A PHYTOSOCIOLOGICAL STUDY OF THE WOODY, FOREST VEGETATION OF THE CYPRESS HILLS

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A PHYTOSOCIOLOGICAL STUDY
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The Faculty of Graduate Studies,
University of Saskatchewan.

We, the undersigned members of the Committee appointed to examine the thesis submitted by Richard D. Newsome, B.S. in partial fulfillment of the requirements of the Degree of Master of Science, beg to report that we consider the thesis satisfactory both in form and content.

Subject of Thesis: "A Phytosociological Study of the Woody Forest Vegetation of the Cypress Hills."

We also report that Mr. Newsome has successfully passed an oral examination on the general field of the subject of his thesis.

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INTRODUCTION

The Cypress Hills are a prominent landmark on the Canadian Great Plains. Their sudden and considerable rise above the general landscape brings with it an equally abrupt vegetal transformation from tawny, semi-arid prairies to green, mesic forests and other, more luxuriant grasslands. The composition of these highland forests and prairies is dissimilar to that of the surrounding vegetations and has its nearest counterpart 200 miles away in the Rocky Mountains of Alberta and in the Aspen Grove Region adjacent to the Boreal Forest. This outlier is relict of at least early post glacial time and covers a landscape that, in part at least, was spared glacial occupation.

The forces which isolated these relicts have eliminated all but 6 tree species of which Pinus contorta var. latifolia (lodgepole pine) and Populus tremuloides (trembling aspen) are by far the most abundant. Picea glauca var. albertiana (white spruce) and Populus balsamifera (balsam poplar) are common but less abundant, and Betula papyrifera var. subcordata (white birch) and Acer negundo (Manitoba maple) are rare. For convenience, the first 4 species will be referred to as pine, aspen, spruce and balsam poplar respectively. Particularly noticeable is the absence of the genus Abies, an important constituent of most coniferous regions. Festuca scabrella is the most abundant grass of this elevated prairie and, together with Potentilla fruticosa, is largely responsible for its physiognomy.

Numerous spring-fed streams emanate from these uplands, providing the only available surface water for many miles. The lush vegetation of the Cypress Hills sustains this brook flow by stabilizing its watersheds and is, in turn, sustained by these same waters. Man, attracted to the hills by the timber and grazing land they offer, and needing this source of water, has sought to exploit their resources and to manage them for his own purposes. The variety and inconstancy of past management efforts attests to a lack of basic knowledge concerning the relationships of this vegetation to its components and to its habitat. A working knowledge of the climate, soils and vegetation of the Cypress Hills has yet to be synthesized.

The purpose of the present study has been to examine the distribution of the woody, forest species in an attempt to determine the basic interrelations between the forest communities. This is a preliminary analysis of limited scope, designed to test methods and to clarify problems in preparation for a more comprehensive study. The field work was conducted during the summer, 1961. Quantitative data were gathered from 26 stands, distributed to include as much variation as occurs in composition, slope, exposure, altitude and topographic position.

LITERATURE REVIEW

There have been relatively few botanical studies conducted within the Cypress Hills and these, most commonly, have been incidental extensions of investigations that pertain more specifically to other areas. A comprehensive description of the prairies on the surrounding plains and lower slopes has been provided by Coupland (1950, 1961) who viewed these as a series of faciations within the Mixed Prairie (Stipa-Bouteloua Association). Sandy loam sites in the Brown Soil Zone support a Stipa-Bouteloua Faciation, which gives way on more mesic sites to the Stipa-Bouteloua-Agropyron Faciation. This latter community extends into the dark-brown soil zone at higher altitudes but is replaced there, on well developed soils of intermediate texture, by the Stipa-Agropyron Faciation. This last variant is the most mesic of the three faciations and is dominated by _Stipa spartea_ var. _curtiseta_ and _Agropyron dasystachyum_, with _Stipa comata_ and _Agropyron smithii_ as abundant secondary species. _Bouteloua gracilis_ supersedes _Agropyron_ spp. in importance in the other two faciations, and in the Stipa-Bouteloua Faciation the Agropyrons contribute relatively little to the cover.

Above 4000', in the black soil zone, grassland sites are occupied by the Festuca scabrella Association (Coupland and Brayshaw, 1953). _Festuca scabrella_ contributes 57-60% of the cover of this prairie but _Potentilla fruticosa_ often gives it a physiognomy that contrasts with the appearance of this association in the Aspen Parkland (Coupland 1961; Moss and Campbell 1947; and Coupland and Brayshaw 1953). This is the Submontane Prairie of Clark _et al_. (1942).

The forests of the Cypress Hills were cited by Rowe (1959) as Boreal Forest outliers, and included within the Lower Foothills Forest (Section B-19a) and the Aspen Groves (B-17) of the Boreal Region. Moss (1955) labelled these "Boreal-Cordilleran Transition Forests" and Breitung (1954) emphasized their cordilleran relationships. The term "boreal" and "cordilleran" are, perhaps, arbitrarily applied but, in view of the mountainous distribution of Pinus contorta var. latifolia, Picea glauca var. albertiana and Betula papyrifera var. subcordata, and considering the ubiquitous distribution of the remaining tree species, the present writer favors the cordilleran affiliation.

Cormack (1945), Kagis (1951) and Gimbarzevsky (1955) presented qualitative descriptions of segments of the forested area from a silvicultural viewpoint, and Maini (1960) studied 12 Populus tremuloides sites in Saskatchewan in his investigation of the ecology of that species. Forest distribution with respect to topography, the influence of fire, successional sequences and growth rate variation according to site quality are discussed by each of these authors.

The flora of the Cypress Hills has been catalogued by Breitung (1954) and included in more general taxonomic works by Budd (1957), Moss (1959) and Breitung (1957). The orchids (Cormack 1948) and bryophytes (Bird 1962) have received individual taxonomic treatment.

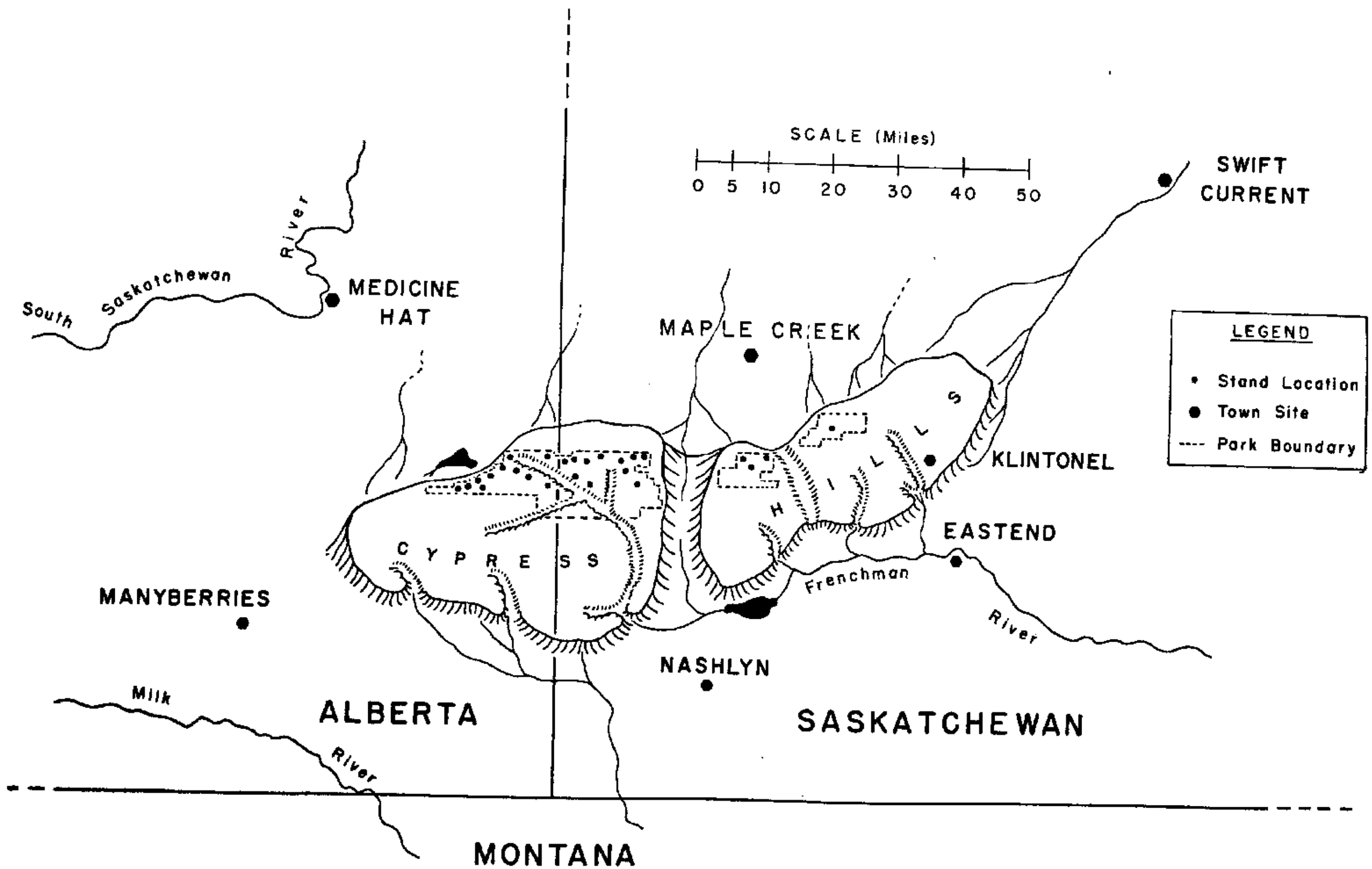
DESCRIPTION OF STUDY AREA

Location and Topography

The Cypress Hills extend for 82 miles, along an east-west axis, over the southern Canadian Plains in southwestern Saskatchewan and southeastern Alberta, 45 miles north of Montana and the United States border (Fig. 1). Their 4810' summit near Elkwater, Alberta is 2730' above Medicine Hat, Alberta, 25 miles to the northwest, and is the highest Canadian elevation between Labrador and the Rocky Mountains. From this summit, elevations decline gradually to the east, nearly three quarters of the Hills' length being in Saskatchewan. Eastend, Saskatchewan was so named because it is commonly taken as the approximate eastward limit of the Cypress Hills but their structure and geologic formations continue northeastward from this hamlet as a low ridge of hills, well blended with the rolling terrain of that region. The hills seldom exceed 15 miles in width and more often are 10 miles or less, giving a total area of about 1000 square miles.

Bold 1000-1500' escarpments edge much of the western and northern flanks and the eastern limit rises abruptly in a 400' scarp, but the southern margin grades imperceptibly into the plains through a series of sloping benches. The upland surface is undulating to hilly and rather well dissected in the east, but levels into a broad, flat plateau in the west, where dissecting forces have cut deeper but with less lateral planation. Headward erosion has been advanced mainly by streams draining to the south and many of these, such as Battle Creek, head almost back to the north escarpment, whereas,

Figure 1. Outline map of southeastern Alberta and southwestern Saskatchewan, showing general location of study areas in the Cypress Hills.


SCALE (Miles)
0 5 10 20 30 40 50
SWIFT CURRENT
MEDICINE HAT
South Saskatchewan River
MAPLE CREEK
LEGEND
Stand Location
Town Site
Park Boundary
KLINTONEL
EASTEND
CYPRESS HILLS
Frenchman River
MANYBERRIES
NASHLYN
ALBERTA
SASKATCHEWAN
Milk River
MONTANA

cutting from the north has been slight.

Wide valleys, coursing north and south, divide the Cypress Hills in Saskatchewan into three buttes. The valley through which Provincial Highway 21 was built, separates the eastern from the central butte, and this section is isolated from the western butte by the Gap, a local name for the valley in which Gap and Oxarart Creeks have their headwaters. The western butte is fairly continuous with the Alberta highlands except that the winding valley of Battle Creek heads so far to the north that it nearly severs the hills again. The gaps were broadened and given their present shape, as were the northern and western scarps, by Pleistocene glaciers and their meltwaters (Russell 1951).

The Cypress Hills ridge forms part of the continental divide between waters that empty into Hudson Bay and those that are carried to the Gulf of Mexico. Drainage to the north, theoretically, is by way of local streams into the South Saskatchewan River and then into Hudson Bay, but this flow is invariably restricted to internal drainage systems of intermittent streams and alkaline lakes and very little of this northbound water actually reaches the South Saskatchewan River. Contrariwise, the effluence through the southern drainage system is sufficient to continuously feed the Frenchman River which empties via the Milk and the Missouri Rivers into the Mississippi River and thence into the Gulf of Mexico.

Climate

Kendrew and Currie (1955) described the Cypress Hills region as being continental, with long, cold winters and cool, dry summers separated by very short spring and autumn seasons. Mean daily temperatures were used by these authors to delimit the seasons; 42°F. marking the transition into and out of summer and 32°F. performing this function for the winter season. Based on these criteria, summer and winter each persist for five months; April and October, respectively, being the spring and fall months. January has the coldest mean temperature and July has the warmest. The extreme temperature range recorded at Swift Current, Saskatchewan varies from -51°F. to +110°F.

The plains south of the hills are semi-arid, averaging 10" precipitation or less per year, but the totals increase north and west of there to a sub-humid status. The Cypress Hills receive more precipitation than any other location in this region (Kendrew and Currie 1955) with snow contributing 25% of the total. Seventy percent is received during the summer, the majority of this percentage falling in May and June. The period December through February is the driest. Snow deposition in the Cypress Hills area averages in excess of 50" annually, while other nearby localities receive less than 40", but the ground throughout the region is usually white from early November to mid-April.

The climate is further characterized by a predominance of sunny days and a frequency of strong, westerly winds which combine to seriously reduce the effective precipitation. Calm days are rare, and the prevailing winds, particularly the Chinook winds, strongly modify other climatic elements. "Chinook" is a local name applied to westerly winds that are noticeably warm and dry and usually of moderate to high velocity, but lacking precise definition (Kendrew and Currie

1955). The impact of these winds is made all the more obvious by the contrasting conditions that immediately precede and follow them. Local temperatures may rise and fall through 50°F. and long-accumulated snow quickly disappears, often by sublimation.

The Cypress Hills are situated in what is locally known as the "Chinook Belt", implying that chinook winds are more common here than elsewhere. The exact nature of their influence within the Cypress Hills is unknown, partly because of the limited climatic data for the Cypress Hills per se. At present, there is no year-round meteorological station within the hills of more than two years duration, except at Klintonel, near the eastern end. Stations in the provincial parks record temperature, wind and precipitation data from May till September and the Department of Transport has recently established several stations on the benchland that will provide useful information in the future.

A meteorological station was operated at the Battle Creek Ranger Station in the West Block, Saskatchewan, from 1919 to 1931. Kagis (1951) has compared data accumulated at this station with that recorded at Swift Current, Saskatchewan during the same period. The average annual precipitation for these 13 years was 18.5" at the ranger station and 13.5" in Swift Current. The minimum and maximum records at Battle Creek, and their years, were 13.4" (1919) and 30.5" (1927). The corresponding figures for Swift Current were 10.0" (1931) and 20.3" (1927). The mean annual temperatures for the period were 36°F. at the ranger station and 38°F. in Swift Current.

Data compiled from Canada Department of Transport records (1948) for stations nearest to the Cypress Hills are listed in Table 1.

Table 1. Climatic data for stations in the region of the Cypress Hills.

Station	Elevation	Years operated	1*	2	3
Klintonel, Sask.	3500'	36	57	16.7"	37°F.
Medicine Hat, Alta.	2144	55	126	12.8	42
Maple Creek, Sask.	2507	23	109	13.5	40
Nashlyn, Sask.	3100	37	88	10.8	37
Swift Current, Sask.	2440	52	106	14.9	39

*1. Average frost-free period (days)
2. Average annual precipitation (inches)
3. Average daily mean temperature for the year (°F.)

Higher elevations appear consistently cooler and have a shorter growing season. A 14-year record at Cypress Park, given in this same source, indicates that frosts can occur as late as July 12 and as early as July 17. The longest frost-free season on record was 96 days (May 30 to September 3), but the average is 46 days (June 18 to August 3). Precipitation appears to increase with elevation also, but the low average recorded at Nashlyn points out the need for more records of local reinfall and for more complete records generally.

Soils

Soil surveys for southern Saskatchewan and Alberta have been completed (Mitchell et al. 1944 and Wyatt et al. 1941) and the following comments are derived primarily from the reports of these surveys. The Cypress Hills occur within the brown soil zone and grassland sites on lower slopes have soils of this description. Higher on the slopes, the soils are dark brown and above 4000' black soils have developed, providing an example of vertical zonation. The dark brown soils on the Saskatchewan side have been classified as the Cypress Association and described as being of medium texture, developed on Tertiary sediments modified by glaciation. These occur mostly on nearly level to hilly sites and most commonly are loams and clay loams. Profiles are usually well developed, except that beds of loose pebbles and conglomerate sometimes are found close to the surface. Dark brown soils on the Alberta side have not been classified but appear to fit the general description of the Cypress Association.

Black soils occupy extensive tracts on the high, flat plateaux but can also occur as low as 3900' under well developed grasslands. In Alberta, these originated from a mantle of fine loessal materials that overlie conglomerate and gravel. This mantle is 2-5' deep near the "head of the mountain" and thins to the east, being only 4-6" deep at the Alberta-Saskatchewan border. The "A" horizon is 10" thick on the deep mantle and becomes thinner as the mantle depth lessens. No lime layer has been found to a 24" depth and it usually is too stony to probe deeper. Whether the black soils on the Saskatchewan side are related is unknown as these have yet to be described.

The upland soils of the Saskatchewan area are classed as the Dissected Plateaux Complex and include a variety of zonal and miscellaneous types. Grey soils (podsolic) have been found under some forested stands but these appear to be rare, the more common forest profile being azonal or truncated. Gravels frequently occur within 1 or 2 inches of the surface under pine, and aspen is often found on black or degraded black soils.

Geology

R. G. McConnell (1866) undertook the first comprehensive geological survey of the Cypress Hills, gave an account of their stratigraphy, discovered and described the conglomerate beds that underlie their summit plateaux, and set forth the first hypothesis to account for their preservation. The details and concepts originally presented by McConnell have been refined and modified by numerous, more recent studies (see Kupsch 1959) but Furnival (1950), Russell (1951) and Kupsch (1956) constitute the three principle modern references to the geology of the Cypress Hills. The description below is a summary of current opinion and information on their stratigraphy, origin and preservation.

A structural profile of the Cypress Hills would present to view a remnant of an anticlinal fold, plunging to the east, and consisting of six stratigraphic units resting upon a base that continues well beyond the hill boundaries (Russell 1951). The base is the Bearpaw Formation, the surface strata upon which Pleistocene deposits on the surrounding plains are strewn. The overlying units, in an upward sequence, are the Eastend, Whitemud, Battle, Frenchman, Ravenscrag, and Cypress Hills Formations. McConnell (1866) described the Cypress Hills Formation as consisting of water-worn pebbles, cobbles and boulders, mainly of chert and quartzite, interbedded in marl, silt and sandstone. Lower formations consist mostly of fine sands, shales, silts and lignite. The Bearpaw through the Frenchman formations are of Cretaceous age; the Ravenscrag and the Cypress Hills being of Tertiary age, Paleocene and Oligocene respectively. The upper six formations have been eroded from the surrounding plains (Lawson 1925) and their continuance here as a positive relief feature is, perhaps, the geologic aspect of these hills of greatest ecologic consequence.

Coincident with the Rocky Mountain revolution were many local uplifts which Furnival (1950) believes gave rise, in the Oligocene Epoch, to the Cypress Hills and their contemporaries, eg. the Sweet Grass Hills, the Little Rocky Mountains and the Bearpaw Mountains. Uplands had existed on the Cypress Hills location in pre-Oligocene time but by late Eocene these had been down-wasted and the site was occupied by a broad turbulent stream, flowing eastward from the Rocky Mountains. This powerful flow transported, and eventually deposited, generous quantities of sand, gravel and boulders which, under pressure and with the addition of finer particles, became cemented into conglomerate rock. Subsequently, in the Oligocene, the river bed was folded and uplifted, producing what Lawson (1925) and Alden (1932) have described as the Cypress Plain. The conglomerate, designated by Williams and Dyer (1930) as the Cypress Hills Formation, capped the surface of this plain.

Uplift exposed the conglomerate to heightened erosive activity which, after penetrating the cap rock, quickly abraded the lower sedimentary strata. These agents have now obliterated the entire plain except one isolated plateau, the Cypress Hills. A layer of conglomerate, grading from a 125' thickness in the east to 25' in the west, still caps the summit plateaux. The conglomerate rock has a variable hardness. It is commonly in lenticular beds and generally loosely cemented, and it is agreed that, while small outcrops of this rock are exceptionally erosion resistant, the formation as a whole is not sufficiently hard to account for the preservation of this plateau. Russell (1951) asserted that the Cypress Hills have continued into present time essentially because of their fortuitous position as a structural high, with drainage continually diverted away from, rather than across, their structure. The conglomerate has played a secondary role in that it has adequately resisted the lessened erosive forces.

Pleistocene History

The high plateau west of the Gap, and its attendant slopes, was never covered by Pleistocene glaciers. McConnell (1866) who first recorded this observation, stated that the unglaciated terrain extended upward from the 4400' contour and, during glacial periods, was probably a nunatak, reaching 400' above the glaciers and occupying nearly 83 square miles. Whether or not this nunatak served as a glacial refugium has provoked considerable speculation but the question remains unsettled. Evidence now available favors the interpretation that the relict vegetation migrated from the Rocky Mountains in post glacial time but, even if this is granted, it does not eliminate the possibility of a glacial refugium, for the invading vegetation could have incorporated or displaced glacial relicts. Further consideration of this problem will be limited to a summary of its more pertinent aspects.

Breitung's (1954) list of the Cypress Hill's flora totals 664 vascular species, of which none are endemic and 85 are distinctly cordilleran in origin. The remaining species include representatives of the Boreal Forest, the Aspen Parkland and the Fescue Prairie. These have affinities that are less clearly defined because many of the "boreal" species are also present in the foothill forests of southwestern Alberta (Moss 1955), and the Aspen Parkland and the Fescue Prairie border the cordilleran as well as the boreal forests. Hence, in considering the origin of this vegetation, a past connection with the Rocky Mountains can be assumed but contact with the northern boreal vegetation is not at all certain.

The apparent lack of endemic species is indicative of short-term isolation and is a strong argument against a pre-glacial interpretation of this flora. Contact with the Rocky Mountains in the post glacial period would most likely have occurred soon after the break-up of the Wisconsin ice sheet and prior to the onset of the warm, dry climate of the hypsithermal (Deevey and Flint 1957). Kupsch (1960) concluded that final ice recession near Herbert, Saskatchewan began about 10,000 years ago. In the Cypress Hills, it commenced earlier, possibly 15,000 years ago as suggested by some radiocarbon dates (Kupsch, personal communication). As the ice retreated, accumulated meltwater was discharged through eastward flowing drainage systems whose channels could have provided migratory routes, and whose debris-laden waters could have transported disseminules for western and cordilleran species. Löve (1959) considered this model to have been effective in extending cordilleran vegetation eastward, and it coincided in time with her estimate of the arrival of western species in Manitoba. Glacial stream channels occur close enough to the Cypress Hills to have provided migrating species easy access to their slopes.

Knowledge of post glacial conditions and vegetational migrations on the northern plains is exceedingly sparse, but Kupsch (1960) has presented evidence that coniferous forests did exist near Herbert, Saskatchewan in the early post glacial period. Whether these were part of a boreal zone migrating northward, or an eastern extension of cordilleran elements is unknown. Pollen of <u>Picea glauca</u>, <u>Picea mariana</u>, <u>Pinus</u> spp. and <u>Abies</u> spp. was identified but these species and genera could be assigned equally well to either forest type.

Objections to accepting a post glacial origin for the Cypress Hills flora are based largely on negative considerations, and stem primarily from the present lack of information, but they never-the-less have considerable merit. <u>Pinus contorta</u>, for example, forms hybrids with <u>Pinus banksiana</u> where their ranges overlap in north central

Alberta (Moss 1955). An eastward extension of P. contorta to the Cypress Hills, or to Herbert, Saskatchewan, or particularly into Manitoba, would have placed it in close juxtaposition to P. banksiana, if intermingling did not occur, and evidence of their hybridization could be expected. No such evidence has yet been reported for Manitoba or the southern edge of the boreal forest in Saskatchewan, and there is no suggestion of P. banksiana in samples from the Cypress Hills but Argus has examined trees near the south-eastern end of Lake Athabaska that are intermediates of these two species (personal communication)[1/]. This latter location is considerably east of the present range of P. contorta (Critchfield 1957; Smithers 1961) and suggests a prior, more eastward limit but intermediates have not been reported from the intervening area and the significance of this find can not yet be assessed. Further study of these and other species may reveal additional areas of hybridization and thus help to clarify post glacial migrations and fluctuations of species ranges.

Similarly, autecological studies and closer taxonomic scrutiny of the Cypress Hills flora may yet disclose endemic species, or, these may be located as the more remote valleys are explored. It is reasonably certain that cordilleran species had opportunity to reach the Cypress Hills in post glacial time but it can not be assumed that boreal species had the same opportunity. Many species probably did reach the Hills after ice recession but this generalization can not be extended to the entire flora.

Recent History

French fur traders who visited the Cypress Hills in the early 1800s were the first white men to explore this region (Eggleston 1951),

1/ Personal Communication. Dr. George Argus, Curator, W.P. Fraser Herbarium, University of Saskatchewan. 1962.

but many Indian tribes had begun to rely on the game and other resources the area provided at a much earlier date. These traders referred to the lodgepole pine (Pinus contorta) as "cypre", mistaking it for the jack pine (P. banksiana) of eastern Canada, and their name for the hills, "montagne de cypre", has subsequently been transformed to "Cypress Hills". The area became part of the Canadian Dominion in 1870 with the transfer of Hudson Bay Company lands to Canadian sovereignty, and in 1906 a small acreage was set aside as a Dominion Forest Preserve. The size of the preserve had been considerably enlarged, mostly by acquisition of private holdings, when control was transferred to the provinces in 1931 and this expansion is still being continued.

The Saskatchewan preserve, administered now by the Department of Natural Resources, includes 106 square miles, divided into three blocks, one being in each of the three topographic sections. The Alberta preserve, a 77 square mile area, is a single block of land, continuous with the West Block of the Saskatchewan preserve, and is operated by the Department of Lands and Forests. Most of the forests, plus the high plateau grasslands, are within the preserve boundaries but sites have been set aside for recreational purposes and permits are issued for grazing and mowing. Forestry operations are restricted primarily to cutting lodgepole pine and aspen for poles, posts, rails and firewood, but some spruce is harvested for lumber.

METHODS AND PROCEDURES

Criteria and Definitions

Criteria for stand selection were enumerated with as much detail as possible prior to the initiation of field work in order that the subjectivity of field decisions might be reduced to a minimum. It became apparent during this process that, while the meaning of certain terms were generally accepted, their precise limits varied and that the objectives of this study necessitated that their limits be clarified. The following definitions have, therefore, been adopted:

Woody vegetation: Included are all species which possess a perennial stem above the soil surface. Four classes are recognized: tree, sapling, seedling and shrub.

Tree: A woody, plant having a trunk that measures 3.7" diameter (12 square inches basal area) or greater, at breast height.

Sapling: A member of a species whose mature habit is a tree and whose present trunk measures less than 3.7" diameter but at least 1.0", at breast height.

Seedling: A member of a species whose mature habit is a tree and whose present trunk measures less than 1.0" at breast height. (Root suckers fall within this definition, albeit with their mode of origin being dismissed.)

Shrub: Any woody plant not included within the definitions given for a tree, sapling or seedling.

Forest: A tract of vegetation, a majority of the dominants of which are trees, growing sufficiently close together to provide a closed canopy.

Closed canopy: The condition in which tree branches are interwoven to the extent that at least an estimated 60% of the forest floor is overhung by the canopy.

Since this study has been restricted to considerations of forest vegetation, certain common communities of the Cypress Hills were excluded. Among these, in addition to grasslands, were the extensive areas of *Pinus contorta* and *Populus tremuloides* which are canopied entirely by sapling-sized individuals. Pine savanna and shrub communities were, of course, also excluded.

A forested site was accepted for study only if it met the following additional qualifications. Its size must be sufficient to allow the procurement of an adequate sample with the methods employed. One and one-half acres proved to be a minimum sufficient size and, while no upper size limit was set, uniform areas in excess of 10 acres were not found. The site must also display at least a minimum homogeneity of composition, slope and exposure, and evidence of disturbance (eg. by fire, cutting, flooding and/or cattle gazing) eliminated a site from consideration, unless these factors were judged to have been light and not to have exercised severe disturbance in the present tree generation. If disturbances were present but localized, they were bypassed by 30 feet, and stand margins were accorded the same interval to avoid edge effects.

Field Procedures

Trees were measured by the point-center quarter method (Cottam and Curtis 1956). This involved sectioning the area around a point into 4 quadrants, the direction of traverse serving as one bisecting axis and the second being drawn perpendicular to the first. In each quadrant, the distance to the nearest tree was measured and recorded, under the name of its taxon, together with its basal area at breast height. Eighty trees were measured in each stand.

Saplings, seedlings and shrubs (except 4 low-growing shrub species) were sampled by a circular quadrat having a 6' radius. Seedlings and saplings were counted and shrub species were noted for presence within the quadrat. The shortcomings of a circular quadrat are recognized but its accuracy was deemed sufficient for this preliminary study, particularly in view of the speed with which it could be employed. The four shrubs referred to above (*Arctostaphylos uva-ursi*, *Juniperus horizontalis*, *Linnaea borealis* var. *americana* and *Vaccinium caespitosum*) produced mats or were otherwise too abundant to be sampled by the circular quadrat and were checked for presence in a $\frac{1}{4}$-M^2 quadrat.

These methods were employed in a sequence that began with a reconnoitering of a stand and the selection of a compass line as the direction of traverse. The first point was objectively selected by tossing a quadrat stick over the shoulder and succeeding points were placed along the compass line at a predetermined interval. A surveyor's pin, placed in the soil at each point, served as the center of the circular quadrat, and the $\frac{1}{4}$-M^2 quadrat was nested at the pin in the leading, right quadrant. Twenty-five quadrats were required to obtain an adequate sample of the saplings, seedlings and shrubs, and seeing that an adequate tree sample required only 20 points, tree measurements were omitted at every fifth point. Since one traverse of a stand was not sufficient, additional lines were established parallel to the first but separated to avoid overlap of sample areas.

These measurements provided frequency data for all four classes of plants but are comparable only between classes measured by the same method. For example, a frequency measurement from the $\frac{1}{4}$ meter quadrat is not equivalent to one from the circular quadrat. Density figures were obtained for trees, saplings, and seedlings, and dominance values were provided for trees. The density figures, though obtained by different methods, are directly comparable.

Stand slopes were measured with an abney level, and exposures were determined by compass reading, both being allowed a 5° range of tolerance. All recorded exposure values have been corrected for magnetic declination. Stand altitudes were read from a topographic map and their physiographic positions were classified, using pre-selected catagories; eg. uplands, upper slope, mid-slope, etc. Soil horizons were measured and a soil sample was obtained by pooling aliquots from three locations within each stand. In each instance, the mulch was removed and the sample taken from the upper 6" of the solum. Plant specimens were collected and placed in the W.P. Fraser Herbarium at the University of Saskatchewan. Nomenclature is according to Moss (1959).

Treatment of the Data

Stands had been selected to provide a spectrum of physiographic positions against which compositional variation could be analyzed. Raw field data were summarized and converted to quantitative analytical characteristics (eg. frequency and density) but these express the status of species only within a single stand and do not, in themselves, describe variation between stands. Therefore, a composite index was required to compare the intra-stand qualities of a series of stands and to incorporate their differences into a measure of inter-stand variation. Motyka's (1950) index of similarity functions in this capacity and was employed in conjunction with the ordination techniques of Curtis and his co-workers (Bray and Curtis 1957; Maycock and Curtis 1960) to describe patterns of floristic variation which could then be compared to the physiographic spectra.

Motyka's index makes use of an analytical character (frequency, for example) to provide a coefficient of similarity between two stands, constructed by the formula $C = \frac{2W}{A + B}$. "A" equals the sum of frequency values in the first stand, "B" equals this sum in the second, and "W" is the sum of the shared frequency values for species common to both stands. If two stands were composed of an identical species composition, with each species having the same frequency in both stands, "C" would equal 1.0, since $2W = A + B$. On the other hand, $C = 0$ when two stands are devoid of common species. In practice, the coefficient is multiplied by 100, providing an index range from 0 to 100.

Each stand was compared with each other stand in this manner, using frequency values, to produce the 325 similarity coefficients presented in the matrix of Table 2. Similarity coefficients, when subtracted from 100, became coefficients of dissimilarity which can be translated into linear units to represent the relative distances which separate stands (Bray and Curtis 1957). Two stands perfectly alike have a similarity coefficient of 100 and a dissimilarity of zero, but such a perfect fit is not expected in practice; 85% being accepted as a near maximum similarity. Zero similarities do occur, however, providing complete separation of two stands.

When two stands are selected as the end-points (reference stands) of an axis, and their coefficient of dissimilarity is used as the length of the axis, all other stands can be positioned along this axis at points which represent, simultaneously, their dissimilarities to both reference stands. The longer the axis, the better will be the separation of unlike stands, provided, of course, that the reference stands are representative of whatever extremes exist within the vegetation. The sums of similarity coefficients for each stand point out which stand has the least similarity to all other stands, and since this stand marks the end-point of floristic variation along one gradient within the sample population, it can be accepted as the first reference stand. The stand with the greatest dissimilarity to the first reference stand must, then, embody a floristic quality that represents the opposite, measured extreme along this gradient, and will serve as the second reference stand. Stand No. 127 had the lowest sum of similarity coefficients (Table 2), and Stand No. 118 possessed the greatest dissimilarity (96.6 units) to Stand No. 127.

The matter of positioning stands along the axis is essentially

Table 2 (Cont'd.). Matrix of similarity coefficients based on frequency values for saplings, seedlings and shrubs.

Stand number	118	119	120	121	122	123	124	125	126	127	128	129	130
101													
102													
103													
106													
108													
109													
110													
111													
112													
113													
114													
115													
116													
118	-												
119	66.7	-											
120	23.3	52.8	-										
121	23.6	52.7	67.2	-									
122	69.2	53.1	28.4	33.3	-								
123	30.8	44.1	51.2	58.1	37.5	-							
124	21.1	35.7	37.9	49.3	27.7	75.6	-						
125	38.4	55.6	57.6	57.8	40.5	57.2	54.9	-					
126	2.4	25.3	48.1	58.6	15.0	49.5	36.5	37.2	-				
127	3.4	21.3	31.1	47.3	20.6	33.3	19.9	26.0	55.9	-			
128	11.1	42.0	53.5	60.9	18.3	54.6	53.4	55.1	43.1	35.3	-		
129	16.2	18.4	32.1	35.1	18.3	67.7	56.4	30.3	41.8	26.5	38.6	-	
130	26.7	21.2	27.1	41.5	35.5	41.1	31.7	36.4	34.6	27.5	42.6	45.8	-
Stand total	859.9	1133.9	1172.6	1242.2	934.0	1415.9	1181.9	1226.0	993.0	707.8	1098.5	1074.5	951.7

Table 2. Matrix of similarity coefficients based on frequency values for saplings, seedlings and shrubs.

Stand number	101	102	103	106	108	109	110	111	112	113	114	115	116
101	-												
102	33.4	-											
103	52.5	35.5	-										
106	51.7	53.3	64.7	-									
108	49.9	48.1	55.3	62.2	-								
109	39.5	60.2	44.6	64.9	79.0	-							
110	45.2	55.9	50.6	72.3	71.2	78.5	-						
111	58.5	26.7	62.1	60.4	40.6	42.9	49.4	-					
112	35.2	40.9	25.1	61.5	37.3	45.8	50.2	56.5	-				
113	73.4	41.2	71.5	70.9	57.1	50.6	64.2	60.0	44.9	-			
114	67.7	47.3	64.9	70.3	66.4	63.0	70.8	57.4	52.6	75.9	-		
115	56.6	44.6	62.9	82.0	61.2	58.4	67.0	61.6	60.6	68.8	74.6	-	
116	64.7	24.0	56.0	46.0	43.5	34.9	44.6	51.4	23.8	69.2	60.0	43.2	-
118	51.0	14.8	41.4	40.8	28.4	32.0	42.4	53.3	24.7	59.0	45.1	34.7	59.4
119	59.7	20.3	50.9	56.2	34.1	39.6	47.5	71.1	52.3	59.8	51.8	52.9	48.8
120	56.9	24.1	65.3	57.7	44.1	34.8	39.5	70.3	58.1	54.1	54.8	60.7	41.9
121	45.6	39.2	61.4	66.2	47.4	40.4	50.6	54.8	64.6	23.7	63.2	68.5	31.2
122	52.2	22.8	47.7	47.1	27.9	33.1	43.9	48.4	28.6	40.4	45.2	43.2	55.1
123	45.2	56.3	56.2	79.9	71.7	74.9	77.8	53.7	51.4	60.3	67.7	76.3	43.8
124	29.5	56.7	37.3	63.9	67.0	78.6	73.9	43.3	48.7	43.0	55.3	61.6	23.0
125	41.9	35.3	44.4	56.1	43.8	51.5	58.2	66.7	59.0	55.1	54.3	60.9	51.8
126	37.7	44.5	42.5	56.0	36.9	35.1	34.8	33.3	49.8	48.4	47.2	54.8	24.0
127	22.8	25.0	31.8	36.7	17.7	19.8	19.2	28.4	41.7	34.5	28.6	36.2	17.3
128	29.4	48.1	77.7	56.4	38.1	47.7	50.0	51.3	72.5	35.1	47.8	56.3	19.6
129	34.1	54.4	44.6	55.8	70.4	67.7	68.1	29.4	36.1	49.6	52.8	49.7	34.6
130	28.1	51.3	40.0	46.0	44.1	40.5	47.6	24.5	47.8	43.8	48.0	41.9	35.4
Stand total	1162.4	1003.9	1246.9	1479.0	1243.4	1258.0	1373.4	1256.0	1169.7	1354.5	1432.7	1439.2	1047.2

a geometric problem which Beals (1960) has analyzed in terms of the Pythagorean theorem (Figure 2). This relationship is particularly useful because it provides a co-ordinate that accurately designates stand positions along an axis, but use of the formula is subject to the following limitations:

1. (dA^2) must be equal to or less than $(L^2 + dB^2)$.
2. $(dA + dB)$ must be greater than or equal to (L).

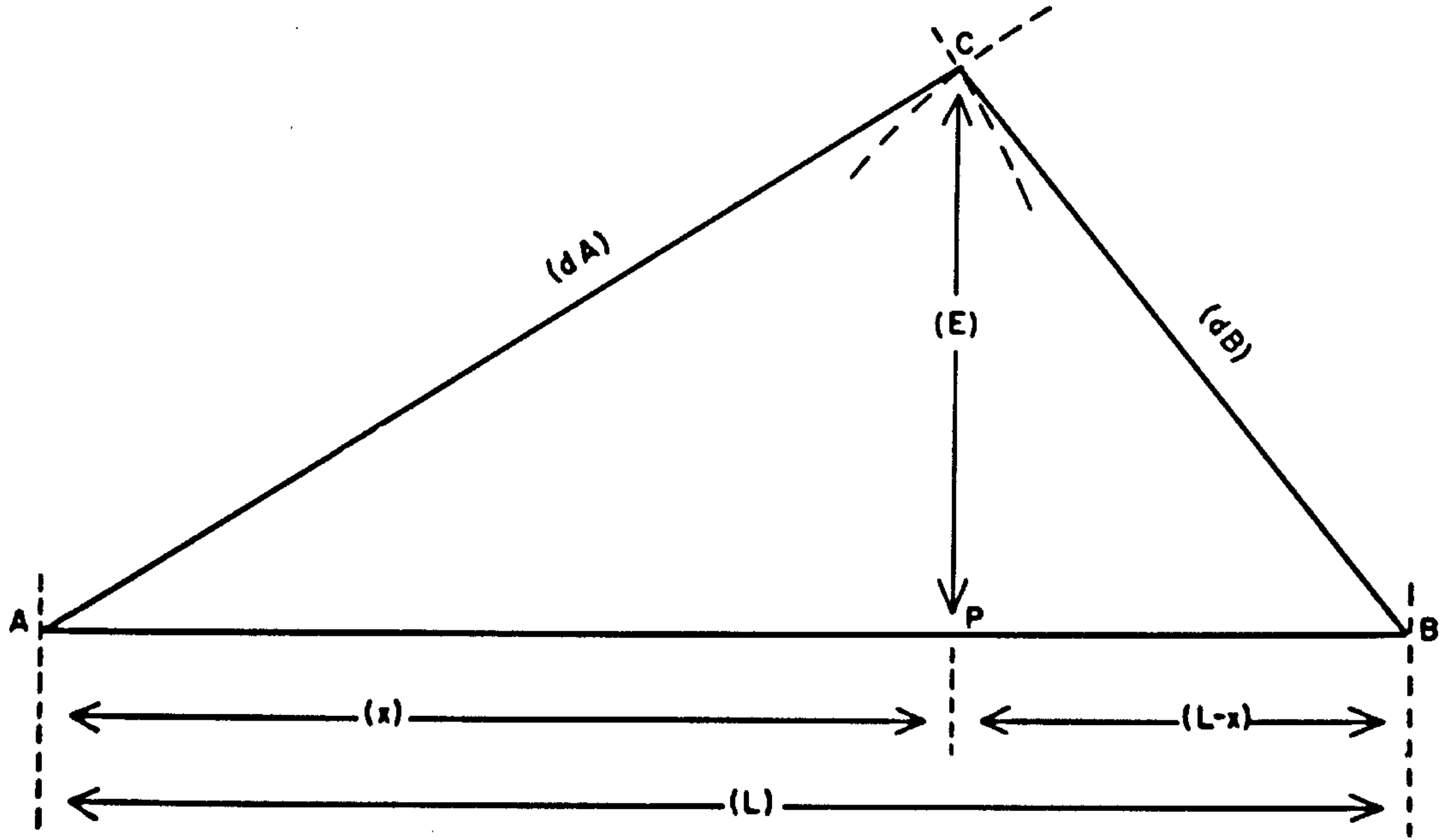
If the first condition is violated, the stand will fall beyond the limits of the axis. This limitation is most apt to arise in constructing secondary or tertiary axes (see below) where the choice of reference stands is somewhat restricted. If (L) is greater than (dA + dB), the dissimilarity axes can not intersect; no apex will exist; and, hence, the stand can have no co-ordinate. No situation has been reported in the literature in which this latter condition would not be met and it may be merely a geometric limitation with no vegetational significance.

Stands with very little similarity may occur close together on an axis. A stand with zero similarity to both reference stands will be positioned at the mid-point of the axis; a position similarly occupied by a stand with 50% similarity to each reference stand. If the reference stands represent end-points of the variability of an environmental factor or factor complex, those stands which are primarily influenced by this factor ought to fall directly on, or near, the axis. Stands which are primarily influenced by other factors will be positioned further away from the axis. The point at which a stand "falls" is at the apex of triangle ABC of Figure 2, and the altitude of this triangle is a measure of the goodness of fit of a

Figure 2. Illustration of the geometric model used to position stands along ordination axes. Adapted from Beals (1960).

A = Reference stand No. 1.
B = Reference stand No. 2.
C = Stand to be positioned along the AB axis.
dA = Dissimilarity of Stand C to Stand A.
dB = Dissimilarity of Stand C to Stand B.
L = Dissimilarity of Stand A to Stand B.
P = Position of Stand C on the AB axis. (by projection from the arc intersection at C).
e = A measure of the goodness of fit of Stand C to the AB axis. The lower the value of "e", the better the fit.

$$X = \frac{L^2 + (dA)^2 - (dB)^2}{2L}$$


C
(dA)
(E)
(dB)
A
P
B
(x)
(L-x)
(L)

stand on that axis. The shorter the altitude, the better the fit, and conversely, as the altitude lengthens, the control exerted by the axis in question lessens. A stand that bears 50% similarity to both reference stands has a perfect fit on the axis (e = 0); but "e" is at a maximum, and fit is the poorest, when a stand has a 100% dissimilarity to both reference stands. Both stands in this example have, however, the same co-ordinate position.

In the present study, the degree of dissimilarity between closely positioned stands was great enough to warrant the construction of a second axis. By common notation, the first axis is labelled the X-axis; the second is the Y-axis; and the third, if needed, is the Z-axis. If the X-axis represents the gradient of one controlling factor, or factor complex, and certain stands are poorly associated with this axis, they, presumably, are controlled by a second set of factors and the stand with the poorest fit on the first axis can be used as a reference stand for the second (Y) axis. The second reference stand for the Y-axis ought to have as great a dissimilarity to the first as possible but it is also necessary that these two stands be in close juxtaposition on the X-axis. These restrictions are necessary in order that the Y-axis embody the full measured range of the Y-axis factors. Stands located near the ends of an axis are more likely to be controlled by factors operating along that axis than are stands placed nearer to its mid-point. Conversely, secondary factors are probably non-limiting near the ends of an axis, but these have equal opportunity to be limiting near the mid-point. Hence, stands in which both extremes of the Y-axis factors are limiting will probably occur close together, and near the center of the X-axis.

Various methods have been described for selecting the second reference stand for secondary axes, but that employed by Bray and Curtis (1956) best fulfilled the conditions imposed by this study. This method limits the stands eligible for selection to those that occur within a zone equal to 10% of the X-axis on either side of the first Y-axis reference stand. Stand No. 2 had the poorest fit on the X-axis, and Stand No. 20 was selected as the second reference stand. The Y-axis is 75.9 units long and stand positions along it were determined in the same manner as that used for X-axis positions.

Each stand now has two co-ordinates which combine to place it on a plane bounded by the X and the Y axes. This two dimensional ordination appeared to provide adequate dispersal of the stands so a tertiary axis was not constructed. If a third axis had been required, a new means of selecting reference stands would have to have been adopted. The stand with the poorest fit on the Y-axis was Stand No. 18, a reference stand on the X-axis, and rather than producing a Z-axis, the procedures used here would simply have reproduced the X-axis.

Comparison of Three Ordinations

The question arose as to which analytical value was most capable of characterizing a stand; i.e., would density and frequency produce the same ordinations? Three separate ordinations were calculated in an attempt to resolve this question for the present study. The values used were: 1. percent frequency for all woody vegetation, 2. percent frequency for forms sampled by the circular quadrat, and 3. density (number per acre) of trees, saplings and seedlings. A two dimensional ordination was necessary in each case to achieve adequate separation of dissimilar stands, and then stand positions along each axis were compared by rank correlation (Table 3). Values of "t", calculated for the correlation coefficients, appear extraordinarily high and, perhaps, can best be used on a comparative basis. For example, the relationship $X_1 = X_2 = Y_3$ and $X_3 = Y_1 = Y_2$ are much more probable than $X_1 = X_3$ even though the table of "t" lists this latter relationship as significant at the 1% level of probability. On this basis, it can be stated that $X_1 \neq Y_1$, $X_2 \neq Y_2$, and $X_3 \neq Y_3$; each axis of a single ordination is, in fact, an independent axis. Stand sequence is certainly not the only important aspect of an ordination axis but interstand distances, for example, which are equally important, are not as subject to statistical comparison.

It was also true that one axis in each ordination graded from spruce to pine, with aspen in the middle, while the other axis separated the aspen from the coniferous stands. Analysis of these three ordinations suggested that they were essentially the same ordination and that quadrat frequency was as capable of characterizing these stands as any other measurement available. In as much as it was the most readily calculated value and had not been previously used by itself in the construction of a forest ordination, it was adopted as the basis of the ordination presented herein. It should be noted that in using this value, two segments of the measured vegetation did not figure in determining stand positions. These were: trees (measured by the point-center quarter method) and prostrate shrubs (measured by the $\frac{1}{4}$ meter quadrat).

Table 3. Comparison of the axes of three ordinations by rank correlation of stand positions. Subscripts designate the ordination to which axes belong. Ordinations are based on: 1. frequency values for all woody species, 2. frequency values for saplings, seedlings and shrubs, and 3. density (number per acre) of trees, saplings and seedlings. Significance levels: *** - .001, ** - .01, * - .05.

		X_1	X_2	X_3	Y_1	Y_2	Y_3
X_1	r	-	-.92**	+.51**	-.26	-.38	-.90**
	t		11.48***	2.91**	1.34	2.05	10.11***
X_2	r		-	-.37	+.14	+.33	+.86**
	t			1.94	0.70	1.69	8.23***
X_3	r			-	-.72**	-.69**	-.34
	t				5.04***	4.70***	1.70
Y_1	r				-	+.95**	+.16
	t					14.74***	0.81
Y_2	r					-	+.31
	t						1.58
Y_3	r						-
	t						

Soil Analysis

All analyses were conducted on soils which had previously been air dried and passed through a 2 mm. sieve to remove small roots, pebbles and debris. Water-retaining capacity was determined by the Hilgard cup method (Curtis. 1956). In this procedure, the upper receptacle of the cup is filled with soil, tapped to settle the soil but not to compact it, and the cup is placed in a pan of water. The water level is adjusted so as to just moisten the lower soil surface, in order that the soils may be thoroughly wetted by capillary action. When the soils have been saturated, the cups are removed from the water, the excess moisture is allowed to drain away, and the soils are dried at 105°C. for 72 hours. Three weighings are made, to ascertain: 1. cup weight, 2. cup + wet soil weight and, 3. cup + oven-dry soil weight. Water retaining capacity is calculated from the formula:

$$WRC = \frac{\text{wet weight - oven-dry weight}}{\text{oven-dry weight - cup weight}} \times 100$$

The water retained is expressed as a percent by weight of the oven-dry soil. Two replicates were run, the average difference between replicates being 3.2%, and the average values were taken for use. This measure of water retention is an approximation of field capacity, but, while it gives a value that is less than saturation, it may exceed field capacity because of the lack of control over the quantity that drains away.

Soil texture was determined by the Bouyoucos (1951) hydrometer method. Three texture classes (sand, silt and clay) were separated and expressed as a percent by weight of the total weight. This is not as accurate a method as the pipette method but it is considered sufficiently accurate for comparative purposes (Toogood and Peters 1953) and has the advantage of being more rapid.

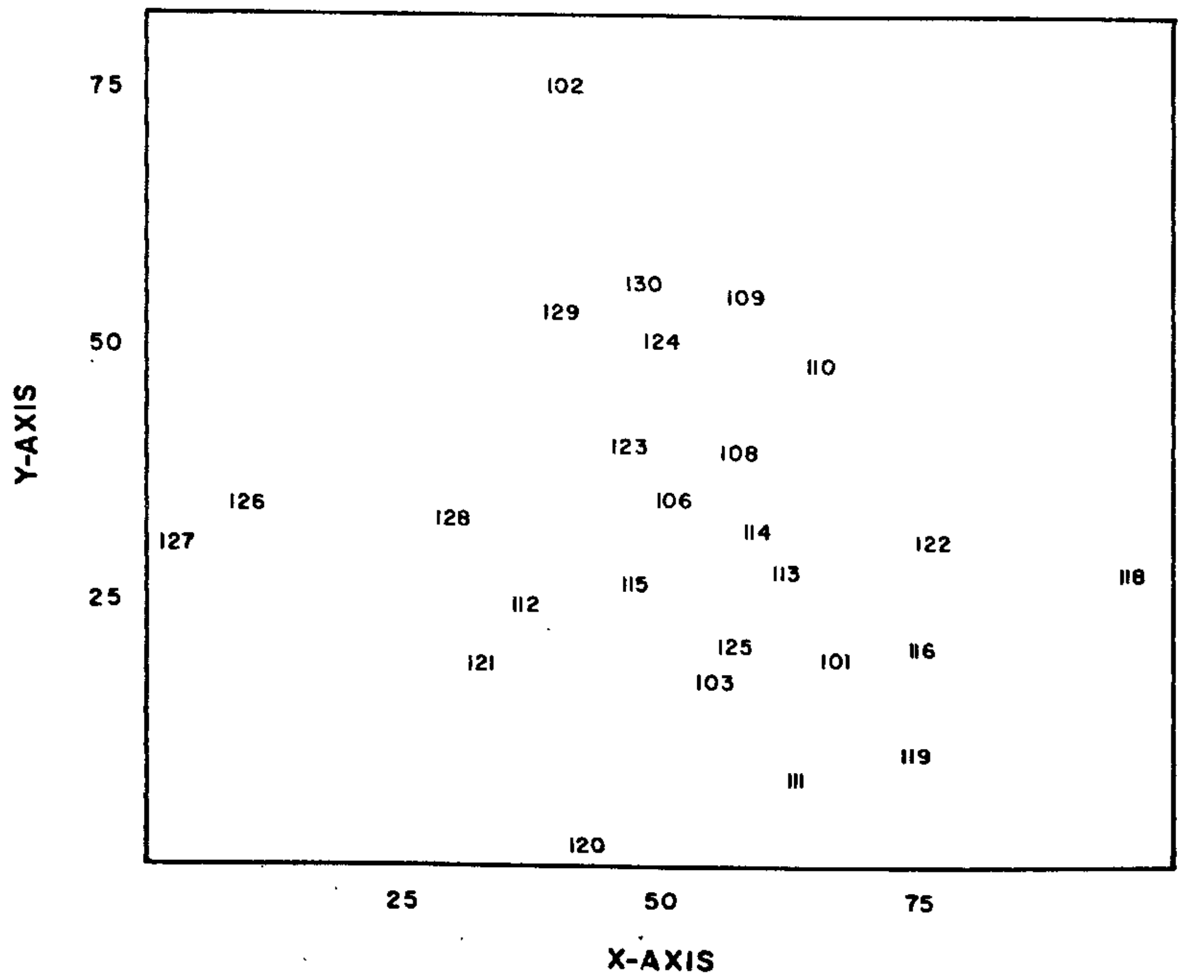
RESULTS

Tree Species

Forested sites in the Cypress Hills consist, most commonly, of a mosaic of relatively small areas (1-5 acres) within which the canopy is composed exclusively, or nearly so, of a single species. Thus, since only four tree species contribute to the canopies, the forest physiognomy is highly similar. Stands in which second ranked species have frequencies of less than 10% will be considered as "pure" stands, and "mixed" stands can be understood to have at least one secondary species that achieves a frequency of 10% or higher. This is a useful, if somewhat arbitrary, distinction. Each recorded tree contributed 5% to the frequency of its species and, since chance encounters with isolated individuals did occur, this distinction separates such isolates from species that can effectually be designated as secondary.

Of the 26 stands sampled, 4 are pure pine, 6 are pure aspen, and the remaining 16 are mixed stands with varied combinations of species numbers and rank sequences. Spruce and aspen are each present in the canopies of 22 stands, and pine and balsam poplar occur in 15 and 14 respectively. No pure spruce stands were found; nor any in which balsam poplar is the first ranked species. Stand positions within the two-dimensional ordination are shown in Figure 3, and their co-ordinates are listed in Table 4. The paucity of tree species makes the use of relative values impractical, thus eliminating the use of importance values and making it necessary to treat density, frequency and dominance individually.

Figure 3. Distribution of stands within the ordination. Numbers shown in the figure are stand numbers.



102
130
109
129
124
110
123
108
126
106
128
127
114
122
113
118
115
112
125
121
101
116
103
119
111
120
75
50
25
Y-AXIS
25
50
75
X-AXIS

Table 4. Stand co-ordinates for the X and Y ordination axes.

Stand no.	Ordination axis X	Ordination axis Y
101	66.7	21.0
102	39.8	75.9
103	54.6	18.5
106	50.9	35.7
108	56.8	40.8
109	57.7	55.5
110	64.9	49.3
111	63.5	8.4
112	36.5	26.5
113	61.8	29.1
114	59.1	33.1
115	47.3	27.9
116	75.2	22.1
118	96.6	28.9
119	74.6	10.8
120	42.4	0
121	32.5	20.7
122	76.0	32.5
123	46.5	41.1
124	49.3	51.0
125	57.0	22.2
126	9.1	35.4
127	0	32.2
128	29.1	34.4
129	39.9	54.6
130	47.7	57.3

Density

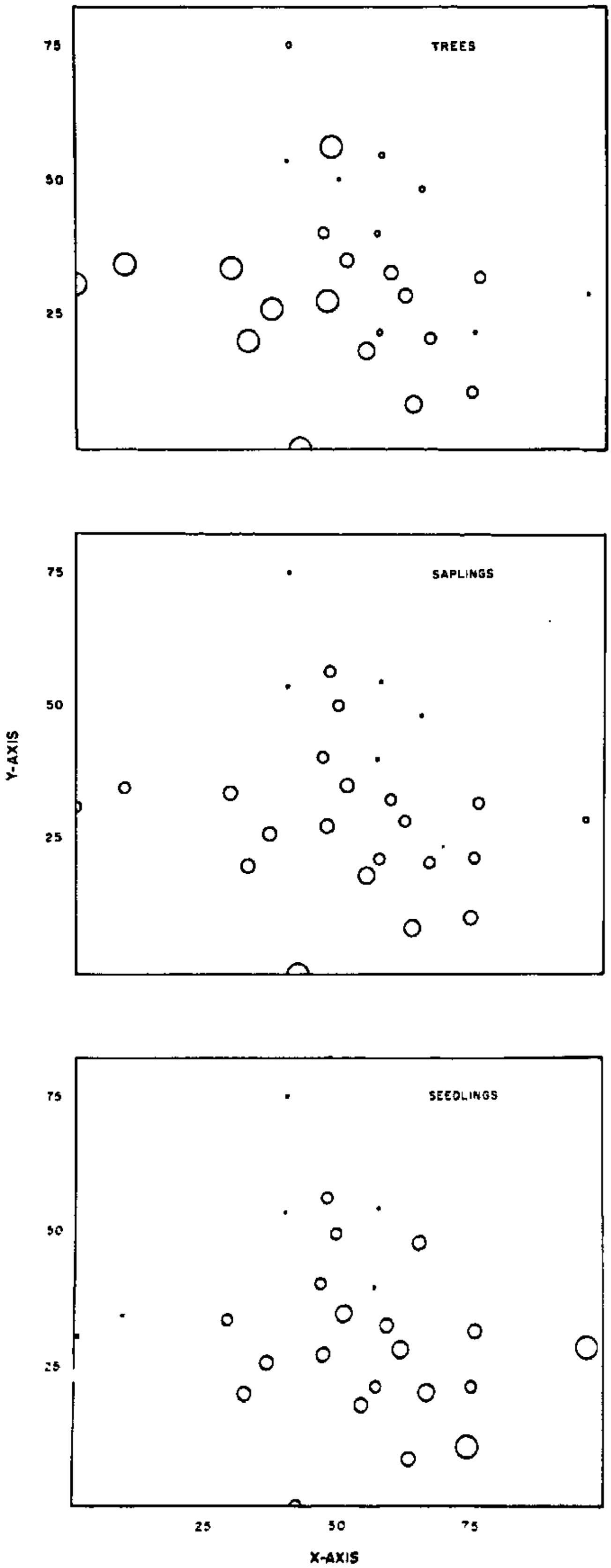
Tree density values (Table 5) are not randomly distributed within the ordination (Figures 4, 5, 6, and 7) but, rather, the high density values for each species are clustered, forming separate centers of prominence for pine and aspen and a combined center for spruce and balsam poplar. Tree densities decrease continuously toward the periphery of these centers but each species displays a unique pattern, particularly as regards its reproductive stages, and these can best be described by considering the species individually.

High density values for spruce trees are centered in the lower, left quarter of the ordination (Figure 4) and decline sharply to the right and upward away from this center. Stand No. 130 appears to disrupt this pattern and others that will be described but it would, perhaps, be moved from this region on a tertiary axis. This assumption is based on the dissimilarity that exists between Stand No. 130 and those adjacent to it (Table 2). At the border of the center of spruce tree density, especially along the right, lower edge, is a zone of high sapling density, and still further to the right is a zone of high seedling density. Spruce seedlings achieve a considerably higher density than do the saplings or trees; this reduction with size, and probably with age, being evident in the field as dead spruce saplings become more common as the canopy is filled with spruce. Spruce seedlings and saplings are most abundant under pine and achieve a slightly lower production under mixtures of pine and aspen (compare Figures 4, 5 and 6). These figures also demonstrate that peak density values for spruce seedlings and saplings do not coincide, which contrasts with the reproductive pattern for aspen.

Table 5. Density values for tree species. Values given are the number per acre.

Stand	Picea glauca			Pinus contorta			Populus balsamifera			Populus tremuloides		
	Tree	Sapling	Seedling	Tree	Sapling	Seedling	Tree	Sapling	Seedling	Tree	Sapling	Seedling
101	8	31	570	571	31	31				38		277
102										718	755	8509
103	182	478	293	436						16	15	154
106	66	200	524				18		77	395	31	509
108										1027	77	1865
109										1150	108	1326
110			277				13		15	996		1372
111	218	570	231	653	46	15						15
112	324	170	524	5			9		15	32		123
113	53	108	1249	433					62	46		663
114	102	46	385	133		15				579	139	262
115	234	154	385	98			53	15	62	219	31	570
116		15	31	1155		15						46
118			1264	1155		15						
119	12	293	1125	928		15						62
120	528	740	123	149	15		9			18		200
121	409	324	339	20			33			58	15	432
122	20	31	170	1499	77							15
123	19	62	46				25			450	46	786
124		15	123	10						785	154	1619
125		15	15	939	93	15				24		308
126	511	108					207		247			1696
127	463	93					24		31			
128	773	173	96							20		135
129							38		15	971		1603
130	559	15	15				9		15	100		185

Figure 4. Phytosociological behavior of Picea glauca based on density values (number per acre). The density range is divided into six classes, each successively higher class being represented by a larger circle. Class intervals: less than 50; 51-100; 101-250; 251-500; 501-1000; and more than 1000 per acre. Absence of a species in a particular stand is indicated by a solid circle.


TREES
SAPLINGS
SEEDLINGS
75
50
25
Y-AXIS
25
50
75
X-AXIS

High densities for pine trees (Figure 5) are nearly double that effected by spruce, and are positioned in the lower, right quarter of the ordination nearly contiguous to the spruce center. The pine density center is smaller than that occupied by spruce but it is similarly delimited by a sudden drop in values at its left and upper margins. Pine reproduction is poor on forested sites but is best near the margin of its tree density center. Pine seedlings and saplings are present in far fewer stands than either spruce or aspen, are limited to significantly lower density levels, and are restricted almost entirely to stands with a predominantly pine canopy.

Aspen densities, shown in Figure 6, are centered in an upper, central position within the ordination and achieve a stocking level that is intermediate between that of pine and spruce. The center of aspen tree density extends into the zone separating the spruce and pine centers and then declines abruptly toward the sides but aspen continues, at a low level, to the base of the ordination. Aspen reproduces at a relatively high rate, comparable to that for spruce, and gives indication of fairly successful reproduction, but in contrast to this latter species, it does best under its own canopy. The sapling zone is smaller than the seedling zone, suggesting that seedling (actually sucker) mortality is higher under spruce and pine.

Balsam poplar (Figure 7) is associated primarily with spruce, secondarily with aspen, and appears rather restricted to a zone between the centers of prominance of these two species but the absence of stands in this sample in which balsam poplar is the leading dominant may account for this apparent restriction. That such stands occur is certain, but these have been severely disturbed by beaver wherever

Figure 5. Phytosociological behavior of _Pinus contorta_ based on density values (number per acre). The density range is divided into six classes, each successively higher class being represented by a larger circle. Class intervals: less than 50; 51-100; 101-250; 251-500; 501-1000; and more than 1000 per acre. Absence of a species in a particular stand is indicated by a solid circle. Pine seedlings are represented only in the lowest class, and saplings occurred only in the lowest 2 classes.

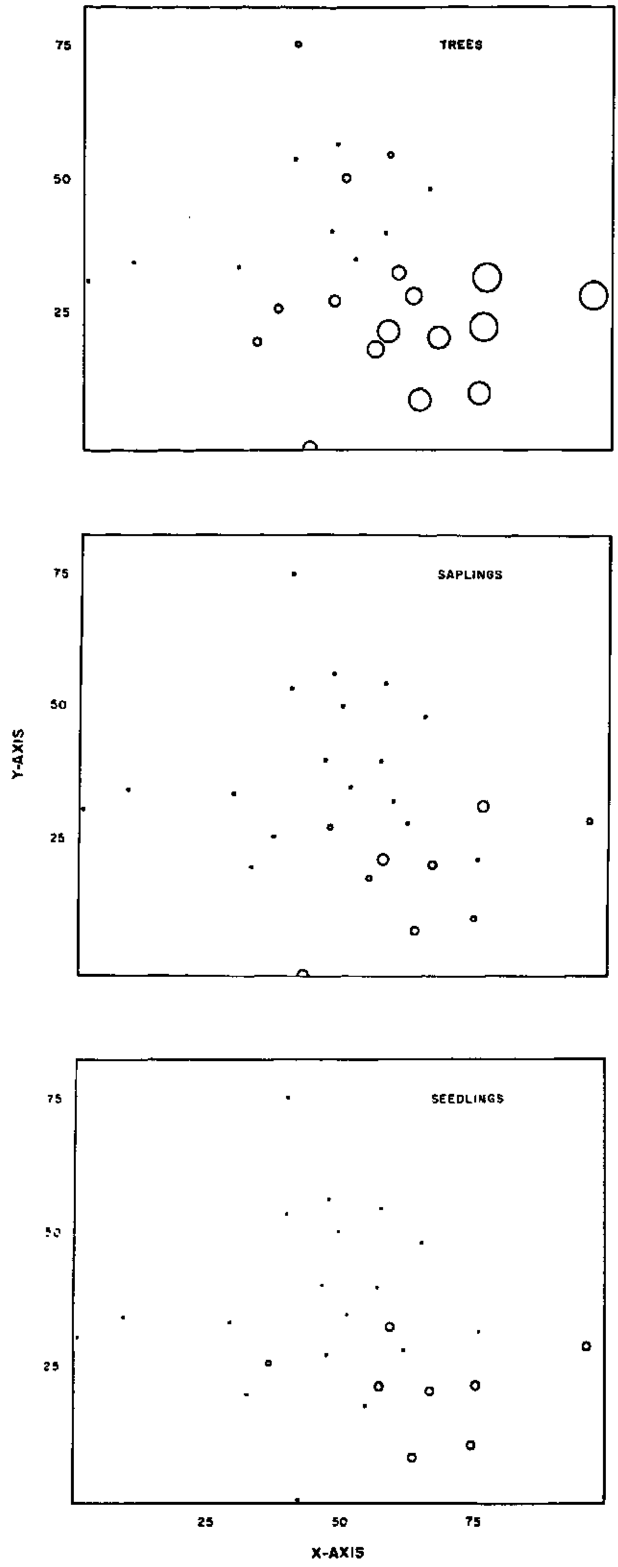

TREES
SAPLINGS
SEEDLINGS
75
50
25
Y-AXIS
X-AXIS

Figure 6. Phytosociological behavior of _Populus tremuloides_ based on density values (number per acre). The density range is divided into six classes, each successively higher class being represented by a larger circle. Class intervals: les than 50; 51-100; 101-250; 251-500; 501-1000; and more than 1000 per acre. Absence of a species in a particular stand is indicated by a solid circle. The density of aspen seedlings in Stand No. 102 (topmost circle) is in a class by itself; 8500 per acre.

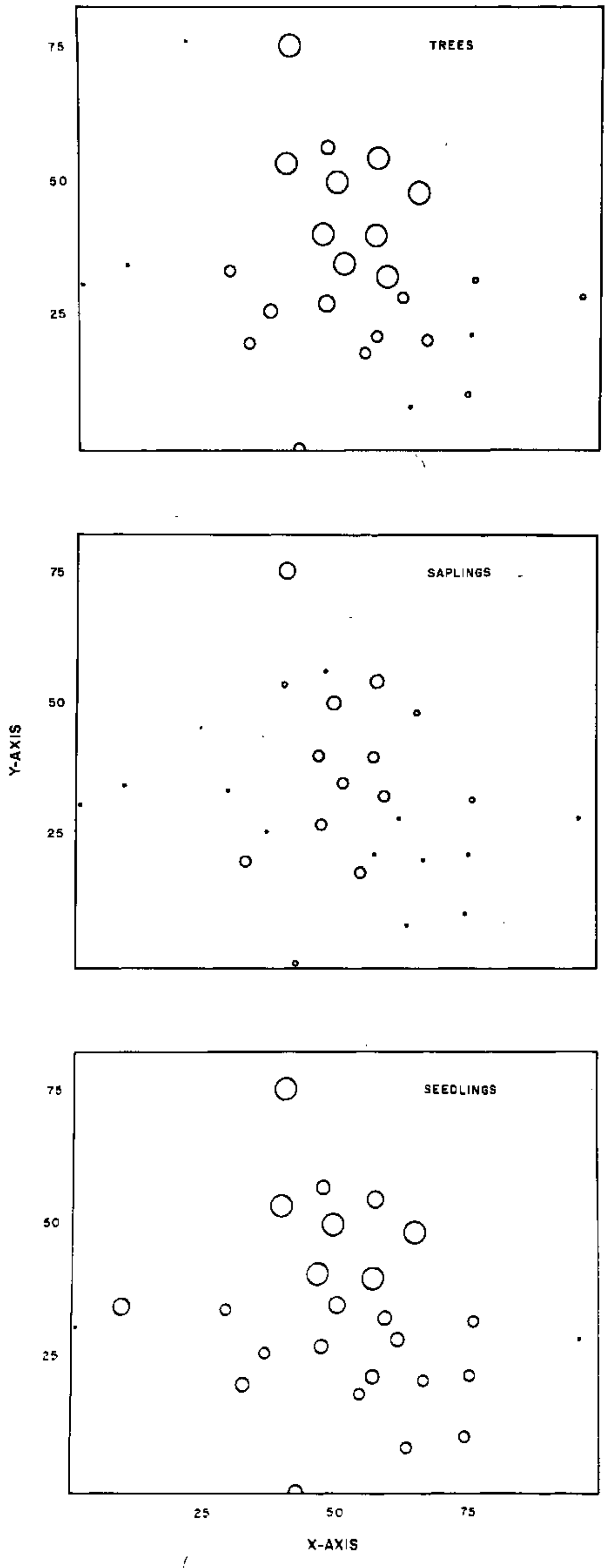
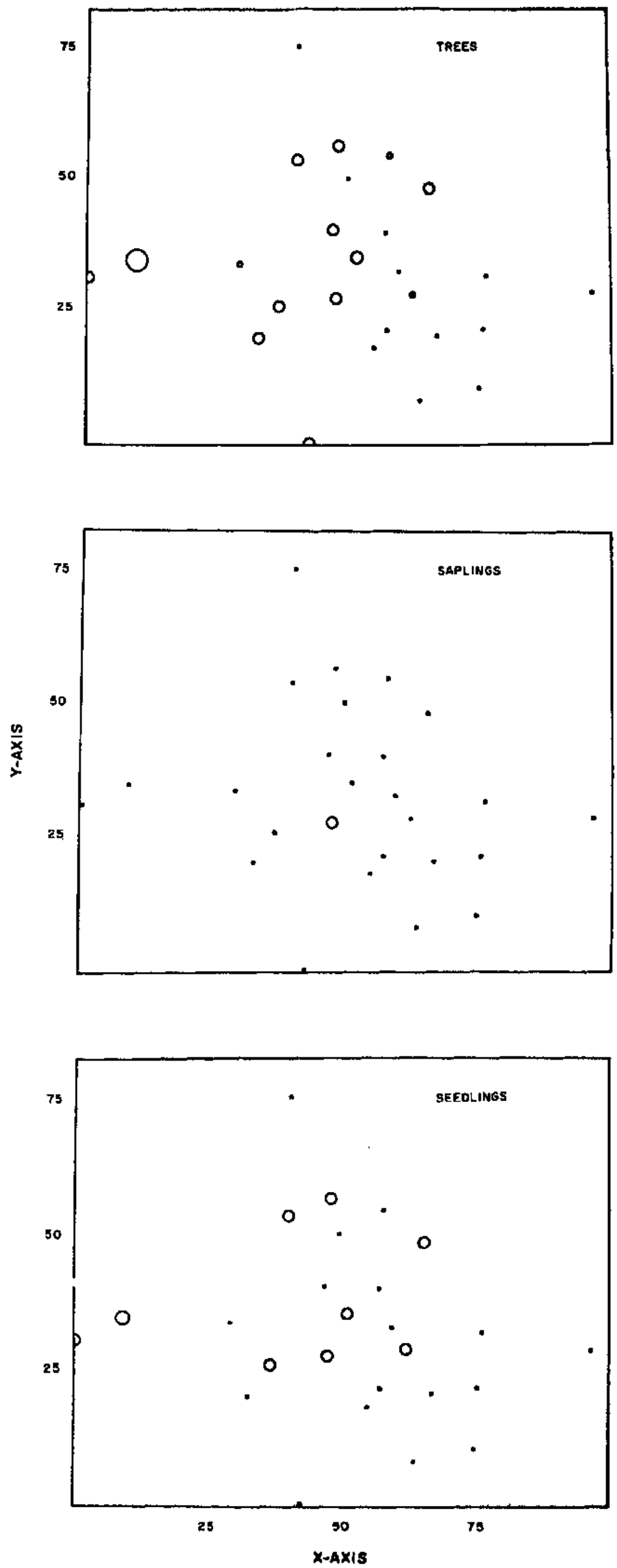

TREES
SAPLINGS
SEEDLINGS
75
50
25
Y-AXIS
25
50
75
X-AXIS

Figure 7. Phytosociological behavior of _Populus_ _balsamifera_ based on density values (number per acre). The density range is divided into six classes, each successively higher class being represented by a larger circle. Class intervals: less than 50; 51-100; 101-250; 251-500; 501-1000; and more than 1000 per acre. Absence of a species in a particular stand is indicated by a solid circle. Balsam poplar is represented only in the lower 3 classes.



TREES
SAPLINGS
SEEDLINGS
Y-AXIS
X-AXIS
75
50
25

encountered thus far. "Disturbance" in this instance involved the felling of most of the trees. Saplings of this species were recorded in only 1 of the 26 stands, and seedlings were encountered in only 9 stands. Balsam poplar reproduction is best in gaps within areas of spruce dominance and under a mixed spruce-balsam poplar canopy.

Frequency

The highest frequency measured for mature balsam poplar was 70% in a single stand, but spruce, pine and aspen are sufficiently dominant that a 100% frequency was recorded for each of these species in several stands (Table 6). The centers of high frequency for tree species are triangularly arranged within the ordination and are generally coincident with the density centers (compare Figures 8, 9, 10 and 11 with Figures 4, 5, 6 and 7). However, the frequency centers occupy larger areas and density values thus begin to decline within areas of uniformly high frequency. Otherwise, frequency patterns for trees and reproductive stages are equivalent to their corresponding density patterns.

Dominance

Frequency and density measurements are assignable to constant points of reference (percent and number per unit area) which allows the prominence of a species in a stand to be expressed in terms of these characteristics by a single number which can be used for comparative purposes. Basal area measurements, however, are interpretable only on a relative basis, as a series of totals based on an equal number of measurements or as a statistic derived from a normal population (eg. mean basal area). Relative values, as noted

Figure 8. Phytosociological behavior of *Picea glauca* based on percent frequency. The frequency range is divided into 4 classes, each having an interval of 25% and each being represented by a circle whose size is proportional to the frequency level. The smallest open circle indicates "presence"; the solid circle indicates "absence".

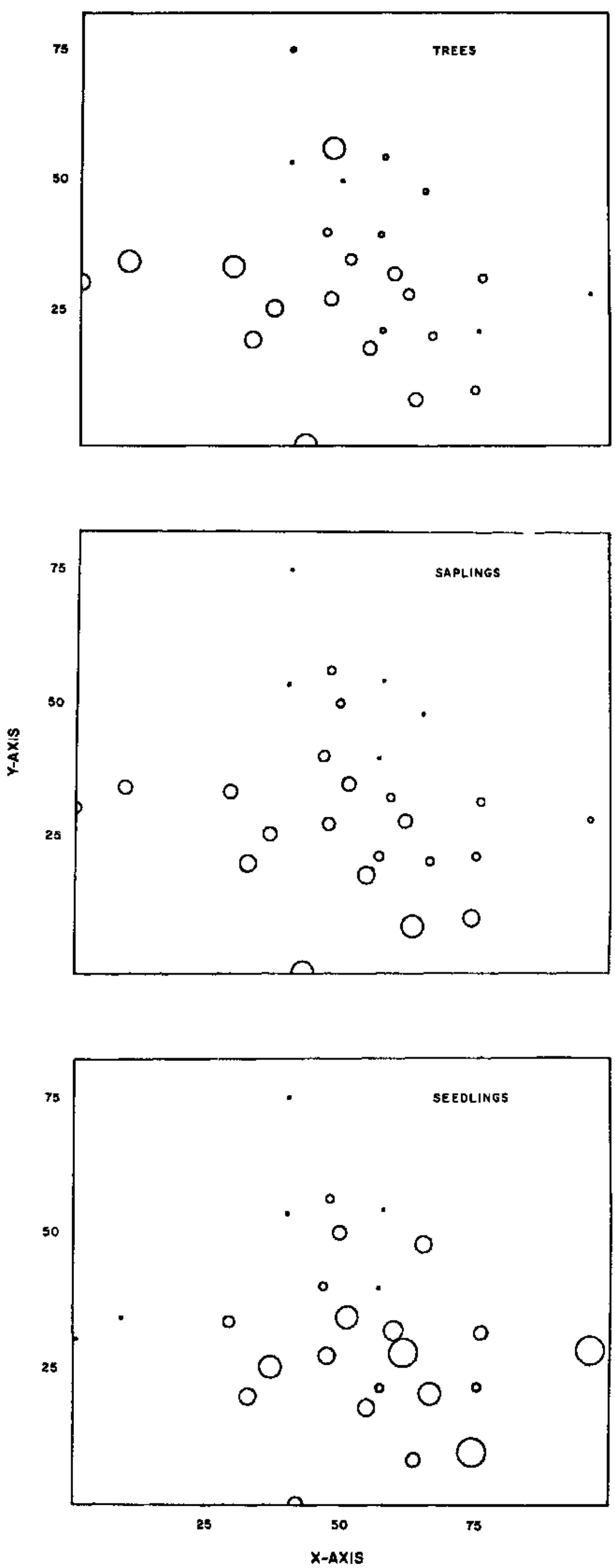

TREES
SAPLINGS
SEEDLINGS
75
50
25
Y-AXIS
25
50
75
X-AXIS

Figure 9. Phytosociological behavior of *Pinus contorta* based on percent frequency. The frequency range is divided into 4 classes, each having an interval of 25% and each being represented by a circle whose size is proportional to the frequency level. The smallest open circle indicates "presence"; the solid circle indicates "absence". Pine seedlings and saplings are represented only in the lowest class and as "present".

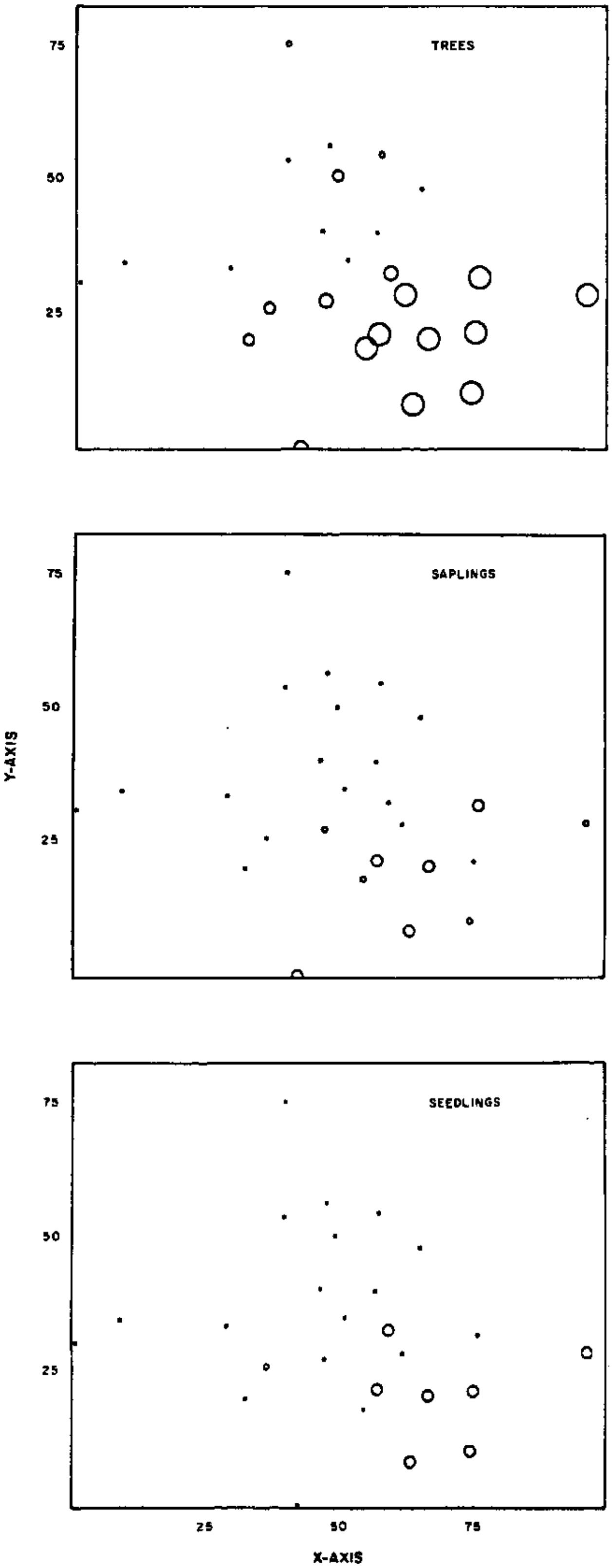
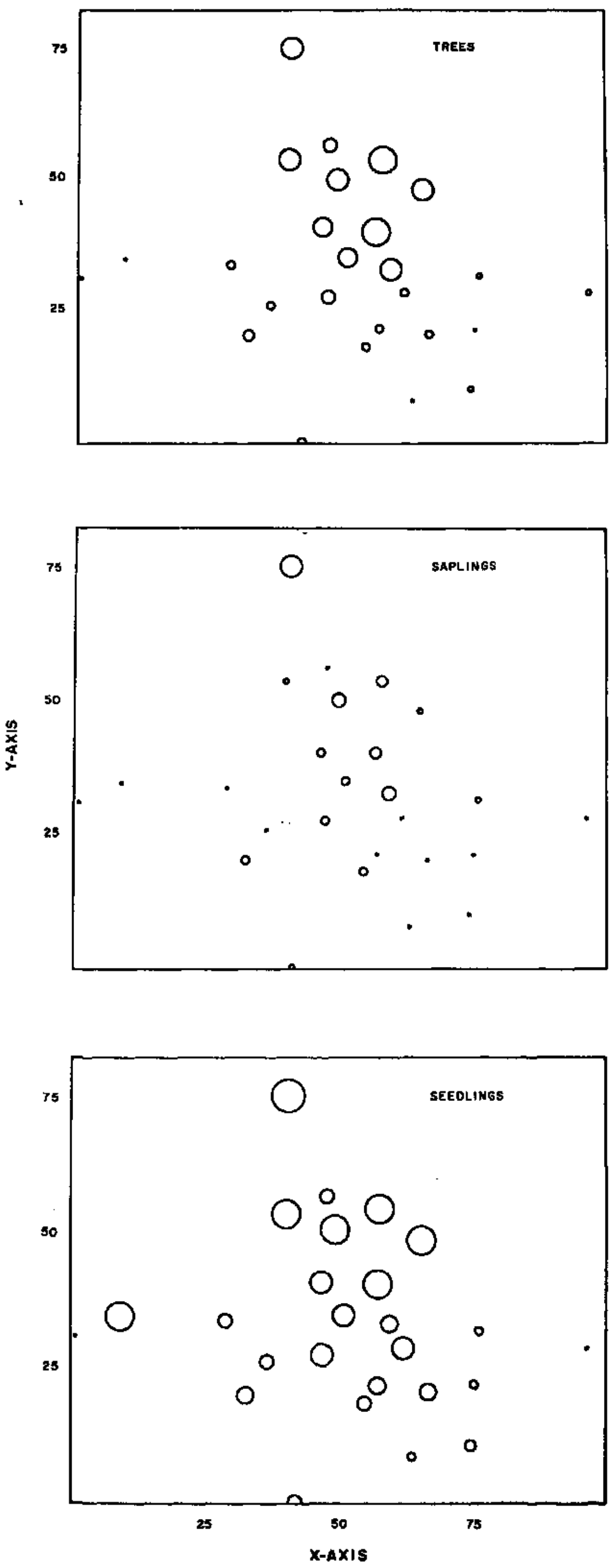
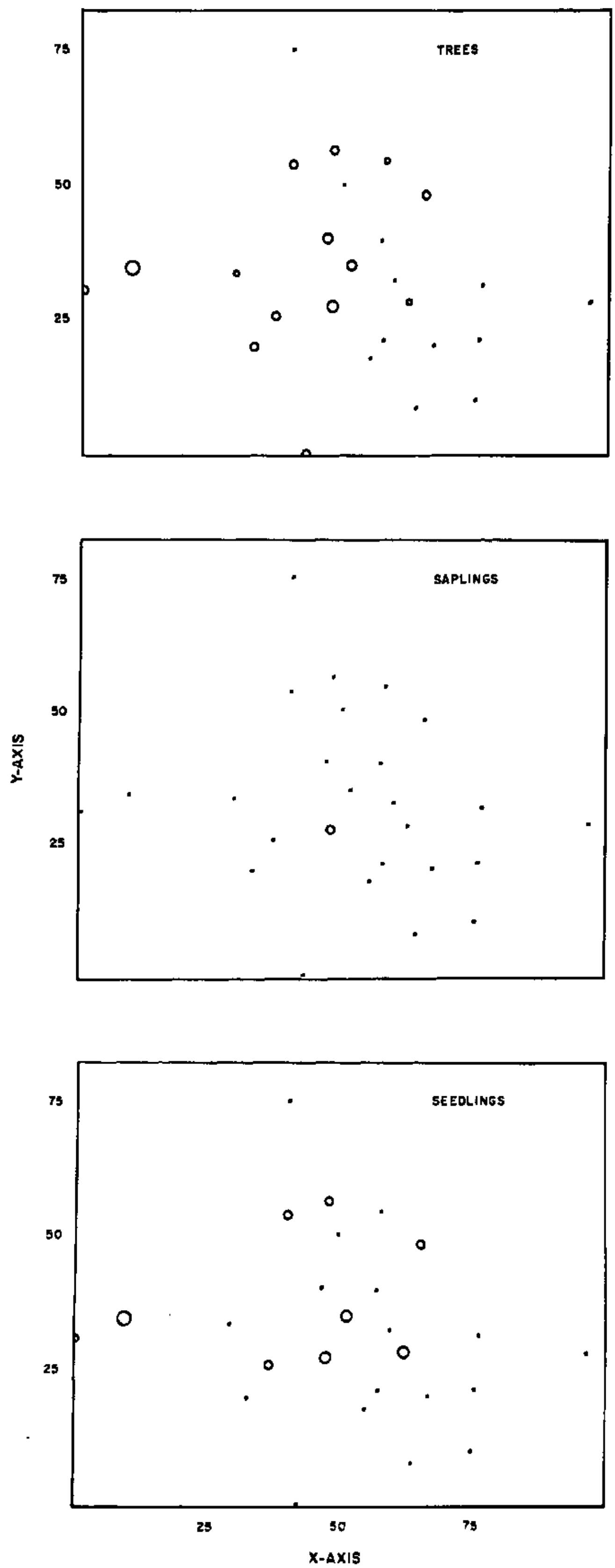

TREES
SAPLINGS
SEEDLINGS
Y-AXIS
X-AXIS
75
50
25
25
50
75

Figure 10. Phytosociological behavior of Populus tremuloides based on percent frequency. The frequency range is divided into 4 classes, each having an interval of 25% and each being represented by a circle whose size is proportional to the frequency level. The smallest open circle indicates "presence"; the solid circle indicates "absence".



TREES
SAPLINGS
SEEDLINGS
75
50
25
Y-AXIS
25
50
75
X-AXIS

Figure 11. Phytosociological behavior of _Populus balsamifera_ based on percent frequency. The frequency range is divided into 4 classes, each having an interval of 25% and each being represented by a circle whose size is proportional to the frequency level. The smallest open circle indicates "presence"; the solid circle indicates "absence". Balsam poplar saplings were encountered only in 1 stand.



TREES
SAPLINGS
SEEDLINGS
75
50
25
Y-AXIS
25
50
75
X-AXIS

Table 6. Percent frequency values for tree species. "P" indicates presence when not otherwise sampled.

Stand	*Picea glauca*			*Pinus contorta*			*Populus balsamifera*			*Populus tremuloides*		
	Tree	Sapling	Seedling	Tree	Sapling	Seedling	Tree	Sapling	Seedling	Tree	Sapling	Seedling
101	5	8	52	100	8	8				15		12
102	P			P						100	56	92
103	65	60	32	95	P					10	4	24
106	40	36	52				15		16	95	8	56
108	P									100	16	88
109	P			P			P			100	28	68
110	P		48				5		4	100	P	76
111	65	68	28	100	12	4						4
112	100	32	36	5		P	10		4	30		24
113	25	16	64	95			P		4	25		44
114	45	12	36	45		4				100	16	32
115	85	28	32	45	P		25	4	12	70	8	48
116		4	8	100		4						4
118		P	88	100	P	4				P		
119	5	40	92	100	P	4				P		12
120	95	80	16	50	4		5			10	P	28
121	100	44	32	15			20			25	4	40
122	5	8	44	100	16					P	P	4
123	15	16	12				20			100	8	76
124		4	20	5						100	32	88
125	P	4	4	100	16	4				10		48
126	100	24					70		36			64
127	100	16					15		8			
128	100	30	20				P			10		25
129							5		4	100	P	80
130	100	4	4				5		4	45		32

previously, could not be used, and since the number of trees of a species measured in each stand was not constant, total basal area also was eliminated. Basal area measurements exhibited an extremely skewed distribution (Table 7) thus refuting the hypothesis that they were derived from a normally distributed population and nullifying the use of mean basal area. No other statistic was found which allowed basal areas to be characterized by a single number, but an inspection of the range of basal areas and their distribution within the ordination suggested that tree sizes were ordered by this positioning of stands and that size frequency could be used to depict this ordering.

Accordingly, 5 size classes were established to cover the recorded range of basal areas (12-420 square inches), but class intervals were based on diameters rather than basal areas in order to avoid the effects of the logarithmic rate of increase of the latter. Basal areas were converted to diameters (range = 3.7 to 23.0 inches) to facilitate handling the data and, in each stand, the diameter values were tallied in their appropriate classes. Separate tallies were kept for each species present (Table 8). Eighty trees were measured in each stand; thus the total tally for each stand is 80 = 100%. Raw tallies, for each species in each stand, were then converted to percentages, giving the percent of the trees in a stand that are of a particular species and size (Table 9). In Stand No. 101 for example, 47.5% of the trees are <u>Pinus contorta</u> with a diameter between 3.7 and 7.0 inches. The sum of the percentages total 100 for each stand; not for each species in a stand.

In order to study the distribution of tree sizes within the ordination, size class percentages were used to construct ideograms

Table 7. Distribution of tree sizes from 4 selected stands among 10 size classes. Table values are the number of trees recorded per species per size class. Eighty trees were measured in each stand.

Stand	Size class	1	2	3	4	5	6	7	8	9	10	Diameter Range	Diameter Mean
	Basal area (sq. in.)	12-15	20-35	40-60	65-90	95-120	130-170	180-220	230-270	280-330	340-390	12-390	-
	Diameter (in.)	3.7-5.0	5.1-7.0	7.1-9.0	9.1-11.0	11.1-13.0	13.1-15.0	15.1-17.0	17.1-19.0	19.1-21.0	21.1-23.0	3.7-23.0	-
111		15	27	18	13	5	2					3.7-15.0	7.4
112		7	26	9	15	7	8	5	1		2	3.7-23.0	9.3
123		2	24	32	15	3	2		1	1		3.7-21.0	8.3
125		12	40	21	5	2						3.7-13.0	6.7

Table 8. Number of trees per species per diameter size class. Values for each stand were separated in order that the figures for each species could be grouped. Eighty trees were measured in each stand. Stands listed in the table include only those in which a species was encountered in sampling.

Pinus contorta

Stand no. Class	Diameter interval	101	103	111	112	113	114	115	116	118	119	120	121	122	124	125
1	3.7-7.0	38	13	28	-	11	4	1	50	61	55	11	1	70	-	50
2	7.1-11.0	34	42	27	-	46	5	7	30	19	24	6	2	9	-	26
3	11.1-15.0	2		5	1	8	3	5							1	2
4	15.1-19.0						1									
5	19.1-23.0															

Populus tremuloides

Stand no. Class	101	102	103	106	108	109	110	112	113	114	115	120	121	123	124	125	128	129	130
1	5	58	2	39	67	69	65	7	5	51	12	2	5	25	54	2	2	55	10
2		22		27	13	10	14		2	6	17		4	44	25			22	2
3														4					
4																			
5																			

Table 8 (Cont'd.). Number of trees per species per diameter size class. Values for each stand were separated in order that the figures for each species could be grouped. Eighty trees were measured in each stand. Stands listed in the table include only those in which a species was encountered in sampling.

Picea glauca

Stand no. Class	101	103	106	109	111	112	113	114	115	119	120	121	122	123	126	127	128	130
1	1	11	4	-	14	25	8	9	13	1	30	25	1	1	26	20	31	8
2		9	5	-	4	24		1	8		23	22		-	17	28	30	35
3		3	2	1	2	13			2		7	12		-	9	16	17	20
4						6			7			4		1	3	10		4
5						2			1					1	2	2		

Populus balsamifera

Stand no. Class	106	110	112	115	120	121	123	126	127	129	130
1	2	-	1	1	1	3	-	3	1	2	1
2	1	1	1	6		2	4	11	3	1	
3								7			
4								1			
5								1			

Table 9 (Cont'd.). Percentage of trees per stand that occur within each of the 5 size classes (Data of Table 8 converted to percentages).

Picea glauca

Stand no. Class	101	103	106	109	111	112	113	114	115	119	120	121	122	123	126	127	128	130
1	1.25	13.75	5.0	-	17.5	31.25	10.0	11.25	16.25	1.25	37.5	31.25	1.25	1.25	32.5	25.0	38.75	10.0
2		11.25	6.25	-	5.0	30.0		1.25	10.0		28.75	27.5		-	21.25	35.0	37.5	43.75
3		3.75	2.5	1.25	2.5	16.25			2.5		8.75	15.0		-	11.25	20.0	21.25	25.0
4						7.5			8.75			5.0		1.25	3.75	12.5		5.0
5						2.5			1.25					1.25	2.5	2.5		

Populus balsamifera

Stand no. Class	106	110	112	115	120	121	123	126	127	129	130
1	2.5	-	1.25	1.25	1.25	3.75	-	3.75	1.25	2.5	1.25
2	1.25	1.25	1.25	7.5		2.5	5.0	13.75	3.75	1.25	
3								8.75			
4								1.25			
5								1.25			

Table 9. Percentage of trees per stand that occur within each of the 5 size classes (Data of Table 8 converted to percentages).

Pinus contorta

Stand no. / Class	101	103	111	112	113	114	115	116	118	119	120	121	122	124	125
1	47.5	16.25	35.0	-	13.75	5.0	1.25	62.5	76.25	68.75	13.75	1.25	87.5	-	62.5
2	42.5	52.5	33.75	-	57.5	6.25	8.75	37.5	23.75	30.0	7.5	2.5	11.25	-	32.5
3	2.5		6.25	1.25	10.0	3.75	6.25							1.25	2.5
4						1.25									
5															

Populus tremuloides

Stand no. / Class	101	102	103	106	108	109	110	112	113	114	115	120	121	123	124	125	128	129	130
1	6.25	72.5	2.5	48.75	83.75	86.25	81.25	8.75	6.25	63.75	15.0	2.5	6.25	31.25	67.5	2.5	2.5	68.75	12.5
2		27.5		33.75	16.25	12.5	17.5		2.5	7.5	21.25		5.0	55.0	31.25			27.5	2.5
3														5.0					
4																			
5																			

(Figure 12) for each species in a stand that contributed at least 10% to the total basal area of that stand and these were subsequently plotted on the ordination (Figures 13, 14 and 15). Size class No. 1 is present in all ideograms and since the vertical axis extends only into size classes that are present, the longer the vertical axis, the greater is the range of tree sizes present. Conversely, the longer the horizontal axis, the greater is the percent contributed by that size class. Also, the greater the area occupied by an ideogram, the greater is the contribution of that species to the total basal area of a stand.

Comparison of Frequency, Density and Dominance Patterns

When the figures for frequency, density and dominance are compared along the X-axis (Figures 5, 9 and 13) it can be observed that, initially, pine increases in size as density decreases and frequency remains constant. This is followed by a sharp decline in frequency while the percentage of trees in intermediate size classes increases. Aspen exhibits an increase in size toward the lower end of the Y-axis (Figure 14) accompanied by a decrease in density (Figure 6) which, in turn, is succeeded by an increase in the relative importance of the smallest size class. This latter increase is matched by an increase in density and followed by a decrease in frequency (Figure 10) with a consequent decline in the overall importance of aspen. In this last stage, those trees present are in the smallest size class.

Within zones predominated by aspen and/or pine, spruce is abundant as seedlings and saplings (Figures 4 and 8) but low percentages of small spruce trees also occur (Figure 15). Spruce

Figure 12. Model for constructing ideograms to demonstrate tree diameter relationships within the ordination. The percentage for each size class designates the percent of the trees in a stand that are of a particular species and size. Since each ideogram represents the diameter contribution of a single species, the sum of the percentages for a single ideogram usually is less than 100. In Stand 000 (Fig. 12) 15% of the trees are of Species A, and of a size that places them in Size Class IV (15.1-19.0" d.b.h.). The 15% is plotted along the scale line for Size Class IV, (as shown in Step 1). Percentages for other size classes are similarly plotted, and the lines are enclosed as in Step 2. The ideogram (Step 3) can then be positioned on the ordination (see Figs. 13, 14 and 15) for comparative purposes.

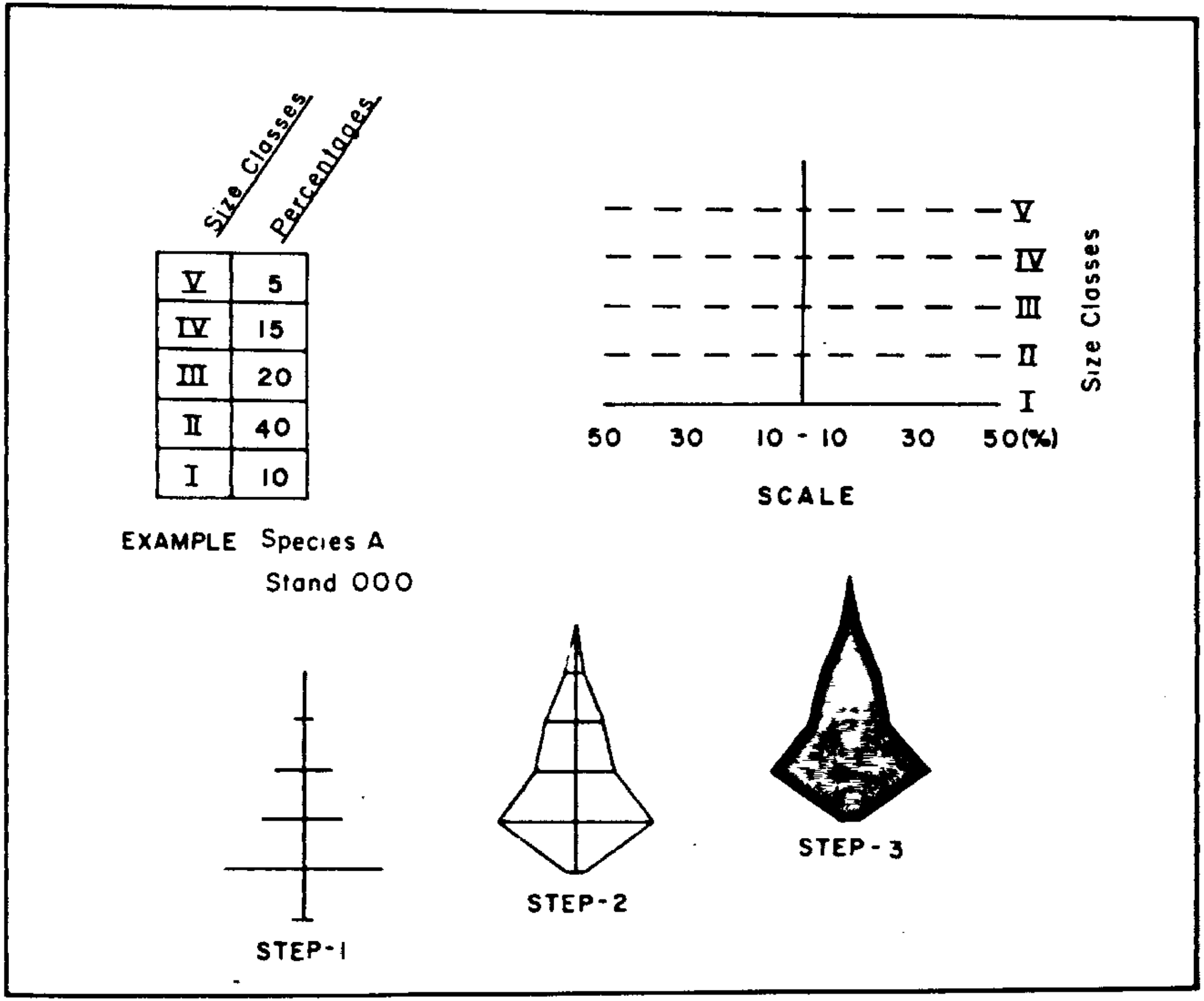

Size Classes
Percentages
V 5
IV 15
III 20
II 40
I 10
EXAMPLE Species A
Stand OOO
V
IV
III
II
I
Size Classes
50 30 10 - 10 30 50(%)
SCALE
STEP-1
STEP-2
STEP-3

Figure 13. Plot of ideograms for *Pinus contorta* against the ordination. See Figure 12 for details of ideogram construction. Solid circles mark the location of stands in which pine contributes less than 10% of the basal area. Each ideogram has Size Class I at its base.

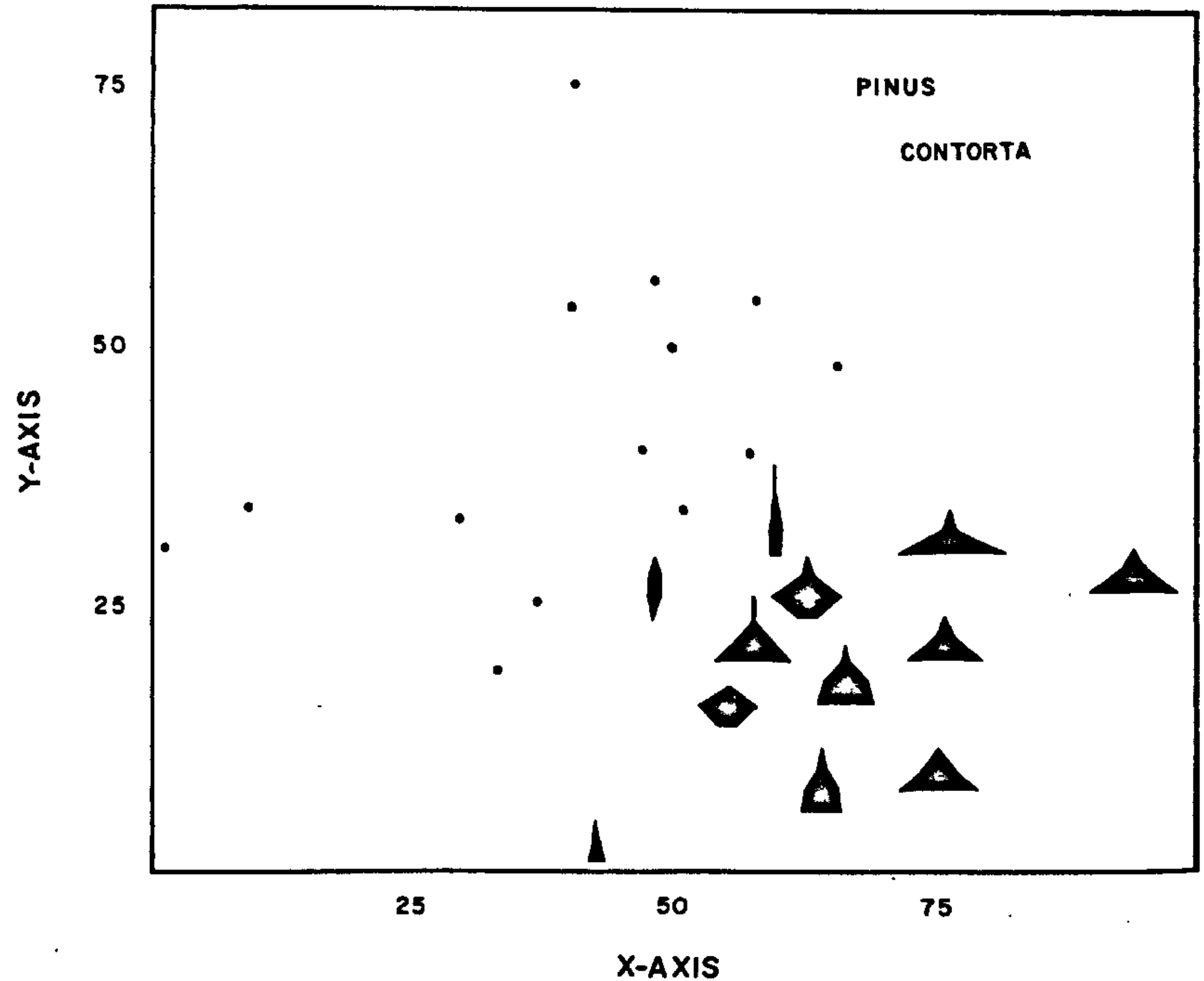

PINUS
CONTORTA
Y-AXIS
75
50
25
25
50
75
X-AXIS

Figure 14. Plot of ideograms for *Populus tremuloides* against the ordination. See Figure 12 for details of ideogram construction. Solid circles mark the location of stands in which aspen contributes less than 10% of the basal area. Each ideogram has Size Class I at its base.

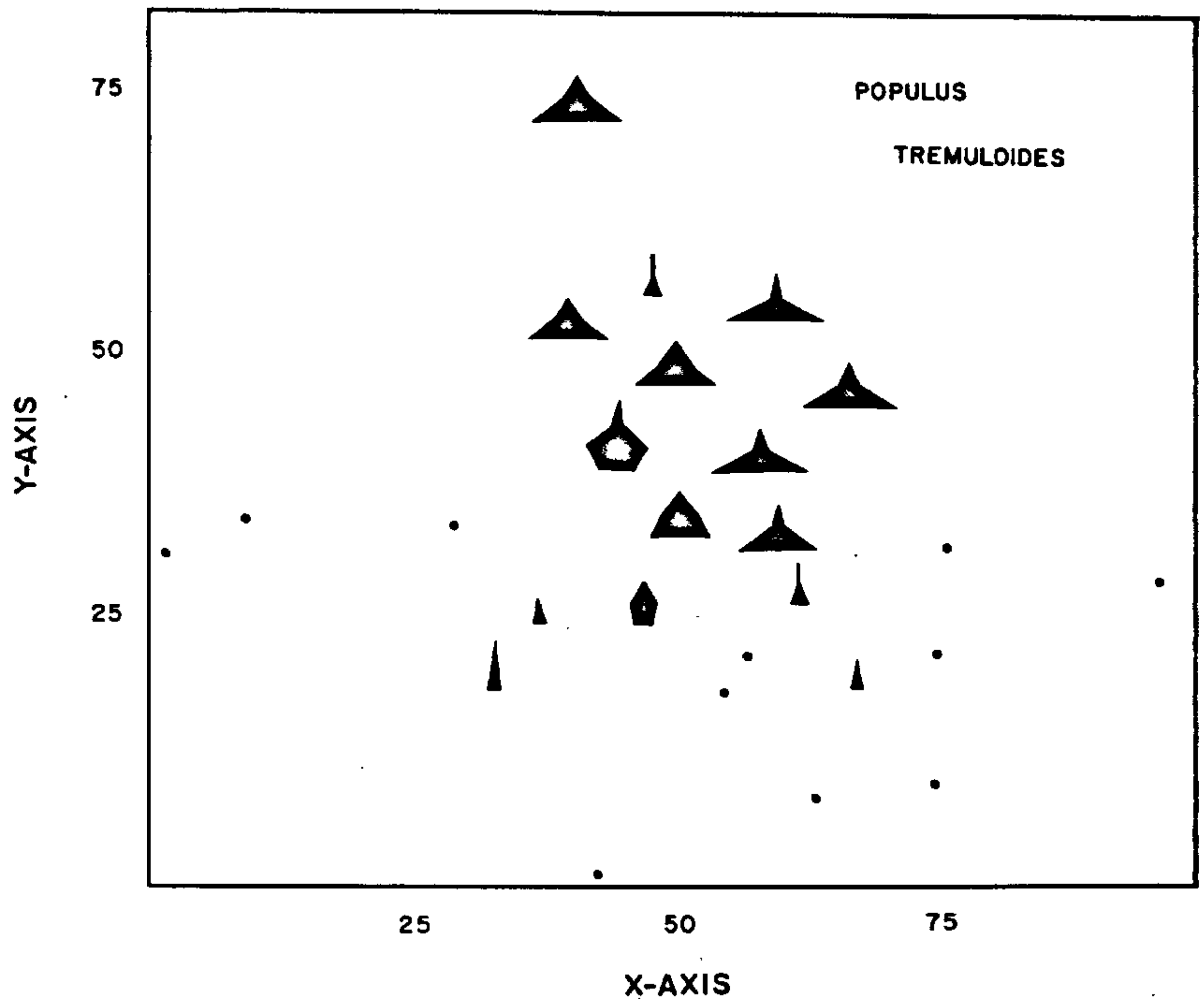
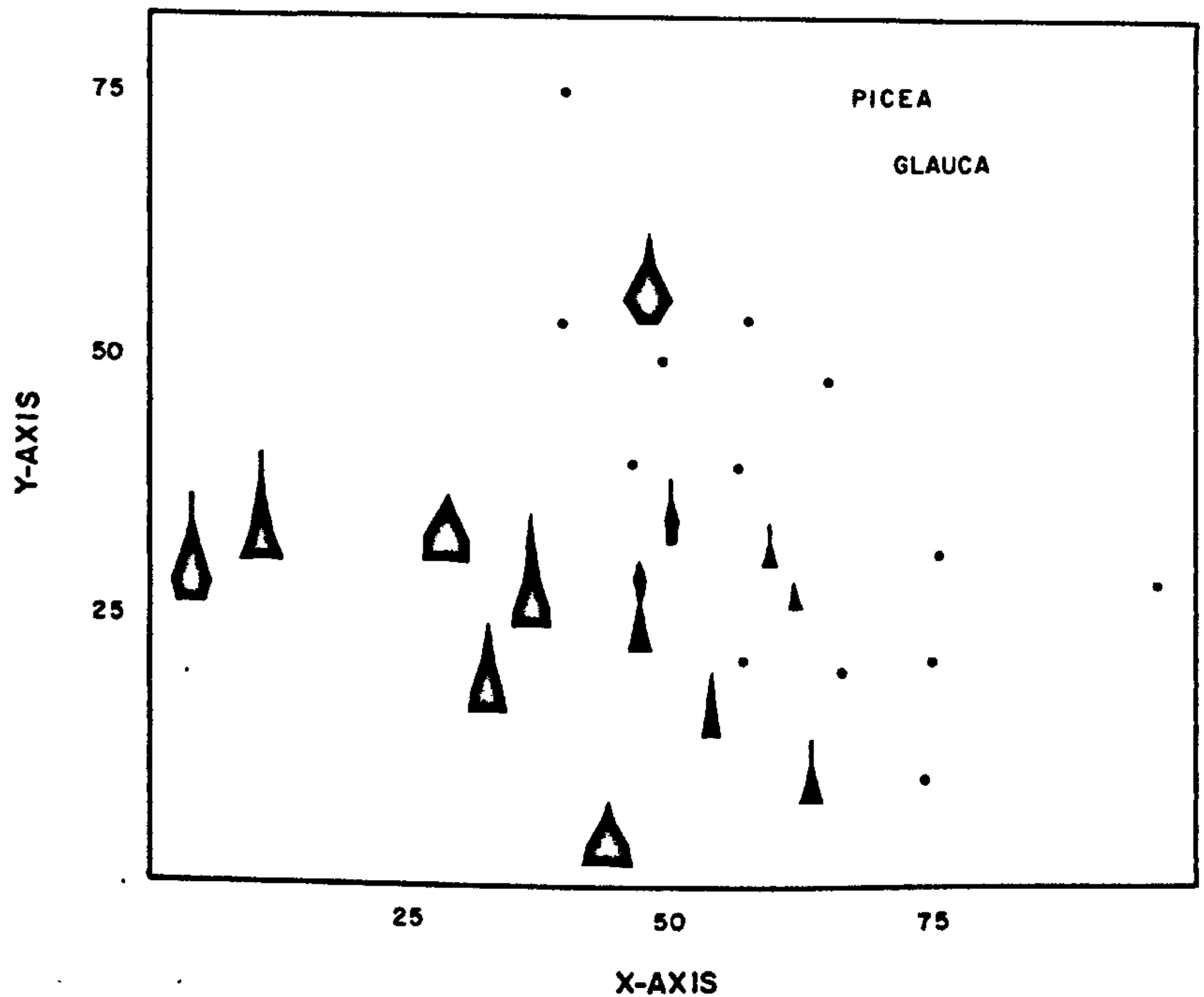

POPULUS
TREMULOIDES
75
50
25
Y-AXIS
25
50
75
X-AXIS

Figure 15. Plot of ideograms for *Picea glauca* against the ordination. See Figure 12 for details of ideogram construction. Solid circles mark the location of stands in which spruce contributes less than 10% of the basal area. Each ideogram has Size Class I at its base.


PICEA
GLAUCA
75
50
25
Y-AXIS
25
50
75
X-AXIS

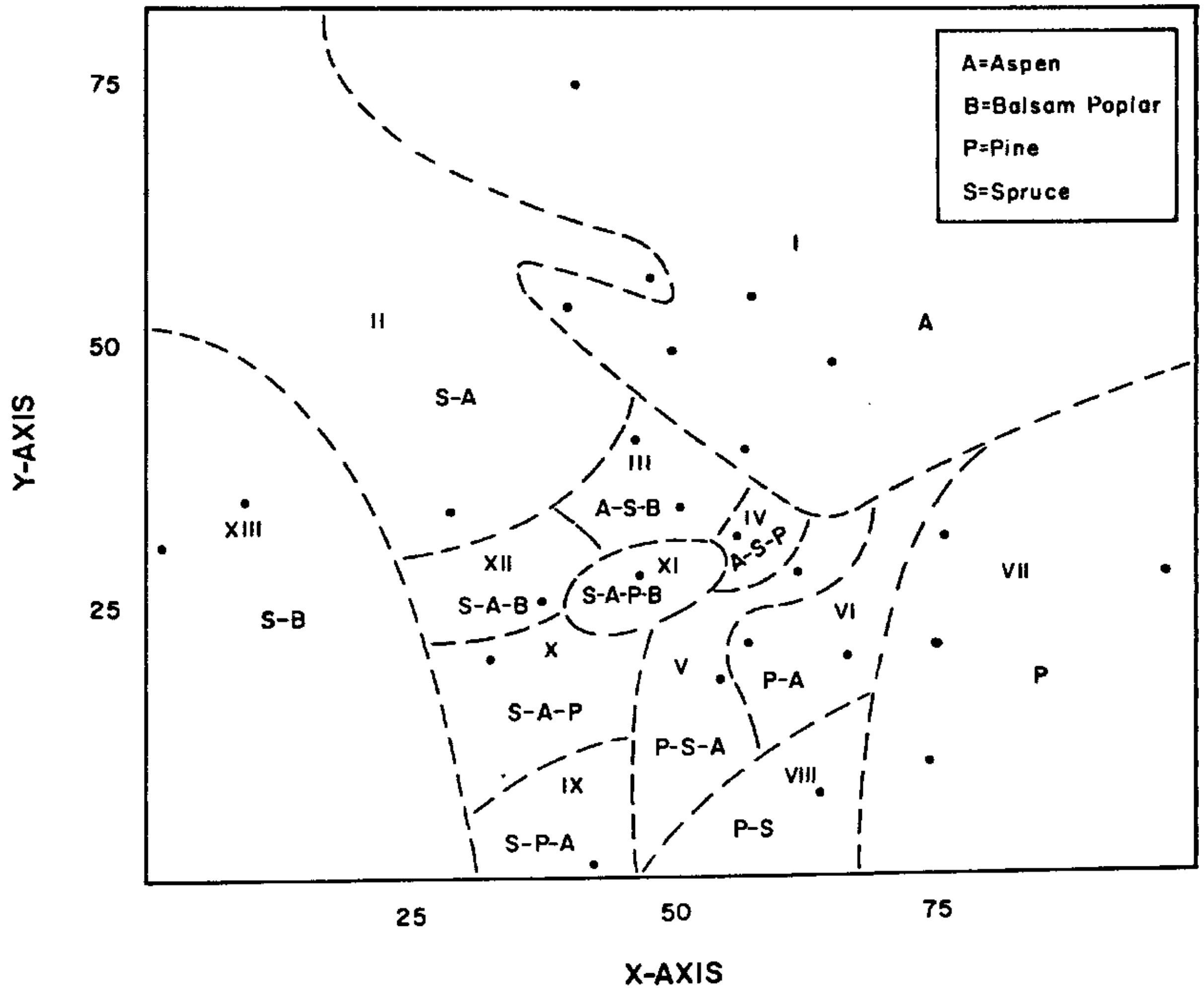
increases in dominance to the left, along the X-axis, and attains sizes considerably larger than those attained by either aspen or pine. As size increases, frequency increases to 100% and remains at this level. Density increases also, but begins to lessen as a majority of the trees become included in the top three size classes. Size increase is interrupted by at least one relative increase in smaller trees but the overriding trend in spruce diameters is one of increase to the left.

Further Analysis of the Ordination

Pure stands occur near the margin of the ordination while, toward its center, stands are increasingly mixed. The extent to which this mixing follows an orderly pattern was investigated by arranging frequency values for all canopy species in a stand in order of descending rank (eg. Stand No. 103: pine - 95, spruce - 65, aspen - 10, balsam poplar - 0: ref. Table 6). Lines were then drawn to separate stands in which pine is the first ranked species from all other stands. Stands in which spruce and aspen ranked first were treated similarly, dividing the ordination into three major areas and these parts were then subdivided into a total of 13 sectors in such a manner that all stands in a given sector are canopied by the same species in identical rank sequence.

The sectioning that resulted from this analysis is illustrated in Figure 16. The focal point of canopy complexity is Sector XI, occupied by a single stand, and the only stand in which all four tree species contributed significantly to the canopy. The number of canopy species is reduced toward the margin of the ordination and a stepwise reduction in the rank of spruce and pine along the X-axis

Figure 16. Division of the ordination into sectors, giving sector numbers (Roman numerals), stand locations (solid circles) and the rank sequence of tree species within each sector. The symbol of the first ranked (highest % frequency) species is at the left.


A=Aspen
B=Balsam Poplar
P=Pine
S=Spruce
I
A
II
S-A
III
A-S-B
IV
A-S-P
XI
S-A-P-B
XII
S-A-B
X
V
P-A
VI
VII
P
XIII
S-B
S-A-P
P-S-A
VIII
IX
S-P-A
P-S
75
50
25
Y-AXIS
X-AXIS

(in opposite directions), and of aspen along the Y-axis is demonstrated. Balsam poplar is restricted to Sectors III, XI, XII, and XIII and is consistently the lowest ranked species.

The purpose of Figure 16 is to present a graphic illustration of the phytosociological patterns which emerged in the analysis of this two-dimensional ordination. The degree of sectioning, the shape and position of lines, and the resultant configuration are arbitrary, but the figure does demonstrate the increasing phytosociological complexity of the stands from the periphery toward Sector XI. The object of this figure is utilitarian and not classificatory and it is not intended that sectors be considered as vegetational units.

Shrub Species

It is now evident that the circular quadrat employed in this study is not sufficiently sensitive for future, more definitive studies but it has, none-the-less, provided data that are adequate for comparative purposes. All shrub species exhibit frequency patterns which include centers of high frequency, tapering through peripheral areas of low frequency into areas of absence, but species differ with respect to the location and size of these centra, the level of frequency achieved and their percent presence. The sectioning illustrated in Figure 16 can be used to point up this variation.

Determination of Sectors of Peak Frequency

Each of the 34 species of shrubs encountered in quadrat samples have frequency peaks which could be characterized by plotting the location of the two highest frequency values (Table 10) recorded for that species. A species may have identical frequency values in two

Table 10. Percent frequency values for shrub species. "P" indicates presence in the stand but not encountered in quadrat samples.

Stand no. / Species	101	102	103	106	108	109	110	111	112
Amelanchier alnifolia	P	28	24	36	100	96	100	20	12
Arctostaphylos uva-ursi	4	28			P	24	8	16	12
Betula occidentalis									
Clematis verticellaris	80	P	96	52	88	8	12	48	4
Cornus stolonifera	P	4	16	20					8
Crataegus chrysocarpa		P			P	40			
Crataegus douglasii		P		4	32				
Eleagnus commutata									
Juniperus communis var. depressa	24	4	8					28	P
Juniperus horizontalis	P	4							
Linnaea borealis var. americana	88		68	8	20			4	8
Potentilla fruticosa		56	P						
Prunus pensylvanica		P			72	24	4		
Prunus virginiana	4	8	16	24	100	76	20		16
Ribes hudsonianum									4
Ribes lacustre	12	28	P	16	32	24			20
Ribes oxyacanthoides - R. setosum	P	8	52	4	16				
Rosa acicularis	72	64	68	56	76	64	84	24	
Rosa woodsii	40	40	28	84	64	72	84	92	96
Rubus acaulis									8
Rubus pubescens	36		4	24	8				8
Rubus strigosus	16	44	20	44	76	72	84	4	4
Salix bebbiana	50	P	P	8	4				
Salix discolor									4
Salix lasiandra									
Salix pseudomonticola									P
Salix scouleriana	P		4						
Shepherdia canadensis	56	P	20	12	36	32	16	52	28
Sorbus scopulina	P								
Spiraea lucida	80	4	76	84	92	80	100	76	12
Symphoricarpos albus	8	88	28	72	96	96	100	36	72
Symphoricarpos occidentalis		P		20		P	4		
Vaccinium caespitosum	32	4	4		4	12	P		
Viburnum edule	60	P	44	8	44	4			4

Table 10 (Cont'd.). Percent frequency values for shrub species. "P" indicates presence in the stand but not encountered in quadrat samples.

Stand no. / Species	113	114	115	116	118	119	120	121	122
Amelanchier alnifolia	28	60	56	8	4	4	4	28	
Arctostaphylos uva-ursi	20	4	P	8	24	20	P		8
Betula occidentalis									
Clematis verticellaris	64	40	84	44	4	8	80	8	8
Cornus stolonifera	P		4				16	32	
Crataegus chrysocarpa									
Crataegus douglasii									
Eleagnus commutata									
Juniperus communis var. depressa	P		P	4	P	12	20	12	
Juniperus horizontalis									P
Linnaea borealis var. americana	48	68	36	80	44	96	56	48	24
Potentilla fruticosa				4					
Prunus pensylvanica							P		
Prunus virginiana	4	16	24					20	
Ribes hudsonianum									
Ribes lacustre		4	8	4		P		P	4
Ribes oxyacanthoides - R. setosum									
Rosa acicularis	88	88	32	92	52	28	P	4	56
Rosa woodsii	36	64	88	16	P	80	92	68	4
Rubus acaulis									
Rubus pubescens	20	48	40			4	12	40	4
Rubus strigosus	20	16	12				P		
Salix bebbiana	4		4	24	P	4	8	4	P
Salix discolor									
Salix lasiandra									
Salix pseudomonticola								4	
Salix scouleriana		4							
Shepherdia canadensis	40	44	P	32	40	76	24	4	
Sorbus scopulina									
Spiraea lucida	100	100	96	100	92	80	48	44	84
Symphoricarpos albus	28	88	72	P		8	44	64	16
Symphoricarpos occidentalis									
Vaccinium caespitosum	32	12	16	64	36	32	P		4
Viburnum edule	24	72	8	28	P	8	60	40	P

Table 10 (Cont'd). Percent frequency values for shrub species. "P" indicates presence in the stand but not encountered in quadrat samples.

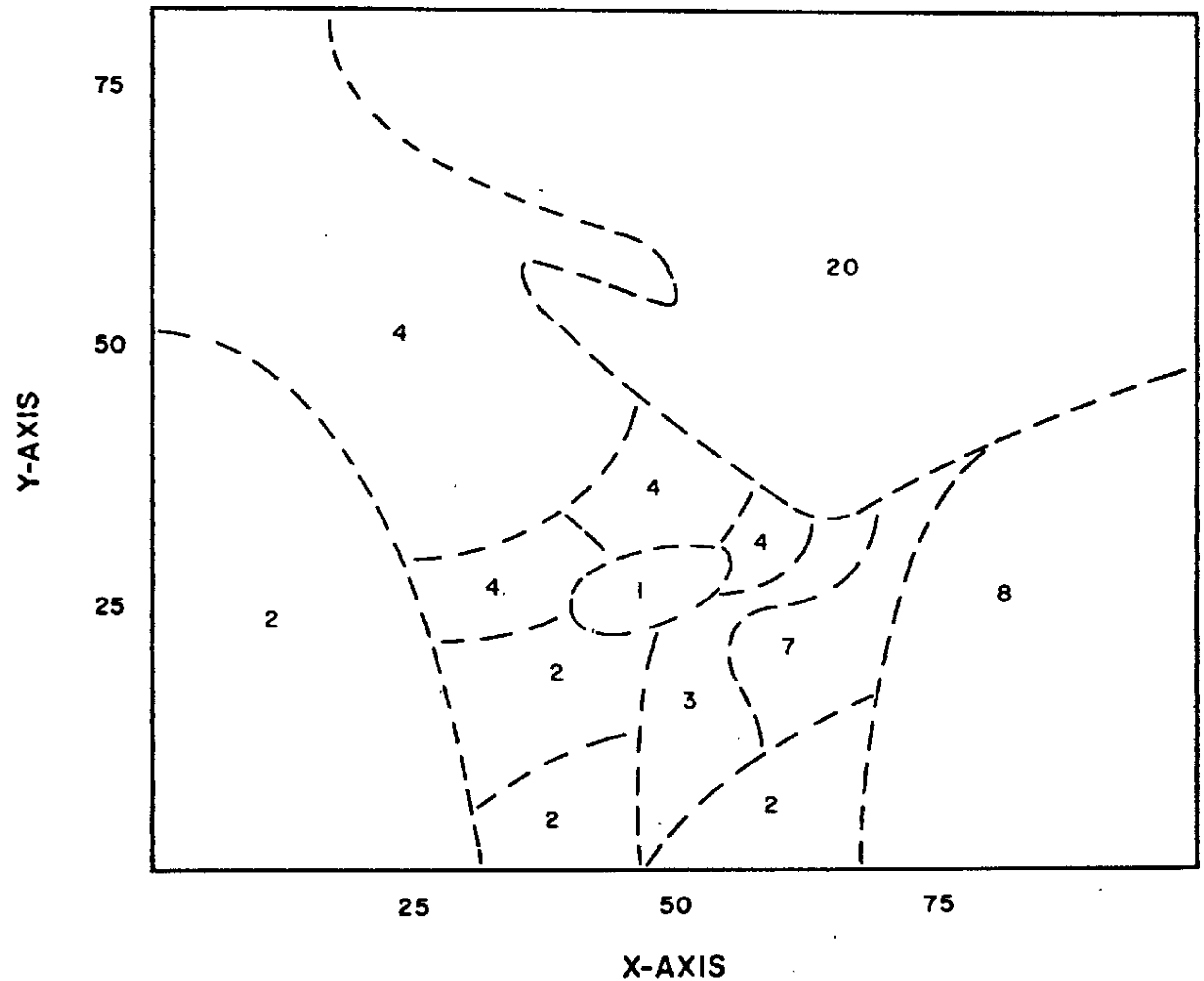
Stand no. / Species	123	124	125	126	127	128	129	130
Amelanchier alnifolia	52	76	20	8	20	40	92	8
Arctostaphylos uva-ursi		P	20	P		5		
Betula occidentalis						15		
Clematis verticellaris	52			32	8	P	64	
Cornus stolonifera	32			24	32	10	24	4
Crataegus chrysocarpa	8	4					8	
Crataegus douglassi							64	
Eleagnus commutata						10		
Juniperus communis var. depressa	4	P	20			20		
Juniperus horizontalis			P			P		
Linnaea borealis var. americana				20				
Potentilla fruticosa								
Prunus pensylvanica		32					P	
Prunus virginiana	44	52	20	8	4	10	56	20
Ribes hudsonianum						4		
Ribes lacustre	12	12		16	8	25	8	
Ribes oxyacanthoides - R. setosum	8							4
Rosa acicularis	44	4	P			5	96	80
Rosa woodsii	88	92	96	40	P	90	24	
Rubus acaulis								
Rubus pubescens	8			52	24			8
Rubus strigosus	76	68	P	20	4		92	
Salix bebbiana	P		4	P		15		P
Salix discolor								
Salix lasiandra						P		
Salix pseudomonticola						P		
Salix scouleriana								
Shepherdia canadensis	4		28			10	24	8
Sorbus scopulina							16	
Spiraea lucida	100	76	100					4
Symphoricarpos albus	96	100	40	44	28	95	96	76
Symphoricarpos occidentalis	8	44						
Vaccinium caespitosum			20				4	P
Viburnum edule	8			24	8		4	

or more stands (for example: Symphoricarpos albus - 100% in Stands 110 and 124, and 96% in Stands 108, 109, 123 and 129) in which case, all 6 stands together comprise the one peak area for Symphoricarpos albus. After all species had been examined in this manner, the number of shrubs that "peak" in each stand was counted and these values were summed for each of the 13 sectors (Figure 17). Twenty-eight species reach their peak frequency within the sectors in which aspen is the first ranked species. Of these, 12 peak only within these sectors, 10 have their high values extended into sectors where aspen occurs as a second ranked species, and the highest frequencies of 10 species are restricted to the sector of pure aspen stands (Sector I). Shrub species which achieve their peak frequencies under an aspen canopy most often reach a higher frequency and a higher percent presence than do species which peak under other canopy types. In addition, a majority of those with medium and low level frequencies also peak where aspen is ranked first in the canopy. Thirteen species peak under a predominantly pine canopy; five such peaks being limited to these sectors. Where spruce ranks first in the canopy, 13 shrubs reach their maximum frequency, with 6 of these peaks being restricted here. These data are summarized in Table 11.

Frequency Distribution of Shrub Species

The frequency distributions of 9 shrub species, selected as being representative of the principal distribution patterns encountered, are illustrated in Figures 18, 19, 20 and 21. Each species, however, exhibits a pattern that is unique to that species. Some, such as Elaeagnus commutata, Symphoricarpos occidentalis and Potentilla fruticosa are known to achieve their best development

Figure 17. Division of the ordination into sectors, giving the number of shrub species that achieve their peak frequency within each sector.



75
50
25
Y-AXIS
25
50
75
X-AXIS
20
4
4
4
4
1
2
2
2
3
7
8
2

Table 11. Percent presence for shrub species and characteristics of their distributions within the ordination. Canopy species are listed in order of rank sequence. A = aspen; P = pine; S = spruce.

Species	% Presence	Section(s) of peak frequency	Leading canopy species of peak sections	Highest frequency levels
Amelanchier alnifolia	96.3	I	A	100
Arctostaphylos uva-ursi	73.1	I, VII	A, P	28
Betula occidentalis	3.9	II	S	15
Clematis verticellaris	92.4	I, VII	A, P	96
Cornus stolonifera	57.7	I, III, X, XIII	A, S	32
Crataegus chrysocarpa	19.3	I	A	40
Crataegus douglasii	14.4	I	A	64
Eleagnus commutata	3.9	II	S	10
Juniperus communis var. depressa	61.6	VI, VIII	P	28
Juniperus horizontalis	19.3	I	A	4
Linnaea borealis var. americana	61.6	VII, VI	P	96
Potentilla fruticosa	11.5	I	A	56
Prunus pensylvanica	27.0	I	A	72
Prunus virginiana	77.0	I	A	100
Ribes hudsonianum	7.7	I, II	A, S	4
Ribes lacustre	73.1	I	A	32
Ribes oxyacanthoides - R. setosum	27.0	I, V	P, A	52
Rosa acicularis	88.5	I, VII	A, P	96
Rosa woodsii	96.3	I, II, VIII, IX	A, S, P	96
Rubus acaulis	3.9	II	S	8
Rubus pubescens	61.6	IV, XIII	S, A	52
Rubus strigosus	65.5	I	A	92
Salix bebbiana	69.3	VI, VII	P	50
Salix discolor	3.9	II	S	4
Salix lasiandra	3.9	II	S	P
Salix pseudomonticola	11.5	X	S	4
Salix scouleriana	11.5	VI, V	P, A	4

Table 11 (Cont'd.). Percent presence for shrub species and characteristics of their distributions within the ordination. Canopy species are listed in order of rank sequence. A = aspen; P = pine; S = spruce.

Species	% Presence	Section(s) of peak frequency	Leading canopy species of peak sections	Highest frequency levels
Shepherdia canadensis	84.7	VI, VII	P	76
Sorbus scopulina	7.7	I	A	16
Spiraea lucida	84.7	I, III, IV, V VI, VII, X	A, P, S	100
Symphoricarpos albus	96.3	I, III	A	100
Symphoricarpos occidentalis	23.1	I, III	A	44
Vaccinium caespitosum	65.5	VII	P	64
Viburnum edule	80.8	IV, VI, IX	P, A, S	72

Figure 18. Phytosociological behavior of three high-frequency shrub species which have their peak frequencies in a central and left-of-center position within the ordination. Percent frequency for shrub species is divided into 5 classes, each having an interval of 20%, and each successively higher percentage class being represented by a larger circle. The smallest open circle indicates "presence"; the solid circle indicates "absence".

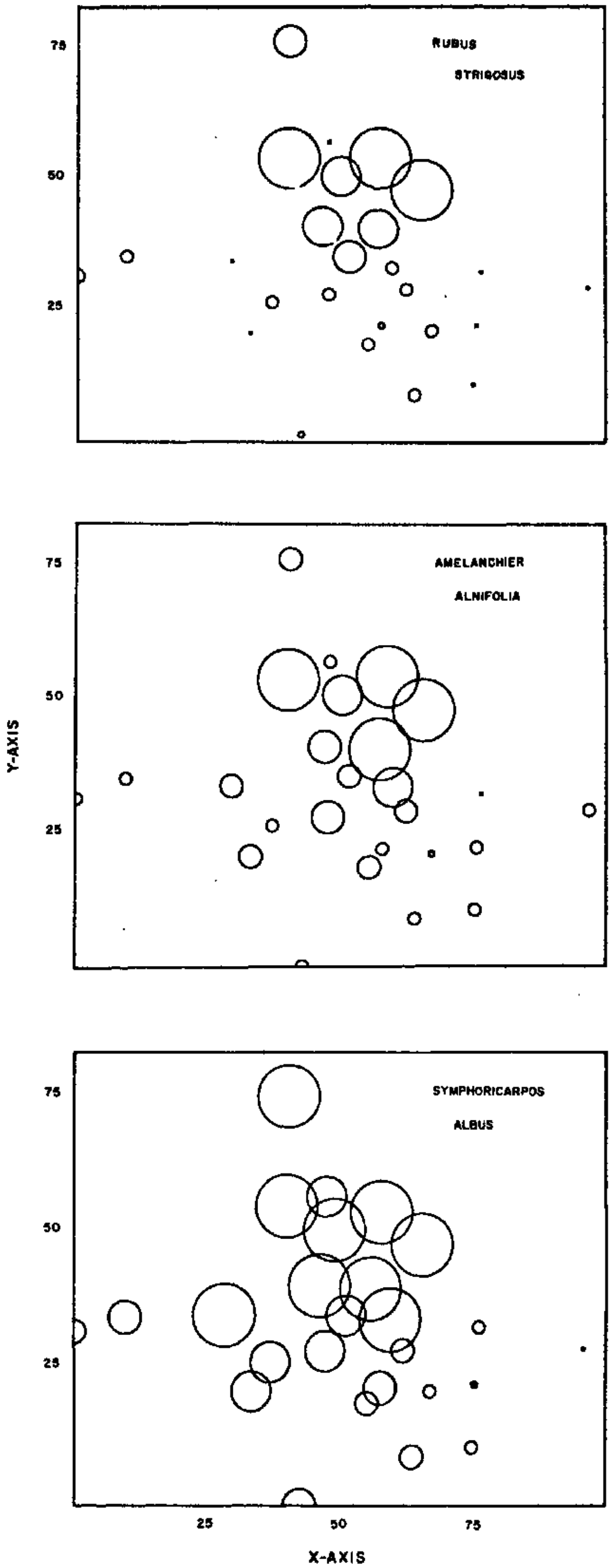
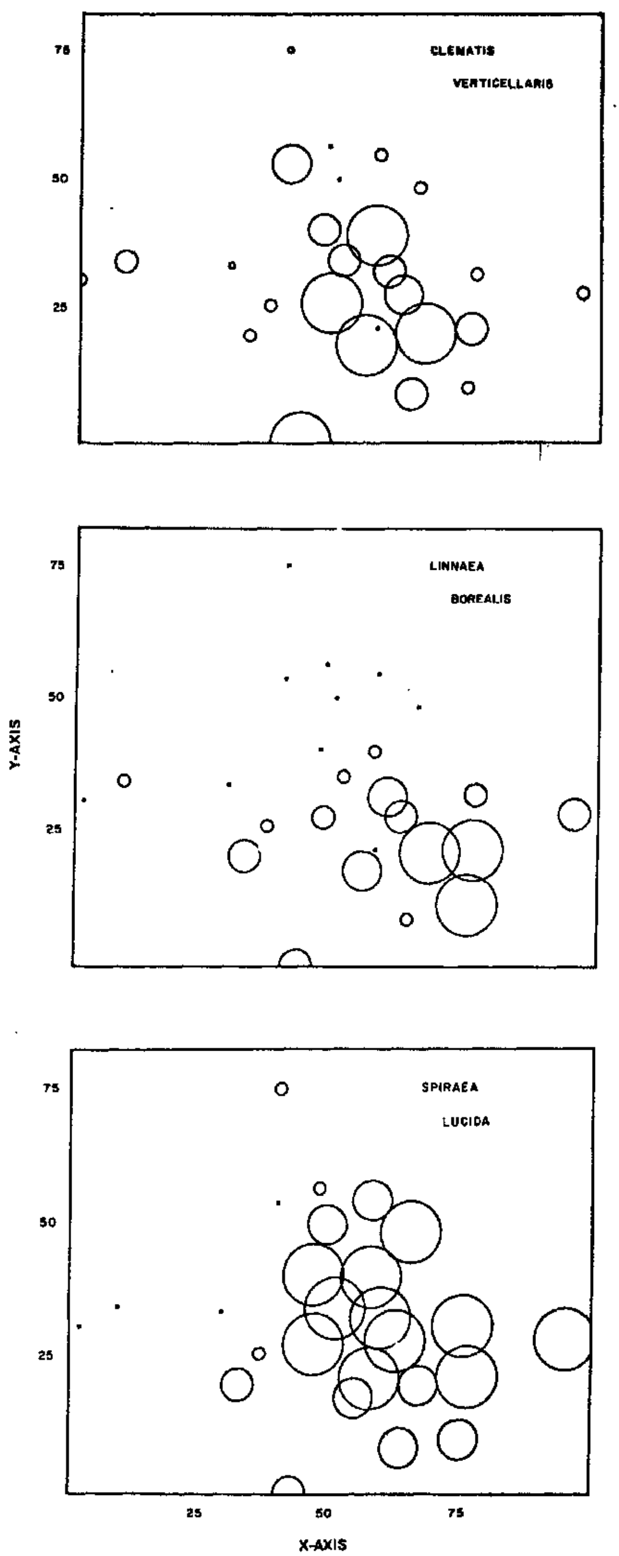
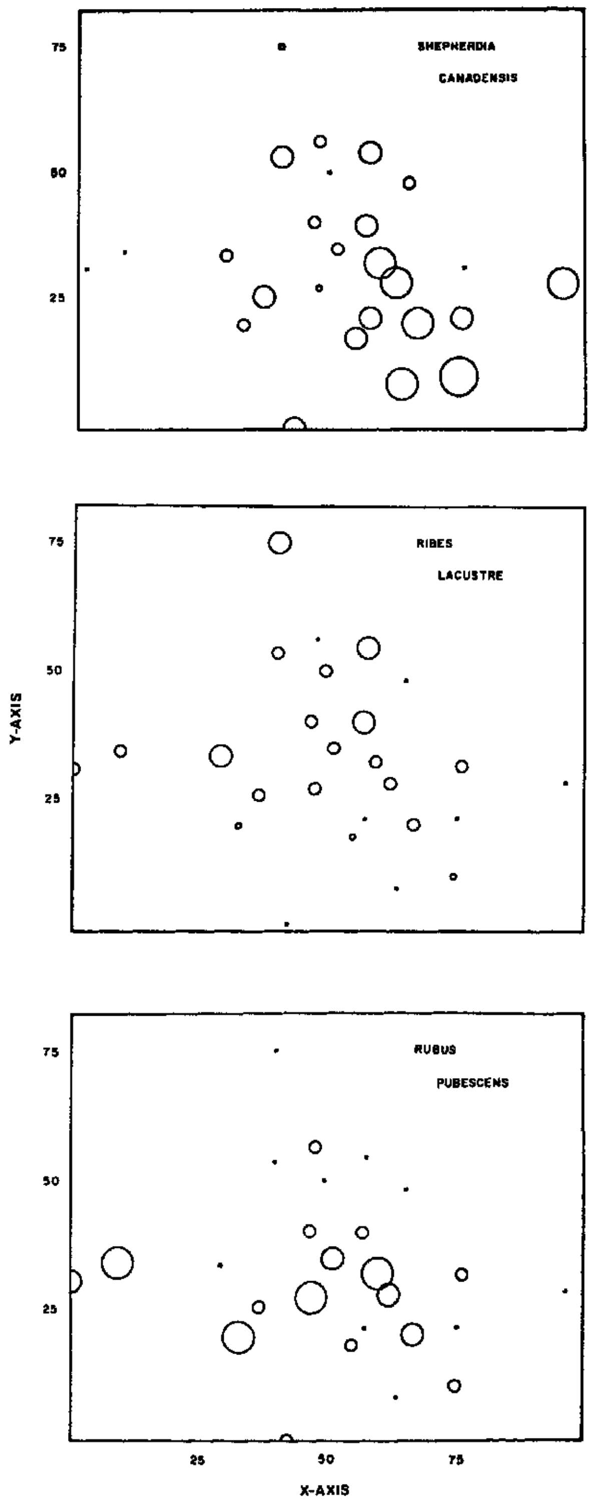

RUBUS
STRIGOSUS
AMELANCHIER
ALNIFOLIA
SYMPHORICARPOS
ALBUS
75
50
25
Y-AXIS
25
50
75
X-AXIS

Figure 19. Phytosociological behavior of three high-frequency shrub species which have their peak frequencies in a central and right-of-center position within the ordination. Percent frequency for shrub species is divided into 5 classes, each having an interval of 20%, and each successively higher percentage class being represented by a larger circle. The smallest open circle indicates "presence"; the solid circle indicates "absence".



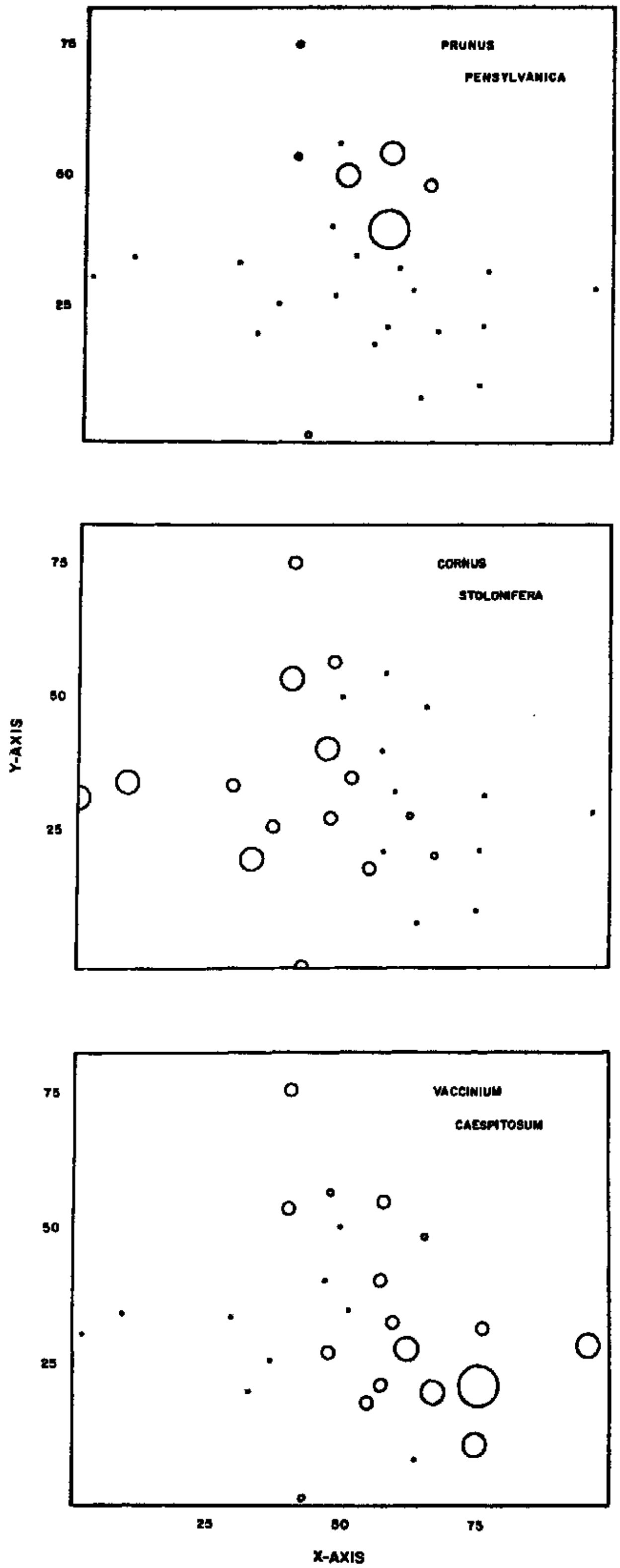
CLEMATIS
VERTICELLARIS
LINNAEA
BOREALIS
SPIRAEA
LUCIDA
Y-AXIS
X-AXIS
75
50
25

Figure 20. Phytosociological behavior of three medium-frequency shrub species which are rather widely distributed within the ordination. Percent frequency for shrub species is divided into 5 classes, each having an interval of 20%, and each successively higher percentage class being represented by a larger circle. The smallest open circle indicates "presence"; the solid circle indicates "absence".



SHEPHERDIA
CANADENSIS
RIBES
LACUSTRE
RUBUS
PUBESCENS
75
50
25
Y-AXIS
25
50
75
X-AXIS

Figure 21. Phytosociological behavior of three shrub species which show restricted distributions within the ordination. Percent frequency for shrub species is divided into 5 classes, each having an interval of 20%, and each successively higher percentage class being represented by a larger circle. The smallest open circle indicates "presence"; the solid circle indicates "absence".


75
60
25
PRUNUS
PENSYLVANICA
75
50
25
Y-AXIS
CORNUS
STOLONIFERA
75
50
25
VACCINIUM
CAESPITOSUM
25
50
75
X-AXIS

in non-forested sites, but such sites have not been examined sufficiently to state whether or not other species of limited forest occurrence behave similarly. Species which have a moderate percent presence, eg. Vaccinium caespitosum, Linnaea borealis var. americana and Juniperus communis might have some indicator value but most are too widely distributed for this purpose.

Environmental Factors

Ordination axes represent compositional gradients that are assumed to be influenced by environmental gradients, and while vegetal composition is determined by many interrelated factorial complexes, one of these may exercise a controlling influence. It is further assumed that factors operating along the primary and secondary axes are those that exercise such a controlling influence. Association of factors with ordination gradients is not sufficient for a cause and effect interpretation, but it is a prerequisite to such an interpretation. The following analysis is an attempt to associate certain components of the physical environment with the ordination axes.

Behavior of Individual Factors within the Ordination

Components of the physical environment that were measured for each stand are catalogued in Table 12, and include two designations which pertain to the compass direction in which stands are bared. "Exposure" applies to the direction one faces when in the stand and sighting down-slope, at right angles to the slope of the stand. "Face" is used here to designate the "exposure" of the landscape in the general region of a stand as measured from a topographic map. The exposure and face

Table 12. Stand environmental characteristics. * - Water retaining capacity. These values are averages of two replicates. ** - See text and Figure 22 for explanation of this term. *** - These are corrected compass readings.

Stand no.	Altitude (ft.)	Slope	Exposure***	Face**	Soil W.R.C.*	Soil texture (% by wt.) Sand	Silt	Clay	Topographic position
101	4100	27°	320°	45°	123	59.0	20.6	20.4	upper slope
102	4100	5°	120°	135°	161	27.4	41.5	31.1	upland
103	4300	35°	325°	360°	136	52.4	29.0	18.6	upper slope
106	4250	15°	325°	45°	115	44.0	26.9	29.1	lower slope
108	3950	12°	225°	225°	111	56.6	24.8	18.6	lower slope
109	4300	15°	90°	135°	143	52.0	25.0	23.0	mid slope
110	4200	20°	140°	225°	106	30.6	38.8	30.6	mid slope
111	4400	8°	185°	270°	125	38.4	34.9	26.7	upper slope
112	3750	7°	10°	45°	111	42.5	28.8	28.7	lower slope
113	4300	12°	225°	270°	109	43.3	40.5	16.2	mid slope
114	4300	18°	280°	270°	126	38.9	30.5	30.6	mid slope
115	4400	15°	330°	360°	148	38.3	41.1	20.6	mid slope
116	4250	12°	285°	360°	102	41.4	36.4	22.2	upland
118	4350	5°	335°	45°	61	41.6	42.3	16.1	lowland
119	4400	5°	340°	45°	134	25.6	37.2	37.2	upland
120	4350	37°	300°	360°	123	34.3	39.0	26.7	upper slope
121	4350	30°	55°	45°	69	43.2	38.5	18.3	upper slope
122	4650	15°	95°	360°	87	44.5	34.9	20.6	mid slope
123	4250	20°	5°	45°	181	34.6	42.2	23.2	lower slope
124	4500	20°	75°	90°	150	26.6	35.7	37.7	mid slope
125	4500	30°	195°	180°	93	55.4	26.3	18.3	mid slope
126	4100	10°	320°	315°	121	24.2	42.1	33.7	lower slope
127	4000	0	0	360°	100	44.4	28.8	26.8	flood plain
128	4300	20°	130°	180°	91	23.1	41.6	35.3	mid slope
129	3800	15°	45°	45°	108	36.2	41.2	22.6	lower slope
130	4100	8°	270°	45°	86	30.5	40.9	28.6	lower slope

of three hypothetical stands are compared in Figure 22 in order to demonstrate that the two qualities are not necessarily equivalent and, hence, warrant being distinguished.

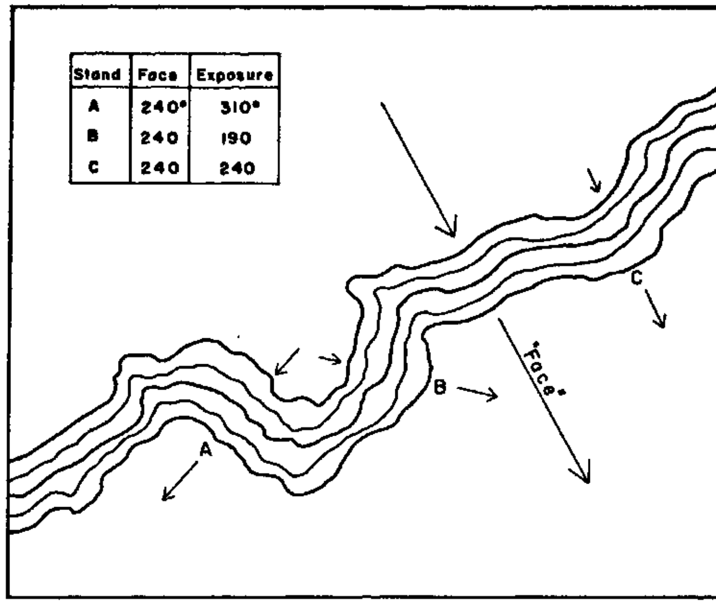
Construction of Factor Indices

Individual factors, when plotted against the ordination, failed to yield meaningful patterns. This is not too surprising, however, since varied combinations of the individual components could effect similar conditions. An increase in either insolation, slope or soil porosity, for example, would reduce moisture availability just as effectively as a decrease in precipitation. It seemed advisable then, to reduce the measured values to indices in order that various factor combinations could be studied. The restriction of forests to altitudinal positions well above the surrounding plains and the evidence that moisture availability increases with elevation, leads to the supposition that moisture may be a limiting factor. Considering also that each of the measured factors is capable of influencing the moisture regime of a site, each was scaled to a moisture-availability index.

A separate scale, ranging from 1 (dry) to 10 (wet), was constructed to cover the recorded variation for each measured environmental factor (Figures 23, 24 and 25). The incorporation of a common index range into each scale allowed independent field measurements to be reduced to comparable index values which could then be summed to provide physiographic index values for the stands. The values assigned to positions along the scales are based on the estimated ability of each factor to influence the moisture regime. These estimates were assigned by the present writer on the basis of field experience

Figure 22. An illustration distinguishing "face" and "exposure" as used in this thesis. The shorter arrows mark the exposure directions of the individual stands, while the longer arrow marks the "face" of the regional terrain.

Figure 23. Scales used to reduce face and exposure values to physiographic index values. (See Fig. 22 for the distinction between these factors.). Face values are adjusted to the nearest 45° compass reading, providing a discontinuous series. A stand with a face of 135° has an index value of 6. Exposure values are not adjusted, providing a continuous series. A stand with an exposure of 135° has an index value of 6.



Stand	Face	Exposure
A	240°	310°
B	240	190
C	240	240

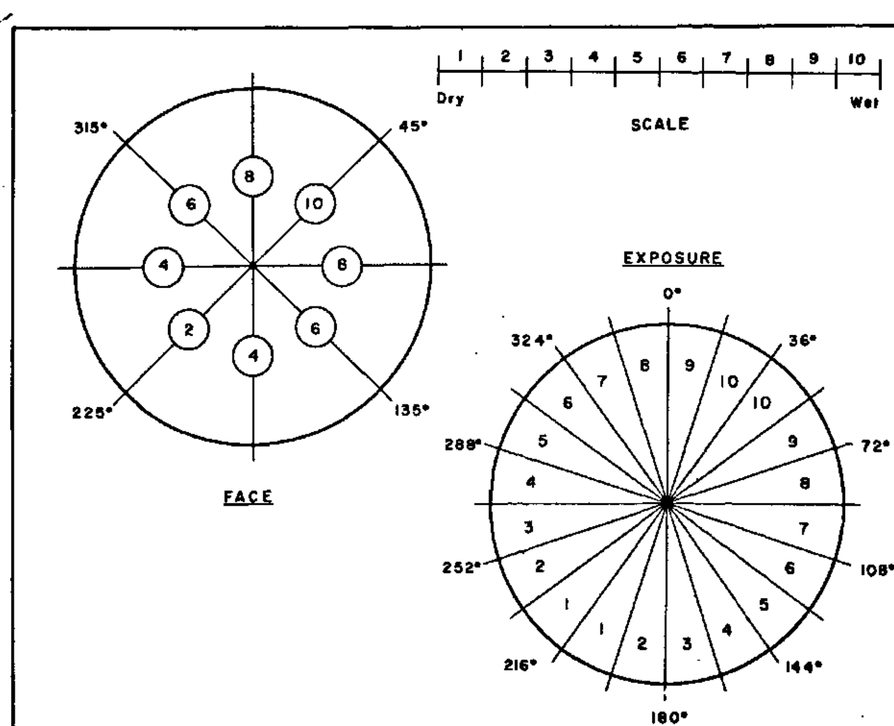


Figure 24. Scales used to reduce slope, altitude and topographic position values to physiographic index values. Scales are constructed to cover the measured range of variation. A scale for physiographic values is given in Figure 23. A stand having a slope of 30°, an altitude of 4000', and occurring on an upper slope would have index values of 4, 3, and 2.

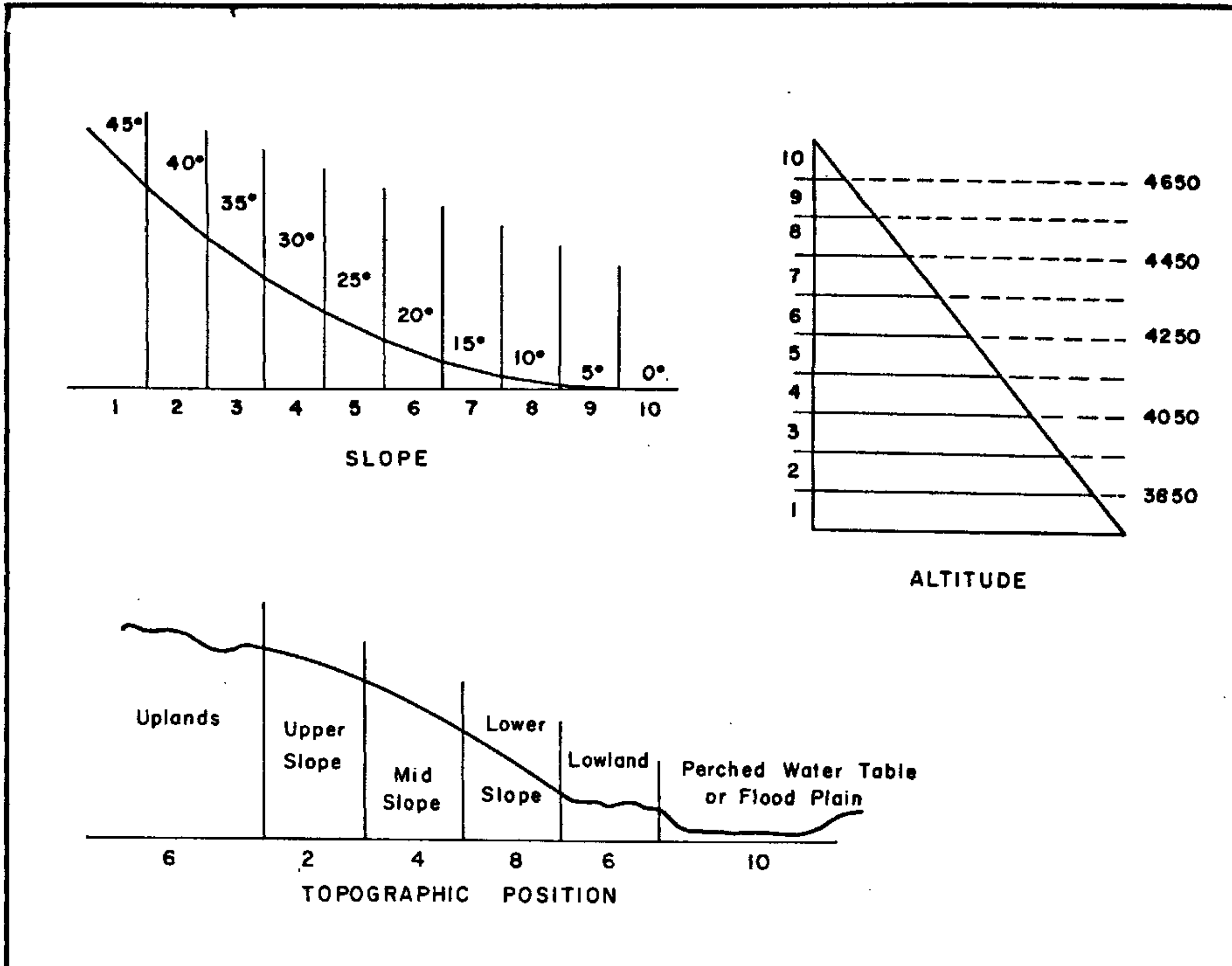

45°
40°
35°
30°
25°
20°
15°
10°
5°
0°
1 2 3 4 5 6 7 8 9 10
SLOPE
10 9 8 7 6 5 4 3 2 1
4650
4450
4250
4050
3850
ALTITUDE
Uplands
Upper Slope
Mid Slope
Lower Slope
Lowland
Perched Water Table or Flood Plain
6 2 4 8 6 10
TOPOGRAPHIC POSITION

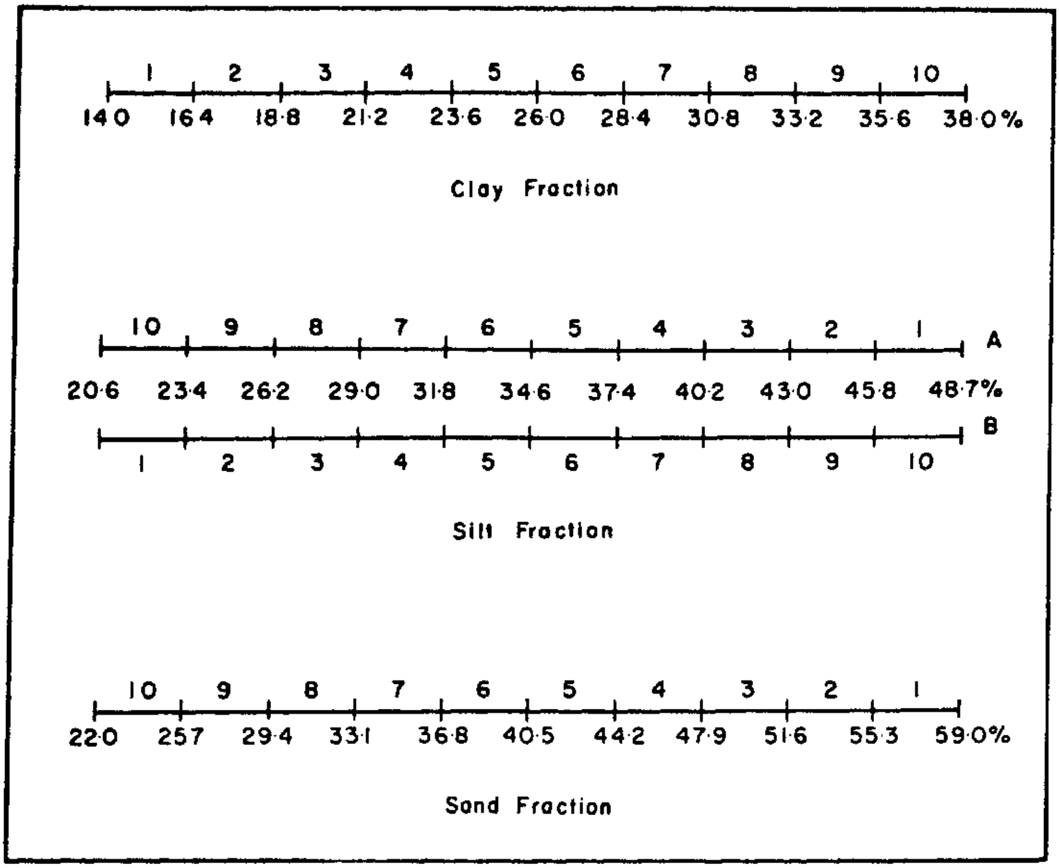
Figure 25. Scales used to reduce soil texture and water retaining capacity values to physiographic index values. Scales are constructed to cover the measured range of variation. A scale for physiographic values is given in Figure 23.

Use of the Soil Texture Scale:

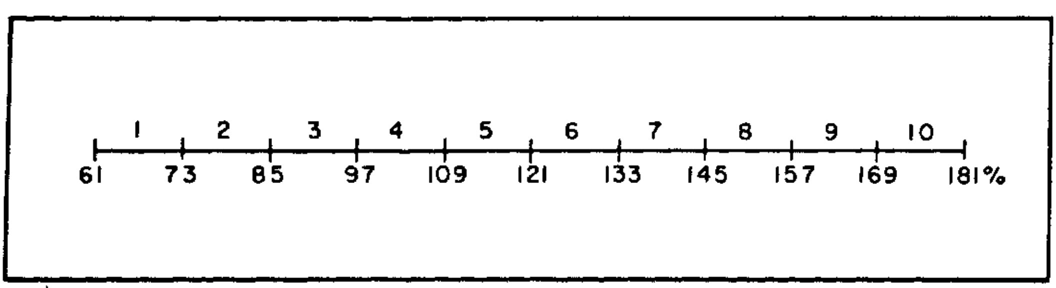
When the sand % exceeds the clay %, use the lower scale for silt (Scale B).
When the sand % is less than the clay %, use the upper scale for silt (Scale A).
When the sand % = the clay % (± 5%), use an index of 5 for silt.

$$\text{Texture index} = \frac{\text{clay index} + \text{sand index} + \text{silt index}}{3}$$

A soil having 20% clay, 30% silt and 50% sand would have a clay index of 3; a silt index of 4; a sand index of 3; and a soil texture index of 3.3.



Soil-Texture Scales



Water-Retaining-Capacity Scale

plus published studies. These are linear scales, each class having an equal increment, though certain factors, such as water retaining capacity (WRC), are known to function on a logarithmic rather than a linear basis. A logarithmic relationship is known for only a few of the included factors, however, and the use of two scalar bases would unduly complicate their combination. If either axis represents a moisture gradient, it is reasonable to assume that this would be demonstrated by linear scales, less precisely but adequately, even for factors which function logarithmically.

The ranges for 5 variables were readily divisible into 10 classes. The exposure scale (Figure 23), for example, is divided into twenty units of 18° beginning at 216° but each class comprises two units since equivalent physiographic positions occur both to the left and to the right of 216°. The "face" and topographic position scales, however, have 5 and 6 classes respectively, because this seemed as fine a division as was practical.

The soil texture index (Figure 25) is founded on the rationale that a high WRC is associated with a high clay, but a low sand, content. Therefore, scales for these two fractions should be read in opposite directions. If the clay content exceeds the sand content, silt would lower the WRC and the silt scale should be read in the same manner as that for sand (i.e. use silt scale A). The silt content in Stand No. 124 (Table 12), for example, equals 35.7% and since the clay percent (37.7%) is greater than the sand percent (26.6%) the silt index for the stand is 5. On the other hand, if the sand fraction is the greater of the two, silt would increase the WRC and its scale should be read like that for clay (i.e. use silt scale B).

Stand No. 101, in which the sand percent (59.0%) exceeds the clay percent (20.4%), has a silt content of 20.6% and a silt index of 1. When sand and clay are in about equal proportions, silt performs at an intermediate level and has been assigned an index value of 5. The formula:

$$\frac{\text{clay index} + \text{silt index} + \text{sand index}}{3} = \text{texture index}$$

is provided to incorporate the three fraction values into one soil texture value which, if subtracted from the WRC index, provides an estimate of the influence of organic matter in the moisture regime. This index of soil moisture compared favorably with the formula used to place soils in named texture classes (Table 13). Stand index values are listed in Table 14.

Plot of Index Values Against the Ordination

Index values were plotted individually (Figure 26) and collectively (Figure 27) against the ordination. Each factor presents a novel pattern or no pattern but there is a suggestion that Sectors V, VI, VIII, IX and X are dry to dry-mesic (Figure 27). Two series of factor combinations were erected to test their combined influences. In series 1 (Table 15 and Figure 28), factors were removed one at a time from the total, and the sub-totals of the remaining 6 factors were plotted (Single Factor Elimination). For series 2, each factor was rated according to its apparent importance in the moisture regime and a rank sequence was established. Each factor was then removed from the total in the sequence established, without replacing those previously removed (Cumulative Factor Elimination).

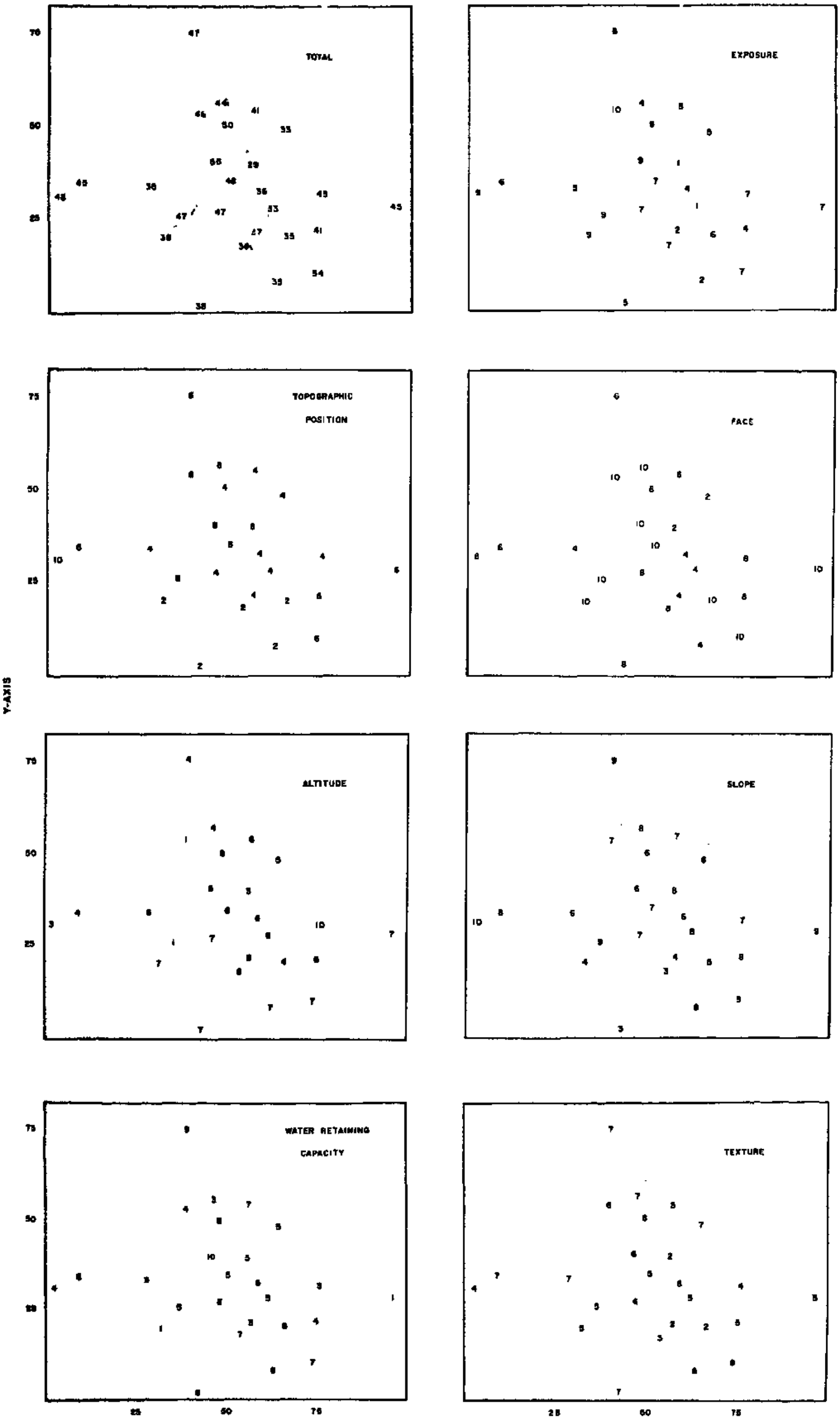
Table 13. Comparison of soil texture index values with named soil texture classes.

Texture class	Index value	Stand no.
Clay Loam	8	119
Clay Loam	8	124
Clay Loam	7	110
Clay Loam	7	102
Clay Loam	7	120
Clay Loam	7	126
Clay Loam	7	128
Clay Loam	7	130
Clay Loam	6	114
Loam	6	111
Loam	6	115
Loam	6	123
Loam	6	129
Loam	5	106
Loam	5	112
Loam	5	113
Loam	5	116
Loam	5	118
Loam	5	121
Loam	4	122
Loam	4	127
Sandy Clay Loam	3	109
Sandy Clay Loam	2	101
Sandy Loam	3	103
Sandy Loam	2	108
Sandy Loam	2	125

Table 14. Physiographic index values for the stands. These values were derived by applying the values in Table 12 to the scales in Figures 23, 24 and 25.

Stand no.	Altitude	Slope	Exposure	Face	Soil W.R.C.	Soil texture	Topographic position	Total
101	4	5	6	10	6	2	2	35
102	4	9	6	6	9	7	6	47
103	6	3	7	8	7	3	2	36
106	6	7	7	10	5	5	8	48
108	3	8	1	2	5	2	8	29
109	6	7	8	6	7	3	4	41
110	5	6	5	2	4	7	4	33
111	7	8	2	4	6	6	2	35
112	1	9	9	10	5	5	8	47
113	6	8	1	4	5	5	4	33
114	6	6	4	4	6	6	4	36
115	7	7	7	8	8	6	4	47
116	6	8	4	8	4	5	6	41
118	7	9	7	10	1	5	6	45
119	7	9	7	10	7	8	6	54
120	7	3	5	8	6	7	2	38
121	7	4	9	10	1	5	2	38
122	10	7	7	8	3	4	4	43
123	6	6	9	10	10	6	8	55
124	8	6	8	8	8	8	4	50
125	8	4	2	4	3	2	4	27
126	4	8	6	6	6	7	8	45
127	3	10	9	8	4	4	10	48
128	6	6	5	4	3	7	4	35
129	1	7	10	10	4	6	8	46
130	4	8	4	10	3	7	8	44

Figure 26. Plot of physiographic index values against the ordination. The total of the index values of each stand is plotted in the upper, left illustration, while numbers in the remaining illustrations are index numbers for individual factors.



TOTAL
EXPOSURE
TOPOGRAPHIC POSITION
FACE
ALTITUDE
SLOPE
WATER RETAINING CAPACITY
TEXTURE
Y-AXIS
X-AXIS

Figure 27. Plot of the total of the physiographic index values for each stand, against the ordination. Sector lines and numbers (Roman numerals) are added for comparison with Figure 16.

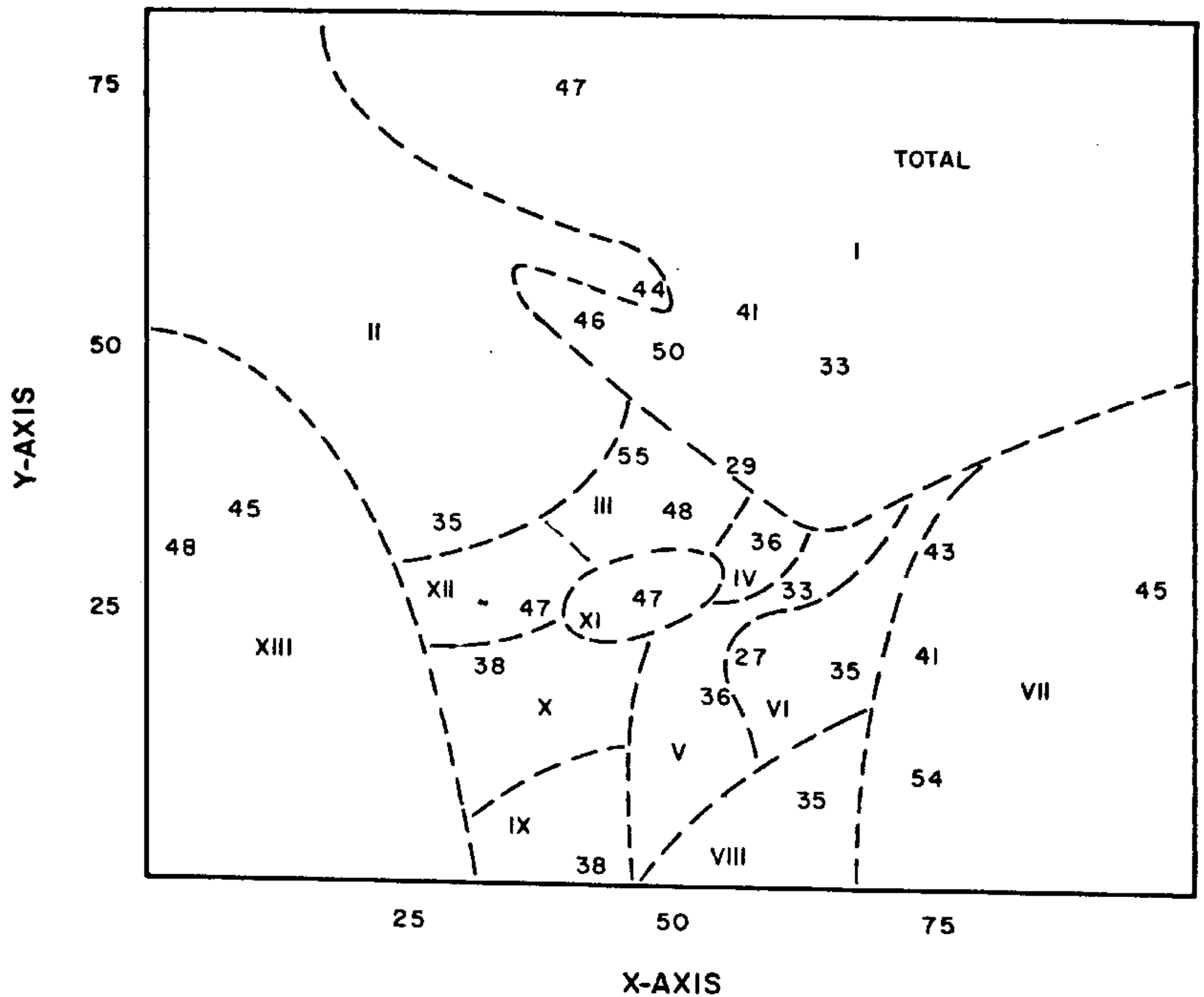
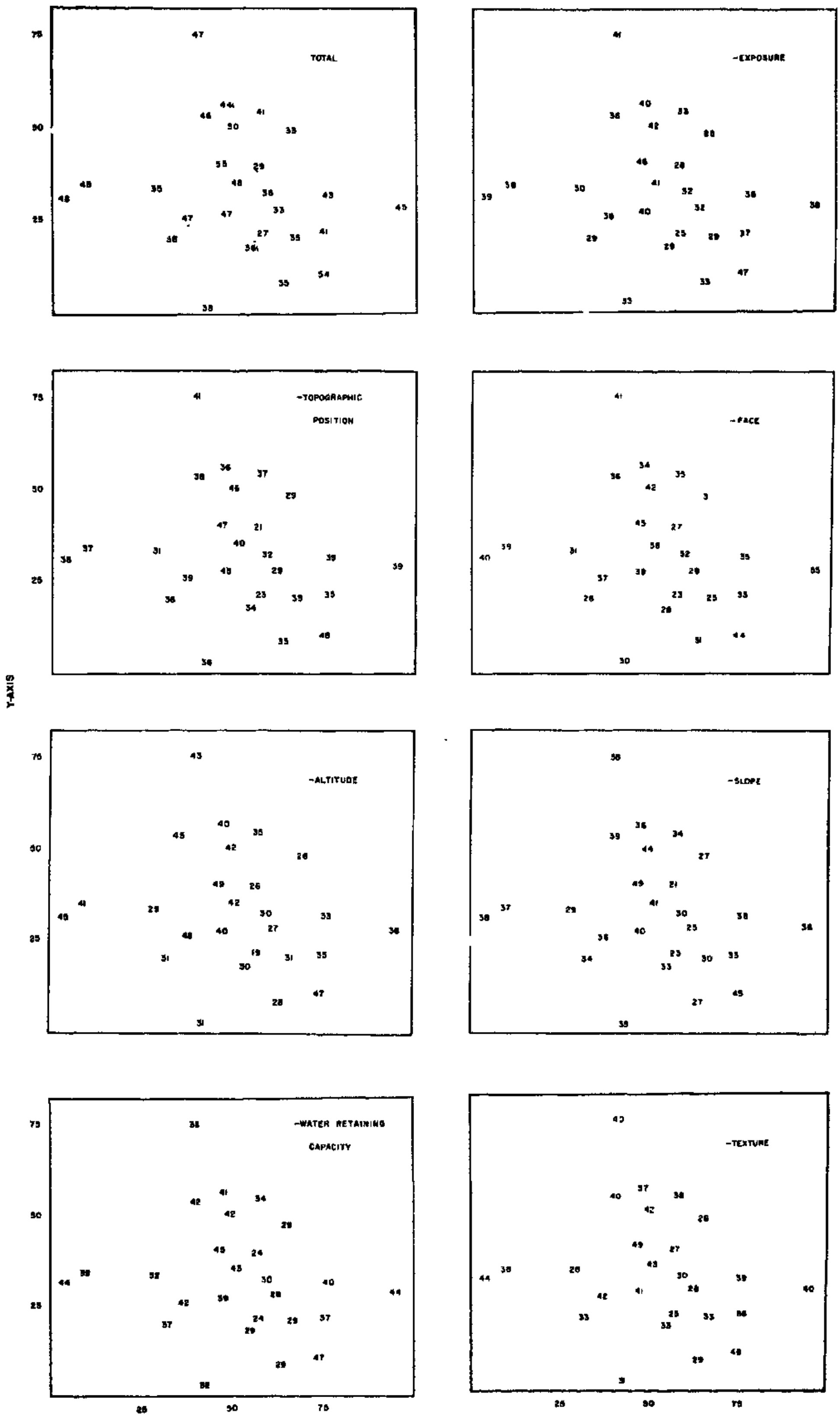

TOTAL
47
I
II
44
46
41
50
33
55
29
III
48
36
35
45
48
XII
47
IV
33
43
45
25
XI
47
XIII
38
27
35
41
X
36
VI
VII
V
54
35
IX
38
VIII
75
50
25
Y-AXIS
X-AXIS

Table 15. Physiographic index values in the Single Factor Elimination Series. Values listed are the remainders after the removal of individual factors from the stand totals.

Stand no.	Total	-Altitude	-Slope	-Exposure	-Face	-Soil W.R.C.	-Soil texture	-Topographic position
101	35	31	30	29	25	29	33	33
102	47	43	38	41	41	38	40	41
103	36	30	33	29	28	29	33	34
106	48	42	41	41	38	43	43	40
108	29	26	21	28	27	24	27	21
109	41	35	34	33	35	34	38	37
110	33	28	27	28	31	29	26	29
111	35	28	27	33	31	29	29	33
112	47	48	36	36	37	42	42	39
113	33	27	25	32	29	28	28	29
114	36	30	30	32	32	30	30	32
115	47	40	40	40	39	39	41	43
116	41	35	33	37	33	37	36	35
118	45	38	36	38	35	44	40	39
119	54	47	45	47	44	47	46	48
120	38	31	35	33	30	32	31	36
121	38	31	34	29	28	37	33	36
122	43	33	36	36	35	40	39	39
123	55	49	49	46	45	45	49	47
124	50	42	44	42	42	42	42	46
125	27	19	23	25	23	24	25	23
126	45	41	37	39	39	39	38	37
127	48	45	38	39	40	44	44	38
128	35	29	29	30	31	32	28	31
129	46	45	39	36	36	42	40	38
130	44	40	36	40	34	41	37	36

Figure 28. Plot of physiographic index values against the ordination, (single factor elimination series). Values plotted are the stand totals minus the factor indicated.



TOTAL
-EXPOSURE
-TOPOGRAPHIC POSITION
-FACE
-ALTITUDE
-SLOPE
-WATER RETAINING CAPACITY
-TEXTURE
Y-AXIS
X-AXIS
25
50
75

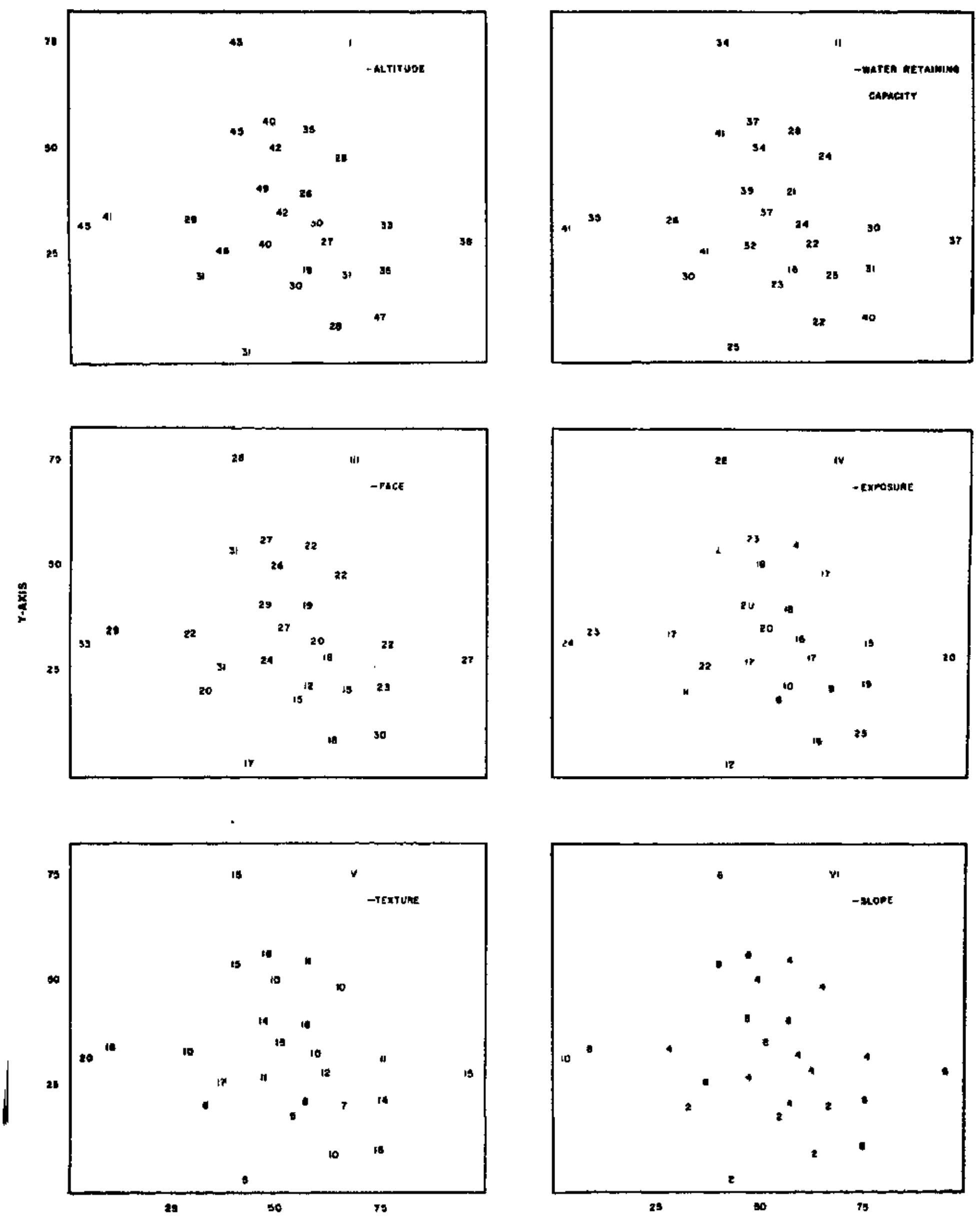
The remainders at each step of this manipulation (Table 16) were likewise plotted against the ordination (Figure 29).

The combination of these 7 physiographic variables presents a pattern of reduced moisture availability, centered on a dry to dry-mesic region in Sectors V, VI, VIII, IX and X. It is clear, then, that physiographic differences are associated with compositional changes but since these sectors are encircled by mesic to wet-mesic stands, the physiographic pattern obviously does not have a monomodal grade along either of the primary axes. It is evident, therefore, that, while the X-axis and the Y-axis are strongly associated with vegetal gradients, they do not represent moisture availability gradients, and that the physiographic pattern is not associated with the principal vegetational patterns.

Table 16. Physiographic index values in the Cumulative Factor Elimination Series. Values listed are the remainders after factors have been cumulatively removed from stand totals. Factors are listed (left to right) in the sequence of removal. "-Slope" = "Topographic Position" in Table 14.

Stand no.	Total	-Altitude	-Soil W.R.C.	-Face	-Exposure	-Texture	-Slope
101	35	31	25	15	9	7	2
102	47	43	34	28	22	15	6
103	36	30	23	15	8	5	2
106	48	42	37	27	20	15	8
108	29	26	21	19	18	16	8
109	41	35	28	22	14	11	4
110	33	28	24	22	17	10	4
111	35	28	22	18	16	10	2
112	47	46	41	31	22	17	8
113	33	27	22	18	17	12	4
114	36	30	24	20	16	10	4
115	47	40	32	24	17	11	4
116	41	35	31	23	19	14	6
118	45	38	37	27	20	15	6
119	54	47	40	30	23	15	6
120	38	31	25	17	12	5	2
121	38	31	30	20	11	6	2
122	43	33	30	22	15	11	4
123	55	49	39	29	20	14	8
124	50	42	34	26	18	10	4
125	27	19	16	12	10	8	4
126	45	41	35	29	23	16	8
127	48	45	41	33	24	20	10
128	35	29	26	22	17	10	4
129	46	45	41	31	21	15	8
130	44	40	37	27	23	16	8

Figure 29. Plot of physiographic index values against the ordination, (cumulative factor elimination series). Factors are numbered (Roman numerals) in sequence of estimated increasing importance in the moisture regime, and are removed from the total in this sequence. Values plotted are the stand totals minus the sum of the removed values, including the factor indicated. Example: III (-Face). Values plotted = stand totals minus (altitude + WRC + face). Note that IV (-slope) is equal to Topographic Position (see Figure 26).


I —ALTITUDE
II —WATER RETAINING CAPACITY
III —FACE
IV —EXPOSURE
V —TEXTURE
VI —SLOPE
Y-AXIS
X-AXIS
25
50
75

DISCUSSION

The goals of this study have been to examine the phytosociological interrelations of the forests of the Cypress Hills and to probe their basic dynamics. Analysis of the floristic composition of the woody vegetation of 26 stands has demonstrated a pattern of continuous variation, linking pine, aspen and spruce forests into one ordered system. This section is a discussion of the factors controlling this system and an attempt to place the results of this study into a perspective with the total vegetation.

Delimiting the Possible Controlling Factors

The ordinated system has two possible sources of control; the physical environment (allogenic factors) or the vegetation itself (autogenic factors). If the vegetation is under autogenic control, the system displayed is successional and it can be concluded that little of the forest vegetation has achieved a steady state. If, on the other hand, allogenic factors are in control, the system can be interpreted as a reflection of individual species tolerances to existing environmental gradients, and it can be concluded that most of the vegetation has achieved a steady state. These two categories are sufficiently distinct for the present analysis though they may not be entirely mutually exclusive. The argument for allogenic control will be presented first, followed by evidence of autogenic control.

Argument for Allogenic Control

Vegetations respond to the simultaneous interaction of all allogenic factors but only certain of these approach limiting levels in any one instance. The location of the Cypress Hills on the Great Plains within a continental climate is one in which moisture is very often limiting. Rowe (1956) states, with reference to the southern edge of the Boreal Forest in the Prairie Provinces, that "soil moisture is probably the most important determinant of growth, and variations in moisture regime are always reflected in variations of the vegetation". Moisture availability hinges on the interplay of three physical factors; moisture received, soil conditions and temperature. Moisture received as precipitation is not necessarily available to plants since part of the water may percolate too rapidly through the soil, be bound too strongly to soil particles, be lost as run-off, etc. and the local moisture supply is further regulated by temperature, particularly as it varies with topographic differences. South-facing slopes, in the northern hemisphere, receive greater insolation than north-facing slopes and, hence, tend to be drier because of increased evaporation. Degree of slope also helps to regulate the quantity of water that soaks into the soil. Whittaker (1960) suggests that "differentiation in relation to topography and the patterning in relation to patterns in topography ... are general characteristics of vegetation".

The conclusions to be drawn from these considerations are that moisture is the allogenic factor most likely to be limiting in the Cypress Hills and that topography and soils are the prime regulators of moisture-availability. If the moisture supply is limiting forest development, the ordered vegetal pattern ought to be associated with a physiographic gradient based on moisture availability.

The Physiographic Index

A plot of the physiographic index established that stands which, because of their topographic position, slope, exposure, etc., were classed as dry, are grouped within the ordination but are bordered on three sides by more mesic stands. Neither the X-axis nor the Y-axis, singly or in combination, represents a physiographic gradient and there is, thus, a lack of correlation between the vegetal and physiographic patterns. This index, admittedly, has weaknesses, such as its failure to account for variation in precipitation received, for differential snow deposition and for depth to the water table, each of which could contribute sufficient local moisture to override the influence of the included factors. The influence exerted by these omitted factors will remain unknown until data concerning them are available, or until a more sophisticated index has been constructed but they appear not to be so influential as to invalidate this index. If their importance were of that magnitude, some stands with south or steep slopes could be expected to have ordinated positions among the more mesic stands. Stand No. 128, a mixture of spruce and aspen on a south slope, is the only stand with an index value in the dry range that is so ordered and even this is a borderline case. As additional sites are studied, the weight of these factors may be accentuated, but within the present study it seems that they could only increase the moisture availability to sites that are already classed as mesic or wet.

Further Considerations of Topography

The forest relationships of the Cypress Hills are part of a broader web involving the interaction between forest and grassland, and an exploration of forest dynamics must necessarily take cognizance of the forest-prairie interrelations. An hypothesis that purports to explain the dynamics of part of this system must fit whatever hypotheses pertain to the entire system. There are, therefore, two facets of the vegetation that must be considered: (1) the persistence of the relict vegetation, and (2) the distribution of relict communities throughout the hills.

It has been suggested that the fescue prairie and the conifer and aspen forests of the Cypress Hills are relicts of some past era (Breitung 1954) and the persistence of a relict is known to require of its habitat some compensating factor that affords it a competitive advantage over the neo-vegetation (Clements 1934). The transition from mixed prairie, through fescue prairie and aspen parkland, to conifer forests further north in Alberta and Saskatchewan, is accompanied by an improved moisture regime (Borchert 1950). Increased elevation in the Cypress Hills appears to accomplish the same effect through lower temperatures and increased precipitation, as evidenced by the weather data from Klintonel and Battle Creek. Direct evidence to support this contention is fragmentary but it is reasonably sufficient to cite an improved moisture regime as the probable compensating factor.

The distribution of relict communities within the relict area, however, is quite a different matter and the control on each site need not be the same. The distribution of climatic elements throughout the hills has yet to be studied and it is not known, for example, whether or not the highest elevations receive more precipitation than intermediate elevations, or whether or not there exists a precipitation cline from east to west. Daily and seasonal temperature distributions likewise are unknown. In short, there is no direct evidence [illegible] f moisture in the distribution of the relict species and communities.

The more obvious distribution of communities suggests control by topography and, hence, by moisture availability, but there are cogent, though perhaps less obvious evidences that contradict this suggestion. The high, flat benchlands at 4800' elevation are occupied primarily by black soils, supporting fescue prairie and are presumed to be kept in grassland because strong winds, Chinook and otherwise, remove snow cover and dessicate the land. To the east, at lower elevations, the black soils are replaced by dark brown and brown soils; the fescue prairie gives way to the mixed prairie; and grasslands, generally, occupy a greater percent of the land. These trends suggest a gradient of increasing moisture from east to west, with the western end being still too dry to support forest growth on the plateau. Consider, then, the fescue prairie sites studied by Coupland and Brayshaw (1953). These are located at an altitude between 4100 and 4200', on black soils; 1100' above the surrounding plains and 600' below the top of the hills. Pine and aspen forests occur on the benchlands at the 4100' contour under ostensibly the same wind conditions that prevail higher up. This point is difficult to reconcile with the argument that moisture availability increases with altitude unless one accepts the possibility that the vegetation has not yet achieved its maximum potential, that forests could occupy some areas that are presently in grassland.

Forested slopes in the eastern third of the hills are almost exclusively aspen, the coniferous species being restricted to sporadic occurrences of single trees along streams and gullies. On lower slopes, and extending out onto the plains, aspen groves follow drainage channels, with grasslands on the interfluves. In the western, more forested region, spruce grows principally along creeks, springs and flood plains, and balsam poplar, where present, occupies similar habitats. Pine forests are most commonly found on north-facing slopes and in deep ravines, with south-slopes and hillcrests being areas of aspen and grassland. Even so, the argument for topographic control is not irrefragable. The crests of forested slopes may support aspen, shrub or grassland communities, but pine may also border these crests and extend out onto the bench. Pine savannas exist on the highest bench and spruce appears on a few steep, south-facing slopes. North-facing slopes are mostly forested but some of these are grassed.

The vegetation is best described as a mosaic. Small clusters of spruce interrupt larger areas of pine or aspen, and patches canopied by one or another of these species alternate irregularly over the landscape. Boundaries are abrupt; grasslands are recurrent; and, occasionally, a mixed forest canopy appears. A patchwork array is, however, intrinsic to both coniferous forests and to ecotones, so the mere alternation of forests and grasslands, or of one forest canopy with another, is not very instructive as to the factors controlling the array. The pattern in the Cypress Hills is regular enough to demonstrate some topographic control but not sufficiently regular that topography may be cited as the primary control.

Argument for Autogenic Control

The second possible source of control for the ordered system is succession and, whereas the ordination axes do not correlate well with a physiographic gradient, they are satisfactorily associated with the expected pattern of a successional gradient. Trembling aspen and lodgepole pine are relatively short-lived, shade intolerant, pioneer species in contrast to the longer-lived white spruce. Still, white spruce possesses the pioneer traits of being intolerant of its own shade and lacking reproductive capability in a conifer mulch. It does, however, reproduce successfully under aspen and, to a lesser extent, under pine. Being longer-lived than the other two species, spruce will replace them in succession. The path of succession outlined by the ordination is described in the following paragraphs.

Description of the Successional Sequence

The initial forest canopy may be pine, aspen, or possibly a mixture of both depending on the circumstances of its origin. Aspen and pine can each reproduce under the others canopy, though only to a slight degree in the case of pine, and in mixed stands it is not always clear whether they began simultaneously or whether one followed the other. Trunk diameters will sometimes provide an answer but age-size comparisons have received only sufficient study to question the validity of assuming that this correlation can be used. Succession from aspen to spruce can be accomplished without the introduction of pine but the pine to spruce sequence seems invariably to include aspen.

Early stages, regardless of the tree species involved, are accompanied by increases in tree sizes and a decrease in their density, this latter change usually being finally accomplished by wind action. Pine reproduction is absent or slight in all but the initial stages but aspen suckers develop well under both aspen and pine once the overstory has been sufficiently thinned. Spruce germination becomes noticeable as the initial stock is thinned and the importance of spruce rises as the second generation matures. Spruce reproduction remains high as long as the overstory is predominantly pine and/or aspen but as spruce fills the canopy all tree reproduction becomes restricted to gaps. Spruce diameters continue to increase but density, after the initial increase, begins to decline.

Concomitant with changes in canopy species are those associated with species of lower strata. Shrub layers have their richest and most varied development under aspen canopies, in marked contrast to the depauperate appearance of this stratum in young pine stands. Shrub composition is enriched as pine stands mature, however, and certain shrubs, including _Linnaea borealis_, _Vaccinium caespitosum_, _Spiraea lucida_ and _Arctostaphylos uva-ursi_ achieve their best development under pine canopies. The shrub layer is depleted again as succession continues toward spruce but _Rubus pubescens_ and _Cornus stolonifera_ increase in prominence. Associated particularly with early stages in succession from aspen are: _Prunus pensylvanica_, _Symphoricarpos occidentalis_ and _Crataegus_ spp. Most shrubs that occur under aspen persist until the spruce canopy is well developed and, even then, appear in gaps. Some of the more conspicuous species in this group are: _Symphoricarpos albus_, _Prunus virginiana_, _Ribes lacustre_, _Rubus strigosus_ and _Amelanchier alnifolia_. _Rosa_ spp. are ubiquitous and _Shepherdia canadensis_, _Viburnum edula_ and _Clematis verticellaris_ appear to do best under mixed canopies.

Further Considerations of Succession

The progress of succession described above differs in detail from that given by Cormack (1953, 1956) for the coniferous forests of the Alberta Rocky Mountains but agrees well with Rowe's (1956) description of the boreal forest. Cormack emphasizes the development of a dense, tall shrub layer as the spruce-fir forests mature and the absence of this layer in the Cypress Hills is undoubtedly due to the absence of its component species: Menziesia glabella, Vaccinium membranaceum, Lonicera glaucescens and Rhododendron albiflorum being the most conspicuous members in addition to the genus Abies.

If the floristic pattern demonstrated by the ordination is succession, the X-axis and the Y-axis may both represent time, with the differences between them reflecting the circumstances of origin of the initial stages. The earliest stages in forest succession were omitted because of the limited scope of this study but these can be initiated in a variety of habitats, eg. shrub thickets, prairie or marsh. It remains for further study to determine whether development along an axis is related to the cause of forest initiation, to the habitat in which it is initiated, to the initial tree species present, or to a combination of these variables. The question that yet needs to be answered for this study is: If the forests are under autogenic control, and if spruce would naturally replace pine and aspen, why are aspen and pine so widespread and spruce so scarce? The answer to this question can best be approached by reviewing the factors which have exerted control over the vegetation.

Factors Controlling Vegetational Development

The extant forest vegetation originated for the most part following a fire in 1885 (Cormack 1945). Isolated trees and a few groves along flood plains or in otherwise sheltered locations survived, but all other forest canopies are 78 years or younger. However, forest succession probably never had progressed to the point of reducing pine and aspen to a minor status in favor of widespread spruce forests, for, as spruce matures, windfall and disease exact their toll, producing gaps in the canopy which can subsequently be reoccupied by seedlings of various genera. Gap phase replacement is the rule rather than the exception in coniferous forests and gap production is aggravated in hilly terrain by microclimatic and physiographic diversity. Gaps are occasioned by fire as readily as by disease or windfall, and fire was likely a common event prior to settlement in the 1880's. The conclusion of Borchert (1950) that "grassland climates favor fire, just as they favor grasses whether there are fires or not" allows for frequent fires on the surrounding plains, with or without the aid of the Indian, and in all likelihood such fires periodically ignited the forests as well.

Spruce reproduction is hindered by fire. Rowe (1953) found that burned seed beds delayed germination of white spruce seeds nearly two months, and that delayed germination promoted increased winter mortality through failure of the seedlings to harden. Lodgepole pine and aspen, contrarily, are favored by fire. Cones of P. contorta var. latifolia do not open until exposed to sufficient heat (Critchfield 1957). Cameron (1953) states that 45.5°C. (103°F.) is required to melt the bonding material on the cone scales but direct insolation at 40°C. can flex the upper scales, leaving the rest of the cone closed. Fire further aids pine reproduction by removing litter and allowing the seedling root to reach mineral soil, though under certain circumstances lodgepole pine may fail to germinate after fire (Smithers 1961). Aspen reproduction in the Cypress Hills is accomplished primarily by means of suckers (Maini 1960) arising from a horizontal component of the root system that extends through the upper 12" of the soil to a considerable distance from the parent. Fire stimulates dense and rapid suckering but direct insolation, eg., via openings in the canopy, or at the edge of groves, can also stimulate sucker production.

The role of fire in grasslands is a long-argued topic but no information has been gathered relative to its effect on the fescue prairie in the Cypress Hills. Moss and Campbell (1947) support the idea that fire has been a prime factor in retarding the advance of trees and shrubs onto this prairie in northern Alberta, and the statement of these two authors that "burning may bring about dessication of the fescue tussocks" has apparently been interpreted by Breitung (1954) to mean that "successive burning tends to eliminate the fescue grassland". The present dominance of Festuca scabrella in this Cypress Hills grassland has been noted by both Breitung (1954) and Coupland (1961). Thus, Breitung's interpretation leads to the conclusion that since Festuca scabrella is abundant at present, it could not have been eliminated and, hence, fires must always have been infrequent. The validity of his interpretation remains in question but a strong circumstantial argument can be made for infrequent burning of the fescue prairie in the Cypress Hills. Its position on the high plateau offers some protection from fires originating on the surrounding plains. The prevailing westerly and northwesterly winds would all but eliminate the sweep of fire up the gradual climb from the east and south, and, since the steep escarpments on the north and west are heavily forested, fires approaching from these directions would tend to be intense, thoroughly scorching the ground and thereby reducing the fire hazard for a considerable period of time. This argument assumes that fire initiation was more common on the surrounding plains than on the high plateau, and this seems justified in view of the cooler, moister conditions at the higher elevation. As regards forest invasion of prairie, infrequent fires appear capable of retarding this event but may not eliminate it completely.

There have been few fires since 1885 and since these were generally limited in extent and intensity, 1885 marks the cessation of fire as a major ecological force in the Cypress Hills. It would appear that the cessation of fire ought to have allowed an expansion and re-establishment of forests whereever there were habitats favorable to forest growth but, while there is some indication that forests have recently expanded, time, an essential factor in this regard, has been short and additional restraining influences have been active. Agricultural activities began in the Cypress Hills region in 1880 (Saskatchewan Dept. Nat. Res. 1962), ranching was introduced about 1884 (Cormack 1945) and widespread selective cutting took place about 1927 (Kagis 1951). Red squirrels (Tamiasciurus hudsonicus hudsonicus), introduced into the Cypress Hills Provincial Park (Saskatchewan) in 1950, gather and consume enormous caches of pine and spruce cones, and have multiplied so successfully that, by 1960, the 10 original animals had expanded to an average density of 6.7 animals per acre within a 40 acre census area (Dirschl, 1960). They have now dispersed throughout the forested region of the Cypress Hills, and while their influence on coniferous species has not been measured, it does not appear likely that forest expansion is fostered by their activities.

Outbreaks of the forest tent caterpiller (Malacosoma disstria) stripped the leaves from aspen forests over vast areas of the Cypress Hills in 1923-26, 1944-45 and 1958-61 (Hildahl et al. 1960) and fungal diseases, such as that caused by Marssonina spp.[2], also periodically defoliate aspen forest canopies. While evidence of increased mortality as a result of these attacks is inconclusive, terminal and radial growth increments are lessened and, perhaps more importantly, the effects of an open canopy on the understory are unknown. These two agents may be classed as natural forest components but they do retard succession by sapping aspen vitality, and thus prolong the duration of present stages. They are included here to emphasize the importance of time; a successional requirement that has not been met.

Final Argument and Conclusions

There has been little ecological study conducted in the Cypress Hills and most of this has been qualitative in nature. Grasslands throughout most of the hills have yet to be studied and the stability of the forest-grassland margin is undetermined. The quantitative data presented in this paper, having been drawn entirely from forested sites, can only be applied to forest dynamics but these, in conjunction with qualitative observations, do allow for a few speculative comments on the total vegetation.

The application of ordination techniques to quantitative data

2/ Identified by H. Zalasky, Research Officer, Forest Pathology Laboratory, Canada Agriculture Research Station, Saskatoon, from specimens collected by the author.

has demonstrated that these forest communities constitute a vegetational continuum (Curtis 1950) that is presently under successional control. If allowed to continue without disturbance, spruce would theoretically succeed aspen and pine and the predominance of these latter two species would diminish, but windfall and disease, as integral components of coniferous forests, would perpetuate the mosaic pattern, allowing earlier stages to redevelop. Whether pine or aspen would be included in this re-establishment is uncertain because of their restricted reproductive capabilities.

The cessation of fire has unquestionably reduced the ability of lodgepole pine to perpetuate itself and red squirrels may well have hindered this function even further. The ecological significance of aspen, a major tree species of this area, being limited to vegetative means of reproductiom is worthy of serious consideration. Suckering may allow existing stands to expand under favorable circumstances but the species is at a distinct disadvantage in the colonization of distant sites. As spruce forests become more widespread, for example, the chance of aspen occupying gaps is lowered and occupancy by other species could preclude the establishment of aspen for lengthy periods, even if it later does become available. In view of the severe reproductive limitations of the tree species present, future development of these forests even if undisturbed by man, remain problematical in the absence of fire.

The qualitative evidence available connotes a degree of topographic control but the immaturity of the vegetation and its history of disturbance is cause to view apparent indications of this control with suspicion. Persistence of the relict communities requires that some line of potential topographic control exists but it is quite possible that boundaries are not presently limited by this potential. While there is no reason to believe that forests could occupy all of the Cypress Hills, there is evidence that forests could expand at the expense of the grasslands under the existing climate. It is concluded, therefore, that this forest vegetation has not achieved a steady state and that its progress toward this end is most probably under autogenic control.

SUMMARY

The Cypress Hills' forests, dominated by Picea glauca (white spruce), Pinus contorta var. latifolia (lodgepole pine) and Populus tremuloides (trembling aspen), are outliers of the Aspen Parkland and coniferous forest zones that border the Northern Great Plains of Canada. The purpose of this study was to determine the composition of woody species within these forests and to examine the pattern of its variation.

Twenty-six stands, incorporating as wide a range of floristic and habitat variability as possible, were selected for study. Trees were sampled by the point center quarter method, but a circular quadrat having a 6' radius and a $\frac{1}{4}$ M^2 quadrat proved better suited for sampling other woody forms. The measurements taken provided percent frequency data for all classes of woody plants, density values for trees, saplings and seedlings, and dominance figures (basal area at breast height) for trees. A two-dimensional ordination provided the basic system for compositional analysis and interpretation.

Three separate ordinations, based on (1) percent frequency of all woody species, (2) percent frequency of saplings, seedlings and shrubs, and (3) density of trees, saplings and seedlings, were erected and were found to be essentially the same ordination. This suggested that frequency and density, of either the canopy or the woody understory species, or both, are equally capable of characterizing these stands. The ordination based on quadrat frequency was selected for demonstration herein and its analysis lead to the following conclusions.

Floristic composition (of woody species) varies continuously in a pattern that links communities of pure aspen and pine to a community dominated by white spruce but having balsam poplar (Populus balsamifera) as a secondary species. This admixture of balsam poplar is not understood and reasons for this uncertainty are discussed. Lodgepole pine reproduction in the absence of fire is negligible and, while aspen does invade naturally thinned pine areas, it propagates best under its own canopy. White spruce, however, reproduces most successfully under aspen or mixed aspen and pine and, thus, eventually will replace these other 2 species in the canopy. Shrub species are most varied and abundant under an aspen canopy but certain species achieve their optimum development under pine or spruce.

Forest development appears to be controlled by the vegetation itself and, while some potential physiographic control may be present, it does not appear to be limiting at this time. The strength of this conclusion rests upon the validity of the assumption that factors which exert prime control over the vegetation are those which function along the primary ordination axes. Since these axes do not correspond to a physiographic gradient but are, however, satisfactorily associated with a successional gradient, it is concluded that physiography has not become limiting and that forest development is presently limited only by successional factors.

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APPENDIX A

Scientific and common names of species included in this study.

Scientific name	Common name
Acer negundo	Manitoba Maple
Amelanchier alnifolia	Saskatoon-berry
Arctostaphylos uva-ursi	Common Bearberry
Betula papyrifera	White Birch
Betula occidentalis	Water Birch
Clematis verticellaris	Purple Clematis
Cornus stolonifera	Red Osier Dogwood
Crataegus chrysocarpa	Hawthorn
Crataegus douglasii	Hawthorn
Elaeagnus commutata	Silver-berry
Juniperus communis	Ground Juniper
Juniperus horizontalis	Creeping Juniper
Linnaea borealis	Twin-flower
Picea glauca	White Spruce
Pinus contorta	Lodgepole Pine
Populus balsamifera	Balsam Poplar
Populus tremuloides	Trembling Aspen
Potentilla fruticosa	Shrubby Cinquefoil
Prunus pensylvanica	Pin Cherry
Prunus virginiana	Choke Cherry
Ribes hudsonianum	Wild Black Currant
Ribes lacustre	Bristly Black Currant
Ribes oxyacanthoides	Wild Gooseberry
Ribes setosum	Wild Gooseberry
Rosa acicularis	Prickly Rose
Rosa woodsii	Common Wild Rose
Rubus acaulis	Dwarf Raspberry
Rubus pubescens	Dewberry
Rubus strigosus	Wild Red Raspberry
Salix bebbiana	Beaked Willow
Salix discolor	Pussy Willow
Shepherdia canadensis	Canadian Buffalo-berry
Sorbus scopulina	Mountain Ash
Spiraea lucida	White Meadowsweet
Symphoricarpos albus	Snowberry
Symphoricarpos occidentalis	Buckbrush
Vaccinium caespitosum	Dwarf Bilberry
Viburnum edule	Low-bush Cranberry
Viburnum trilobum	High-bush Cranberry