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Balsam Poplar (*Populus balsamifera*; Salicaceae) Beyond the Tree Line in the Western Canadian Mainland Arctic (Northwest Territories)

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ABSTRACT. Balsam poplar is the northernmost tree species in North America, with a reported range that extends generally to the tree line across the continent and beyond the tree line in Alaska, where extralimital stands growing in Arctic ecosystems on the North Slope have been documented and studied. Here we summarize existing information and report new data on extralimital stands of balsam poplar from the Arctic ecozone in the northeastern mainland Northwest Territories. These occurrences extend the geographical and ecological range of the species fully into the mainland Canadian Arctic. In this region, balsam poplar is known from four sites: two in Tuktut Nogait National Park and two along the Hornaday and Brock rivers just beyond the northwestern Park boundary. Balsam poplar was first reported from two of these sites more than 50 years ago, but those data have not been considered in most subsequent floristic and ecological work. A balsam poplar grove in Tuktut Nogait National Park consists of four discrete stands of shrubby plants growing on a low ridge adjacent to the Hornaday River; their tallest ramets measure 1.1 – 1.86 m. A larger grove along the edge of the lower Brock River consists of three large stands, the tallest ramets measuring 3.5 – 4 m. The boreal and subarctic regions of the Northwest Territories and Nunavut have large areas where balsam poplar has not been documented by herbarium specimens, including most of the forest-tundra and tree-line zones. Collections from these areas and other potential extralimital sites in the Canadian Arctic are urgently needed to document the current distribution of balsam poplar. Such data could serve as a baseline for assessing potential future alteration of the range of this species as a result of climate change.

Key words: balsam poplar, tree line, Arctic, Northwest Territories, *Populus balsamifera*, floristics, phytogeography, climate change

RÉSUMÉ. Le peuplier baumier est l'espèce arborescente qui pousse le plus au nord de l'Amérique du Nord. Son aire d'extension s'étendrait généralement jusqu'à la limite forestière du continent et au-delà de la limite forestière de l'Alaska, où des peuplements extralimites qui croissent dans les écosystèmes arctiques ont été répertoriés et étudiés sur le versant nord. Nous résumons ici des données recueillies antérieurement et publions de nouvelles données sur les peuplements extralimites de peupliers baumiers de l'écozone arctique se situant dans la partie continentale nord-est des Territoires du Nord-Ouest. Ces occurrences ont pour effet d'étendre la portée géographique et écologique de l'espèce entièrement sur la partie continentale de l'Arctique canadien. Dans cette région, le peuplier baumier se retrouve dans quatre emplacements : deux d'entre eux se trouvent dans le parc national Tuktut Nogait et les deux autres, le long des rivières Hornaday et Brock, juste au-delà de la limite nord-ouest du parc. Le peuplier baumier a été signalé dans deux de ces emplacements il y a plus de 50 ans, mais ces données n'ont pas été considérées dans la plupart des études floristiques et écologiques subséquentes. Un bocage de peupliers baumiers du parc national Tuktut Nogait consiste en quatre peuplements discrets de végétation arbustive poussant sur une dorsale basse adjacente à la rivière Hornaday; les plus grands ramets y mesurent de 1,1 à 1,86 mètre. Un bocage plus volumineux le long du rivage de la rivière Brock inférieure est composé de trois gros peuplements, où les ramets les plus grands mesurent de 3,5 à 4 mètres. Les régions boréale et subarctique des Territoires du Nord-Ouest et du Nunavut sont dotées de grandes sections où le peuplier baumier n'a pas été répertorié dans les échantillons d'herbiers, ce qui comprend la plus grande partie de la toundra forestière et les zones de limite forestière. Il faudrait procéder promptement à la collecte d'échantillons de ces régions et d'autres emplacements extralimites potentiels de l'Arctique canadien afin de pouvoir consigner la répartition actuelle du peuplier baumier. De telles données pourraient servir de point de référence pour évaluer la modification éventuelle de l'aire d'extension de cette espèce, modification attribuable au changement climatique.

Mots clés : peuplier baumier, limite forestière, Arctique, Territoires du Nord-Ouest, *Populus balsamifera*, floristique, phytogéographie, changement climatique

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INTRODUCTION

The Arctic tree line is typically defined as the northern limit of the subarctic forest-tundra or tundra-taiga interface, the transitional zone between the closed-canopy continuous boreal forest to the south and the treeless Arctic tundra to the north (Hustich, 1953, 1979; Payette et al., 2002; Fig. 1). In tree-line studies, "tree" is typically used as a functional term to identify the northernmost position of arboreal (tree-like) growth that is 2–5 m or greater in height (e.g., Hustich, 1979; Payette, 1983; Timoney et al., 1992; Payette et al., 2002). By contrast, the tree species line is the northern limit of a tree species in any of its growth forms, including scraggly bushes, low scrub, seedlings, or prostrate mats, which can occur beyond the tree line (Hustich, 1953, 1979; Payette, 1983; Payette et al., 2002). In the context of climate change, understanding the past and present distributions of the tree line, tree species lines, and the geophysical parameters that affect them is of considerable interest (e.g., Nichols, 1976; Elliott and Short, 1979; Cooper, 1986; Caccianiga and Payette, 2006), particularly given the accumulating evidence that many tree-line regions in Canada and the world are advancing (e.g., Gamache and Payette, 2005; Caccianiga and Payette, 2006; Harsch et al., 2009).

Collections documenting new records and range extensions for Arctic plant species are fairly common following regional floristic inventories, particularly in Arctic areas that have not been thoroughly explored botanically (e.g., Cody, 1996; Cody et al., 1984, 1989, 1992; Soper and Powell, 1985; Bennett et al., 2010). Observations of outlier or disjunct populations (occurrences beyond the main range of a species) of tree and other large woody species growing beyond the tree line (e.g., *Picea glauca* (Moench) Voss; some species of the willow genus, *Salix* L.) have generated considerable attention given their unusual presence in the typically treeless North American Arctic landscape. Examples include studies by Johansen, 1919, 1924; Soper, 1933; Polunin, 1937; Maycock and Matthews, 1966; Edlund, 1983; Edlund and Egginton, 1984; Cooper, 1986; Payette and Delwaide, 1994; Elsner and Jorgenson, 2009; see Holm (1922) for a review of the many reports of northern spruce groves in accounts of the early Arctic explorers. Documentation and study of such extralimital occurrences can provide useful insights into their distributions, niches, and environments, and potentially the distribution and composition of post-glacial vegetation in Arctic regions (Maycock and Matthews, 1966). Such baseline data may help us to understand how these northern species and their ecosystems responded to changing climate in the past, and how they might respond to the warmer Arctic climate that is predicted for the coming decades (e.g., Feng et al., 2011). Here we report new data and summarize existing information on extralimital stands of the tree species balsam poplar from the northeastern Northwest Territories, extending the geographical and ecological range of balsam poplar into the mainland Canadian Arctic.

BALSAM POPLAR IN NORTHERN NORTH AMERICA

Balsam poplar (*Populus balsamifera* L., Salicaceae) is the northernmost tree species in North America, and with such species as *Larix laricina* (Du Roi) K. Koch, *Picea mariana* (P. Mill.) B.S.P. and *P. glauca*, it forms the northern tree line on the continent (Payette and Lavoie, 1994). Balsam poplar is a broad-leaved deciduous species found in floodplains, bottomlands, and other moist lowland areas distributed across Canada and the adjacent northeastern United States, from Newfoundland and Labrador to northern and eastern British Columbia, Yukon, and Alaska (e.g., Viereck and Foote, 1970; Porsild and Cody, 1980; Zasada and Phipps, 1990; Payette, 1993); the species is also known from the adjacent southeastern Chukotka Peninsula, Russia (Katenin, 1980). At the tree line, balsam poplar grows along river floodplains and on dry, south-facing slopes (Landhäusser et al., 1996). With its wind-mediated long-distance dispersal mechanism, balsam poplar is predicted to become more dominant north of the tree line as the climate warms (e.g., Landhäusser and Wein, 1993).

Although balsam poplar generally ranges to the tree line, disjunct populations have been reported from Arctic regions well beyond the tree line. The best known of these are on the North Slope of Alaska, where multiple well-documented balsam poplar groves of considerable stature occur along rivers to more than 100 km north of the tree line (69°28′ N) (Wiggins and Thomas, 1962; Viereck and Foote, 1970; Murray, 1980; Edwards and Dunwiddie, 1985; Bockheim et al., 2003; Viereck and Little, 2007). In Alaska, the tree line is usually defined by *Picea glauca* (Brandt, 2009), but some sources have based it on the northern limit of balsam poplar on the North Slope (e.g., Kankaanpää et al., 2001). Two extralimital Alaskan balsam poplar groves have been studied in considerable detail: one is located at the confluence of Cache Creek and the Canning River (69°25′ N, 146° W) (Dunwiddie and Edwards, 1984; Edwards and Dunwiddie, 1985), and the other is along a tributary of the Ivishak River called "Cottonwood Creek" (69°06′ N, 147°53′ W) (Bockheim et al., 2003).

Extralimital stands of balsam poplar are less well known in Canada. In the eastern Canadian mainland Arctic, a few stands are known from the shrub tundra at Saglek fjord, Newfoundland and Labrador (58°28′46″ N, 63°14′03″ W; Payette, 1983, 1993). In Nunavut, extralimital balsam poplar is known from a single location found nearly a century ago during the Canadian Arctic Expedition, 1913–18 (Johansen, 1924). A few small twigs from "trees … about ten feet [ca. 3 m] high" with "trunks [that] attained the thickness of a finger" growing at Gully Creek just above Escape Rapid in the Coppermine River valley were collected by R.M. Anderson (*Anderson 756* [CAN]) in winter when "all but the upper twigs were hidden by snow…." (Johansen, 1924:49c). This depauperate collection was originally reported as *P. tremuloides* Michx. (Macoun and Holm, 1921; Johansen, 1924), though Holm (1922) also considered that it could be *P. balsamifera*. Porsild and Cody

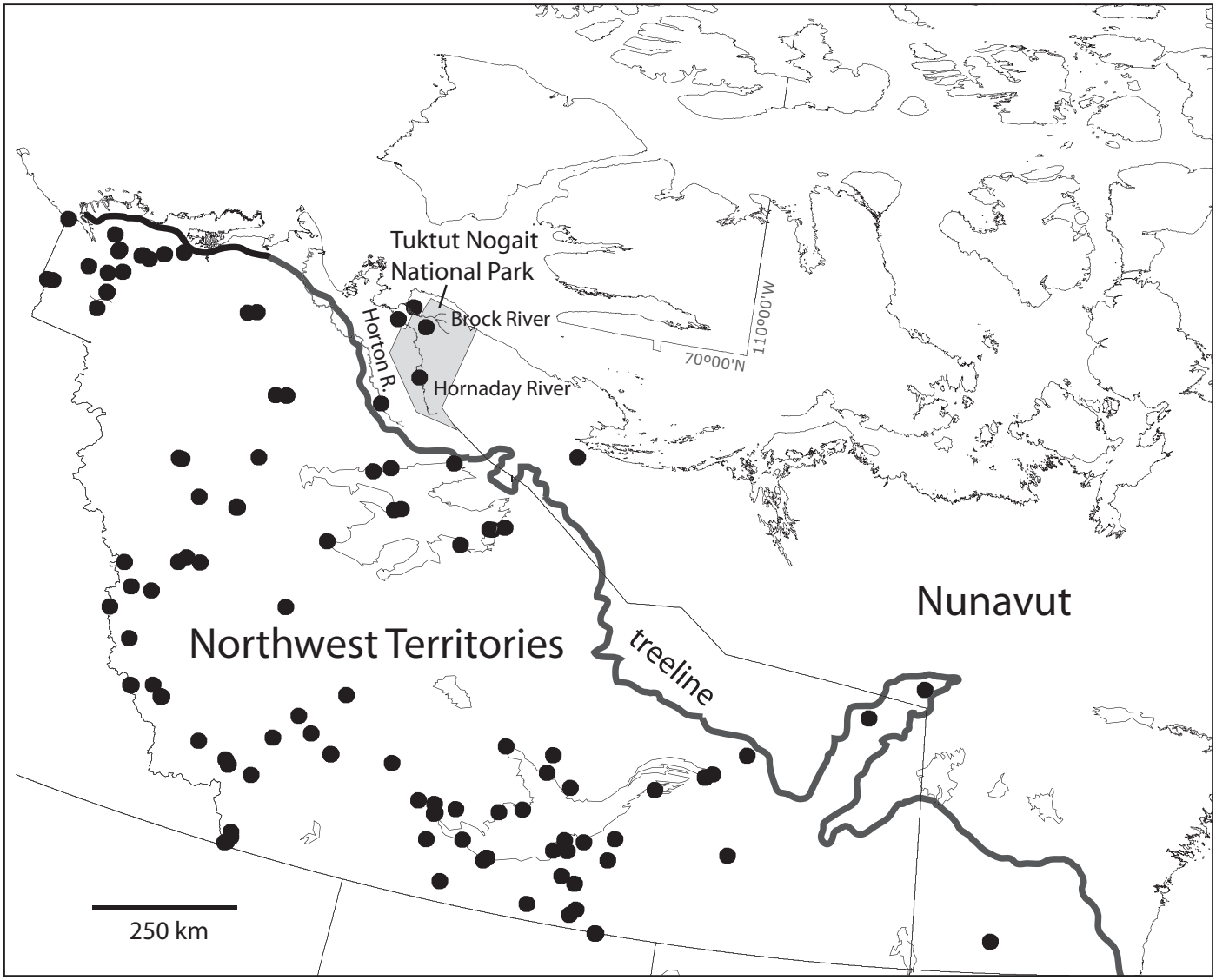

FIG. 1. Distribution of balsam poplar in the Northwest Territories and Nunavut as documented by herbarium specimens.

(1980) reported the collection as *P. balsamifera*, a determination that likely is correct (G.W. Argus, pers. comm. 2011). Better collections of the species are needed from this region to document its occurrence there unambiguously.

A few extralimital stands of balsam poplar are known from the Northwest Territories, but none has been studied in detail. In Porsild and Cody (1980), Porsild reported that in the 1930s, he observed a grove of tree-sized balsam poplar in the Old Man Lake area (68˚58′ N, 132˚17′10″ W) adjacent to the Eskimo Lakes east of the Mackenzie Delta (also see Cody, 1965a); this site was included on the distribution map in that study. Ritchie (1987:36) referred to this stand as the "northernmost tree-form arboreal species in the Mackenzie Delta." This stand is in Canada's Southern Arctic Ecozone (Ecological Stratification Working Group, 1995), essentially at the forest-tundra boundary as delimited by Timoney et al. (1992) and Spear (1993). We are not aware of a voucher specimen for this location, but we include it on our map (Fig. 1) on the authority of Porsild and Ritchie.

In 1951, the geographer J. Ross Mackay observed and made collections of extralimital balsam poplar in the Southern Arctic Ecozone in the Northwest Territories. He discovered the species at three sites in the Melville Hills south of Darnley Bay: along the lower Brock River approximately 8 miles (ca. 13 km) east of its mouth; along the lower Hornaday River 16 miles (ca. 26 km) southeast of its mouth; and scattered along the valley of the lower course of Rummy Creek, a small tributary that runs from Rummy Lake into the Hornaday River west of La Roncière Falls (Mackay, 1958; Fig. 1). These sites are adjacent to the present-day northwestern boundary of Tuktut Nogait National Park. Mackay (1958) stated that the largest trees, of height unknown to him, had been cut by humans for use as drying poles and other purposes; it is not clear from his writing whether he observed cut logs at all sites, or only at specific sites. Data from the herbarium specimens collected by Mackay to document the groves along the Brock and Hornaday rivers (*R. Mackay s.n.*, Table 1) were published

TABLE 1. Specimen citations for extralimital balsam poplar in Tuktut Nogait National Park and vicinity, Northwest Territories. Measurements are reported with the units given on the herbarium specimens.

Site	Location / Elevation	Collection date	Voucher specimen (Herbarium)	Habitat description
Along Brock River, ca. 8 mi directly E of its mouth	69°22′52″ N, 123°05′22″ W	25 July 1951	*R. Mackay s.n.* (DAO–198912, DAO–198913[1])	see main text
16 mi SE of the mouth of the Hornaday River, on a creek flowing into it	ca. 69°09′22″ N, 123°17′15″ W	30 August 1951	*R. Mackay s.n.* (DAO–198913[1])	some trees reach diameter of 4–5 inches
W of Tuktut Nogait National Park, N side of lower Brock River	69°22′52″ N, 123°05′22″ W / 70 m	25 July 2009	*L.J. Gillespie, L.L. Consaul & R.D. Bull 9292* (CAN)	see main text
Tuktut Nogait National Park: Akluk Creek	69°13′01″ N, 122°57′27″ W / 280 m	31 July 2004	*P. Achuff 7515* (CAN)	small, shrubby patches on lower slope
E side of Hornaday River	68°19′21″ N, 121°54′25″ W / 396 m	11 July 2009	*L.J. Gillespie, J.M. Saarela, L.L. Consaul, R.D. Bull, J. Boxwell & C. Hunter 8965* (CAN)	see main text

[1] This is a mixed sheet with three separate Mackay collections: the two cited here and one from the Horton River noted in the main text and cited in the appendix.

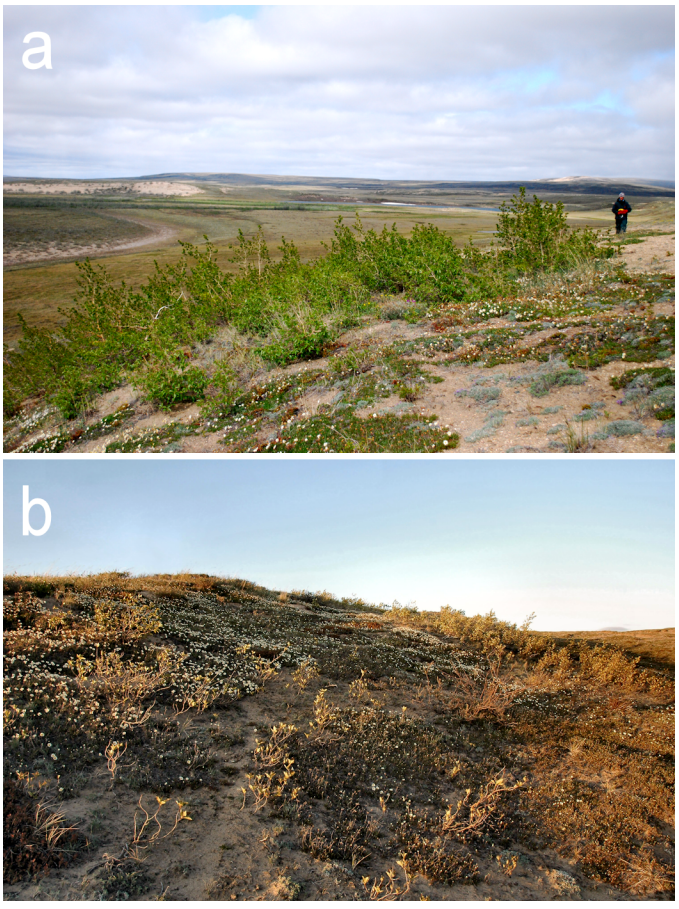

FIG. 2. Arctic balsam poplar growing on a raised terrace adjacent to the Hornaday River in Tuktut Nogait National Park, Northwest Territories, Canada. Two of four discrete stands present at this location are shown: (a) stand 1; (b) stand 2. Photo credits: J.M. Saarela (a), R.D. Bull (b).

by Cody (1965b), who noted that east of the Anderson River, balsam poplar extends farther north than spruce. The Rummy Creek site(s) do not appear to be documented by herbarium specimens. Despite the publications by Mackay (1958) and Cody (1965b), these Arctic occurrences appear to have been largely overlooked, as they are not mentioned in subsequent scientific literature or included on most later distribution maps for balsam poplar (e.g., Hultén, 1968; Viereck and Foote, 1970; Zasada and Phipps, 1990; Farrar, 1995; Eckenwalder, 2010). An exception is the study by Porsild and Cody (1980), who mapped Mackay's balsam poplar sites. However, the small size of their distribution maps makes it difficult to interpret these sites as occurring in the Arctic beyond the tree line; we suspect this to be the reason that these records have otherwise escaped notice.

Balsam poplar was not reported in the first major study of the flora of the Melville Hills region (i.e., Paulatuk, Tuktut Nogait National Park and vicinity, adjacent Nunavut), which was conducted as part of a natural resource inventory to determine the region's suitability as a national park (Zoltai et al., 1992). On the basis of extensive collections made by S.C. Zoltai and G.W. Scotter, Cody et al. (1992) reported some 237 vascular plant taxa for the region; however, they did not mention balsam poplar. These researchers did not encounter this conspicuous species at the 41 geographically disparate Arctic sites they visited, suggesting that its presence in the area is quite restricted. More recently, in 2004, Peter Achuff collected balsam poplar at Akluk Creek in the northwestern segment of Tuktut Nogait National Park, where he observed small, shrubby patches of the species on a lower slope. His collection (*Achuff 7515* [CAN], Table 1) is the first record for the species in Tuktut Nogait National Park.

NEW ARCTIC BALSAM POPLAR GROVES IN THE NORTHWEST TERRITORIES

While collecting plants in July 2009 for a floristic inventory of Tuktut Nogait National Park and vicinity (J.M. Saarela and L.J. Gillespie, unpubl. data), we encountered

two balsam poplar groves growing fully in Arctic ecosystems. The first grove (represented by the collection *Gillespie et al. 8965*, Table 1) was found adjacent to the Hornaday River some 3 km (air) upstream from its confluence with the Little Hornaday River (Fig. 2). This previously unreported site is the second documented occurrence of balsam poplar within Tuktut Nogait National Park and the only one that we encountered while travelling along a 155 km stretch of the Hornaday River from the southern Sahtu region of the Park (67˚59′29″ N, 121˚32′28″ W) to Uyarsivik Lake (68˚52′07″ N, 122˚49′18″ W). This grove consisted of four small, discrete stands of shrubby and low-scrub balsam poplar in sandy soil along the side and near the top of a low ridge (elevation: 396 m) (Table 2) that borders a string bog (see Surveys and Mapping Branch, 1980). Balsam poplar at this site did not occur on the floodplain of the Hornaday River, which is braided in this area. The first stand was approximately 160 m to the east of the Hornaday River. Stands 1 and 2 were separated by 82 m (bearing 30.034˚) as measured from the center of each stand, stands 2 and 3 by 133 m (bearing 11.917˚), and stands 3 and 4 by 131 m (bearing 6.024˚). Vegetation cover varied in stand 1, ranging from under 5% along some of the sandy ridge slopes to 90%–100% amongst the largest ramets. We observed animal burrows within stands 1 and 3. We observed no evidence of sexual reproduction, as no catkins were present. Each stand consisted of ramets of varying size, with the largest ramets distributed roughly in the center of each stand and the smallest ramets, which appeared to be suckers, distributed towards the edges of the stands. The stand closest to the Hornaday River had a SW-facing aspect and the largest ramets in the grove (Table 2). The heights of the tallest ramets in each of the stands ranged from 1.1 to 1.86 m (Table 2). The dominant species in this poplar grove was the mat-forming *Dryas integrifolia* Vahl (Rosaceae). Other associated species included *Arctous rubra* (Rehder and E.H. Wilson) Nakai (Ericaceae); *Artemisia borealis* Pallas (Asteraceae); *Bromus pumpellianus* Scribn. (Poaceae); *Potentilla* L. sp. (Rosaceae); *Hedysarum americanum* (Michx.) Britton, *Oxytropis arctobia* Bunge (Fabaceae); *Salix niphoclada* Rydb. (Salicaceae); and *Stellaria longipes* Goldie (Caryophyllaceae). These are all fairly common tundra species in the area, and none was unique to this poplar grove.

The second balsam poplar grove (represented by the collection *Gillespie et al. 9292*, Table 1) was found along the edge of the lower Brock River just outside the boundary of Tuktut Nogait National Park (Fig. 3). This is the same grove that Mackay encountered 60 years earlier in 1951; he indicated that "trees up to 12 feet [ca. 3.7 m] high and two inches [ca. 5 cm] in diameter two feet [ca. 0.6 m] above ground grew with willows and juniper (*Juniperus communis*) on the left bank of the Brock River 10 miles [ca. 16.1 km] from its mouth" (Mackay, 1958:102). At this site, we observed three large stands that ranged in size from 600 to 1500 m^2 (Table 3). The tallest trees in each stand ranged in height from 3.5 to 4 m (Table 3), very similar to the heights observed by Mackay (1958) and considerably larger than the tallest plants at the Hornaday River site. Female catkins with developing fruits were present on the five largest trees in stand 1, as documented in the voucher specimens we collected. Balsam poplar is a dioecious species; thus, the presence of fruits indicates that both sexes are present and that sexual reproduction is occurring at the Brock River site. However, we do not know whether the fruits reach maturity at the site or whether seeds are able to germinate and survive. In the first Brock River stand, balsam poplar was growing in a fairly dense, roughly 2 m high thicket with the large shrubby willow species *Salix alaxensis* (Andersson) Coville and several other willows, including *S. glauca* L. var. *stipulata* Floderus, *S. hastata* L., and *S. richardsonii* Hook. Other species at this stand included *Anemone richardsonii* Hook. (Ranunculaceae); *Anticlea elegans* (Pursh) Rydb. var. elegans (Melanthiaceae); *Arctous rubra*; *Arnica angustifolia* Vahl subsp. *angustifolia* (Asteraceae); *Dasiphora fruticosa* (L.) Rydb. (Rosaceae); *Juniperus communis* L. subsp. *depressa* (Pursh) Franco (Cupressaceae); *Platanthera obtusata* (Banks ex Pursh) Lindl. (Orchidaceae); *Senecio lugens* Richardson (Asteraceae); and *Shepherdia canadensis* (L.) Nutt. (Elaeagnaceae). We did not fully inventory associated species at stands 2 and 3, but in general they were similar in composition but less diverse than in stand 1. They included *Juniperus communis*, growing adjacent to and at the edge of the stands and known only from one other site in the region (La Roncière Falls in Tuktut Nogait National Park), as well as *Shepherdia canadensis*, *Salix* species as in stand 1, *Anticlea elegans*, *Anemone richardsonii* and *Orthilia secunda* (L.) House subsp. *obtusata* (Turcz.) Böcher (Ericaceae). The ages of individual ramets are unknown (we did not have the proper equipment to take core samples from which to obtain age estimates). We do not know if the stands in each grove comprise one or several clones, or if the two groves are genetically distinct.

DISCUSSION

Collectively, the earlier and new Arctic balsam poplar collections from Tuktut Nogait National Park and vicinity summarized here document a considerable extension to the species' northeastern range (Fig. 1) previously indicated in multiple authoritative works (Hultén, 1968; Viereck and Foote, 1970; Zasada and Phipps, 1990; Farrar, 1995; Eckenwalder, 2010). Even though Porsild and Cody (1980) mapped the extralimital sites known to them, these Arctic occurrences have been ignored. The nearest known occurrence of balsam poplar to the south is in the Horton River valley, as noted by Mackay (1958), who made a collection "west of the tree limit on Horton River by about 15 miles [ca. 24 km]" (*Mackay s.n.* [DAO]). This site is some 83 km southwest (bearing -146.217˚) of the Hornaday River site. The nearest collections to the west are from the lower Anderson River valley (*Scotter 6437* [DAO] and *Kesting &*

TABLE 2. Locations and size characteristics of a balsam poplar grove on a low ridge adjacent to the Hornaday River in Tuktut Nogait National Park, Northwest Territories, Canada. Measurements are approximate.

Stand no.	Location	Elevation (m)	Height of tallest ramet (m)	Mean height of five tallest ramets (cm)
1	68°19′20.7″ N, 121°54′24.9″ W	396	1.86	181 ± 0.13
2	68°19′23.0″ N, 121°54′28.5″ W	389	1.1	72 ± 0.28
3	68°19′27.2″ N, 121°54′29.7″ W	392	1.12	81 ± 0.18
4	68°19′28.8″ N, 121°54′30.9″ W	391	1.5	121 ± 0.23

TABLE 3. Locations and size characteristics of a balsam poplar grove adjacent to the Brock River northwest of Tuktut Nogait National Park, Northwest Territories, Canada. Measurements are approximate.

Stand no.	Location	Elevation (m)	Stand extent (m^2)	No. of ramets	No. of ramets > 1 m tall	No. of ramets < 1 m tall	Height of tallest tree (m)	Diameter at ca. 0.75 m of tallest tree (cm)	Catkins (pistillate) present
1	69°22′55.1″ N, 123°05′28.1″ W	60	30 × 20	200	95	95	4	12	Yes
2	69°22′52.0″ N, 123°05′22.3″ W	69	60 × 25	250	175	< 100	3.5	10	No
3	69°22′50.6″ N, 123°05′10.2″ W	68	40 × 20	70	60	< 30	3.5	8	No

Barton 34 [UBC]), some 250 km from the western boundary of Tuktut Nogait National Park, where Kesting (1996) noted that balsam poplar was growing at the tree line near the northern edge of its range. The Coppermine River valley site in Nunavut noted earlier is the nearest known location to the east, a distance of some 280 km from the Hornaday River site. Additional extralimital balsam poplar groves growing at their ecological extreme in western Canada are likely scattered along rivers in the northwestern mainland Arctic. These groves should be looked for and documented by herbarium specimens.

Specimens in herbaria unambiguously document the distributions of plant species in time and space. To determine the range of balsam poplar in the Northwest Territories and Nunavut as documented by specimens, we mapped the locations of some 140 balsam poplar specimens (each representing a unique number or collecting event) housed in six major Canadian herbaria (ALTA, CAN, DAO, MT, UBC, WIN; abbreviations according to Thiers, continuously updated). A few of these collections have been published in earlier floristic works (e.g., Raup, 1936, 1947; Porsild, 1950; Cody, 1965a), but most have not. Primary occurrence data for these specimens are thus provided in full in Appendix 1. Compared with the map in Porsild and Cody (1980), our map uses smaller dots and an area restricted to the territories, more clearly identifying sites where balsam poplar has—and perhaps more critically, has not—been collected. The distribution depicted in our map (Fig. 1) is very similar to that in Porsild and Cody (1980), which is to be expected since most of the underlying specimen data are the same. Indeed, the majority of balsam poplar specimens from the Northwest Territories and Nunavut (80%) included here were collected during the 1940s–70s, whereas very few collections (7%) apparently have been made since Porsild and Cody (1980) published their flora more than 30 years ago (Fig. 4). Balsam poplar is fairly well documented by collections from such regions as the lower Mackenzie River, Great Slave Lake, a few arms of Great Bear Lake, the Mackenzie Mountains, and Nahanni National Park Reserve, yet there remain vast regions where the species has been collected infrequently or not at all (Fig. 4). Major distribution "gaps" include the large region between Great Slave Lake and Great Bear Lake, boreal regions north of Saskatchewan and Manitoba, and much of the inland northwestern Northwest Territories (Fig. 4). Critically, very few collections have been made throughout much of the forest-tundra zone and along the tree line (see Timoney et al., 1992 for boundaries). Collections and basic ecological data from these areas are urgently needed to document the current locations and population densities of balsam poplar, particularly along the edges of its northern range. Such data can be used as a baseline to help us understand potential changes in the species range and population densities in response to climate change.

Discovery of any species beyond its known or expected range naturally prompts questions about its origins. Stands of balsam poplar in the Northwest Territories mainland Arctic may have originated from wind-dispersed seeds produced by more southerly populations. Such recent recruitment into the low Arctic might seem unlikely, given recent experimental evidence that demonstrated low germination and seedling survival for balsam poplar when grown in dry lichen-heath tundra, mesic acidic tussock tundra, and wet acidic shrub tundra (Hobbie and Chapin, 1998); however, if balsam poplar's preferred riparian habitat had been included in the experiment, the species might have fared better, and the results might have been different. It is also plausible that these extralimital occurrences of balsam poplar may be relicts of warmer post-glacial Holocene vegetation communities (we did not observe sub-fossil snags that might corroborate this hypothesis). Considerable paleoecological evidence indicates that the distributions of balsam poplar and the tree line extended considerably farther north in northern Alaska and northwestern Canada during the late Pleistocene and early Holocene than at present. A shift

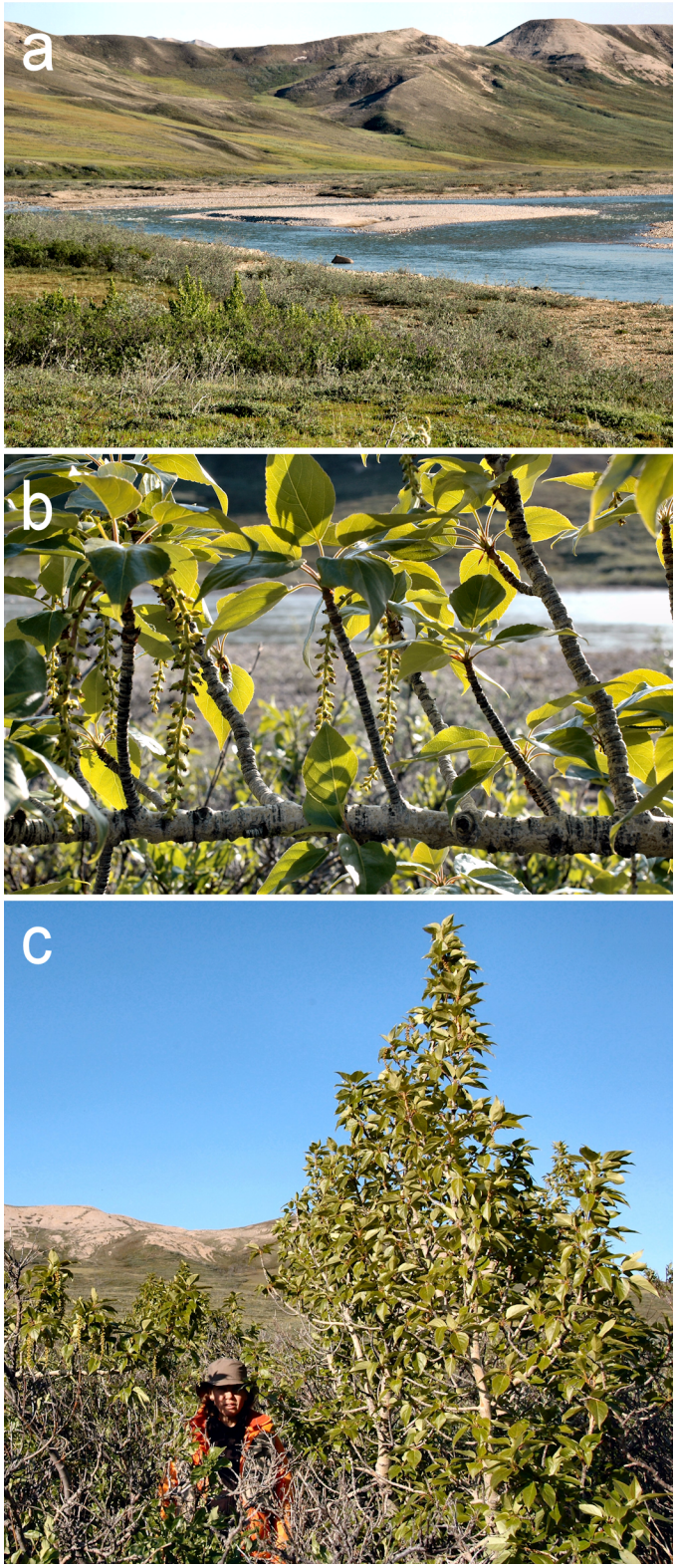

FIG. 3. Arctic balsam poplar growing along the lower Brock River in northeastern Northwest Territories, Canada: (a) poplar grove; (b) catkins; (c) a large balsam poplar ramet. Photo credits: R.D. Bull.

from forest to present-day tundra conditions has occurred since the mid-Holocene (e.g., Ritchie, 1987; Payette, 1993; Burn, 1997; Mann et al., 2002; Payette et al., 2002).

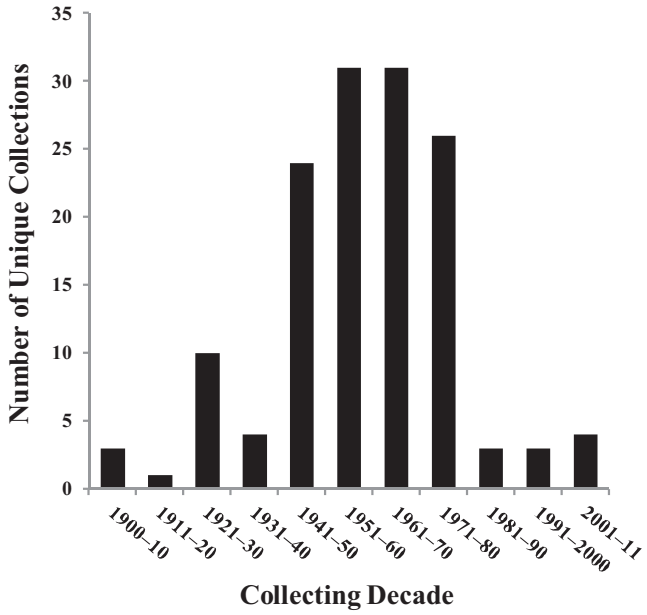

FIG. 4. Bar graph of the number of collections of balsam poplar made in the Northwest Territories and Nunavut per decade from 1900 to 2011, based on herbarium specimens in ALTA, CAN, DAO, MT, UBC, and WIN. Herbarium acronyms follow Thiers (continuously updated).

Whatever their origins, extralimital populations of balsam poplar in and around Tuktut Nogait National Park occur at the edge of the geographical and ecological range of the species in the Northwest Territories and Nunavut. Future research should investigate whether the current warming trend is affecting their growth and distribution, as Bochheim et al. (2003) suggested for the Alaskan Arctic stands. It would also be useful to better our understanding of their ecology, demography, and genetic structure within and among populations in the region, in comparison to the Alaskan North Slope stands, and throughout the range of balsam poplar (e.g., Breen et al., 2009; Keller et al., 2010; Olson et al., 2010). Similar comparative studies of their ecophysiology and phenology could also provide new insight (e.g., Landhäusser et al., 1996; Soolanayakanahally et al., 2009; Keller et al., 2011). Since the whole-genome sequencing of *Populus trichocarpa* (Tuskan et al., 2006), the first sequenced tree genome, poplar has been established as an important model organism for genomic studies. Inclusion of Canadian Arctic balsam poplar genotypes in future work is likely to improve our understanding of variation in this broadly distributed, ecologically variable, and economically important species, the northern range of which may soon expand in response to climate change.

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REFERENCES

Bennett, B.A., Catling, P.M., Cody, W.J., and Argus, G.W. 2010. New records of vascular plants in the Yukon Territory VIII. Canadian Field-Naturalist 124:1–27.

Bockheim, J.G., O'Brien, J.D., Munroe, J.S., and Hinkel, K.M. 2003. Factors affecting the distribution of *Populus balsamifera* on the North Slope of Alaska, U.S.A. Arctic, Antarctic, and Alpine Research 35(3):331–340, doi:10.1657/1523-0430(2003)035[0331:FATDOP]2.0.CO;2.

Brandt, J.P. 2009. The extent of the North American boreal zone. Environmental Reviews 17(1):101–161.

Breen, A.L., Glenn, E., Yeager, A., and Olson, M.S. 2009. Nucleotide diversity among natural populations of a North American poplar (*Populus balsamifera*, Salicaceae). New Phytologist 182(3):763–773, doi:10.1111/j.1469-8137.2009.02779.x.

Burn, C.R. 1997. Cryostratigraphy, paleogeography, and climate change during the early Holocene warm interval, western Arctic coast, Canada. Canadian Journal of Earth Sciences 34(7):912–925.

Caccianiga, M., and Payette, S. 2006. Recent advance of white spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Québec, Canada). Journal of Biogeography 33(12):2120–2135, doi:10.1111/j.1365-2699.2006.01563.x.

Cody, W.J. 1965a. Plants of the Mackenzie River Delta and Reindeer Grazing Preserve. Ottawa: Canada Department of Agriculture. 56 p.

———. 1965b. New plant records from northwestern Mackenzie District, N.W.T. Canadian Field-Naturalist 79:96–106.

———. 1996. Additions and range extensions to the vascular plant flora of the Northwest Territories, Canada. Canadian Field-Naturalist 110:260–270.

Cody, W.J., Scotter, G.W., and Zoltai, S.C. 1984. Additions to the vascular plant flora of Bathurst Inlet, Northwest Territories. Canadian Field-Naturalist 98:171–177.

———. 1989. Vascular plant flora of the Wager Bay region, District of Keewatin, Northwest Territories. Canadian Field-Naturalist 103:551–559.

———. 1992. Vascular plant flora of the Melville Hills Region, Northwest Territories. Canadian Field-Naturalist 106:87–99.

Cooper, D.J. 1986. White spruce above and beyond treeline in the Arrigetch Peaks regions, Brooks Range, Alaska. Arctic 39(3):247–252.

Dunwiddie, P.W., and Edwards, M.E. 1984. The dendrochronological potential of *Populus balsamifera* in northern Alaska. Tree-Ring Bulletin 44:45–52.

Eckenwalder, J.E. 2010. 1. *Populus* Linnaeus. In: Flora of North America Editorial Committee, eds. Flora of North America, Vol. 7. Magnoliophyta: Salicaceae to Brassicaceae. Oxford and New York: Oxford University Press. 5–22.

Ecological Stratification Working Group. 1996. A national ecological framework for Canada. Report and national map at 1:7 500 000 scale. Ottawa: Agriculture and Agri-Food Canada, Research Branch, Centre for Land and Biological Resources Research, and Hull: State of the Environment Directorate, Environment Canada. 125 p.

Edlund, S.A. 1983. Reconnaissance vegetation studies on western Victoria Island, Canadian Arctic Archipelago. Current Research, Part B, Geological Survey of Canada, Paper 83-1B:75–81.

Edlund, S.A., and Egginton, P.A. 1984. Morphology and description of an outlier population of tree-sized willows on western Victoria Island, District of Franklin. Current Research, Part A, Geological Survey of Canada, Paper 84-1A:279–285.

Edwards, M.E., and Dunwiddie, P.W. 1985. Dendrochronological and palynological observations on *Populus balsamifera* in northern Alaska, U.S.A. Arctic and Alpine Research 17(3):271–277.

Elliott, D.L., and Short, S.K. 1979. The northern limit of trees in Labrador: A discussion. Arctic 32(3):201–206.

Elsner, W.K., and Jorgenson, J.C. 2009. White spruce seedling (*Picea glauca*) discovered north of the Brooks Range along Alaska's Dalton Highway. Arctic 62(3):342–344.

Farrar, J.L. 1995. Trees in Canada. Markham: Fitzhenry & Whiteside Limited, and Ottawa: Natural Resources Canada. 502 p.

Feng, S., Ho, C.-H., Hu, Q., Oglesby, R.J., Jeong, S.-J., and Kim, B.-M. 2011. Evaluating observed and projected future climate changes for the Arctic using the Köppen-Trewartha climate classification. Climate Dynamics, doi:10.1007/s00382-011-1020-6.

Gamache, I., and Payette, S. 2005. Latitudinal response of subarctic tree lines to recent climate change in eastern Canada. Journal of Biogeography 32(5):849–862, doi:10.1111/j.1365-2699.2004.01182.x.

Harsch, M.A., Hulme, P.E., McGlone, M.S., and Duncan, R.P. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters 12(10):1040–1049, doi:10.1111/j.1461-0248.2009.01355.x.

Hobbie, S.E., and Chapin, F.S., III. 1998. An experimental test of limits to tree establishment in Arctic tundra. Journal of Ecology 86(3):449–461, doi:10.1046/j.1365-2745.1998.00278.x.

Holm, T. 1922. Contributions to the morphology, synonymy, and geographical distribution of Arctic plants. Report of the Canadian Arctic Expedition 1913–18, Vol. 5, Botany, Part B:1B–135B.

Hultén, E. 1968. Flora of Alaska and neighbouring territories: A manual of the vascular plants. Stanford: Stanford University Press. 1008 p.

Hustich, I. 1953. The boreal limits of conifers. Arctic 6(2):149–162.

———. 1979. Ecological concepts and biographical zonation in the North: The need for a generally accepted terminology. Holarctic Ecology 2:208–217.

Johansen, F. 1919. The forest's losing fight in Arctic Canada. Canadian Forestry Journal 15:303–306.

———. 1924. General observations on the vegetation. Report of the Canadian Arctic Expedition 1913–18, Vol. 5, Botany, Part C:1C–85C.

Kankaanpää, P., Huntington, H.P., and Program for the Conservation of Arctic Flora and Fauna (CAFF). 2001. Arctic flora and fauna: Status and conservation. Helsinki: Edita. 266 p.

Katenin, A.E. 1980. American species *Populus balsamifera* L. (Salicaceae) and *Viburnum edule* (Michx.) Rafin. (Caprifoliaceae) in the south-eastern part of Chukotka Peninsula. Botanicheski Zhurnal (Moscow & Leningrad) 65:414–421.

Keller, S.R., Olson, M.S., Silim, S., Schroeder, W., and Tiffin, P. 2010. Genomic diversity, population structure, and migration following rapid range expansion in the balsam poplar, *Populus balsamifera*. Molecular Ecology 19(6):1212–1226, doi:10.1111/j.1365-294X.2010.04546.x.

Keller, S.R., Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Olson, M.S., and Tiffin, P. 2011. Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). American Journal of Botany 98(1):99–108, doi:10.3732/ajb.1000317.

Kesting, S.F. 1996. Potential insolation and plant communities through treeline in the lower Anderson River Valley, N.W.T., Canada. MSc thesis, The University of British Columbia, Vancouver, British Columbia. 75 p.

Landhäusser, S.M., and Wein, R.W. 1993. Postfire vegetation recovery and tree establishment at the Arctic treeline: Climate-change—vegetation-response hypotheses. Journal of Ecology 81(4):665–672.

Landhäusser, S.M., Wein, R.W., and Lange, P. 1996. Gas exchange and growth of three Arctic tree-line tree species under different soil temperature and drought preconditioning regimes. Canadian Journal of Botany 74(5):686–693.

Mackay, J.R. 1958. The Anderson River map area, N.W.T. Canada Department of Mines and Technical Surveys Geographical Branch, Memoir 5:1–137.

Macoun, J.M., and Holm, T. 1921. Vascular plants. Report of the Canadian Arctic Expedition 1913–18, Vol. 5, Botany, Part A:1A–50A.

Mann, D.H., Peteet, D.M., Reanier, R.E., and Kunz, M.L. 2002. Responses of an Arctic landscape to late glacial and early Holocene climatic changes: The importance of moisture. Quaternary Science Reviews 21:997–1021, doi:10.1016/S0277-3791(01)00116-0.

Maycock, P.F., and Matthews, B. 1966. An Arctic forest in the tundra of northern Ungava, Quebec. Arctic 19(2):114–144.

Murray, D.F. 1980. Balsam poplar in Arctic Alaska. In: Rutter, N.W., and Schweger, C.E., eds. The ice-free corridor and peopling the New World. Canadian Journal of Anthropology 1(1):29–32.

Nichols, H. 1976. Historical aspects of the northern Canadian treeline. Arctic 29(1):38–47.

Olson, M.S., Robertson, A.L., Takebayashi, N., Silim, S., Schroeder, W.R., and Tiffin, P. 2010. Nucleotide diversity and linkage disequilibrium in balsam poplar (*Populus balsamifera*). New Phytologist 186(2):526–536, doi:10.1111/j.1469-8137.2009.03174.x.

Payette, S. 1983. The forest-tundra and present tree lines of the northern Quebec-Labrador Peninsula. In: Morisset, P., and Payette, S., eds. Tree-line ecology. Nordicana 47:3–23.

———. 1993. The range limit of boreal tree species in Québec-Labrador: An ecological and palaeoecological interpretation. Review of Palaeobotany and Palynology 79(1-2):7–30, doi:10.1016/0034-6667(93)90036-t.

Payette, S., and Delwaide, A. 1994. Growth of black spruce at its northern range limit in Arctic Quebec, Canada. Arctic and Alpine Research 26(2):174–179.

Payette, S., and Lavoie, C. 1994. The Arctic tree line as a record of past and recent climatic changes. Environmental Reviews 2:78–90.

Payette, S., Eronen, M., and Jasinski, J.J.P. 2002. The circumboreal tundra-taiga interface: Late Pleistocene and Holocene changes. Ambio 12:15–22.

Polunin, N. 1937. The birch 'forests' of Greenland. Nature 140:939–940, doi:10.1038/140939a0.

Porsild, A.E. 1950. Vascular plants of Nueltin Lake, Northwest Territories. National Museum of Canada Bulletin 118:72–83.

Porsild, A.E., and Cody, W.J. 1980. Vascular plants of continental Northwest Territories, Canada. Ottawa: National Museums of Canada. 667 p.

Raup, H.M. 1936. Phytogeographic studies in the Athabaska-Great Slave Lake region. 1. Catalogue of the vascular plants. Journal of the Arnold Arboretum 17:180–315.

———. 1947. The botany of southwestern Mackenzie. Sargentia 6:1–275.

Ritchie, J.C. 1987. Postglacial vegetation of Canada. Cambridge: Cambridge University Press. 178 p.

Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Drewes, E.C., and Schroeder, W.R. 2009. Enhanced assimilation rate and water use efficiency with latitude through increased photosynthetic capacity and internal conductance in balsam poplar (*Populus balsamifera* L.). Plant, Cell & Environment 32(12):1821–1832, doi:10.1111/j.1365-3040.2009.02042.x.

Soper, J.D. 1933. Solitudes of the Arctic. Canadian Geographical Journal 7:102–115.

Soper, J.H., and Powell, J.M. 1985. Botanical studies in the Lake Hazen region, northern Ellesmere Island, Northwest Territories, Canada. National Museums of Canada Publications in Natural Sciences 5. 67 p.

Spear, R.W. 1993. The palynological record of Late-Quaternary Arctic tree-line in northwest Canada. Review of Palaeobotany and Palynology 79(1-2):99–111, doi:10.1016/0034-6667(93)90040-2.

Surveys and Mapping Branch. 1980. District of Mackenzie, Northwest Territories, Series A 701, Map 97 A/7, Edition 1. Ottawa: Department of Energy, Mines and Resources.

Thiers, B. Continuously updated. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. http://sciweb.nybg.org/science2/IndexHerbariorum.asp. Archived by WebCite® at http://www.webcitation.org/5wq8VzTQ9.

Timoney, K.P., La Roi, G.H., Zoltai, S.C., and Robinson, A.L. 1992. The High Subarctic forest-tundra of northwestern Canada: Position, width, and vegetation gradients in relation to climate. Arctic 45(1):1–9.

Tuskan, G.A., DiFazio, S., Jansson, S., Bohlmann, J., Grigoriev, I., Hellsten, U., Putnam, N., et al. 2006. The genome of black cottonwood, *Populus trichocarpa* (Torr. & Gray). Science 313(5793):1596–1604, doi:10.1126/science.1128691.

Viereck, L.A., and Foote, J.M. 1970. The status of *Populus balsamifera* and *P. trichocarpa* in Alaska. Canadian Field-Naturalist 84:169–173.

Viereck, L.A., and Little, E.L., Jr. 2007. Alaska trees and shrubs, 2nd ed. Fairbanks: University of Alaska Press. 359 p.

Wiggins, I.L., and Thomas, J.H. 1962. A flora of the Alaskan Arctic slope. Toronto: University of Toronto Press. 425 p.

Zasada, J.C., and Phipps, H.W. 1990. *Populus balsamifera* L., balsam poplar. In: Burns, R.M., and Honkala, B.H., eds. Silvics of North America, Volume 2: Hardwoods. Washington, D.C.: U.S. Forest Service. 518–529.

Zoltai, S.C., Sirois, J., and Scotter, G.W. 1992. A natural resource survey of the Melville Hills region, Northwest Territories. Technical Report Series No. 135. Yellowknife: Canadian Wildlife Service, Western and Northern Region.

APPENDIX 1: Voucher specimen data documenting the distribution of *Populus balsamifera* in Nunavut and the Northwest Territories. Measurements are reported with the units given on the herbarium specimens. DBH = diameter at breast height.

Specimen data are organized by territory (Nunavut and Northwest Territories). Within the Northwest Territories, a subset of the collections is organized by geographical regions (boldfaced) in which the collections were made (e.g., Eskimo Lakes, Fort Providence, Fort Simpson, etc.) as determined from herbarium labels. Specimens listed first are from isolated sites and are not organized in broader geographical regions. Collection data for each specimen are listed in the following order: general collection location, comments made by the collector(s), elevation, geographical coordinates, collection date, collector(s) and collection number, herbarium and herbarium accession number. Herbarium acronyms follow Thiers (continuously updated). Entries reflect collection data as presented on herbarium labels; entries are incomplete in cases where label data are lacking.

NUNAVUT: Gully Creek just above Escape Rapids, E side of Coppermine River, 67.617˚ N, 115.483˚ W, 1916, *R.M. Anderson 756* (CAN–40681); Josie's Bay, a westerly arm of Windy Bay, Nueltin Lake, 60.5˚ N, 99.5˚ W, 18 Jul 1947, *F. Harper 2330* (CAN–40667); tributary to Thelon River, 12 mi from Thelon, trees to 25 ft, DBH 4″, many young trees, including seedlings less than 3 ft high, 64.5˚ N, 102.083˚ W, 1 Apr 1956, *J.S. Tener s.n.* (CAN–52932).

NORTHWEST TERRITORIES. 1 mi S of the Mountain River-Mackenzie River confluence, 62.667˚ N, 128.833˚ W, 21 Aug 1973, *W. Friesen 1872* (CAN–446964); 3 mi N of the outlet of Lockhart River, 63.15˚ N, 107.867˚ W, 30 May 1900, *J.W. Tyrrell 23133* (CAN–40675); 8 mi below Hornby's Bend, Thelon River, 63.96˚ N, 103.907˚ W, 29 Jul 1952, *J.S. Tener 181* (CAN–219863); Aklavik, elev. 7.5 m, 68.233˚ N, 134.233˚ W, 07 Jul 1963, *V.J. Krajina, K. Wade & R. Kuramoto 63070753* (UBC–V110523); along the lower Anderson River, 68.483˚ N, 128.783˚ W, Jun 1994, *S. Kesting & K. Barton 34* (UBC–V212425); Aubry Lake, N arm, E shore, small tree 4–5 m high, 67.333˚ N, 126.417˚ W, 13 Jun 1976, *R.R. Riewe & J. Marsh 18* (CAN–433306); Aubry Lake, N arm, E side, 67.333˚ N, 126.417˚ W, 20 Jul 1976, *R.R. Riewe & J. Marsh 264* (WIN–31381); Bear Creek, a tributary of Rat River, elev. 1000 ft, 67.717˚ N, 136.2˚ W, 24 Jun 1973, S.*L. Welsh & J.K. Rigby 12045* (CAN–381492); Blachford Lake, mid W shore, tall tree, 62.2˚ N, 113.5˚ W, 25 Jun 1961, *G.W. Scotter 1007* (DAO–198907); Canol Road (Hwy. 6), 6 Sep 1971, *R.G.H. Cormack s.n.* (ALTA–41937); delta of the Horn River, Mills Lake, 61.5˚ N, 117.716˚ W, 18 Aug 1956, *C.D. Bird 187* (ALTA–21439, DAO–198911); E bank of E Channel, Mackenzie River, small grove of trees in protected spot in valley at base of hills, trees 12 ft, DBH 1 1/2″, first poplar noted travelling south on river, 68.917˚ N, 134.55˚ W, 02 Jul 1957, *W.J. Cody & D.H. Ferguson 9802* (DAO–198943); E shore of Slave River, 7 mi N of mouth of Salt River (Camp 11), trees up to 100 ft with 14″ DBH, this specimen 18 ft, 3″ DBH, 60.217˚ N, 112.8˚ W, 11 Aug 1955, *H.H. Day 33* (DAO–198920); Enterprise – Mackenzie River Highway, near game warden's cabin on SE shore of Kakisa Lake, tree to 15 ft, 60.933˚ N, 117.717˚ W, 21 Jun 1959, *J.W. Thieret & R.J. Reich 4619* (DAO–198919, CAN–298095); Little Doctor Lake, small tree 8 ft high, 61.8677˚ N, 123.333˚ W, 08 Aug 1961, *W.J. Cody & K.W. Spicer 12090* (DAO–198909); Logan Mountains, Flat River Valley, ca. 2 km S of Tungsten, elev. 1500 m, 61.967˚ N, 128.283˚ W, 13 Aug 1981, *J.G. Harris 1545* (ALTA–88314); Mackenzie Bison Sanctuary, elev. 190 m, 61.5˚ N, 117˚ W, 27 Jul 1987, *D.L. Smith 87–040* (ALTA–94032); Mackenzie River, just S of mouth of Blackwater River, 63.95˚ N, 124.167˚ W, 14 Jul 1970, *W.J. Cody 18877* (DAO–601643, MT); Mackenzie Valley, beside Hume River 16 mi WNW of Mountain River Camp, mature tree some 20 m high, 65.733˚ N, 129.35˚ W, 28 Jun 1972, *D.E. Reid 465* (CAN–407586); Macmillan Pass, near the Yukon border along the Canol corridor within 5 km W of Camp 222, elev. 1300 m, 63˚ N, 130˚ W, 07 Aug 1993, *K. Harper 7* (ALTA–98232); McDougall Pass, floodplain of Rat River, 1 mi S of Horn Lake, 67.733˚ N, 136˚ W, 14 Jul 1962, *P.M. Youngman & G.D. Tessier 122* (CAN–273828); McTavish Arm, fiords on the E shore, elev. 800–900 ft, common as a low shrub on gravelly slopes, 66.167˚ N, 117.5˚ W, 11 Aug 1928, *A.E. Porsild & R.T. Porsild 5344* (CAN–40673, MT); N shore of Smith Arm (Canoe Creek Harbour), 66.667˚ N, 122˚ W, 20–22 Jul 1928, *A.E. Porsild & R.T. Porsild 4994* (CAN–40672); Norman Wells Pipeline, ca. 430 km S from Norman Wells, near Ebbutt Hills, 62.317˚ N, 122.717˚ W, 16 Jul 1986, *K.L. MacInnes 86–100* (DAO–595990); on island 10 mi N of British Columbia–NWT boundary, 60.167˚ N, 123.7˚ W, 03 Jul 1959, *W.W. Jeffrey 169* (CAN–291823); on the E side of

the East Channel, 12 mi N of Inuvik, ca. 8.5 m tall, 68.360˚ N, 133.725˚ W, 02 Jul 1971, *H. Hernandez 283* (ALTA–41142); Point Separation, Mackenzie River, 67.6˚ N, 134.083˚ W, Jun 1888, *McConnell s.n.* (CAN–40677); Porter Lake, small trees forming a band along sandy beach, small trees to 5 ft in height, 61.5167˚ N, 108.1˚ W, 27 Jul 1966, *W.J. Cody 15502* (DAO–198946); Rocher River settlement at mouth of Taltson River, tree 25 ft tall, DBH 4″, 61.383˚ N, 112.75˚ W, 01 Aug 1965, *W.J. Cody 14345* (DAO–198931); Sans Sault, beside Hume River, Mackenzie River, 16 mi WNW of the Mountain River Camp, mature tree some 20 m high, 65.733˚ N, 129.217˚ W, 28 Jun 1972, *D.E. Reid 465* (ALTA–77267, ALTA–77268); small lake 4 mi NE of Cameron Hills, tree 25 ft tall, DBH 4″, 60.333˚ N, 117˚ W, 15 Aug 1965, *W.J. Cody 14810* (DAO–198936); small unnamed lake on Rutledge River, young tree 8 ft tall, 61.167˚ N, 111.883˚ W, 10 Aug 1966, *W.J. Cody 16125* (DAO–198945); small unnamed lake on S side of Horn Plateau, small trees to 10 ft in height, 61.983˚ N, 119.3667˚ W, 03 Jul 1970, *W.J. Cody 18623* (DAO–603555); south of Campbell Lake, East Channel, elev. 50 ft, 67.917˚ N, 133.983˚ W, 15 Aug 1965, *M. Aleksiuk 65081502* (UBC–V113088); East Channel, south of Campbell Lake, 50 ft, 67.917˚ N, 133.983˚ W, 30 Jul 1965, *M. Aleksiuk 65073016* (UBC–V113128); Thubun Lake, tree 12 ft tall, 61.517˚ N, 111.767˚ W, 31 Jul 1950, *W.J. Cody 14298* (DAO–198934); vicinity of Brintnell Lake, on or near Camp Point, along Frost Creek, tree 20 ft high, 3″ in diameter, 62.083˚ N, 127.583˚ W, 28 Jun 1939, *H.M. Raup & J.H. Soper 9315* (CAN–268503, ALTA–22214); vicinity of Eldorado Mine, Port Radium, E end of McTavish Arm, above McDonough Lake, shrub to 3 ft high, 66.083˚ N, 118.033˚ W, 07 Jul 1948, *H.T. Shacklette 2862* (CAN–200328); Wood Buffalo National Park, mile 105–110, Hwy. 5, ca. 30 mi SE of Nyarling River, 60.267˚ N, 114.168˚ W, 31 Aug 1970, *D.G. Despain & G.H. LaRoi 240* (ALTA–30791); Yellowknife River Power House, 62.667˚ N, 114.25˚ W, 07 Aug 1949, *W.J. Cody 3299* (DAO–198928); west of the tree limit on Horton River by about 15 mi, trees grew to almost 1 ft in diameter, 67˚42′ N, 123˚00′ W, 1951, *J.R. Mackay s.n.* (DAO-198913). **Eskimo Lakes**: Eskimo Lake Basin, narrows between 3rd and 4th lake, occasional in sheltered spots where tree-like, 10–20′ tall, 68.75˚ N, 133˚ W, 20 Aug 1927, *A.E. Porsild & R.T. Porsild 3026* (CAN–40668); Portage Point, E side of westernmost lake, small trees to 8 ft, 68.767˚ N, 133.267˚ W, 12 Aug 1957, *W.J. Cody & D.H. Ferguson 10823* (DAO–198941); Reindeer Grazing Preserve, Island in Anderson River, 5 ft tall, 68.55˚ N, 128.467˚ W, 05 Jul 1965, *G.W. Scotter 6437* (DAO–198929); Reindeer Grazing Preserve, small knolls, 68.9˚ N, 132.683˚ W, 01 Aug 1966, *G.W. Scotter 10308* (DAO–198944); W side of lake, trees 2–25 ft, 68.75˚ N, 133.317˚ W, 11 Aug 1957, *W.J. Cody & D.H. Ferguson 10735* (DAO–198942). **Fort Providence**: 61.35˚ N, 117.65˚ W, 06 Jul 1951, *A.A. Lindsey 168* (CAN–216257); near Royal Canadian Corps Signals buildings, small tree, 8 ft, 61.367˚ N, 117.6333˚ W, 04 Jul 1955, *W.J. Cody & J.M. Matte 8556* (DAO–198917). **Fort Simpson**: tree 30 ft, DBH 6″, 61.867˚ N, 121.367˚ W, 01 Jun 1955, *W.J. Cody & J.M. Matte 8008* (ALTA–23090); airport, tree 12 ft, DBH 2″, 61.367˚ N, 117.633˚ W, 09 Jun 1955, *W.J. Cody & J.M. Matte 8136* (DAO–198918); behind Royal Canadian Corps Signals buildings, tree 30 ft, DBH 6″, 61.867˚ N, 121.367˚ W, 01 Jun 1955, *W.J. Cody & J.M. Matte 8008* (DAO–198915); Indian village of Mackenzie River ca. 30 mi downstream from Fort Simpson, tree 30 ft, 62.1˚ N, 122.167˚ W, 11 Jun 1955, *W.J. Cody & J.M. Matte 8171* (DAO–198910); road in front of Experimental Farm, tree 40 ft, DBH 6″, 61.866˚ N, 121.367˚ W, 29 Jun 1955, *W.J. Cody & J.M. Matte 8444* (DAO–198916, MT); vicinity of Fort Simpson, 20 ft tall, 62.85˚ N, 121.383˚ W, 11 Jun 1939, *H.M. Raup & J.H. Soper 9068* (CAN–268502). **Fort Smith**: tree 18 ft, 60˚ N, 111.883˚ W, 26 Jun 1950, *W.J. Cody & C.C. Loan 4027* (DAO–198938), 8 ft, ♂, 3570 (DAO–198953); 12 ft, ♀, *W.J. Cody & C.C. Loan 3571* (DAO–198954, MT); trees 12–35 ft, 60˚ N, 111.883˚ W, 09 Jun 1950, *W.J. Cody & C.C. Loan 3775* (DAO–198952), 3776 (DAO–198951), 3777 (DAO–198950), 3778 (DAO–198949, MT), 3779 (DAO–198948, MT), 3780 (DAO–198955); 60˚ N 111.9167˚ W, 20 Jun 1940, *A. Dutilly 8024* (MT). **Great Bear Lake**: Etacho Point (Big Point), 66˚ N, 121.5˚ W, 24 Aug 1928, *A.E. Porsild & R.T. Porsild 3487* (CAN–40670); Fort Franklin, 65.183˚ N, 123.467˚ W, 12–13 Jun 1928, *A.E. Porsild & R.T. Porsild 3200A* (CAN–40669, ALTA 29552); N shore of Dease Arm, 67.033˚ N, 119.833˚ W, 23–26 Jun 1928, *A.E. Porsild & R.T. Porsild 4696* (CAN–40671); N shore of Smith Arm, Olmsted Bay, low bushes 1–3 ft high, 66.533˚ N, 122.583˚ W, 16–21 Jul 1928, *A.E. Porsild & R.T. Porsild 5059* (CAN–40674); Sawmill Bay, NE tip of Leith Peninsula, not exceeding 1 ft high, 65.717˚ N, 118.9˚ W, 16 Jul 1948, *H.T. Shacklette 3071* (CAN–200329); Scented Grass Hills Peninsula, S shore of Etacho Point, low, more or less prostrate bushes, 18″ high on side of dune, 66.05˚ N, 121.25˚ W, 11–21 Jul 1949, *A.E. Porsild 17019* (CAN–127619); Cameron Bay, 66.0833˚ N 117.9167˚ W, 28 Jul 1940, *A. Dutilly 28253* (MT). **Great Slave Lake**: East Channel, Hay River, tree ca. 1–15 m tall at maturity, 60.85˚ N, 115.7˚ W, 03 Jun 1951, *W.H. Lewis 232* (DAO–198925, UBC–V72779); Brabant Island, tree 8–15 m tall, 61.05˚ N, 116.583˚ W, 31 Jul 1951, *W.H. Lewis 1047* (DAO–198921); Fairchild Point, 62.717˚ N, 109.167˚ W, 18 Aug 1927, *H.M. Raup 492* (CAN–310818); Fort Reliance, E end of Great Slave Lake, 62.713˚ N, 109.165˚ W, 02 Jul 1949, *A.L. Wilk 4* (ALTA–5549); Hay River, S shore of Great Slave Lake, 12 Jul 1949, 60.85˚ N, 115.7˚ W, *E.H. Moss 8841* (ALTA–5545), 8842 (ALTA–5544); Long Island, tree 10–18 m tall, 61.717˚ N, 114.883˚ W, 30 Jun 1951, *W.H. Lewis 845* (DAO–198923); Moraine Point, shrub 2–3 dm tall, 61.6˚ N, 115.633˚ W, 30 Jun 1951, *W.H. Lewis 498* (DAO–198924, UBC–72682); near Fort Resolution, 61.167˚ N, 113.667˚ W, 12 May 1900, *J.W. Tyrrell 23132* (CAN–40676); NW shore of Great Slave Lake between Jones Point and Fort Rae, 62.65˚ N, 115.833˚ W, 1925, *R. Bedford s.n.* (CAN–268035);

old settlement, Hay River, tree 10 m, 60.85˚ N, 115.7˚ W, 28 Jul 1951, *W.H. Lewis 987* (DAO – 198922); S shore of Great Slave Lake, Hay River, 60.8015˚ N, 115.799˚ W, 12 Jul 1949, *E.H. Moss 8841* (DAO – 198956), 8842 (DAO – 198927); shore of E end of McLeod Bay, E end of Great Slave Lake, near Ft. Reliance, 62.717˚ N, 109.167˚ W, 26 Jun 1965, *G.B. Rossbach 6353* (CAN – 329774); Snowdrift (Lutsel K'e), at E end of Great Slave Lake, tree 15 ft, 62.4˚ N, 110.75˚ W, 12 Aug 1965, *W.J. Cody 14734* (DAO – 198933); W shore of Yellowknife Bay, 6 mi S of town of Yellowknife, tree 12 ft, DBH 2 1/2″, ♀, 62.3669˚ N, 114.3347˚ W, 04 Jun 1949, *W.J. Cody 2212* (DAO – 198947, MT); vicinity of Old Fort Reliance, 62.783˚ N, 108.917˚ W, 07 Aug 1927, *H.M. Raup 496* (CAN – 310817). **Liard River**: island in Liard River 15 mi SW of Fort Liard, over-mature tree 60 ft high, DBH 15″, 60.0833˚ N, 123.783˚ W, 21 Jul 1961, *W.J. Cody & K.W. Spicer 11522* (DAO – 198908, 2 sheets, UBC – V111390); island in Liard River S of Fort Liard, elev. 725 ft, 60.061˚ N, 123.843˚ W, 17 Aug 1994, *H.J. Kubiw & D.W. Cowell 1004* (DAO – 684084); Mackenzie Lowlands, Liard River valley, Liard River, shingle bar 5 mi above Liard-Kotaneelee confluence, 60.25˚ N, 123.75˚ W, 12 Jul 1959, *W.W. Jeffrey 163* (CAN – 260966). **Mackenzie Mountains**: elev. 4000 ft, 29 Jul 1960, *E.W. Arnold 100* (UBC – V119953); by hotspring on N branch of Twitya River, elev. ± 4000 ft, trees 50 – 60 ft tall, DBH to 12″, 63.8˚ N, 129.867˚ W, 09 Jul 1972, *W.J. Cody & F.M. Brigham 20649* (DAO – 620671); Canada Tungsten Mine, grove around picnic area by hotspring meadow, 1 mi S of mine, 61.967˚ N, 128.25˚ W, 03 Aug 1967, *K.W. Spicer 1650* (DAO – 198957, 2 sheets); Canol Road, Mile 202 from Mackenzie River site 35 road adjacent, 63.467˚ N, 129.351˚ W, 14 Jul 1977, *L. Kershaw & G.P. Kershaw 524* (DAO – 304784); June Lake, trees 12 – 25 ft in height, DBH 1 – 4″, elev. 3700 ft, 63.516˚ N, 128.667˚ W, 31 Jul 1967, *W.J. Cody 17139* (DAO – 198959, ALTA – 105202); Keele and Ekwi River, elev. 2500 ft, 64.1˚ N, 128.133˚ W, 15 Jul 1963, *E. Kvale & K. Haggard 266f* (DAO – 198914); Keele River at Canadian Wildlife Service Camp, shrub 2 ft tall, elev. 1400 ft, 64.208˚ N, 127.417˚ W, 17 Jul 1970, *W.J. Cody 18885* (DAO – 601848, MT); Keele River, "Slew Lick," 1500 – 1900 ft, small trees 3 – 10 ft in height, 64.216˚ N, 127.916˚ W, 26 Jun 1971, *W.J. Cody & G.W. Scotter 19163* (DAO – 616081); margin of hot springs, elev. 4000 ft, 29 Jul 1960, *E.W. Arnold 100* (CAN – 264890); on N flank of Carcajou Range, Florence Lake, trees to 20 ft, elev. 1400 ft, 65.233˚ N, 128.217˚ W, 16 Jul 1972, *W.J. Cody & F.M. Brigham 20987* (DAO – 620725); S Nahanni River area, Deadman Valley, near cabin, elev. 1050 ft, 69.25˚ N, 124.5˚ W, 27 Jun 1970, *G.W. Scotter 12398* (DAO – 604486); S Nahanni River drainage, Rabbitkettle Lake, young tree, 6 ft tall, elev. 2050 ft, 61.95˚ N, 127.217˚ W, 10 Aug 1967, *W.J. Cody & K.W. Spicer 17907* (DAO – 198960); S Nahanni River Valley, Rabbitkettle Hot Spring, elev. 2100 ft, 61.95˚ N, 127.183˚ W, 12 Jul 1972, *W.J. Cody & F.M. Brigham 20900* (DAO – 620684, MT). **Mackenzie River Delta**: 21 Jul 1966, *D. Gill 07216610* (UBC – V132788); E branch, Reindeer Lake, 68.833˚ N, 136.417˚ W, Aug 1953, *E.H. McEwen 50* (CAN – 226067); Inuvik, 67.917˚ N, 133.983˚ W, 08 Aug 1966, *Owen-Larsen 218* (UBC – V171519); Jackfish Creek, 28 mi S of Inuvik, 68.217˚ N, 134.983˚ W, 04 Aug 1966, *J.D. Lambert s.n.* (DAO – 641029); Williams Island opposite Reindeer Station, trees 9 – 15 ft, small stands, scattered, 68.667˚ N, 134.167˚ W, 18 Jun 1957, *W.J. Cody & D.H. Ferguson 9635* (ALTA – 105203, DAO – 198940); Williams Island, opposite Reindeer Station, tree 14 ft, DBH 2 1/2″, 68.667˚ N, 134.167˚ W, 14 Jul 1957, *W.J. Cody & D.H. Ferguson 10037* (DAO – 198939, UBC – V197775). **Nahanni National Park**: Rabbit Kettle Lake, midway N side, 61.954˚ N, 127.2167˚ W, 29 Jun 1975, *A.H. Marsh 5270* (DAO – 137391); S bank of Flat River, near Mackenzie Mountains, 61.467˚ N, 125.6˚ W, 22 Jul 1975, *S. Talbot T5041 – C* (CAN – 395551); S Nahanni River, Deadman Valley, Prairie Creek fan, 61.25˚ N, 124.45˚ W, 21 Jun 1976, *H.M. Kershaw 384* (DAO – 147184); base of Twisted Mountain, 206 m, shrub 25 – 50 cm, 61.2˚ N, 123.667˚ W, 11 Jul 1975, *S.S. Talbot T5008 – 16* (DAO – 157683); Prairie Creek alluvial fan, Deadman Valley, 21 Jul 1976, 61.25˚ N, 124.45˚ W, *H.M. Kershaw 1399* (ALTA – 83048). **Norman Wells**: bank overlooking Mackenzie River, 65.267˚ N, 126.817˚ W, 30 Jul 1953, *W.J. Cody & R.L. Gutteridge 7678* (DAO – 198926, UBC – V85926); Norman Wells Quad., vicinity of lodge, 66.183˚ N, 126.667˚ W, 11 Jul 1971, *G.W. Argus & W.N. Chunys 8065* (CAN – 570863); top of bank overlooking Mackenzie River, 65.282˚ N, 126.831˚ W, 30 Jul 1953, *W.J. Cody & R.L. Gutteridge 7678* (ALTA – 5551); tree 15 – 20 ft, 65.267˚ N, 126.85˚ W, 21 Jun 1969, *G.E. Shewell 68* (DAO – 603103); W edge of airport, SW of fuel area, 67.283˚ N, 126.8˚ W, 14 Jul 1974, *J.K. Rigby 30* (CAN – 399282). **Slave River**: Le Grand Detour, S side of Slave River, in stand of old trees to 60 ft in height and DBH 18″, young tree 18 ft in height, DBH 2″, 60.317˚ N, 112.617˚ W, 24 Jul 1950, *W.J. Cody 13858* (DAO – 198937); lowlands on E side of Slave River, ca. 2 mi W of Hook Lake camp, 60.717˚ N, 112.808˚ W, 24 Jul 1975, *H.W. Reynolds 333* (DAO – 154920); N end of Long Island, old sawmill site, DBH 5″, tree 30 ft tall, 60.8˚ N, 113.25˚ W, 2 Aug 1965, *W.J. Cody 14438* (DAO – 198932); N side of Slave River, 8 mi above Ring Lake, young trees to 20 ft in height, 61.2˚ N, 113.217˚ W, 05 Aug 1965, *W.J. Cody 14505* (DAO – 198930); Slave River delta, Jean River, young tree 12 ft tall, 61.3677˚ N, 113.3667˚ W, 07 Aug 1965, *W.J. Cody 14557* (DAO – 198935).