

SPECIES VERSATILITY IN SHORE HABITATS

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MATERIALS FOR THE present paper are derived from notes and plant collections made during seven field seasons in the years 1926–30, 1932, and 1935, in the Athabaska-Great Slave Lake region of northwestern Canada. In the course of this work shoreline vegetation was described at approximately 130 places. Seventy-nine of these were on the shores of sloughs, ponds, and small lakes, while the remaining 51 were on the shores of the larger lakes (Athabaska and Great Slave) or on river banks and deltas. The following discussion deals primarily with the vascular flora, though reference is made on occasion to lichens and mosses.

A part of the material was published in the author's "Botanical investigations in Wood Buffalo Park" (1935). Itineraries of the seven expeditions will be found in this paper and in others dealing with the vascular flora and its distribution (Raup, 1930b, 1936, 1941). A brief account of the vegetation of Shelter Point, Lake Athabaska, was published in 1928, and a paper on the shore vegetation at Fort Reliance, Great Slave Lake, in 1930(a). The most complete sets of supporting plant collections are at the National Herbarium of Canada in Ottawa, and at the Harvard University Herbaria in Cambridge, Massachusetts.

Most of the vegetational data for the present study were gathered along transects selected because they showed differences or similarities when compared in the field with other transects. The differences were recorded first in terms of species' *presence* or *absence*, and second in terms of *primary* and *secondary* species. In common ecological parlance the primary species in an assemblage would be termed "dominants." They are the ones that give a specific form, color, or other characteristic to an assemblage of plants by which the latter is readily distinguished visually from those adjoining it. All other species in the assemblage are regarded as secondary. Usually the primary species are those that predominate in numbers of individuals, but in sparse vegetative cover or in tree or shrub vegetations the populations of primary species may be smaller than those of secondary species. The selection of primary species was done by eye.

A general view of the shore floras of the region shows them occupying an extraordinary number of lakes, ponds, and sloughs that dot the landscapes. They are numerous in the great deltas and flood plains of the lower Athabaska, Peace, and Slave rivers, but are especially abundant on the crystalline and metamorphic rocks of the Canadian Shield. Travelers for many years have noted the large numbers of small bodies of water along their routes, but full realization of their extent awaited the advent of aerial photographic mapping. An area of 16 square miles (4 miles square) selected at random in the country north of Lake Athabaska con-

tains over 100 ponds and lakes large enough to appear on a map scaled at 4 miles to one inch. The number of smaller water bodies can only be conjectured, but a conservative estimate would be another 100. The ponds and small lakes throughout this region are infinitely variable in shape, size, and depth. The large lakes also present a wide variety of shorelines, from almost vertical rock cliffs to wide shelving beaches of sand, mud, or shingle. Further variation is found in the morainic and karst topography west of the Slave River, in flood-plain sloughs and deltas, and in the saline flats that border the Salt and Little Buffalo rivers. However these bodies of water were formed and whatever their subsequent history, their abundance and the large proportion of the total flora they harbor force us to consider their marginal plant life as one of the most important elements in the vegetation of the region.

When this study was begun in 1926, major emphasis was placed on the "development of the vegetation." The units of study were to be "communities" or "associations" of plants described in terms of form and floristic content. The "development" was largely confined to the theory of succession among communities, leading to more or less stable climax or climaxes. Time scales for the processes were not clearly defined, but it was assumed that the present state of the vegetation could be rationalized by projection of these processes backward to the disappearance of the last glacial ice.

The vascular flora of the region was not well enough known in 1926 to cover the needs of such a vegetational study. This applied not only to the less common species but also to many abundant ones which, as "dominant" species, gave form and character to "communities." Consequently the collection and identification of the species was the first necessity. Between 1926 and 1935 the known vascular flora of the region was thus increased by about 30%. Most of the new records were range extensions, for the region has very little endemism.

The writer's earliest papers on the region reflect the above frame of reference (1928, 1930a & b, 1935). After the field season of 1935 this frame became almost wholly inadequate.

A determined effort was made to use "communities" or plant "associations" as the basic units of study. This could be effective only if the assemblages of species, or at least of the so-called "dominant" species, were largely repetitive within such habitat complexes as could be defined with the knowledge and facilities at hand. Because the identity of the "communities" rested upon floristic composition, it was thought that they probably had some form of internal organization among mutually compatible species which added validity to their use as study units.

Wide variation in species composition of the shore assemblages began to appear in the early work on Great Slave Lake (1927). Seventeen small bodies of water were studied on Fairchild Point, a peninsula about 10 miles long in this lake. Each of these ponds was unique, either in the arrangement of its vegetation zones or in the "dominant" species composition of the zones. The field seasons in the Wood Buffalo Park (1928-

30) brought out even greater variability, not only among the many ponds and small lakes that were studied, but also within habitats on the shores of individual bodies of water. A lake about 10 miles long on the upland west of the Slave River required eight transects for a fair sampling of its shore vegetation. Twenty-eight different "communities" of vascular plants were described in these transects, involving 20 "dominant" species. Field experience strongly suggested that in the region as a whole the study of more pond and lake shores would yield more different "communities," more zonal variations in the vegetation, and additional "dominant" species.

The use of the "community" or "association" as the basic unit for the study of the shore vegetation became extremely doubtful. Nonetheless, these terms continued to be used (Raup, 1934, 1935), and the complexity was in part avoided by annotated descriptions of assemblages believed to be "typical" of the various habitats. Maximum confusion was reached in the 1935 season when many shores around the whole of Lake Athabaska were examined, particularly those of the intricate lagoon systems on the south shore. Here no two of the hundreds available for study seemed to have the same "community" structures and contents.

The idea of orderly successional development among "communities" had to be greatly restricted in space and time. The last cover of glacial ice did not retreat steadily, but in stages so that land surfaces available for colonization by plants were of varying ages. Owing to the general topography of the region and the geography of its drainage systems, there had been large variations in the levels of its major lakes and in the development of its flood-plain and delta systems (see below; also Raup, 1930b, 1931, 1946, and Cameron, 1922). Lengths of time during which physical habitats could remain relatively stable, and in which long-term biological successions could have occurred began to be notably shortened. A high water level seen at Lake Athabaska in 1935 was maintained throughout the growing season, and effectively drowned all the shore "successions" that were described in prior years. The frequency of such floods has been estimated recently by Stockton and Fritts (1973; see below), and it is not unlikely that time periods during which the shores of this lake can remain physically stable are shorter than the life spans of most of the perennial plants that make up the shore vegetation. If this is the case, successions in this vegetation are reduced to fragments which, if they exist at all, have indeterminate beginnings and ends.

The extent to which analogues of these findings can be seen in the shores of smaller upland lakes and ponds is unknown. Many of these smaller water bodies are held up by morainic dams, are deposited at different times, have varying materials, and erode at different rates. Extreme cases occur in the karst topography west of the Slave River, where fluctuations in pond levels of 10 to 30 feet are not uncommon, giving rise to curious "duplications" of shore zonations at different levels in the same sink hole. Here the fluctuations are due to unpredictable changes in the movement of ground water through the underlying cavernous gypsum.

With the failure of the "community" as a viable, repetitive unit for

study and rationalization of the shore vegetation, and with the greatly restricted use of biological succession for interpreting the development of this vegetation, it became necessary to construct some other frame of reference. The present paper explores the use of the species as the basic study unit. There is abundant precedent for this in the literature of floristic plant geography (cf. Raup, 1942; Wulff, 1943; Cain, 1944; Böcher, 1954). But there is less precedent in ecological plant geography, which has been concerned primarily, during the present century, with the structure, physiology, and "dynamics" of "communities" (cf. Gleason, 1926; Cain, 1947). The use of species as study units has been greatly stimulated since the 1920's by research on ecotypic variation within species and by the realization that taxonomically defined species contain biotypes and ecotypes that behave differently in their relations to environments (Tureson, 1922, 1925, 1927, 1929; Hultén, 1937a; Clausen, Keck, & Hiesey, 1940; Mayr, 1964). The implications of this research for the geography of plants were rather thoroughly reviewed by Cain in his "Foundations of plant geography" (1944).

In the present paper the term "community" is replaced by "assemblage," which carries fewer connotations of relationships among species that are unknown or nonexistent. The terms "primary" and "secondary," though not common in ecological literature, are not new in the sense in which they are used here. They were so used by Hultén in his "Flora of the Aleutian Islands" (1937b).

THE VASCULAR FLORA AND ITS SHORE HABITATS

The total known vascular flora of the Athabaska-Great Slave Lake region numbers approximately 750 species. The shore flora contains 424 of these, or about 57% of the total. Seven species are excluded from the following studies. Three appear to be endemic or so localized that their ranges and local behavior are not well known. The other four, though they have wide ranges southward in the continent, are apparently sporadic in the southern part of our region. Thus the number for the total shore flora in the following analyses will be 417.

Species units used here are those in the author's catalogue of the flora of the region (1936) except for a few additions and changes made by more recent students. Sixty-three families are represented in the shore flora, and 177 genera. Twelve of the families are represented by 10 or more species each and supply two thirds of the flora (262 spp., 63%). The same families supply a similar proportion of all the primary species (93 spp., 64%). The 12 families are as follows (numbers in parentheses indicate first the total number of species and second the number of primary species): Cyperaceae (59-23), Compositae (38-5), Gramineae (37-22), Salicaceae (23-14), Rosaceae (18-7), Ranunculaceae (16-1), Zosteraceae (15-7), Juncaceae (13-3), Ericaceae (12-10), Caryophyllaceae (11-0), Scrophulariaceae (10-0), Saxifragaceae (10-1). Half of these families

produce five or less of the primary species so that nearly half of all the primary species in the flora come from only six of the families. These families are among those that have been most poorly collected in boreal America, because their numerous species are not commonly recognized in the field and usually have been lumped together as "willows," "grasses," "sedges," "rushes," or the last three simply as "gramineous" plants. The genus *Carex* alone has 40 species in this flora, 14 of which were noted as primary in one or more assemblages. The Gramineae are represented by 10 genera and 37 species, among which 22 were primary. *Salix* has 21 species, of which 13 were primary. Of the 14 species of *Potamogeton*, six were found to be primary. The preceding four groups, which probably are the most frequently "generalized" by students of vegetation, contain more than one fourth of the shore flora of this region, and about 38% of all the primary species that give the shore scape its characteristic features.

A common arrangement of shore vegetation in the region has four major "form types." First there is a zone of aquatics, both submerged and emergent. Inshore from this is usually a zone of some kind of wet meadow made up principally of grasses, sedges, and rushes. The third landward zone is mainly of upright or decumbent shrubs. Finally there is a marginal zone of upright shrubs and trees which merges with the surrounding forest. For purposes of study and analysis this is an oversimplification. It gives no indication of the wide variation that occurs from one body of water to the next, or even on different shores of the same lake or pond. For purposes of analysis, therefore, 10 types are recognized, although it is probable that with further field work more would be found. Because the 10 types all occupy sites that differ in moisture regime, substrate or topographic position, they are considered as habitat-vegetation complexes, and the term "habitat" will be used for them in most cases. In the following list the numbers in parentheses are the approximate numbers of different assemblages seen in each type.

The term "muskeg" refers to vegetations that develop in undrained depressions with beds of hygrophytic mosses.

1. Aquatic habitats, with submerged and/or emergent plants (29).
2. Saline or brackish sloughs or wet meadows (15).
3. Muskeg grass-sedge meadows, with moss substrata (35).
4. Open (treeless) shrub muskegs (37).
5. Shrub-tree borders of muskegs (32).
6. Damp to wet sand and/or gravel on shores of rivers and ponds or on the lower beaches of large lakes (12).
7. Vegetation of upright shrubs and trees on upper beaches of large lakes (41).
8. Grass-sedge meadows on river flood plains or local river deposits, with silt or silt and thin moss substrata (49).
9. Shrub-tree borders of meadows on flood plains or local river deposits (25).
10. Vegetation of herbs and low or trailing shrubs on middle beaches of large lakes (22).

Data are not available from which to describe with any degree of precision the physical and nutritional properties of these habitats. The arrangement (from 1 to 10) of the preceding list approximates, from greatest to least, a scale of moisture availability. Factors of physical disturbance are obvious in such places as the lower and middle beaches of large lakes and in local river deposits. Currents and waves are active in summer, and at the spring break-up of ice there is much scouring of shores along the large rivers. Ice-push on the shores of the large lakes displaces large quantities of material. Further, the levels of the large lakes are known to change by several feet owing either to flooding from the main rivers or to gale winds. The middle beaches are commonly of sand, which is moved by dry westerly winds. Though frost heaving and thrusting no doubt occur in many of the soils, their distribution and the variations in their intensity are not known. Water supply to upland ponds and muskegs varies greatly with precipitation, and in dry summers fire is known to run through some muskegs and grass-sedge meadows. It may be that such sites, apparently rather stable, are more susceptible to disturbance than is yet known.

TOPOGRAPHY OF THE REGION

The topography, geological structure, soils, and general climatic features of the Athabaska-Great Slave Lake region were reviewed at some length in an earlier paper (Raup, 1946). This material will not be repeated except in a broad outline intended to clarify discussions of the geographic ranges of species.

The region is divided into two major subregions by a boundary running generally from S-SE to N-NW. Geologically this boundary is between Precambrian rocks to the east and Paleozoic or younger rocks to the west. The western area is underlaid by Silurian, Devonian, and Cretaceous sedimentary rocks, its surfaces mantled with wide expanses of morainic deposits, sand plains, ancient lake beds of clayey silt, and river alluvium. Outcrops of limestone, shale or gypsum are few. Topographically this area has representatives of two physiographic provinces. There are extensive alluvial lowlands in the broad valleys of the main rivers (the Peace, Athabaska, Slave, Buffalo, Little Buffalo, and Hay rivers) which make up the Mackenzie Lowland Province, with altitudes ranging from about 500 to about 700 feet above sea level in our area. This includes the wide deltas of these rivers at Athabaska and Great Slave lakes. Above it to the west of the Slave River, margined in places by well-defined limestone escarpments about 400 feet high, is a broad plain that gradually slopes upward to the southwest and is part of the Alberta Plateau Province. Much of this area is underlaid by gypsiferous rocks, on which an extensive karst topography is developed. At the west and southwest margins of our area are outliers of the Cretaceous portion of the Alberta Plateau, rising to altitudes of 2500 to 3000 feet above sea level.

The dividing boundary runs northward along the eastern margin of the

lower Athabaska River valley, crosses the western end of Lake Athabaska, and then follows the eastern margin of the Slave River lowland to Great Slave Lake. It appears again on the eastern shore of the north arm of this lake.

East of this boundary is the Laurentian Plateau Province, or "Canadian Shield." In our area its highest altitudes reach to about 1700 feet above the sea. It is characterized by abundant outcrops of Precambrian rocks, and by thin and scattered deposits mainly of morainic materials and beach or glacio-fluvial sands and gravels. South of Lake Athabaska, with occasional representatives on the north shore, is a large area of sandstones and quartzites, the weathering of which has produced the extensive beaches, dunes, and sand plains that border the lake on the south. Between the Athabaska and Great Slave lakes, and around the east arm and east shore of the north arm of the latter, are many areas of ancient Precambrian, highly metamorphosed sedimentary rocks. Finally there are the granitic and gneissic rocks that are so wide-spread in the Canadian Shield that the ancient metamorphic rocks appear as "islands" interspersed among them.

Drainage systems on both sides of the boundary are poorly developed, giving rise to a multitude of undrained or poorly drained depressions, which in this region contain shallow ponds and lakes and a great variety of sloughs, muskegs, and grass-sedge meadows. The muskegs are most extensive on the uplands, while sloughs and meadows are most abundant on the flood plains and deltas of the large rivers, where meandering streams have produced a plethora of abandoned channels containing lakes and ponds. Small bodies of water are most abundant on the Canadian Shield east of the boundary, where basins in the resistant rocks have for the most part remained intact since the glacial ice receded.

Major features of the region are the two large lakes, Athabaska and Great Slave. The first is approximately 190 miles long, about 35 miles wide, and as presently mapped lies almost entirely in the Precambrian area. Formerly it had a large western extension over Paleozoic rocks and a southward extension up the Athabaska River valley, but these have been largely filled by alluvial deposits from the Athabaska and Peace rivers, leaving some shallow bodies of water, the largest of which are now mapped as Lakes Mamawi and Claire. Great Slave Lake is about 350 miles long from southwest to northeast. Its basin crosses the major boundary noted above, with a broad western portion on Paleozoic rocks. In an earlier period the western part was wider and had a long extension up the present valley of the lower Slave River. This has been filled with alluvium carried also from the Peace and Athabaska. The great alluvial deposits of these rivers are well known for the immense amounts of driftwood they contain.

The present level of Lake Athabaska is about 690 feet above the sea, and Great Slave Lake is at about 495 feet. Earlier levels in post-glacial time have been placed at about 800, 1100, and 1600 feet above the sea (Cameron, 1922; see also Raup, 1946). The higher levels are believed to have been formed at stages in the retreat of the glacier during which the water from the Peace and Athabaska rivers was impounded by glacial ice

before the latter had released the normal flow through the upper Mackenzie River valley.

That major changes have occurred in the levels of the large lakes is evident in the abandoned gravel or sand beaches found high in the neighboring hills. These were measured to at least 240 feet above the current lake level on the north shore of Lake Athabaska, and they have been reported up to about 600 feet around the eastern arm of Great Slave Lake. They run in an apparently continuous series down to the present shores. It was assumed in our early studies of vegetation on the northwest shore of Lake Athabaska that the lowering of the lake was still going on, although very slowly and probably not rapidly enough to have much effect upon the development of shore vegetation. Evidence that the water level fluctuated to some extent was seen in September, 1932, when a southwest gale temporarily lowered it about four feet near the western end of the lake. Other evidence was in heavy driftwood found on broad sand beaches several feet above the existing lake level, but this was thought to be due to storm waves or ice-push. Raised barrier beaches, on the other hand, were believed to be the result of the long-term, though gradual, lowering of the general level of the lake.

Measurements that later pertained to lake levels were made in 1926 of the plant zonation on shore rocks at Lake Athabaska (L. C. Raup, 1930). Four well-defined zones were seen, the lowest of which is a dark-colored crust of *Verrucaria nigrescens* (vertical width ca. 9 inches). The second zone, also a dark crust, consists of the same *Verrucaria* plus *Dermatocarpon miniatum* (vertical width ca. 5 feet). The third is gray in color, the primary species being *Rhizocarpon geminatum*, *Physcia caesia*, and *Lecanora cinerea* (vertical width ca. 2 feet). The fourth and uppermost zone forms a transition to the neighboring upland. On rocky headlands the primary species here are *Parmelia saxatilis* and *Gyrophora Muhlenbergii*. Where there is much sand on the upper beaches *Stereocaulon tomentosum* appears. Measurements of these zones and their heights above the lake level were made at 14 stations along the shore at Shelter Point, ranging from vertical cliffs to gently sloping shores of boulders, gravel, or sand. Heights of the zones above the lake were essentially the same, suggesting that they were related to the general water level rather than to wave or ice action, which would vary with the exposure of the shore. But lichens grow very slowly, and it was impossible to say whether they marked a general, though gradual, fall in the level of the lake.

There were major floods in the Athabaska and Peace rivers during the Spring of 1935. In normal flow the Athabaska empties into the western part of Lake Athabaska and its water is carried through the western end to the Slave River. Most of the normal flow from the Peace River goes directly into the Slave, but there are reversible channels in its delta by which some flood water gets into Lake Athabaska and thence into the Slave. The floods in these main rivers in 1935 were so great that the level of Lake Athabaska was raised 6.5 feet above that seen by our field parties in 1926 and 1932. This took it above the two lowermost lichen zones and

about a foot into the third zone, as shown by examination of the stations measured in 1926. Similar lichen zones were seen on the shores of Great Slave Lake, but here they were much narrower, suggesting similar high water episodes that have a smaller magnitude.

A recent study of water levels in Lake Athabaska (Stockton & Fritts, 1973), based on analyses of the growth rings of trees, shows that relatively large fluctuations of level have occurred in the past. Some gauge measurements of flow in the Peace and Athabaska rivers for the years 1935 to 1967 were available, with a few from the lake itself, and from the data the authors estimated the levels of the lake for these years. A peak level of about 693.2 feet above sea level is their estimate for 1935. They then projected their analysis backward in time to 1810. Their estimate for 1926, the year in which our field party made its first measurements, was about 687 feet. If this is approximately correct, the difference in 1935 would have been about 6 feet, while our actual measurements showed 6.5 feet. The frequency of these high water levels is not known with precision. The projected estimates of Stockton and Fritts show a similar peak in 1921 and somewhat higher ones in 1908 and 1900. From this time back to the mid-1830's, large fluctuations apparently occurred, but at levels for the most part below 690 feet. From about 1821 to the mid-1830's, several peaks were again high (ca. 692 to ca. 693.5 feet).

THE PRIMARY SPECIES

Of the 417 species considered in the shore flora, 145 were noted in one place or another as primary in their assemblages; that is, they were sufficiently abundant or prominent to give the assemblages their distinctive form and appearance. Some of them were found as single primary species, but more were members of combinations, with others having approximately equal rank in their respective assemblages. The disposition of the primary species in this respect is as follows:

74 spp.	Found only in combinations of 2-4 spp. each	}	134 spp.	Found in combinations
60 spp.	Found in combinations or as single primary spp.			
11 spp.	Found only as single primary spp.		71 spp.	Found as single primary spp.

The 134 primary species found in combinations represented 180 different assemblages. Another 71 assemblages were characterized by single primary species, making the total number of different assemblages seen in the shore vegetation 251. The total number of assemblages described was 550. An estimate of the number of times a given assemblage was repeated in the course of the field observations was thus about 2.2. This, of course, is an average. Some of the assemblages were unique, while others were seen

several times. Owing in part to varying areas among the 10 habitat complexes, and in part to the varying extent of field studies among them, the numbers of different assemblages seen in them is far from uniform, ranging from about 12 on wet sand or gravel shores to as many as 49 in flood-plain meadows. Further, they add up to 297, which is 46 more than the total of 251 previously mentioned. The discrepancy is due to the 46 having been seen in more than one of the habitats.

The following 10 primary species were found in 95 of the 180 combinations recognized (numbers of combinations in parentheses). In making these combinations they were associated with 59 other primary species.

<i>Alnus incana</i> subsp. <i>tenuifolia</i> (19)	<i>Betula papyrifera</i> subsp. <i>humilis</i> (13)
<i>Salix planifolia</i> (18)	<i>Ledum groenlandicum</i> (12)
<i>Chamaedaphne calyculata</i> (16)	<i>Myrica Gale</i> (11)
<i>Carex aquatilis</i> (15)	<i>Populus balsamifera</i> (11)
<i>Equisetum fluviatile</i> (13)	<i>Juncus balticus</i> var. <i>littoralis</i> (10)

The second 10 species, in order of decreasing numbers of combinations, were found in 33 and added 16 to the number of associated species.

<i>Picea mariana</i> (9)	<i>Nuphar variegatum</i> (8)
<i>Carex rostrata</i> (9)	<i>Calamagrostis canadensis</i> (8)
<i>Salix Bebbiana</i> (9)	<i>Equisetum pratense</i> (7)
<i>Empetrum nigrum</i> (9)	<i>Arctostaphylos Uva-ursi</i> (7)
<i>Equisetum arvense</i> (8)	<i>Salix glauca</i> var. <i>acutifolia</i> (7)

Thus the 20 primary species found in the largest numbers of combinations ranging from 7 to 19, inclusive, appeared in 128 of the 180 combinations observed. In these assemblages they were associated with 75 of the 134 primary species that were seen in combinations. All of the second 10 species noted above were included among those associated with the first 10. Thus the total number of primary species involved in the 128 assemblages was 85, or 63.4% of all species found in combinations.

These observations raise some questions about the relations of primary species to their habitats. If 145 of them were to be distributed evenly throughout the 10 habitats described above, they would average about 14 in each. If it is assumed that there is a close and restrictive relationship of these species to their habitats, then either there are many undetected microhabitats within each of the 10, or there are possibly 14 primary species that have the same environmental requirements and have been randomly distributed throughout each of the 10 habitats.

With present or foreseeable knowledge of these habitats, it would be possible to make a small number of subdivisions in some of them, such as on the beaches of large lakes or in some of the muskegs; however, definition of the theoretical 14, adding up to 145 in all, seems impracticable, even with the most modern techniques of analysis. The problem is further complicated by the fact that the number 14 is far from realistic. When the numbers of primary species noted in each of the habitats are

added together, the total is 251 (See FIGURE 13), indicating that nearly three fourths of them (106) were growing in more than one of the habitats, and about one fourth in as many as 5 to 7 different habitats (see below). Nearly half of them (66) had reached primary status in more than one habitat. In a relatively uniform site, such as the flood-plain grass-sedge meadow, 30 primary species were seen, and in the muskeg grass-sedge meadow there were 40.

The tendency of the primary species to spread widely throughout the habitats suggests that the possibility of finding appreciable numbers of them having similar restrictive environmental requirements is remote. It also suggests a third alternative: that the habitat relations of a great many of the species are not narrowly restrictive and that the species have wider latitude in their selection of habitats than is commonly assumed for them.

Another question arises with respect to compatibility among species growing together as "co-primaries" in their respective assemblages. If the compatibility is assumed to be to any extent restrictive, it becomes difficult to rationalize when 134 of the primary species are found in 180 different combinations of 2 to 4 each, and when individual primary species are seen in combination with as many as 19 different ones.

HABITAT TOLERANCES OF THE SPECIES

The term "tolerance" is used here in the sense of "versatility" or "flexibility" on the part of species with respect to the differing kinds of habitats in which they were found. These terms are equivalent to "ecological amplitude," which has been used commonly in ecological literature. Interpretations of species versatility with respect to habitat have been primarily physiological in the literature of ecology, and they have been based largely on the idea that limiting factors in the environment may be recombined in such a way that species can live in differing habitats. Varying competition among species is thought to play a major role. A clear statement of this idea has been published by Küchler (1967).

In the total shore flora (417 spp.), 165 species were found in one habitat only. Thus more than half the flora (60.5%) showed capacity to live in two or more kinds of habitat. FIGURE 1 shows the general distribution of species in terms of this capacity. FIGURE 1A contains the distribution in four groups: species found in 1, 2, 3 to 4, and 5 to 7 habitats. The last three of these are added together in FIGURE 1B to show the contrast between those found in only one habitat and those in 2 to 7.

Methods of analysis used for the text figures and tables in the present paper aim only at relative comparisons of the behavior of species with respect to their occupancy of habitats. They are meant merely to illustrate a group of ideas thought to be useful for a rationalization of the shore vegetation.

The method of computing percentages, unless otherwise stated, will be uniform throughout the following analyses. The base numbers for the

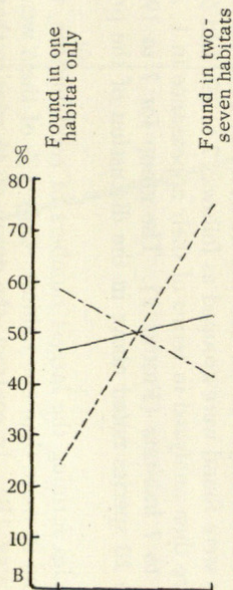
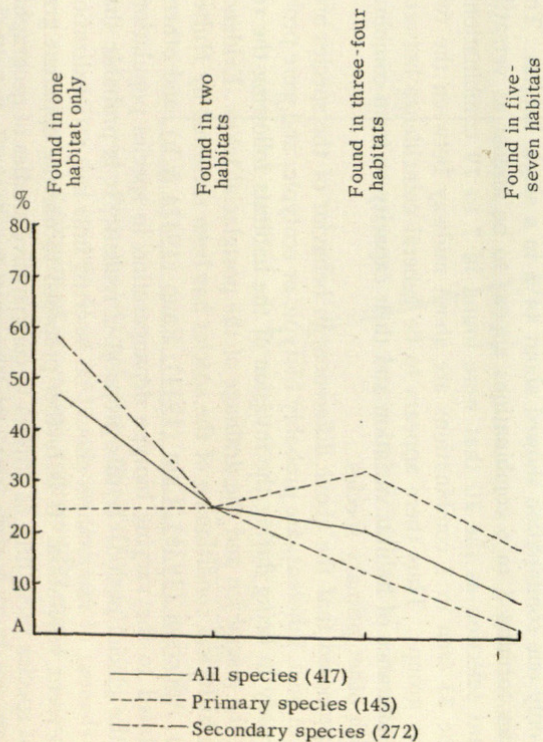


FIGURE 1 (left). Distribution of shore species with respect to the number of habitats in which they were found. Percentages based on the total numbers of all species, primary species, and secondary species. FIGURE 2 (right). Distribution of 134 primary species, found in varying numbers of combinations with other primary species, with respect to the number of habitats in which they were found. Base numbers for percentages are the total numbers of primary species found in 7 to 19, 3 to 6, 2, and 1 combinations.

percentages will be the total numbers of species within the groups being analyzed. In FIGURE 1, for example, there are three base numbers. Where the whole shore flora is concerned and it is desirable to know how all the species in this flora are apportioned in a range of the numbers of habitats occupied, the base number is 417. Similarly, for the primary and secondary species the numbers are 145 and 272 respectively.

The primary species are relatively almost as abundant among those found in 5 to 7 habitats as among those found in only one (FIGURE 1A). The secondary species, on the other hand, though with more than twice the percentage of the primary species confined to one habitat, are represented among those found in 5 to 7 habitats by only about $1/8$ the percentage of the primary species. Thus, in the shore flora as a whole, the primary species show far more tolerance of habitat variation than do the species that have secondary roles in the assemblages. They are more versatile in finding shore habitats in which they can grow. In some of these differing habitats they retain their primary position, while in others they join the secondary species.

The capacity of 134 of the primary species to form combinations may be analyzed in the same way. To do this the numbers of combinations in which the species were found were grouped as follows: 7 to 19, 3 to 6, 2, 1. These groups were then analyzed in terms of their appearance in 1, 2, 3 to 4, 5 to 7, and 2 to 7 habitats (FIGURE 2). The group for 7 to 19 combinations are the 20 species noted above in the discussion of the primary species.

Of the 20 species forming the largest numbers of combinations, nearly all were also found in more than one habitat. Only 5% of them were seen in only one (FIGURE 2B). In contrast, the group of 46 species that were seen in only one combination showed about 44% in a single habitat. The 35 species forming 3 to 6 combinations appear to be almost as versatile in habitat selection as the 20 that were found in 7 to 19 combinations, while the 33 seen in 2 combinations are about midway between the two preceding groups. Thus there appears to be general coincidence between species' tolerance of habitat variation and their capacity to form combinations with other primary species.

It is proposed that the above differences in behavior of the species are, at least in part, inherent, are probably biotypic or ecotypic, and were probably already in being during the invasion of the habitats following the retreat of the glacial ice and the drainage of the postglacial lakes. Evidence for such historical conditioning of the species has been reviewed by Hultén (1937a), Anderson (1936), Cain (1944), Raup (1947a & b), and others. It is related to the varying biotype depauperation in species populations during the glacial period. If this proposal is realistic, it is probable that a large element of randomness should be inserted into any rationalization of the present vegetation. It is further proposed to use the apparent gradients of species versatility as criteria in comparative studies of geographic range patterns, the behavior of the life-forms of the plants, and the floras of the various habitats.

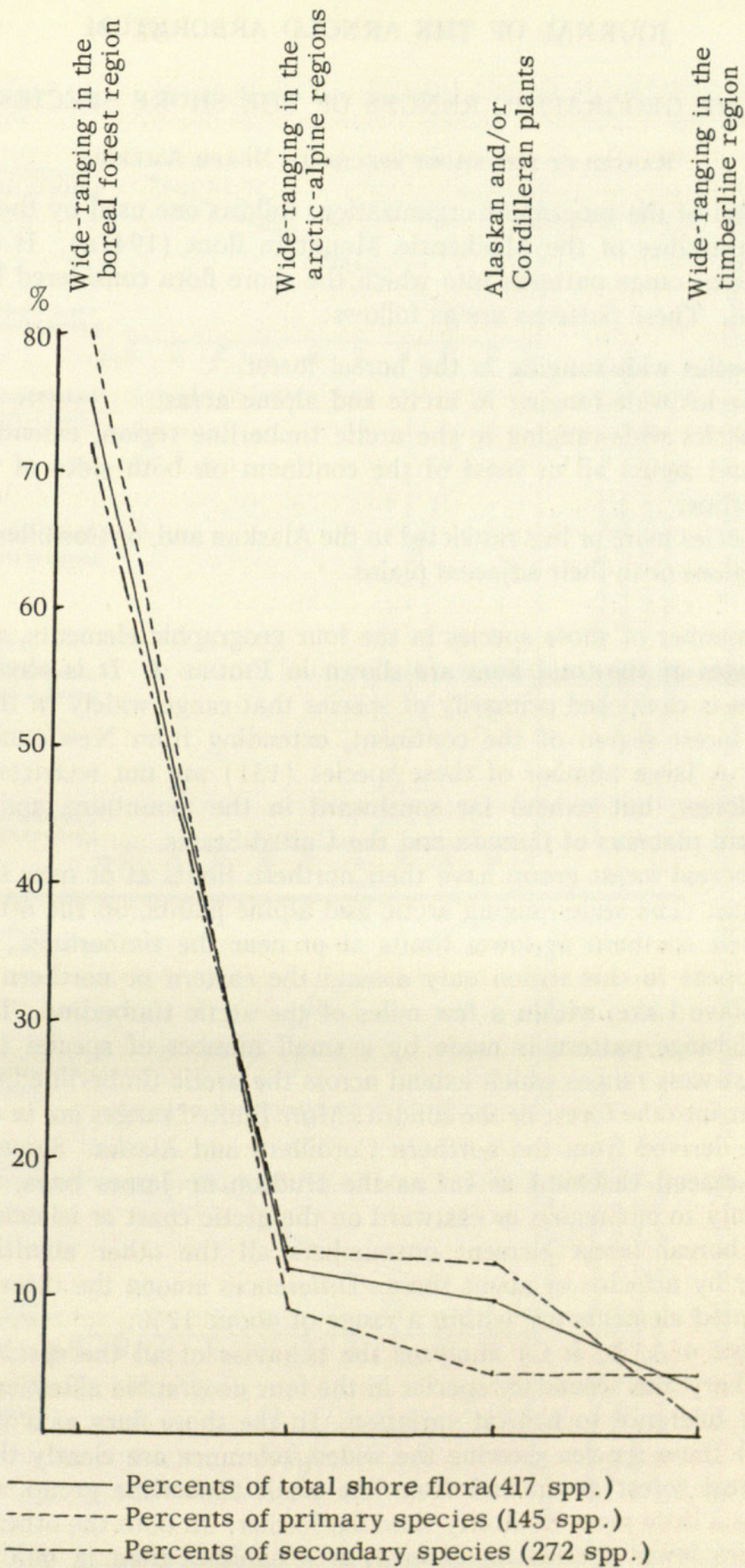


FIGURE 3. Proportional representation in the shore flora of the four major geographic elements in the vascular flora of boreal America.

THE GEOGRAPHIC RANGES OF THE SHORE SPECIES

RANGES OF THE SHORE SPECIES IN NORTH AMERICA

The first of the geographic organizations follows one used by the present writer in studies of the Mackenzie Mountain flora (1947a). It contains four general range patterns into which the shore flora considered here can be placed. These patterns are as follows:

1. Species wide-ranging in the boreal forest.
2. Species wide-ranging in arctic and alpine areas.
3. Species wide-ranging in the arctic timberline region, extending in a band across all or most of the continent on both sides of the timberline.
4. Species more or less restricted to the Alaskan and/or Cordilleran regions or to their adjacent plains.

The number of shore species in the four geographic elements, and their percentages of the total flora are shown in FIGURE 3. It is obvious that this flora is composed primarily of species that range widely in the boreal conifer forest region of the continent, extending from Newfoundland to Alaska. A large number of these species (131) are not restricted to the boreal forest, but extend far southward in the mountains and interior plains and plateaus of Canada and the United States.

The boreal forest group have their northern limits at or near the arctic timberline. The wide-ranging arctic and alpine plants, on the other hand, have their southern or lower limits at or near the timberlines. Most of them appear in this region only around the eastern or northern parts of Great Slave Lake, within a few miles of the arctic timberline. The "timberline" range pattern is made by a small number of species that have wide east-west ranges which extend across the arctic timberline but do not reach far into the forest or the tundra. More limited ranges are in a floristic element derived from the northern Cordillera and Alaska. Some of these species extend eastward as far as the Hudson or James bays, but most reach only to our region or eastward on the arctic coast or islands.

The boreal forest element outnumbers all the other affinities taken together by a factor of about three. Differences among the three less well represented elements are within a range of about 12%.

FIGURE 4(A, B, & C) analyzes the behavior of all the species and of the primary and secondary species in the four geographic affinities in terms of their tolerance to habitat variation. In the shore flora as a whole (all species) those species showing the widest tolerance are clearly those from the boreal forest group and from the small timberline group, the latter showing a little more flexibility than the former. In both the other affinities there are fewer species found in 2 to 7 habitats than in one, with the Alaskan-Cordilleran group a little more versatile than the arctic-alpine. The primary species all show high tolerance ratings but are also in two groups. The most versatile are the Alaskan-Cordilleran and timberline

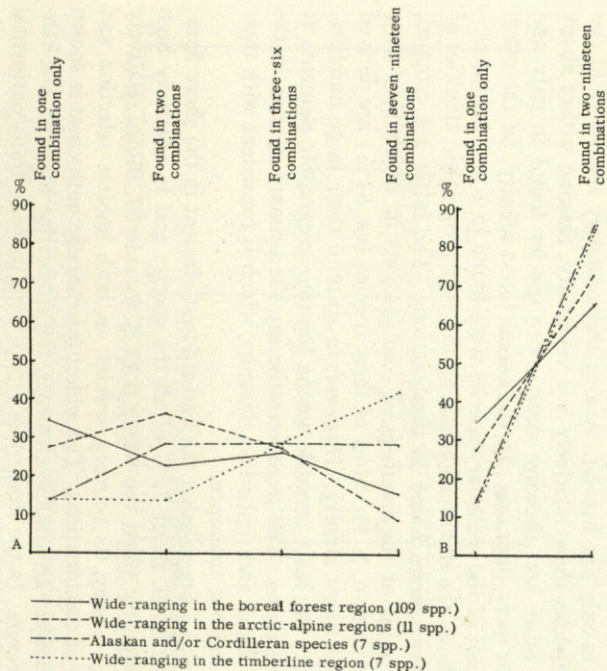
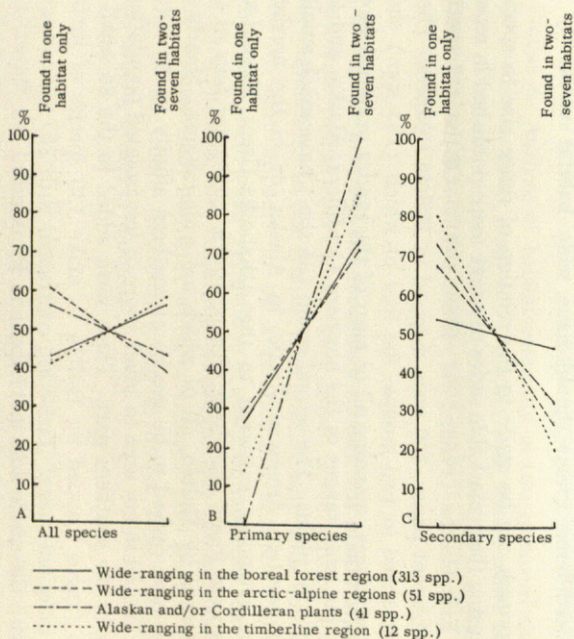


FIGURE 4 (left). Analyses of the four major geographic elements in the shore flora with respect to the numbers of habitats in which their species were found. Percentages based on the total numbers of all species, primary species, and secondary species derived from each geographic element. FIGURE 5 (right). Analyses of the four major geographic elements in the shore flora with respect to the numbers of combinations seen among the 134 primary species that were found in combinations. Percentages based on the total numbers of combination-forming primary species in each geographic element.

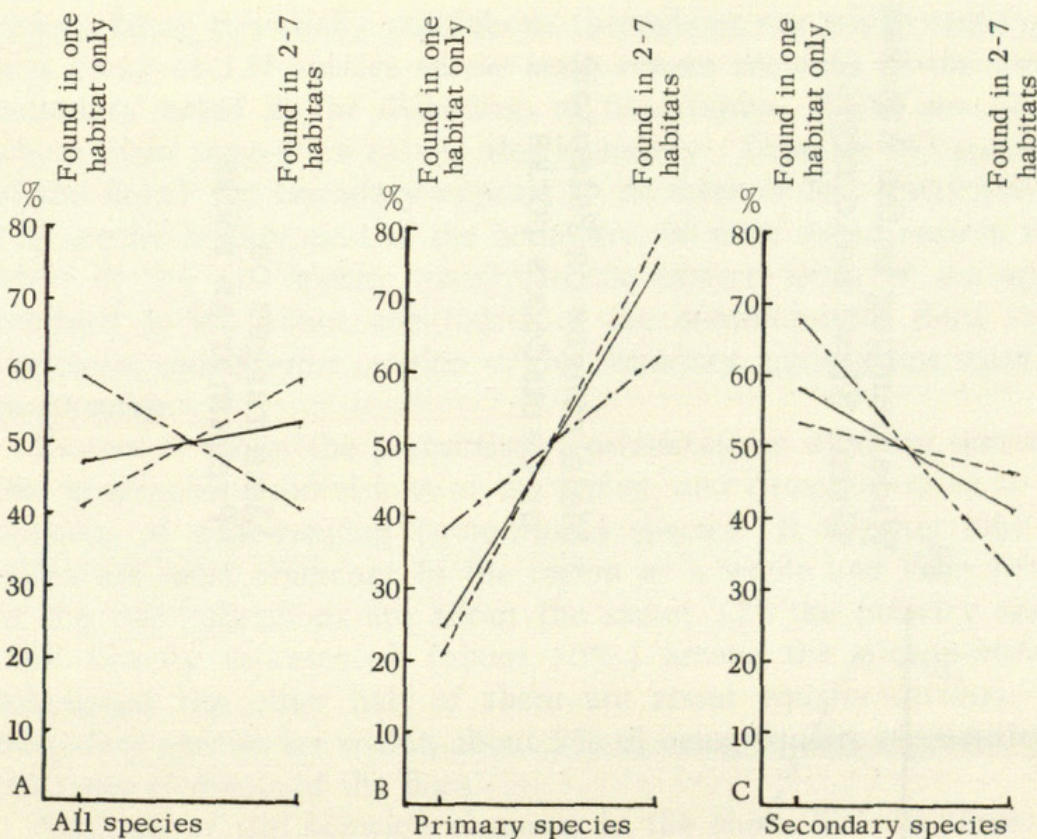
groups, with many more found in 2 to 7 habitats than in only one. The other two affinities form the other group, nearly equaling each other and showing about two and a half times as many of the more flexible species as were found in only one habitat. Among the secondary species all of the three lesser affinities show relatively low versatility, ranging within about 10% of each other and showing many more species found in only one habitat than in more than one. In the boreal forest affinity, on the other hand, nearly half of the secondary species were found in 2 to 7 habitats.

FIGURE 5 shows the distribution among the four geographic affinities of the 134 primary species found in combinations. The latter are grouped, as before, in terms of the numbers of combinations in which they were found (7 to 19, 3 to 6, 2, 1). Most of these species (ca. 81%) are derived from the boreal forest affinity. However, in spite of their large numbers, these species are the least versatile among the four geographic elements at forming combinations. The most versatile are the primary species in the Alaskan-Cordilleran and timberline elements, which is consistent with their versatility in habitat tolerance.

FIGURES 4 and 5 suggest that the boreal forest element in the shore flora, though it contributes about 75% of all the species and is relatively high in habitat versatility when the whole flora is considered, shows relatively low versatility among its primary species, in both habitat selection and the formation of combinations. The widest tolerance in both cases is shown by the two smallest geographic elements, the timberline and the Alaskan-Cordilleran groups. In the timberline group, with its wide transcontinental range, this is understandable, but why all of the seven primary species in the Alaskan-Cordilleran group should have wide habitat versatility is unknown.

Another approach can be made to the relation of range size to species versatility by using the remarkable series of range maps published in recent years by Dr. Eric Hultén (1958, 1962, 1968, 1971). Of the 417 species treated in the present paper, 369 were mapped in Hultén's papers. These species were arranged in two groups, the first of which (283 spp.) show wide continental ranges, spanning all or most of the tundra or boreal forest regions, or having wide ranges in the northern Cordillera, Alaska, and the neighboring interior plains. The second group (86 spp.) have much smaller ranges: in the western American Arctic, in Alaska, or in the northern Cordillera but extending eastward to the Athabaska-Great Slave Lake region. Maps were found elsewhere (Raup, 1947a, 1959) for four of the species not treated by Hultén, all of which are wide-ranging. Nearly all of the 44 remaining proved to be species of southern affinity in the boreal forest region, limited in our area to small, more or less isolated populations, most of them in the southern part. These were added to the 86 small or discontinuous ranges mapped by Hultén to make 130 species of limited or distinctly marginal range. These are contrasted with 287 wide-ranging species and with the whole flora (417 spp.) in FIGURE 6.

The relative versatility shown by the whole flora in FIGURE 6 (solid line) is equivalent to that shown in FIGURE 1B. In the whole flora, as well



- Total shore flora (417 spp.)
- Species with wide continuous ranges in tundra or boreal forest regions of North America (287 spp.)
- · - · - Species with relatively small range areas in northwestern America, or with much disrupted ranges, or with main ranges farther south and represented here by more or less isolated marginal populations (130 spp.)

FIGURE 6. Analysis of habitat versatility in two groups of species, one with large continuous range areas and the other with much smaller or discontinuous ranges. Data mainly from Hultén (1958, 1962, 1968, 1971). Base numbers for percentages are the total numbers for all, primary, and secondary species in each of the geographic groups.

as among the primary and secondary species, the plants with small or discontinuous ranges are considerably lower in versatility, as reflected by their populations in our region, than species with wide continuous ranges. Because there appears to be a relationship between “primaryness” in species and their wider versatility, it could be expected that a segment of the flora showing low versatility would provide proportionally fewer primary species than one with wider tolerance. This proves to be the case here, for the more restricted group is about 29% primary while the wide-ranging group is about 38%.

SPECIES RANGES WITHIN THE ATHABASKA-GREAT SLAVE LAKE REGION

Although the bulk of the shore flora is of species that range widely in northern America, there are many that have more or less limited ranges within our region. There are 170 species that are ubiquitous, their popu-

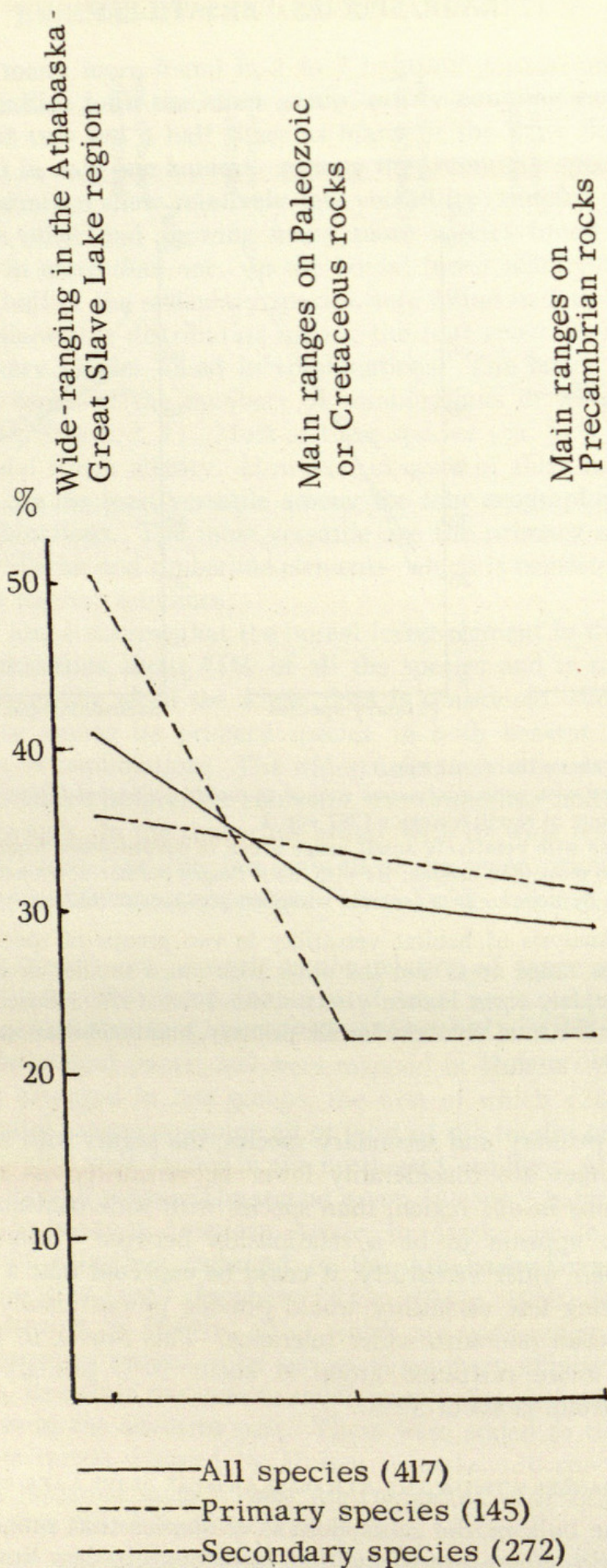


FIGURE 7. Analysis of the shore flora with respect to its local distribution within the Athabaska-Great Slave Lake region. Percentages based on total numbers of all species, primary species, and secondary species.

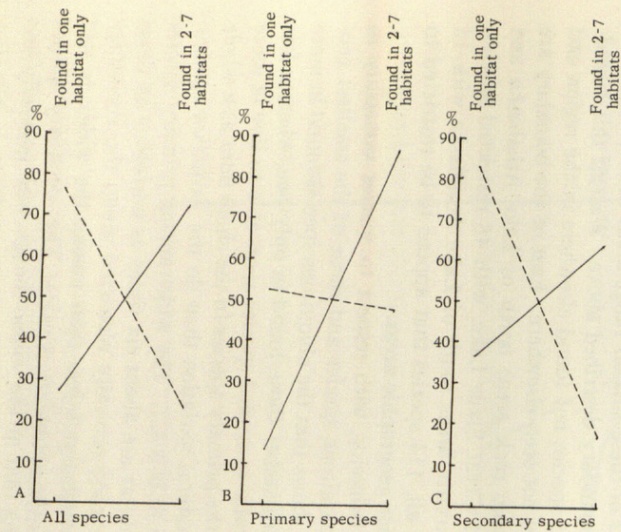
lations being essentially continuous throughout our whole region. Second is a group of 127 species whose main ranges are west of the major N-S boundary noted in the discussion of topography. Third are 120 species whose main ranges are east of this boundary. Thus for 247 species (59% of the flora) the boundary appears to be more or less restrictive. Of the 127 species mainly west of the boundary, 90 were found *only* in this area, while of the 120 species mainly in the eastern area, 94 are apparently confined to it. About one fourth of the nonubiquitous flora (63 spp.), therefore, shows some overlap of the boundary, usually not more than 10 to 20 miles.

FIGURE 7 shows the percentage representations of shore species in the two geographic subdivisions of the region, and compares them to the proportions of wide-ranging (ubiquitous) species. It appears that (1) the wides are most abundant in the region as a whole and their proportions in the two subregions are about the same; (2) the primary species are most heavily represented (about 50%) among the wides, while in the subregions the other half of them are about equally divided; (3) the secondary species are within about 5% of being equally represented among the three elements of the flora.

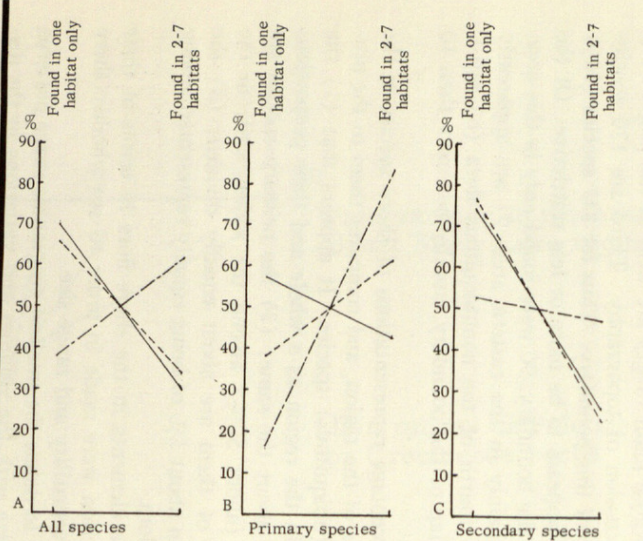
Analyses of the nonwide elements in the shore flora in terms of their versatility in habitat selection were made in order to see whether there were correlations between versatility and range size.

First an effort was made to define the smallest geographic range patterns that would be commensurate with the volumes and variations in the distribution of field data. Four of these smaller range areas were defined, two on each side of the major boundary described above. West of this boundary are the uplands with 13 species not found elsewhere in the region and the lowlands with 38 species not seen elsewhere. East of the boundary are the granitic and metamorphic rock areas north of Lake Athabaska and around the eastern parts of Great Slave Lake, with 48 restricted species, and the sandstone and quartzite areas south of Lake Athabaska with 15 species. Thus there are, in all, 114 species that appear to be restricted to one or another of these lesser geographic areas.

FIGURE 8 compares the behavior, with respect to species versatility in habitat tolerance, of the ubiquitous species and those of the smallest geographic extent. FIGURE 8A shows that the ubiquitous species found in more than one habitat greatly outnumber those found in only one, whereas less than half of the geographically restricted species seem able to live in more than one. As noted earlier the primary species in the shore flora as a whole show greater tolerance of habitat variation than do the secondary species. This is reflected in FIGURE 8(B & C). The wide-ranging primary species found in more than one habitat are about six times as numerous as those found in only one. In the geographically restricted group the versatility of the primary species, though much less than among the wides, is still much greater than that of the secondary species. The secondary species show a contrast approaching that of the wides, though with generally less versatility in evidence.



— Wide-ranging species in the Athabaska-Great Slave Lake region (170)
 - - - Species having greatly restricted ranges, i.e. missing in all but one or another of the minor subregions (114)



— Species found only in areas underlain by Paleozoic or Cretaceous rocks, or by alluvium derived from these rocks (90)
 - - - Species found only in areas underlain by Precambrian rocks (94)
 . . . Species with main ranges over Paleozoic and/or Cretaceous, or over Precambrian rocks, but with some overlap of these ranges (63)

FIGURE 8 (left). Analyses, with respect to habitat versatility, of 170 species of wide continuous range within the Athabaska-Great Slave Lake region and of 114 species apparently restricted to much smaller areas within the region. Percentages based on numbers for all species, primary species, and secondary species found in each geographic group. FIGURE 9 (right). Analyses, with respect to habitat versatility, of species found only on one side or the other of the Paleozoic-Precambrian boundary and of species with main ranges on one side or the other, but with some overlap of the boundary. Percentages based on numbers of all species, primary species, and secondary species in each geographic group.

Analogous results appear when the ubiquitous species are eliminated and only those species whose main ranges lie on one side of the major boundary or the other are considered. In FIGURE 9 the two wholly restricted groups and the group with some boundary overlap are analyzed and compared in terms of relative tolerance of habitat variation. About half of the overlapping species have their main ranges to the east, and the other half to the west of the boundary. The species with overlapping ranges appear to have much higher tolerance ratings than do those in the more restricted areas. Consistent with the preceding analysis (FIGURE 8), the least differences are among the primary species. It is notable that only three of the overlapping primary species are primary on both sides of the boundary, and it is suggestive that primary species found only east of the boundary have considerably wider habitat tolerance than those confined to the area west of the boundary.

It was shown earlier that the number of combinations formed among primary species appeared to reflect their relative versatility in habitat selection. The nonubiquitous species noted as primary only west or east of the major N-S boundary are analyzed in FIGURE 10 for their combination-forming proclivities and are compared to those of the overlapping primary species. FIGURE 10 is analogous to FIGURE 9B. The overlapping species show proportionately many more combinations than do those found only in one or the other of the two major subregions.

The data from analysis of the species' geographic patterns indicates a positive correlation between size of range and versatility in the occupance of habitats. In the flora as a whole species derived from the largest ranges show the largest proportions of the more versatile species (FIGURES 4A & 6). Relations to size of range are more striking when the behavior of plants ubiquitous in our region is compared to that of species greatly restricted in range (FIGURE 8). In the latter the primary species show even fewer growing in more than one habitat than in one.

The relation of habitat versatility to a prominent vegetative boundary is shown in FIGURE 9, where the nonubiquitous species that do not cross the boundary are compared with those that do cross it for relatively short distances. The latter show notably greater habitat versatility than the former.

LIFE-FORMS IN THE SHORE FLORA

The shore flora of the region is here classified in six rather generalized life-form groups:

1. Trees: all single-stemmed woody plants.
2. Shrubs: all multiple-stemmed woody plants, whether upright, decumbent, or trailing.
3. Perennial herbs with only fibrous roots as underground organs: mostly caespitose plants; term usually shortened in the following text to "perennials with fibrous roots" or "fibrous-rooted perennials."

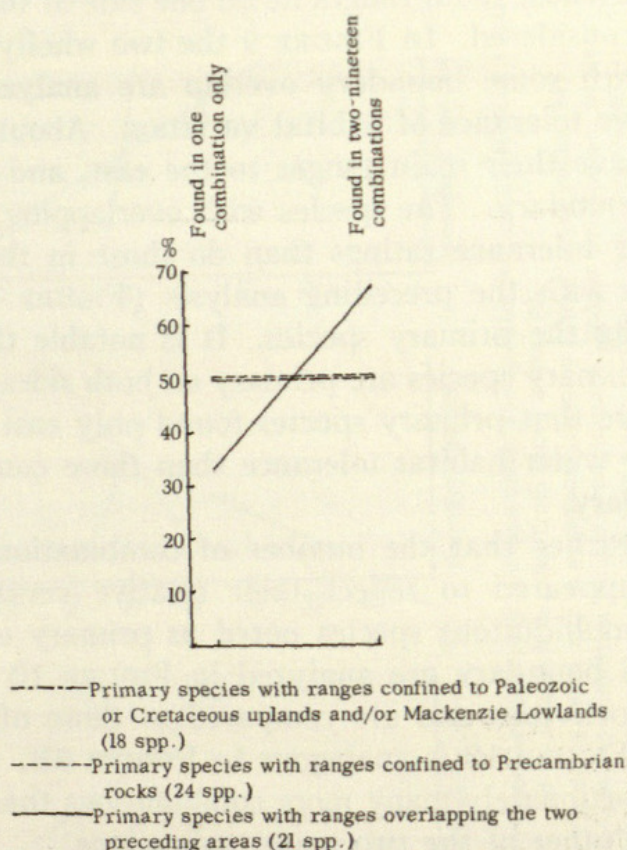


FIGURE 10. Analysis of the primary species in FIGURE 9 with respect to the numbers of combinations in which they were found. Percentages based on the total numbers of primary species found in combinations and restricted to or overlapping the two subregions.

4. Perennial herbs with caudexes, rhizomes, runners, stolons, or with stems that root at the nodes: this group brings together most of the plants that have means of vegetative propagation by underground or aboveground organs; term usually shortened in the following text to "perennials with rhizomes" or "rhizomatous perennials."
5. Perennial herbs with taproots, bulbs, corms, tubers, or turions: these plants have storage organs, but no means of vegetative traveling; term commonly shortened to "taprooted perennials" in the following text.
6. Annual or biennial herbs.

FIGURE 11 (solid line) shows the numbers of species in the above life-form categories and their percentage representation in the whole shore flora. Perennial herbs with rhizomes, caudexes, etc. are predominant, comprising a little over half of the total flora, with about three times as many species as fibrous-rooted perennials and nearly four times as many

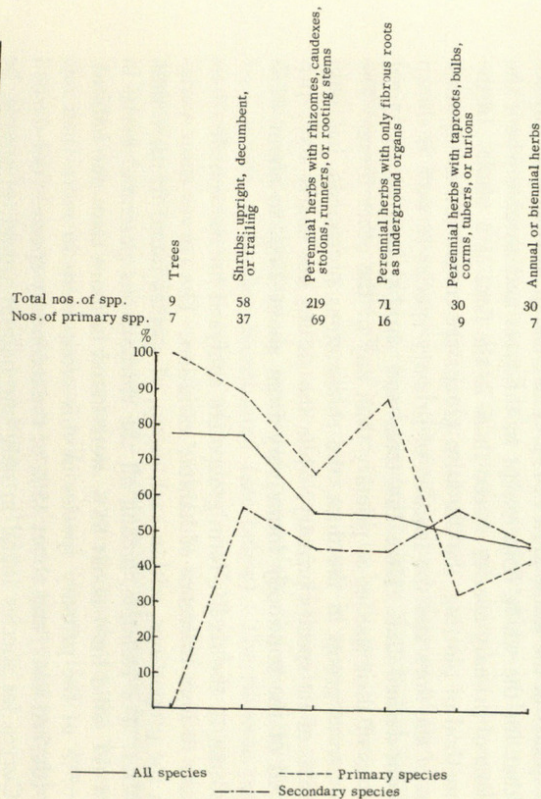
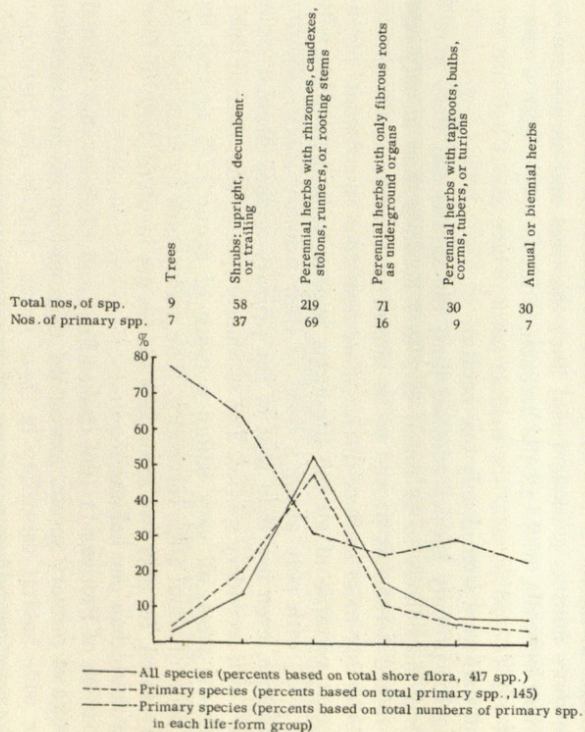


FIGURE 11 (left). Proportional representation of life-forms among all species and all primary species in the shore flora; also the proportions of primary species in each life-form group. FIGURE 12 (right). Analysis of life-forms for relative versatility in the occupation of more than one habitat. Percentages based on the numbers of all species, primary species, and secondary species in each life-form found growing in more than one habitat (2 to 7).

as the shrubs. Tree species are least numerous, while taprooted plants and the annual-biennial group come between the trees and the shrubs.

The primary species in FIGURE 11 are plotted in two ways. The dashed line shows the percentages of the life-forms based on the total number of primary species in the whole flora (145). The trend of this curve resembles closely that for the whole flora except in the trees and shrubs, where the proportions of primary species exceed those in the flora as a whole. In the second method of plotting, the life-form groups are considered as separate elements of the flora and the fraction of primary species in each is shown by the dot-dashed line. Here the trees and shrubs show much larger proportions of their species as primary than any of the other forms. The most numerous group in the flora, the rhizomatous perennials, has only about 30% of its species primary, while the shrubs are nearly 65% primary. All of the nonwoody forms vary from about 24% to about 32% primary.

In FIGURE 12 the six life-form groups are analyzed for the contributions they make to high tolerance of habitat variation. The curves show variations in the proportions, within each group, of species found in more than one habitat. For example, among all the rhizomatous perennial herbs in the flora (cf. solid line) about 55% were found in more than one habitat. About 67% of the primary species in this group were in more than one habitat (dashed line), and about 45% of the secondary species (dot-dashed line). Curves for species found in only one habitat would, of course, be mirror images of these.

In the shore flora as a whole (solid line) the trees and shrubs are by far the most versatile, while all the herbaceous forms vary within a range of about 9% (47–56%) near the median point, where about half are versatile and half were seen in only one habitat.

Among the primary species (dashed line) the shrubs and trees were 9 to 10 times more likely to be found in 2 to 7 habitats than in only one. Fibrous-rooted perennials proved to be almost as tolerant as the shrubs, and considerably more so than the far more numerous rhizomatous perennials. Least versatile of all the life-forms appear to be perennials with taproots, etc., with only about a third of their primary species showing wide tolerance, even less than that of the primary annual-biennial group or of their own secondary species. The secondary species (dot-dashed line), excepting the trees, all vary within a range of about 12% around the median point of about 50% versatility. The percentages for trees probably are exaggerated, for only two secondary species are involved, both of them found in more than one habitat.

Comparison of FIGURES 11 (dot-dashed line) and 12 shows that the high percentages of primary species among the trees and shrubs are consistent with the wide habitat versatility in these forms. But in the herbaceous forms the coincidence does not occur. Although the primary species among these forms show only small differences around 25–30%, they differ widely in versatility, from about 35% among taprooted species to about 87% among fibrous-rooted perennials.

Analyses of the life-forms of the primary species in the four geographic affinities of the shore flora were also made to show the incidence of varying habitat versatility among them. In the predominant boreal forest element, the tolerance ratings are not much different from those seen in FIGURE 12, though rhizomatous perennials show somewhat less versatility. The timberline element, though small, also reflects the ratings in FIGURE 12. The most striking departure from this pattern was found in the arctic-alpine affinity, which deserves particular attention.

In the 14 primary species of the arctic-alpine element of the shore flora, the taprooted and fibrous-rooted perennials have the greatest flexibility in habitat selection, with all of them found to be living in more than one habitat. The shrubs, with three times as many in more than one habitat as in one, are second in the scale of tolerance. If those in the arctic-alpine element are considered as taprooted perennials, the most tolerant group here would be further accentuated (see below). The rhizome perennials have an intermediate rating with about 63% found in more than one habitat. There are, of course, no trees from this affinity, and no primary annual or biennial plants.

It may be useful to contrast the findings on life-forms here with those in the high Arctic. For comparison, a study made in the Mesters Vig district of Northeast Greenland will be used (Raup, 1969). The classification used there was based on the writer's own observations supplemented by those of Gelting (1934) and Böcher (1938).

In the part of Greenland covered by the above studies there are no trees, and woody plants are limited to low or trailing shrubs. Following the practice of Gelting, all of the shrubs (11 spp.) were classified as taprooted perennials. It may be that many of the shrubs in the Athabaska-Great Slave Lake region could be so treated, but not enough is known of their root systems to justify such a classification. Also absent in the Mesters Vig district, as in most of Northeast Greenland, are nearly all annual and biennial herbs. Thus comparison of the two floras must be limited to the perennial herbs. In the Mesters Vig area the classification was as follows:

Species with fibrous roots predominant	64 (41.6%)
Species with taproots or short, oblique rhizomes	65 (42.2%)
Species with well-developed underground rhizomes	25 (16.2%)

Approximate equivalents of these groups in the Athabaska-Great Slave Lake region are:

Perennial herbs with rhizomes, caudexes, etc.	219 (68.4%)
Perennial herbs with fibrous roots	71 (22.2%)
Perennial herbs with taproots, bulbs, etc.	30 (9.4%)

The species with taproots and fibrous roots are the predominant forms in the arctic flora at Mesters Vig, while rhizomatous species so numerous in the region studied here are reduced to about 16% of the flora. It is possible that the high versatility shown by the fibrous and taprooted species

in the arctic-alpine element of our flora reflects the predominance of these forms in the arctic tundra. A large proportion of this element was found in the areas nearest the arctic timberline.

In the Alaskan-Cordilleran element there are only seven primary species, but it is notable that the taprooted plants have a high rating for versatility, as in the tundra, and that the rhizomatous perennials are even lower in the scale than in the arctic-alpine element.

ANALYSES OF VEGETATION TYPES IN THE SHORE FLORA

FIGURE 13 shows the number of species found in each of the 10 habitat-vegetation complexes defined earlier, and the percentage of the total shore flora found in each (solid line). The numbers of primary species in each habitat are also shown, with the percentage of total primary species (145) in each (dashed line).

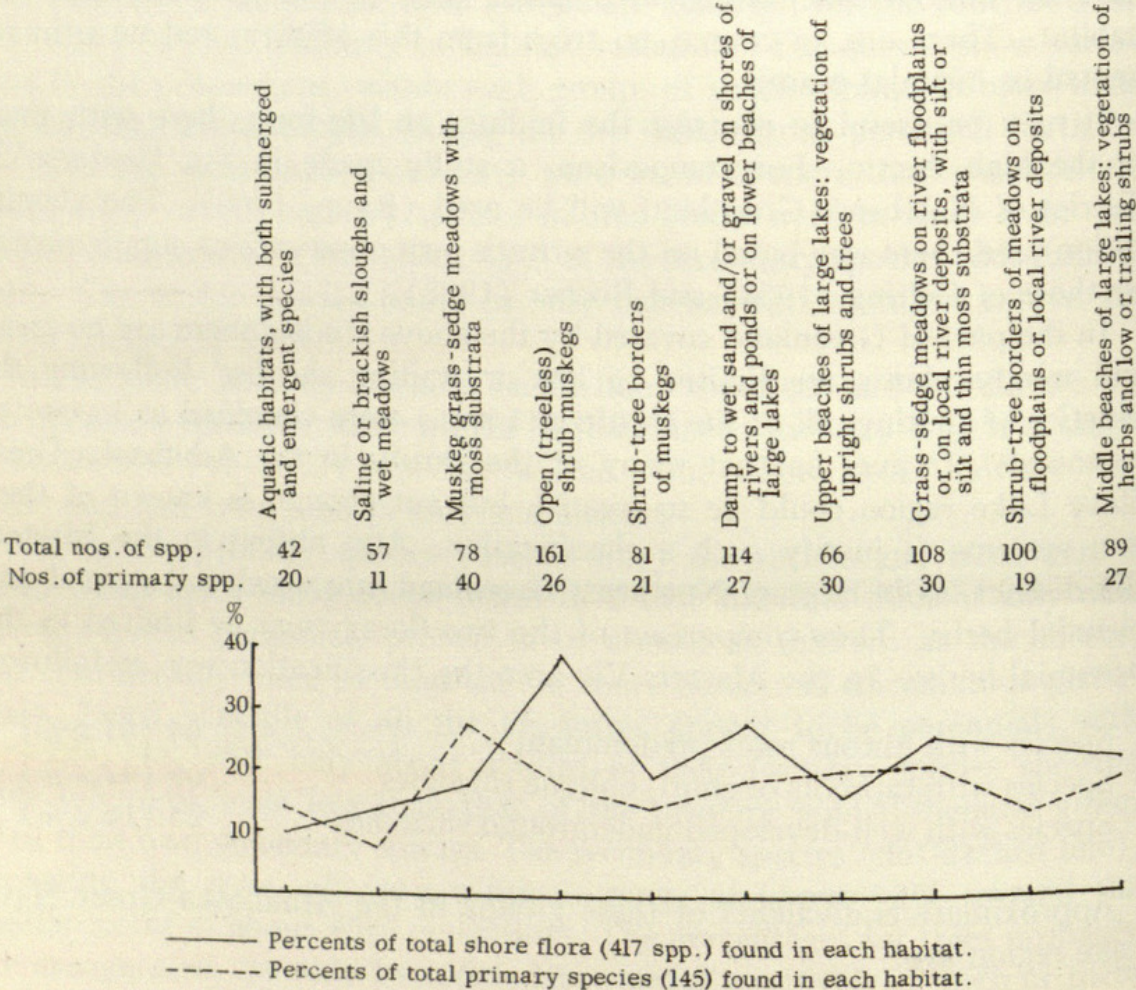


FIGURE 13. Proportional representation of all species and of all primary species among ten shore habitats.

Reasons for the variation in numbers of species found in the 10 habitats are not clear. The variations might be due to sampling differences, but if this were true the habitats in which the largest numbers of different assemblages were described should show the largest numbers of species. This

correlation, however, does not occur. The treeless shrub muskeg, for example, had the largest number of species (161), seen in 37 different assemblages, while the flood-plain meadows, with the largest number of different assemblages (49), had only 108 species listed. The next largest number of species was in the damp to wet sandy shores of lakes and rivers (114) and was noted in the smallest number of different assemblages (12).

A somewhat better coincidence is with the probable areas occupied by the habitats. No accurate figures are available for this, but it is probable that shrub muskegs occupy more area in the shore vegetation than any other type. A tentative scale of areas, based on the writer's field observations, is given below. The habitats are listed from largest to smallest, with the numbers of species, from greatest to least, listed on the right as they occur in the areas.

1. Treeless shrub muskegs	1
2. Flood-plain meadows	3
3. Shrub-tree borders of flood-plain meadows	4
4. Damp to wet sand or gravel lake and river shores	2
5. Shrub-tree borders of muskegs	5
6. Muskeg meadows	8
7. Shrubs and trees on upper lake beaches	7
8. Aquatic habitats	10
9. Middle beaches of large lakes	6
10. Saline or brackish habitats	9

The correlation here is far from complete, but it suggests that size of area may have some significance.

Addition of the numbers of species in the 10 habitats gives a total of 896, which is a little over twice the number in the shore flora and indicates the extent to which in general, the species showed their habitat versatility.

FIGURE 14 gives the proportional representation, in each of the 10 habitats, of the primary and secondary species that were found in more than one habitat (2 to 7). The base numbers for percentages in both are the total floras of the habitats. Curves for species found in only one habitat would be mirror images of those in FIGURE 14.

Reasons for variations in the proportions of more versatile species from one habitat to another, ranging from about 20% to 100%, can only be suggested with present knowledge of the habitats and without more information on the gradient of versatility that seems to exist among the plants. It is probable that there is an inverse relationship between gradients of structural and physiological specialization on one hand, and of habitat versatility on the other. The most highly specialized species in the shore flora probably are the aquatics and the halophytes, and FIGURE 14 shows them to be at the bottom of the scale of versatility.

A certain amount of specialization for resistance to desiccation is to be expected, if the above reasoning is tenable, toward the dry end of the moisture gradient. If the halophytes were considered specialized for physiological dryness, they could be placed at the opposite side of the graph in FIGURE 14 and would accentuate the drop in versatility that is suggested

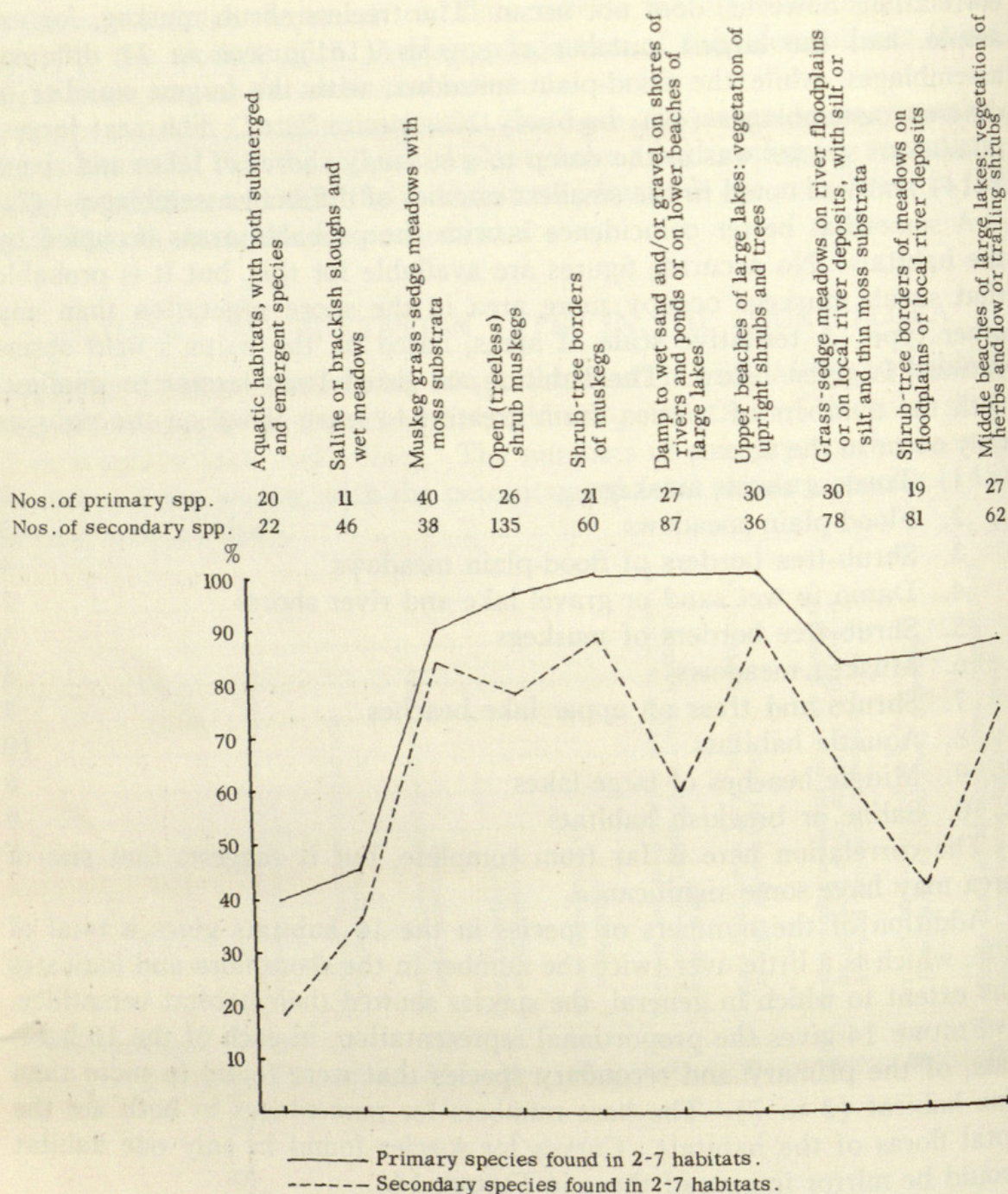


FIGURE 14. Analyses of shore habitat floras with respect to the habitat versatility of the primary and secondary species found in them. Base numbers for percentages are the numbers of primary and secondary species in each habitat.

by the three vegetations at the drier end of the gradient. The high versatility shown by the muskeg floras, the vegetation of the upper beaches, and wet sand or gravel shores would be expected, as would lowered flexibility in the flood-plain meadows and their shrub-tree borders. The latter sites are subject to flooding in spring or early summer, but become relatively dry in mid- or late summer. Their silty alluvial soils are fairly well drained after the floods recede, and most of them do not have thick moss mats to hold water and retard evaporation. Their shrub-tree borders usually are on low levees where drainage is better than in the meadows.

The middle beaches of the large lakes are the driest sites on the shores owing to their topographic position, their exposure to winds, and their coarse-textured soils.

Most of the high versatility in FIGURE 14 is in vegetations containing large percentages of the upright shrubs and trees of the flora. FIGURE 12 and TABLE 1 (below) indicate that these forms, wherever they occur, show high versatility. It is probable that their presence has influenced the trends of the curves in FIGURE 14.

Seventy-nine of the 145 primary species in the shore flora (54.5%) were found to be primary in only one or another of the 10 habitats. Thus nearly half of the primary species noted in any one habitat were likely to appear as primary in at least one other and possibly in six others. Of the 66 species found to be primary in more than one habitat, most were seen in 2 (46), 15 in 3 to 4, and 5 in 5 to 7. All but one of the 20 primary species found in the largest numbers of combinations (7 to 19) are among the more versatile of the primary species. The exception is *Nuphar variegatum*, a highly specialized aquatic.

TABLE 1. Analysis of habitat floras for their percentage representations of life-forms. Numbers in parentheses are for primary species.

	Aquatic habitats, with both submerged and emergent species	Saline or brackish sloughs and wet meadows	Muskeg grass-sedge meadows with moss substrata	Open (treeless) shrub muskegs	Shrub-tree borders of muskegs	Damp to wet sand and/or gravel on shores of rivers and ponds or on lower beaches of large lakes	Upper beaches of large lakes: vegetation of upright shrubs and trees	Grass-sedge meadows on river floodplains or on local river deposits, with silt or silt and thin moss substrata	Shrub-tree borders of meadows on floodplains or local river deposits	Middle beaches of large lakes: vegetation of herbs and low or trailing shrubs
Nos. of species	42 (20)	57 (11)	78 (40)	161 (26)	81 (21)	114 (27)	66 (30)	108 (30)	100 (19)	89 (27)
Trees	0 (0)	1.8 (0)	0 (0)	3.1 (0)	7.4 (4.9)	6.1 (2.6)	13.6 (9.1)	0.9 (0)	6.0 (1.0)	6.7 (0)
Shrubs	0 (0)	10.5 (0)	5.1 (3.8)	21.7 (9.9)	37.0 (17.3)	16.7 (7.0)	39.4 (25.8)	9.3 (0)	35.0 (12.0)	29.2 (9.0)
Perennial herbs with fibrous roots	9.5 (0)	12.3 (3.5)	19.2 (6.4)	17.4 (0.6)	7.4 (0)	20.2 (4.4)	12.1 (1.5)	14.8 (1.9)	8.0 (0)	14.6 (4.5)
Perennial herbs with rhizomes	71.4 (31.0)	52.6 (12.3)	67.9 (37.2)	48.4 (5.0)	39.5 (3.7)	41.2 (8.8)	27.3 (7.6)	62.0 (23.1)	48.0 (6.0)	34.8 (13.5)
Perennial herbs with taproots	16.7 (14.3)	3.5 (1.8)	3.8 (3.8)	6.8 (0.6)	7.4 (0)	7.9 (0)	6.1 (1.5)	3.7 (0)	3.0 (0)	10.1 (2.2)
Annual and biennial plants	2.4 (2.4)	19.3 (3.5)	3.8 (0)	2.5 (0)	1.2 (0)	7.9 (0.9)	1.5 (0)	9.3 (2.8)	(0) (0)	4.5 (1.1)

The predominance of perennial herbs with rhizomes, caudexes, etc., noted earlier, appears again in TABLE 1, where the 10 habitat floras are analyzed in terms of life-forms. They show the highest percentages in all but one of these floras. The exception is among the trees and upright shrubs on the upper beaches of large lakes, where they are least represented. They are most abundant in the grass-sedge meadows and in aquatic habitats, in which they range between 62 and 71% of the floras. Except on the upper beaches noted above, they do not fall below about 35% in any of the habitats.

Next in descending order of abundance are the shrubs, which of course reach their largest percentages in the shrub muskegs and in the shrub-tree borders of meadows and lake beaches. In these habitats they range between 21 and about 40% of the species. In the meadows they range from 5 to about 10%. The middle beaches of large lakes have a larger proportion of shrubs than the shrub muskegs, but most of them are decumbent or trailing, while in the muskegs most are upright.

Third are fibrous-rooted perennial herbs, ranging from about 8% to about 20% of the habitat floras. They have their lowest percentages in aquatic and shrub-tree border habitats, and their highest in muskeg grass-sedge meadows and in the damp to wet sand and gravel shores of lakes and rivers. They have a relatively large percentage (14.6) on the middle beaches of large lakes, where they represent a tundra element of the flora in which their life-form is much more common than in our region.

Perennial herbs with taproots, bulbs, corms, tubers or turions range, with two exceptions, from 3% to about 8% of the floras. The exceptions are in aquatic and middle beach habitats, at the two ends of the moisture gradient. They are relatively prominent among the aquatics because some of these plants perennate by detached winter buds (turions). On the middle beaches, with 10.1%, they are mainly taprooted plants which, like the fibrous-rooted species, represent the tundra flora in which plants with taproots are abundant.

Many of the most characteristic plants of saline or brackish habitats in this region are annuals, and the category of annual or biennial herbs has its highest percentage in these sites (19.3). In all the others they range from 1.2 to 9.3%, in most of them below about 5%. All of the habitats in which their percentages are above about 5% are located mainly in the lowlands along the main rivers, which have been the major travel routes since the early fur trading days. Many of the annuals in the shore flora are introduced weeds, so that it is not surprising to find relatively large proportions of this form in the flood-plain meadows and on river banks. Since the field work was done for this paper there has been much more travel away from the old routes, notably eastward into the Canadian Shield. It is probable that annual and biennial weed species have increased in numbers and distribution during the last 40 years.

The trees have minor roles in most of the habitats, although they have some prominence in the shrub-tree borders of muskegs and meadows, and particularly on the upper beaches of large lakes. They were found in small

numbers, as seedlings or very small trees, in all the other habitats except in open water and in muskeg meadows.

TABLE 1 gives the percentages of primary species produced by each of the life-forms in the various habitats. The only life-form that had primary species in all of the habitats is that of rhizomatous perennial herbs. In general, the forms that showed very low representations in one or more of the habitats produced no primary species or very few. On the other hand, rhizomatous perennials which showed consistently high percentages of all species produced some very low numbers of primary species. As might be expected, these were in the shrub muskegs, the shrub-tree borders, and in the saline or brackish habitats.

It was noted earlier that by far the largest geographic element in the shore flora is a group of 313 species that range widely in the boreal forest region, nearly all of them reaching across the northern part of the continent from Newfoundland to Alaska (FIGURE 3). The predominance of this affinity appears again in TABLE 2, where the representations of the

TABLE 2. Analysis of habitat floras for their percentage representations of the four major geographic elements of the shore flora. Numbers in parentheses are for primary species.

	Aquatic habitats, with both submerged and emergent species	Saline or brackish sloughs and wet meadows	Muskeg grass-sedge meadows with moss substrata	Open (treeless) shrub muskegs	Shrub-tree borders of muskegs	Damp to wet sand and/or gravel on shores of rivers and ponds or on lower beaches of large lakes	Upper beaches of large lakes: vegetation of upright shrubs and trees	Grass-sedge meadows on river floodplains or on local river deposits, with silt or silt and thin moss substrata	Shrub-tree borders of meadows on floodplains or local river deposits	Middle beaches of large lakes: vegetation of herbs and low or trailing shrubs
Nos. of species	42 (20)	57 (11)	78 (40)	161 (26)	81 (21)	114 (27)	66 (30)	108 (30)	100 (19)	89 (27)
Boreal forest	95.2 (47.6)	80.7 (19.3)	78.2 (42.3)	75.2 (12.4)	81.5 (19.8)	71.9 (21.1)	77.3 (34.8)	88.9 (26.9)	85.0 (17.0)	62.9 (15.7)
Arctic-alpine	2.4 (0)	1.8 (0)	12.8 (2.6)	13.7 (0.6)	7.4 (1.2)	15.8 (0.9)	9.1 (4.5)	0.9 (0)	3.0 (0)	18.0 (11.2)
Alaskan-Cordilleran	2.4 (0)	15.8 (0)	3.8 (2.6)	6.8 (0.6)	4.9 (2.5)	8.8 (0.9)	10.6 (4.5)	10.2 (0.9)	10.0 (2.0)	12.4 (1.3)
Timberline	0 (0)	1.8 (0)	5.1 (3.8)	4.3 (2.5)	6.2 (2.5)	3.5 (0.9)	3.0 (1.5)	0 (0)	2.0 (0)	6.7 (2.6)

four major geographic elements of the flora are noted as they appear in the ten habitats used in the present study. There is wide variation in their distribution among the habitats.

The boreal forest group shows a range of representation of about 33%. It is highest in aquatic habitats and lowest in the shrub muskegs and on the middle beaches of the large lakes. Other relatively high points are reached in the lowland meadows and in the shrub borders of these meadows. Another relatively low point is on the wet to damp sand or gravel beaches and river shores. All the other habitats have median percentages, ranging from about 77 to 81. The primary species produced by the boreal forest group vary from this pattern, although the highest percentage is also reached in the aquatic habitats. Their lowest point is in the shrub muskegs. Relatively high percentages appear in the grass-sedge muskeg meadows and in the shrub-tree borders of the upper beaches of large lakes. Though this element makes one of its largest contributions in the lowland meadows and their borders, its primary species in these sites are median. The reverse proportions appear on the upper beaches and in muskeg meadows, where the element has produced relatively large percentages of primary species.

The second major element of the shore flora, derived from wide-ranging arctic-alpine plants, contains 51 species. It makes very small contributions to the saline and aquatic habitats, none at all to lowland meadows, and only minor ones to the shrub-tree borders of these meadows. In the last two of these, the boreal forest plants are heavily represented. On the other hand, the element shows the highest percentage on the middle beaches of the large lakes, where the boreal forest group was near its lowest point. It is relatively high in damp to wet sand or gravel beaches and in muskegs, and in both of these habitats the boreal forest group is median. Thus the arctic-alpine species, in general, complement the boreal forest group in their distribution, suggesting that in general the wet sand and gravel beaches, the middle beaches of the large lakes, and possibly some of the muskegs most closely resemble the arctic habitats, while the lowland meadows and the shrub-tree borders more closely resemble habitats in the boreal forest region.

Primary species in the arctic-alpine element show very low percentages except in the middle and upper beaches of the large lakes, particularly in the former. This further suggests the general predominance of the boreal forest element, which is represented not only by the largest number of species, but also by a large proportion of the primary species. The unique position of the middle beaches is shown by the fact that the arctic-alpine group supplies almost as many primary species there (within about 5%) as the much more numerous boreal forest group.

The last two geographic affinities to be considered are the Alaskan-Cordilleran group, with 41 species, and the timberline group, with only 12 species. Both make only small contributions to the flora, but they differ considerably. The Alaskan-Cordilleran plants are most numerous on the middle beaches and in the saline or brackish habitats, and are relatively common on the sand and gravel shores and in the lowland meadows or their borders. Their lowest proportions are in the aquatic habitats, the muskegs and muskeg borders. Judged by distributions in the preceding

two elements, this proportion is indicative of the mixed boreal forest and arctic-alpine character of the Alaskan-Cordilleran element. It will be seen that the Alaskan-Cordilleran group contributes very small numbers of primary species to the vegetation (less than 5%) and none at all to the saline and aquatic habitats. The timberline group is by definition also a mixed one, bridging the arctic timberline. Compared to the Alaskan-Cordilleran element, it contributes, relatively, many more primary species.

SUMMARY AND DISCUSSION

This study deals with the shore vegetation of lakes and rivers in the Athabaska-Great Slave Lake region of northwestern Canada. It is based on about 130 transects that extended from open water to the shrub-tree borders. Ten habitat-vegetation complexes are defined to embrace the principal variations that were found. Definitions of the habitats are based mainly on differences in local topography, substrata, and moisture regimes. Vegetative components are defined physiognomically as grass-sedge meadows, treeless shrub muskegs, shrub-tree borders, etc. Within the habitats the vegetation is described in terms of assemblages of vascular plant species which are visibly different from one another owing to the abundance and/or prominence of one or more "primary" species. All other species in the assemblages are considered "secondary."

In the course of the field work 424 species of vascular plants were noted, seven of which were eliminated from the analyses because they were endemic or marginal and their behavior was not sufficiently known. Assemblages described numbered 550. Of these, 251 were found to differ from one another in their primary species composition. Thus the average number of times a given assemblage was repeated was 2.2.

One hundred and forty-five of the shore species were noted as primary in one or more of the different assemblages in which they occurred. All but 11 of them (134 spp.) were found in varying combinations of two to four species each, and 60 of these were also found as single primary species in their assemblages. The 134 primary species formed 180 different combinations. Twenty of these species were found in 7 to 19 combinations each, involving 75 other primary species and accounting for 128 of the 180 combinations observed.

With so little repetition among the assemblages, the feasibility of generalizing or rationalizing the vegetation in terms of these assemblages becomes remote. The large number of different combinations among the primary species suggests that most of the latter have very wide latitude in their "choice" of associates. It suggests a greatly reduced probability that species compatibility, or some kind of obligate relationship among species, has much effect upon the primary composition of the assemblages.

Coefficients of species' group relations to habitat, or of "preferred" associations among species, could be derived statistically, but the scale of refinement thus achieved would be far from commensurate with the scale of our present or foreseeable knowledge of the habitats; nor would it be

commensurate with our limited understanding of differences in behavior known to occur among the species.

About 60% (252) of all the shore species were found growing in more than one of the 10 habitats, some of them in as many as 5 to 7 (FIGURE 1). The "most successful" species — those that were found to be primary in the assemblages — were drawn mainly from those species growing in more than one habitat. It is proposed that the number of different habitats used by a given species is a rough index of its inherent tolerance or versatility ("ecological amplitude") in adjusting to habitat variation. It is suggested that the primary species have attained this rank at least in part because they are inherently more versatile than the secondary species. Their versatility appears to apply to both physical and biological habitats, for the primary species growing in the greater number of different habitats also formed the greater number of combinations with other primary species (FIGURE 2).

Size of geographic range appears to be correlated with differing tolerances of habitat variation. In general, the larger the continuous range, the greater the incidence of wide tolerance among the species. This is suggested by analysis of the major geographic elements of the flora (FIGURES 4, 5, & 6), but is shown more clearly by species that have more or less limited ranges within the Athabaska-Great Slave Lake region (FIGURES 7 & 8). A major floristic boundary shows much greater tolerance among the species that cross it even for short distances than among those that do not (FIGURES 8 & 9).

Wide versatility in habitat occupancy is not evenly distributed among life-forms of the plants. In the shore flora as a whole the trees and shrubs are the most versatile, while the herbaceous plants form a second group that do not differ greatly among themselves (FIGURE 12). The primary species in this group, however, show notable differences. Perennials that have fibrous roots as underground organs show considerably more versatility than the much more numerous perennials with caudexes, stolons, runners, or rooting stems. They are nearly as versatile as the primary shrubs. Least versatile are the perennials with taproots, bulbs, corms, tubers, or turions. Primary annual and biennial species are also very low in the scale of tolerance.

The life-forms of species in different geographic affinities show some notable variations from the above. Plants whose general ranges are arctic-alpine have appreciably greater versatility in their fibrous-rooted and taprooted perennials than is shown by these forms in the boreal forest or timberline affinities. This difference is shared in part by the Alaskan-Cordilleran affinity, which has in it an arctic-alpine element. It is probable that the wider tolerance in these forms reflects their predominance in the arctic tundra.

Variations in the incidence of wide versatility in the floras of the 10 habitats is shown in FIGURE 14. An explanation of the variation can only be suggested. It may be assumed that the most highly specialized species

in the flora, morphologically and physiologically, are the aquatics and the halophytes. If this is the case, they are the least likely to be found in other habitats and should show the least versatility, as they do in FIGURE 14. By the same reasoning, there should be some effects of specialization for partial desiccation toward the drier end of the moisture gradient. This is suggested among the last three of the habitats on the right side of the figure, where percentages of widely tolerant species are appreciably lower than in the preceding five habitats.

In view of the findings in this paper, it appears that the shore species of the Athabaska-Great Slave Lake region are behaving not so much as members of "communities" in which there are necessary relationships to specific habitats or to other species, but as populations of individual species that have found, perhaps in part by chance, sites that are satisfactory to them. Their adaptation to site seems to have considerable flexibility, which varies from one species to another. The flexibility is most pronounced among the primary species — those that give form and color to supposed "communities" and make the shore vegetation look the way it does. The present paper, therefore, has dealt primarily with the behavior and distribution of species rather than of "communities." The term "community" is replaced by "assemblage," which carries fewer implications of relationships that are nonexistent or unknown.

Only the effects of differences in versatility among the species are apparent, in local or regional behavior and distribution. It is presumed that the differences are due to biotypic or ecotypic variations within the populations which, in turn, have been conditioned historically. Such variations are known to occur in species that have been studied cytotaxonomically and experimentally (Turesson, 1922, 1925; Anderson, 1936; Clausen, Keck, & Hiesey, 1940; Mayr, 1964; Johnson & Packer, 1965). Their probable significance in the study of "dominance," and in the concept of "niche" in ecological systems, has been stated by McNaughton and Wolf (1970). The genetic differentiation of plant populations within small areas has been discussed by Bradshaw (1972), who concludes that "the ecological amplitude of most species . . . has a strong genetical component." Further understanding of the ecological and geographic behavior of the vegetation discussed here will depend in large measure upon investigations of its history and the processes of its inheritance. The starting point for this is at the species level.

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