9558

Seed Zone Delineation for Jack Pine in the Former Northwest Region of Ontario Using Short-term Testing and Geographic Information Systems

W.H. Parker and A. van Niejenhuis

Lakehead University
Faculty of Forestry
Thunder Bay, Ontario
P7B 5E1

1996

NODA • EDNO
CANADA
ONTARIO
Northern Ontario Development Agreement
Entente de développement du nord de l'Ontario
Forestry • Foresterie

Funding for this report has been provided through the Northern Ontario Development Agreement's Northern Forestry Program.

Canadian Cataloguing in Publication Data

Parker, W.H.

Seed zone delineation for jack pine in the former northwest region of Ontario using short-term testing and geographic information systems

(NODA/NFP technical report; TR-35)
Includes an abstract in French.
Includes bibliographical references.
"Funding for this report has been provided through the Northern Ontario Development Agreement's Northern Forestry Program."
ISBN 0-662-24954-2
DSS cat. no. Fo29-42/35-1996E

1. Jack pine—Seeds—Ontario, Northern.
2. Jack pine—Seedlings—Ontario, Northern.
3. Jack pine—Breeding—Ontario, Northern.
I. Van Niejenhuis, A. (Annette)
II. Great Lakes Forestry Centre.
III. Title.
IV. Series.

SD397.P575P37 1996 634.9'751 C96-980448-2

Catalogue No. Fo29-42/35-1996E
ISBN 0-662-24954-2
ISSN 1195-2334

Copies of this publication are available at no charge from:
Publications Services
Natural Resources Canada
Canadian Forest Service
Great Lakes Forestry Centre
P.O. Box 490
Sault Ste. Marie, Ontario
P6A 5M7

Microfiche copies of this publication may be purchased from:
Micro Media Inc.
Place du Portage
165, Hotel-de-Ville
Hull, Quebec J8X 3X2

Parker, W.H.; van Niejenhuis, A. 1996. Seed zone delineation for jack pine in the former Northwest Region of Ontario using short-term testing and geographic information systems. Nat. Resour. Can., Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, ON. Tech. Rep. NODA/NFP TR-35. 34 p.

ABSTRACT

To obtain a better understanding of the pattern of adaptive variation of jack pine *(Pinus banksiana* Lamb.) that would improve existing seed transfer guidelines, a short-term provenance test was carried out for 102 seed sources collected from the furthest northwestern portion of Ontario. Seed sources were grown in common environments at a greenhouse for one season (1994) and at three field trials for two growing seasons (1993–1994). A total of 32 biological variables was determined for each seed source, including seedling heights, needle flushing dates, the timing of shoot elongation, and relative freezing damage. Significant levels of interprovenance variation were present for 21 of these variables. Graphic analysis of the pattern of variation indicated that sources from the northwestern portion of the collection area had the slowest height growth. A gradual cline in needle flushing date was present from the southwest to the northeast; the more southern sources flushed later. Multiple regressions were run for each of the 32 variables against 12 climatic variables interpolated for each of the seed sources using a geographic information system (GIS). Data from 1951–1980 were obtained from nearby weather stations. Large coefficients of variation (up to 0.72) were obtained for some variables. Principal components analysis (PCA) was used to summarize the main components of variation, and the PCA axis scores for the seed sources were regressed against climatic variables. Mean May daily maximum temperature, May precipitation, extreme minimum temperature, and number of frost free days were good predictors of PCA summary scores. The regression equations were used to model the patterns of adaptive variation, and these patterns were graphically reproduced as contour maps using GIS. A series of focal point seed zone maps were produced by GIS intersection of the regression based contour maps. Based on these maps a summary of the pattern of adaptive variation in jack pine was used to produce a recommendation for breeding zone boundaries for Zone 1 of the Ontario Tree Improvement Board.

RÉSUMÉ

Pour mieux cerner le profil de variation adaptative de *Pinus banksiana* qui permettrait d'améliorer les lignes directrices actuelles relatives au transfert des graines, un test de provenance à court terme a été appliqué à 102 sources de graines prélevées dans la partie nord-ouest la plus éloignée de l'Ontario. Toutes les graines ont été cultivées en commun dans une serre pendant une saison (1994) et dans 3 essais au champ pendant 2 saisons de croissance (1993 et 1994). Au total, on a déterminé 32 variables biologiques pour chaque source de graines, dont la hauteur des semis, les dates de pousse des aiguilles, la chronologie de l'élongation des tiges et les dommages relatifs dus au gel. Des degrés appréciables de variation interprovenance ont été observés pour 21de ces variables. L'analyse graphique du profil de variation indique que les sources venant de la partie nord-ouest de l'aire de prélèvement montrent la plus faible croissance en hauteur. Les dates de pousse des aiguilles décrivaient un cline graduel du sud-ouest au nord-est; la pousse est survenue plus tard pour les sources les plus au sud. Des analyses de régression multiple ont été effectuées pour chacune des 32 variables selon 12variables climatiques interpolées pour chaque source de graines au moyen d'un système d'information géographique (SIG). Des données allant de 1951 à 1980 ont été obtenues de stations météorologiques voisines. D'importants coefficients de variation (jusqu'à 0,72) ont été notés pour certaines variables. La méthode d'analyse en composantes principales (ACP) a été employée pour résumer les principales composantes de la variation et les résultats de l'axe ACP de chaque source de graines ont été soumis à une analyse de régression selon les variables climatiques. Les moyennes de température maximale quotidienne de mai, de précipitations de mai, detempérature minimale extrême et du nombre de jours sans gel se sont avérées de bons prédicteurs des résultats sommaires de l'ACP. Les équations de régression ont servi à construire les profils de variation adaptative qui ont été représentés graphiquement sous forme de cartes d'isolignes par SIG. Une série de cartes focalisées des zones de provenance des graines ont été produites par intersection SIG des cartes d'isolignes fondées sur la régression. Le résumé du profil de variation adaptative du pin gris obtenu à partir de ces cartes a été employé pour formuler une recommandation sur les limites de la zone d'amélioration génétique de la zone1 de l'Institut de recherche forestière de l'Ontario.

TABLE OF CONTENTS

SEED ZONE DELINEATION FOR JACK PINE IN THE FORMER NORTHWEST REGION OF ONTARIO USING SHORT-TERM TESTING AND GEOGRAPHIC INFORMATION SYSTEMS

INTRODUCTION

The current opinion in Ontario is that when a forest is harvested, seedlings derived from the original stand should be used whenever possible to naturally or artificially regenerate that site. Thus, the new forest is as well adapted to the site as the harvested stand, the genetic base of that stand is preserved, and current levels of biodiversity are maintained. When it is not possible to use the germ plasm from the original stand, the intent is to only use seedlings that are well adapted to the site. For this reason, seed zone boundaries intended to reduce the possibility of using maladapted seed for reforestation have been put in place in northern Ontario. These boundaries correspond to Hills (1959) site classification system and administrative district boundaries (Ontario Ministry of Natural Resources 1987). These seed zones are thought to reflect general adaptive variation since they correspond to broad changes in climate, and in some cases vegetation. Unfortunately, they are not based on demonstrated patterns of adaptive variation. Although the patterns of adaptive variation are somewhat different for at least two of Ontario's commercial species (Parker et al. 1994, van Niejenhuis 1995), only one set of seed zones is currently applied to all tree species regardless of their ecological and adaptive differences. In all cases seed collected anywhere within a zone is considered suitable to reforest sites within the zone, but not in adjacent or more distant zones.

Jack pine *(Pinus banksiana* Lamb.) is a leading forest crop species in Ontario, where it comprises 25 percent of the planting stock used in artificial regeneration, and where its cone collection exceeds that of any other conifer species (Ontario Ministry of Natural Resources 1991). In the Northwest Region alone, the 1992 requirement for direct seeding of jack pine was 973.24 million seeds (Coles and White 1992). Not all of this seed requirement can be derived from parent stands, so improved guidelines for seed transfers, based on patterns of adaptive variation of jack pine, will enhance the future forest.

In an earlier study, a method to produce site-specific 'focal point seed zones' was developed for jack pine based on seed sources sampled from that area of northern Ontario that centers around Lake Nipigon (Parker 1992). Five stages were needed to define the focal point seed zones: (i) intensive sampling of naturally established stands to gather the seed sources (or provenances) to be tested; (ii) establishment of short-term growth and freezing tests to compare the collected seed sources in a common test environment; (iii) summarization of the comparative data by multivariate statistics; (iv) graphical reconstruction of the data by the construction of three-dimensional models, or trend surfaces, by geographic information systems (GIS) software, where the x- and y-axes are the geographic coordinates of the sample sites and each z-axis represents a component of adaptive variation; and (v) delineation of individual focal point seed zones by the construction of contour maps for each of the multivariate axis trend surfaces, and subsequent intersection of the contours to yield a polygon(s) or seed zone.

The static seed zone boundaries currently employed in Ontario are in need of reevaluation and subsequent refinement. Considerable activity has been directed toward this goal in recent years.[1] As tree improvement moves into advanced generation stages, precise matching between genotype and site will become critical. While the focal point seed zone approach was developed to match suitable seed sources and a particular geographic point, the method also provides the information needed to refine the boundaries of static seed zones such as those currently employed in northern Ontario. This is because the resulting seed zones for jack pine are based on demonstrated levels of adaptive similarity unique to the species.

This study was designed to apply the already developed focal point seed zone methodology to jack pine in the furthest northwestern portion of Ontario. The goals of the project were: (i) to improve the knowledge of adaptive variation of jack pine in this region; (ii) to develop a rapid, operational method of site-specific seed source selection based upon GIS techniques; and (iii) to refine the existing pattern of breeding zone boundaries for the region. It was anticipated that four end products would result from this work: namely, (i) a database summarizing adaptive variation in jack pine for the Northwest Region; (ii) a computer protocol running on ARC/INFO to be used to determine, as needed, focal point seed zones for any location in the northwestern portion of Ontario; (iii) a handbook of focal point seed zones, based upon a systematic grid of focal points, which could be used to make routine seed transfer decisions for jack pine in the area; and (iv) a map of refined breeding zone boundaries based upon the biology of jack pine.

---

[1] Joyce, D. Ontario Ministry of Natural Resources, Ontario Forest Research Institute, Sault Ste. Marie, ON. Pers. comm.

Adaptive Variation in Jack Pine

Jack pine is found primarily in the Boreal Forest Region of Canada. Its range extends from the Mackenzie River in the Northwest Territories across much of Alberta, Saskatchewan, Manitoba, Ontario, Quebec, New Brunswick, and Nova Scotia. As well, its range extends into the United States in Maine, New Hampshire, and New York, and around the Great Lakes in Michigan, Indiana, Illinois, Wisconsin, and Minnesota.

Throughout its range, jack pine occupies sites having diverse climatic, edaphic, and topographic conditions. Mean annual temperatures vary from -5°C to 9.5°C, and mean minimum temperatures vary from -20°C to -45°C or lower. Precipitation varies from 13 to 58 cm during the 60 to 170 day growing season (Rudolf 1958). Soils associated with jack pine are commonly sandy; however, loam or shallow soils over bedrock or even organic soils may also be colonized by this species (Rudolph and Yeatman 1982).

Due to the economic importance and the broad ecological amplitude of jack pine, considerable research has been directed at investigating its patterns of adaptive variation. These studies have included range-wide provenance tests to determine the broad patterns of geographic variation, and more restricted local provenance tests to determine the most desirable sources for artificial regeneration programs.

Range-wide provenance studies of jack pine, including 99 provenances from throughout the range, were established in 1962 (*cf.* Rudolph and Yeatman 1982 for a summary and list of references). Growth measured in these tests has shown a broad clinal pattern that follows the environmental gradients of photoperiod, and the length and temperature of the growing season. Regressions of seedling weights on growing degree-days lead Yeatman (1966) to distinguish between populations east and west of 91° longitude. Yeatman (1966) also reported that cold hardiness was related to the latitude of seed origin in the range-wide provenance tests.

Regional trials also indicate clinal variation in jack pine, although a more complex pattern has been reported for north central Ontario (van Niejenhuis 1995). Local sources did not always produce the best height results, nor were southern sources consistently tallest in common garden trials.

MATERIALS AND METHODS

The various methods used here to establish focal point seed zones for jack pine are illustrated as a flow diagram in Figure 1. The general approach is to model variation detected in short-term common garden tests by regression against important climatic variables so that the modeled seed zones directly correspond to environmental variation. For this project two separate databases had to be established: (i) a database containing the results of comparative growth and freezing tests for different seed sources,

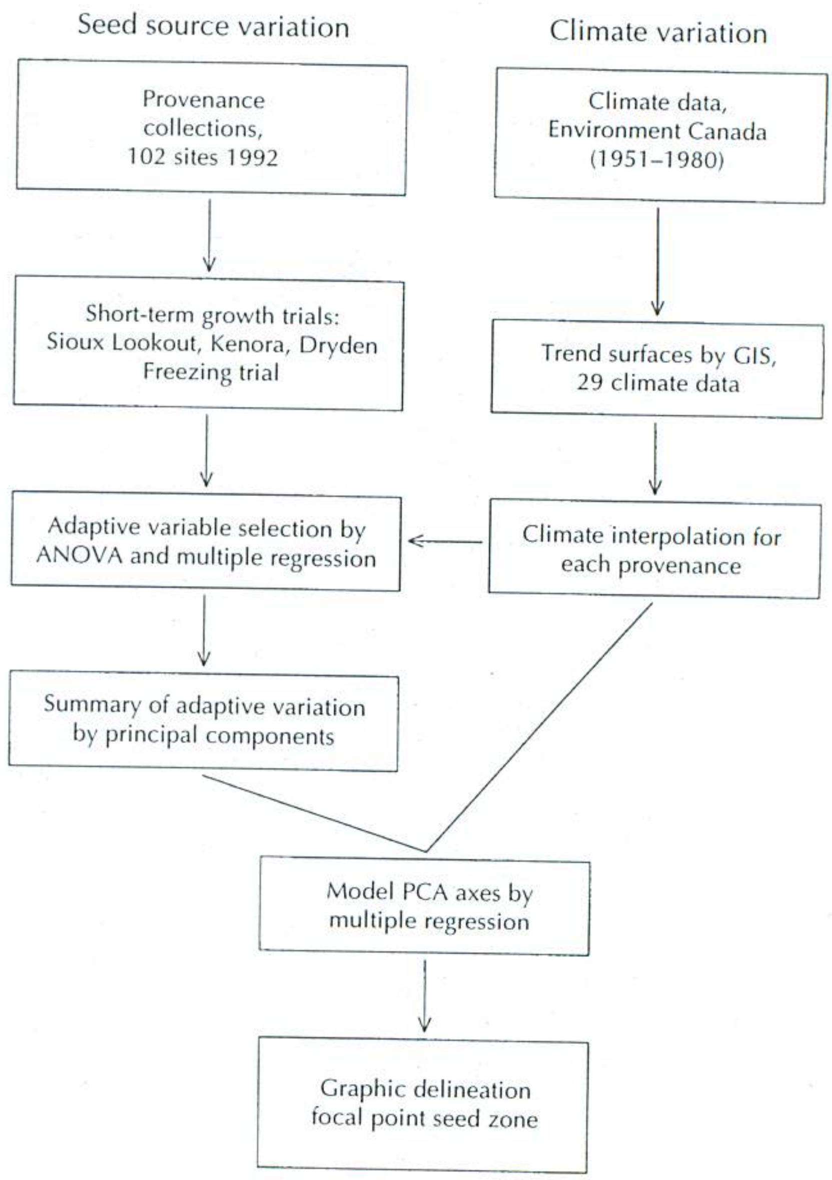

Figure 1. Methods used to establish focal point seed zones.

and (ii) a database consisting of historical climatic data for the area from which the seed sources were collected. These two databases are equally important. The value of the end product, or the actual seed zones, depends upon the quality of each database.

Stand Collections

Collections of jack pine cones, together with vegetation and soils data, were gathered in the summer of 1992 from that portion of northwestern Ontario extending from a longitude of approximately 90° (to the northeast of Quetico Provincial Park) west to the Ontario–Manitoba border, and from the Ontario–Minnesota border north to approximately 51°. The study area formed a rectangle of approximately 400 km east to west, and 350 km north to south. Within this area 102 jack pine stands of natural origin (fire origin) were selected for sampling (Fig. 2). The sampled stands represent the broad ecological amplitude of jack pine within this portion of its range.

At each seed source, vegetation and soil data were determined following the Ontario Forest Ecosystem Classification (FEC) system (Sims et al. 1989). The vegetation type (V-type) for each site was then classified, based upon the vegetation found in a 10-m x 10-m undisturbed plot. Classification of the soil types (S-types) was based upon soil horizons found in a 1-m x 1-m x 1-m soil pit (Table 1). Of the 38 V-types recognized in northwestern Ontario, seven predominantly jack pine V-types were included in the sampled stands. These included V-types 17 and 18, jack pine mixedwood types; and V-types 28 to 32, essentially pure conifer stands dominated by jack pine. Fourteen different S-types were represented among the 102 seed sources, ranging from very coarse (S1, S7, and SS5) to fine (S6, S10, and SS7). Both shallow and deep mineral soils were included.

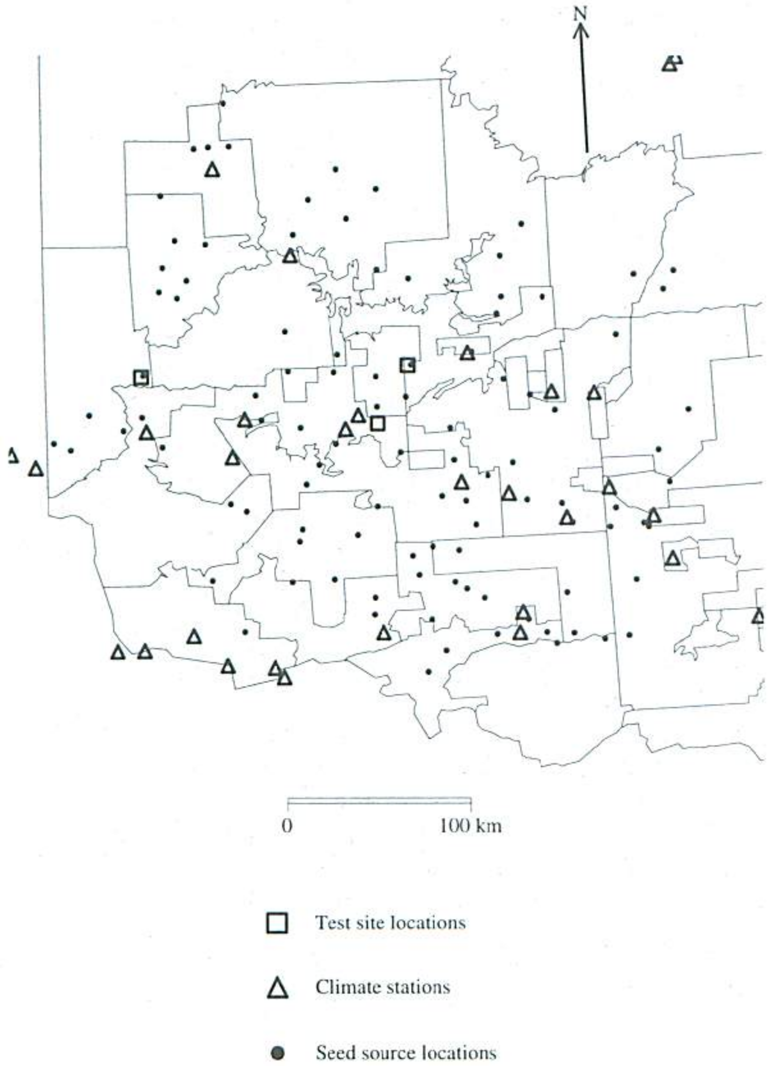

Figure 2. Map of climate stations, seed sources, and test locations.

At each of the 102 collection sites, at least ten dominant jack pine trees with adequate numbers of serotinous seed cones in the upper crown were randomly chosen. Selected trees were separated by a distance of at least 20 m so as to minimize the probability of including siblings. Each jack pine selected was felled, measured, and aged, and cones that had matured the previous fall (1991) were collected. Average ages of these stands varied from 47 to 120 years (Table 1).

Climatic Data

Climatic data for the period 1951–1980 were obtained from 58 Ontario weather stations (Environment Canada 1982a, 1982b, 1982c), 18 Manitoba weather stations (Environment Canada 1982b, 1982c, 1982d), and 10 Minnesota weather stations (Gale Research Company 1985) within and surrounding the study area (Fig. 2). In total, 29 climatic variables were selected for use in examining adaptive variation. These included annual and monthly means corresponding to the growing season for climatic variables affecting tree growth and survival (i.e., precipitation, temperature, growing degree-days, and heating degree-days), and spring and fall frost dates (Table 2). For each of the 102 seed sources, climatic data were interpolated using geographic information system (GIS) techniques. Individual climatic values for each of the 102

Table 1. Site and collection data summary for 102 stands of jack pine.

Site	Age		Height (m)		DBH* (cm)		Latitude			Longitude			Elev	V-	S-
	Mean	S.D.	Mean	S.D.	Mean	S.D.							(m)	type	type
1	66.6	8.45	19.24	1.93	22.72	2.85	49°	41'	48"	92°	55'	38"	360	28	S2
2	55.5	4.03	19.07	0.65	22.54	3.05	50°	8'	15"	92°	53'	11"	424	29	S7
3	74.1	2.38	19.71	1.52	32.22	5.15	49°	25'	15"	92°	8'	50"	460	17	SS6
4	70.3	1.42	20.78	1.14	26.18	3.04	49°	30'	30"	91°	48'	0"	440	29	S2
5	69.1	3.14	19.79	1.42	22.75	2.24	50°	9'	45"	90°	46'	10"	440	18	S8
6	65.5	2.46	18.80	1.12	22.59	2.79	50°	22'	15"	91°	18'	30"	410	29	S2
7	74.0	3.30	16.51	0.87	18.01	1.94	50°	27'	15"	90°	36'	10"	415	32	S7
8	115.2	6.84	22.06	1.81	28.64	3.39	50°	22'	15"	90°	23'	0"	440	18	SS4
9	67.5	5.25	17.85	1.52	20.31	2.10	50°	7'	15"	91°	52'	10"	390	31	S2
10	52.2	0.79	16.22	1.11	16.65	2.36	50°	27'	30"	90°	17'	45"	410	32	SS5
11	71.7	0.95	21.47	1.34	25.18	2.68	49°	53'	30"	91°	27'	0"	410	31	S2
12	89.3	5.42	20.83	1.46	23.64	2.01	48°	49'	14"	92°	16'	23"	502	17	S10
13	62.4	2.72	18.15	1.18	22.10	2.34	49°	2'	17"	92°	58'	42"	388	18	n.a.
14	76.4	2.17	18.82	1.01	23.80	2.26	49°	1'	57"	93°	17'	42"	433	31	SS7
15	105.1	16.72	0.05	2.31	31.59	4.90	49°	17'	21"	93°	12'	18"	510	18	SS1
16	73.3	2.79	17.87	1.30	21.65	3.91	49°	15'	5"	92°	47'	29"	551	18	SS6
17	91.8	3.43	17.92	1.44	23.49	1.46	49°	13'	50"	93°	13'	47"	414	17	SS2
18	57.3	4.81	16.25	1.14	20.27	3.94	48°	51'	26"	92°	41'	38"	402	18	SS7
19	65.0	2.40	16.61	1.52	18.83	1.75	48°	56'	26"	92°	41'	4"	426	17	SS6
20	51.9	1.79	17.84	1.02	23.43	2.94	48°	56'	26"	92°	41'	5"	426	17	SS6
21	99.3	2.75	19.30	2.15	24.79	2.01	49°	3'	6"	93°	53'	47"	426	28	S10
22	82.1	1.29	18.03	1.79	25.27	2.74	49°	44'	7"	95°	3'	52"	436	17	SS5
23	53.1	0.99	15.92	0.88	22.77	1.85	50°	3'	46"	94°	22'	41"	387	32	SS5
24	65.2	5.94	18.81	1.29	28.27	2.62	49°	51'	21"	94°	23'	41"	375	17	S7
25	74.2	1.23	18.78	2.44	23.88	2.92	49°	47'	31"	94°	32'	8"	385	31	SS5
26	83.4	6.02	17.35	2.43	25.73	3.72	49°	42'	3"	94°	56'	3"	355	17	SS7
27	110.8	5.85	15.25	2.08	27.04	2.96	49°	52'	15"	94°	47'	35"	356	17	SS5
28	89.5	3.69	16.00	2.16	23.58	3.99	49°	42'	25"	94°	14'	54"	373	30	SS1
29	53.7	2.95	14.88	1.81	18.77	1.82	49°	23'	10"	93°	37'	21"	370	31	SS5
30	53.7	2.95	14.50	2.53	19.12	2.98	49°	25'	27"	93°	44'	23"	345	18	SS7
31	77.6	3.10	17.48	1.06	20.79	2.33	50°	3'	3"	92°	55'	12"	399	29	S3
32	95.3	5.83	13.25	1.78	24.03	2.52	49°	49'	35"	93°	29'	23"	377	30	SS1
33	54.3	3.27	14.00	1.88	18.97	3.65	49°	38'	33"	92°	26'	30"	418	30	SS4
34	70.1	4.43	18.51	1.06	20.20	4.52	48°	54'	49"	91°	52'	46"	463	32	S1
35	68.9	2.73	17.81	1.49	20.72	2.91	48°	47'	49"	91°	33'	53"	465	32	SS5
36	76.2	6.87	19.23	1.98	24.95	2.61	48°	55'	1"	91°	16'	3"	413	32	SS6
37	87.5	2.33	19.81	0.77	24.57	2.18	49°	9'	1"	92°	2'	41"	442	28	SS5
38	87.0	3.71	19.56	1.51	24.16	2.09	48°	42'	59"	91°	14'	10"	440	30	SS4
39	62.6	3.24	18.33	1.19	20.34	2.60	48°	57'	49"	92°	0'	10"	465	17	SS5
40	85.0	4.81	20.70	1.20	28.82	2.28	48°	40'	40"	91°	0'	43"	481	30	SS4
41	93.9	3.83	15.82	2.35	19.53	2.41	49°	10'	42"	92°	14'	14"	394	29	SS1
42	59.7	4.00	18.81	0.98	25.42	3.12	48°	59'	58"	92°	5'	9"	450	32	S1
43	68.2	2.25	19.62	1.57	21.03	2.86	48°	39'	58"	92°	10'	43"	410	18	S1
44	60.9	5.82	17.06	0.95	22.53	1.74	48°	33'	55"	92°	19'	16"	428	30	SS1
45	63.6	1.07	17.47	2.19	19.60	2.15	48°	43'	57"	91°	47'	50"	350	28	SS2
46	80.3	5.89	17.94	1.51	20.13	1.45	48°	4'	16"	91°	21'	58"	263	32	S2
47	93.1	3.80	17.30	2.07	20.84	2.01	49°	8'	15"	92°	23'	24"	415	30	SS1
48	67.3	4.95	17.21	2.06	19.63	1.96	49°	2'	34"	92°	20'	57"	334	32	S10
49	90.8	7.34	16.21	2.17	20.09	3.78	48°	43'	41"	91°	25	59"	427	32	SS2
50	64.3	2.00	17.33	1.81	17.53	2.06	50°	18'	2"	91°	39	41"	373	18	SS4
51	95.0	2.31	20.77	1.78	24.28	3.13	50°	35'	4"	91°	36'	34"	NA	29	S2

(cont'd)

Table 1. Site and collection data summary for 102 stands of jack pine. (concl.)

Site	Age		Height (m)		DBH* (cm)		Latitude	Longitude	Elev	V-	S-
	Mean	S.D.	Mean	S.D.	Mean	S.D.			(m)	type	type
52	69.0	7.85	16.73	2.15	18.54	2.01	50° 4' 14"	92° 19' 51"	324	30	S2
53	57.3	3.92	19.23	1.90	21.26	2.30	50° 23' 1"	91° 37' 10"	470	32	S1
54	77.8	8.87	21.46	0.91	20.63	1.21	49° 54' 48"	92° 22' 50"	458	29	S1
55	84.8	1.23	18.17	1.18	18.88	1.76	50° 44' 1"	91° 25' 55"	397	32	SS4
56	79.9	3.66	18.23	1.23	19.80	2.69	50° 1' 15"	92° 36' 14"	570	29	S2
57	71.4	5.89	19.13	1.27	20.35	1.75	49° 58' 36"	91° 38' 19"	365	29	S1
58	66.2	2.57	17.85	0.86	17.56	1.73	49° 21' 16"	91° 15' 43"	492	32	S2
59	79.7	1.70	17.31	1.42	18.76	1.71	49° 33' 50"	91° 36' 31"	475	32	SS5
60	71.3	4.06	19.36	1.35	21.90	2.40	49° 48' 32"	91° 16' 7"	446	32	S2
61	64.2	2.04	17.50	1.18	18.71	1.75	49° 35' 32"	92° 2' 39"	485	29	S1
62	102.8	7.92	21.67	0.81	25.61	3.48	49° 44' 59"	92° 3' 29"	487	32	S2
63	72.3	4.76	18.57	1.34	22.90	2.69	49° 23' 32"	91° 58' 22"	485	32	SS4
64	74.0	4.30	16.32	1.13	15.98	1.91	49° 16' 27"	91° 54' 30"	489	32	S2
65	77.8	2.44	18.75	1.48	20.61	3.38	49° 22' 52"	91° 31' 12"	506	29	S2
66	71.9	4.12	14.98	1.01	16.27	2.31	49° 15' 31"	91° 11' 34"	477	29	SS4
67	120.0	3.10	12.74	1.30	17.42	1.24	50° 56' 32"	94° 12' 48"	458	30	SS2
68	74.9	5.18	15.51	1.43	18.19	2.18	50° 32' 47"	92° 33' 27"	358	32	S2
69	55.8	1.14	17.61	1.01	19.51	2.04	50° 29' 46"	92° 19' 1"	345	29	S2
70	75.6	4.00	16.03	2.02	17.64	1.78	51° 10' 18"	93° 39' 52"	298	32	S2
71	74.8	1.03	15.95	0.61	19.36	2.34	50° 48' 9"	92° 46' 16"	454	32	SS5
72	65.2	4.89	17.45	1.22	18.58	2.14	50° 56' 25"	92° 31' 60"	448	32	S6
73	94.4	1.71	19.23	1.18	22.32	2.81	51° 23' 2"	93° 42' 7"	510	29	S1
74	71.1	5.65	17.65	1.01	17.33	1.73	51° 10' 16"	93° 49' 43"	375	30	S2
75	46.9	3.03	16.92	0.83	21.49	3.60	50° 44' 2"	93° 11' 27"	410	29	S1
76	76.7	3.80	18.09	1.14	18.55	2.37	51° 9' 53"	93° 56' 25"	537	32	S2
77	71.3	0.82	18.86	1.05	22.56	3.25	51° 2' 38"	92° 50' 7"	461	18	SS5
78	78.0	4.94	18.65	0.86	18.89	2.16	50° 54' 5"	93° 3' 40"	353	32	S6
79	88.2	2.62	21.53	1.72	21.32	2.12	50° 39' 16"	93° 12' 31"	362	32	SS5
80	83.7	4.50	16.62	1.27	17.79	1.37	50° 26' 23"	94° 6' 12"	417	29	SS5
81	78.1	6.40	20.28	2.14	23.81	3.89	50° 28' 19"	94° 14' 35"	259	18	SS6
82	75.2	6.83	20.81	1.30	22.04	2.95	50° 35' 26"	94° 12' 50"	453	29	S6
83	82.3	1.16	18.55	1.12	20.05	2.84	50° 31' 31"	94° 1' 35"	406	32	S2
84	92.7	7.54	11.85	1.89	17.11	3.44	50° 43' 23"	94° 6' 34"	389	30	SS1
85	77.1	2.42	17.57	1.28	20.07	2.82	50° 42' 3"	93° 52' 28"	340	29	S5
86	81.4	9.96	14.33	2.67	18.65	3.63	50° 15' 33"	93° 16' 54"	416	30	SS1
87	91.5	14.33	18.38	1.73	21.57	5.73	50° 3' 47"	93° 16' 9"	449	17	S6
88	66.8	3.011	9.37	0.71	18.59	1.57	49° 18' 55"	90° 51' 41"	423	n.a.	S1
89	51.9	0.741	5.27	0.85	19.93	3.83	49° 13' 59"	90° 39' 50"	649	29	S1
90	58.8	1.69	20.30	2.27	20.26	2.17	48° 57' 34"	90° 44' 59"	445	32	S2
91	75.8	2.74	17.86	1.28	20.32	1.31	49° 34' 52"	90° 30' 39"	555	29	SS5
92	61.7	4.72	18.59	1.07	17.61	2.24	49° 25' 21"	90° 26' 47"	478	n.a.	S2
93	84.0	n.a.	17.73	1.32	16.12	1.35	49° 46' 5"	90° 15' 57"	370	18	SS4
94	58.7	3.27	17.98	1.26	19.96	1.63	49° 13' 30"	90° 54' 48"	635	32	S1
95	64.1	2.56	21.07	3.22	21.44	2.06	49° 12' 48"	90° 37' 34"	502	32	S1
96	70.4	4.22	16.92	1.70	20.69	2.56	49° 46' 56"	93° 11' 29"	505	29	S1
97	118.9	2.38	19.35	1.36	28.19	4.46	49° 30' 19"	93° 9' 46"	290	32	SS4
98	72.2	2.80	16.90	1.13	17.69	1.86	49° 56' 55"	93° 31' 31"	400	29	SS4
99	85.6	10.97	16.02	1.28	17.99	1.44	49° 35' 51"	93° 3' 41"	300	30	SS1
100	73.9	5.38	16.84	1.37	17.49	1.44	49° 23' 10"	92° 38' 7"	450	32	SS4
101	93.7	9.03	19.85	1.80	23.25	3.54	48° 41' 17"	90° 49' 60"	480	17	S3
102	70.3	3.09	19.22	1.54	19.74	2.26	49° 52' 16"	92° 36' 18"	411	29	S6

* DBH = diameter at breast height.

Table 2. Summary of the climatic data interpolated by GIS for the 102 jack pine seed sources.

Climate variable	Minimum	Maximum	Mean
Mean temperatures (°C)			
Annual	-0.59	2.60	1.31
April	-0.13	3.47	1.91
May	7.81	10.72	9.46
June	14.16	16.11	15.28
July	17.05	19.19	18.26
August	15.34	17.58	16.70
September	9.77	11.86	10.89
Mean maximum temperatures (°C)			
April	5.93	9.92	7.91
May	13.96	17.70	15.98
June	20.22	22.87	21.44
July	23.20	25.45	24.34
August	21.32	24.00	22.58
September	14.42	17.95	16.06
Mean minimum temperature (°C)			
January	-27.64	-22.76	-24.74
Extreme temperatures (°C)			
Minimum	-49.37	-41.52	-45.26
Maximum	34.96	42.08	37.94
Temperature sums			
Growing degree-days (>5°C)	1205.63	1683.54	1508.85
Heating degree-days (<18°C)	5748.96	6813.40	6193.51
Growing season			
Last spring frost	May 17	June 16	May 29
First fall frost	Aug. 27	Sept. 26	Sept. 14
Frost free days	70.94	130.68	107.13
Mean precipitation (cm)			
Total annual	56.62	80.45	69.07
Annual snow	152.90	262.08	199.91
April	3.11	5.38	4.38
May	4.69	7.86	6.55
June	7.78	11.47	9.28
July	7.03	10.20	9.21
August	7.53	11.24	8.94
September	5.68	9.98	7.82

collection sites were interpolated from continuous three-dimensional trend surfaces generated by the TIN (triangulated irregular network) subpackage of ARC/INFO (Environmental Systems Research Institute Inc. 1992). The locations of the weather stations serve as the corners of the triangles. This technique provides estimates of the recent climate at each seed source based on averages, but cannot give the actual climate data for each source as it does not account for local fluctuations in the climatic gradients due to elevational gradients, aspect, and other topographical features.

For all variables, the climatic data for the 102 seed sources displayed a large amount of variation throughout the collection area (Table 2). The amount of climatic heterogeneity observed is striking, particularly for those variables related to timing of the growing season.

Establishment of the Short-term Tests

Cones from each jack pine at each site were individually processed for the extraction of seed, and equal numbers of seed per tree were bulked by site. Cleaned seed was then weighed and recorded for ten replicates of five seeds each per site.

Seedlings to be outplanted in the field and greenhouse trials were grown in leach tubes at the Lakehead University (Thunder Bay, Ontario) greenhouse in a mixture of 3 parts peat, 3 parts vermiculite, and 1 part perlite by weight. Seeding of jack pine for the field trials was completed on 8 April 1993; seeding for the greenhouse trial was completed on 5 May 1993. Seedlings were watered twice or three times a week. An 11-41-8 soluble seedling starter fertilizer was applied at a rate of 50 ppm nitrogen from the third to the fifth week after seeding, followed by fertilization using 20-8-20 soluble seedling special fertilizer at a rate of 100 ppm nitrogen from Week 6 to Week 13, and 8-20-30 soluble seedling finisher fertilizer at a rate of 65 ppm nitrogen from Week 14 to Week 16. Seedlings were cultured under extended light periods of 18-hr days. This schedule was maintained until the field trial stock was moved from the greenhouse to a shade house on 12 July 1993.

In the summer of 1993, common garden tests including seedlings of all 102 seed sources were established near the Fifth Creek Seed Orchard in the Kenora District (W 94°23'30", N 50° 3'14"), at the Goodie Lake North Seed Orchard in the Sioux Lookout District (W 92°21'23", N 50° 4'12"), and at the Dryden Tree Nursery (W 92°36'7", N 49°47'18"). At each of these locations field trials were planted. These consisted of three blocks of ten replicates per seed source arranged in a completely randomized design. Field trials were planted at Sioux Lookout on 4–5 August, at Kenora on 12–13 August, and at Dryden on 17–18 August. A freezing trial of a single complete randomized block with 25 replicates from each seed source was established on 24–25 August at the former Thunder Bay Forest Nursery (W 89°23'57", N 48°21'48") to provide material for frost hardiness tests. As well, a greenhouse trial consisting of a single, completely randomized block with 25 replications from each seed source was established at the Dryden Tree Nursery. These seedlings were transplanted from the leach tubes into 3-L pots by 29 September. This stock was overwintered in a shade house and brought into a greenhouse on 26–27 April 1994.

Data Collection

The first height measurements (i.e., 1993 heights) were made before flushing began in 1994. The Dryden greenhouse trial was measured on 28 April, and the field trials were measured during the first and second week of May. Daily measurements were made of the candle lengths (i.e., current year shoots or leaders with flushing or elongating needles) from mid-May until mid-June, when needle flushing had occurred. The needle flushing date was also recorded for each seedling at all trials (i.e., the date that the first needle emerged from a fascicle). Measurements of the candle lengths continued every second day until the end of June; they were then recorded at weekly intervals until early August. Final candle measures and total heights were recorded for all seedlings at all trials during the second week of August, 1994. Total heights for 1993 and 1994 were also recorded for the freezing trial on 3 May 1994, and 5 November 1994, respectively.

For each jack pine seedling in each trial, phenological data, including elongation initiation date, elongation cessation date, and duration of elongation in days, were estimated. The shoot elongation measurements were fitted to a growth equation described by Rehfeldt and Wykoff (1981):

$$Y = \frac{1}{1 + be^{(-rX + c/X)}}$$

or

$$ln\left(\frac{1}{Y} - 1\right) = ln(b) - rX + c\left(\frac{1}{X}\right)$$

where: Y is the proportion of the total elongation observed by day X, and ln (b), r, and c are regression coefficients.

A multiple linear regression algorithm was written following the methods of Sokal and Rohlf (1981) to calculate the regression coefficients and coefficients of multiple determination (r-squared), and to plot the growth curves.

Regression of the elongation data for each seedling allowed estimates for the time of elongation initiation (i.e., the day on which 3 mm of cumulative growth had occurred), and the time of elongation cessation (i.e., the day on which all but 5 mm of the growth had occurred) (Rehfeldt and Wykoff 1981). Duration was then calculated as the difference between these two estimated dates.

Needle flushing date was the third phenological variable examined. The date when the developing needles had swelled to open their fascicles was transformed to the number of days after 30 April for each seedling in each trial.

Freezing Tests

Three comparative freezing damage trials were conducted in the fall of 1994. Current year needles were collected and bulked from ten seedlings of each seed source. Nine replicates of 20 needles from each seed source were placed in labeled bags. These included three controls, three of a first treatment temperature, and three of a second treatment temperature. These were cooled at a rate of 2°C per hour in a programmed chest freezer and maintained for 2.5 hours at treatment temperatures varying from -8°C on the earliest date of 15 September to -38°C on the last date of 12 October 1994. Needles were then thawed, placed in labeled vials, and distilled water was added. Electro-conductivity measurements of electrolyte leakage (Colombo et al. 1984) were used to assess freezing damage. Percent damage was assessed relative to control samples maintained at 5°C, and the resulting data were arcsin transformed prior to analysis. In this manner comparative freezing damage data were obtained for the 102 sources for six different freezing treatments.

Data Analysis

Each of the measured biological variables was analyzed by ANOVA to determine the amount of variation expressed among seed sources. For the greenhouse trial and freezing tests, each of which consisted of only one block, one-way ANOVAs were run, and the coefficients of intraclass correlation were calculated (Sokal and Rohlf 1981) to determine the extent of differentiation among the 102 seed sources. The model used was:

$$Y_{ij} = \mu + A_i + \varepsilon_{ij}$$

where: i = 1 to 102 seed sources;

j = 1 to 25 replicates per seed source;

Y_{ij} = measured variable value of replication j of seed source i;

μ = the population mean;

A_i = the random effect of seed source i; and

ε_{ij} = the random effect of replication $_j$ of provenance i.

Similarly, for the three field trials, two-way ANOVAs were run and the results were presented as percents of variation attributable to seed sources, blocks, and seed source x block interactions. The model used was:

$$Y_{ijk} = \mu + A_i + B_j + (AB)_{ij} + \varepsilon_{ijk}$$

where: i = 1 to 102 seed sources;

j = 1 to 3 blocks;

k = 1 to 10 replicates for each seed source in each block;

Y_{ijk} = measured variable value of replication k of the block j of seed source i;

μ = the population mean;

A_i = the random effect of seed source i;

B_j = the random effect of block j;

$(AB)_{ij}$ = the interaction effect in the subgroup representing the $_i$ th seed source and the $_j$ th block; and

ε_{ijk} = the random effect of replication k of block j of seed source i.

All growth and freezing variables were screened by simple and multiple linear regression against 12 of the climatic variables interpolated by GIS from 1951–1980 climatic data (Table 2). The 12 climatic variables were average annual precipitation, average annual snowfall, extreme maximum temperature, average maximum daily temperature in July, average annual temperature, average minimum daily temperature in January, extreme minimum temperature, growing degree-days (>5°C), heating degree-days (< 18°C), average annual number of frost free days, date of the last spring frost, and date of the first fall frost. Biological test variables, which demonstrated significant differentiation among seed sources ($\alpha < 0.05$) and which showed significant regressions against the climatic data ($\alpha < 0.05$), were selected for multivariate analysis. The rationale for the double screening was: (i) that variables with little or no between-source variation in common garden tests are not useful in determining seed zones, and (ii) that the components of adaptive variation on which seed zone decisions should be based will show a strong correspondence with the local climates of the seed source locations. As a result, 21 of the 32 measured variables were retained: namely, 11 growth, 8 phenological, and 2 freezing damage.

Seed source mean values for the 22 variables were analyzed using principal components analysis (PCA) (based on the correlation matrix) to summarize the main components of variation in the data set. New summary variables consisting of principal component scores were calculated for each main axis of variation. These PCA summary variables were reproduced graphically as contour maps by GIS to show patterns of geographic variation. Additional multiple linear regressions of these PCA summary variables were run against climatic data interpolated for the 102 sources. Preliminary regressions were run using a backwards stepwise procedure with a probability for removal of an explanatory climatic variable set at the 0.05 level. For these regressions against the PCA axes, the full complement of 29 climatic variables was used (Table 2). To avoid overfit regressions, variables with tolerances considerably less than 0.1 or t values less than 2.0 were eliminated (Wilkinson et al. 1992) and the regressions were rerun. These simplified regressions were then used to model the main PCA axes. Scores predicted by the regressions were calculated for each of the 102 seed sources. These scores were standardized to have means of 0 and standard deviations of 1 to allow for a direct graphic comparison to the actual PCA scores. These predicted scores were then graphically reproduced as contour maps by GIS to summarize the modeled pattern of geographic variation. All PCAs and regressions were run using Systat (Wilkinson et al. 1992).

Additional (GIS) contour maps were made of several individual biological variables. Selection of these variables was based upon a relatively high percentage of variation being expressed among seed sources and a good fit to the climatic data. For comparison purposes, additional contour maps were prepared of the climatic variables that were retained in the regression equations against the first two PCA axes.

A series of focal point seed zone maps was prepared for the sampled area of northwestern Ontario following procedures described by Parker (1992). Focal point locations were chosen every 12 minutes of latitude and 20 minutes of longitude, thus constituting a systematic grid of the sample area. Z-scores for the focal point locations were determined on each of the two trend surfaces corresponding to the first two modeled PCA axes. Then, for each focal point, two new contour maps were constructed with the base levels (zero values) set to the z-scores and the contour intervals set to 0.5 standard deviations. These two new contour maps were then overlaid, and the contour intervals intersected. Zones of simultaneous similarity were identified by shading patterns. In this way, a shaded zone represented a minimum level of adaptive similarity on both modeled PCA axes. Eight of the resulting focal point seed zone maps were chosen to highlight the pattern of adaptive variation for the area. The entire set of 184 focal point seed zones is presented in a separate volume (Parker 1995). Based on these results, a further map was prepared to summarize the major zones of black spruce adaptive variation for the area from which the seed sources were sampled. This map was provided as a recommendation for breeding zones for jack pine in the region.

RESULTS

Single Variable Analyses

Differences were evident in the growth response of the seedlings among the various test environments. Seedlings tested in the greenhouse flushed their needles earlier and had a longer growing season of 74 days than did those in the three outdoor trials, which had growing seasons ranging from 57 to 64 days (Table 3). Seedling heights at the end of the 1993 growing season were similar for all of the tests, but growth was superior after the 1994 growing season at the Dryden and former Thunder Bay forest nurseries. Grand means were of 21.2 cm and 24.6 cm, respectively. These were compared to the height growth at the Kenora and Sioux Lookout trials, with means of 17.8 cm and 18.2 cm, respectively. At each test the start of elongation preceded the date of needle flushing, but only by 1.5 days in the greenhouse trial as opposed to 9 to 15 days in the three field tests.

Provenance differentiation was evident under all test conditions. The largest components of variation (20–38 percent) expressed among provenances were observed for the freezing trials (Table 3). In general, low to moderate (6–12 percent) fractions of variation were expressed among provenances for seedling heights at the three field trials, and the situation was similar for dates of needle flushing (3–15 percent). Due to a more controlled environment, more variation was expressed among seed sources for heights and flushing dates in the greenhouse. Phenological variables related to shoot elongation showed little or no variation among the 102 seed sources, with the exception of the start of growth in the greenhouse. Two trends are evident in the height growth and needle flushing results. First, the level of provenance differentiation was greatest in the most favorable environment, the greenhouse; lower in the two nursery situations; and lowest in the less favorable Kenora and Sioux Lookout trials. Second, the level of differentiation between provenances indicated by seedling height growth diminished with time in the greenhouse and nursery trials, but increased at the Kenora and Sioux Lookout trials.

The percentages of variation expressed by blocks in the three blocked test designs were very low to moderate (0–6 percent). Both height variables and flushing dates were sensitive to block effects in some but not all cases (Table 3). The block x seed source interaction term generally accounted for none or small (0–2 percent) fractions of the total variation.

Four contour maps depicting seedling height and increment growth (Figs. 3–6), and four additional maps showing needle flush dates (Figs. 7–10), are presented to show the gradual changes in adaptive variation throughout the seed collection area, and to illustrate the differences in the pattern that appear at the different test sites related to genotype x site interaction. In all four cases the most northwestern seed sources showed the slowest height growth. The most rapid growing seed sources occurred as a band or in patches from east to west across the central to south central portion of the collection area. However, within this area of rapidly growing seed sources, there exist many local irregularities of slower growing sources. A comparison of the four figures shows that some seed sources may grow rapidly at some test sites and slowly at others.

The four contour maps that illustrate variation among seed sources in the dates of needle flushing (Figs. 7–10) are more uniform than those showing height growth. Although the actual dates and the duration of the flushing period differ, in all cases there is a gradual trend (clinal) from the southwest to the north or northeast; the northern sources flushed earlier and the southern sources flushed later.

Both simple linear and backwards stepwise multiple linear regression analyses were run for all test variables against 12 climatic variables. Coefficients of determination (r^2) and the independent climatic variables are provided in Table 4 for all of the regressions that were significant ($a < 0.05$). All 12 climatic variables were good predictors for at least some of the dependent biological variables in the regressions. Whereas the ANOVA results indicated only low to moderate amounts of variation expressed among seed sources, much of this variation correlated with the climate for both the height and some phenological variables. Flushing dates had the highest r^2 values; simple linear regressions accounted for as much as 59 percent of the variation and multiple regressions accounted for up to 72 percent. However, the situation was reversed for the freezing variables, which showed relatively large components of variation expressed among seed sources and none to low levels of variation explained by climate. This was a surprising result since the variation among seed sources displayed in the freezing trials normally would be expected to correlate with temperature and growing season variables.

Multivariate Analyses

Principal components analysis of the 21 selected variables showed that the first and second axes overshadowed all the rest, accounting for 38 and 14 percent, respectively (Table 5). Thus, these two axes expressed a little more than one-half of the total variation; the other 19 axes

Table 3. Means, standard deviations, and percentages of variation expressed among 102 seed sources (provenances) of *Pinus banksiana*.

Variable	Mean[a]	S.D.[a]	Provenances (%)	Block (%)	Interaction (%)
Greenhouse					
GH94 flush date[b]	6.78	1.41	17.05	-	-
GH94 start date[b]	5.30	4.79	8.05	-	-
GH94 stop date[b]	79.43	12.01	0 ns[c]	-	-
GH94 increment (cm)	3.30	1.40	4.98	-	-
GH93 height (cm)	10.24	1.61	21.02	-	-
GH94 height (cm)	18.86	3.30	12.74	-	-
Dryden					
DR94 flush date[b]	23.81	2.05	14.54	2.49	1.52
DR94 start date[b]	14.58	3.95	0.35 ns	2.39	0
DR94 stop date[b]	78.25	14.01	0.70 ns	1.78	0
DR94 increment (cm)	5.58	2.68	5.58	1.66	0.65
DR93 height (cm)	13.11	2.36	12.20	1.25	0.53
DR94 height (cm)	21.15	3.72	10.67	3.64	0.66
Kenora					
KE94 flush date[b]	28.35	3.04	3.36	5.96	0.38
KE94 start date[b]	13.10	4.03	0.47 ns	0.25	0
KE94 stop date[b]	71.72	20.58	0.12 ns	0.09	0
KE94 increment (cm)	3.35	1.96	4.90	0.11	0.21
KE93 height (cm)	12.88	2.31	6.29	0.24	2.08
KE94 height (cm)	17.83	3.51	9.42	1.57	0.30
Sioux Lookout					
SL94 flush date[b]	28.53	2.47	6.04	2.71	0
SL94 start date[b]	17.75	2.99	0.75	0.52	0.96
SL94 stop date[b]	74.85	17.37	0.21 ns	0	1.12
SL94 increment (cm)	3.73	2.37	3.38	5.58	0
SL93 height (cm)	12.23	2.23	6.45	2.19	0.98
SL94 height (cm)	18.23	3.95	6.82	5.46	0.18
Thunder Bay Forest Nursery					
TB93 height (cm)	12.23	2.42	7.44	-	-
TB94 height (cm)	24.62	6.27	3.87	-	-
Freezing trials					
Frz1 Temp2[d]	4.81[e]	2.33	32.24	-	-
Frz1 Temp3[d]	11.38	7.42	26.53	-	-
Frz2 Temp2[d]	14.92	3.82	36.44	-	-
Frz2 Temp3[d]	17.72	5.29	19.62	-	-
Frz3 Temp2[d]	9.62	1.48	37.88	-	-
Frz3 Temp3[d]	10.74	2.18	35.75	-	-

[a] Based on 102 seed source values.

[b] Number of days starting on 1 May.

[c] Not significant ($a > 0.05$).

[d] Freezing trial dates and temperatures: Frz1 Temp2 was -8°C on 15 September; Frz1 Temp3 was -14°C on 15 September; Frz2 Temp2 was -18°C on 28 September; Frz2 Temp3 was -25°C on 28 September; Frz3 Temp2 was -28°C on 12 October; Frz3 Temp3 was -38°C on 12 October.

[e] Percent damage relative to control samples.

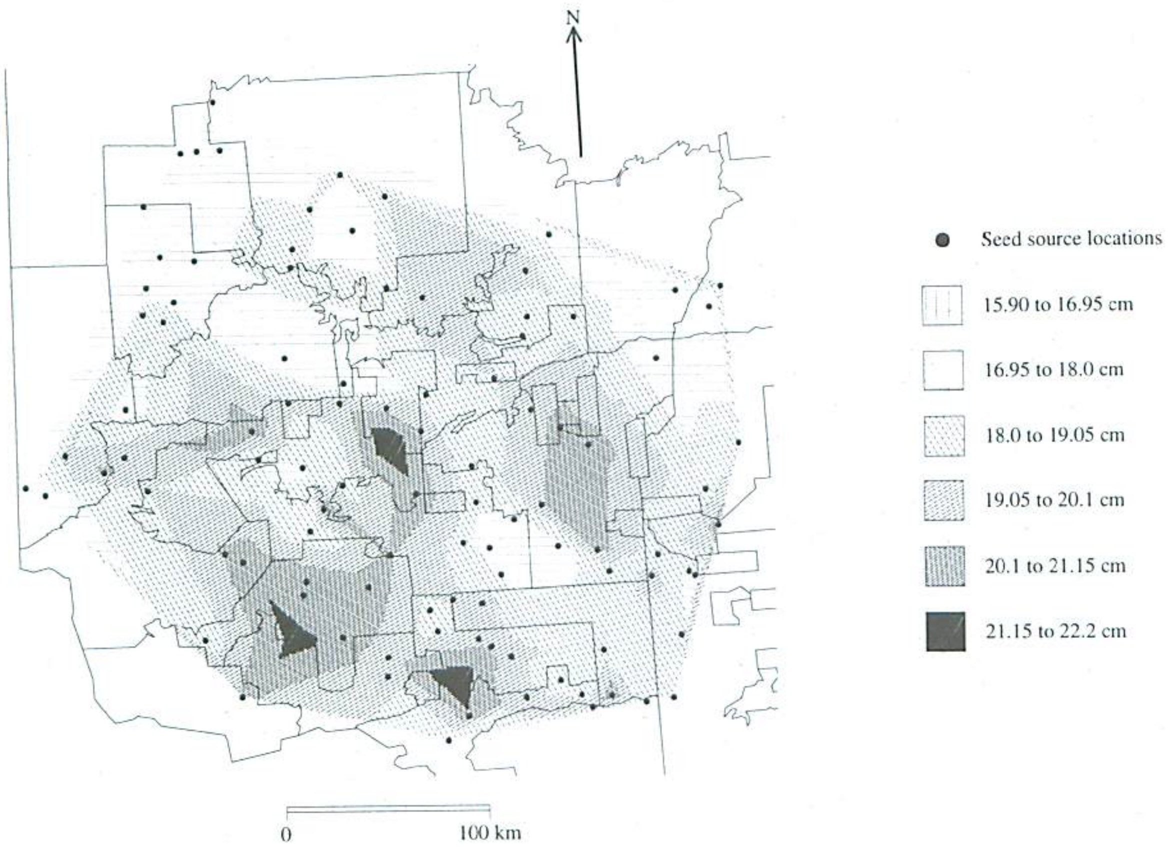

Figure 3. Greenhouse—1994 height.

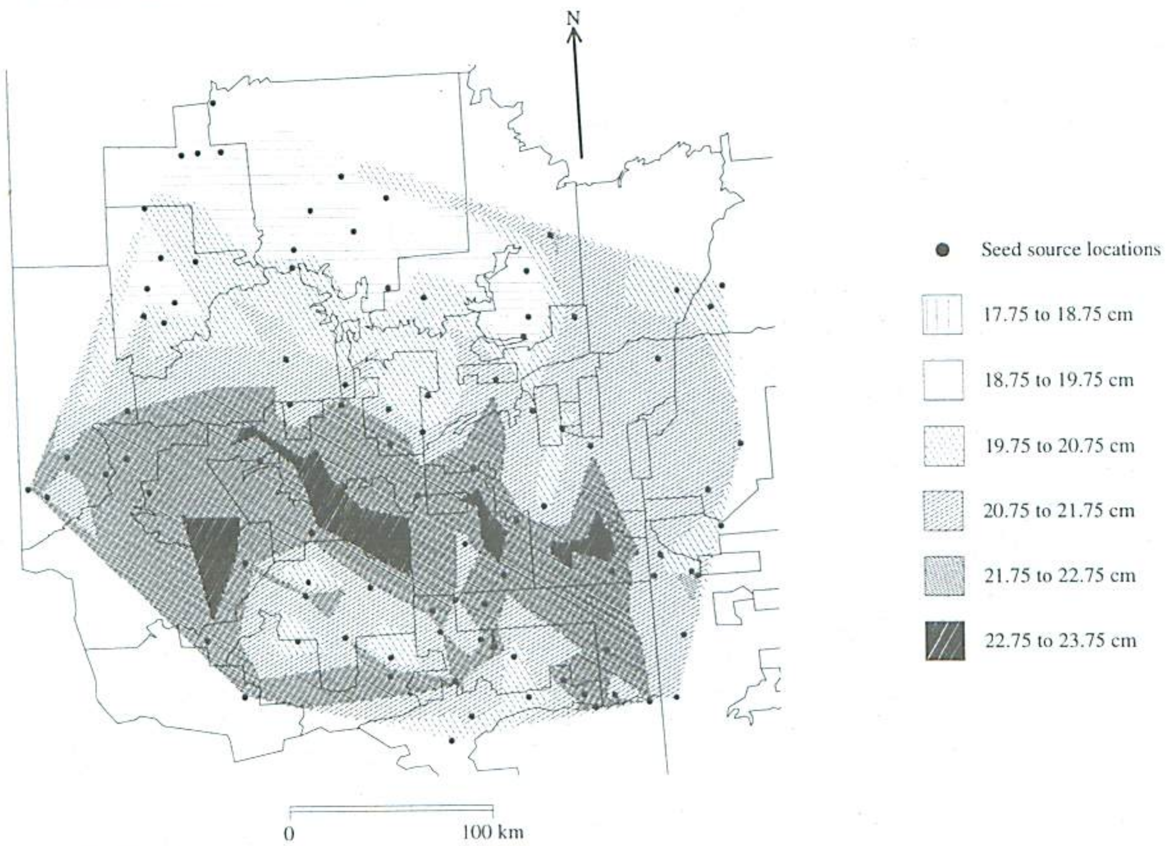

Figure 4. Dryden—1994 height.

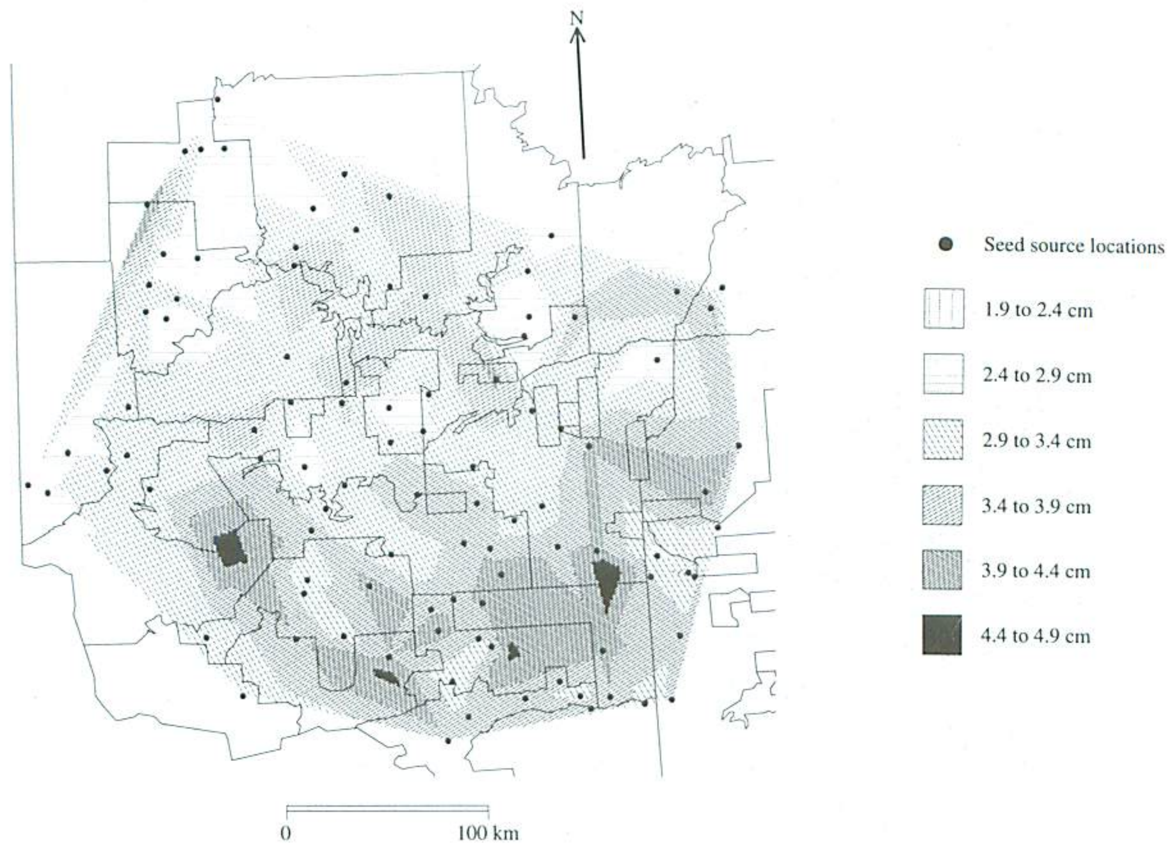

Figure 5. Kenora—1994 increment.

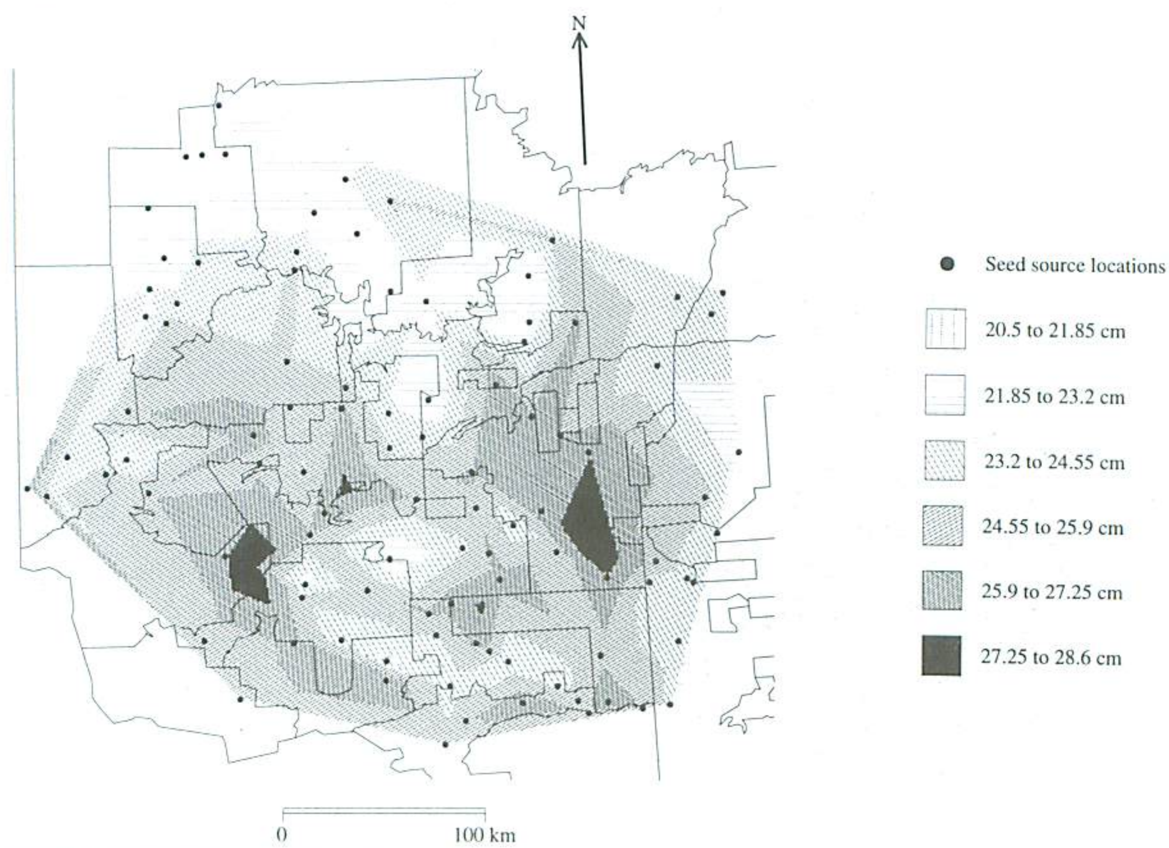

Figure 6. Thunder Bay—1994 height.

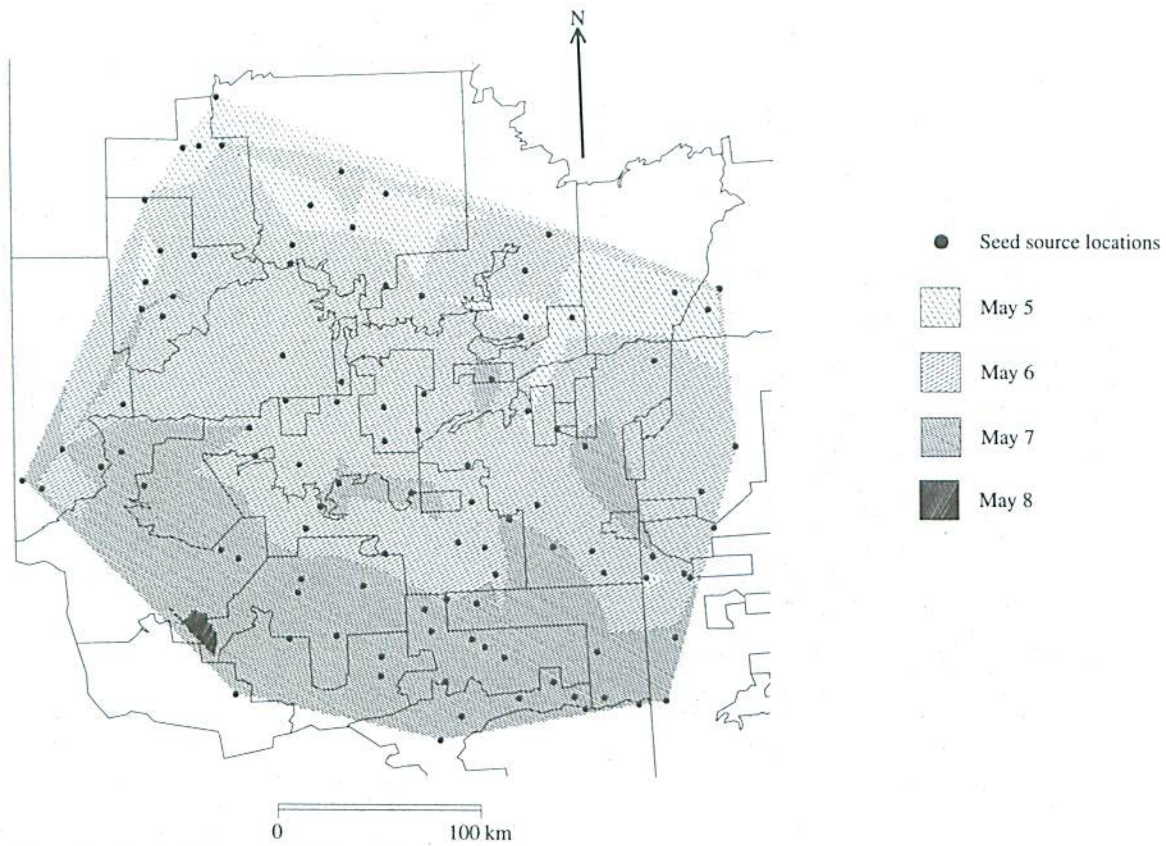

Figure 7. Greenhouse—1994 needle flush date.

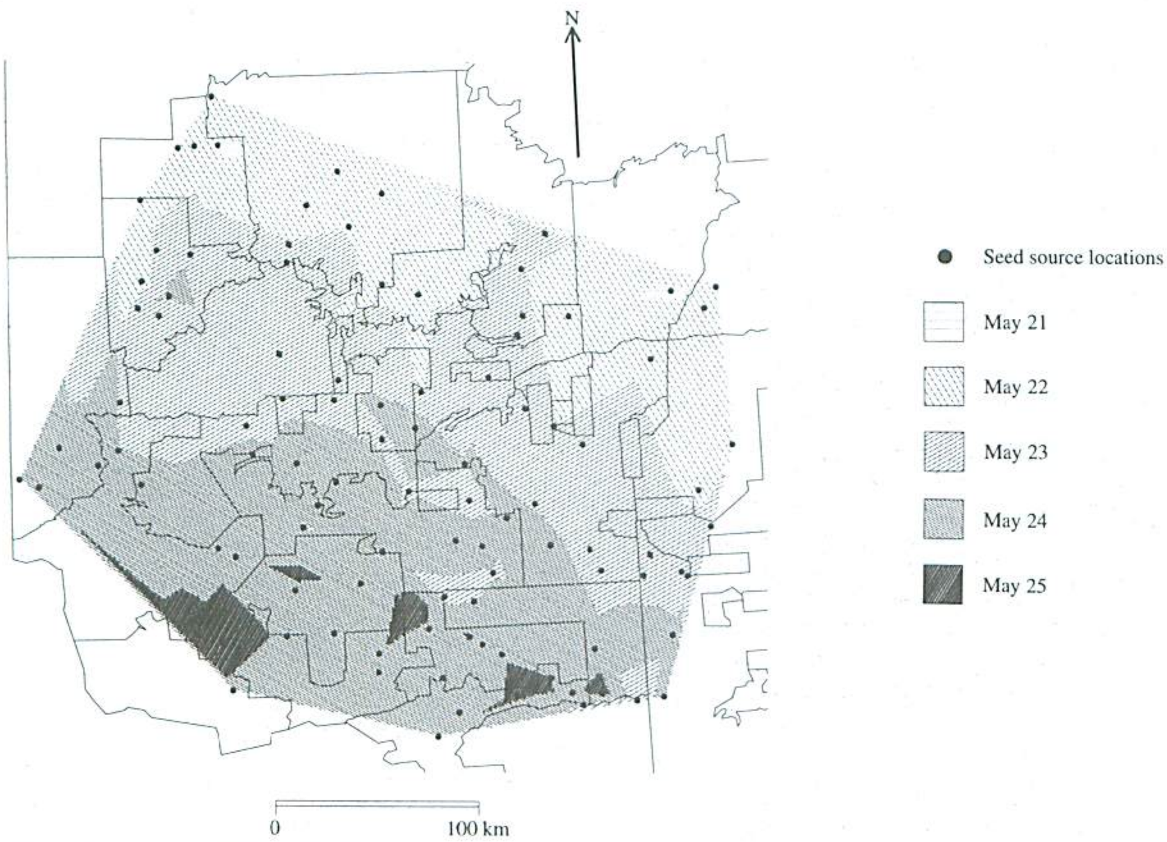

Figure 8. Dryden—1994 needle flush date.

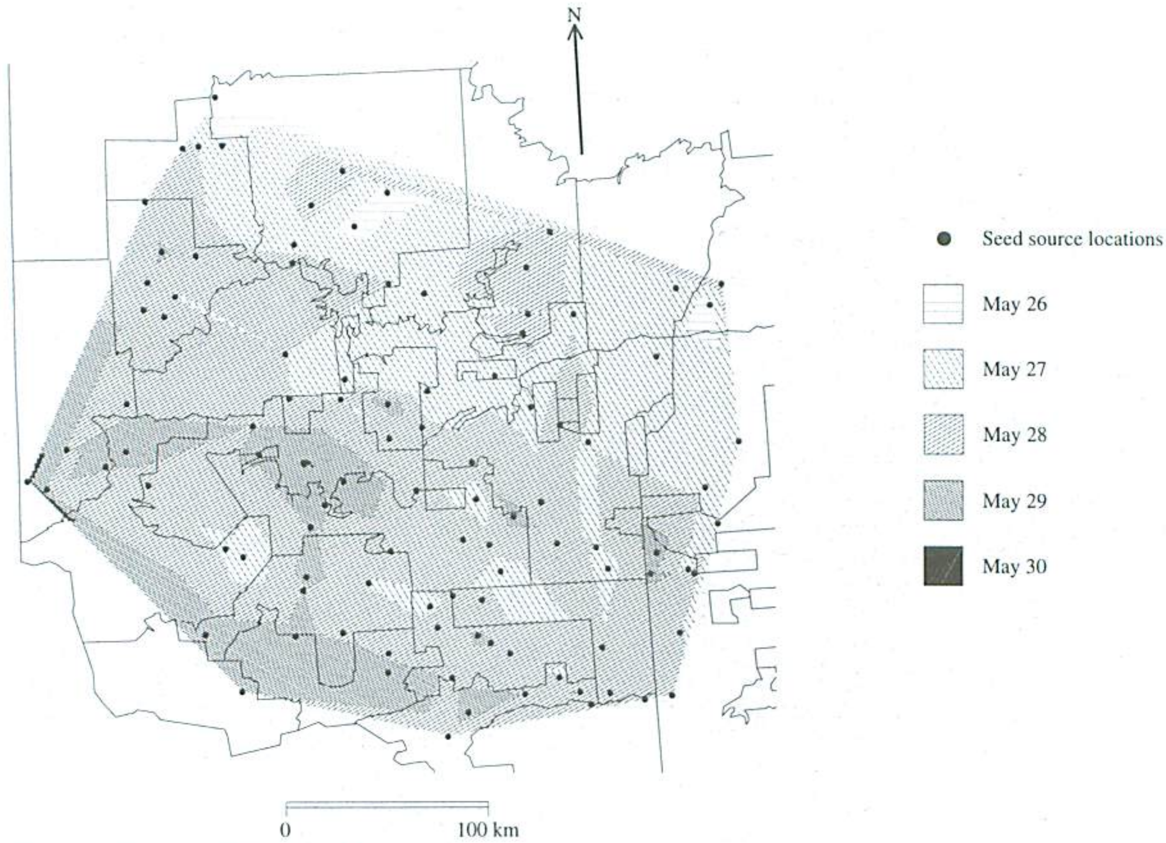

Figure 9. Kenora—1994 needle flush date.

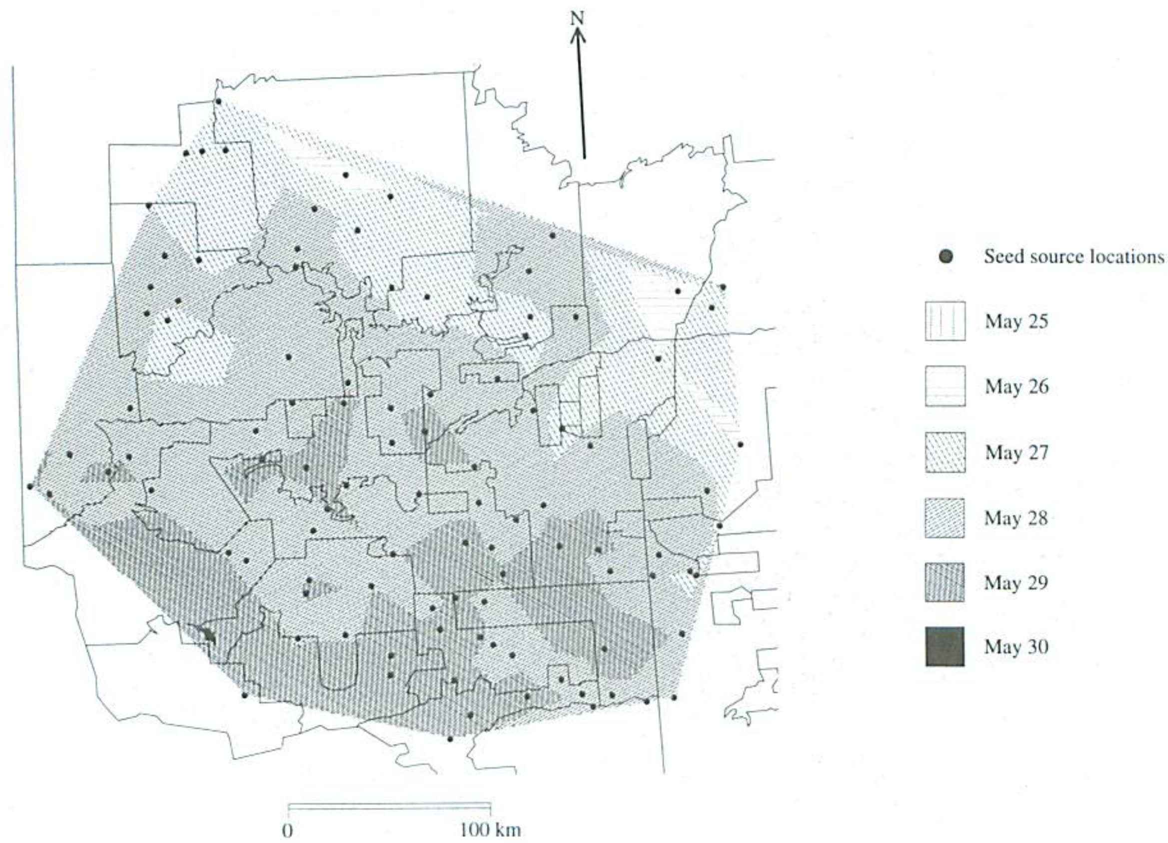

Figure 10. Sioux Lookout—1994 needle flush date.

Table 4. Results of simple linear and backwards stepwise multiple linear regression: Individual test variables against 12 climatic variables.[a]

	Simple regression		Multiple regression	
Biological variable	Climate variable	R^2	Climate variable	R^2
Greenhouse				
GH94 flush date	JANT	0.28	MAXT	0.72
	JULYT	0.56	MEANT	
	MAXT	0.12	FALLF	
	MEANT	0.58		
	SNOW	0.13		
	GROWDD	0.22		
	HEATDD	0.52		
	FALLF	0.08		
	FFD	0.04		
GH94 start date	JANT	0.10	JULYT	0.43
	JULYT	0.40	SNOW	
	MAXT	0.10		
	MEANT	0.36		
	PRECIP	0.08		
	SNOW	0.27		
	GROWDD	0.26		
	HEATDD	0.38		
GH94 stop date	—	0.00	—	0.00
GH94 increment	JANT	0.24	JANT	0.45
	JULYT	0.32	MEANT	
	MAXT	0.12	FALLF	
	MEANT	0.35		
	SNOW	0.07		
	GROWDD	0.13		
	HEATDD	0.32		
	FALLF	0.04		
GH93 height	JANT	0.19	JANT	0.25
	JULYT	0.12	FALLF	
	MEANT	0.14		
	PRECIP	0.07		
	HEATDD	0.08		
GH94 height	JANT	0.25	JANT	0.33
	JULYT	0.18	FALLF	
	MAXT	0.04		
	MEANT	0.22		
	PRECIP	0.05		
	GROWDD	0.06		
	HEATDD	0.18		
Dryden				
DR94 flush date	JANT	0.24	PRECIP	0.71
	JULYT	0.59	HEATDD	
	MAXT	0.10	SPRINGF	
	MEANT	0.59	FALLF	
	SNOW	0.19		
	GROWDD	0.32		
	HEATDD	0.61		
	FALLF	0.05		
DR94 start date	JULYT	0.04	MEANT	0.05
	MEANT	0.05		
	SNOW	0.05		
	GROWDD	0.04		
	HEATDD	0.05		

(cont'd)

Table 4. Results of simple linear and backwards stepwise multiple linear regression: Individual test variables against 12 climatic variables.[a] (cont'd)

	Simple regression		Multiple regression	
Biological variable	Climate variable	R^2	Climate variable	R^2
DR94 stop date	—	0.0	—	0.0
DR94 increment	JULYT	0.14	MEANT	0.34
	MAXT	0.08	HEATDD	
	MEANT	0.11	FALLF	
	PRECIP	0.04		
	HEATDD	0.01		
	SPRINGF	0.08		
	FALLF	0.16		
	FFD	0.12		
DR93 height	JANT	0.08	JANT	0.32
	JULYT	0.12	MAXT	
	MEANT	0.14	MEANT	
	MINT	0.09	PRECIP	
	PRECIP	0.04		
	GROWDD	0.05		
	HEATDD	0.12		
DR94 height	JANT	0.12	JANT	0.46
	JULYT	0.18	MEANT	
	MEANT	0.21	MINT	
	MINT	0.10	PRECIP	
	PRECIP	0.06		
	GROWDD	0.06		
	HEATDD	0.18		
Kenora				
KE94 flush date	JANT	0.04	HEATDD	0.25
	JULYT	0.18		
	MEANT	0.22		
	SNOW	0.15		
	GROWDD	0.20		
	HEATDD	0.25		
KE94 start date	—	0.0	—	0.0
KE94 stop date	—	0.0	—	0.0
KE94 increment	JANT	0.06	MAXT	0.30
	JULYT	0.05	MINT	
	MAXT	0.07	GROWDD	
	MEANT	0.06	HEATDD	
	PRECIP	0.08		
	SPRINGF	0.04		
	FALLF	0.06		
	FFD	0.05		
KE93 height	MEANT	0.04	MINT	0.13
	HEATDD	0.05	FALLF	
KE94 height	JANT	0.06	MEANT	0.14
	JULYT	0.07	PRECIP	
	MEANT	0.08		
	MINT	0.06		
	HEATDD	0.06		
Sioux Lookout				
SL94 flush date	JANT	0.17	JANT	0.52
	JULYT	0.41	PRECIP	
	MAXT	0.06	HEATDD	
	MEANT	0.38		

(cont'd)

Table 4. Results of simple linear and backwards stepwise multiple linear regression: Individual test variables against 12 climatic variables.[a] (concl.)

Biological variable	Simple regression: Climate variable	R^2	Multiple regression: Climate variable	R^2
SL94 flush date (concl.)	SNOW	0.13		
	GROWDD	0.26		
	HEATDD	0.42		
SL94 start date	PRECIP	0.05	PRECIP	0.05
SL94 stop date	—	0.0	—	0.0
SL94 increment	PRECIP	0.06	MINT	0.21
	SPRINGF	0.09	FALLF	
	FALLF	0.12		
	FFD	0.11		
SL93 height	JANT	0.04	MINT	0.26
	MEANT	0.04	PRECIP	
	MINT	0.12	GROWDD	
	PRECIP	0.07	FALLF	
SL94 height	JANT	0.07	JANT	0.24
	JULYT	0.05	MINT	
	MEANT	0.08	FALLF	
	MINT	0.08		
	PRECIP	0.07		
	HEATDD	0.06		
Thunder Bay Forest Nursery				
TB93 height	MAXT	0.04	MINT	0.16
	MINT	0.08	FALLF	
TB94 height	JANT	0.10	MINT	0.37
	JULYT	0.14	PRECIP	
	MEANT	0.14	HEATDD	
	MINT	0.05	FALLF	
	PRECIP	0.06		
	HEATDD	0.12		
	FALLF	0.07		
Freezing Trials				
Frz1 Temp2	—	0.0	—	0.0
Frz1 Temp3	—	0.0	—	0.0
Frz2 Temp2	—	0.0	—	0.0
Frz2 Temp3	—	0.0	—	0.0
Frz3 Temp2	JANT	0.06	JULYT	0.12
	JULYT	0.12		
	MAXT	0.05		
	MEANT	0.10		
	SNOW	0.04		
	GROWDD	0.06		
	HEATDD	0.12		
Frz3 Temp3	JULYT	0.10	JULYT	0.14
	MAXT	0.04	SPRINGF	
	MEANT	0.05		
	SNOW	0.05		
	HEATDD	0.07		
	SPRINGF	0.05		
	FALLF	0.07		
	FFD	0.06		

[a] MEANT = mean annual temperature, JULYT = mean maximum daily temperature in July, JANT = mean minimum daily temperature in January, MINT = all-time extreme minimum temperature, MAXT = all-time extreme maximum temperature, GROWDD = growing degree-days, HEATDD = heating degree-days, SPRINGF=date of last spring frost, FALLF = date of first fall frost, FFD = number of frost free days per year, PRECIP = mean total annual precipitation, and SNOW=mean annual snowfall.

expressed the remainder. This result indicates that the individual test variables are highly intercorrelated.

All variable loadings were positive on the first PCA axis. These ranged from values of 0.34 for freezing variables to 0.83 for growth variables. Loadings for phenological variables were intermediate (Table 5). The high loading values for the height growth variables, in conjunction with the uniformly positive signs for all the loadings, indicate that the first axis is generally a descriptor of growth potential (i.e., seed sources with the greatest potential for growth generally had the highest growth at each of the test sites). Since the loadings for the six phenological variables were also positive, it is evident that the sources having the greatest growth potential flushed later and started and stopped elongation later. Similarly, the positive loadings for the freezing variables on the first axis indicate that the seed sources with the greatest growth potential suffered the highest frost damage in the last freezing trial on 12 October, since they hardened off later in the fall.

All but one of the test variables make substantial contributions to the second PCA axis, but the loadings have mixed signs. The loadings for greenhouse, flushing, and freezing variables were positive, while height growth variables at the field trials were negative (Table 5). While the biological significance of this axis is less obvious than the first, it apparently reflects relative winter hardiness of the seed sources, or at least that portion of hardiness independent of growth potential. The opposite polarity of the variable loadings implies that less frost hardy sources with a higher growth potential generally showed reductions in height growth at the field trials but not the greenhouse trial. The negative loadings for start of growth at the Kenora and Sioux Lookout tests indicates that elongation was delayed for the less hardy seed sources, but needle flushing was not.

Table 5. Results of principal components analysis of 21 growth, phenological, and freezing variables for 102 jack pine seed sources.

PRINCIPAL COMPONENTS		
PCA axis	1	2
Eigenvalues	7.93	2.87
Percent variation	37.75	13.65
Cumulative variation	37.75	51.40
VARIABLE LOADINGS		
Greenhouse		
GH94 needle flush date	0.76	0.42
GH94 elongation start date	0.52	0.40
GH94 increment of leader growth	0.58	0.50
GH93 height	0.47	0.36
GH94 height	0.56	0.48
Dryden		
DR94 needle flush date	0.70	0.44
DR94 elongation start date	0.50	0.02
DR93 height	0.74	-0.25
DR94 height	0.83	-0.21
Kenora		
KE94 needle flush date	0.39	0.45
KE94 elongation start date	0.48	-0.27
KE93 height	0.70	-0.39
KE94 height	0.75	-0.42
Sioux Lookout		
SL94 needle flush date	0.64	0.35
SL94 elongation start date	0.45	-0.31
SL93 height	0.69	-0.46
SL94 height	0.70	-0.47
Thunder Bay Forest Nursery		
TB93 height	0.60	-0.31
TB94 height	0.79	-0.19
Freezing trials		
Frz3 Temp2 (-28°C on 12 October)	0.34	0.38
Frz3 Temp3 (-38°C on 12 October)	0.35	0.30

Correlations were calculated among the first two PCA axes and the full set of 29 climatic variables (Table 6). Remarkably, all but three correlations against the first PCA axis (last spring frost, July precipitation, and August precipitation) were significant. This result demonstrates the high level of intercorrelation of the climatic variables and the large component of adaptive variation expressed by the first PCA axis. Similarly, all but three growing season variables and four precipitation variables were significantly correlated with the second PCA axis. The strongest correlations generally occurred between monthly average maximum temperatures and either PCA axis, although very strong correlations were also observed for spring precipitation (April and May) with the first PCA axis.

Figures 11 and 12 are GIS-generated contour maps that graphically summarize the geographic pattern of variation expressed among the 102 seed sources, based upon principal component axis scores for the first two PCA axes; contour intervals for each are one standard deviation. Generally, the higher positive scores on the first axis, indicating higher growth potential, occur in the

Table 6. Correlation of PCA Axes 1 and 2 scores with 29 climatic variables.

PCA AXIS	1		2	
Climate variable	R	Probability	R	Probability
Mean temperatures				
Annual	0.63	0.00	0.46	0.00
April	0.60	0.00	0.44	0.00
May	0.50	0.00	0.44	0.00
June	0.38	0.00	0.38	0.00
July	0.23	0.02	0.28	0.00
August	0.27	0.01	0.35	0.00
September	0.45	0.00	0.47	0.00
Mean maximum temperatures				
April	0.59	0.00	0.50	0.00
May	0.66	0.00	0.52	0.00
June	0.60	0.00	0.50	0.00
July	0.63	0.00	0.51	0.00
August	0.58	0.00	0.51	0.00
September	0.60	0.00	0.50	0.00
Mean minimum temperature				
January	0.48	0.00	0.30	0.00
Extreme temperatures				
Minimum	0.24	0.02	-0.26	0.01
Maximum	0.21	0.04	0.35	0.00
Temperature sums				
Growing degree-days	0.36	0.00	0.43	0.00
Heating degree-days	-0.60	0.00	-0.50	0.00
Growing season				
Last spring frost	0.09	ns	-0.05	ns
First fall frost	-0.29	0.00	-0.04	ns
Frost free days	-0.19	0.05	0.01	ns
Mean precipitation				
Total annual	0.22	0.03	-0.21	0.03
Annual snow	-0.26	0.01	-0.34	0.00
April	0.57	0.00	0.26	0.01
May	0.51	0.00	-0.04	ns
June	0.37	0.00	-0.07	ns
July	-0.00	ns	-0.15	ns
August	0.07	ns	-0.34	0.00
September	0.21	0.04	-0.16	ns

southwestern portion of the sampled area. The more negative scores indicating reduced growth potential occur in the northeastern portion (Fig. 11). The similarity to the maps based on flushing dates (Figs. 7–10) is high. Within this generalized cline of variation there are a few scattered local irregularities, although these may reflect scores of individual seed sources deviating by chance from the true population mean values.

The pattern of variation of the second axis PCA scores is similar at the southwestern and northeastern extremes (i.e., the higher positive scores indicating reduced hardiness occur in the southwestern portion of the sampled

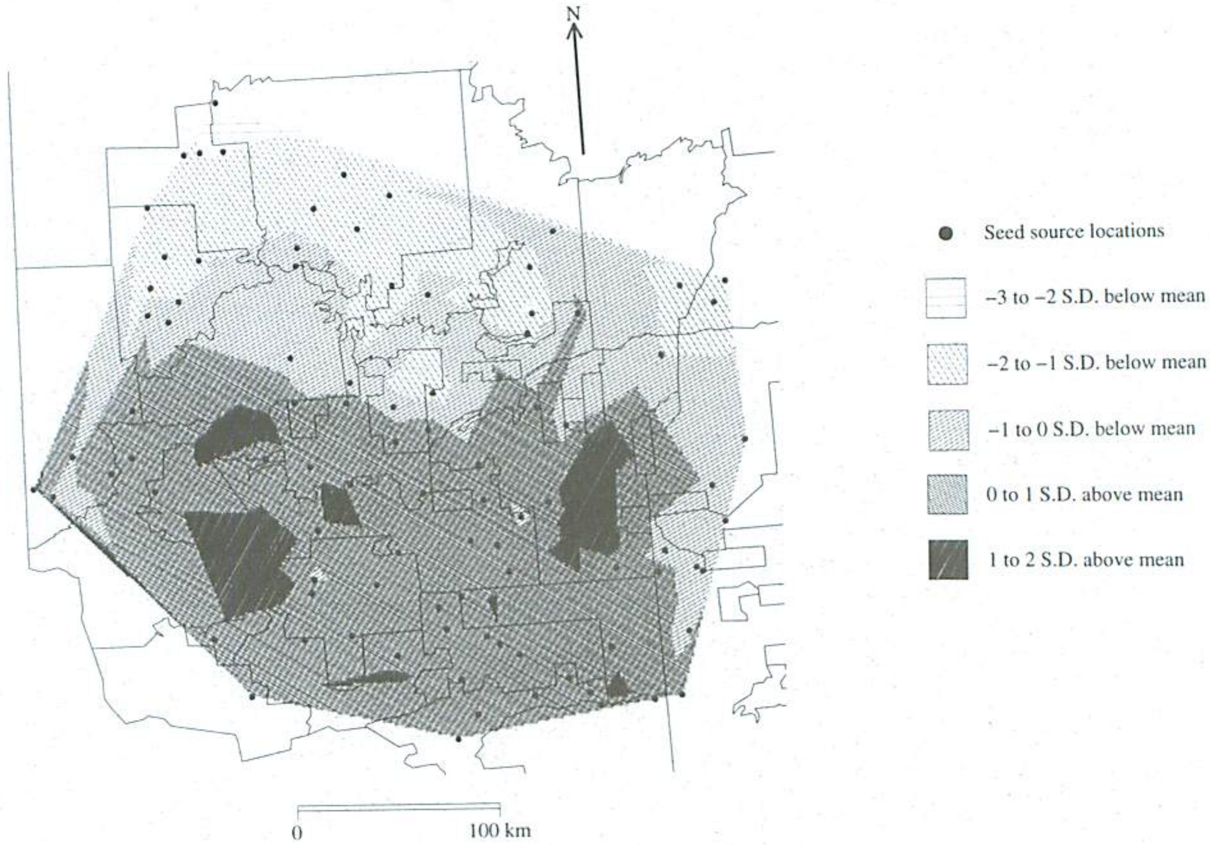

Figure 11. Principal Components—Axis 1.

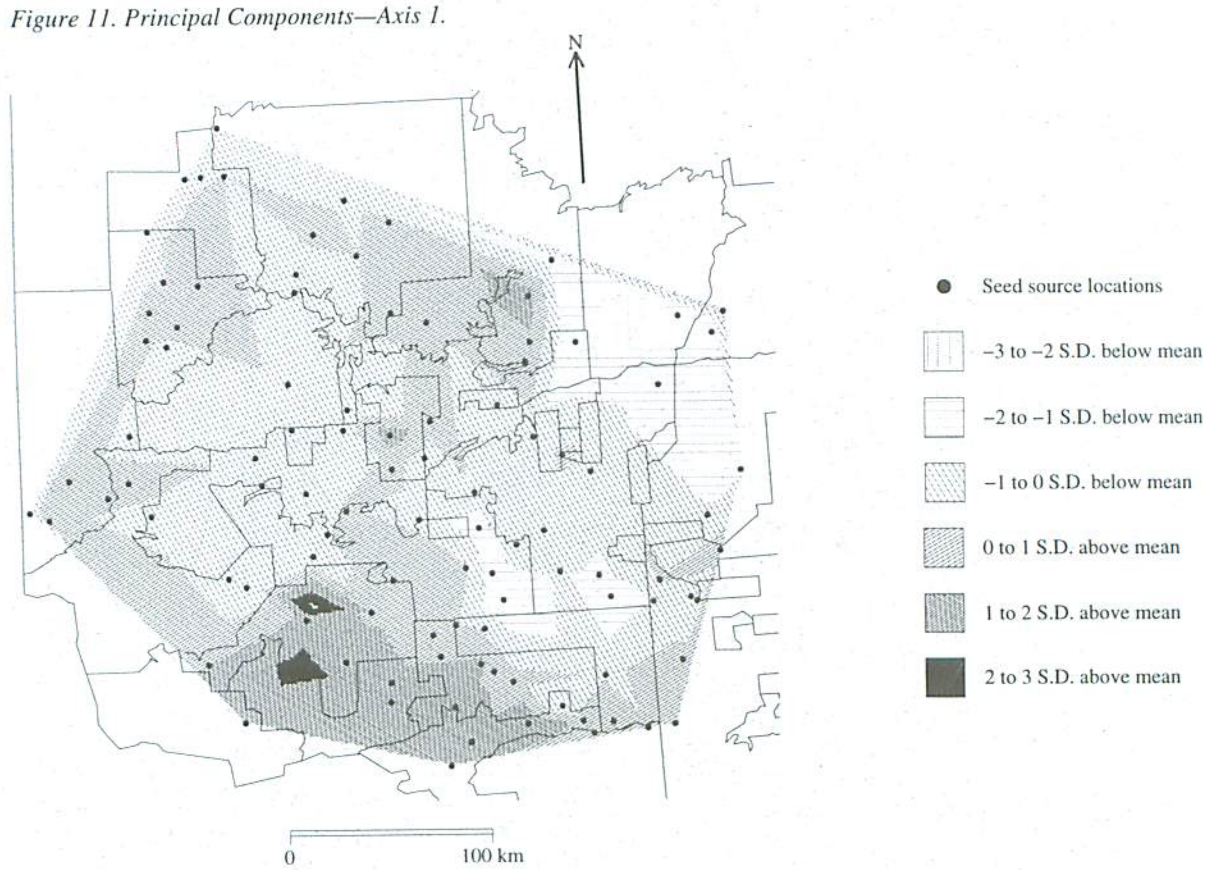

Figure 12. Principal Components—Axis 2.

area)(Fig. 12). However, in the middle of the collection area there is a more longitudinal pattern, with zones of greater and lesser hardiness alternating across the region.

Due to the high level of intercorrelation among the 29 climatic variables, many combinations of these produced good predictive regression equations for the first two PCA axes. Two were chosen for presentation due to their high predictive ability coupled with relatively small numbers of independent variables retained in the equations (Table 7). Regression of the first PCA axis against mean May daily maximum temperature, May precipitation, and extreme minimum temperature had an r^2 value of 0.68; thus, sources with high May temperatures coupled with greater amounts of May precipitation and warmer winters had higher scores on the first PCA axis. Generally, this corresponded to a higher growth potential.

The regression of the second PCA axis against extreme minimum temperature, the number of frost free days, and the daily maximum temperature for May had an r^2 value of 0.40 (Table 7). In this case seed sources with more frost free days and higher May temperatures had higher scores on the second axis. Generally, this signified greater hardiness. As was true for the regression against the first PCA axis, the variable extreme minimum temperature also remained in the equation. However, its sign was negative, which is the opposite of what would intuitively be expected.

Contour maps of the four climatic variables retained in the two regression equations are presented to compare against the individual and PCA summary variables (Figs. 13–16). The contour map for daily May maximum temperature reveals a great similarity to the maps showing dates of needle flush (Figs. 7–10) as well as the first PCA axis (Fig. 11). An obvious southwest to northeast cline exists across the collection area, ranging from 18°C in the south to 14°C in the north.

The contour map for extreme minimum temperature indicates that the lowest temperatures (ranging to -50°C) are recorded both in the northern and southern extremes (Fig. 14). This observation explains why this variable took the unexpected polarity in the regression against the second PCA axis. In the central portion of the range the minimum values are generally higher, ranging to -41°C, but follow a longitudinal, intermittent pattern of warmer and cooler temperatures. This alternating longitudinal pattern in the midportion of the range shows similarity to the pattern for the second PCA axis over the same area.

The contour map showing the pattern of May precipitation (Fig. 15) reveals a pronounced clinal effect from relatively low precipitation levels in the northwest (5 cm) to larger amounts in the southeast (7–8 cm). The contour map for frost free days is more irregular (Fig. 16). The lowest values, of only 70 days, are seen in the southeast; the highest values, ranging to 130 days, occur in the west. Again, the general clinal trend is longitudinal, and shows alternating patches of increasing and decreasing numbers of frost free days from east to west.

Figures 17 and 18 are GIS-generated contour maps that graphically summarize the geographic pattern of variation expressed among the 75 seed sources, based upon the axis scores predicted by the two multiple linear regressions in Table 7. Again, contour intervals for each are one standard deviation. In each case the overall correspondence to the contour maps based on the actual PCA scores (Figs. 11 and 12) is very close. The differences correspond mainly to the smoothing of the clinal pattern of genetic variation by elimination of the local seed source irregularities evident in Figures 11 and 12.

Table 7. Results of regression of PCA for Axes 1 and 2 against climatic variables for 102 jack pine seed sources.

Dependent variable	Independent variables	Coefficient	Tolerance	t*	P**
PCA Axis 1	Constant	-7.53			
$r^2 = 0.68$	Extreme minimum temperature	0.18	0.99	5.40	0.00
	May mean daily maximum temperature	0.74	0.95	10.10	0.00
	Mean May precipitation	0.06	0.95	6.96	0.00
PCA Axis 2	Constant	-24.02			
$r^2 = 0.40$	Extreme minimum temperature	-0.23	0.69	-4.34	0.00
	Frost free days	0.02	0.67	3.52	0.00
	May mean daily maximum temperature	0.69	0.96	6.96	0.00

*t = student's t statistic.
**P = Probability.

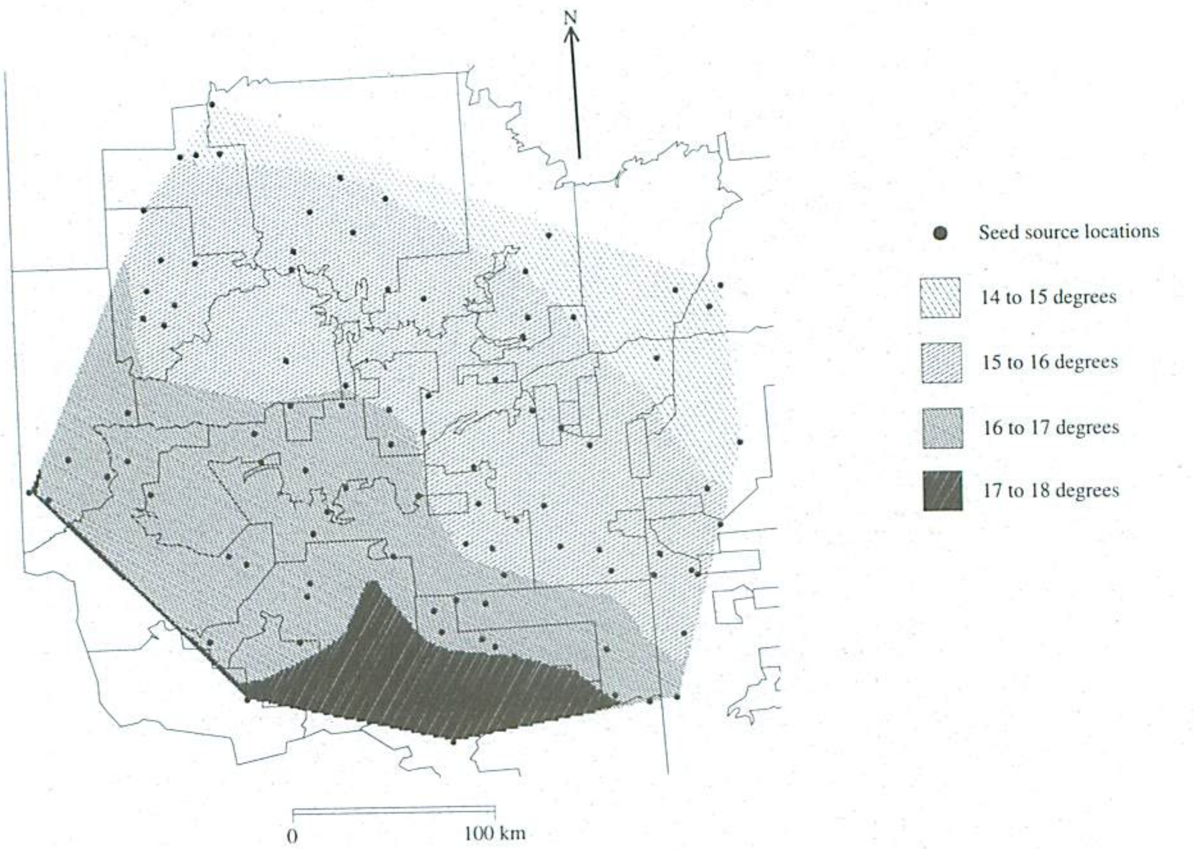

Figure 13. Mean May daily maximum temperature.

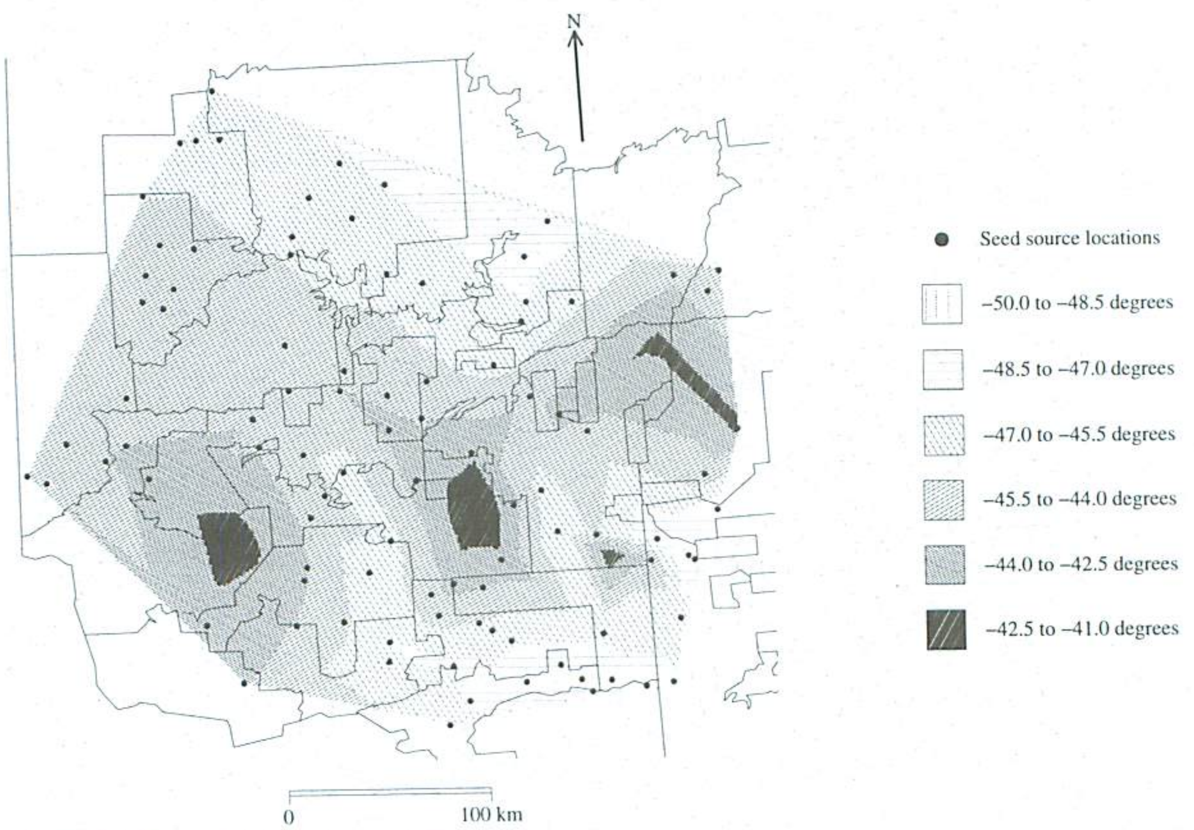

Figure 14. Extreme minimum temperature.

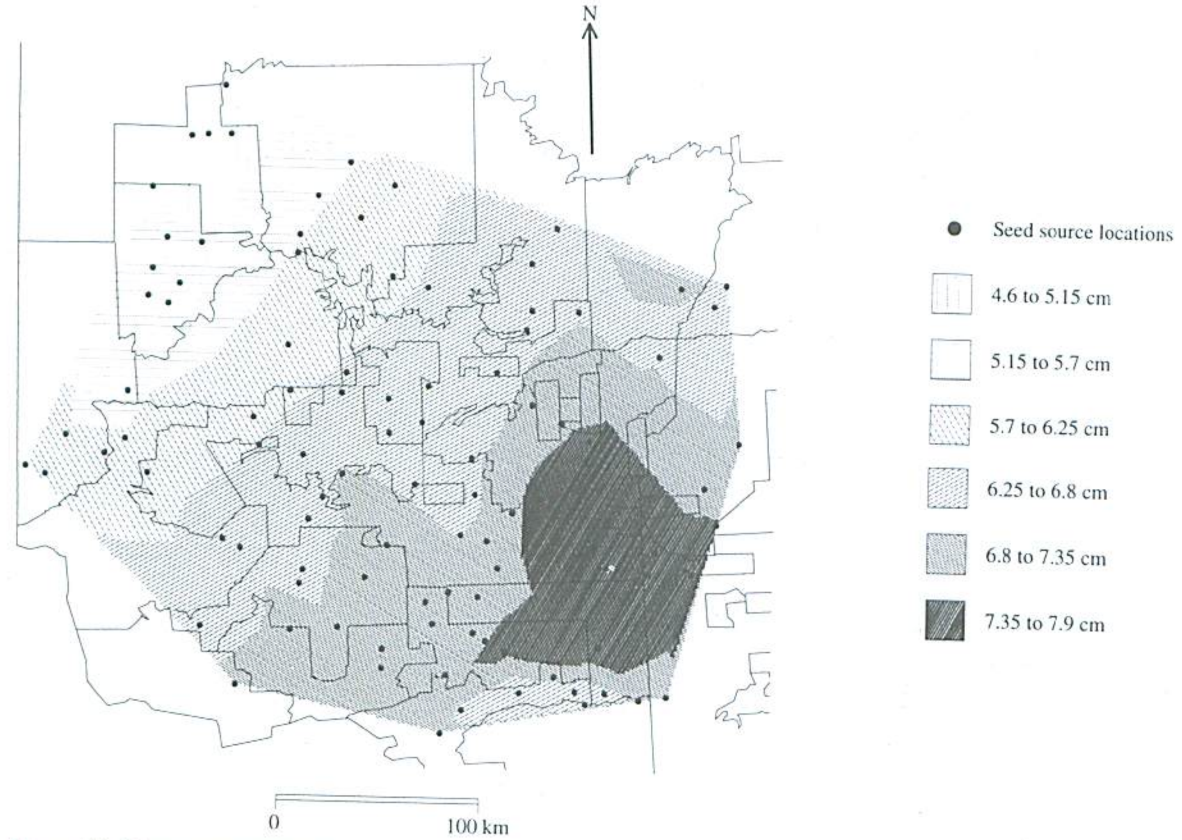

Figure 15. Mean May precipitation.

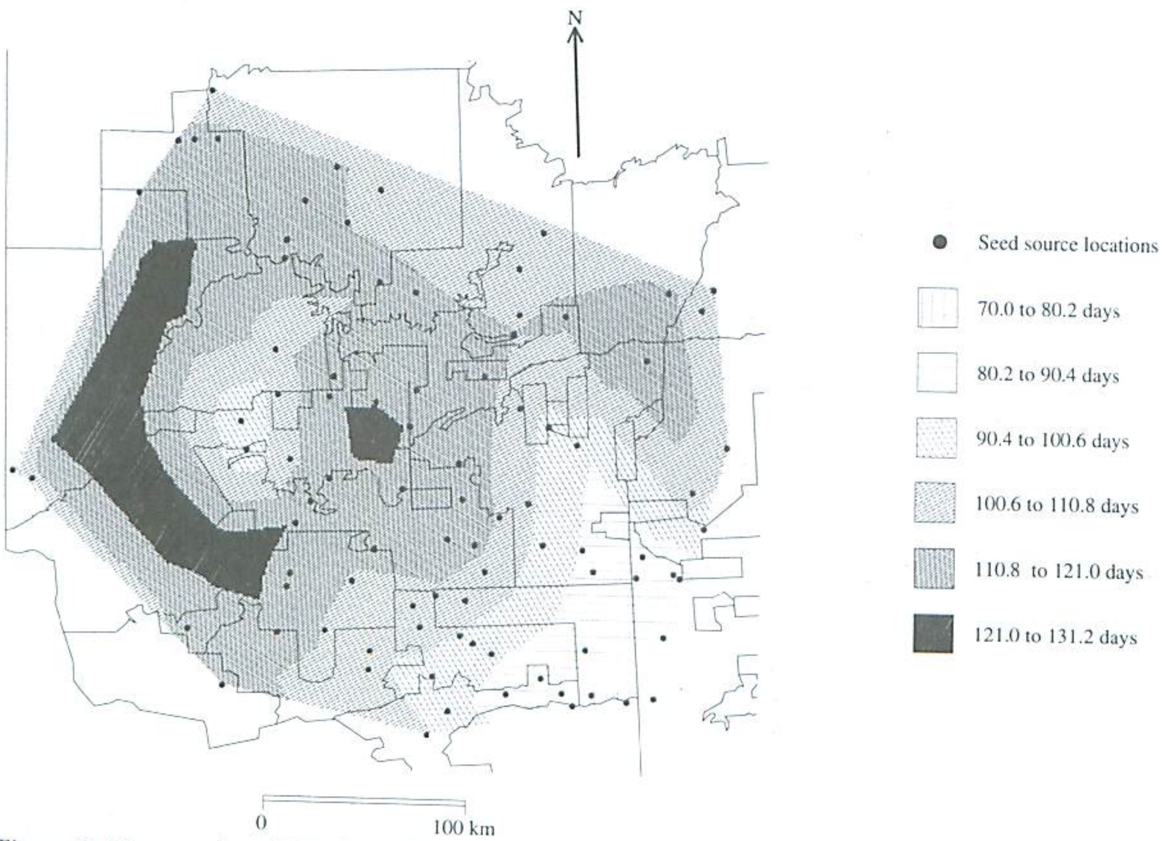

Figure 16. Mean number of frost free days.

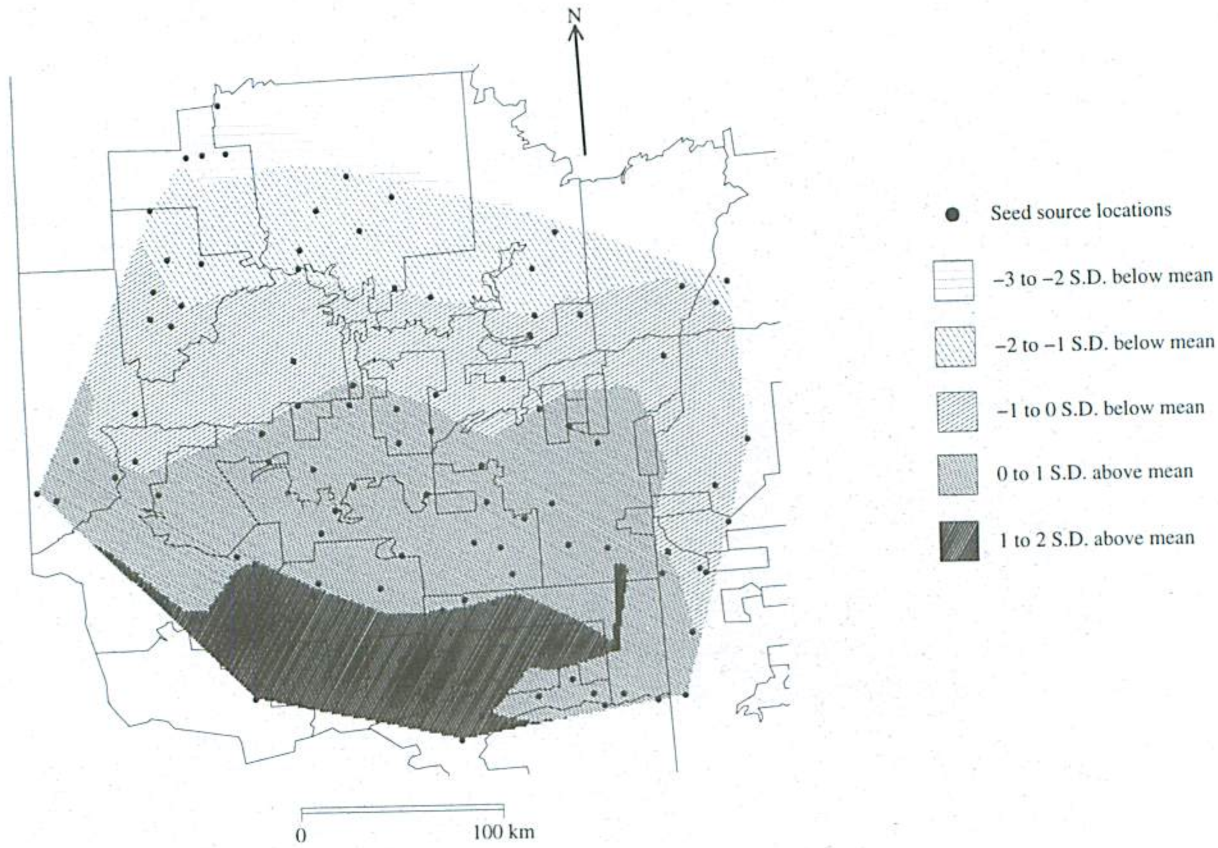

Figure 17. Regression model of PCA Axis 1.

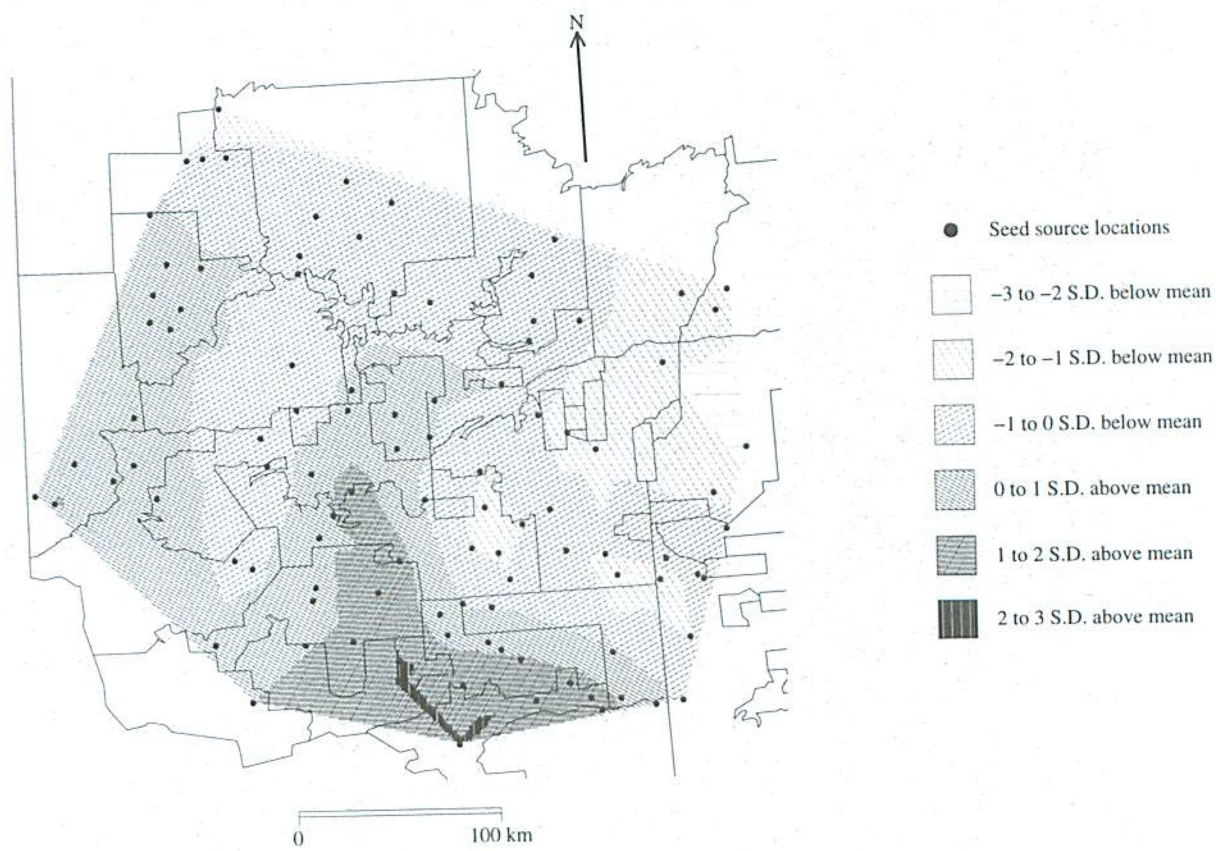

Figure 18. Regression model of PCA Axis 2.

Focal Point Seed Zones

The products of the r^2 values obtained from regressions (Table 7) and the percents of variation accounted for by the PCA axes (Table 5) provide an approximate percentage of the total amount of the variation expressed among seed sources that could be accounted for by the climatic variables. These products for the first and second PCA axes are 25.7 and 5.5 percent, respectively. Thus, a total of 31 percent of the variation was used to generate focal point seed zones. A much greater magnitude of adaptive variation is expressed by the first axis compared to the second. This suggests that perhaps this component should be weighted more highly than the second in making seed transfer decisions. However, both components were considered equally for the calculation of focal point seed zones because the two components are independent of each other due to the nature of PCA, and either may act like the weakest link in a chain.

To determine the focal point seed zones for this project a program was written in ARC/INFO AML language (Environmental Services Research Institute Inc. 1992). To run, the program requires the input of geographic coordinates of the focal point(s) in the form of an ASCII text file (one point per line, decimal degrees, and longitude first separated from latitude by a space), and outputs a focal point seed zone map(s) in the form of a Postscript file. For the program to run successfully, several ARC/INFO coverages (i.e., the database derived from this project) must be available.

Although the entire systematic grid of 184 focal point seed zones are included in Parker (1995), eight of these zones are presented here, as they are generally representative for the seed source collection area (Figs. 19–26). In each case the hatched areas represent levels of adaptive similarity to the focal point, as indicated simultaneously by the first and second regression-based PCA axes; the denser the hatching, the greater the similarity. The Ontario provincial borders with Manitoba and Minnesota limit the extent of the zone maps in the west and south; the border line in the figures represents the limit of their extent for the rest of the study area. Figure 19 illustrates a zone based on a focal point from the south central part of the range (48° 36' N, 92° 20' W). As is true for all but the most northerly zones, represented by Figures 25 and 26, this figure generally represents a band of adaptive similarity ranging from the northwest to the southeast. Simultaneously, it winds in a serpent-like fashion north and south. The major trend is determined by the first PCA axis; the secondary sinuoid pattern is the result of the second PCA axis.

Figures 20 and 21 show similar sinuoid patterns somewhat to the north of the first focal point seed zone. Figures 22 and 23 show a more northerly zone of similarity, but one which also has the characteristic twisting shape. It is clear for each of these two pairs of example zones that the focal points do not have to be geographically close to produce similar zones. Figure 24 is based on a focal point from the east central portion of the study area (49° 36' N, 90° 20'W). In this case the zone of similarity tends to be more restricted to the eastern portion of the map, although the snake-like pattern from northwest to southeast is still discernible.

Figures 25 and 26, the most northerly focal point seed zones, generally show latitudinal bands of similarity with a fairly sharp transition between them. The northernmost zone is very restricted compared to the others, although this in effect is partly artificial because it occupies the end of the cline. If the limits of the map went further north, the zone would probably also extend further to the north.

Breeding Zone Recommendation

Figure 27 is presented to summarize the adaptive variation in jack pine seed sources evident from the focal point seed zone determinations. The area of primary interest is Zone 1 of the Ontario Tree Improvement Board (OTIB), or the area of the Lake of the Woods–English River Seed Management Association. Since a number of seed collections for this project were made to the east of this zone, a portion of OTIB Zone 2 is also included within the map limits. The **sawtooth** line in the map represents the boundary between these two zones. Unlike all of the preceding maps, which were produced by a computer using GIS software, this map was prepared manually after examining all focal point seed zones produced following the systematic grid. The boundaries are intended to represent areas of fairly abrupt transition in terms of the expressed patterns of adaptive similarity. The map indicates two northern zones represented as east–west bands, a central sinuoid band running from the west central portion of the range to the southeast, an eastern zone that penetrates sharply toward the center of the study area, and a fifth southern zone that undulates north and south until it ceases near the southeast corner. These zones are not intended to represent, nor should they be interpreted as, static seed zones. The development of focal point seed zones makes static seed zones obsolete. Thus, the volume of 184 focal point seed zones (Parker 1995) should be consulted to make jack pine seed transfers within OTIB Zone 1. Instead, the boundaries separating the five zones in Figure 27 indicate where the clines of adaptive variation are the steepest. They are presented here to serve as a guide for the refinement of breeding zones for jack pine tree improvement programs in OTIB Zone 1.

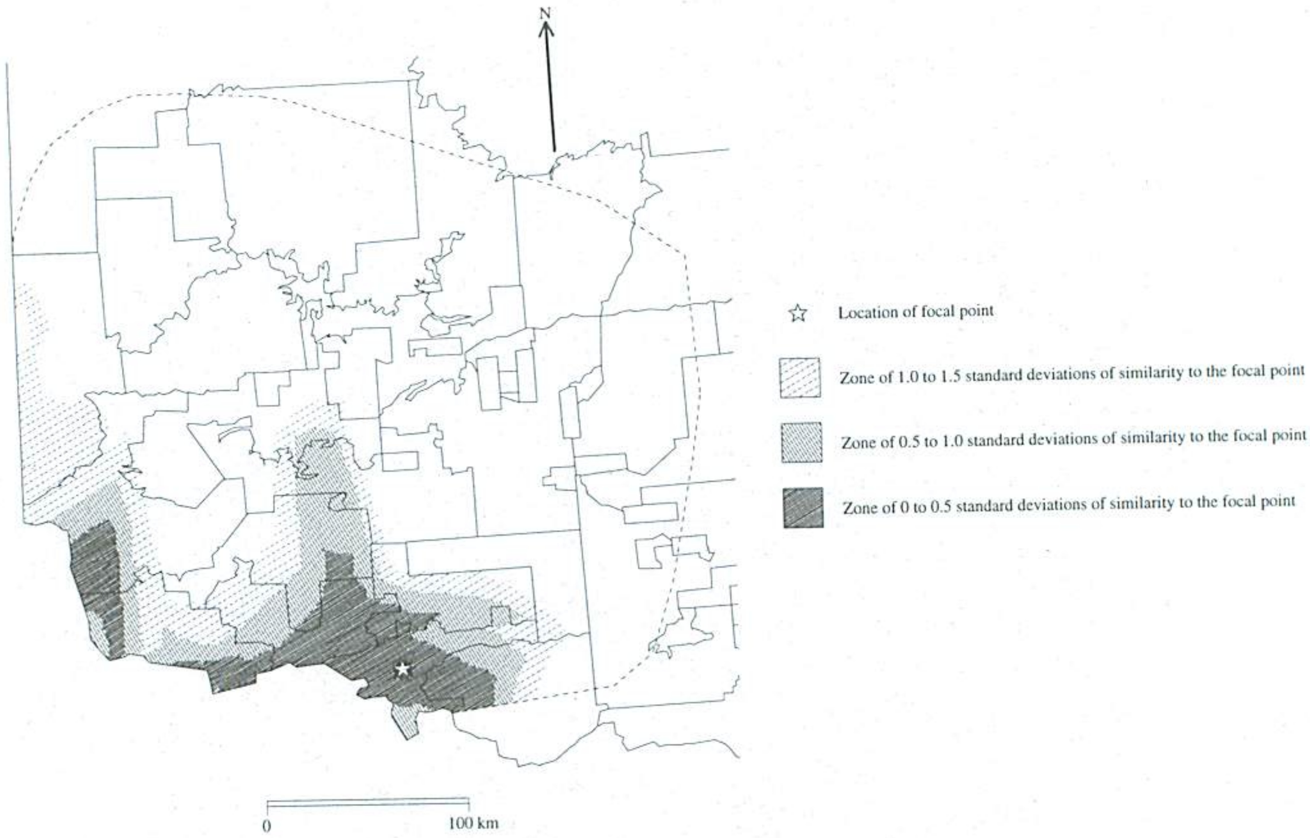

Figure 19. Jack pine focal point seed zone—48.60 N 92.33 W.

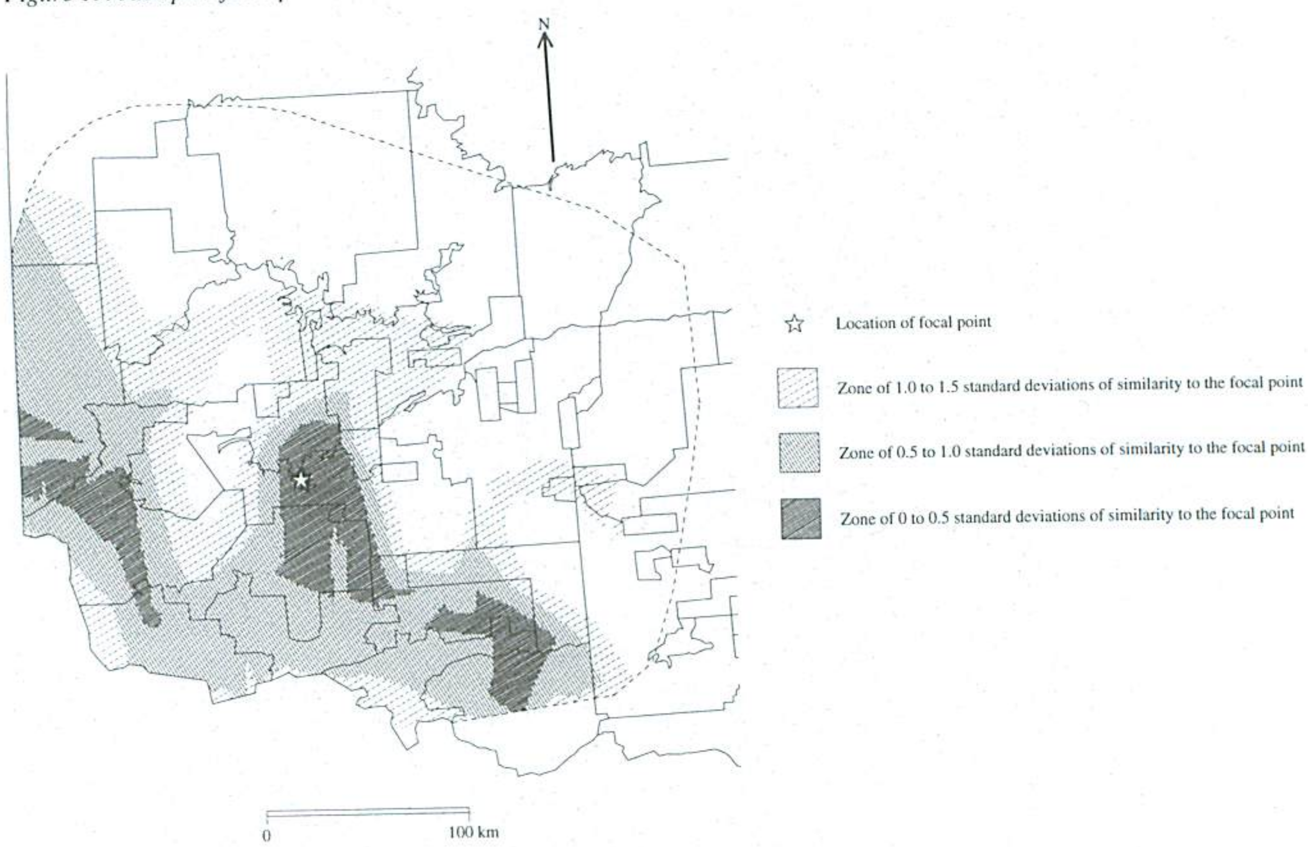

Figure 20. Jack pine focal point seed zone—49.60 N 93.00 W.

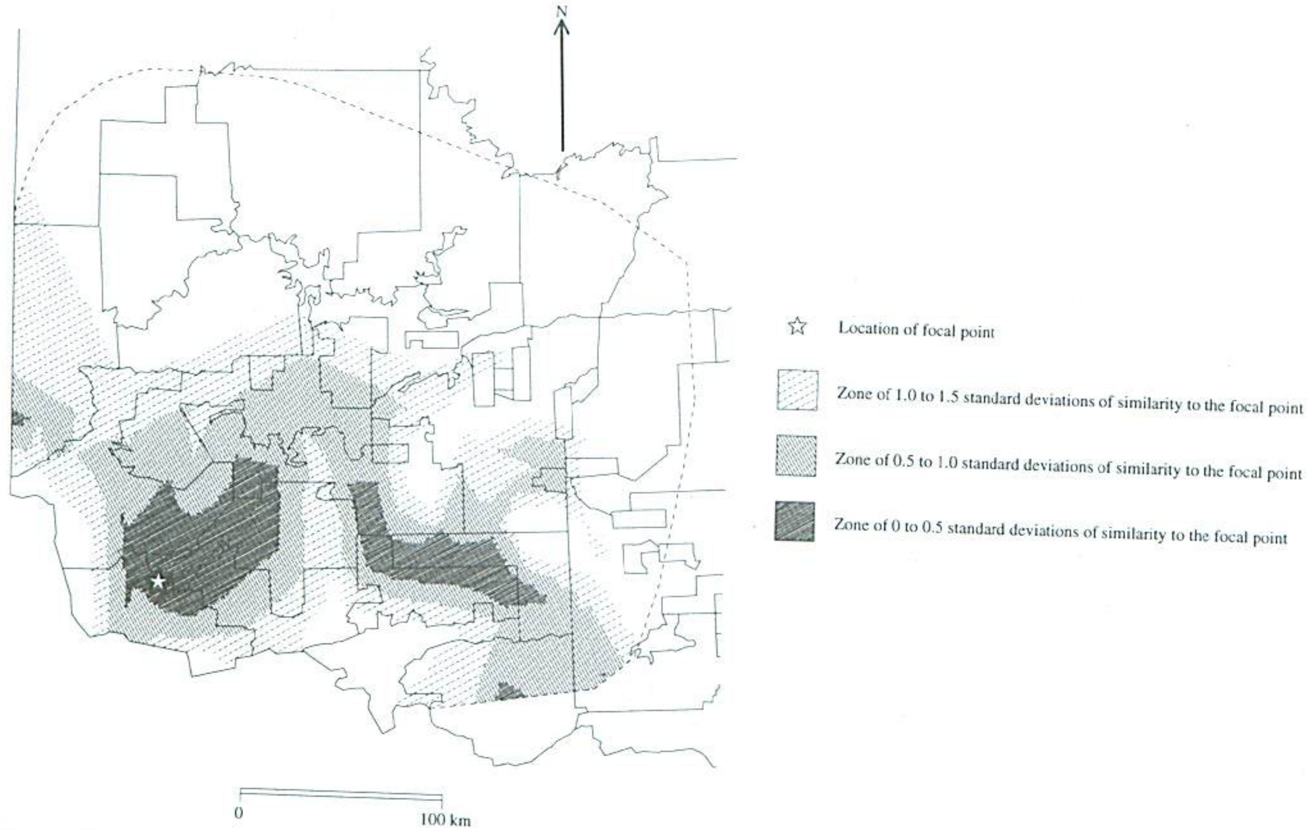

Figure 21. Jack pine focal point seed zone—49.00 N 94.00 W.

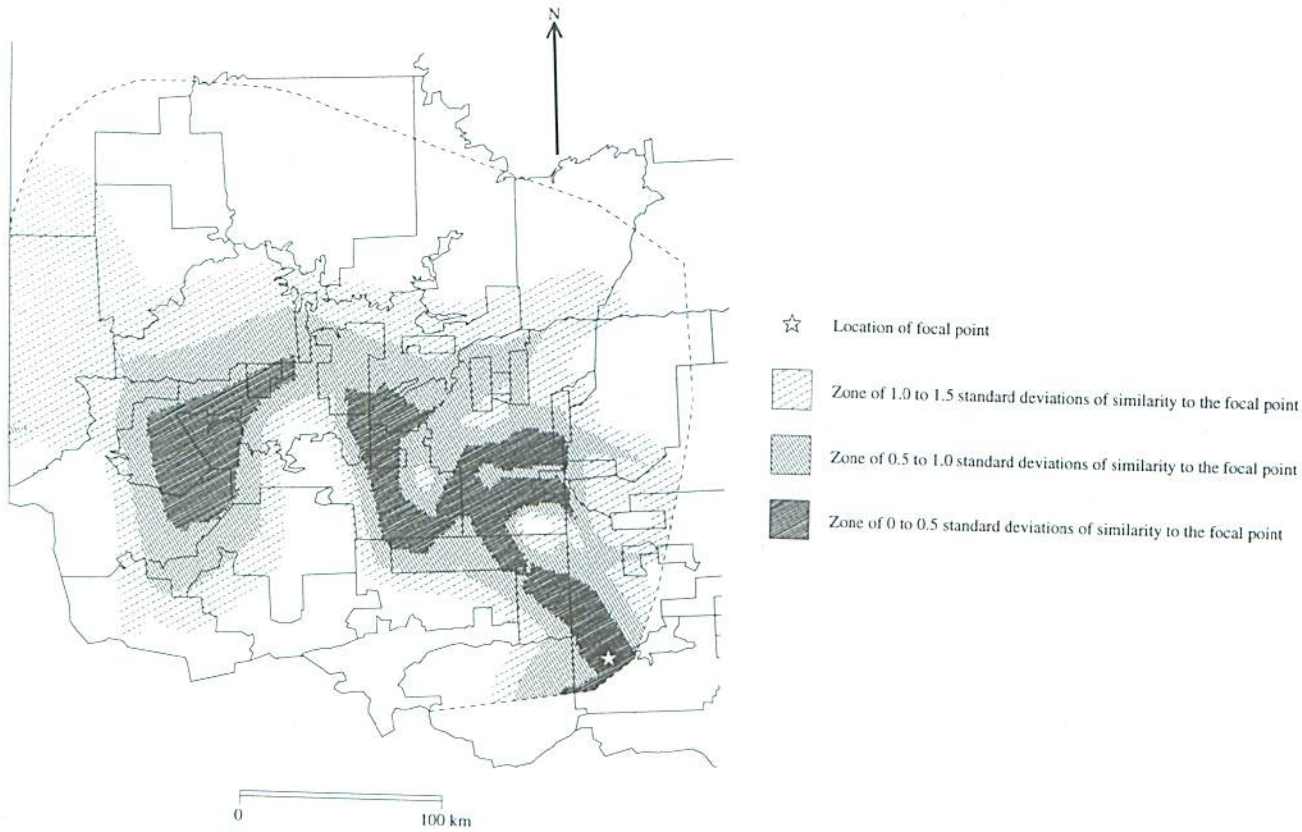

Figure 22. Jack pine focal point seed zone—48.60 N 90.67 W.

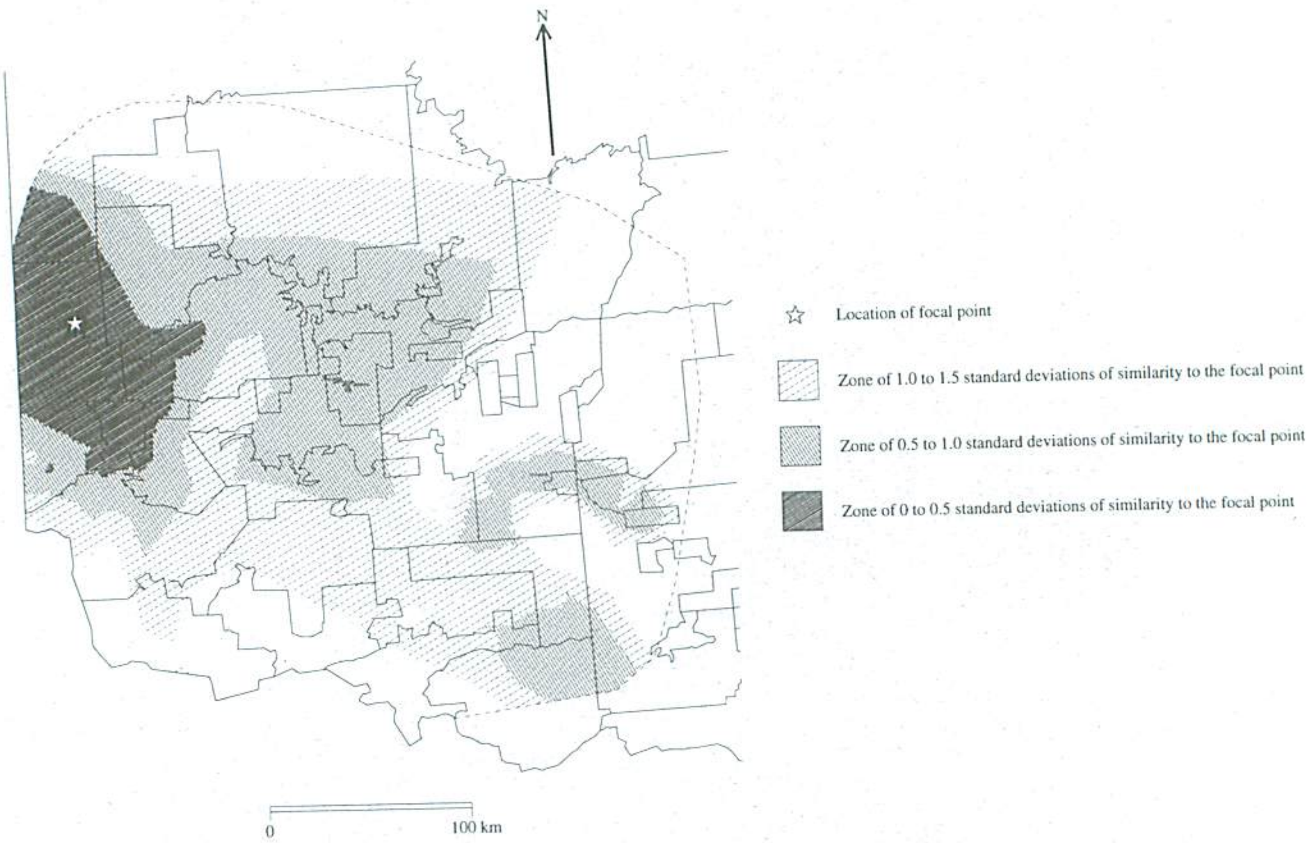

Figure 23. Jack pine focal point seed zone—50.40 N 94.67 W.

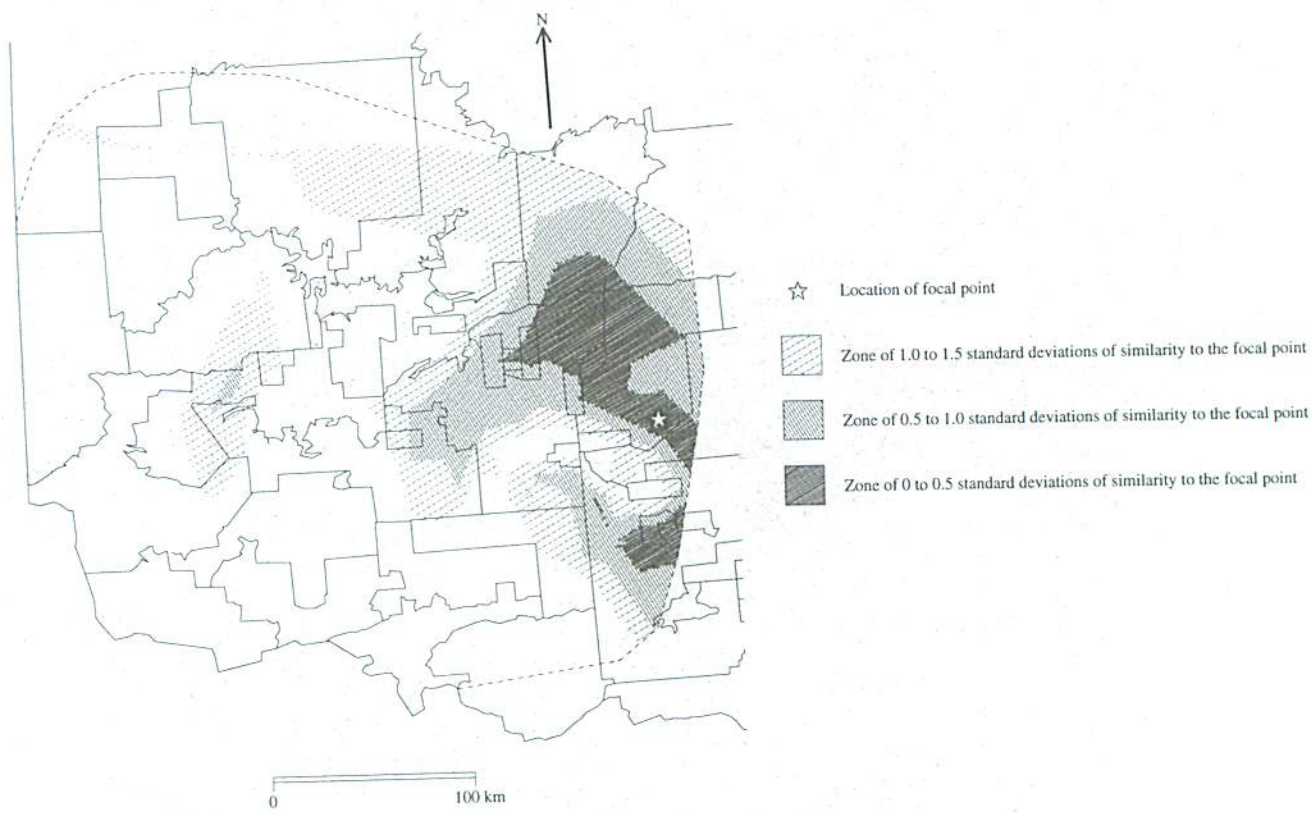

Figure 24. Jack pine focal point seed zone—49.60 N 90.33 W.

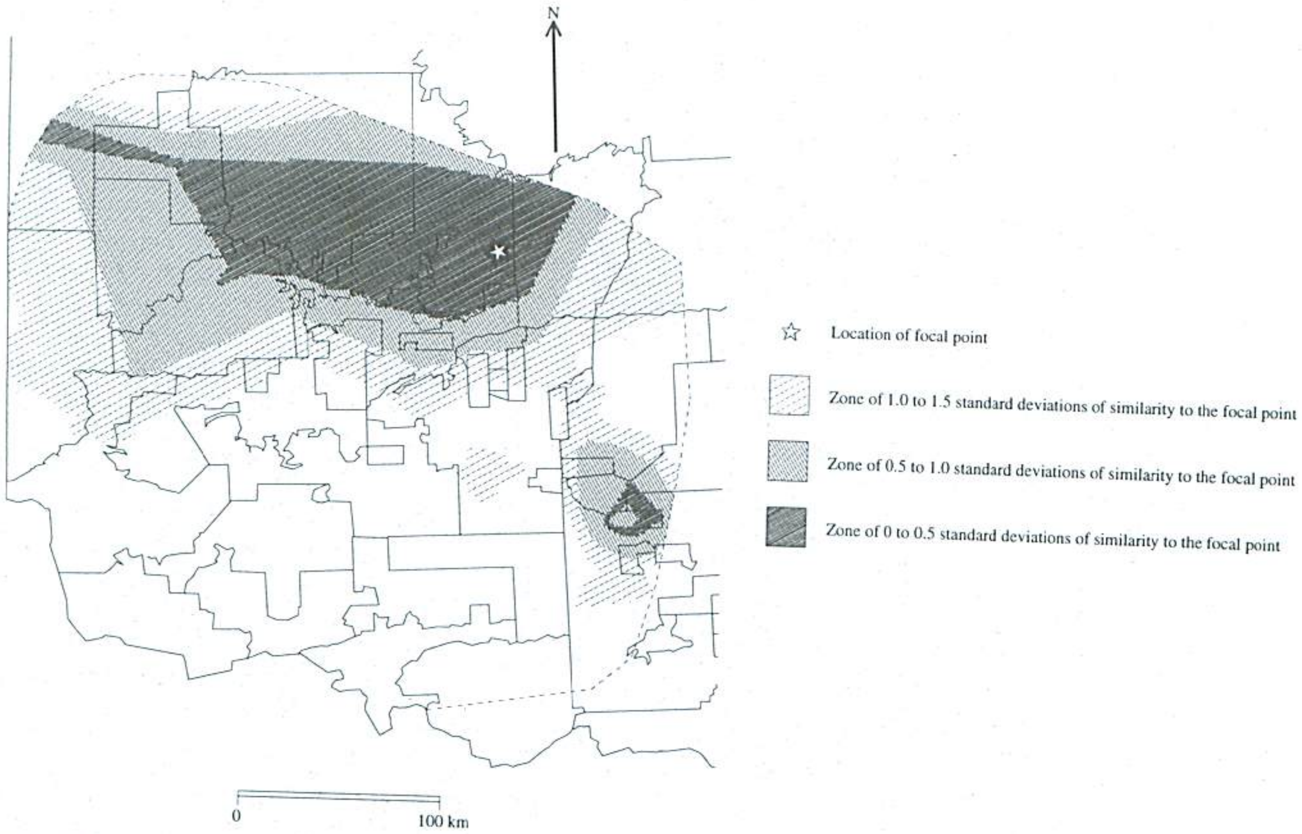

Figure 25. Jack pine focal point seed zone—50.60 N 91.33 W.

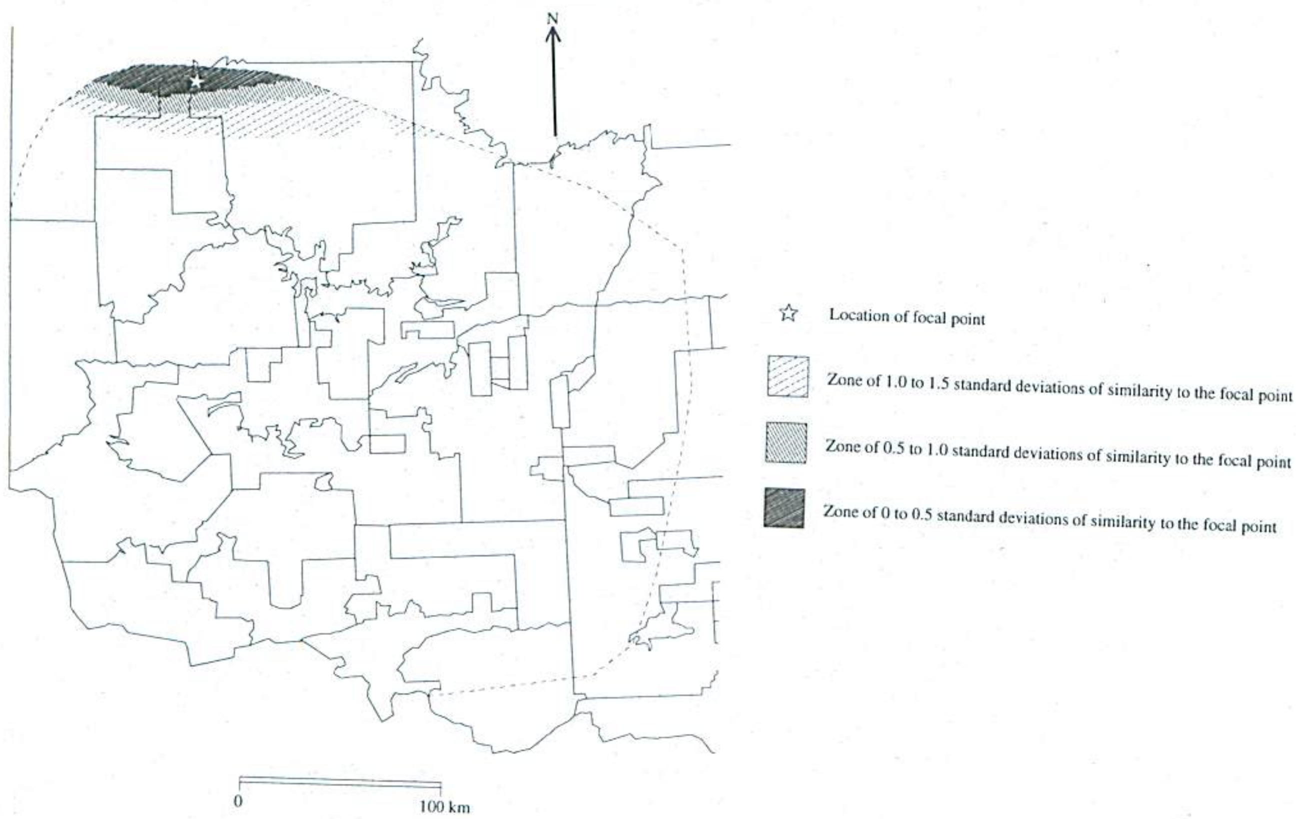

Figure 26. jack pine focal point seed zone—51.40 N 93.67 W.

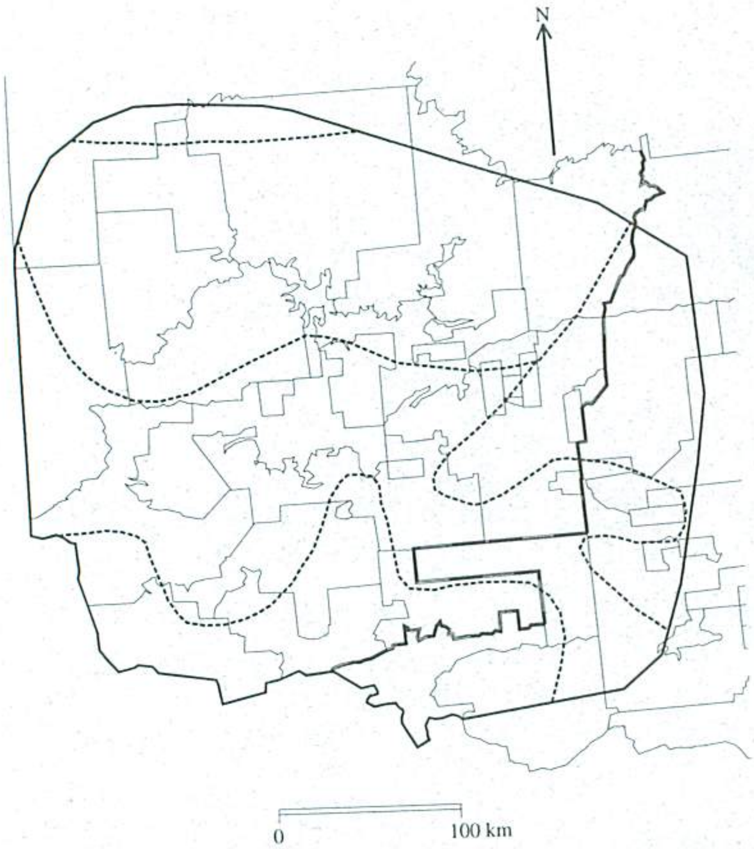

Figure 27. OTIB Zone 1 Jack pine breeding zone recommendation.

DISCUSSION

Adaptive Variation in Jack Pine

As indicated in the introduction, other studies have shown that geographic variation in jack pine is clinal and that its pattern correlates with various environmental variables. As expected, the results of this project show a similar pattern for this important boreal species.

This assessment of adaptive variation in jack pine starts with the collection of seed sources from naturally established stands, and is followed by the measurement of their progeny in common environment tests, subsequent analysis, and summary of the data by multivariate statistical methods. Finally, graphical reproduction of the patterns of variation is generated by GIS computer software. Both biological and climatic data are available only for individual geographic points, and a critical step is the expansion of this data into three-dimensional trend surfaces so that it can be interpolated for focal points anywhere within the target area. The ARC/INFO algorithm used was the TIN subroutine, which constructs triangles between geographic points. The faces of the triangles form the three-dimensional trend surface. Numerous other subroutines are available that will 'smooth' the surface of the three-dimensional model. Quite possibly some of these may produce more accurate results than the TIN subroutine, but they were not used for this project because at this stage it was preferable to employ the simplest and most readily determined interpolation technique. It is clear from the magnitude of the r^2 values that were observed for the regressions among biological and climatic variables (Tables 4, 6, and 7) that acceptable results were obtained with the TIN subroutine.

The successful investigation of adaptive variation depends upon being able to demonstrate differences among provenances. Greater components of variation were expressed among seed sources of jack pine at the Dryden greenhouse and nursery tests as compared to the other growth tests at Kenora and Sioux Lookout (Table 3). This difference results from the elimination of competition and the more uniform environments for the Dryden trials. There is still a significant component of variation expressed at the other trials, but it is a smaller fraction of the total because of the introduction of additional sources of variation. Height measures and dates of needle flushing showed greater among-source variation than did the phenological variables related to the period of shoot elongation. From this it appears that date of needle flush is more strictly genetically programmed than is the initiation of shoot extension (i.e., local fluctuations in microclimate have more effect in regulating the start of shoot elongation). The dates when growth ceased showed no component of variation expressed among seed sources. This was probably the result of jack pine's capacity for lammas growth, which was extensive at all tests in the late summer of 1994.

The relatively large components of variation expressed among sources for each of the freezing trials are anomalous (Table 3). The lack of a significant association (Table 4) for four of the six freezing variables indicates that the differences do not reflect adaptations to local climate, as would be expected. Presumably the bulk of the observed differences reflect a genotype x freezing-trial-conditions interaction.

Greater r^2 values were determined for the regressions based on the Dryden greenhouse and nursery trials. As indicated earlier, this results from a cleaner expression of the genetic component of variation expressed among seed sources in the absence of fewer sources of confounding variation. Generally, the dates of needle flushing produced the highest r^2 values at all of the trials showing strong associations with temperature variables. At the two Dryden trials more than 70 percent of the total variation in needle flush date was explained by the multiple regressions.

The multiple regressions equations for PCA Axes 1 and 2 are each based on three climatic variables, two of which are common to both equations. The first PCA axis, which was interpreted to reflect the growth potential of the sources, was predicted by temperature and precipitation at the start of the growing season (May), as well as by the coldest temperatures of winter. The second PCA axis, thought to reflect hardiness of the sources, also depended on early growing season temperature and extreme winter cold. In addition, however, it depended on a variable related to the length of the growing season—the number of frost free days. An earlier study of jack pine adaptive variation from an area of northwestern Ontario east of the present study area was recently completed using the same methodology described here (Parker 1994 a,b). In that study, only two climatic variables, extreme maximum temperature and May mean temperature, were used to predict the first PCA axis. Three variables; namely, total precipitation, August mean temperature, and date of the last spring frost, were used for the second equation. It is possible that these differences in climatic variables between the two studies are at least partially the result of the local populations, or seed sources, responding to different selection pressures corresponding to a geographically variable climate. However, the differences in the variables may also be more apparent than real (i.e., the climatic variables are so intercorrelated that either set of independent climatic variables will predict the other set of PCA axes to a reasonable extent).

Comparison of the regressions of PCA axes against climatic variables for jack pine data in this project and the previous one (Parker 1994 a,b) shows another interesting difference. In the former study the first and second axes accounted for 27 and 20 percent of the total variation with r^2 values of 0.43 and 0.30, respectively. This compared to 38 and 14 percent with r^2 values of 0.68 and 0.40, respectively, for the present study. The higher r^2 values indicate that greater confidence can be placed on the focal point seed zones produced for jack pine in this present study since the higher values are likely the result of more accurate biological and climatic data. In particular, since the climatic trends are less complex as the distance increases from Lake Superior and Lake Nipigon, it is probable that the interpolation technique was more accurate for the present study. Another less likely possibility for the differences in r^2 values would be that jack pine populations have become more finely adapted to their environment in the extreme western portion of Ontario as compared to the areas on either side of Lake Nipigon.

Focal Point Seed Zones for Jack Pine in OTIB Zone 1

The philosophy underlying the development of the focal point seed zone technique described in this report corresponds to the current opinion in Ontario that local seed sources are best for reforestation. Since the technique is multivariate, being based on numerous growth, phenological, and freezing damage variables, the resulting zones delineate areas of broadly based adaptive similarity. Thus, an indeterminate range of seed sources with adaptive characteristics similar to those of the focal point are identified, as demonstrated in common environment trials. However, it must be kept in mind that these similarity zones definitely do not identify the seed sources that will give the best height growth at each selected focal point. This approach cannot be used to maximize height growth due to genotype x environment interaction. If desired, the raw height growth data could be used for this purpose for limited parts of the sample area centering around the vicinity of the Kenora, Sioux Lookout, and Dryden field trials. Nonetheless, due to the diversity of both the growth variables and tests determined for this study, seed sources with the greatest growth potential in a favorable climate can be identified based on the first PCA axis scores (Figs. 11 and 17).

Seed zone boundaries for any species should be located in such a way that genotype (G) x environment (E) interactions do not exist among seed sources located within each zone. This concept is analogous to what happens when focal point seed zones are delineated by intersecting contour maps based on PCA axes. Seed sources with closely matched scores on first and second PCA axes (analogous to no G x E interaction) constitute the focal point seed zones. Sources closely matched on one axis but differing on the other (analogous to a G x E interaction) constitute separate zones.

Once the biological data were summarized by PCA, multiple regression was used to model the summarized data. The reason for this additional regression step was that seed zones should be based on demonstrated patterns of adaptive variation and, to demonstrate that the pattern of variation is truly adaptive, it must correlate with the local environments of the seed sources. Thus, by modeling the principal components based on environmental variation, the inclusion of nonadaptive variation components occurring in the common garden and freezing tests will be avoided. For example, stock and planting irregularities, measurement errors, inbreeding, maternal effects of seed weight, and factors related to setting up the freezing trials may be major sources of variation. Since these sources of variation normally will not correlate with the environments of the seed sources, they will be excluded if seed zones are based on predictable adaptive variation derived from regressions against environmental variables.

Comparison of the maps based on the modeled first and second PCA axes (Figs. 17 and 18), with the maps based on the actual axes (Figs. 11 and 12), shows a smoothing effect (i.e., the clines of variation were reproduced, but the local irregularities, often produced by a single seed source, were removed). As a result the focal point seed zone maps produced from these modeled PCA axes generally represent a truer adaptive pattern owing to the removal of noise (i.e., nonadaptive variation) from the actual data set. Very similar focal point seed zone maps could have been made based on the actual PCA results, but the noise effects would have led to the occurrence of small, spurious, disjunctive areas of adaptive similarity on the maps.

The overall assumption of this regression-based approach is that the 31 percent of the total variation that was explained jointly by the first and second PCA axis regression equations is sufficient to delineate seed zones for jack pine. This assumption is justified because this approach only models the adaptive variation expressed between seed sources, and because 30 percent is actually quite high compared to the levels of variation expressed among provenances for individual variables as demonstrated by the univariate ANOVAs (Table 3).

Forest managers are becoming increasingly concerned about the effects of projected global warming on the growth of future forests. Since focal point seed zones are based on species' adaptations to local climates, the results may help avoid future maladaptation resulting from such global warming. If it were possible to predict future values for the four climatic variables used to develop the two PCA axes (Table 7), then seed sources could be identified to match the anticipated climate shift. Seed from these sources could then be used in reforestation efforts. Although this approach sounds appealing and may become technically possible in the future, it may not be advisable. Regenerating trees matched to future climates might leave the seedlings maladapted and potentially unable to compete and survive in the critical early stages of their life cycle.

A current goal in forest management is to preserve biodiversity. While the present range of jack pine certainly is not limited or threatened, it is important to conserve genetically unique populations. Obviously, identification of these populations is the first step to conservation, but this task is formidable. The more specialized a species has become in terms of its adaptive variation, the more difficult the task. The focal point seed zone approach, besides providing a guide to best match seed transfers, is a practical and efficient way to identify the distribution and size of these adaptively specialized species subunits. The information provided in this report should be helpful in devising an in situ gene conservation scheme for jack pine.

Breeding Zones for OTIB Zone 1

The focal point seed zone approach, which is used here to make the best match between seed sources and particular geographic points, also provides the information needed to refine the location and boundaries of geographically contiguous breeding zones needed in tree improvement orchard and breeding programs. Advanced generation tree improvement will require precision matches between site and genotype. The focal point seed zones mapped in Figures 19 to 26 show very specific levels of geographic discontinuity in adaptive pattern. Thus, the establishment of fixed zone boundaries can be counterproductive. In spite of this, the focal point seed zone approach provides the best means currently available for the task since it identifies the true adaptive pattern for a species. The more effectively a breeding zone can be delineated, based on a true adaptive pattern, the more effectively the genotype x environment interaction can be reduced.

The recommended breeding zone boundaries shown in Figure 27 were drawn to summarize the trends observed in the complete collection of 184 focal point seed zone maps (Parker 1995). They were located subjectively at the locations where the rate of change seemed to be the greatest (i.e., where the clines were the steepest). A comparison of these boundaries with the maps based on the first two PCA axes (Figs. 17 and 18) shows obvious similarities; the contour lines on the PCA maps roughly correspond to the suggested breeding zone boundaries. As well, the climatic variable maps (Figs. 13 to 16) also show obvious similarities, particularly for mean May daily maximum temperature, and these maps also could have been used to prepare the breeding zone boundaries. This latter approach has been the best method available when biological comparison data were not available. The problem with that approach is to decide which climatic variables should be weighted, if any, and to guess how flat the clines are for the targeted species.

ACKNOWLEDGMENTS

Funding for this project was provided under the Northern Ontario Development Agreement, Northern Forestry Program. Cooperation with Brian Sykes and Diana Callaghan, Canadian Forest Service, was appreciated. As well, the contributions of the scientific authority, Dennis Joyce, were welcome. Bob White, Regional Seed Management

Specialist, assisted with much of the logistical work. Information and advice provided by Paul Charrette, Ontario Tree Improvement Board Specialist, was also useful.

The assistance of local Ontario Ministry of Natural Resources (OMNR) personnel and company personnel was invaluable throughout this study. Rick Reynolds and Murray Fergusen of Avenor, together with Ed Iskra of the OMNR in Dryden, assisted in the initial provenance collection. OMNR personnel in area, district, and regional offices assisted as required throughout the project. These included Al Matthews and Jim Young of Sioux Lookout; Dave Lawson of Ignace; Bob McColm, Mike Webber, and John Munroe of Atikokan; Gord Pyzer, Richard Shwedack, and John Norrish of Kenora; Mike Willick of Fort Frances; Tim Taylor and Trevor Park of Red Lake; and Ross Johnston of Thunder Bay. Company personnel, including Paul Jewiss, Colin Hewitt, and Jim Parsons of Rainy River Forest Products in Fort Frances; Dale Munro of Rainy River Forest Products in Kenora; Jim Cassan and Ted Aho of Avenor in Thunder Bay; Gary McKibbin of Avenor in Ear Falls; and Cam Paterson and Al Brailsford of Mckenzie Forest Products in Sioux Lookout were generous sources of required information as well as in-kind support.

This work would not have been possible without the dedication of our crews over three seasons. Provenance collections were made in 1992 by Bill Buchanan, Michael McCarthy, Tony VandeWeghe, Michael Goodfellow, Karen Duffy, Darren Kempe, Allan Plourde, and Andrew Madge. Nancy Luckai assisted in the stock production. Outplanting of the trials in 1993 was completed by Dorothy Dobrik, Brian Gauthier, Susan Boyes, and Robert May. Thanks to the fire crews from Sioux Lookout, Dryden, and Kenora who also assisted with outplanting. The trials were measured throughout the summer of 1994 by Brent Horton, Scott Longridge, Spooner Prentice-Collins, Dave Schroeder, Susan Boyes, and Jennifer Pringlemeir. A number of Lakehead University forestry students assisted with the frost hardiness tests.

The assistance and cooperation of Rendy Burns at the Dryden Tree Nursery was greatly appreciated. As well, Mark Campbell, Brian Saar, and the rest of the staff at the Dryden Tree Nursery supported this work. Space was also made available to us by Paul McAlister at the former Thunder Bay Tree Nursery. Special thanks are extended as well to Paul Sirman for providing housing at Rushing River Provincial Park, to the staff of the Dryden Tree Nursery for providing housing, and to the Sioux Lookout OMNR for providing housing.

The cooperation of all parties involved made this project a success. The in-kind assistance was readily available from all sources. Much credit must go to everyone involved throughout the project.

LITERATURE CITED

Coles, J.F.; White, R.G. 1992. Seed management co-op. Zone 1. Seed management plan 1992/93–1996/97. Ont. Min. Nat. Resour., Toronto, ON. Unpublished document.

Columbo, S.J.; Webb, D.P.; Glerum, C. 1984. Frost hardiness testing: An operational manual for use with extended greenhouse culture. Ont. Min. Nat. Resour., Maple, ON. For. Res. Rep. 110.

Environment Canada. 1982a. Canadian climate normals 1951–1980: Temperature and precipitation. Ontario. Atmospheric Environment Service, Downsview, ON. 254 p.

Environment Canada. 1982b. Canadian climate normals 1951–1980: Degree days. Vol. 4. Atmospheric Environment Service, Downsview, ON.

Environment Canada. 1982c. Canadian climate normals 1951–1980: Frost. Vol. 6. Atmospheric Environment Service, Downsview, ON.

Environment Canada. 1982d. Canadian climate normals: 1951–1980: Temperature and precipitation. Prairie Provinces. Atmospheric Environment Service, Downsview, ON.

Environmental Systems Research Institute. 1992. ARC/INFO user's guide. Redlands, CA.

Gale Research Company. 1985. Climates of the States. Vol. 1. Alabama to New Mexico. Detroit, MI. 758 p.

Hills, G.A. 1959. A ready reference to the description of the land of Ontario and its productivity. Ontario Department of Lands and Forests, Division of Research, Toronto, ON. Preliminary report.

Ontario Ministry of Natural Resources. 1987. Tree improvement master plan for Ontario. Queen's Printer for Ontario, Toronto, ON.

Ontario Ministry of Natural Resources. 1991. Statistics 1989–1990. Toronto, ON 106 p.

Parker, W.H. 1992. Focal point seed zones: Site specific seed zone delineation using geographic information systems. Can. J. For. Res. 22:267–271.

Parker, W.H. 1994a. Focal point seed zones of black spruce and jack pine. Zone 2 edition. Private printing for Ontario Tree Improvement Board. Lakehead University, Thunder Bay, ON. 123 p.

Parker, W.H. 1994b. Focal point seed zones of black spruce and jack pine. Zone 3 edition. Private printing for Ontario Tree Improvement Board. Lakehead University, Thunder Bay, ON. 131 p.

Parker, W.H. 1995. Focal point seed zones of jack pine. Zone 1. Private printing for Ontario Tree Improvement Board. Lakehead University, Thunder Bay, ON. 98 p.

Parker, W.H.; van Niejenhuis, A.; Charrette, P. 1994. Adaptive variation in *Picea mariana* from northwestern Ontario determined by short-term common environment tests. Can. J. For. Res. 24:1653–1661.

Rehfeldt, G.E.; Wykoff, W. R. 1981. Periodicity in shoot elongation among populations of *Pinus contorta* from the northern Rocky Mountains. Ann. Bot. 48:371–377.

Rudolf, P.O. 1958. Silvical characteristics of jack pine *(Pinus banksiana)*. USDA For. Serv., Lake States For. Exp. Stn., St. Paul, MN. Res. Pap. 61. 31 p.

Rudolph, T.D.; Yeatman, C.W. 1982. Genetics of jack pine. USDA For. Serv., Washington, DC. Res. Pap. WO-38. 60 p.

Sims, R.A.; Towill, W.D.; Baldwin, K.A.; Wickware, G.M. 1989. Field guide to the forest ecosystem classification for northwestern Ontario. Ont. Min. Nat. Resour., Toronto, ON. 191 p.

Sokal, R.R.; Rohlf, F.J. 1981. Biometry: The principles and practice of statistics in biological research. Second edition. W.H. Freeman and Company, San Francisco, CA. 859 p.

van Niejenhuis, A. 1995. Genecology of jack pine in north central Ontario. MScFor. Thesis. Lakehead University, Thunder Bay, ON.

Wilkinson, L.; Hill, M.; Vang, E. 1992. Systat: Statistics, Version 5.2. Systat, Inc., Evanston, IL.

Yeatman, C.W. 1966. Geographic variation in jack pine *(Pinus banksiana* Lamb.) seedlings. Ph.D. Thesis. Yale University, New Haven, CT.