The extent of the North American boreal zone

J.P. Brandt

Abstract: The circumpolar boreal zone is one of the world's major biogeoclimatic zones, covering much of North America and Eurasia with forests, woodlands, wetlands, and lakes. It regulates climate, acts as a reservoir for biological and genetic diversity, plays a key role in biogeochemical cycles, and provides renewable resources, habitat, and recreational opportunities. Poor agreement exists amongst scientists regarding this zone's delimitation and the areal extent of boreal forests, even though the zone has been well-studied. This paper reviews the literature on the phytogeography of the zone and makes use of a geographic information system (GIS) and published maps to delineate a current map of the North American boreal zone and the hemiboreal subzone, which is a transitional area lying immediately to the south of the boreal zone that is usually included in the boreal zone by Europeans but excluded by North Americans. On the basis of the map described here, the boreal zone covers about 627 million ha, or 29% of the North American continent north of Mexico. If the hemiboreal subzone, at 116 million ha, is included, then 34% of the same area is covered. Forests and other wooded land (362 million ha) cover 58% of the North American boreal zone on the basis of current forest inventory data. With forests and other wooded land of the hemiboreal subzone (68 million ha) factored in, this percentage remains basically unchanged. Values reported in this paper are compared with other published statistics. Important sources of error contributing to differences in areal statistics are discussed.

Key words: boreal forest, hemiboreal, map, North America, phytogeography.

Résumé : La zone boréale circumpolaire constitue une des zones biogéoclimatiques les plus importantes du monde et comprend une bonne partie des forêts, des milieux boisés, des terres humides et des lacs de l'Amérique du Nord et de l'Eurasie. Elle régularise le climat, agit comme réservoir de diversité biologique et génétique, joue un rôle dans les cycles biogéochimiques et fournit des ressources renouvelables, des habitats et des opportunités récréatives. Il existe peu de consensus parmi les scientifiques quant à la délimitation de cette zone et sur l'étendue des forêts boréales, bien qu'on ait passablement étudié cette zone. Cet article révise la littérature sur la phytogéographie de la zone et utilise le système d'information géographique (GIS) ainsi que les cartes publiées pour définir une cartographie actuelle de la zone boréale nord-américaine et de la sous-zone hémiboréale qui constitue une aire de transition située immédiatement au sud de la zone boréale; les Européens incluent cette région dans la zone boréale, contrairement aux Nord-Américains qui l'excluent. Sur la base de la carte présentée ici, la zone boréale couvre 627 millions ha ou 29 % du continent nord-américain, au nord du Mexique. Si on inclut les 116 millions ha de la sous-zone hémiboréale, on atteint une couverture de 34% de la même région. Les forêts et autres terrains boisés (362 millions ha) couvrent 58% de la zone boréale nord-américaine, sur la base des données actuelles des inventaires forestiers. Si on inclut les forêts et autres surfaces boisées de la sous-zone hémiboréale (68 millions ha), ce pourcentage demeure globalement inchangé. Les valeurs rapportées dans ce document se comparent à d'autres statistiques publiées. Cet article discute les sources d'erreur importantes contribuant aux différences des statistiques des superficies.

Mots-clés : forêt boréale, hémiboréale, carte, Amérique du Nord, phytogéographie.

[Traduit par la Rédaction]

1. Introduction

The circumpolar boreal biome or zone is one of the world's largest and most important biogeoclimatic areas. It covers a large portion of North America and Eurasia with coniferous forests and woodlands, wetlands, and lakes. With its extensive forests, the boreal zone provides food and renewable raw materials for human consumption and use; provides habitat for wildlife, arthropods, fungi, and microorganisms; acts as a reservoir for the maintenance of biological and genetic diversity; regulates regional and global climates; sequesters carbon; cycles nutrients; purifies air and water; controls erosion; and provides multiple, unique, and abundant opportunities for recreational activities. The boreal zone is also culturally and spiritually important to indigenous peoples. Because of the fibre and other renewable resources within its forests, the non-renewable mineral and energy resources below ground, the hydroelectric potential of boreal rivers, and the large areas it covers, the circumpolar boreal zone is vitally important to the economies of Canada, Finland, Norway, Russia, and Sweden. The boreal zone is also an important source of raw materials in China, Kazakhstan, and Mongolia, even though forests cover a relatively small proportion of the areas of these countries (Finch 1999; UNECE 2000*a*; Wang et al. 2001; Kushlin et al. 2003).

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There are large discrepancies in the literature as to the extent of forests within the circumpolar boreal zone. Similar problems affect the definition of other forests worldwide (see Table 13.4 in Williams 2003). Most maps of the boreal zone are of such low resolution that they are of little value for estimating areal extent. Furthermore, the methodologies and terminologies of various phytoclimatologists, phytogeographers, and phytosociologists have varied substantially, resulting in differing opinions as to the exact limits of the boreal zone in various regions (Hämet-Ahti 1981; Tuhkanen 1984). For example, there is a global, quasi-latitudinal belt, which is usually considered a subzone, lying to the south of the typical boreal zone. This subzone is often called the hemiboreal subzone (Ahti et al. 1968; Tuhkanen 1984). Scandinavian scientists and some Russian scientists tend to include the hemiboreal subzone in the boreal zone because of its floristic affinity to the latter zone (Ahti et al. 1968; Tuhkanen 1984; Hytteborn et al. 2005). On the *Map of the Natural Vegetation of Europe* (Bohn et al. 2004), the hemiboreal zone is considered temperate (personal communication, Udo Bohn, Bundesamt für Naturschutz, Germany, 6 November 2008). North American scientists do not, however, recognize this subzone; areas in North America that Scandinavian scientists have recognized and mapped as being in the hemiboreal subzone have been placed in either the boreal or temperate zone by North American scientists. Also, papers on forests in the boreal zone (or global forests in general), on forest fires, and on the global carbon budget, as well as reports from various environmental organizations, have provided widely different estimates of various parameters used to describe the boreal zone and its forests. These often-conflicting reports have caused confusion amongst scientists, governmental and non-governmental organizations, and the public as to the exact nature and extent of the boreal zone. Language barriers also impede an understanding of the boreal zone as the relevant literature has been written in several different languages (e.g., Chinese, English, Finnish, French, Japanese, Korean, Mongolian, Norwegian, Swedish, and Russian).

When J.S. Rowe published his *Forest Regions of Canada* in 1972 it was viewed as an accurate depiction and description of Canadian forests at a national scale (Krajina 1973*b*) and it continues to be cited in the current scientific literature. Two newer national maps, *Ecoclimatic Regions of Canada* [Ecoregions Working Group (EWG 1989)] and *Ecozones of Canada* [Ecological Stratification Working Group (ESWG 1995)], have gained some acceptance more recently. The former map was used by Scott (1995) in his thorough book on Canada's vegetation and also by researchers working on Canada's carbon budget model during the 1990s (e.g., Kurz et al. 1992; Kurz and Apps 1999). ESWG (1995) provides an historic overview and the rationale for their map and that of EWG (1989). The map of Viereck and Little (1972) is the most recent map of vegetation types in the boreal zone in Alaska.

Geographic information systems (GIS) have improved our ability to produce spatially accurate maps. This technology, however, is limited by the accuracy and resolution of the accessed spatial data. Several recent vegetation studies within the boreal zone and other recently developed spatial data sets provide new data that can be used in combination with a GIS to develop an improved map of the North American boreal zone.

The objectives of this paper are to (*i*) review the North American literature pertaining to the phytogeography of the boreal zone; (*ii*) use a GIS to compare and contrast existing maps of the zone; (*iii*) develop a revised map of the North American boreal zone and the hemiboreal subzone using consistent criteria and the most current information; and (*iv*) provide descriptive statistics on the areal extent of the boreal zone and the hemiboreal subzone based on the new map. No attempt has been made to map boundaries of subzones based on some aspect of the vegetation, temperature, or oceanity-continentality within the boreal zone as others have attempted (e.g., Ahti et al. 1968; Rowe 1972; Tuhkanen 1984). Such subdivisions are beyond the scope and intent of this paper. A new map and the corresponding statistics of the North American boreal zone can be viewed as a significant step toward providing scientists, regulators, and environmental groups with a common baseline or standard with which to measure changes in attributes and conservation efforts for a substantial portion of the circumpolar boreal zone. A baseline map is especially important because of the anticipated changes expected within the zone resulting from climate warming as well as the negative effects of various industrial sectors or other anthropogenic activities that are likely to have an additive or synergistic impact.

2. Terminology

As mentioned earlier, the literature describing the circumpolar boreal zone and its boundaries with adjacent vegetation zones (arctic, temperate) is written in several different languages. Even within the literature written in English there are inconsistencies in the use of terms, with some authors using the same term for different things or using different terms for the same things (Hustich 1966; Löve 1970; Tuhkanen 1984; Sjörs 1999). Many of the discrepancies in the areal statistics of the zone relate to differences in the methodologies used to estimate areas and in the definitions of the following terms: *forest*, *forest land*, *forested land*, *timberland*, *unforested land*, *closed forest*, *open forest*, *forest-tundra*, and *other wooded land*. Some environmental groups use novel terms like *frontier forests* and *intact forests* (e.g., Bryant et al. 1997). In some jurisdictions, qualifying terms such as *reserved* or *unreserved*, *timber-productive* or *timber-unproductive land*, or *stocked* or *unstocked* are used to describe forest land in national forest inventories. For the sake of clarity I have provided definitions for the terms that are most relevant to this review in Appendix A. For terms related to areal statistics I have taken the definitions used in some of the latest Food and Agriculture Organization (FAO) reports (FAO 2001, 2006) because these have been vetted by experts in different countries.

3. Overview of the boreal zone

Because of the predominance of forests in the boreal landscape, the zone has often been referred to as the *boreal forest* in North America or the *taiga* (Hoffmann 1958) in Russia. The boreal zone, however, includes closed forests, other wooded land, and naturally treeless areas including alpine areas on mountains, heathlands in areas influenced by maritime climatic conditions, and some grasslands in drier areas. In North America, the boreal zone stretches from Greenland to Newfoundland and across northern Canada into Alaska. In Eurasia, the boreal zone is distributed throughout most of Scandinavia and Russia and includes parts of China, Kazakhstan, and Mongolia. Although the location of both the northern and southern boundaries of the boreal zone is the subject of debate (Tuhkanen 1984), the boreal zone's northern boundary in both North America and Eurasia is generally accepted as the southern limit of the tundra; its southern boundary is generally coincident with the northern limit of temperate forests, or grasslands (steppes). In both the north and south, the boundary depends primarily on topography, local climate, and edaphic conditions.

Ecologically, the North American landscape presently occupied by the boreal zone is relatively young. As recently as 21 400 calender years ago at the peak of the Wisconsin glaciation, almost all of the northern half of the continent was covered with ice, excluding parts of the Yukon Territory, the Northwest Territories, and Alaska (Dyke et al. 2003). As the continental glaciers melted during the next 15 000–16 000 years, newly deglaciated land was colonized by tree species growing in refugia south of the ice margin. Fossil-pollen data have been used to infer past distributions of several tree taxa, including *Abies*, *Betula*, *Larix*, *Picea*, and *Pinus* in North America from 21 000 years ago to modern time (Williams et al. 2004). Presently in North America, coniferous trees such as *Picea glauca*, *Picea mariana*, *Larix laricina*, *Abies balsamea*, and *Pinus banksiana* dominate the boreal zone but large areas are also covered by shade-intolerant deciduous trees such as *Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera*, either in pure stands or, more commonly, intermixed with conifers. In the western reaches of the boreal zone, *Pinus contorta* var. *latifolia* and *Abies lasiocarpa* cover extensive areas. The distribution of several tree species of significance in the context of this paper are depicted in Figs. 1–4.

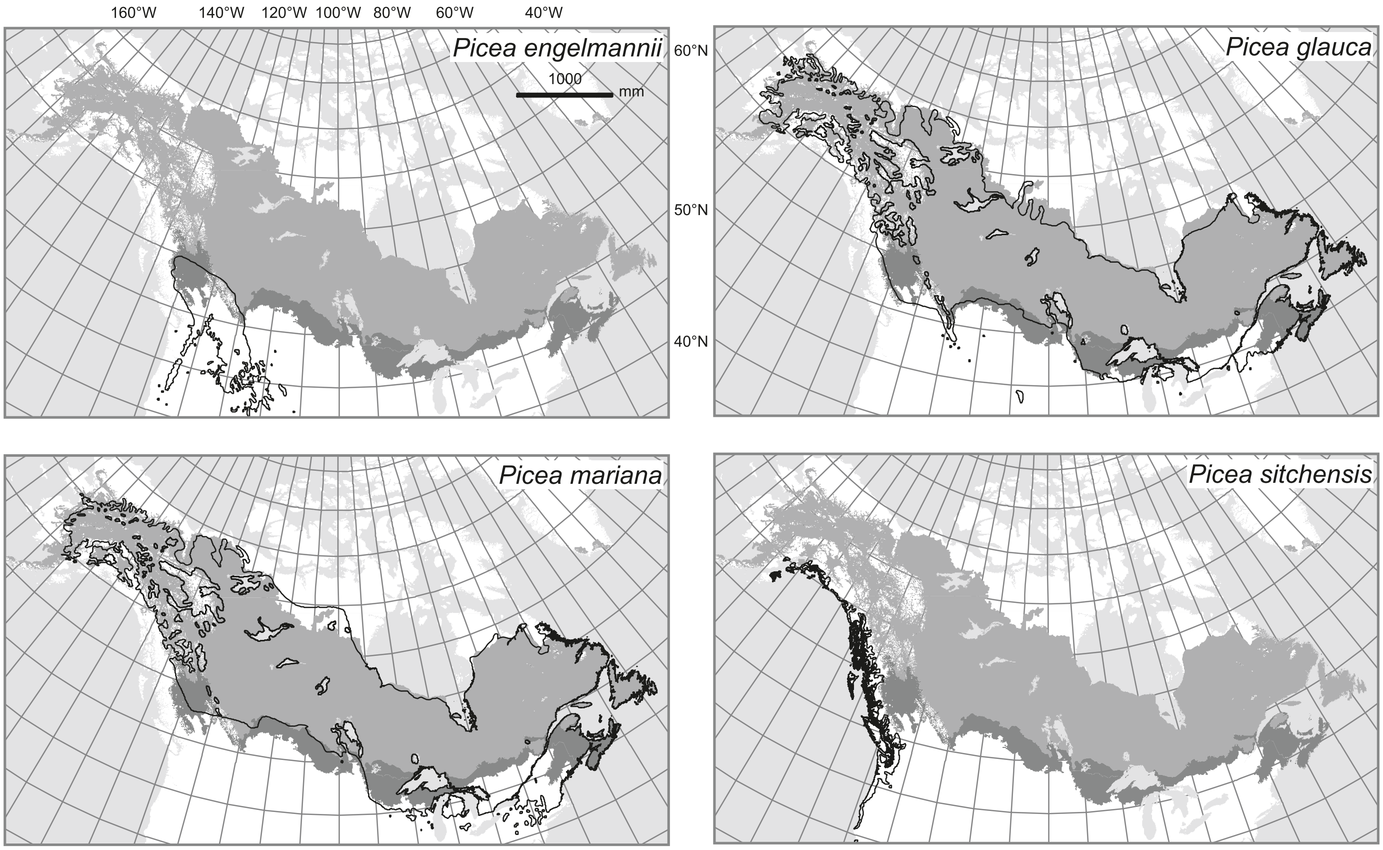
The North American tree species currently distributed in the boreal zone can be divided into two groups: a cordilleran group whose present distribution originated from one or more western refugia at the end of the Wisconsin glaciation, and an eastern group originating from one or more eastern refugia. In many cases there are closely related species in the two groups. For example, *Picea engelmannii* is a cordilleran species generally found at elevations above 1830 m whose range extends north into western Canada (Fig. 1). *Picea glauca* is considered an eastern boreal species with a transcontinental distribution (Fig. 1); it is found at elevations below 1220 m (Achuff and La Roi 1977; Pfister et al. 1977; Farrar 1995). In the western cordillera, hybrids between the latter two species are generally found between 1220 and 1830 m (Achuff and La Roi 1977). Recent research, however, has demonstrated that the taxonomic status of the two *Picea* species and their hybrids and the zone of hybridization or introgression remain controversial (Rajora and Dancik 2000; Strong and Hills 2006). Similarly, *Pinus contorta* var. *latifolia* could be considered a western cordilleran species whose range extends into the boreal zone, whereas *Pinus banksiana* is an eastern boreal species (Fig. 2); these species hybridize where their ranges overlap (Critchfield 1985). The range of *Pinus contorta* var. *latifolia* has been expanding northward (MacDonald and Cwynar 1985) and may have been more extensive in earlier post-glacial time but this species was displaced by *Pinus banksiana* as the latter species moved westward from eastern refugia, except at higher elevations in northern and northeastern Alberta where outlying populations of *Pinus contorta* var. *latifolia* remain (Critchfield 1985). *Abies lasiocarpa* is a western cordilleran species and *Abies balsamea* is its eastern boreal counterpart, which is restricted to elevations <1200 m in Alberta where the ranges of the two species overlap (Achuff and La Roi 1977). In each of the three pairs of trees described above, these closely related trees were probably isolated in widely separated eastern and western North American refugia one or more times during each of the continental glaciations of the Pleistocene, although the locations of these refugia remain speculative (Parker et al. 1981; Critchfield 1985; Palmer and Parker 1991; Rajora and Dancik 2000; Godbout et al. 2005; Strong and Hills 2006). A somewhat similar situation occurs in eastern North America where *Picea mariana* and *Picea rubens* hybridize naturally. *Picea mariana* is a transcontinental boreal species often found in lowlands (Fig. 1) (Viereck and Johnston 1990; Farrar 1995). Recent evidence suggests that there may have been refugia in both eastern and western Canada for this species (Jaramillo-Correa et al. 2004). *Picea rubens* is restricted to eastern North America and is often found at higher elevations although in the Atlantic Maritimes and near the St. Lawrence River this tree species is abundant at low elevations (Blum 1990). The present distribution of tree species in the boreal zone is probably a function of their post-glacial history and their superior cold hardiness in a boreal climate (Sakai and Larcher 1987). For a more detailed review of various aspects of the climate, ecology, floristics, and history of the circumpolar boreal zone the reader is referred to Larsen (1980), Ritchie (1987), Elliot-Fisk (1988), Kuusela (1990), Hytteborn et al. (2005), and Weber and Van Cleve (2005).

4. Past approaches to delineating the boreal zone

The various schemes used to classify global vegetational and climatic zones are all human constructs. The utility of any given scheme is dependent, to a large degree, on the needs of the user (Sims et al. 1996*b*). There is no right or wrong scheme unless the criteria used to identify the various zones are applied incorrectly or inconsistently. In any of these schemes it is difficult to provide a single all-encompassing definition for a particular zone. For instance, species in the tree stratum and vegetation in the other strata vary across the North American and Eurasian landscapes as do many other diagnostic features. Climatic factors also vary across the landscape. As will be discussed later in this section, no single climatic parameter or index works equally well in all areas of any one zone.

Mueller-Dombois and Ellenberg (1974) describe three main approaches for classifying vegetation based on: (*i*) properties of the vegetation itself including those systems using physiognomic and structural criteria, floristic criteria, or numerical relation criteria; (*ii*) properties outside the vegetation including habitat or environment, the geographical

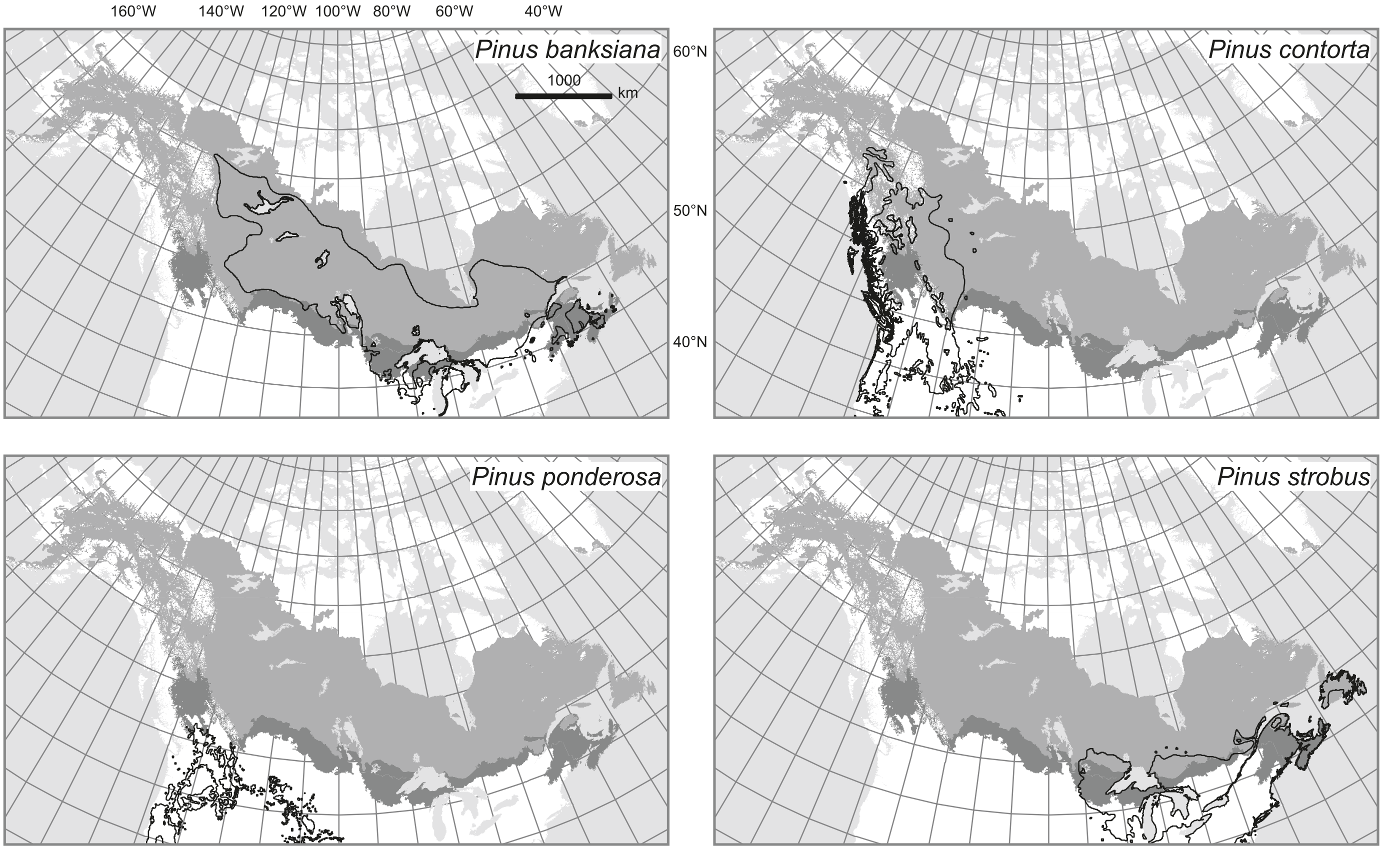
Fig. 1. The distribution of *Picea engelmannii*, *Picea glauca*, *Picea mariana*, and *Picea sitchensis* in North America (adapted from Little 1971). The gray-scale used to depict the boreal zone (medium gray), the hemiboreal subzone (dark gray), alpine areas within the boreal zone or hemiboreal subzone (white), oceans and large freshwater lakes (light gray), and other land areas outside the boreal zone (white) is the same in all subsequent figures.



location of communities, or those where the final stage in vegetation development (climax) is presumed; and (*iii*) properties combining vegetation and the environment. Classification is merely the sorting procedure (i.e., the taxonomic framework) that groups similar vegetation units on the basis of certain prescribed attributes (Moore and Chapman 1986; Banner et al. 1996). Mapping is the mechanism by which the spatial distribution of these groups is depicted (Moore and Chapman 1986; Banner et al. 1996). There are several considerations for mapping: purpose of the map, scale, the method of characterizing the mappable unit in the classification scheme, and characteristics of the area to be mapped (Küchler 1967; Moore and Chapman 1986). For more information on methods for and approaches to classifying and mapping vegetation or land, the reader is referred to Mueller-Dombois and Ellenberg (1974), Moore and Chapman (1986), and Sims et al. (1996*a*).

The circumpolar boreal zone is widely accepted in phytoclimatology, phytogeography, and phytosociology (Tuhkanen 1984; Spribille and Chytrý 2002) but specialists in each of these fields of study have taken different approaches to defining this zone. For example, Hare (1954) defines the "boreal conifer zone" as the circumpolar forest that spans Alaska, Canada, and Eurasia and occupies the so-called subarctic belt. Hare's boreal conifer zone generally corresponds climatically to the Köppen subprovinces, Dc and Dd, or to the range of potential evapotranspiration 31–52 cm on Thornthwaite's scale of thermal efficiency (Thornthwaite 1948). Phytogeographers have utilized various climatic, edaphic, floristic, ecological, and phytosociological criteria to describe the boreal zone, which they consider to be the bioclimatic area covered primarily by coniferous forests and lying between the northern arctic polar zone and the southern temperate zone (Ahti et al. 1968; Tuhkanen 1984). Phytogeographers from different countries, however, have generally used different approaches and definitions. For example, Japanese and Soviet scientists have traditionally focussed primarily on trees, the Fennoscandians have paid more attention to understory vegetation and bryophytes, and the Canadians have placed more emphasis on physiognomical features, at least at a national scale (i.e., Rowe 1972) (Hämet-Ahti et al. 1974; Tuhkanen 1984). More recently, most countries are focussing classification and mapping efforts on hierarchical schemes at various scales using ecological approaches (e.g., in Canada, EWG 1989; ESWG 1995; Saucier et al. 1998; British Columbia Ministry of Forests and Range [BCMFR 2006] (Sims et al. 1996*a*). Phytosociologists who use the Braun-Blanquet approach to vegetation classification (Braun-Blanquet et al. 1939) generally recognise the *Vaccinio-Piceetea* class of vegetation as synonymous with Eurasian and North American boreal and subboreal coniferous forests (Peinado et al. 1998; Spribille and Chytrý 2002; Kolbek et al. 2003). Peinado et al. (1998) developed a list of circumpolar boreal taxa, but there are some problems with this list (Spribille 1999).

Fig. 2. The distribution of *Pinus banksiana*, *Pinus contorta*, *Pinus ponderosa*, and *Pinus strobus* in North America (adapted from Little 1971).



Various climatic parameters and indices have been used to model the boundaries of the boreal zone. Climate is the primary factor affecting the distribution of vegetation on the planet; secondary factors include terrain, edaphic conditions, and the historical distribution of plants (Tuhkanen 1984; Woodward 1987; Prentice 1992). All of these factors affect energy flow and productivity in ecosystems (Oechel and Lawrence 1985; Bailey 1988). Where moisture is not limiting, energy input and productivity increase from the northern arctic zone through the boreal zone to the more southern temperate zone. At the scale of zones, however, changes in vegetation types along a climatic gradient are gradual until some climatic threshold is breached, at which point changes can become rapid (Tuhkanen 1984). Interannual variation in climate and local changes in topography and soils act on vegetation at ecotones to make zone boundaries and boundaries between different forest or vegetation types diffuse or abrupt, depending on the gradient of the environmental factor affecting the change.

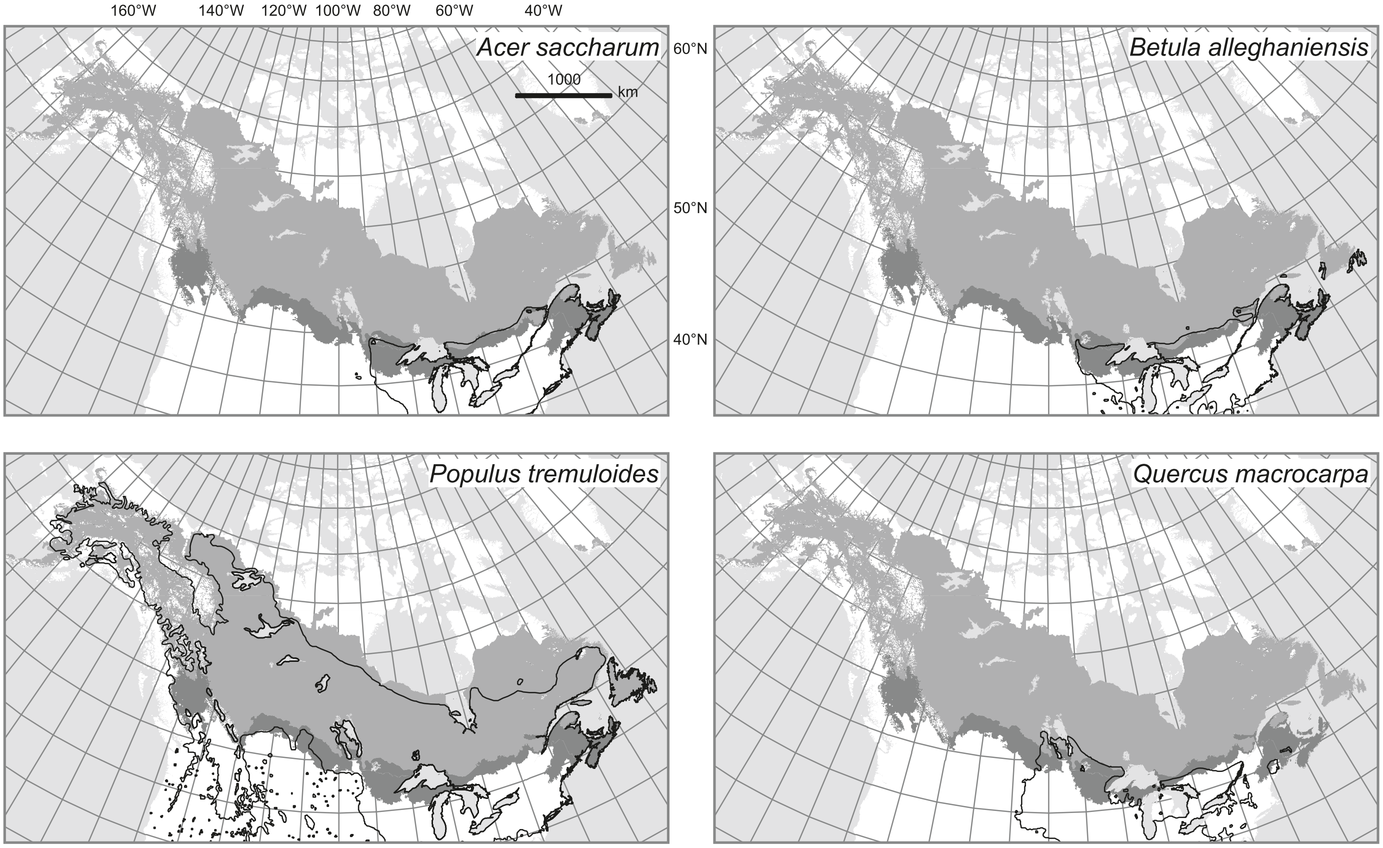
The climatic parameters and indices that have been used to delineate the boreal zone include mean annual temperature, warm or cold season temperatures, the Nordenskjöld line[2], the length of the growing season, effective temperature or frost sums, biotemperature, potential evapotranspiration and moisture indices, the Conrad index of continentality, and growing-season precipitation (Nordenskjöld 1928; Conrad 1946; Holdridge 1947, 1959; Thornthwaite 1948; Tuhkanen 1980, 1984; Arris and Eagleson 1994; Hogg 1994).

Temperature is the most important climatic parameter affecting the northern boundary of the boreal zone and some portions of the southern boundary. Various workers have tried to delimit the boreal zone using different indices of temperature, particularly those related to summer or winter warmth, or extreme summer or winter cold. These parameters or indices, however, can show substantial variation in time and space (Hustich 1966; Tuhkanen 1980). Additionally, meteorological stations across the northern circumpolar regions are few and data sets extend back only a few decades in most cases.

Tuhkanen (1980) assessed the fit of several climatic isopleths in relation to the tree limit in Canada; all of them provide a reasonable fit to the tree limit. The isotherm for a warm-month mean of 10 °C, which is generally considered the mean temperature below which tree growth is not possible (Andersson 1902; Supan 1903; Köppen 1920; Walter 1973; Wolfe 1979), provides a poor fit for the northern tree limit on the basis of Canadian data; however, the 11 °C isotherm provides a good fit in eastern Canada whereas the 12 °C isotherm fits well in western Canada (Tuhkanen 1980). According to Hopkins (1959), the isotherm for a warm-month mean of 10 °C also provides an inadequate fit to the tree limit in western Alaska. Here, the climates of the coastal spruce-hemlock forests and of the interior boreal zone differ primarily in severity of winters; the boundary appears to lie between –12 °C and –9 °C for the minimum

[2] A limit for the northern boundary of the boreal zone along which the expression $v = 9 - 0.1k$ holds, where v represents the mean temperature (°C) of the warmest month, and k represents the mean temperature (°C) of the coldest month.

Fig. 3. The distribution of *Acer saccharum*, *Betula alleghaniensis*, *Populus tremuloides*, and *Quercus macrocarpa* in North America (adapted from Little 1971).



mean temperature in winter (Hopkins 1959). The northern tree limit in Eurasia corresponds with the 10 °C to 12 °C July isotherm (MacDonald et al. 2000).

Along some of the boreal forest's southern boundary, the shift in dominance from needle-leaved conifers to broadleaf deciduous trees corresponds generally to a warm-month mean of 20 °C (Wolfe 1979). The boreal–temperate boundary can also be approximated by the 3 °C mean annual temperature isotherm in Europe, Asia, and North America (Wolfe 1979). The reader should be aware, however, that there are problems relating these indices of temperature to ecological and physiological mechanisms that limit the distribution of trees in cold and warm climates (Oechel and Lawrence 1985; Kullman 1990; Bonan and Sirois 1992; Sykes et al. 1996).

Yim and Kira (1975) correlated the distribution of forest trees on the Korean peninsula with both warm and cold indices (degree-day summations); there was close agreement between the Korean high-elevation, subarctic forest zone (as mapped by Yim 1968) and a warmth index of <55. Some consider these high-elevation forests as outliers of the boreal zone. A warmth index was then used by Yim (1977) to compare and contrast seven vegetation maps of the Korean peninsula. Hämet-Ahti et al. (1974) applied Kira's warmth indices to Finnish forests and found that indices <20 correspond to their northern boreal subzone, values between 30 and 40 correspond to their southern boreal subzone, and values >40 to their hemiboreal subzone. There is also strong agreement between critical isopleths of Kira's warmth indices and well-known phytogeographical boundaries in forests of northeastern Eurasia (Grishin 1995).

Hare and Ritchie (1972) and Timoney (1988) discuss the correspondence of the Canadian tree limit and the closed forest boundaries with annual absorbed and annual net radiation values; the tree limit corresponds generally to the 0.75×10^9 J·m^{-2} annual net radiation isorad whereas the closed forest boundary corresponds to about the 1.26×10^9 J·m^{-2} annual net radiation isorad. Hare and Ritchie (1972) also depict data for Alaska using Hopkins' (Hopkins 1959) state vegetation map.

A relatively recent effort to describe the circumpolar boreal zone cartographically is that of Tuhkanen (1984). He used climate data from about 2000 meteorological stations distributed in the northern hemisphere to determine threshold values of several climatic indices (Table 1) that correlate well with the subzones described by Ahti et al. (1968) for northwestern Europe (Tuhkanen 1984). These threshold values were then applied globally to delineate the circumpolar boundaries of each of the subzones. However, both Tuhkanen's method of data interpolation between meteorological stations for each of the indices and his cartographic method for applying lines to his map are unclear. Tuhkanen's map agrees generally with various regional maps produced by earlier workers (see later discussion).

Classifying large vegetational zones using climatic criteria alone is problematic because such data are sparse or lacking, some climatic parameters are difficult to measure, critical threshold values have not often been defined, and no single climatic parameter or index works equally well across a zone (Daubenmire 1956; Pojar et al. 1987), but some modern techniques applied to recent climate data sets have dem-

Fig. 4. The distribution of *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, and *Tsuga mertensiana* in North America (adapted from Little 1971).

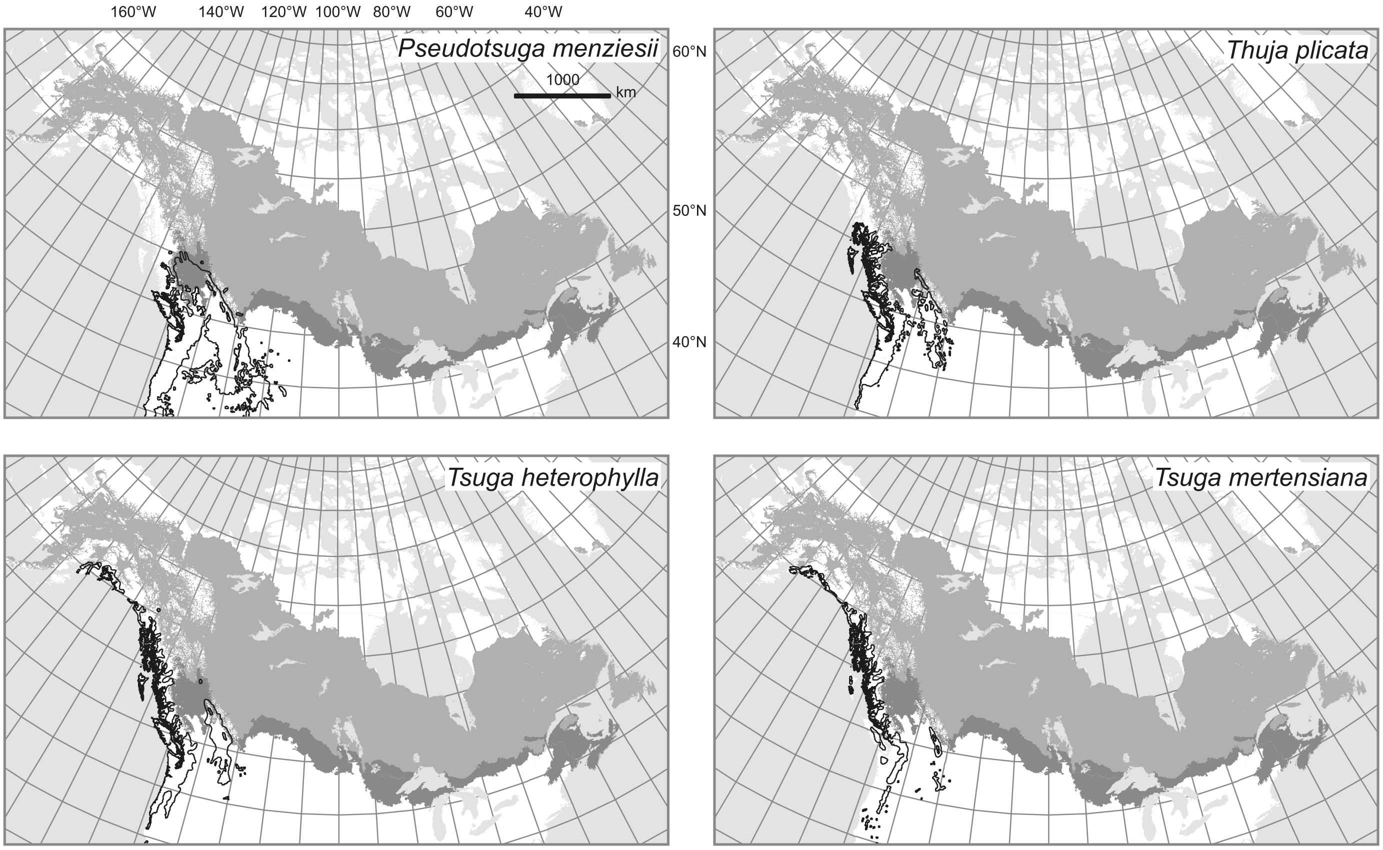


Table 1. Climatic parameters used to describe boreal vegetational boundaries after Tuhkanen (1980, 1984).

Zone or subzone	Growing season (days)	Effective temperature sum (°C)	Potential evapotranspiration (mm)	Biotemperature (°C)
Arctic–boreal	100	15	320	2.5
Boreal–hemiboreal	175	42	520	6.25
Hemiboreal–temperate	205	48	575	7.5

onstrated their utility for similar applications (e.g., McKenney et al. 2001, 2006). Another consideration is that extremes in weather (i.e., roughly greater than one standard deviation from the mean) are probably more important in the distribution of plants than mean climatic conditions (Daubenmire 1956; George et al. 1974; Sakai 1983; Sakai and Larcher 1987; Brandt et al. 2004). Although vegetation established during favourable climatic periods can often endure extremes that occur at occasional intervals (Daubenmire 1956), there have been cases in North America in which extensive forest dieback has been associated with such events (Auclair et al. 1992; Braathe 1995; Hogg et al. 2002, 2005). The critical issue related to extreme events and plant distribution is probably the frequency with which extreme events occur (Graumlich 1993; Tardif et al. 2001).

Classification systems based on floristics also have problems. At the simplest level, single, easily recognized plants can be used to order plant communities; these have some utility for certain purposes (Mueller-Dombois and Ellenberg 1974) but cannot be applied to broader geographic areas (Tuhkanen 1984). The concept of plant association is widely accepted by phytosociologists for classification purposes but the term is applied differently in various parts of the world. A generally agreed definition accepted at the Third International Botanical Congress in Brussels in 1910 was that it is a plant community of definite composition, presenting uniform physiognomy, and growing in uniform habitat conditions (Daubenmire 1968; Mueller-Dombois and Ellenberg 1974). Since that time interpretations have varied about the inclusiveness of a plant association. Thus, according to Allaby (1998), an association is (*i*) a plant community that is united physiognomically and floristically in the American and British phytosociological traditions; or (*ii*) a basic unit of vegetation, an abstract entity that is defined floristically from field data in the tradition of the Zurich-Montpellier school of phytosociology, as described by J. Braun-Blanquet. The former tradition is considered a divisive method (i.e., starts with large and heterogeneous units that are then subdivided) while the latter an agglomerative method (i.e., starts with small units that are then combined into successively larger, more heterogeneous units) (Daubenmire 1968; Moore and Chapman 1986). Regardless of the approach, problems arise if plant communities with similar floristic composition are grouped but their climates, soils, physiognomy, or ecology are different, a concern raised by Daubenmire (1968), Ahti et al. (1968), Mueller-Dombois and Ellenberg (1974), and Tuhkanen (1984).

The best approach would seem to be one that takes advantage of floristic, climatic, edaphic, and historic data to delineate broad vegetation zones. Accurate classification and mapping of plant communities on the basis of these factors can alleviate some of the problems of demarcation between vegetation zones (Ahti et al. 1968; Hämet-Ahti 1988). Substantial advances have been made in this regard during the last several decades (e.g., Sims et al. 1996*b*); however, humans constantly alter vegetation. Care must be used in inferring potential vegetation boundaries (Rowe 1996). Excellent examples of classification and mapping systems in North America that consider multiple factors include the hierarchical systems developed by the B.C. Ministry of Forests and Range on the basis of ideas and work of V.J. Krajina and his students (BCMFR 2006), and the Quebec ministère des Ressources naturelles (Saucier et al. 1998). These latter systems, among others, were used to create the new map of the boreal zone in the present paper. Before the new map is presented, however, it is instructive to briefly review some ecophysiological issues in the boreal zone; these issues affect the distribution of trees in the boreal zone and hemiboreal subzone, which in turn was considered in the development of the new map.

5. Ecophysiological issues in the boreal zone and hemiboreal subzone

Knowledge of the ecophysiological responses of a plant at its different life stages is vital to understanding the various factors affecting the plant's distribution (Kullman 1983; Woodward 1987). In general, a plant's tolerance to cold, and its heat, chilling, and moisture requirements play critical determining roles in where plants are found (Samish 1954; Walter 1973; Kramer and Kozlowski 1979; Woodward 1987; Prentice et al. 1992). I will review key causal factors and the physiological responses of trees at the forest–tundra, boreal–hemiboreal, and hemiboreal–temperate ecotones.

At the forest–tundra ecotone, *Picea glauca* and *Picea mariana* are two extremely winter hardy boreal species. The primordial shoot, needles, and tissues of the cortex and xylem of these two species can survive exposure to temperatures as low as –80 °C (Sakai and Weiser 1973; Sakai 1983). The ability to harden is primarily under genetic control but the degree of hardening can also be affected by the plants' health, their nutritional status, and the degree of development achieved during the growing season (e.g., reduced carbohydrate reserves because of a curtailed growth period) (Larcher and Bauer 1981). Woodward (1987) also suggests that growing season length is critical to tree survival at the tree limit, a view that is supported by data from Wardle (1968), Baig and Tranquillini (1976), Black and Bliss (1980), and Larcher and Bauer (1981). In the studies of Wardle (1968) and Baig and Tranquillini (1976), short and cool growing seasons did not allow needles to fully mature, rendering them susceptible to winter desiccation. At low temperatures, the photosynthetic production of many plants is inhibited by a reduction in the velocity of enzymatically catalyzed photosynthetic reactions, but boreal conifers can achieve up to 60% of their optimal CO_2 uptake at temperatures between 5 and 10 °C (Pisek 1973; Larcher and Bauer 1981). In a study of the reproductive ecology of *Picea mariana* at the tree limit near the Mackenzie River delta (physical features and communities identified in the text are depicted in Fig. 22) in northwestern Canada, temperatures <15 °C limited seed germination (Black and Bliss 1980). These temperatures were identified as the most important factor controlling the tree's distribution but other critical factors that had a negative impact included a short growing season, low annual precipitation (water stress in seedlings determined seedling survival), high wind abrasion, reduced germination of seeds and seed size because of poor growing conditions during cool summers, and rapid destruction of seeds in the soil (i.e., reductions in the seed bank) (Black and Bliss 1980). Reduced reproductive capacity of *Larix laricina*, *Picea glauca*, *Picea mariana*, and *Betula* spp. because of cold temperatures was observed near the tree limit in the Northwest Territories (Elliott 1979), northern Quebec (Sirois 2000), and Greenland (Sulkinoja 1990).

Picea mariana has an advantage over *Picea glauca* in that the former species maintains a relatively constant seed population that is not destroyed by fire, is little affected by the burn interval, and accumulates on the tree over a period of years (Black and Bliss 1980). *Picea mariana* is also able to regenerate vegetatively through layering (Black and Bliss 1980). *Picea glauca* relies on regeneration from seed, which is released annually; thus, it must seed over longer distances from survivors that have escaped the fire (Black and Bliss 1980).

The deciduous habit may also provide a competitive advantage at the tree limit because of reduced metabolic costs associated with the maintenance of evergreen needles and the risk of damage to overwintering needles (Schulze 1982; Hadley and Smith 1989; Gower and Richards 1990). Examples of this occur at the tree limit in some places in Eurasia as well as at the elevational tree limit on some mountains. This is generally not the case at the forest–tundra ecotone in North America, however, as *Larix laricina* rarely forms the tree limit, and, in the case of Greenland, only deciduous species occur because conifers were extirpated during the first widespread glaciation of the island (Ødum 2003).

At the boreal–hemiboreal ecotone, the boundary can be divided into broad geographical areas where either temperature or moisture acts as the primary limiting factor in the distribution of the characteristic tree species.

Temperatures in much of the North American boreal zone commonly fall to –40 °C or lower during winter (Brandt et al. 2004; McKenney et al. 2006). Plant cells exposed to freezing temperatures can die either from dehydration owing to extracellular freezing of water or from the formation of intracellular ice, which damages cell membranes (Levitt 1980; Ziegler and Kandler 1980). Plants can use three strategies to survive freezing: they can tolerate extracellular freezing; can avoid freezing by supercooling, or can undergo extraorgan freezing (Ishikawa and Sakai 1982; Sakai and Larcher 1987). Plants that use supercooling to tolerate low temperatures are restricted to areas where temperatures do not fall substantially below –40 °C (George et al. 1974, 1977, 1982; Burke et al. 1976; Becwar et al. 1981; George and Burke 1981). Boreal and alpine plants, which are the species most tolerant of low temperatures, survive extreme cold by tolerating extracellular freezing whereas many temperate species rely on supercooling (Becwar et al. 1981; George et al. 1982; DeHayes 1992; Zwiazek et al. 2001).

The freezing resistance of *Abies balsamea*, *Abies lasiocarpa*, *Larix laricina*, *Picea engelmanii*, *Picea glauca*, *Picea mariana*, *Pinus banksiana*, and *Pseudotsuga menziesii* was investigated by Sakai (1983). In this study, the primordial shoot, needle, cortex, and xylem of the more continental boreal *Pinus banksiana*, *Larix laricina*, *Picea glauca*, and *Picea mariana* were all equally frost hardy, surviving temperatures as low as –70 °C and immersion in liquid nitrogen after prefreezing to –40 °C. The next most hardy species was *Abies balsamea*, whose primordial shoot was hardy to temperatures of about –56 °C whereas its other tissues were hardy to –70 °C. The western cordilleran species *Abies lasiocarpa* and its common associate *Picea engelmanii* were about equally hardy, with the primordial shoot, needle, and xylem hardy to temperatures between about –44 °C and –54 °C. *Pseudotsuga menziesii* was the least hardy of the North American conifers tested, with its shoot and xylem tissues hardy to –30 °C and its cortex hardy to –40 °C. In both *Abies lasiocarpa* and *Picea engelmanii*, the limit of their cold hardiness suggests that these two species use supercooling to avoid freezing (Becwar et al. 1981; Sakai 1983). The frost hardiness of buds and needles of different species within the genera *Pinus* and *Larix* was also studied (Sakai 1983). Of the North America members of these two genera, *Pinus banksiana*, *Pinus contorta*, *Pinus strobus*, and *Larix laricina* were all equally hardy; *Pinus ponderosae* and *Larix occidentalis* were hardy only to –30 °C. The buds, needles, and xylem of *Pinus strobus* are as frost hardy as those of typical boreal tree species (George et al. 1974; Sakai 1983) but *Pinus strobus* is susceptible to winter desiccation (Sakai 1970, 1983). Thus, the range of *Pinus strobus* does not extend far northward into the typical boreal zone (Fig. 2). In Cupressaceae (e.g., *Thuja*), the shoot and flower primordia are encapsulated by a few green or brown bud scales in contrast to boreal conifers of Pinaceae that have 40 or more scales and resin covering the entire bud surface to counter winter desiccation (Sakai 1983).

Tissues of the boreal hardwoods, *Populus tremuloides* and *Betula papyrifera,* do not supercool (George et al. 1982; Gusta et al. 1983), unlike those of many temperate eastern deciduous hardwoods (e.g., *Acer saccharum*, *Betula alleghaniensis*, *Quercu rubra*), which use this method to avoid freezing (George et al. 1974, 1977, 1982; George and Burke 1981). *Quercus macrocarpa*, *Ulmus americanum*, *Fraxinus nigra*, and *Fraxinus pennsylvanica* are the most winter hardy of the eastern North American hardwoods and all are found farther north than the typical temperate hardwoods (George et al. 1974; Gusta et al. 1983). Gusta et al. (1983) speculate that there may be differences in the elasticity of these four species' cell walls or in properties of their plasma membranes or a combination thereof that allow them to survive lower temperatures. The distribution of *Acer saccharum*, *Betula alleghaniensis*, and *Quercus macrocarpa* is depicted in Fig. 3. The same cold hardiness relationships hold for eastern Eurasia (Sakai 1978) where the potential frost resistance of deciduous trees increases along a north-south climatic gradient from the subtropics to the boreal zone (Sakai and Larcher 1987). Although various organs and tissues of species of the cool-temperate zone are hardy to –30 °C, those of species of the boreal zone are hardy to –70 °C. Frost splitting may also be an important factor in determining the northern limit of certain tree species. The deciduous genera *Acer* and *Quercus* and some species of *Betula* are most susceptible to frost cracks, followed by *Fraxinus*, *Ostrya*, and *Ulmus*, whereas conifers and deciduous hardwoods native to interior Alaska, Canada, and eastern Siberia are able to withstand conditions that produce this defect in less hardy species (Sakai and Larcher 1987).

Another weather event that may play an important role in the distribution of tree species at the boreal–hemiboreal ecotone is the occurrence of late winter or early spring thaw–freeze cycles that have been linked to regional diebacks (Auclair et al. 1990, 1992, 1996; Pomerleau 1991; Bertrand et al. 1994; Braathe 1995; Cox and Malcolm 1997; Zhu et al. 2000; Bourque et al. 2005). Dieback events have been reported for *Betula alleghaniensis*, *Acer saccharum*, and *Picea rubens* in the hemiboreal subzone of eastern North America during the 20th century (Barter 1949; Canada Department of Agriculture 1953; Braathe 1957; Johnson et al. 1986; DeHayes 1992; Auclair et al. 1997). Dieback events in these species may be indicative of their susceptibility to unusual weather events at the northern limits of their ranges. *Betula alleghaniensis* and *Acer saccharum* help to define the northern limit of the hemiboreal subzone across much of the Great Lakes region whereas stands of *Picea rubens* are common in hemiboreal stands in eastern North America where it appears to have arrived relatively recently (Lindbladh et al. 2003). In *Betula*, thaw–freeze events can cause xylem cavitation and root damage, rendering roots incapable of generating the pressure necessary to refill the cavitated xylem (Cox and Malcolm 1997). During the thaw, tissues in *Betula* shoots and roots deharden, which predisposes the tissues to freezing when the temperature drops again (Cox and Zhu 2003). *Picea rubens* also dehardens during thaws but it is the foliage that is damaged during the refreeze (DeHayes 1992; Perkins et al. 1993; Perkins and Adams 1995; Strimbeck et al. 1995). In contrast, boreal *Abies balsamea* does not deharden under the same climatic conditions (DeHayes 1992; Strimbeck et al. 1995). Drought has also been suggested to be a factor in dieback (Johnson et al. 1986; Payette et al. 1996), but the dieback may be a response to drought stress in trees previously injured during thaw–freeze events (Auclair et al. 1996).

In the western Canadian interior, drought appears to be the critical factor affecting the distribution of trees in the transition from the boreal zone to the hemiboreal subzone and from the hemiboreal subzone to the grasslands. *Larix laricina*, *Picea glauca*, *Picea mariana*, and *Pinus banksiana* are common in the southern portion of the boreal zone of the Prairie Provinces. These species are gradually replaced by *Populus tremuloides* in the aspen parkland region and the conifers eventually disappear altogether (Zoltai 1975), except on azonal sites such as sheltered, north-facing slopes of river valleys. Mature *Picea glauca* is drought tolerant, demonstrated by the survival of planted trees in many areas of the Canadian Prairies (Hogg and Schwarz 1997). Natural regeneration of *Picea glauca*, however, is affected by drought as the species requires a period during which the soils remain moist (Hogg and Bernier 2005; Hogg and Wein 2005). *Populus tremuloides* has the ability to re-sprout from its roots if the above-ground stems are killed by drought. This may explain the tree's distribution farther south into the aspen parkland region (i.e., into the hemiboreal subzone) (Hogg 1994). There is also a close relationship between moisture availability and the boundaries of both the boreal zone and the aspen parkland in the Canadian interior (Hogg 1994). The southern limit of the boreal zone in this region corresponds closely with the zero isopleth of monthly mean precipitation minus monthly potential evapotranspiration; the southern limit of the aspen parkland corresponds with the –15 cm isopleth of the same index (Hogg 1994). Thermal characteristics of climate correspond poorly with regional vegetation boundaries (Hogg 1994). Conifers and hardwoods differ in that coniferous sapwood may be readily recharged with water after rain whereas the water-conducting column in hardwoods may be disrupted when water is unavailable, causing cavitation (Siau 1971). In conifers, only individual tracheids are affected by drought because bordered pits in the tracheid walls close in response to the pressure gradient created by a water deficit (Woodward 1987). This prevents gas bubbles from passing to other conducting elements and interrupting water transport (i.e., cavitation) (Woodward 1987). In *Populus tremuloides*, however, when the vapour pressure deficit increases, stomatal conductance is reduced (Dang et al. 1997; Hogg and Hurdle 1997; Hogg et al. 2000). This mechanism allows this drought-tolerant hardwood to maintain leaf and stem water potential above a critical threshold, thus avoiding xylem cavitation (Hogg et al. 2000; Frey et al. 2004). Thaw–freeze events can also induce cavitation but conifers appear to be resistant to this type of cavitation as well (Sperry and Sullivan 1992).

At the hemiboreal–temperate ecotone, unseasonably cold temperatures may also play a role in the distribution of several temperate tree species but there is limited evidence of this for the few species that have been investigated. The reproductive capacity of temperate species may be diminished by unseasonably cold temperatures. Frost resistance in the overwintering seeds of *Quercus rubra* is limited to temperatures above –15 °C (Sakai and Larcher 1987). The flowers of the European *Quercus robur* and the western North American *Pseudotsuga menziesii* are sensitive to frosts (Larcher and Bauer 1981; Timmis 1977). In Europe, the northern limit of *Tilia cordata* is controlled by low temperatures during flowering, when they restrict pollen-tube growth, and during summer, when they hinder seed development (Pigott and Huntley 1978, 1980, 1981). Late spring frosts during the growing season can have a dramatic negative impact on growth and can lead to mortality of susceptible species such as *Fagus grandifolia*, *Fraxinus americana*, *Prunus serotina*, *Pseudotsuga menziesii*, and *Quercus rubra* (Tryon and True 1966, 1968; Timmis 1977; Rast and Brisbin 1987; Reich and van der Kamp 1993).

In the western interior the location of the grassland – deciduous forest ecotone is generally attributable to climatic factors, with local variation controlled largely by edaphic factors, topography, fire, differential migration rates of some taxa, and survival of relicts in favourable habitats (Davis 1977; Hildebrand and Scott 1987). Drought appears to be the critical climatic factor affecting the distribution of trees in the transition from the hemiboreal subzone to the temperate grasslands (Hogg 1994).

6. Creation of a new map of the boreal zone

6.1. Vegetation zones defined

Five major bioclimatic zones have generally been recognized in the northern hemisphere: arctic, boreal, temperate, subtropical, and tropical. The latter two zones do not bound the boreal zone and will not be considered further. The ***arctic zone*** is defined primarily by the absence of trees, the occurrence of continuous permafrost, and the presence of tundra vegetation dominated by low-growing shrubs, herbaceous plants, mosses, and lichens (Walker et al. 2002). The tree limit is used by the latter researchers as the southern boundary of the arctic zone in their *Circumpolar Arctic Vegetation Map*. Unfortunately, Walker et al. (2002) do not list their sources for their boundary in North America or Eurasia.

The ***boreal zone*** is defined as the broad, circumpolar vegetation zone of high northern latitudes covered principally with forests and other wooded land consisting of cold-tolerant trees species primarily within the genera *Abies*, *Larix*, *Picea*, or *Pinus* but also *Populus* and *Betula*; the zone also includes lakes, rivers, and wetlands, and naturally treeless areas such as alpine areas on mountains, heathlands in areas influenced by oceanic climatic conditions, and some grasslands in drier areas. In North America, the boreal zone can be divided into either two or three sub-zones on the basis of the vegetation: the forest-tundra (or subarctic or hemiarctic) at the north; the continuous boreal forest (consisting of closed forests, and open forests or woodlands) generally occupying the mid portion, and the hemiboreal (or sub-boreal) at the south. Like Walker et al. (2002), the tree limit defines the northern boundary of the forest-tundra. The continuous boreal forest subzone is defined by the dominance of closed and open forests consisting of cold-tolerant trees species (i.e., tolerant of temperatures of –80 °C or lower, Table 2) primarily within the genera *Abies*, *Larix*, *Picea*, or *Pinus* but also *Populus* and *Betula*. Although other features such as podzolic soils, surplus moisture leading to runoff in rivers and creeks, stable lake levels, the formation of wetlands or peatlands, and permafrost are also considered to have some diagnostic utility for parts or all of the boreal zone (Sjörs 1963; Ahti et al. 1968; Walter 1973; Hogg 1994; Hogg and Bernier 2005), these are not considered in this paper. The ***hemiboreal subzone*** is defined by the co-occurrence of cold-intolerant tree species, cold-tolerant tree species, and species with intermediate cold-tolerance, with the cold-tolerant species contributing substantially to the forest cover. Although I concur with many other North American scientists who do not distinguish a hemiboreal subzone lying south of the continuous boreal forest subzone because of the occurrence of many temperate deciduous tree species in the subzone, I have mapped the former subzone to determine its areal extent in the second half of this paper. The reader is given the choice whether to include the subzone, as some Europeans do, or exclude it from the map of the North American boreal zone. The ***temperate zone*** is defined by the dominance on most sites of tree species intolerant of

Table 2. Lowest temperature (°C) withstood without injury by selected North American trees (adapted from White and Weiser 1964; Sakai 1970; Sakai and Weiser 1973; George et al. 1974; DeHayes et al. 1990; DeHayes 1992; Silim and Lavender 1994).

Species	Bud	Cortex	Leaf	Xylem	Susceptibility to winter desiccation
Cold tolerant					
Abies balsamea	–80	–80	–80	–80	na
*Betula papyrifer*a	–80	–80	–	–80	na
Fraxinus nigra	na	na	–	below –54	na
Larix laricina	–80	–80	–	–80	na
Picea glauca	–80	–80	–80	–80	low
Picea mariana	–80	–80	–80	–80	low
Pinus banksiana	–80	–80	–80	–80	low
Pinus contorta var. *latifolia*	–80	–80	–80	–80	moderate
Pinus resinosa	–80	–80	–80	–80	na
Populus tremuloides	–80	–80	–	–80	na
Populus balsamifera	–80	–80	–	–80	na
Ulmus americana	–80	–80	–	below –54	na
Intermediate cold tolerance					
Abies lasiocarpa	–40	–80	–80	–80	mod. low
Picea engelmanii	–60	–70	–70	–70	moderate
Picea rubens	na	na	–57	na	low
Pinus strobus	–80	–80	–80	–80	high
Quercus macrocarpa	–60	–60	–	–46	na
Thuja occidentalis	–80	–80	–80	–80	high
Tsuga canadensis	–60	–60	–60	–60	na
Cold intolerant					
Abies amabilis	–20	–40	–30	–40	na
Acer saccharum	–80	–80	–	–43	na
Acer rubrum	–30	–30	–	below –54	na
Betula alleghaniensis	na	na	–	–45	na
Fraxinus pennsylvanica	–40	–70	–	–54	na
Larix occidentalis	–40	–50	–	–50	na
Picea sitchensis	–30	–60	–40	–60	na
Pinus ponderosa	–35	–50	–40	–50	na
Pseudotsuga menziesii var. *glauca*	–30	–40	–40	–40	na
Quercus rubra	na	below –70	–	–40	na
Thuja plicata	–30	–40	–30	–40	na
Tsuga heterophylla	–20	–20	–20	–20	na
Tsuga mertensiana	–25	–20	–20	–20	na

Note: na, not available; –, not applicable.

extremely cold winter temperatures (i.e., they require temperatures above –45 °C to survive; see Table 2). The interior of both continents is arid and no temperate forests exist in the latitudinal belt to the south of the boreal zone where they would exist if temperature were the only critical factor governing their presence. Instead, the temperate zone in continental situations is occupied by grasslands, whose occurrence is dictated more by drought (moisture availability). The hemiboreal subzone in the continental interior consists of grasslands interspersed with drought-tolerant hardwoods, mainly *Populus tremuloides* but also some *Quercus macrocarpa*.

6.2. Source maps and approach

The maps of North America's boreal zone and its forests were scanned, digitized, and converted to GIS coverages. Maps by Rowe (1972), Marschner (1974), Finley (1976), EWG (1989), Comer et al. (1995*b*), ESWG (1995), Saucier et al. (1998), FAO (2001), Olson et al. (2001), Natural Regions Committee (NRC 2006), and BCMFR (2006) were available as GIS files. Other maps, listed later in this paper in the regional descriptions, were consulted but were not digitized because (*i*) these maps had insufficient or inadequate control points to properly geo-reference them for GIS input; (*ii*) they lacked sufficient detail to warrant digitization; (*iii*) they were of the same pedigree as an acceptable existing map; (*iv*) they were superceded by a more recent map; or (*v*) they were adjacent to but outside the boreal zone. All coverages were converted to the same projection and datum.

The GIS was used to view and compare the boundaries of the 32 maps of the boreal zone. Table 3 summarizes various aspects of these maps including scale, the methods and materials used to create them, and the criteria used by the au-

Table 3. Summary information on maps referenced in the delineation of the boreal zone in various regions of North America. Maps are listed by author in chronological order.

Map and scale	General subject and areal extent	Terminology used for zones, subzones, regions, cover types, etc.	Synopsis of methods and materials	Criteria used for delineation
Shantz and Zon (1936) 1:8 000 000	Natural vegetation types of the US	Spruce-fir; jack, red, and white pines; birch-beech-maple-hemlock; oak; etc.	Not described	Vegetation types
Cunningham and White (1941) 1:1 778 000	Forest types of northern Michigan	Pine; spruce-fir; hardwood; conifer swamp; etc	Forest inventory based on transects 16 km apart	Forest types
Braun (1950) 1:5 517 000	Forest regions and sections of the eastern US	Hemlock-white pine-northern hardwoods region; maple-basswood forest region; beech-maple forest region; mixed mesophytic forest region; etc.	Not described. However, Braun does note that she used Halliday's (Halliday 1937) boreal forest boundary.	Forest types
Moss (1952) 1:4 800 000	Parkland and grassland vegetation of northern Alberta	Parkland vegetation on dark soils	Reconnaissance combined with a limited number of detailed ground surveys.	Vegetation and soil types
Hare (1959) 1:3 721 000	Vegetation zones of northern Quebec and Labrador	Forest; lichen-dominated tundra; sedge-dominated tundra; forest-tundra; woodland	Reduced from a series of 1:500 000 sketch maps based on interpretation of 1:40 000 or 1:60 000 air photographs.	Vegetation cover types and land forms
Bird (1961) 1:5 473 000	Aspen parkland of the Canadian prairie provinces	Aspen parkland	Ground surveys and input from provincial forestry officers	Southern boundary based on distribution of aspen groves; northern boundary based on the southern limits of spruce and jack pine.
Sjörs (1963) 1:29 556 000	Vegetation zones of northeast North America	Arctic zone; boreal zone; boreo-nemoral zone; nemoral zone; woodland steppe zone; etc.	Not described	Forest types
Semenova-Tyan-Shanskaya (1964) 1:20 000 000	Vegetation types of North America	Arctic type vegetation; boreal type vegetation, within which there are 13 different zones; nemoral type vegetation, within which there are 10 different zones; etc.	Not described	Vegetation types
Janssen (1967) 1:40 000 000	Major vegetation formations of Minnesota and adjacent areas	Boreal forest; aspen parkland; coniferous-deciduous forest; deciduous forest; prairie.	Not described	Forest types
Little (1971) 1:26 667 000	Distribution maps of conifers and important hardwoods in North America	Not applicable	Redrawn from working maps and other maps based on ground surveys and locality information from herbarium specimens.	Geographical area where individual species occur naturally, exclusive of changes resulting directly or indirectly from the actions of humans since the European settlement of North America.
Arno and Habeck (1972) 1:5 161 000	Natural distribution of alpine larch	Not applicable	Not described	Not described

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Table 3 (*continued*).

Map and scale	General subject and areal extent	Terminology used for zones, subzones, regions, cover types, etc.	Synopsis of methods and materials	Criteria used for delineation
Rowe (1972) 1:6 336 000	Forest regions in Canada	Boreal forest region; Great Lakes-St. Lawrence forest region; Acadian forest region; subalpine forest region; montane forest region; deciduous forest region; Columbia forest region; coast forest region.	Minor revision of Rowe (1959), which was revised from Halliday (1937). The 1959 version was drawn by W.G.E. Brown with regional input from many scientists and forestry officers.	Forest region conceived as a major geographic belt or zone, characterized vegetationally by a broad uniformity both in physiognomy and in the composition of the dominant tree species.
Viereck and Little (1972) 1:5 000 000	Vegetation types of Alaska	Closed spruce-hardwood forest; open low growing spruce forests; treeless bogs; coastal spruce-hemlock forests; etc.	Compiled by senior author based on information from five previously published maps, most notably the map of Spetzman (1963), as well as personal observations and experiences.	Vegetation types
Marschner (1974) 1:500 000	Original vegetation of Minnesota	Grassland; brushland; hardwood forest; pineries; bogs and swamps. Within each of these broad categories there are several vegetation types.	Compiled in 1930 by Marschner using US General Land Office notes, descriptions, and maps from the original land surveys completed between 1850 and 1905.	Vegetation types
Zoltai (1975) 1:3 030 000	Southern limit of conifers on the Canadian prairies	Limits of white spruce, black spruce, tamarack, jack pine, and lodgepole pine, and the parkland–boreal transitional zone	Vehicle survey using existing roads 6.5 km apart as transects across the region.	Presence of individual conifers; presence of at least one coniferous species for the parkland–boreal transitional zone.
Finley (1976) 1:500 000	Original vegetation of Wisconsin	Boreal forest; mixed coniferous-deciduous forest; deciduous forest; grassland and brush; and wetland vegetation. Within each of these broad categories there are several vegetation types.	Compiled using US General Land Office notes, descriptions, and maps from the original land surveys completed between 1832 and 1866.	Vegetation types
Oswald and Senyk (1977) 1:2 500 000	Ecoregions of the Yukon Territory	Twenty-two ecoregions are described.	Landsat imagery, aerial photography, aerial surveys, ground surveys, and existing physiographic, climatic, and geological maps	Presence or absence of tree species, the occurrence and surface expression of permafrost, and topography.
Archibold and Wilson (1980) 1:4 444 000	Vegetation zones of southern Saskatchewan	Transitional forest; aspen parkland; grassland	Township-level classification using 1:80 000 aerial photography; transitional forest boundary based on Zoltai (1975).	Townships classified as aspen parkland based on the presence of at least 2–3 aspen groves in each section (2.59 km^2).

Table 3 (*continued*).

Map and scale	General subject and areal extent	Terminology used for zones, subzones, regions, cover types, etc.	Synopsis of methods and materials	Criteria used for delineation
Payette (1983) 1:8 696 000	Vegetation zones of northern Quebec and Labrador	Tundra; forest tundra; boreal forest	Transects along meridians and at each 30' between meridians where complex vegetation patterns occurred; also used aerial photography, aerial surveys, and ground surveys. Mapping based on the spatial distribution of tree species and coniferous formations defined on a structural or physiognomic basis.	Boreal forest corresponds with closed forests and open woodlands growing on mesic and xeric sites in valleys and on hills. Forest-tundra contains natural openings in the forest cover and stunted trees are characteristic features of these sites; these were used as diagnostic criteria. Northern limit of forest-tundra corresponds to trees with an upright form and a height of ≥5 m.
Feilberg (1984) 1:5 000 000	Vegetation zones of southern Greenland	Arctic zone; subarctic zone.	Not described explicitly but it appears the map was developed by overlaying distribution maps of critical species. Distribution maps were based on locality data and ground surveys.	Subarctic zone corresponded with occurrence of *Betula pubescenes* and *Salix* copses as well as *Sorbus groenlandica*, *Elocharis quinqueflora*, and *Sagina nodosa*.
Tuhkanen (1984) 1:47 619 000	Circumboreal climatic-phytogeographical zones	Arctic zone; hemiarctic zone; boreal zone (including northern boreal, middle boreal, southern boreal, and hemiboreal subzones); temperate zone.	Correlated threshold values of several climatic indices with subzones described by Ahti et al. (1968) for northwestern Europe. Threshold values were then applied globally using climate data from about 2000 meteorological stations to delimit boundaries of zones and subzones. Tuhkanen's method of data interpolation between meteorological stations and his cartographic method for applying lines to his map are unclear.	Threshold values of climatic indices: biotemperature, potential evapotranspiration, effective temperature sum, and length of the growing season.
Kingsley (1985) 1:8 089 000	Forest types of northeastern US	Spruce-fir; white-red pine-hemlock; maple-beech-birch; aspen-birch; etc.	Developed from forest types compiled as part of the most recent forest inventory and analysis.	Forest types
Timoney (1988) 1:5 847 000	Forest-tundra vegetation of the Northwest Territories and northern Manitoba	Tree:upland tundra cover ratios	Aerial photography at 1:50 000 to 1:70 000 taken between 1950 and 1980 covering 24% of the study area; ground truthing followed. Cover data input into mapping software to generate grid matrices, from which contour maps were drawn that depict percentage cover.	Northern limit of forest-tundra corresponds with the northern limit of trees ≥3–4 m (>0.1% cover or a ratio of tree:upland tundra cover of 1:1000). Southern limit of forest tundra corresponds to a ratio of tree:upland tundra cover of 1000:1.

Table 3 (*continued*).

Map and scale	General subject and areal extent	Terminology used for zones, subzones, regions, cover types, etc.	Synopsis of methods and materials	Criteria used for delineation
EWG (1989) 1:7 500 000	Ecoclimatic regions of Canada	Ten ecoclimatic provinces (e.g., arctic, subarctic, boreal, cool temperate, subarctic cordilleran, etc.) and 73 ecoclimatic regions (e.g., high subarctic, Atlantic high boreal, perhumid mid-boreal, etc.)	A hierarchical system with two levels developed by the Ecoregions Working Group, composed of various federal, provincial, and territorial government departmental representatives.	Ecoclimatic regions are broad areas characterized by distinctive ecological responses to climate, as expressed by vegetation and reflected in soils, wildlife, and water. Ecoclimatic provinces identify broad areas that show similarities on a much more general level. Vegetation development shows greater affinities within a province than between neighbouring provinces.
Godman et al. (1990) 1:22 222 000	Distribution of *Acer saccharum* in North America	Not applicable	Not described explicitly but it appears the map was modified from the map for the same species from Little (1971).	Not described
Comer et al. (1995*a*, 1995*b*) Digital data	Original vegetation of Michigan	Spruce and fir; jack pine; lowland conifer; aspen and birch; white, red, and jack pine; maple, beech, and birch; etc.	Compiled using US General Land Office notes, descriptions, and maps from the original land surveys completed between 1816 and 1856.	Vegetation types
ESWG (1995) 1:7 500 000	Terrestrial ecozones and ecoregions of Canada	Fifteen ecozones (e.g., taiga plains, taiga shield, boreal cordillera, boreal plains, boreal shield, Atlantic maritime, etc.) and 217 ecoregions	A hierarchical system with three levels (ecozones, ecoregions, and ecodistricts, with the latter not included in the map) developed by the Ecological Stratification Working Group. Various federal, provincial, and territorial government agencies as well as environmental interest groups and the private sector were consulted during development. Other published map resources were also used.	Ecozones are areas representative of large and generalized ecological units characterized by interactive and adjusting abiotic and biotic factors. Ecoregions are areas characterized by distinctive regional ecological factors, including climatic, physiography, vegetation, soil, water, fauna, and land use.
Saucier et al. (1998) Digital data 1:250 000	Ecological regions of Quebec	Three vegetation zones (e.g., northern temperate, boreal, arctic), six vegetation subzones (e.g., deciduous forest, mixed forest, continuous boreal forest, taiga, forest tundra, low-arctic), ten bioclimatic domains, etc.	A hierarchical system with 11 levels whose cartographic boundaries match. Each level is defined by a set of ecological factors. Boundaries are based on ecological plots, forest inventory plots, data analysis, elevation data, and other existing maps.	Criteria varied with different levels. For example, a vegetation zone is characterized by the physiognomy of the plant formations reflecting major climatic differences (i.e., the tree limit marks the boundary between the boreal and arctic zones).

Table 3 (*continued*).

Map and scale	General subject and areal extent	Terminology used for zones, subzones, regions, cover types, etc.	Synopsis of methods and materials	Criteria used for delineation
FAO (2001) Digital data intended to be used at a scale of 1:40 000 000 (data for Canada derived from ESWG (1995)	Ecological zones of the world	Five domains (e.g., polar, boreal, temperate, etc.) and 20 ecological zones (e.g., boreal coniferous forest, boreal tundra woodland, boreal mountain systems, etc.)	A hierarchical system developed by FAO in cooperation with various agencies and governments. Whenever possible, the system used existing data to generate boundaries depicted in the map. For example, boundaries of the various ecological zones in Canada are based largely on the ecozone and ecoregion boundaries of ESWG (1995).	Criteria varied with different domains and ecological zones. For the boreal domain, the area required temperatures higher than 10 °C for up to 3 months. For the boreal ecological zones, the intended criteria were based on vegetation physiognomy or elevation. However, the actual criteria used were dependent on the criteria of the existing map system. In the case of Canada, the criteria used were those of ESWG (1995).
Olson et al. (2001) Digital data	Terrestrial ecoregions of the world	Nine realms (e.g., nearctic, palearctic, etc.), 14 biomes (e.g., boreal forests – taiga, temperate coniferous forests, temperate broadleaf and mixed forests, temperate grasslands, savannas, and shrublands, etc.), and 867 ecoregions	A hierarchical system with three levels (realms, biomes, ecoregions). The system used published regional biogeographic classification schemes. Data and consultations from regional experts were important in final delineations. For example, boundaries of the various biomes in Canada are based largely on the ecozone and ecoregion boundaries of ESWG (1995).	Criteria used were dependent on the criteria of the existing classification scheme. For Canada, the criteria used were those of ESWG (1995).
BCMFR (2006) Digital data. Scales vary from 1:20 000 to 1:600 000.	Biogeoclimatic ecosystem classification of British Columbia	Fourteen biogeoclimatic zones (e.g., boreal white and black spruce, subboreal spruce, sub-boreal pine, spruce-willow-birch, etc.) each of which has several subzones	A hierarchical system developed by the B.C. Ministry of Forests and Range on the basis of ideas and work of V.J. Krajina and his students. Biogeoclimatic units are the result of climatic classification and represent classes of ecosystems under the influence of the same regional climate. The biogeoclimatic subzone is the basic unit. Subzones are grouped into zones, regions, and formations, and divided into variants. A biogeoclimatic subzone has a distinct climax plant association on zonal sites. Boundaries are based on plot sampling, data analysis, ground and aerial surveys, and elevation data. The map is a work in progress and scale varies in different parts of the province.	Criteria based on climate, vegetation, and site characteristics. Vegetation of mature ecosystems is emphasized because it is considered the best integrator of the combined influence of the environmental factors affecting a site.

Table 3 (*concluded*).

Map and scale	General subject and areal extent	Terminology used for zones, subzones, regions, cover types, etc.	Synopsis of methods and materials	Criteria used for delineation
NRC (2006) Digital data at 1:250 000	Natural regions and subregions of Alberta	Six natural regions (e.g., boreal forest, parkland, foothills, Rocky Mountain, etc.) and 21 subregions (e.g., lower boreal highlands, upper boreal highlands, subalpine, montane, etc.)	A hierarchical system developed by the Natural Regions Committee. The committee used a GIS to overlay climate, soil, vegetation, wetland distribution, elevation and remote sensing data to delineate boundaries. Input was also received from government, industry, and academia as well as previously published classification schemes. Inconsistencies, anomalies, and conflicts were resolved with personal knowledge and additional ground surveys.	Not explicitly described. Although several sources of data were used, the critical factor or factors used for delineation were dependent on the natural region or subregion (e.g., elevation and vegetation in the subalpine natural subregion or soils in the parkland natural region).

Note: EWG, Ecoregions Working Group; ESWG, Ecological Stratification Working Group; FAO, Food and Agriculture Organization; BCMFR, British Columbia Ministry of Forests and Range; NRC, Natural Regions Committee.

thors of the maps to delineate boundaries. To develop a revised map of the North American boreal zone and the hemiboreal subzone using consistent criteria and the most current information, I used the map of Rowe (1972) for Canada and the map of Viereck and Little (1972) for Alaska as a starting point because these two maps are generally perceived as being accurate for the scale at which they are depicted and they are still widely used in the scientific literature even though they are 37 years old. One of the limitations of both maps that is not widely recognized or acknowledged is that the authors describe only briefly the materials and methods they used to compile their maps (Table 3). Thus, I replaced an ecotone boundary depicted on the older maps with a boundary depicted by a more recent study when (*i*) the more recent study used a criterion the same as or similar to a criterion used in the present paper, and (*ii*) the more recent study provided a thorough description of materials and methods that should allow repeatable results. Two examples of studies that meet both of these conditions are those of Timoney (1988) and Payette (1983). In some situations the scale or resolution of data also became a factor; I gave preference to maps at larger scales and data of higher resolution. For boundaries for which a more recent study was not found and for which other data were not readily available, the default boundary was that of either Rowe (1972) or Viereck and Little (1972). The hemiboreal subzone is mapped by neither Rowe (1972) nor Viereck and Little (1972). For this subzone, boundaries were selected from studies compatible with this paper's definition and meeting the two conditions listed above. Table 4 lists the maps that were viewed in the GIS for each boundary and region considered in this paper. There were maps and studies in addition to those reviewed in the present paper that the reader might find useful to learn more about the distribution of vegetation and ecological conditions in particular regions. These are listed by region in Appendix B.

There are problematic areas that defy classification on the basis of the definitions and criteria used in this paper. These include treeless coastal areas and islands, mountain areas that result in belts of vegetation, and outliers of distinct vegetation found at different elevations than the surrounding areas. Coastal areas and islands covered with heaths (i.e., treeless), having cool climates moderated by the ocean (i.e., eastern Labrador, parts of Newfoundland, the Aleutians), and lying adjacent to the boreal zone are placed within the boreal zone (Meades 1983; Yurtsev 1994; Talbot et al. 2006). Belts of vegetation in mountain areas have traditionally been classified as montane, subalpine, or alpine. In this paper, assignment of mountain areas adheres to the following rules to the extent possible given the available data. (*i*) If the lowest elevations of the valley fall within the boreal zone, then forests at higher elevation are also in the boreal zone; areas above the tree limit are classified as alpine but within the boreal zone. Thus, areal statistics for the boreal zone include treeless, alpine areas but the statistics for these alpine areas are reported separately (like water, see Table 6). (*ii*) If the lowest elevations of the valley fall within the hemiboreal subzone, then forests at higher elevation consisting of cold-tolerant species are placed in the boreal zone, otherwise (i.e., forests consisting of species of intermediate cold-tolerance) they are classi-

Table 4. Maps referenced in the delineation of the boreal zone in various regions of North America for the three ecotones considered in this paper. Maps are listed in chronological order.

	Forest–tundra ecotone					Boreal–hemiboreal ecotone			Hemiboreal–temperate ecotone		
	Greenland	Northern Labrador and Quebec	North-western Canada	Yukon Territory and Mackenzie Mountains	Alaska	Atlantic Maritimes and Great Lakes	Western interior	Western cordillera	Atlantic Maritimes, NE US, and Great Lakes	Western interior parkland	Western cordillera
Shantz and Zon (1936)									X		
Cunningham and White (1941)									X		
Braun (1950)						X	X		X		
Moss (1952)							X			X	
Hare (1959)		X									
Bird (1961)							X			X	
Sjörs 1963)		X				X			X		
Semenova-Tyan-Shanskaya (1964)		X	X	X	X	X	X	X	X	X	X
Janssen (1967)							X		X	X	
Little (1971)											X
Arno and Habeck (1972)											X
Rowe (1972)		X	X	X		X	X	X	X	X	X
Viereck and Little (1972)					X						
Marschner (1974)						X			X		
Zoltai (1975)							X				
Finley (1976)						X			X		
Oswald and Senyk (1977)				X							
Archibold and Wilson (1980)							X			X	
Payette (1983)		X									
Feilberg (1984)	X										
Tuhkanen (1984)	X	X	X	X	X	X	X	X	X	X	X
Kingsley (1985)									X		
Timoney (1988)			X								
EWG (1989)		X	X	X		X	X	X	X	X	X
Godman et al. (1990)						X					
Comer et al. (1995*b*)						X			X		
ESWG (1995)		X	X	X		X	X	X	X	X	X
Saucier et al. (1998)		X				X			X		
FAO (2001)		X	X	X	X	X	X	X	X	X	X
Olson et al. (2001)		X	X	X	X	X	X	X	X	X	X
BCMFR (2006)								X			X
NRC (2006)							X	X		X	X

fied as hemiboreal. Areas above the tree limit are treated as alpine; these alpine areas are included in the boreal zone when forests immediately below these areas are classified as boreal, or are included in the hemiboreal subzone when the forests immediately below these areas are classified as hemiboreal. (*iii*) If the lowest elevations of the valley fall within the temperate zone, then forests at higher elevation are classified as being in the hemiboreal subzone if they consist of species of intermediate cold-tolerance and are contiguous with the hemiboreal subzone. If they are not contiguous with forests classified as being in the hemiboreal zone then they are considered montane or subalpine subzones or belts of the temperate zone. Areas above the tree limit are treated as alpine; these alpine areas are included in the hemiboreal subzone when the forests immediately below these areas are classified as hemiboreal. In British Columbia, there are several outlying areas of vegetation usually lying in isolated valleys that are distinct from the surrounding vegetation; these outliers are included in the same zone or subzone as the surrounding vegetation. For example, there are valleys covering a relatively small area with temperate species (i.e., *Thuja plicata* and *Tsuga heterophylla*) in northwestern British Columbia east of Skagway, Alaska, that are included in the boreal zone. Other outliers in non-mountainous terrain found at different elevations and with vegetation distinct from surrounding areas are treated similarly; these outliers are also included in the zone or subzone of the surrounding areas. Examples include the Cypress Hills in southern Alberta and Saskatchewan, which is placed in the temperate zone, and the Spruce Woods in Manitoba, which is placed in the hemiboreal subzone.

6.3. Locating ecotones

6.3.1. Arctic – forest–tundra ecotone

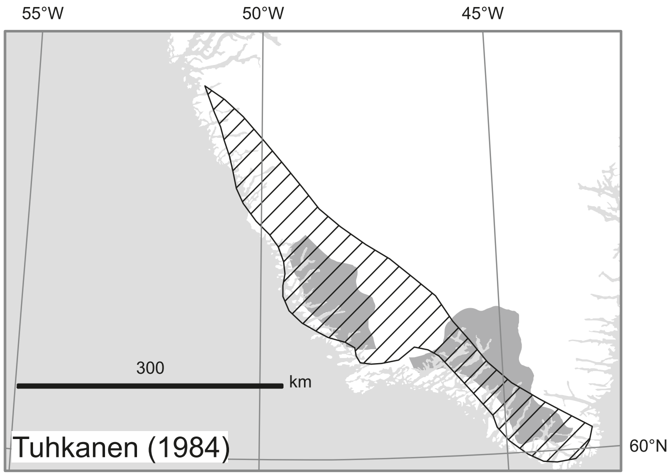
The forest-tundra ecotone is a transitional area between the continuous forests of the boreal zone and the tundra of the arctic zone. The northern tree limit is generally considered to be the boundary between the boreal and arctic zones and is the criterion used in this paper as the boreal zone's northern boundary. There is another tree limit, which will be treated separately within the framework of this paper; it occurs between the subalpine belt and the alpine belt on mountains, and its elevation approaches the elevation of the northern tree limit poleward for any given longitude (Lamb 1985). Alpine areas within the limits of the boreal zone across North America as defined in this paper were also mapped to the extent possible with existing data so that areal statistics on these areas could be reported as well. The northern and elevational tree limits represent the same processes: a cooling of climate resulting in conditions unfavourable for tree growth, reproduction, and survival (Ahti et al. 1968; Löve 1970; Tuhkanen 1984). Climatic conditions along the northern tree limit or at the elevational tree limit, however, are not necessarily the same along their length and the cold tolerances of the various species making up the tree limit at these locations may be different (Hämet-Ahti 1979; Tuhkanen 1984; Sakai and Larcher 1987). A problem with trying to map the northern tree limit with various isotherms and climatic indices is that they are interpolated abstractions, which may vary latitudinally over several hundreds of kilometres from year to year (Hustich 1966; Tuhkanen 1980). Climate also varies at centennial and millenial scales. The effect of these variations is reflected in the tree limit. In northwestern and northeastern Canada the tree limit has receded as the climate has cooled since its mid-Holocene temperature maximum (Ritchie 1987). More recently, since the end of the Little Ice Age (ca. 1850) it appears that the tree limit has advanced up mountain slopes and northward at the forest-tundra ecotone in response to climate amelioration (Lescop-Sinclair and Payette 1995; Scott et al. 1987*a*; Kullman 1986). Fire and its interactions with climate can also have a dramatic effect on the forest-tundra ecotone through deforestation (Hustich 1966; Zoltai and Pettapiece 1973; Payette 1983; Payette and Gagnon 1985; Filion et al. 1991; Payette et al. 2001; Heikkinen et al. 2002; Karlsson et al. 2007). Humans have caused considerable local deforestation at the tree limit near settlements in North America and Europe (Ritchie 1960; Hustich 1966; Ball 1987; Kullman 1979; Tuhkanen 1980; Karlsson et al. 2007). Insect defoliators have been important at the tree limit in Scandinavia (Seppälä and Rastas 1980; Heikkinen et al. 2002) but no pests are known to cause significant mortality at the forest-tundra ecotone in North America. All of the factors listed above contribute to a tree limit that is stable neither in time nor in space in North America and Eurasia.

The tree species at the forest-tundra ecotone vary across North America. They are *Betula pubescens* ssp. *tortuosa* and *Sorbus groenlandica* in Greenland, predominantly *Picea mariana* but also *Larix laricina* and *Picea glauca* in northern Canada, and *Picea glauca* in Alaska (Hustich 1966; Black and Bliss 1980; Tuhkanen 1980; Payette 1983; Scott et al. 1987*b*). There are several locations where small groups of small *Populus balsamifera* occur north of the general tree limit of the forest-tundra ecotone, most notably in Labrador (Elliot and Short 1979; Payette 1983), the Northwest Territories (Ritchie 1987), and Alaska (Viereck and Little 1975).

6.3.1.1. Boundaries

6.3.1.1.1. Greenland — The boundary of Feilberg's (Feilberg 1984) subarctic zone (for consistency I have used lower case letters for all names of zones, subzones, vegetation types, etc. of other authors) was used as the boundary of the forest-tundra ecotone in Greenland (Fig. 5) for three reasons. First, Feilberg's definition of his subarctic zone meets this paper's criterion for the forest-tundra ecotone (Table 3). Second, Feilberg's boundary provides greater resolution than the only other map of the region (i.e., that of Tuhkanen 1984). Finally, he provides a thorough description of his methods (Table 3). Feilberg's placement of southwestern Greenland in the boreal zone is in agreement with Böcher (1963, 1979), Hämet-Ahti and Ahti (1969), Hämet-Ahti (1981), Tuhkanen (1984), and Yurtsev (1994). The native vegetation of southwestern Greenland consists of *Betula pubescens*, *Alnus crispa*, and *Sorbus groenlandica*, as well as several boreal forest-floor species including *Copti trifolia*, *Pyrola minor*, *Orthilia secunda* ssp. *obtusata*, *Linnaea borealis* ssp. *americana*, and *Ledum groenlandicum* (Böcher 1963, 1979; Ødum 2003).

Fig. 5. Boreal zone adapted from Feilberg (1984) in southern Greenland and Tuhkanen's (1984) hemiarctic subzone (diagonal hatching).

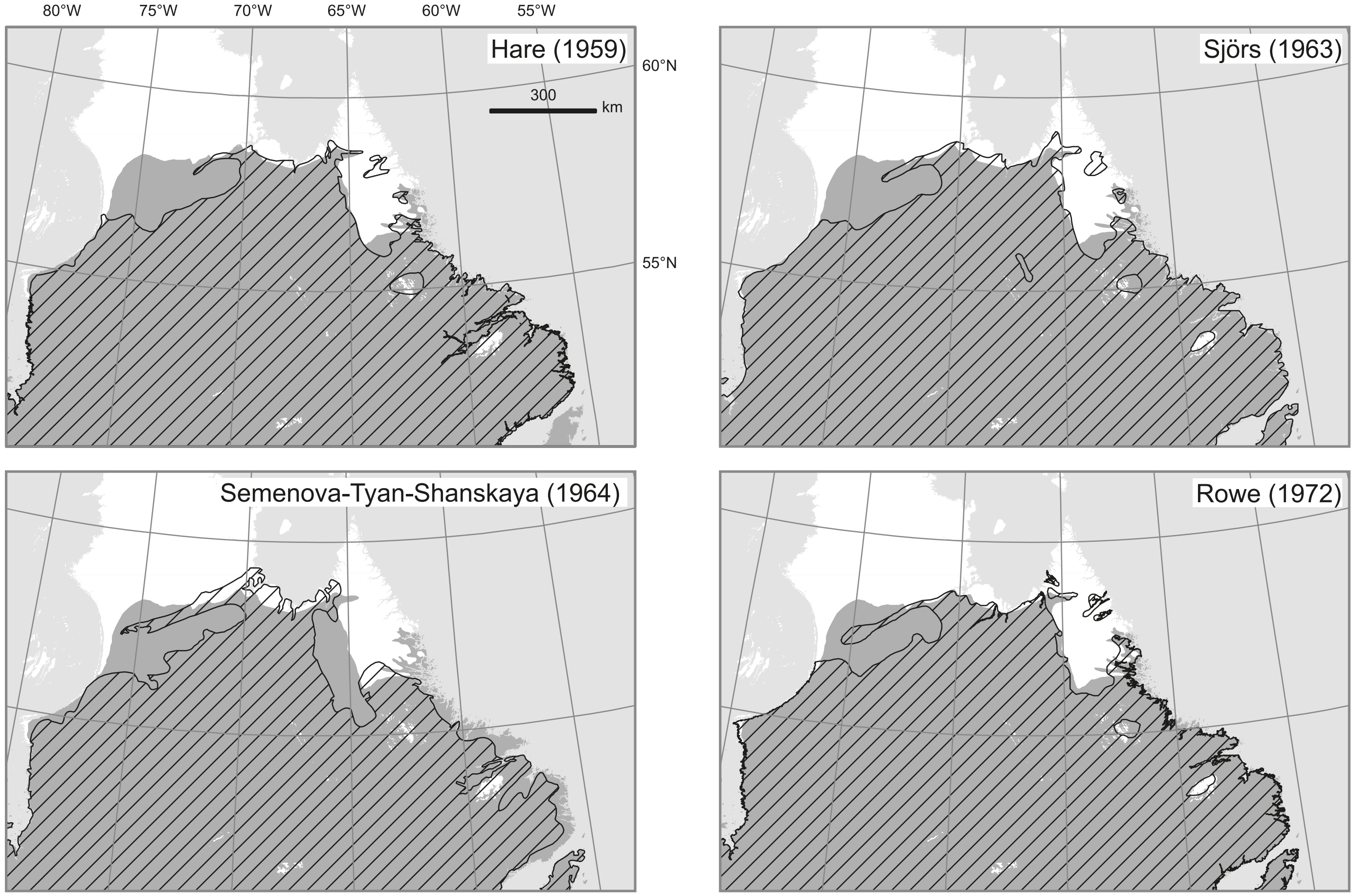


Trees 4–7 m high with stem diameters up to 20 cm are confined to protected valleys (Böcher 1979; Ødum 2001). Norse settlement and animal husbandry have had a large impact on the native vegetation (Böcher 1979; Fredskild and Ødum 1990; Aas and Faarlund 2001; Ødum 2003). In addition to the native boreal species, several non-native tree species have been grown successfully in the region for over 100 years (Ødum 1979, 2001, 2003), providing supporting evidence for the region's placement in the boreal zone rather than in the arctic zone. The best adapted species include *Larix sibirica*, *Abies lasiocarpa*, *Picea engelmannii*, *Pinus pumila*, *Picea abies*, *Pinus sylvestris*, and *Picea glauca* and its hybrids with *Picea engelmannii* and *Picea sitchensis*. I am unaware of any literature that indicates whether or not these tree species have reproduced naturally at any of these sites.

6.3.1.1.2. Northern Labrador and Quebec — The northern tree limit mapped by Payette (1983) was used as the northern boundary of the boreal zone in northern Labrador in the present paper (Fig. 6) and that of Saucier et al. (1998), which was adapted from Gerardin (1980), Richard (1987), Lavoie and Payette (1994), and Grondin et al. (1996), was used in Quebec. However, when the boundary of Saucier et al. (1998) is compared with that of Payette (1983) it is apparent that the former authors have largely used Payette's (Payette 1983) boundary for much of northern Quebec from Hudson Bay to Ungava Bay (Fig. 7). The major difference is that Saucier et al. (1998) have included in their forest-tundra the area on the plateau surrounding Lake Nedlouc (Plateau du Lac Nedlouc), which Payette (1983) classifies as "tundra-forest tundra"on his map. Grondin et al. (1996) also includes this plateau in the forest-tundra of the boreal zone. The boundaries of Payette (1983) and Saucier et al. (1998) were chosen because these researchers used the same criterion as the present paper. Payette's methods are also well-described and repeatable (Table 3). He used transects along meridians at 30-min intervals and along parallels near Hudson Bay, aerial photography, and aerial surveys to map the tree limit in this region. To the southeast, islands along the Atlantic coast off Labrador and Newfoundland and extensive areas on the island of Newfoundland proper are treeless and covered primarily by heathlands (Rowe 1972; Daman 1983; Meades 1983); these areas are also included in the boreal zone. There are several mountain ranges that are distributed across the interior of Labrador and Quebec whose peaks lie above the tree limit. These include but are not limited to the Chic-Chocs, Groulx, and Otish mountains (Monts Chic-Chocs, Monts Groulx, and Monts Otish), Manitou Mountain (Mont Manitou), and uplands near Schefferville in Quebec, and the Mealy mountains and the upland near Harp Lake in Labrador. Digital elevation data (Natural Resources Canada [NRCan 2001*a*] and tree-limit elevation data from several published studies (Brown 1979; Gray and Brown 1979; Lamb 1985; Pauwels 2005; Quebec 2008) were used to more accurately place these alpine areas.

The boundaries of Hare (1959) and Rowe (1972) are similar to those in Payette's map (Payette 1983) in northern Labrador and to those in the map of Saucier et al. (1998) in Quebec but the two former maps are far more conservative with respect to the area of the forest-tundra (Fig. 6). Hare (1959) relied on 1: 50 000 scale aerial photography to develop his map. Both Hare (1959) and Rowe (1972) exclude large areas of forest-tundra north and south of Minto Lake (Lac Minto) to the east of Hudson Bay and the former author also excludes a substantial area of forest-tundra along the Leaf River (Rivière aux Feuille). In Labrador, both Hare (1959) and Rowe (1972) place the treeless, higher elevation areas in the Mealy Mountains and near Harp Lake in the tundra zone. The boundary presented by Sjörs (1963) is similar to that of Rowe (1972) and Hare (1959). Semenova-Tyan-Shanskaya's (Semenova-Tyan-Shanskaya 1964) boundary is similar to Rowe's (Rowe 1972) in northwestern Quebec but does not coincide with the boundary of Saucier et al. (1998) near Minto Lake, in northeastern Quebec, and near the Quebec-Labrador border. Tuhkanen's (Tuhkanen 1984) northern boundary for his hemiarctic subzone is too general when compared with the boundaries of Payette (1983) and Saucier et al. (1998) (Fig. 7); he also excludes areas of the boreal zone near Minto Lake and along the Leaf River. EWG's (EWG 1989) northern boundary for its high subarctic ecoclimatic region follows the boundary of Saucier et al. (1998) reasonably well between Hudson Bay and Ungava Bay, but southeast of Ungava Bay and into northern Labrador it is conservative with respect to the area of the tundra compared with the boundary described by Saucier et al. (1998) and Payette (1983). Similarly, the northern boundary of the taiga shield ecozone of ESWG (1995) generally agrees with the boundary of Saucier et al. (1998) near Hudson Bay and in northeastern Quebec; however, near Ungava Bay and in northern Labrador these boundaries coincide poorly with the boundaries in the maps of Saucier et al. (1998) and Payette (1983). In these two latter areas, extensive areas of tundra are included in the boreal zone by ESWG (1995). FAO (2001) and Olson et al. (2001) use the various ecoregion boundaries of ESWG (1995) to generate their polygons; FAO (2001) regroups the ecoregions of ESWG (1995) into either its boreal tundra woodland or boreal coniferous forest ecological zones. The northern boundary of FAO's boreal tundra woodland ecological zone in this region is the same as the northern boundary of ESWG's

Fig. 6. Boreal zone adapted from Payette (1983) and Saucier et al. (1998) in northern Labrador and Quebec compared with relevant zones or subzones of other pertinent studies (diagonal hatching).

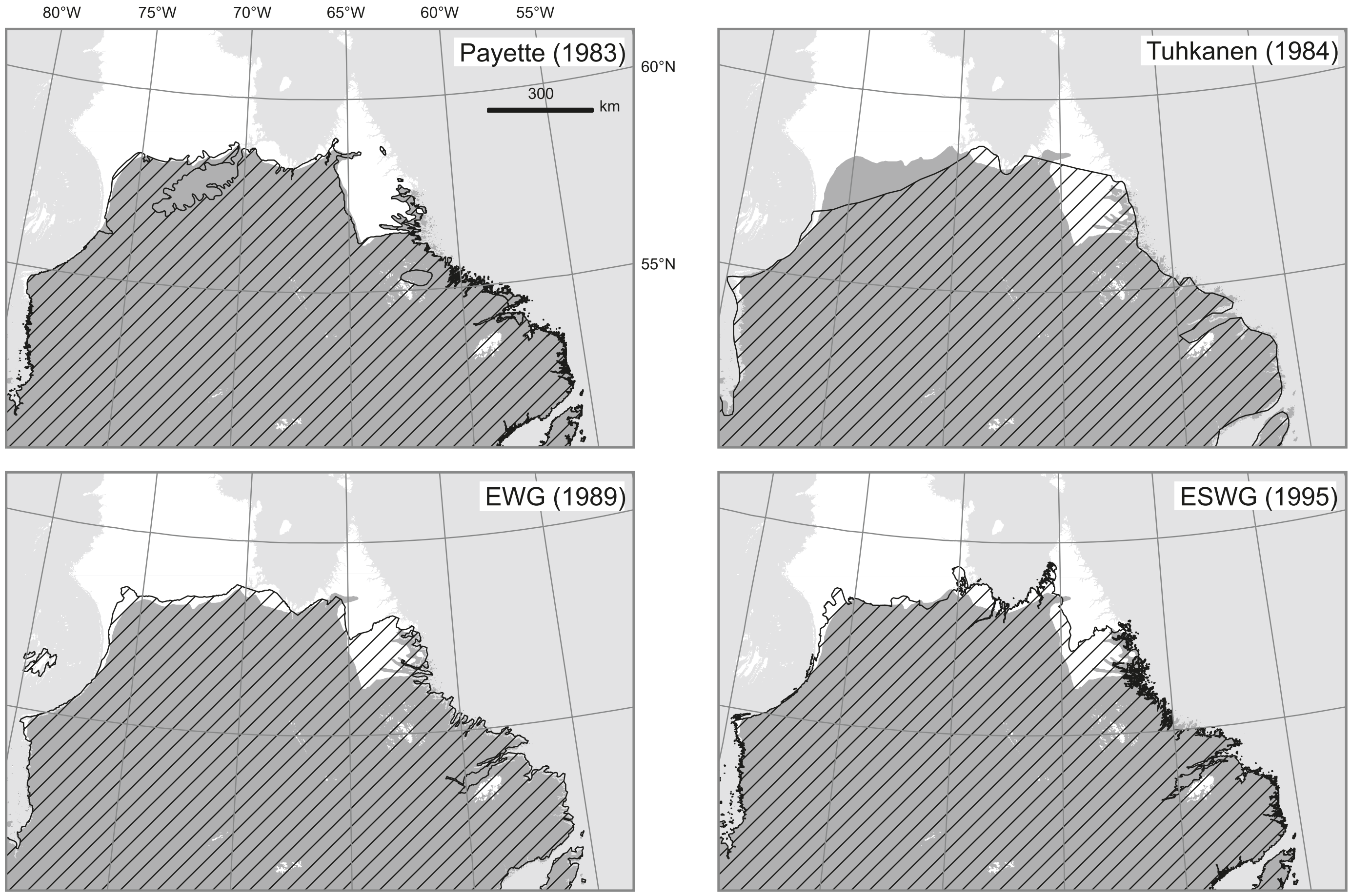


(ESWG 1995) taiga shield ecozone. Olson et al. (2001) also use the northern boundary of the taiga shield ecozone (ESWG 1995) for their eastern Canadian Shield taiga ecoregion.

6.3.1.1.3. Northwestern Canada — James Bay and Hudson Bay define the northern limits of the boreal zone in Ontario (Fig. 8). There is a narrow coastal belt along the shores of both of these bays a few kilometres wide that is treeless (Sjörs 1961). The northern tree limit as one goes west from Churchill, Manitoba, on the west coast of Hudson Bay to the border between the Yukon Territory and the Northwest Territories is adapted from Timoney (1988) (Figs. 8, 9, 10, 11). However, several relatively small outlying patches of trees to the north of the boundary are excluded as well as a few patches of tundra south of the boundary (Figs. 8, 10). Timoney et al. (1992) also published a smaller scale map with the same boundaries as Timoney (1988). Like the methods of Payette (1983) and Saucier et al. (1998), Timoney's (Timoney 1988) methods are well-described and repeatable. He used aerial photography and ground truthing as well as definitions similar to those of Payette (1983) to map the northern tree limit west of Hudson Bay.

The northern boundary of zones 6 and 7 of Semenova-Tyan-Shanskaya (1964) (see Appendix C for a description of Semenova-Tyan-Shanskaya's zones cited in the present paper) east of the Mackenzie River delta generally runs south of this paper's boundary, especially between the Thelon River and Hudson Bay and between the Mackenzie River delta and the Horton River (Figs. 8, 10). West of the delta, the northern boundary of zone 7 differs from this paper's boundary and excludes extensive areas of forest-tundra near the border between the Yukon Territory and the Northwest Territories. Similarly, Rowe's (Rowe 1972) boundary differs from this paper's boundary immediately west of the Mackenzie River delta as well as south and southeast of the Tuktoyaktuk and north of Great Bear Lake where Rowe excludes substantial areas of forest-tundra (Fig. 10). Running southeast from Great Bear Lake, Rowe's and this paper's boundaries coincide reasonably well, except northeast of Ennadai Lake where Rowe excludes a large area of forest-tundra. Tuhkanen's (Tuhkanen 1984) northern boundary for his hemiarctic subzone generally follows this paper's boundary but it lies too far south between the Mackenzie River delta and Great Bear Lake, and it does not capture the northward extension of the tree limit along the Thelon River between Great Slave Lake and Hudson Bay (Figs. 8,10). The boundary of EWG (1989) corresponds reasonably well with that of this paper, except to the east and west of the Thelon River and east of the Mackenzie River delta (Figs. 9, 10). The northern boundary for ESWG's (ESWG 1995) taiga shield ecozone east and west of the Thelon River is similar to EWG's boundary (Fig. 9). On either side of the Mackenzie River delta, the boundary of the ESWG's taiga plains

Fig. 7. Boreal zone adapted from Payette (1983) and Saucier et al. (1998) in northern Labrador and Quebec compared with relevant zones or subzones of other pertinent studies (diagonal hatching).



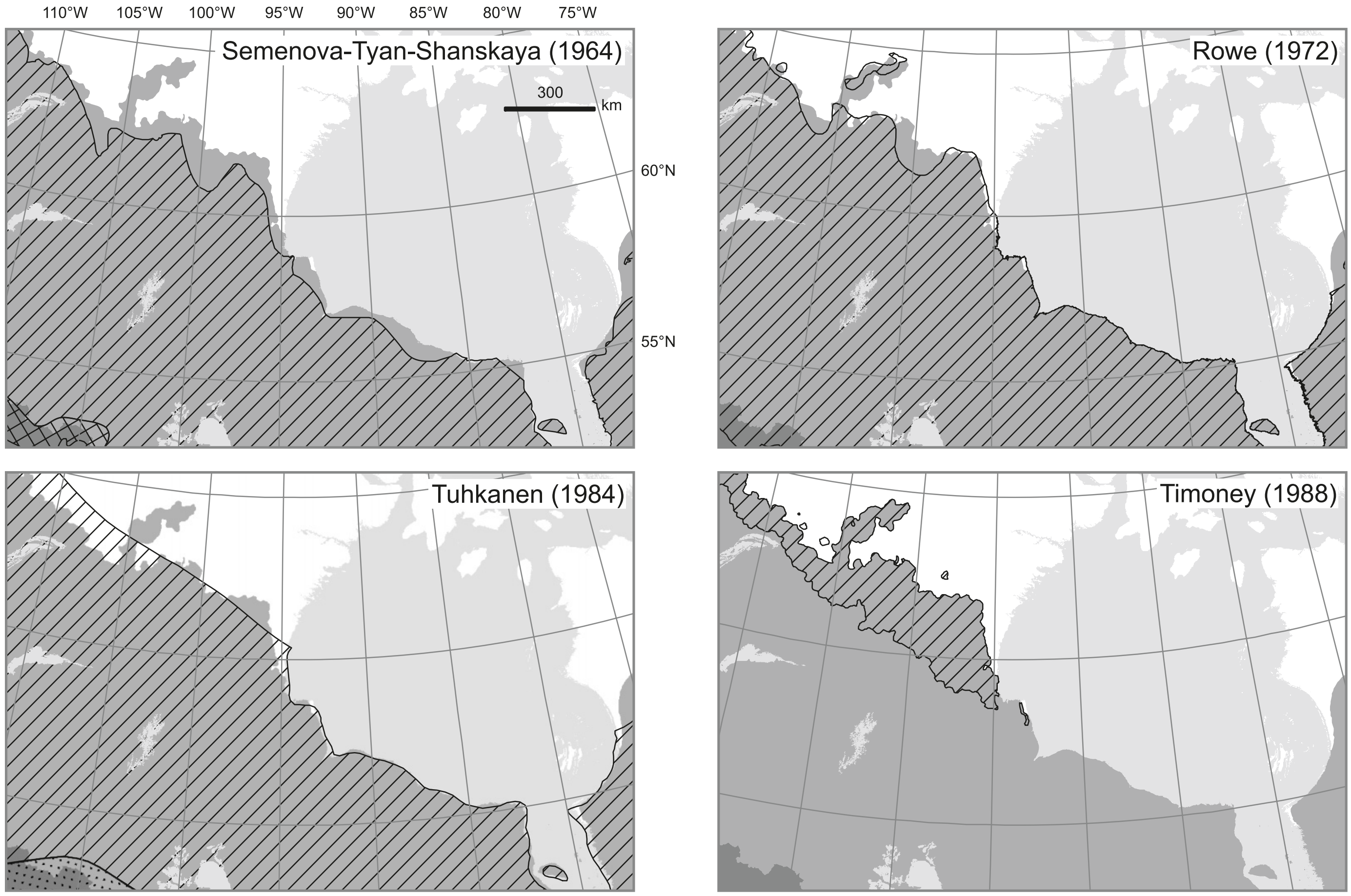
ecozone coincides poorly with this paper's boundary (Fig. 11). FAO (2001) and Olson et al. (2001) use the various ecoregion boundaries of ESWG (1995) to generate their polygons. The northern boundary of FAO's boreal tundra woodland ecological zone in this region is the same as the northern boundary of ESWG's (ESWG 1995) taiga plains and taiga shield ecozones. Olson et al. (2001) also use the northern boundary of the taiga plains and taiga shield ecozones (ESWG 1995) for their Northwest Territories taiga and northern Canadian Shield taiga ecoregions, respectively.

6.3.1.1.4. Yukon Territory and Mackenzie Mountains — The regional and local topography of the Yukon Territory and Mackenzie Mountains section of the boreal zone is complex because several mountain ranges dissect this vast area. In mountainous terrain the climate, as affected by altitude, is one of the most important factors dictating the tree limit, but factors such as aspect, slope, cold air drainage, precipitation, and soil also have an influence. To improve on the accuracy of previous maps of the region listed in Table 4, digital elevation data (NRCan 2001*a*), the ecoregion map of Oswald and Senyk (1977), and tree-limit elevation data from various regional studies (Porsild 1945; Drew and Shanks 1965; Douglas 1974; Oswald and Senyk 1977; Ritchie 1982; MacDonald 1983; Cwynar and Spear 1991; Szeicz and MacDonald 1995; Szeicz et al. 1995) were used to delineate the northern tree limit as well as alpine areas above the elevational tree limit in each of the ecoregions of Oswald and Senyk (1977) and the Mackenzie Mountains of the Northwest Territories. The results of this process are the boundaries of the northern tree limit and alpine areas depicted in Fig. 10.

The new map for the boreal zone in this area depicts alpine distribution at a higher spatial resolution than any of the earlier maps. This conclusion is reached on the basis of comparisons between the alpine areas depicted in this paper, those of the Earth Observation for Sustainable Development (EOSD) land cover data from the Canadian Council of Forest Ministers' National Forest Information System Web site (http://nfis.org/web_portals/themed_e.shtml), and those visible on high-resolution imagery of Google™ Earth. The higher spatial resolution is important for the areal statistics reported later. Although alpine areas above the tree limit are more accurately depicted in the new map than in other maps of the region, these areas are included in the boreal zone, unlike the approach of Semenova-Tyan-Shanskaya (1964), Rowe (1972), EWG (1989), and Olson et al. (2001) (Figs. 10, 11).

6.3.1.1.5. Alaska — In Alaska, the Pacific Ocean brings relatively warm moist air to the southern coastal areas whereas the Beaufort, Bering, and Chukchi seas bring cold air to the western and northern coastal areas (Hare and Hay 1974; Fleming et al. 2000). The region is dissected by the

Fig. 8. Boreal zone adapted from Timoney (1988) in north-central Canada compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.

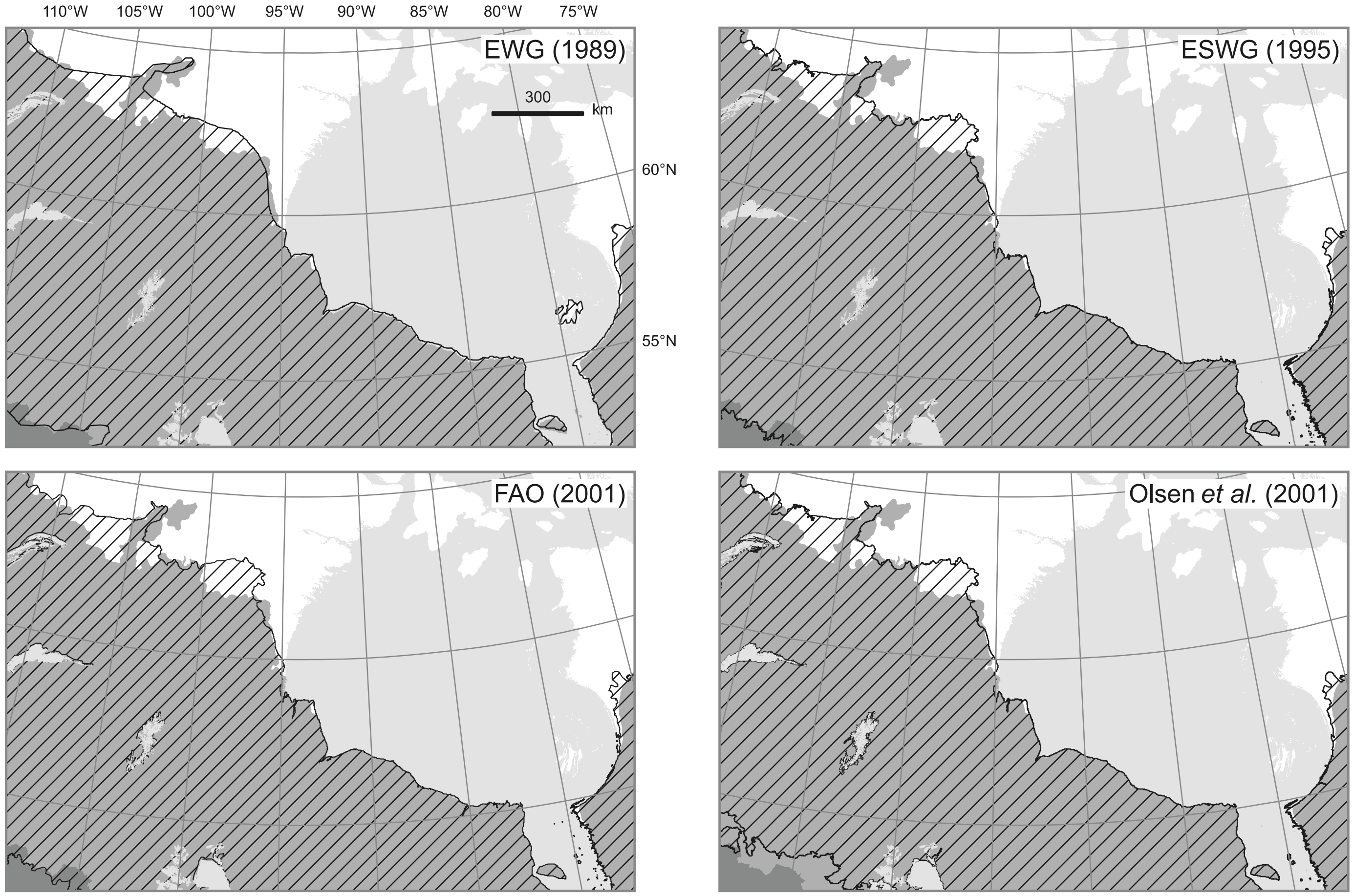


Brooks Range in the north, and in the south the Saint Elias Range, Wrangell Mountains, Chugach Mountains, Kenai Mountains, Talkeetna Mountains, and the Alaska Range separate Pacific coastal areas from the interior. The weather systems formed over the four bodies of water interact with the mountain ranges to determine the geographical distribution of the boreal zone in Alaska.

In the present paper the boundaries of the boreal zone in this region (Fig. 12) were adapted from the scheme of Viereck and Little (1972) and Yurtsev (1994). The boreal zone includes the following vegetation types as described by Viereck and Little (1972): closed spruce-hardwoods; open, low-growing spruce; and treeless bogs. However, because of the various mountain ranges distributed across Alaska and the small scale of the map of Viereck and Little (1972), digital elevation data and tree-limit elevation data from several published studies (Thompson 1969; Hettinger and Janz 1974; Anderson 1975; Denton and Karlén 1977; Viereck et al. 1983; Goldstein et al. 1985; Cooper 1986; Short et al. 1986; Sveinbjörnsson et al. 1995; Suarez et al. 1999; Lloyd and Fastie 2002; Epting and Verbyla 2005) were used to delineate the northern tree limit as well as alpine areas above the elevational tree limit. There were also several small outliers mapped by Viereck and Little (1972) that were excluded from the boreal zone (Fig. 12). The boreal zone in this region also includes the Alaska Peninsula and the Aleutian Islands because the vegetation in these areas has many boreal taxa but lacks trees (i.e., treeless heaths) (Yurtsev 1994; Talbot et al. 2006). The treeless condition of this peninsula and the Aleutian Islands cannot be explained by thermal characteristics of the regional climate, which is generally wet with moderate temperatures and little seasonal variation (the eastern Aleutians are warmer and wetter than the western Aleutians), except at higher elevations on mountain slopes (Bruce and Court 1945; Raup 1945; Hare and Ritchie 1972). Consequently, both Hämet-Ahti (1981) and Tuhkanen (1984) include these areas in the boreal. *Picea sitchensis* trees have been successfully grown and have produced seedlings on the Aleutian island of Amaknak but other afforestation efforts on the islands have met with varied success, with failures, however, largely resulting from poor selection of seedlings and sites (Viereck 1979; Alden 2000; LaBau and Alden 2000).

The boreal zone in Alaska corresponds generally with zones 6 and 7 on Semenova-Tyan-Shanskaya's (Semenova-Tyan-Shanskaya 1964) map in the north but poorly in the west and south (Fig. 12). Semenova-Tyan-Shanskaya (1964) also depicts extensive alpine areas, which are excluded from the boreal zone on Semenova-Tyan-Shanskaya's map. As elsewhere, Tuhkanen's (Tuhkanen 1984) smoothed northern boundary for his hemiarctic subzone generally coincides with the northern boreal zone boundary in this region (Fig. 12). However, Tuhkanen's northern boreal subzone includes tundra areas in western Alaska and his middle boreal

Fig. 9. Boreal zone adapted from Timoney (1988) in north-central Canada compared with relevant zones or subzones of other pertinent studies (diagonal hatching).



subzone includes temperate coastal forests in southern Alaska. FAO's (FAO 2001) boreal tundra woodland and boreal mountain system ecological zones in Alaska generally overlap with this paper's boreal zone but the boundaries of the zones lack detail and exclude large areas along the Alaska Peninsula (Fig. 12). The boundaries of the boreal forest – taiga biome of Olson et al. (2001) exclude substantial areas of the boreal zone in the north and southwest and much of the lower elevation forests in the more mountainous interior (Fig. 12).

6.3.2. Boreal–hemiboreal ecotone

The hemiboreal subzone as defined by some Europeans exists as a continuous belt across North America and Eurasia. Proximity to oceans on the eastern and western flanks of these land masses results in relatively warm and moist weather systems, which ameliorate the regional climates. Thus, the southern boreal zone merges into temperate deciduous forests in eastern North America and eastern and western Eurasia. These three transitional regions are referred to as the boreo-nemoral zone of Sjörs (1963). In western North America, boreal forests merge into temperate cordilleran forests consisting primarily of conifers. The temperate interior of both continents is occupied by grasslands. Thus, the hemiboreal subzone is represented by aspen parkland or steppe forests whose occurrence is dictated more by the availability of moisture than by temperature.

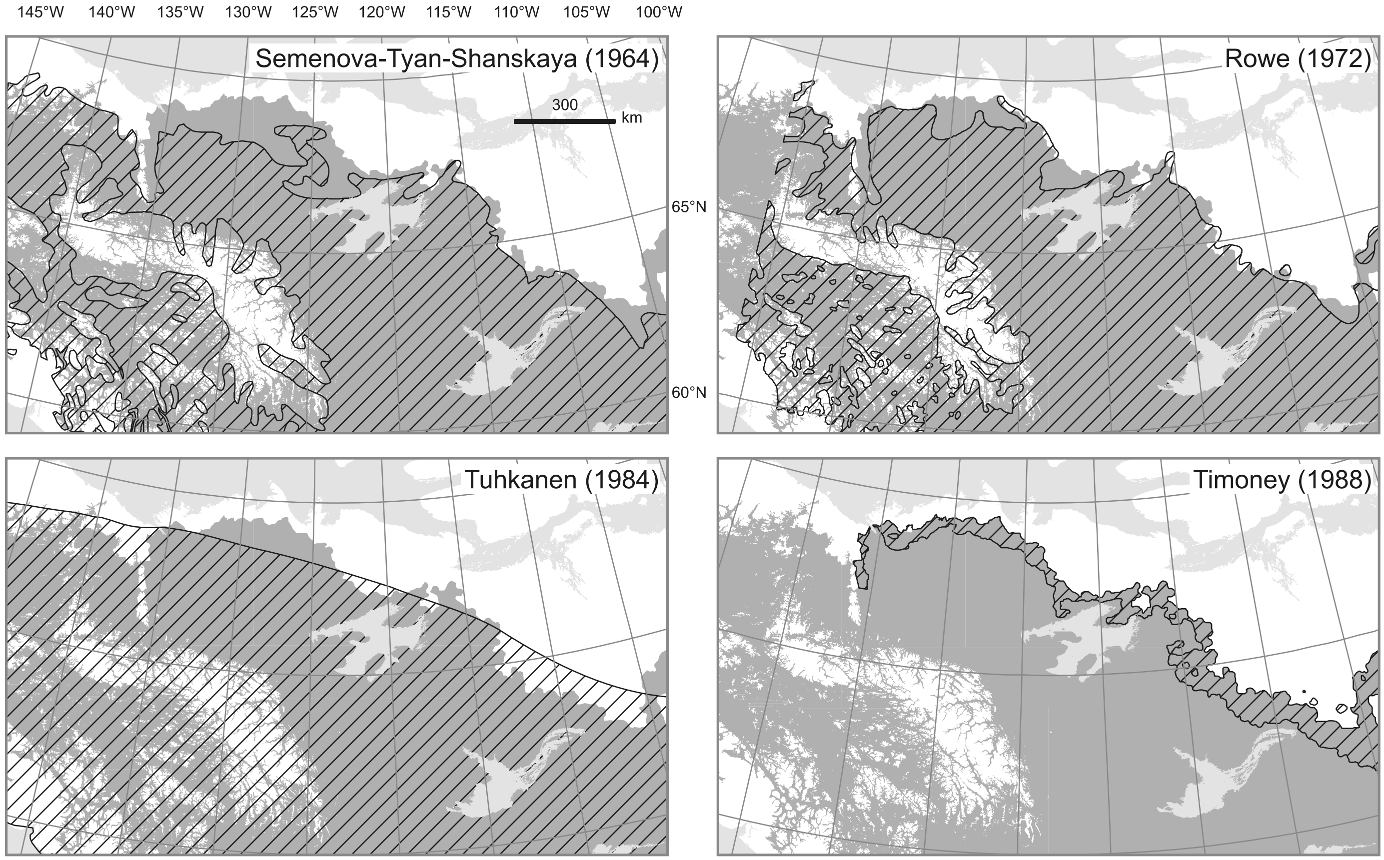
Although I concur with Rowe (1972) and many other North American scientists who do not distinguish a hemiboreal subzone lying south of the boreal zone, I have mapped the subzone to determine its areal extent in the second half of this paper. The reader is given the choice whether to include the subzone, as some Europeans do, or exclude it from the map of the North American boreal zone.

6.3.2.1. Boundaries

6.3.2.1.1. Atlantic Maritimes and Great Lakes — The boreal zone and hemiboreal subzone in the eastern and interior parts of North America are shown in Figs. 13–18. The southern boundary of the boreal zone used in eastern North America is that of Halliday (1937) in Newfoundland and Ontario as modified by Rowe (1972) and Saucier et al. (1998) in Quebec (Figs. 13, 16, 17). The French islands of Saint Pierre and Miquelon south of Newfoundland are also included in the boreal zone. At the Ontario-Quebec border, a minor amount of edge-matching was required. Contour lines were followed from Quebec into Ontario to match the boundaries. Boundaries of Saucier et al. (1998) are based on ecological plots, forest inventory plots, data analysis, elevation data, and other existing maps.

The distribution of *Acer saccharum* (Little 1971; Godman et al. 1990; Farrar 1995) and *Betula alleghaniensis* (Little 1971; Erdmann 1990; Farrar 1995) (the distribution of both

Fig. 10. Boreal zone adapted from Timoney (1988) and digital elevation data in northwestern Canada and from Viereck and Little (1972) and digital elevation data in eastern Alaska compared with relevant zones or subzones of other pertinent studies (diagonal hatching).

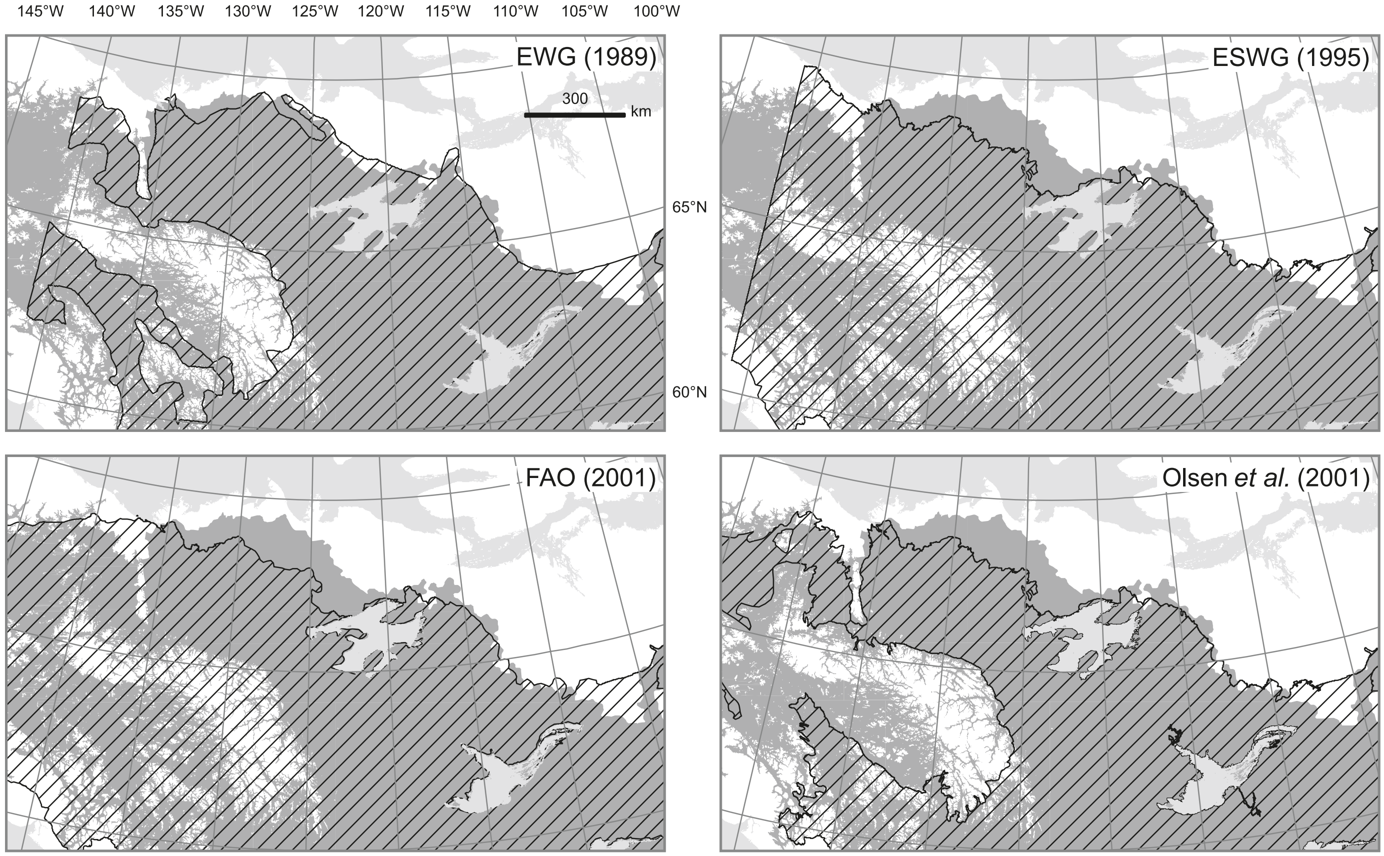


species is depicted in Fig. 3) extends north of Rowe's boundary east of Lake Superior in Ontario but according to Halliday (1937) and Rowe (1959, 1972) this area (section B.7, Missinaibi-Cabonga of Rowe) contains only scattered individuals or more or less isolated stands with these two species mixed with *Pinus strobus* and *Pinus resinosa*. The northern limit of *Betula alleghaniensis* was used by Halliday (1937) to delineate the northern boundary of the Great Lakes St. Lawrence forest region (Halliday and Brown 1943). However, a careful inspection of their distribution map of *Betula alleghaniensis* or of Erdmann's (Erdmann 1990) and Farrar's (Farrar 1995) more recent maps for the same species shows that the northern limit of this species does not coincide well with the northern boundary of Halliday's (1937) Great Lakes St. Lawrence forest region.

In Quebec, the southern boundary of the boreal zone north of the St. Lawrence River mapped by Saucier et al. (1998) coincides reasonably well with the northern limit of *Acer saccharum* as mapped by Little (1971) and Godman et al. (1990). Rowe's (Rowe 1972) boundary in Quebec lies substantially south of the boundary depicted by Saucier et al. (1998). Halliday's (Halliday 1937) boreal boundary was used as the northern boundary of Braun's (1950) hemlock-white pine-northern hardwoods region (Figs. 13, 16, 17). Sjörs' (Sjörs 1963) southern boundary for his southern boreal subzone in this region is almost exactly that of Rowe (1972) including two pockets of the boreal zone on the Gaspé Peninsula (Figs. 13, 16). GIS evidence suggests that Sjörs (1963) used Rowe's (1959) boundaries for his map of northeastern North America because the boundaries on the two maps are similar.

From the Atlantic Maritimes to the west side of Lake Superior, the boundaries of zone 10 and zone 11 of Semenova-Tyan-Shanskaya's (Semenova-Tyan-Shanskaya 1964) southern taiga correspond poorly to the boundaries of the present paper because these zones include areas with temperate species (Figs. 13, 16, 17). Tuhkanen's (Tuhkanen 1984) generalized southern boundary for his southern boreal approximates the southern boundary of the present paper's boreal zone except west of Lake Superior (Figs. 14, 16, 18). The maps of both EWG (1989) and ESWG (1995) correspond poorly with the southern boundary of the present paper's boreal zone (Figs. 14, 15, 16, 18). ESWG (1995) appears to have given little consideration to the vegetation of the boreal shield ecozone because much of its southern portion is covered by temperate deciduous species. Also, all of the Gaspé Peninsula lies within ESWG's Atlantic maritime ecozone, which contrasts with the placement of the region's higher elevation forests in the boreal zone by Saucier et al. (1998). Olson et al. (2001) do not separate boreal forests from mixedwood forests on the Gaspé Peninsula; thus, the entire peninsula lies within their boreal forests – taiga biome (Fig. 15). In Quebec and in Ontario east of Lake Superior, the southern boundary of the boreal forests – taiga biome of Olson et al. (2001) lies substantially north of the present paper's boundary (Figs. 15, 16). Northwest of Lake Superior, however, the southern boundary of the boreal forests – taiga biome of Olson et al. (2001) corresponds reason-

Fig. 11. Boreal zone adapted from Timoney (1988) and digital elevation data in northwestern Canada and from Viereck and Little (1972) and digital elevation data in eastern Alaska compared with relevant zones or subzones of other pertinent studies (diagonal hatching).

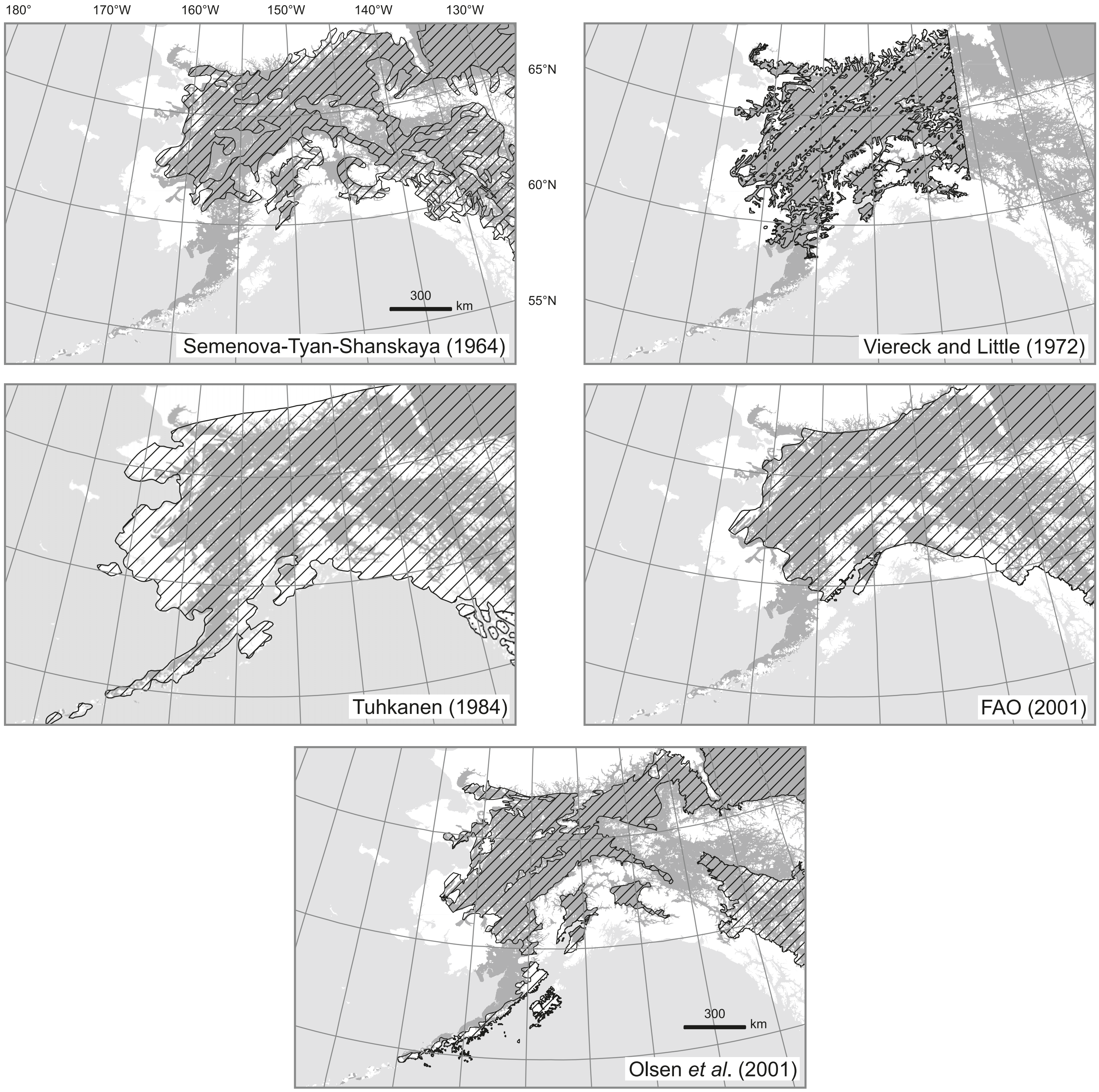


ably well with the present paper's boundary (Fig. 16). The southern boundaries of the FAO's (FAO 2001) boreal ecological zones are similar to those of Olson et al. (2001) except for the Gaspé Peninsula, which the FAO includes in its temperate ecological zone.

6.3.2.1.2. Western Interior — Zoltai (1975) mapped the southern limits of the distribution of *Larix laricina*, *Picea mariana*, *Picea glauca*, *Pinus banksiana*, and *Pinus contorta* var. *latifolia* in the southern Prairie Provinces using a series of transects (Table 3). A new line was generated on the basis of the presence of at least two of these five boreal conifers using Zoltai's data. This line is the southern boundary of the boreal zone in this region, except in southwestern Alberta and southeastern Manitoba, which fell outside Zoltai's study area. Thus, the new line generated from Zoltai's data was edge-matched with the boundary of the foothills natural region of NRC (2006) in southwestern Alberta and with Rowe's (Rowe 1972) boreal forest region boundary in southeastern Manitoba (Figs. 17, 19). Although the Spruce Woods in Manitoba has several boreal conifers it is excluded from this paper's boreal zone because it is an outlier surrounded by aspen parkland.

The boundary between Bird's (Bird 1961) aspen parkland and the boreal zone generally follows the present paper's boundary across the region except in eastern Saskatchewan and in west-central Alberta (Figs. 17, 19). The northern and eastern boundary of zone 16 on the map of Semenova-Tyan-Shanskaya (1964) corresponds generally with the southern boundary of the boreal zone depicted in the present paper in Manitoba and Saskatchewan (Fig. 17). It excludes, however, the boreal forests on Riding Mountain in Manitoba. Semenova-Tyan-Shanskaya's (Semenova-Tyan-Shanskaya 1964) map also corresponds poorly with the map in the present paper in west-central and southwestern Alberta (Fig. 19). The parkland – boreal forest transitional zone of Zoltai (1975), which he includes in the boreal zone on the basis of the presence of at least one of *Larix laricina*, *Picea mariana*, *Picea glauca*, *Pinus banksiana*, and *Pinus contorta* var. *latifolia*, places the southern boundary of the boreal zone substantially to the south, especially between Lake Winnipeg and Lake Winnipegosis, western Saskatchewan, and Alberta (Figs. 18, 19). Rowe (1972) includes the aspen parkland transitional area in his boreal forest region; consequently his boundary for the boreal zone lies substantially south of the present paper's boundary (Figs. 17, 19). Archibold and Wilson (1980) use the southern boundary of the parkland – boreal forest transitional zone of Zoltai (1975) as their southern boundary for the boreal zone in Saskatchewan (Fig. 18). Tuhkanen's (Tuhkanen 1984) southern boreal boundary corresponds poorly with the boundaries depicted in the present paper for this region (Figs. 18, 20). The boundaries of both EWG (1989) and ESWG (1995) correspond closely with the present paper's boundary, except in eastern Saskatchewan and in west-central Alberta where both EWG's and ESWG's boreal zone boundary lie to the north (Figs. 18, 20). The degree of correspondence is the same for the map of FAO (2001) because they use the boundaries of ESWG (1995).

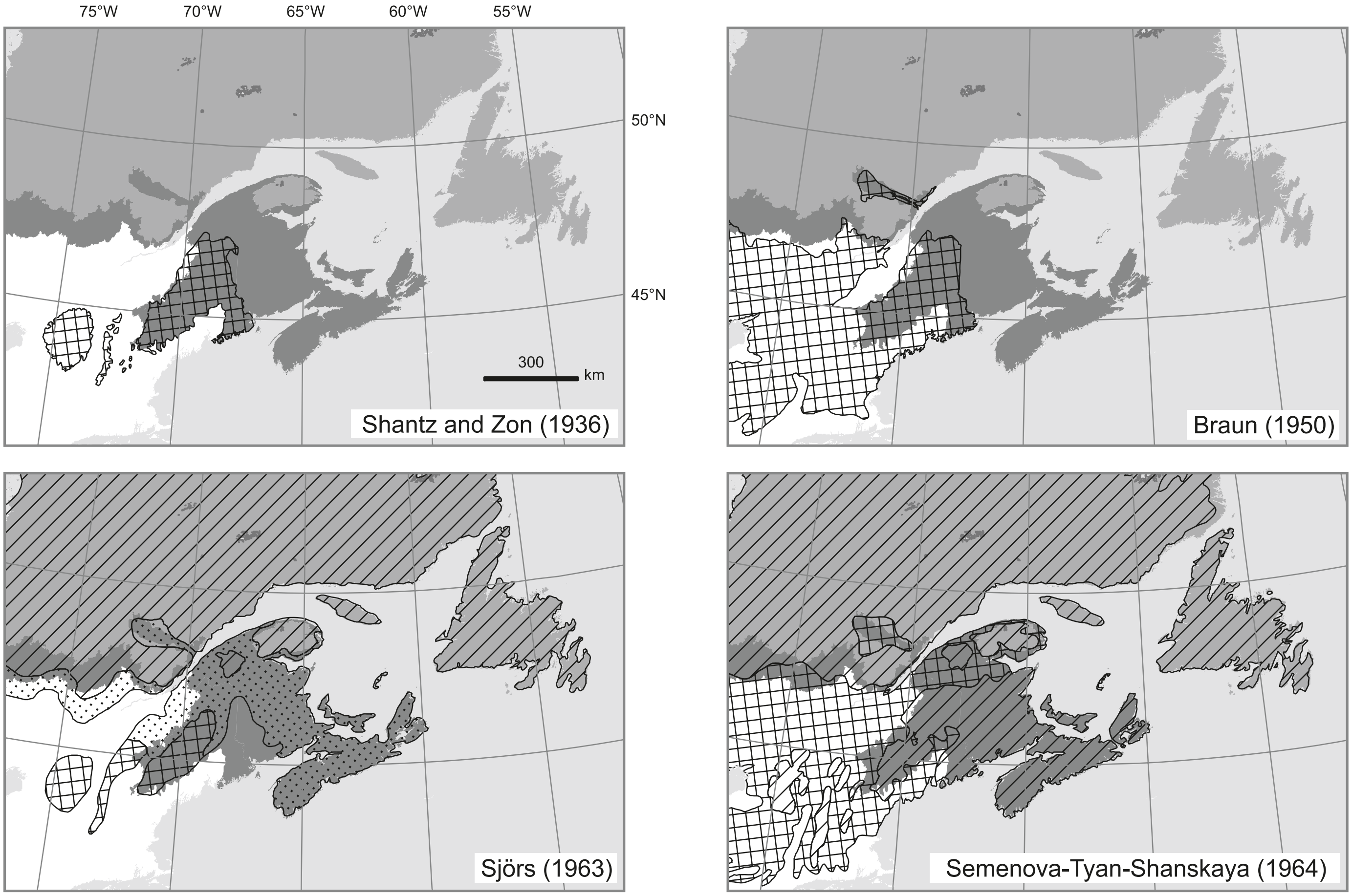
Fig. 12. Boreal zone adapted from Viereck and Little (1972), Yurtsev (1994), and digital elevation data in Alaska compared with relevant zones or subzones of other pertinent studies (diagonal hatching).



Olson et al. (2001) place their boundary for the boreal zone substantially north of the boundary in the present paper (Figs. 18, 20), excluding large areas (i.e., most of the boreal transition and the interlake plain ecoregions of ESWG) with cold-tolerant boreal conifers. NRC's (NRC 2006) boundary for the boreal zone in Alberta is essentially the same as ESWG's (ESWG 1995) boundary.

6.3.2.1.3. Western Cordillera — The task of delineating the boundaries of the boreal zone and the hemiboreal subzone is complicated by the mountainous terrain of British Columbia and western Alberta. In many valleys several distinct vegetation types may occur as relatively narrow horizontal belts from valley bottom to mountain peak. Although factors such as elevation and aspect play important roles in the distribution of vegetation, it is the movement of air masses over and around the successive mountain ranges that play the critical role in this region. The precise nature of these air masses and their eastward movement across the cordilleran region is depicted and described in detail by Bryson and Hare (1974); what follows is a synopsis of their paper. The coast mountains act as a barrier, deflecting

Fig. 13. Boreal zone and hemiboreal subzone adapted from Shantz and Zon (1936), Rowe (1972), and Saucier et al. (1998) in the Atlantic Maritimes, Quebec, and the northeastern US compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.

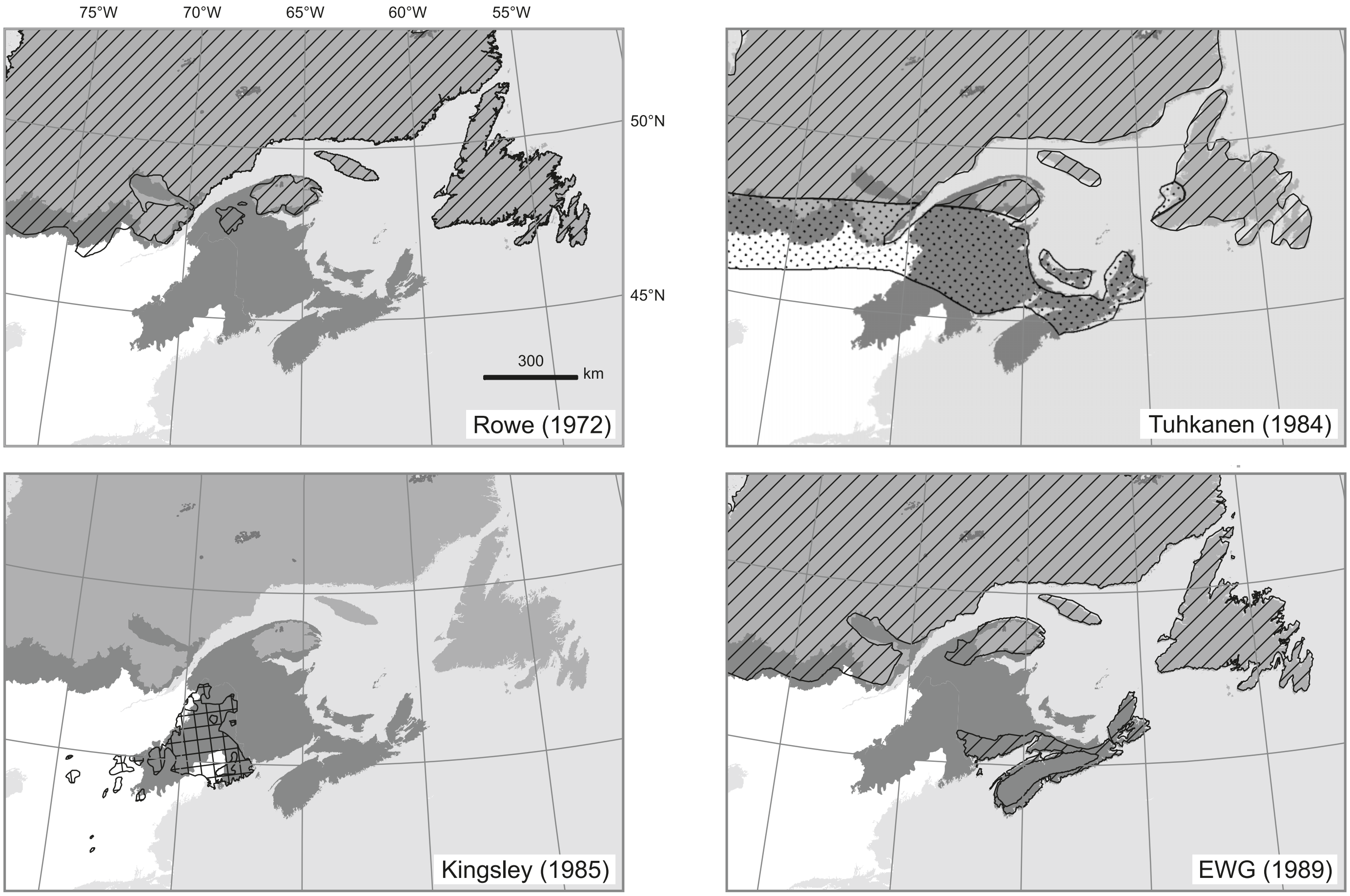


westerly winds to the north or south unless the winds have sufficient strength to cross the crests of these mountains. There are, however, three routes that allow normal low-level westerly flow: along the coast near 45–50°N where maximum westerlies occur; through the gap provided by the Columbia River – Snake River – Wyoming basin; and through the lower region near the Mexican-US border. The first route at 45–50°N results in the maximum eastward penetration of the westerlies from the Pacific Ocean and has a strong influence on regional flora of relevance to this paper (Daubenmire 1943; Hansen 1948; Daubenmire and Daubenmire 1968; Peet 1988; Barbour and Christensen 1993; Brouillet and Whetstone 1993). Daubenmire (1943) referred to this region of maximum eastward penetration of the westerlies as a "climatic peninsula." The latitude and characteristics of the westerlies change with the seasons. As the moist Pacific air masses move east over western North America, they rise over a series of mountain ranges, each time releasing precipitation on the windward side of these obstacles and resulting in a rain shadow on the leeward side of these ranges. Consequently, the oceanic influence decreases after crossing each range. There is a large intermountain basin in British Columbia. This basin can be penetrated by cold air from east of the Rocky Mountains. Occasionally the cold air is trapped here for several days or, more often, rapidly flushed by the westerlies resulting in a more moderate climate than east of the continental divide. In winter, the topographic roughness in the basin results in strong northward and northwestward airflow as the air moves toward the subpolar low. In summer, the basin is filled with dry air that originates in the Pacific anticyclone.

These seasonal movements of the Pacific airstream and the mountainous terrain of the western cordillera result in a unique phytogeographical area where conifers dominate over hardwoods in both temperate and boreal climates (Waring and Franklin 1979). The coastal areas of Oregon, Washington, British Columbia and southeastern Alaska where the maritime conifers such as *Abies amabilis*, *Abies grandis*, *Picea sitchensis, Thuja plicata, Tsuga heterophylla*, and *Tsuga mertensiana* are found are temperate rain forests (the distribution of the latter four species is depicted in Figs. 1, 4). The eastward extension of this temperate climate into the interior (i.e., the climatic peninsula) is coincident with the range of *Thuja plicata* and *Tsuga heterophylla*. Northeastern British Columbia and western Alberta lie east of the cordilleran divide where the oceanic influence is minimal and arctic air dominates the landscape. The climate of the large intermountain basin in central British Columbia is generally intermediate between the predominantly temperate forests to the west and south and boreal forests to the north and northeast.

Although the entire length of the Rocky Mountains has been divided into four north-south divisions on the basis of

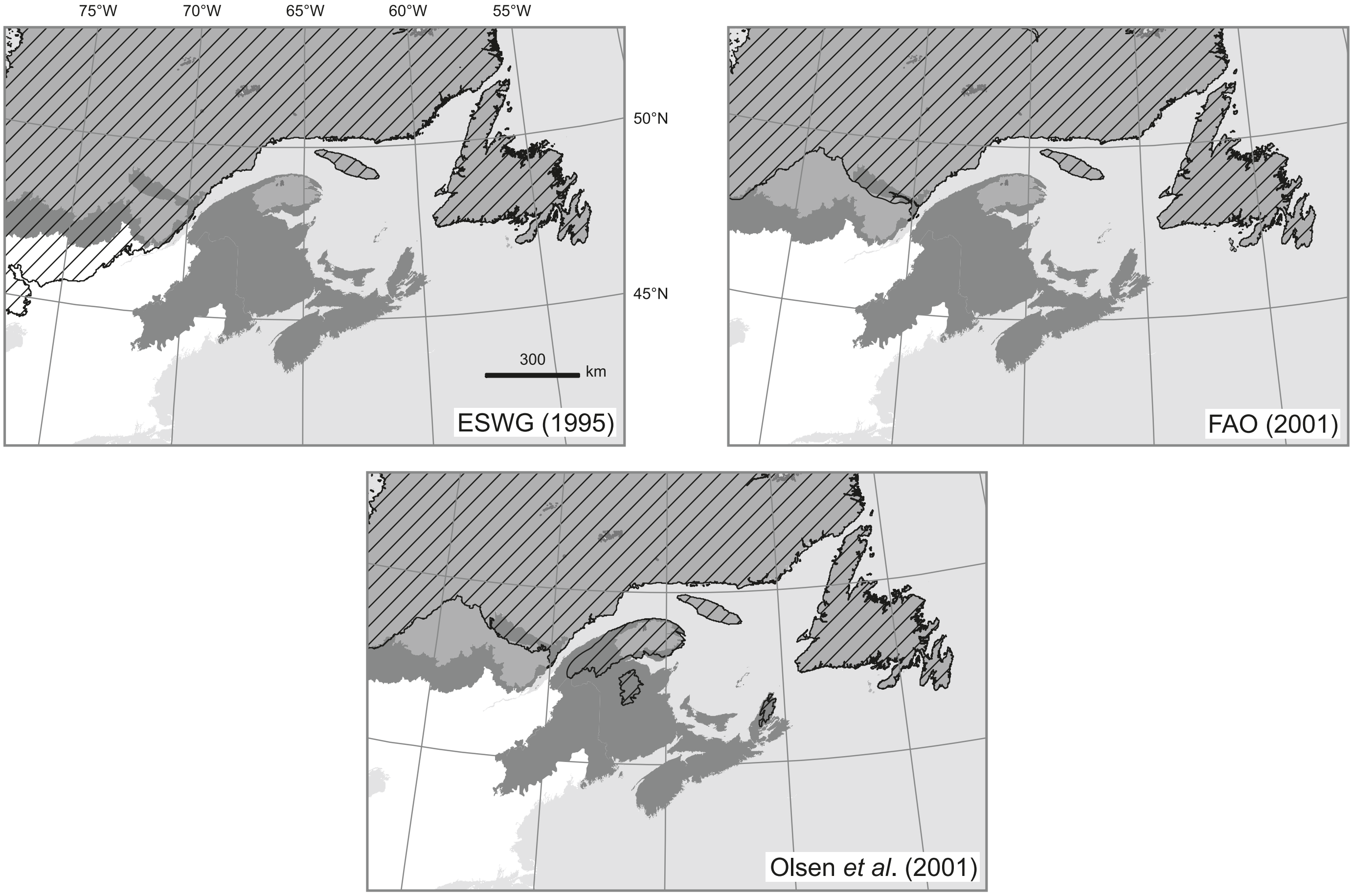
Fig. 14. Boreal zone and hemiboreal subzone adapted from Shantz and Zon (1936), Rowe (1972), and Saucier et al. (1998) in the Atlantic Maritimes, Quebec, and the northeastern US compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.



conspicuous floristic differences (Daubenmire 1943), the division between the two most northern are of relevance to this paper. The presence of *Picea mariana*, *Alnus viridis*, *Viburnum edule*, and *Amelanchier florida* differentiates Daubenmire's (Daubenmire 1943) northern and far northern divisions and according to NRC (2006) this boundary should be placed at the upper Red Deer River drainage, at least on the east side of the continental divide in the Rocky Mountains. Peet (1988) also divides the Rockies into four regions with the boundary between the far northern and the northern lying about 53°N. According to Barbour and Christensen (1993), Peet's (Peet 1988) far northern region is most closely related to the interior continental boreal zone. Peet's northern region commonly includes *Larix lyallii* and *Pinus albicaulis* (see Barbour and Christensen 1993), both of which are limited to areas south of the North Saskatchewan River drainage in the Rocky Mountains of Alberta (NRC 2006). On the basis of NRC's information, the boundary between Peet's far northern and northern regions should be placed south of 53°N, at least on the east side of the continental divide in the Rocky Mountains (Peet's Fig. 3.1 would seem to indicate this as the boundary lies farther north on the west side compared with the east side of the Rockies). On the west side of the Rocky Mountains in the same vicinity as above, *Pinus flexilis* and *Larix lyallii* are restricted to southeastern British Columbia (Coupé et al. 1991; Arno and Habeck 1972). Daubenmire's (Daubenmire 1943) northern division is part of the climatic peninsula discussed earlier. Because the oceanic influence along the peninsula diminishes with each crossing of a major mountain range, the components of the vegetation mosaic also change in an east-west direction across the Rockies. Additionally, the coastal influence is insignificant on the leeward slopes, resulting in differing climates and vegetation (Daubenmire 1943). In southwestern Alberta, the climatic influence of the storm track along the peninsula is manifested by a more pronounced summer-dry and winter-wet precipitation regime, slightly higher total precipitation, and somewhat milder temperatures compared with conditions to the north (Ogilvie 1962). The northern boundary of this peninsula in Canada on the east side (leeward) of the Rockies may be indicated by the floristic discontinuity noted by Ogilvie (1962, 1963) at the Wilkinson Summit at about 50°14′N, or, more likely, at the upper Red Deer River drainage, as indicated by NRC (2006). The southern Canadian Rocky Mountains are closely related physiographically and floristically to the northern US Rocky Mountains across the Canada-US border (Habeck 1987).

Thus, the boreal zone in this region, depicted in Fig. 19, is as follows: In the foothills and Rocky Mountains east of the continental divide in Alberta, the boreal zone includes NRC's (NRC 2006) upper and lower foothills subregions

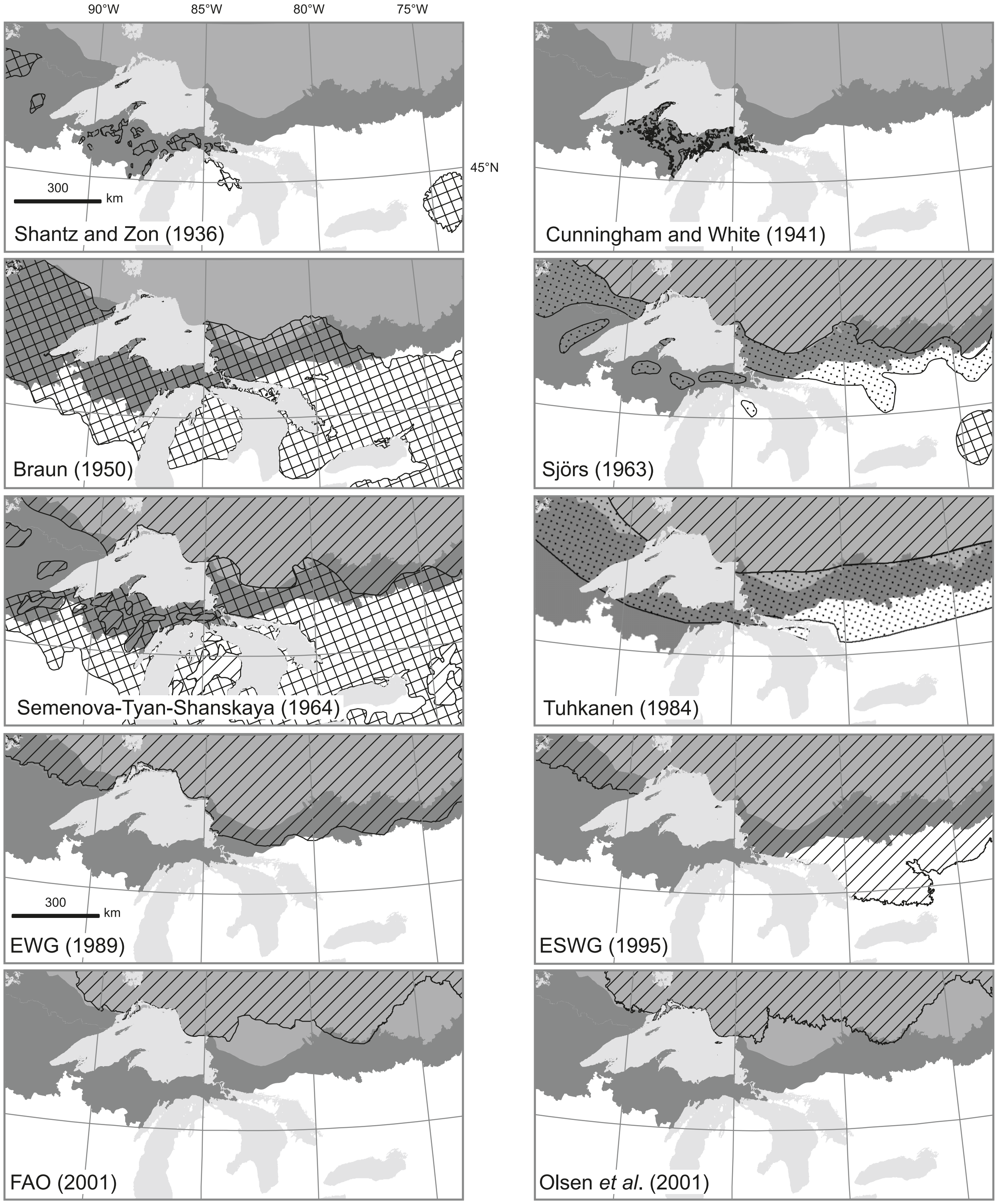
Fig. 15. Boreal zone and hemiboreal subzone adapted from Shantz and Zon (1936), Rowe (1972), and Saucier et al. (1998) in the Atlantic Maritimes, Quebec, and the northeastern US compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.



and the subalpine natural subregion north of the upper Red Deer River near the continental divide (at about 51°38′N). Floristically, the foothills forests have much in common and are contiguous with the lower elevation forests to the east, although as elevation increases *Picea glauca* is replaced by *Picea engelmannii*, *Abies balsamea* by *Abies lasiocarpa*, and *Pinus banksiana* by *Pinus contorta* (Moss and Pegg 1963; Achuff and La Roi 1977; Strong 2002). In the subalpine forests north of the North Saskatchewan River, *Larix lyallii* and *Pinus albicaulis* are uncommon and about 40 km south, at the upper Red Deer River drainage, several understory plants drop out in the subalpine natural region (Achuff 1989; NRC 2006). Thus, north of the upper Red Deer River drainage the influence of the boreal zone is more prominent with increased incidence of typical boreal species (i.e., *Picea mariana*, *Larix laricina*, *Vaccinium vitis-idaea*, and *Ledum groenlandicum*) (Achuff 1989; NRC 2006). In British Columbia, the boreal white and black spruce and the spruce-willow-birch biogeoclimatic zones of BCMFR (2006) are included in the present paper's boreal zone as both their flora and climate show strong affinities to the boreal zone, which is supported by information outlined in Krajina (1965, 1973*a*, 1973*b*, 1975), Pojar and Meidinger (1991), Delong et al. (1991), and Pojar and Stewart (1991). The sub-boreal pine-spruce and the sub-boreal spruce biogeoclimatic zones are included in the hemiboreal subzone. Steen and Demarchi (1991) and Meidinger et al. (1991) provide a thorough description of the ecological conditions of these latter two biogeoclimatic zones. Meidinger et al. (1991) consider the forests of the sub-boreal pine-spruce and the sub-boreal spruce biogeoclimatic zones as transitional between the true montane forests of *Pseudotsuga menziesii* var. *glauca* to the south and the boreal forests to the north. Klinka et al. (2002) note that the climate of this zone is less continental than that of the boreal white and black spruce biogeoclimatic zone. In northern British Columbia and east of the Rocky Mountains in British Columbia, forests of the Engelmann spruce – subalpine fir biogeoclimatic zone (most of subzones mv, mvp; some of subzones wv, wvp north of 59°7′N) that are contiguous with forests of the boreal white and black spruce and the spruce-willow-birch biogeoclimatic zones are placed in the present paper's boreal zone.

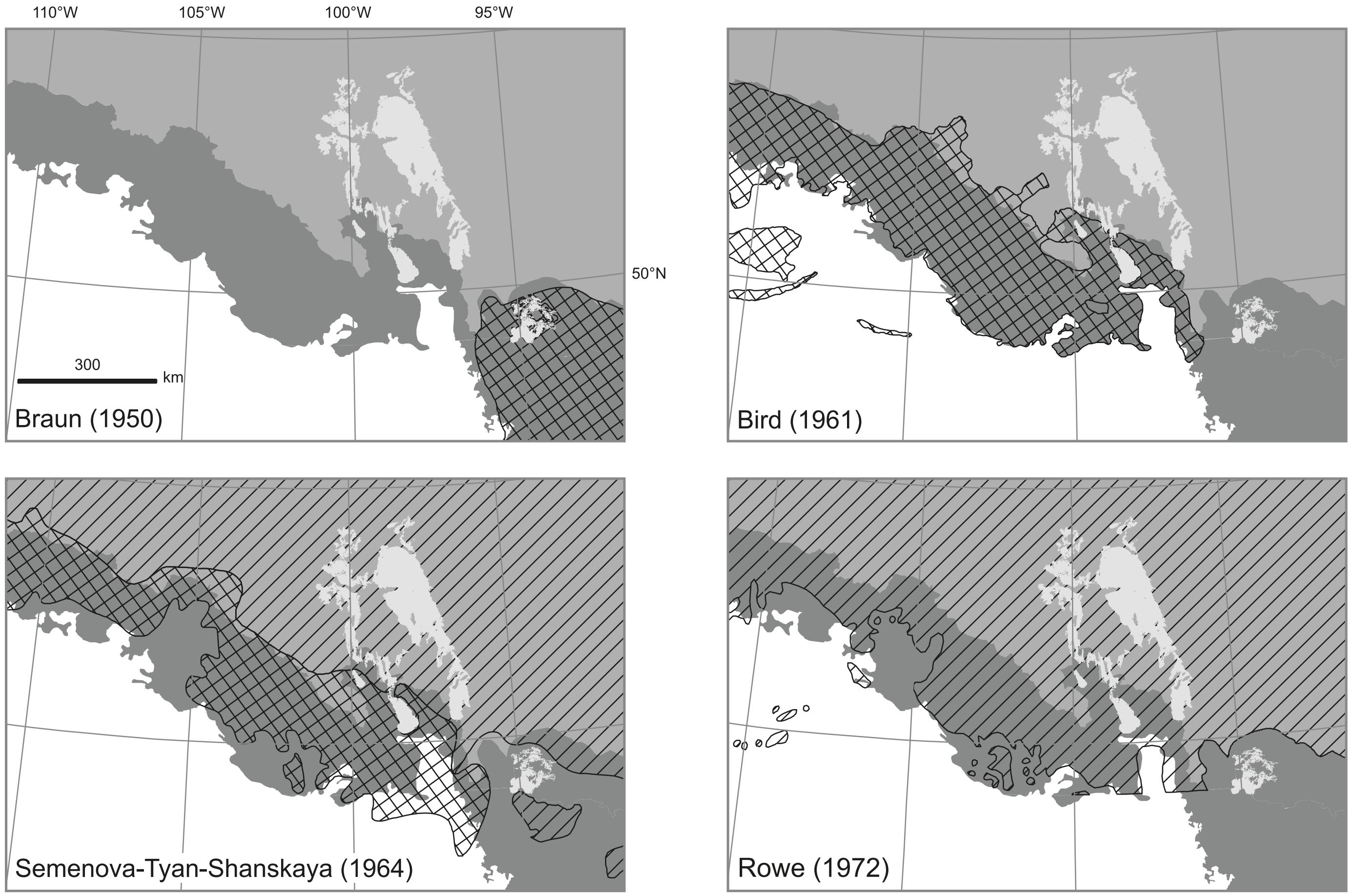
The map of NRC (2006) was produced at a scale of 1:250 000 (Table 3). Contour lines based on data from a provincial digital elevation model were used in many cases to delineate ecological boundaries. The map of BCMFR (2006) is a result of detailed surveys and mapping. About 60% of the province was mapped at a scale of 1:20 000, about 30% at 1:250 000, and the remainder at 1:600 000. None of the maps by Semenova-Tyan-Shanskaya (1964), Tuhkanen (1984), Rowe (1972), ESWG (1995), FAO

Fig. 16. Boreal zone and hemiboreal subzone adapted from Rowe (1972), Marschner (1974), Finley (1976), Comer et al. (1995*b*), and Saucier et al. (1998) in the Great Lakes region and Quebec compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.



(2001), or Olson et al. (2001) (Figs. 19, 20) approach the scale or accuracy of the maps by either NRC or BCMFR. Zone 12 of Semenova-Tyan-Shanskaya (1964) includes substantial areas in southern British Columbia, Montana, Idaho, and Washington that are south of the boreal zone depicted in the present paper (Fig. 19). Alpine areas above the tree limit are inaccurately mapped, which is the same for each of the other maps of the region. Rowe's (Rowe 1972) boreal forest region in western Canada corresponds generally with the boreal zone depicted in the present paper (Fig. 19) but he

Fig. 17. Boreal zone and hemiboreal subzone adapted from Bird (1961), Rowe (1972), Marschner (1974), Zoltai (1975), Finley (1976), Archibold and Wilson (1980), and the Natural Regions Committee (NRC 2006) in the North American interior compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.



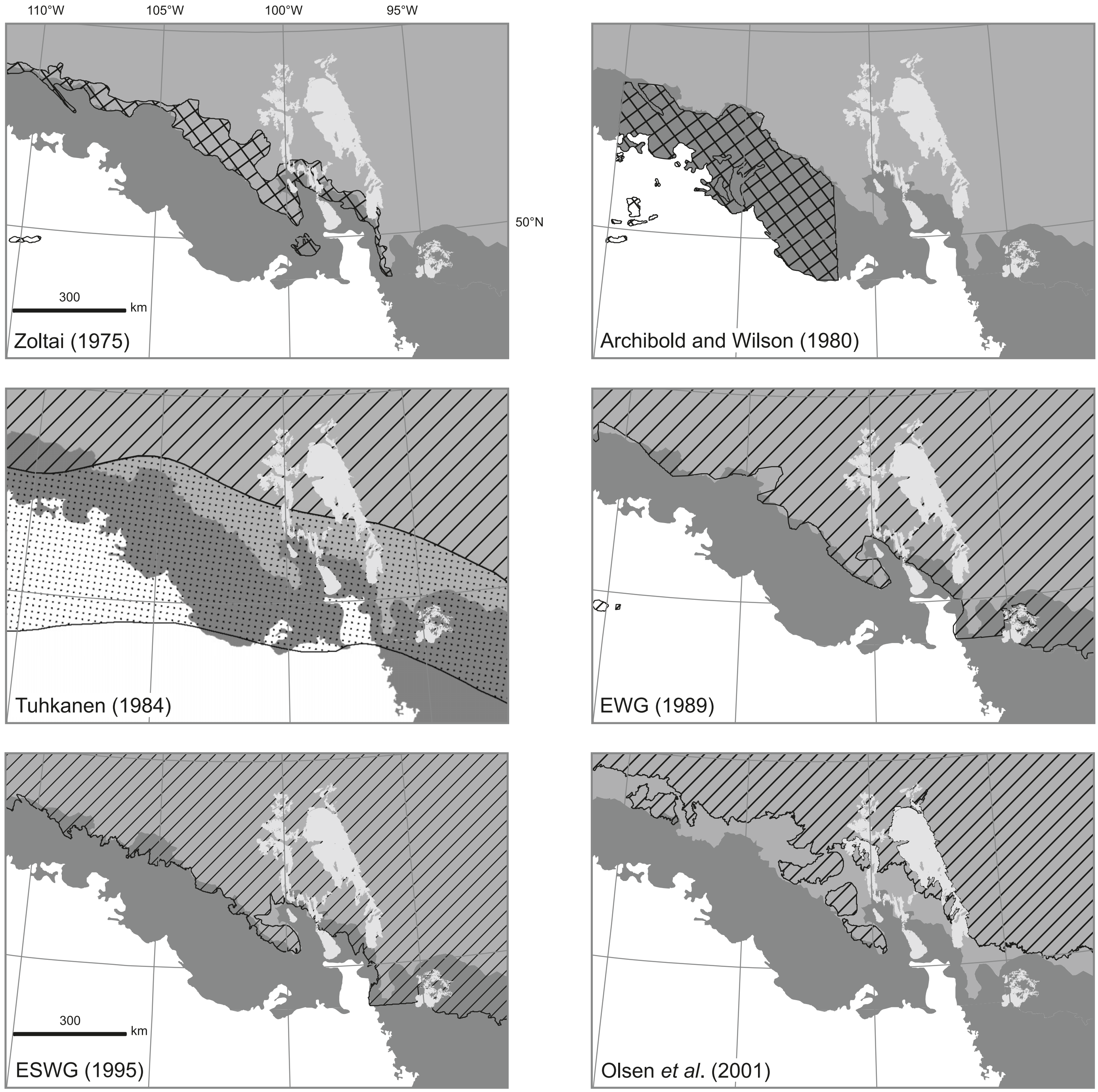
distinguishes a subalpine forest region in eastern British Columbia and southwestern Alberta. The boreal ecoclimatic provinces and regions on EWG's (EWG 1989) map correspond poorly with the present paper's boreal zone in interior British Columbia (Fig. 20). ESWG's (ESWG 1995) map coincides generally with the present paper's boreal zone (Fig. 20). ESWG places much of southern interior British Columbia in their montane cordillera ecozone. The taiga plains, boreal plains, and boreal cordillera ecozones of ESWG (1995) correspond, in part, to the boreal tundra woodland, boreal coniferous forest, and boreal mountain system ecological zones of FAO (2001). In the map of Olson et al. (2001) (Fig. 20), their boreal forests – taiga biome in the cordilleran region corresponds, in part, to the taiga plains and boreal cordillera ecozones of ESWG (1995) but the area corresponding to the Peace lowland ecoregion of ESWG (1995) has been placed in the temperate grasslands, savanna, and shrublands biome and most of the remaining area in the region considered to be part of the boreal zone in this paper along the foothills to the east of the Rockies has been placed within the temperate coniferous forests biome.

6.3.2.1.4. Alaska — The boreal zone in this region is adapted from the scheme of Viereck and Little (1972) and Yurtsev (1994) and includes most of interior Alaska, the Alaska Peninsula, and the Aleutian Islands. The coastal spruce-hemlock forests of Viereck and Little (1972) are considered part of the temperate zone of western North America in the present paper. There is no transitional hemiboreal subzone in Alaska because the boreal and temperate zones are separated by alpine areas and icefields along the coastal mountains. Hare and Ritchie (1972) consider these Alaskan coastal forests as a "low-temperature, low-energy differentiate'' of the more southern temperate variant in coastal British Columbia, Washington, and Oregon. Tuhkanen (1984) places the Alaskan coastal forests in his middle boreal zone.

6.3.3. Hemiboreal–temperate ecotone

Southward through the hemiboreal subzone the frequency of cold tolerant conifers diminishes. In the temperate zone, deciduous hardwoods dominate in the east and maritime conifers in the west. Moderately cold-tolerant conifers, such as *Tsuga canadensis*, *Picea rubens*, *Pinus strobus*, and *Thuja occidentalis* in eastern North America and *Picea engelmanii*, its hybrid with *Picea glauca*, and *Abies lasiocarpa* in western North America, can also be found in the hemiboreal subzone mixed with the cold tolerant conifers, depending to a large degree on local site conditions. In eastern North America it appears that the greater photosynthetic capacity of deciduous tree species gives them a competitive advantage

Fig. 18. Boreal zone and hemiboreal subzone adapted from Bird (1961), Rowe (1972), Marschner (1974), Zoltai (1975), Finley (1976), Archibold and Wilson (1980), and the Natural Regions Committee (NRC 2006) in the North American interior compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.

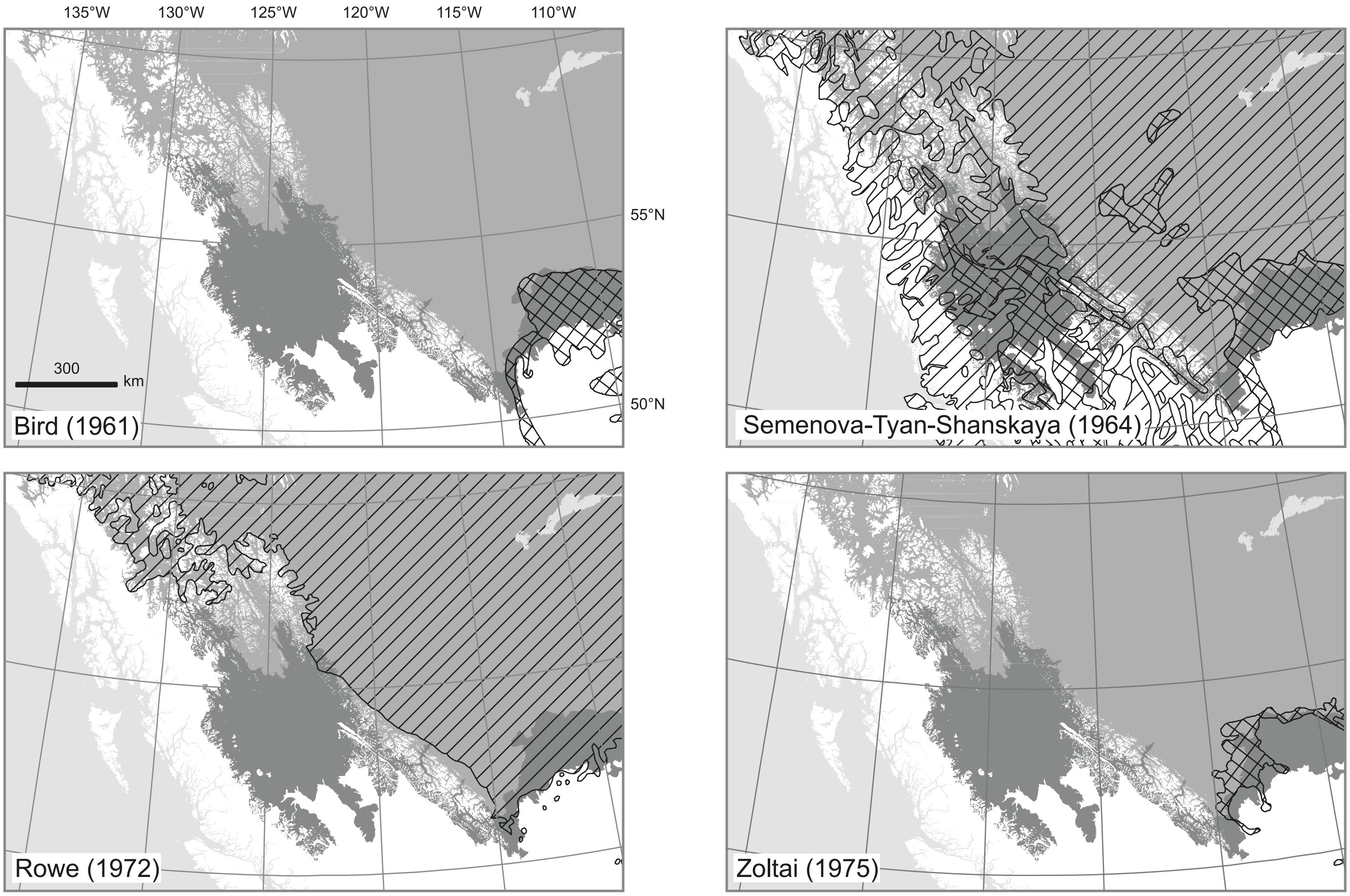


over boreal species, provided that unseasonably cold temperatures no longer limit the deciduous species (Woodward 1987; Barbour and Christensen 1993; Arris and Eagleson 1989, 1994). Temperate trees have higher productivity (Arris and Eagleson 1994) at the cost of cold hardiness, whereas boreal conifers have lower productivity but greater cold hardiness (Woodward 1987). Consequently, the poleward limit for any given species is probably temperature limited, whereas the limit in the equatorial direction is probably competitive exclusion (Woodward 1987). Boreal trees can grow in the temperate zone where factors other than climate allow for their occurrence. Conversely, temperate trees can grow in the boreal zone where topography allows a microclimate favourable to their survival and growth.

6.3.3.1. Boundaries

6.3.3.1.1. Atlantic Maritimes, Northeastern US, and Great Lakes — In the Atlantic Maritimes and the northeastern US, the hemiboreal subzone, depicted in Fig. 13, includes Rowe's (Rowe 1972) Acadian forest region and most of the

Fig. 19. Boreal zone and hemiboreal subzone adapted from Zoltai (1975), the Natural Regions Committee (NRC 2006), and the British Columbia Ministry of Forests and Range (BCMFR 2006) in western North America compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.

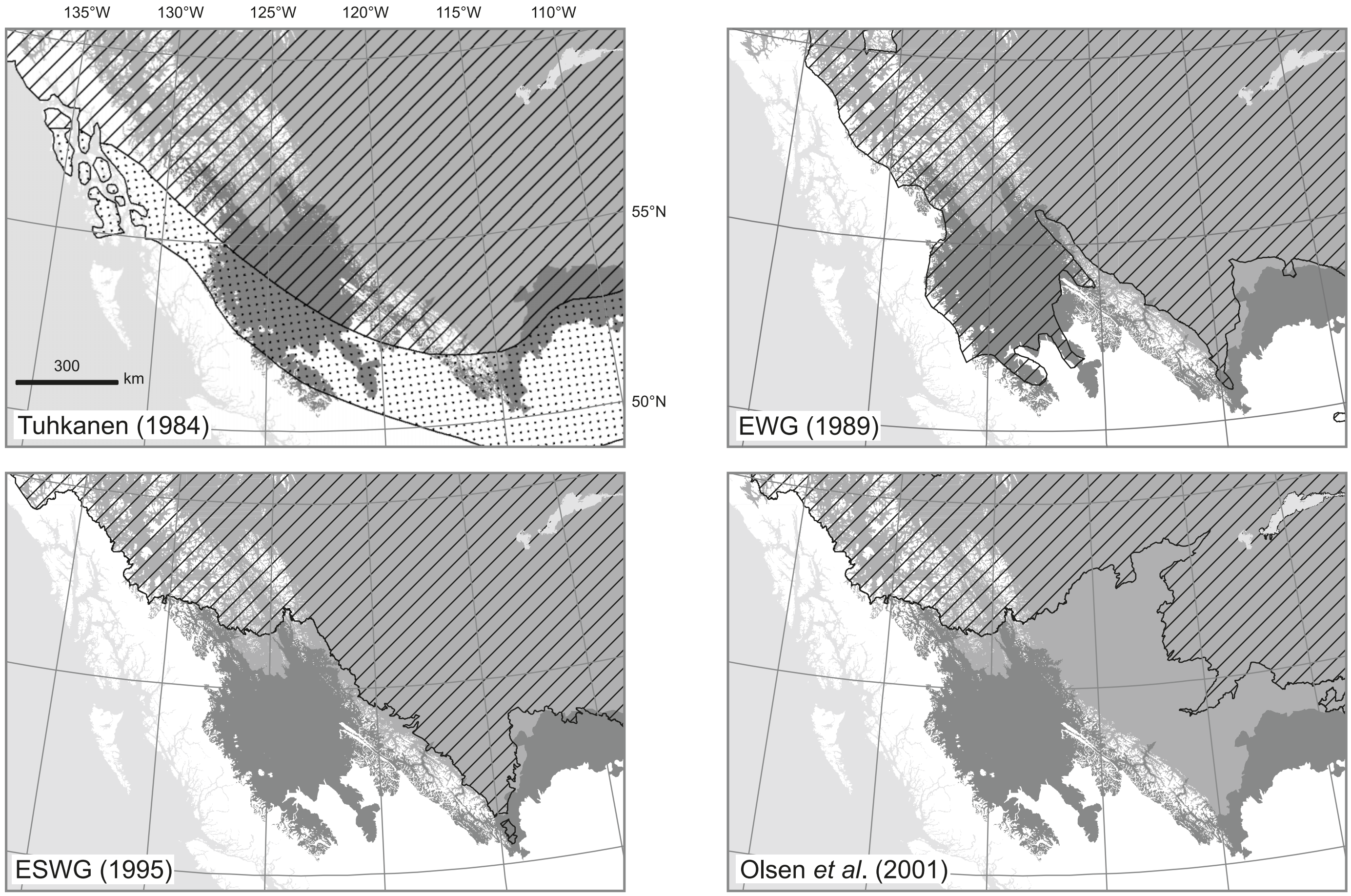


so-called "spruce-fir forest vegetation type" of Shantz and Zon (1936) that is contiguous with forests of the former forest region (Figs. 13 and 14). The patches of higher elevation spruce-fir forests in the Adirondack Mountains of New York, the Green Mountains of Vermont and Massachusetts, and the White Mountains of New Hampshire mapped by Hawley and Hawes (1912), Bray (1915), Dana and Greeley (1930), Westveld (1930, 1956), and Hotchkiss (1932) are not considered part of the hemiboreal subzone as these are outliers. The "spruce-fir forest vegetation type" in much of the Appalachian region of the US actually consists of two forest types: a mixedwood forest occurring at elevations of 550–760 m and primarily consisting of *Picea rubens*, *Abies balsamea*, *Tsuga canadensis*, *Pinus strobus*, *Pinus resinosa*, *Acer saccharum*, and *Betula alleghaniensis*; and a true *Picea-Abies* forest occurring at elevations above 760–800 m (Dana and Greeley 1930; Westveld 1930; Braun 1950; Bormann et al. 1970; Siccama 1971, 1974; Spear 1989; Cogbill and White 1991). In the case of the mixedwood forest, the latter five species gradually drop out of the species mix as elevation increases and the spruce-fir zone is approached; the tree-limit species is *Abies balsamea* (Braun 1950; Bormann et al. 1970; Leak and Graber 1974; Spear 1989; Cogbill and White 1991). Forests below 550 m are dominated by temperate deciduous species (Braun 1950). Shantz and Zon (1936) place their "spruce-fir forest vegetation type" in the boreal zone, but both the *Picea-Abies* forest type and the lower-elevation mixedwood forest type have more affinity with the forests of Halliday's (Halliday 1937) and Rowe's (Rowe 1972) Acadian forest region (Braun 1950; Oosting and Reed 1944; Oosting and Billings 1951; Davis 1966; Bormann et al. 1970; Siccama et al. 1970; Lorimer 1977; Bailey 1995). *Picea rubens*, in particular, cannot be considered a boreal species as its tolerance to cold is limited (Table 2).

In Quebec, the hemiboreal subzone includes the mixed forest vegetation subzone of Saucier et al. (1998) (Figs. 13, 16). It also includes land subregion 3d-S (Collines du Mont-Mégantic) of the deciduous forest vegetation subzone considered by Saucier et al. (1998) to be transitional between the sugar maple-yellow birch and the balsam fir-yellow birch bioclimatic domains. Edge-matching was required at the Quebec-Maine border near Megantic Mountain. Thus, contour lines were followed from Quebec into Maine to match the various polygons taken from Shantz and Zon (1936) and from Saucier et al. (1998).

In the Great Lakes region of Ontario (Figs. 16, 17), Rowe's (Rowe 1972) sections L.9–L.12 are included in the present paper's hemiboreal subzone. These areas can be considered transitional because of the abundance of boreal coni-

Fig. 20. Boreal zone and hemiboreal subzone adapted from Zoltai (1975), the Natural Regions Committee (NRC 2006), and the British Columbia Ministry of Forests and Range (BCMFR 2006) in western North America compared with relevant boreal (diagonal hatching), hemiboreal (stippled), or other (cross hatching) zones or subzones of other pertinent studies.



fers here (Maycock and Curtis 1960; Rowe 1972; Jackson et al. 2000). In Michigan, Minnesota, and Wisconsin (Figs. 16, 17), pre-settlement forests of spruce, pine, and mixedwoods mapped by Marschner (1974), Finley (1976), and Comer et al. (1995*a*, 1995*b*) have been included in the hemiboreal subzone. These forests have been included because they are similar to Canadian hemiboreal forests on the opposite side of the Great Lakes on the basis of data presented by Daubenmire (1936), Cunningham and White (1941), Braun (1950), Buell and Cantlon (1951), Buell and Niering (1957), Maycock and Curtis (1960), Maycock (1961), Janssen (1967), Janke et al. (1978), Frelich and Reich (1995), Schmidt et al. (1996), and Friedman et al. (2001). Edge-matching was required at the Ontario-Quebec border. Contour lines were followed from Quebec into Ontario to match the boundaries.

Although Braun (1950) does not map a hemiboreal zone, she does recognize the transitional nature of the northern portion of her hemlock – white pine – northern hardwoods region. She also recognizes the affinities between the red spruce–mixedwoods of much of New England and those of the Canadian Atlantic region. In the Atlantic Maritimes, Sjörs (1963) excludes Rowe's section A.4 and most of section A.10. He also excludes much of the red spruce – mixedwoods of upland Maine from his hemiboreal zone and instead classifies these areas as "sub-alpine and montane belts of non-boreal mountains" (Fig. 13). In Quebec, Sjörs' boreo-nemoral zone lies substantially to the south of the present paper's hemiboreal zone. To the east of the Great Lakes in Ontario, Sjörs' (Sjörs 1963) boreo-nemoral zone is more extensive than that presented for the hemiboreal subzone here (Fig. 16). Semenova-Tyan-Shanskaya (1964) does not recognize a hemiboreal zone, although in the Canadian Atlantic region (Fig. 13) zone 10 corresponds well with Rowe's (Rowe 1972) Acadian forest region. Semenova-Tyan-Shanskaya's zone 14 approximates the uplands of New York and New England (Fig. 13) but also includes the entirely different uplands of the Gaspé Peninsula and northwestern Newfoundland in the same zone. Although Tuhkanen's (Tuhkanen 1984) hemiboreal subzone is substantially wider latitudinally than the subzone mapped in the present paper to the west and east of the Great Lakes (Figs. 14, 16), it excludes large areas of the Canadian Atlantic region and the northeastern US. The map of Kingsley (1985), which is based on a relatively recent forest inventory, provides a relatively current depiction of the distribution of the spruce-fir forest type in the northeastern US (Fig. 14). The maps of ESWG (1995) and FAO (2001) do not recognize a hemiboreal subzone or equivalent (Figs. 15, 16). The approach of Olson et al. (2001) is similar, at least at the level of biomes, but these authors do identify some distinct areas (e.g., eastern forest – boreal transition ecoregion) within the temperate broadleaf and mixed forests biome as transitional between this biome and the boreal forests – taiga biome; however, the boundaries of the ecoregion differ from those in the present paper.

6.3.3.1.2. Western Interior Parkland — The southern boundary of the hemiboreal subzone in this region is adapted from the southern boundary of the aspen parkland as mapped by Bird (1961) in Manitoba, Archibold and Wilson (1980) in Saskatchewan, and NRC (2006) in Alberta as the central parkland and foothills parkland natural subregions, although, in Saskatchewan and Manitoba, several outliers mapped by these workers are excluded from the hemiboreal zone (Figs. 17, 19). The boundary of the parkland in Minnesota (Fig. 17) is adapted from the boundaries depicted by Marschner (1974). Both Ewing (1924) and Janssen (1967) consider the aspen parkland in Minnesota to be the terminus of the broader forest–grassland transition that extends into Canada. The aspen parkland in this state extends from about the Wild Rice River (a tributary of the Red River) in Mahnomen County north to the Canadian border as a narrow belt about 10–50 km wide from east to west (Ewing 1924). In Canada, the aspen parkland areas in northwestern and northern Alberta and British Columbia in the Peace River region, as mapped in detail by Moss (1952) and which can also be seen on several of the other maps of the region, are not included in the hemiboreal subzone. The occurrence of these outliers of grassland and aspen parkland is related more to the distribution of solonetzic soils than climate (Moss 1952; Krajina 1973*a*; Redmann and Schwarz 1986; Wilkinson and Johnson 1983). These areas may be relicts of grasslands that were more widely distributed earlier in post-glacial times and that have been perpetuated until recently by regular burning by indigenous peoples (Moss 1952; Nelson and England 1971; Anderson and Bailey 1980; Bailey et al. 1990). The southern boundary of the parkland delineated by Bird (1961) corresponds well with the boundary adapted from Archibold and Wilson (1980) in Saskatchewan but lies substantially to the south of NRC's (NRC 2006) boundary in Alberta (Figs. 17, 19). Bird (1961) depicts aspen parkland extending through southwestern Alberta into Montana, on the basis of studies by Moss (1944, 1955) and Lynch (1955). Lynch considers Glacier County in Montana as the terminus of the aspen parkland in the west; these aspen stands are floristically similar to those of the more northern aspen parkland of the Canadian Prairie Provinces (Looman 1987) but the climate is considerably warmer (i.e., temperate). The boundary of Semenova-Tyan-Shanskaya (1964) in Manitoba (Fig. 17) is too general as zone 16 includes grassland areas whereas in Saskatchewan the boundary lies substantially north of the boundary adapted from Archibold and Wilson (1980), and in west-central and southwestern Alberta (Fig. 19) it deviates greatly from the boundary of NRC (2006). The parkland boundaries depicted by Rowe (1972) correspond fairly well with the boundaries of the present paper in Manitoba and Alberta (Figs. 17, 19), but Rowe considers these forests to be boreal. He also excludes substantial areas of the parkland in Saskatchewan mapped by Archibold and Wilson (1980). The hemiboreal subzone of Tuhkanen (1984) in this region corresponds poorly with the present paper's depiction of the subzone (Figs. 18, 20). Tuhkanen excludes a relatively large area of parkland in east-central Alberta and Saskatchewan but includes most of the grasslands south of the parkland to the Canada-US border and forests consisting of cold-tolerant boreal species in southern Manitoba. ESWG (1995) delineates the parkland in its aspen parkland ecoregion but lumps it into the prairies ecozone, which is not considered a boreal ecozone. The southern boundaries of ESWG's aspen parkland ecoregion coincide poorly with those of the present paper in Manitoba and Saskatchewan but well in Alberta. The map of FAO (2001) does not include a distinct parkland region; this area falls within its temperate steppe ecological zone, of which the northern boundary follows that of the prairies ecozone of ESWG (1995). The boundary in the map of Olson et al. (2001) corresponds poorly with the present paper's boundary in the region because Olson and colleagues place the entire parkland region in their temperate grasslands, savannas, and shrublands biome (Figs. 18, 20). They also include in the same biome a large area of northern Alberta and a smaller area of British Columbia (Fig. 20). The latter two areas correspond to the Peace lowlands ecoregion of ESWG (1995), the ecoregion in which some of the grasslands and parklands mapped by Moss (1952) are located.

6.3.3.1.3. Western cordillera — In Alberta, NRC's (NRC 2006) montane natural subregion north of the height of land separating the Livingstone River and Highwood River watersheds (Wilkinson Summit at about 50°11′N) to the Athabasca River valley near Jasper is included in the hemiboreal subzone (Fig. 19). *Pseudotsuga menziesii* var. *glauca* are mixed with cold-tolerant boreal species in many of the forests in this natural subregion. The subalpine natural subregion from the Wilkinson Summit north to the upper Red Deer River drainage is also included in the hemiboreal subzone. At the Wilkinson Summit and near the upper Red Deer River watershed, strong floristic discontinuities have been noted by Ogilvie (1962, 1963), Achuff and La Roi (1977), and NRC (2006). Although the Rocky Mountain region of Alberta has, on average, the coolest summers, shortest growing season, highest mean annual precipitation, and the most snow in winter of any natural region in the province, the montane natural subregion is distinguished by having milder winters than most other subregions in Alberta and by the strong influence of warm Pacific air masses and frequent chinook or föhn winds (NRC 2006). In British Columbia, areas within BCMFR's (BCMFR 2006) sub-boreal spruce and sub-boreal pine-spruce biogeoclimatic zones are included in the hemiboreal subzone. Isolated patches of these forests are not included in the hemiboreal subzone if they are surrounded by forests consisting of cold-intolerant tree species characteristic of the temperate zone. Subalpine forests in the Engelmann spruce-subalpine fir biogeoclimatic zone of BCMFR (2006) that are contiguous with either the lower elevation sub-boreal spruce or sub-boreal pine-spruce biogeoclimatic zones in British Columbia are also included in the hemiboreal zone. These subalpine forests are climatically intermediate between boreal forests to the north and lower elevation temperate *Pseudotsuga menziesii* var. *glauca* forests (personal communication, Del Meidinger, British Columbia Ministry of Forests and Range, 3 November 2008). Subalpine forests on the windward side of the Coast Mountains (e.g., mountain hemlock biogeoclimatic zone) are excluded from the hemiboreal zone because the vegetation structure, the milder climate as influenced by warm Pacific air, the heavy snow that prevents the ground from freezing, and the humic podzols are all completely different from those of the interior subalpine forests east of the crest of the Coast Mountains (Krajina 1973*a*, 1975). Parts of the montane spruce biogeoclimatic zone of BCMFR (2006) that exist as outlying patches within the sub-boreal spruce or sub-boreal pine-spruce biogeoclimatic zones are also included in the hemiboreal subzone. The bunchgrass, coastal Douglas-fir, coastal western hemlock, interior cedar-hemlock, interior Douglas-fir, and ponderosa pine biogeoclimatic zones of BCMFR (2006) are considered temperate in this paper except for a few relatively small outlying areas of the interior cedar-hemlock biogeoclimatic zone. Classification of the previous six biogeoclimatic zones as temperate is consistent with the positions of Habeck (1987), Franklin (1988), and Peinado et al. (1997). The forest types in these biogeoclimatic zones extend considerably south and are also similar to those described by Daubenmire (1943, 1952), Fonda and Bliss (1969), and Pfister et al. (1977) for Washington, Oregon, Idaho, Montana, and Wyoming. The cold tolerance (Table 2) and the frost hardiness of typical species in the aforementioned biogeoclimatic zones, such as *Larix occidentalis*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Thuja plicata*, *Tsuga heterophylla*, and *Tsuga mertensiana*, are typical of the degree of hardiness of northern temperate species (Sakai and Weiser 1973; Sakai 1983; Grossnickle 1992; Whitlock 1995; Fiedler and Lloyd 1995; Schaberg et al. 2005). The distribution of the latter five species is depicted in Figs. 2 and 4.

The map of NRC (2006) was produced at a scale of 1:250 000 and the map of BCMFR (2006) was derived from maps of scales ranging from 1:20 000 to 1:600 000; the other maps applicable to the region do not approach the scale or accuracy of these recent maps. Zone 12 of Semenova-Tyan-Shanskaya (1964) includes substantial areas where temperate species dominate in southern British Columbia, Montana, Idaho, and Washington that are south of the present paper's hemiboreal zone (Fig. 19). Daubenmire (1956) considers subalpine forests in Washington and Idaho as taiga, and Peet (1988) considers the spruce-fir forests along the entire length of the Rocky Mountains as a southern extension and modification of the boreal zone. I disagree with all three of the latter authors as there is a clear floristic and climatic gradient latitudinally through British Columbia. Rowe's (Rowe 1972) map (Fig. 19) does not recognize a hemiboreal subzone but instead distinguishes a subalpine forest region and a montane forest region from his boreal forest region. Some areas within Rowe's subalpine and montane forest regions correspond with the hemiboreal subzone mapped in the present paper. Tuhkanen's (Tuhkanen 1984) hemiboreal subzone generally lies farther to the south than the present paper's hemiboreal zone (Fig. 20); it also includes forests with temperate species. EWG's (EWG 1989) map (Fig. 20) does not include a hemiboreal subzone. The montane cordillera ecozone of ESWG (1995) includes all of the present paper's hemiboreal subzone, large areas of boreal forest in the north and east, and temperate forests consisting of cold-intolerant tree species in the south. Similarly, the temperate mountain system global ecological zone of FAO (2001) and the temperate coniferous forests biome of Olson et al. (2001), both of which partly use the boundaries of ESWG's montane cordillera ecozone, also include large areas of forests consisting of cold-tolerant boreal species. The maps of ESWG (1995) and Olson et al. (2001) are depicted in Fig. 20.

6.4. Comparisons with Eurasian boreal zone

There are similarities in the genera making up the northern tree limit at the forest-tundra ecotone in North America and Eurasia. In Eurasia, moving from east to west, the predominant tree species at the tree limit are *Pinus pumila*, *Larix gmelinii* (= *Larix dahurica*), *Larix sibirica*, *Picea obovata*, *Pinus sylvestris*, and *Betula pubescens* (Hämet-Ahti 1963; Hustich 1952, 1966; Tuhkanen 1980; Grishin 1995; Kremenetski et al. 1998; MacDonald et al. 2000). The tree limit in Greenland, Iceland, and northern Scandinavia is represented by the same species, *Betula pubescens*, although the taxonomy of species remains in doubt (Hämet-Ahti 1987; Sulkinoja 1990). *Pinus sylvestris* often grows in association with *Betula pubescens* in northern Scandinavia (Hustich 1966). Nowhere in North America do *Pinus* species reach the northern tree limit (Fig. 2). For much of Eurasia, *Larix* species are the most prevalent trees at the tree limit (Hustich 1952, 1966; Kremenetski et al. 1998). The deciduous habit of both *Larix* and *Betula* species may allow trees of these genera to extend farther north than the boreal evergreen conifers. Like *Populus balsamifera*, *Populus suaveolens* grows as small trees scattered on flood plains along with *Chosenia arbutifolia* near the northern tree limit in far eastern Eurasia (Hustich 1966; Tuhkanen 1980; Grishin 1995).

Several researchers have compared and contrasted the boreal forests of eastern Canada with those of northwestern Eurasia. The flora of the forests and peatlands in the boreal zone in eastern Canada is similar to the flora of the forests and peatlands of northern Europe, with a large proportion of the vascular and cryptogamic species common to both regions (Sjörs 1961; Ahti 1964). There are also strong similarities in forest types (as defined by Cajander 1926) and the distribution and types of peatlands (Kalela 1962*a*, 1962*b*).

In the hemiboreal subzone, the mixedwood forests of eastern North America, Europe, and the Asian Far East are similar on the basis of the tree genera they contain (i.e., *Tsuga*, *Fraxinus*, *Quercus*, *Pinus*, *Picea*, *Tilia*, *Acer*) as well as other floristic characters (Hare 1954; Kalela 1962*a*, 1962*b*; Sjörs 1963; Tuhkanen 1984; Rowe 1972; Grishin 1995). In Scandinavia, the northern limit of *Quercus robur* is usually considered as the boundary between the boreal zone and hemiboreal subzone and generally corresponds with *limes norrlandicus* (Fries 1948; Hustich 1960), but in Russia the southern boundary of the boreal zone is drawn some distance farther south by the Russians (e.g., Lavrenko and Sochava 1954; Isachenko et al. 1988; Belov et al. 1990) than the northern limit of *Quercus robur* (Sjörs 1963). Along *limes norrlandicus*, which runs from southern Norway and Sweden east-south-eastwards to the Urals, members of *Acer*, *Fraxinus, Quercus*, and *Tilia* replace the dominant conifers, although some *Picea abies* and *Pinus sylvestris* remain (Fries 1948; Hare 1954). Similarly, *limes labradoricus* is the name suggested for the boundary in North America where the typical boreal *Picea-Abies* forest transitions to a forest dominated by *Acer saccharum*, *Betula alleghaniensis*, *Pinus strobus*, *Pinus resinosa*, *Fagus grandifolia*, *Tsuga canadensis*, *Tilia americana*, and species of *Quercus* and *Fraxinus*, although, again, boreal *Picea glauca*, *Picea mariana*, *Abies balsamea*, and *Pinus banksiana* remain relatively abundant (Hustich 1960; Hare 1954; Hustich 1949 refers to this floristic boundary as the "southern main treeline"). The northern limit of *Acer saccharum* in eastern North America (Fig. 3) could be used as a similar indicator of the southern boundary of the boreal zone in this region. *Acer saccharum*, however, is more winter hardy than the European *Quercus robur* on the basis of hardiness trials in Canada (Ouellet and Sherk 1967; Davidson et al. 1994; NRCan 2001*b*) and horticultural information (Partyka et al. 1980). Thus, the presence of the two species does not necessarily indicate equivalent climatic conditions for the southern boundary of the boreal zone in North America and Europe. *Betula alleghaniensis*, another common associate of *Acer saccharum*, whose distribution (Fig. 3) is important in delineating the boreal zone's southern boundary in the Great Lakes region (Halliday and Brown 1943), is also more winter hardy than *Quercus robur* (Davidson et al. 1994; Dirr 1998). The southern boundary of the boreal zone in Ontario could be placed more precisely with detailed digital forest inventory maps that depict the current distribution of the temperate *Acer saccharum* and *Betula alleghaniensis* and the boreal *Picea glauca*, *Picea mariana*, *Pinus banksiana*, and *Larix laricina*; this approach is similar to the one described by Hämet-Ahti (1988). One problem to this approach, however, is that the current distribution of these tree species may be different than pre-European settlement conditions, a situation observed by Jackson et al. (2000).

The aspen parkland of the Prairie Provinces and aspen-oak forests of southern Manitoba and northern Minnesota appear to be similar to the steppe forests of southern Russia east of the Ural Mountains and northern Kazakhstan, Mongolia, and the Russian Far East on the basis of information given by Lavrenko and Sochava (1954), Sjörs (1963), Rowe (1972), Hämet-Ahti (1981), Tuhkanen (1984), Nimis et al. (1994), and Kushlin et al. (2003). *Quercus macrocarpa* (North America) and *Quercus mongolica* (Asia) grow in similar forests under similar climatic conditions and appear to be equally hardy to cold (Sakai and Larcher 1987). In central Alberta and Saskatchewan there are patches of *Pinus banksiana* forests, which occupy sandy aeolian and fluvial deposits. These forests range in size from several hundred to tens of thousands of hectares. Similar *Pinus sylvestris* forests are found at similar sites and latitudes in Russia and Kazakhstan (Isachenko et al. 1988; Belov et al. 1990; Lavrenko and Karamysheva 1993; Kushlin et al. 2003).

7. Extent of boreal zone and hemiboreal subzone

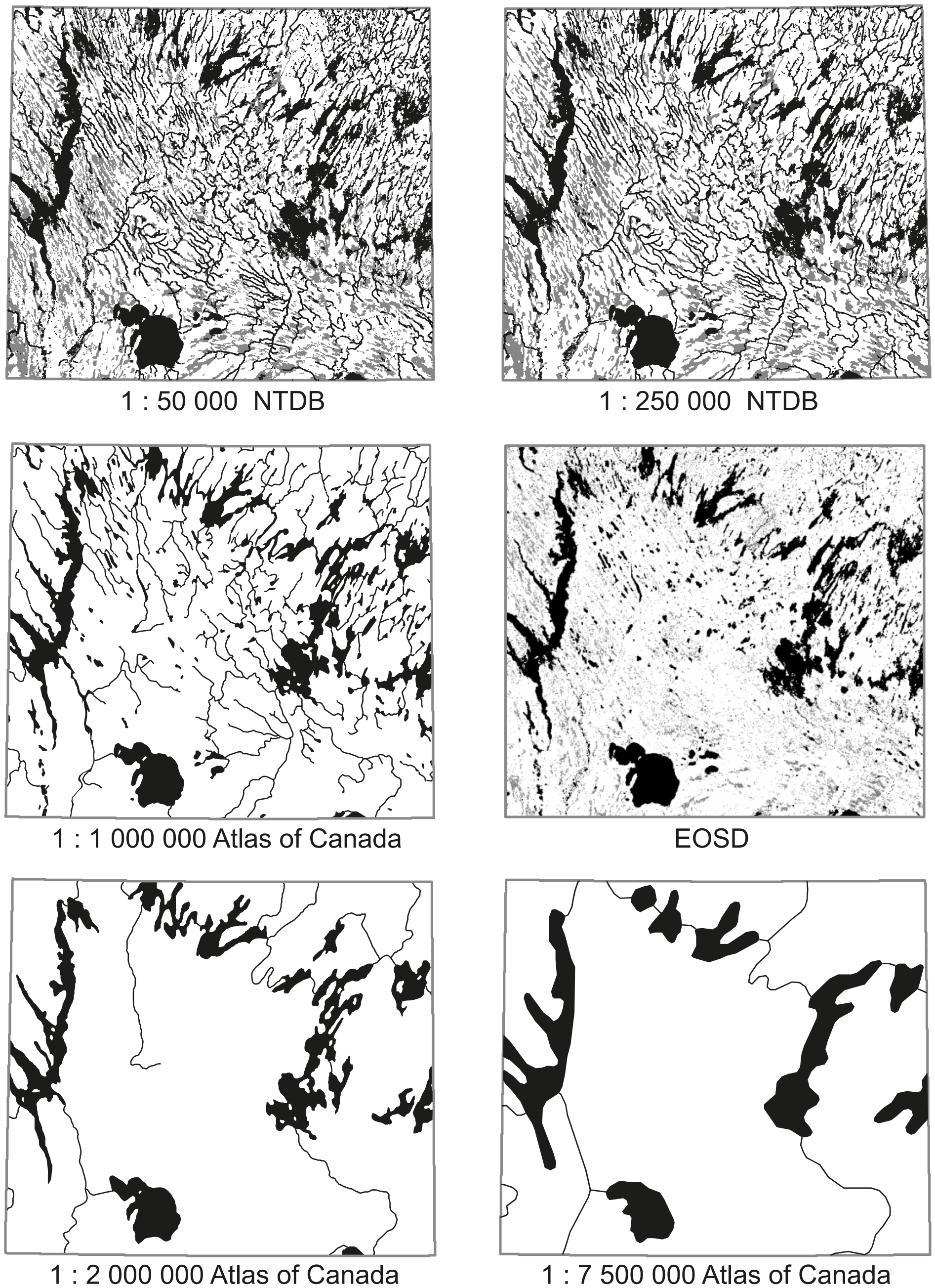
7.1. Determination of areal statistics

Once the boundaries of the boreal zone were selected at the three ecotones, polygons between these boundaries were dissolved in the GIS. The resulting coverage was then projected with the Albers equal-area conic projection with two standard parallels set at 47.5°N and 54.5°N and with the central meridian set at 113°W. The reference layer for the Canadian portion of North America was from the *Atlas of Canada* (1:1 000 000). The reference layer for the Greenland and Saint Pierre and Miquelon portions of North America was from the Environmental Systems Research Institute (1:1 000 000), whereas comparable data for the US was from the 2005 edition of the *National Atlas of the U.S.* (1:2 000 000). The hydrology layer for Canada and the US was from the *Atlas of Canada* (1:1 000 000) and the *National Atlas of the U.S.* (1:2 000 000), respectively. Rivers in the hydrology layer exist as lines (i.e., they have only one dimension: length); thus, 20-m buffers were assigned to the lines to estimate the area of these features. Total area of the boreal zone, area of inland water (including rivers), and, by subtraction, total land area were determined with the GIS. Statistics on forests, other wooded land, and other land for Canada were generated by intersecting this paper's boreal zone and hemiboreal subzone coverage with the data of Canada's Forest Inventory (CanFI, version 2001) (personal communication, Mark Gillis, Manager, National Forest Inventory, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, January 2009). For Alaska and the Great Lakes and northeastern region in the US, the coverage was intersected with satellite-derived forest cover data available at the US Geological Survey (http://edc2.usgs.gov/glcc/fao/index.php).

7.2. Sources of error related to mapping

The reader should be aware of three possible sources of error in areal determinations related to mapping: scale, conversion of analogue maps to digital format, and map projection. The analogue and digital maps used to construct this paper's boreal zone map varied greatly in scale (e.g., 1:20 000 to 1:8 000 000); the majority of the maps were at a scale of about 1:5 000 000. Generalization occurs in cartography because of five related procedures: selective omission, simplification, combination, exaggeration, and displacement (Keates 1996). Of these five procedures, selective omission and simplification are affected by scale and are most important in the context of the present paper. Selective omission refers to the restriction in display of the feature or phenomenon of the map's theme and is generally a function of scale, geographical density, and relative importance (Keates 1996). For example, the extent of rivers and lakes depicted on a map at 1:50 000 cannot be displayed on a map at 1:1 000 000 without compromising the legibility of the smaller scale map (Fig. 21). This, in turn, has an impact on the areal statistics of the extent of land and water derived from the two different maps (Table 5). Additionally, both linear features and outlines presented on a map need to be made less complex than the reality they depict and this is also dependent on scale (Keates 1996). This aspect is apparent when comparing the maps at various scales in Fig. 21. In the studies of Bird (1961), Zoltai (1975), Payette (1983), Timoney (1988), and Archibold and Wilson (1980), aerial photography, aerial surveys, ground surveys, or all three methods were employed to collect the data on which the maps in these publications were based. Presumably the data were captured on relatively large- or medium-scale maps

Fig. 21. Rivers and lakes depicted at various scales from the *Atlas of Canada* and from National Topographic and Earth Observation for Sustainable Development databases for an arbitrary region in central Saskatchewan bounded by 55°N and 56°N latitude and 106°W and 108°W longitude.



and then reduced to the scale depicted in the publications. During this process, linear features would have been omitted, simplified, or both.

Conversion of analogue maps to digital format involves several steps. The analogue map must be scanned. The map projection of the analogue map must then be identified so that a reference layer in the GIS with the same map projection as the analogue map can be opened. The map must be registered by adding control points and transforming the scanned map to the coordinate system of the control points on the reference layer. Next, the scanned map must be georectified. Finally, the spatial information of the scanned map is input into the GIS with heads-up digitizing. One of the key problems in the above steps is that often the map projection of the analogue map is not known and the scanned map must be rubber-sheeted (a GIS term referring to the process of digitally stretching the map) to fit the reference layer. Rubber-sheeting introduces error.

A map is a visual representation of part or all of the earth's surface and the success of this representation depends on the map projection chosen to produce the map (Pearson 1990). The earth is an oblate spheroid and both spheres and spheroids have been used to model the earth. Spheres and spheroids have undevelopable surfaces (i.e.,

Table 5. Areas of rivers and lakes estimated from different databases of different scale for an arbitrary region in central Saskatchewan bounded by 55°N and 56°N latitude and 106°W and 108°W longitude.

	Rivers		Lakes
Source data	Buffer width of lines representing rivers in the database[a] (m)	Area (ha)	Area (ha)
1:50 000 National Topographic Database	30	21 261	227 158
1:250 000 National Topographic Database	40	23 617	225 994
1:1 000 000 *Atlas of Canada*	70	21 880	210 365
1:2 000 000 *Atlas of Canada*	100	7549	166 655
1:7 500 000 *Atlas of Canada*	150	7397	169 737
EOSD (25-m resolution raster land-cover data)		219 862[b]	219 862[b]

Note: EOSD, Earth Observation for Sustainable Development.

[a]Rivers in the various databases are represented by lines. Widths were assigned to these lines by placing a buffer around them in the GIS to estimate their area. Buffer widths increase down the column because only progressively larger rivers are shown on maps as scale decreases.

[b]The value reported from the EOSD land-cover database represents areas classified as water (i.e., rivers and lakes).

they are three-dimensional shapes that cannot be developed onto a plane without distortion (Pearson 1990)). Distortion can occur in area, linear dimensions, angle, or shape, and minimizing distortion of one type leads to increased distortion in the others (Pearson 1990). There are three distinct types of projection: equal-area, conformal, and conventional (Pearson 1990). Equal-area projections preserve the ratio of areas on earth to corresponding areas on a map but they introduce distortion in distance and angle, with the latter suffering the most distortion (Pearson 1990). Equality of areas between the earth and the map (i.e., equal-area) is useful for depicting comparative areal extents of things such as the amount of forest or lakes in different countries, a situation in which distortion in shape and linear scale is acceptable (Fenna 2007). The best equal-area projection for a long narrow strip on the earth (i.e., not exceeding 30°–35° latitude) at about middle latitudes and parallel to a latitude is the Albers equal-area conic (Pearson 1990; Snyder 1993; Kennedy and Kopp 2000). However, Maling (1973) notes that it is difficult to find any projection to depict Canada or Russia in which linear or area distortion is less than 3% or angular deformation is less than 3°–5°. The map developed in this paper was projected with Albers equal-area conic projection and standard parallels set at 47.5°N and 54.5°N.

7.3. Areal extent

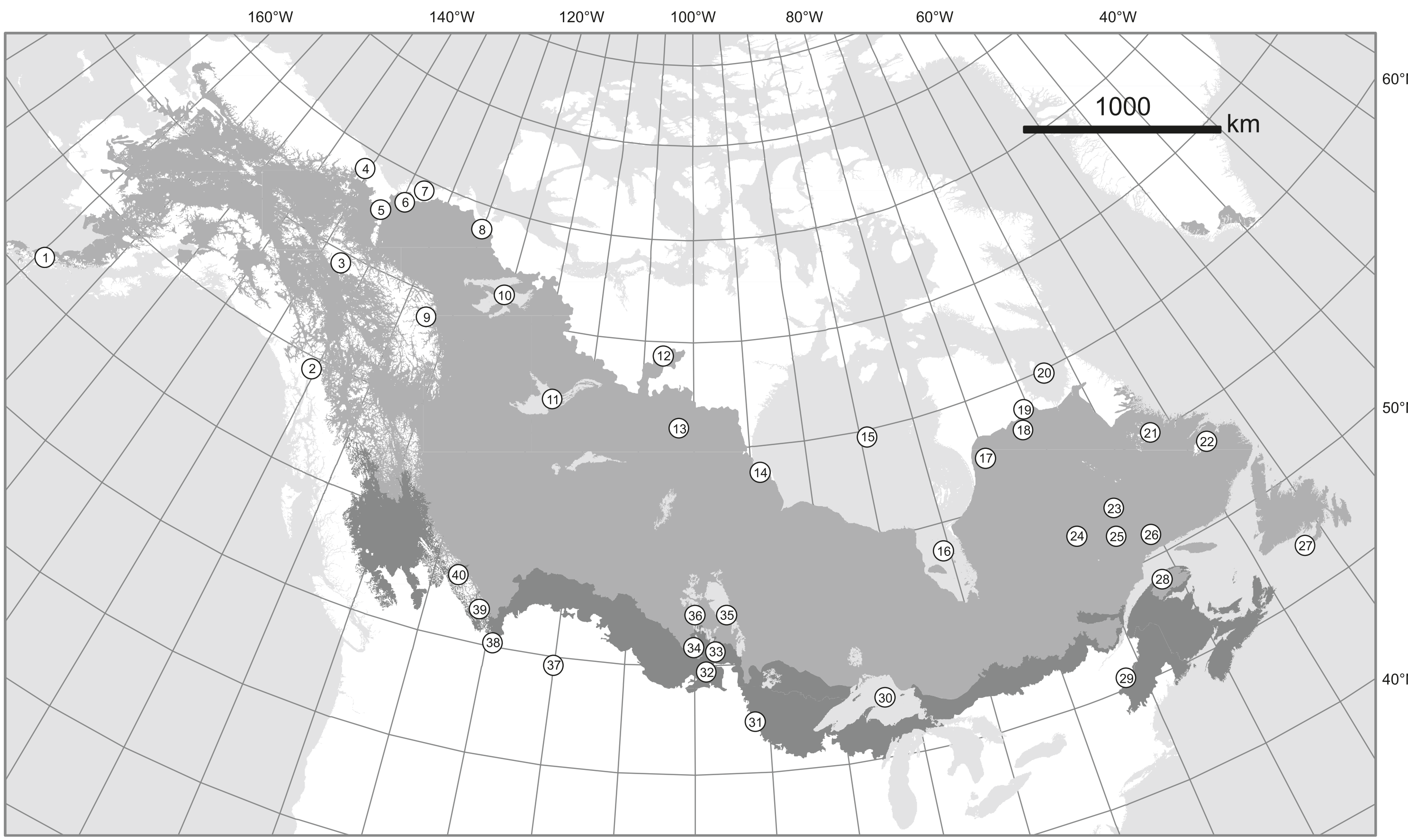
The North American boreal zone and the hemiboreal subzone are depicted in Fig. 22[3] and their areal extent is summarized in Table 6. The boreal zone covers about 627 million ha, or 29% of the total area covered by Canada, Greenland, Saint Pierre and Miquelon, and the US. If the hemiboreal subzone, at 116 million ha, is included in the boreal zone, then 34% of the North American continent north of Mexico is covered. Eighty-eight percent of the North American boreal zone lies within Canada, a figure that decreases to 86% with the hemiboreal subzone factored in. For Canada and the US, total areas of the boreal zone and the hemiboreal subzone reported in Table 6 are not the totals of the respective areas for forest land, other wooded land, non-forest land, alpine land, and area of water because total areas were determined independently with a GIS. The total area for the Canadian boreal zone using CanFI data and this paper's map is just over 537 million ha, which is 2.7% smaller than the value of 552 million ha reported in Table 6. CanFI data are derived from 48 sources, including management, regional, and reconnaissance-level inventories, satellite imagery, and other surveys (Power and Gillis 2006). CanFI contains 102 120 summary units, which vary in size from 2800 ha to 90 000 ha (average, 9 600 ha) depending on the data source (Power and Gillis 2006). During compilation of CanFI, stand-level data were aggregated to fewer and standardized records, including a scale change from about 1:20 000 to 1:20 000 000 (Power and Gillis 2006). Consequently, small differences in total areas for the Canadian portion of the boreal zone and the hemiboreal subzone are to be expected between values derived from CanFI data and those derived from the GIS and this paper's map because the two processes are entirely different. A similar situation applies to the Canadian hemiboreal areas and the US boreal and hemiboreal areas (see Table 6).

The area currently covered by forest and other wooded land accounts for about 58% of the boreal zone, whereas non-forest land, which includes wetlands, barren ground, and other areas without trees, covers 26%. Alpine land covers 5% and lakes and rivers cover 9%. When the hemiboreal subzone is included in the boreal zone, these percentages for forest and other wooded land, non-forest land, alpine land, and water remain basically unchanged.

For the most part, there is little variation in the total area of the boreal zone and hemiboreal subzone in Canada and the US between the different boreal maps that depict all or much of North America (Table 7). The exceptions are the areas based on Tuhkanen's (Tuhkanen 1984) map. His North American totals for the boreal zone and the hemiboreal subzone are substantially higher (8% and 10%, respectively) than the values for the same areas calculated from the present paper's map because he includes substantial areas with temperate tree species or grasslands. The most conser-

[3] Supplementary data for this article are available on the journal Web site (http://er.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3914. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Fig. 22. The boreal zone and the hemiboreal subzone in North America. Physical features and communities identified in the text: 1, Aleutian Islands; 2, Skagway; 3, Ogilvie Mountains; 4, Firth River; 5, Richardson Mountains; 6, Mackenzie River delta; 7, Tuktoyaktuk; 8, Horton River; 9, Mackenzie Mountains; 10, Great Bear Lake; 11, Great Slave Lake; 12, Thelon River; 13, Ennadai Lake; 14, Churchill; 15, Hudson Bay; 16, James Bay; 17, Minto Lake; 18, Lake Nedlouc plateau; 19, Leaf River; 20, Ungava Bay; 21, Harp Lake; 22, Mealy Mountains; 23, Schefferville; 24, Otish Mountains; 25, Groulx Mountains; 26, Manitou Mountain; 27, Saint Pierre and Miquelon; 28, Chic-Chocs Mountains; 29, Megantic Mountain; 30, Lake Superior; 31, Wild Rice River; 32, Spruce Woods; 33, Lake Manitoba; 34, Riding Mountain; 35, Lake Winnipeg; 36, Lake Winnepegosis; 37, Cypress Hills; 38, Wilkinson summit; 39, upper Red Deer River; 40, Jasper.



vative map of the boreal zone is that of Olson et al. (2001) because they classify large areas in the western interior as their temperate grasslands, savannas, and shrublands biome even though much of these areas were largely covered with cold-tolerant boreal conifers before European settlement.

Various areal statistics relating to Canada and its forests have been published (Table 8). Substantial variation exists in the national statistics as well in statistics for the boreal zone. The statistic with the least variation in Table 8 is that for the total area of Canada (CV = 0.6%). The largest difference is only –1.5% smaller than this paper's value for this parameter. The land area of Canada is slightly more variable (CV = 2.7%), with the largest difference being +8.1% greater than this paper's value for this parameter. Statistics related to forest land and other wooded land, however, are considerably more variable (12.8% ≤ CV ≥ 49.7%), with some values differing by more than 50%. Most notable in this regard are the values reported by Kuusela (1990), Iremonger et al. (1997), and Shvidenko and Apps (2006).

Three papers have attempted to estimate the amount of forest and other wooded land in the circumpolar boreal zone: Kuusela (1990), FAO (2001), and Burton et al. (2003). The total areas of forest and other wooded land in these three publications are 1.474 billion ha, 1.444 billion ha, and 1.150 billion ha, respectively. The list of countries that were deemed to fall at least partly in the boreal zone varied among the three publications and it is unclear whether or not a consistent approach to zonation was used, especially regarding treatment of the hemiboreal subzone. The most inclusive publication in terms of countries with at least some boreal forests is the report by FAO in 2001, although this report had the lowest estimate of the global area of forest and other wooded land. Burton et al. (2003) do not include forests in northeastern China, northern Mongolia, and Kazakhstan that could be classified as falling within the boreal zone or hemiboreal subzone, and Kuusela (1990) excludes forests in China and Mongolia. With these caveats in mind as well as the sources of error described earlier for mapping, forest and other wooded land in boreal North America could cover as little as 25% or as much as 32% of the circumpolar boreal zone. If the North American hemiboreal subzone is included, then the comparable percentages range from 29% to 37% of the circumpolar boreal zone. For boreal Canada, forest and other wooded land could represent as little 21% or as much as 27% of the circumpolar boreal zone's forest and other wooded land. Again, if the hemiboreal subzone is included in the Canadian boreal zone, then these percentages range from 24% to 31%. Of course, all these percentages depend on how the circumpolar boreal zone is mapped and how its extent is determined.

8. Discussion and conclusions

The map of the North American boreal zone and hemiboreal subzone should be considered a refinement of the maps of Rowe (1972) and Viereck and Little (1972). Boundaries on these maps were altered based on more recent studies that have provided well-described methods. These changes, however, reflect an improvement in technology and data sets rather than a shift due to environmental or anthropogenic factors. Thus, the map of the North American boreal zone and hemiboreal zone in the present paper should be considered the baseline map against which future changes can be measured.

Development of interpolated climate data sets on an extensive grid like those developed and used by Thompson et al. (1999), Fleming et al. (2000), and McKenney et al. (2001, 2006) will likely provide an opportunity to better characterize the climate of the boreal zone and the hemiboreal subzone when used in combination with the present paper's map. Such a characterization is required so that any future changes related to climate can be better quantified. The work of Thompson et al. (1999) can also be extended to refine the current relations between climate and the distribution of plant taxa strictly within the boreal zone.

The world's vegetation zones are in a state of flux at centennial, millennial, and longer time-scales as a result of climate variability. In terms of the boreal zone, forest development has varied across North America as a function of the timing of deglaciation and latitudinal position (Ritchie 1987). The tree limit was considerably farther north about 5 000 years ago in western Canada and about 3 000 years ago in eastern Canada (Ritchie 1987). Much of the North American boreal zone and hemiboreal subzone is relatively young because it was covered with continental glaciers not long ago. Since that time, plants have reacted to changes in climate as individual taxa (Huntley and Webb 1988; Prentice 1992; Jackson et al. 1997) resulting in plant associations at different points in time during past 21 000 years that have no floristic analogue today; a conclusion reached on the basis of analysis of extensive pollen and macrofossil data (Overpeck et al. 1992; Williams et al. 2004). Plant associations have varied continuously, appearing, then disappearing through time (Jackson et al. 1997; Williams et al. 2004). Vegetation development since the last glacial maximum can be divided into four stages: full-glacial stage between 21 000 and 17 000 years ago when vegetation development was relatively stable; transitional stages during the late glacial (16 000–11 500 years ago) and early Holocene (11 500–8 000 years ago); and a return to relative stability during the mid- to late Holocene (7 000–500 years ago) (Williams et al. 2004). Rates of vegetation change were greatest between 15 000 and 8 000 years ago and during the past 500 years when European settlement of the continent becomes apparent in the pollen record (Williams et al. 2004).

The areal extent of forest and other wooded land before European settlement of the continent is unknown, especially in those areas where most of the original vegetation has been altered because of agricultural development (e.g., aspen parkland where grasslands were interspersed with groves of aspen). However, the map developed in the present paper can be used in conjunction with other data to assess some of the other changes that have occurred since that time. The boreal zone is often viewed as a relatively pristine environment little affected by humans. There are many anthropogenic activities that occur or have occurred in the boreal zone; these need to be quantified and their impact assessed. For example, how much of the boreal zone and hemiboreal subzone has been converted to agricultural land? How much area has been affected by urbanization, roads, railways, and utility corridors? What has been the impact of mining and hydroelectric development? How much

Table 6. Areal extent (in thousands of hectares) of the North American boreal zone and hemiboreal subzone.

	National				Boreal zone						Hemiboreal subzone					
Nation	Total area	Land area	Inland water	Forest & other wooded land	Total area	Forest land	Other wooded land	Non-forest land	Alpine land	Area of water	Total area	Forest land	Other wooded land	Non-forest land	Alpine land	Area of water
Canada	997 822[a]	909 538	88 284[b]	402 085[b]	551 979[c]	223 468[d]	83 667[d]	151 677[d]	24 229[e]	54 100[f]	85 844[c]	44 753[d]	1942[d]	29 579[d]	2120[e]	5836[f]
Greenland	216 609[g]	40 650[g]	395[g]	8[h]	1595[c]	0[h]	8[h]	1570[i]	0	15	0	0	0	0	0	0
Saint Pierre & Miquelon (France)	23[j]	22	1[h]	3[h]	23[c]	3[h]	0[h]	20[h]	0	1[h]	0	0	0	0	0	0
United States	982 663[k]	916 192[k,l]	66 471[k]	303 208[m]	73 701[c]	47 324[i]	7456[i]	9753[i]	8218[e]	1282[n]	29 880[c]	20 333[i]	4[i]	3 302[i]	0[o]	6454[n]
Column total	2 197 117	1 866 402	155 151	705 304	627 298	270 795	91 131	163 020	32 447	55 398	115 724	65 086	1946	32 881	2120	12 290

[a]Determined with a GIS and the 1:1 000 000 map of Canada from the *Atlas of Canada* projected with Albers equal-area conic projection and standard parallels set at 47.5°N and 54.5°N.

[b]From Canada's Forest Inventory (CanFI, version 2001).

[c]This value is not the total of areas reported for forest land, other wooded land, non-forest land, alpine land, and area of water because it was determined independently of the latter four areas using a GIS and the boreal zone or hemiboreal subzone map projected with Albers equal-area conic projection and standard parallels set at 47.5°N and 54.5°N.

[d]Determined with a GIS by intersecting the boreal zone and hemiboreal subzone map and Canada's Forest Inventory (CanFI, version 2001).

[e]Determined with a GIS and the boreal zone and hemiboreal subzone map. The area reported does not include areas of lakes and rivers; the areas of the latter two features are included in the area of water.

[f]Determined with a GIS by intersecting the boreal zone and hemiboreal subzone map and the 1:1 000 000 hydrology map from the *Atlas of Canada*.

[g]From Weng (1995), who used a 1:2 500 000 map of Greenland and the Sanson-Flamsteed equivalent projection.

[h]From Food and Agriculture Organization (FAO 2006).

[i]Determined with a GIS by intersecting the boreal zone and hemiboreal subzone map and forest type map developed as part of the Global Forest Resources Assessment in 2000. The latter forest type map is available at the US Geological Survey's Global Land Characterization Web site (http://edc2.usgs.gov/glcc/glcc.php).

[j]Determined with a GIS and ESRI's 1:1 000 000 Map of the World projected with Albers equal-area conic projection and standard parallels set at 47.5°N and 54.5°N.

[k]From the World Factbook (Central Intelligence Agency. Available from www.cia.gov/library/publications/the-world-factbook/ [accessed September 2007].

[l]The difference between the value in this table and that reported by Smith et al. (2004) (2 263 230 000 acres or 915 917 000 ha) is probably due to rounding errors when converting from acres to hectares (i.e., 1 ha = 2.471 acres).

[m]From Smith et al. (2004).

[n]Determined with a GIS by intersecting the boreal zone and hemiboreal subzone map and the 1:2 000 000 hydrology map from the *National Atlas of the United States*.

[o]There is some area above the tree limit on Mount Washington, Mount Adams, and Mount Katahdin, but these areas are not significant.

Table 7. Total area (in thousands of hectares) of the boreal zone and the hemiboreal subzone based on this paper's map and maps of several other studies dealing with the North American continent, Canada, or Alaska. Studies are listed in reverse chronological order.

	Boreal zone					Hemiboreal subzone			
Study	Canada	Greenland	Saint Pierre &Miquelon (France)	United States	North America	Canada	United States	North America	Total North America
This paper	551 979	1595	23	73 701	627 298	85 844	29 880	115 724	743 022
FAO (2006)[a]	525 667	0	24	69 669	595 336	na	na	na	na
Olson et al. (2001)[b]	461 131	0	na	49 706	510 837	na	na	na	na
ESWG (1995)[c]	581 930	na	na	na	na	na	na	na	na
EWG (1989)[d]	555 940	na	na	na	na	na	na	na	na
Tuhkanen (1984)[e]	557 246	3356	na	116 325	676 927	123 428	13 599	137 027	813 955
Rowe (1972)[f]	530 814	na	na	na	na	na	na	na	na
Viereck and Little (1972)[g]	na	na	na	57 060	na	na	na	na	na
Semenova-Tyan-Shanskaya (1964)[h]	510 953	na	na[i]	69 587	580 540	na	na	na	na

Note: Total area was determined with a GIS and Albers equal-area conic projection with standard parallels set at 47.5°N and 54.5°N. The reference layer for the Canadian portion of North America was from the *Atlas of Canada* (1:1 000 000). The reference layer for the Greenland portion of North America was from the Environmental Systems Research Institute (1:1 000 000), whereas comparable data for the United States were from the *National Atlas of the United States.* (1:2 000 000). FAO, Food and Agriculture Organization; na, not applicable; ESWG, Ecological Stratification Working Group; EWG, Ecoregions Working Group.

[a]Includes the boreal coniferous, boreal mountain, and boreal tundra ecological zones.

[b]Includes the boreal forest/taiga biome.

[c]Includes the Hudson plains, boreal cordillera, boreal plains, boreal shield, taiga cordillera, taiga plains, and taiga shield ecozones.

[d]Includes the boreal ecoclimatic provinces and ecoclimatic regions.

[e]Includes the hemiarctic, northern boreal, middle boreal, southern boreal, and hemiboreal subzones.

[f]Includes the boreal forest region.

[g]Includes the closed spruce-hardwoods, open, low-growing spruce, and treeless bogs vegetation types.

[h]Includes zones 6–14 of the boreal type vegetation.

[i]These islands appear on the map of Semenova-Tyan-Shanskaya (1964) but it is difficult to discern their colour, which identifies the zone to which they belong.

Table 8. Areal statistics (in thousands of hectares) for Canada based on this paper and other studies, which are listed in reverse chronological order.

	National						Boreal zone						
Study	Total area	Land area	Inland water	Forest and other wooded land	Forest land	Other wooded land	Total area	Forest and other wooded land	Forest land	Other wooded land	Non-forest land	Alpine land	Area of water
This paper	997 822	909 538	88 284	402 085	310 134	91 951	551 979	307 135	223 468	83 667	151 677	24 229	54 100
FAO (2006)	997 061	922 097	74 964	402 085	310 134	91 951	nr	nr	226 398	nr	nr	nr	nr
Shvidenko and Apps (2006)[a]	nr	921 500	nr	501 800	466 300	35 500	nr	nr	345 100	nr	nr	nr	nr
Burton et al. (2003)	982 932	nr	nr	nr	nr	nr	580 426	430 260	164 795[b]	nr	nr	nr	nr
Goodale et al. (2002)	nr	nr	nr	404 000	316 000	88 000	nr	nr	nr	nr	nr	nr	nr
FAO (2001)	997 061	922 097	74 964	417 584	244 571	173 013	nr	304 836	178 537	nr	nr	nr	nr
UNEP (2001)[a]	nr	983 400	nr	nr	368 651	nr	nr	nr	nr	nr	nr	nr	nr
UNECE (2000*b*)	997 061	921 543	75 518	417 584	244 571	173 013	nr	nr	nr	nr	nr	nr	nr
Kurz and Apps (1999)	nr	nr	nr	404 200	nr	nr	nr	307 100	nr	nr	nr	nr	nr
Iremonger et al. (1997)	nr	nr	nr	547 886	nr	nr	nr	nr	nr	nr	nr	nr	nr
Apps et al. (1993)	nr	nr	nr	nr	nr	nr	nr	304 000	nr	nr	nr	nr	nr
Kurz et al. (1992)	nr	nr	nr	nr	nr	nr	nr	303 717	nr	nr	nr	nr	nr
Kuusela (1990)	nr	916 700	nr	nr	nr	nr	nr	436 400	nr	nr	nr	nr	nr
Coefficient of variation	0.6%	2.7%	8.4%	12.8%	23.8%	49.7%	–	18.3%	29.3%[c]	–	–	–	–

Note: FAO, Food and Agriculture Organization; nr, not reported; UNEP, United Nations Environment Programme; UNECE, United Nations Economic Commission for Europe.

[a]Shvidenko and Apps (2006) and UNEP (2001) use the same definitions as FAO (2001, 2006).

[b]This is the area of timber productive land.

[c]The value reported by Burton et al. (2003) was not included in the determination of this coefficient of variation.

of the zone and subzone is directly and indirectly “disturbed” by these latter activities? How much of the zone and subzone is protected? In areas subjected to forest management, how much of the area is uncut, cut once, or cut two or more times? Environmental groups have attempted to address some of these issues (e.g., Lee et al. 2006; Stanojevic et al. 2006, etc.); these topics should be subjected to further scientific examination.

Given the circumpolar boreal zone’s importance to the economies of many nations and its key role in regulating global and regional climates and biogeochemical cycles, it is vital we increase our understanding of the boreal and the effects of human development in the zone. Scientists, regulators, and environmental groups can use the map and the corresponding statistics of the North American boreal zone in the present paper to create a common baseline or standard against which future changes in the North American boreal zone and the success of conservation efforts can be measured. The mapping of the North American boreal zone in the present paper should be considered an important first step in a longer-term process of mapping the circumpolar boreal zone. The approach outlined in this paper could be applied to developing a map of, and comparable statistics for, the Eurasian portion of the zone.

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Appendix A

Terminology

Association	A characteristic assemblage of species that are considered a unit of vegetation (Moore and Chapman 1986). The concept has been treated differently by North Americans and Europeans (Mueller-Dombois and Ellenberg 1974; Allaby 1998).
Azonal	A term originally developed in Russian geobotany that applies to plant communities that are controlled primarily by soil conditions (Mueller-Dombois and Ellenberg 1974).
Biome	A biogeographical subdivision that reflects the ecological and physiognomic character of the vegetation and is equivalent to the concept of major plant formations in plant ecology, but is defined in terms of all living organisms and of their interaction with the environment, not just the dominant vegetation (Allaby 1998).
Boreal	Pertaining to the north (from Boreas, the Greek god of the north wind) (Allaby 1998).

Boreal climate A climate associated with the boreal or taiga forest zone of North America. Winters are long and cold with mean temperatures below 6 °C for 6–9 months, whereas summers are short with mean temperature of the warmest month >10 °C (Allaby 1998).

Closed forest A forest in which trees and the understory vegetation cover ≥40% of the ground. These forests can be managed or unmanaged and the trees may have been harvested more than once and regenerated either naturally or by planting (see also UNEP 2001).

Ecotone A transitional area where characteristics of adjacent plant communities or ecological systems intergrade; these characteristics are uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems (Braun 1950; Gosz 1993; Allaby 1998). In the ecotone there is a mosaic pattern, which consists of variation in the number and sizes of patches that represent the 2 vegetation types (Gosz 1993). An ecotone will occur where a reversal in competitive abilities occurs owing to the changing physical environment of the plants (Arris and Eagleson 1994). Ecotones can be broad where critical environmental conditions change gradually or they can be narrow where conditions change abruptly (Risser 1995). Broad ecotones always present problems in interpretation of boundaries because of the overlapping of vegetational features (Braun 1950). Ecotone boundaries appear to be in a state of flux at centennial to millennial time scales (e.g., Bird 1961; Archibold and Wilson 1980; Lescop-Sinclair and Payette 1995; Lloyd and Fastie 2003).

Forest A land area with trees >5 m in height and a canopy cover of >10%, or with trees able to reach these thresholds in situ. It excludes land that is predominantly under agricultural or urban use. Areas under reforestation that have not yet reached but are expected to reach a canopy cover of >10% and a tree height of >5 m are included, as are temporarily unstocked areas that have been deforested as a result of human intervention or natural causes and that are expected to regenerate. It includes forest roads, fire breaks and other small open areas, and forests in national parks and other protected areas (FAO 2001, 2006). Generally, forest area = area of closed forests + area of open forests + area of plantations; where area of plantations = area reforested + area afforested (FAO 2001).

Forest limit The northern limit of forest stands located in the northernmost parts of the forest-tundra (Payette 1983). The closed-crown forest stands or open woodlands in the forest limit may include several hundred trees and can be well circumscribed on the landscape. This term is synonymous to Hustich's (Hustich 1966) *physiognomic forest-line*.

Forest–tundra A transitional area where patches of tundra of various sizes occur on uplands between forest stands (Payette 1983; Timoney et al. 1992). Tree growth and regeneration are generally poor. The southern boundary of this area is the northern limit of continuous closed-crown forests or open woodlands; the northern boundary is the northern tree limit (Payette 1983; Timoney et al. 1992). Other names have been used for the same general transitional area with similar types of vegetation and physiognomy (Löve 1970; Tuhkanen 1984). In this paper it is synonymous with the *subarctic zone* of Löve (1970) and the *hemiarctic zone* of Ahti et al. (1968) and Tuhkanen (1984).

Inland water The area of major rivers, lakes, and water reservoirs.

Land area The total area of a country, excluding areas under inland water bodies.

Open forest A forest in which trees and understory vegetation are discontinuous and cover 10-40% of the ground.

Other land The land area not classified as forest or other wooded land as defined in this section. It includes agricultural land, meadows, pastures, urban areas, and barren land.

Other wooded land The land area not classified as forest with an area greater than 0.5 ha; with trees >5 m in height and a canopy cover of 5–10%, or with trees able to reach these thresholds in situ; or with a combined cover of shrubs, bushes and trees >10% (trees not able to reach >5 m at maturity in situ, e.g., dwarf or stunted trees (FAO 2001)). It excludes land that is predominantly under agricultural or urban land use (FAO 2001, 2006).

Physiognomy The appearance of vegetation, such as height, colour, luxuriance, and leaf size and shape (Mueller-Dombois and Ellenberg 1974; Moore and Chapman 1986).

Phytogeography The study of the geography of plants, particularly their distribution at different taxonomic levels. Patterns of distribution are interpreted in terms of climatic and anthropogenic influence, but above all in terms of earlier continental configurations and migration routes (Allaby 1998).

Phytosociology The classification of plant communities based on floristic rather than life-form or other considerations. These schemes currently use computer-based methods such as ordination (Mueller-Dombois and Ellenberg 1974; Allaby 1998).

Plantation A forest established by planting or seeding in the process of afforestation or reforestation using a non-native tree species, or a forest that is intensively managed with one or two regularly spaced native species of the same age.

Sector A meridional division of a zone based on gradients of oceanity (or continentality) (Ahti et al. 1968; Tuhkanen 1984). The term is synonymous with Rowe's (Rowe 1972) *section*.

Total area The total land area of a country and areas under inland water bodies, excluding offshore territorial waters.

Tree limit The northern limit of trees with a normal, upright growth-form and attaining some minimum height (≥5 m, Payette 1983; ≥3 m, Timoney et al. 1992; >2 m, Kullman 1979, 1989). Hustich (1966), Sveinbjörnsson (2000), and many other Europeans use the term *treeline*.

Tree species limit — The northern-most occurrence of a tree species, regardless of growth form (Payette 1983; Timoney et al. 1992). Thus, tree species that are shrub-like or have krummholz form are included in this limit.

Zonal — A term originally developed in Russian geobotany that applies to plant communities that are controlled primarily by current climatic conditions of a larger region on soils with mesic properties (Mueller-Dombois and Ellenberg 1974; Allaby 1998).

Zone — A region with similar, characteristic vegetation and soils that may be approximately bounded by lines of latitude (Ahti et al. 1968; Tuhkanen 1984; Allaby 1998). The term *zone*, as applied by Tuhkanen (1984), is synonymous with *subzone*, as used by Ahti et al. (1968); both are similar to Rowe's *forest region* (see Rowe 1959) although Rowe generally excludes alpine areas from his regions. Sjörs (1999) provides remarks on zonal and subzonal nomenclature and he compares his terminology with that of Ahti et al. (1968) and Tuhkanen (1984).

Appendix B

Table B1. Other relevant maps and studies

Maps (Reference)	Studies (Reference)
Northern Labrador and Quebec	
(Lescop-Sinclair and Payette 1995)	(Bouchard et al. 1987)
(Payette 1975)	(Charest et al. 2000)
(Payette 1976)	(Hustich 1949)
(Rousseau 1952)	(Lamb 1980)
(Rousseau 1968)	(Lamb 1984)
(Wilton 1964)	(Lavoie and Payette 1992)
	(Morneau and Payette 1989)
	(Payette 1993)
	(Simon 2005)
Northwestern Canada	
(Ritchie 1959)	(Clarke 1940)
(Ritchie 1960)	(Hansell and Chant 1971)
(Rühland et al. 2003)	(Jeffrey 1964)
	(Johnson 1975)
	(Kershaw 1977)
	(Landhäusser and Wein 1993)
	(La Roi 1967)
	(Larsen 1965)
	(Larsen 1971)
	(Larsen 1974)
	(Lindsey 1952)
	(Maini 1966)
	(Raup 1936)
	(Ritchie 1956)
	(Ritchie 1962)
	(Ritchie 1984)
	(Zoltai and Pettapiece 1973)
Yukon Territory and Mackenzie Mountains	
(Collins and Sumner 1953)	(Birks 1977)
	(Clark and Lauriol 1997)
	(Cwynar and Ritchie 1980)
	(Hettinger et al. 1973)
	(Kojima 1996)
	(MacHutchon 2001)
	(MacHutchon and Wellwood 2003)
	(Porsild 1951)
	(Raup 1945)
	(Stanek 1980)
	(Stanek et al. 1981)

Table B1 (*concluded*).

Maps (Reference)	Studies (Reference)
	(Zoltai and Pettapiece 1973)
Alaska	
(Collins and Sumner 1953)	(Lutz 1956)
(Hutchison 1967)	(Raup 1945)
(Joint Federal-State Land Use Planning Commission for Alaska 1973)	(Swanson 2003)
(Taylor and Little 1950)	(Van Cleve et al. 1983*b*)
(Viereck and Little 1975)	(Viereck 1975)
(Van Cleve et al. 1983*a*)	(Viereck 1979)
	(Viereck et al. 1992)
Atlantic Maritimes, Northeastern US, and Great Lakes	
	(Carleton and Maycock 1978)
	(Carleton and Maycock 1980)
	(Copenheaver and Abrams 2002)
	(Davis 1980)
	(Foster 1992)
	(Sjörs 1963)
	(Whitney 1987)
Western Interior	
(Harrison 1934)	(La Roi 1967)
	(La Roi and Stringer 1976)
	(Looman 1987)
	(Rowe 1956)
	(Swan and Dix 1966)
Western Cordillera	
(Franklin and Dyrness 1969)	
(Ogilvie 1990)	

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Appendix C. Description of the zones of Semenova-Tyan-Shanskaya (1964) cited in the present paper

Zone 6: pretundra spruce and larch-spruce, and in places larch woodland and spruce-fir northern taiga forest (*Picea mariana*, *Picea glauca*, *Larix laricina*, *Abies balsamea*) with sections of birch (*Betula papyrifera*) and aspen (*Populus tremuloides*), and tundra patches, understory shrubs (*Alnus crispus*), and sphagnum bogs.

Zone 7: mountain and foothill spruce, fir, and larch (*Picea glauca*, *Abies lasiocarpa*, *Larix laricina*) woodland with understory shrubs (*Alnus crispus*, *Betula glandulosa*) and mountain-tundra, rock, and meadow associations with birch (*Betula papyrifera*) and aspen (*Populus tremuloides*).

Zone 10: southern taiga spruce-fir (*Picea mariana*, *Picea glauca*, *Abies balsamea*) forests and pine (*Pinus banksiana*, *Pinus strobus*) with sections of broadleaf species (*Acer saccharum*, *Betula alleghaniensis*, *Fraxinus nigra*) and cedar (*Thuja occidentalis*).

Zone 11: pine-dominated southern taiga forest (*Pinus strobus*, *Pinus resinosa*, *Pinus banksiana*) with sections of deciduous species (*Acer saccharum*, *Acer spicatum*, *Betula alleghaniensis*) mixed with forests of *Picea mariana* and *Thuja* [*canadensis*], and also *Larix laricina* bogs.

Zone 12: high mountain spruce and spruce-fir forest and subalpine woodland (*Picea glauca*, *Picea mariana*, *Picea engelmannii*, *Abies lasiocarpa*). Areas with larch (*Larix occidentalis*) and understory shrubs, alpine meadows and rock.

Zone 14: mountain spruce and spruce-fir forests (*Picea mariana*, *Picea rubens*, *Abies fraseri*, *Thuja occidentalis*) with admixture of *Betula alleghaniensis* and *Sorbus americana* in combination with alpine meadows and understory shrubs (*Rhododendron catawbiense*, *Alnus viridis*).

Zone 16: aspen (sparse forest) parkland of *Populus tremuloides* and *Populus deltoides* with some *Populus balsamifera*, *Ulmus americana*, *Fraxinus nigra*, *Fraxinus pennsylvanica*, and *Acer negundo*.