Taxonomy, History, and Biogeography of the Contortae (*Pinus* spp.)

Dahl Winters

Biol 561 – Ecological Plant Geography

Introduction

The Contortae is a subsection of the subgenus *Pinus*, which contains the diploxylon pines (those having two vascular bundles per needle vs. one). The other subgenus is *Strobus*, and together, *Pinus* and *Strobus* comprise one of the most successful plant families to date – the Pinaceae. Representatives of the wind-dispersed, wind-pollinated Pine family can be found in abundance on every continent except Antarctica, but the subsection Contortae stands out from other pines given their special adaptations to grow in places even other pines cannot.

The Contortae is a four-species monophyletic clade comprised of *Pinus virginiana* (Virginia pine), *P. clausa* (sand pine), *P. banksiana* (jack pine), and *P. contorta* (lodgepole pine). These four species occupy an important niche in each of their ranges – that of an early seral species, adapted to dry, relatively nutrient-poor soil conditions where few other tree species can compete. If not for these trees, which often form pure stands where fire is a common disturbance and the soil is infertile, there would be little in the way of forest habitat for animals. Humans would not be able to make use of the pulpwood they provide.

Though very closely related, the range sizes of these species are widely divergent, from Sand pine being isolated mostly to northern Florida, to Lodgepole pine, which occupies one of the widest ranges of environmental conditions in North America. However, taken together, their combined range spans a sizable portion of North America, from the west coast all the way to the east, and from the northern Canadian treeline all the way south to Mexico, exempting the Great Plains region and desert areas of the Southwest. The only places on the continent they do not grow are where their physiological limits are exceeded by weather too cold or too dry, or where the soil is too fertile or fine, limiting their range by interspecific competition.

This paper will discuss the historical and environmental reasons for the current distribution of each member of the Contortae, as well as give some insight into possible future distributions of these four pine species.

Classification History and Taxonomy

Pinus virginiana

Virginia pine was first described on April 16, 1768 in the eighth edition of The Gardeners Dictionary as *Pinus virginiana* Mill, and this is the name it still has today.[1] It was also described as *Pinus virginiana* var. *echinata* (Mill.) Du Roi[2] in 1771, and *Pinus inops* Aiton[3] in 1789. No subspecies are recognized.

Pinus clausa

The first description of *Pinus clausa* was in the 10th Census of the United States, as *Pinus clausa* Vasey.[4] It was also described as *Pinus inops* var. *clausa* Chapm. ex. Engelm. in 1877, and as *Pinus clausa* (Chapm. ex Engelm.) Sarg. in 1884. Today, it is known as *Pinus clausa* (Chapman ex Engelm.) Vasey ex Sarg.[5] Two subdivisions of this species are recognized: Choctawhatchee sand pine (*P. clausa* var. *immuginata*), and Ocala sand pine (*P. clausa* var. *clausa*).

[1] Pinus virginiana P. Miller, Gard. Dict., ed. 8. n. 9. 1768 [16 Apr 1768]
[2] Pinus virginiana var. echinata (Mill.) Du Roi, Obs. Bot. Sist. 44. 1771.
[3] Pinus inops Aiton, Hort. Kew. 3: 367. 1789.
[4] From w3TROPICOS: http://mobot.mobot.org/W3T/Search/vast.html
[5] Pinus clausa (Chapman ex Engelmann) Vasey ex Sargent, Rep. For. N. America 9:199. 1884.

Pinus banksiana

Pinus banksiana was described in 1803 as *Pinus banksiana* Lamb.[6] It was again described in 1850 as *Pinus banksiana* Lindl. & Gord.[7] The species was named after Sir Joseph Banks (Seymour 1982). As early as 1789, it was recognized as *Pinus divaricata* (Aiton) Gordon & Sudw. It has also been known as *Pinus divaricata* (Ait.) Dumont.-Cours., *Pinus sylvestris* var. *divaricata* , *Pinus* sylvestris L. var. *divaricata* Aiton, *Pinus banksiana* Lamb. forma *procumbens* J.Rousseau, *Pinus hudsonica* Parl. in DC., *Pinus hudsoni* Poir. in Lam., *Pinus rupestris* F.Michx., *Pinus divaricata* (Aiton) Gordon & Sudw. forma *procumbens* (J.Rousseau) B.Boivin, and *Pinus banksiana* Lamb. var. *annae* Schwer.[8]

Pinus contorta

Pinus contorta was described as *Pinus contorta* Dougl. in Loudon's Encyclopedia of Trees.[9] It was also described in 1838 as *Pinus contorta* Douglas ex Loudon,[10] and in 1866 as *Pinus contorta* Bol.[11] Today, the species is known as *Pinus contorta* Dougl. ex Loud. There are four geographically distinct varieties, which have all had a history of different names (the most current is at the top):

1. Bolander Beach Pine (western California, Mendocino County, only)
Pinus contorta Dougl. ex Loud. var. *bolanderi* (Parl.) Vasey
Pinus contorta Dougl. ex Loud. ssp. *bolanderi* (Parl.) Critchfield

2. Shore pine, beach pine (North American west coast)
Pinus contorta Dougl. ex Loud. var. *contorta*
P. contorta var. *hendersoni* Lemmon, Erythea 2:176. 1894.
P. divaricata var. *hendersonii* Boiv. Nat. Can. 93:272. 1966. = var. *contorta*.

3. Lodgepole pine (throughout the intermountain west)
Pinus contorta Dougl. ex Loud. var. *latifolia* Engelm. ex S. Wats.[12]
Pinus contorta Dougl. ex Loud. ssp. *latifolia* (Engelm. ex S. Wats.) Critchfield[13]
Pinus divaricata (Ait.) Dum.-Cours. var. *hendersonii* (Lemmon) Boivin
Pinus divaricata (Ait.) Dum.-Cours. var. *latifolia* (Engelm. ex S. Wats.) Boivin[14]
P. tenuis Lemmon[15]

4. Sierra lodgepole pine (Sierra Nevada region only)
Pinus contorta Dougl. ex Loud. var. *murrayana* (Grev. & Balf.) Engelm.[16]
Pinus contorta Dougl. ex Loud. ssp. *murrayana* (Grev. & Balf.) Critchfield[17]
Pinus murrayana Grev. & Balf.[18]

---

[6] Pinus banksiana Lambert, A Description of the Genus Pinus 1: 7, plate 3. 1803.
[7] Pinus banksiana Lindl. & Gord. -- in Journ. Hort. Soc. v. (1850) 218, partim.
[8] Natural Resources Canada. Plant Hardiness Site. http://www.planthardiness.gc.ca/plant_chklist.pl?speciesid=1003671
[9] Pinus contorta Dougl. -- in Loud. Encyc. Trees, 975. f. 915.
[10] Pinus contorta Douglas ex Loudon -- Arbor. Frutic. Brit. 4: 2292 (figs. 2210-2211). 1838 [1 Jul 1838]
[11] Pinus contorta Bol. -- Proc. Calif. Acad. Sci. 3: 227. 1866.
[12] P. contorta var. latifolia Engelm. in Wats. Bot. King Exp. 331. 1871.
[13] P. contorta ssp. latifolia Critchf. M. M. Cabot Found. Pub. no. 3:107. 1957.
[14] P. divaricata var. latifolia Boiv. Nat. Can. 93:272. 1966.
[15] *P. tenuis* Lemmon, Erythea 6:77. 1898. = var. *latifolia*.
[16] *P. contorta* var. *murrayana* Engelm. in Wats. Bot. Calif. 2: 126. 1880.
[17] *P. contorta* ssp. *murrayana* Critchf. M. M. Cabot Found. Pub. no. 3:106. 1957.
[18] *P. murrayana* Balf. in A. Murr. Bot. Exp. Oreg. (Rep. no. 8) 2, no. 740, illus. 1853.

Morphology

The Contortae, as diploxylon pines, all have two leaf vascular bundles. They also have persistent fascicle sheaths, 2 needles per fascicle, medial needle resin ducts, thick cone scales, variable umbo prickles, articulate seed wings, and a dorsal umbo position (Gernandt et al 2005). Their evergreen needles are between ¾ to 3 inches length. All species are monoecious (male and female parts found on the same plant, but on different flowers). However, the form of each species varies.

P. clausa is the shortest (20-40 feet), with a bushy crown, scrubby form and upward-angled branches. *P. virginiana* is a small to medium-sized tree up to 70 feet tall with a flat, sparse crown. *P. banksiana* is much like *P. virginiana* in form, but can grow up to 80 feet tall with a small, irregular grown. *P. contorta* is more tall and slender than the other three, with a narrow, loose crown up to 80 feet tall, but can be short and scrubby in varieties growing along the Pacific Coast. On both *P. virginiana* and *P. banksiana*, dead branches and cones persist on the trunk for several years. Additional differences between the species are summarized (Table 1).

Table 1: Summary of Species-Specific Characteristics

	P. virginiana	***P. clausa***	***P. banksiana***	***P. contorta***
Needle length	1.5-3 inches	2-3 inches	¾-1.5 inches	1.5-3 inches
Needle color	Yellow-green	Yellow-green	Yellow-green	Yellow-green to green
Cone length	1.5-2.5 inches	2-3.5 inches	1.5-2 inches	1-2 inches
Cone color	red-brown	reddish brown to gray-brown	light brown but graying with age	light brown to brown
Cone prickle	umbo armed with a sharp, needle-like prickle	armed with a short, stout prickle	apophysis round and umbo armed with a small prickle	apophysis armed with a short spine
Cone shape	Conical to ovoid	Often clustered	Curved	Often asymmetrical; lumpy near the base
Cone persistence	Persistent; mature in the fall	Persistent and remaining closed	Serotinous, persisting for several years	May remain closed for several years
Twig properties	Slender; buds gray-brown, narrowly ovoid.	Slender	Very resinous, narrowly ovoid buds.	Needles persistent for several years; buds narrowly ovoid, reddish brown, resinous.
Twig color	Green changing to purple-green with a glaucous bloom	Reddish to gray-brown	Yellow to greenish brown when young, gray-brown with age	Orange-brown, turning darker with age

Habitat

Soils and climate are the two major determinants of distribution for the Contortae. Soil is important because its properties (parent material, porosity, texture, decomposition rate) control nutrient and water supply to the trees. Temperature is important since some of the Contortae (*P. banksiana* and *P. contorta*) are more cold-adapted than the others. Below is a summary of important soil and climate requirements.

Table 2: Summary of Soil Types[19]

	P. virginiana	***P. clausa***	***P. banksiana***	***P. contorta***
Soils	Spodosols and inceptisols derived from marine deposits, crystalline rocks, sandstones, shales, and even limestone. Grows best on clay, loam, or sandy loam, and poorly on serpentine, shallow shaly, or very sandy soils.	Sandy entisols of marine origin (developed during the Pleistocene) that are well-drained to excessively-drained, infertile, and acid to strongly-acid.	Usually on sandy spodosols and entisols, though also grows on loamy soils, thin soils over Canadian Shield granites and metamorphic rocks, over limestones or permafrost, or on peats. Grows best on acid, sandy soils, tolerates dry, infertile soils, and grows poorly if at all on calcareous soils.[20]	Widely-varying soil types but usually moist and mostly inceptisols or alfisols in the interior forests. Best growth where soil parent materials are granites, shales, or coarse-grained lavas.

Table 3: Summary of Climate[21]

	P. virginiana	***P. clausa***	***P. banksiana***	***P. contorta***
Overall Climate	Humid across most of the range.	Hot summers with much rain; mild, dry winters.	Eastern range with a maritime climate; elsewhere, continental climate of short, warm-cool summers, very cold winters, and low rainfall.	A wide variety of climatic conditions.
Mean annual rainfall	890-1400 mm	1250-1550 mm	250-1400 mm	250-5000 mm
Mean annual temp	n/a	21 to 22 °C	-5 to 4 °C	-3 to 18 °C
Mean max temp of hottest month	21 to 24 °C	32 to 33 °C	29 to 38 °C	27 to 38 °C
Mean min temp of coldest month	-4 to 4 °C	4 to 8 °C	-46 to -21 °C	-57 to 7 °C
Absolute minimum temp	n/a	> -17 °C	> -55 °C	> -60 °C

Classification trees have been generated by the US Forest Service for eastern US tree species to help point out the most important environmental predictors of tree distribution (Prasad et al. 2007). Despite

[19] Obtained from http://www.na.fs.fed.us/pubs/silvics_manual/

[20] Pines of Silvicultural Importance. Compiled from the *Forestry Compendium*, CAB International. CABI Publishing, 2002.

[21] Data obtained from: Pines of Silvicultural Importance. Compiled from the *Forestry Compendium*, CAB International. CABI Publishing, 2002.

measuring a variety of climate, soil, and chemical variables on a number of Forest Inventory Analysis (FIA) sites, only a few soil and climate properties matter most to the distribution of the Contortae, with soil being of greater importance.

P. banksiana

A large majority, 97.1%, of all *P. banksiana* occurrences in the FIA database have three variables in common. The first is the percentage of soil passing sieve No. 200 (fine) being greater than 12.65%, which indicates that 87.35% of the soil was coarser (sandier) than the pores of the sieve. The second is a mean annual temperature greater than 6.5°C. Together, these variables are found in 82.3% of all occurrences. Another 14.8% of observations occur where the soil type is less than 71.5% entisol.

P. virginiana

Soil type (< 11.5% ultisol), mean July temperature (> 25.5 degrees C), and depth to bedrock (> 13.95 cm) were common to 83.2% of *P. virginiana* occurrences in the FIA database. Since most of the soils throughout the Southeast can be classified as ultisol, this may be one reason why *P. virginiana* has high importance values only in limited areas. The remaining 16.8% of occurrences fall on sites where the mean July temperature is less than 25.5 degrees C. On these cooler sites, a new variable becomes important: potential soil productivity. Almost 9.3% of the remaining occurrences are found where soil productivity is low, falling beneath 5.05 square meters of timber per hectare. Since Virginia pine is a poor competitor with other plants on fertile, fine-textured, moist soils, it makes sense that it is found on drier, nutrient-poor sites.

P. clausa

The model reliability for this species is not as good as with Virginia or Jack pine. However, 95.5% of occurrences have 2 soil-related variables in common. First, the percentage of soil passing through the No. 200 (fine) sieve was greater than 6.8%. Second, the susceptibility of the soil to water erosion was greater than 0.15, indicating very sandy, erodable sites.

P. contorta

No classification tree was done for *P. contorta*, but soil type is equally important for this species. Like jack pine, lodgepole pine also forms pure stands on sandy soil. The difference between the two is that lodgepole pine is intolerant of lime. On well-leached, sandy, non-calcareous soils, such as river terraces and flood plains, only *P. banksiana* forms pure stands (Porsild and Cody 1980).

Historical Phylogeography

Using fossil records and molecular clock techniques, we now try to deduce the historical phylogeography of the Contortae and explain how this roughly 80 million year old subsection of the genus *Pinus* came to be in its present distribution. The resulting timeline (Fig. 1) is still very speculative, as the best genetic and fossil data have still not resolved the divergence times between *P. contorta* and *P. banksiana*, and when extinct species related to *P. contorta* first appeared. Still, the sources described in this section have helped to narrow these timeframes somewhat. They are given in yellow on the timeline.

The story of the Contortae begins in the early Cretaceous, 100-120 million years ago, when North America and Eurasia were united into the single Laurasian landmass (Fig. 3a). We know this from the work of Krupkin et al. (1996), who used chloroplast DNA restriction sites to determine phylogenetic relationships among the subgenus *Pinus*, which includes the Contortae. Their results suggest that the progenitor of the North American clade of the subgenus *Pinus* split off from the Eurasian clade roughly

120 million years ago. Later work by Lopez et al. (2002) give an approximate lineage divergence date of 104 Ma (with 95% confidence limits of 61 Ma and 169 Ma).

The dates vary tremendously, and this is likely due to the nature of the vicariance event that split North American and Eurasian *Pinus*. During the Cretaceous, it was warm with no ice at the poles. Cool and warm temperate forest existed throughout eastern Eurasia and into western North America.[22] The Cretacean Sea separating eastern and western North America took a while to form, but eventually caused the pines of Laurasia to diverge into two groups, one east and one west of the sea. On the western side of the sea, the North American progenitor became isolated from the rest of the Eurasian clade for much of the mid to late Cretaceous (Krupkin et al. 1996). The common ancestor of the Contortae then speciated from this progenitor roughly 76-81 MY ago (Krupkin et al. 1996). Lopez et al. (2002) suggest that this common ancestor later migrated from Eurasia into North America via the Beringian corridor (Fig. 2).

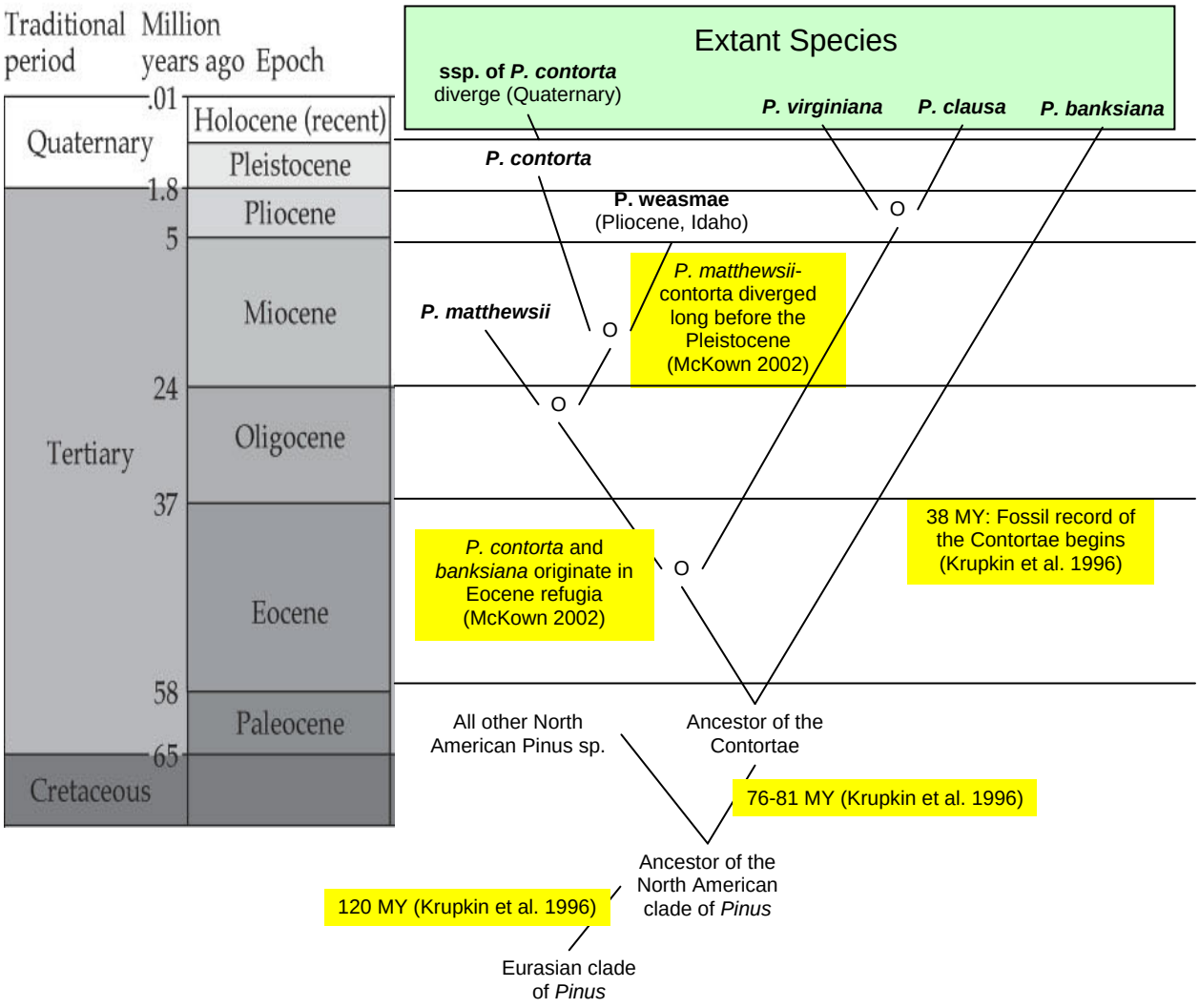


Figure 1. Proposed evolutionary timeline of the Contortae, based on best available evidence.

[22] Scotese, C.R. 2000. PALEOMAP Project. http://www.scotese.com/lcretcli.htm.

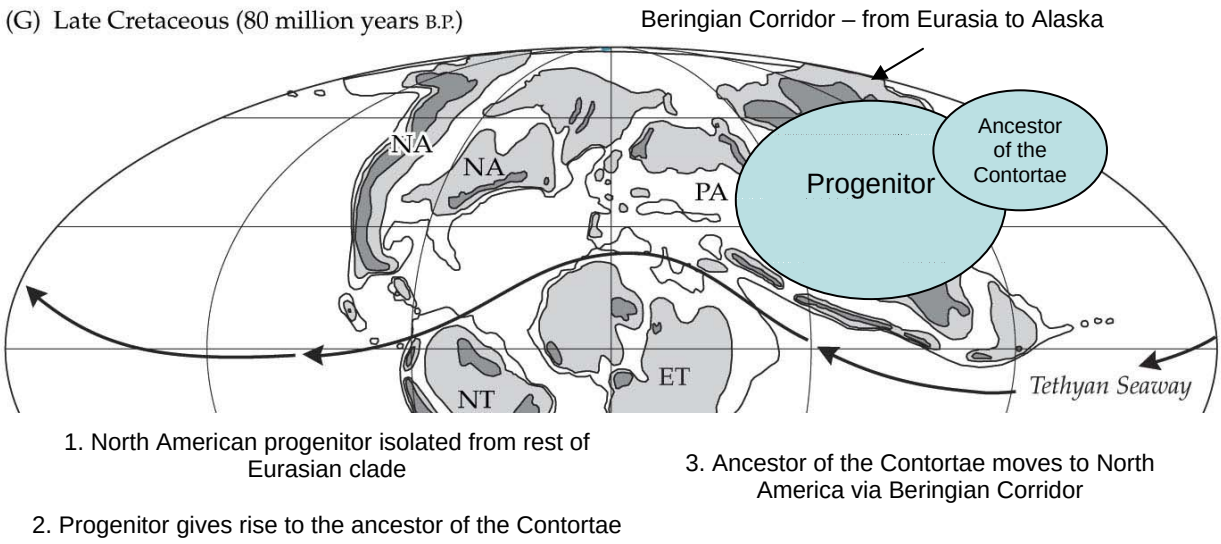


Figure 2: Proposed migration route leading to establishment of the Contortae in North America.

Upon arriving, the common ancestor would have found itself in much the same range that lodgepole pine occupies today, which might lead us to believe that *P. contorta* was the first species to branch off from the ancestral population. However, plastid DNA studies suggest that *P. banksiana* may have been the first to diverge (Lopez 2002). Two of three cladograms resulting from these studies suggest that *P. virginiana* is more closely related to *P. contorta* than to *P. banksiana*, while one suggests *P. virginiana* is more closely related to *P. banksiana* (Lopez 2002). We also know that *P. virginiana* and *P. clausa* are the most closely related of the four species (Gernandt et al. 2005). Thus, either jack or lodgepole pine was the first to split from the common ancestor of the Contortae.

The evolutionary divergence of *P. contorta* and *P. banksiana* has previously been attributed to range disruptions caused by Quaternary glaciations (Critchfield 1984). However, recent molecular studies suggest that this divergence occurred long before the Quaternary. During the Eocene, the Contortae were apparently divided into northern and southern refugia (McKown 2002). These were not glacial refugia, but refugia from the heat. It was even warmer in the far north than during the Cretaceous, and considerably warmer than today (Figs. 3d, e). Cold-tolerant members of the Contortae likely found themselves isolated to high-altitude areas throughout the northern portions of North America where soils were dry and relatively infertile. Over time, isolation led to speciation. McKown (2002) suggests that *P. banksiana* and *P. contorta* originated in the northern refugium.

It is only in the late Eocene that the fossil record of the Contortae begins (38 MY); everything prior to this point has been inferred from genetic studies. At the onset of Pleistocene glaciation, pine habitat became fragmented by ice, isolating populations again, this time in ice-free glacial refugia. It is during the Pleistocene that fossil records become abundant, and also when *P. contorta* is thought to have evolved into its four geographically distinct subspecies (Krupkin et al. 1996). Upon the most recent deglaciation, *P. contorta* began migrating northward. It is likely that *P. contorta* ssp. *latifolia* is still migrating northward in northwestern Canada (MacDonald and Cwynar, 1985).

No literature exists on the speciation event that led to *P. virginiana*, but it had to have shared a common ancestor with *P. banksiana* and *P. contorta* in the Eocene. Given its lower tolerance for cold compared to these other two species, *P. virginiana* may have originated in a more southerly refugium, and perhaps one that was already near the eastern portion of North America. Later, in the Oligocene when the climate cooled (Fig. 3f), it would have made its way farther south to stay within the warm temperate

region, distancing itself from the other two species. In the Miocene, when the middle of North America grew more arid (Fig. 3g), Virginia pine would have been effectively isolated from lodgepole pine to the west, and the appearance of a new cool temperate climate zone to the north would also isolate it from Jack pine.

Not much is known about Jack pine between the Eocene and the Pleistocene. However, during the last full glacial, Jack pine persisted on the infertile coastal plain soils of the Southeastern US and was absent from the interior until 11,000 years ago owing to blocking ice in Lake Michigan. Following glacial retreat, its western spread was rapid, at an average rate of 400 m/yr. Though Virginia pine also likely persisted in the same range as Jack pine during the full glacial, they had long since separated as distinct species, and thus did not hybridize.

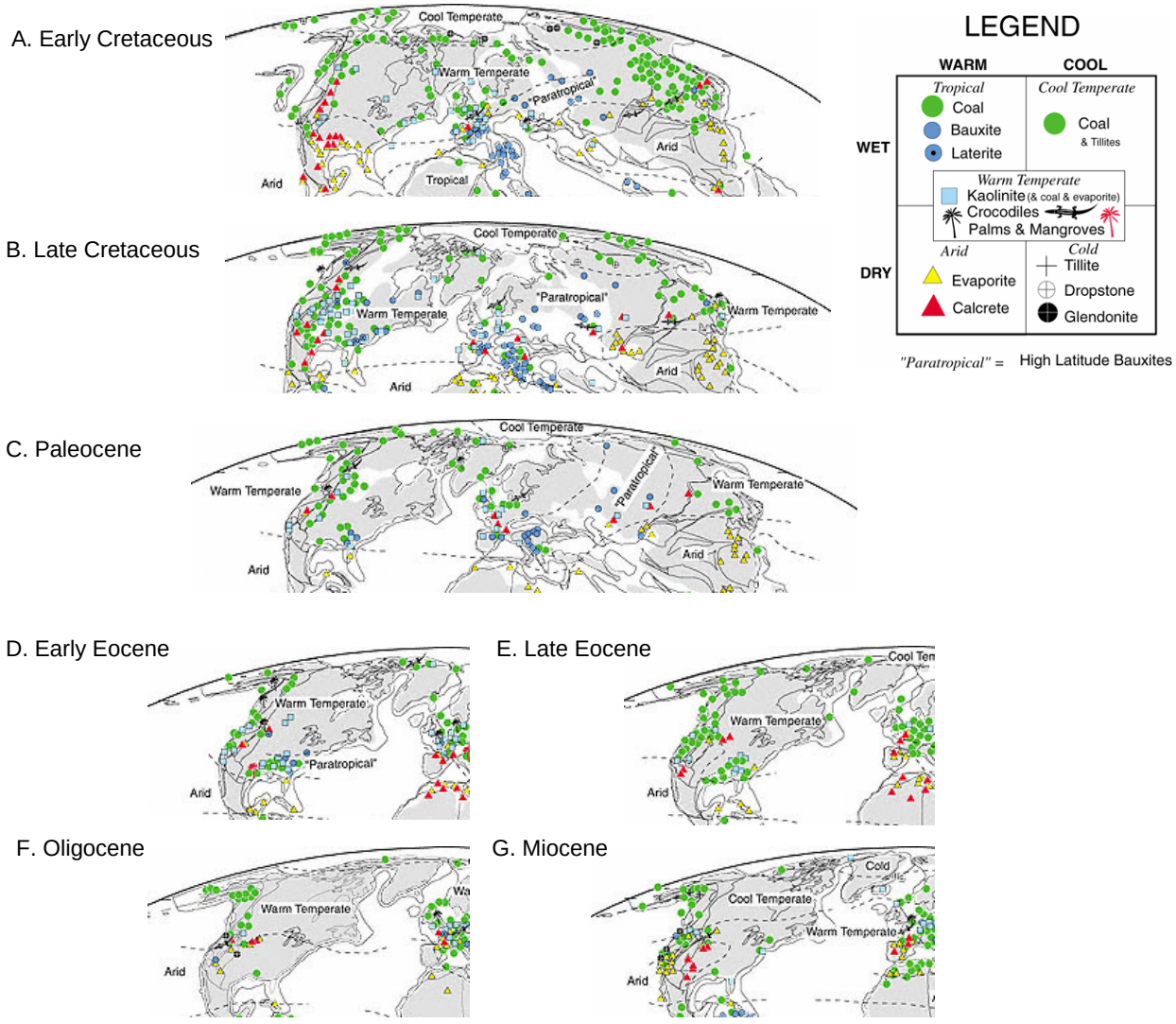


Figure 3. Paleoclimatic conditions during the evolution of the Contortae. Adapted from Scotese, C.R. 2000. PALEOMAP Project. http://www.scotese.com/lcretcli.htm.

Finally, Virginia and sand pine likely split during the end of a recent glacial, when their common ancestor occupied a range in the far southeastern US near northern Florida. Upon deglaciation, the ancestors of Virginia pine migrated northward, following the warmer temperatures. However, the

ancestors of sand pine persisted in the scrubby habitat of northern Florida, being better adapted than *P. virginiana* to living on the young, dry northern Florida sands that developed during the Pleistocene.

Virginia pine later became divided into northwest and southeast races by the Appalachian mountain chain (Parker et al. 1997). Genetic evidence suggests that the origin of the genetically homogeneous northwestern population is not due to a postglacial migration from the southeast, but due to prolonged isolation, possibly throughout the Pleistocene, from the southeastern population (Parker et al. 1997).

Today, Virginia pine is only kept from crossing with Sand pine by considerable geographic separation. If Virginia pine had moved down into Florida at the last glacial maximum, it would have freely hybridized with Sand pine. Thus, they must have had separate refuges during the last glacial (Parker et al. 1997).

Extinct Species

Species of the Contortae had northern refugia in North America during the Eocene (McKown 2002). One such unglaciated refugium, the Bluefish Basin of the northern Yukon Territory in Canada, was home to *P. matthewsii*,[23] an extinct species most closely related to *P. contorta*. The northern Yukon was warmer in the late Tertiary than today, allowing the range of *P. matthewsii* to extend further north than the present range of *P. contorta* (McKown 2002), where it lived in dense forest cover dominated by spruce, soft pines, and birch. Like *P. contorta*, *P. matthewsii* may have been a pioneer, shade-intolerant species. It has small fossil seeds with long wings that allowed its seeds to be dispersed further by wind, noted as a typical adaptation of pioneer species (McKown 2002).

This extinct species provides another clue for the evolutionary timeline of the Contortae. Since the fossil remains of *P. matthewsii* are more similar to *P. contorta* than to *P. banksiana*, we can infer that *P. banksiana* and *P. contorta* likely diverged long before the late Tertiary.

Another more recently extinct species, *Pinus weasmae* Miller, is known from one ovulate cone from the Pliocene of Idaho. This species was described as being similar to both *P. contorta* and *P. banksiana*, and existed just prior to the Pleistocene (McKown 2002). Exactly when it arose or went extinct is unknown, as well as any other occurrences of this species.

Current Distribution

A major purpose of this paper was to synthesize all credible observations of the four Contortae species into one source, to make it easy to deduce how and why the geographic distributions of these species vary. This section begins first with the overall map of the distribution of the Contortae, followed by more detailed descriptions from NatureServe of the population status in each state.

The overall map (Fig. 4) shows each verified county occurrence in a different color. Primary colors were chosen so that overlapping colors would represent potential sites of hybridization. For each color, dark shades represent county occurrences obtained from herbaria or expert sources (textbooks, expert-vouchered observations). Light shades represent county occurrences obtained from the USDA Plants database. Overlaid on each species' range is its range boundary.

[23] Full name: *Pinus matthewsii* sp. nov. McKown, Stockey et Schweger (McKown 2002).

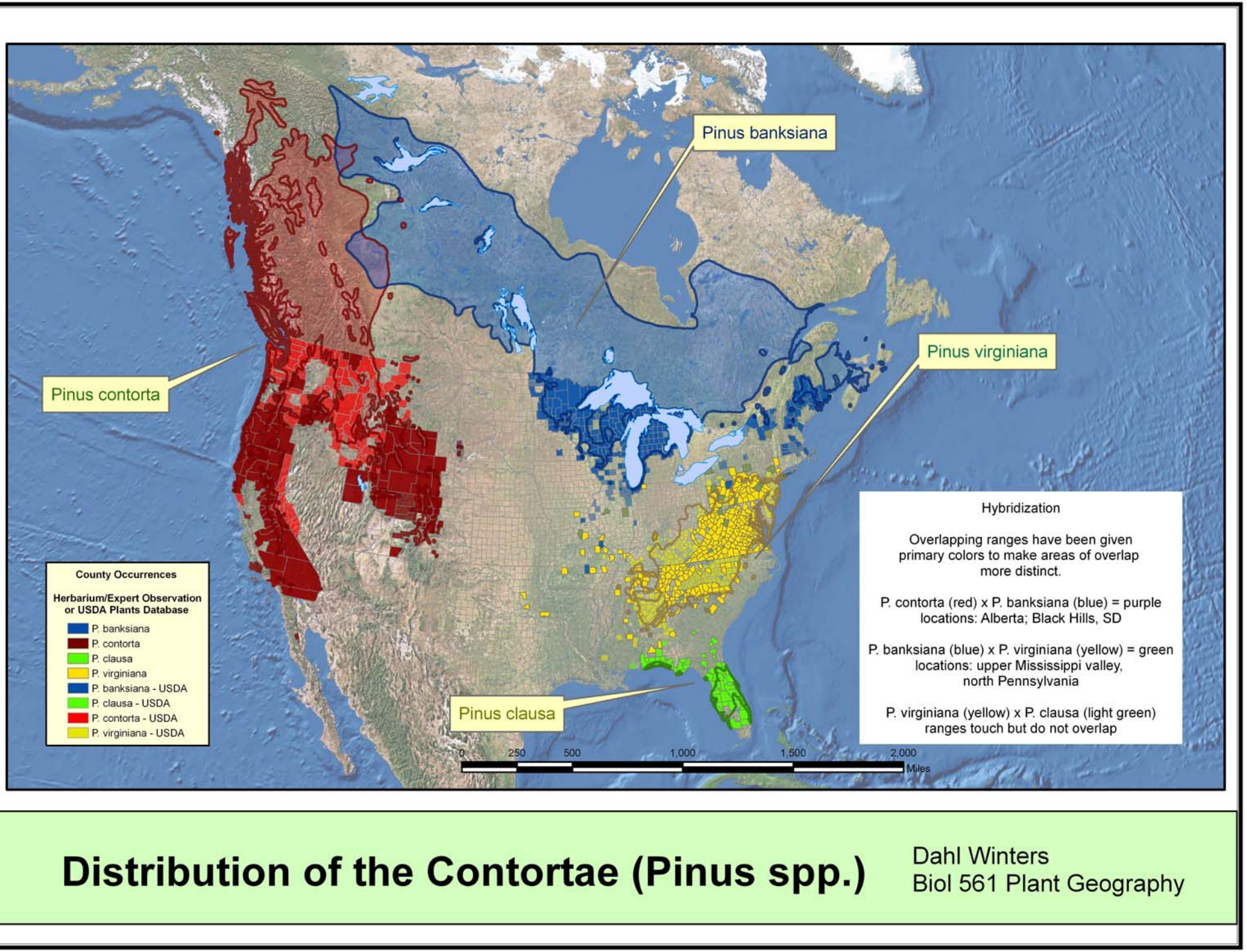
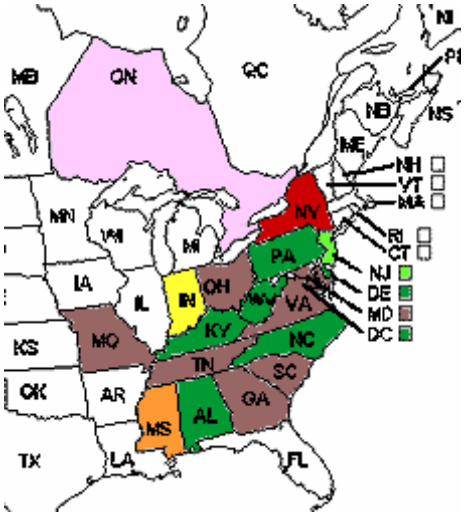


Figure 4: Distribution of the Contortae.

Pinus virginiana



Virginia pine is found throughout the southeastern and midatlantic portions of the US. Populations of conservation concern exist in three states: Indiana, where it is vulnerable; Mississippi where it is imperiled, and New York, where it is critically imperiled (NatureServe). In Maryland, it is commonly found on dry, sterile soils, especially abandoned farm fields (Brown and Brown, 1972). It is found in almost every county in Virginia, which may help to lend its common name. This species is also found as an exotic in Ontario, which is far north of its natural range (Little).

State/Province Conservation Status

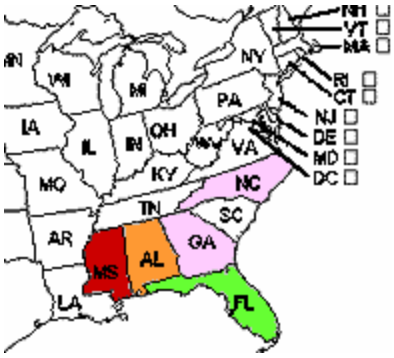
- SX: Presumed Extirpated
- SH: Possibly Extirpated
- S1: Critically Imperiled
- S2: Imperiled
- S3: Vulnerable
- S4: Apparently Secure
- S5: Secure
- Not Ranked/Under Review (SNR/SU)

Conservation Status

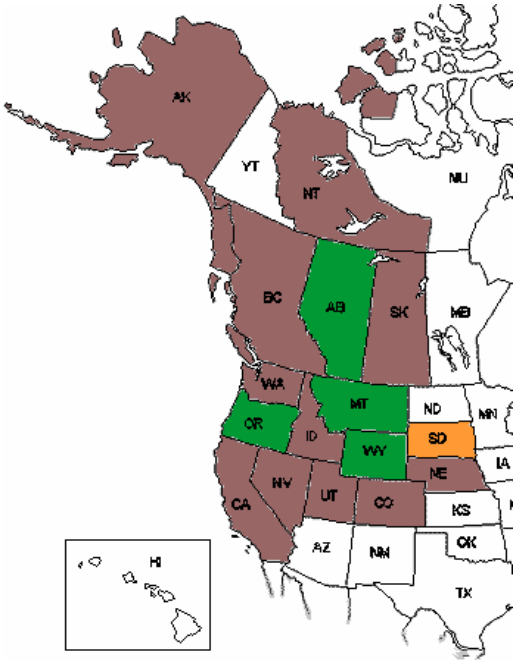
Not Applicable (SNA)

- Exotic
- Hybrid without Conservation Value

Pinus clausa



Sand pine is found predominantly on dry, deep sands in northern Florida (Wunderlin 2003), but populations exist throughout five states. Choctawhatchee sand pine (*P. clausa* var. *immuginata*) is found in northwestern Florida to southern Alabama, while Ocala sand pine (*P. clausa* var. *clausa*) is in peninsular Florida. Imperiled populations exist in Alabama and critically imperiled populations exist in Mississippi (NatureServe). This species is also found as an exotic in Georgia and North Carolina, where its range abuts the southern limit of Virginia pine but does not overlap (at least at the county level). If their ranges did happen to overlap, hybrids are possible. Hybrids of Virginia pine and Ocala sand pine *(Pinus clausa* var. *clausa)* have been made under controlled conditions with either species as the seed parent. However, controlled crosses of *P. virginiana* with jack pine *(P. banksiana)* and lodgepole pine *(P. contorta)* have not been successful.[24]



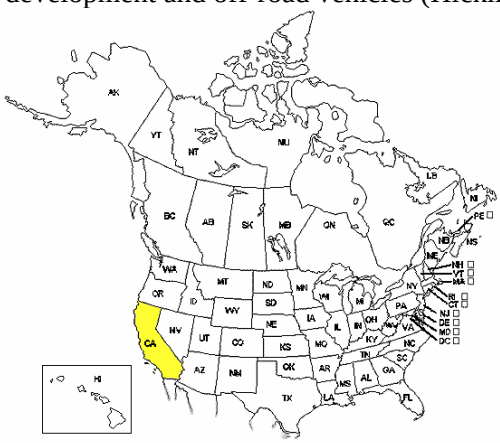
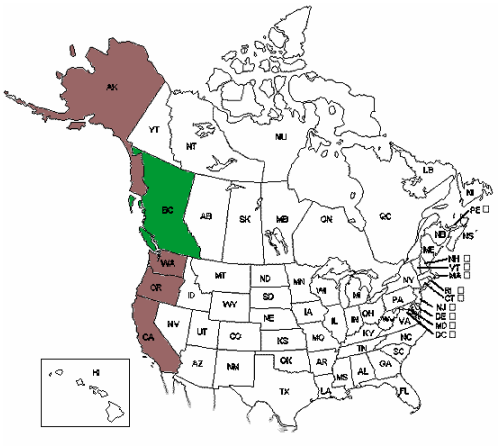
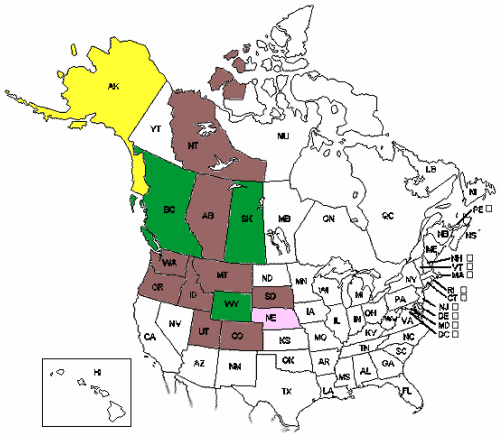
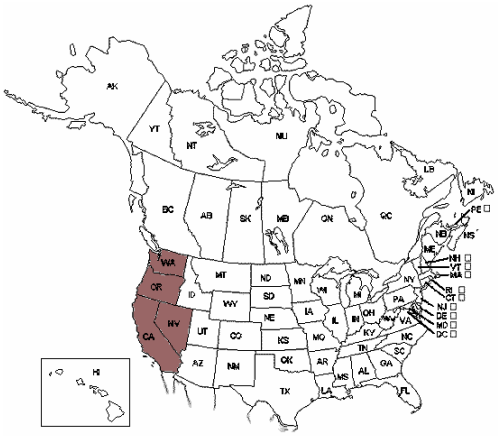
Pinus contorta

Lodgepole pine is the only member of the Contortae isolated to western North America. It occupies a large range of environmental conditions along the West Coast and Rockies regions, as far south as northern Baja California and as far north as the Yukon. To the east, its range intersects with *P. banksiana* in two locations: Alberta, and the Black Hills of South Dakota. There, *P. contorta* var. *latifolia* forms hybrids of intermediate morphology with *P. banksiana* in central

[24] http://www.na.fs.fed.us/pubs/silvics_manual/Volume_1/pinus/virginiana.htm

Alberta (Moss 1983). Only in South Dakota do imperiled populations exist, in the Black Hills region (NatureServe).

Varieties of P. contorta

Bolander's beach pine (*P. contorta* var. *bolanderi*) forms a pygmy forest on coastal claypan soils in Mendocino County, CA. It is threatened by development and off-road vehicles (Hickman 1993) 	*Pinus contorta* var. *contorta* exists only along the west coast of North America. 
Pinus contorta var. *latifolia* is the most geographically extensive variety. Though a vulnerable population exists in Alaska, its exotic status in the Great Plains state of Nebraska is indicative of its survival ability under a wide range of environmental conditions. 	Murray's lodgepole pine (*P. contorta* var. *murrayana*) is found only in the Sierra Nevada mountains. 

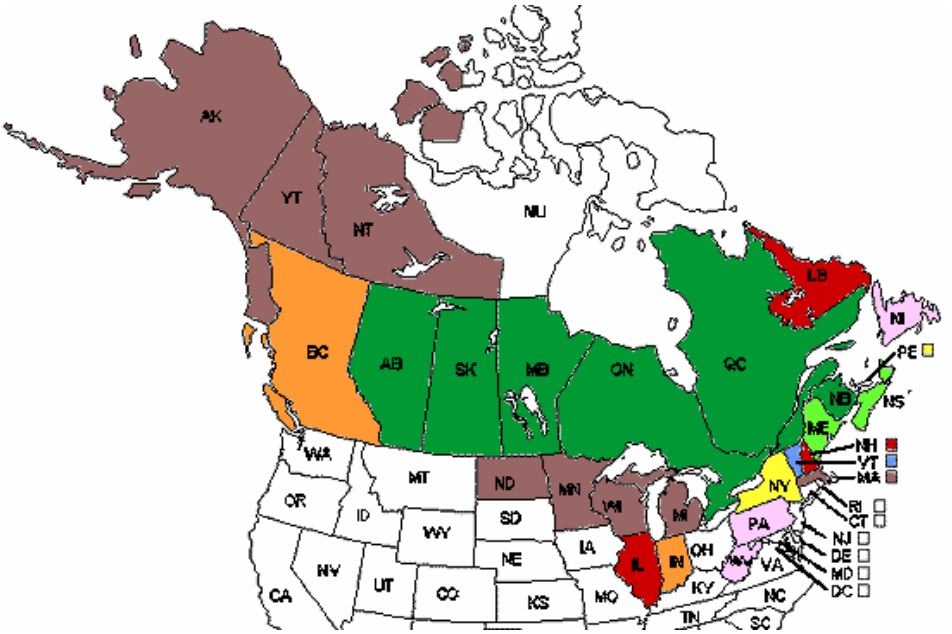
Pinus banksiana

Jack pine is primarily found throughout the Canadian boreal forest region, as well as the northcentral to northeastern portions of the United States. It grows farther north than any other American pine and is the most widely distributed pine species in Canada.[25] Populations of conservation concern are located along the fringes of its natural range: there are vulnerable populations in New York and Prince Edward

[25] http://www.na.fs.fed.us/pubs/silvics_manual/Volume_1/pinus/banksiana.htm

Island, imperiled populations in Indiana and British Columbia, and critically imperiled populations in Illinois, New Hampshire, and Labrador (NatureServe). Though jack pine has possibly been extirpated in Vermont, it is an exotic in Newfoundland, Pennsylvania, and West Virginia.

P. banksiana is largely found in Canada, but makes it into the US in areas to the east and west of the Great Lakes. The range of *P. banksiana* and *P. virginiana* overlap in both these regions, with a greater southern overlap extending down the Mississippi River valley into Missouri. In Pennsylvania, jack pine has been introduced as forest plantations by the Bureau of Forestry and the Game Commission (Rhodes and Klein 1993).



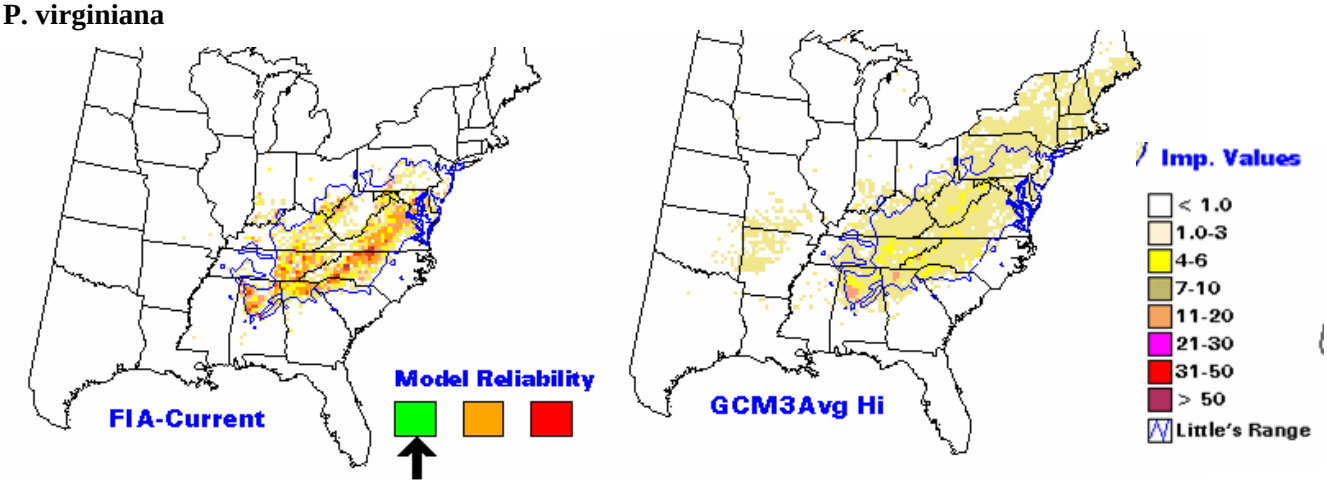
The presence of Jack pine in the Black Hills of South Dakota is an interesting case (McGregor and Barkley, 1977). Jack pine seeds are rather heavy and typically disperse no greater than 100 m from the parent tree.[26] This makes dispersal exceedingly unlikely if Jack pine were unable to grow in the calcareous soils of the northern Great Plains. However, given its tolerance for calcareous soil, it may have migrated there during deglaciation from neighboring southern interior populations. Then, as the climate continued to warm and grassland expanded throughout the Great Plains, Jack pine was trapped in the Black Hills as a relic population, able to thrive due to the cooler, high-elevation temperatures as well as the alfisol soils present.

Future Distributions

Given the importance of greenhouse-driven climate change on vegetation throughout north America, models have been done to predict changes in tree species importance values due to a doubling of CO_2. Below are the results of one such prediction for three Contortae species, done by the Forest Service (Prasad et al. 2007). On the left are the current distributions of each species, taken from the Forest Inventory Analysis (FIA) database. On the right is the average of three GCM models (Hadley, PCM & GFDL) for the high carbon scenario.

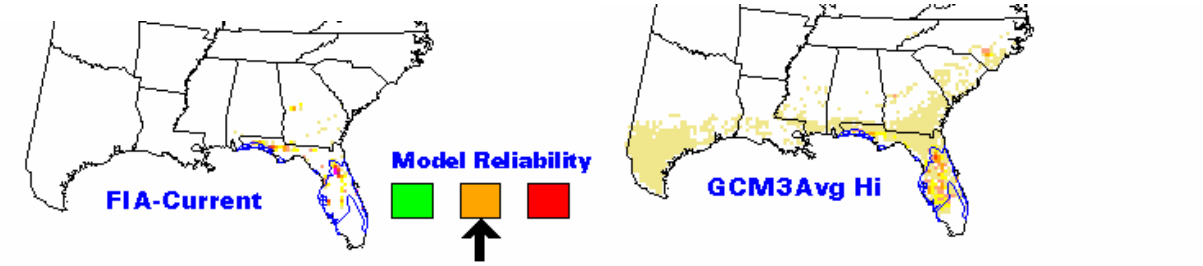
[26] Pines of Silvicultural Importance. Compiled from the *Forestry Compendium*, CAB International. CABI Publishing, 2002.

P. virginiana



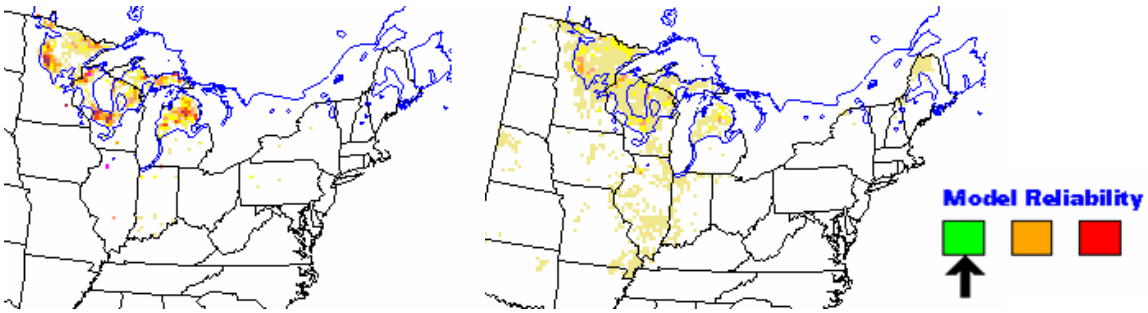
The model suggests a northward and westward expansion of Virginia pine's range, with a concomitant reduction of importance values at the core of its range. Occurrences of *P. virginiana* in Missouri and Arkansas are not shown on the FIA map, but interestingly there are several county occurrences in Missouri that fall within the area predicted by the three GCM models (Fig. 4).

P. clausa



Sand pine is also predicted to undergo a northward and westward range expansion, though the model reliability is less than that of Virginia pine. It will still continue to have a high importance value in places where it is already abundant, namely north-central Florida.

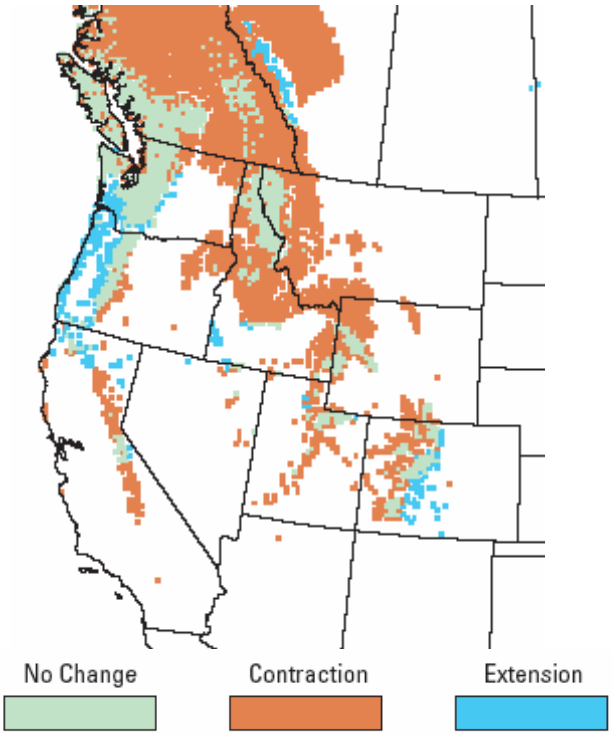
P. banksiana



Jack pine is predicted to undergo a southward migration along with a decrease in importance value over much of the northern Midwest. Why it is the only member of the Contortae to migrate southward is a good question. Given what we know of its environmental preferences, this southward migration would only take place where sandy, infertile soils exist. Such places would be difficult to come by in this highly fertile agricultural region of America.

P. contorta

Under a different model than used for the previous three species, lodgepole pine is predicted to undergo a severe range contraction over much of its range, along the entire Rocky Mountain region and in the Sierra Nevada Mountains.[27] The major areas where no change is predicted are along the Pacific Northwest and eastern slope of the Colorado Rockies; bordering these places are locations where range extensions are predicted.



Summary

The Contortae have grown on North American soil for the past 80 million years. They occupy the basal position to all other North American pines. They grow as pioneer species on dry, infertile soils that few other trees can survive on, increasing the productivity and wildlife value of the land. Dramatic climate changes have occurred in their past that have caused some species to go extinct, but others managed to find refugia, remain isolated for long periods of time, and form new species or varieties in the process. Despite upcoming climate change, it is anticipated that the Contortae as a whole will still occupy a large portion of the North American landscape. Lodgepole pine may suffer a contraction of its range, but the ranges of *P. virginiana*, *clausa*, and *banksiana* are predicted to expand, ensuring a good chance of their future survival.

[27] US Geological Survey. Changes in Species Distribution Between Present-Day Simulated Distribution and Simulated Distribution Under 2xCO2 Climate. http://pubs.usgs.gov/circ/1998/c1153/c1153_4.htm

References

Critchfield, W.B. 1984. Impact of the Pleistocene on the genetic structure of North American conifers. *Proc. North American Forest Biology Workshop*. 8: 70-118.

Cwynar, L.C. & MacDonald, G.M. 1987. Geographical variation of lodgepole pine in relation to population history. *Am. Nat.*, 129: 463-469.

Gernandt, D.S., López, G.G., García, S.O., Liston, A. 2005. Phylogeny and classification of *Pinus*. Taxon 54(1): 29-42.

Krupkin, A.B., A. Liston; S. H. Strauss. 1996. Phylogenetic Analysis of the Hard Pines (*Pinus* subgenus *Pinus*, Pinaceae) from Chloroplast DNA Restriction Site Analysis. *American Journal of Botany* 83(4): 489-498.

MacDonald, G.M. & Cwynar, L.C. 1985. A fossil pollen-based reconstruction of the late Quaternary history of lodgepole pine (*Pinus contorta* ssp. *latifolia*) in the western interior of Canada. *Can. J. Forest. Res.*, 15: 1039-1044.

Parker, K. C., Hamrick, J. L., Parkers, A. J., and Stacy, E. A. 1997. Allozyme diversity in *Pinus virginiana* (Pinaceae): Intraspecific and interspecific comparisons. *Am. J. Botany* 84: 1372–1382.

Pines of Silvicultural Importance. Compiled from the *Forestry Compendium*, CAB International. CABI Publishing, 2002.

Prasad, A. M., L. R. Iverson., S. Matthews., M. Peters. 2007-ongoing. A Climate Change Atlas for 134 Forest Tree Species of the Eastern United States [database]. http://www.nrs.fs.fed.us/atlas/tree, Northern Research Station, USDA Forest Service, Delaware, Ohio.

Map References

(**none** means none of the 4 Contortae species were found in the reference)

USDA. PLANTS database http://plants.usda.gov
The NatureServe Explorer database. http://www.natureserve.org/explorer/.

Southeastern US (North Carolina, South Carolina, Virginia, West Virginia, Tennessee, Georgia, Kentucky)

Weakley, A.S. 2007. Flora of the Carolinas, Virginia, and Georgia, and Surrounding Areas. UNC Herbarium, North Carolina Botanical Garden. http://herbarium.unc.edu/flora.htm.
NCU Atlas of the Southeastern United States. http://www.herbarium.unc.edu/seflora/.

New England (Connecticut, Massachusetts, Maine, New Hampshire, Vermont, Rhode Island)

Angelo, R. & D.E. Boufford. 1996-7. Atlas of the flora of New England: Pteridophytes and gymnosperms. Rhodora 98:1-79; Poaceae. Rhodora 100:101-233. Monocots except Poaceae and Cyperaceae Rhodora 102:1-119. http://neatlas.huh.harvard.edu/
Magee, D. W. & H.E. Ahles. 1999. Flora of the Northeast: A manual of the vascular flora of New England and Adjacent New York. University of Massachusetts Press.
Seymour, F.C. 1982. The flora of New England

Alaska
Hulten, E. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press, CA.

Arizona
Kearney, T.H. and R.H. Peebles. 1960. Arizona Flora. California. **(none)**

California
Calflora: Information on California plants for education, research and conservation. [web application]. 2007. Berkeley, California: The Calflora Database [a non-profit organization]. Available: http://www.calflora.org/. (Accessed: Nov 25, 2007)
Hickman, J.C., ed. 1993. The Jepson Manual: Higher plants of California. University of California Press.

Colorado
Specimen database of Colorado vascular plants.
http://cumuseum.colorado.edu/Research/Botany/Databases/search.php
Colorado vascular plants by county.
http://cumuseum.colorado.edu/Research/Botany/Databases/county_species.html

Florida
Wunderlin, R.P. 2003. Guide to the vascular plants of Florida. Second edition. Univ. Press of Florida.
Wunderlin, R.P. and B.F. Hansen. Atlas of Florida vascular plants. http://www.plantatlas.usf.edu/

Georgia
Jones, S.B. & N.C. Coile. 1988. The distribution of the vascular flora of Georgia. Dept. Botany, Univ. Georgia, Athens.

Idaho
Hitchcock, C.L., A. Cronquist, M. Ownbey and J.W. Thompson. 1955-1969. Vascular plants of the Pacific Northwest. U. Washington Press.
Scott, R.W. 1995. The alpine flora of the Rocky Mountains. Vol. 1. Middle Rockies. U. Utah Press.

Illinois
Iverson, L.R., D. Ketzner, and J. Karnes. 1999. Illinois Plant Information Network. http://www.fs.fed.us/ne/delaware/ilpin.html. Illinois Natural History Survey and USDA Forest Service.
Illinois Natural History Survey vascular plant co0llection database.
http://ellipse.inhs.uiuc.edu:591/INHSCollections/plantsearch.html
Mohlenbrock, R.H. & D.M. Ladd. 1978. Distribution of Illinois vascular plants. S. Ill. Univ. Press, Carbondale, Ill.
Swink, F. & G. Wilhelm 1994. Plants of the Chicago region. 4th ed. Morton Arboretum.

Indiana
Deam, C.C. 1940. Flora of Indiana.

Iowa
Roosa, D.M., M.J. Leoschke, L.J. Eilers. 1989. Distribution of Iowa's endangered and threatened vascular plants. Iowa Dept. Nat. Res. **(none)**

Kansas
Stephens, H.A. 1969. Trees, shrubs and woody vines in Kansas. Univ. Pr. Kansas. **(none)**

Louisiana
MacRoberts, D.T. 1989. A documented checklist and atlas of the vascular flora of Louisiana. Bull. Mus. Life Sciences #7-9, La. State Univ. Shreveport. 3 vols. **(none)**

Maryland
Brown, R.G. and M.L. Brown. 1972. Woody plants of Maryland. Univ. Maryland.
Flora of the Washington - Baltimore area. http://persoon.si.edu/DCFlora/

Michigan
Voss, E.G. 1972, 1985, 1996. Michigan flora. Cranbrook Inst. Sci

Minnesota
McGregor, R.L. & T.M. Barkley (eds.). 1977. Atlas of the flora of the Great Plains. Iowa
Ownbey, G.B. and T. Morely. 1991. Vascular plants of Minnesota: a checklist and atlas. Univ. Minn. Press, Minneapolis.

Mississippi
Lowe, E.N. 1921. Plants of Mississippi: a list of flowering plants and ferns. Miss. State Geological Survey. Bull. 17.
Pullen Harbarium specimen database. http://herbarium.olemiss.edu/projects.html

Missouri
Steyermark, J. 1962. Flora of Missouri. Iowa State Univ. Press, Ames.
Atlas of Missouri vascular plants.
http://biology.missouristate.edu/Herbarium/atlas/atlas_of_missouri_vascular_plant.htm

Montana
McGregor, R.L. & T.M. Barkley (eds.). 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames.
Scott, R.W. 1995. The alpine flora of the Rocky Mountains. Vol. 1. Middle Rockies. U. Utah Press.

New Jersey
Hough, M.Y. 1983. New Jersey wild plants. Private Printing. **(none)**

New Mexico
Martin, W.C. 1980. A flora of New Mexico. 2 vols. J. Cramer. **(none)**
McGregor, R.L. & T.M. Barkley (eds.). 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames

New York
Magee, D. W. & H.E. Ahles. 1999. Flora of the Northeast: A manual of the vascular flora of New England and Adjacent New York. University of Massachusetts Press.
New York Flora Atlas. http://www.nyflora.org/atlas/atlas.htm

North Dakota
McGregor, R.L. & T.M. Barkley (eds.). 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames.

Ohio
Fisher, T.R. 1988. The Dicotyledoneae of Ohio. Part 3. Asteraceae. Ohio State Univ. Press.

McCance, R.M. and J.F. Burns. 1984. Ohio endangered and threatened vascular plants: abstracts of state-listed taxa. Div. Nat. Areas, Dept. Nat. Res., Columbus, OH. **(none)**

Oklahoma

McGregor, R.L. & T.M. Barkley (eds.). 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames.

Oklahoma vascular plants database. http://www.biosurvey.ou.edu/atlasdesc.html

Oregon

Hitchcock, C.L., A. Cronquist, M. Ownbey and J.W. Thompson. 1955-1969. Vascular plants of the Pacific Northwest. U. Washington Press.

Oregon Vascular Plant Database http://ocid.nacse.org/cgi-bin/qml/herbarium/plants/vherb.qml

Pennsylvania

Pennsylvania Flora Project. http://www.paflora.org/

Rhodes, A.F. and W.M. Klein Jr. 1993. The vascular flora of Pennsylvania: an annotated checklist and atlas. Amer. Phil. Soc., Philadelphia, PA.

South Carolina

South Carolina Plant Atlas, http://cricket.biol.sc.edu/herb/

South Dakota

McGregor, R.L. & T.M. Barkley (eds.). 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames.

Tennessee

Atlas of Tennessee vascular plants. http://tenn.bio.utk.edu/vascular/vascular.html

Chester, E.W., B.E. Wofford, R. Kral, H.R. DeSelm & A.M. Evans. 1993. Atlas of Tennessee vascular plants. Vol. 1. Pteridophytes, gymnosperms, angiosperms: monocots. Misc. Publ. 9, Center for Field Biology, Austin Peay State Univ., Clarksville, TN 37044.

Utah

Albee, B.J., L.M. Shultz & S. Goodrich. 1988. Atlas of the Vascular Plants of Utah. Occ. Publ. Utah Mus. Nat. Hist. #7. 670 pp. (Online version: http://www.nr.usu.edu/Geography-Department/utgeog/utvatlas/ut-vascatlas.html)

Scott, R.W. 1995. The alpine flora of the Rocky Mountains. Vol. 1. Middle Rockies. U. Utah Press.

Virginia

Harvill, A.M., T.R. Bradley, C.E. Stevens, T.F. Wieboldt, D.M.E. Ware, D.W. Ogle, G.W. Ramsey & G.P. Fleming. 1992. Atlas of the Virginia flora, Third edition. Virginia Bot. Assoc., Burkeville, Va.

Digital atlas of the Virginia flora. http://www.biol.vt.edu/digital_atlas/

Washington

Hitchcock, C.L., A. Cronquist, M. Ownbey and J.W. Thompson. 1955-1969. Vascular plants of the Pacific Northwest. U. Washington Press.

West Virginia

P.J. Harmon, D. Ford-Werntz, and W. Grafton, eds. 2006. Checklist and atlas of the vascular flora of West Virginia. West Virginia Division of Natural Resources, Wildlife Resources Section, Elkins, WV. 381 p

Wisconsin
Swink, F. & G. Wilhelm 1994. Plants of the Chicago region. 4th ed. Morton Arboretum. [PB and PV]
Wisconsin State Herbarium, with multiple map options. http://www.botany.wisc.edu/herbarium/
Freckman Herbarium http://wisplants.uwsp.edu/

Wyoming
McGregor, R.L. & T.M. Barkley (eds.). 1977. Atlas of the flora of the Great Plains. Iowa State Univ. Press, Ames.
Scott, R.W. 1995. The alpine flora of the Rocky Mountains. Vol. 1. Middle Rockies. U. Utah Press.
Atlas of the vascular plants of Wyoming. http://www.sbs.utexas.edu/tchumley/wyomap/atlas.htm

Canada

Alberta
Moss, H.H. 1983. Flora of Alberta, Second edition.

British Columbia
Electronic atlas of the plants of British Columbia http://www.eflora.bc.ca/

Labrador
Rousseau, C. 1974. Geographie floristique du Quebec-Labrador. Presses Univ. Laval, Quebec.

Maritime Provinces
Roland, A.E. and E.C. Smith. 1969. The flora of Nova Scotia. Proc. Nova Scotian Inst. Sci.

Newfoundland
Rouleau, E. & G. Lamaneux. 1992. Atlas of the vascular plants of the island of Newfoundland and the islands of Saint-Pierre-et-Miquelon. Fleurbec, Quebec.

Northwest Territories
Porsild, A.E. & W.J. Cody. 1980. Vascular plants of continental Northwest Territories, Canada. Nat. Mus. Canada.

Ontario
Argus, G. et al. 1987. Atlas of the rare vascular plants of Ontario. Canadian National Museum of Natural Science. **(none)**

Quebec
Rousseau, C. 1974. Geographie floristique du Quebec-Labrador. Presses Univ. Laval, Quebec.