VEGETATION OF THE SOUTHERN BOREAL FOREST IN SASKATCHEWAN AND MANITOBA

by

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Abstract

The vegetation of that part of the southern boreal forest which occupies the Cretaceous uplands in western Manitoba and central Saskatchewan has been studied, with particular attention to communities in which Picea glauca (Moench) Voss. is a component. As a background to the vegetational studies, the glacial and post-glacial history of the flora is first discussed, and it is argued that the boreal flora of this area probably survived the last glaciation along the southern and southwestern periphery of the continental ice sheet rather than in the Great Lakes refugium.

The autecology of each of the eight principal tree species is examined as a basis for the understanding of their relative abilities to compete, survive and enter into the composition of the various forest types. The forest communities are sorted into series based primarily on moistness of site, and within each series recognizable "noda" or "forest types" (in the Russian sense of the term) are defined by means of the dominant trees and by characteristic constant species of the undergrowth. The successional relationships of numerous communities are examined and it

is concluded that very few can be designated as stable, chiefly due to the frequency of fire which prevents development of the vegetation to a final steady state. However on extreme sites relatively permanent communities occur, and on non-extreme sites where physiographic features provide protection from fires, fragments of the fundamental Abies & Picea/Hylocomium-Rubus forest type are found.

An outline is given of a generalized descriptive scheme which can be applied to all stands in the southern boreal forest. It is based on the physiognomy and moisture preferences of undergrowth species.

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INTRODUCTION

The forest vegetation of west-central Canada has not yet been studied in any detail, or described except in the most general terms. With progressive settlement of the forest fringe, and with continuing logging activity and the inevitable fires, it is becoming increasingly more difficult to find undisturbed examples of the mature vegetation, and this lends urgency to the need for botanical and ecological work in the area. The purpose of the present project was to examine and study a comprehensive sample of stands in the accessible and economically important forest belt which stretches from the Cretaceous Uplands of western Manitoba across central Saskatchewan, describing the composition and structure of the forest types, as well as their ecological and successional relationships.

The size of the area covered made necessary some limitations in the scope of the work, and attention was concentrated primarily on the vegetational communities of highest immediate importance, namely, the mature upland forests which have white spruce and aspen as their major components. The field work was carried out in the years 1949 to 1954 inclusive, as an accompaniment of studies of white spruce reproduction, white spruce forest types, and the productive potentialities of forest sites.

The study has been organized into seven chapters which deal in turn with, field methods, a general description of the area, post-glacial history of the vegetation, the autecology of the tree species, the conceptual basis for the vegetational studies, the description of the forest communities and their successional relationships, and finally, a generalized scheme for the description of forest stands in this particular area.

Because of the broad nature of the studies it has not been feasible to consolidate in one section a review of related research work by other investigators, and therefore discussions of relevant literature have been included within the text, wherever most appropriate.

The nomenclature of higher plants follows Fernald (1950) for the most part. Where other names have been used, authorities are given only the first time that each name appears in text or tables. The nomenclature of the mosses follows Grout (1940) and Andrews (1940).

I

METHODS

Considerable assistance in the location of suitable study areas was received from men in the provincial Forest Services of both Manitoba and Saskatchewan, as well as from co-workers in the Federal Forestry Branch. At each selected locality a preliminary rapid reconnaissance of the forests was made in order to gain an idea of the variability in forest sites and forest communities. Aerial photographs, and forest cover-type maps prepared by the provinces, proved very useful at this stage. Stands for closer examination were then selected so as to sample observed differences in composition and in stage of development of the vegetation on the various sites. Wherever possible, undisturbed forests were compared with adjacent cut-over and burned-over areas as a means of gauging probable successional trends.

A plan for the collection of field data, outlined in a previous publication (Rowe, 1953), was followed. Briefly, the unit of detailed study was a plot, square or rectangular, and usually of one-tenth or one-fifth acre in size (the latter is the usual sample plot size in forestry work). The plots were usually laid out in such a way as to include homogeneous samples of vegetation and site. On each plot a complete study of the total plant community was made. All trees were tallied by inch-diameter classes for the interpretation of stand structure and of density, and the heights and ages of representative individuals were measured for rate of growth data. Tree seedlings and saplings were closely examined as to rooting habits, ages and heights, rates of growth, and position relative to differences in micro-site. A study of stand genesis was made by investigating the surface medium on which the oldest trees had become established, and this was augmented by examinations of the humus layer for signs of fire and windthrow.

The minor vegetation within each plot was examined in 20 milacre quadrats which were evenly spaced, as the advantages of random sampling are not important in studies such as these (Oosting, 1948, p. 50). The quadrat size (6.6 feet by 6.6 feet) is large compared to that used in grasslands or other communities where the individual species are small, but it proved suitable for the simultaneous sampling of all forest undergrowth strata: shrubs, herbs and mosses. On the basis of data from three mixed spruce-aspen stands, the milacre quadrat was found to approximate the minimum size of quadrat calculated by Cain's (1938) method. Also, diagrams of frequency, based on data taken in numerous 20-quadrat samples, approximated Raunkiaer's normal J-shaped curve, with a relatively few species in the 81 to 100 per cent class and many in the

1 to 20 per cent class. Quadrat size was therefore suitable for the discrimination of the four or five most important species in each sample plot.

The cover-abundance of each species was estimated within each quadrat using Braun-Blanquet's 6-point scale, although in the last year a modification was introduced to effect a separation of the species of low cover-abundance. The modified scale is as follows:

5 - covering 76 to 100 per cent of the ground
4 - covering 51 to 75 per cent of the ground
3 - covering 26 to 50 per cent of the ground
+2 - covering 16 to 25 per cent of the ground
2 - covering 6 to 15 per cent of the ground
+1 - covering 3 to 5 per cent of the ground
1 - covering 1 to 2 per cent of the ground
+ - covering less than 1 per cent of the ground.

Species not found in the quadrats but observed elsewhere on a given plot were also noted in order to provide the complete data for determination of constance.

In compiling the data for each plot, a card summary of the vegetation was prepared by listing the species in decreasing order of importance, using the frequency and cover-abundance data. The examination of many hundreds of quadrats showed that, in general, the species of highest frequency are also those of greatest cover-abundance, and therefore frequency alone is usually sufficient as an index of the relative importance of plant species in any community, provided that the quadrat size is suitable. The completed cards made possible a rapid comparison of the numerous sample plots, and facilitated the grouping of stands according to similarities in composition and structure.

On each plot, notes were made concerning those features of site believed to be related significantly to the vegetation. Topographic position and its probable effect on local climate (ecoclimate) through slope, aspect and exposure were noted. The morphology of soil profiles was carefully examined and described, and simple field tests were made to determine the texture and acidity of horizons. In some instances monoliths of characteristic profiles were collected for later study, and smaller samples were brought in from the field for laboratory analysis of texture, acidity, and moisture equivalent.

In addition to the intensive studies of sample plots as outlined above, a great many other forest stands and their sites were examined in a less detailed way.

II

GENERAL DESCRIPTION OF THE AREA

Physiography

The vegetation with which these studies are concerned occupies the eastern part of the plain which extends from the Manitoba Cuesta (Cretaceous escarpment) through Saskatchewan, thence rising gradually to the foothills of the Rocky Mountains. Physiographically, the area is a part of the Great Plains section of the Interior Continental Plain, and it corresponds in general to the forested eastern and northern parts of the Second Prairie Level (Putnam, 1952).

The relief of the area is not extreme except locally in the eastern part. It is chiefly a result of pre-glacial erosion of the soft bedrock shales, which produced such features as the Cretaceous escarpment and associated hills (Riding Mountain, Duck Mountain, Porcupine Hills, Pasquia Hills and Wapawekka Hills) in the vicinity of the Manitoba-Saskatchewan boundary, and of the Missouri Coteau farther to the west. Subsequent glaciation modified the landscape, in some places sharpening the relief (as on the escarpment face at the eastern and northern sides of the Hills) and in others reducing it by planation and the deposition of drift. The highest points on the Cretaceous Hills are 2,500 feet to 2,700 feet above sea level, compared to a general elevation of less than 1,000 feet on the Manitoba lowlands to the east and north below the scarp. Immediately to the west of the Hills there is a less pronounced decrease in altitude to below the 2,000-foot contour, but continuing westward there is a gradual rise across Saskatchewan and Alberta to the foothills of the Rocky Mountains. A discussion of the "landforms" within the southern boreal forest in central Saskatchewan has been given by Mitchell, et al (1950).

In general the topography is rolling, with locally rougher morainic deposits on the uplands and with locally smoother glacio-lacustrine deposits on the lowlands. Well-entrenched rivers carry the drainage waters of the Plains east and northeast to the Churchill and Nelson Rivers.

Vegetation

The forest vegetation of the area has been classified as the "Mixedwood Section" (Halliday, 1937) of the transcontinental "Boreal Forest: Picea-Larix Formation" (Weaver and Clements, 1929). The name "Mixedwoods" refers to the prevalence of mixed stands of *Populus tremuloides* (Aspen), *Populus balsamifera* (Balm of Gilead, or balsam poplar), *Picea glauca* (white spruce), *Betula papyrifera* (paper birch) and *Abies balsamea* (balsam fir). Other important tree species which enter into the composition of the various forest communities are *Pinus banksiana* (jack pine), *Picea mariana* (black spruce) and *Larix laricina* (tamarack). The position of this forest section relative to neighbouring vegetation is shown in Fig. 1.

Rousseau (1952) has pointed out that the subarctic zone with its characteristic park-like forest and *Cladonia* ground-cover (the "Taiga" or "Hudsonian Lichen Woodland") should be clearly differentiated from the temperate zone with its exploitable, floristically rich, close forests. If this be done in the northern part of Manitoba and Saskatchewan, then the boreal forest proper to the south can be divided into two major vegetational areas by a line which roughly follows the surface contact between the Cretaceous uplands and the Palaeozoic and Precambrian lowlands, corresponding to the division between the Mixedwood section and the Hyper-Churchill, Northern Coniferous Forest, and Manitoba Lowlands sections (Halliday, 1937). South and west of this line in the area to be treated in the following paper, poplar and white spruce are the prominent trees in the forest communities, while on the lower and leveler terrain to the north and east black spruce is the primary dominant and the importance of hardwood species is much reduced. The two parts can be called respectively the "Southern Boreal Forest" and the "Northern Boreal Forest". The former term is preferred to "Mixedwoods" in this study because of its geographic connotation. To make it even

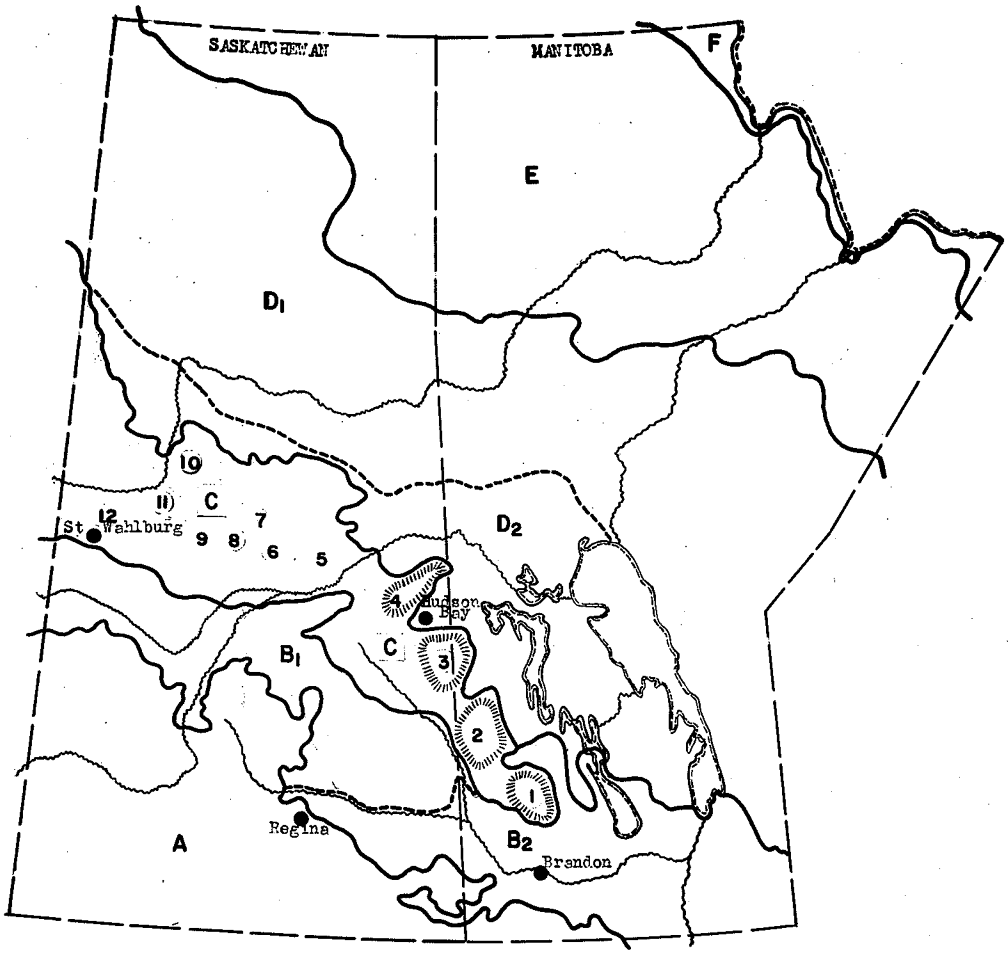

Fig. 1. Map of Saskatchewan and Manitoba showing vegetational zones (A to F), and the location of the principal areas (1 to 12) in the southern boreal forest where studies were made. Explanation (Halliday's symbols bracketed):

A Grassland
B_1 Aspen Woodland (B.17)
B_2 Aspen-oak Woodland (B.16)
C Southern Boreal Forest (B.18 - "Mixedwoods")

1	Riding Mountain	7	Bittern Creek
2	Duck Mountain	8	Waskesiu
3	Porcupine Hills	9	Big River
4	Pasquia Hills	10	Dore Lake
5	Torch River	11	Green Lake
6	Candle Lake	12	Loon Lake

D_1 Northern Boreal Forest, Precambrian Section (B.21, B.22)
D_2 Northern Boreal Forest, Palaeozoic Lowlands Section (B.15, B.20)
E Taiga (B.27)
F Tundra

more specific, the Southern Boreal Forest is defined as including a coniferous element, thus distinguishing it from the Aspen Woodland which along the southern edge forms an ecotone between boreal forest and grassland.

The southern boreal forest appears to the traveller as a constantly changing pattern of poplar and of spruce-poplar stands on the uplands, and of coniferous stands (spruce and tamarack) on the poorly drained lowlands. The open upland forests are "rich" floristically, with abundant shrubs and herbs forming a tall, dense undergrowth on the deep soils that are, for forestry purposes at least, relatively fertile. In patches of closer-canopied forest, where the spruce component is high, the clean forest floor with low herbs and mosses can be seen, a condition most commonly encountered on the lowlands. Areas of excessively drained soils are usually occupied by jack pine, with a low shrub and herb undergrowth.

Climate

Detailed information on climatic conditions over the area as a whole is scanty, as there are few settlements where weather records have been kept within the forested region. There are however indications that the southern boreal forest belongs within one climatic unit which extends from central-western Manitoba to northern Alberta. A glance at generalized climatic and vegetational maps for the area (for example see Putnam, 1952, pp. 347-351) shows the close correspondence of the two.

According to Thornthwaite's climatic classification, the southern boreal forest belongs to the microthermal climatic type and is placed in the dry, subhumid province (Sanderson, 1948). Mr. G. Brown of the Federal Forestry Branch at Ottawa, and Mr. H. Cameron (until recently, employed by the Federal Forestry Branch), have kindly provided the descriptive climatic data shown in Table I, obtained in large part by interpolation in the maps of the Climatological Atlas of Canada (Thomas, 1953).

The general description in Table I needs to be modified in several respects to convey a truer picture of climatic variations within the area. According to Sanderson (1948) the moisture deficiency north of a line running approximately from Edmonton to Prince Albert and The Pas is less than 4 inches, due to decreasing evaporation at the higher latitude. The seasonal moisture deficiency for the extensive uplands (above the 2,000-foot contour) which occur in the east and west must also be considerably lower than the average, although there are no climatic records for them. As an example, the Cretaceous Hills along the Manitoba-Saskatchewan boundary are almost certainly more humid than the neighbouring lowlands, and this is indicated by a consistent difference of several inches in yearly

TABLE I

CLIMATIC DATA FOR THE SOUTHERN BOREAL FOREST

(B.18 MIXEDWOOD SECTION)

Mean Annual Total Precipitation	19 - 17	inches
Mean Annual Rainfall	14 - 11	"
Mean Rainfall March April May	2.4 - 1.5	"
June July August	7.0 - 9	"
September October November	2.5 - 2	"
Mean Annual Snowfall	45 - 55	"
Mean Annual Temperature	35° - 30°	
Mean Annual Maximum	90° - 94°	
Mean Annual Minimum	-40° - -50°	
Mean Daily Temperature - April	35° - 31°	
Mean Daily Temperature - July	65° - 62°	
Mean Daily Temperature - October	35° - 38°	
Mean Annual Total Hours of Bright Sunshine	2100-2000	hours
Average Annual Potential Evaporation - Thornthwaite	19.5 - 21	inches
Average Annual Water Deficiency - Thornthwaite	4 - 6	"

precipitation between weather stations on the Riding Mountain National Park and those of the surrounding towns at lower elevations. The seasonal pattern of precipitation is another important factor, and it has been pointed out that there is apparently a higher autumnal rainfall in eastern than in western Saskatchewan, with the probability of increased moisture storage in soils of the former district (Mitchell, et al, 1950). A great store of relevant information concerning the variability of climate in the west is contained in Currie's Monograph on Climates of the Prairie Provinces and Northwest Territories (1953, 1954).

Soils

There is a remarkably clear correspondence latitudinally between patterns of climate, vegetation and soil in the Prairie Provinces. The climatic and vegetational zonation from the steppe lands of southwestern Saskatchewan and southeastern Alberta through prairie and forest to the tundra in the north and northeast is matched by the zonation of Brown, Black, Podzolic Grey and Tundra soils. The southern boreal forest of western Manitoba, central Saskatchewan and northern Alberta corresponds closely to the podzolic grey wooded group of soils.

The process responsible for the development of the grey wooded soils is podzolization or, more accurately, decalcification. It is first a solution process by which the carbonates mainly responsible for the stability of grassland soils are removed from the solum, and then a decomposition-eluviation process. Under the influence of cool climate and forest cover, an organic layer accumulates on, rather than in, the surface soil. Slow decomposition, chiefly by fungi, yields acid products which in leaching downward remove the basic cations. Acid weathering of the soil minerals commences, releasing iron and aluminum which in ionic and combined forms move downward in the profile. Humic and clay colloids also migrate, and a leached siliceous acid horizon (bleicherde) develops. Below the eluviated horizon, the colloidal organic matter, the compounds of iron and aluminum, and the clay are precipitated.

Recent papers reviewing the literature on the grey wooded soils in western Canada and presenting new descriptive data on some of the profile variants in Saskatchewan and Manitoba are those by Moss and St. Arnaud (1955) and by Ehrlich (1955). The information available shows that the grey wooded profiles are developed predominantly on somewhat calcareous, glacial or post-glacial deposits. The following features are characteristic: Under the humus layer (variable in composition and thickness) the A_1 horizon is thin or absent. The bleached, acid, platy A_2 horizon is well developed, its depth significantly related to texture and calcareousness of parent material. Analyses have shown that the A_2 horizon is lower in content of clay, bases and sesquioxides than the B horizons, although higher in content of silica and silt. In the B horizons the accumulation of materials eluviated from the A horizons is reflected in darker (brown) colours, heavier texture, and frequently in a nutty or blocky structure.

The podzolization process is not strongly expressed in grey wooded soils, due primarily to the limited leaching which is in turn contingent on moderate rainfall, calcareousness of parent material, and nature of the vegetation. As a general statement "The grey wooded soils differ from the podzols in exhibiting a higher range in pH values and a correspondingly higher base status. They show less accumulation of organic matter and greater accumulation of clay in the B horizons. They also exhibit greater structural development" (Moss and Arnaud, 1955, p. 307).

Intrazonal associates of grey wooded soils are: swamp podzols (depression podzols), fen and meadow soils (wiesenboden), and peats. Solonetzic variants of the grey wooded profiles--characterized by a thin leached A_3 horizon under a dark A_1 and A_2, and by a tough, columnar B horizon--have been recognized in Saskatchewan and northern Alberta. The genesis of the latter soils is not understood, although apparently they have developed in the hydromorphic position on shaly parent material.

Further reference to soils is made in Chapter V where relationships of site and forest vegetation are discussed.

III

HISTORY OF THE AREA IN RELATION TO THE FLORA

It is certain that the entire area now occupied by forest vegetation in Manitoba and in central and northern Saskatchewan was glaciated many times during the Pleistocene epoch. In the Wisconsin Glacial Age the ice pushed into the Dakotas south of Manitoba, into southern Saskatchewan, and into southern Alberta (Bretz, 1943), leaving evidence on its retreat in the form of numerous end moraines and lateral moraines of which one of the best known (Mankato phase of the Cary substage) trends northwest through western North Dakota, southern Saskatchewan and eastern Alberta, following roughly the crest of the Missouri Coteau. At this time all plant life must have been completely displaced from our area, returning from west, south and east as the glacier melted and the land surface was exposed. The origin of the present flora and its affinities with eastern, western and southern elements, constitutes a problem of considerable interest, bearing as it does on such questions as past climatic conditions, areas of refuge where species survived glaciation, and post-glacial migrations.

To set the problem in perspective, reference should be made to Hultén's "Outline of the history of arctic and boreal biota during the Quaternary Period" (1937). In this study, Hultén showed that when the ranges of many present-day arctic and boreal plant species are superimposed, regions of overlap representing centres of species' concentration appeared. Furthermore, these so-called "centra" were found to coincide with areas known to have escaped glaciation in Pleistocene times, and therefore represent "refugia" or source areas from which plants radiated during the inter-glacials. Hultén located centra in northeastern Siberia and the Amur-Manchurian region, in northern Japan, and around the northern part of the Bering Sea (the latter of particular importance as a primary source area for the North American boreal flora), in the Yukon Valley, the Arctic American coast, the Arctic Archipelago, and the central Rocky Mountains. However, no groups of plants "could be formed having their centres in northern Europe or western Siberia, or in Northeastern America or in the country between Yukon Valley and the Great Lakes." (Hultén, 1937, p. 25).

From the northwest then, according to this hypothesis, came the original boreal flora of North America, achieving wide distribution before or during the long Yarmouth (D) inter-glacial. With the advent of the subsequent Illinoian or maximal ice advance the ranges of the various plants are believed to have been drastically reduced. The principal survival areas at that time, as well as during the final glacial age (Wisconsin), are believed to have been the Atlantic Coastal Shelf, the southern edge of the ice front (particularly the area south of the Great Lakes), and the Cordilleran region (particularly the Yukon River Valley).

The fact that Hultén's centra coincide with unglaciated areas is sufficient proof that his thesis of refugia from which plants radiated, forming their "progressive equiformal areas", is soundly based. However there has been considerable controversy over the interpretation of the present-day ranges of species in terms of these source areas within a time scale. (See for example Raup, 1947; Butters and Abbe, 1953.) One difficulty of course is the lack of basic knowledge which still exists concerning the areas occupied by many boreal plants. As an example, *Cynoglossum boreale* and *Listera auriculata* have been listed recently as disjunct between British Columbia and Ontario (Scoggan, 1950), although the writer has collected the former near Big River, Saskatchewan (Specimen No. 525) and the latter near Singoosh Lake, Manitoba (Specimen No. 668). Similarly, the following species which are common throughout our area appear from Raup's dot maps (1947) to be absent and therefore disjunct: *Carex canescens*, *Potentilla fruticosa*, *Heracleum lanatum*, *Cornus canadensis*, *Moneses uniflora* and *Pyrola virens* (Raup's nomenclature).

Hultén's interpretations of major disjunctions are largely in terms of glacial or inter-glacial reductions, and possibly the most serious criticism of his work is that he tends to neglect the possibility of significant post-glacial happenings. In examining the discontinuous distributions of some British plant species, Pigott and Walters (1954) argue that the observed disjunctions have been brought about in recent (post-glacial) times by a combination of climatic change and of competition from an encroaching forest vegetation. Essentially the same argument is advanced by Butters and Abbe (1953) to explain the presence of certain rare species in Cook County, Minnesota.

One of the few studies dealing in part with the distributions and post-glacial migrations of species in our area was made by Halliday and Brown (1943). Maps were prepared showing not only the ranges of important trees in Canada, but also their relative abundances from place to place, and this information was used as a basis for the interpretation of refugia and migrations. It should be noted that although the authors took Hultén's hypothesis as a point of departure for their discussion, they attempted to use a criterion of centre of origin which Hultén avoided, namely relative abundance. The validity of this criterion has been examined by Cain (1944) who, after quoting Hultén's objection to it, concludes that "dominance and density are frequently highly irrelevant in this respect". Thus for example, using the data of Halliday and Brown, the fact that *Abies balsamea* is most abundant in the lower St. Lawrence valley and the Maritime provinces but very scarce in western Canada does not necessarily place its centre of origin at the Eastern Continental Shelf refugium. It is more likely that the true explanation, an ecological one, is contained by inference in the statement that: "the abundance of fir throughout Canada will be found to resemble quite closely the map of mean annual rainfall (Halliday and Brown, 1943, p. 364). Also, the high relative abundance of *Pinus banksiana* in the Lake States--interpreted as indicating its centre of dispersal--suggests more than anything else conditions suited to the perpetuation of this species: a long fire history, and extensive areas of sandy and stony soils. It is not impossible that jack pine was present in Alberta in Cary times, for Hansen (1952) reported 38 per cent pine pollen (species unknown) with 62 per cent spruce pollen at the bottom of a peat profile ("3.8 meters deep") in an area well east of the present range of lodgepole pine near Smith, Alberta.

Raup (1946) also has accepted the idea of a primary source area south of the Great Lakes from which, following deglaciation, came the "eastern" boreal element to repopulate the Athabasca-Great Slave Lake Region. The same premise appears in his examination of the flora of southwestern Mackenzie (Raup, 1947). However, there is no reason to believe that the so-called "eastern" element in northern Alberta and Saskatchewan and in Mackenzie is a recent arrival from the east. It may actually have come from the south, following the retreating edge of the glacier, a point that will be discussed more fully a little later.

The distances which pine and fir are assumed to have travelled from their postulated refugia, since deglaciation opened the route, makes the hypothesis of origin centres in the east appear at least doubtful. According to this idea, jack pine, for example, must have moved from south of the Great Lakes to its present western limit near Great Bear Lake (roughly 1,800 miles) in about 11,000 years--a migration rate of one mile every six years <u>against prevailing winds and river currents</u>. In any case the anomalous ranges of balsam fir and jack pine, the former reaching only to northern Alberta and the latter to the western Northwest Territories, should be considered in the light of the fact that their western limits occur near where their vicariants (alpine fir and lodgepole pine, respectively) appear. The limit to westward migration may therefore have been imposed, not so much by a lack of time for dispersal from eastern refugia since deglaciation, as by a complex of factors involving climatic conditions, competition, and possibly reduced vigour in the marginal populations due to hybridization. Moss (1949, 1953) has reported apparent hybridization between jack pine and lodgepole pine, and between balsam fir and alpine fir, in Alberta. It is appropriate to mention here that the western variety of white spruce, Picea glauca var. albertiana (S.Brown) Sarg., is probably a product of hybridization with Picea engelmannii Parry (Wright, 1955).

Problems of the origin of our particular flora will not be easily solved. It is evident that distributional data alone without supplementary information on ecological and historical factors may be deceptive (Böcher, 1951). Butters and Abbe (1953) have raised the question "of the value of elaborate analyses of contemporary ranges, especially when the tacit assumption is made that they are static." They go on to say: "direct comparisons of contemporary distribution patterns are likely to be just as misleading as the old comparative morphology of living plants often was in arriving at sweeping phylogenetic conclusions". The phytogeographer needs in addition to distributional data the information provided by studies of palynology, ecology, experimental taxonomy, and Pleistocene geology, in order to trace the floristic history of an area.

In the following discussion an attempt has been made to draw together the writer's field observations and relevant information from various sources in order to suggest a few possibilities as to the immediate origin of the flora in the area concerned. No pretense to completeness is made since the primary aim of the study was ecological rather than phytogeographical. Nevertheless some suggestive clues have appeared which may at least aid in interpreting the larger picture of the future, and it is thought worth-while to set them down here, particularly since little has appeared to date concerning the phytogeography of this area. Some of the problems have been touched on by Löve and Löve (1954) working in the Agassiz Basin, and by Moss (1955) in Alberta. Valuable research on the fossil pollen of bogs has been done in the latter province (Erdtman and Lewis, 1931; Hansen, 1949a, 1949b, 1952) but not elsewhere, and a fruitful field for study along similar lines exists in Saskatchewan and Manitoba. In the farther northwest Raup (1946, 1947) has discussed the probable origins of vegetation in the Athabasca-Great Slave Lake Region and in southwestern Mackenzie.

It is not generally believed today that the advancing ice was fronted by a tundra zone, ahead of which extended the forest zones in cliseral sequence. Potzger (1953) among others has pointed out that "in many pollen profiles from Ontario and Minnesota, across Wisconsin, Michigan, south to Indiana and Ohio, eastward to New Jersey, Connecticut and southern Maine, no one has been able to find absolute evidence of a tundra at the border of the continental ice sheets of Tazewell, Cary, and Mankato times....." From another point of view, it might be supposed that had the vegetation zones moved southward ahead of the ice they should also have followed its retreat northward, an event that would surely have resulted in the isolation of many relict species in favourable microhabitats far south of their appropriate zones today. A study of the flora of North Dakota, just south of Manitoba and eastern Saskatchewan, by Rudd (1951) convinced her that the northern coniferous forest did not migrate into the aspen parkland and prairie of that area during recent glacial and post-glacial times. It is noteworthy too that the Turtle Mountain, a Tertiary highland in southwestern Manitoba, shows little evidence in its present flora of a past invasion by the coniferous forest, although single reports of _Drosera_ _rotundifolia_ L. (Stevens, 1950) and _Salix_ _pedicellaris_ var. _hypoglauca_ (Scoggan, 1952) are intriguing. Before leaving this subject it should in justice be pointed out that the species characteristic of the coniferous forest are by definition those which cannot exist outside it. Therefore the failure to find indicators of a previous coniferous forest points only to the obvious fact that the forest does not exist today, which does not rule out the possibility that it may have been present in the not distant past. However in the absence of conclusive proof in the form of fossil evidence for the hypothesis of coniferous forest migration over the uplands ahead of the ice, it may be assumed on climatic grounds that such did not take place.

One piece of vegetation in south-central Manitoba whose origin has been interpreted at variance with the above is the isolated Picea glauca (white spruce) "parkland" forest (Spruce Woods Forest Reserve) which occupies a raised delta southeast of Brandon. The delta was formed in an early stage of Glacial Lake Agassiz by the Assiniboine River. Bird (1930) accepted the idea of forest retreat before the ice and of advance in its wake, and suggested that during the latter movement a fragment of the spruce forest remained on the delta where local edaphic conditions proved favourable for its survival. However it is significant that no relict spruce community occupies the similarly formed sandy deposits in the Souris basin to the southwest of Brandon, and a glance at the drainage patterns of the two areas immediately suggests the reason for the difference in vegetation. The Assiniboine River flows to its old delta from a forested zone in the northwest, while the Souris River approaches its old delta from a prairie zone in the southwest. It seems likely therefore that white spruce arrived at the Assiniboine delta via what the writer believes was a main route of migration of boreal species, namely a southeastwardand eastward-trending river valley. Additional evidence for the valley-migration hypothesis as opposed to the zonal-movement hypothesis is found in the fact that *Pinus banksiana* (jack pine), the one conifer best suited ecologically to the sand delta habitat, is entirely absent from the Spruce Woods Forest Reserve, or at least it was until introduced by man early in the present century. Pine of course is not adapted to survival in the riparian habitat and hence would not be expected as a constituent of communities migrating via river valleys. Its presence would be expected however if the boreal forest had moved southward and then northward en masse. More puzzling perhaps is the absence of *Abies balsamea* (balsam fir), a tolerant species well suited to dispersal via rivers and lakes. Its absence may be due to a lack of mesophytic upland habitats in the delta area.

Further to the above, Mr. C.B. Gill of the Manitoba Forest Service, has drawn my attention to an interesting book: "The Company of Adventurers" (Cowie, 1913), a series of reminiscences of the author when he was in the service of the Hudson's Bay Company from 1867-74. Speaking of old Fort Ellice, which was located on the Assiniboine River in western Manitoba near the point where the peri-glacial Qu'Appelle coulée system joins the Assiniboine from the west, Cowie remarks on a palisade of *spruce* pickets surrounding the Fort (p. 183). A few pages later in describing his trip from Fort Ellice westward to Fort Qu'Appelle (up the Qu'Appelle valley) he says: "The cart trail from the fort led first through what might be called--comparatively speaking--a wooded country, in which among the prevailing poplar a stray oak and a chance spruce might be seen" (p. 196). No white spruce extend this far down the Assiniboine today nor is any to be seen in the Qu'Appelle valley, and although the accuracy of these reminiscences are certainly questionable there is the suggestion that isolated patches of white spruce may have persisted in the lower Assiniboine valley until very recently. Mention will again be made of the significance of the valley habitat when problems of glacial and post-glacial survival and migration are examined.

Returning to a consideration of the glaciation of our area, the scant evidence available suggests that the ice sheet impinged directly on the resident vegetation in its southward and southwestward movement from the Keewatin centre, successively obliterating coniferous forest and aspen woodland in its advance into the prairie. Then as now the southern Canadian plains lay in the rain shadow of the Rocky Mountains and therefore the opinion has been expressed that no drastic climatic changes sufficient to alter the vegetation from prairie to forest accompanied glaciation of or possibly aspen parkland.

Geological history since Late Wisconsin time suggests that the chief immediate source of the boreal forest flora in Alberta, Saskatchewan, and western Manitoba was not the area south of the Great Lakes. It seems fairly certain that the lowlands east of the Cretaceous scarp in Manitoba and North Dakota provided an effective barrier to plant migrations from the east throughout much of the last glacial age, since it must have been successively occupied by ice, water, or swamp and marsh, depending on the phases of glacial advance or retreat. Each time a glacier was nourished in the north, natural drainage was blocked and lakes must have resulted in the Manitoba lowlands. With the advance of the glacier the lakes would shrink, only to reappear as the ice withdrew from the basin. Following withdrawal of the ice load from lands east of the Agassiz basin there may have been short periods during which the lag in crustal uplift allowed drainage to take place into the Great Lakes area, but it is hardly likely that during such periods the basin would be completely free of water.

Rudd (1951) believed that during Late Wisconsin glaciation the ice barrier in the lowlands east of the Cretaceous scarp (Agassiz Basin and present Red River valley) was effective in preventing migration of the boreal coniferous forest westward from Minnesota, at a time when climatic conditions might have been sufficiently modified by proximity of the glacier to allow this event. She has made the further suggestion that: "Other northern or Canadian species, because of their limited distribution, so far as available records indicate, appear to have invaded North Dakota from the northeast relatively recently, perhaps only since the removal of the Lake Agassiz barrier" (italics my own).

Dr. J.A. Elson has kindly provided the relevant information on recent surface geology which forms the basis of the following paragraphs. Radiocarbon dates from Iowa indicate that the ice extended that far south (Cary advance?) somewhere between 12,120±530 to 13,300±900 years ago. At that time ice doubtless filled the Palaeozoic lowlands of central Manitoba. Between roughly 12,500 and 11,000 years ago the deglaciation of the lowlands took place, Lake Agassiz I formed and drained, and Lake Agassiz II came into existence. At the time of the latter event (Valders advance?) it is assumed that "the ice margin stood no farther south than The Pas Moraine,..., and probably extended southeast from the north end of Lake Winnipeg to, roughly, Port Arthur or even farther south." How long Lake Agassiz II existed is not yet known. On the basis of artifacts of known age (Agate Basin projectile points) distributed around it but not in it, the inference can be made that the Lake was filled to the Campbell strandline (and hence extended southward to the outlet at Lake Traverse, Minnesota) about 7,000 years ago. A radiocarbon date in alluvium in the Red River valley at Robbin, Minnesota, indicates that sometime prior to 2,684±200 years ago the lake was drained. Since the Thermal Maximum has been placed at about 4,000 to 6,000 years ago by various investigators, it is likely that Lake Agassiz II was in existence through at least the beginning of the post-glacial xerothermic period.

The configuration of end moraines in Manitoba and Saskatchewan indicates that the ice receded northwestward and northward across the prairies west of the Manitoba Escarpment at a time when the Lake Agassiz basin was filled. Thus an open road for plant invasion from the west existed long before the barrier of ice and water disappeared in the east. Indeed, even today the Lake Agassiz basin is a region of prairie, swamp and lake, across which the movement of forest species must be very difficult. Migration of forest elements via strandlines on the southern and western edges of the basin was probably not possible since this route traverses the prairie. During the xerothermic period the southern migration route would have been particularly hazardous. In addition it should be remembered that disseminules from the east would have to advance against prevailing winds and river flow. Both of these forces would however favour invasion from the west.

A consideration of the source of the present northern forest flora should not neglect the possibility that most if not all of its constituent species actually survived along the edge of the ice sheet on the line between the foothills of the Rocky Mountains and the Agassiz basin. To champion this viewpoint does not necessarily involve arguing for the hypothesis of cliseral movement of vegetation zones parallel to the ice front, since a much more convincing hypothesis can be substituted for it, viz., that the peri-glacial rivers and lakes which formed along the ice margin as the glacier advanced or retreated provided favourable local habitats for the temporary survival of the flora, while also providing avenues of ready dispersal as old drainage systems were abandoned or obliterated by the ice and new patterns of streams and lakes were established. Normal drainage to the northeast was interrupted by the continental glaciers and new channels had to be established eastward and southward. In some places drainage held close to the edge of the retreating ice while in others the river channels grew headward, following their retreating glacial source. Thus were formed the picturesque and sometimes spectacular coulée systems which trend generally from northwest to southeast or from north to south across the western plains today. Boivin (1953) has published a short discussion of some of the major coulée systems in western Canada, and he has made the significant suggestion that "ces coulées ont joué un rôle important dans la recolonisation végétale de la Prairie canadienne pendant et après la fonte du glacier continental". The north-facing slopes of these old rivers and their associated lakes must have provided particularly suitable conditions for the survival of the boreal flora, and thus played an equally important role in the recolonization of the northern forest area.

Evidence in support of this viewpoint is found in the present flora of the coulées. Although many now wind as dry channels through prairie or parkland, they preserve a vegetation on their shaded southern sides which resembles that encountered in the more northern forests. For example, the following moist, tall-shrub type of aspen stand was found in a tributary of the Qu'Appelle coulée system near Watrous, Saskatchewan (Table I).

TABLE II

YOUNG ASPEN STAND ON THE NORTH-FACING SLOPE OF A DEEP COULEE: MANITOU BEACH, SASKATCHEWAN

Tree layer dominant: Populus tremuloides, stems 2" to 6" D.B.H., 30' to 40' tall

Tall shrub layer (4' to 6' tall) very prominent:

Abundant: Corylus cornuta

Common: Cornus stolonifera, Prunus virginiana, P. pensylvanica, Amelanchier alnifolia

Herb layer prominent:

Abundant: Aralia nudicaulis

Common: Viola rugulosa, Aster ciliolatus, Pyrola asarifolia

Occasional species:

Actaea rubra,
Agropyron subsecundum (Link.) Hitchc.,
Apocynum androsaemifolium, Carex deweyana,
Chamaenerion spicatum (Lam.) S.F. Gray,
Cornus canadensis,
Disporum trachycarpum S. Wats.,
Elymus innovatus Beal., Fragaria virginiana,
Galium septentrionale R.& S.,
Gentiana amarella, Lathyrus ochroleucus,
Linnaea borealis var. americana,
Lonicera dioica var. glaucescens,
Moehringia lateriflora (L.) Fenzl.,
Pyrola secunda, Rosa acicularis,
Rubus idaeus, R. pubescens,
Salix bebbiana (?), Schizachne purpurascens,
Smilacina stellata, Solidago lepida,
Symphoricarpos albus, S. occidentalis,
Viburnum edule, Vicia americana.

Although the vegetation on the plains surrounding the coulée is "Mixed Prairie", the above described community is practically identical with many poplar stands in the boreal forest zone, for example, in the Riding Mountain National Park, Manitoba.

Even more convincing is the fact that fragments of the spruce forest can be found straggling down the valleys of present-day rivers which flow from forest into parkland or prairie. Excellent examples are to be seen in Alberta in particular, for example in the Bow River valley south of Gleichen, and on a tributary of the Battle River near Castor. On the Assiniboine River spruce can be found below Sturgis in Saskatchewan, and reference has already been made to the coniferous forest on the old Assiniboine delta near Brandon.

Additional evidence is Wickenden's report (1930) of spruce cones and leaves, resembling those of white spruce, in inter-glacial deposits at Johnstone Lake in south-western Saskatchewan. The description of the fossil find shows that the spruce fragments, although lying between two dissimilar tills (hence "inter-glacial deposits"), are actually associated with sand, silt and shell fossils indicating alluvial deposition. When it is further noted that the location is in or adjacent to the southwest side of the Altamont moraine and that Johnstone Lake is one of a chain of lakes outside the moraine marking the course of a former peri-glacial river, the fossil spruce appears as evidence of a coniferous forest on the river, either near that point or farther upstream.

In a personal communication, Elson has reported that he found considerable wood during examinations, in 1955, of sediments of the Assiniboine delta deposited approximately 11,000 to 12,500 years ago in an early stage of Glacial Lake Agassiz "when the ice margin probably extended from Winnipeg to Roblin". A collection of peat buried with some of these deposits yielded pollen of the following tree genera: Picea (mainly P. mariana), Pinus (mainly P. banksiana), Betula, Larix, Alnus, Salix, Populus. The report on Elson's peat sample, prepared by J. Terasmae, palaeontologist with the Geological Survey of Canada, states that the microfossil evidence suggests a cold climate and scattered tree coverage. Thus the contention of Upham (1895) that Lake Agassiz received driftwood only in its later stages is refuted as is Raup's argument that "southern Alberta, Saskatchewan and Manitoba were also devoid of forests during late Wisconsin time", and that forests "must not have appeared in this region until the ice had left the Lake Agassiz basin, and until after the lake had been drained" (Raup, 1946, p. 78).[x]

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x Footnote on following page

FOOTNOTE

Further information was obtained too late to be incorporated in the text. Another of Dr. Elson's peat samples, radiocarbon dated 12,400 $\pm$ 240 years (No. Y165), collected on the western side of the Lake Agassiz basin (SW 35-9-9 W. Prin.M.) has been analyzed by Dr. J. Terasmae. A part of his report is quoted: "The assemblage of non-arboreal pollen suggests open conditions, and combined with the arboreal pollen, colder than the present. White spruce is dominant although black spruce is present. Low pine value (Jack pine type) has little significance. Some of the birch pollen is of the dwarf birches. The spruce growth may have been of local nature."

Also, Dr. Elson kindly sent four samples of wood collected from Lake Agassiz beds on the western side of the basin, and these have been identified at the Forest Products Laboratory, Ottawa, as Picea (probably P. mariana), Ulmus americana, Fraxinus sp. and Larix laricina.

Granted that habitats suitable for survival of the northern forest flora existed in shaded valleys cooled by the proximity of ice and glacial melt-water, the question naturally arises as to whether or not the flora could take advantage of these habitats, moving into them as they became available and migrating out rapidly enough to escape obliteration. The answer is emphatically in the affirmative for most of the boreal species, and this is proved by the very complete flora found on islands in the northern lakes. All the tree species of the coniferous forest, and their minor vegetation associates, are apparently able to travel considerable distances (several miles at least) over water, doubtless aided by wind and by animals. The writer watched white spruce seed falling on Clear Lake, in the Riding Mountain National Park, in September of 1955, and observed that it was moved about easily on the surface of the water by wind currents. A strong west wind on September 8 swept seed from the entire lake into the east bay, and the waves breaking on the shore were black with it. A small experiment later showed that the seeds will easily stay afloat for two weeks or more in quiet water, so there is little doubt that coniferous seed can be carried long distances rather rapidly by wind and water currents on lakes and rivers. "Cold soaking" of coniferous seed is not harmful, in fact it has much the same effect as prolonged stratification in overcoming dormancy (Crossley and Skov, 1951).

It must be admitted that it is difficult to fit the heliophytic and xerophytic species, typified by _Pinus banksiana_, _Hudsonia tomentosa_, _Sibbaldiopsis tridentata_ (Soland.) Rydb., and others, into the preceding picture. Such plants are not adapted to survival along shaded river banks in competition with mesophytic species. Areas of persistence were probably sandy terraces and outwash adjacent to the rivers, open sandy and gravelly beach ridges adjacent to lakes, pre-glacial sand dunes, and similar habitats. Rapid dispersal may have taken place parallel to the edge of the retreating ice sheet, on the exposed, competition-free mineral soil, as proposed by Godwin (1949) in his discussion of post-glacial migrations.

Summing up, it seems reasonable to assume that the flora of the northern coniferous forest survived in large part at least along the complex reticulated systems of peri-glacial rivers and lakes formed successively as the ice advanced or retreated. Edaphically and climatically favourable habitats were provided for mesophytic species by valley bottoms and by north-facing slopes of river banks and lake shores, for even in a predominantly prairie climate the cooling effects of shade and of glacial melt-water would favourably modify these habitats. The presence of moving water adjacent to the local refugia provided the means of rapid movement of propagules, thus guaranteeing survival under the unstable, constantly changing conditions of drainage along the moving ice margin. It would be deduced from this hypothesis that where the flora was exterminated due to such vicissitudes as ice advance or local ponding, replenishment would normally take place from the westward and northwestward, following both the natural lines of drainage and the direction of the prevailing winds. Therefore a movement of western elements to the east would be expected, even though the marginal vegetation might maintain itself reasonably well in some places. Thus the hypothesis of survival of the northern coniferous forest flora in peri-glacial drainage channels can be integrated with the hypothesis of a source area in western Alberta.

Consideration will now be given to the ranges of some plants of our own and neighboring areas in the light of the preceding discussion. The species which will be mentioned are those which have come to the writer's attention during field work in Manitoba and Saskatchewan; in other words they are conspicuous plants, although this conspicuousness stems not from abundance but rather from presence in the east and absence in the west, or vice-versa. They may be thought of as representative of larger groups which a thorough floristic study would identify, and this assumption is one premise of the following section. A second premise which logically follows from the known geological youthfulness of the area is that species of limited range are either static or expanding at the present time, that is, their present distributions do not represent contractions from formerly larger areas.

It is first of all notable that the Lake Agassiz basin does actually mark a definite floristic boundary. A few of the species well known in the eastern coniferous forest but not crossing the Agassiz lowlands are:

Aster macrophyllus	Lycopodium lucidulum
Clintonia borealis	Mitchella repens
Comptonia peregrina	Oxalis montana
var. asplenifolia	Pinus resinosa
Hepatica triloba	Pinus strobus
Kalmia angustifolia	Viburnum cassinoides

Generally speaking, few of the eastern coniferous forest species appear to be advancing westward into the upland forests of our area. However, a group of interesting species has entered the Agassiz basin, and some members have established themselves at isolated stations on or adjacent to the Cretaceous uplands of the western side. These are probably recent arrivals since the drainage of Lake Agassiz II.

Aralia hispida	Pteridium aquilinum var. latiusculum
Arceuthobium pusillum	Streptopus roseus
Diervilla lonicera	Taxus canadensis
Epigaea repens	Thuja occidentalis
Gaultheria procumbens	Vaccinium angustifolium
Malaxis brachypoda	

The strongest recognizable migrant element which appears on the west side of the Agassiz basin shows marked affinities with the eastern deciduous forest. This element is mainly riparian, and it probably invaded from the south after the comparatively recent re-establishment of drainage to the north. Although well-developed in river valleys, the steep slopes of the Cretaceous scarp, and on the south-facing slopes of hills in the eastern part of our area, it contributes little to the vegetational make-up of the forests in which the conifers are constituents. Some of the well-known species in this group are:

Acer negundo	Prunus nigra
Amphicarpa bracteata	Psedera quinquefolia
Asarum canadense	Rhus typhina
Athyrium filix-femina var. Michauxii	Rudbeckia laciniata
	Sambucus pubens
Celastrus scandens	Viburnum rafinesquianum
Cornus alternifolia	Viola pensylvanica var. leiocarpa
Corylus americana	
Menispermum canadense	Vitis vulpina
Mimulus ringens	

A few species related to the preceding group have pushed westward onto the Cretaceous uplands, some reaching to eastern Saskatchewan. They form a minor although locally important element in the upland forests. Examples are:

Acer spicatum	Milium effusum var. cisatlantica
Anemone riparia	
Anemone quinquefolia var. interius	Smilax lasioneura
	Trillium cernuum
Aquilegia canadensis	Viburnum lentago
Lonicera oblongifolia	

Along the southern edge of our area, particularly although not exclusively in the aspen woodland, there appear some species which are usually considered to be of eastern origin. These may well have survived south of the ice-sheets, associated then as now with the aspen forest.

The following are good examples:

Botrychium virginianum	Pyrola elliptica
Corallorhiza striata	Rhamnus alnifolia
Corylus cornuta	Rhus toxicodendron
Lathyrus venosus var. intonsus	Sanicula marilandica
Osmorhiza longistylis	Spiraea alba
Prenanthes alba	Thalictrum dasycarpum

Turning now to the western extremity of the forest section, a perusal of the species' lists published by Moss in his study "Forest Communities in Northwestern Alberta" (1953) is instructive. The first impression of one who has studied the forests in western Manitoba and in Saskatchewan is that a remarkable floristic similarity exists in the boreal forest of the three provinces. Only a very few species listed in the article just referred to can be classed as a strictly confined Cordilleran element, the best examples being *Pinus contorta* Loudon var. *latifolia* Engelm. and *Spiraea lucida* Dougl. both however found in the Cypress Hills. Quite a number of species designated as western or Cordilleran, some of considerable importance in the forest vegetation, range eastward varying distances beyond Alberta:

Achillea sibirica
Aquilegia brevistyla
Arabis lyrata var. kamchatika
Arceuthobium americanum Nutt.
Arnica cordifolia Hook.
Aster conspicuus Lindl.
Aster umbellatus var. pubens
Astragalus tenellus
Betula fontinalis Sarg.
Betula papyrifera Marsh. var. neolaskana (Sarg.) Raup
Castilleja raupii Penn.
Castilleja rhexifolia Rydb.
Delphinium glaucum Wats.
Disporum trachycarpum
Elymus innovatus
Ribes oxyacanthoides
Salix arbusculoides Anders.
Salix lasiandra Benth.
Salix scouleriana Barratt.
Senecio eremophilus Richards.

This group could doubtless be expanded considerably. From it an argument for the importance of migration "drift" into our area from the west could be developed since there is apparently no similar group from the east which has so successfully integrated itself into the various vegetation communities of the upland forests. As previously pointed out, what appear to be the chief eastern invaders belong to the deciduous rather than the coniferous forest element, and they show little present tendency to move from the valleys, scarps and south slopes, and to integrate with the vegetation of the upland forests.

One last small group of plants with a puzzling distribution merits attention. It includes species which have been reported on the Precambrian Shield in northwestern Saskatchewan (Raup, 1946) but which in our area are only found in and adjacent to the Agassiz basin. Four have come to the writer's attention, namely:

Chimaphilla umbellata var. occidentalis	Cypripedium acaule
Coptis groenlandica	Sarracenia purpurea

The remaining species are widely distributed. They form the matrix of the vegetation over the entire area and are responsible for the remarkable floristic homogeneity mentioned previously. Because of their extensive distributions they suggest little as to the recent sources of our flora, and nothing is to be gained by listing them here. Reference can be made to the succeeding sections and particularly to Table XXXIX where many of the important species contributing to the various vegetational communities are listed.

IV

AUTECOLOGY OF THE TREE SPECIES

A knowledge of the autecology of dominant plant species goes a long way toward explaining the genesis and organization of the communities in which they occur. Therefore a short treatment from this viewpoint of the trees which dominate vegetation in the southern boreal forest will now be presented. Well-known sylvical characteristics will not be stressed, for they can be found summarized in numerous forestry books and bulletins. Emphasis will rather be placed on certain habits believed to be of particular significance for competition and survival. Much of the following information has been derived from the writer's own studies, but supplementary data have been obtained from a few key sources to which reference is made.

Populus tremuloides (Aspen)

Aspen is a pioneer species, intolerant of shade but rapid-growing in full sunlight. Its abundance in the aspen woodland and in the adjacent "Mixedwood" forest reflects an aggressiveness there which is apparently lacking farther north, and suggests that the species is best adapted to the deep, comparatively warm soils of the southern boreal forest zone. Nash (1951) has pointed out that in northern

Manitoba the growth of poplar (aspen) is favoured by southern exposure where presumably insolation is the critical factor. On wet, peaty soils aspen rarely survives, and on dry sandy or gravelly soils it does poorly compared to jack pine and white spruce (Heinselman and Zasada, 1955), but on moist to very moist loamy and clayey soils it forms fine stands. Strongly leached till soils do not appear to be so favourable for aspen as weakly leached (calcareous) tills, although here the reason may relate to the greater competitive ability of conifers on the former sites.

Aspen combines with white spruce to form the majority of the forest cover-types in our area. In these types balsam poplar, white birch, and balsam fir are often minor constituents. It associates with jack pine on soils that are not excessively dry. Because it avoids organic soils it is found with black spruce and tamarack only where the latter species occupy upland sites.

Aspen produces light seed prolifically by which means it is able to invade such habitats as moist mineral soil on severely burned areas, new alluvium, or pond margins where the water has lately receded. But where a perennial vegetation is already established (the usual condition in the forest) preventing growth from seed, aspen perpetuates itself vegetatively from root sprouts or "suckers". Suckering usually follows removal of the contributed by the dense shrub-and-herb vegetation that usually develops in such old stands may be an unfavourable contributing factor.

Light surface fires stimulate the sprouting of aspen, but severe fires which burn away the humus layer may seriously impair ability to sprout by damaging the surface roots. However the species usually regenerates more or less prolifically after any type of fire, hence is known as a "fire" tree. Its wide distribution and abundance in the southern boreal forest bear witness to the importance of fire in the history of the vegetation of our area.

Aspen is not so long-lived as the spruces. Probably 150 years is a maximum age under the most favourable conditions, but this age-potential is rarely realized due to its susceptibility after about 60 years to trunk rot, particularly by Fomes igniarius (L.) Gill. Consequently stands are usually overmature before 100 years, and fire or some other form of disturbance is necessary to renew them. The largest aspen trees yet seen by the writer, growing on the north side of the Porcupine Forest Reserve, were up to eighteen inches in diameter at breast height and measured 100 feet tall.

The lateral roots of aspen are firmly anchored in the ground, and in digging soil pits it is common to encounter large ones, one inch to three inches in diameter, in the A_2 and B horizons. Because of this secure rooting, strong winds break the trunk rather than uproot the species, and it does not "plough" the forest floor as windthrown spruce does.

Aspen is a primary food species for many of the larger animal influents of the forest. Beaver eliminate it along rivers and lakeshores, hastening the succession in these fringe habitats toward pure coniferous types. Moose, elk and deer browse the young trees, particularly during the winter, and the writer has seen extensive areas in the Riding Mountain National Park where aspen has been killed out by these animals.

<u>Populus balsamifera (Balsam Poplar)</u>

Balsam poplar is not an important constituent of upland stands. It resembles aspen in its intolerance to shade, modes of regeneration, and rapid initial growth rate. It differs in its greater aggressiveness on very moist sites, and seems to be peculiarly adapted to invasion, growth and regeneration on silty alluvial deposits. Remarkable stands of this species are reported on the flood plains of the Carrot and Saskatchewan Rivers near The Pas, where diameters of 4 feet at breast height have been commonly measured, and diameters of 5 feet to 9 feet estimated. Associates include all our tree species with the possible exception of jack pine and tamarack.

It appears to be a longer-lived tree than aspen, possibly because it is more resistant to fungal decay. Its sap has a very high content of calcium carbonate, and although no one has investigated the physiological significance of this fact it may be assumed that its litter is likewise high in lime and therefore "soil improving".

The root sprouts of balsam poplar are similar to those of aspen but are coarser and faster-growing on very moist sites. The writer has observed that sprouting from the stump also occurs on occasion, and this is unknown for aspen. The vegetative shoots appear to be less palatable to animals than those of aspen, and thus biotic influences may determine what "consociation" is formed when the two species are competing for the same ground. Tolerance to low temperatures may also be of significance when competition between the two poplars is considered, for evidence has been found at the Riding Mountain of frost damage to aspen suckers when adjacent balsam poplar suckers remained apparently unharmed. Little is known concerning the root system of balsam poplar. It is assumed to be similar to that of aspen, and Pulling (1918) defined it as "flexible but deep".

Betula papyrifera (Paper Birch)

Birch is also a pioneer species, in this respect behaving like the poplars. It seems to be more shadeenduring than aspen, but it requires full sunlight for best growth. The species has a wide tolerance of site which allows it to enter into the composition of most forest types. Although it reaches its best development on intermediate sites with the typically upland trees, it also grows on dry sands with pine and on wet peat with tamarack and black spruce. In the latter association, and in communities of the far north, the variety neoalaskana may be involved more often than the type variety, but this problem has not been sufficiently studied as yet. Although present throughout the area under discussion, paper birch is not very abundant except on the eastward- and northward-facing slopes of the Cretaceous escarpment, in Manitoba and in eastern Saskatchewan, where a "birch belt" occurs. Through most of the "belt" the species is associated with varying amounts of aspen and white spruce, although locally it may form small pure stands.

The reproductive potential of birch by means of seed is high, for mature trees produce large quantities of the light, winged fruits almost every year. These are well adapted to wind dispersal and to subsequent development into seedlings, as they are larger and heavier than poplar seeds. The seedling birch have much the same preference of habitat as white spruce, and they can be found growing in the forest on decayed logs and stumps, on wet peaty humus and on moist light-textured soils. They are very palatable to members of the deer family and are often severely browsed.

Birch is usually considered a "fire" tree due to its rapid invasion of severely burned areas, however fire can hardly be the primary cause of the extensive "birch belt" on the scarps of the Riding Mountain, Duck Mountain, Porcupine Hills and Pasquia Hills. The writer believes that another causative agency is also important in the genesis of birch stands in our area, namely erosion of slopes, the effect of which is evident on the face of the Cretaceous escarpment as well as on the steep sides of rivers and creek valleys. Instability of slopes, associated usually with seepage, provides a favourable seed-bed of moist to wet mineral soil where the seedlings become established, and apparently the root systems of the developing trees are able to cope with conditions of soil movement which are sufficient to eliminate or at least severely hamper the growth of other trees. The roots are wide-spreading through the upper mineral soil, and the stumps have a well-known reputation for firmness when land is being cleared.

Once established, birch can maintain itself by sprouting from the root collar, although not from the roots. Second-growth stands often show grouped trunks, a number of stems having grown from the base of each of the original single trees. Thus single-stem stands always indicate a genesis of the type from seed.

Not much is known concerning the life-span of birch in our area. The trunks apparently remain sound even when of large size (diameters of 18 inches D.B.H. and heights of 80 feet are not uncommon), and probably ages in excess of the average for aspen are commonly reached. The association of single-stem birch with spruce 140 years to 160 years old in the Pasquia Hills suggests an equal age for the birch.

Picea glauca (White Spruce)

White spruce is a tree of wide ecological amplitude. Its distribution east and west across the continent and from timber-line to the southern limit of the boreal forest reflects a remarkable ability to tolerate extremes of drought and moisture, heat and cold, and suggests the presence of considerable genetic diversity within the species. It is most abundant in the southern boreal forest, being largely replaced to the north of our area by black spruce and jack pine, and southward by aspen, although in river valleys and along lake shores it extends itself significantly into both neighbouring zones.

White spruce is able to pioneer on open land without benefit of cover and although usually preceded in such habitats by hardwood species it is not absolutely dependent on them for its own survival as the commonly held "nurse crop" idea supposes. Its tolerance of shade is such that it can invade and eventually supplant hardwood stands, provided that surface conditions are favourable.

Like most trees it makes its best growth on permeable, moist soils, or on wetter soils if the ground water is moving. It appears to be most aggressive on moist, strongly leached tills where the leached layer (A_2 horizon) is deep and light in texture (sandy loam or loam). On moist calcareous tills where profiles tend to be shallow it does not compete so successfully with aspen. White spruce can survive on more extreme sites than aspen however. Not only is it able to establish itself successfully on "raw" mineral soil, but also it can be seen today at the southern edge of the forest invading and replacing native prairie vegetation on gravelly kames, eskers, old beach ridges and deltaic deposits. At the wet end of the scale, it grows successfully on fen or muck soils at the edges of rivers, creeks and sloughs. It is evident from the foregoing that white spruce can grow in association with all other tree species over a wide range of sites, and its presence can confidently be expected in most forest types excepting only black spruce stands on deep peats, and jack pine stands on the driest sand soils.

The regeneration problem of white spruce in our area has been studied and reported on by Rowe (1955) and some of the more significant findings are briefly summarized here. Spruce is entirely dependent for its continued survival on seed which it usually begins to produce between 40 years and 60 years of age, the variation being related to such factors as stand density and vigour of the individual tree. Moderate crops are borne at irregular intervals, usually every 3 years or 4 years, and when heavy fruiting occurs the amount of seed produced is tremendous, as a single tree may easily bear 15,000 cones, each containing 50 or more seeds. Despite this reproduction potential, spruce does not easily invade established forest communities because the delicate seedlings produced from the small seed cannot compete with the large, vigorous perennial herbs and shrubs of the forest floor. Mechanical competition is also a factor in survival, and crushing by the annual fall of poplar leaves in hardwood stands accounts for much of the mortality of the invading conifer.

In general, light surface fires produce unsatisfactory conditions for spruce reproduction because they stimulate renewed growth of competing herbs, shrubs and hardwood trees. The best conditions for germination and survival are provided by moist media free of aggressive competitors, such being well-decayed wood (logs and stumps), wet muck soils (drained beaver meadows, etc.) and mineral soil exposed where severe fires have completely consumed the humus layer. The latter is thought to be of major importance in the genesis of densely stocked upland spruce stands. Formerly it was supposed that all seed was shed in fall and early winter soon after the cones ripened, but the writer has found that a small amount is regularly retained on the trees in a small number of cones until the autumn. This persistent seed source may have considerable significance for regeneration following spring and summer fires.

White spruce is a comparatively long-lived tree. It outlasts many of the species with which it may initially be associated: the poplars, birch, tamarack and pine. The oldest merchantable specimens examined by the writer in Saskatchewan showed about 275 annual rings, an exceptional age for a tree usually considered mature at about 120 years. Heights up to 125 feet have personally been measured, and a reputable forester has reported that a tree felled in the Porcupine Reserve measured 140 feet on the ground. The usual diameters of trees in good stands run from 18 inches to 30 inches D.B.H., although exceptional diameters of 4 feet or more have been measured. Site conditions determine to a large extent the age to which a tree lives as well as its size, for where growth is rapid, maturity is reached early and decays of root and butt soon appear.

The root system of white spruce is flexible and well adapted to secure survival on many different sites. An extensive plate-like system of laterals occupies the humus layer and surface mineral soil, while from the primary lateral roots vertical "sinkers" descend to tap deeper moisture sources. Thus the tree can survive above a high water table (the vertical roots are not developed) or it can reach down to the moist zone in surface-dry soils. In competition with the deeper-rooted hardwoods the surface root mat of spruce is very efficient as it can make the most of any precipitation penetrating the canopy. Both birch and poplar doubtless suffer from the severe root competition of spruce in "Mixedwood" stands, for the process of elimination of the hardwoods can sometimes be observed even before crown competition has developed.

Of all the forest trees, the spruces (both white and black) suffer least from animal depredations. Squirrels cut down the cones, and varying hares (Lepus americanus) sometimes trim back the shoots of seedlings and saplings, but most herbivorous animals bypass the spruces in favour of more palatable species.

One last feature of importance should be noted. It concerns phenology as this relates to low temperature resistance in the spring of the year, and may be stated in the following comparative terms: White spruce in our area is distinctly less frost-tolerant than black spruce due to its habit of earlier growth. Records from the Riding Mountain area show that where the two species are associated on the same sites there is a consistent difference of about 7 days to 10 days in the dates when their growth commences. White spruce is first, its buds breaking dormancy and then producing flowers and new leaves. The tender early shoots are very often killed by frosts in late May or in early June when black spruce is still in the bud stage. Whether the pollen and the female flowers are also injured by early frosts has not yet been studied but such is very likely. The writer has found white spruce seedlings killed or badly injured by frosts in low areas (frost "pockets") and has also observed in the same locations healthy undamaged black spruce seedlings of equal size. Among foresters, black spruce is known to be superior to white spruce in its resistance to cold and it is recommended for use in the reforestation of areas liable to frost in the spring and summer. Here then is a factor of considerable importance which may provide a simple explanation of the success of black spruce in competition with white spruce on low, wet sites. It is rather surprising that white spruce apparently is more hardy and vigorous than black spruce at the edge of the tundra (Raup, 1946; Hustich, 1949; 1954). The difference in behaviour of the two species between our area and the far northwest and northeast suggests possible genetic differences (Hustich, 1954), an approach to the studies of which might first be made through observations of phenology.

Picea mariana (Black Spruce)

Black spruce is as widely distributed as white spruce although it has quite different ecological habits. It does not do well on warm, dry or fresh sites. Over much of its range it is confined to poorly drained peat-filled basins where it grows in association with Sphagnum mosses and ericaceous shrubs. But where the moisture regimes of upland sites are favourable, this species often invades successfully beyond the margin of the muskegs, forming densely stocked superior stands. The black spruce upland type, or "feather moss type" as it is commonly called, is a primary community farther northward (in the Northern Coniferous Forest) particularly on areas of low relief where the bedrock is covered with glacio-lacustrine deposits, but it is common locally in our area on cooler sites. The requisite conditions for its genesis appear to be three: a moist to very moist soil usually with low relief, proximity to a seed source sufficient for mass invasion (for example, near muskegs), and fire to clear the ground for invasion.

Usually black spruce grows in pure stands no matter what site it occupies, but mixed stands do occur, for example with tamarack on wet peats, and with aspen, white spruce, balsam fir and jack pine on the uplands. The latter species is by far the commonest associate, a fact which at first sight is puzzling as black spruce and jack pine are generally considered to be far removed ecologically from one another and to be adapted to quite different sites. Close examination of black spruce-pine types has shown that usually the pine occupies slight rises between spruce "flats", so that the two species tend to alternate in bands rather than to mix evenly. At the borders of swamps too, the black spruce is sometimes associated with pine. The two species have three significant features in common which may explain their juxtaposition: precocious fruiting, persistent cones from which seed is released in large quantities by fire, and frost tolerance, the latter stemming at least in part from a tardy initiation of growth in the spring. These adaptations for survival in the face of recurrent fire and frost are probably adequate to explain the association of the two species on cool upland sites as well as at swamp borders, and at the same time to explain why white spruce and balsam fir are less frequently found with black spruce in place of the pine. From the foregoing an interesting question arises as to whether or not students of palynology are correct in their interpretation of the occurrences of jack pine pollen and spruce pollen as correlatives of warm, dry climate, and of cool, humid climate, respectively (Sears, 1948). Possibly the behaviour of these species at the southern edges of their ranges has prejudiced opinion concerning their more general behaviour.

The fruiting habits of black spruce have been suggested in the preceding paragraph. Viable seed is produced at an earlier age than white spruce, and large amounts are held in the dense mass of persistent, semi-serotinous cones at the tops of the trees. In cutting down the cones, squirrels shape the "club tops" so typical of black spruce stands.

The writer examined a 35-year-old burn on the Riding Mountain where thicket regeneration of both spruce species was present. Many black spruce already bore cones although white spruce had none. Seed was collected from the former, and it was found to germinate and grow well. In all likelihood therefore, another fire in this place would eliminate white spruce and bring a pure black spruce stand into being, as no other seed would be present.

Black spruce reproduces vegetatively by "layering", particularly in open stands on wet organic soils. On upland sites where denser stocking is the rule and where the trees grow rapidly, lower branches are soon self-pruned and no layering is possible. Recently "rootlings" (root sprouts) have been reported (LeBlanc, 1955) but these are evidently of little importance for the continued existence of the species.

The best conditions for germination and for survival of seedlings are provided by moist mineral soil, peat and decayed wood. Neutral or slightly alkaline fen and muck soil is apparently much less favourable. The seedlings are tolerant of shade, being able to persist and grow under poplar or pine.

The longevity of black spruce depends on severity of environmental conditions, and it is true for this as for all trees that the slower the rate of growth the greater the potential age. Thus stunted swamp-grown trees may reach ages in excess of 200 years, but vigorous upland-grown trees mature at about 100 years and begin to die soon thereafter. Stems never reach the size attained by good white spruce, and it is exceptional to encounter individuals exceeding 15 inches D.B.H. and 75 feet in height.

The root system has been classified as "inflexibly shallow" (Pulling, 1918; Bannan, 1940). It is plate-like without strong vertical extensions, admirably adapting the species for growth on wet sites but making it very susceptible to windthrow.

<u>Pinus banksiana</u> (Jack Pine)

Jack pine is a shade-intolerant, fast-growing species which is particularly suited both for survival on dry porous soils and for regeneration following fire. It is abundant in our area as pure stands wherever extensive sandy soils occur, but it is also found on heavier-textured, calcareous soils in mixture with aspen, paper birch and white spruce. The association of pine with black spruce on areas of low relief and at the border of swamps has been mentioned in the previous section, as has the fact that in these places the pine usually occupies the slightly higher and drier parts of the terrain. There are several recognizable sites where pine does not appear. Two are very wet, namely the deep, acid peats where black spruce and tamarack are found, and the fen and muck soils where white spruce is successful. The third is best described as the prairie site, for the vegetation of these areas rather than their soil moisture or texture appears to be the best correlative of the jack pine's absence. Sands and gravels on which prairie vegetation has previously produced shallow Black-Earth profiles are almost always occupied by white spruce rather than by jack pine, and the latter species is apparently unsuited to the invasion of native grassland. This fact probably explains why white spruce rather than pine marks the southern border of the Mixedwood forest, spruce being the first conifer seen in travelling northward from prairie to woodland.

Jack pine bears its first cones at a very early age, sometimes when only 10 years to 15 years old. Precocious production of seed gives the species an advantage over the other conifers if fires recur at short intervals. It has been noticed that the first cones often open on the trees, and the early scattering of seed doubtless helps to fill in the juvenile stand. Older trees have serotinous cones, although occasionally a specimen with open cones has been found in our area. The closed-cone habit conserves the seed, and a supply is always present on the trees. The right conditions for dispersal are provided by fire, as heat breaks the resin bond binding the cone scales and allows them to flex and release the seed. Fire also provides the most favourable seed-bed for pine, namely, mineral soil free of competing vegetation.

Seedlings grow rapidly on suitable sites, far surpassing balsam fir and both the spruce species in the first few decades. As with the other fast-growing trees, maturity is reached at a comparatively early age. On dry, sandy soils, jack pine is considered mature at 60 years to 80 years, but on moist, heavier-textured soils where the best stands are formed (for example on clay-loam tills) good growth continues to 100 years or more. Sound trees with an age of 160 years have been found on moist clay-loam till on the Riding Mountain, and in the same area stands up to 90 feet tall with diameters up to 20 inches at breast height are occasionally found.

The root system of jack pine is generally believed to be wide-spreading and strong in the vertical plane (Bannan, 1940). This adaptation assists survival on dry soils where moisture supplies lie deep. On very moist sites the vertical roots do not develop and the pine relies on its lateral system in much the same manner as white and black spruce (Day, 1945).

The cold hardiness of pine has already been mentioned, and foresters know it as a species better suited than white spruce to early planting, due to its resistance to frost. Of additional significance may be the slow development of the pine flowers in the spring, as shown by a later pollen release than black spruce (in turn later than white spruce and fir).

The twigs and leaves are relished by rodents and members of the deer family, and pine suffers much from browsing and bark girdling, particularly in the seedling stage. The biotic factor may sometimes be effective in checking the reproduction of this species.

Abies balsamea (Balsam Fir)

Balsam fir is the most mesophytic, shade-tolerant conifer in our area. It is also the species most adversely affected by fire, and its limited distribution and abundance are probably related to the twin factors of low precipitation and high incidence of fire. Here it should be noted that all the tree species discussed up to this point can be classed as "fire" species with obvious adaptations for reproduction following burning. Fir on the other hand is usually found in greatest abundance in locations where protection against fire (and possibly against spring frosts?) is afforded by the proximity of water or by topographic features, for example, on islands, in the vicinity of lakes and sloughs, and in valleys.

Balsam fir apparently is best suited to moist or very moist sites where a humus layer has been built up by pioneer species. All the other conifers make their best initial growth on mineral soil, provided that the moisture regime is satisfactory, and fir alone appears to illustrate Clementsian "Succession" following the ameliorating influence or "Reaction" of prior species on the habitat. Because of its particular site requirements, balsam fir is not found on dry soils and peat, hence is rarely associated with jack pine or with black spruce and tamarack. Most commonly it is found in overmature white spruce stands where lesser amounts of birch and poplar may also be present. Occasionally the fir dominates open stands of spruce and poplar where a dense undergrowth of shrubs and herbs indicates rich moist soil.

Fewer cones are produced by fir than by spruce of similar size. The seeds fall during autumn and winter as the deciduous cone scales are shed, and none is retained on the crowns for so long a period as on the spruces and pine.

Vegetative reproduction by layering of the lower branches is common, particularly when the parent stems are young, scattered and of bushy form. In denser, older stands the lower branches are soon shed and layering is not possible.

The tolerant seedlings of fir have the ability to survive under conditions of shade which effectively prevent establishment of any other tree species. In undisturbed coniferous stands it alone reproduces to any extent, and therefore it fits the concept of a "climax" species. But because of the frequency of fires and other forms of disturbance which are advantageous to the reproduction of the hardwoods, the spruces and pine, balsam fir rarely develops to a point of dominance except on limited areas.

Despite its "climax" attributes, balsam fir is surprisingly short-lived and the writer has encountered very few sound individuals over 100 years of age in the forest. Generally rots are present in butt and trunk after about 70 years, and the writer's field observations suggest that this tree has a shorter life expectancy than any of the other species. The largest specimens measured during these studies were up to 95 feet tall with maximum diameters of 20 inches at breast height. The oldest single tree was 121 years at breast height.

The phenology of fir is very similar to that of white spruce, both species shedding pollen and initiating vegetative growth at about the same time in late May or early June. Spring frosts often kill the newly flushed needles, just as with white spruce, and some investigators are of the opinion that of the two species, fir is the more susceptible to frost damage (personal communication, Dr. J. Farrar, Petawawa Forest Experiment Station, Ontario). The root systems of the two species are also similar, although there are indications that after the seedling stage is past the roots of spruce are better branched and more extensive than those of fir (Moore, 1922). Probably in the rooting habit lies a partial explanation of the lesser degree of drought tolerance of the latter species.

Balsam fir is palatable to deer, and it is a preferred winter food plant. Several old forestry reports from the Pasquia Hills mention browsing as a reason for the poor growth of fir in comparison to spruce. There are indications at the Riding Mountain and Duck Mountain that seedlings and saplings may actually be killed by repeated browsing, and possibly biotic influences are of great importance in the failure of fir to exhibit greater aggressiveness in some districts.

Larix laricina (Tamarack)

Tolerance to shade is generally inversely related to rate of growth, and tamarack, our most intolerant tree species, is also the most rapidly growing one. In the far north this species is comparatively common on upland sites, but in our area it is only abundant on wet organic soils where competing trees cannot survive. Its commonest location is at the edges of swamps or bogs, backed by white spruce in the former habitat (on muck or fen soil) and by black spruce in the latter (on acid peat). Occasionally tamarack moves out of the wet lowlands and is found scattered through upland stands of poplar, spruce and fir. Its presence then indicates either prior fire or locally very moist soil conditions.

Tamarack regeneration is almost entirely from seed, and cone crops are borne periodically in numbers large or small. The seedlings are frost-tolerant and hardy, but they are very susceptible to insect attack and to browsing by animals. The varying hare finds tamarack particularly palatable, and several old forestry reports state that when "rabbits" were plentiful (in 1914-15, 1924-25) the tamarack advance growth suffered relatively greater damage than that sustained by any other tree species including poplar and fir.

The root system of tamarack is not wide-spreading compared, for example, to pine, and it is shallow rather than deep even on well-drained soils (Day, 1945). The roots are able to tolerate submergence in water for considerable periods of time, hence the adaptation of the species to wet sites.

Mature trees may reach a large size on suitable upland sites, and the writer has seen isolated specimens 18 inches in diameter and 75 feet tall. In swamps and muskegs such growth is never made.

The foregoing outline of the autecology of the eight tree species which dominate the forest vegetation in our area shows some of the adaptations and advantages which allow each species to invade, become established, and compete successfully on particular sites under particular circumstances. It is very significant that all, with the possible exception of balsam fir, can be classed as "pioneer" species, capable of colonizing bare mineral soil when this is exposed to fire, windthrow of trees, river deposition, or other causes, although they differ in their subsequent abilities to compete.

V

A BASIS FOR THE VEGETATIONAL STUDIES

In travelling through the southern boreal forest one gets the strong impression that disturbance, by fire in particular, is here a basic ecological fact. There is evidence on every hand: the existence of extensive even-aged stands of trees, the scarcity of old forests except where protected by natural fireguards such as swamps and lakes, abundant charcoal in the humus layers of almost all stands, and even occasional charcoal lines in soil profiles, marking severe post-fire erosion. Recent history too records widespread fires, back to the particularly dry period of 1885-90, and even earlier. The factor of instability introduced by recurrent fires makes difficult the recognition of stable or relatively permanent ("climax") communities. Most of the vegetation appears young, and its history of development seldom includes a period of modification and amelioration of habitat by prior communities. On the contrary, the factors of greatest importance to the genesis and maintenance of most of the contemporary vegetation in our area (as to all young vegetation) appear to be two:

1. The particular opportunities for invasion which followed the destruction of the original vegetation, depending on the severity of the fire (i.e., on the extent to which it produced a suitable seed-bed and

reduced the competition factor), on the availability of species which survived, and on their reproductive potential for mass invasion.

2. The competitive ability of invading species, depending on such factors as frost resistance, tolerance, rooting habits, rate of growth, and longevity.

Both the opportunities for invasion and the competitive ability of invading plants are strongly influenced by suitability of habitat. Therefore the direct influence of habitat, or "site" in forestry parlance, is more or less clearly reflected in the composition and structure of the majority of our forest communities, and the study of sites is a natural accompaniment of the study of the vegetation, providing a basis for understanding, comparing and relating the various communities. It is worth noting here that the simplicity of the flora in this area contributes to the close "fit" of vegetation to site as there are few possible dominants or combinations of dominants in tree, shrub, herb or moss layer for any given environment. This suggests excellent possibilities for the use of plant indicators, in contrast to floristically richer regions.

Forest Sites

The essence of ecology, the "whole" approach, has often been overlooked or obscured due to the natural bias that follows from a specialization in one particular field. The student who sets out to understand rather than merely describe the phenomena in such fields as pedology, or climatology, or plant sociology, finds himself inevitably led into a study of the other disciplines, and the implications of this fact are proof of the inter-relatedness of biotic and abiotic phenomena. It is a truism that organisms and their environments are inseparably related. Together, at a given time and place, the living and non-living are associated as interacting parts of ecosystems (Tansley, 1935; Sjors, 1955) or "biogeocoenoses" (Sukachev, 1954) which are the basic realities with which ecological study is concerned. The natural bias of the plant scientist toward explanations of vegetation in terms of the constituent plants should not obscure the equal and essential importance of habitat or site.

According to traditional ecological thought in America, vegetation develops primarily under the influence of regional climate, terminating in a "climatic climax". Where the theoretical development is prevented by particular environmental conditions (usually related to the nature of substratum), additional categories are provided such as "subclimax", "preclimax", and "postclimax" (Weaver and Clements, 1938). The latter categories correspond to the "edaphic climaxes" of some authors, and Odum (1953, p. 196) suggests that: "For a given region it is convenient, although somewhat arbitrary, to recognize a single climatic climax which is in equilibrium with the general climate, and a varying number of edaphic climaxes which are modified by local conditions of the substrata." This is very close to the British "polyclimax" position, and it was essentially Nichols' approach to the classification of the vegetation of Northern Cape Breton Island in 1917. Every stable community is in equilibrium with physiography of course, and the "climatic climax" is actually the edaphic climax of non-extreme sites (Cain, 1947), i.e., of loamy, moderately drained soils on undulating topography (Daubenmire, 1952). Seen from this viewpoint, a classification of sites becomes a necessary adjunct to the study and classification of vegetation.

It is difficult if not impossible to make sense of vegetation without considering habitat, and the reverse is also true. Nevertheless attempts to describe and classify one or the other as separate entities are continually being made. The strictly vegetational approach to the study of plant communities cannot solve the problems of observed variations in place and time, while the strictly environmental approach is defeated by the fact of compensatory features which allow the development of similar communities on what appear to be different sites. Only the unity, vegetation-site, is amenable to study and understanding.

A system for the description and classification of sites, well suited to the ecologists' needs, has been proposed by Hills (1950, 1952, 1955). Formulated with a view to widespread application, the system takes into account all significant parts of "total site" (the biotic as well as the abiotic), although it emphasizes the relatively stable geomorphic portion of environment. Basic units are defined in terms of factors which are of known importance to plant growth, viz., soil moisture, ecoclimate, nutrients, and pore pattern of soil profile (including fabric of the parent material). Larger mappable units, called "landtypes", are envisaged as patterns of basic sites, the latter coinciding with recognizable patterns of vegetation.

It is rarely possible to measure directly the factor complex of basic sites, and recourse to indicators is necessary. For example, the soil moisture regime of a given homogeneous area is judged on the basis of topographic position, pore pattern, and profile development of the soil, while ecoclimate is judged from relief, topographic position, aspect, and exposure. Biotic features play a considerable role too in the interpretation and assessment of moisture regime, ecolimate, and nutrient regime, but Hills observes that too little is known at present about the ecology of plants to bring out their full indicator value. Although the site units are a synthesis of a number of inter-related and as yet imperfectly understood variables, they provide the necessary frame of reference for ecological studies.

The selected environmental features that are used to describe the basic site units are rated on scales according to their departure from defined standards. A quotation illustrates the definition of the normal "fresh" or standard moisture regime: "In the site region in which the University (of Toronto) Forest is situated, an adequate supply of available moisture may be held in a good-structured loam which is sufficiently sloping to prevent the accumulation of excess moisture, except for short periods. In such a soil the rainfall common to this region will move so slowly through the rooting zone that the trees growing in it will receive a constant supply except in very dry seasons. The maximum development of A_2 and B horizons in these soils indicates a maximum chemical reaction brought about by an optimum balance of soil moisture, aeration and temperature. The lack of a glei horizon indicates the absence of excess moisture. Such a soil is said to be fresh...." (pp. 10 and 11, Hills and Brown, 1955). The comparison of the regimes of many unit areas with the established standard regime shows departures toward the drier or wetter extremes as indicated by variations in such features as depth and colour of soil horizons, presence or absence of incipient gleization, and position on slope, and from such comparisons a scale or gradient of intensity is defined. As the scale is used to classify new sites, it is constantly being checked and refined. In a similar manner intensity gradients are defined empirically for ecoclimate, nutrient regime, and pore pattern of substratum.

In the present study, Hills' concepts were applied to the description of each unit forest area which was usually a plot of one-tenth- or one-fifth-acre in size, chosen for apparent homogeneity of forest vegetation and site. Scales used to rate ecoclimate, moisture regime, pore pattern of parent material, and calcareousness of soils on each unit site were developed by modification of Hills' scales as field work progressed. Ecoclimate was simplified to the four-point scale shown in Table III.

TABLE III

ECOCLIMATE SCALE FOR THE DESCRIPTION OF FOREST SITES IN THE SOUTHERN BOREAL FOREST OF SASKATCHEWAN-MANITOBA

Symbol	Explanation
2	Warmer than normal--ridgetops, south and southwest slopes. Exposure to drying winds.
4	Normal--undulating plains, good cold-air drainage.
6	Cooler than normal--north and northeast slopes.
8	Colder than normal--depressions without outlets, flats, muskegs and peat bogs. Poor cold-air drainage.

Moisture regimes were defined primarily on the basis of profile development, although topographic position and soil texture were also used. Table IV shows the scale, with examples of profile characteristics on well-drained moderately calcareous tills.

TABLE IV

MOISTURE REGIME SCALE FOR THE DESCRIPTION OF FOREST SITES

Symbol	Explanation	Profile characteristics on unmodified, moderately calcareous, clay-loam till
0	Very dry[x]	Dark A_1 horizon; shallow prairie type of soil.
1	Dry	Weak "grey wooded" profile, A_2 horizon narrow, not prominent.
2	Moderately fresh	Free lime carbonate at less than 18 inches depth in profile.
3	Fresh (Standard)	Strong (zonal) profile. A_1 narrow if present. A_2 maximal. B nutty, rich brown. Lime carbonate at 1 1/2- to 2-feet depth.
4	Moderately moist	Good profile, but A_1 prominent. A_2 narrower than standard. B slightly duller brown, less structure. Incipient gleization below solum (in C).
5	Moist	A_1 cloddy granular, A_2 not apparent. Aggregates of B horizon dull brown within and without. Incipient gleization at bottom of solum (in B).
6	Very moist	A_1 prominent, black granular (fen soils), or A_2 prominent, gleyed (swamp podzol). Gleization to top of mineral soil.
7	Wet	Organic cap (A_0) plus A_1 exceeds 12-inch thickness. Free water at 1- to 2-feet depth.
8	Very wet	No profile. Permanent saturation in organic cap at 1- to 2-feet depth.
9	Saturated	Muskegs, bogs. Organic hydrosols.

x - Underlined regimes are those selected as most relevant for site descriptions in this study.

The scale of soil pore patterns is shown in Table V. Nutrient regime has been simplified to a scale based primarily on calcareousness of soils in Table VI.

TABLE V

PORE PATTERN SCALE FOR THE DESCRIPTION OF FOREST SITES

Symbol	Explanation
0	Coarse sands, sandy gravels--extremely rapid drainage.
1	Medium sands, gravelly loams.
2	Sandy loams, very fine sands--rapid drainage.
3	Light loams, well-decomposed peats.
4	Loams--moderate drainage.
5	Clay loams, compact silt loams
6	Massive clays, muck--slow drainage.

TABLE VI

SCALE OF SOIL CALCAREOUSNESS FOR THE DESCRIPTION OF FOREST SITES

1. Highly calcareous--shallow profiles. Lime carbonate accumulation usually less than 12 inches from surface in well-drained position.

2. Moderately calcareous--moderately deep profiles. Lime carbonate accumulation at 1 1/2- to 2-feet depth in well-drained position.

3. Weakly calcareous--deep profiles. Lime carbonate accumulation at 2 to 3 or more feet in depth in well-drained position.

4. Non-calcareous--no lime carbonate in profile.
   (a) Siliceous
   (b) Argillaceous.

In the field, basic unit sites were described in the order: ecoclimate, moisture regime and pore pattern, using the symbols as a short-hand method of notation. For example, "2:1:4" refers to a site warmer than normal (a south or southwest slope), with a dry moisture regime (due to degree of slope, exposure) on a medium-textured (loam) parent material. During the studies, similarities in vegetation became apparent, particularly between sites closely related by moisture regime and to a lesser extent by parent material (porosity and calcareousness) and eco-climate. Thus a basis was provided for first grouping the variable data and then making tentative generalizations concerning the relationships of the different communities.

Forest Soils

When the numerous forest communities from all parts of the area studied were grouped within moisture "series" for purposes of comparison, it was found that similarities in stand to stand composition were more pronounced on the moister half of the moisture gradient than on the drier half, presumably because in the former groupings the influence of excessive water in the soil usually outweighs all other factors of site and is reflected directly in the vegetation. But where moisture regime is critical, the influences of modifying factors such as soil depth, porosity and calcareousness become important, complicating the relationship between vegetation and the moisture gradient. Thus a consideration of soils beyond their simple relationships to defined moisture gradients is necessary for an understanding of the patterning of vegetation, particularly on dry and fresh sites.

The importance of calcareousness of parent material as a modifying factor in soil profile genesis is stressed by all pedologists. Its influence is reflected in the thickness and rate of decomposition of the humus layer, in depth and structure of mineral horizons, and in total depth of solum. Therefore it is evident that the relative calcareousness of the glacial drift on which grey wooded soils are developed has considerable significance for vegetational studies.

From east to west across the southern boreal forest there is, in general, a marked decrease in calcareousness of parent material, related to the various advances of the glaciers and to the geological strata over which they passed. High-lime drift is found on the east side of the Cretaceous highlands as well as in the re-entrant valleys formed by westward erosion into the scarp. On the uplands themselves--the Riding and Duck Mountains, the Porcupine and Pasquia Hills--the glacial deposits are only moderately calcareous due to dilution of the transported palaeozoic limestone detritus by the underlying Cretaceous shales.

In most of central Saskatchewan the drift is even less calcareous, while in the westernmost part of that province tills of very low lime-carbonate content are found. The comparison of soils on the Cretaceous Hills with those of central Saskatchewan is of most importance to the present discussion, as the easterly high-lime drift (characteristic of rather level glacio-lacustrine deposits, and belonging with the very moist and wet series of sites) is limited in extent within the area studied, while the western Saskatchewan low-lime drift bears a vegetation similar to that of the weakly calcareous drift in central Saskatchewan.

Scarcely any work has been done in Manitoba and Saskatchewan on the description and classification of soils outside the agricultural districts. However the provincial Soil Surveys have done considerable mapping of soil associations adjacent to the boundaries of the Forest Reserves (see in particular Mitchell et al, 1944, 1950) providing numerous clues as to what may be expected within them, and several studies of a general nature which were earlier referred to are particularly valuable for an understanding of forest sites. The available literature suggests what field experience clearly shows, namely that important differences exist between soils of the Cretaceous uplands in western Manitoba and those of central Saskatchewan. For example, in both areas the Waitville association (grey podzolic loam and clay-loam soils developed on undifferentiated boulder clay) has been mapped, but in the west the well-drained associate is usually a much deeper soil than in the east. Some of the differences in development can be illustrated by comparing two profiles which, although not of the Waitville association, are typical in a general way of the soils of east and west according to the writer's experience.

The first example is a soil examined on the north side of the Porcupine Hills under a forest cover of mature white spruce and aspen.

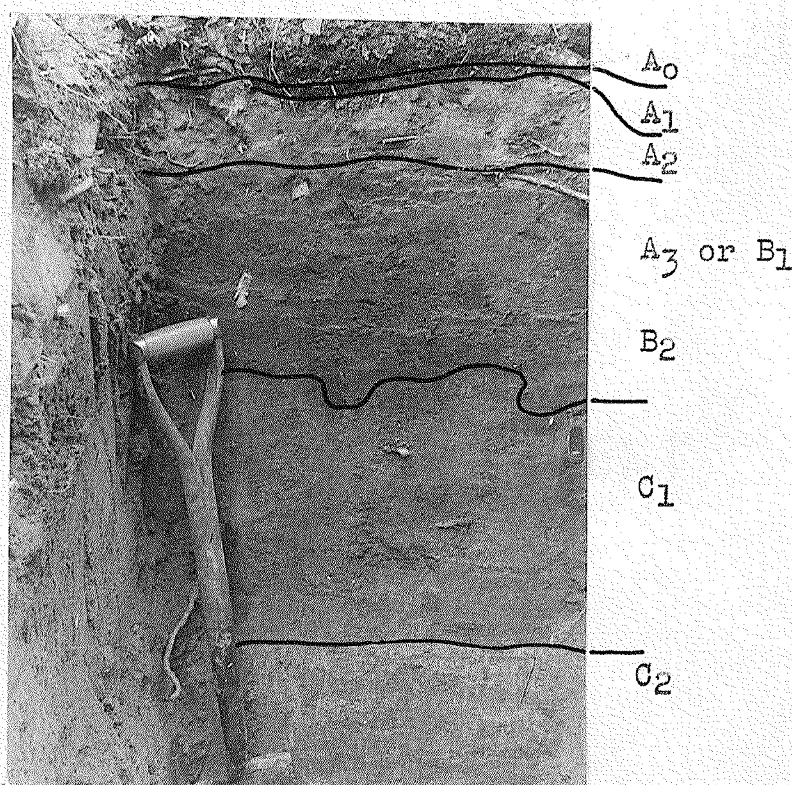


Fig. 2. Shallow grey wooded profile, moderately calcareous phase. Porcupine Reserve, Saskatchewan.

PROFILE DESCRIPTION

A_0 horizon: 3" dark brown felty humus under a loose leaf litter. pH 6.6.

A_1 horizon: 1/2" grey black loam.

A_2 horizon: 4-6" brownish grey to grey loam, distinct platy structure. pH 5.4.

A_3 or B_1 horizon: 3" grey brown sandy clay loam, weakly platy to fine nuciform structure. pH 5.3.

B_2 horizon: 6" brown clay loam, medium nutty to cloddy-granular at the bottom, containing scattered small stones. pH 6.8. Free lime carbonate at base of B_2 at 20" depth.

C_1 horizon: 14" light brown silty clay loam, laminated (lamina about 1/16" thick). Some lenses of rusty sandy loam. pH 7.4.

C_2 horizon: light brown silty clay loam to silt loam with streaks of free lime carbonate, becoming darker brown and stony below 48". pH 7.4+.

This soil is typical of many examined on the Riding Mountain, the Duck Mountain, and the Porcupine Forest Reserve. On the moderately calcareous silty clay-loam till, a shallow profile has been formed, with free lime carbonate at a depth of little more than 1 1/2 feet. The leached horizon (A_2) is thin, but the zone of accumulation (B horizon) is relatively thick and of a heavier texture than the parent material. The result is a rich "surface-moist" soil, i.e., one which holds its moisture reserves close to the surface. The combination of surface moistness and a low degree of leaching makes these soils particularly favourable for the luxuriant growth of minor species on the forest floor (Fig. 3).

Fig. 3. Minor vegetation under Picea-Populus on a moderately calcareous grey wooded soil. Porcupine Forest Reserve, Saskatchewan (same plot as Fig. 2). Note presence of Petasites palmatus, Smilacina stellata, Fragaria virginiana, Symphoricarpos albus, Rubus pubescens.

The second example is a soil examined several miles south of the settlement of Green Lake, Saskatchewan, under a cover-type of mature spruce with scattered aspen (Fig. 4).

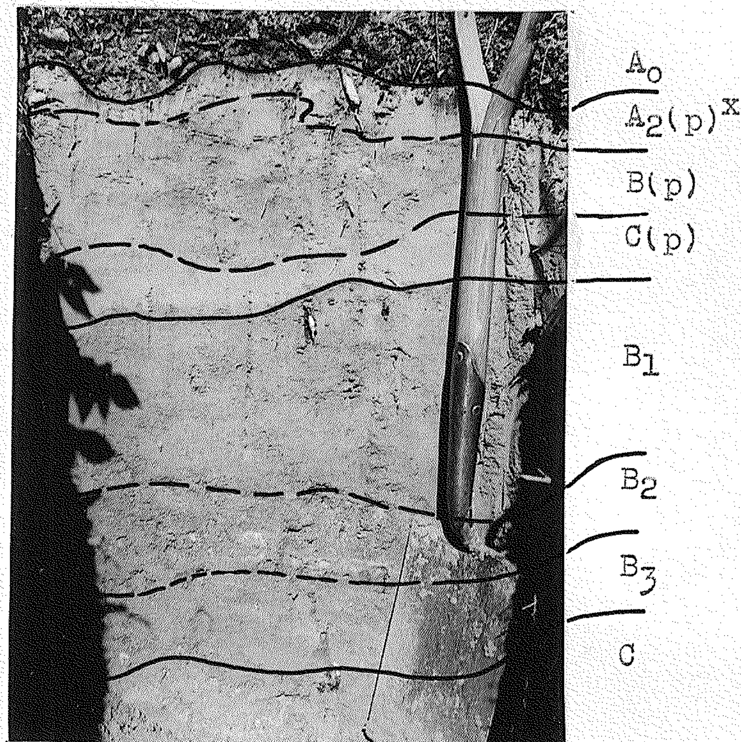


Fig. 4. Deep grey wooded profile, weakly calcareous phase. Green Lake, Saskatchewan.

x - Horizon of podzol profile.

PROFILE DESCRIPTION

A_o horizon: 3"- 4" dark brown fibrous humus under a loose leaf litter, pH 5.0.

A_1 horizon: 0-1/2" black sandy loam, speckled with white silica grains. Few chips of charcoal.

A_2 horizon: 9"- 10", showing secondary podzolization as follows:

$A_2(p)$: 1"- 2" grey very fine sand, slightly melanized under the A_1, single grain structure. pH 5.0.

B(p): 6"- 7" brownish grey very fine sand with a faintly mottled appearance, weakly platy. pH 5.4.

C(p): 2" grey very fine sand. pH 6.0.

B_1 horizon: 9" brown very fine sandy loam, weakly cloddy-granular, plastic when moist. pH 5.6.

B_2 horizon: 4"- 6" brown sandy and gravelly loam (a lens intrusion). pH 6.0.

B_3 horizon: 12" light brown loam, somewhat gravelly. pH 6.4. Free lime carbonate at the base of the B_3 at 41" depth.

C horizon: light brown compact stony loam. pH 7.4.

This profile is representative of many soils in the forested areas of central Saskatchewan, for example in the Torch River Reserve, at Candle Lake and Montreal Lake, and at Green Lake and Big River. The soil-forming processes working on a weakly calcareous till have produced a deep, acid, leached (A_2) horizon which in this particular profile shows evidences of secondary podzolization. The entire B horizon in the sample profile is light in texture, and is underlain at about 3 1/2 feet by a zone of lime carbonate accumulation. Frequently the parent material of these soils consists of two geological strata, an upper loamy till (ablation moraine) in which the solum is developed, overlying a compact clay loam or clay (lodgement till). Such soils although excellent for forest growth are frequently "surface-dry", a condition reflected in a somewhat sparse ground cover of the minor vegetation (Fig. 5).

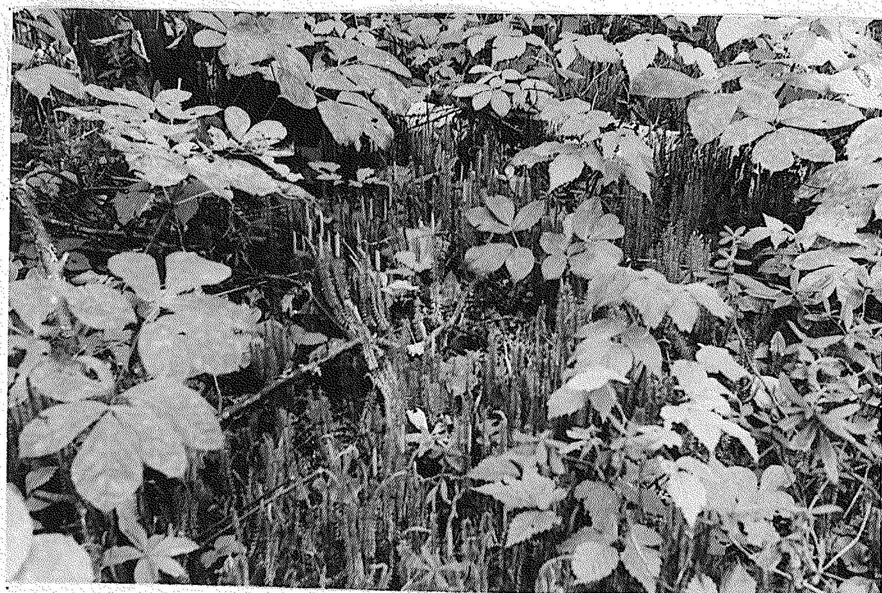


Fig. 5. Minor vegetation under Picea-Populus on a weakly calcareous, deep, grey wooded soil. Green Lake, Saskatchewan (same plot as Fig. 4). Note presence of *Lycopodium annotinum*, *Ledum groenlandicum*, *Aralia nudicaulis*, *Cornus canadensis*.

The deep phase of the grey wooded soils showing no apparent modification of the A_2 horizon is apparently more frequent than the podzol "double" profile on weakly calcareous drift, but the latter type is sufficiently common to merit a few further remarks. The present tentative theory is that following leaching of bases and the lowering of pH during formation of the grey wooded soil, secondary weathering commences and a podzol develops within the A_2. According to a personal communication from

Mr. H. C. Moss of the Saskatchewan Soil Survey, it is usually the light-textured deposits which give rise to podzol-like ("double") profiles, while heavier, more calcareous deposits are associated with the typical grey wooded podzolic profiles. Significantly, both kinds of profiles may occur in the same general area, and a distinct climatic (zonal) difference does not seem to be responsible for the observed differences. In this connection, "double" profiles have also been found locally on light-textured deposits on the Cretaceous Hills, in close association with the much more common shallow grey wooded soils.

One other factor, time, may have played a significant role in the differentiation of deeper profiles westward and northwestward from the Cretaceous Hills. Local glaciers were probably maintained on the higher elevations of the Hills for a considerable period after the lower lands to the west were freed of ice and exposed to the soil-forming processes, and thus the shallower soils of the former locality may be comparatively young.

It might seem that the site distinction between the moderately calcareous "shallow" soils and the weakly calcareous "deep" soils could best be handled by assigning a moisture regime one unit higher to the first than to the second. This would be a practical approach for some forestry purposes--regeneration studies, for example--where attention is focused on the surface horizons. However, so far as growth of the dominant trees is concerned, all horizons including the parent material are important, and there is good evidence that under similar climatic conditions many of the deep, grey wooded soils are superior to the shallow, grey wooded soils for the reproduction and growth of conifers. The reason is probably to be found in relative moisture availability of the entire profile, the deeply leached, weakly calcareous soils being superior in this respect to the shallow, heavier-textured, moderately calcareous soils. In a subhumid climate such as prevails through the southern boreal forest, particularly where during the growing season the pattern of precipitation is one of light showers alternating with periods of high surface evaporation, the coarser-textured soils are actually superior to fine-textured soils for the growth of deep-rooted plants (Stoeckeler and Bates, 1939). Comparing the two soil profiles just described, the Green Lake profile (predominantly very fine sand and loam) is probably superior to the Porcupine Hills profile (predominantly clay loam) for the growth of white spruce, for the following reasons:

(a) Greater total storage of free water in the former (lower hygroscopic coefficient).

(b) Deeper penetration of moisture, therefore less surface loss by evaporation (particularly important when rain falls intermittently in small quantities).

(c) Deeper root development (a result of deeper moisture penetration) placing part of the root system beyond the zone liable to dessication by evaporation.

The broad difference in soil sites between east and west as outlined above is not without its exceptions. It has been pointed out that deep profiles (sometimes "double") are found on the Cretaceous uplands, while shallow profiles on locally calcareous deposits are found farther westward. But in general the distinction appears to be valid, and it is reflected in the following characteristic differences in the vegetation.

1. On the dry and fresh sites, a greater aggressiveness of white spruce where soils are deep and strongly leached rather than shallow, with the opposite true for aspen and for tall shrubs such as *Corylus cornuta*, *Viburnum trilobum*, and *Prunus pensylvanica*.
2. A jack pine component more common on the deep than on the shallow soils.
3. Denser and floristically "richer" undergrowth in forests on the shallow (surface moist) than on the

deep (surface dry) soils, with species such as *Corylus cornuta*, *Aralia nudicaulis*, *Petasites palmatus*, *Disporum trachycarpum*, *Symphoricarpos albus*, characterizing the former and *Alnus crispa*, *Vaccinium myrtilloides*, *Lycopodium* spp. and *Ledum groenlandicum* characterizing the latter, even under a poplar canopy.

4. A tendency for the formation of even-aged coniferous stands on the deep soils and for the formation of uneven-aged mixedwoods on the shallow, richer soils, this doubtless related to the different conditions of competition and moisture encountered by coniferous seedlings on the two types of forest floor.

Vegetational Units

An acceptable system for the classification of vegetation has yet to be worked out. No general agreement on the basic units of vegetation exists, and many are the definitions of "plant associations" . This indicates the complexity of vegetation--there doubtless are as many different kinds of associations as there are different kinds of species. One suspects however that while the genetic approach is being utilized more and more in the study of species, the analogous approach in the study of vegetation is not being given sufficient attention. As previously pointed out, the site complex as a genetic factor is commonly neglected.

Vegetational units are distinguished one from another by real or apparent discontinuities, and studies of the causes of discontinuities aid an understanding of the genesis and status of the units. The following outline is presented to clarify the genetic background of vegetational entities.

Causes of vegetational
discontinuity and continuity

1. Abrupt environmental discontinuity, e.g., sudden changes in surface geology or in topography and local climate as commonly seen in mountainous terrain.
   (a) Usually accompanied by abrupt vegetational discontinuity with a narrow ecotone at the zone of abrupt environmental change.
   Disturbance such as fire, often stops at the line of environmental change, further sharpening the apparent vegetational discontinuity.
   (b) Compensatory features on either side of the zone of abrupt environmental change may widen the ecotone and blur the differences on either side of it, resulting in a lesser degree of vegetational discontinuity than study of habitat alone would suggest.

(c) The degree of apparent vegetational discontinuity may vary according to composition and stage of development of the communities occupying the adjacent habitats. Early seral stages may be similar, although more advanced stages may be entirely different.

2. Gradual environmental change, e.g., slow geographic changes in climate or in relief, as commonly seen on the interior continental plains.

(a) Usually accompanied by gradual vegetational change. Vegetation forms a "continuum" (c.f. "cline", "catena") corresponding to gradient change in soil moisture, radiant energy, etc.

(b) More or less abrupt vegetational change may accompany gradual environmental change, due to:

1) Disturbance (pyric, biotic, etc.) which leads to the juxtaposition of:

a) Different seral communities.

b) Communities of equal seral status but dissimilar due to accidents of post-disturbance invasion. For example, different "consociations".

2) Competition, whose influence may show itself at some point on the environmental gradient in the sudden and complete change from dominance by one

species to dominance by another. Commensal species change with the change in dominants, and distinct zonation appears, as at the edge of a pond.

3) Historical factors which control migration. The removal of isolating barriers or change in climate, may allow dominants to advance, as at the tree line in Alaska.

3. <u>Method of sampling</u> may give a false picture of continuity or discontinuity.

(a) Where abrupt vegetational discontinuity exists, insufficient sampling in the ecotone and on either side of it may create a false picture of gradual change (continuum).

(b) Where there is gradual vegetational change, sampling at widely separated points on the gradient may apparently show more or less different vegetations which are assumed to be discontinuous. Actually the broad ecotones form as valid vegetational units as the "discrete" segments of the continuum which they join.

The above outline suggests reasons for the different patterning of vegetation from place to place. In a recent paper Curtis (1955) has reported that a study of prairie communities" referred to by Curtis (1955) or the "noda" analogous to "taxa") of Poore (1955). The latter designation carries no implications as to discreteness of the units, and it is therefore a useful way to refer to communities while their successional and spatial relationships are being worked out.

In forestry, any combination of dominating trees in a stand is usually referred to as a "Cover-type" or more simply as a "Type", neither term having any connotation beyond the immediate one of species composition. "Forest Type" on the other hand has been defined in various ways. The writer uses this term in the sense advocated by Sukachev (1954): "A forest type is a combination of forest plots (individual forest biogeocenoses) which are homogeneous by the composition of the arboreus stock, by the other layers of vegetation and fauna, by the complex of site factors (climatic, soil and hydrological), by the relationship between the plants and environment, by the processes of reproduction, and by the trend of changes within them. Hence in similar economic conditions these plots require the same forestry measures." This definition, in its stress on stand-to-stand similarity in minor vegetation and site factors, resembles that of the Finnish forest (site) type (Cajander, 1926) although differing by also specifying stand-to-stand similarity in composition of the tree component.

The forest types (in the Russian sense) which will presently be described are abstract communities that have been established from the observation, study and comparison of many concrete stands. They are conceived as noda within environmental and successional series. Inevitably a degree of subjectivity has entered into their definition by the very fact that in the field a selection of study areas had to be made, some stands being accepted and others rejected. This defect is inherent in all synthesizing vegetational studies, and if unrecognized and unacknowledged it can be very misleading.

An immediate problem in working up the vegetational data concerned the methodology to be adopted. The exclusive use of dominants, as stressed in much American ecology, is a practical approach for the definition of large units of vegetation ("Formation", "Association", "Consociation"), but for smaller communities it is not always adequate. According to Braun-Blanquet (1951) the abstract plant "association" is best characterized by species of high fidelity to the individual stands. This is a useful approach, one which is particularly appropriate for the discrimination of communities which occupy distinctly different habitats, such as acid peat bogs, rock ledges, and serpentine soils. As the basis for a universal system of description however, the idea has been criticized by Poore (1955), on the grounds that the fidelity of species to many communities is a result either of limited sampling or of the arbitrary rejection of conflicting descriptive material. Poore found in his studies of mountain communities that the use of several constant species provided a satisfactory means of characterizing the "noda". "Although it is not denied that the constants are usually more wide-ranging species than the faithful, they are not ubiquitous, and <u>combinations of constants</u> are quite adequate to define a community precisely" (Poore, 1955, p. 648). The term "ubiquitous" is relative to many different things--to the species concerned, to the unit of vegetation defined, to the ranges of sites and the sizes of area that are compared. Within the frame of reference of these studies some species did appear to be nearly ubiquitous, and therefore it seemed that the indiscriminate use of constant species might give unsatisfactory results. For this reason although constant species were used in describing communities, an attempt was made to select those of highest fidelity according to field observation. The forest types have therefore been described by dominant tree species and by "characteristic" constant species of the undergrowth.

VI

FOREST COMMUNITIES AND SUCCESSIONAL RELATIONSHIPS

In this chapter the vegetation is treated within six environmental divisions or series, a method that has frequently been adopted for forest description. Each series represents a significant segment of the moisture gradient, from very dry and dry to fresh, moist, very moist and wet. Within the series, the oldest and most mature forest stands encountered in the field are first described and examined as to stability, and the seral or temporary communities are then discussed. Wherever possible, recognizable forest types are described.

Very Dry Series

No detailed examinations were made of the composition and development of forest communities in the very dry series, as emphasis in the present study was on types of greater economic importance. The following is therefore a very general treatment of the forests which occupy porous, excessively drained soils. Only two tree species--jack pine and white spruce--contribute significantly to the cover-types of this series, for aspen, paper birch and black spruce are poorly adapted to droughty sites, while fir, balsam poplar and tamarack are entirely unsuited and never appear.

There seems to be a good basis for distinguishing the sites and communities of white spruce from those of pine, at least along the southern boundary of the forests, for the former species is usually associated with elements of a prairie flora on calcareous sands and gravels, while the latter species is associated with an ericaceous flora on pure sands. The difference is apparently one of comparative nutrient regime, with the richer (calcareous) soils favouring a prairie vegetation into which spruce is able to move, and the poorer (siliceous) soils incapable of supporting any but the most xerophytic and least demanding of trees and minor species. The ability of jack pine to invade established prairie is for some reason inferior to that of spruce, and although scattered pine have been observed in _Festuca scabrella_ prairie at Riding Mountain, Manitoba, and at Hudson Bay, Saskatchewan, it is commoner to find white spruce under these conditions. Experimental seeding in the Duck Mountain Forest Reserve has also indicated that white spruce may become established in grassland where pine fails.

Parkland White Spruce

The invasion of native prairie by spruce can be observed in many places along the southern border of the mixedwood forests. This does not imply that the prairie climate is everywhere suitable for an invasion of the northern forest today; it signifies only that local habitats favourable for invasion of spruce do exist, these being the porous soils which, at the forest edge, usually bear a "preclimax" prairie vegetation. Initial establishment of spruce probably has taken place during a series of relatively wet years, allowing the seedlings to root deeply before the return of normal drought conditions.

Fig. 6. The invasion of white spruce on a native prairie. Riding Mountain National Park, Manitoba.

Commonly the spruce trees are widely scattered, and the somewhat modified prairie vegetation persists between them. Infrequently a few aspen, of poor form and unhealthy appearance, are present. The following community was growing on an old strand-line of Glacial Lake Agassiz near Hudson Bay, Saskatchewan (Table VII).

TABLE VII

DESCRIPTION OF A PICEA/AGROPYRON COMMUNITY

Parkland white spruce - Very dry, grass-herb (prairie) type.
Riding Mountain National Park, Manitoba.
Physiographic site: 2 : 0 : 1.
Soil: Shallow Black Earth profile on calcareous gravel.

Dominant species: Picea glauca widely scattered, limby to the ground, stems many-aged up to 70 years, heights to 65 feet.
Populus tremuloides represented by a few short crooked individuals full of trunk rot.

Tree regeneration: Scattered seedlings in the grass, but no signs of mass invasion.

Minor species: Predominantly grass and herbs, although scattered shrubs and tall herbs give a ragged appearance to the ground vegetation.

Abundant: Agropyron subsecundum, Arctostaphylos uva-ursi, Fragaria virginiana

Common: Species of the forest and forest border:

Achillea millefolium
Agastache foeniculum
Amelanchier alnifolia
Calamagrostis inexpansa
Campanula petiolata A.DC.
Elymus innovatus
Galium septentrionale
Hedysarum alpinum var. americanum
Hieracium canadense
Juniperus communis
Lathyrus ochroleucus
Lilium umbellatum
Lonicera dioica var. glaucescens
Maianthemum canadense var. interius
Rosa sp.
Schizachne purpurascens
Shepherdia canadensis
Smilacina stellata
Thalictrum venulosum

Species of the prairie:

Anemone cylindrica
Anemone multifida
Antennaria campestris
Aster laevis
Bromus pumpellianus Scrib.
Comandra richardsiana
Danthonia spicata
Drymocallis agrimonioides (Pursh.) Rydb.
Erigeron glabellus
Festuca saximontana
Festuca scabrella
Heuchera richardsonii
Juniperus horizontalis
Oxytropis gracilis (A.Nels.) K.Schum.
Poa interior Rydb.
Rudbeckia hirta
Stipa richardsoni Link.
Viola adunca
Zizia aptera

The parkland forests of the Spruce Woods Forest Reserve are very similar in structure and composition to the stand just described, although developed on calcareous sandy deltaic deposits. The comparative adaptations of spruce and aspen to droughty sites can be clearly seen in the Reserve, for the latter species grows chiefly in moist depressions while the former is found established over the sides and tops of the sandhills as well. Brief reference to the flora and fauna of this area has been made by Bird (1927).

In some of the parkland forests examined, mass invasion from neighbouring seed-trees has resulted in dense thickets of spruce whose individual stems remain small in size due to the deficiency of moisture. The shade of the conifers has eliminated the intolerant prairie flora, but surface drought has largely prevented replacement by tolerant forest species. Consequently a "needle cover" type has formed, with scarcely a minor species showing on the forest floor except for a rare individual of *Maianthemum canadense* var. *interius*, *Pyrola secunda*, *Schizachne purpurascens* or *Corallorhiza trifida*. This type of stand is found on the Riding and Duck Mountains.

It is probable that the prairie and the parkland spruce alternate in time on some sites, probably in phase with climatic cycles. On the Riding Mountain several small areas which presently support a typical native prairie flora were found with unmistakable signs that scattered trees had grown there before. The evidence was the presence of decayed wood. The positions of old logs were usually marked by lines of Rosa acicularis.

Farther northward the spruce parkland on very dry gravelly soils appeared floristically poorer than in the south, presumably because there has been no ready access to a prairie flora. For example, on a gravelly beach ridge at Dore Lake, Saskatchewan, the following species were scattered through the open spruce stand:

Agropyron pauciflorum (Schwein.) Hitch.
Amelanchier alnifolia
Arctostaphylos uva-ursi
Artemisia caudata
Campanula petiolata
Cladonia rangiferina (L.) Web.
Comandra richardsiana
Cornus canadensis
Elymus innovatus
Festuca saximontana
Hieracium canadense
Hierochloe odorata
Lonicera dioica var. glaucescens
Maianthemum canadense var. interius
Oryzopsis pungens
Poa interior
Sibbaldiopsis tridentata
Prunus pensylvanica
Rhytidium rugosum
Rosa sp.
Schizachne purpurascens
Vaccinium myrtilloides
Vaccinium vitis-idaea var. minus

A parkland spruce forest type can perhaps be defined on a strictly physiognomic basis, but taxonomically it does not seem that sufficient stand-to-stand homogeneity exists.

Pine Sands

The only truly distinctive pine types occur on these driest sites, where other tree species are unable to survive. Stands are patchy in structure with numerous openings, and their park-like appearance is accentuated by a low, sparse ground vegetation in which ericaceous species (especially Arctostaphylos uva-ursi) and Cladonia rangiferina are prominent (Fig. 7).

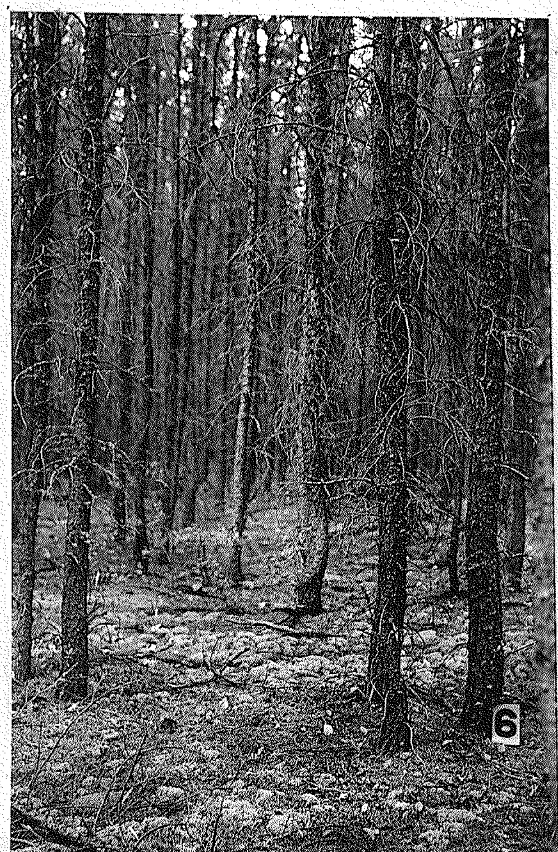


Fig. 7. Pinus banksiana stand with a ground cover of of Cladonia rangiferina-Arctostaphylos uva-ursi.

Under the conditions of excessive drainage and siliceousness of parent material, the only visible profile development is a faint bleaching of the upper two or three inches of sand (A_2 horizon) just beneath the thin, dry humus layer. The dryness of the sites predisposes them to frequent burning.

No attempt was made in this study to define variants of the very dry, pine sand forest on the basis of the minor vegetation. Considerable differences from stand to stand have been observed, doubtless related to frequency of fire, stand age and density, and the availability of species for invasion. However, a common physiognomy and, to some extent, a common floristic composition was noted, and it is believed that the general description in Table VIII defines a recognizable forest type.

Under present climatic conditions the Pinus/Arctostaphylos-Cladonia community is apparently a stable forest type. It cannot be replaced by other tree species for they are unable to grow on the sterile, dry soils. On the other hand it seems to be quite capable of reproducing itself either with or without the assistance of fire, the latter possibility resulting from the frequent although as-yet-unexplained opening of cones on scattered large trees as well as on most small trees. In a sense then it is also a fundamental forest type. Succession is from pine to pine, although frequent fires may prevent the formation of stands for long periods of time.

TABLE VIII

DESCRIPTION OF THE PINUS/ARCTOSTAPHYLOS-CLADONIA FOREST TYPE

Pine sand community - Very dry, low shrub-and-lichen type.
Southern Boreal Forest, Saskatchewan.
Typical physiographic site: 2 : 0 : 0.
Soil: Weakly podzolic, medium to coarse sand.

Dominant tree: Pinus banksiana

Constant minor species:

Arctostaphylos uva-ursi	Festuca saximontana
Cladonia rangiferina	Maianthemum canadense var. interius
Oryzopsis pungens	

Other species, listed approximately in order of decreasing importance (based on presence in 10 stands):

Fragaria virginiana	Melampyrum lineare
Vaccinium myrtilloides	Artemisia caudata
Lycopodium complanatum	Rosa sp.
Sibbaldiopsis tridentata	Antennaria campestris
Galium septentrionale	Hieracium canadense
Solidago hispida	Vaccinium vitis-idaea var. minus
Solidago nemoralis	Linnaea borealis var. americana
Elymus innovatus	Arceuthobium americanum
Arabis lyrata var. kamchatica	Anemone patens
Aster laevis	Carex foenea
Comandra richardsiana	Selaginella densa
Lathyrus ochroleucus	Spiranthes gracilis

On moister sites, jack pine is associated with a minor vegetation very different in character from the one described above. Medium and tall shrubs are more frequent, and numerous herbaceous species which commonly grow under white spruce and aspen appear. It is doubtful therefore whether these moister types are stable, a point to be further discussed in the next section.

Dry and Fresh Series - Moderately Calcareous Soils

(1) Dry Series

Forest communities of the dry series are developed on sites which although more favourable for tree growth than those of the very dry series, have nevertheless a moisture deficiency due to excessive porosity of the soil or to slope and aspect. Dryness is indicated by less than maximal growth in height of the trees, by a feeble development in stratification of the undergrowth even where the forest canopy is open, and by poorly defined or very shallow soil profiles.

The same two species found on very dry sites--white spruce and jack pine--are dominant on the dry sites as well. Aspen, paper birch and black spruce occur occasionally, either alone or as associates of spruce and pine, but being less well adapted than the latter species they are not persistent where competition is effective. Within this series there is evidence that white spruce has the potential ability to survive wherever pine does, but it is questionable as to whether or not the reciprocal relationship holds, and gravelly tills are a particularly doubtful site for pine. For this reason white spruce is the only species considered to form stable types in the dry series.

In the Riding Mountain National Park, numerous examples of white spruce forests on dry stony drift can be found. The young trees often show a rapid initial growth but they mature early and seldom reach a height of more than 70 feet. Typically they taper rapidly and carry their limbs to the ground. Minor vegetation is low, giving the stands a very park-like appearance. Most undergrowth plants are less than six inches tall, although flowering stems may be higher. Figs. 8, 9 and 10 show the trees, the minor vegetation and a soil profile of a typical stand, and Table IX is a description of the plot where the pictures were taken.

Fig. 8. Two-storied stand of Picea glauca on a dry site. Riding Mountain National Park, Manitoba.

Fig. 9. Minor vegetation associated with a spruce stand on a dry site. Riding Mountain National Park, Manitoba. Note the abundance of Elymus innovatus and Fragaria virginiana.

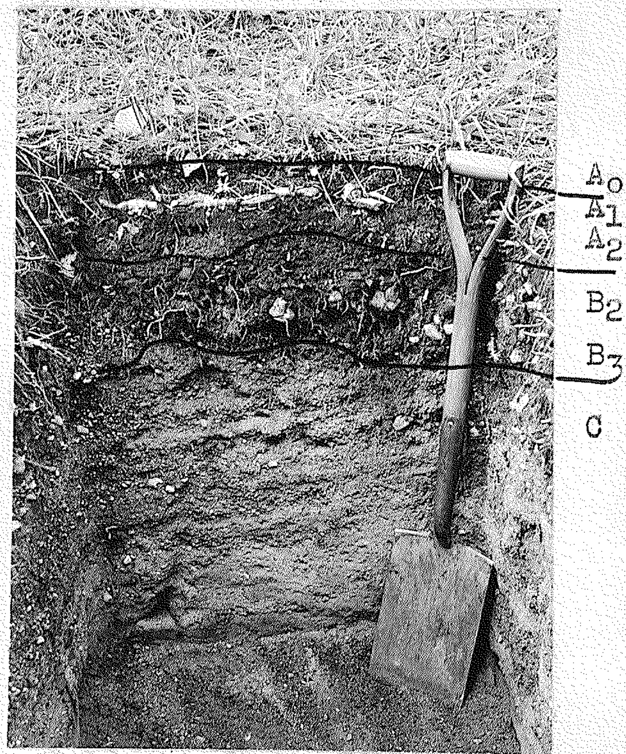


Fig. 10. Soil profile under a <u>Picea</u>/<u>Elymus</u>-<u>Fragaria</u> community. Riding Mountain National Park, Manitoba.

PROFILE DESCRIPTION

A_0 horizon: 1" dark brown mottled leaves and spruce needles.

A_1 horizon: 1" black granular sandy loam.

A_2 horizon: 1" very dark grey, granular sandy loam.

B_2 horizon: 4" dark brown, stony clay loam.

B_3 horizon: 5" dark grey brown stony loam. Free lime carbonate at base of B_3 at 12" depth.

C horizon: Light yellowish brown fine gravel, calcareous, weakly stratified.

TABLE IX

DESCRIPTION OF A PICEA GLAUCA COMMUNITY ON A DRY SITE

White spruce - Dry, low grass-herb type.
Plot No. 301, Riding Mountain National Park, Manitoba.
Physiographic site: 2 : 1 : 1.
Soil: Shallow, grey wooded profile on calcareous fine gravel.

Dominant species: Irregular stand of Picea glauca, uneven-aged, up to 70 feet tall at 90 years of age. Scattered small Populus tremuloides.

Minor species: Forest floor clean-looking, with abundant low grasses and herbs but no conspicuous shrubs. The species are listed within each frequency class in order of decreasing importance as determined by studies of cover-abundance in 20 milacre quadrats.

Frequency 100-85%

Oryzopsis asperifolia
Maianthemum canadense var. interius
Fragaria virginiana
Elymus innovatus
Galium septentrionale
Lathyrus ochroleucus
Symphoricarpos albus
Rosa acicularis
Hieracium canadense

Frequency 80-65%

Thalictrum venulosum
Aster ciliolatus
Calliergonella schreberi

Frequency 60-45%

Linnaea borealis var. americana
Carex sp.
Achillea millefolium
Aster laevis

Frequency 40-25%

Lonicera dioica var. glaucescens
Agastache foeniculum
Vicia americana
Smilacina stellata
Taraxacum sp.
Brachythecium salebrosum
Hylocomium splendens
Antennaria parvifolia Nutt.
Solidago hispida
Viola adunca

Table IX cont.

Frequency 20-5%

Schizachne purpurascens	Prunus virginiana
Zizia aptera	Campanula petiolata
Amelanchier alnifolia	Galium triflorum
Pyrola secunda	Artemisia gnaphalodes
Vaccinium caespitosum	Aralia nudicaulis
Drymocallis agrimonioides	Lathyrus venosus
Lilium umbellatum	Prenanthes alba
Thuidium recognitum	Rhytidiadelphus triquetrus
Dicranum rugosum	Ceratodon purpureus
Juniperus communis	Pohlia nutans

The structure of this stand indicates an initial invasion of the site by a few trees and a later seeding in of the gaps. Some of the minor species are indicative of an earlier prairie history (e.g., Zizia aptera, Artemisia gnaphalodes), while the presence of scattered mosses shows the trend toward reduced light on the forest floor. It is notable that tall shrubs such as Corylus cornuta are unimportant constituents.

Spruce communities with low grass-herb undergrowth on dry sites are sufficiently common and recognizable to be characterized as a distinct forest type. Constance data from ten stands are shown in Table X.

TABLE X

THE COMPOSITION OF THE PICEA/ELYMUS-FRAGARIA FOREST TYPE

Within each Constance class the species are listed in order of decreasing importance (first the left column, then the right) as determined from quadrat studies of frequency and cover-abundance in all stands.

Constance 100 and 90%

Fragaria virginiana
Galium septentrionale
Rosa acicularis
Oryzopsis asperifolia
Elymus innovatus
Maianthemum canadense var. interius
Thalictrum venulosum
Aster ciliolatus
Lathyrus ochroleucus
Symphoricarpos albus
Achillea millefolium
Taraxacum sp.
Lonicera dioica var. glaucescens
Vicia americana
Amelanchier alnifolia
Carex sp.
Hylocomium splendens

Constance 80 and 70%

Schizachne purpurascens
Agastache foeniculum
Hieracium canadense
Viola adunca
Zizia aptera
Linnaea borealis var. americana
Calliergonella schreberi
Lathyrus venosus
Pyrola asarifolia
Pyrola secunda
Solidago hispida
Corylus cornuta
Prenanthes alba

Constance 60 and 50%

Chamaenerion spicatum
Cornus canadensis
Lilium umbellatum
Aster laevis
Vaccinium vitis-idaea var. minus
Comandra pallida
Rubus pubescens
Smilacina stellata
Ribes hirtellum
Campanula petiolata
Sanicula marilandica
Solidago lepida

Plus 62 additional species of Constance 40% and less.

The name *Picea/Elymus-Fragaria* has been given to this forest type, for although in Table X *Elymus innovatus* is outranked in frequency by four species, it is more characteristic of dry sites than they are.

In the Duck Mountain Forest Reserve occasional stands of jack pine of the low grass-herb type were found on dry till ridges or on the south-facing slopes of valleys. The minor vegetation of these stands was very similar to that found under spruce on similar sites. Compare for example the following community (Table XI) and the constant species in Table X.

Eighteen of the twenty-one species listed as abundant or common in this *Pinus/Elymus-Fragaria* stand occur with a constancy of 50 per cent or higher in the *Picea/Elymus-Fragaria* forest type. Under aspen also, the minor vegetation is very similar to what is found in these dry, coniferous types. Apparently the minor vegetation is true to the site regardless of which tree species dominates, a usual condition on poor sites with open forest types, and the basis of Cajander's theory of forest types (Cajander, 1926).

TABLE XI

DESCRIPTION OF A PINUS/ELYMUS-FRAGARIA COMMUNITY

Jack pine - Dry, low herb type.
Singoosh Lake, Duck Mountain, Manitoba.
Physiographic site: 2 : 1 : 4.
Soil: Shallow, grey wooded profile on a clay-loam till slope.

Dominant species: Pinus banksiana in an open, even-aged stand, 65 years of age and 55 feet tall.

Minor species: A grass and herb undergrowth. Shrubs not prominent.

Very abundant: Elymus innovatus

Abundant: Fragaria virginiana
Aralia nudicaulis

Common:

Actaea rubra	Chamaenerion spicatum
Anemone riparia	Lathyrus ochroleucus
Agastache foeniculum	Prenanthes alba
Lilium umbellatum	Galium septentrionale
Sanicula marilandica	Petasites palmatus
Thalictrum venulosum	Cornus canadensis
Schizachne purpurascens	Linnaea borealis var. americana
Solidago hispida	
Oryzopsis asperifolia	Maianthemum canadense var. interius

Occasional:

Vaccinium myrtilloides	Achillea sibirica
Amelanchier alnifolia	Corylus cornuta
Hieracium canadense	Shepherdia canadensis
Lathyrus venosus	Diervilla lonicera
	Alnus crispa

Successional Relationships

Removal of the overstory trees on dry sites usually brings *Elymus innovatus* into even greater prominence, and open areas are often completely dominated by this western grass. Frequently *Elymus* occurs in mixture with *Arctostaphylos uva-ursi* and with typical prairie grasses and herbs, forming communities intermediate between those of the very dry and the dry series.

White spruce is apparently the tree best suited to the dry sites. It occasionally forms closed stands, and although the individual trees may not be large they effectively shade the ground and reduce the role of the minor vegetation. Examination of a one tenth-acre plot in one such stand showed that the most striking change in comparison to adjacent more open stands was a great reduction in abundance of *Elymus innovatus* and an increase of the feather mosses *Hylocomium splendens* and *Calliergonella schreberi*. The moss mat although thin was prevalent over all the plot, indicating its dependence on shade rather than on soil moisture. A sparse feather-moss type of white spruce vegetation is probably the final stage in development within the dry series, followed no doubt by disintegration of the stand and a return to a park-like stage with *Elymus innovatus* prominent.

(2) Fresh Series

Forest types of the fresh series are typical of the rolling uplands on the Cretaceous Hills. Each of the eight native tree species is able to make good growth on the grey wooded soils which develop in the well-drained position on the prevalent calcareous tills, but competition reduces the importance of all but white spruce and aspen. Minor vegetation is generally dominated by a vigorous tall-shrub stratum (with *Corylus cornuta* prominent) beneath which a rich herb flora is found. The aggressiveness of aspen, and the vigour of the minor vegetation on fresh sites is a deterrent to the establishment of white spruce. Consequently where the latter species is available, mixed stands are normally formed. Often there is a slow replacement of the aspen by the spruce, giving rise to uneven-aged stands which nevertheless maintain the relatively open structure imposed on them by the prior aspen community. In such stands the shrub and herb minor vegetation is able to persist and there is no trend toward a feather moss "shaded floor" type.

Fig. 11 shows an old spruce stand on an island in Singoosh Lake, Duck Mountain Forest Reserve, and Fig. 12 shows the interior of the same stand.

A description of the stand shown in Figs. 11 and 12 will be given next (Table XII) to illustrate a possible trend of the successional process on fresh sites.

Fig. 11. Stands of Picea glauca (island in right foreground) and Picea-Populus (left background) at Singoosh Lake, Manitoba.

Fig. 12. Overmature Picea glauca with undergrowth of Rubus idaeus. (Interior of the stand on Singoosh Lake island, Manitoba.)

TABLE XII

DESCRIPTION OF AN OVERMATURE WHITE SPRUCE STAND (PICEA/RUBUS) ON A FRESH SITE

White spruce - Fresh, medium-shrub type.
Plot No. 111, Duck Mountain Forest Reserve, Manitoba.
Physiographic site: 4 : 2-3 : 5.
Soil: Grey wooded profile on moderately calcareous clay-loam till.

Dominant species: Picea glauca most important; an open stand 50-140 years of age, 4-27 inches D.B.H., up to 85 feet tall.
Abies balsamea secondary, up to 65 years of age, 1-13 inches D.B.H., and up to 60 feet tall.
Scattered Betula papyrifera, Populus balsamifera, Picea mariana, Pinus banksiana.

Tree regeneration: Abundant seedlings and saplings of balsam fir, scattered saplings of birch and poplar, rare spruce seedlings.

Minor vegetation: A conspicuous stratum of wild raspberry, about 3 feet tall. Its prominence is indicative of a gradually opening canopy which is exposing the coniferous humus layer to increased light and warmth.

Very abundant: Rubus idaeus

Abundant:	Mertensia paniculata	Cornus canadensis
	Aralia nudicaulis	Galium septentrionale
	Rosa acicularis	Ribes hirtellum
Common:	Viburnum edule	Rubus pubescens
	Schizachne purpurascens	Amelanchier alnifolia
	Chamaenerion spicatum	Lonicera dioica var. glaucescens
	Calamagrostis canadensis	Ribes glandulosum
	Linnaea borealis var. americana	Carex sp.
	Mitella nuda	Galium triflorum
	Symphoricarpos albus	Petasites palmatus
	Fragaria virginiana	Moehringia lateriflora
	Maianthemum canadense var. interius	Viola rugulosa
Occasional:	Ribes triste	Urtica gracilis
	Cornus stolonifera	Vicia americana
	Agropyron subsecundum	Taraxacum sp.
	Aster ciliolatus	Achillea millefolium
	Pyrola asarifolia	Disporum trachycarpum

The history of the tree component of the stand is known back to 1921, and the changes which have occurred during the last thirty years are shown in Fig. 13.

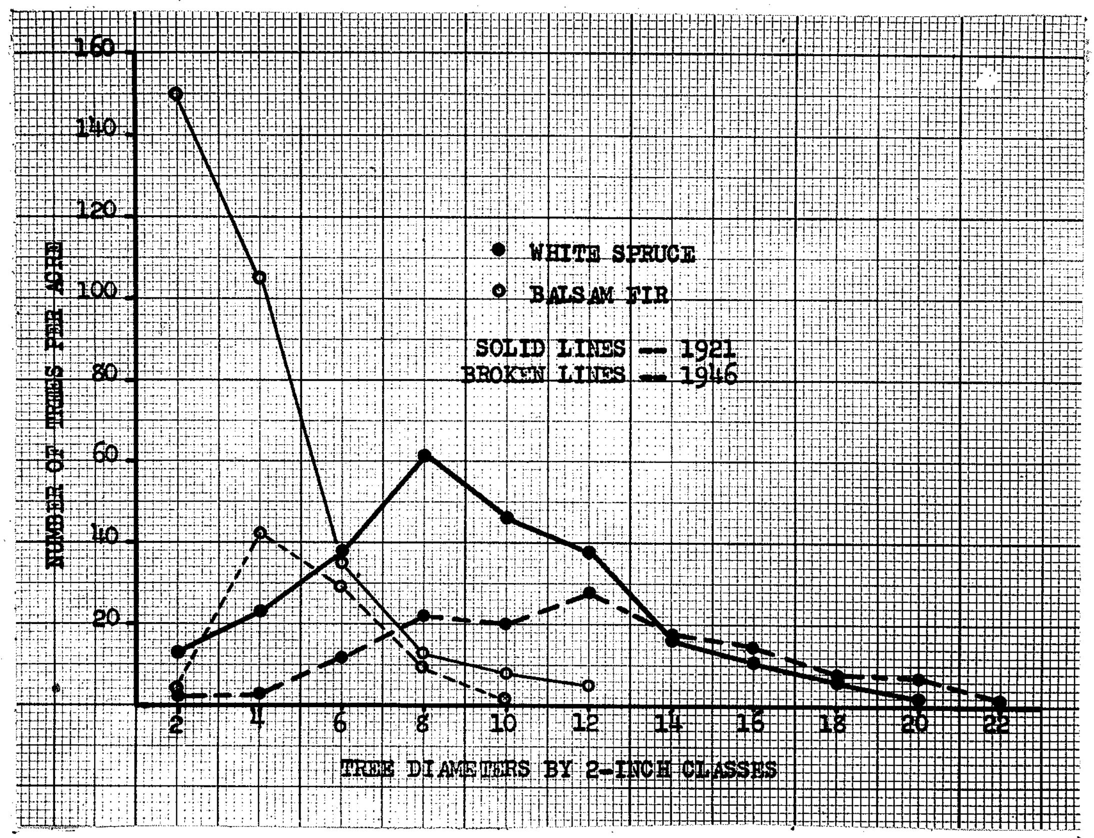


Fig. 13. Tree composition of a spruce stand in 1921 and in 1946. Singoosh Lake, Manitoba. (Note: These graphs are not regression lines.)

The most important point to note is the decrease of fir in all size classes since 1921. This apparently indicates a poor ability of the species to compete on fresh sites, a point of considerable significance when the "climax" status of fir in the Mixedwood forest is argued. It is of interest too that by 1950 all aspen had disappeared from the stand.

Regeneration studies at the same locality showed that the forest had its genesis after a severe fire (circa 1810) which destroyed a stand of large trees and burned away most of the surface humus. The spruce and scattered pine seeded in on exposed mineral soil. Under the stand as examined in 1951 only fir appeared to be regenerating to any extent, although its seedlings and saplings had an unthrifty appearance due partly at least to browsing. Small balsam poplar suckers were found here and there, and rotted logs supported many small birch saplings, but only one or two white spruce seedlings were located. Unless such a stand is burned over it seems likely that it will become more and more open and brushy as the spruce dies out. There was no indication that any of the tree species could form a self-maintaining (fundamental) forest type on this site.

Successional relationships of younger communities

With few exceptions, all forest stands in the fresh series have their genesis in fire. The severity of the burn has a profound influence on the subsequent forest due to differences in the habits of reproduction of the two main tree species, aspen and white spruce. The extreme possibilities, light (i.e., non-severe) fires and severe fires, will be taken up in turn.

(a) Succession following light fires

Crown fires, or light surface fires which merely burn over the top of the humus layer, stimulate the suckering of aspen and encourage a vigorous growth of perennial minor species on the forest floor. The severe competition factor effectively prevents the rapid invasion of spruce, for the small, delicate seedlings of the latter species cannot compete either above ground for light or below ground for moisture with the numerous well-established perennial shrubs and herbs. Therefore a pure poplar stand generally develops.

It is interesting to note that different vegetational communities are predisposed in varying degrees to fire and to severity of burning. Fires tend to be light in poplar stands because of the luxuriant broad-leaved undergrowth. Only in spring is there dry fuel on the ground, and at that time the humus layer can rarely be consumed by fire because it is moist except on the surface. Consequently the cycle, poplar stand → light burn → poplar stand, and so on, tends to recur, and spruce is effectively excluded at almost every stage.

The effect of a light fire in an aspen or aspen-spruce stand is comparable to that of clear cutting; the trees are removed but the minor vegetation is unchanged. Shrubs and herbs quickly sprout from their roots and form, with the new aspen sprouts, a community very similar to the previous one. Usually there is an increase in the relative abundance of some species such as Chamaenerion spicatum, Lathyrus venosus and Fragaria virginiana in response to the changes in light, moisture and nutrients, but the actual composition of each community depends largely on what plants were originally present, and the historical aspect is doubtless most important to the explanation as to why different species dominate the undergrowth strata from stand to stand.

The commonest dominant of the undergrowth in poplar communities in the fresh series is Corylus cornuta, a shrub which is widespread through the southern boreal forest (Fig. 14).

On the basis of field observations there seems to be a recognizable, temporary or stable, aspen forest type characterized by Corylus cornuta, Aralia nudicaulis, Viola rugulosa, Oryzopsis asperifolia and Lathyrus venosus. In Table XIII a summary of the composition of fifteen aspen stands, each with a vigorous Corylus stratum, is presented.

Fig. 14. *Corylus cornuta* forming the dominant ground cover under mature aspen, Riding Mountain National Park, Manitoba.

TABLE XIII

THE COMPOSITION OF THE POPULUS/CORYLUS-ARALIA-VIOLA-ORYZOPSIS FOREST TYPE

Within each constance class the species are listed in order of decreasing frequency as determined by the examination of 200 quadrats.

Constance 100 and 90%

Corylus cornuta
Aralia nudicaulis
Maianthemum canadense var. interius
Rosa acicularis
Aster ciliolatus
Fragaria virginiana
Mertensia paniculata
Viola rugulosa
Oryzopsis asperifolia
Symphoricarpos albus
Galium septentrionale
Cornus canadensis
Prunus virginiana
Galium triflorum
Lathyrus venosus
Viburnum edule
Chamaenerion spicatum
Vicia americana
Amelanchier alnifolia

Constance 80 and 70%

Petasites palmatus
Thalictrum venulosum
Rubus idaeus
Lathyrus ochroleucus
Sanicula marilandica
Carex sp.
Lonicera dioica
Disporum trachycarpum
Pyrola asarifolia
Actaea rubra
Cornus stolonifera
Calamagrostis canadensis

Constance 60 and 50%

Heracleum maximum
Elymus innovatus
Solidago lepida
Ribes triste
Ribes hirtellum
Taraxacum sp.
Viburnum trilobum
Agropyron subsecundum
Smilacina stellata
Prunus pensylvanica
Schizachne purpurascens
Mitella nuda

Plus 63 species of Constance less than 40%.

A moister variant of this type that deserves recognition due to its better productive potential for white spruce has a high incidence of *Mitella nuda* and *Cornus canadensis* associated with *Corylus* and *Aralia*. In the *Populus/Corylus-Aralia-Mitella-Cornus* community the *Corylus* grows very tall, sometimes up to six or eight feet.

As aspen stands mature and the individual trees begin to die, the shrub stratum becomes denser but apparently there is no radical change in composition of the undergrowth. In such circumstances it is rare to find that the old stand is regenerating itself. Table XIV shows the composition of an old stand in which only scattered trees remained, and where very few young root sprouts were found.

In an occasional locality one aspen stand was found to have suceeeded another without any signs of the interposition of fire. Possibly windthrow of the parent trees was the initiating cause as it seems that some form of disturbance is always necessary for the genesis of new poplar stands.

TABLE XIV

DESCRIPTION OF A DECADENT, OPEN STAND OF ASPEN ON A FRESH SITE

Aspen - Fresh, tall shrub type.
Riding Mountain National Park, Manitoba.
Physiographic site: 2 : 3 : 5.
Soil: Grey wooded profile on moderately calcareous, silty clay-loam till.

Dominant species: Populus tremuloides widely scattered, overmature. Many dead "snags". A few root sprouts.

Minor species: Shrub layer strongly developed, 4 to 5 feet tall, dominated by Corylus cornuta.

Within the frequency classes, species are listed in order of decreasing importance as determined by quadrat studies of cover-abundance.

Frequency 100-85%

Corylus cornuta
Aralia nudicaulis
Rubus idaeus
Fragaria virginiana

Frequency 80-65%

Viola rugulosa
Galium triflorum
Galium septentrionale
Heracleum maximum
Mertensia paniculata
Maianthemum canadense var. interius

Frequency 60-45%

Rosa acicularis
Aster ciliolatus
Lathyrus ochroleucus
Elymus canadensis
Vicia americana
Rubus pubescens

Frequency 40-25%

Bromus ciliatus
Sanicula marilandica
Calamagrostis canadensis
Oryzopsis asperifolia
Moehringia lateriflora
Solidago lepida
Taraxacum sp.
Thalictrum venulosum
Prunus virginiana
Carex deweyana
Agropyron subsecundum

Frequency 20% and less

Disporum trachycarpum	Brachythecium salebrosum
Petasites palmatus	Ceratodon purpureus
Smilacina stellata	Cornus stolonifera
Amelanchier alnifolia	Crataegus chrysocarpa
Symphoricarpos albus	Prunus pensylvanica
Aster umbellatus var. pubens	Ribes hirtellum
Lathyrus venosus	Picea glauca seedlings
Urtica gracilis	Poa sp.
Elymus innovatus	Anemone canadensis
Schizachne purpurascens	Anemone quinquefolia
Cornus canadensis	Chamaenerion spicatum
	Prenanthes alba
	Lysimachia ciliata

The invasion of established aspen stands by white spruce following light fires can occur, but it is usually a slow process because relatively few niches where the seedlings can survive are available on fresh sites. The most important niche for initial invasion is decayed wood, as few other species are adapted to grow on it. Consequently spruce sometimes slowly "dribbles" into poplar stands where the decayed remains of former trees provide a suitable substratum. Another invasion niche of some importance is provided by mossy hummocks at the bases of the aspen trees where, as on decayed logs and stumps, moisture conditions are favourable and the dangers of smothering by the autumnal fall of broad leaves are minimized. Fig. 15 shows the distribution of stems in a mature aspen stand where white spruce was found to be invading, and where in time an open, uneven-aged spruce stand will be formed.

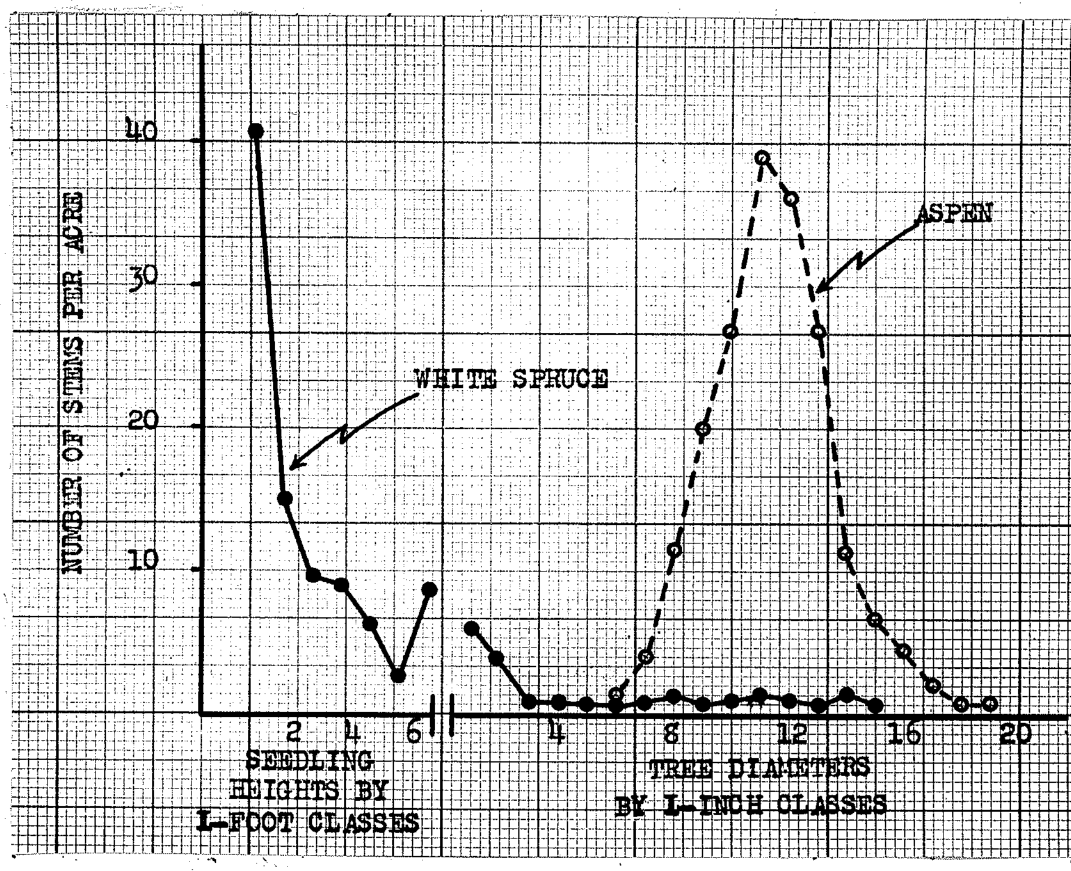


Fig. 15. The invasion of a mature aspen stand by white spruce. The distribution of spruce seedlings is given by one-foot height classes and the distribution of trees by one-inch diameter classes. Data from a tally of three acres of the type. (Note: These graphs are not regression lines.)

(b) Succession following severe fires

Severe ground fires which burn away the humus layer favour establishment of spruce by simultaneously destroying competing plants and baring a mineral soil seed-bed. Many examples of spruce stands which have regenerated after fire have been observed and some have been referred to previously (Rowe, 1955, pp. 18, 19). Various factors other than climatic conditions per se dispose forest stands to severe ground fires, the most important ones being a high needle-leaf content of the humus layer and a texture and structure of the underlying mineral soil conducive to rapid drainage at the surface. Therefore complete destruction of the humus layer by fire is more frequent in coniferous stands than in hardwood stands, and on sandy surface soils than on clays. In mixed stands it has been observed that ground fires often burn away all humus under spruce while only lightly burning the surface under adjacent aspen, and thus spruce regeneration is favoured where spruce grew before, just as aspen is favoured where it formerly existed.

The effect of a severe ground fire is to destroy almost all the resident forest vegetation, for most species (including poplar) have their perennating parts in or just beneath the humus layer. A few small studies made by the writer are pertinent to this point. In one experiment, one hundred samples of humus layer (12 inches by 12 inches by 4 inches) were collected under a mature mixed spruce-and-aspen stand early in the spring. The samples, placed in open frames and watered throughout the summer, produced the typical flora of the mixedwood stand, an indication that the perennating parts of most of the forest floor species are in the humus layer. During the same period observations at points where the samples had been lifted showed that only a few species had survived removal of the humus layer, these including *Vicia americana*, *Lathyrus ochroleucus*, and *Galium septentrionale*. Other plants rapidly invaded the bared mineral soil from adjacent undisturbed humus, particularly the stoloniferous species *Fragaria virginiana* and *Rubus pubescens*. Excavation of the underground parts of *Vicia americana*, *Lathyrus ochroleucus* and *Lathyrus venosus* showed the reason for the success of these legumes after destruction of the humus layer. All possess deep roots and rhizomes in the mineral soil from which new stems can rapidly be produced.

The species of the open communities which form on exposed mineral soil after fires can be classed in three groups, as follows:

(i) Species with deep perennating parts:
E.g., *Vicia americana*, *Lathyrus venosus*, *Lathyrus ochroleucus*, *Galium septentrionale*, *Apocynum androsaemifolium*, *Mertensia paniculata*, *Chamaenerion spicatum*, *Rosa acicularis*. *Populus tremuloides* belongs partly here, for severe fires seldom eliminate it entirely.

(ii) Species spreading rapidly by vegetative means:
E.g., *Populus tremuloides*, *Fragaria virginiana*,

Rubus pubescens, Arctostaphylos uva-ursi, Smilacina stellata.

(iii) Species with mobile seeds (many ruderals): E.g., Taraxacum dumetorum, Sonchus arvensis, Lactuca pulchella, Solidago hispida, Cirsium arvense, Salix bebbiana, Aster ciliolatus, Achillea millefolium, Hieracium canadense, Erigeron canadense, Gentiana acuta, Geranium bicknellii, Ceratodon purpureus and Funaria hygrometrica. Picea glauca belongs with this group.

The invasion of spruce, aspen and the pioneer minor species on severely burned areas gradually results in the formation of a new humus layer in which the more mesophytic species Aralia nudicaulis, Viola rugulosa, Petasites palmatus, Sanicula marilandica, Cornus canadensis, etc. become established.

Corylus cornuta does not invade areas where spruce has established itself equally with aspen, presumably due to unfavourable light conditions. Instead Aralia nudicaulis, slightly more tolerant than the Corylus, often comes to the fore (Fig. 16).

The soil associate accompanying the community in Fig. 16 is shown in Fig. 17.

Fig. 16. Aralia nudicaulis dominating the minor vegetation in a patch of white spruce. Riding Mountain National Park, Manitoba.

A closer cover of spruce is in turn less favourable to tall herbs such as Aralia, and then the lower, more tolerant species such as Cornus canadensis, Linnaea borealis var. americana and Pyrola spp. become distinctive in the minor vegetation. A recognizable temporary forest type (Picea-Populus/Cornus-Linnaea-Pyrola) is described in Table XV on the basis of ten mixed stands in which spruce predominated over aspen.

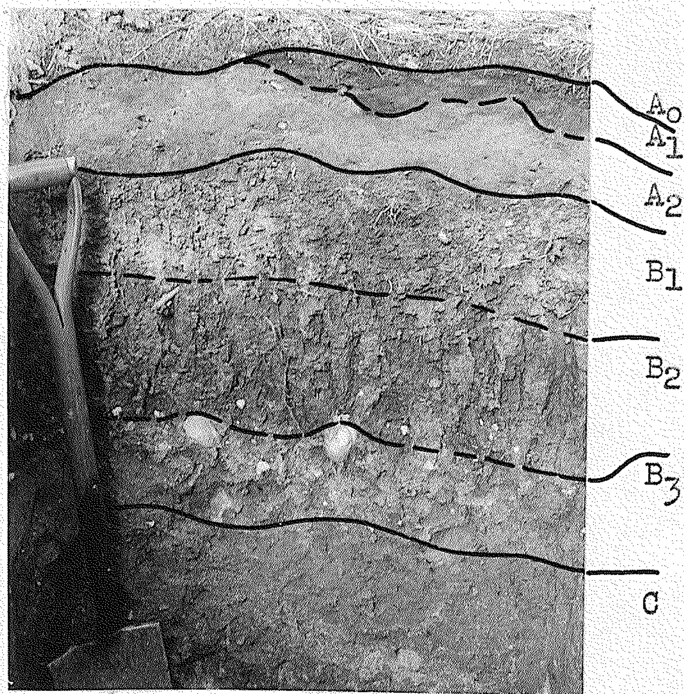


Fig. 17. Fresh associate of the "Granville" grey wooded soil association. Riding Mountain National Park, Manitoba.

PROFILE DESCRIPTION

A_0 horizon: 1 1/2" dark brown mottled humus.

A_1 horizon: 0-1" dark grey to black loam, some charcoal flecks.

A_2 horizon: 3-4" brownish grey loam, platy structure.

B_1 horizon: 6" brown clay loam, granular to fine nutty.

B_2 horizon: 8-10" dark brown clay loam, weakly columnar, breaking to medium nutty aggregates.

B_3 horizon: 2-4" yellowish brown clay loam, stony, weak nutty to granular structure, with free lime carbonate at base (at 20-24" depth).

C horizon: greyish brown silty clay loam, moderately calcareous, fragments of shale and limestone abundant.

TABLE XV

THE COMPOSITION OF THE PICEA-POPULUS/CORNUS-LINNAEA-PYROLA FOREST TYPE

Within each Constance class the species have been listed in order of decreasing frequency as determined on the basis of 100 milacre quadrats.

Constancy 100 and 90%

Cornus canadensis
Mertensia paniculata
Fragaria virginiana
Rosa acicularis
Petasites palmatus
Aralia nudicaulis
Aster ciliolatus
Linnaea borealis var. americana
Mitella nuda
Rubus pubescens
Maianthemum canadense var. interius
Elymus innovatus
Pyrola asarifolia
Symphoricarpos albus
Pyrola secunda

Constancy 80 and 70%

Galium septentrionale
Viola rugulosa
Oryzopsis asperifolia
Viburnum edule
Chamaenerion spicatum
Lathyrus ochroleucus
Lonicera dioica var. glaucescens
Disporum trachycarpum
Calliergonella schreberi
Ribes triste
Ribes hirtellum
Amelanchier alnifolia
Cornus stolonifera
Mnium spp.

Constancy 60 and 50%

Corylus cornuta
Thalictrum venulosum
Carex sp.
Schizachne purpurascens
Hylocomium splendens
Galium triflorum
Viola renifolia
Equisetum arvense
Pyrola virens
Solidago hispida
Sanicula marilandica
Dicranum rugosum
Corallorhiza trifida
Actaea rubra

Plus 53 others of Constancy 40% and less.

The average community just described is a seral stage which will give way to a spruce type as the aspen mature and die. Although a tendency has been observed for the patchy development of a feather moss stratum (Calliergonella schreberi, Hylocomium splendens, Dicranum rugosum) in the most shaded parts of intermediate-aged spruce and spruce-aspen stands (60 to 80 years), older stands usually show little evidence of further development in this direction, as has earlier been mentioned. In some stands the herb and shrub vegetation seems to have become denser rather than thinner with advancing age, due in all probability to increased side-light as suppressed spruce and mature poplar die and fall throughout the stand.

In support of the contention that spruce stands do not necessarily develop to a feather moss type, reference will be made to a small spruce stand on the Riding Mountain where tree measurements have been made since 1921. When three 1/4-acre study plots were marked out in 1921 by G. Tunstell and C. Gill, notes were taken stating that the stand contained "mainly spruce, some poplar (aspen), a few birch and some dead tamarack". Furthermore it was stated that no underbrush was present, the minor vegetation "being mainly moss 2 to 4 inches thick (presumably in patches), bunch berry (Cornus canadensis) and hound's tongue (Mertensia paniculata)." Fig. 18, a photo taken in 1921, shows the dense spruce and the minor vegetation in which *Aralia nudicaulis*, *Fragaria virginiana*, *Petasites palmatus* and *Rubus pubescens*, as well as the above-mentioned *Cornus* and *Mertensia*, can be discerned.

Fig. 18. Dense white spruce with a sparse herb and moss ground vegetation. Riding Mountain National Park, Manitoba. 1921.

The vegetation thirty-one years later (in 1952) is shown in Fig. 19. The similarity of the latter picture to Fig. 12, the overmature spruce stand at Singoosh Lake, is notable.

Fig. 19. The spruce stand of Fig. 18 as seen in 1952, with a herb and shrub ground cover.

In the 31-year interval the forest changed from a sparse moss-and-herb type to a predominantly shrub-and-herb type. The most important species at present (as determined by examination in 1953) are Rubus idaeus, *Aralia nudicaulis*, *Cornus canadensis* and *Petasites palmatus*. *Corylus cornuta* is present, with *Linnaea borealis* var. *americana*, *Pyrola virens*, *Rubus pubescens*, *Mertensia paniculata*, and many other herbs.

Some of the different kinds of stands arising after severe or light fires have now been discussed. Many other kinds, intermediate in character, are formed due to variations in fire intensity, composition of original stands, suitability of season for regeneration, and so forth. Thus every conceivable mixture of white spruce and aspen can be found in the fresh series, along with a great many different age-class distributions. If a stand is predominantly aspen (common after light fire), and spruce slowly invades over a long period, the final result is an open uneven-aged coniferous stand. Where invasion by spruce is sudden and complete (common after severe fire) a more closed, even-aged coniferous stand will result. This is the type of stand whose development has been discussed by Kabzems (1952).

Probably the commonest condition arises when, due to variability in intensity of fire, in local climate and in reproductive potential, a patchwork forest of spruce, aspen and their mixtures is formed. Sixty to seventy years after the initiation of such a forest there is usually a secondary intra-stand invasion of the aspen by the spruce. Kagis (1954) observed this process in a mixedwood stand

and suggested that it could be related to "stand-opening" as aspen declined after about 60 years. This may be one predisposing factor, but there is another of equal or greater importance, namely the initiation of seed production by the spruce after approximately the same interval of time.

The diameter distribution of a mature, mixed spruce-and-aspen stand on the Riding Mountain is shown in Fig. 20 as an illustration of stand structure resulting from the above-mentioned developmental process.

Note in Fig. 20 the normal distributions by diameter size classes of aspen and balsam poplar and paper birch, indicating an even-aged hardwood component in the stand. On the other hand, the distribution of the spruce by diameter size classes indicates unevenness of age of the softwood component. The mode of the distribution curve for the older spruce is apparently around the 9- to 12-inch diameter classes, and this can be visualized if a leg extending from the 8-inch diameter class toward the lower left of the graph is added (dotted line from the arrow). The shape of the left-hand side of the spruce curve indicates the presence of young trees. The old stand is 100 to 110 years old, and if it is assumed that appreciable seed production began when the older spruce were 50 to 60 years of age, then there has been a period of 50 years for the establishment of the "ingrowth" represented by the left-hand side (1 to 8 inches diameters) of the curve.

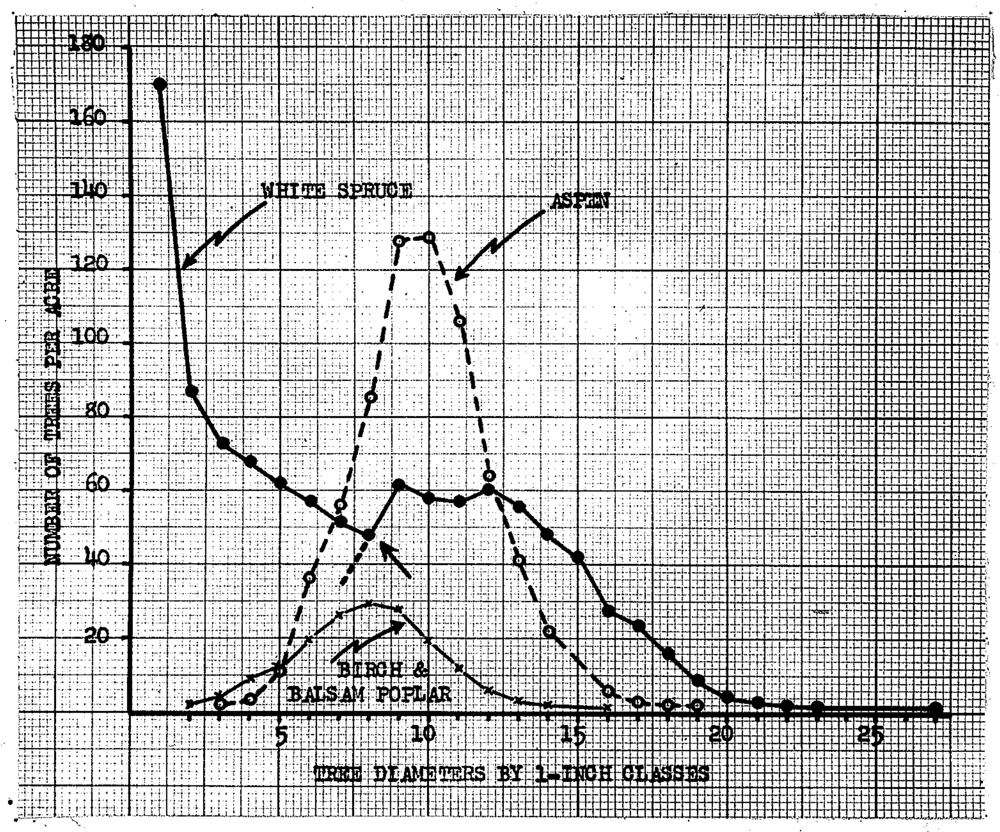


Fig. 20. The diameter distribution of the tree species in a mature mixed forest. Riding Mountain N ational Park, Manitoba. The data are from a complete tally of 100 acres of the type. (Note: These graphs are not regression lines.)

The vegetation of this mature mixed stand was sampled by 1,000 small circular plots, each one half a meter in size, distributed systematically over the 100-acre area. The topography is undulating, and a minority of the plots fell in moist to wet localities. However the great majority of the plots sampled upland sites, and therefore the data are presented in summary form in Table XVI as representative of the vegetation under mature mixed spruce-and-aspen on fresh sites.

TABLE XVI

DESCRIPTION OF THE MINOR VEGETATION IN A MATURE MIXED FOREST OF SPRUCE, POPLAR AND BIRCH
RIDING MOUNTAIN NATIONAL PARK, MANITOBA

The 70 commonest minor species are listed in order of decreasing frequency in 1,000 sample plots.

<u>Frequency above 80%</u>

Fragaria virginiana

<u>Frequency 80 to 60%</u>

Aster ciliolatus
Petasites palmatus
Aralia nudicaulis
Rubus pubescens
Mertensia paniculata
Galium septentrionale
Calamagrostis canadensis

<u>Frequency 60 to 40%</u>

Maianthemum canadense var. interius
Cornus canadensis
Rosa acicularis
Symphoricarpos albus
Oryzopsis asperifolia

Table XVI cont.

Frequency 40 to 20%

Pyrola asarifolia
Thalictrum venulosum
Lathyrus ochroleucus
Brachythecium salebrosum
Elymus innovatus
Corylus cornuta
Mnium spp.
Viola rugulosa
Carex spp. chiefly
C. deweyana

Frequency less than 20%

Smilacina stellata
Rubus idaeus
Aster umbellatus var. pubens
Mitella nuda
Vicia americana
Chamaenerion spicatum
Galium triflorum
Taraxacum spp.
Equisetum arvense
Populus tremuloides suckers
Sanicula marilandica
Solidago lepida
Lonicera dioica var. glaucescens
Pyrola secunda
Schizachne purpurascens
Anemone canadensis
Prenanthes alba
Achillea millefolium
Ribes hirtellum
Halenia deflexa
Hieracium canadense
Amelanchier alnifolia
Lathyrus venosus
Heracleum maximum
Anemone quinquefolia
Anemone riparia
Viburnum edule
Ribes triste
Bromus ciliatus
Viola renifolia
Luzula multiflora
Moehringia lateriflora
Apocynum androsaemifolium
Mentha arvensis
Gentiana acuta
Stachys palustris
Climacium americanum
Actaea rubra
Pyrola elliptica
Viola sp.
Prunus virginiana
Thuidium recognitum
Linnaea borealis var. americana
Aster puniceus
Petasites sagittatus
Solidago hispida
Agastache foeniculum
Calliergonella schreberi

Plus 50 additional spp. of minor importance.

Dry and Fresh Series - Weakly calcareous soils

The differences between the shallow, moderately calcareous soils characteristic of the Cretaceous highlands in the vicinity of the Manitoba-Saskatchewan boundary and the deeper, weakly calcareous soils which are common in central Saskatchewan have been briefly outlined before. Both support forests consisting mostly of aspen, white spruce and their intermixtures, but important differences in stand structure and in composition of accompanying vegetation can be discerned which in the writer's opinion justify their separation.

The deep, leached surface horizon (A_2) of soils on the weakly calcareous drift confers on them many of the characteristics of sandy porous soils. To the agriculturist, interested in the growth of shallow-rooted annual cereals, many of the soils would probably be classed as impoverished and somewhat arid, but for forestry purposes such is not the case as they provide good to superior conditions for the reproduction and growth of spruce and pine. The well-drained surface allows rapid drying of the humus layer which is a predisposing factor to its complete destruction when fires occur, and the consequent exposure of mineral soil in turn facilitates invasion by the conifers. Impoverishment of the surface horizon by strong leaching--indicated by the depth to free lime carbonate in the soil, by strong acidity in the upper horizons and frequently by secondary podzolization of the A_2 horizon--probably favours the survival of coniferous seedlings in composition with the more demanding broad-leaved herbs, shrubs and trees. Thus the favourability of these soils for spruce and pine as compared to shallower, more calcareous (richer) soils is reflected in the higher incidence of forest stands in which the coniferous component is both even-aged and dense. Once established, the subsequent rate of growth of conifers is also good, particularly on the fresh sites, and a reason in terms of favourable moisture storage and availability has earlier been suggested.

Some of the species which assume greater importance on the deeply leached soils than on the shallower, more calcareous soils are the ericaceous species *Vaccinium myrtilloides*, *V. vitis-idaea* var. *minus*, and *Ledum groenlandicum*. The club mosses, *Lycopodium* spp., also become prominent, and such species as *Geocaulon lividum* and *Habenaria orbiculata* frequently appear, not only under coniferous cover but also under hardwoods. It is an interesting although puzzling fact that where the above-mentioned species occur on the more calcareous soils, they are usually associated with much moister conditions of site. On the other hand some species more commonly associated with dry pine sites in the eastern area are prominent in spruce and poplar as well as pine stands to the west. Such are *Alnus crispa*, *Vaccinium caespitosum* and *Arctostaphylos uva-ursi*.

(1) Dry Series

White spruce, jack pine, and aspen, alone or in mixture, compose the stands of the dry series. Only fragmentary examples of forests belonging to this series were found during these studies. An example of a spruce-aspen stand is given in Table XVII.

The open forests of the dry series resemble those which have been described farther east on the Cretaceous Hills, in that *Elymus innovatus* is the most abundant minor species. This grass carpets the ground, particularly under aspen and pine, but it is associated with species less common on comparable sites to the eastward, such being *Arctostaphylos uva-ursi*, *Vaccinium* spp., *Sibbaldiopsis tridentata* and *Alnus crispa*.

TABLE XVII

DESCRIPTION OF A PICEA-POPULUS COMMUNITY ON A DRY, DEEP GREY WOODED SOIL

White spruce and aspen - Dry, mixed herb-and-shrub type.
Loon Lake, Saskatchewan.
Physiographic site: 4 : 1-2 : 4.
Soil: Deep grey wooded profile on weakly calcareous, stony clay-loam till.

Dominant species: Picea glauca in an open stand, with individual trees up to 70 feet tall at 85 years of age.
Populus tremuloides of poor form, stems up to 55 feet tall.

Minor species: No distinct stratification in the undergrowth. Variable ground cover.

Abundant:	Linnaea borealis var. americana	Cornus canadensis
	Chamaenerion spicatum	Arctostaphylos uva-ursi
	Shepherdia canadensis	Calliergonella schreberi
	Elymus innovatus	Hylocomium splendens
		Viburnum edule
Common:	Aralia nudicaulis	Corylus cornuta
	Aster ciliolatus	Vaccinium caespitosum
	Aster conspicuus	Vaccinium myrtilloides
	Rosa acicularis	Vaccinium vitis-idaea var. minus
	Ledum groenlandicum	
Occasional:	Calamagrostis canadensis	Rubus pubescens
	Schizachne purpurascens	Vicia americana
	Achillea millefolium	Populus tremuloides suckers
	Fragaria virginiana	Amelanchier alnifolia
	Gentiana acuta	Mitella nuda
	Galium septentrionale	Eurhynchium strigosum
	Hieracium canadense	Viola renifolia
	Disporum trachycarpum	Lonicera involucrata
	Mertensia paniculata	Betula papyrifera seedlings
	Maianthemum canadense var. interius	Taraxacum sp.
	Petasites palmatus	Goodyera repens
	Pyrola secunda	Salix discolor
	Pyrola asarifolia	Lonicera dioica var. glaucescens
	Symphoricarpos albus	Castilleja rhexifolia
	Lathyrus ochroleucus	Spiranthes romanzoffiana

In the dry series the same situation of similarity in ground flora, whether under white spruce, pine, aspen or their mixtures, was observed on the weakly calcareous as on the moderately calcareous soils. Therefore it is logical to assume that white spruce could replace both aspen and pine on the dry series of sites given sufficient time and an absence of fire.

(2) Fresh Series

The dominants of forest stands of the fresh series on weakly calcareous soils include aspen, white spruce, balsam fir, jack pine, balsam poplar and black spruce. The last three trees usually occur either scattered or as small patches in stands of the other species. The sites are particularly favourable for the regeneration of white spruce and, in association with it, of balsam fir. Spruce-fir stands appear to have more stability than on comparable moisture regimes of more calcareous soils.

The description of an overmature spruce-fir forest studied near Bittern Creek, Saskatchewan is first given (Table XVIII). This stand is typical of the *Picea-Abies/Hylocomium-Rubus* forest type, to which reference will be made later under the Moist and Very Moist Series.

TABLE XVIII

DESCRIPTION OF AN OLD PICEA-ABIES FOREST ON A FRESH SITE

White spruce and balsam fir - Fresh, feather moss type.
Plot No. 327, Bittern Creek, Saskatchewan.
Physiographic site: 4 : 3 : 4.
Soil: Deep grey wooded profile, developed in weakly calcareous ablation moraine (stony loam) over lodgement till (stony clay).

Dominant trees: _Picea glauca_ 1 to 27 inches in diameter, up to 115 feet tall, and 170 years old.
Abies balsamea 1 to 18 inches in diameter, up to 85 feet tall, 80 years old.
Picea mariana, a few scattered small trees, 1 to 10 inches in diameter. A few _Betula papyrifera_. No _Populus_ spp.

Tree Regeneration: Abundant seedlings and saplings of fir in stand openings. Scattered spruce seedlings on decayed logs.

Minor species: The presence of a great deal of decayed wood--logs and stumps--has resulted in a "moist" moss ground flora. Under the closed coniferous canopy the moss stratum is prominent, but in stand openings caused by the death of old trees _Rubus idaeus_ dominates the undergrowth.

Species are listed below, within frequency classes, according to their decreasing frequency and cover-abundance as determined by examination of 20 milacre quadrats.

Frequency 85-100%

Hylocomium splendens
Calliergonella schreberi
Hypnum crista-castrensis
Abies balsamea seedlings

Frequency 65-80%

Eurhynchium strigosum
Moss sp. (Hypnum haldanianum?)
Mitella nuda

Frequency 45-60%

Linnaea borealis var. americana
Dicranum flagellare
Mnium sp.

Table XVIII cont.

Frequency 25-40%

Rubus idaeus	Eurhynchium diversifolium
Cornus canadensis	Betula papyrifera seedlings
Dicranum rugosum	Chamaenerion spicatum
Pohlia nutans	Rubus pubescens
Aralia nudicaulis	Trientalis borealis
Maianthemum canadense var. interius	Polytrichum juniperinum
Pyrola secunda	Dicranum bergeri

Frequency 5-20%

Ribes triste	Oncophorus wahlenbergii
Lycopodium annotinum	Viburnum edule
Galium triflorum	Goodyera repens
Moneses uniflora	Dryopteris spinulosa
Pyrola virens	Carex sp.

Fig. 21 shows the distribution by two-inch diameter classes of the spruce and fir components in a one-acre sample of the forest.

It appears that the community here may be a stable or even a fundamental forest type. Fir has been reproducing well, although not to the exclusion of the larger and longer-lived spruce. The occurrence of the latter species in the small diameter classes indicates a probability that it has been reproducing at a rate sufficient for its maintenance in the community. The large amount of moist decayed wood on the forest floor is a significant factor so far as continued regeneration of spruce is concerned.

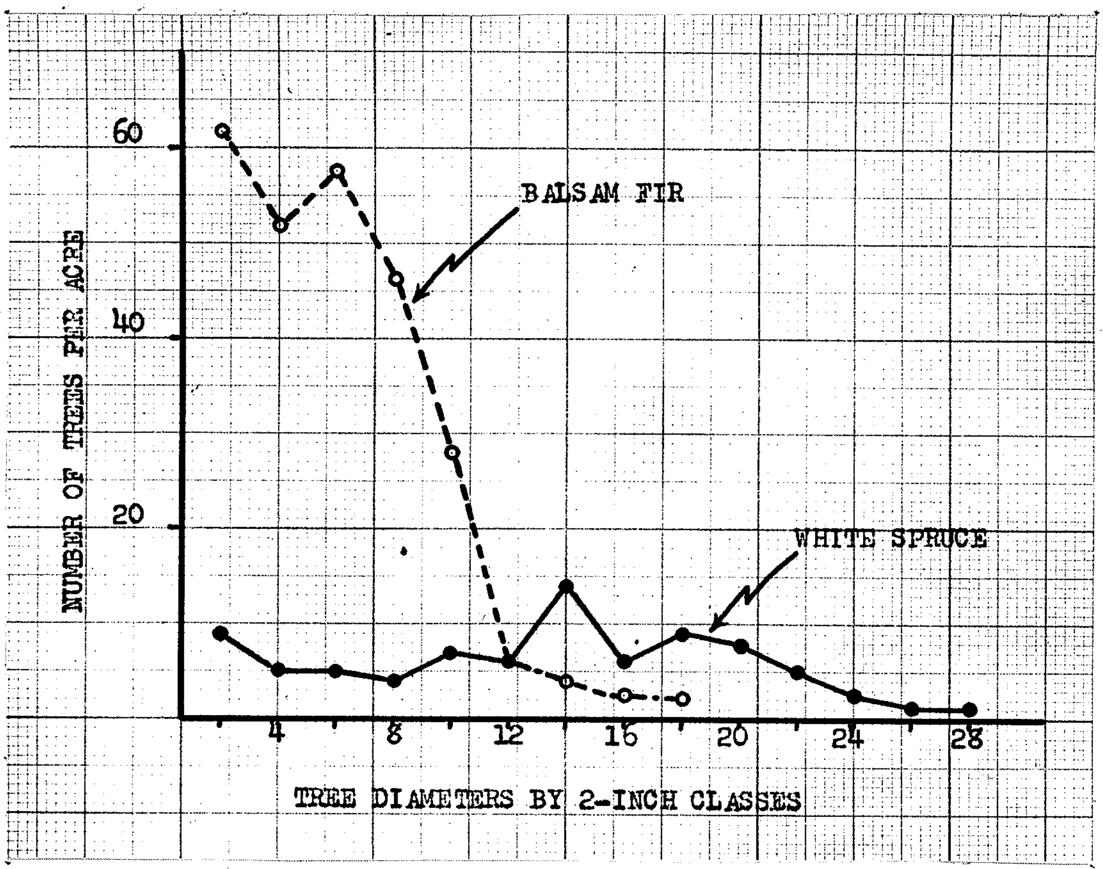


Fig. 21. The diameter distribution of spruce and fir in an old coniferous stand. Bittern Creek, Saskatchewan.
(Note: These graphs are not regression lines.)

Successional relationships of younger communities:

The successional relationships of the vegetation in the fresh series are much the same throughout our area. A common end point of forest succession (in the absence of fire) is apparently a spruce or spruce-and-fir forest of variable stability. Due to the more favourable conditions for the establishment of spruce which exist on the deep, weakly calcareous soils, there is a greater tendency here than on shallower more calcareous soils for the development of even-aged, closed types of coniferous stands. A closer canopy and a less vigorous herb stratum than on the more calcareous soils is in turn conducive to the genesis of feather moss forest floors, and with these the regeneration of balsam fir is quite commonly associated.

On the deep grey wooded soils, forest types of similar composition and structure to those discussed earlier for the more eastern part of the area are to be found, for example: pure poplar stands, poplar with spruce slowly "dribbling in", open stands of fairly even-aged spruce-and-poplar with regeneration of the former species filling in under the latter, and closed stands of even-aged spruce-poplar in which the successional trend to a feather moss coniferous type can clearly be seen. Examples of some of these common communities will now be given.

By far the most common forest in Saskatchewan and in Manitoba is the pure aspen type, a result of frequent fires. In young aspen stands, tall herbs often form the most noticeable stratum, but after about 40 years a pronounced tall-shrub stratum usually dominates the undergrowth. Table XIX gives an example of a mature aspen stand which developed after a severe fire.

TABLE XIX

DESCRIPTION OF A MATURE ASPEN STAND ON A FRESH, DEEP, GREY WOODED SOIL

Mature aspen - Fresh, tall shrub type.
Plot No. 131, Torch River Forest Reserve, Saskatchewan.
Physiographic site: 4 : 3 : 3-4.
Soil: A deep, grey wooded ("double") profile developed on weakly calcareous glacio-lacustrine deposits (very fine sandy loam with interbedded thin bands of clay.

Dominant trees: Populus tremuloides 6 to 11 inches D.B.H., up to 80 feet tall, 88 years old.
Scattered Betula papyrifera 1 to 2 inches D.B.H.

Tree regeneration: Scattered seedlings and saplings of Picea glauca, all rooted in decayed wood.

Minor species: A strongly developed shrub stratum 6 to 8 feet tall consisting of Corylus cornuta and Alnus crispa, with a lower stratum of herbs and Diervilla lonicera.

Species are listed within each frequency class in order of decreasing frequency and cover-abundance, as determined by the study of 20 milacre quadrats.

Frequency 100-85%

Corylus cornuta
Aralia nudicaulis
Cornus canadensis
Maianthemum canadense var. interius
Rosa acicularis
Diervilla lonicera

Frequency 80-65%

Rubus pubescens
Trientalis borealis
Rubus idaeus
Ribes triste
Mitella nuda

Frequency 60-45%

Viburnum edule
Alnus crispa
Ribes glandulosum
Galium triflorum
Pyrola asarifolia

Table XIX cont.

Frequency 40-25%

Calamagrostis canadensis	Linnaea borealis var. americana
Carex sp.	Petasites palmatus
Aster ciliolatus	Mertensia paniculata

Frequency 20-5%

Viola rugulosa	Cornus stolonifera
Oryzopsis asperifolia	Ledum groenlandicum
Actaea rubra	Schizachne purpurascens
Galium septentrionale	Equisetum arvense
Lycopodium annotinum	Lathyrus ochroleucus
Lycopodium obscurum	Apocynum androsaemifolium
Amelanchier alnifolia	Chamaenerion spicatum
	Disporum trachycarpum

Fig. 22 shows the soil profile under this stand.

This natural stand of Populus/Corylus-Alnus-Diervilla was found to resemble closely a number of artificial stands created by the logging out of spruce from spruce-aspen mixedwoods in the Torch River area. The tall-shrub stratum evidently develops rather quickly where light conditions are favourable. A further relationship, suggestive of developmental trends, was found with some open coniferous types (white spruce and balsam fir) where the stand openings were dominated by Corylus cornuta and Alnus crispa (with Diervilla lonicera very abundant under the Alnus in one stand) and where the closed canopy parts had a low herb and moss ground cover.

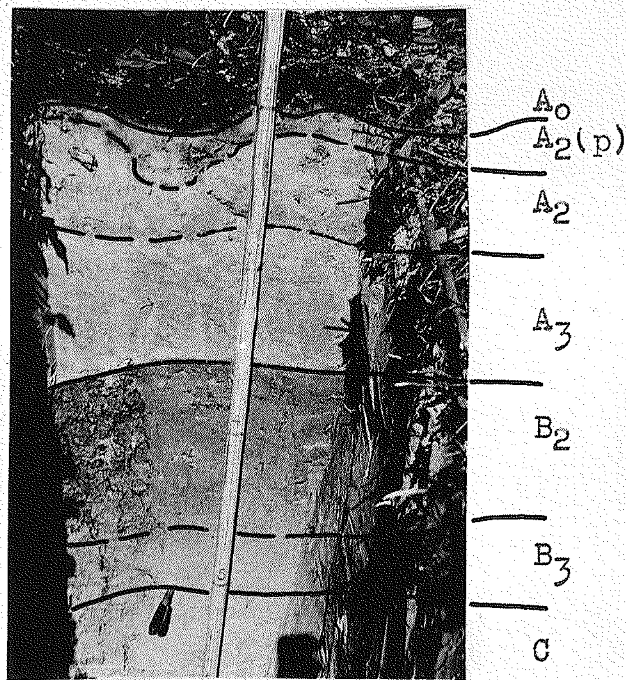


Fig. 22. Soil profile under a fresh, Populus/Corylus-Alnus-Diervilla community. Torch River Forest Reserve, Saskatchewan.

PROFILE DESCRIPTION

A_0 horizon: 2-3" dark matted mor.

A_2(p) horizon: 1-3" pinkish grey, loamy sand.

A_2 horizon: 6-10" faintly blotchy, light yellowish brown, very fine sandy loam. Weakly laminated structure.

A_3 horizon: 4-6" light brown very fine sandy loam with fine rusty crenulate lines of clay.

B_2 horizon: 8" brown clay, compact, somewhat stony.

B_3 horizon: 8" light brown friable clay loam. Some small streaks of free calcium carbonate at 40" depth.

C horizon: light grey to very pale brown silty clay below 48" depth.

In moister variants of open "fresh" forests, *Corylus cornuta* usually replaces *Alnus crispa*. A fine example of a mature spruce stand from which most of the poplar had died, but which still maintained a tall-shrub (*Corylus*) stratum, is given in Table XX.

Earlier, reference has been made to an aspen forest type on moderately calcareous soils, *Populus*/*Corylus*-*Aralia*-*Viola*-*Oryzopsis*, and to a moister variant, in which *Mitella nuda* and *Cornus canadensis* are prominent. The stand described in Table XX has the latter type of undergrowth (*Corylus*-*Aralia*-*Mitella*-*Cornus*) although associated with an open stand of spruce rather than aspen. Similar stands, in which spruce where present always showed an excellent rate of growth, have been found on the Cretaceous uplands as well as in central Saskatchewan. There is here an indication that except on the dry and fresh sites the differences in vegetational communities between the eastern and western parts of our area are very small.

TABLE XX

DESCRIPTION OF A MATURE OPEN STAND OF PICEA/CORYLUS ON A SUPERIOR FRESH TO MOIST SITE

White spruce - Fresh, tall-shrub type.
Plots Nos. 323, 324, Love, Saskatchewan.
Physiographic site: 4 : 3-4 : 4.
Soil: Deep, grey wooded profile on weakly calcareous glacio-lacustrine deposits (very fine sandy loam over modified clay till).

Dominant trees: Picea glauca, a moderately open stand of trees 4 to 20 inches D.B.H., up to 110 feet tall at 100 years of age--an excellent rate of growth. Populus tremuloides mostly dead. Populus balsamifera and Abies balsamea present as scattered individuals.

Tree regeneration: Numerous seedlings and saplings of fir, mostly in scattered patches or thickets. A few spruce seedlings on decayed wood, and a few birch and poplar saplings where the canopy has opened.

Minor vegetation: A pronounced Corylus stratum, 4 to 6 feet tall, dominates the undergrowth.

Species are listed below in order of decreasing frequency and cover-abundance within each frequency class as determined by the study of 40 milacre quadrats.

Frequency 100 to 85%

Corylus cornuta
Mitella nuda
Aralia nudicaulis
Cornus canadensis
Mertensia paniculata
Rubus pubescens
Petasites palmatus
Mnium spp.
Fragaria virginiana
Maianthemum canadense var. interius
Galium triflorum

Frequency 83 to 65%

Ribes triste
Linnaea borealis var. americana
Viburnum edule

Table XX cont.

Frequency 63 to 45%

Cornus stolonifera	Rubus idaeus
Brachythecium salebrosum	Carex sp.
Pyrola asarifolia	Calliergonella schreberi

Frequency 43 to 25%

Oryzopsis asperifolia	Galium septentrionale
Ribes hirtellum	Aster ciliolatus
Hylocomium splendens	Eurhynchium strigosum
Viola renifolia	Symphoricarpos albus
Rosa acicularis	Circaea alpina

Frequency 23% and less

Lonicera dioica var. glaucescens	Actaea rubra
Trientalis borealis	Chamaenerion spicatum
Calamagrostis canadensis	Goodyera repens
Pyrola secunda	Smilacina stellata
Agropyron subsecundum	Solidago lepida
Bromus ciliatus	Taraxacum sp.
Lathyrus ochroleucus	Climacium americanum
Amelanchier alnifolia	Dicranum flagellare
Cinna latifolia	Pohlia nutans
Lonicera involucrata	Ribes glandulosum
Dicranum rugosum	Shepherdia canadensis
Viola rugulosa	Elymus innovatus
Apocynum androsaemifolium	Schizachne purpurascens
Equisetum arvense	Heracleum maximum
Hypnum crista-castrensis	Trillium cernuum
Moss sp.	Thalictrum venulosum
Prunus virginiana	Rhytidiadelphus triquetrus
Disporum trachycarpum	Thuidium recognitum

Turning once again to more typical fresh sites, a summary of the composition of four mixed stands, each with a high spruce component, will next be given. The stands are representative of even-aged forests found after severe fire and they were selected for similarities in soil (deeply leached, very fine sandy loams) and in age

(80 to 90 years). On the basis of these data and other observations, a Picea glauca/Cornus-Linnaea-Vaccinium forest type is tentatively defined (Table XXI).

TABLE XXI

THE COMPOSITION OF THE PICEA(POPULUS)/CORNUS-LINNAEA-VACCINIUM FOREST TYPE

Dominant trees: Picea glauca 2 to 12 inches D.B.H., up to 70 feet tall at 80 years of age.
Populus tremuloides 3 to 9 inches D.B.H., equal in age and height to the spruce, but fewer stems.
Scattered individuals of Pinus banksiana, Picea mariana, Abies balsamea and Populus balsamifera.

Minor species: A pronounced herb-and-moss undergrowth.

The species are listed in decreasing order of cover-abundance as determined by the study of 40 milacre quadrats, supplemented by ocular estimates.

Very abundant:

Cornus canadensis
Hylocomium splendens
Linnaea borealis var. americana
Calliergonella schreberi

Abundant:

Maianthemum canadense var. interius
Hypnum crista-castrensis
Oryzopsis asperifolia
Petasites palmatus
Rubus pubescens
x Vaccinium myrtilloides

Common:

Rosa acicularis
Mitella nuda
Aralia nudicaulis
x Trientalis borealis
Viola renifolia
Aster ciliolatus
Viburnum edule
x Vaccinium vitis-idaea var. minus
x Ledum groenlandicum
Fragaria virginiana
x Lycopodium complanatum
Brachythecium salebrosum
Galium septentrionale
x Alnus crispa
Chamaenerion spicatum
Goodyera repens
Lathyrus ochroleucus
Ribes triste

Table XXI cont.

Occasional:

x Vaccinium caespitosum	x Geocaulon lividum
Pyrola asarifolia	Symphoricarpos albus
Elymus innovatus	Alnus rugosa
Lonicera dioica var. glaucescens	Corylus cornuta
Dicranum rugosum	Mertensia paniculata
Schizachne purpurascens	Habenaria orbiculata
Calamagrostis canadensis	Cornus stolonifera
Achillea millefolium	Shepherdia canadensis
Hieracium canadense	Agropyron subsecundum
Pyrola secunda	Apocynum androsaemifolium
x Lycopodium annotinum	x Arctostaphylos uva-ursi
Solidago hispida	Carex sp.
Mnium sp.	Equisetum arvense
Pyrola virens	Solidago lepida
Polytrichum juniperinum	Vicia americana
Amelanchier alnifolia	Rhytidiadelphus triquetrus
	Drepanocladus uncinatus
	Eurhynchium diversifolium

x - The characteristic species are marked with an asterisk to facilitate comparison with Table XV which summarizes the constancy data for similar stands on moderately calcareous soils.

A picture of a patch of the ground cover from one of the plots on which Table XXI is based is shown in Fig. 23.

In older stands the trend toward a complete moss cover on the forest floor has been observed, accompanied by the dying out of poplar and the appearance of much balsam fir regeneration. The moss flora brings with it a characteristic low-herb flora in which the orchids Goodyera repens, Habenaria obtusata and Habenaria orbiculata are usually distinctive. In the final stage, which is a feather moss type of spruce and fir forest as in Table XIX, the Vaccinium and Lycopodium species typical of the earlier stages may not appear, possibly due to the lessening influence of the mineral soil as the humus layer thickens and decayed wood accumulates on the forest floor. Reduced light intensity is doubtless a significant factor also in the elimination of these and many other minor species.

Fig. 23. Some of the characteristic species in the ground cover of the Picea(Populus)/Cornus-Linnaea-Vaccinium forest type. Torch River Forest Reserve, Saskatchewan.
Note presence of Vaccinium myrtilloides, Ledum groenlandicum, Cornus canadensis, Lycopodium complanatum, and one of the Agaricaceae.

Several less important although fairly common forest types will now be mentioned. They are the forests formed by jack pine and black spruce, both of which species find conditions favourable for invasion when fire clears the humus from the surface of fresh, strongly leached soils. Seed availability after fire, and superior adaptation to cooler than normal ecoclimate, probably assists the local establishment of these species to the exclusion of white spruce.

Upland black spruce stands are usually very dense and for this reason they typically have a complete feather moss ground cover. Observations suggest that Calliergonella schreberi is the most prominent moss on sites toward the drier side of fresh, with Hylocomium splendens of greater importance toward the moister side (Fig. 24).

Fig. 24. Minor vegetation typical of some dense upland black spruce stands. Torch River Forest Reserve, Saskatchewan.
Note the abundance of Calliergonella schreberi and the presence of Trientalis borealis, Cornus canadensis, Ledum groenlandicum and Linnaea borealis var. americana.

The mosses, and the occasional herbs and shrubs noted in the moss mat of several upland black spruce stands, are listed below in decreasing order of importance:

- Calliergonella schreberi
- Hylocomium splendens
- Cornus canadensis
- Lycopodium annotinum
- Mitella nuda
- Linnaea borealis var. americana
- Pyrola secunda
- Ledum groenlandicum
- Petasites palmatus
- Rosa acicularis
- Lycopodium complanatum
- Lycopodium obscurum
- Dicranum rugosum
- Hypnum crista-castrensis
- Aralia nudicaulis
- Lonicera dioica var. glaucescens
- Viola renifolia
- Vaccinium vitis-idaea var. minus

In one 65-year-old black spruce stand that was studied, the ground was criss-crossed with the white trunks of dead birch (Betula papyrifera), all individuals having died when about 2 to 4 inches in diameter. Evidence of a similar elimination of birch has frequently been found in dense white spruce stands also, indicating a poor ability of the species to compete with conifers in closed stands.

A mixture of jack pine with black spruce on upland sites is common, the two species coexisting due to the fact that the intolerant pine is faster growing and extends above the black spruce canopy. The mixture invariably represents a transitional stage in development toward a black spruce type. Commonly the undergrowth is dominated by feather mosses, Vaccinium species, and the plants previously listed as occasional in upland black spruce stands.

Several examples of open pine stands, encountered on fresh sites in western Saskatchewan, had the typical understory associates *Alnus crispa*, *Elymus innovatus*, *Vaccinium myrtilloides*, *V. vitis-idaea* var. *minus* and *Ledum groenlandicum*, with other more ubiquitous species such as *Cornus canadensis*, *Fragaria virginiana* and *Maianthemum canadense* var. *interius*. A few denser pine stands shaded the ground sufficiently for the development of a complete cover of *Calliergonella schreberi*, and in the moss mat occasional individuals of *Linnaea borealis* var. *americana*, *Goodyera repens* and *Pyrola secunda* were found. Examination of the soils suggested no differences from adjacent areas occupied by aspen and white spruce, although slope and aspect provided evidences of cooler than normal ecoclimate. Such pine types are probably the result of accidents of seeding following disturbance.

At this point reference should be made to a forest type which, although occurring on the Cretaceous highlands, has many points of similarity to some of the open forests just described. It can be designated the *Pinus/Alnus-Lycopodium* forest type. The following description (Table XXII) is based on an examination of four stands, ranging in age from 70 to 120 years old, in the Riding Mountain and Duck Mountain Forest Reserves.

TABLE XXII

DESCRIPTION OF THE PINUS/ALNUS-LYCOPODIUM FOREST TYPE

Jack pine - Fresh to moist, tall shrub type.
Four stands, Riding Mountain and Duck Mountain
Usual physiographic site: 6 : 4-5: 5.
Soil: Grey wooded profiles on moderately calcareous, stony clay-loam till.

Dominant tree: Pinus banksiana. Excellent growth shown by old stands, with trees up to 18 inches D.B.H. and 85 feet tall.

Minor vegetation: A pronounced stratum of Alnus crispa, 5 to 7 feet tall, the clumps evenly spaced, almost as if planted (hypodispersion).

Beneath the Alnus there is a low herb and moss vegetation, in which Calliergonella schreberi, Lycopodium annotinum and Cornus canadensis are distinctive.

Species are listed below in order of decreasing abundance as determined by an examination of 20 milacre quadrats supplemented by ocular estimates.

Very abundant:	Alnus crispa	
Abundant:	Cornus canadensis	Rosa acicularis
	Calliergonella schreberi	Rubus pubescens
	Linnaea borealis var. americana	Petasites palmatus
	Lycopodium annotinum	Maianthemum canadense var. interius
	Pyrola asarifolia	Rubus idaeus
Common:	Fragaria virginiana	Symphoricarpos albus
	Elymus innovatus	Galium triflorum
	Schizachne purpurascens	Galium septentrionale
	Aralia nudicaulis	Viburnum edule
	Aster ciliolatus	Luzula acuminata
	Chamaenerion spicatum	Mitella nuda
	Dryopteris spinulosa	Hylocomium splendens
	Pyrola secunda	Oryzopsis asperifolia

Table XXII cont.

Occasional:

Dicranum rugosum	Hieracium canadense
Lonicera dioica var. glaucescens	Arctostaphylos uva-ursi
Ribes glandulosum	Campanula petiolata
Vaccinium myrtilloides	Achillea millefolium
Rhamnus alnifolia	Anemone canadensis
Calamagrostis canadensis	Solidago hispida
Actaea rubra	Taraxacum sp.
Corallorhiza trifida	Oryzopsis pungens
Lathyrus ochroleucus	Lycopodium complanatum
Vaccinium caespitosum	Lycopodium clavatum
Viola adunca	Equisetum scirpoides
Goodyera repens	Ribes triste
Polytrichum juniperinum	Vicia americana
Carex pedunculata	Mertensia paniculata
	Potentilla fruticosa

A relationship of this type to some of the fresh, upland coniferous stands in central Saskatchewan is suggested not only by the abundant species but also some of the rarer ones--for example, Vaccinium caespitosum, V. myrtilloides and Lycopodium complanatum. The surprising feature of the type is that it usually occurs on moist sites, that is, on areas of low relief and poor drainage, rather than on dry to fresh sites as the pine and alder components would suggest. In some places scattered white spruce, black spruce and poplar are mixed with the pine, and it is notable that the spruce shows an excellent rate of growth. Possibly the type has been shaped primarily by local climate (cooler than normal) rather than by soil moisture regime or nutrient regime, as its distribution compared to communities with the typical *Corylus-Aralia-Viola* substrata appears to be topographically determined. It is undoubtedly a temporary type, dependent on recurring fire for its maintenance.

Moist and Very Moist Series

Forest communities of the moist, very moist and wet series can be distinguished rather easily as a group from those of the fresh and dry series by characteristics of soil and of vegetation. In the soil, the appearance of an A_1 (humus-darkened) horizon just beneath the humus layer, accompanied by a dulling of the brown colours in the B horizon and by signs of incipient gleization at its base, have been chiefly used in setting a boundary between the two large site groups. Recognizable changes in the composition of the vegetation also accompany the transition from sites with inadequate or barely adequate moisture for good tree growth to those with an excess. For example, there is a decided shift in dominance by minor species, as exemplified by the increased importance of *Cornus stolonifera* over *Corylus cornuta*, and of *Mertensia paniculata* over *Viola rugulosa*. In the tree stratum, jack pine becomes a much less important member of the forest communities, while black spruce, balsam poplar, paper birch and balsam fir increase in frequency of occurrence. The moister soil surfaces favour survival of coniferous seedlings with the frequent result that dense stands are formed, under which "feather moss" ground-cover appears at an early age. The local formation of pure fir stands is also favoured, a very uncommon situation on fresh sites.

Within the moist to wet portion of the environmental gradient however, it has proved difficult to find characteristics of soil and vegetation that can be used to draw the line between the moist series and the very moist series. If variability of communities is any criterion, there is truly a vegetational continuum on these sites! Although the unique features of most of the communities examined in these studies on moist and very moist sites are such as to cast doubt on the advisability of attempting to group and generalize except on a local basis, there is one forest type which was found to occur rather frequently although not extensively in most localities. It is the white spruce (or spruce and fir) forest type characterized by a mossy floor in its shaded parts. Reference has already been made to an example in the fresh series (Table XVIII).

The reason why this recognizable type occurs over a broad range of sites can be understood by an examination of the conditions which apparently favour its development. Absence of fire seems to be a prime necessity, and only very rarely in the entire area has the writer found a mixture of young spruce and fir growing under an aspen canopy soon after fire. (In one burned area where the above conditions prevailed, a neighbouring stand of mature fir had provided the source of seed, and invasion had taken place on the incompletely burned humus of a prior coniferous forest.) Without fire to renew their growth, the intolerant hardwoods die and the normal conversion to a white spruce forest takes place on many sites. Concurrently the humus layer thickens as needles, twigs, cones and tree trunks fall, and although rate of accumulation (and of decomposition) is related to moistness, coolness, nutrients, etc., the composition of the accumulating surface humus is largely independent of site. Whether the underlying soil is fresh, moist or very moist, the debris on its surface develops a sameness of character, provided that the appropriate cover has been maintained for a sufficiently long period. This is doubtless the key to the formation of the same forest undergrowth on many different sites, and it is a good example of the reaction of dominant plants on initially different habitats to finally produce a similar degree of mesophytism on all.

In Table XXIII a summary of the species composition in eight stands of white spruce, each showing the characteristic "feather moss" floor, is presented. The stands were mature and appeared to be very similar, although soil examinations indicated that the physiographic site range was from fresh to very moist. This forest type has been named Picea/Hylocomium-Viola-Trientalis, as Viola renifolia and to a lesser extent Trientalis borealis are characteristically present in the Hylocomium mat.

Referring to the "Moss spp." listed with a constance of 50 per cent in Table XXIII it should be explained that the richness of the moss, lichen, and liverwort flora in particular stands is directly related to the amount of decaying wood present. The larger mosses such as Hylocomium splendens, Calliergonella schreberi, Hypnum crista-castrensis and Dicranum rugosum are capable of growing on substrata other than rotting wood, but numerous smaller species are not. In the latter group some of the commonest species collected on various plots during these studies were: Heterophyllium haldanianum, Dicranum flagellare, Pohlia nutans, Hypnum reptile, Oncophorus wahlenbergii, Plagiothecium striatellum and Ptilidium ciliare.

TABLE XXIII

THE COMPOSITION OF THE PICEA/HYLOCOMIUM-VIOLA-TRIENTALIS FOREST TYPE

Within each Constance class the species are arranged in decreasing order of importance as determined by quadrat studies of frequency supplemented by ocular estimates of cover-abundance.

Constance 100 and 88%

Hylocomium splendens
Linnaea borealis var. americana
Calliergonella schreberi
Rubus pubescens
Mitella nuda
Cornus canadensis
Aralia nudicaulis
Rosa acicularis
Ribes triste
Viola renifolia
Goodyera repens
Chamaenerion spicatum

Constance 75 and 62%

Viburnum edule
Maianthemum canadense var. interius
Mnium spp.
Dicranum rugosum
Pyrola virens
Petasites palmatus
Equisetum arvense
Galium septentrionale
Mertensia paniculata
Schizachne purpurascens
Pyrola secunda
Trientalis borealis
Pyrola asarifolia
Ribes hirtellum
Moneses uniflora

Constance 50 and 38%

Moss spp.--chiefly Heterophyllium haldanianum and Dicranum flagellare
Fragaria virginiana
Hypnum crista-castrensis
Galium triflorum
Symphoricarpos albus
Carex spp.
Eurhynchium diversifolium
Circaea alpina
Aster ciliolatus
Lonicera dioica var. glaucescens
Cornus stolonifera
Amelanchier alnifolia
Lonicera involucrata
Ribes glandulosum
Rubus idaeus
Bromus ciliatus
Lathyrus ochroleucus
Thuidium recognitum
Polytrichum juniperinum
Actaea rubra
Vicia americana
Peltigera spp.

Plus 60 species of Constance 25% and less.

Balsam fir is frequently an associate of the Picea/Hylocomium-Viola-Trientalis forest type. Its seedlings are able to establish themselves where those of white spruce cannot--on the shaded forest floor, among the mosses and low herbs (Fig. 25).

Fig. 25. Ground cover in an old Picea-Abies stand. Reserve, Saskatchewan. Note the seedlings of fir scattered through the mat of Hylocomium splendens, with Cornus canadensis, Viola renifolia, Rubus pubescens, Mitella nuda and other spp.

As openings develop in the forest canopy due to the death of overmature trees, the fir increases in abundance, and in very old stands it becomes the most prominent tree. Such old fir-spruce stands when seen from a distance have an uneven silhouette due to the appearance of the spire-like tops of scattered large spruce above the general fir canopy.

In Table XXIV the constance of minor species in twelve coniferous stands, each having balsam fir as an important constituent, is given.

TABLE XXIV

THE COMPOSITION OF THE PICEA-ABIES/HYLOCOMIUM-VIOLA-TRIENTALIS FOREST TYPE

Within each Constance class the species are arranged in decreasing order of importance as determined by quadrat studies of frequency supplemented by ocular estimates of cover-abundance.

<u>Constancy 100 to 80%</u>

Hylocomium splendens
Calliergonella schreberi
Linnaea borealis var. americana
Cornus canadensis
Mitella nuda

<u>Constancy 75 to 65%</u>

Aralia nudicaulis
Rubus pubescens
Petasites palmatus
Viola renifolia
Ribes triste
Equisetum arvense
Mertensia paniculata
Trientalis borealis
Maianthemum canadense var. interius

<u>Constancy 60 to 50%</u>

Circaea alpina
Rosa acicularis
Hypnum crista-castrensis
Viburnum edule
Galium triflorum

<u>Constancy 40 to 30%</u>

Rhytidiadelphus triquetrus
Mnium spp.
Schizachne purpurascens
Fragaria virginiana
Viola rugulosa
Symphoricarpos albus
Aster ciliolatus
Galium septentrionale
Ribes hirtellum
Polytrichum juniperinum
Pyrola virens
Carex spp.
Lonicera dioica var. glaucescens
Rubus idaeus
Lycopodium annotinum
Pyrola asarifolia
Pyrola secunda
Ribes lacustre
Actaea rubra
Ledum groenlandicum
Amelanchier alnifolia

Plus 56 additional species of Constancy 25% and less.

A comparison of the last two tables (Tables XXIII and XXIV) shows the similarity in species composition of the feather moss types of white spruce and of spruce-fir. The similarity also extends to stands of upland black spruce, a type that will be discussed later. With the exception of the mosses and *Peltigera* spp., the species of highest fidelity to these coniferous types are the following:

Viola renifolia	Moneses uniflora
Trientalis borealis	Pyrola virens
Goodyera repens	Vaccinium vitis-idaea var. minus
Linnaea borealis var. americana	Geocaulon lividum
Habenaria obtusata	Dryopteris disjuncta
Habenaria orbiculata	Lycopodium annotinum
Corallorhiza striata	Equisetum scirpoides

In all forests where the feather-moss carpet of *Hylocomium splendens*, *Calliergonella schreberi*, *Dicranum rugosum* and *Hypnum crista-castrensis* is prominent, the favourable conditions for its development seem to be provided by the inter-related complex of shade, surface coolness and absence of mechanical competition from broad-leaved trees, shrubs and herbs. That moistness of sub-stratum is not directly important is indicated by the formation of the feather moss layer under some closed coniferous stands on excessively drained soils. (Locally cooler-than-normal ecoclimate probably favours this development.) Also, studies of the ecology of some of the mosses (*Hylocomium splendens* by Tamm, 1953; *Polytrichum commune* and *Atrichum* *angustatum* by Anderson and Bourdeau, 1955) have shown that they apparently obtain their water needs from above (rain, fog and dew) rather than from below. Nevertheless soil moistness undoubtedly exerts an indirect beneficial effect through its cooling and humidifying influence on the eco-climate of the ground surface, and this is reflected in the particularly luxuriant development of the feather mosses under coniferous stands at the borders of swamps and on north-facing slopes.

An examination of the coniferous types which lack the feather moss stratum is instructive. Stands having an open structure, even though very old, maintain a shrub-and-herb minor vegetation and show no tendencies to pass to the moss-and-low-herb type. Shrubs and tall herbs are probably unfavourable to the development of the moss stratum for the same reason that hardwood trees are unfavourable, i.e., because of the smothering effect of their annual leaf fall.

One densely stocked, mature white spruce stand which appeared to have all the necessary qualifications for a feather moss floor, namely, shade and moistness, was found to have instead a dense herbaceous ground-cover. This must have stemmed from fertility of substratum--at that particular place a calcareous degrading meadow soil--and it seems probable that the moss floor will develop sooner on nutrient-poor than on nutrient-rich soils, other things being equal. The inference has previously been made that this is one reason for the rarity of the feather moss type of spruce stand on the relatively fertile, fresh, moderately calcareous soils. The feather mosses are also absent in over-dense stands, and instances have been seen where nothing but a needle floor existed beneath mature white spruce. The shade and the needle fall of thickets of balsam fir are also unfavourable, and vigorous regeneration of fir is usually accompanied by a bare needle floor. Occasional patches of mature fir have been found with sufficient density to maintain the needle floor, but it is more usual to find the typical moss mat under fir as under spruce.

It follows from the foregoing that the feather moss floor under spruce or spruce-fir requires a particular history of stand development for its genesis, and the maintenance of a certain stand cover and composition for its continued existence. The feather moss type is therefore a developmental stage, although one which appears to have "climax" attributes due to its recognizability and to its duration and stability relative to earlier stages (e.g., to the poplar-spruce stage). Inevitably however the forest canopy opens, and this is fatal to the characteristic ground flora as increased light allows the development of shrubs and herbs with which the feather mosses cannot co-exist. The moss floor may not be restored for a long time, depending on how rapidly balsam fir and spruce invade the openings--the former species usually forming thickets on the decomposing humus, and the latter appearing as scattered single stems on decayed logs and stumps (Fig. 26).

Fig. 26. Uneven-aged Picea-Abies forest, Riding Mountain National Park, Manitoba. A feather moss (closed) type in the background and a shrub-herb (Rubus idaeus-Chamaenerion spicatum) stand opening in the foreground. Note the thicket of fir regeneration behind the shovel.

The final stage or steady state of the vegetation therefore appears to embrace a mosaic of patches which alternate in time and place until fire intervenes. The patches are: spruce and fir with a feather moss floor, fir with or without a feather moss floor, and openings dominated either by brambles (chiefly Rubus idaeus and

Ribes spp.) or by fir regeneration. Such a vegetation, the Abies-Picea/Hylocomium-Rubus forest type, is pictured in Fig. 27.

Fig. 27. An old stand of Abies-Picea showing a mosaic of vegetational patches. Torch River Forest Reserve, Saskatchewan.
Note the fir regeneration (at left), and Rubus idaeus in stand openings (centre right). In the left background there is a closed-forest feather moss type.

The feather moss-dominated vegetation of the closed coniferous stands or patches has been previously discussed. To complete the picture, an example of the vegetation of the open patches which develop in overmature coniferous forests is shown in Table XXV.

TABLE XXV

DESCRIPTION OF AN OVERMATURE, OPEN STAND OF ABIES-PICEA ON A MOIST TO VERY MOIST SITE

White spruce-balsam fir - Very moist, shrub and herb type.
Madge Lake, Saskatchewan.
Physiographic site: 4 : 5-6 : 5.
Soil: A grey-black profile on moderately calcareous, stony clay-loam till.

Dominant trees: Uneven-aged _Abies balsamea_ and _Picea glauca_ in pure patches and intermixed. Many stand openings with much decayed wood (logs and stumps) on the ground.

Tree regeneration: Thickets of _Abies balsamea_ regeneration here and there. Scattered seedlings of _Picea glauca_ rooted in decayed wood.

Minor species: Dense tangles of brambles, chiefly _Rubus idaeus_ and _Ribes hirtellum_, also some pure patches of fern (_Pteretis pensylvanica_ and _Athyrium filix-femina_).

Species are listed below in decreasing order of abundance, based on ocular estimates.

Abundant:	Rubus idaeus	Impatiens capensis
	Ribes hirtellum	
Common:	Athyrium filix-femina var. michauxii	Circaea alpina
	Mertensia paniculata	Cornus canadensis
Occasional to Rare:		
	Rosa acicularis	Calamagrostis canadensis
	Viburnum edule	Ribes glandulosum
	Urtica gracilis	Aralia nudicaulis
	Viola renifolia	Carex sp.
	Galium septentrionale	Cinna latifolia
	Galium triflorum	Viola rugulosa
	Mitella nuda	Fragaria virginiana
	Actaea rubra	Dryopteris disjuncta
	Stachys palustris	Dryopteris spinulosa
	Cornus stolonifera	Mnium sp.
	Agropyron subsecundum	Thuidium recognitum
	Sorbus decora	Polytrichum juniperinum
	Pteretis pensylvanica	

Other communities and successional tendencies

Some examples which illustrate the variability in forest communities of the moist and very moist series will now be mentioned.

Mature and overmature undisturbed stands of white spruce were examined at Dore Lake, Saskatchewan. The trees were large, frequently two feet in diameter at breast height and 100 to 110 feet tall, and as old as 180 years. Development had been through the usual mixedwood stage, evidence of which could be seen in the numerous poplar snags scattered through the stands. There were indications that balsam fir was increasing, and young growth of this species was becoming prominent in some places under the spruce.

Apparently there is no *Corylus cornuta* in the Dore Lake area and the absence of this shrub from all cover-types is a striking feature to one familiar with the forests of the Cretaceous highlands. Instead, *Viburnum edule*, *Cornus stolonifera*, *Alnus rugosa* and *Ribes* spp.--indicative of moist to very moist soils--were prevalent. In most of the stands which were examined the undergrowth was dominated by herbs, and the feather mosses, although present, nowhere formed a continuous carpet.

The soils had been formed in what appeared to be a weakly calcareous, stony ablation moraine over a compacted, tight lodgement till. Conditions of slow drainage associated with the underlying till resulted in conditions of excess moisture as indicated by soil colouration and composition of minor vegetation.

In Table XXVI a summary of the vegetation in nine stands of mature and overmature spruce at Dore Lake is given. All stands were moderately dense, and most of them contained a small component of balsam fir. It proved difficult to select species of the ground flora that could be used to characterize moist forests of spruce or spruce-poplar. The three species that have been tentatively selected to describe these types are Mitella nuda, Petasites palmatus and Mertensia paniculata.

The composition of the vegetation in these stands at Dore Lake is remarkably similar to that reported by Moss (1953) for a white spruce stand at Lesser Slave Lake in Alberta.

A mature spruce, fir and poplar stand in the Torch River Forest Reserve is next described (Table XXVII).

The similarity of this stand to the Dore Lake forests is apparent from a comparison of Tables XXVI and XXVII. The trees in both forests were very large, probably due to the open stand structure imposed by a prior "mixed-wood" stage, and this same stand structure appeared to provide the possibility for self perpetuation of the type.

TABLE XXVI

THE COMPOSITION OF THE PICEA/MITELLA-PETASITES-MERTENSIA FOREST TYPE

Within Constancy classes the species are arranged in decreasing order of importance as determined by ocular estimate of cover-abundance in the nine stands.

<u>Constance 100 and 88%</u>

Aralia nudicaulis
Cornus canadensis
Linnaea borealis var. americana
Mitella nuda
Rosa acicularis
Rubus pubescens
Viburnum edule
Mertensia paniculata
Petasites palmatus
Maianthemum canadense var. interius
Ribes hirtellum
Ribes triste
Galium septentrionale
Viola renifolia
Lonicera dioica var. glaucescens

<u>Constance 77 and 66%</u>

Cornus stolonifera
Pyrola secunda
Calliergonella schreberi
Hylocomium splendens
Equisetum arvense
Rubus idaeus
Pyrola asarifolia
Actaea rubra
Galium triflorum
Amelanchier alnifolia
Mnium spp.

<u>Constance 55 and 44%</u>

Elymus innovatus
Trientalis borealis
Ribes glandulosum
Lathyrus ochroleucus
Dicranum flagellare
Eurhynchium strigosum
Fragaria virginiana
Ribes lacustre
Lycopodium annotinum
Alnus rugosa
Equisetum sylvaticum
Calamagrostis canadensis
Aster ciliolatus
Hypnum crista-castrensis
Brachythecium salebrosum

Table XXVI cont.

Constance 33, 22 and 11%

Chamaenerion spicatum	Pylaisia polyantha
Dryopteris disjuncta	Polytrichum juniperinum
Circaea alpina	Carex spp.
Dryopteris spinulosa	Ledum groenlandicum
Pohlia nutans	Symphoricarpos albus
Eurhynchium diversifolium	Shepherdia canadensis
Drepanocladus uncinatus	Salix bebbiana
Rhytidiadelphus triquetrus	Anemone canadensis
Alnus crispa	Geocaulon lividum
Achillea millefolium	Equisetum scirpoides
Dicranum rugosum	Heracleum maximum
Lonicera involucrata	Goodyera repens
Sorbus decora	Geum macrophyllum
Impatiens capensis	Pyrola virens
Urtica gracilis	Vicia americana

TABLE XXVII

DESCRIPTION OF A MATURE STAND OF PICEA/MITELLA-PETASITES

White spruce - Moist, herb and moss type.
Plot No. 132, Torch River Forest Reserve, Saskatchewan.
Physiographic site: 4 : 5 : 5.
Soil: A deep grey-black profile developed on weakly calcareous clay-loam till.

Dominant trees: *Picea glauca* of all sizes, 1 to 30 inches in diameter at breast height, up to 120 feet tall, 175 years old.
Scattered *Picea mariana* (3 to 12 inches D.B.H.), *Abies balsamea* (up to 18 inches D.B.H.), *Populus balsamifera* and *Populus tremuloides* (up to 20 inches D.B.H.).

Tree regeneration: Abundant seedlings and saplings of *Abies balsamea* on the forest floor; scattered seedlings and saplings of *Picea glauca* on decayed wood.

Minor species: Species are listed in order of decreasing frequency and cover-abundance within each frequency class, as determined by the study of 20 milacre quadrats.

Frequency 100-85%

Cornus canadensis
Petasites palmatus
Aralia nudicaulis
Viburnum edule
Rubus pubescens
Mitella nuda

Frequency 80-65%

Hylocomium splendens
Calamagrostis canadensis
Abies balsamea seedlings
Linnaea borealis var. americana
Lycopodium annotinum
Galium septentrionale
Lathyrus ochroleucus

Frequency 60-45%

Fragaria virginiana
Ribes sp. (triste?)
Maianthemum canadense var. interius
Viola renifolia
Mertensia paniculata
Rosa acicularis

Table XXVII cont.

Frequency 40-25%

Equisetum arvense	Rubus idaeus
Calliergonella schreberi	Chamaenerion spicatum
Picea glauca seedlings	Ribes hirtellum
Galium triflorum	Lonicera dioica var. glaucescens
Symphoricarpos albus	Pyrola asarifolia

Frequency 20-5%

Oryzopsis asperifolia	Corylus cornuta
Schizachne purpurascens	Elymus innovatus
Aster ciliolatus	Equisetum sylvaticum
Actaea rubra	Hieracium canadense
Pyrola secunda	Trientalis borealis
Amelanchier alnifolia	Ledum groenlandicum
Achillea millefolium	Carex sp.
Equisetum scirpoides	Vaccinium myrtilloides
Vicia americana	Viola sp.
	Solidago hispida

On the northern and eastern sides of the Porcupine and Pasquia Hills numerous small streams descending from the swampy uplands are responsible for moist to very moist slope sites. Here a mixed forest of poplar, spruce and fir is found, with considerable paper birch component (the "birch belt"). The excellence of these sites is reflected in a tall, vigorous shrub vegetation of Acer spicatum, Corylus cornuta and Cornus stolonifera, which in some places forms a nearly impenetrable tangle. Areas of seepage and surface flooding are recognized by abundant Equisetum species in the herbaceous stratum. Unfortunately no plot studies of the type were made, but in Fig. 28 the tree composition of a mature spruce-birch forest on the north side of the Pasquia Hills is shown. Only the trees 4 inches D.B.H. and larger were tallied, but the diameter distributions of the four species indicate a probable trend toward a coniferous (fir-spruce) type. However, the birch may be able to maintain itself on the very moist slopes, and the possibility of a relatively stable mixed forest on these sites cannot be dismissed.

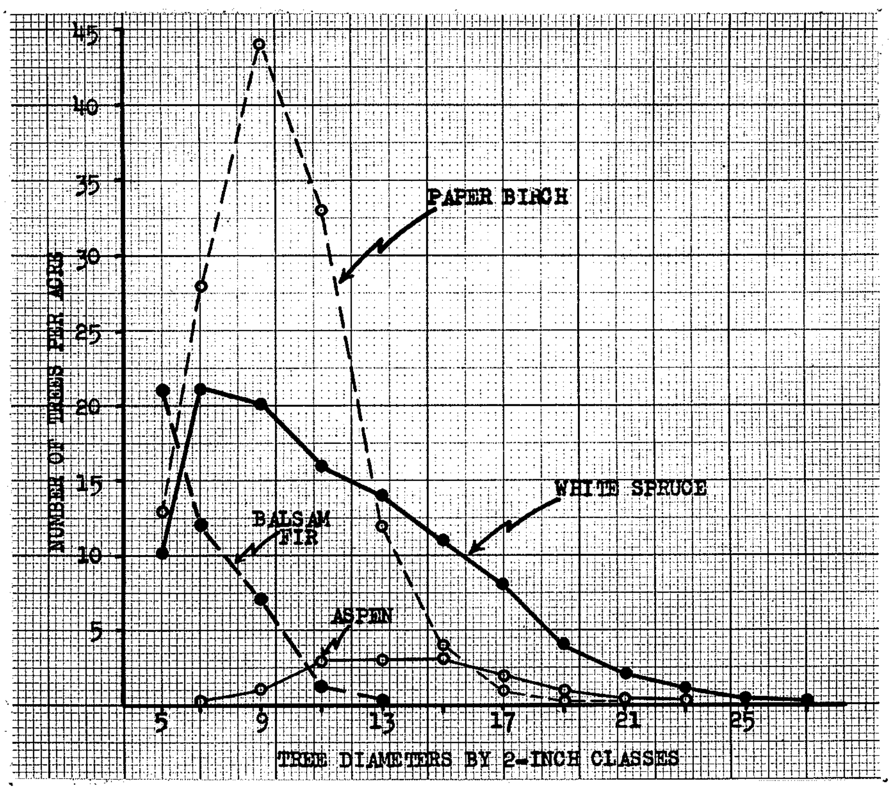


Fig. 28. The diameter distribution of tree species in a mature mixed forest on a very moist site. Pasquia Hills, Saskatchewan. The data are from a tally of 18 acres of the type. (Note: These graphs are not regression lines.)

Several mature forests on alluvial deposits were examined north and east of Hudson Bay, Saskatchewan . This area is a part of the Manitoba lowlands and was at one time covered by Glacial Lake Agassiz. On the flanks of the Cretaceous Hills (Pasquia and Porcupine Hills) the former levels of the post-glacial lake are marked by a series of sandy beach ridges, and streams descending from the uplands dissect them at right angles. A fertile strip of calcareous alluvium has been deposited along the sides of the streams and this provides a favourable site for the growth of poplar and spruce. Within the rectangular areas formed by the beach lines and the intersecting streams, the swampy land is vegetated by sedges and rushes, black spruce, or wet variants of the spruce-poplar forest.

Along the lower sides of the beach ridges and on the fertile alluvium (both very moist sites) conditions are ideal for the luxuriant growth of tall shrubs, particularly *Acer spicatum* and *Cornus stolonifera*. Even when spruce invades, the shrub stratum seems to be persistent.
Table XXVIII is based on two mature stands of white spruce and balsam fir examined on the east side of the Pasquia Hills.

TABLE XXVIII

DESCRIPTION OF TWO MATURE PICEA-ABIES STANDS ON MOIST ALLUVIUM

White spruce and fir - Moist, tall shrub type.
Plot Nos. 530, 531A, Pasquia Reserve, Saskatchewan.
Physiographic site: 4 : 5 : 4.
Soil: Grey-black profile on calcareous silty alluvium over sandy beach deposits.

Dominant trees: Picea glauca, uneven-aged in patches with some stems about 220 years, 148 years and 115 years old. Individual stems up to 26 inches D.B.H. and 119 feet tall.
Abies balsamea up to 16 inches D.B.H., 120 years old and 70 feet tall.
Scattered Betula papyrifera 4 to 13 inches D.B.H., and Populus balsamifera up to 22 inches D.B.H.

Tree regeneration: Dense thickets of Abies balsamea seedlings and saplings covering the ground in stand openings. No spruce.

Minor vegetation: A 60 to 80 per cent cover of Acer spicatum 6 to 8 feet tall, with low herbs beneath. Mosses associated with the coniferous patches.

Very abundant: Acer spicatum

Abundant:

Circaea alpina
Hylocomium splendens
Mitella nuda
Rubus pubescens
Cornus canadensis
Linnaea borealis var. americana
Aralia nudicaulis

Common:

Calliergonella schreberi
Mnium sp.
Rhytidiadelphus triquetrus
Rubus idaeus
Ribes triste
Ribes lacustre
Viola renifolia
Galium septentrionale
Mertensia paniculata
Maianthemum canadense var. interius
Trientalis borealis
Equisetum arvense
Corylus cornuta

Table XXVIII cont.

Occasional:

Hypnum crista-castrensis	Pyrola asarifolia
Eurhynchium diversifolium	Rosa acicularis
Dryopteris disjuncta	Sorbus decora
Goodyera repens	Lathyrus ochroleucus
Equisetum sylvaticum	Aster ciliolatus
Moneses uniflora	Petasites palmatus
Amelanchier alnifolia	Viola rugulosa
Symphoricarpos albus	Viburnum edule
Actaea rubra	Ribes hirtellum
Hieracium canadense	Achillea sibirica
Schizachne purpurascens	Rhamnus alnifolia
Pyrola secunda	Lonicera oblongifolia

Similar stands were found near Armit, on the north side of the Porcupine Hills. There large scattered spruce grew on very moist, strongly calcareous alluvium, with a tangled shrub understory of *Acer spicatum* and *Cornus stolonifera* six to eight feet tall, and an herb stratum in which *Mertensia paniculata*, *Petasites palmatus*, *Thalictrum dasycarpum*, *Rubus pubescens*, *Equisetum arvense*, *Pteretis pensylvanica*, *Viola rugulosa* and *Aralia nudicaulis* were prominent. In several stands the tall shrubs were rare and only tall herbs covered the ground under the spruce. It was interesting to note that several species usually associated with mature spruce forests were not present, namely *Cornus canadensis*, *Linnaea borealis* var. *americana* and *Maianthemum canadense* var. *interius*. Periodic flooding rather than the excess of lime carbonate in the soil may explain their absence. In any event there were no indications that natural succession would lead to a low herb and feather moss type on these rich sites.

In the same district, excellent aspen stands occupied sites similar to the above where spruce had not yet invaded or was only in the early stages of invasion. The tall shrubs showed phenomenal development under the aspen, reaching heights of ten to fifteen feet in some places. In Table XXIX the common species in one such aspen stand are shown; those marked with an asterisk were also present under spruce on adjacent sites.

TABLE XXIX

MINOR SPECIES ASSOCIATED WITH POPULUS TREMULOIDES ON A RICH, VERY MOIST ALLUVIAL SITE

Shrubs

x Cornus stolonifera
Acer spicatum
x Prunus virginiana
Amelanchier alnifolia
Corylus cornuta
Viburnum trilobum
Alnus rugosa
x Acer negundo
Rubus idaeus
x Ribes triste
Ribes hirtellum
Rosa acicularis

Tall and Medium Herbs

Calamagrostis canadensis
Cinna latifolia
x Anemone canadensis
x Solidago gigantea
x Aralia nudicaulis
Disporum trachycarpum
x Trillium cernuum
x Equisetum arvense
x Mertensia paniculata
x Smilacina stellata

Low Herbs

x Galium triflorum
x Circaea alpina
x Rubus pubescens
x Mitella nuda
x Fragaria virginiana
Anemone quinquefolia
Pyrola secunda

The presence of Populus tremuloides rather than Populus balsamifera in association with the undergrowth just listed is at first sight surprising. The latter species is usually considered the characteristic tree of very moist alluvium. During these studies the writer encountered very few pure balsam poplar stands, and it was noticeable that aspen often occupied sites which appeared to be better suited to the former species. Alternatively it was not uncommon to find stands dominated by balsam poplar on fresh, upland sites. The alluvial sites north of the Pasquia Hills where balsam poplar grows to a very large size were not examined in this study.

No matter which species dominates on moist to very moist sites, whether balsam poplar or aspen. the accompanying minor vegetation is much the same. In the eastern area referred to above, Acer spicatum was prominent on moist till slopes and alluvium. But throughout the study area as a whole, Cornus stolonifera was the more characteristic species on moist and very moist sites. In Table XXX a summary of the constance of minor species in ten poplar stands, each with Cornus stolonifera dominating the undergrowth, is presented. As Equisetum spp. are frequently present with the Cornus stolonifera, the forest type is called Populus/Cornus-Equisetum.

TABLE XXX

THE COMPOSITION OF THE POPULUS/CORNUS-EQUISETUM FOREST TYPE

Within Constance classes the species are arranged in decreasing order of importance as determined by quadrat studies of frequency supplemented by ocular estimates of cover-abundance.

<u>Constance 100 and 90%</u>

Cornus stolonifera
Equisetum arvense
Fragaria virginiana
Rubus pubescens
Mertensia paniculata
Petasites palmatus
Mitella nuda
Ribes triste
Galium triflorum
Symphoricarpos albus

<u>Constance 80 and 70%</u>

Aralia nudicaulis
Rubus idaeus
Aster ciliolatus
Maianthemum canadense var. interius
Smilacina stellata
Bromus ciliatus
Viola rugulosa
Anemone canadensis
Ribes hirtellum
Viburnum edule
Pyrola asarifolia
Actaea rubra
Amelanchier alnifolia
Calamagrostis canadensis

<u>Constance 60 and 50%</u>

Rosa acicularis
Cornus canadensis
Corylus cornuta
Galium septentrionale
Linnaea borealis var. americana
Carex sp.
Chamaenerion spicatum
Prunus virginiana
Vicia americana
Agropyron subsecundum
Circaea alpina
Stachys palustris
Lonicera dioica var. glaucescens
Heracleum maximum
Viola renifolia
Schizachne purpurascens

Plus 63 additional species of Constance 40% and less.

In addition to <u>Cornus stolonifera</u> there is another species which locally at least dominates the ground flora on moist to very moist sites, giving a distinctive appearance to many stands of poplar and poplar-spruce. It is the tall grass, <u>Calamagrostis canadensis</u>. Following fires or logging this species often spreads rapidly forming a meadowland type of vegetation which persist even after the forest has been re-established (Fig. 29).

Fig. 29. An open <u>Populus-Picea</u> forest with abundant <u>Calamagrostis canadensis</u> undergrowth. Riding Mountain National Park, Manitoba. Note <u>Salix</u> sp. at left.

On the Riding Mountain, numerous examples of the Calamagrostis canadensis type of forest have been examined, and there is apparently little difference in the composition of the vegetation whether associated with aspen, balsam poplar or open stands of white spruce. In Table XXXI a summary of the species composition in eight stands is presented. The type has been designated as Populus (or Populus-Picea)/Calamagrostis-Aster-Anemone, the latter two names from Aster umbellatus var. pubens and Anemone canadensis.

The soil profile associated with a stand of Picea-Populus/Calamagrostis is shown in Fig. 30. The blackening of the surface horizon (A_1) is doubtless due to the Calamagrostis roots.

TABLE XXXI

THE COMPOSITION OF THE POPULUS-PICEA/CALAMAGROSTIS-ASTER ANEMONE FOREST TYPE

Within each Constance class, species are arranged in order of decreasing importance as determined by a study of 10 to 20 milacre quadrats in each of eight stands.

Constance 100 and 88%

Calamagrostis canadensis
Galium septentrionale
Rosa acicularis
Mertensia paniculata
Thalictrum venulosum
Fragaria virginiana
Aster ciliolatus
Rubus pubescens
Vicia americana
Maianthemum canadense var. interius
Petasites palmatus
Carex spp.
Aster umbellatus var. pubens
Smilacina stellata
Ribes hirtellum
Rubus idaeus
Lathyrus ochroleucus
Heracleum maximum
Solidago lepida
Symphoricarpos albus
Chamaenerion spicatum
Sanicula marilandica
Amelanchier alnifolia
Anemone canadensis
Achillea millefolium
Pyrola asarifolia
Lonicera dioica var. glaucescens
Taraxacum sp.

Constance 75 and 62%

Corylus cornuta
Oryzopsis asperifolia
Viola rugulosa
Aralia nudicaulis
Elymus innovatus
Agastache foeniculum
Salix bebbiana
Cornus canadensis
Schizachne purpurascens
Comandra pallida

Constance 50 and 38%

Equisetum arvense
Petasites sagittatus
Petasites vitifolius
Stachys palustris
Viola sp.
Galium triflorum
Mentha arvensis
Moehringia lateriflora
Mnium spp.
Prenanthes alba
Hieracium canadense
Lysimachia ciliata
Zizia aptera
Aster puniceus
Bromus ciliatus
Actaea rubra
Cirsium muticum
Mitella nuda
Thuidium recognitum
Cornus stolonifera
Ribes triste
Viburnum edule
Lilium umbellatum

Plus 37 additional species of Constance 25 and 12%.

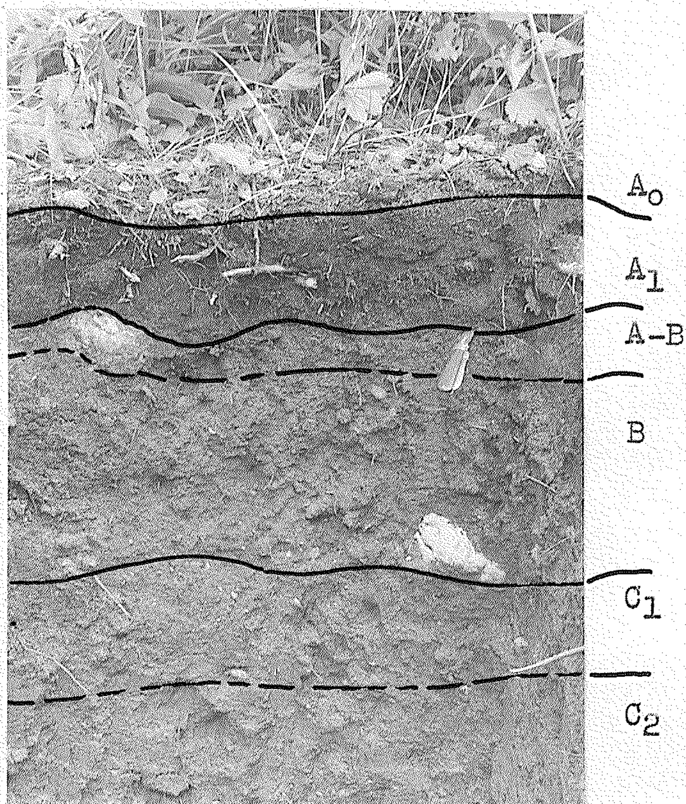


Fig. 30. Soil profile under a moist to very moist Picea-Populus/Calamagrostis-Aster-Anemone community. Riding Mountain National Park, Manitoba.

PROFILE DESCRIPTION

A_o horizon: 2-3" dark brown humus passing gradually into the A_1 (mull-like).

A_1 horizon: 3-4" black granular clay loam

A-B transition: 2" grey, granular clay.

B horizon: 12" dark grey to greyish brown, faintly mottled clay, cloddy structure. Free lime carbonate at 20" depth.

C_1 horizon: 10" mottled greyish brown wet silty clay, granular.

C_2 horizon: Mottled rusty brown and grey, stony silty clay. Moderately calcareous.

At no place in the *Calamagrostis* type, even where the spruce has formed a close stand, has there been observed any signs of a transition to the feather moss type, and the reason may possibly be traced to the underlying heavy-textured soils which are subject to surface flooding in the spring.

Some of the results of severe fire on moist and very moist sites were observed in the vicinity of Reserve and Bertwell, in the Porcupine Forest Reserve of Saskatchewan. Frequent fires have destroyed stands of various ages and compositions in this area, producing many different types which could be related in successional series. In 1937 the summer was so dry that the deep humus layers which had developed on the normally moist to very moist sites were burned away entirely, exposing mineral soil. Twelve years later, in 1949, studies of several such areas showed the presence of scattered young aspen, abundant *Salix bebbiana* and *S. discolor*, and an open herbaceous vegetation in which *Taraxacum* sp., *Vicia americana*, *Epilobium angustifolium* and *Aster ciliolatus* were prominent. Many white spruce seedlings 4 to 20 inches tall were growing in the mineral soil. In 1954 the minor vegetation had consolidated and completely covered the ground, and *Vicia americana* had assumed the position of most abundant herb. Meanwhile the spruce had grown rapidly, and it seemed probable that the future development would be to a feather moss spruce type via an herbaceous type of spruce-poplar, the entire process probably requiring about 80 years more for its completion.

A list of species pioneering on mineral soil on fresh sites has been previously given on pages 137 and 138. Based on a study of ten separate areas, the following species can be listed as characteristic of clean-burned areas on moist to very moist sites:

Salix bebbiana	Lysimachia ciliata
Salix discolor	Anemone canadensis
Salix petiolaris	Lathyrus palustris
Calamagrostis canadensis	Equisetum arvense
Deschampsia caespitosa	Potentilla norvegica
Agrostis scabra	Habenaria hyperborea
Erigeron philadelphicus	Parnassia palustris
Senecio pauperculus	Carex aurea
Cirsium muticum	Funaria hygrometrica
Achillea sibirica	Marchantia spp.
Solidago lepida	

Wherever fire had only burned the upper part of the humus layer, aspen and balsam poplar stands were found with their usual mesophytic undergrowth. The primary shrub in all cases was <u>Cornus</u> <u>stolonifera</u> although Viburum edule was abundant in some stands. The abundance of spruce seedlings ranged from none to many in different stands, and the entire range of forest communities from pure poplar, to mixed spruce-poplar, to spruce with scattered poplar, could be seen in the formative stages.

A last community to be described on moist and very moist sites is the feather moss black spruce type. A"fresh" variant has already been described (pp. 168 and 169) on weakly calcareous soils, but the moister community on level clay uplands or at the borders of bogs and muskegs is of commoner occurrence. Apparently it is a fire type, and there is ample evidence that these even-aged stands usually have their genesis immediately following severe ground fires.

The distribution of the type is significant. Relative to the incidence of coniferous forests dominated by white spruce, it increases in frequency northward, and on the shallow tills and lacustrine deposits of the Precambrian Shield area it is a major forest type. The latitudinal increase is paralleled by an altitudinal increase as well, and on the highest elevations of the Cretaceous Hills the upland black spruce forest is prominent. The relationship here may be topographic as well as climatic, for the tops of the hills are nearly level, hence poorly drained. A picture of a typical stand is shown in Fig. 31, and in Table XXXII a stand description is given.

Note that the soil was frozen under this stand in July, and thus a high water table was maintained into mid-summer. Reference to frozen layers in the soil of various forest stands, and to the significance of the phenomenon to forest sites, has been made by Rowe (1953).

Fig. 31. A mature stand of Picea mariana/Hylocomium on a very moist upland site. Duck Mountain Forest Reserve, Manitoba.

The increased importance of the Picea mariana/Hylocomium-Calliergonella forest type northward and at higher altitudes suggests the effect of climatic conditions in its genesis. The known frost resistance of the species possibly confers on it an advantage over other trees on the cooler sites. Certainly in the normal and warmer-than-normal ecoclimates (south slopes, for example) of the southern coniferous forest region black spruce does not establish itself in competition with white spruce, even where moisture conditions are favourable. The problem needs further study however, particularly in relation to the relative incidence of fires in areas where the type occurs as compared to those where it is absent.

TABLE XXXII

DESCRIPTION OF THE PICEA MARIANA/HYLOCOMIUM-CALLIERGONELLA STAND ON A VERY MOIST SITE

Black spruce.- Very moist, feather moss type.
Plot No. 11, Duck Mountain, Manitoba.
Physiographic site: 6 : 6 : 4.
Soil: A Grey-black profile under a thick humus layer, developed on a moderately calcareous silt loam. The soil frozen at 18" depth on July 26, 1954.

Dominant tree: Picea mariana in an almost pure stand, the stems densely crowded, 2 to 8 inches D.B.H. and up to 40 feet tall at 60 years of age.
Scattered Picea glauca, Pinus banksiana, Abies balsamea and Populus spp.

Minor species: Feather mosses form a continuous ground cover. Few shrubs and herbs.

Very abundant:

Hylocomium splendens	Calliergonella schreberi
	Hypnum crista-castrensis

Occasional:

Mitella nuda	Linnaea borealis var. americana
Lycopodium annotinum	Mertensia paniculata
Pyrola secunda	Trientalis borealis
	Rubus pubescens

Rare:

Moneses uniflora	Cornus canadensis
Equisetum scirpoides	Petasites palmatus
Corallorhiza trifida	Dicranum rugosum
Aquilegia brevistyla	Lonicera villosa var. solonis
Rosa acicularis	Ranunculus lapponicus
Viburnum edule	Viola renifolia
Ledum groenlandicum	Listera cordata
Ribes triste	

The feather moss *Picea mariana* community very often develops through a pine or a pine-spruce stage. The gradual replacement of pine stands by the black spruce can be observed on many cool moist sites, particularly to the northward although also quite commonly on the highest parts of the uplands throughout the area. The type does not appear to be self-perpetuating, at least in any immediate sense, and in overmaturity, as the trees die, it tends toward the open, brushy *Rubus idaeus* type. At the latter stage a few examples of invasion by scattered fir and white spruce have been observed, but this may be of only local significance.

Wet Series

The wet series includes all forest types developed on sites which at some prior time were too wet for tree growth. In other words it comprises the later stages of the hydrosere--the treed stages of the succession which takes place as streams and ponds are slowly filled under the influence of vegetation. The soils of the wet series are therefore highly organic in nature, having been built up primarily from plant remains.

It is usually assumed that the observed vegetational zones at the edge of a pond or stream correspond also to developmental stages in time. If this be true, and it is a logical assumption, then indications are that the successional stages through which vegetation proceeds in transforming areas of water to organic soil are many and varied, for numerous different zonation patterns can be found. Depth of water, currents, wave action, nutrient regime, aspect and exposure of the shore, biotic influences, available flora, and many other factors influence the formation and sequence of development of hydrophytic communities, hence the diversity of the site-vegetation units which often appear in the vicinity of one small lake or stream.

Plant succession in the wet series culminates in forests dominated by white spruce, black spruce or tamarack, with small amounts of paper birch, aspen, balsam poplar, and balsam fir. Although the reasons for the differences in the successional series are obscure, it seems that the deposits frequently formed in shallow drainage channels, ponds or lakes, which comprise the group of hydromorphic soils called "fen", "wiesenboden" and "muck", are more favourable for the ultimate invasion of white spruce than of black spruce, while the deep "raw" peats such as result primarily from the accumulation of moss remains are more favourable for the latter than for the former species. Tamarack apparently is tolerant of either site and can be found intermingled in, or as a zone on the wetter side of, both white and black spruce stands.

White Spruce Forests

Throughout the entire area covered by these studies, dense stands of white spruce frequently occur as patches and strips along the edges of ponds and creeks on meadow, fen and muck soils. On the east side of the Porcupine Hills Forest Reserve, extensive areas of the "swamp spruce" type form a mosaic with sedge and grass meadows on lacustrine clay flats, and here a study of the vegetation and its successional relationships was made.

A typical stand is shown in Fig. 32 and the description of a similar stand is given in Table XXXIII.

Fig. 32. A stand of "swamp spruce", *Picea glauca*, at the edge of a *Carex* meadow. Reserve, Saskatchewan.

TABLE XXXIII

DESCRIPTION OF A STAND OF "SWAMP SPRUCE", PICEA GLAUCA

White spruce - Herb and moss type.
Plot No. 523, Bertwell, Saskatchewan.
Physiographic site: 6 : 7 : 5.
Soil: A black peaty meadow profile developed on modified, calcareous, silty clay.

Dominant species: Picea glauca, dense stand with stems 1 to 15 inches D.B.H., up to 70 feet tall at 115 years of age. A few scattered stems of Populus tremuloides. No tree regeneration.

Minor vegetation: Dominated by Equisetum arvense about one foot tall, like a green haze over the forest floor, and an almost continuous moss stratum of Hylocomium-Calliergonella.

Very abundant: Equisetum arvense

Abundant: Linnaea borealis var. americana
Hylocomium splendens
Calliergonella schreberi
Mitella nuda

Common:
Symphoricarpos albus
Lonicera dioica var. glaucescens
Rosa acicularis
Cornus stolonifera
Viburnum edule
Ledum groenlandicum
Ribes glandulosum
Ribes hudsonianum
Salix discolor
Lonicera involucrata
Betula glandulosa
Rhamnus alnifolia
Shepherdia canadensis
Agropyron subsecundum
Thalictrum venulosum
Aralia nudicaulis
Chamaenerion spicatum
Heracleum maximum
Petasites sagittatus
Mertensia paniculàta
Petasites vitifolius
Mentha arvensis
Habenaria orbiculata
Fragaria virginiana
Cornus canadensis
Goodyera repens
Maianthemum canadense var. interius
Pyrola asarifolia
Taraxacum sp.
Galium triflorum
Moneses uniflora
Rubus pubescens
Viola renifolia
Rhytidiadelphus triquetrus
Dicranum rugosum
Mnium sp.
Thuidium recognitum

Table XXXIII cont.

Occasional:

Halenia deflexa	Solidago lepida
Cypripedium calceolus var. pubescens	Spiraea alba
Galium septentrionale	Impatiens capensis
Smilacina stellata	Lathyrus palustris
Pyrola virens	Parnassia palustris var. neogaea
Anemone canadensis	Hypnum crista-castrensis
Cirsium muticum	Aulacomnium palustre

The undergrowth of the swamp border white spruce forests is distinctive chiefly because of the abundance of Equisetum species, especially Equisetum arvense (although E. sylvaticum, E. pratense and E. scirpoides are also important), in association with the moss and low herb flora.

Sufficient stands were seen with the same general composition to suggest that a recognizable forest type Picea/Equisetum-Hylocomium, can be defined. Table XXXIV gives a summary of the composition of ten stands of this type.

TABLE XXXIV

THE COMPOSITION OF THE PICEA/EQUISETUM-HYLOCOMIUM FOREST TYPE

Within each Constance class the species are arranged in order of decreasing importance, based on cover-abundance as determined by quadrat studies supplemented by ocular estimates.

Constance 100 and 90%

Equisetum arvense
Hylocomium splendens
Linnaea borealis var. americana
Rubus pubescens
Aralia nudicaulis
Galium triflorum
Rosa acicularis

Constance 80 and 70%

Mitella nuda
Cornus canadensis
Calliergonella schreberi
Viola renifolia
Ribes triste
Dicranum rugosum
Fragaria virginiana
Mertensia paniculata
Ribes hirtellum
Calamagrostis canadensis
Hypnum crista-castrensis
Viburnum edule
Lonicera dioica var. glaucescens
Moneses uniflora
Goodyera repens

Constance 60 and 50%

Mnium spp.
Aulacomnium palustre
Maianthemum canadense var. interius
Petasites palmatus
Ribes glandulosum
Rubus idaeus
Equisetum scirpoides
Chamaenerion spicatum
Symphoricarpos albus
Cornus stolonifera
Aster ciliolatus
Agropyron subsecundum
Rhytidiadelphus triquetrus
Pyrola virens
Smilacina stellata
Amelanchier alnifolia
Habenaria obtusata
Galium septentrionale

Table XXXIV cont.

Constance 40 and 30%

Carex sp.	Rhamnus alnifolia
Lycopodium annotinum	Bromus ciliatus
Pyrola secunda	Mentha arvensis
Ledum groenlandicum	Habenaria orbiculata
Circaea alpina	Achillea sibirica
Alnus rugosa	Aster puniceus
Petasites sagittatus	Actaea rubra
Petasites vitifolius	Pyrola asarifolia
Lonicera involucrata	Shepherdia canadensis
Trientalis borealis	Solidago lepida
Taraxacum sp.	Cirsium muticum

Plus 57 additional species of Constance 20 and 10%.

Numerous variants of the swamp-border spruce type were encountered, due presumably to such differences in local habitat as are caused by fluctuating water levels, thickness of organic soil, nutrient status of substratum, and density of tree cover. In most stands the _Equisetum_ component of the ground flora was consistently present and abundant, but the moss component, more sensitive to differences in site, was variable. _Hylocomium splendens_, the usual associate of _Equisetum arvense_, was replaced partly or entirely by _Climacium americanum_ or _Aulocomnium palustre_ on some of the wetter sites. In a few of the faster-growing stands _Mnium cuspidatum_ was the predominant moss and its abundance seemed to be paralleled by an increase in _Circaea alpina_. In these stands there were signs of periodic flooding of the surface and of a consequent accumulation of mineral matter in the organic soil.

Fig. 33 shows the ground cover in a stand opening of the Picea/Equisetum type where Mnium spp. are abundant rather than Hylocomium.

Fig. 33. The ground cover in an opening of the Picea/Equisetum type. Riding Mountain National Park, Manitoba. Note presence of Mertensia paniculata, Rubus idaeus and Ribes spp. with the Equisetum arvense.

On the drier side, there was evidence that with the accumulation of litter, and the gradual build up of the forest floor, the transition to a spruce and fir forest would take place. An example of a community which had reached this stage via a meadow stage is given in Table XXXV, while a soil profile illustrating the same succession is shown in Fig. 34.

TABLE XXXV

DESCRIPTION OF A PICEA-ABIES/EQUISETUM-HYLOCOMIUM FOREST STAND

White spruce and balsam fir - Wet, herb and moss type.
Plot No. 56, Reserve, Saskatchewan.
Physiographic site: 6 : 7 : 5.
Soil: Under a thick humus layer there is a shallow, black, meadow profile developed on highly calcareous, modified till.

Dominant trees: Closed stand of Picea glauca 3 to 20 inches D.B.H., up to 80 feet tall at 180 years of age. Abies balsamea very numerous in the 1- to 6-inch diameter classes, up to 10 inches D.B.H., with maximum height and age of 75 feet and 90 years.

Tree regeneration: Abundant seedlings and saplings of Abies balsamea, and scattered seedlings of Picea glauca, the latter invariably rooted in decayed wood. Considerable numbers of Betula papyrifera seedlings, also on decayed wood.

Minor vegetation: A continuous carpet of feather mosses, with Equisetum and low herbs prominent.

Within frequency classes the species are listed in order of importance based on cover-abundance in ten milacre quadrats.

Frequency 100 and 90%

Hylocomium splendens
Cornus canadensis
Equisetum arvense
Linnaea borealis var. americana
Calliergonella schreberi
Mitella nuda

Frequency 80 and 70%

Ribes triste
Aralia nudicaulis
Lycopodium annotinum
Carex sp.
Rubus pubescens
Viola renifolia

Frequency 60 and 50%

Betula papyrifera seedlings
Equisetum scirpoides

Table XXXV cont.

Frequency 40 and 30%

Alnus rugosa	Ledum groenlandicum
Rosa acicularis	Galium triflorum
Ribes glandulosum	Moneses uniflora
	Gaultheria hispidula

Frequency 20 and 10%

Circaea alpina	Sorbus decora
Pyrola virens	Rhytidiadelphus triquetrus
Trientalis borealis	Geocaulon lividum
Ribes hirtellum	Mertensia paniculata
Salix sp.	Petasites palmatus
Calamagrostis canadensis	Vaccinium vitis-idaea var. minus
Agropyron subsecundum	Dryopteris disjuncta
Dicranum rugosum	Thuidium recognitum
Aulacomnium palustre	Hypnum crista-castrensis
Goodyera repens	Aster puniceus
Habenaria obtusata	Cirsium muticum
Maianthemum canadense var. interius	Solidago lepida
Habenaria hyperborea	Corallorhiza trifida
Viburnum edule	Habenaria orbiculata

Successional Relationships

Swamp border stands of white spruce such as those just described have undoubtedly succeeded a wet meadow stage. The evidence is frequently preserved in the humus, in the form of abundant snail shells and the broad leaves of paludal plants. Present zonation of the vegetation suggests that one probable sequence is the following, from stage 1 to stage 6:

1. In open water, *Nuphar variegatum*, *Potamogeton* spp., *Lemna trisulca*, etc.

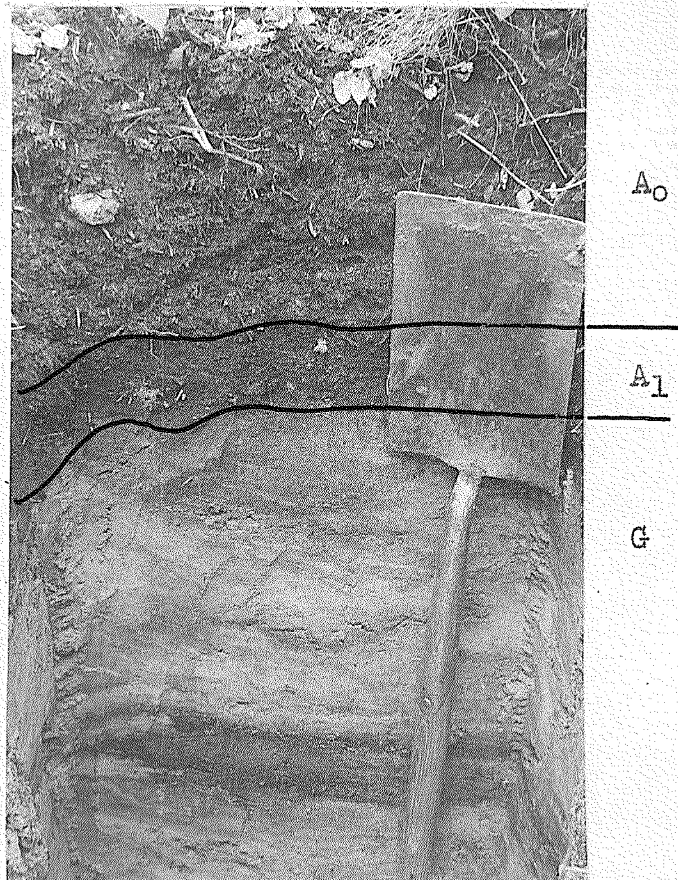


Fig. 34. Soil profile on a very moist to wet site under a Picea-Abies/Equisetum community. Torch River Forest Reserve, Saskatchewan. Note tuft of Equisetum arvense at top right.

PROFILE DESCRIPTION

A_o horizon: 12-14" wet, peaty humus, chiefly built up from coniferous needles. Full of tree roots.

A_1 horizon: 3-4" wet mucky black loam, representing a former meadow or fen soil.

G horizon: Gleied loam, showing irregular dark humus staining and yellowish grey mottling.

2. Typha latifolia.

3. Carex species, particularly Carex aquatilis, C. atherodes, C. rostrata.

4. The meadow grasses Scolochloe festucacea, Phalaris arundinacea, and Calamagrostis neglecta, plus an abundant herb flora including Aster puniceus, A. salicifolius, Galium trifidum, Scutellaria epilobifolia, Petasites sagittatus, Rumex mexicanus, Epilobium lineare, Sium suave, Triglochin palustris, Lycopus uniflorus, Mentha arvensis, Potentilla palustris.

5. Salix species, particularly Salix petiolaris, S. serissima, S. bebbiana.

6. Picea glauca.

Apparently invasion by spruce in the final stage can take place rapidly, because most of the stands were found to be even-aged and dense. Possibly establishment has taken place in one or two favourable years during the drier part of the climatic cycle.

Black spruce was rarely found with white spruce on the meadow or fen soils of the wet, swamp-border sites, but tamarack was frequently an associate. In several places, stands were examined where tamarack formed a distinct zone (Larix/Carex community) on the wetter side of the white spruce as shown in Fig. 35, thus representing an earlier successional stage in the hydrosere.

Fig. 35. Zonation of Larix laricina and Picea glauca at the edge of a Carex swamp. Riding Mountain National Park, Manitoba.
The zonation is: Pond - Typha zone - Carex zone (Carex atherodes, C. aquatilis) - Salix zone - Larix zone - Picea zone.

The chief species found in the Larix and Picea communities shown in Fig. 35 are compared in Table XXXVI.

Severe fires can occur on normally wet sites during periods of drought, burning away the humus down to the mineral horizon or to a level of saturation. With the return of normal precipitation the burned areas are swamped, a condition aggravated by the drastic reduction in transpirational losses accompanying destruction of the forest. The vegetation then returns to the early, wet-meadow stage, and the slow succession back to forest begins.

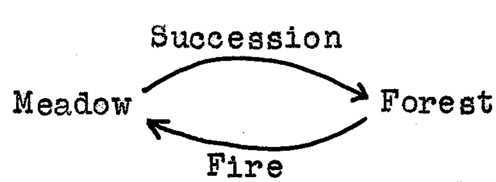
TABLE XXXVI

COMPARISON OF SPECIES IN ADJACENT STANDS OF LARIX LARICINA AND PICEA GLAUCA AT THE BORDER OF A SWAMP

The first group of species in each column is of greatest importance in that community.

Larix/Carex	Picea/Equisetum
Climacium americanum	Hylocomium splendens
Aulacomnium palustre	Equisetum arvense
Mnium spp.	Cornus canadensis
Carex canescens	Mitella nuda
Carex disperma	Rubus pubescens
Rubus arcticus	Linnaea borealis var. americana
Smilacina trifolia	Lycopodium annotinum
	Viola renifolia
Rhamnus alnifolia	Calamagrostis canadensis
Ribes glandulosum	Ribes glandulosum
Caltha palustris	Ribes hirtellum
Mitella nuda	Chamaenerion spicatum
Polygonum sp.	Rosa sp.
Lysimachia thyrsiflora	Viburnum edule
Potentilla palustris	Lonicera dioica var. glaucescens
Galium triflorum	Galium triflorum
Galium trifidum	Ribes triste
Moneses uniflora	Moehringia lateriflora
Dryopteris cristata	Fragaria virginiana
Geum macrophyllum var. perincisum	Rhytidiadelphus triquetrus
Pyrola asarifolia var. purpurea	Calliergonella schreberi
Betula papyrifera seedlings	Dryopteris cristata

Much evidence of this cycle



was found in the Porcupine Reserve. Reference has already been made to snail shells and paludic plants preserved in the humus under mature forests. Usually charcoal was mixed with these indicators of a former meadow stage, and indeed charcoal seemed to be as common on the wet sites as on the moist or fresh sites. In the Reserve meadows, charred wood was found buried in the fibrous organic soils, and in several places whole logs were found, thus indicating a prior forest stage. A final piece of evidence was provided by the examination in 1949 and again in 1954 of a "swamp spruce" stand which had been partly burned in 1942. At the first examination, the forest vegetation (including many seedling white spruce) seemed to be successfully reinvading on the exposed mineral soil, but five years later the entire burn had become a wet _Carex_ swamp and no elements of the forest flora could be found in it.

Less severe fires which kill the trees but do not destroy the organic soil are often followed immediately by a return of the forest. The pioneer tree on the humus of lightly burned areas was usually paper birch rather than poplar. Pure birch stands with a spruce and fir understory were found in several localities, the slower-growing conifers having seeded in at about the same time as the birch. As on many of the moist and very moist sites, so on wet sites the birch does not usually last very long, and the dead white stems, standing or on the ground, were a conspicuous feature in a number of older coniferous stands. A common line of succession is therefore through a birch stage to the Equisetum-Hylocomium type of Picea or Picea-Abies.

A unique site in the wet series comprises the shallow drainage channels of till and glacio-lacustrine deposits. Small intermittent or permanent streams wind through the channels, bordered by thickets of speckled alder (Alnus rugosa) rooted in the wet black soils. The specificity of alder to these alluvial, muck soils and its rarity on the meadow and fen soils suggests a relationship between the presence of the species and moving water. Wilde et al (1954) have described some of the characteristics of muck soils under alder in the Algoma District of Ontario.

The composition of the Alnetum is shown in the following list, based on an examination of four communities:

Alnus rugosa (dominant)
Caltha palustris
Rhamnus alnifolia
Ribes glandulosum
Ribes hudsonianum
Ribes lacustre
Glyceria striata var. stricta
Cinna latifolia
Sium suave
Viola renifolia
Viola palustris
Cirsium muticum
Geum macrophyllum var. perincisum
Cardamine pensylvanica
Dryopteris cristata
Urtica gracilis
Equisetum arvense
Equisetum scirpoides
Impatiens capensis
Circaea alpina
Chrysosplenium ionese
Mnium cuspidatum
Mnium affine
Climacium americanum

As soil accumulates in the Alnus swales white spruce can be found invading in locally favourable places, especially along the outer edges of the channels. The result is the formation of a rather open spruce forest, occurring as a narrow border along the edges of the shallow drainage channels. Ribes species flourish and patches of Alnus rugosa persist. An example is shown in Fig. 36.

Fig. 36. An open stand of Picea/Ribes-Alnus on muck soil. Torch River Forest Reserve, Saskatchewan.

This community is called the Picea/Ribes-Alnus forest type. The individual spruce trees of the type sometimes grow to a large size, influenced in all probability by inflow of enriched ground water from the adjacent slopes.

Black Spruce Forests

A close examination of black spruce types on wet sites, and of the tamarack communities associated with them, was not within the scope of the present study, and therefore only a few general observations are given here.

Scattered mixed stands of black spruce and white spruce are found occasionally on well-decomposed, organic soils, but pure stands of the former species on wet sites are largely confined to the raw moss-peat type of deposit. Here the widely distributed *Picea mariana/Sphagnum* forest type is characteristic.

Many of the mosses, herbs and low shrubs found in the white spruce forests on moist to wet sites also grow in the sphagnous black spruce forests, for example the common feather mosses and *Equisetum* spp., *Pyrola* spp., *Rubus pubescens*, *Mitella nuda*, *Mertensia paniculata*, *Cornus canadensis* and *Linnaea borealis* var. *americana*, but the species listed in Table XXXVII are more faithful to the *Picea/Sphagnum* community and serve to characterize it.

In the drier variants of the *Picea/Sphagnum* type, *Ledum groenlandicum* increases in abundance, provided that the tree canopy is not too dense. Other ericaceous shrubs--*Chamaedaphne calyculata*, *Kalmia polifolia* and *Andromeda polifolia*--are not so common as *Ledum* in the bogs and muskegs of the southern boreal forest, although their importance increases northward. A typical open stand of black spruce with abundant Ledum is shown in Fig. 37, and the ground cover of the same stand is shown in Fig. 38.

TABLE XXXVII

SOME PREFERENTIAL SPECIES OF THE PICEA MARIANA/SPHAGNUM FOREST TYPE

Sphagnum capillaceum	Spiranthes romanzoffiana
Sphagnum fuscum	Vaccinium vitis-idaea var. minus
Sphagnum magellanicum	Rubus arcticus
Sphagnum tenerum	Smilacina trifolia
Sphagnum recurvum	Ledum groenlandicum
Rubus chamaemorus	Eriophorum spissum
Vaccinium oxycoccus	Carex paupercula
Drosera rotundifolia	Carex gynocrates
Gaultheria hispidula	Carex capillaris
Orchis rotundifolia	Carex vaginata

Fig. 37. A shrub and moss type of black spruce (Picea/Ledum-Sphagnum). Riding Mountain National Park, Manitoba.

Fig. 38. The ground cover in a <u>Picea/Ledum-Sphagnum</u> stand. Note the presence of <u>Ledum groenlandicum</u>, <u>Sphagnum</u> spp., and <u>Vaccinium vitis-idaea</u> var. <u>minus</u>.

Considerable evidence has been found in support of Moss's (1953) contention that the natural succession of the "black spruce-peat moss association" is to a "black spruce-feather moss association". In one black spruce-feather moss stand on the Riding Mountain, the lower humus layer was found to be composed of sphagnous peat. In another stand on the Duck Mountain, the feather mosses could be seen encroaching on the sphagnum mounds. Table XXXVIII describes the latter stand.

TABLE XXXVIII

DESCRIPTION OF A DRY PHASE OF THE PICEA MARIANA/LEDUM COMMUNITY

Black spruce - Wet, moss (peat) type.
Plot No. 113. Duck Mountain, Manitoba.
Physiographic site: 8 : 7 : 4.
Soil: Half Bog (shallow peat) profile, consisting of 2 1/2 feet of sphagnous and woody peat over a gleid stony clay.

Dominant trees: Picea mariana 1 to 12 inches D.B.H., up to 150 years old. The stand had been partially cut.

Tree regeneration: Scattered seedlings of Picea mariana, Abies balsamea, Betula papyrifera and Larix laricina.

Minor species: Abundant Ledum with feather mosses on hummocks of Sphagnum.

Species are listed below within frequency classes in order of decreasing importance as determined by studies of cover-abundance in ten milacre quadrats.

Frequency 100 and 90%

Ledum groenlandicum
Calliergonella schreberi
Vaccinium vitis-idaea var. minus
Dicranum rugosum

Frequency 80 and 70%

Equisetum sylvaticum
Geocaulon lividum

Frequency 60 and 50%

Gaultheria hispidula
Sphagnum spp.

Frequency 40 and 30%

Moneses uniflora
Equisetum arvense

Table XXXVIII cont.

Frequency 20 and 10%

Ribes triste	Fragaria virginiana
Rubus pubescens	Hylocomium splendens
Vaccinium oxycoccus	Carex sp.
Cladonia rangiferina	Chamaenerion spicatum
Salix sp.	Orchis rotundifolia
Marchantia sp.	Habenaria obtusata

The succession from Sphagnum to feather moss ground cover does not mean that the former community is a necessary antecedent of the latter, for it has been pointed out earlier that most black spruce-feather moss types are formed, following ground fires, on moist mineral soil rather than on peat.

This concludes the description of forest communities within the environmental series.

Discussion

The review of forest communities that has just been given raises a number of interesting points concerning the development of vegetation. Some of these will be briefly discussed, after which a review of relevant studies by other workers will be given.

(1) Development of Vegetation

It is first of all evident that throughout the area as a whole there is no convergence of succession to one "Climax" forest type. Even if the "Climax" be defined more inclusively as a mosaic of communities (Jones, 1945) or as a pattern of populations corresponding to the pattern of environmental gradients (Whittaker, 1953) the problem remains as to what particular mosaics or patterns represent developmental end points. Disturbance by fire is such an integral part of the ecology of the forest that ultimate communities are seldom realized, and indeed it may be questioned as to whether the eight resident tree species are capable of forming fundamental or steady-state communities on many sites. For example, there is evidence that some poplar stands if undisturbed would die without replacement, and that some white spruce types on fresh, calcareous soils might also in time give place to brushy, sparsely treed vegetation. Again, the fate of upland stands of black spruce is uncertain, and fire is probably necessary to perpetuate the type.

On the other hand there are certain noda in the vegetation pattern which are sufficiently permanent on particular sites to be characterized as "climax" or "fundamental", although fire may still be an active agent in their perpetuation. On extreme sites, in particular, persistent communities are formed which owe much of their recognizability to dominance by a single tree species. Such are the pine and the spruce forest types on very dry and dry sites (Pinus/Arctostaphylos-Cladonia and Picea/Elymus-Fragaria), the white spruce forest type on meadow and fen soils (Picea/Equisetum-Hylocomium), the black spruce forest type on moss peat (Picea mariana/Sphagnum, or Picea/Ledum-Sphagnum), and the tamarack forest type on poorly consolidated organic soils (Larix/Carex). The less extreme sites--fresh, moist and very moist--show a great deal more variability in vegetational patterning, due to the fact that more than one tree species can occupy them and that successional development is an immediate possibility. One nodum with "climax" attributes is the mosaic fir-spruce forest type (Abies-Picea/Hylocomium-Rubus) that occurs over a considerable range of sites and which may represent an approximation of the steady state, with the fir continuously reproducing on the coniferous humus or in the moss mat, and the spruce (plus small numbers of paper birch in some localities) reproducing in stand openings on the decayed remains of former trees.

There is nothing inevitable about the development of the Abies-Picea/Hylocomium-Rubus community on non-extreme sites. Wherever it occurs its genesis can be traced to a coincidence of conditions which favoured the initial establishment of white spruce seedlings in sufficient numbers for the ultimate development of closed coniferous stands, and also favoured the formation of the moss ground-cover and the invasion of balsam fir. The prime necessity--the mass invasion of an area by white spruce--is prevented by a number of circumstances, chief among which is competition from broad-leaved trees, shrubs and herbs. The competition factor itself is intensified by a variety of processes which stem from site, vegetation, and historical circumstances, such as frequent fires, light (crown) fires, shallow calcareous soils, warm local climate, the composition and structure of prior non-coniferous communities, etc. Hence the relative rarity of the Abies-Picea/Hylocomium-Rubus forest type, and the preponderance of stands of hardwoods and of mixed hardwoods and conifers in the southern boreal forest.

The developmental trends, on different sites, in stands with varying mixtures of poplar and spruce need more study. In the absence of fire some mixed forests undoubtedly pass to white spruce types as the hardwood component dies. On moist sites there is evidence of a further trend toward a spruce-fir type, for example in the Dore Lake forests, although whether such stands are capable of sufficient intra-stand reproduction to form closed, feather moss types is problematical. On other sites the conditions of habitat, or the vegetational structure and composition, may possibly favour the perpetuation of open forests with herb or shrub-herb undergrowth, as for example on the rich slopes and alluvial sites of the Pasquia-Porcupine Reserve areas.

Practical forestry interest in developmental trends does not go beyond the spruce-hardwood communities, as the best spruce saw timber is found in the mature mixed stands or in coniferous stands which have only recently emerged from the mixed stage. In older forests the incidence of cull, due to butt and trunk rots of the spruce, increases concurrently with an increase in the proportion of the "weed tree" balsam fir, and exploitation becomes less profitable.

It is often said that white spruce makes its best growth in association with poplar. This is another way of saying that white spruce grows best in the same places where poplar also thrives, i.e., on the fresh to very moist sites. Poplar is rarely able to tolerate conditions on very dry, dry and wet sites, and it is here that white spruce in pure stands grows rather poorly. Pure stands of spruce sometimes occur on the intermediate sites as well but almost invariable evidence can be found that poplar was present in the earlier stages of development. In some circumstances the poplar may have a deleterious effect on the growth of smaller spruce, a result of mechanical abrasion of the tops of the latter species as it grows into the hardwood canopy (Kagis, 1952). However in several indirect ways the poplar is probably instrumental in assisting growth to large sizes of individual spruce. Its presence as a diluent in all stands on intermediate sites frequently prevents the establishment in excessive numbers of spruce seedlings. Any tendencies toward overcrowding and stagnation are thus prevented in the young stands, and in later life the death of the poplar produces results akin to a silvicultural thinning, yielding increased space, light, nutrients and moisture for continued growth of the maturing spruce.

In terms of soils and sites, the best growth of individual white spruce trees has been observed on deep, permeable, fresh and moist soils. Loams and very fine sandy loams having solum depths of three or four feet are particularly favourable. On sites where the ground water either is moving or is frequently replenished spruce grows very well on many different kinds of soils, and therefore alluvium and the slopes of hills are excellent spruce sites whether the moisture regime is moist, very moist or wet.

(2) Related studies by other workers

Considerable information on the forest vegetation of Manitoba and Saskatchewan is contained in old forestry reports (some dating back to the beginning of the century) dealing with timber cruises, rate of growth surveys, working plans and general silviculture. Several of the most interesting and instructive are "The Riding Mountain Forest Reserve" by J. R. Dickson (1909), and "Silvical Report on Riding and Duck Mountain Forest Reserves" by Tunstell, Gill and Kuhring (1922), the latter containing an excellent account of the silvics of the forest tree species. Most of the reports are prefaced by only very general descriptions of the forest vegetation, as the writers were either not interested in ecology or had insufficient time to write down their observations in detail. However a few men did actually set out to describe and classify the forest vegetation in a more ambitious way, and their pioneer work deserves recognition.

Connell (1920) wrote a thesis (unpublished) entitled "Forest types of eastern Saskatchewan" in which he discussed the climax and seral vegetation of an area studied only in part by the writer, namely the north side of the Porcupine Hills, the Pasquia Hills and the Palaeozoic and Precambrian Lowlands immediately to the north. Following the concepts of Nichols (1918), he took the whole area as one "Climatic Formation" and divided it into eight "Edaphic Formations": Boulder Clay Slope, Sand Plain, Rock Outcrop, Lacustrine Clay, Poorly drained (drift) Flat, Undrained Swamp, Drained Swamp, Flood Plain--each supporting an "Association Complex" (called also a "Forest Type") consisting of the temporary and climax associations appropriate for that particular site. Thus he recognized a number of "Edaphic Climax Association Types", but he selected only one as the "Regional Climax Association Type", it representing "the highest degree of mesophytism which the climate of the region permits". This is precisely Odum's suggested approach as expressed earlier (p. 76). Connell gave short descriptions of the various "Association Types", classifying them firstly in either the Xerarch (upland) or Hydrarch (lowland) successional series, and secondly as belonging to either the Prisere or the Subsere.

Connell's work was not intensive and for most Association Types he described little more than the tree composition, but because his classification has a physiographic basis it is possible to match it with the results of this study. His Sand Plain Association Type with its stable climax of _Pinus banksiana_ belongs in the Very Dry Series. The Rock Outcrop Type occurs only north of our area. The Boulder Clay Slope Association Type doubtless corresponds to segments of the Fresh, Moist and Very Moist

Series. Here Connell defined his Regional Climax Association Type, made up of _Picea glauca_ (75 per cent of stand), _Abies balsamea_ (10 per cent), and the hardwoods _Betula papyrifera_, _Populus tremuloides_ and _P. balsamifera_ (15 per cent), with a pronounced moss stratum on the forest floor, and such herbs as _Cornus canadensis_, _Trientalis borealis_, and _Maianthemum canadense_. This is the typical _Picea-Abies/Hylocomium_ forest type described in the present paper. The _Populus/Corylus_ community on some of these sites was considered a stable sub-climax by Connell. The rest of his Association Types fall in the Very Moist and Wet Series, and although some of them are poorly defined, it is possible to recognize communities similar to the feather moss types of white and black spruce at the borders of swamps and bogs, the _Sphagnum_ type of black spruce, and the open shrubby types of hardwoods and white spruce on alluvium.

Halliday (1929, 1930) studied the forests of the Cretaceous Hills in western Manitoba and eastern Saskatchewan, and developed a classification on the basis of the minor vegetation. In this he was strongly influenced by the work of Cajander (1926). Four "Forest Classes" were recognized and these were subdivided into "Forest Types" (sensu Cajander) on the basis of dominance by particular layer communities. The following is a brief outline of his classification:

1. Grass-Herb Forest
   (a) Shrub type. Typical of hardwood stands on high ground.
   (b) Herb type. Typical of mixedwood stands on well-drained slopes and flats.
2. Moist Moss Forest
   (a) Hylocomium type. Complete feather moss cover, scattered herbs and shrubs. Typical of coniferous stands, especially white spruce and balsam fir.
   (b) Transition (Hylocomium/Grass-Herb) type. Typical of coniferous stands with small amounts of hardwood species.
3. Wet Moss Forest
   (a) Hypnum type. Black spruce with occasional tamarack and white spruce.
   (b) Sphagnum type. Complete Sphagnum cover, scattered herbs. Typical of black spruce and black spruce-tamarack stands.
   (c) Ledum Muskeg type. Labrador tea and Sphagnum in hillocks. Non-merchantable black spruce with occasional tamarack.
   (d) Tamarack Moor type. Wet grass and reeds. Typical of open tamarack stands.
   (e) Low Moor type. Open muskeg and floating bog. Characterized by swamp birch.

4. Dry Moss and Lichen Forest

   (a) Heath type. Abundant ericaceous dwarf shrubs and lichens. Typical of jack pine forests, with occasional black spruce.

   (b) Transition (Heath-Hylocomium) type. Typical of jack pine and black spruce mixtures at the borders of bogs.

This is quite a comprehensive classification, one into which most forest communities in our area can be fitted without difficulty. A criticism, however, is that while it is fairly detailed for the moss types, it provides only two categories for the much more important grass, herb and shrub types. The latter types need to be defined either taxonomically or in terms of moisture regime if they are to have any precise meaning. Halliday did not develop the classification further, nor did he attempt to describe the vegetation of the types or to show their relationships to one another either physiographically or successionally.

Halliday (1935) made a study of vegetation and sites on a limited forest area in the Riding Mountain National Park. His aim was to investigate the forest conditions of the locality, with particular reference to the relationship of tree growth to site conditions as expressed through the lower vegetation, and to this end nineteen plots sampling a variety of cover-types were examined in detail. The communities were fitted into the following classification, again following Cajander (1926) and Ilvessalo (1929).

1. Meso-hygrophile or Hygrophile Forest. Shrub forest with tall herbs, poor in mosses.
2. Mesophile Transition. Herb-grass forest with some tall herbs and shrubs, irregular moss cover.
3. Mesophile Forest. Moist-moss communities, with abundant fernworts and hydrophytic shrubs.
4. Hydrophile Forest. Wet-moss communities, with Sphagnum or aquatic mosses on peat or muck.

The difficulties which accompany attempts to apply an *a priori* classification are well exemplified in this study. It has been shown in the previous section that some grass and herb (Mesophile Transition) forests on the Riding Mountain are dry (*Elymus* type) and some are very moist (*Calamagrostis* type), and they cannot be realistically classed together. Furthermore, shrub communities are variable in the same way, as are the moss communities, and it is hardly possible to sort them out in any reasonable way unless cognizance is taken of other features such as cover-type and site. The study contributed some interesting data concerning the composition of individual stands, although its value from the standpoint of classification of forest sites and vegetation is small.

The only other work of importance in similar forests has been done farther to the west. Moss (1953, 1955) reported on the forest communities in northwestern Alberta, an area very similar geographically and floristically to our own. As would be expected therefore, his descriptions apply equally well to many stands in Saskatchewan and Manitoba. He treated each of the prevalent single-species cover-types as associations or consociations, defining variants on the basis of ground-cover. In the white spruce association, the following four faciations (variants) were recognized:

1. Needle cover faciation; minor vegetation scarce or lacking. This is a type that can develop on many sites provided that conditions have been favourable for the prolific regeneration of white spruce, black spruce or fir.
2. Grass-shrub faciation, characterized by Elymus innovatus, Aster conspicuus, Shepherdia canadensis and Alnus crispa. This corresponds closely to spruce types in the Dry Series on weakly calcareous soils.
3. Shrub-herb faciation, with a prominent shrub stratum (Viburnum edule, Rosa spp., Ribes spp.) and luxuriant herb strata (Linnaea borealis var. americana, Rubus pubescens, Cornus canadensis, Mitella nuda, etc.)
   This is like some of the moist spruce forests recognized in these studies, sufficiently open (i.e., diluted with poplar) to prevent the formation of a moss stratum and yet dense enough to shade out the tall shrubs and many of the tall herbs. The "good

regeneration" in older stands referred to by Moss may represent the intra-stand invasion earlier referred to, which coincides with the falling out of the poplar and the attainment of maximum seed production by the first generation spruce.

4. Feather moss faciation, characterized by Hylocomium splendens, Calliergonella schreberi and other mosses, plus Equisetum spp. and Cornus canadensis.

The reported presence of Equisetum spp. suggests that this faciation corresponds in part to the Picea/Equisetum-Hylocomium forest type of the Very Moist and Wet series, otherwise to the similar closed types in the fresh and moist series. Moss considered the feather moss faciation as the end point of succession in the spruce association (barring fire), and there is certainly a trend in this direction on many sites. Since the development and maintenance of the feather moss stratum depends primarily on coniferous cover, the above is an expression of the tendency toward normal stand density, i.e., open spruce stands tend to close with age, and over-dense stands (needle cover faciation) tend to become somewhat more open. It is by no means sure that all open stands do "fill in" with age however, particularly where environmental conditions favour broad-leaved competitors.

In connection with the question raised by Moss concerning succession of the black spruce-feather moss association to the white spruce association, or vice versa, it is probable that one or the other species is favoured under different climatic and soil conditions. Within the area of the present study the relative competitive ability of black spruce apparently increases from south to north, and it is probable that Kabzems (1952) had the more northern areas in mind when he stated that black spruce succeeds the white spruce.

Farther to the north and west Raup (1946, 1935) has described the forest types of the Athabaska-Great Slave Region and adjacent northern Alberta. Moss (1953, 1955) has compared Raup's forests with those of northwestern Alberta, and his remarks concerning differences and similarities apply equally well for our area. Raup recognized three kinds of white spruce forest:

1. Park-like White Spruce

   This is actually a subarctic ("Taiga") type, and it is probably comparable to spruce communities in far northern Manitoba and Saskatchewan. It is similar in physiognomy of tree layer to our Parkland Spruce, although the undergrowth of the two community types is distinctly different, with only a few species in common, e.g., Juniperus horizontalis, Arctostaphylos *uva-ursi*, and *Hedysarum alpinum* var. *americanum*. It is interesting that Raup found spruce rather than pine on stony ridges (lake beaches), a situation akin to that of our area.

2. Flood Plain White Spruce

This resembles the spruce stands observed on very moist alluvium in the southern boreal forest. It begins as a poplar type with tall shrubs, and progresses to a spruce type in which a "loose mat of mosses is formed" and the shrubs and herbs are largely shaded out. The relatively poor development of the moss mat may be due to a number of factors as suggested previously, namely, a relatively open canopy due to the structure imposed on the spruce forest by a prior poplar component, a rich soil favouring persistent herb and shrub growth even as the canopy closes, and intermittent flooding with a consequent deposition of thin layers of new alluvium.

3. Upland Mesophytic White Spruce

This category covers all upland forests except those occupied by Park-like White Spruce. It is therefore too broad a grouping to convey much information on the character of particular cover-types and sites. Apparently the feather moss type, featuring *Hypnum crista-castrensis* rather than *Hylocomium splendens* is prevalent.

Raup reports that succession on the uplands following light (crown) fires is directly back to spruce, but following severe (ground) fires it is to aspen (or to aspen-pine). This is exactly the opposite to what has been observed in our area on upland sites, and it points to the dangers of generalizing for large areas.

A few of the other forest communities in the Athabaska-Great Slave Lake Region are homologous with ours. The sand plains jack pine type (Pinus/Arctostaphylos-Cladonia) is there, and also the black spruce bog forest (Picea/Sphagnum-Ledum). Balsam Fir-White Spruce forests are less widely distributed than with us, being "confined to the immediate valleys of streams and to local terraces within valleys". Raup's description indicates that the type is largely confined to alluvium, whereas in the southern boreal forest the fir is much more common on upland sites.

In another paper which deals with the vegetation along the Alaska highway, Raup (1945) has mentioned the relationship between upland black spruce, heavy soils (lacustrine and till clays) and frozen ground. He has suggested that the shade of the forest maintains a frozen subsoil which in turn is responsible for a high water table. The same coincidence of vegetation-site characteristics has been observed in the Duck Mountain Forest Reserve, where in 1954 the ground remained frozen at least in patches under upland black spruce until midsummer. This relationship between ground frost and vegetation may be very important on many heavy-textured soils throughout the boreal forest region.

Across the Lake Agassiz basin in the boreal forest of the east, the published descriptions of the vegetation show many points of resemblance to the vegetation of the southern boreal forest in Manitoba-Saskatchewan. Particularly is this true of coniferous types. Reference will be made to only two examples. Cooper's (1913) classic description of the Climax forest of Isle Royale, pictures a fir-spruce-birch forest very similar to some of the *Abies-Picea/Hylocomium-Calliergonella* communities in this area, although floristic differences are apparent. For example, *Thuja occidentalis* is associated with the tree dominants on Isle Royale, while *Taxus canadensis*, *Clintonia borealis*, *Oxalis acetosella* and other eastern species appear in the undergrowth. Northward from the Great Lakes the floristic differences become less, and with the deletion of very few minor species Hustich's (1955) short accounts of some spruce-fir stands at Moose River, near James Bay, could apply to feather moss and herb types of *Picea-Abies* in the southern boreal forest.

Having mentioned some of the relationships to west and east, it only remains to consider the north and south contacts of the southern boreal forest. Scarcely any ecological work has been done northward on the palaeozoic and precambrian lowlands, although in recent years a number of floristic surveys of selected areas have been carried out in northern Manitoba and Saskatchewan, chiefly, by taxonomists of the Canadian National Museum. It is known that in the "northern boreal forest" the importance of white spruce and aspen is much reduced relative to the role these species play in the southern boreal forest, and also that there is a reciprocal increase in the importance of black spruce, jack pine and tamarack. There are indications too in the inventory reports of the Provincial Forest Services that paper birch is generally more abundant than aspen on the precambrian shield, and that fir and balsam poplar are relatively unimportant constituents of the vegetation.

On its southern side, the boreal forest is fringed by a belt of aspen woodland which is first a continuous forest and then, nearer the prairies, a groveland or parkland interspersed with grassy patches. The aspen woodland has been studied in Manitoba by Bird (1930) and in Alberta by Moss (1932). From these published papers as well as from personal observations, it is clear that the aspen woodland is closely related floristically to the poplar stands of the southern boreal forest, although differing from them in the relative incidence of certain secondary plant species. A comparison of the species tallied in twenty-four aspen stands in the southern boreal forest proper with those tallied in sixteen stands south of it has indicated that in the aspen woodland there are only a few characteristic species. Examples of these are:

Symphoricarpos occidentalis	Smilax lasioneura
Pyrola elliptica	Rhus radicans var. rydbergii
Aster laevis	Corylus americana
Thalictrum dasycarpum	Viburnum lentago
Anemone riparia	

Probably more distinctive is the absence or comparative rarity of species which are common in poplar stands to the north. Examples are:

Cornus canadensis	Linnaea borealis var. americana
Petasites palmatus	Calamagrostis canadensis
Mertensia paniculata	Prunus pensylvanica
Mitella nuda	Shepherdia canadensis
Ribes triste	

In a general and none too exact sense the southern boreal forest can be envisaged as an intergrade between the northern boreal (coniferous) forest and the aspen woodland. Many of its coniferous stands with their low herb and moss vegetation show a marked similarity floristically (and presumably in structure also) to northern types, while the close affinities of its shrub and tall herb hardwood types to those of the aspen woodland have just been mentioned. A further interesting comparison or analogy can be made between succession following fire on upland sites in the southern boreal forest (poplar → poplar-spruce → spruce) and the zonation from south to north of aspen woodland, "Mixedwoods", and coniferous forest.

VII

A GENERAL DESCRIPTIVE SCHEME FOR FOREST VEGETATION

The task of describing vegetational communities is not easy. The investigator is confronted with the fact that no two stands are exactly alike; variability due to vegetational development and site differences occurs on every hand. Usually the method followed is to describe selected "representative" stands (as has been done in the previous chapter) fully aware at the same time that no one will encounter in the field the exact conditions described. From the study of several hundred stands, the writer has selected for description those forest communities which he believes illustrate the range of interplay of three variables: site, species composition and successional status. At the same time an effort has been made to define communities which, due to the recurrence of similar historical circumstances and similar site patterning, show general similarities of composition and structure. These are the defined forest types. Still, much of the vegetation has of necessity been left out, and a great number of intermediate and variant communities remain undescribed. It would be very useful, particularly to the practising forester, to have a general descriptive scheme that could be applied in the field to each and every stand encountered, and in the following pages such a scheme for use in the southern boreal forest is outlined.

The attribute of vegetation which lends itself most readily to description is physiognomy (Du Rietz, 1931; Dansereau, 1951) and a comparison of the structure of the forest undergrowth in various stands during these studies suggested one very helpful approach. Where sites are neither extremely dry nor wet, the undergrowth of pioneer forest stands (poplar, birch, or even pine, at times) characteristically shows a high proportion of tall shrubs and/or tall herbs. In marked contrast is the clean forest floor under pure spruce or spruce-fir stands, characterized by mosses and low herbs. It is interesting to note that if a list of the forest flora from non-extreme sites is divided into three groups on the basis of height alone as follows--tall shrubs and herbs (higher than three feet and one foot, respectively), medium shrubs and herbs (one to three feet and four inches to one foot), low herbs and mosses (generally lower than four inches)--then the species in the tall and low groups are precisely those which stand out in deciduous forest (poplar) stands and in coniferous (chiefly spruce) stands, respectively. The middle group is not so specific as to cover-type preference, its species characterizing many kinds of stands.

The principal factor controlling the structure of the undergrowth is light, for although temperature, root competition, litter accumulation, and other soil characteristics exert a subsidiary effect, their main influence is on composition rather than on stratification. A poplar canopy allows much more light to penetrate to the forest floor than does a spruce canopy, consequently tall shrubs are able to flourish under the former but not under the latter forest. In a comparable way, an open stratum of tall shrubs may allow tall herbs to survive, while a dense stratum eliminates all but the most tolerant. It is a fairly sound generalization that the relative height of the forest undergrowth species bears an inverse relationship to tolerance, since plants of low stature must be adapted to shade in order to survive. For example, the series: Corylus cornuta → Aralia nudicaulis → Cornus canadensis → Calliergonella schreberi (tall shrub → tall herb → low herb → moss) is clearly one of increasing tolerance to shade.

In order to illustrate the change in vegetative structure with increasing shade, an analysis was made of the comparative cover-abundance of the shrub, herb, and moss layers in stands representative of the successional series: poplar - poplar-spruce - spruce-poplar - spruce. The data were drawn from 400 milacre quadrats examined in 20 forest stands on fresh and moist sites. Fig. 39 shows the calculated percentage of total cover that the various layers contributed in this particular sample.

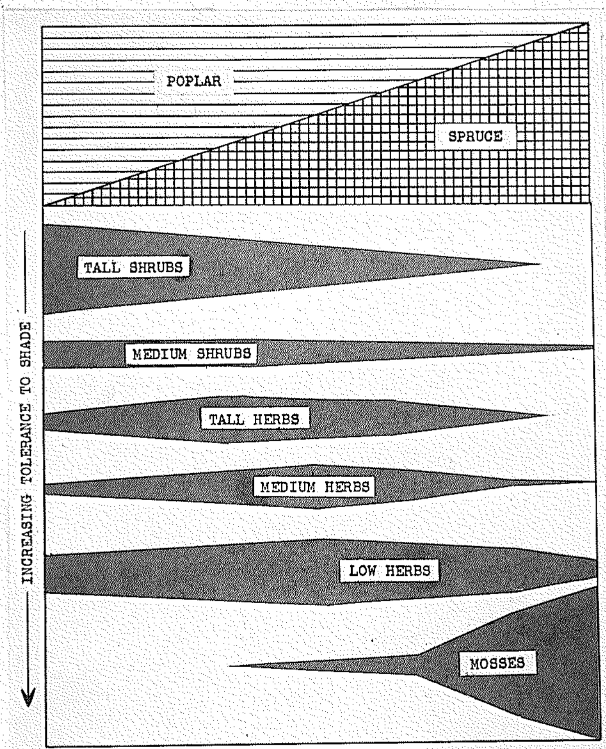


Fig. 39. The relative cover-abundance of the undergrowth strata in mature stands of poplar, poplar and spruce, and spruce.

Note that the percentage of cover contributed by tall shrubs decreases steadily from poplar through mixed-wood to spruce stands, while the percentage of cover contributed by mosses rises abruptly as mixed stands change to spruce. Note also that the cover-abundance of tall herbs is inversely related to that of tall shrubs in the poplar and poplar-spruce communities, reaching a high point in the latter. Medium shrubs decrease slowly from poplar to spruce, some few being very persistent even where light intensity is very low, e.g., Viburnum edule and Ribes spp. Herbs of medium height have their best development in mixed stands. The low-herb stratum is strong in all communities, particularly in the mixed; its conspicuousness in spruce stands is due to the absence of the higher, herb and shrub strata which tend to conceal it elsewhere.

A second feature useful in describing stands is found in the relationship between the forest plants and the soils which support them. In so far as single soil factors can be separated from the environmental complex and treated as "causes", soil moisture is probably the most important modifier of competitive ability and growth, and variations in moisture regime are always reflected in variations of vegetation. To determine the moisture regime of a site is not always easy even after the time-consuming examination of the complete soil profile. Topographic position and texture of mineral material are frequently good indicators, as also are plants when their habits are sufficiently understood.

In 1949, after two years of field work in the Cretaceous Hills area of the southern boreal forest, a tentative table was drawn up ranking many of the species on a four-point moisture-preference scale (Rowe, 1950). Subsequently, additional observations made during the course of these studies under various conditions of physiography led to a partial revision of the table, and to the use of five main moisture groups: Dry (including Very Dry), Fresh, Moist, Very Moist, and Wet. The picture which has gradually been developed of the moisture preferences of the common forest species, relative to one another, provides a means of judging the moisture relations of particular stands.

Using these two features, structure of vegetation and moistness of site as indicated by the species present, it is possible to characterize every forest stand with a short descriptive epithet as was done, for example, in the tables describing particular forest communities in the previous chapter. Considerable information on density and successional status is conveyed at the same time. Mention of the "dry, low grass-and-herb type" immediately calls to mind the open, limby stands of pine or spruce which pioneer on excessively drained soils, just as the "moist moss type" suggests the dense, comparatively stable stands of spruce or spruce-fir on flats and lower slopes. When describing stands in this generalized manner, the names of the dominant trees are always included.

Note that the characterization of stands according to structure of the undergrowth stresses what is particularly evident to the observer's eye. Thus a "tall shrub type" may actually include tall-herb and low-herb strata, although these may not be mentioned because they are not readily seen. Where two or more strata are conspicuous the description can include them all, for example, "the moist, tall-shrub and moss type of pine forest" (Pinus banksiana/Alnus crispa-Calliergonella schreberi).

The Vegetation Table

As an aid to more exact descriptions of plots and stands particularly in the forests of the Riding and Duck Mountains, a field sheet was prepared on which the common forest species were located with reference to height on one co-ordinate axis and to moisture preference on the other. In using this field sheet the investigator checks off the plant species which occur on the area being studied, noting as well the prominent stratum or strata which contribute to the physiognomy or "look" of the stand. Relevant notes on environmental factors (soil, topographic position, aspect, etc.) are also taken. Table XXXIX shows the vegetation part of the field sheet, as revised after one summer's use, with the relationship of tree species to moisture gradient indicated at the top of the page.

It should be immediately emphasized that the position occupied by each species in the table does not represent its only possible niche in natural communities. Consider the vertical scale: from top to bottom of the page are listed tall shrubs (more than three feet tall), medium shrubs (one to three feet tall), tall herbs (more than one

TABLE XXXIX

VEGETATION TABLE FOR THE SOUTHERN BOREAL FOREST

The species are arranged by strata in the vertical dimension and by moisture preference in the horizontal dimension Species having little indicator value so far as moisture is concerned are underlined, and species characteristic of coniferous types are marked with an asterisk.

VEGETATION STRATA	VERY DRY AND DRY FOREST xerophytic species	FRESH FOREST xero-mesophytic species	MOIST FOREST mesophytic species	VERY MOIST FOREST meso-hydrophytic species	WET FOREST hydrophytic species
	← Pinus banksiana →			← Larix laricina →	
	← Picea glauca →				
	← Betula papyrifera →				
		← Populus balsamifera →			
			← Picea mariana →		
		← Populus tremuloides →			
			← Abies balsamea →		
TALL SHRUBS (3 ft. plus)	Alnus crispa Elaeagnus commutata Salix humilis Shepherdia canadensis	Amelanchier alnifolia Corylus cornuta Prunus pensylvanica Prunus virginiana	Acer spicatum Sorbus decora Viburnum trilobum	Acer negundo Cornus stolonifera Salix bebbiana Salix discolor	Alnus rugosa Salix petiolaris Salix pyrifolia
	....	....	....	....	....
MEDIUM SHRUBS (1 ft. to 3 ft.)	+ Hudsonia tomentosa Juniperus communis	Diervilla lonicera Rosa acicularis Symphoricarpos albus Symphoricarpos occidentalis + Vaccinium myrtilloides	Lonicera dioica var. glaucescens	+ Ledum groenlandicum Lonicera involucrata Lonicera villosa var. solonis Ribes glandulosum Ribes hirtellum Ribes triste Rubus idaeus Viburnum edule	+ Andromeda polifolia Betula glandulosa + Chamaedaphne calyculata + Kalmia polifolia Rhamnus alnifolia Ribes hudsonianum Ribes lacustre Spiraea alba
TALL HERBS AND GRASSES (1 ft. plus)	Agastache foeniculum Anemone cylindrica Hedysarum alpinum var. americanum Hieracium canadense Lathyrus venosus Lilium umbellatum Potentilla arguta	Agropyron subsecundum Anemone riparia Apocynum androsaemifolium Aralia nudicaulis Chamaenerion spicatum Disporum trachycarpum Lathyrus ochroleucus Sanicula marilandica Thalictrum venulosum	Achillea sibirica Aquilegia canadensis Osmorhiza longistylis Solidago lepida	Anemone canadensis Aster umbellatus var. pubens Calamagrostis canadensis Cinna latifolia Heracleum maximum Pteretis pensylvanica Solidago gigantea Thalictrum dasycarpum Urtica gracilis	Arnica chamissonis Aster junciformis Aster puniceus Cirsium muticum Eupatorium maculatum Glyceria borealis Impatiens capensis Petasites sagittatus Petasites vitifolius Sium suave

	Potentilla arguta	Lathyrus ochroleucus Sanicula marilandica Thalictrum venulosum		Pteretis pensylvanica Solidago gigantea Thalictrum dasycarpum Urtica gracilis	Petasites sagittatus Petasites vitifolius Sium suave
MEDIUM HERBS AND GRASSES (4 in. to 1 ft.)	Achillea millefolium Aster laevis Astragalus alpinus Astragalus striatus Erigeron glabellus Castilleja rhexifolia C omandra pallida Elymus innovatus Equisetum hyemale Gentianella amarella Habenaria bracteata Heuchera richardsonii Melampyrum lineare Oryzopsis asperifolia Poa interior Polygala senega Rudbeckia hirta Solidago nemoralis Zizia aptera	Aquilegia brevistyla Aster ciliolatus Corallorhiza maculata Corallorhiza striata Galium septentrionale Prenanthes alba Schizachne purpurascens Smilacina stellata Vicia americana Viola rugulosa	Bromus ciliatus Mertensia paniculata Osmorhiza obtusa Petasites palmatus	Dryopteris cristata Dryopteris disjuncta Dryopteris spinulosa + Geocaulon lividum Habenaria hyperborea Lysimachia ciliata Poa palustris Valeriana septentrionalis	Caltha palustris Equisetum arvense Equisetum pratense Geum macrophyllum Geum rivale Lathyrus palustris Mentha arvensis Parnassia palustris var. neogaea Senecio pauperculus Stachys palustris
LOW HERBS AND GRASSES AND SHRUBS (Less than 4 in.)	Antennaria campestris Antennaria petaloidea + Arctostaphylos uva-ursi Danthonia spicata Houstonia longifolia Festuca ovina Juniperus horizontalis + Lycopodium complanatum Oryzopsis pungens Polygala paucifolia + Sibbaldiopsis tridentata Solidago hispida Spiranthes gracilis Vaccinium caespitosum Viola adunca	Anemone quinquefolia Corallorhiza trifida Fragaria virginiana + Lycopodium obscurum Maianthemum canadense var. interius Pyrola asarifolia Pyrola secunda	Carex deweyana + Coptis groenlandica Corallorhiza trifida Cornus canadensis Fragaria vesca + Goodyera repens + Linnaea borealis var. americana Lycopodium annotinum Moehringia lateriflora Monotropa uniflora + Pyrola virens Rubus pubescens + Trientalis borealis + Vaccinium vitis-idaea var. minus + Viola renifolia	Circaea alpina + Equisetum scirpoides Galium triflorum + Gaultheria hispidula + Habenaria obtusata + Habenaria orbiculata + Listera cordata Mitella nuda + Moneses uniflora + Ranunculus lapponicus	Carex capillaris + Carex disperma Carex gynocrates Chrysosplenium ioense + Drosera rotundifolia Galium trifidum Ranunculus abortivus + Rubus acaulis + Rubus chamaemorus + Smilacina trifolia Stellaria longifolia + Vaccinium oxycoccus Viola nephrophylla Viola palustris
MOSSES AND LICHENS	Ceratodon purpureus + Cladonia rangiferina Polytrichum piliferum	Brachythecium salebrosum Polytrichum juniperinum Rhytidiadelphus triquetrus	+ Calliergonella schreberi + Dicranum rugosum Eurhynchium strigosum Eurhynchium diversifolium Peltigera spp.	+ Hylocomium splendens + Hypnum crista-castrensis Thuidium recognitum	Aulacomnium palustre Camptothecium nitens Climacium americanum Drepanocladus uncinatus Mnium cuspidatum + Sphagnum spp.

foot tall), medium herbs (four inches to one foot tall), low shrubs and herbs (less than four inches tall), and the moss and lichen layer. Obviously there are numerous plants which can take their places, according to growing conditions, in more than one of these arbitrarily defined strata. The aim has been, however, to make the scale conform as closely as possible to the average physiognomy of the vegetation as observed in numerous forest stands throughout the eastern part of the Mixedwood Forest Section, and in most cases it has not been difficult to decide where any given species should be placed. More importance has been attached to the position of the vegetative foliage than to the flowering parts, and species such as *Elymus innovatus*, *Aster ciliolatus*, and *Mertensia paniculata*, which in flowering extend into the tall-herb layer, are nevertheless ranked as medium herbs.

The position of a species relative to the horizontal moisture-preference scale is not meant to be interpreted in a hard and fast way either. Plants of wide tolerance may be found in all sorts of communities, from dry to wet sites. However, most of the species exhibit a preference for one moisture regime (their "apparent optimum") over others, reflecting this preference in greater abundance and vigour, and it is expedient here to pigeon-hole each according to the moisture column of closest fit. Intensive studies would make possible the subdivision of moisture-preference classes, as the finer responses of species relative to one another were distinguished, but for present purposes a five-point division of moisture gradient is considered adequate.

The sampling unit in forestry work is usually a one-tenth- or one-fifth-acre plot. On such limited areas, particularly when cover-type and site conditions are relatively homogeneous, it has been found from quadrat studies that 40 to 50 species of minor plants are usually present (plus a number of rarer bryophytes and lichens which are not considered here). When these species are checked off on the table, a certain scatter pattern is obtained depending on the nature of the overstory, successional stage of the community, and the moistness of the site. It is often quite apparent from the presence pattern thus obtained that the weight of the community is concentrated in a particular part of the table, and this facilitates the characterization of stands by physiognomy and moisture regime.

Table XXXIX can be interpreted as a general description of many communities, indicating as it does the probabilities of certain plants entering into the constitution of the vegetation in response to environmental variations. It represents an attempt to come to terms both with the important fact that a segregation of species occurs in relation to gradients of light and moisture, and with the corollary that ecologically similar species may replace one another on equivalent sites. It suggests in a very broad way what may be expected so far as floristic composition is concerned under various degrees of crown closure and soil moisture.

One important qualification is necessary. The table places together all species which are somewhat similar in height, growth habit and moisture preference, but this does not mean that they are necessarily ecological equivalents or even that they are found together in nature. To further refine the table for descriptive purposes it would be necessary to mark those species which commonly occur together, thus suggesting more exactly the probable composition of communities under particular conditions of cover-type and site. A rather broad division has been made in the table by marking with an asterisk those species which are largely confined to coniferous forests.

The table also indicates something of the developmental trends in forest communities. The course of succession on many upland sites from poplar or pine to spruce (or to spruce-fir) is marked by a diminution of light on the forest floor. As previously mentioned, the pioneer communities are characterized by an open canopy which allows tall shrubs and tall herbs to flourish beneath (provided that moisture and nutrients are adequate). The more advanced communities--the white spruce (or white spruce-fir) and black spruce--with their closer canopies make conditions unsuitable for survival of all except the most tolerant undergrowth: the mosses and low herbs. With some exceptions then, which are mentioned below, the top half of the table contains the species characteristic of pioneer open forest types, while the lower half contains those species characteristic of the coniferous types, many of which stand farther along in the successional series. The exceptions occur mainly in the Dry column, and many of the low species of dry sites are intolerant of much shade. As an example, Arctostaphylos uva-ursi and Sibbaldiopsis tridentata, both low shrubby "heath" plants, are often found forming a carpet in dry open pine types, but they are absent or at least very rare where the shade factor is high. Other exceptions to the generalization are exemplified by the shade tolerance of some medium shrubs such as Viburnum edule and Rosa acicularis, and of some tall and medium herbs such as Aralia nudicaulis and Petasites palmatus.

The most tolerant herbs of the forest are those listed as low herbs in the Fresh, Moist and Very Moist columns. Some of these species occur in communities of poplar or pine where they grow under the taller shrubs and herbs, and their prominence in the denser coniferous stands is a result of the shading out of the higher layer communities which concealed them in the earlier successional communities. Fig. 39 illustrates this very well. On the other hand, certain of the low herbs show a high fidelity to spruce and fir stands only.

The mosses are the most tolerant of all species, successional development from the more or less open pioneer stands to the close coniferous forest is marked by an increase in importance of this lowest layer community, culminating in the predominantly moss type. Mention has been made of the special forest community which is distinctive because of the virtual absence of any undergrowth species: the "needle cover type"(Moss, 1953). Needle cover is maintained under densely stocked coniferous stands, where light is of low intensity and root competition is presumably of high intensity.

It is worth pointing out that the prominent stratum of the undergrowth in mixed and coniferous stands is a fair index of stocking or stand density, and in many cases it is possible to interpret shrub types as indicating understocking, and needle cover or moss types as indicating overstocking.

Forest Vegetation Types

A short outline of some of the commoner forest communities of the southern boreal forest will now be given, by way of summary of the preceding chapter, using the physiognomy and moisture scheme. The series of communities, from shrub-layer prominent to moss-layer prominent, will be taken up under each moisture class, with brief mention of some of the typical species participating.

(1) The Very Dry and Dry Series of forests, occurring on excessively drained soils, are characterized predominantly by low, grass-herb-shrub vegetation under jack pine or white spruce. Examples are the low-heath (*Arctostaphylos*) pine types on sand plains and dunes, and the prairie or "park" types (*Festuca*-*Agropyron*) on gravelly outwash or on the beach ridges of post-glacial lakes, these latter types being the result of recent invasion of prairies by spruce. Exceptionally dry sites carry considerable *Cladonia* spp., usually under pine although sometimes under spruce. On slightly less dry sites a few examples of tall-shrub pine communities have been seen, featuring *Alnus crispa* and (in one place) *Salix humilis*. In the Nisbet Forest Reserve, Saskatchewan, there is a remarkable dry-herb type of pine stand with an understory of *Thermopsis rhombifolia* (Nutt.) Richards, a leguminous herb.

Possibly the most frequent species in the Dry Series is the Cordilleran grass Elymus innovatus, which in association with Arctostaphylos uva-ursi, Shepherdia canadense and numerous species characteristic of semi-open woodland, forms a characteristic ground vegetation on appropriate sites under pine, aspen and spruce forests from western Manitoba to western Alberta.

(2) The Fresh Series on well-drained soils includes many shrub and herb types, while moss types are uncommon. Tree species are mainly jack pine, white spruce, aspen, birch, plus their mixtures. Corylus cornuta is a common tall shrub in the Fresh Series particularly along the southern part of the Mixedwood Section, while on the plateaux of the Cretaceous Hills and in the northern districts, Alnus crispa becomes prominent as Corylus declines. Other tall shrubs--Prunus virginiana, P. pensylvanica, Crataegus chrysocarpa and Amelanchier alnifolia--characterize many aspen, pine and spruce stands, often in association with Corylus. Medium shrubs which sometimes contribute a well-defined stratum to forests of pine or poplar are Vaccinium myrtilloides and Diervilla lonicera.

The absence of shrubs, whether due to a failure of invasion after destructive fires or to the eliminative action of a closing canopy, may allow herbs to come to the fore. Common tall herbs forming pure dominant strata under poplar, pine, spruce, or mixedwoods are Aralia nudicaulis and Chamaenerion spicatum, associated in turn with Actaea rubra, Disporum trachycarpum, Apocynum androsaemifolium and Viola rugulosa. Under dense canopies, particularly where spruce dominates, low-herb types are prevalent. A layer community of Maianthemum canadense var. interius, Pyrola spp., Fragaria virginiana, Galium septentrionale, Oryzopsis asperifolia, plus Cornus canadensis and Rubus pubescens is usual in such cirumstances.

(3) In the Moist Series (soils only moderately drained) all layer communities may become prominent in association with various mixtures of all tree species. Where the forest stands are such that considerable light penetrates the canopy, tall shrubs often play a primary role in the undergrowth. In the eastern part of the Mixedwood Forest Section, particularly in the Cretaceous escarpment area, Acer spicatum is a characteristic shrub under stands of aspen and aspen-spruce. Corylus cornuta continues to be abundant but with it appear Viburnum trilobum and scattered Sorbus decora. Similarly Aralia nudicaulis and Chamaenerion spicatum are common in tall-shrub types although their association with more mesophytic species such as Solidago lepida, Mertensia paniculata, Petasites palmatus and Heracleum maximum is significant of a trend toward the moister than fresh soils.

In coniferous stands, a low-herb vegetation is usual, with a high percentage of the cover contributed by *Cornus canadensis*, *Linnaea borealis* var. *americana*, *Viola renifolia*, *Mitella nuda*, *Rubus pubescens* and *Petasites palmatus*. While the herb type of undergrowth is common in young coniferous stands, the feather moss stratum apparently develops only with age and is rarely present until stands are more than 70 years old. The development of the forest moss floor is accompanied by the appearance of such species as *Trientalis borealis*, *Goodyera repens* and *Pyrola virens*, in addition to the other low herbs present in the previous stage of development.

(4) The *Very Moist Series* on imperfectly drained soils includes many physiognomic types. All tree species enter into the possible cover composition, although jack pine and tamarack are relatively unimportant.

The tall shrub which characterizes many stands of aspen, balsam poplar and white spruce is *Cornus stolonifera*. *Salix* species also contribute to the tall-shrub stratum, particularly on burned-over areas. Medium-shrub types are frequent, with *Viburnum edule*, *Rubus idaeus* and *Ribes* spp. particularly important in mature and overmature coniferous stands. *Calamagrostis canadensis* with *Aster umbellatus* var. *pubens*, *Anemone canadensis*, *Cinna latifolia*, forms a distinctive tall-herb stratum in some open poplar and poplar-spruce forests. Pteretis pensylvanica and Athyrium filix-femina are sometimes prominent on very moist alluvium.

In the closer spruce and spruce-fir stands, herb types feature the same species as in the moist series, but Equisetum species begin to appear, with Circaea alpina, Geocaulon lividum, Dryopteris spp., Habenaria spp. A moss stratum forms early in the life of such stands, and the older forests almost invariably show a more or less continuous carpet of Hylocomium splendens with Calliergonella schreberi, Dicranum rugosum and Hypnum crista-castrensis.

(5) The Wet Series on soils of poor drainage and high organic content includes forests composed chiefly of white and black spruce and tamarack. The latter is the species most tolerant of excessive soil moisture, hence its pioneer role in the forest invasion of peats. On the firmer and slightly drier peaty deposits, formed in areas of stagnating ground water, black spruce is the typical tree. White spruce shows a tendency to colonize muck or fen soils which are apparently formed under the influence of various conditions such as alkalinity of substratum, grass and sedge vegetation, and moving ground water.

The commonest tall-shrub type is characterized by Alnus rugosa, associated usually with tamarack and white spruce. Tall Salix species are not uncommon in the Wet Series, but their intolerance to shade tends to reduce their significance speedily in the physiognomy of developing forests. The medium-shrub types of black spruce are well known, particularly those characterized by *Ledum groenlandicum*, *Chamaedaphne calyculata*, *Kalmia polifolia* and *Andromeda polifolia*. With white spruce, *Ribes* spp. *Rubus idaeus* and *Rhamnus alnifolia* are common medium-shrub associates. Tall herbs are rarely prominent in stands of larch and black spruce, but the open variants of the swamp border white spruce stands sometimes show a conspicuous layer of *Cirsium muticum*, *Aster puniceus*, *Sium suave*, and others. *Carex* spp. characterize many tamarack and spruce stands. There is one readily recognizable medium-herb type in which *Equisetum arvense* is abundant. It is usually associated with mosses and with the same low herbs that appear in the Very Moist Series. Well-defined moss types are common, with *Hylocomium splendens*, *Climacium americanum*, *Aulacomnium palustre* and *Mnium* spp. on the fen and muck soils with white spruce and tamarack, and *Sphagnum* species or *Camptothecium nitens* in the deep peats with black spruce.

Groups of Species as Indicators of Moistness of Site

Those who are thoroughly familiar with the vegetation of a particular region are often able to judge the moisture relations of any given community with considerable accuracy. Unfortunately the approach through experience is not possible for everyone, and a more objective method which all may use is highly desirable. The vegetation table offers some help, for if the moisture-preference groupings are soundly based, as the author believes they are, then anyone with a moderate knowledge of the flora should be able to interpret the moisture relations of a particular area from the species present. To take an artificial example, a site supporting Cornus stolonifera, Ribes hirtellum and Dryopteris cristata ("Very Moist" species), should have similar moisture conditions to one supporting Viburnum edule, Mitella nuda and Hylocomium splendens (also "Very Moist" species), even though the forest cover on the two areas may differ in quality and quantity. Unfortunately the species making up actual plant communities never fall nicely into one moisture-preference column as in this example, and therefore it is difficult by inspection alone to determine what moisture regime is indicated.

To circumvent this difficulty, various methods were tested in an attempt to derive for any given sample of forest vegetation a single numerical index, based on the distribution of the species as checked on the table. The following practical and theoretical considerations guided the development of a "vegetation moisture index":

(1) For maximum usefulness the method must be simple-- not much more than recognition of the plant species can be expected of those who will use it. Therefore, if possible,

an index must be derived from presence or absence of species rather than from features such as cover and density which are difficult to assess without quadrat or line-intersect studies.

(2) Certain accommodating species occupy practically all habitats within a given forest district. The broad ecological amplitude of such species (here called "ubiquists") renders them more or less useless as indicators. Little weight should be given to them when calculating a moisture index, even though they may be very prominent constituents of the vegetation. Preliminary studies are necessary to determine which species fall into the category of "ubiquist".

(3) Rare plants (defined as those which in quadrat studies have the very lowest frequencies and cover-abundances, or which in presence studies are not readily found) should be used very cautiously if at all in working out a moisture index, as the danger is always present that members of this group are ephemeral invaders from outside the community.

(4) The ecological amplitude of species listed in the very moist and wet columns is, in general, narrower than that of species on the drier side of the table. In other words, the former are better indicators than the latter and should be given more weight when calculating an index. Why this should be so is not well understood, but it is

apparent in the field that the more mesophytic and hydrophytic species are tied rather closely to their appropriate habitats, while species which are able to tolerate drier conditions are not by that fact necessarily confined to the drier sites.

The method which was adopted as giving the most satisfactory results assigned a weight of 1, 2, 4, 8 and 16 to species which occur in the Dry, Fresh, Moist, Very Moist and Wet columns, respectively. Ubiquists are omitted from the calculations, as also are rare species, except in particular circumstances. The geometric increase of values is a recognition of the greater significance of species on the wetter side of the table. Steps in the calculations are as follows:

(1) A special field sheet, drawn up in the same form as the vegetation table and listing the important forest species of the district in their appropriate moisture-preference columns, is used. Ubiquists, identified from preliminary studies, are specially marked, so that they can be readily kept apart from the others in subsequent calculations. A place is provided for noting the dominant and secondary strata of the undergrowth ("tall shrub", etc.) which characterize each stand.

(2) The investigator checks off all the species which he finds in the particular stand being studied. In practice

it has been found preferable to enter beside each species an ocular estimate of cover-abundance, since this increases the value of the list for other phytosociological purposes. By specifying in field instructions that on each plot a minimum number of species (usually 25) must be listed in addition to the ubiquists, an adequate sample is assured.

(3) On completion of the tally, the species in each of the five moisture columns are summed, and the totals are weighted by multiplying by the appropriate number, whether 1, 2, 4, 8 or 16. At this stage the ubiquists are excluded, and the rare species are used only when their omission would reduce the sample below 20 species.

(4) The figures from all columns are now summed, the total is divided by the number of species entering into the previous calculations, and the quotient is multiplied by 10 to eliminate the decimal. The resulting figure is the Vegetation Moisture Index, abbreviated hereafter as the VMI.

The VMI was worked out for various forest sample areas in Manitoba and Saskatchewan during the field season of 1954, and it was found that stands in which white spruce is a constituent species segregated along an index gradient from 15 (driest) to 80 (wettest). Three examples are shown in Table XL.

TABLE XL

THE FOREST VEGETATION OF THREE SITES, ILLUSTRATING THE DERIVATION OF VEGETATION MOISTURE INDICES

A. Plot 500 - Duck Mountain Forest Reserve, Manitoba.
Open white spruce and aspen stand on excessively drained till.
Dry, grass-herb community (Elymus-Fragaria-Arctostaphylos).

"Very Dry and Dry": 14 species (plus 3 rare)

4	Elymus innovatus	1	Aster laevis
2	Arctostaphylos uva-ursi	1	Comandra richardsiana
1	Agastache foeniculum	1	Oryzopsis asperifolia
1	Hedysarum alpinum var. americanum	1	Polygala senega
		1	Oxytropis gracilis
1	Potentilla arguta	1	Viola adunca
1	Astragalus alpinus	+	Lilium umbellatum
1	Halenia deflexa	+	Solidago hispida
1	Anemone multifida	+	Antennaria campestris

"Fresh": 5 species

1	Amelanchier alnifolia	1	Vicia americana
1	Lathyrus ochroleucus	1	Viola rugulosa
1	Thalictrum venulosum		

"Very Moist": 1 species

1 Salix bebbiana

"Ubiquists": 6 species

3	Fragaria virginiana	1	Galium septentrionale
1	Rosa acicularis	1	Schizachne purpurascens
1	Aster ciliolatus	1	Smilacina stellata

Sum of the weighted values of the species in each moisture group:

$$(14 \times 1) + (5 \times 2) + (1 \times 8) = 32$$

VMI: $32/(14 + 5 + 1) = 1.6 \times 10 = \underline{\underline{16}}$.

B. Plot 512 - Duck Mountain Forest Reserve.
Mature white spruce and birch, on moderately drained till.
Moist, tall shrub-and-herb community (Corylus-Aralia-Mitella).

"Dry" species: 1 (plus 1 rare)

1	Oryzopsis asperifolia	+	Elymus innovatus

"Fresh" species: 3 (plus 4 rare)

3	Corylus cornuta	+	Prunus virginiana
1	Symphoricarpos albus	+	Actaea rubra
1	Lathyrus ochroleucus	+	Chamaenerion spicatum
		+	Pyrola secunda

"Moist" species: 7 (plus 1 rare)

2	Mertensia paniculata	1	Viola renifolia
2	Petasites palmatus	1	Linnaea borealis var. americana
2	Cornus canadensis		
2	Rubus pubescens	+	Sorbus decora
1	Pyrola virens		

"Very Moist" species 8(plus 1 rare)

2	Viburnum edule	1	Ribes triste
2	Circaea alpina	1	Rubus idaeus
2	Mitella nuda	1	Galium triflorum
1	Cornus stolonifera	+	Dryopteris cristata
1	Ribes hirtellum		

"Ubiquists": 6 (plus 1 rare)

3	Aralia nudicaulis	1	Fragaria virginiana
1	Rosa acicularis	1	Maianthemum canadense var. interius
1	Aster ciliolatus		
1	Galium septentrionale	+	Schizachne purpurascens

Sum of the weighted values of species in each moisture group:

$$(1 \times 1) + (3 \times 2) + (7 \times 4) + (8 \times 8) = 99$$

VMI: $99/(1 + 3 + 7 + 8) = 5.2 \times 10 = \underline{\underline{52}}.$

Table XL cont.

C. Plot 510 - Duck Mountain Forest Reserve.
Mature white spruce, on poorly drained (muck) soil.
Wet, herb-moss type (<u>Equisetum</u>-<u>Mnium</u>).

"Fresh": 1 species (plus 1 rare)

1	Disporum trachycarpum	+	Chamaenerion spicatum

"Moist": 3 species

2	Mertensia paniculata	1	Petasites palmatus
2	Cornus canadensis		

"Very Moist": 11 species (plus 2 rare)

5	Mnium spp.	1	Circaea alpina
3	Mitella nuda	1	Galium triflorum
1	Viburnum edule	1	Habenaria obtusata
1	Ribes hirtellum	1	Moneses uniflora
1	Ribes triste	+	Ribes glandulosum
1	Anemone canadensis	+	Poa palustris
1	Heracleum maximum		

"Wet": 2 species (plus 2 rare)

5	Equisetum arvense	+	Ribes hudsonianum
1	Carex disperma	+	Stachys palustris

"Ubiquists": 4 species

1	Aralia nudicaulis	1	Schizachne purpurascens
1	Aster ciliolatus	1	Fragaria virginiana

Sum of the weighted values of species in each moisture group:

$$(1 \times 2) + (3 \times 4) + (11 \times 8) + (2 \times 16) = 134$$

VMI: $134/(1 + 3 + 11 + 2) = 7.9 \times 10 = \underline{79}$.

If there were some objective method of determining the soil moisture regimes of given homogeneous areas, then it would be possible to check the reliability of the VMI's, but none such exists. The system proposed by Hills (1950, 1952) to which reference has earlier been made is one of the least subjective which can be used, as it derives moisture regimes of sites primarily from the study of soil profile development, pore pattern of parent material, and topographic position--all determinable with a fair degree of exactitude. Basic work along these lines was carried out in conjunction with quadrat studies of minor vegetation on one-tenth-acre forest sample plots at the Riding Mountain Forest Experimental Area in 1952, hence a comparison was possible of soil moisture regimes according to Hills' method, and of VMI's as later worked up from the quadrat frequency-abundance data. Table XLI shows the results from Plots 301 to 316, inclusive, the VMI's being based on the 25 most frequent species, exclusive of ubiquists, on each plot.

TABLE XLI

COMPARISON OF SOIL MOISTURE REGIMES AND VEGETATION MOISTURE INDICES ON SIXTEEN ONE-TENTH-ACRE PLOTS

Plot Number	Soil Moisture Regime	Vegetation Moisture Index	Remarks
301	0	22	
308	1	18	
303	1	23	
316	1	23	
306	1	24	
313	2	28	
304	2	30	--- Slope community
307	2-3	28	
312	3	29	
305	3	32	
310	4	41	--- Uneven surface
309	4-5	39	
311	5	46	
302	5	49	
314	5	64	--- Depression in plot
315	6	65	

A rather good correspondence between increasing moisture regime and increasing vegetation moisture index is shown. There are doubtless a number of reasons why the two scales do not coincide. The soil moisture regimes were determined from the examination of single soil pits, in other words, they represent "point" studies, while each VMI was derived from the areal study of an entire plot. For this reason the best coincidence is to be expected on very homogeneous plots, and the poorest on those of irregular surface or on slopes, as the notes in the table suggest. Also, the use of plant species as indicators is not straightforward. A complicating fact is that each species reflects a slightly different environment according to size and to depth or preference of rooting. Small species are influenced by surface conditions while large species usually are influenced by deeper as well as the shallow soil horizons. Thus the small herbs on well-leached, surface-dry soils may reflect more xerophytic conditions than do the associated tall shrubs and herbs, but on the same sites if much decayed wood lies on the ground, the comparative moisture indications of the small and large plants may be reversed. In general however there is a good correspondence between moistness of site and the associated elements of the vegetation, although common sense cannot be dispensed with both in working up the VMI and interpreting its usefulness in particular situations.

Two additional facts support the contention that the proposed method of determining a Vegetation Moisture Index for site, using the groupings of species shown in the Vegetation Table, will be found useful in the field. The first is that communities on long slopes segregate out as expected, with a relatively low VMI on the upper slope and a relatively high VMI on the lower slope. As an example, the following VMI's were calculated on five plots sampling the forest on a north-facing hillside in the Duck Mountain Forest Reserve--36, 43, 42, 44 and 48--this representing the sequence from a birch stand on the upper slope to a spruce stand on the lower slope.

The second fact is that samples of different vegetation growing on apparently similar sites work up to very similar VMI's. For example, it is not uncommon to find patchy forest types in which well-stocked areas with a shade-type flora alternate with small, more open areas where better light conditions allow the development of richer vegetation. Provided that the patches are not so large as to cause marked differences in such factors as tree-root distribution, surface temperature, and moisture, it has been found that the VMI's of the various patches usually fall within half a dozen units of one another.

It is not claimed that the vegetation moisture index provides more than a rough measure of site conditions, yet it apparently has possibilities which could be improved upon by more exact knowledge of the ranges and tolerances of the minor forest plants. Used in conjunction with Hills' soil sites (op. cit.) it may prove to have considerable value, as it can be called upon where soil conditions are difficult to interpret, or where the emphasis is on rapid reconnaissance. For a given district it would seem feasible to correlate soil moisture regimes and VMI's so that both might be used together or interchangeably. In Table XLII an equivalency is tentatively suggested for the Riding Mountain-Duck Mountain area at the southeastern extremity of the Mixedwood Forest Section, based on the comparisons of soil moisture regimes determined in the field and VMI's worked up from the forest vegetation lists.

TABLE XLII

EQUIVALENCE OF VMI CLASSES AND SOIL MOISTURE REGIMES IN UPLAND FORESTS OF THE RIDING MOUNTAIN-DUCK MOUNTAIN AREA

VMI Classes (Rowe)	Moisture Regimes (Hills)	General Moisture Class
Less than 25	0, 1	Very Dry and Dry
25-28	2	Moderately Fresh
29-34	3	Fresh
35-42	4	Moderately Moist
43-52	5	Moist
53-65	6	Very Moist
More than 65	7, 8	Wet

As a comment on the foregoing Table XLII, it might be supposed that all "Dry" plots should place in the 10 to 20 VMI range and all "Wet" plots in the 80 to 160 range. However, in almost every kind of forest community there has been found a scattering of "Fresh" and "Moist" species whose presence tends to raise the VMI of the dry and lower the VMI of the wet plots. Therefore the data in hand suggested that all VMI's less than 25 should be designated as "Dry" and all greater than 65 as "Wet". The intermediate classes have been made of unequal width, increasing by 4, 6, 8, 10 and 13 units, respectively, in recognition of the theoretical tendency toward a geometrical increase in VMI which follows from the geometrical increase in weight given to each succeeding moisture class.

The vegetation table, the vegetation moisture index, and the index classes (above), have all been drawn up with a view to usability in the eastern part of the B.18 Forest Section, particularly in stands of white spruce and aspen. Studies in other forest sections, or studies which emphasize other types, would require that new tables be devised to take account of the significant species. For example, work confined to jack pine types would require a considerable expansion of the left-hand side of the table, since species in the two right-hand columns (very moist and wet) would be largely omitted. The same general approach could be used however.

Discussion

Various classifications of forest types and forest sites have been built around the concept of gradients in environmental factors, as the following examples illustrate. Heimburger (1934) refers to early work by Pogrebnjak who "plotted the natural limits of distribution of certain plants on two axes representing the main edaphic factors of growth, namely mineral soil fertility and moisture".

Thus a series from poor-to-rich nutrient status was combined with a series from dry-to-wet moisture regime, and the scheme was applied to yield classes for forest trees. A similar approach to the classification of forest communities in Russia can be seen in the work of Sukachev (1928).

More recently Anderson (1952) classified "locality units" on a co-ordinate system, using six fertility and four moisture groups. The resulting site classes were named after the predominant plant species usually occurring on them. Tore Arnborg (1950) used a similar system in a forest site classification for northern Sweden, with five moisture classes (arid, dry, fresh, moist, wet) and four nutrient-regime classes which, from poorest to best, are indicated by dominance of the following: ericaceous shrubs, oak fern with ericaceous shrubs, herbs with ericaceous shrubs, and herbs. Working in New Brunswick, Long (unpublished, 1952) has also outlined a forest type-and-site classification dividing the three stable forest associations of the Acadian Research Area into moisture types (dry, fresh, moist and wet) on the basis of the "apparent moisture requirements" of the vegetation. Still another worker exploring along similar lines is Lossee (1954), who has prepared a tentative site classification for the Abitibi Experimental Area based partially on plant indicators as they relate to gradients of soil moisture within three fertility series. In addition to the above examples drawn from forestry literature, many more references could be quoted to illustrate the considerable interest which is presently being shown by ecologists in "gradient analysis" as an approach to specific problems of vegetation (see for example, Whittaker, 1954).

It cannot be expected that the distribution and growth of plants will always show a neat correlation with gradients in the intensity of particular factors, as compensatory influences in the environment plus variable ecological tolerances in the plants will tend to conceal much of the relationship. Nevertheless, detectable responses of plants to factor variations do occur, and careful study by appropriate techniques will disclose them.

The responses of plants to variations in intensity of light and of moisture have been discussed at some length in the main body of this chapter. Two environmental factors, or rather factor-complexes, whose gradients might be correlated with plant indicators, are soil fertility and ecoclimate. Mention has already been made of fertility series set up by some investigators for purposes of site classification. Much of the reported work is highly subjective however, partly because the concept of fertility is poorly defined and partly because of a lack of knowledge of the optimal nutrient requirements for tree growth. A recent article by Wilde (1955) illustrates an improved approach to the problem.

The other factor-complex, ecoclimate, has been little studied in relation to plant indicators. One fruitful line of research is the study of plant distributions, as the range of a species suggests the climatic conditions to which it is adapted. Thus within the boreal forest the warmer sites are often characterized by plant migrants from the eastern deciduous forest, while colder sites are inhabited by arctic-alpine plants. A second approach can be made through studies of phenology, for the periodicity of leafing, flowering, etc., is closely related to climatic influences.

The suggestion is made here that the methods used in the development of a Vegetation Moisture Index might also be applied in working out indices of other important factors or factor-complexes. The approach is as follows: First determine, as exactly as possible, the relative positions of the plant species along a gradient from low intensity to high intensity of the selected environmental factor. As previously pointed out, this requires intensive field work, combining close observation and good judgement with whatever instrumental measurements and analyses are appropriate. Next, divide the gradient into classes or series, and assign empirical weights to each. When calculating the final index from given samples of vegetation, take into account only the species whose significance in respect to the factor concerned is reasonably assured.

SUMMARY

1. Very few detailed studies of the forest vegetation of west-central Canada have yet been made. The purpose of the present project was to examine and describe the composition, structure and ecological relationships of some of the more important forest communities in western Manitoba and in Saskatchewan. The work was carried out in twelve main localities, from the Riding Mountain in the east to Loon Lake in the west.

2. The area of study, here called the "Southern Boreal Forest", extends from the Cretaceous escarpment westward to Alberta. It lies within a dry, subhumid climatic province, with a total annual precipitation of 17 to 19 inches and an average annual moisture deficiency (Thornthwaite) of 4 to 6 inches. The forests are dominated by eight principal tree species, _Populus tremuloides_, _Picea glauca_, _Populus balsamifera_, _Picea mariana_, _Betula papyrifera_, _Pinus banksiana_, _Abies balsamea_ and _Larix laricina_, of which the first two are of most importance in the forests of upland sites. The soils are of the grey wooded (podzolic) group, developed on deep, more or less calcareous, glacial and post-glacial deposits.

3. The unit of detailed study was a plot, square or rectangular and of one-tenth- or one-fifth-acre in size, so located as to sample a homogeneous forest-site unit.

On each plot a complete study of the total forest community was made, using accepted ecological methods. Significant features of site, including ecoclimate, moisture regime, pore pattern of substratum and calcareousness of soil, were studied in relation to vegetational patterning. In addition to the intensive studies of several hundred sample plots, a less detailed examination was made of many other forest stands and their sites.

4. The southern boreal forest corresponds to one homogeneous floristic province. The centre of origin of the migrant flora which came to this area following Wisconsin glaciation has generally been placed eastward in the vicinity of the Great Lakes, although there is evidence of an unglaciated survival area in the foothills of western Alberta. In the light of what is now known concerning glacial and post-glacial history, it seems unlikely that the flora of the southern boreal forest emanated from southeast of the Lake Agassiz basin. Rather, evidence is produced to support the contention that the forest survived in large part at least along the southern and western borders of the last continental ice sheet, occupying the favourable sites provided by valley sides and shores of peri-glacial rivers and lakes. New fossil evidence of the presence of spruce, pine and tamarack on the west side of Glacial Lake Agassiz during its initial stage shows conclusively that

important boreal elements were already present on the western plain in Late Wisconsin times, when ice and water in the Agassiz basin must have constituted an effective barrier against plant migration from the east. The present distribution of certain shrubs and herbs points to the importance of species "drift" into the area from the west.

5. The autecology of the eight tree species is discussed with particular attention to habits which are believed to be of special significance for competitive ability and survival: site preferences, habits of reproduction, rooting behaviour, tolerance to shade and cold, palatability to animals, and length of life. All the trees are adapted to survive recurring fires with the exception of fir, the latter species alone apparently depending on prior forest communities to prepare conditions of humus and shade favourable for its invasion.

6. The theoretical approach adopted in order to "make sense" of the diversity in the vegetation is outlined with emphasis on the ecosystem concept. The necessity of including site within the framework of vegetational studies is argued, and a system for describing unit sites using ecoclimate, soil moisture regime, pore pattern of soil parent material, and calcareousness of soil is presented. Within the area studied one distinct site difference stems from the greater amount of lime carbonate in the parent

materials of soils in the eastern than in the western sector. The question of discreteness of vegetational units is examined, and it is shown that many different circumstances may contribute to the appearance of either the discrete community or the continuum. The abstract "forest type", in the Russian sense, is adopted as the unit of forest description. In these studies the forest type is defined by the dominant trees and by characteristic constant species of the undergrowth. The forest vegetation and its successional relationships are described within environmental "series" based on moistness of site. Examples of vegetation and of typical soil profiles are shown pictorially.

7. In the Very Dry Series a Picea/Agropyron community is formed wherever white spruce invades native prairie. On nutrient-poor sands, a stable Pinus/Arctostaphylos-Cladonia forest type is usual.

8. In the Dry Series on moderately calcareous grey wooded soils a stable Picea/Elymus-Fragaria forest type is defined, and on these sites stands of Pinus and Populus frequently have the same kind of undergrowth as the spruce. In closer coniferous stands, the grass-herb vegetation is partly replaced by feather mosses. In the Fresh Series on moderately calcareous soils, old forests from which the hardwoods have died are frequently open shrubby types (Picea/Rubus). Younger stands which originate after light

(crown) fires are mostly of the Populus/Corylus-Aralia-Viola-Oryzopsis forest type. This may slowly be invaded by white spruce with the eventual formation of an open, uneven-aged coniferous type. Young spruce-dominated stands--the Picea (Populus)/Cornus-Linnaea-Pyrola forest type--sometimes appear after severe ground fires. There is evidence that such stands may not develop into feather moss types as they mature.

9. On weakly calcareous (deep) grey wooded soils, the forest communities toward the drier side of the moisture gradient are characterized by the presence of ericaceous shrubs, Lycopodium spp. and Alnus crispa. In the Dry Series, Elymus innovatus is usually abundant under spruce, pine and aspen. In the Fresh Series, closed coniferous stands of the Picea (Abies)/Hylocomium-Calliergonella forest type are sometimes formed. Young tall-shrub types of aspen and white spruce are common, and where the spruce component is prominent, the Picea (Populus)/Cornus-Linnaea-Vaccinium forest type can be recognized. Feather moss types of black spruce and pine occur infrequently. A Pinus/Alnus-Lycopodium forest type on the moist sites of moderately calcareous soils resembles some of the communities formed on fresh sites of the weakly calcareous soils.

10. On all soils in the Moist and Very Moist Series, Picea and Abies/Hylocomium-Viola-Trientalis forest type may

form if conditions favour the mass invasion of the conifers. With advancing age, the community develops into a mosaic *Abies*-*Picea*/*Hylocomium*-*Rubus* forest type consisting of patches of old conifers with a moss undergrowth, and of stand openings dominated by brambles (*Rubus idaeus* and *Ribes* spp.) or by fir regeneration. Spruce (and sometimes paper birch) regenerates sparsely on decayed logs and stumps. This is a self-perpetuating steady-state, a fundamental or "climax" community. More open communities are frequently of the *Picea*/*Mitella*-*Petasites*-*Mertensia* forest type. On "rich" alluvial and slope sites the open forest type may be stable due to the vigorous undergrowth which effectively prevents mass invasion by the conifers. The *Populus*/*Cornus*-*Equisetum* community is a common young forest type; the *Populus*-*Picea*/*Calamagrostis*-*Aster*-*Anemone* forest type is of more local occurrence. Feather moss black spruce communities are found on upland sites under conditions of cool ecoclimate.

11. The Wet Series includes all forest on soils which at some prior time were too wet for tree growth. A *Picea* (*Abies*)/*Equisetum*-*Hylocomium* forest type is recognized on meadow or fen soils, and a *Picea*/*Ribes*-*Alnus* forest type on muck soils. The tamarack forest type (*Larix*/*Carex*) on poorly consolidated organic soils, and the black spruce forest type (*Picea*/*Sphagnum*) on deep peat are briefly mentioned.

12. There is no single "climax" community toward which all forest development trends. Different sites have their appropriate vegetational patterns which are stable, or not, according to a variety of circumstances. The trends within mixed stands on the various sites require more study.

13. A review of relevant work by other investigators is given. A close correspondence can be seen between the vegetation of the southern boreal forest in Manitoba-Saskatchewan and that of Alberta as described by Moss.

14. A generalized descriptive scheme is developed for communities in the southern boreal forest, based on physiognomy and moistness of site as reflected in the composition of undergrowth. Stands are described, for example, as dry low-herb types, fresh tall-shrub types, or moist moss types. A vegetation table designed to facilitate the characterization of communities is given, and its use as a general description of many forest communities and of their successional relationships is briefly outlined.

A method of deriving an index of site moistness from the species present in a given stand, using the vegetation table, is presented. Finally, it is suggested that similar methods might be used to derive indices of soil fertility and ecoclimate for use in stand description and forestry research.

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