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The High Subarctic Forest-Tundra of Northwestern Canada: Position, Width, and Vegetation Gradients in Relation to Climate

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ABSTRACT. A phytogeoclimatic study of the high subarctic region of Canada between Hudson Bay and the Cordillera at the northern Yukon–Mackenzie border was undertaken to provide a verifiable and quantitative synthesis of forest-tundra vegetation ecology. Three field seasons of vegetation and terrain studies provided ground truth for a grid of 1314 black-and-white air photos that cover *ca.* 24% of the forest-tundra and adjacent low Subarctic and low Arctic. Air photos were analyzed for percentage cover of nine vegetation-terrain types, bedrock and parent materials, landforms, and elevations. The forest-tundra, as bounded by the 1000:1 and 1:1000 tree:upland tundra cover isolines, spans an average 145 ± 72 km (median 131 km) and increases in width from northwest to southeast. The transition from 10:1 to 1:10 tree:upland tundra cover occupies one-fourth to one-half the area of the forest-tundra. Regional slope of the land probably accounts for much of the variation in width of the forest-tundra. Southern outliers of forest-tundra in the northwest are found mainly in areas of high elevation. Across much of the northwest, steep vegetation gradients occur near the northern limit of trees. North of Great Slave Lake, steep vegetation gradients shift from the northern to the southern half of the forest-tundra and maintain this position eastward to Hudson Bay. The forest-tundra of the northwest receives roughly three-fourths the mean annual net radiation available to the southeast and central districts.

Key words: air photos, boreal, climate, ecology, forest-tundra, high Subarctic, Northwest Territories, plant geography, tree line, vegetation

RÉSUMÉ. On a entrepris une étude phytogéoclimatique de la zone de l'Extrême-Subarctique canadien comprise entre la baie d'Hudson et la cordillère, située à la frontière du Yukon-Mackenzie, en vue d'offrir une synthèse vérifiable et quantitative de l'écologie végétale de la forêt-toundra. Trois saisons d'étude de végétation et de terrain ont fourni des données de vérification pour une grille de 1314 clichés aériens en noir et blanc, recouvrant environ 24 % de la forêt-toundra et de la zone avoisinante du Bas-Subarctique et du Bas-Arctique. On a analysé les clichés en vue de déterminer le pourcentage de couverture de neuf types de végétation-terrain, de roche de fond et de matériaux mères, de configurations et de niveaux. La forêt-toundra, délimitée par les isarithmes du rapport entre le couvert d'arbres et celui de toundra des hautes terres de 1000 pour 1 et 1 pour 1000, recouvre une bande de largeur moyenne de 145 ± 72 km (131 km de médiane) et s'élargit en allant du nord-ouest vers le sud-est. La transition du rapport du couvert d'arbres à celui de toundra des hautes terres entre 10 pour 1 et 1 pour 10 occupe de un quart à la moitié de la zone de forêt-toundra. La pente régionale du terrain y est probablement pour beaucoup dans la variation de la largeur de la forêt-toundra. Les îlots méridionaux de forêt-toundra dans le Nord-Ouest se trouvent principalement dans les zones de haute altitude. Dans une grande partie du Nord-Ouest, des gradients de végétation brusques se trouvent près de la limite septentrionale des arbres. Au nord du Grand Lac de l'Esclave, des gradients de végétation brusques passent de la moitié septentrionale à la moitié méridionale de la forêt-toundra et conservent cette position vers l'est jusqu'à la baie d'Hudson. La forêt-toundra du Nord-Ouest reçoit environ les trois quarts de la radiation nette annuelle moyenne disponible pour les régions du sud-est et du centre.

Mots clés: clichés aériens, boréal, climat, écologie, forêt-toundra, Extrême-Subarctique, Territoires du Nord-Ouest, géographie de la végétation, ligne des arbres, végétation

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INTRODUCTION

In recent years, interest in the forest-tundra, or "tree line," has risen due to concern over the effects of global warming. The forest-tundra may be a sensitive indicator of climatic change (Kellogg and Zhao, 1988). Recent studies predict a northward migration of the forest-tundra of from 300 to 400 km in eastern Canada to negligible distances in the far northwest of Canada (Zoltai, 1988) and an overall shrinkage of 58% due to northward encroachment by grassland and boreal forest (Rizzo, 1988).

Prior to the study completed by Timoney (1988), there had been no comprehensive study of the vegetation and terrain of the subarctic forest-tundra west of Hudson Bay. Numerous authors have reported on vegetation, terrain, and climate relationships in localized areas of the subarctic (e.g., Larsen, 1965; Hardy and Associates, 1976; Zoltai and Johnson, 1978; Zoltai *et al.*, 1979; Bradley *et al.*, 1982; Ritchie, 1962, 1984). Differences in aims, terminology, methodology, and interpretation, however, may make direct comparisons difficult among areas studied by different authors.

Although tree-line maps have been produced, in one form or another, by various authors (e.g., Hustich, 1966; Thomas, 1969; Hare and Ritchie, 1972; Rowe, 1972; Larsen, 1974; Noble, 1974; Nichols, 1976; Elliott-Fisk, 1983; Edlund, 1987; Thannheiser, 1987; Ecoregions Working Group, 1989), many studies have been based on a minimum of ground and airborne observations. Primary works in which original data are presented are few. Much of the geographic ecology of northern vegetation is derivative, based on secondary sources of data.

The forest-tundra, the tree line, and other subarctic-arctic boundaries have been defined more often than they have been mapped. Mackay (1969) has pointed to the limited value of debating the merits of the various boundary criteria. A veritable "Babel of nomenclatures" of subarctic terminology (Hare and Ritchie, 1972) exists (see, for example, Blüthgen, 1970; Hustich, 1966, 1970, 1979; Löve, 1970; Ahti, 1980; Atkinson, 1981; Payette, 1983; Timoney, 1988:Appendix 7; Larsen, 1989; Ecoregions Working Group, 1989). Thus it is often unclear, or left unstated, what data were used and what criteria were applied to delimit the tree line, tree limit, or the northern and southern limits of the forest-tundra.

Of various criteria used to delimit the forest-tundra, emphasis has been placed on the height, stem density, and growth forms of tree species (e.g., Payette, 1974; Scott *et al.*, 1987) and the typical vegetation and soils of mesic or upland sites

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(e.g., Bradley *et al.*, 1982; Ecoregions Working Group, 1989). Recently, Larsen (1989:23) has defined the forest-tundra transition as "that land where . . . unbroken forest occupies less than 75% of the land surface above the water table (upland), *or* less than 75% of the area is unbroken tundra, i.e., 25% of the land area or more is occupied by an admixture of forest and tundra. . . ."

Universal agreement as to where the Arctic begins will probably never be reached; redefinition to suit individual objectives of study may always be required (Larsen, 1989). Four vegetation regions were sampled in this study: high boreal, low subarctic, high subarctic, and low arctic (*cf.* Bradley *et al.*, 1982; Timoney, 1988:Table 1, Appendix 7; Ecoregions Working Group, 1989).

The high boreal closed crown forest region was sampled little. Based on widely applicable criteria observable on air photos, it is characterized by closed crown conifer forest on both upland and lowland mineral soils and open crown conifer forest over bedrock. Treed peat plateaus and bogs are typical in the lowlands. Mixed-wood forests with aspen and balsam poplar are absent, although both species are present as trees (see mid-boreal ecoregion of Bradley *et al.*, 1982).

The transition to the low subarctic open crown forest region is marked by the southern limit of zonal open crown conifer forests on the well-drained mineral soils of uplands. Open crown forest or treeless rockland is found over bedrock; peat plateaus and palsas are typical (Bradley *et al.*, 1982).

The high subarctic forest-tundra is the landscape mosaic of zonal tree and tundra vegetation composing a transition region lying poleward of the low subarctic open crown forest region and southward of the low arctic tundra region. It is bounded on the south by the *southern limit* (<0.1% cover) of *upland tundra* and to the north by the *northern limit* (<0.1% cover) of *trees ≥3-4 m* tall.

The ratio of tree:upland tundra cover may be used to both quantify spatial vegetation change and to delimit the zonal boundaries. The cardinal boundaries of the forest-tundra may be delimited as the 1000:1 (south), 1:1 (central), and 1:1000 (north) tree:upland tundra cover isolines. Between these limits, forest and tundra co-dominate in a mosaic with subordinate bog-fen and sedge meadow wetland, dwarf birch-willow shrubland, lichen rockland, burned forest, and eroding terrain. A physiognomic transition occurs across the forest-tundra, from closed and open crown forests in the south to single-stemmed and clonal woodlands and thickets, either in discrete groves or as forest-tundra vegetation mosaics. Forest-tundra tree stems assume a range of plastic, climatically determined growth forms from protected or southern sites to exposed or northern sites; these are: symmetrical crown, flagged, whorled, supra-nival skirted, infra-nival fruticose, and mat (Payette, 1974). Dwarf ericad/lichen and medium shrub/ericad tundras are typical of the Precambrian Shield; *Dryas*-legume/lichen and medium shrub/*Dryas*-legume tundras are typical west of the Shield. The southern limit of conspicuous upland equiforms (polygons, nets, circles) correlates closely with the southern limit of the forest-tundra, particularly on the Shield (Timoney, 1988).

The low arctic tundra is characterized by medium and low shrub, lichen, and tussock tundras, sedge meadows, and peat polygon areas (ice wedge polygons). Upland equiforms are prevalent; peat plateaus are absent. Its southern limit is marked by the northern limit of trees ≥3-4 m tall (= 1:1000 tree:upland tundra isoline). Dwarf spruce (<3 m tall) are occasional in the low arctic tundra but are not readily observable on air photos.

This paper delimits and describes quantitatively the dominant zonal vegetation cover of the high subarctic forest-tundra west of Hudson Bay and relates these findings to climate. The object of this study is to provide a testable delimitation of the subarctic forest-tundra of Canada west of Hudson Bay. It is hoped that the results will prove useful as a baseline against which present and future vegetation change in the western Canadian Subarctic may be compared.

STUDY REGION

The study region includes the high subarctic forest-tundra in the Northwest Territories and Manitoba and parts of the adjoining low subarctic and low arctic regions (Fig. 1).

Geology

The study region may be divided physiographically and geologically into two great parts (after Geological Survey of Canada, 1968, 1969; Bostock, 1976): a core of Precambrian (mostly igneous and metamorphic) rocks forming the Shield, and a surrounding crescent of younger sedimentary rocks forming the Borderlands.

The majority of the Shield has been metamorphosed. While Archean granitic gneisses constitute much of the bedrock, about 40% of the Shield is composed of Archean sediments and metasediments (paragneisses and paraschists), basic and intermediate volcanics and metavolcanics, granites, and Proterozoic sandstones (Geological Survey of Canada, 1968).

The northwest is physiographically and geologically diverse. The Horton and Anderson plains lie north and northwest of Great Bear Lake and form the Arctic Slope, where drainage is directly to the Arctic Ocean. The southern parts of both areas are underlain by Ordovician-Silurian and middle Devonian carbonates. The northern portions of both areas are underlain by Cretaceous shales, siltstones, and mudstones (Geological Survey of Canada, 1968; Bostock, 1976).

The Colville Hills are located northwest of Smith Arm, Great Bear Lake. There, Ordovician-Silurian and middle Devonian carbonates and shales project 300 m above the surrounding plains and reach elevations up to 675 m asl.

The Great Bear Plain is underlain by lower Cretaceous shales, with smaller amounts of Ordovician-Silurian carbonates and related rocks east of McVicar Arm and non-marine sandstone and related rocks on Cape MacDonnel. Most of its surface lies below 300 m asl, but the Scented Grass Hills and Grizzly Bear Mountain reach elevations of about 450 m.

The Mackenzie Delta division presents a complex surface of Tertiary and Quaternary sediments and includes not only the present delta, but remnants of former delta and fluvial and marine deposits that form the present Arctic Coastal Plain (Geological Survey of Canada, 1968, 1969; Bostock, 1976).

Parent Materials

Over 99% of the study region was glaciated during the Pleistocene. The glacial deposits of the study region are Late Wisconsinan, and till constitutes about 75% of these deposits. Glaciofluvial deposits are widespread but usually of limited area. Lacustrine deposits and lacustrine reworked tills are found around Great Slave and Great Bear lakes and the Thelon, Dubawnt, and upper Kazan rivers (Geological Survey of

Canada, 1967; Bradley *et al.*, 1982). Alluvium is important in large river valleys, such as the Mackenzie, Coppermine, and Thelon rivers. Colluvium is found locally in actively eroding areas (Zoltai *et al.*, 1979). Organic materials are prevalent on the Arctic Coastal Plain, the Hudson Bay Lowlands, and locally elsewhere.

Tills of the Canadian Shield, generally 2-8 m thick, are complex both in lithology (see Geology above) and mineralogy; they are most often non-calcareous, coarse grained, and have low clay content. Tills derived from granitic rocks are of sandy loam and loamy sand texture (Scott, 1976).

Red tills are found in central Keewatin and adjacent eastern Mackenzie District, where red beds of the Proterozoic Dubawnt Group have been eroded and dispersed in all directions from the vicinity of the Keewatin ice divide (Scott, 1976).

Tills in the northwest (Prairie-Mackenzie province of Scott, 1976) fall into two lithological types: weak and generally poorly consolidated shale, siltstone, and sandstone; and better-consolidated carbonate and related Paleozoic rocks. Thickness of northwestern tills varies; a typical texture is loam to clay loam.

Soils

Cryoturbation and low temperatures and permeabilities in the typical fine-textured soils of the northwest result in a prevalence of orthic, regosolic, and gleysolic turbic cryosols (Tarnocai, 1973; Zoltai and Tarnocai, 1974; Clayton *et al.*, 1977; Tedrow, 1977; Canada Soil Survey Committee, 1978).

Orthic and eluviated dystric brunisols on well-drained sites and gleyed dystric brunisols and gleysolic turbic cryosols on imperfectly and poorly drained sites predominate across much of the forest-tundra of the Shield. Northward, brunisolic and regosolic turbic cryosols are common (Hardy and Associates, 1976; Clayton *et al.*, 1977; Bradley *et al.*, 1982; Timoney, 1988).

Fibric and mesic organic cryosols are typical of bog and residual peats and sedge fen peats respectively (e.g., Zoltai and Tarnocai, 1974; Hardy and Associates, 1976; Bradley *et al.*, 1982; Ritchie, 1984), and are most prevalent along the Arctic Coastal Plain and in the Hudson Bay Lowlands.

Climate

The median summer position of the arctic front has been widely referenced as a correlate of "tree line" (see Bryson, 1966; Barry, 1967; Hare, 1968). Yet the arctic front is difficult to define, and at most times there is no sharp boundary between arctic and Pacific air (F.K. Hare, pers. comm. 1986). On average, fairly warm and moist Pacific air predominates to the west of this zone, and cold arctic air predominates on the ground to the east (Hare, pers. comm. 1986). Arctic airstreams dominate the forest-tundra for ≥10 months of the year (Bryson and Hare, 1974).

Climatic analyses for July by Bryson (1966:Figs. 14-17, 19) indicate that the forest-tundra is dominated by the following air masses: a) from the Cordillera to north of Great Bear Lake, cool Pacific air (40-80% frequency) originating over Alaska-Yukon; b) north and northeast of Great Bear Lake, Alaska-Yukon (35-40%), eastern arctic (25-30%), and western arctic air (20-30%); c) the central forest-tundra, Alaska-Yukon air (35-45%) to the south and eastern arctic (25-40%) and

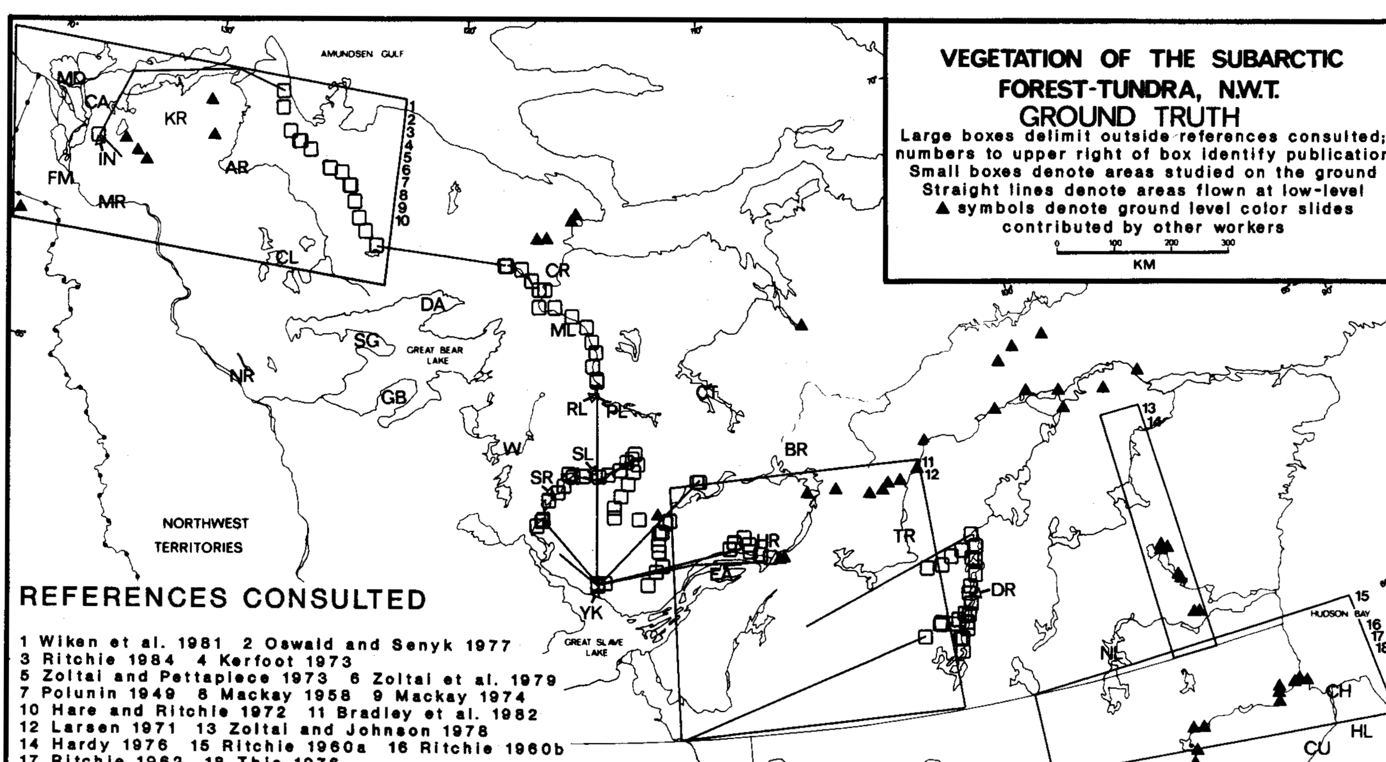

FIG. 1. Sources of ground truth for the study region. Place-names are plotted as: Anderson River (AR); Back River (BR); Caribou Hills (CA); Churchill (CH); Churchill River (CU); Colville Hills (see Colville Lakes area); Colville Lake (CL); Contwoyto Lake (CT); Coppermine River (CR); Dease Arm (DA); Dubawnt River (DR); East Arm (EA); Fort McPherson (FM); Grizzly Bear Mountain (GB); Hoarfrost River (HR); Hudson Bay Lowlands (HL); Inuvik (IN); Kugaluk River (KR); Mackenzie Delta (MD); Mackenzie River (MR); Muskox Lakes (ML); Norman Range (NR); Nueltin Lake (NL); Point Lake (PL); Redrock Lake (RL); Scented Grass Hills (SG); Snare Lake (SL); Snare River (SR); Thelon River (TR); Wopmay River (WR); Yellowknife (YK).

western arctic air (10-30%) to the north; d) southern Keewatin and northern Manitoba, eastern arctic air (40-50%) originating over the Arctic Archipelago and Alaska-Yukon air (25-40%).

The subarctic forest-tundra of Canada west of Hudson Bay lies between the July mean isotherms of 10-13°C and within the July mean isotherms of 4.5-7.0°C at the 850 mbar level (about 1.5 km aloft; Table 1). Mean daily air temperatures for the forest-tundra rise to 0°C by about 7-31 May, with the 0° threshold reached earliest in the central district. The frost-free period ranges from 50 to 80 days, with the fewest frost-free days found to the north and northwest of Great Bear Lake. The frost-free period at ground level may be only half that of the air; for subarctic Siberia, the frost-free period for the air is 60-90 days, but only 30-60 days at ground level (Dolgin, 1970). Mean daily air temperature falls to 0°C by about 1 October for much of the forest-tundra, with the northwest sector cooling about one week earlier and the central sector cooling to 0°C about one week later. Mean annual air temperature for the forest-tundra lies between −10 and −6.5°C east of Great Bear Lake and between −10.5 and −9°C westward to the Mackenzie Delta (Fletcher and Young, 1978).

Measured values for rain and especially snowfall in the Subarctic are probably underestimates on the order of 10-50% (Hare, 1971). Mean annual measured precipitation is light, ranging from about 25-40 cm in the southeast to 20-28 cm in the central district and 18-34 cm in the northwest. Measured snowfall over southern Keewatin and northern Manitoba ranges from 80 cm near the limit of trees to >200 cm in the Hudson Bay Lowlands. In the northwest, snowfall is variable. Highest values are recorded in the Mackenzie valley at Fort McPherson (235 cm), but in general the area receives 85-180 $cm \cdot yr^{-1}$. Between the northwest and southeast extremes, the central forest-tundra receives about 100-130 cm snow per year (Atmospheric Environment Service, 1982b).

TABLE 1. Summary of relevant climatic parameters for longitudinal districts of the subarctic forest-tundra of western Canada*

	Northwest	Central	Southeast
April net radiation ($cal \cdot cm^{-2} \cdot day^{-1}$)	15-35	30-70	25-75
Mean annual absorbed solar radiation ($kcal \cdot cm^{-2} \cdot yr^{-1}$)	52-55	53-63	55-63
Mean annual net radiation ($kcal \cdot cm^{-2} \cdot yr^{-1}$)	11-18 (x~15)	13-25 (x~21)	14-25 (x~20)
July mean air temp. @ screen level (C)	10-13	11-13	11-13
July mean air temp. @ 850 mb level (C)	4.5-6.5	4.5-7	6-7
Mean annual air temp. @ screen level (C)**	−10.5 to −9	−10 to −6.5	−10 to −7
Mean annual heating deg-days (0°C base)			
N half forest-tundra	3400-4100	2800-3500	3000-3600
S half forest-tundra	2800-3400	2300-2800	2600
Frost-free period (days)	50-65	55-80	70-75
Median last date of winter snow cover > 2.5 cm	15-31 May	15-31 May	21 May -7 June
Mean date of rise of mean daily air temp. to 0°C	15-31 May	7-31 May	15-31 May
Mean date of fall of mean daily air temp. to 0°C	25 Sept.	5 Oct.	1 Oct.

*"Northwest" extends from Yukon border to east side of Great Bear Lake; "Central" extends from east side of Great Bear Lake to Keewatin border (exclusive of central Thelon area); "Southeast" includes southern Keewatin and northern Manitoba. Values are approximations to be used for comparison; data interpolated from Hare and Hay (1974) unless noted otherwise.
**Fletcher and Young (1978) and Hare and Hay (1974), by calculation.

METHODS

Field Methods

Ground truthing of air photo interpretation was conducted during the summers of 1982-84. Travel was by canoe across and along the forest-tundra transition. Study sites, other sources of ground truth information, and place-names used in the text are detailed in Figure 1. Common and scientific names of vascular plants follow Porsild and Cody (1980). Tree, upland tundra, and tall shrub stands were examined using line transects run through representative communities, along which 30-70 quadrats were placed randomly. Species presence and percentage cover were estimated for non-tree species using 0.25 m^2 quadrats.

Trees (dbh ≥10 cm) were sampled with 25 m^2 circular plots, saplings (2.5 cm ≥ dbh <10 cm) with 12.5 m^2 semi-circular plots, transgressives (dbh <2.5 cm, ht. ≥ 0.2 m) with 6.25 m^2 quarter circle plots, and seedlings (ht. <0.2 m, and rooted) with the 0.25 m^2 quadrats used for the ground layer. Presence, density, dbh, height, cover, and age (increment cores) were determined for trees and saplings. Height was determined with a clinometer, and crown cover was estimated by the average maximum radius of the stem branches. All but age were also determined for transgressives and seedlings.

A representative soil pit was analyzed by horizon for thickness, color, texture, structure, consistence, horizon boundary, roots, pH, drainage, and parent material, and nearby vegetation and terrain were described.

Special transects were designed to augment tree data without the use of detailed stands. Species, dbh, height, cover, and age were determined for 10-20 selected trees or saplings. Relevés (~0.1 ha) were used primarily in the lowlands. Species presence was noted and cover classes were estimated.

Laboratory Methods

A matrix of 1314 National Air Photo Library (Ottawa) black-and-white photos was established. Air photos, at scales from 1:50 000 to 1:70 000, were taken between 1950 and 1980, with 68% taken prior to 1962. Although the imagery is dated, the quality is good. Correcting for the small amount of stereo overlap, the air photos cover about 260 000 km^2, or *ca.* 24% of the the study region.

Air photos were analyzed at 6× magnification with a stereo-microscope. The following information was gathered for each photo: a) percentage cover of tree, upland tundra, tall shrub (≥1.5 m), treeless wetland, and burned forest vegetation types was estimated visually, as was percentage cover of rockland (semi-barren bedrock), eroding terrain, water, and unsuitable (due to focus, clouds, etc.); notes accompanied each category; b) vegetation region (using presence/absence of tree and upland tundra vegetation and the landscape criteria given in Timoney, 1988:Table 1); c) prominent surficial features, such as parent materials, glacial landforms, beaded streams, rilled peat plateaus; d) the longitude and latitude of the center of each photo; e) mean, maximum, and minimum elevation and relief were estimated by plotting the photo on a 1:250 000 NTS topographic map; f) bedrock type was determined by reference to Geological Survey of Canada maps and publications or other reports; g) physiographic division (Bostock, 1976).

Air photo cover percentages were adjusted to percentage of land surface by algorithms correcting for percentage of water and unsuitable. Photo positions were transformed to a Lambert Conformal map projection, and the air photo cover data were then passed to Surface II software (Sampson, 1978). Surface II was used to generate 360 × 180 grid matrices, from which contour maps were drawn that depict percentage cover of the vegetation-terrain types. In order to show local detail, averaging was kept to a minimum (six neighbor photos). Checking of the contour maps with unaveraged air-photo data and ground truth indicates the normal accuracy of the isolines to be ±15 km.

Climatic data are based primarily on pattern matching of the forest-tundra region with the climatic maps of Hare and Hay (1974: climatic normal period 1931-60; global and net radiation 1957-64 and 1957-65 respectively). The accuracy of synoptic climatic isopleths for Canada varies from a few tens of kilometres to even a few hundreds of kilometres for the Arctic (F.K. Hare, pers. comm. 1986). Temperature-related isopleths are perhaps accurate to ± 0.5° latitude (±55 km); the degree of smoothing of isopleths is also important to consider (R.G. Barry, pers. comm. 1986). Maps of frost-free period, snow cover disappearance, etc., may be accurate to ±1° latitude (Barry, pers. comm. 1986). Climatic data used from Fletcher and Young (1978) are based on the 1948-73 period; supplementary weather station data (Atmospheric Environment Service, 1982a,b) use the 1951-80 period. Fortuitously, most of the air photos were taken either near the end or the mid-point of the climatic normal period.

RESULTS AND DISCUSSION

Width of the High Subarctic Forest-Tundra

The forest-tundra transition zone (exclusive of the Cordillera, Mackenzie Delta, and Thelon valley) averages 145 km wide (median 131 km) but varies greatly (S.D. ± 72 km, n=36; Figs. 2, 3). In the western half of the study region from east of the Mackenzie Delta to north of Yellowknife, the forest-tundra spans 112 ± 41 km (median 105 km, n=18); the eastern forest-tundra spans 179 ± 81 km (median 151 km, n=18). Regional minima are reached a) on the lower Anderson River (47 km); b) north of Dease Arm (Great Bear Lake); and c) north of the East Arm (70 km). Greatest widths are found between the Dubawnt River and central Manitoba-Keewatin (228-338 km). The forest-tundra of the northwest is significantly narrower than that of the southeast (Mann-Whitney test, p=0.009) — i.e., about 65% as wide. The marked west-to-east widening is especially evident between Great Slave Lake and central Manitoba-Keewatin.

It is difficult to compare these figures with other forest-tundra regions in the world as delimitation methods differ. In eastern Canada, exclusive of coastal areas, the forest-tundra varies greatly in width from 45 to 355 km (as mapped by Payette, 1983:Fig. 3). In the Soviet Union, the forest-tundra (after Lavrenko and Sochava, 1954) varies from 20 to 200 km wide, with most areas spanning 40-140 km.

Those who disagree with using absolute limits of trees and upland tundra as boundaries for the forest-tundra might wish

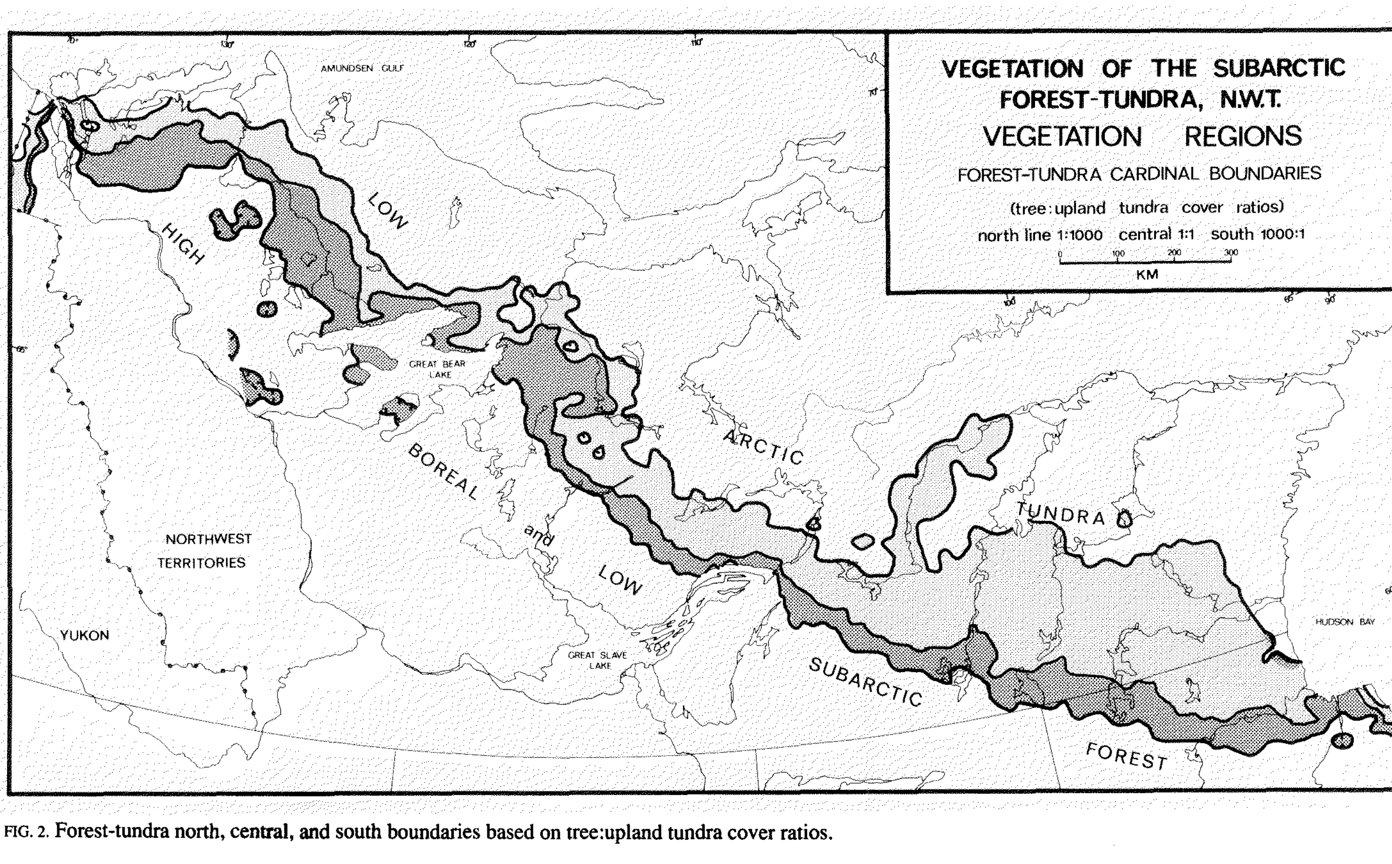

FIG. 2. Forest-tundra north, central, and south boundaries based on tree:upland tundra cover ratios.

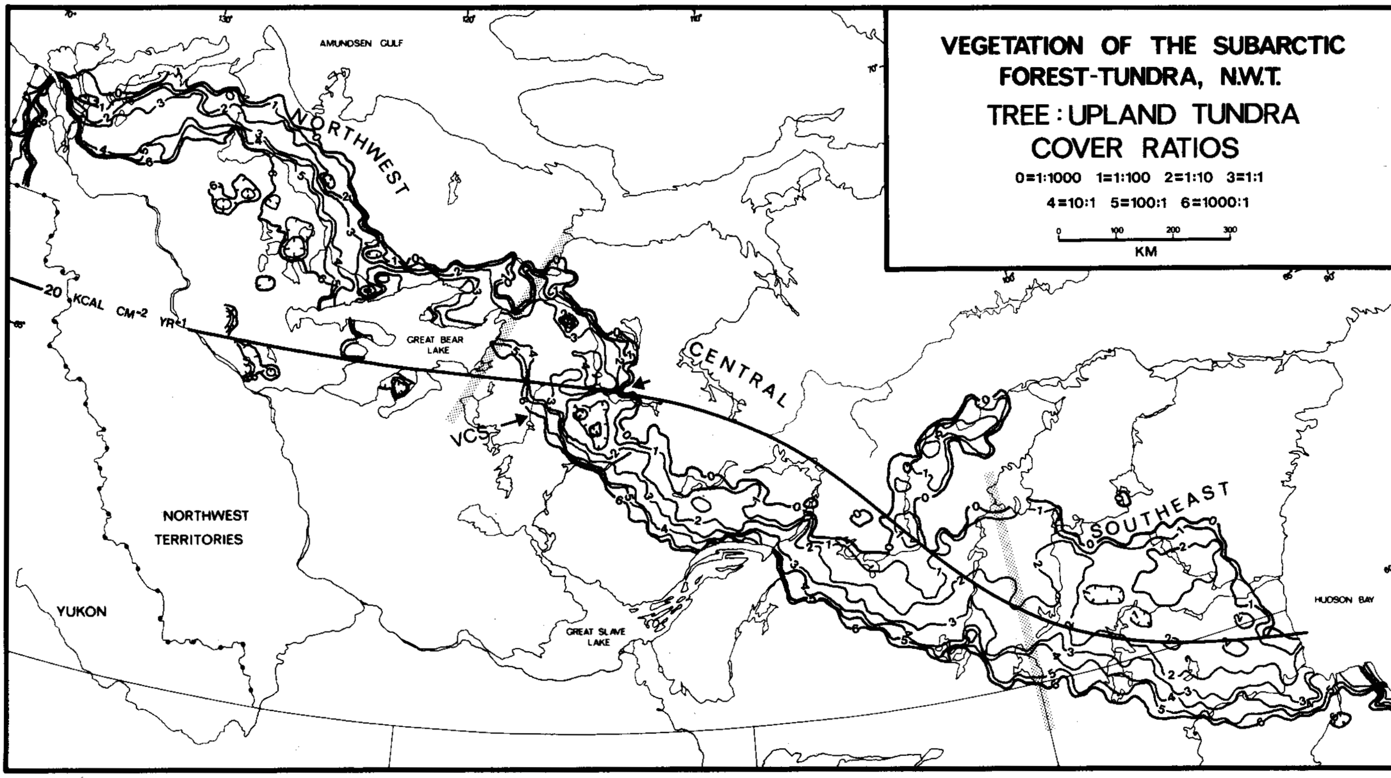

FIG. 3. Percentage cover of trees:upland tundra for the forest-tundra of western Canada. The 20 kcal·cm^{-2}·yr^{-1} annual net isorad (after Hare and Hay, 1974) is overlaid for climatic comparison. VCS axis highlights an abrupt transition in vegetation, climate, and soils within the forest-tundra.

to apply narrower ratios. Use of rational limits of 1:100 and 100:1 (lines 1 and 5 in Fig. 3), for example, would narrow the contiguous forest-tundra by about 10% (range 2-60%) and cut off the middle Thelon River from the contiguous forest-tundra. In other words, the 1:100 to 100:1 band spans about 90% of the forest-tundra.

Boundary limits for tree:upland tundra cover of 1:10 and 10:1 (lines 2 and 4 in Fig. 3) would narrow the forest-tundra by approximately 45-75%; i.e., this band occupies 25-55% of the forest-tundra. This narrowly bounded forest-tundra would range in width from about 30 to 75 km from east of the Mackenzie Delta to the northeast side of Great Bear Lake, 20 to 95 km from northeast of Great Bear Lake to the East Arm of Great Slave Lake, 20 to 70 km from the East Arm to west of the Dubawnt River, 40 to 100 km from the Dubawnt River to central Keewatin-Manitoba, and 40 to 55 km in northeast Manitoba (outside of the Hudson Bay Lowlands).

Regional slope of the land probably accounts for much of the variation in the width of the forest-tundra. North of Dease Arm, Great Bear Lake, and in the central district from the Snare River southeast to the East Arm of Great Slave Lake, elevations rise from south to north or southwest to northeast, parallel to the vegetation gradient. Evidently a strong topoclimatic gradient is created by the northward rise of elevation, eliciting steep vegetation gradients (Fig. 4). Conversely, northward decrease in elevation may help explain the northward extension of trees in the Thelon River area and the great breadth of the forest-tundra in southeast Mackenzie District and Keewatin. In eastern Canada, Hare (1950) suggested that the northward fall of elevation in Labrador-Ungava has the effect of partially offsetting the normal northward fall of temperature. As a result the thermally correlated zonal divisions of the boreal forest are wide there.

FIG. 4. Northward rise of elevation contributes to steep vegetation gradients north of the East Arm, Great Slave Lake. Mixed open crown forests of white and black spruce yield dominance to dwarf birch-willow/ericad upland tundras over short distances; the fall from 1000:1 to 1:1 tree:upland tundra cover may span only 15-18 km here; view to NE from between Lac La Prise and Lockhart River, at 108°44′W, 62°57′N; mean elevations here are ~395 m asl, or 240 m above the level of Great Slave Lake; 12 April 1990.

Southern outliers of the forest-tundra are recognized by disjunct areas of upland tundra. Most occur in the northwest (Figs. 2, 3) and they are due mainly to high elevations (e.g., Grizzly Bear Mountain, Norman Range, Scented Grass Hills). Within the contiguous forest-tundra, depression contours denote localities where tree cover falls to low or zero cover (e.g., Caribou Hills, highlands between Snare and Redrock lakes, west of Muskox Lakes, north of Nueltin Lake) in areas of high elevation and/or stony, shallow, or nutrient-poor soils

(Fig. 3). In the extreme southeast near the Churchill River, the hachured contour approximates where tree cover falls to <1% due to almost complete dominance by treeless wetland (upland tundra is absent).

Locations of Steep Vegetation Gradients

When the position of the 1:1 tree:upland tundra isoline (Fig. 2) is considered relative to the north and south limits, general trends appear. In the western half of the study region (west of Yellowknife), the relative positions of the cover contours vary greatly, but the 1:1 contour usually lies closer to the northern than to the southern limit of the forest-tundra. This indicates that high tree cover extends well to the north, then rapidly falls to zero. Erratic changes in the relative positions of the north, 1:1, and south lines in the west are likely due to major variations in elevation, parent material, and perhaps to fire history (e.g., east of Inuvik).

On an ENE axis running from the middle Wopmay River to western Point Lake, relative dominance of tree and upland tundra vegetation undergoes a dramatic change (VCS axis, Fig. 3). The change is correlated with a steep gradient in the radiation climate (see Radiation Budget, below) and a shift from sedimentary rocks overlain by relatively nutrient-rich loamy cryosols in the northwest to crystalline rocks overlain by nutrient-poor sandy brunisols in the southeast.

Northwest of this axis, most vegetation change takes place in the northern half of the forest-tundra; white spruce, *Dryas integrifolia*, calciphilic legumes and Carices, and arctic indicators are characteristic. Southeast of this axis, tree cover falls rapidly (upland tundra increases rapidly) in the southern half of the forest-tundra, then extends well to the northward in a dominantly tundra landscape; black spruce, dwarf birch, acidophilic ericads, and boreal-subarctic indicators are characteristic.

The southward plunge of the forest-tundra north of Great Slave Lake may in part result from both edaphic restrictions imposed upon the vegetation by the shallow, sandy brunisols of the Shield and upon the reproductive ecology of the dominant tree species. Available soils data (Timoney and Zoltai, unpubl. data) compared with nutrient deficiency levels for conifers (Lowry, 1972; Morrison, 1974) indicate that levels of soil nitrogen, calcium, and magnesium are likely deficient for white spruce on Shield till soils derived from acidic crystalline bedrock. The shift from white to black spruce dominance at the VCS axis is further noteworthy in that optimal germination of white spruce seeds occurs between 12.8-15.6°C (57-58% during 21-day trials) vs. 20°C (41%) for black spruce (Fraser, 1971; Black, 1977). Between 10 and 12.8°C (approximately the mean July air temperature range for the forest-tundra), 26 and 57% of white spruce seeds germinated (Fraser, 1971) vs. 0 and 5% for black spruce (Black, 1977). Thus, black spruce may be unable to reproduce by seed in the northwest, while white spruce may be limited by soil nutrient deficiencies on the Shield.

Vegetation and Climate Relationships

East/west of the Cordillera and of Hudson Bay, boreal to low arctic vegetation zones and relevant climatic isotherms and isorads show an oblique NW-SE orientation. In contrast with the typical W-E orientation of vegetation and climatic zones across the circumpolar North, the oblique orientation in western Canada results from the N-S Cordilleran barrier to zonal flow (J.C. Ritchie, pers. comm. 1988), leading to a SW-NE progression of spring. In northern Canada, the Cordillera restricts Pacific air dominance in July to the southwestern Mackenzie District (Bryson, 1966). Linkage between snow cover, vegetation, and radiative climate is strong, such that change to one results in adjustment of all components (e.g., Hare and Ritchie, 1972; Lettau and Lettau, 1975; Rouse, 1984; Rizzo, 1988). Vegetation-climate linkage has been implicated in intensifying the effects of the Sahelian drought of 1968-73 and in the desertification of subtropical semi-arid regions since the mid-Holocene (Hare, 1979).

Due to their lower albedo, forest stands at tree line have a substantially larger annual net radiation than adjoining tundra stands; the balance between tundra and forest stands strongly affects the regional radiation environment (Rouse, 1984). As such, steep or gentle gradients in tree and upland tundra cover should be mirrored by those of climate and snow cover. Some examples follow.

Mean July air temperature on the ground and at the 850 mb level, mean date of rise of daily mean air temperature to 0°C, and mean length of frost-free period (from Hare and Hay, 1974) all show steeper gradients in the northwest than in the southeast. The zone of mixing of modified Pacific and arctic air masses is narrow in the northwest and broad in the southeast (Bryson, 1966). April net radiation (Hare and Hay, 1974) in the southeast decreases sharply (from south to north) in the southern part of the forest-tundra. This likely correlates with the steep transition from dark canopy forest to snow-covered tundra seen in the southern third of the forest-tundra there.

Mean July air temperature on the ground and mean length of frost-free period decrease most rapidly in the northwest at the northern limit of the forest-tundra. This may be due both to the proximity of cold ocean waters off the arctic coast and to landscape feedback with the correspondingly steep vegetation gradient in the northern forest-tundra there. Summer air temperatures averaged 7°C colder for onshore than for offshore winds along the coast of Hudson Bay (Rouse and Bello, 1985).

Distance from the 1:1 tree:upland tundra cover isoline (Fig. 2) is correlated significantly with degree-days above 10°C for 25 boreal to arctic weather stations in western Canada (after Atmospheric Environment Service, 1982a; Spearman's rho, $r=-0.904$, 23 d.f., $p<<0.0001$). Comparison of weather station data with the forest-tundra boundaries indicates degree-day (10°C) values of ~140-300 for the northwest and ~170-330 for the southeast; the 1:1 tree:upland tundra isoline corresponds approximately to values of ~200-250 degree-days.

The correspondence between vegetation and climatic gradients appears to break down, however, when mean annual absorbed global solar radiation and mean annual net radiation are compared to contours of tree and tundra cover. These critical radiation parameters show steeper gradients over the southeast than over the northwest (Hare and Hay, 1974). Thus the apparent paradox arises that the forest-tundra of the northwest, which generally spans only 60-140 km, occupies a zone where net radiation gradients are gradual. In contrast, the forest-tundra of Keewatin and northern Manitoba spans 228-338 km, yet occupies a zone of steep radiation gradients.

The apparent paradox can be partially resolved when narrower tree:upland tundra ratios are used for comparison with radiation gradients (Fig. 3). In the southeast, the transition from a ratio of 10:1 tree:upland tundra cover in the south to 1:10 in the north takes place in 40-100 km. Relative to the overall width of the forest-tundra in the southeast, this vegetation gradient is steep and, moreover, takes place in the southern third of the forest-tundra, where the mean annual net radiation gradient is also steep.

Notwithstanding the clear vegetation-climate correlations, synoptic climate cannot be expected to account for the variability in the dominant vegetation cover within the forest-tundra (evident in Fig. 3). Nor can synoptic climate fully account for the great width of the forest-tundra in the southeast and the steep transitions in many places elsewhere. This variability derives from local and regional differences in topoclimate, parent materials and soils, bioclimatic feedbacks, and fire history.

Radiation Budget

Mean annual heating degree-days (0°C base; Table 1) for the forest-tundra indicate that the northwest is colder than central and southeast districts. By approximation, the northern limit of much of the forest-tundra southeast from Great Slave Lake to Hudson Bay is nearly as warm as the southern limit of the forest-tundra in the northwest. The southern portion of the forest-tundra across much of the central district is anomalously warm.

Upland tundra and tree cover gradients are oriented at a steeper NW-SE diagonal than critical thermal and radiation gradients (Fig. 3; *cf.* Hare and Hay, 1974), indicating that the forest-tundra of the northwest receives less warmth and photosynthetic energy than the forest-tundra of central and southeast districts. The northwest forest-tundra, for example, functions on roughly three-fourths the mean annual net radiation available to central and southeast districts (Table 1). Due to its higher forest cover relative to central and southeast districts (Figs. 2, 3), and therefore lower average albedo, the northwest may have a more favorable net radiation balance than synoptic climate data indicate.

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