from the forest border.

	Eigenvector			Confidence	
	1	*2*	*3*	*% Level*	*No. Obs.*
Black spruce	-.81	-.24	-.18	99	25
White spruce	.85	-.15	-.30	99	12
Jack pine	-.73	-.01	.13	99	12
Aspen	-.51	-.53	-.30	n.s.*	10
Rock field	-.89	.16	.04	99	14
Low meadow	.11	-.72	-.44	95	7
Tussock muskeg	-.53	.45	.28	n.s.*	9

*±.53 with 12 observations would be significant at the 95% level.

is led to the conclusion that the plant species are not responding directly to these specific air mass types but rather to a northern and southern climatic component, or in other words their geographical orientation in respect to air mass source regions. It must be indicated that the climatology of the region is not to be described as simply a combination of the air mass frequencies as presented here since there are other factors to be considered, among them such influences as the direction of resultant winds (Bryson 1966), wave structure of frontal zones, gradual air mass modification during movement from region to region, and so on; air mass frequency is but one of the measurable parameters indicative of the prevailing climatic regime in a given area.

Another parameter of some interest is the correlation between eigenvector coefficients and distance from the forest border. Since the forest border coincides with a climatic frontal zone (Bryson 1966), this relationship demonstrates the increasing or decreasing importance of species in the eigenvector as this frontal zone is approached from central portions of the air mass regions (see Table 5).

Since second eigenvector species in low meadow communities are the most significant in terms of these air mass relationships, the species are listed additionally in Table 2.

The dominance relationships of the species highly correlated in frequencies with the frequencies of the air mass types are of particular interest. In the black spruce and white spruce communities and in the rock field community especially, the species with highest correlations with air mass frequencies are consistently among the dominant species in the sampled stands. To illustrate this, the average frequency values in black spruce community stands of species highly correlated with arctic air are given in Table 6 and the dominance relationships of these species in the individual stands sampled are shown in Table 7. Similarly the dominance relationships of species in the rock field community are given in Table 8. In Tables 7 and 8 the species listed are those that appear as one of the 4 leading dominants (possessing highest frequency values) in at least one stand of the number of study areas indicated in column 1.

It is apparent that in the black spruce community the species showing highest relationships to arctic air mass frequencies are those that attain dominance in

TABLE 6. Average frequencies (for method of calculation see text) in stands of each study area of species of importance in the first component and highly correlated positively* with arctic air mass frequencies. Black spruce understory communities.

	Betula glandulosa	*Empetrum nigrum*	*Ledum decumbens*	*Ledum groenlandicum*	*Salix glauca*	*Vacinnium uliginosum*	*Vaccinium vitis idaea*	Average	Number samples (stands)
Clinton-Colden	90	100	100	60	30	90	100	81	1
Kazan River	85	65	65	95		65	95	67	1
Artillery Lake	53	71	39	73	8	73	98	59	8
Colville Lake	47	32	40	67	18	68	93	52	3
Ennadai Lake	50	49	24	60	5	75	85	50	18
Inuvik	53	35	15	73	3	90	76	49	2
Ft. Reliance	7	41	8	71	19	60	77	41	7
Dubawnt Lake	65	43	25	40	10	40	43	39	2
Florence-Carcajou	40	28	17	32	3	66	37	33	5
Churchill		50		40		40	100	33	1
Yellowknife	2	8	11	83	8	7	96	31	5
Wapata Lake		2		86			96	26	16
Otter Lake	10			81			88	26	5
Black Lake		8		90			71	24	5
Ilford	3	9		80			75	24	9
Lynn Lake	1	1	2	74		1	79	22	16
Ft. Providence	1	25	17	77	3	25		21	5
God's Lake				75			40	16	1
West Hawk Lake				88			45	16	2
Rocky Lake	12			41			33	12	9
Waskesiu Lake				47			37	12	3
Remi Lake				85				12	1
Trout Lake				80				11	3
Raven Lake				62			2	9	5
Klotz Lake				40			3	6	4
Clear Lake				37			7	6	3
Bagley-Pike Bay				43				6	2

*The exception is *Ledum groenlandicum* included here to illustrate its significance as a widespread and generally abundant species.

the community at least in the more northern areas. Dominant species in the rock field community are those with a high degree of correlation with Pacific air; these are species which attain dominance in the more southern tundra areas. In the tussock muskeg community the relationship becomes less apparent; none of the species showing high correlation with an air mass type are among the first ten

TABLE 7. Dominance relationships of species in black spruce communities.

	Number of Areas in Which Species Occurs As a Dominant	Number of Individual Stands according to Rank of Species			
		1st	*2nd*	*3rd*	*4th*
Ledum groenlandicum	25	44	35	18	8
Vaccinium vitis idaea	19	63	22	10	
Picea mariana (seedlings*)	13	2	4	13	20
Rubus chamaemorus	12	7	8	8	9
Vaccinium oxycoccos	10	4	4	5	2
Betula glandulosa	11	3	3	6	9
Empetrum nigrum	10	2	8	4	8
Cornus canadensis	9	7	2	5	3
Linnaea borealis	8	2	3	3	6
Vaccinium uliginosum	8	9	8	10	7
Vaccinium myrtilloides	7	1	2	10	3
Geocaulon lividum	7		3	4	6
Chamaedaphne calyculata	7	3	2	3	2
Equisetum sylvaticum	6	4	1	6	5
Equisetum scirpoides	6	2	2	5	1
Equisetum arvense	6	1	1	2	5
Kalmia polifolia	6	1	2	1	3
Maianthemum canadense	5	2	1	2	

(39 additional species unlisted are each one of first four dominants in at least one stand).

TABLE 8. Dominance relationships of species in rock field communities. Those marked with asterisk are highly correlated with Pacific air masses.

	Number of Areas in Which Species Occurs As a Dominant	Number of Individual Stands			
		1st	*2nd*	*3rd*	*4th*
**Vaccinium vitis-idaea*	9	32	13	6	2
**Ledum decumbens*	7	12	8	9	9
**Vaccinium uliginosum*	7	9	4	9	7
**Arctous alpina*	7	6	7	8	2
**Empetrum nigrum*	5	4	7	7	10
Betula glandulosa	5	3	5	10	2
**Loiseleuria procumbens*	4		1	6	3
Hierochloe alpina	4	4			2
Cassiope tetragona	3	10	1	4	2
Dryas integrifolia	3	3	1		4
Saxifraga tricuspidata	3			3	
Salix herbaceae	2	3			2
Salix arctica	2	3	6	2	
Lupinus arctica	2	1			
Polygonum viviparum	2				3
Salix glauca	2			1	1
Rhododendron lapponicum	2			1	1
Luzula confusa	1	1	2	5	3

(12 additional species unlisted are each one of first four dominants in at least one stand).

dominants in the community. Dominance and air mass relationships in the low meadow community are even less discernible.

Some additional air mass relationships of some significance can be seen in the rock field community. In the data of Table 5, species are listed according to relationships to Pacific air masses and dominance in the community. It is of interest that the species in the rock field community highly correlated with arctic air do not attain dominance. These species, which include *Salix glauca, S. reticulata, S. arctica, Luzula confusa, Arctous alpina, Cassiope tetragona, Dryas integrifolia, Polygonum viviparum, Carex atrofusca, Arctagrostis latifolia,* and *Eriophorum angustifolium* are species with strong arctic affinities and obviously do not attain dominance in the rock field community near the forest border but only much farther to the north. This absence of arctic species in the tundra of low (latitude) arctic regions has been noted previously by the author (Larsen 1967, 1971). In place of these species are those wide-ranging species attaining dominance at the northern edge of the forest and the southern edge of the tundra (see black spruce and rock field dominants mentioned above).

In the remaining forest communities, the species attaining dominance are as follows (those marked with asterisk are also those possessing a high correlation with an air mass type):

White spruce — **Vaccinium vitis idaea, *Empetrum nigrum, *Cornus canadensis, Linnaea borealis, *Rubus pubescens, *Betula glandulosa, Mitella nuda, *Ledum groenlandicum;*

Jack pine — *Vaccinium myrtilloides, *V. vitis idaea, Ledum groenlandicum, Linnaea borealis, Arctostaphylos uva-ursi, *Maianthemum canadense, Picea mariana* (seedlings);

Aspen — *Maianthemum canadense, Cornus canadensis, Aralia nudicaulis, Linnaea borealis.*

DISCUSSION AND SUMMARY

It is apparent that the frequencies of certain species found in each of the 7 communities possess striking correlative relationships to the frequencies of air mass types. There are 63 species that possess the requirements of both relatively high loading values and high correlations of frequency values with the frequency of an air mass type. Some of these 63 species are of importance in only one community, others are present in two or more communities, or as many as five in the case of *Vaccinium vitis-idaea.* These latter species are found in both forest and tundra over a wide geographical area.

It is of some interest, additionally, that only in the black spruce and white spruce forest communities and the rock field tundra community do those species with high air mass correlations attain a consistently dominant position in the sampled stands of these communities. It appears that, for indicator purposes, these communities then become of the greatest significance in attempting correlations between vegetation and climate in these regions. As field ecologists well know, variability in vegetation is often so great as to virtually preclude high correlations between vegetational composition and environmental parameters. It is perhaps of some ecological significance that northward there are communities in which at least some species may be found to be correlated with macro-climatic parameters. From the evidence available here, it would appear that the greatest difficulty in correlating environmental factors with vegetational structure would be encountered in the communities of the lower slopes and meadows and, by inference, the shorelines and marshes. Perhaps one could have foretold that this would be the case since the physical characteristics of abundant water might itself tend to override other environmental influences. The significance for paleo-climatological work is also apparent.

Perhaps most interesting are those 7 species which correlate with opposing air mass types in different communities. Each is correlated with arctic air when it occurs in either the black or white spruce community and with Pacific air (with one exception) when it is a component of the rock field or tussock muskeg community. Because of this regularity in pattern, the explanation is readily apparent. These species are the ubiquitous species which range widely through forest and tundra. They increase in frequency northward through the forest and then decrease northward beyond the forest border in the tundra communities. In the former case they correlate positively with arctic air, in the latter positively with Pacific air. The species of this group, including *Empetrum nigrum, Ledum decumbens, Rubus chamaemorus, Vaccinium uliginosum,* for example, attain highest frequencies in the communities of the forest-tundra ecotone where they are dominants in a floristically depauperate vegetation (Larsen 1967, 1971). Whether uniquely adapted or simply widely tolerant of harsh and variable conditions, they provide an interesting group for further study.

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REFERENCES

BRYSON, R. A. 1966. Air masses, streamlines, and the boreal forest. *Geographical Bulletin,* 8 (3): 228-69.

COTTAM, G., and J. T. CURTIS. 1956. The Use of Distance Measures in Phytosociological Sampling. *Ecology,* 37: 451-60.

CURTIS, J. T. 1959. *The vegetation of Wisconsin.* Madison: The University of Wisconsin Press. 657 pp.

GREIG-SMITH, P. 1964. *Quantitative Plant Ecology,* (Second Edition). Washington: Butterworths Inc. 256 pp.

HUMBOLDT, A. VON. 1807. *Ideen zu einer Geographie der Pflanzen nebst einem, Naturgemalde der Tropenlander.* Tubingen.

LARSEN, J. A. 1965. The vegetation of the Ennadai Lake area, N.W.T.: Studies in Arctic and Subarctic Bioclimatology. *Ecological Monographs* 35 (1): 37-59.

——— 1967. Ecotonal plant communities of the forest border, Keewatin, N.W.T., Central Canada. *University of Wisconsin, Department of Meteorology, Technical Report No 32.*

——— 1971. Vegetation of the Fort Reliance-Artillery Lake area, N.W.T.: Studies in Arctic and Subarctic Bioclimatology. *The Canadian Field Naturalist.* In Press.

MCINTOSH, R. P. 1967. The continuum concept of vegetation. *The Botanical Review,* 33 (2): 130-87.

SCHIMPER, A. F. W. 1903. *Plant geography upon a physiological basis.* Oxford: Clarendon Press, 830 pp.

WARMING, E. 1909. *Oecology of plants.* England: Oxford Press. Translated from Groom and Balfour from Plantesamfund, Danish edition, 1895. German editions, 1896, 1902. 422 pp.