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REPRODUCTIVE ECOLOGY OF *PICEA MARIANA* (MILL.) BSP., AT TREE LINE NEAR INUVIK, NORTHWEST TERRITORIES, CANADA¹

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Abstract. *Picea mariana* predominates in even-aged stands of fire origin at the forest-tundra ecotone near Inuvik, Northwest Territories, Canada. Growth rates of *P. mariana* decrease with increasing latitude and density although growth rates do not change significantly along the ecotone. Field measurements of water relations, when compared with laboratory determinations of leaf water potentials vs. net photosynthesis, suggest no water stress related photosynthetic reduction for mature trees during 1976. Maximum and minimum leaf water potentials for mature trees were -0.6 and -2.1 MPa on 4 August and 1 July, respectively. Winter measurements of water relations also suggest no water stress. In contrast, 1st-yr seedlings demonstrated sensitivity to water stress with high rates of mortality at low levels of water loss.

A macro-mesoclimatic gradient of 4°C was found across the tree line (135-km study transect). *Picea mariana* seed production and germination are limited by this environmental gradient to ≈ 40 km south of modern forest line. Germination and survivorship are also affected by microenvironments within a well-developed soil hummock terrain. The lower cardinal germination temperature of 15°C was the determinant of germination timing and success. Seed production estimates suggested little effect on stand reproduction with burn intervals of 100–200 yr. Shorter or longer burn intervals are believed to reduce stand reproduction. Reduced seed longevity, complete stand destruction by wild-fire, and apparent destruction of seed in the soil restrict establishment to 1–8 yr after fire. This may cause local extermination of the species or out-of-equilibrium tree line positions under conditions of deteriorating environment.

Key words: fire; forest-tundra; germination; *Picea mariana*; survivorship; tree line; water relations.

INTRODUCTION

Studies of the causal factors of species distribution are most effectively carried out near the species' limits. The study of *Picea mariana* (Mill.) BSP. at its northern limit is of particular interest because of its wide distribution within the boreal forest and its importance as a tree line species in numerous geographic regions.

Previous tree line studies have been of a vegetational (Larsen 1965, 1971a), palynological (Ritchie and Hare 1971, Nichols 1975, Ritchie 1976, 1977), or climatological nature (Bryson 1966, Larsen 1971b, Hare and Ritchie 1972). Considerable speculation on the interaction of species was presented in these studies, as there was minimal autecological information concerning the key species. In addition, these studies operated in a sometimes confusing scheme from which we have chosen terminology following Love (1970) and Hustich (1966) for this study. For example, as used here, the subarctic zone ranges from tree line to closed boreal forest and includes forest-tundra in the north and open boreal forest in the south.

Along with the demarcation of tree and forest lines there has also been a search for the causal mechanisms, among the earliest of which was Halliday and Brown's (1943) correlation of 10°C mean July temperature with tree line. Hopkins (1959), in response to this correlation for Alaska, introduced the degree day concept to separate Alaskan vegetational zones environmentally. Bryson (1966) and Larsen (1971b) extended the degree day concept in the correlation of frequency of major air mass occurrences and vegetational boundaries. Hare and Ritchie (1972) noted changes in energy budgets and net production associated with the vegetational zones and cautioned that, "This relationship works as an interlocking system rather than as a simple control of vegetation by climate: the structure of the vegetation, because of its effect on albedo and aerodynamic roughness, markedly influences climate."

Investigations into causal factors of tree line must also include the effects of past tree line movements which have occurred at varying rates and irregular intervals from the last proglacial event. Migration of boreal forest tree species to present tree line position began from proglacial positions (14,000–15,000 radiocarbon yr BP) in the United States and southwestern Canada (Whitehead 1973, Ritchie 1976). These migrating forest species invaded a postglacial "tundra" (12,900–11,600 yr BP) occupied by *Betula*, *Shepherdia canadensis*, and *Artemisia* in western Canada (Ritchie

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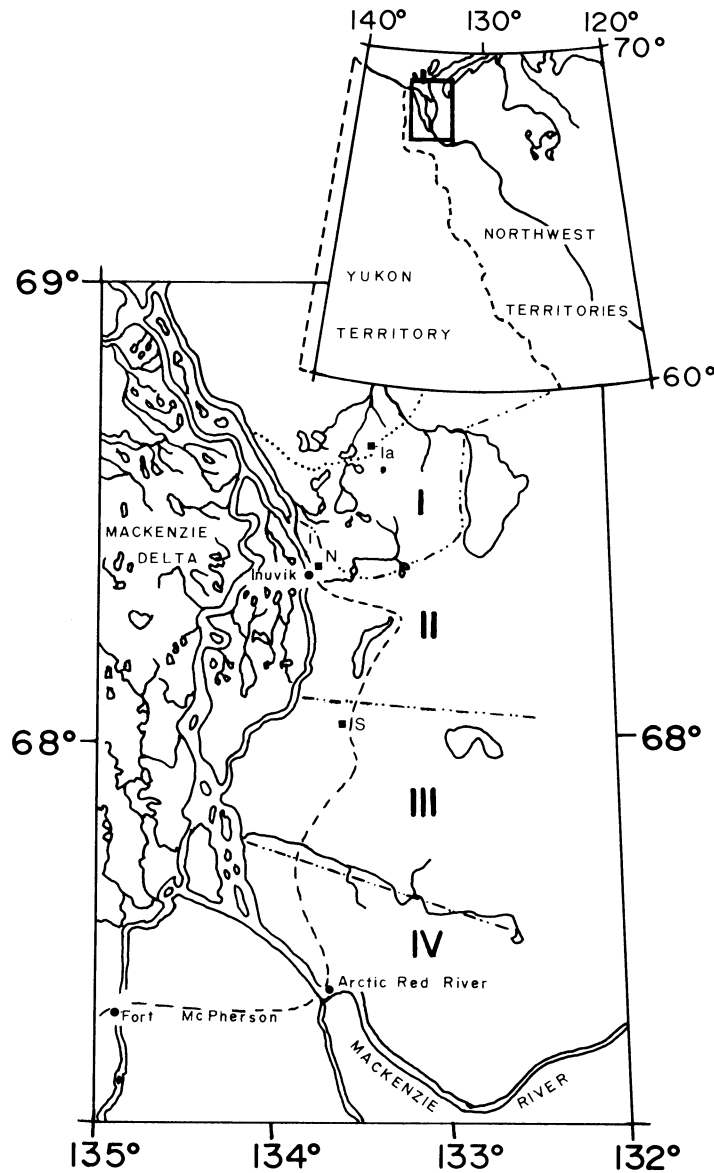


FIG. 1. Map of study sites. (—●—●— = boundaries of study regions; --- = Dempster highway; = the approximate position of tree line; S, N, and Ia mark instrument stations [■]).

and Hare 1971, Ritchie 1976, 1977) similar to the proglacial assemblages described for interior Alaska (Matthews 1974). Forests were present by 6,200 yr BP (Nichols 1975) and were probably present immediately after deglaciation in the District of Keewatin by 8,000 yr BP (Bryson et al. 1969). Ritchie (1976) suggested possible establishment on the stagnant ice and till surface to explain this rapid appearance. Similar invasions occurred between 11,600 and 8,500 yr BP in the northwest District of Mackenzie with the establishment of a "continuous spruce forest" by 8,500 yr BP on the Tuktoyaktuk Peninsula 100 km north of modern tree line (Ritchie and Hare 1971). This continuous

spruce forest remained until 5,500 yr BP near Tuktoyaktuk or 4,800 yr BP in central Keewatin (Nichols 1975), and is believed to be in response to higher summer mean temperatures ($+5^{\circ}$ and $+4^{\circ} \pm 1^{\circ}\text{C}$, Ritchie and Hare 1971, Nichols 1976, respectively). *Picea* (palynologists are able to identify only the taxon *Picea* and cannot separate species), in response to climatic change in the Hypsithermal, was probably 300 km north of its modern position in Keewatin and reached the Beaufort Sea in the District of Mackenzie. After 5,500 yr BP, Ritchie and Hare report a reduction in tree cover and from 4,000 yr BP to the present, dwarf birch-heath tundra has dominated the Tuktoyaktuk

Peninsula. Nichols (1975) reported a similar but rapid retreat of tree line after 4,800 yr BP in Keewatin. But unlike the Tuktoyaktuk area, there was an advance between 4,500 and 3,500 yr BP. Forests subsequently retreated in Keewatin ≈ 100 km south of modern positions by 2,100 yr BP. Amelioration of the climate, $\approx 1,200$ –1,000 yr BP caused an advance of tree line 100 km followed by retreat 600 yr ago to approximately its modern distribution.

Nichols also reported the occurrence of "wide-spread broadly synchronous fires" at 3,500 and 600 yr BP with immediate replacement by tundra vegetation. These observations are supported by earlier observations and dates for buried soil and charcoal horizons north of modern tree line in the District of Keewatin (Bryson et al. 1965, Sorenson et al. 1971). These fires are believed to be indicative of climatic change, specifically the southward movement of cool, dry arctic air, and are differentiated from fires after which recovery of forests occurred within 50 yr.

Outliers of *Picea* currently in the forest-tundra zone are generally considered relict from these past advances of forest line (Larsen 1965, Nichols 1976). However, reported invasions of forest-tundra or tundra by trees are found (Griggs 1934, Marr 1948, Hansell and Chant 1971). These reported invasions unfortunately are difficult to interpret or have been reevaluated in view of increased knowledge of glacial history (see Nichols 1976). Retreat of forest line and apparent destruction of forest by fire during this retreat posed questions concerning the role of fire. The role of fire at tree line is also of interest due to the widespread occurrence of burning in closed and open boreal forest (Heinselman 1973, Rowe and Scotter 1973, Viereck 1973, Johnson and Rowe 1975) and less frequent burning of tundra and forest-tundra vegetation (Wein 1976).

Questions have been raised concerning the biology of tree establishment following disturbance (Mackay 1970, Rouse and Kershaw 1971) and the physiology of the established trees (Vowinckel et al. 1975). There has been speculation concerning environmental limitations on seed production and seedling establishment of *Picea glauca* (Nichols 1976) and *P. mariana* (Larsen 1965, 1974) at tree line in North America, and other tree line species in Asia (Tikhomirov 1962). However, investigations of photosynthesis (van Zinderen Bakker 1974, Vowinckel et al. 1975) and water relations (van Zinderen Bakker 1974, Marchand and Chabot 1978) in *P. mariana* have shown adaptations for survival in stressed environments.

Dominance of forest line and forest-tundra vegetation in the lower Mackenzie Valley by *P. mariana* (Rowe 1972) and reduced importance of *P. glauca* and *Larix laricina* compared to eastern regions adjacent to Hudson Bay (Marr 1948, Ritchie 1959, 1960), raised the question: Why is *P. mariana* successful at this forest line and what are the controlling environmental

factors? This question bears not only on past regional distribution of *P. mariana* and its associated environment, but also on the vegetational pattern observed by Zoltai and Pettapiece (1974) on a microtopographic scale. These questions were pursued with the knowledge that recent climatic warming during the past two centuries "may have been too small to move the 'seedling treeline' northwards beyond the present woodland-tundra ecotone which was previously established under substantially warmer conditions. Thus, the hypothesis of the historically established position of some modern tree lines implies that a consistently successful establishment of spruce seedlings due to that recent warming should also be searched for within the present northern woodlands, not just in the southern tundra" (Nichols 1976: 42).

This study was undertaken to elucidate autecological factors controlling the limit of *P. mariana* at tree line and to provide a baseline of information on climatic effects for this species. Autecological factors investigated were: (1) the role of water relations and photosynthesis in determining the success of germ-lings (first season seedlings), seedlings, and mature trees, (2) germination potential and production of seed, (3) germination and seedling establishment, (4) growth of seedlings to mature trees, and (5) the role of climate and fire interval in the success of the species.

SITE DESCRIPTIONS

Locations

Study areas were located along a north-south transect ($\approx 133^{\circ}30'W$, $67^{\circ}40'N$) from 40 km north of Inuvik, District of Mackenzie, Northwest Territories to the community of Arctic Red River ($\approx 67^{\circ}25'N$) (Black 1977). This 135-km transect was divided a posteriori into four ecologic regions (Fig. 1) based upon growth and reproductive potential for *Picea mariana*. Regions defined on the study transect were ≈ 40 km wide and encompassed an area within which vegetation was considered homogeneous for that region.

Region I (latitude $68^{\circ}40'$ to $68^{\circ}24'N$) was within the forest-tundra north of forest line. Region II (latitude $68^{\circ}24'$ to $68^{\circ}08'N$) was the northernmost limit of open boreal forest and was delimited based on limited growth and reproduction of *P. mariana* in established vegetation. Regions III and IV (latitudes $68^{\circ}08'$ to $67^{\circ}46'$ and $67^{\circ}46'$ to $67^{\circ}25'N$, respectively) were those in which reliable reproduction of stands was recorded in conjunction with generally improved growth rates. Instrumentation, tree growth analysis, burn scar and cone production sites were located in each ecologic region.

Instrumentation sites were located on burns in Regions II and III. Both sites were burned in 1968 by separate fires. Sites were chosen in upland areas of free drainage where burning had exposed mineral soil

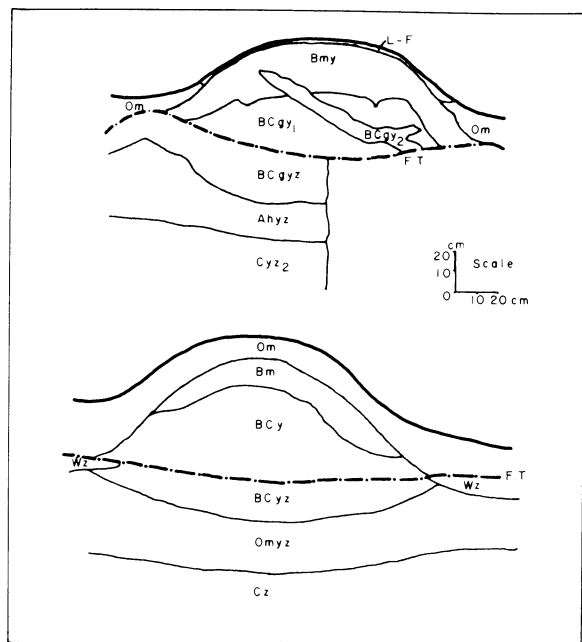


FIG. 2. Hummock sections redrawn from Zoltai and Tarnocai (1974). The top section is from the north end of the study transect and the bottom section southeast of Arctic Red River. Soil horizon symbols are after the Canadian Soil Classification System with the addition of y for cryoturbated layers and W indicating >95% water; F.T. designates the frost table; z indicates frozen horizon. In the Canadian Classification System, L-F and Om are organic horizons in order of increasing decomposition. Lower case suffixes g and h stand for gleyed or mottled and organically enriched horizons, respectively. All other symbols are similar to United States (Seventh Approximation) designations. Hummock top microsites are found on the relatively level center of each individual hummock. Hummock side microsites are continuous with top microsites and are found on the sloped side of an individual hummock. Hummock trough microsites are found in the relatively level area between two or more hummocks and again, are continuous with hummock side microsites.

and where *P. mariana* seedlings occurred. These were the intensive meso- and microclimatic instrumentation sites and also seed and seedling trial sites. Mesoclimate was used in the sense of within-stand climate. Microclimate here refers to the climate of microsites or plots on representative hummocks. Macroclimate refers to regional climate either within defined regions or in a general sense for the Inuvik area. An intensive mesoclimatic site (Site Ia; Fig 1) was added during 1976 in Region I.

Representative sites (19) spanning all available age classes were chosen for growth analysis in all regions (see Black 1977). Dominant age classes in Regions II, III, and IV were 8, 29, 86, 102, 182, and 250+ yr since burning. Only 250+ yr-old sites were found in Region I. All sites were restricted to till with hummocky soil development.

Geology

Bedrock geology, of minor importance due to complete Wisconsinan glaciation, changes from unconsolidated Tertiary sands and gravels of the Reindeer Formation in Region I to Ordovician-Devonian limestones and dolomitic limestones outcropping in Region II (Monroe 1972). Region III and IV bedrock is composed of undivided shales and sandstones of the Cretaceous or Devonian Imperial Formation outcropping only at the Rengleg and Mackenzie Rivers.

Glacial advances during the early Wisconsinan or possibly pre-Wisconsinan stadials traversed the entire study area reaching into the eastern Richardson Mountains and along the north Yukon coast as far as Herschel Island (Hughes 1972). Late Wisconsinan advances also probably covered the study area. Deglaciation of the northern sectors, specifically the Tuktoyaktuk Peninsula occurred before $12,900 \pm 170$ radiocarbon yr BP (Ritchie and Hare 1971), and a minimum ice-free age of $8,200 \pm 300$ yr BP was given for the Inuvik area (Hughes 1972). These glacial events left the region covered with broad morainal plains of low relief (Hughes et al. 1972).

Soils

Soils in the study region are classified as Brunisolic or Regosolic Turbic Cryosols in the Canadian classification system and Pergelic Ruptic-Histic Cryaquepts in the United States classification system. These classifications reflect the limited soil development which occurs throughout the region as a result of continuous permafrost and cryoturbation of the fine-textured tills. The dominant patterned ground found with *P. mariana* stands was nonsorted circles in Washburn's classification (Washburn 1956) or referred to as hummocky terrain (Zoltai and Tarnocai 1974). This earth hummock form (Figs. 2 and 3) is believed to have developed during a past climatic change (Brown 1969), though Zoltai (1975a) has shown that active hummock movement has occurred in the recent past, suggesting a continuous active development. Each hummock consists of a mineral soil core with organic-rich horizons of varying thickness on the tops and in the troughs between hummocks.

Hummocks also show changing morphologies within a burn cycle (Zoltai and Tarnocai 1974). Postfire exposure of the mineral soil core, general reduction of the peat cover, and blackening of the surface result in melting of ice-rich layers and in hummock subsidence. Increasing plant and peat cover reverse the trend and the active layer decreases in thickness. These changes afford a variety of environmental conditions for post-fire establishment and subsequent plant growth.

Vegetation

Vegetational changes within *Picea mariana/Vaccinium uliginosum* (nomenclature follows Cody 1965,



FIG. 3. Recently burned (1968) *Picea mariana*/*Vaccinium uliginosum* forest showing the distribution of soil hummocks and trees in the trough areas in late May 1975.

Holmen and Scotter 1971, and Ahti et al. 1973 for vascular plants, mosses, and lichens, respectively) open boreal forest are minor along the study transect from tundra to forest vegetation (Black and Bliss 1978). Only Regions I and II exhibit floristic and quantitative affinities to tundra regions and in general, understory assemblages are not different from tundra communities. Dominant in the region are open canopy *P. mariana* forests with understory shrubs of *Salix glauca*, *S. pulchra*, and *Vaccinium uliginosum*. Cryptogamic ground covers change in a consistent sequence with time since burning (Black and Bliss 1978), from the colonizing species *Bryum pseudotriquetrum*, *Ceratodon purpureus*, and *Polytrichum juniperinum* to *Aulacomnium turgidum*, *A. palustre*, and *Tomentypnum nitens*. Approximately 120 yr after burning the ground cover changes to include a lichen component dominated first by *Cladina mitis* and later by mixtures of *C. mitis*, *C. rangiferina*, and *C. alpestris* (= *C. stellaris*). This vegetation type appears to have corollaries throughout the lower Mackenzie Valley (Strang 1973, Reid 1974, Ritchie 1974, Zoltai 1975b and Bird et al. 1977) on similar substrates. Along streams *Picea glauca* is the dominant tree associated with *Alnus* spp. and *Salix* spp. though both *P. glauca* and *Larix laricina* may rarely be found in mature, open boreal forest.

Macroclimate

Macroclimate of the study area is transitional between the Taiga, Continental Tundra, and Marine Tundra Climatic Zones (Burns 1973), the result of the interaction of major air masses. Winter months are dominated by Continental Arctic air (cA) over northern Canada, which retreats and modifies in summer months to Cold Maritime Arctic (cmA) and Maritime

Arctic air (mA). These modified summer air masses are associated with the Beaufort Sea and the stagnant polar ice cap. The frontal formation of these summer air masses (cmA and mA), with Maritime Polar (mP) or rarely Maritime Tropical (mT) air, occurs commonly near the study area. Bryson (1966) first associated the northern limits of boreal forest with this frontal pattern and Larsen (1971b) expanded on this thesis. The proximity of Arctic air masses at all times results in cool summers, long, cold winters, low precipitation, and steep gradients of temperature and precipitation increasing north to south. Important macroclimatic averages are the 13.3°C July mean and -29.4°C January mean temperatures with 260 mm average annual precipitation of which 67% is received as snow. Snow release (<2.5 cm) generally occurs by 20 May and recordable snow depths (>2.5 cm) generally occur by 10 October.

METHODS

Meso- and microclimates

Meso- and microclimates were monitored during summer months in 1975 and 1976 for instrumented sites (Sites N and S; Fig. 1) in Regions II and III. Temperature and humidity were measured continuously with a hygrothermograph (Belfort Instrument Model 5-594) housed in a white, louvered shelter (Vogel and Johnson 1965) and calibrated at 6-d intervals using a sling psychrometer. Temperature profiles on a representative soil hummock were measured at 1-h intervals using a Grant Model D. Multipoint Recorder and thermistor probes. Probes with self-aspirating shields were installed at 150, 50, and 5 cm above the hummock and 5 cm above the side and trough of the same hummock. Probes were also installed -3 cm into

the hummock at the same top, side, and trough locations. Supplementary spot readings of surface temperature every 6 d were made with an Infrared Thermometer (Barns Engineering Model PRT-10) during 1976 and at -5, -10, and -15 cm with thermocouples read with a microvoltmeter and electronic reference junction (Wescor Model MJ-55) for both years.

Wind speeds were measured at 1 m (top of the shrub layer) with a three-cup totalizing anemometer (Belfort Instrument Model 5-349). Wind profiles were measured with a hot-wire anemometer (Hastings-Raydist Model AB-27) and unidirectional probe at 1, 0.5, 0.3, 0.2, 0.1, 0, -0.1, and -0.2 m (0 was the hummock top and minus values were in the trough). Bias in the readings was avoided by recording 10 replicates of readings at 15-s intervals and reporting the mean. Precipitation was recorded with a wedge-type precipitation gauge (Edwards Manufacturing Model Tru-Chek) mounted with orifice opening 50 cm above the ground.

Soil water was measured gravimetrically at 6-d intervals for surface samples (0 to -2.5 and -2.5 to -5 cm) and water potential equivalent estimated from desorption curves using a pressure plate apparatus (Soil Moisture Equipment). Soil water at -5 and -10 cm was measured with Spanner type thermocouple psychrometers with ceramic cups (Wescor) read at 6-d intervals with a microvoltmeter. Active layer depth was measured monthly at 1-m intervals for 50 points along a transect with a 1.2-cm diameter rod, recording also the relative hummock position of each probing.

During 1976, an additional instrumentation site (Site Ia) was established in Region I. Hygrothermograph, totalizing anemometer, and precipitation gauges were installed and serviced at monthly intervals. Temperature data reduction consisted of daily maximum, daily minimum, hourly determined daily mean, and maximum-minimum determined daily mean temperatures. Three-day mean, monthly mean, and degree day calculations were made using missing data supplied by linear calibrations of regional sites to the Inuvik airport. Precipitation was expressed in 6-d and 3-mo totals and wind as monthly averages.

Water relations

All psychrometric determinations of water potential were made using a Spanner type chamber psychrometer (Mayo 1974), and were read with a Wescor MJ-55 microvoltmeter after the application of a 10-s (8-mA) cooling current. Psychrometer measurements were made in triplicate, equilibrated at least 12 h for total leaf potential and 2 h for combined osmotic and matric potentials in a room temperature water bath. Data presented were temperatures corrected to 25°C (Brown 1970) and were expressed in the standard model of water relations. Combined osmotic and matric potentials were determined after freezing of the original needle sample in liquid nitrogen (-196°C) and turgor

was calculated by subtracting combined osmotic and matric potentials from total leaf potential.

Water contents of each psychrometer sample were determined after measurement of combined osmotic and matric potentials. All water contents were expressed as a percent of sample dry mass after oven drying at 80°C for 24 h. These were the standard techniques for all measurements of water status and only deviations from these techniques will be mentioned below.

Measurements of seasonal trends in the water relations of *Picea mariana* were made on three individuals near Inuvik at 6-d intervals during 1976. Samples of the same 5, 3, and 1 m tall trees were taken between 1500 and 1800 Mountain Standard Time (MST) on rainless days during summer months to maximize stress measured. Psychrometers were loaded and closed in the field and returned to the laboratory for measurement after a 12-h equilibration time. Winter samples were transported frozen and sampled under laboratory conditions 1-2 d later.

Photosynthesis

Effects of water deficit on rates of net assimilation (P_{net}) were investigated using four "season (\approx 3-mo growing season)" old greenhouse-grown *P. mariana* seedlings. Flats of seedlings were maintained in a controlled environment chamber and watered only at Day 0 and Day 9. An "open" infrared gas analysis system was used for all gas exchange measurements (Sestak et al. 1971) and in all samples entire seedlings were enclosed in the sample chamber. Differential measurements of gas exchange were determined with a Beckman Model 865 infrared gas analyzer (IRGA) which spanned 30 ppm full scale and recorded continuously. Zero and span of the IRGA were checked using gases standardized after Bate et al. (1969) before each sampling run; gas flow was measured with Gilmont No. 1 flowmeters. Leaf temperature was recorded continuously with leaf thermocouple clips attached to abaxial surfaces. Temperature control of the cuvette was provided by the enclosing controlled environment chamber.

Photosynthetically active radiation was measured continuously using a quantum sensor supplied by Lambda Instruments (Lincoln, Nebraska). Lighting was provided by fluorescent tubes in the controlled environment chamber and supplemented by a 1000-W quartz-iodide lamp which was rheostatically controlled.

Germination response to temperature

All seed-bearing cones were stored at -3°C before seeds were germinated. No cold treatment was required due to previous overwintering. Seeds were extracted by soaking the cone in hot tap water for 6 h, drying at 80°C for 8 h, and tumbling to knock the seed

free. Extracted seeds were dewinged and counted into lots of 50 for testing. Seeds were placed on filter paper disks, treated with a mercurial fungicide (Morsodren, Morton Chemicals), and transferred to Petri dishes. Germination was defined as radicle elongation and germinated seeds were removed at 1–2 d intervals. All germination trials were terminated after 3 wk.

Temperature requirements for germination were investigated using two trials of 2–5 yr-old seed collected in Region II during 1975 and 1976. Temperature gradients were provided by a germination bar as in Barbour and Racine (1967) in a controlled environment chamber. Temperature was held constant within $\pm 1^\circ\text{C}$ with four replicates at 5° , 10° , 15° , 17° , 20° , 22° , 25° , 28° , 30° , and 35°C . Thermal contact between the plates and bar was insured by a thin layer of petroleum jelly.

Percent germination data were analyzed using an arcsine transformation and one-way analysis of variance (Sokal and Rohlf 1969). Duncan's multiple range test was used to isolate significant ranges of mean germinations.

Regional germination response

Regional variation in seed germination was investigated using cone samples collected in each of the four designated forest regions. At the time of collection, cones were separated into 1, 2–5, and 5+ yr-old samples. Storage, extraction, germination, and statistical analysis of seed lots were as described previously, except all tests were conducted at 20°C in a controlled environment chamber.

Regional differences in seed size were investigated using four replicates of 50 seeds 2–5 yr of age. Seeds were weighed with wings intact; data are expressed in seeds per kilogram. Data analysis was similar to that for the germination trials.

Germination and mortality response to environment

Microsites within soil hummock topography were chosen to represent the microenvironment encountered by germling *P. mariana* in a postfire subarctic woodland. These were characterized as hummock top, side, and trough microsites by the following criteria: (1) Hummock top microsites were the exposed (after fire) mineral soil core of a discrete soil hummock. Little or no vegetation and no organic material covered the mineral soil. (2) Hummock side microsites were microtopographically lower with an organic covering of increasing thickness away from the hummock top. These were covered with the bryophytes, including *Polytrichum commune*, *P. juniperinum*, *Marchantia polymorpha*, *Ceratodon purpureus*, and *Bryum pseudotriquetrum*. (3) Hummock trough microsites were the lowest and were characterized by a peat soil and by a water table at the soil surface in early June. Veg-

etative cover was similar to the hummock side microsite but with more luxuriant growth of *Polytrichum*.

No aspect-related pattern was found in the preburn distribution of *P. mariana* trees but nevertheless microsites were chosen minimizing bias with respect to aspect. Living moss and peat were removed to the charred postfire surface in a 4×4 dm area, and all vascular plants were removed from the plots but were subsequently permitted to regrow.

Seed lots from Region II ($33.6\% \pm 5.5$ SD germination 1976 sample) were used in all field trials. Seeds (250 seeds per plot) were hand sown into 2×2 dm plots within 3 wk after snow release in 1975 (14 June, Site N and 12 June, Site S) and within 2 wk in 1976 (5 June, Site N and 4 June, Site S). Permanent records of recruitment and mortality were made by mapping emerging seedlings with a mapping table as described by Mack and Harper (1977). Plots were remapped at 6-d intervals June through August, and on 28 September 1975, and June through August 1976.

Germination was expressed as percent of the 250-seed lot and mortality as a percent of total germinations per plot. Data analysis consisted of an arcsine transformation of both germination and mortality data within a three-way complete factorial analysis of variance using regional site, microsite, and time as the treatments. Nonsignificant ranges of germination and mortality were determined by Duncan's multiple range test using error mean square generated from one-way analysis of variance for individual microsites. Comparison of means tests were used to test significant differences between summations of germination, mortality, and subgroups of mortality.

Environmental measurements were made as outlined in the previous site descriptions. Qualitative assessment of the hummock microenvironment was made with 10 replicate transplants of 5–7 yr-old seedlings into each microsite. These allowed assessment of possible revegetation by transplants and tested differing hummock positions for established seedling survival.

Tree growth

Growth measurements across tree line were made using three replicate 10×10 m plots at each sampling site. Each tree (>1 m in height) was measured for height, and diameter at the stem base and small individuals (<1 m) were counted. All rooted stems with apical dominance, plus stems produced by vegetative reproduction (layering) were included.

Ring counts were made in the laboratory with a dissecting microscope. Six (or more) trees were sectioned at each site and spanned the range in sizes from >1 m to canopy dominants. Seedling ages in young stands were determined by counts of terminal bud scars back to the cotyledons, including years buried by peat.

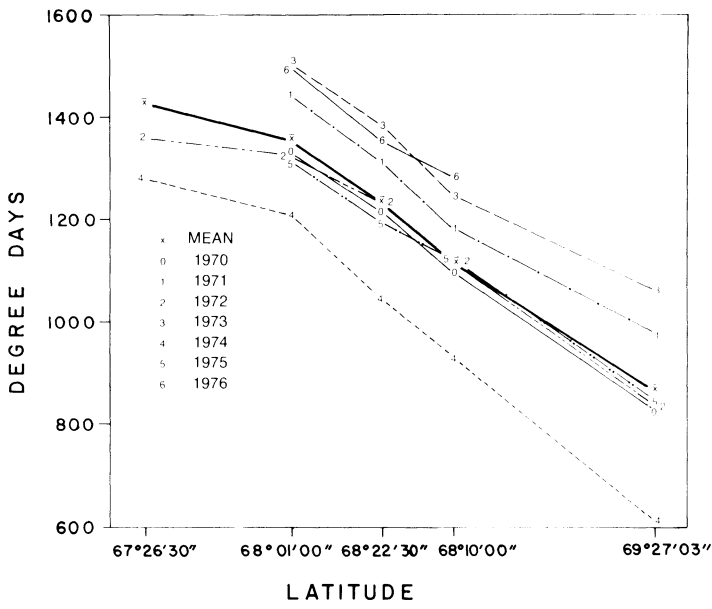


FIG. 4. Degree day summaries (based on 0°C) for study transect, 1970–1976 (69°27'03" = Tuktoyaktuk; 68°10'00" = Site Ia; 68°22'30" = N; 68°01'00" = Site S; 67°26'30" = Ft. McPherson).

Stand origins were dated using burn scar ages collected at stand margins.

Cone production was counted from 87 trees along the transect. All cones in the top 2 m of the crown were separated into 1, 2–5, and 5+ yr-old classes in the laboratory based on branch position relative to the branch buds. Seeds per cone were also determined.

RESULTS

Meso- and microclimates

Mesoclimatic variation from Region I to IV, across tree line, was demonstrated in temperature differences

directly affecting length of the growth season. Degree days (>0°C, Fig. 4) reflected the ≈4°C daily mean difference along the study transect. Distribution of monthly temperatures (Table 1) suggested differing conditions in 1975 and 1976 than were apparent in the degree day calculations; 1975 exhibited a much earlier and warmer spring than average and 1976 a cooler than average spring. Degree day summations suggest that 1976 was a warmer year primarily due to higher fall temperatures.

Precipitation did not vary between sites during the two summers, though annual average precipitation differences exist (129, 260, and 336 mm for Tuktoyaktuk,

TABLE 1. Monthly mean temperatures for 1975 and 1976 at study sites and neighboring airports (°C).

	May	June	July	August	September
1975					
Site N	2.9*	10.6*	13.6	9.7	1.5*
Site S	4.9*	11.5*	13.9	10.6	3.8*
Inuvik airport	3.0	10.6	13.9	10.0	1.7
1976					
Site Ia	0.5*	7.9	12.7*	11.7	5.1*
Site N	1.0*	8.6	14.0	13.1	5.8*
Site S	3.3*	10.3	14.5	12.4	7.4*
Inuvik airport	1.1	8.9	14.2	12.5	5.9
Long-term airport means†					
Tuktoyaktuk	−4.4	4.4	10.6	8.9	2.2
Inuvik	−0.6	10.0	13.3	10.6	2.8
Ft. McPherson	1.7	11.7	15.0	11.7	3.3

* Missing data supplied by site calibrations.
† Means collected from 1941 to 1970 when available.

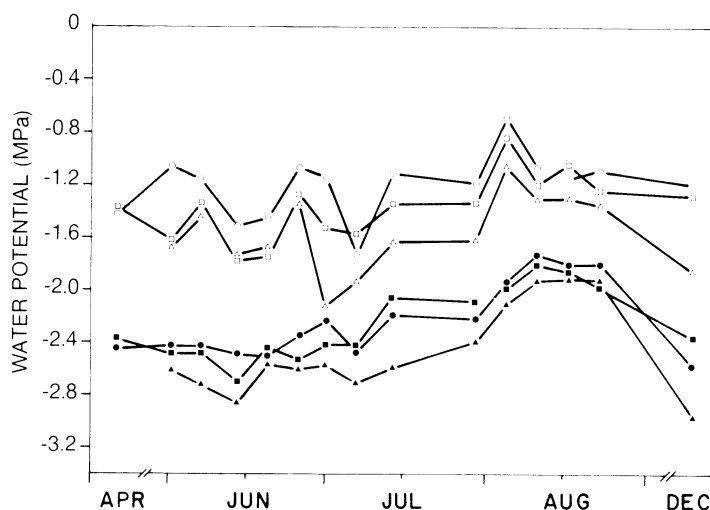


FIG. 5. Seasonal trends in water relations of three *Picea mariana* trees. Total leaf potentials are the open symbols and combined osmotic and matric potentials are closed symbols (\circ and \bullet = 5-m tree; \square and \blacksquare = 3-m tree; \triangle and \blacktriangle = 1-m tree).

Inuvik, and Ft. McPherson, respectively). Precipitation in 1976 was approximately average for the 3-mo study period (98 vs. 93 mm) but June precipitation was twice the average compared to June 1975 reflecting the predominance of arctic air. Summer precipitation in 1975 was lower than average (77 vs. 93 mm).

Humidity was relatively constant throughout the summer months, though it was lowest and most variable during June and July (weekly minima and maxima, 30–50% and 80–100%, respectively). The June and July periods of lower humidity were associated with 30–60% higher wind speed than August, accentuating these drying effects (Black 1977). Average wind speeds at the Inuvik airport follow the same June to August trends though the absolute values differ, reflecting the 10-m recording height. Wind speed in general decreases 25–35% north to south.

Temperature profiles of hummocks suggest earlier spring warming of the hummock top as opposed to peat trough areas (i.e., temperatures of 3.5°, 0°, and 1°C at –15 cm for top, side, and trough microsites, respectively, Site N, 3 June 1976; Black 1977). This is probably the result of improved drainage and the insulating properties of peat. Higher temperatures and higher wind speeds associated with hummock top microsites, grading to lower temperatures and wind speeds in trough areas result in more mesic conditions for plant establishment from hummock top to trough microsites (Black 1977).

Soil water potential at –5 or –10 cm did not go below –0.1 MPa during 1975 or 1976 in any microsite. Droughty soil conditions (soil water potential below –1.5 MPa) were therefore restricted to surface (0 to –5 cm) layers. Droughty soil conditions were most common on hummock tops thus having little effect on

established plants but profound effects on germinating seed.

Active layer depth of the soil hummocks also reflected seasonal macroclimatic and microclimatic differences between 1975 and 1976. The hummock core (top) melted deeper and earlier than associated side and trough areas. This probably resulted from differences in thermal conductivity and latent vs. sensible heat flux of each microsite. Trends in active layer melt in 1975 and 1976 followed spring temperatures with greater June melt in 1975 than 1976. Total active layer depth for all microsites was similar by August in both years (80 and 110 cm, Sites N and S, respectively, 1975; 88 and 115 cm, Sites N and S, respectively, 1976).

Water relations

Water relations of the adult trees follow a similar seasonal response. Fig. 5 presents seasonal water relations and shows minimum water potentials (= maximum stress) occurring for all trees between 13 June and 6 July, a time of high air and low soil temperatures. Lowest total leaf potential (–2.1 MPa) was measured from the suppressed (1-m) tree during a period of high air temperature (18°C) July 1. Maximum leaf potentials of –0.6, –0.8, and –1.1 MPa for the 5, 3, and 1 m tall trees respectively, were measured on 4 August and preceded a needle cast (\approx 10 August).

Combined osmotic and matric potentials showed marked increases from –2.4 to –2.0 MPa beginning 20 June. These increased potentials were associated with bud expansion and pollen cast; both events were delayed in the suppressed tree. Combined osmotic and matric potentials decreased with the onset of winter, while total leaf potential remained stable, reflecting a

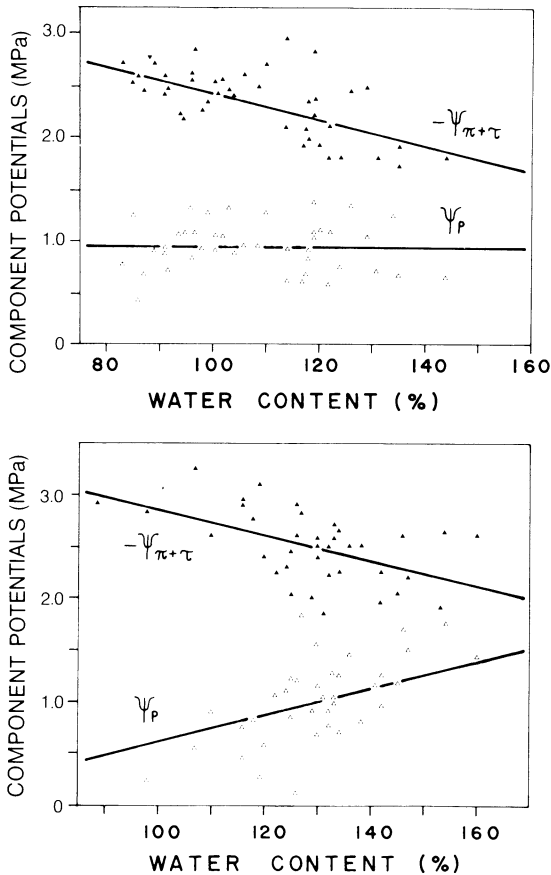


FIG. 6. Field measurements of turgor potential (Ψ_p) and combined osmotic and matric potentials ($\Psi_{\pi+\tau}$) as a function of water content for *Picea mariana* needles (top graph). Comparative laboratory determined values (bottom graph) from water-stressed 3 yr old *P. mariana* (Δ = turgor potential, \blacktriangle = combined osmotic and matric potentials).

change in water relations associated with winter hardness. Osmoregulation by the trees maintained a constant turgor (1.0 MPa), permitting expansion and growth (Fig. 6). Turgor potential remained stable during the growing season through a range in water contents from 83 to 144%. This osmoregulation resulted in a significant correlation ($P < .01$) between water content and total leaf potential for field determinations.

Germling responses to water stress were investigated in controlled environment chambers (M-12, Environmental Growth Chambers, Chagrin Falls, Ohio) using paired flats of greenhouse mix soil and 10-d-old germlings. Temperature (20°C) and illumination (250–300 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ Photosynthetically Active Radiation, PhAR) were held constant. The experimental flat was not watered and sampling of both the experimental and control germlings occurred simultaneously, twice daily. Each sample consisted of six germlings random-

ly chosen from each flat for psychrometric readings and water content.

Water potential of the experimental germlings by day 6 had decreased to -1.0 MPa from the control values of -0.5 MPa (Fig. 7). This decrease in water potential resulted in a 60% mortality which increased to 80% with a continuing decreased water potential to -2.5 MPa. No turgor pressure was measured at -2.5 MPa. After watering, recovery was observed only in individuals which had not wilted during the period of drought. Continued mortality after watering was evident in an additional 12% loss.

The sensitivity of germlings to water stress is demonstrated in Fig. 8. Two points are made: first, the decrease in water content of both the control and experimental samples is interpreted as maturation of the germlings, the result of an increase in dry mass; second, the water content, which resulted in zero turgor pressure and -2.5 MPa combined osmotic and matric potentials in the experimental germlings, was not distinguishable from control water contents. This suggested that small changes in water content resulted in lethal drops in turgor and combined osmotic and matric potentials.

Photosynthesis

Descriptive measurements of P_{net} for six replicates were made to determine optima for subsequent investigation of stress responses. Temperature optima for P_{net} of 4.9 $\text{mg} \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ (Fig. 9) occurred at 15°C at a constant light intensity of 740 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. A broad plateau of responses resulting in P_{net} of 1.5 $\text{mg} \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ and 2 $\text{mg} \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ occurred at 0°C and 35°C, the minimum and maximum measurement temperatures, respectively. Maximum dark respiration measured was 1.9 $\text{mg} \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$ at 30°C (the highest temperature used in the measurements). Respiration was undetectable at 0° and 5°C.

Light response curves (Fig. 10) measured at 15°C show compensation for respiration occurred at 18 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Saturation, when defined as the point at which a 100% increase in irradiance resulted in a <10% increase in P_{net} , occurred at 500 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

Photosynthetic measurements during the water stress investigations were made at 15°C and 740 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The P_{net} of the same two seedlings was monitored while determinations of water content, water potential, combined osmotic and matric potentials, and turgor potential were made on three "neighboring" seedlings. Measurements were made daily until day 5, after which morning and evening measurements were made. Water stress at day 5 of -1.5 MPa leaf water potential resulted in a 50% reduction of P_{net} and day 8 readings of -2.5 MPa leaf potentials resulted in further reduction of P_{net} to zero (Fig. 11). Plots of turgor potential and combined osmotic and matric potentials (Fig. 6) showed no osmoregulation

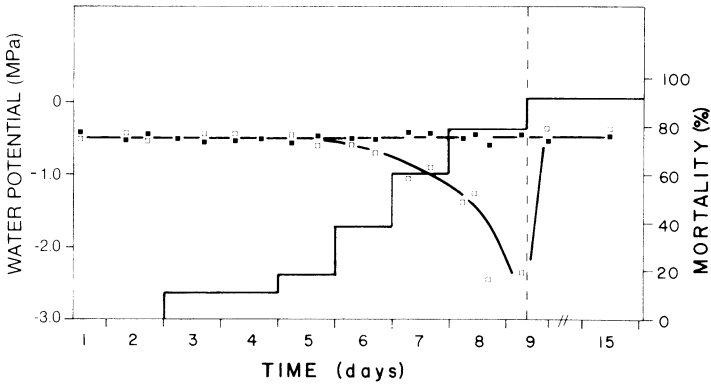


FIG. 7. Total water potential and mortality as a function of time since watering for entire germlings. Watering occurred at day 0 and day 9 for the experimental germlings. Mortality is the step function of percent (■ = control germlings; □ = experimental germlings).

of turgor potential as found in field measurements and a lower correlation ($r = .59$, $n = 41$) compared to field data ($r = .66$, $n = 42$) for the relationship of water content to leaf potential. Leaf water potential after watering of stressed plants recovered within 10 h, but P_{net} remained at 25% of original measurements; 100% recovery of P_{net} was observed after 6 d.

Seed germination

Temperature had a significant effect on germination with highest germination (41%) at 20°C with a nonsignificant reduction at 22°C (38%). Germination occurred at reduced levels at 17°, 25°, and 28° (14–21%) and was inhibited at 5°, 10°, 15°, 30°, and 35° (0–9%). Seed from lower temperature trials (5°, 10°, 15°, and 17°C) germinated when placed in temperatures conducive to germination (20°C), while seed from higher temperature trials (30° and 35°C) did not respond to optimal temperatures.

Germination was highest (28–35%) in 2–5 yr-old seed samples with nonsignificant differences between Regions II, III, and IV (Fig. 1). No germination was observed from Region I, the forest-tundra region. Seed size was not significantly different in the three forest regions, ($0.97\text{--}1.32 \times 10^6$ seeds/kg) but seed was less than one-half as large in the forest-tundra region (2.28×10^6 seeds/kg) ($P < .001$).

Germination in the 5+ yr old seed was not significantly different in the three regions tested (0.5–3.5%). Region IV seed 5+ yr old was inadvertently destroyed before testing. Only seed 5+ yr old germinated (0.5%) from the forest-tundra indicating how rare successful seed-set is in this region.

Seed samples (1 yr old) initiated in 1975 show a gradient of increasing germination from north to south of 0, 1.5, 4, and 7% for Regions I, II, III, and IV, respectively, and a gradient of nonsignificance between them.

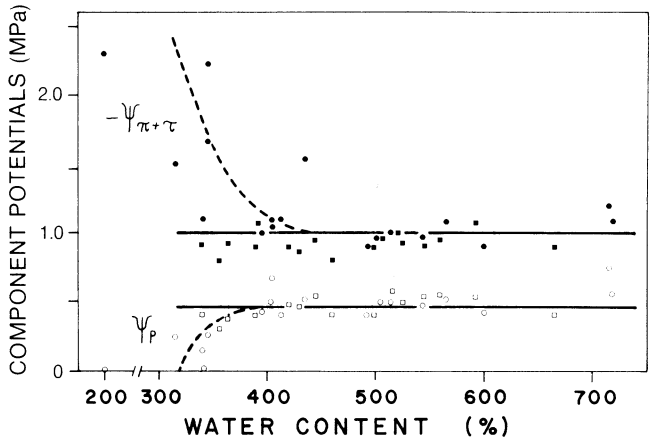


FIG. 8. Combined osmotic and matric potentials (closed symbols) and turgor potential (open symbols) as a function of water content for entire germlings in the stress experiment (○ and ● = experimental germlings; □ and ■ = control germlings).

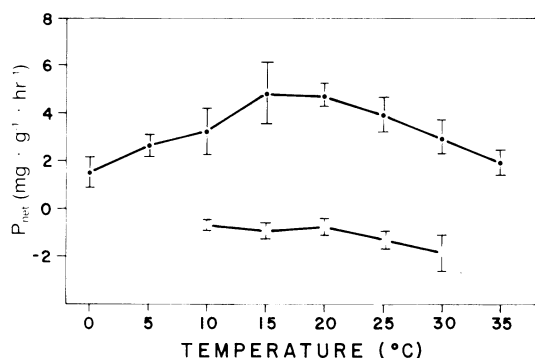


FIG. 9. Temperature response of net photosynthesis and dark respiration for three "season" old seedlings of *P. mariana* (● = light P_{net} response; ○ = dark respiration; bars are 95% confidence intervals).

Field germination

Regional site, microsite, and time interacted in 1975 producing a significant component of variance ($P < .001$), but only interactions of regional site with time and microsite with time were significant in 1976 ($P < .001$ and $P < .025$, respectively). Nonsignificant differences between all germinating sites (Table 2) in 1976 resulted in the change in interaction variances.

Microtopographic effects on germination were similar in 1975 and 1976 with germination restricted to hummock sides and troughs. Seed failed to germinate in 1975 and 1976 on hummock top microsites. Otherwise substrates were not directly responsible for variance in germination between microsites as differences were not significant between total percent germination at the same regional site (Table 2).

Together, regional and microsite temperatures control the initiation of germination. All germination occurred after 3-d mean air temperatures (5 cm above soil surface) were $>15^{\circ}\text{C}$. Temperatures at 5 cm were found more highly correlated ($r = .76$, $n = 70$) with soil surface temperatures than were -3-cm temperatures ($r = .68$, $n = 70$). Air temperature data were used in all comparisons.

Germination peaks occurred before 8 July in 1975 for the hummock side microsite at both regional sites (Table 2). Germination peaks for the trough microsites were delayed compared to side microsites, reflecting a difference in air (0.5°C) and soil ($4\text{--}5^{\circ}\text{C}$) temperatures. Germination was not significant after mid-July (Table 3), even with temperatures in the optimal ranges, due to low soil water content (Fig. 12). Significant germination peaks in 1976 were delayed until the 2nd wk in July or did not occur (trough microsite, Site S) due to low spring temperatures (compare Tables 2 and 3). No significant germination occurred after the 4th wk of July 1976 (Table 3).

Temperature differences between regional sites and

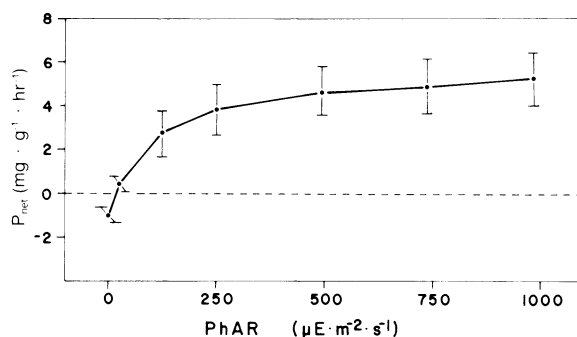


FIG. 10. Net photosynthesis (P_{net}) as a function of light intensity at 15°C for three "season" old seedlings. PhAR = photosynthetically active radiation. (Bars are 95% confidence intervals.)

yearly trials provide information on the germination requirements of *Picea mariana*. The regional mean temperature for June 1975 and 1976 was significantly correlated ($P < .05$) with microsite germination, corroborating the temperature limitation to germination found in laboratory trials. July mean macrosite temperatures were not correlated with germination, due to early July germination dates.

Interpretation of soil water relations data was hampered by the necessity of using composite soil samples. Reductions of soil water to unavailable ranges (-1.5 MPa) in the seedbed (top 1 mm?) were not reflected in the small changes in soil water content in the 0–2.5 cm sample; therefore seed germination was probably prevented by low soil water, well before water contents equivalent to 0.03 MPa were measured. Soil water status probably determined the cessation of germination after mid-July or prevented germination when temperature was not limiting. Surface (0–2.5 cm) soil water content was <-1.5 MPa on all hummock tops throughout 1975 and 1976, only reaching levels of available soil water immediately after precipitation or snow release. The absence of germination on hummock top microsites therefore was the result of unavailable soil water as temperatures were frequently not limiting (see Black 1977). Snowmelt appears to be the only major source of recharge as no discernible difference was detected in microsite soil water content between 1975 and 1976. June 1976 precipitation was double the average for that month. Germination in 1976 was significantly reduced ($P < .01$) from 1975 values in spite of increased precipitation. The interaction of temperature and soil water was critical for germination of *P. mariana*. Microsite temperatures must average $>15^{\circ}\text{C}$ before measurable reduction in soil water content occurs (before 15 July). Laboratory germination trials required 6–10 d for radical elongation, suggesting temperature requirements must be met before 1 July to insure an adequate water supply

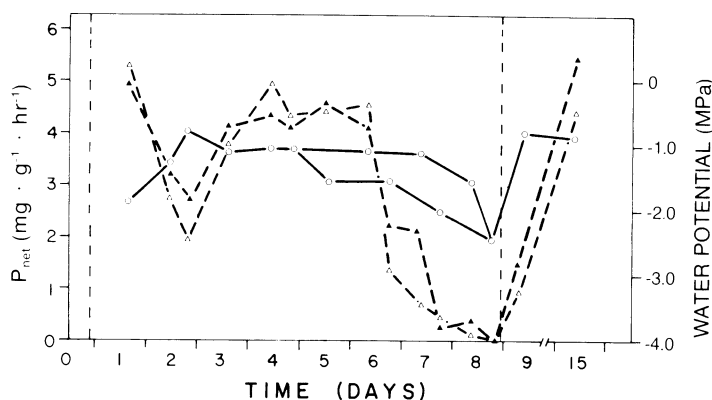


FIG. 11. Net photosynthesis and water potential as a function of time since watering (\blacktriangle = P_{net} of seedling 1; \triangle = P_{net} of seedling 2; \circ = associated total leaf water potentials) split to morning and evening readings. Measurements were on 3 yr old *Picea mariana* seedlings. The vertical dotted lines indicate watering dates.

for establishment. These requirements were not met in 1976, resulting in reduced germination.

Overwintering of viable seed resulted in only 10 seedlings, suggesting destruction of the majority of ungerminated seed (≈ 70 – 90% of viable seed sown).

Field mortality

Regional site, microsite, and time interacted to produce significant components of variance in mortality of the 1975 and 1976 germling populations ($P < .001$ both years). Individual microsites, however, did not experience significant differences in mortality (Table 3), apparently due to low germination, and were dropped from consideration. Mortality percentages did not differ in the microsites after 1 yr but two mortality patterns were apparent (Fig. 13). Both microsites at Site S and the side microsite at Site N show low initial probabilities of 15-d survival (.68) compared to the Site N trough microsite (.96). Reduced trough microsite mortality was the result of cooler temperature and high soil water contents. All summer mortality resulted from water stress induced by high transpiration stress (see physiology section under Results), heat stem girdling as found in other conifers (Baker 1929), or reduced soil water. Summer percent mortality peaked 16 July and 14–19 July (Sites N and S, respectively; Table 2) following 3-d means with maximum temperatures $>30^{\circ}\text{C}$ at 5 cm. Minor mortality peaks occurred before 14 August (Site N) and 17 August (Site S) associated with 24° – 31° and 33° – 42°C microsite maximum temperatures, respectively. Precipitation (up to 15 mm during the growing season) only temporarily reduced mortality (i.e., 8 August 1975, Site N and 11 August 1975, Site S) probably through reduction in temperature rather than increasing soil water.

Overwintering mortality was significant only in the trough microsite (Site N). Abundant needle ice for-

mation as observed 28 September 1975 resulted in burial or uprooting of germlings and high (20%) spring mortality. High soil water content of this microsite reduced summer mortality but promoted needle ice production thereby increasing overwinter mortality.

Minor sources of mortality were mechanical damage by snowfall (2 August 1975), inability to penetrate soil, uprooting or burial by rain splash, and apparent grazing by insects. Germling submergence (snow melt to 5 June 1976 in the trough microsite, Site N), resulted in no observed short-term mortality, indicating the plants were resistant to waterlogging. Germination time had no significant effect on mortality of subpopulations divided a posteriori at 8 July (Site S), 10 July (Site N, side microsite), and 16 July (Site N, trough microsite). Germling age and daily microenvironment apparently were the factors determining mortality. Germination time or microsite had no effect on germling success, suggesting initial germination was the major determinant of stand reproduction.

Tree growth

Seedling age distributions (Fig. 14) suggest stand reproduction occurs only immediately after burning. Section ages however, suggest a much broader age distribution with 10–80 yr discrepancies between ages and burn dates. These discrepancies and increases in age variation were the result of lost annual rings due to burial by peat, suppressed growth, and/or confusion caused by layers. Though these errors would be highly variable between trees, a linear correction ($r = 0.99$, $n = 24$) based on the oldest ring counts in a stand and fire scar sections was developed and applied to all stand ages in the study. This correction was

$$A = 16.9764 + 1.0926SA, \quad (1)$$

where A is the age of the stand (since burning) and SA

TABLE 2. Percent germination and mortality for Sites N and S microsites (msite) in summer 1975 and winter 1975–1976. Undifferentiated groups ($P = .05$) as determined by Duncan's multiple range testing, are underlined. Dotted line under a number indicates that it is significantly different from the adjacent underlined numbers.

		1975												1976		
Site N		June		July				August				Sept	June	Total		
		14	30	6	10	16	22	28	2	8	14	20	27		28	2
Side msite																
Germination (%)	sown	0		2.2	0.9	0.3	0	0.1	0	0	0	0	0	0	0	3.5
Undifferentiated groups																
Mortality (%)		0	0	9.7	16.1	12.2	7.8	9.2	0	6.9	1.5	0	0	0	0	63.4
Undifferentiated groups																
Trough msite																
Germination (%)	sown	0		0.3	0.4	1.5	0.2	0.3	0.5	0.3	0.3	0	0.1	0	0	3.9
Undifferentiated groups																
Mortality (%)		0	0	0	1.4	0	0	0	0	2.1	0	0	0	0	19.8	23.8
Undifferentiated groups																
		1975												1976		
Site S		June		July				August				Sept	June	Total		
		12	29	3	8	14	19	24	30	5	11	17	27		28	2
Side msite																
Germination (%)	sown	0		4.4	3.0	1.2	0.4	0.1	0	0	0	0	0	0	0	9.1
Undifferentiated groups																
Mortality (%)		0	0	6.7	9.4	6.9	1.4	1.6	0.8	0	1.5	0	0	0	0	28.3
Undifferentiated groups																
Trough msite																
Germination (%)	sown	0		2.2	5.0	2.3	0.3	0.3	0	0.1	0	0	0	0	0	10.1
Undifferentiated groups																
Mortality (%)		0	0	4.2	25.2	20.9	4.7	2.8	1.2	0	1.0	0	0.4	0.5		60.9
Undifferentiated groups																

is the section age of the oldest stand members. A single corrected stand age was used for all stand members and the assumption made that all individuals were the same age (± 8.8 yr, SE of estimate).

Stand density was a function of age (Fig. 15) decreasing to a relatively constant stand density (≈ 6000 trees/ha) by 80 yr in age. Density subsequently increased after 200 yr. This increased density resulted from the death and windthrow of dominant trees and increased layering, and was not the result of seedling establishment. Layering appeared sufficient to effect stand replacement in the absence of burning.

Assuming similar patterns of mortality for all stands studied, tree survivorship could be described by one of two possible models (Hett 1971). One was the negative exponential model

$$Y_t = Y_0 e^{-bx}, \tag{2}$$

where Y_t is the number of plants per unit area at time t , Y_0 is the initial numbers of plants, b the mortality rate, and x is age in years. This model assumes mor-

tality was constant through time and was rejected for that reason. The power function model

$$Y_t = Y_0 x^{-b} \tag{3}$$

assumes mortality rates change with time and was felt more appropriate. This model, transformed and fitted to the data from stands < 100 yr old by a least squares technique, gives the relationship

$$\ln Y_t = 7.3606 - 0.7246 \ln X, \tag{4}$$

describing density as a function of age. This relationship (Eq. 3) fitted to the data; though not significantly different from the previous example (Eq. 2) by a-test of homogeneity using a z statistic (Sokal and Rohlf 1969), it nevertheless described a more highly correlated ($r = -.70$ vs. $-.61$, $n = 47$) relationship.

Growth was examined from two points, volume growth ($V = \pi r^2 h/3$) and height growth. Mean volume was calculated for each plot and the correlation of stand density, latitude, and age examined by stepwise linear multiple regression of the form

TABLE 3. Percent germination and mortality for Sites N and S microsites (msite) in summer 1976. Undifferentiated groups ($P = .05$), as determined by Duncan's multiple testings, are underlined. Dotted line under a number indicates that it is significantly different from the adjacent underlined numbers.

Site N	June		July			August					Total
	5	29	5	11	29	4	11	16	22	30	
Side msite											
Germination (%)	sown	0	0.2	0.4	0.4	0.1	0.1	0	0	0	1.2
Undifferentiated groups											
Mortality (%)		0	0	2.8	0	8.3	0	0	0	0	11.1
Undifferentiated groups											
Trough msite											
Germination (%)	sown	0	0.3	0.2	0.5	0	0.1	0	0	0	1.1
Undifferentiated groups											
Mortality (%)		0	0	0	3.3	0	0	0	0	0	3.3
Undifferentiated groups											
Site S	June	July				August					Total
	4	1	7	13	30	5	11	17	23	29	
Side msite											
Germination (%)	sown	0	0.2	0.7	0.1	0	0	0	0	0	1.0
Undifferentiated groups											
Mortality (%)		0	2.8	56.8	0	0	0	0	0	0	59.6
Undifferentiated groups											
Trough msite											
Germination (%)	sown	0	0.3	0.1	0	0	0	0	0	0	0.4
Undifferentiated groups											
Mortality (%)		0	0	0	10.0	0	0	0	0	0	10.0
Undifferentiated groups											

$$Y = a + b_1x_1 + b_2x_2 + \dots b_nx_n, \tag{5}$$

where Y is the dependent variable, a is the intercept, b_1 to b_n are partial regression coefficients, and x_1 to x_n are the independent variables (Steele and Torrie 1960).

The age squared term produced a curvilinear relationship simulating the senescence of the stand with age. Density accounted for 71% of the explained variance, though the magnitude of the standardized partial regression coefficient was 33% stand age (Table 4). Density reduced mean tree volume, both as related to young, dense stands and to overstocked older stands. An investigation of log mean tree volume as a function of log density yielded a significant negative correlation ($r = -.57$, $n = 44$), suggesting intraspecific interference resulting in stand thinning. The slope of the thinning relationship was not significantly different from Yoda's 3/2 thinning law (White and Harper 1970).

Increased latitude (decimal latitude, i.e., $68^{\circ}30' = 68.5^{\circ}$) reduced mean volume as expected in a negative manner. A standardized partial regression coefficient of similar magnitude was found with both latitude and density. Age had the greatest effect ($3\times$) on the regression and was the most useful measure for prediction of stand mean volume.

Stand volumes (Table 5) were generated for each

region using the mean tree volume multiple regression (Table 4) and an average stand density. Stand volume calculated for Region 1 was overestimated tenfold when compared to field data. These values represent a potential never reached due to physical damage by wind abrasion and lower observed tree densities.

Dominant height growth (mean of six tallest trees per plot) and average height growth of stands <200 yr old were not predicted to be significantly different (better), using the same independent variables (age, density, and latitude), than mean tree volume ($R = .85$, $.85$, and $.90$, $n = 47$, 47 , and 53 respectively) by a test of homogeneity using a z statistic (Sokal and Rohlf 1969).

Age accounted for most of the explained variance (89% and 88%, dominant height and mean stand height, respectively) though the magnitudes of age effects differ (Table 4). Average stand height was less a function of age than was stand dominant height, reflected in the magnitude of the standardized partial regression coefficient, and was probably the result of the suppressed cohort population. Dominant tree height tables were generated for each region (Table 5) using the multiple regression (Table 4) and the average density.

No relationship between cone production and age was found other than the fact that cones were first

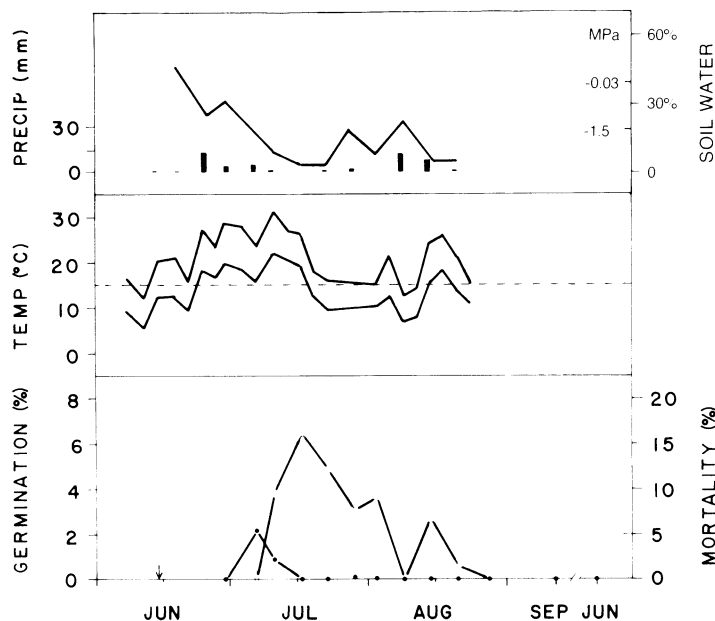


FIG. 12. Environmental, germination, and mortality data from Site N hummock side microsite for 1975. In the top graph the line is soil water content and bars are 6-d sums of precipitation. In the middle graph the lines are 3-d means of maximum temperature (upper) and mean daily temperature (lower). The lower graph shows germination (●), germling mortality (○); date of sowing is marked by an arrow.

produced between 25 and 30 yr and were reliably produced at 85 yr. Tree volume was curvilinearly ($r = .75$, $n = 69$) related to 5-yr cone production by

$$\log C = -1.1393 + 0.6498 \log V, \quad (6)$$

where V is the individual tree volume and C is the number of cones 1–5 yr old. The use of five-year cone production represses annual variation and gives the best estimate of standing seed population. Forest-tundra (Region I) stands were not considered in the regression due to the low and sporadic cone production.

Seed number per cone varied with length by

$$N = 1.6620 + 4.0690L, \quad (7)$$

where L is the cone length (mm) and N is the seed number. No environmental or growth characteristics could be related to cone length or seed number. Consequently, all measures of seed production used 71.8 seeds per cone ($SD = 11.95$, $n = 100$) in the calculation. Seed production was estimated at 6.28×10^5 seeds \cdot ha $^{-1}$ \cdot yr $^{-1} \pm$ ($SD = 2.16$) for stands 80–100 yr old increasing to 13.2×10^5 seeds \cdot ha $^{-1}$ \cdot yr $^{-1}$ ($SD = 3.00$) for stands 100–200 yr old. Stands 200+ yr old

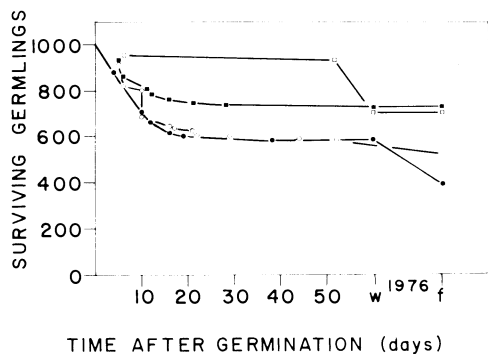


FIG. 13. Survivorship curves for 1975 germlings (● = Site N side microsite; □ = Site N trough microsite; ■ = Site S side microsite; ○ = Site S trough microsite; w = end of winter; f = end of growing season).

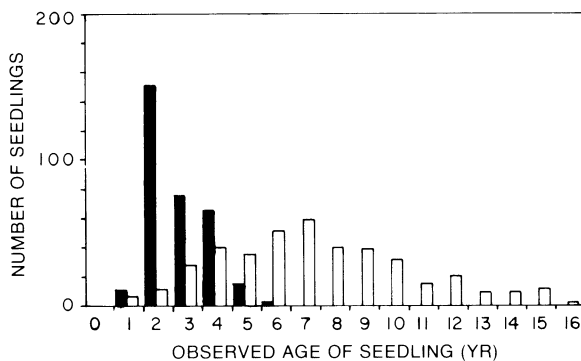


FIG. 14. Age distributions of two stands of seedlings. Solid bars are from Site S, 1968 burn. Open bars are from a 1947 burn (Site IIIh of Black and Bliss 1978) and show increasing error in measurement of age.

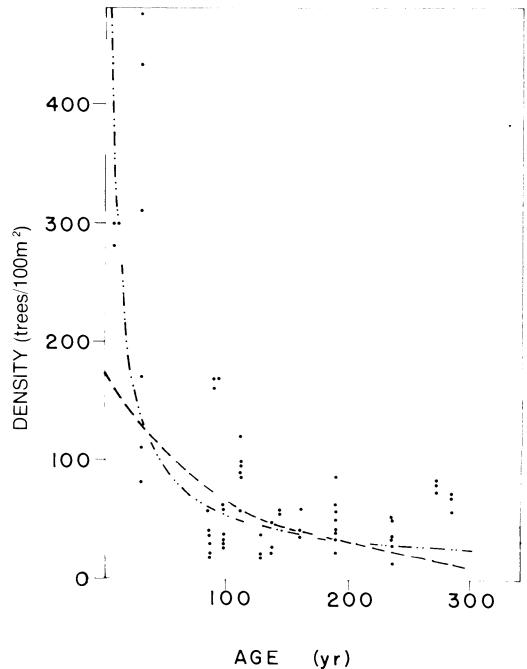


FIG. 15. Tree density as a function of age for all *Picea mariana* stands sampled. — · — · — is a power function fit; — — — is a negative exponential fit. Data points are individual plot values.

were estimated to reduce annual seed production to 6.03×10^5 seeds \cdot ha⁻¹ \cdot yr⁻¹ (SD = 1.40). All seed production estimates were calculated from measured tree volumes and summed by plot.

DISCUSSION

Environmental change and plant response

The climatic gradient and fire interval near tree line interact in controlling the success of *Picea mariana* in the lower Mackenzie Valley. Changes along this climatic gradient in mean daily summer temperatures, length of the growing season, and annual precipitation are important in the reproductive stages of *P. mariana*. Macro-meso climate changes across the study transect are most evident in daily temperatures during the growing season. Temperature means increase north to south $\approx 4^\circ\text{C}$ for the 135-km transect resulting in a vegetational change from self-reproducing forests to forest-tundra, and north of the study area to tundra vegetation.

Soil hummock microenvironment directly influences seedling establishment by restricting *P. mariana* germination to the side and trough areas ($\approx 66\%$) of the hummocky terrain. Temperatures are higher in hummock top microsites than trough microsites (differing by $\approx 1^\circ\text{C}$ air temperature at 5 cm above the surface, $4\text{--}5^\circ\text{C}$ soil temperature 3 cm below the surface) but more importantly, snow release and permafrost

TABLE 4. Multiple regression statistics for log of mean tree volume in thousands of cubic centimetres ($n = 53$), dominant tree height (m; $n = 47$), and mean tree height (m; $n = 47$).

Independent variable	Partial regression coefficient	Standardized partial regression coefficient	<i>t</i>	<i>R</i> ²
Mean tree volume				
Intercept	90.1897			
Density	-0.008531	-0.5457	-5.2	.57
Latitude	-1.3346	-0.4360	-6.7	.73
Age squared	-0.00006575	-1.6392	-4.4	.74
Age	0.02163	1.6418	-4.1	.81
Dominant tree height				
Intercept	183.59858			
Age	0.02698	0.9577	7.5	.65
Latitude	-2.66984	-0.3617	-3.3	.69
Density	-0.005216	-0.2286	-2.6	.74
Mean tree height				
Intercept	130.47496			
Age	0.01888	0.1407	6.9	.63
Latitude	-1.89951	-0.3751	-3.1	.67
Density	-0.0043866	-0.2767	-2.9	.72

melt occurred first in hummock top microsites. Droughty soil conditions develop in hummock top microsites and grade simultaneously to moist soil conditions, often with standing water in June, in the trough microsites.

Vegetation and seedling response was most apparent in early stages after burning where hummock tops would be devoid of vegetation but adjacent troughs were covered with luxuriant growths of mosses in competition with *P. mariana* seedlings. Soil hummocks increase in size and occurrence, south to north, across the gradient of open boreal forest to tundra (Zoltai and Tarnocai 1974). This further restricts tree establishment in northern areas and may affect subsequent seedling growth rates and survival. No evidence was found that tree distribution was influenced by aspect on the hummocks. However, this may be explained by the continuous solar insolation during the germinating period.

Limits to vegetative growth of *P. mariana* at tree line may result from wind abrasion or water stress. Baig and Tranquillini (1976) found water stress and premature needle cast were probably caused by anatomically immature needles in European conifers. They related the poorly developed needles to a shortened growing season near tree line. Needle longevity for forest-tundra trees near Inuvik was reduced compared to trees south of forest line (6 vs. 11 yr), suggesting a similar phenomenon.

However, south of forest line, trends in the water relations of *P. mariana* were found to be similar to those of *P. mariana* and *P. engelmannii* in other studies (Lindsay 1971, van Zinderen Bakker 1974, Marchand 1975, Marchand and Chabot 1978). The high

TABLE 5. Literature reported stand volumes and dominant tree heights for *Picea mariana* sites.

Author	Location	Community type	Age (yr)	Volume (m ³ /ha)	Height (m)		
Black and Bliss 1978*	Region I†	<i>P. mariana</i> / <i>V. uliginosum</i>	50	0.21	0.8		
			100	2.18	2.7		
			150	3.94	4.2		
	Region II†		50	0.47	1.5		
			100	4.81	3.4		
			150	8.69	4.9		
	Region III†		50	1.47	2.5		
			100	15.07	4.4		
			150	27.25	5.9		
	Region IV†		50	3.36	3.2		
			100	34.32	5.1		
			150	62.07	6.6		
Weetman and Harland 1964	Quebec	“Hypno-Picetum”	65	223.0	13.3		
Barney and van Cleve 1973	Fairbanks, Alaska		51		9.4		
			55		10.3		
Jameson 1964‡	Northern Manitoba Saskatchewan	Black spruce/feathermoss	50	34.7	7.6		
			100	143.2	15.8		
		Black spruce/feathermoss	50	15.5	9.8		
			100	117.1	14.6		
			140	185.7	17.7		
		Black spruce/sphagnum	100	83.9	13.1		
			160	95.8	14.6		
		Black spruce/jackpine	140	108.5	15.3		
			Horton and Lees‡ 1961	Foothills in Alberta	“Mesic upland”	50	128.7
		100				268.0	16.8
150	309.3	19.3					
	“Upland transition”	50		69.9	8.0		
		100		191.4	13.7		
		150		229.1	16.1		
	“Shallow bog”	50		23.7	5.0		
		100		120.3	10.6		
		150		152.2	12.4		
Jeglum 1974	Northern Ontario	“Moist forest” “ <i>Picea/Ledum</i> ”				12.2	
					10.1		
				5.9			
		“Muskeg”			4.6		
					1.5		

* Data generated from growth analysis.

† Regions as in this paper. (See Fig. 1.)

‡ Data taken from stand volume and height tables.

winter water content and leaf water potentials agree with observations by Marchand and Marchand and Chabot of *P. mariana* on Mt. Washington, New Hampshire, and suggest winter water relations are not important distributional factors. These high winter values are different from the pattern of winter desiccation in other evergreen species (Lindsay 1971, Wilkenson 1977).

Low leaf water potentials in *P. mariana* were also found by van Zinderen Bakker, who believed that maximum stress occurred with cold soils and high air temperatures. The P_{net} of *P. mariana* showed sensitivity to water stress when compared to *Juniperus virgini-*

ana (Bacone et al. 1976), both by showing photosynthetic reductions at higher leaf water potential and slower recovery rates after the stress period. However, water stress probably did not result in major inhibition of P_{net} during 1976 as leaf water potentials of -1.5 to -2.0 MPa (levels inhibitory to P_{net}) were measured only in the suppressed tree. The unusually low values of the suppressed tree at Inuvik were not surprising in view of the relationship between tree density and water stress found in other conifers (Warmbolt 1971). There was no stress-related needle cast and osmoregulation apparently maintained turgor in all sampled trees (Fig. 6) suggesting a capacity to

tolerate environmental stresses encountered. The absence of water stress inhibitory to photosynthesis also was reported for tree line *P. mariana* by Volwinckel et al. (1975).

Photosynthetic measurements of the Inuvik populations were similar to reported measurements from Alberta (van Zinderen Bakker 1974) and Quebec (Volwinckel et al. 1975). The P_{net} temperature optimum of 15°C was similar for all reported studies. The P_{net} at 0°C and 35°C was between 1 and 2 $mg \cdot g^{-1} \cdot h^{-1}$ for each population but the maximum P_{net} measured ranged from 3.5 to 7.0 $mg \cdot g^{-1} \cdot h^{-1}$ for Volwinckel et al. and van Zinderen Bakker, respectively (5.2 $mg \cdot g^{-1} \cdot h^{-1}$, this study).

Volwinckel et al. speculated that P_{net} was light limited in Quebec as they reported light saturation and light compensation values were twice other literature reports (1000 and 35 $\mu E \cdot m^{-2} \cdot s^{-1}$, Volwinckel et al. 1975; 450 and 12 $\mu E \cdot m^{-2} \cdot s^{-1}$, van Zinderen Bakker 1974; 500 and 18 $\mu E \cdot m^{-2} \cdot s^{-1}$, this study, respectively).

Germling water relations help to explain mortality observed in field trials. The extreme sensitivity of seedlings to water loss controlled plant survival in the hummocky terrain. Sensitivity of germlings to water stress has been used to explain the distribution of *Tsuga canadensis* (Olson et al. 1959), but few if any studies have compared the change in water relations from germling to mature tree and the consequence of this for the species.

Temperature appears of primary importance in controlling germination of *P. mariana*, even in these northern populations. Temperatures <15°C limit seed germination. Similar finds were reported by Fraser (1970) for populations of *P. mariana* from the southern Northwest Territories to Michigan. This inhibition was not reported to be reversible by Fraser. The inhibition and probable death of seed >28°C was less well defined when compared to Fraser's work. Fungal and bacterial activity in temperature ranges limiting to germination may be instrumental in the elimination of viability in buried seed as reported by Johnson (1975), Fraser (1976), and in this study.

Germination reduction of the 1975 seed in a north-to-south gradient correlates with the unusually cool summer of 1974 (Fig. 4). A 1-yr delay in environmental effects on cone initiation in *P. mariana* was previously observed in Ontario (Fraser 1966) and it is probable that such environmental effects extend to germination as well (Teeri 1968 in Marchand and Chabot 1978). Environmental effects on seed development may help explain the reduced germination of 35% in this study from the reported values of 40–60% (Vincent 1965, Zazada 1971). Examining seed size may clarify the problem of reduced germination as reported seed masses of 0.89×10^6 seeds/kg (Vincent 1965) were greater than values in this study, especially for seed from the forest-tundra region. Reduced seed size may

also explain the reduced longevity observed (3% germination at 5 yr in the Inuvik population), for Chai and Hansen (1952) reported germinations of 32% at 5 yr, 8% at 10 yr, and 1% at 15 yr for Minnesota.

As seed matures, concurrent environmental conditions (warm vs. cool summer) may influence subsequent seed longevity and germination. The environment also interferes with germination of the seed through the lower cardinal temperature and in the apparent death of seed in high-temperature regimes. Present temperatures in Region I probably would prevent germination (assuming viable seed). Germination was reduced (9.6%–3.6%, Sites S and N, respectively) over the 40-km distance between Sites S and N in 1975 in response to temperatures above the Inuvik June average (11.5°–10.6°C, Sites S and N, respectively). Germination in 1976 (0.6% and 1.2%, nonsignificant difference, Sites S and N, respectively) was again reduced by temperatures above (10.3°C, Site S) and below (8.9°C, Site N) the Inuvik June mean. Similar differences in field germination from year to year were reported by Place (1955), but were not attributed to any environmental factor.

A reliable and suitable environment for germination becomes important in consideration of the short (5–8 yr) postfire period available for establishment of *P. mariana*. This short period is the result of rapid seed release after fire (Wilton 1963), apparent short seed life (see germination section under Results), and destruction of seed in the soil profile (Johnson 1975, Fraser 1976). Narrow seedling age distributions (Fig. 14) resulting in even-aged stands were also found by Ahlgren (1959) and Wein (1975).

Germination of *P. mariana* was found constant between differing seedbeds in this study. This may result from temperature limitations as most studies report germination success related to seedbeds (Lebarron 1948, Place 1955, Ahlgren 1959, Vincent 1965). Mineral soil or "moist moss" seedbeds are generally favored by *P. mariana* and most authors report improved seedbed conditions with burning. Germination in conifer species appears to be most successful during periods of high soil temperatures and high available soil water, immediately after snow release (Place 1955, Eis 1965, Arnott 1973, this study). Individual precipitation events in summer have minimal effect but snowmelt recharge of the soil in spring is of central importance.

One-year survivorship of *Picea* and *Abies* species was similar (41–60%) in all seedbeds (Place 1955, Ahlgren 1959, and Eis 1965). All authors cite water stress and heat girdling as primary causes of mortality with no mention of winter damage by needle ice. The comparable mortality rates of the Inuvik germlings to other studies implies that the success of establishment (or lack thereof) would be dependent on seed viability and the germination limits imposed by low spring temperatures.

Stand growth and structure

Even-aged stands near tree line support the hypothesis that fire is central to *P. mariana* reproduction. On the contrary, the data of Zoltai (1975b) indicate uneven-aged stands based on stem discs (+10 cm). A considerable age variation can result from inclusion of suppressed individuals and probable differential growth rates of trees in the hummock topography.

The absence of *P. mariana* seed reproduction within established Inuvik stands may also be in contrast to Kershaw and Rouse's (1976) reported increased densities with age, where no separation of layered individuals was made (Kershaw 1978, K. A. Kershaw, *personal communication*). In the present study, the importance of layering was most evident in older stands where layering increased stand density and would certainly replace canopy dominant trees. Strang (1973) working between Fort Good Hope and Inuvik, reported "the open *Picea* forest eventually died out if fire was excluded, to be replaced by an almost tundra-like condition." He ignored the importance of layering. Even in the most northerly stands (stands near instrument site 1a) in this study there is no evidence to suggest elimination of *P. mariana* by fire exclusion.

Changing mortality rates and density-dependent average tree volumes suggested intraspecific interference by *P. mariana* even in an open canopy woodland community. Changing mortality rates have been found in other species both with even (Yarranton and Yarranton 1974) and uneven age distributions (Hett and Loucks 1971), but most studies have dealt with closed canopy species. Yarranton and Yarranton suggested limitations imposed to tree water relations as causal in the observed high mortality rate, but no work with thinning was presented. Further, the slope of the density-dependent tree volume relationship also suggested intraspecific interference. This interference was probably through root interactions. *Picea mariana* roots occur primarily in the mineral soil-peat interface with certain restrictions imposed by the permafrost table (Pettapiece 1974 and R. A. Black, *personal observation*). Extrapolation of the power function describing mortality (0.7246 mortality rate) to the ranges including the germling survivorship experiment (0.7851 ± 0.4238 SD, $N = 4$) gave results not significantly different by comparison. This suggested a seedling population of 350 individuals per 100 m² at 8 yr resulting from 1570 germinations, not unreasonable values.

Stand volumes (Table 5) were 33–50% of literature values for southern upland and poor sites, respectively. Both lower stand densities and smaller trees were responsible for reduced volumes. Densities were comparable to "spruce-lichen woodland" in northern Quebec (Moore and Verspoor 1973) and "Stereocaulon woodland" in the southern Northwest Territories (Kershaw and Rouse 1976) but were lower than south-

ern populations (Horton and Lees 1961) and in Alaska (Barney and van Cleve 1973). Dominant height growth also follows this pattern.

Average tree growth generally decreases south to north but falls short of predicted values by an order of magnitude in Region I (Fig. 1). Annual height growth of individuals in Region I, however, was often double the annual increments from Regions II, III, and IV. These trees appear to be released from competition in the low-density Region I stands. Stand volume reductions are the subsequent result of low seedling establishment densities and deformity by ice abrasion. Therefore tree growth at the forest-tundra ecotone appears to be unrestricted by environment except as the result of low establishment densities.

Seed production, in spite of reduced stand volumes and dominant height growth, was similar to reported values ($5.12\text{--}21.90 \times 10^5$ seeds/ha, Lebarron 1948), though no indication of stand age, growth rates, or methods was given in the early study. Seed production in Lebarron's study was higher in the upland stand ($11.11\text{--}21.90 \times 10^5$ seeds/ha compared to $6.03\text{--}13.2 \times 10^5$ seeds/ha in this study) but further comparison would be tenuous. Initiation of seed production in Inuvik stands is delayed 15–20 yr (Vincent 1965), which extends the critical interval for effective regeneration between fires and generally reduces seed production. Quantity of seed produced, generally decreasing with stand volumes toward tree line, is greatly reduced in forest-tundra areas in response to the deformed nature of the trees. These deformed trees never reach their potential size or density.

Tree growth and seed production appear to reach a plateau between ≈ 100 and 200 yr. This suggests burning within this time frame would have little effect on postfire reproduction. Fires occurring before or after this plateau in seed production may result in reduced stand density. The reduced reproductive potential of stands before 80 yr is the result of fires occurring before the saplings are reproductively mature. This has been observed with wildfire return intervals of 21 yr (Black and Bliss 1978). Reduced reproductive potential after 200 yr results from the death of the canopy dominants and replacement by reproductively immature layers.

Study implications

Temperatures $<15^\circ\text{C}$, the lower cardinal limit for seed germination, are probably the ultimate control of *P. mariana* at tree line and stand reproduction south of forest line. The relatively short period of time (5–8 yr) possible for establishment after a fire accentuates the precarious nature of tree line. This short period for effective establishment is probably due to short seed life in cones and the apparent destruction of ungerminated seed in the soil. Consequently, the lower cardinal temperature for seed germination and limited

time for establishment help explain the rapid retreat of tree line reported by Nichols (1975).

Short-term (1–10 yr) changes in climate could exhaust the seed population before a fire or prevent seed germination after fire and therefore result in large areal changes in vegetation. Major changes in tree cover over large areas may reflect only minor and short-term changes in climate near forest line.

The 50-yr recovery time for forests after fire reported by Nichols (1975) should be reinterpreted in context with the limited establishment time available for *P. mariana* after fire. The apparent 50-yr recovery period probably is the result of the time required before detectable amounts of pollen are produced and recorded in the fossil pollen record. Actually, *Picea* is present throughout this time period as immature individuals.

Climatic reconstruction could possibly be based on the climatic requirements for reproduction of *P. mariana*. Estimated minimum average temperatures for reproduction of *P. mariana* in the District of Mackenzie are 11°, 14°, and 11°C for June, July, and August, respectively. These are temperatures estimated from ≈40 km south of modern forest line and suggest forest line is out of equilibrium with modern climate. Temperatures of 9.5°, 13°, and 10°C are minimum estimates below which no successful establishment would be expected. Degree day values (>0°C) of 1200 and 1330 are upper and lower estimated limits for no establishment and reliable establishment, respectively. These estimates, based on temperature control of seed germination and germination potential, provide a basis for climatic reconstruction, if caution concerning environmental variability is incorporated.

Qualitative information supporting the out-of-equilibrium position of forest line was found by the absence of reproduction following burning in Regions I and II (Black and Bliss 1978) where stands failed to regenerate after a fire occurred in stands originating prior to 1850. These stands probably represent a northward pulse of forest line in response to a warming trend during the 18th and 19th centuries (Nichols 1976). Modern stands reliably regenerate in Regions III and IV, providing the burn interval is of sufficient length to permit seed production of the new forest.

Ritchie and Hare's (1971) 5°C and Nichol's (1976) 4° ± 1°C estimated increases in mean daily summer (June, July, and August) temperatures for ecotonal positions during the Hypsithermal are ≈1°C higher than the estimated temperatures for reliable reproduction. This assumes these estimates were based on the June, July, and August mean temperatures at Tuktoyaktuk and Ennadai Lake (4.4°, 10.6°, and 8.9°; 6.7°, 12.8°, and 11.7°C, respectively). Further in support of these temperature increases was Ritchie and Hare's observation of greater radial increments on a fossil stump from the late Hypsithermal (4,940 ± 140 radi-

ocarbon yr BP), compared to increments from near the modern forest line.

Management of open boreal forest should reflect the plasticity of this dominant tree species. As suggested by the seed production estimates, fire interval has no effect on stand reproduction as long as it is ≈100–200 yr, due to seed retention in cones and constant tree densities. But burning must occur for stand regeneration by seed. The semiserotinous cones of *P. mariana* (Vincent 1965) and small seed size require burning to open the cones and to remove accumulated duff and interfering vegetation for effective establishment. Fire suppression prevents this necessary environmental change and may reduce reproductive potential of a stand in extreme situations (200+ yr).

Management of open boreal forest should also include the revegetation of damaged surfaces (i.e., seismic lines, borrow pits, abandoned roads, and construction and gas well sites). Revegetation by direct seeding of *P. mariana* would be quite unpredictable due to seasonal variation in climate at the northern limit of the species. Improved success might be obtained by light burning of the surface or scarifying and sowing seed onto snow or immediately after spring snow melt. No germination of seed should be expected the 2nd yr after sowing due to apparent destruction of seed in the soil.

In general, direct sowing of cut lines or seismic lines would yield poor results and these areas are best left for natural seeding providing there is a nearby seed source. Vincent (1965) reported seed dispersal dropped to zero ≈100 m from a stand edge. This provides an estimate of the maximum area for natural seeding of *P. mariana* but does not consider dispersal onto snow surfaces. Planting seedlings would increase success rates. Experimental seedlings transplanted into any microsites were found to be 100% successful in all microsites. However, this is a labor-intensive operation on an intact peat mat.

In spite of these restrictions, why does *P. mariana* remain as the most successful conifer at forest line in the Lower Mackenzie Valley? The answer probably lies in its tolerance of burn cycles and of the cold, wet soils. *Picea mariana* maintains a relatively constant seed population which is little affected by the burn interval, is not destroyed by fire, and accumulates on the tree over a period of years. *Larix laricina* and *Picea glauca* on the contrary, release seed annually, maintaining no such seed population, and therefore must seed from survivors over longer distances. The continuous nature of the forests on the flat till plains results in large burned areas and few survivors, which limit and localize the potential seed dispersal of *P. glauca* and *L. laricina*. *Picea mariana* in contrast, floods the burned site immediately after fire with seed stored in cones of previous years, capitalizing on the

reduction in interfering vegetation and improved soil thermal regime (Rouse and Kershaw 1971).

In the absence of burning, a rare occurrence south of forest line, layering of *P. mariana* serves to maintain the species on a site with little evidence of replacement. Mixed tree stands of *P. glauca*, *L. laricina*, and *P. mariana* mature to purely *P. mariana*-dominated stands. Site alteration by peat accumulation and permafrost aggradation restricts root systems to surface horizons. This results in severe growth restriction and stand thinnings. Stand thinning is generally at the expense of *P. glauca* and *L. laricina*. *Larix*, though faster growing than *P. mariana*, appears to be shorter lived (150–180 yr, maximum), especially in mixed stands. Therefore the reproductive alternatives open to *P. mariana* make it persistent in burn cycles of almost any interval and result in its dominance as a tree line species in boreal North America.

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LITERATURE CITED

- Ahlgren, C. E. 1959. Some effects of fire on forest reproduction in northeastern Minnesota. *Journal of Forestry* 57:194–200.
- Ahti, G., G. W. Scotter, and H. Vanska. 1973. Lichens of the reindeer preserve, Northwest Territories, Canada. *Bryologist* 76:48–76.
- Arnott, J. T. 1973. Germination and seedling establishment. Pages 55–56 in J. H. Cayford, editor. Direct seeding symposium. Publication 1339, Canadian Forestry Service, Ottawa, Ontario, Canada.
- Baig, M. N., and W. Tranquillini. 1976. Studies on upper timberline: morphology and anatomy of Norway spruce (*Picea abies*) and stone pine (*Pinus cembra*) needles from various habitat conditions. *Canadian Journal of Botany* 54:1622–1632.
- Baker, F. S. 1929. Effect of excessively high temperatures on coniferous reproduction. *Journal of Forestry* 27:949–975.
- Barbour, M. G., and C. H. Racine. 1967. Construction and performance of a temperature-gradient bar and chamber. *Ecology* 48:861–863.
- Barney, R. J., and K. van Cleve. 1973. Black spruce fuel weights and biomass in two interior Alaskan stands. *Canadian Journal of Forestry Research* 3:304–311.
- Bate, G. C., A. D'Aoust, and D. T. Canvin. 1969. Calibration of infra-red CO₂ gas analyzers. *Plant Physiology* 44:1122–1126.
- Bird, C. D., G. W. Scotter, W. C. Steere, and A. H. Marsh. 1977. Bryophytes from the area drained by the Peel and Mackenzie Rivers, Yukon and Northwest Territories. *Canadian Journal of Botany* 55:2879–2918.
- Black, R. A. 1977. Reproductive biology of *Picea mariana* (Mill.) BSP. at tree line. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Black, R. A., and L. C. Bliss. 1978. Recovery sequence of *Picea mariana*/*Vaccinium uliginosum* forests after burning near Inuvik, Northwest Territories, Canada. *Canadian Journal of Botany* 56:2020–2030.
- Brown, J. 1969. Buried soils associated with permafrost. Pages 115–127 in S. Pawluk, editor. *Pedology and quaternary research*. The University of Alberta Press, Edmonton, Alberta, Canada.
- Brown, R. W. 1970. Measurement of water potential with thermocouple psychrometers: construction and applications. Research Paper INT-80, United States Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Bryson, R. A. 1966. Air masses, streamlines and the boreal forest. *Geographical Bulletin* 8:228–269.
- Bryson, R. A., W. N. Irving, and J. A. Larsen. 1965. Radiocarbon and soil evidence of former forest in the southern Canadian tundra. *Science* 147:46–48.
- Bryson, R. A., W. M. Wendland, J. D. Ives, and J. T. Andrews. 1969. Radiocarbon isochrones on the disintegration of the Laurentide ice sheet. *Arctic and Alpine Research* 1:1–14.
- Burns, B. M. 1973. The climate of the Mackenzie Valley-Beaufort Sea. Volumes I and II. Environment Canada, Climatological Studies 24, Ottawa, Ontario, Canada.
- Chai, T. S., and H. L. Hansen. 1952. Characteristics of black spruce seed from cones of different ages. Minnesota Forestry Notes 2, University of Minnesota, Saint Paul, Minnesota, USA.
- Cody, W. J. 1965. Plants of the Mackenzie River Delta and Reindeer Grazing Preserve. Plant Research Institute, Canadian Department of Agriculture, Ottawa, Ontario, Canada.
- Eis, S. 1965. Development of white spruce and alpine fir seedlings on cutover areas in the central interior of British Columbia. *Forestry Chronicle* 41:419–431.
- Fraser, A. D. 1966. Vegetative and reproductive growth of black spruce (*Picea mariana* [Mill.] BSP.) at Chalk River, Ontario, Canada. *Canadian Journal of Botany* 44:567–580.
- Fraser, J. W. 1970. Cardinal temperatures for germination of six provenances of black spruce seed. Information Report PS-X-23, Canadian Department of Fisheries and Forestry, Ottawa, Ontario, Canada.
- . 1976. Viability of black spruce seed in or on a boreal forest seed bed. *Forestry Chronicle* 52:229–231.
- Griggs, R. F. 1934. The edge of the forest in Alaska and the reasons for its position. *Ecology* 15:80–95.
- Halliday, W. E. D., and A. W. A. Brown. 1943. The distribution of some important forest trees in Canada. *Ecology* 24:353–373.
- Hansell, R. I. C., and D. A. Chant. 1971. Changes in the northern limit of spruce at Dubawnt Lake, Northwest Territories. *Arctic* 24:233–234.
- Hare, F. K., and J. C. Ritchie. 1972. The boreal bioclimates. *Geographical Review* 62:333–365.
- Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* 3:329–382.
- Hett, J. M. 1971. A dynamic analysis of age in sugar maple seedlings. *Ecology* 52:1071–1074.
- Hett, J. M., and O. L. Loucks. 1971. Sugar maple (*Acer saccharum* Marsh.) seedling mortality. *Journal of Ecology* 59:507–520.
- Holmen, K., and G. W. Scotter. 1971. Mosses of the Reindeer Reserve, Northwest Territories, Canada. *Lindbergia* 1–2:34–56.
- Hopkins, D. M. 1959. Some characteristics of the climate in forest and tundra regions in Alaska. *Arctic* 12:214–220.

- Horton, K. W., and J. C. Lees. 1961. Black spruce in the foothills of Alberta. Technical Note 110, Forest Research Branch, Canadian Department of Forestry, Ottawa, Ontario, Canada.
- Hughes, O. L. 1972. Surficial geology of northern Yukon Territory and northwestern District of Mackenzie, Northwest Territories. Paper 69-36, Geological Survey of Canada, Ottawa, Ontario, Canada.
- Hughes, O. L., D. A. Hodgson, and J. Pilon. 1972. Surficial geology. Sheet 106N, 1:125,000, Open File Report 97, Canadian Geological Survey, Ottawa, Ontario, Canada.
- Hustitch, I. 1966. On the forest-tundra and the northern treelines. Report of Kevo Subarctic Station 3:7-47.
- Jameson, J. S. 1964. Preliminary yield tables for black spruce. Manitoba-Saskatchewan. Publication 1064, Forestry Research Branch, Canadian Department of Forestry, Ottawa, Ontario.
- Jeglum, J. K. 1974. Relative influence of moisture-aeration and nutrients on vegetation and black spruce growth in northern Ontario. Canadian Journal of Forestry Research 4:114-126.
- Johnson, E. A. 1975. Buried seed populations in the subarctic forest east of Great Slave Lake, Northwest Territories. Canadian Journal of Botany 53:2933-2942.
- Johnson, E. A., and J. S. Rowe. 1975. Fire in the subarctic wintering ground of the Beverly caribou herd. American Midland Naturalist 94:1-14.
- Kershaw, K. A., and W. R. Rouse. 1976. Impact of fire on forest and tundra ecosystems. Final Report 1975. Arctic Land Use Research Report 75-76-63, Department of Indian Affairs and Northern Development, Ottawa, Ontario, Canada.
- Larsen, J. A. 1965. The vegetation of the Ennadai Lake Area, Northwest Territories: studies in subarctic and arctic bioclimatology. Ecological Monographs 35:37-59.
- . 1971a. Vegetation of Fort Reliance, Northwest Territories. Canadian Field-Naturalist 85:147-178.
- . 1971b. Vegetational relationships with air mass frequencies: boreal forest and tundra. Arctic 24:177-194.
- . 1974. Ecology of the northern continental forest border. Pages 341-369 in J. D. Ivers and R. G. Barry, editors. Arctic and alpine environments, Methuen, London, England.
- LeBarron, R. K. 1948. Silvicultural management of black spruce in Minnesota. Circular 791, United States Department of Agriculture, Washington, District of Columbia, USA.
- Lindsay, J. H. 1971. Annual cycle of leaf water potential in *Picea engelmannii* and *Abies lasiocarpa* at timberline in Wyoming. Arctic and Alpine Research 3:131-139.
- Love, D. 1970. Subarctic and subalpine: where and what? Arctic and Alpine Research 2:63-73.
- Mack, R. N., and J. L. Harper. 1977. Interference in dune annuals: spatial pattern and neighborhood effects. Journal of Ecology 65:345-363.
- MacKay, R. 1970. Disturbances to the tundra and forest-tundra environment of the western Arctic. Canadian Geotechnical Journal 7:420-432.
- Marchand, P. J. 1975. Winter plant-water relations with special reference to alpine treeline. Dissertation. University of New Hampshire, Durham, New Hampshire, USA.
- Marchand, P. J., and B. F. Chabot. 1978. Winter water relations of treeline plant species on Mt. Washington, New Hampshire. Arctic and Alpine Research 10:105-116.
- Marr, J. 1948. Ecology of the forest-tundra ecotone of the east coast of Hudson Bay. Ecological Monographs 18:118-144.
- Matthews, J. V. 1974. Wisconsin environment of interior Alaska: pollen and macrofossil analysis of a 27-meter core from the Isabella basin (Fairbanks, Alaska). Canadian Journal of Earth Sciences 11:828-841.
- Mayo, J. M. 1974. A thermocouple psychrometer chamber for field and laboratory use. Canadian Journal of Plant Science 54:597-598.
- Monroe, R. L. 1972. Bedrock geology. Sheet 197B, Open File Report 120, Canadian Geological Survey, Ottawa, Ontario, Canada.
- Morre, T. R., and E. Verspoor. 1973. Above ground biomass of black spruce stands in subarctic Quebec. Canadian Journal of Forestry Research 3:596-598.
- Nichols, H. 1975. Palynological and paleoclimatic study of the late-Quaternary displacement of the boreal forest-tundra ecotone in Keewatin and Mackenzie. Occasional Paper 15, Institute of Arctic and Alpine Research, Boulder, Colorado, USA.
- . 1976. Historical aspects of the northern Canadian treeline. Arctic 29:38-47.
- Olson, J. S., F. W. Stearns, and H. Niensteadt. 1959. Eastern hemlock seeds and seedlings response to photoperiod and temperature. Bulletin 620, Connecticut Agricultural Experiment Station, New Haven, Connecticut, USA.
- Ormsbee, P., F. A. Bazzaz, and W. R. Boggess. 1976. Physiological ecology of *Juniperus virginiana* in oldfields. Oecologia 23:75-82.
- Pettapiece, W. W. 1974. A hummocky permafrost soil from the subarctic of Northwestern Canada and some influences of fire. Canadian Journal of Soil Science 54:343-355.
- Place, I. C. M. 1955. The influence of seed bed conditions in the regeneration of spruce and balsam fir. Forestry Branch Bulletin 117, Department of Northern Affairs and National Resources, Ottawa, Ontario, Canada.
- Reid, D. E. 1974. Vegetation of the Mackenzie Valley. Part one. Arctic Gas Biological Report Series. Volume 3. Canadian Arctic Gas Study Limited, Calgary, Alberta, Canada.
- Ritchie, J. C. 1959. The vegetation of northern Manitoba. III. Studies in the subarctic. Technical Paper 3, Arctic Institute of North America, University of Calgary, Calgary, Alberta, Canada.
- . 1960. The vegetation of northern Manitoba. VI. The lower Hayes River Region. Canadian Journal of Botany 38:769-788.
- . 1974. Modern pollen assemblages near the arctic treeline, Mackenzie Delta region, Northwest Territories. Canadian Journal of Botany 52:381-396.
- . 1976. The late-Quaternary vegetation history of the western interior of Canada. Canadian Journal of Botany 54:1793-1818.
- . 1977. The modern and late Quaternary vegetation of the Campbell-Dolomite uplands, near Inuvik, Northwest Territories, Canada. Ecological Monographs 47:401-423.
- Ritchie, J. C., and F. K. Hare. 1971. Late-Quaternary vegetation and climate near the Arctic treeline of northwestern North America. Quaternary Research 1:331-342.
- Rouse, W. R., and K. A. Kershaw. 1971. The effects of burning on the heat and water regimes of lichen dominated subarctic surfaces. Arctic and Alpine Research 3:291-304.
- Rowe, J. S. 1972. Forest regions of Canada. Forestry Service Publication 1300, Department of Environment, Ottawa, Ontario, Canada.
- Rowe, J. S., and G. W. Scotter. 1973. Fire in the boreal forest. Quaternary Research 3:444-464.
- Sestak, Z., J. Catsky, and P. G. Jarvis. 1971. Plant photosynthetic production-manual of methods. Dr. W. Junk, The Hague, Netherlands.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California, USA.
- Sorenson, C. J., J. C. Knox, J. A. Larsen, and R. A. Bryson. 1971. Paleosols and the forest border in Keewatin, Northwest Territories, Canada. Quaternary Research 1:468-473.
- Steel, R. G. D., and J. H. Torrie. 1960. Principles and pro-

- cedures of statistics. McGraw-Hill, New York, New York, USA.
- Strang, R. M. 1973. Succession in unburned subarctic woodlands. *Canadian Journal of Forestry Research* 3:140-143.
- Teeri, J. A. 1968. The ecology of subalpine black spruce in New England. Thesis. University of New Hampshire, Durham, New Hampshire, USA.
- Tikhomirov, B. A. 1962. The treelessness of the tundra. *Polar Record* 11:24-30.
- van Zinderen Bakker, E. M., Jr. 1974. An ecophysiological study of black spruce in Central Alberta. Dissertation. University of Alberta, Edmonton, Alberta, Canada.
- Viereck, L. A. 1973. Wildfire in the taiga of Alaska. *Quaternary Research* 3:465-495.
- Vincent, A. B. 1965. Black spruce: a review of its silvics, ecology and silviculture. Publication 1100, Canadian Department of Forestry, Ottawa, Ontario, Canada.
- Vogel, T. C., and P. L. Johnson. 1965. Evaluation of an economic instrument shelter for microclimatological studies. *Forest Science* 11:434-435.
- Vowinkel, T., W. C. Oechel, and W. G. Boll. 1975. The effect of climate on photosynthesis of *Picea mariana* at the subarctic treeline. I. Field measurements. *Canadian Journal of Botany* 53:604-620.
- Wambolt, C. L. 1973. Conifer water potential as influenced by stand density and environmental factors. *Canadian Journal of Botany* 51:2333-2337.
- Washburn, A. L. 1956. Classification of patterned ground and review of suggested origins. *Geological Society of America Bulletin* 67:823-865.
- Weetman, G. F., and R. Harland. 1964. Foliage and wood production in unthinned black spruce in northern Quebec. *Forest Science* 10:80-88.
- Wein, R. W. 1975. Vegetation recovery in arctic tundra and forest-tundra after fire. Arctic Land Use Research Report 74-75-62, Department of Indian Affairs and Northern Development, Ottawa, Ontario, Canada.
- . 1976. Frequency and characteristics of arctic tundra fires. *Arctic* 29:213-222.
- White, J., and J. L. Harper. 1970. Correlated changes in plant size and number in plant populations. *Journal of Ecology* 58:467-485.
- Whitehead, D. R. 1973. Late-Wisconsin vegetational changes in unglaciated eastern North America. *Quaternary Research* 3:621-631.
- Wilkinson, A. J. 1977. Physiological aspects of the cold hardiness of *Ledum groenlandicum*. Thesis. University of Alberta, Edmonton, Alberta, Canada.
- Wilton, W. C. 1963. Black spruce seed fall immediately following fire. *Forestry Chronicles* 39:477-478.
- Yarranton, M., and G. A. Yarranton. 1975. Demography of a jack pine stand. *Canadian Journal of Botany* 53:310-314.
- Zasada, J. C. 1971. Natural regeneration of interior Alaska forests—seed, seedbed, and vegetative reproduction considerations. Pages 231-246 in C. W. Slaughter, R. J. Barney, and G. M. Hansen, editors. *Fire in the northern environment*. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.
- Zoltai, S. C. 1975a. Tree ring record of soil movements on permafrost. *Arctic and Alpine Research* 7:331-340.
- . 1975b. Structure of subarctic forests on hummocky permafrost terrain in northwestern Canada. *Canadian Journal of Forestry Research* 5:1-9.
- Zoltai, S. C., and W. W. Pettapiece. 1974. Tree distribution on perennially frozen earth hummocks. *Arctic and Alpine Research* 6:403-411.
- Zoltai, S. C., and C. Tarnocai. 1974. Soils and vegetation of hummocky terrain. Report 74-5, Environmental-Social Program, Task Force on Northern Oil Development, Ottawa, Ontario, Canada.