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THE
ECOLOGY OF LODGEPOLE PINE IN ALBERTA
and its Role in Forest Succession

by
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K. W. Horton*

Introduction

Forest ecology involves all the factors which influence the composition and development of a forest stand. These factors may be reduced to three major categories—external operative forces, site effects, and species composition. A study of the ecological behaviour of a single species must embrace all these points.

This report presents the findings of such a study of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) in Alberta. It was initiated to provide basic information on the floristics of pine communities, the successional relationships between pine and associated species, and the broad influences of climatic region, stand history and site on pine establishment and development.

Lodgepole pine is the dominant pioneering species in three of the forest regions designated by Halliday (1937) for Alberta, the Montane, the Subalpine and the Foothills Sections of the Boreal Forest. In the mountains, Engelmann spruce (*Picea engelmanni* Parry) is a frequently associated species, and in the foothills, white spruce (*Picea glauca* (Moench) Voss var. *albertiana* (S. Brown) Sarg.) and black spruce (*Picea mariana* (Mill.) BSP.) are frequently associated. Alpine fir (*Abies lasiocarpa* (Hook) Nutt.) is another important tolerant, usually more abundant in the older pine stands. The only other major associated species is aspen (*Populus tremuloides* Michx.), which attains prominence solely in the eastern or lower part of the foothills.

Several allusions may be found in the literature to secondary forest succession in these regions. Among the most relevant references are Bloomberg (1950) and Cormack (1953), who have recognized a general trend on the east slope of the Rockies from lodgepole pine, established following fire, to a spruce-fir climax. To the north and east in the lower foothills, the situation is more complex through the prevalence of mixedwoods and the local lack of fir. Again, however, succession from pine and aspen to spruce is indicated (Moss 1953).

Experiments on various silvical characteristics of lodgepole pine are currently underway in Alberta and it is hoped that the broad background information provided by this investigation, together with the results of those experiments, will clarify the picture of the species' habits.

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METHODS

The extensive distribution of lodgepole pine in Alberta and the number of variables involved in the study necessitated primarily a broad survey approach. Several districts within each of the three forest regions were selected for investigation on the basis of widespread distribution. In each district as many ecologically significant stands were examined as time allowed—stands of various compositions, ages and densities on diverse sites.

Several techniques of examination were used. In the broad survey, observed typical conditions were sampled by selected plots. These were 1/40-acre in size, closely approximating the standard ecological quadrat of 100 square metres. Data collected thereon included diameters, dominant heights and age ranges of each species. Along the centre line of each quadrat a belt transect was used to tally the reproduction and the ground vegetation. Atypical stands of ecological interest were described simply by subjective notes similar to but more general than the plot information. In transitional conditions, "associational transects" were employed. This involved running direct lines across-country and continuously noting the change in tree cover which accompanied a change in site, a subjective method well suited for rough terrain.

In each stand an assessment of site was made, considering local climate and soil moisture in accordance with Hills' method (1952). Soil pits were dug to examine the profile development, texture, and water table depth, while aspect, slope and physiography were used in assessing local climate. In addition the history of every stand was deduced from any available evidence such as age-class structure, increment variations and stump or fire scar occurrences. The nature of the previous stand, the question of local seed sources and the effects of damage agents were also considered, thereby including all the major factors involved in the origin and development of each stand.

This broad survey gave general indications of many trends, some of which required further investigation. Thus in a few selected stands intensive sampling methods were used. Most of this work was done in the Subalpine region, in stands which were in advanced stages of succession from pine to spruce-fir. The line plot system was used to provide quantitative data on certain processes of succession, namely, the effect of site on rate of succession, the age-class structure of spruce and fir established under pine, and the growth and reproductive trends of spruce and fir following natural pine mortality.

The stem analysis technique was also used, particularly in the pine-mixedwood type, to compare relative species competition. It involved selecting competitive pairs of trees of two species, for example a dominant aspen or spruce competing with a dominant pine, or an aspen suppressing a pine of equal age (or vice versa). Each tree was sectioned at 5- or 10-foot intervals, and ring counts enabled height development to be related to age.

RESULTS

This sampling of lodgepole pine in its various regions, habitats and stages of development afforded a general picture of the species' status in Alberta. The extent of the coverage is shown on the map (Figure 1). Within its common range, pine was found to be the dominant subclimax species on practically all sites. The exceptions are well-developed bogs, alluvial valley floors and timberline areas, all of which are special edaphic conditions relatively unimportant on an areal basis.

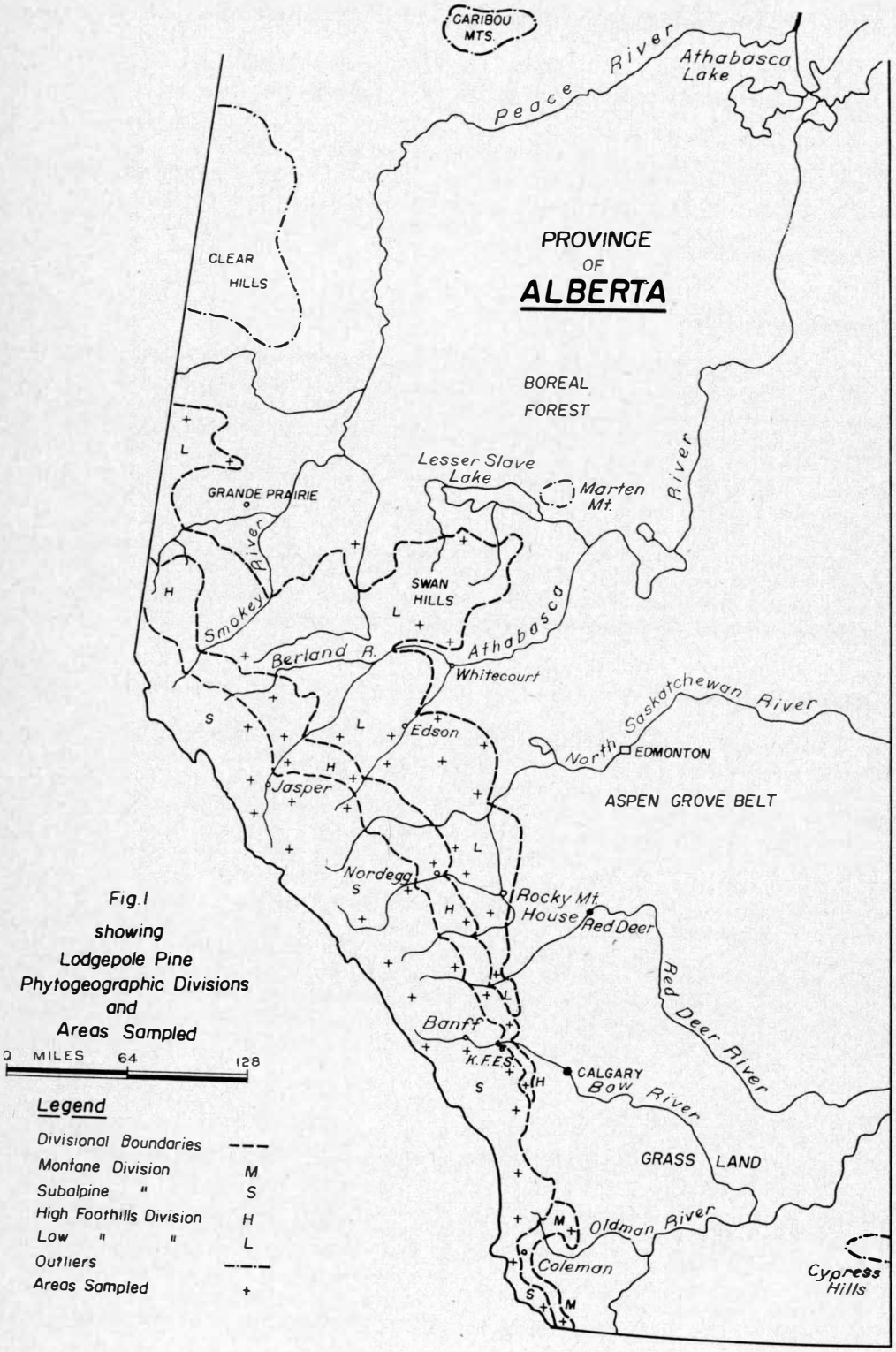


Fig. I
showing
Lodgepole Pine
Phytogeographic Divisions
and
Areas Sampled

Phytogeographical Divisions of Lodgepole Pine

The lodgepole pine community of Alberta is described below in four phytogeographical divisions, each distinguishable on several counts.

Broadly they correspond with Halliday's, but in detail several revisions are made. The tree species mentioned are all associated with pine in various degrees, forming the mosaic of cover types. Figure 1 shows the approximate boundaries of the four divisions. Four known outlying areas of lodgepole pine are also shown. It is significant that each of these occurs on ranges of high hills and plateaux.

Montane Division

This forest is confined to relatively small areas in the southwest corner of the province, where it occupies a middle altitudinal zone between prairie and subalpine vegetation. It appears to be a northern extension of a forest association which is common on the east slope of the Rockies in Montana (Halliday, 1937). It is represented in Halliday's classification as the M-5 section of the Montane region. Lodgepole pine and Douglas fir (*Pseudotsuga menziesia* (Poir) Britton var. *glauca* (Mayr) Sudw.) are the chief tree species. Engelmann spruce, alpine fir and limber pine (*Pinus flexilis* James) form an admixture at higher elevations, and stunted aspen groves and white spruce occur along the grassland fringe. Certain ground vegetation species distinguish the division, prominent among which are *Ribes viscossimum, Berberis repens, Pachystima myrsinites, Xerophyllum tenax, Chimaphila umbellata* and *Viola orbiculata.*

Subalpine Division

This closely corresponds with Halliday's SA 1 Section which includes the Rocky Mountains east of the Great Divide from about 4,500 feet in elevation to timberline. The characteristic tree species is Engelmann spruce but subclimax stands of lodgepole pine predominate. White spruce replaces Engelmann in the lower valleys and hybrid forms of the two species are common in the intermediate zone. Black spruce is present in this division only north of the North Saskatchewan River and then only at lower levels, presumably as a result of intrusion from the foothills along the low Athabasca valley. Alpine fir is a frequent component, particularly in older stands. Douglas fir occurs spasmodically in the three main mountain passes, which distribution suggests intrusion from British Columbia. The poplars attain fairly good development in protected valley sites but seem incapable of competing with the coniferous species on the mountain slopes. Of the lesser flora, *Vaccinium scoparium* and *Menziesia glabella* best characterize the division.

High Foothills Division

Halliday's B 19 or Foothills Section of the Boreal Forest Region, which he describes as an ecotone between boreal and subalpine conditions, has been divided in two on the basis of geographic and vegetative differences. The long, narrow strip of country typified by high, wooded hills and deep valleys, usually between the altitudes of 4,000 and 6,000 feet, comprises the High Foothills Division. Along with lodgepole pine, which is preponderant, typical white spruce (rather than the Engelmann-white spruce complex of the Subalpine) and black spruce are the major species. Black spruce occurs sporadically in the southern

part of the division, becoming frequent above the North Saskatchewan River. Alpine fir is somewhat less prevalent than in the mountains and poplar is again relatively unimportant. Because of its transitional nature there are no characteristic species in the lesser flora here.

Low Foothills Division

Low hills and plateaux between 3,000 and 4,000 feet in elevation in the south and down to about 2,500 feet farther north comprise this division. Though still an ecotone, it much more closely resembles boreal conditions. The outstanding difference between this and the High Foothills Division is the prevalence of mixedwood types. Aspen and, to a much lesser extent, balsam poplar (*Populus balsamifera* L.) are able to compete with lodgepole pine as post-fire pioneers here. White and black spruce are common but alpine fir is comparatively rare. The ground vegetation differs from the other divisions in the prevalence of many elements of the boreal mixedwood forest, such as *Lonicera involucrata*, *Viburnum edule*, *Lathyrus ochroleucus* and *Equisetum sylvaticum*. Three species, *Vaccinium myrtilloides*, *Maianthemum canadense* and *Aralia nudicaulis*, are considered to be indicators of the low foothills.

Ground Vegetation Association

Table 1 is a list of the lesser flora associated with lodgepole pine in its four divisions. It is compiled from assessments made in 404 different stands, representing a great variety of conditions. Because of this variation, a broad subjective form of classifying specific importance is used, a frequency distribution scale as shown. The most significant figures, those which best portray phytogeographic differences, are in bold-face type.

This list coincides for the most part with those compiled by Cormack (1953) for the south, and by Moss (1953) and Raup (1934) for pine associations of northeastern Alberta.

Table 1 indicates that although minor specific differences exist between the divisions, there is a strong similarity in floristic structure and composition. Thus a general lodgepole pine association for the whole might be derived as follows:

Pinus—Picea—Vaccinium—Elymus—Linnæa—Feather moss—Peltigera

The actual species composition varies with site, density of the pine canopy, and stand age, and the resulting combinations are so numerous that it seems pointless to attempt further arbitrary classification. Rather, it would appear to concur with the concept of the vegetational continuum, which envisages a continually varying series of species occurring on an environmental gradient largely controlled by the vegetational interactions. In the lodgepole pine community the most important interaction is succession which is primarily dependent on fire.

TABLE 1

GROUND VEGETATION

Species Associated with Lodgepole Pine in its Four Forest Divisions in Alberta

Species	Montane	Subalpine	High Foothills	Low Foothills
Shrubs				
Ledum groenlandicum	—	2	3	4
Rosa acicularis	2	3	3	**5**
Shepherdia canadensis	2	3	2	2
Vaccinium vitis-idaea	—	2	5	4
V. caespitosum	—	2	3	3
V. myrtilloides	—	—	—	**4**
V. membranaceum	—	2	2	1
V. oreophilum	**3**	1		
V. scoparium	2	**3**		
Menziesia glabella	2	**3**		
Juniperis communis	2	3	2	1
J. horizontalis		1	1	1
Arctostaphylos uva-ursi	2	2	2	2
A. rubra		1		
Salix spp.	2	3	2	3
Alnus crispa	2	2	2	3
Empetrum nigrum		2	**3**	
Spiraea lucida	**5**	2	1	2
Symphoricarpos alba	3	1	1	1
Lonicera involucrata	1	1	1	**3**
L. glaucescens		1		1
L. utahensis	2	1		
Ribes lacustre	2	1	1	2
R. triste				1
R. viscossisimum	**2**			
Rubus ideeus	1	1	1	2
R. parviflorus	**3**			1
Cornus stolonifera		1	1	1
Rhododendron albiflorum		1	1	
Betula glandulosa		1	1	1
Phyllodoce spp.		1		
Viburnum edule		1	1	**3**
Potentilla fruticosa	2	1	1	1
Amelanchier sp.	1			1
Sambucus racemosa				1
Sorbus scopulina			1	1
Acer glabrum	**2**			
Berberis repens	**3**			
Pachystima myrsinites	**2**			
Chiogenes hispidula				**1**

Species	Montane	Subalpine	High Foothills	Low Foothills
Herbs				
Elymus innovatus	—	4	5	4
E. glabrum	**3**	1	—	—
Calamagrostis spp.	1	2	1	4
Other grasses	3	2	1	2
Linnaea borealis	4	5	5	5
Cornus canadensis	3	4	4	5
Arnica cordifolia	4	3	4	2
Epilobium angustifolium	2	2	3	4
Mertensia paniculata		1	3	3
Aster conspicuus	2	2	2	3
A. ciliolatus	1	1	1	3
Petasites palmatus			3	4
Mitella nuda		2	2	3
Pyrola secunda	3	3	2	1
P. asarifolia	3	3	2	3
Moneses uniflora		1		
Fragaria glauca	2	2	2	3
Zygadenus elegans	1	1	2	1
Lycopodium annotinum	1	2	2	2
L. complanatum		1	1	2
L. clavatum				1
Smilacina amplexicaulis	2	1	1	1
Stenanthium occidentale	2	2	2	
Streptopus amplexifolius		1	1	2
Achillea millefolium		1	1	2
Senecio indecorus		1		
Aquilegia spp.		1	1	
Pedicularis bracteosa		1	1	1
P. labradorica			1	1
Hedysarum sulphurescens			1	
Galium boreale		1	1	**3**
Lathyrus ochroleucus	1	1	2	3
Clematis columbiana	1	1	1	
Rubus pubescens			1	**3**
R. pedatus			1	1
Habenaria spp.			1	1
Maianthemum canadense				**4**
Antennaria spp.		1	1	2
Aralia nudicaulis				**2**
Viola rugulosa		1	1	2

Table 1 (cont'd)

Species	Montane	Subalpine	High Foothills	Low Foothills
Mosses and Lichens				
Feather mosses (3 spp.)	3	5	5	5
Thuidium abietinum			1	
Dicranum spp.	2	3	2	3
Polytrichum spp.	1	2	2	3
Mnium spp.	1	1	1	1
Cladonia spp.	2	3	3	2
Peltigera apthosa	3	5	5	4

Scale
Frequency Distribution

1 rare
2 occasionally present
3 often present
4 usually present
5 constantly present

Species	Montane	Subalpine	High Foothills	Low Foothills
Herbs (cont'd)				
Viola orbiculata	**3**			
Equisetum scirpoides		2	2	2
E. sylvaticum				**3**
E. pratense				1
Carex spp.		1	1	2
Dryopteris disjuncta				**2**
Thalictrum occidentale	**4**	1		
Clintonia uniflora	2	1		
Vicia americana	1	1		
Actaea rubra	1			1
Castilleja spp.	1	1	1	2
Geocaulon lividum				1
Xerophyllum tenax	**2**			
Tiarella unifoliata	1	1		
Goodyera spp.	2			1
Chimaphila umbellata	**2**			
Erythronium grandiflorum	2			
Osmorhiza occidentalis	1			
Disporum trachycarpum	1	1		1

Stand History Effects

It seems that the effect of stand history on the vegetative pattern has often been by-passed in ecological studies, perhaps because it is a difficult thing to assess. However, in the region under consideration one factor is all-important—fire. One survey conducted on the east slope showed in effect that 100 per cent of the pine stands were of fire origin (Anon. 1930).

The intensity of fire varies greatly. Sometimes it takes the form of a light ground fire which will skip haphazardly through a stand leaving some parts untouched, some scarred in varying degrees and others completely denuded. This provides a variable overhead seed source for pine reproduction, the nature of which will be dealt with later. Time often eradicates all signs of fire scars leaving only the age differences as evidence of the event. An intense crown and ground fire is more usual in these regions. It sweeps quickly over an area, scorching and thereby killing all vegetation. Many of the serotinous pine cones survive charring and open to disseminate seed by a mechanism that has been described by several authors. (Clements 1910, Mason 1915, Bates 1924, Cameron 1953.)

Examination of stump remains and available fire scars on residual trees often provided a reasonable picture of the former stand. Thus in many immature stands it was possible to assess the age, relative size and density of the pre-fire stand and thereby make a subjective comparison with post-fire tendencies. The general conclusions were as follows:

1. Pine stocking tends to increase after each fire, if the interval between fires is neither very short nor very long.

2. The burning of immature and overmature pine stands will result in great variation in regeneration stocking. Instability of seed production is usual in young stands owing to wide density variations, and in old stands because of a variable rate of succession to climax species.

Among the other species associated with lodgepole pine, black spruce is the only one which possesses the serotinous cone characteristic, enabling the seed to survive fire. Poplar has an even more effective means of perpetuation in its capacity for prolific root suckering in burns. Douglas fir's exceptionally thick bark at maturity enables it to withstand light fires; hence old residuals, acting as seed sources, may often be found in young stands. White and Engelmann spruce and alpine fir, having no other means of surviving intense fires, depend entirely on a residual seed source for regeneration. Their abundance, then, will relate directly to the proximity of such a seed supply. This might appear very haphazard, but in the irregular mountain and foothill terrain refugia are frequent, occurring along river banks or gullies, on cliffs and in bogs and hangmoors. During the investigation many examples were observed of the incidence of spruce and fir in a pine stand increasing steadily towards such a refugium. A relationship between black spruce distribution and the incidence of bogs was particularly evident in the high foothills. In the Red Deer Valley, the southern range limit of black spruce, the species is distinctly confined to the vicinity of bog conditions. Northward from the North Saskatchewan River the frequency of boggy plateaux enables black spruce to intrude onto upland sites to the extent that it often forms a continuous understory beneath lodgepole pine, far outnumbering the white spruce. However, it rapidly disappears on the higher, well-drained slopes.

Historic factors other than fire are of secondary or localized importance in Alberta's pine stands. Logging has been influential only in the low foothills where the demand for pine ties and poles has resulted in considerable partial cutting in the more accessible mixedwood stands. The effect is simply a depletion of the pine content, since the poplar has been left untouched in almost every case. There was no evidence of appreciable windfall damage in any of the pine stands examined. Nor were there indications of extensive catastrophic infestations of forest insects or pathogens on pine.

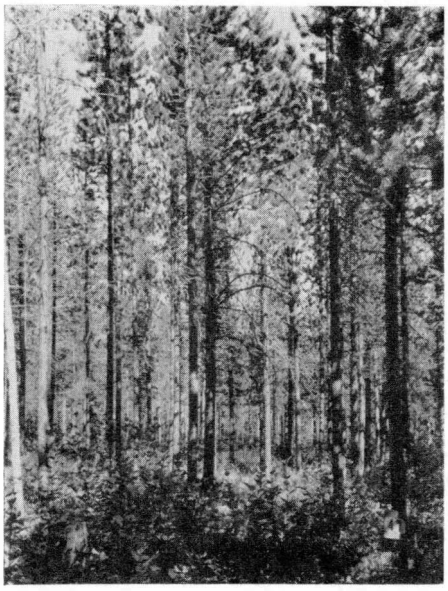
The combined effects of stand history and specific silvical characteristics are reflected in the various forest compositions of the different divisions. In the Montane Division, variable-aged mixtures of residual Douglas fir and younger lodgepole pine are common. In the Subalpine and High Foothills Divisions, there is a predominance of immature pine owing to the extent and frequency of fires, but older stands in various stages of succession to spruce-fir are fairly frequent and patches of "climax" forest more than 300 years of age are not uncommon. It is the Low Foothills Division which displays the most heterogeneous forest cover. Immature stands of aspen and lodgepole pine predominate, each species usually occurring patch-wise in small groves; admixing does occur but to a lesser degree. Fire seems to have been more thoroughly effective in this division as witnessed by the fact that stands more than 100 years of age are unusual, and more than 150 years, very rare. The less combustible poplar has apparently discouraged crown fires while allowing light ground fires which often destroy the canopy of pine and aspen and invariably result in a growth of aspen suckering far more abundant than any pine reproduction which may evolve. Logging disturbance has also favoured increased aspen reproduction. Thus the overall trend in the Low Foothills Division is toward an increase in aspen at the expense of pine.

Reproduction and Resulting Stand Structure

Lodgepole Pine

The ability of lodgepole pine to exist in extremely dense stands is a continual source of amazement to foresters. Literally hundreds of thousands of trees per acre may become established in a burn, and the survival is very high (Horton 1954). Extreme stagnation results in such cases. For example, one 50-year-old stand examined had a dominant height of only 4 feet. Heavy overstocking was found to occur on both mesic and dry sites. The general survey corroborates a previous view that, given a ready seed source and favourable site, pine reproduction following fire will normally tend to be over-dense (Horton 1953). This does not apply where the seed source is scanty or the site adverse. Plates 1A and 1B illustrate the contrasting degrees of stocking that may occur side by side. Rigorous sites often prevent good stocking but only the most extreme can preclude lodgepole pine altogether. It is an unusually adaptable species, having been found to some extent growing to maturity on all soil sites ranging from wet to extremely dry.

As to the manner of pine's seed dispersal, serotinous cones allow seed to survive a fire which, in turn, makes possible the freeing of seed through the heat breaking the adhesive rosin bond. Though a great seed flight follows on the heels of a fire, it is thought that a considerable amount of seed remains in semi-open cones to be freed periodically for some years afterward by fluctuating weather conditions. It was recently shown that the pine regeneration does not all become established in the year following a fire (Horton 1953). Most of it "comes in" over the first three years, yet a noteworthy amount continues to seed



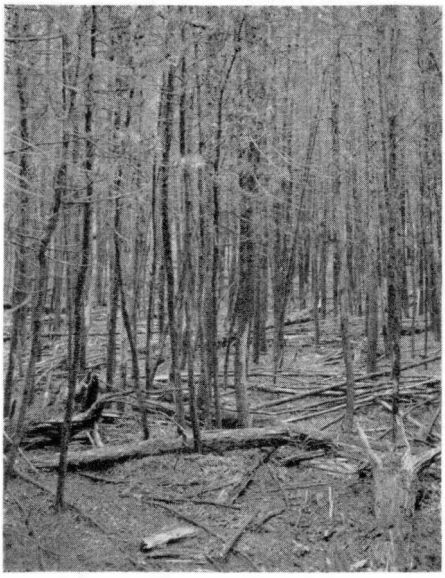


PLATE 1A PLATE 1B

Two 70-year-old lodgepole pine stands on similar conditions showing contrasting stocking, open-grown (1A) and stagnant (1B).

PLATE 2. A two-aged lodgepole pine stand resulting from a light ground fire.

in for several years afterwards. This seemed to be the case generally, since an age range of several years was found in every young stand investigated. It is doubtless a contributing factor to the heavy overstocking which is so common with pine.

There is one condition in which the age range of pine is likely to extend over many years. It obtains when a stand has been lightly burned, leaving a variable cover of residual trees. The result, shown in Plate 2, is usually called a "two-aged stand". Actually, the pine understory which becomes established does so yearly or irregularly until the canopy is complete. In large openings this may take many years. Forty years was the maximum range found in this study. Examples of "three-aged stands", resulting from two light ground fires since the original establishment, were also encountered occasionally. They were usually of patchy stocking, but again, each "age" was represented by a variable range of years. The abundance of the regeneration in every case examined related directly to the degree of opening of the canopy. Where the residuals become more dense, the regeneration becomes correspondingly less dense and more stunted until in well-stocked areas untouched by fire it is absent. This point attests further to the intolerant nature of the species. The best examples of the two-aged stands were found on dry sites. Mesic sites tend to produce a richer ground vegetation in the openings resulting from the light fire, and this appears to diminish the extent of pine seedling establishment.

Natural pine reproduction, not resulting from fire, was found quite frequently but never extensively. It apparently requires two conditions, plenty of light and a dearth of vegetative competition. Thus, in open-stocked pine stands on dry sites it is not uncommon. Also, occasional pine reproduction might be found wherever an exposed ridge or knoll occurs in an otherwise well-stocked stand on a mesic site. In appearance the condition is similar to the above "two-aged stand", but age counts reveal a difference. Natural reproduction does not usually occur in a broad age range but tends to be periodic, generally in two or three age concentrations. This might be explained by the fact that pine has rather exacting requirements for germination and the proper natural conditions are likely to occur only periodically. A limited amount of seed is available annually from trees with non-serotinous cones, which are not uncommon. The natural pine reproduction is usually very much suppressed even where the light intensity seems more than adequate. The most obvious explanation for this is root competition from the parent trees. While this stunting of growth results in a high mortality rate, enough individuals persist and later attain intermediate tree size to ensure the prolongation of succession.

White and Engelmann Spruce

There are few pine stands in the higher divisions that lack a spruce understory to some degree. Often it is merely an occasional seedling or sapling but rarely is it completely absent in a stand. And, in the vicinity of a seed supply, it may form a continuous layer along with alpine fir. Plates 3A and 3B illustrate average understory conditions.

Given a ready seed supply the success of spruce establishment will depend largely on two variables, site and competition. Many examples of spruce's well-known propensity for mesic rather than dry sites were found. Though spruce is rated a tolerant species, the pine overstory is sometimes so dense that spruce reproduction is precluded especially on the drier sites. However, in the usual pine stands, varying from lightly stocked to moderately overstocked, a dense spruce seedling layer may occur.

In general, spruce becomes established over a variable but considerably broader age-range than pine directly following fire. The extent of this range, like the abundance of spruce, depends on the proximity to the seed source first, and favourable conditions second. Again, the pine density is an important factor, since early height growth of pine is much faster than that of spruce. If the pine canopy is open, spruce will continue to "seed in" irregularly until it becomes closed, often a matter of some 40 years: if the pine is initially well-stocked, the spruce age range may be only 10 to 15 years, the time required for the pine to close the canopy. As the stand develops, the self-thinning of pine will allow scattered spruce seedlings to become established. These are mostly confined to rotten log seedbeds (*see* Table 2), owing to the development of a dense feather moss mat which discourages germination elsewhere. Thus, at the early climax stage there is a preponderance of old spruce in the overstory, with scattered intermediate and suppressed trees and with reproduction common in openings which result from the natural mortality of the last pine. As Table 3 shows, the spruce understory at this stage may be uneven-aged.

PLATE 3A

PLATE 3B

Two immature pine stands showing a dense (3A) and a scattered (3B) spruce understory.

Alpine Fir

The same principles involving seed source and initial establishment apply to fir as to spruce. However, there are important differences in behaviour. Fir is the most tolerant of all our species and therefore increases in abundance with stand age. It can reproduce prolifically by two methods, seed and layering. Seedlings were found to occur more frequently than layers but both in general far outnumbered spruce seedlings in older stands. The fecundity of fir reproduction is balanced in some existing stands by damage such as game browsing or spruce budworm defoliation, which often have an appreciable decimating effect.

Table 2 illustrates the seedbed preference of spruce and fir seedlings in a subalpine pine stand which has mainly succeeded to climax (240 years old). The sample involves 389 spruce and 1,162 fir, which represent all the reproduction on 114 randomly-chosen plots, each of 1/200th acre. The fir outnumbered the spruce 3 to 1 and this is a conservative figure because only one layer of each layering clump was counted.

TABLE 2

Seedbed Origin by Per Cent

Species	Rotten Wood	Moss	Mineral Soil	Needles	Unknown	Layers
Spruce	59	20	7	0	14	0
Fir	26	24	4	4	11	31

The preference of spruce seedlings for rotten wood is manifest. Fir is less exacting, germinating equally well on moss or fallen logs. Mineral soil seedbeds are rare in the undisturbed forest but where they do appear, both spruce and fir reproduction favour them.

Table 3 indicates the age-class structures of the spruce-fir understory in an area which includes the 240-year-old stand described above and adjoining stands of about 200 years of age. The data were collected on line plots where the ages of an assortment of trees ranging from seedling to intermediate tree size were determined.

TABLE 3

Age-Class Structure of Spruce-Fir Understory

Age Class	Spruce		Fir	
	No. Trees	Per Cent	No. Trees	Per Cent
1– 50	199	18·6	249	23·4
51–100	300	27·9	340	32·0
101–150	260	24·2	333	31·4
151–200	228	21·3	127	12.0
201–240	86	8·0	13	1·2

The outstanding feature in Table 3 is the unevenness of age in both species. It was observed that in any one site the understory age structure may be irregularly periodic, but in the stand as a heterogeneous whole it is distinctly uneven. Further, the density of the canopy is an obviously important factor, in that the denser the overstory, the less frequent and uneven the understory. These trends are considered to apply at large over the Subalpine and High Foothills Divisions.

Black Spruce

This species becomes established under pine in a manner similar to white spruce. The age range and density of the reproduction depends on the proximity of a seed source, usually a boggy area, and the pine overstory density. It has, however, the advantage of propagating by layering as well as seed. In all of the older stands examined, reproduction of layering origin far outnumbered seedlings. At later stages in stand development this results in uneven-aged clumps of black spruce around each parent tree.

Douglas Fir

Outliers of the interior variety of this species are found locally in Alberta. It appears to prefer dry conditions and usually occurs in lightly stocked stands mixed with pine and stunted aspen. Reproduction is common near residual trees, occurring abundantly in openings and occasionally under a canopy. Most old stands have been lightly burned one or more times and the result is a patchy distribution of uneven-aged Douglas fir interspersed with even-aged groves of pine or aspen.

Aspen

Aspen reproduction occurs in all the divisions of pine but it thrives only in the Low Foothills where it is usually the dominant species. Root suckers may be observed there in almost every stand regardless of age, composition, site or stocking. If there are any aspen in the vicinity dead or alive, reproduction of that species rapidly fills in all the natural stand openings. Browsing and blight were often observed to retard it locally, but seldom completely. Any disturbance such as ground fire, partial cutting or windfall rapidly encourages more suckering.

When fire destroys a mixedwood stand, aspen often becomes established by means of quick sucker growth one to several years before many of the pine seedlings. It consequently has a considerable initial advantage over pine. This was found to apply on a variety of sites, ranging from fairly moist to dry. Aspen reproduction is usually absent on the very moist sites and is less vigorous than pine on the very dry. A particularly dense overhead canopy will preclude the survival of aspen reproduction as it does all other species, but even in such adverse conditions incipient suckers were often observed.

Growth and Resulting Competition

Lodgepole Pine

On an individual tree basis, pine is a relatively slow-growing species but, because dense rather than understocked stands are the rule, the yield is often high. This is well illustrated in the data of Table 4 which were collected during a growth survey of the pine type in the east slope area of Alberta (Anon. 1930).

TABLE 4

Sample of Lodgepole Pine Yield

—	Age Class					
	1-20	21-40	41-60	61-100	101-140	140+
No. of 1/10-acre plots	37	428	196	71	3	4
Average diameter in inches	1·51	2·82	3·45	4·04	6·09	6·27
Total cubic foot volume per acre	93·3	827·8	1,842·2	2,102·8	2,602·2	3,295·5

It is generally accepted that lodgepole pine growth is better in the low foothills than in the higher divisions. This could be the result of better soil conditions and less rigorous climate, or it may reflect the more desirable stocking

that exists in mixed stands as opposed to pure pine stands. The largest lodgepole pine encountered in this investigation was growing under optimum conditions in the low foothills. At 300 years of age the tree had a d.b.h. of 29 inches and a height of 117 feet. In the higher divisions, 15 inches in d.b.h. and 75 feet in height are the approximate maximum dimensions attained by the species.

White and Engelmann Spruce

Spruce occurs as an understory in immature pine stands because it is initially slower growing than pine. Also, it is in many cases younger than the pine, and therefore suppressed from the beginning. However, the growth rate of spruce increases with age faster than that of pine and thus there comes a point when the dominant spruce reach the pine canopy. This is a milestone in the progress of succession. From this point on, spruce becomes increasingly important and pine is on the decline, successionally speaking. The greater the spruce content, the faster will be that decline owing to increased competition. As would be expected, the point of succession varies greatly in different stands. It was found to range from 70 to 160 years, generally occurring around 125 years. The trend is illustrated in Figure 2, in which is compared the height development of a dominant pine and that of a nearby dominant spruce, growing in a typical, mature, subalpine stand on a moderate, well-drained site. The data were obtained by the stem analysis technique, and the curves shown were selected from a number of similar sets as representative of the general trend.

As natural mortality gradually reduces the pine canopy, an increasing number of spruce and fir trees are released. The capacity of the species for release is well recognized but further evidence of this is presented in Table 5, the result of a radial increment examination of a 220-year-old spruce-pine-fir stand in the Subalpine Division. The method used involved selecting spruce and fir trees of various crown classes which were within the former competitive influence of dead pines. These were bored at breast height and the ring growth trends were noted. More than 90 per cent of the releases took place within the last 60 years and were obviously the result of pine mortality. Both species showed release occurring at all ages, but as the data indicate, it was appreciably more frequent in the lower crown classes.

TABLE 5

Radial Growth Release Following Natural Mortality of Pine

Crown Class	Hybrid Spruce		Alpine Fir	
	No. of Trees	Per Cent Released	No. of Trees	Per Cent Released
Dominant	43	23		
Codominant	40	35	15	0
Intermediate	37	76	30	53
Suppressed	23	48	21	57

Additional evidence of release of spruce and fir following the removal of the pine overstory is presented in Table 6. This table shows height release of

advanced growth in a cut-over compared with an undisturbed portion of the same stand as described in Table 5. Parallel transects were run in each condition and all seedlings and saplings of both species encountered were measured as to internodal extension from five years before until five years after logging. The criterion of release was an increase of two or more times the previous growth. Specimens which showed a retardation in height growth since the date of logging were also recorded for comparison.

TABLE 6

Height Growth Trends of Spruce-Fir Advanced Growth

Condition	Species	No. of Trees	Per Cent Retarded	Per Cent Released
Cut-over	Spruce	51	8	53
Cut-over	Fir	51	4	59
Undisturbed	Spruce	51	27	0
Undisturbed	Fir	54	24	6

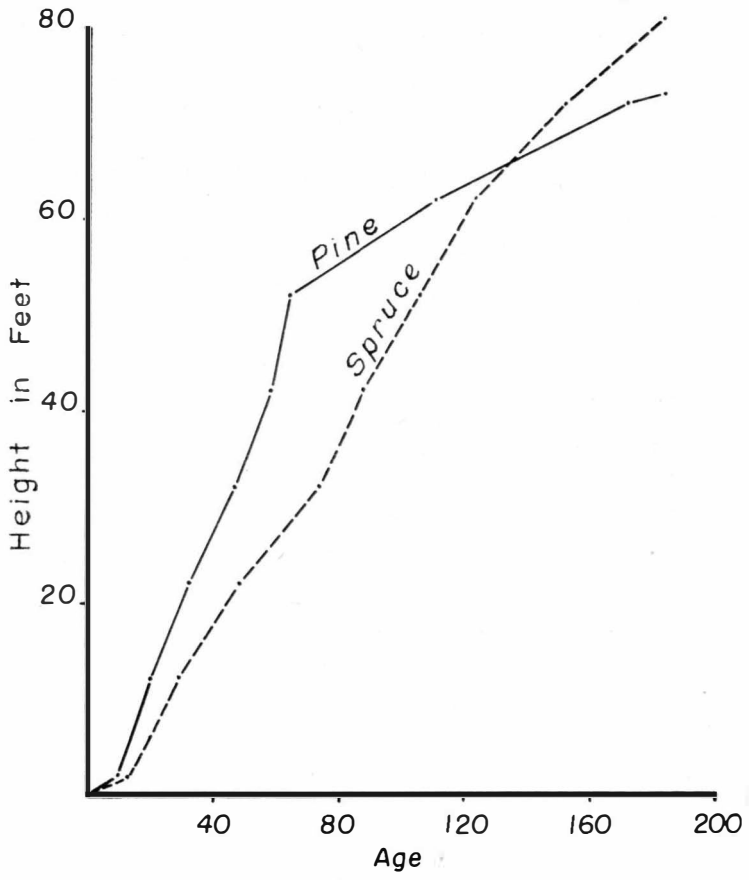


FIGURE 2. Sample relative height growth of dominant pine and spruce.

Other Conifers

Alpine fir does not generally become established in abundance until the pine overstory is well developed. It is therefore usually represented in overmature stands by a suppressed understory. Not until most of the pine content has disappeared will fir come into a dominant position in the stand, and even then its dominance is a result of abundance rather than size, since it never reaches the proportions of spruce.

Douglas fir, in relation to pine, has a growth rate similar to white spruce, according to observations made in stands where the three species occurred together.

Black spruce has the slowest growth rate of all the species associated with pine. A d.b.h. of 8 inches and a height of 40 feet is the usual maximum size attained. During its whole lifespan, therefore, black spruce is suppressed beneath pine on upland sites. Only on moist sites adjoining bogs or hangmoors was it found in any degree of dominance, and this condition seemed to result from stunted pine growth and lack of white spruce rather than from good black spruce development.

Aspen

The inability of aspen to compete with pine in the higher divisions, except on rich sheltered valley sites, has already been noted. Though aspen may be locally abundant on the slopes in recent burns, most of it soon dies out (Horton 1954) and the occasional hanger-on becomes suppressed (*see* Plate 4A). By contrast, aspen's development in the Low Foothills Division is often greater than that of pine initially, as Plate 4B illustrates.

PLATE 4A. A 70-year-old subalpine stand showing aspen suppressed by lodgepole pine.

PLATE 4B. A young stand in the low foothills, showing aspen initially overtopping pine.

This initial growth advantage of aspen in the low foothills is a consequence of the root sucker's ability to spring up during the growing season following a fire and to maintain a rapid early height growth, while pine is relying on the slower processes of seed dispersal, germination and seedling development. However, from a subjective comparison of the many mixedwood stands examined, it

appeared that within 50 years the two species were usually competing equally both in diameter and height growth, and continued so to the point of over-maturity in aspen at approximately 120 years.

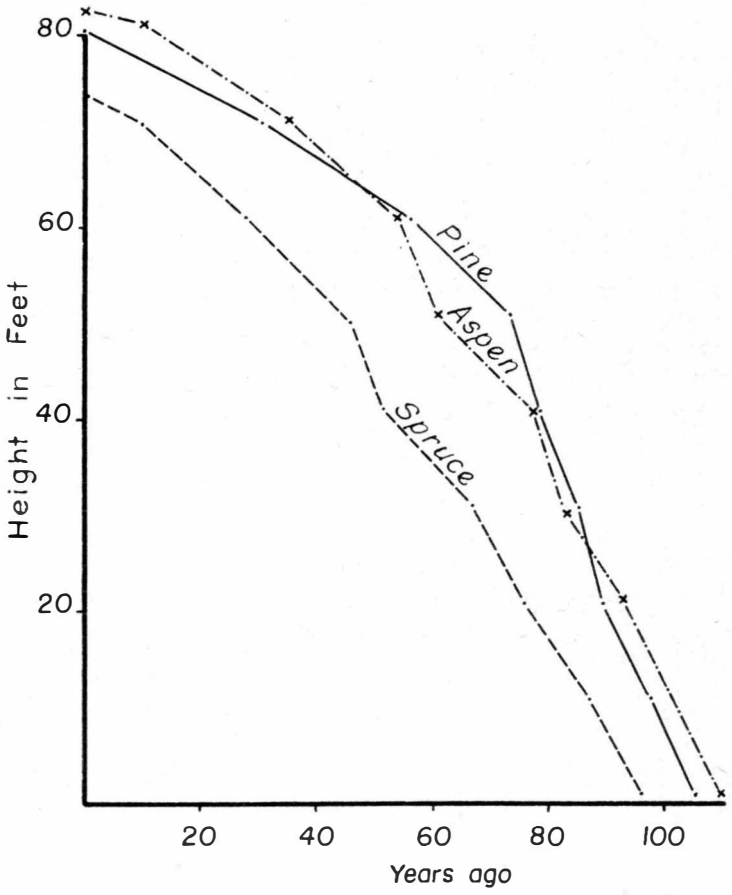


FIGURE 3. Sample height growth of competing dominant aspen, pine, and white spruce.

Figure 3 shows the relative height growth trends of a competing dominant lodgepole pine and an aspen, and a nearby codominant white spruce, as found by stem analyses. Fifty-five selected trees were analysed, including pine, aspen, and spruce of all crown classes, competing with each other in different degrees and occurring on the two most typical sites of the low foothills, i.e. well-drained clay-loam and imperfectly drained clay. The trees of Figure 3 are representative of the general trends found on both sites. Further conclusions resulting from the stem analyses are as follows:

1. Aspen is generally taller than pine for the first 10 to 40 years. Pine subsequently overcomes this lead and, though individual fluctuations may occur in either species, the dominant heights are very similar at maturity.

2. The height growth of an individual pine or aspen is not necessarily reduced by a surrounding predominance of trees of the other species, which is a further indication of equal tolerance.

3. Individual pines or aspens are subject to sudden suppression through increasing direct overhead competition, but suppression is far more common within than between the species.

4. Height growth of spruce in all crown classes is much steadier than that of pine or aspen.

Similar tendencies were apparent in an examination of radial increment of the same trees.

Succession

The specific reactions which result in forest succession in the lodgepole pine region have been discussed. It remains to unite the separate details into a coherent whole. Quantitative evidence of the early successional trends from pioneer to climax species is provided in Table 7. These figures were adapted from an earlier survey of growth rates on the east slope (Anon. 1930).

TABLE 7

Early Successional Trends in Several Forest Types

Age Class	No. of 1/10 Acre Plots	Pine		wS		bS		alF		Poplar	
		p.c. No.	p.c. Vol.	p.c. No.	p.c. Vol.	p.c. No.	p.c. Vol.	p.c. No.	p.c. Vol.	p.c. No.	p.c. Vol.
		Pine type									
1–20	37	97·5	95·8	2·5	4·2	—	—	—	—	—	—
21–40	428	90·3	95·7	1·5	1·0	6·8	1·4	0·2	0·1	1·2	1·8
41–60	196	91·8	94·9	4·6	1·9	1·0	0·7	0·1	0·1	2·5	2·4
61–100	71	80·5	91·7	8·6	3·8	6·8	1·5	—	—	4·1	3·0
101–140	3	73·1	88·3	19·7	9·8	—	—	4·6	1·1	2·6	0·8
		Pine—wS type									
21–40	22	35·4	63·4	57·0	31·2	3·4	1·5	0·4	0·9	3·8	3·0
41–60	32	38·9	66·4	51·8	26·0	1·1	1·2	1·9	1·1	6·3	5·3
61–100	26	31·4	56·9	63·5	39·6	2·0	1·0	1·7	0·9	1·4	1·6
101–140	11	30·7	57·9	62·8	39·2	0·4	0·4	6·1	2·5	—	—
140+	33	27·6	49·3	64·5	46·0	2·8	0·6	4·1	3·6	1·0	0·5
		Pine—bS type									
21–40	19	38·6	71·6	0·9	0·4	59·2	20·2	—	—	1·3	7·8
41–60	20	29·8	61·1	3·0	2·6	59·7	24·8	—	—	7·5	11·5
61–100	6	28·0	67·9	6·9	3·7	61·9	24·2	2·6	2·5	0·6	1·7
		Mixed type (Po, pine and wS)									
1–20	3	14·7	25·0	2·3	1·2	—	—	—	—	83·0	73·8
21–40	52	23·9	46·1	10·6	7·8	4·2	1·7	—	—	61·3	44·4
41–60	39	22·2	40·2	22·1	19·9	5·9	2·2	—	—	49·8	37·7
61–100	6	30·2	46·6	4·4	6·8	14·2	2·6	—	—	51·2	44·0

It will be noticed from Table 7 that:

1. The general tendency in all cover types is for the proportion of spruce and fir to increase steadily with age and the pine and poplar to decrease.

2. In the pine-spruce types the spruce species are proportionately high in numbers but low in volumes, indicating an abundance of small trees. Many of these will later be released to swell the spruce volumes.

3. In the mixed type the poplar decreases and the pine and spruce increase to maturity, at which point additional poplar sucker growth often develops. The sparse poplar in the other types shows an initial increase followed by a rapid decline as stands mature.

That succession does occur in this region is undeniable. It is the rate at which it occurs that is in question. This varies between the divisions and between stands. In the low foothills, succession from poplar and pine to white spruce is evident, but in the early stages only. Fire has been so thorough here that few stands have survived undisturbed for more than 100 years, and stands more than 150 years of age are extremely rare. This means, in effect, that succession and climax are matters of only academic interest in the Low Foothills Division. Raup (1954) has recently expressed this view as applying in other regions. There are scanty bits of evidence which suggest the probable successional trends in mixedwoods barring fire. The aspen reputedly has an average lifespan of 120 years (Moss 1932). This is corroborated by the present study insofar as every aspen more than 100 years of age which was examined showed rot, although radial and height increment was in some instances still vigorous at 115 years. By the time the aspen is breaking up, the most vigorous white spruce have become dominant. There were frequent indications that the pine in the mixedwood groves suffered greater mortality than in the pure pine groves. At any rate, the drastic opening of the canopy would presumably give rise to a new crop of aspen suckers and vigorous spruce growth, thus perpetuating the mixedwoods with an increase in spruce and a decrease in pine.

PLATE. 5. Near-climax Engelmann spruce-alpine fir stand with remnant pine, Subalpine Division.

In the higher divisions fire has been only slightly less thorough, the greater part of the total area having been burned recurrently within a century. However, there are frequent residual patches of older stands which afford examples of various advanced stages in succession. One such stage is shown in Plate 5. Note the numerous lodgepole pine deadfalls, all the result of natural mortality. A few standing live remnants of the former well-stocked pine stands can be seen.

Since competition from the climax species is a major factor in the decline of pine, the more abundant and vigorous the spruce and fir, the faster will be the rate of succession. Pine, then, will persist longer where the original spruce seed sources were scarce. There were strong indications that conditions adverse to spruce development such as high initial pine densities and dry sites retarded succession. To investigate the rationship between site and rate of succession, an intensive line-plot survey was made in a 240-year-old subalpine stand, *i.e.* in the near-climax stage. The results are presented in Table 8.

TABLE 8

Relationship between Site and Rate of Succession

Soil Site	Local Climate	Dom. Ht. Spruce	No. Plots 1/40 Acre	Plots with Pine	Plots with Pine Comprising 20 per cent or more of Basal Area	Species Composition Av. Basal Area		
						Pine	Spruce	Fir
		feet		p. c.	p. c.	p. c.	p. c.	p. c.
Wet	Varying	—	4	75	25	8	74	18
Moist	Varying	74	15	7	0	0	72	28
Mesic	Sheltered	74	13	23	0	1	65	34
Mesic	Normal	72	13	23	8	3	63	34
Mesic	Exposed	70	13	77	54	31	45	24
Dry	Sheltered	—	5	40	40	10	54	36
Dry	Normal	68	23	57	26	13	52	35
Dry	Exposed	67	21	90	86	44	31	25

Using soil moisture and local climate as criteria of site, the drier the combined conditions, the greater is the persistence of pine. The one exception to this trend obtains, suprisingly enough, on the wettest site. This anomaly of scattered, stunted, old pine persisting on the edges of hangmoors and bogs was frequently observed, and serves to emphasize the broad adaptability of the species.

In addition to the factors which increase the length of the sere by prolonging the life of pine, there are those that do so by encouraging natural pine reproduction, namely, dry and open conditions or light ground fires. In the rare cases where pine has persisted to a great age and finally has died before an appreciable spruce-fir content has developed, the drastic opening of the canopy may give rise to some pine reproduction. All such cases studied were small and localized, and there was invariably spruce or fir nearby. Increased reproduction of the latter species was assured, along with a release from suppression of any existing advanced growth.

The remaining silvical gauge of succession is specific longevity. In Table 9 is presented a list of the maximum lifespans of the important species occurring in the higher lodgepole pine divisions, as found in examinations of the oldest stands. It is arbitrary and applies only to the most dominant trees, mortality being possible in the lesser crown classes at any age.

Fig. 4 Diagram of Stand Development in Lodgepole Pine — Aspen

Low Foothills Division

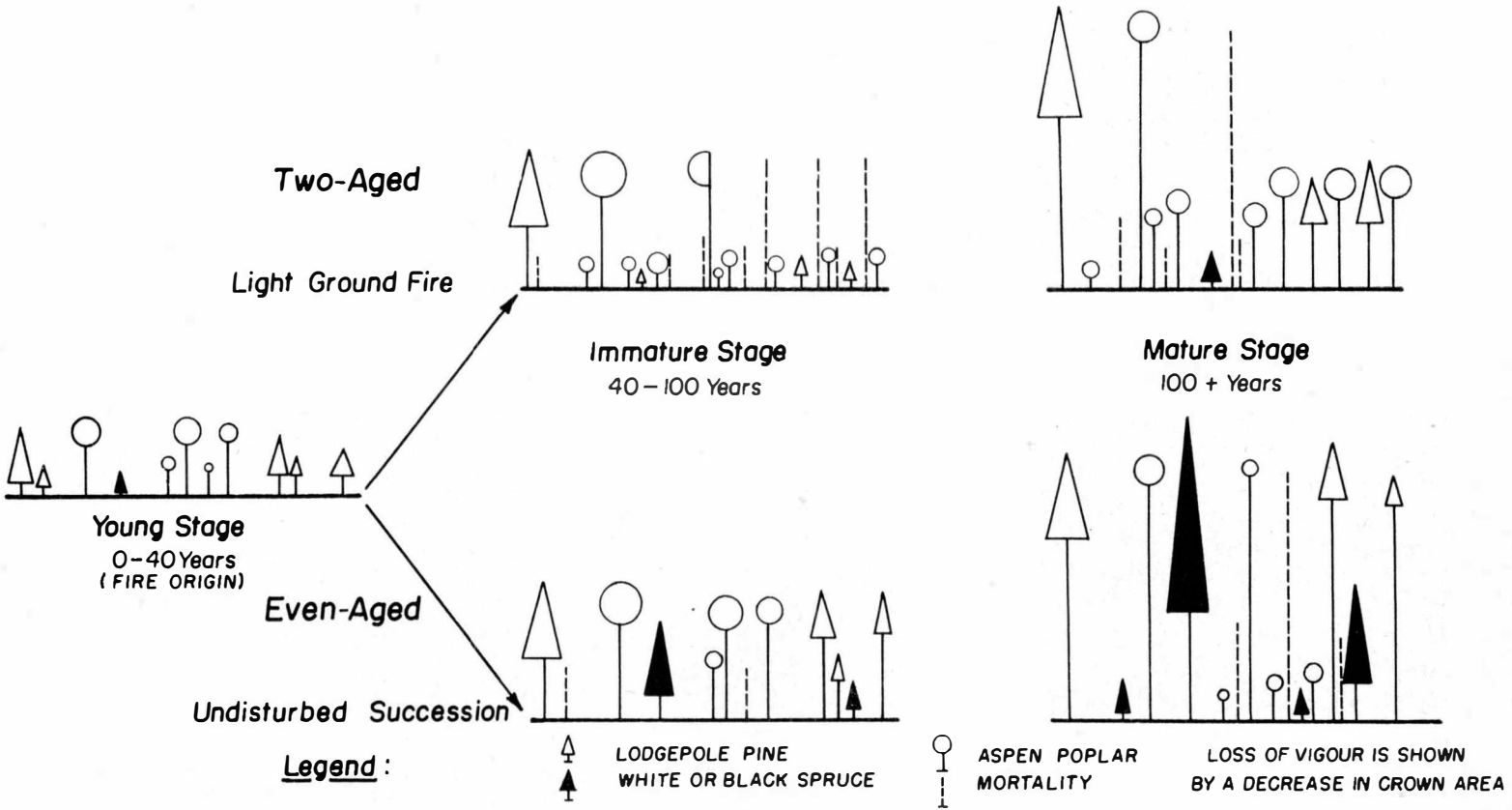


Fig.5 Diagram of Stand Development in Lodgepole Pine

Subalpine Division

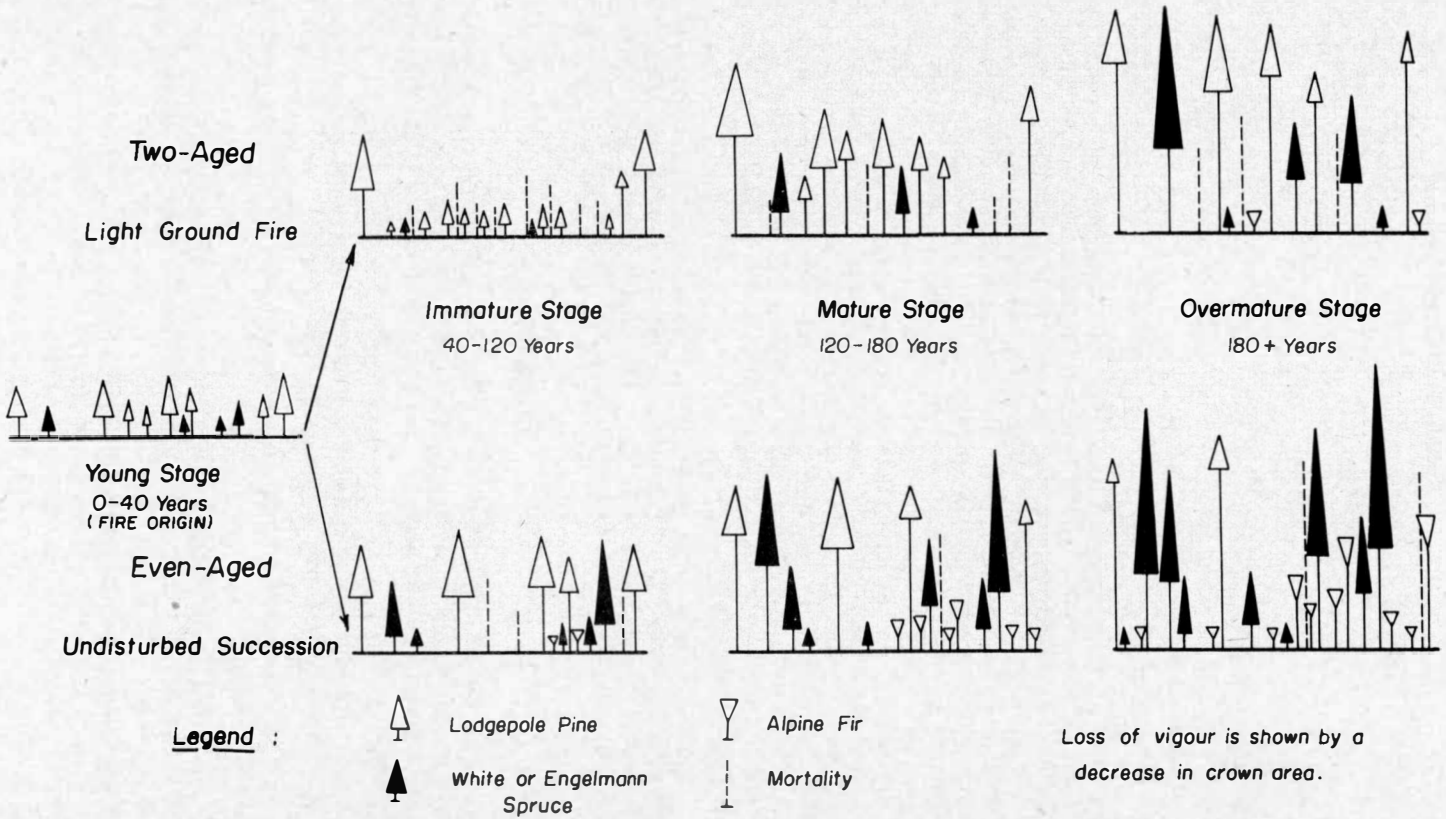


TABLE 9

Specific Maximum Lifespans

Species	Av. Max. No. Years	Max. No. Years
Black spruce	200	250
Alpine fir	200	325
Lodgepole pine	290	375
Douglas fir	300	360
White spruce	300+	400
Engelmann spruce	350	450

In the Subalpine and High Foothills Divisions, succession from pine was found to be complete by 290 years on the average. It varied from 225 to 375, the widest variations occurring in the Subalpine Division where conditions are more diverse. Thus pine has generally disappeared by 300 years, leaving an overstory of old spruce, a variable, uneven-aged, spruce-fir understory and an abundance of reproduction, mainly fir. In the Montane Division, scattered Douglas fir will be present, and in the High Foothills Division, uneven-aged black spruce of layering origin will remain. This is the early stage of the climax community. In the later stage the spruce becomes progressively more uneven-aged as the oldest trees die and scattered reproduction develops, while the fir content increases its prolific reproductive tendencies. However, long before this final stage is reached, fire usually occurs and pine reproduction evolves from seed sources in adjacent younger stands or from individual trees which have persisted within the climax community on dry knolls or like conditions. The cycle then begins anew.

The typical trends in forest succession which have been described are presented pictorially in Figures 4 and 5, representing the Low Foothills and Subalpine Divisions respectively. The latter applies also to the Montane, with the addition of Douglas fir, and to the High Foothills, adding black spruce.

SUMMARY

This study, confined to the range of lodgepole pine in Alberta, recognizes four phytogeographic divisions of that range based on geographic, physiographic, and vegetative differences, i.e. Montane, Subalpine, High Foothills and Low Foothills.

No attempt has been made to subdivide these into pine associations; rather the whole is looked upon as a varying continuum.

Fire is stressed as the primary historic factor determining forest composition and succession.

In the Low Foothills Division, where mixed woods prevail, very few stands have escaped fire for more than 100 years, which means that succession is unimportant. Pine and aspen compete as pioneers there, the aspen having an initial advantage through its rapid-growing root suckers. Pine afterwards overtakes the aspen and the two species in general compete equally to maturity. The occurrence of aspen suckers and lack of pine reproduction in most stands and especially in those which have been lightly burned or cut over, suggests that aspen is increasing at the expense of pine in the division as a whole.

In the three higher divisions, pine has expanded to general dominance through the frequency of fire, but the rougher terrain has provided refugia for residual older stands which give evidence of succession and are a seed source for the dispersal of spruce and fir into the adjoining young pine stands. Succession from pine to Engelmann spruce-alpine fir is indicated for the Subalpine Division. This also applies in the Montane Division with the inclusion of Douglas fir, and in the High Foothills Division with the substitution of white spruce for Engelmann spruce and the addition of black spruce.

The rate of succession varies with the abundance and vigour of the climax species, the initial density of pine, and the site. Pine persists longer on the drier sites. In the Subalpine and High Foothills Divisions, succession from pine was complete by 290 years on the average, varying from 225 to 375 years.

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