Investigation of limestone ecotypes of white spruce based on a provenance test series

Mark R. Lesser, Marilyn Cherry, and William H. Parker

Abstract: Previous laboratory and field studies have presented evidence for the existence of limestone ecotypes in white spruce (*Picea glauca* (Moench) Voss). Remeasurements of the range-wide 410 series of provenance trials were used for further evaluation of the existence of these ecotypes. In 2001, heights were measured of 23 provenances grown at four test sites in Ontario, all located south of 46°N. Bedrock classification for test sites and provenances by limestone or non-limestone parent material was done using a 1993 data set of the Ontario Geological Survey. Analysis of variance revealed significant differences among test sites and provenances only. No significant interactions consistent with the existence of limestone ecotypes were detected. This finding is in contrast to that of an earlier field study that detected a strong interaction between test site and provenance bedrock type ($p < 0.001$). Examination of the relative performance of individual provenances from limestone and non-limestone bedrock types revealed differences in performance at the four different test sites but few instances supporting the existence of limestone ecotypes. Although these more recent results generally support a pattern of between-stand variation in southern Ontario, they do not disprove the existence of limestone ecotypes, owing to the nature of the 410-series test design and the classification of provenances according to bedrock type instead of actual soil analyses.

Résumé : Des études antérieures en laboratoire et au champ ont présenté des indices qui tendent à démontrer l'existence d'écotypes calcaires chez l'épinette blanche (*Picea glauca* (Moench) Voss). Les tests de provenances de la série 410 qui couvrent l'ensemble de l'aire de répartition de cette espèce ont été mesurés à nouveau afin de réévaluer l'existence de ces écotypes. La hauteur a été mesurée en 2001 chez 23 provenances, dans quatre endroits tous situés au sud du 46°N en Ontario. Les tests et les provenances ont été classés en fonction de l'assise rocheuse, roche mère calcaire ou non calcaire, à l'aide de la classification de 1993 de la Commission géologique de l'Ontario. L'analyse de variance a révélé des différences significatives seulement entre les tests et les provenances. Aucune interaction significative compatible avec l'existence d'écotypes calcaires a été notée. Ce résultat contraste avec une étude antérieure au champ qui avait détecté une forte interaction entre les tests et l'assise rocheuse des provenances ($p < 0{,}001$). L'examen de la performance relative de chaque provenance selon le type d'assise rocheuse a révélé des différences de performance dans quatre sites d'essai différents mais bien peu de cas supportent l'existence d'écotypes calcaires. Même si ces résultats plus récents supportent généralement l'existence d'une forme de variation entre les peuplements dans le sud de l'Ontario, ils ne permettent pas de réfuter l'existence d'écotypes calcaires étant donné la nature du dispositif d'essai de la série 410 et la classification des provenances fondée sur le type d'assise rocheuse plutôt que sur de vraies analyses de sol.

[Traduit par la Rédaction]

Introduction

White spruce (*Picea glauca* (Moench) Voss) has a transcontinental range in temperate North America and is adapted to widely diverse climatic and edaphic conditions (Nienstaedt and Zasada 1990). Past studies on adaptive variation of this species have generally concentrated on clinal variation following latitudinal and altitudinal gradients (Nienstaedt and Teich 1972), but some studies have focused on soil-related variation.

In laboratory studies, Farrar and Nicholson (1967) compared limestone- and granitic-origin seed sources grown in nutrient solutions of different calcium concentrations. Their findings showed some evidence of genetic differences between the two groups, but the data contained large amounts of unexplained variation and the study was unreplicated (Nienstaedt and Teich 1972). Cunningham (1971) conducted a study involving different pH levels and calcium concentrations that showed no association between progeny performance and source soil pH or calcium level. A second study conducted by Cunningham (1971) showed evidence of genetic adaptation to soils high in nutrient availability. In that study, progeny stem length and foliar calcium levels were significantly correlated with several parental soil elements.

On the basis of a study that included 12 provenances collected from southern Ontario, Teich and Holst (1974) concluded that limestone ecotypes of white spruce are naturally occurring. Their study included six provenances from soils

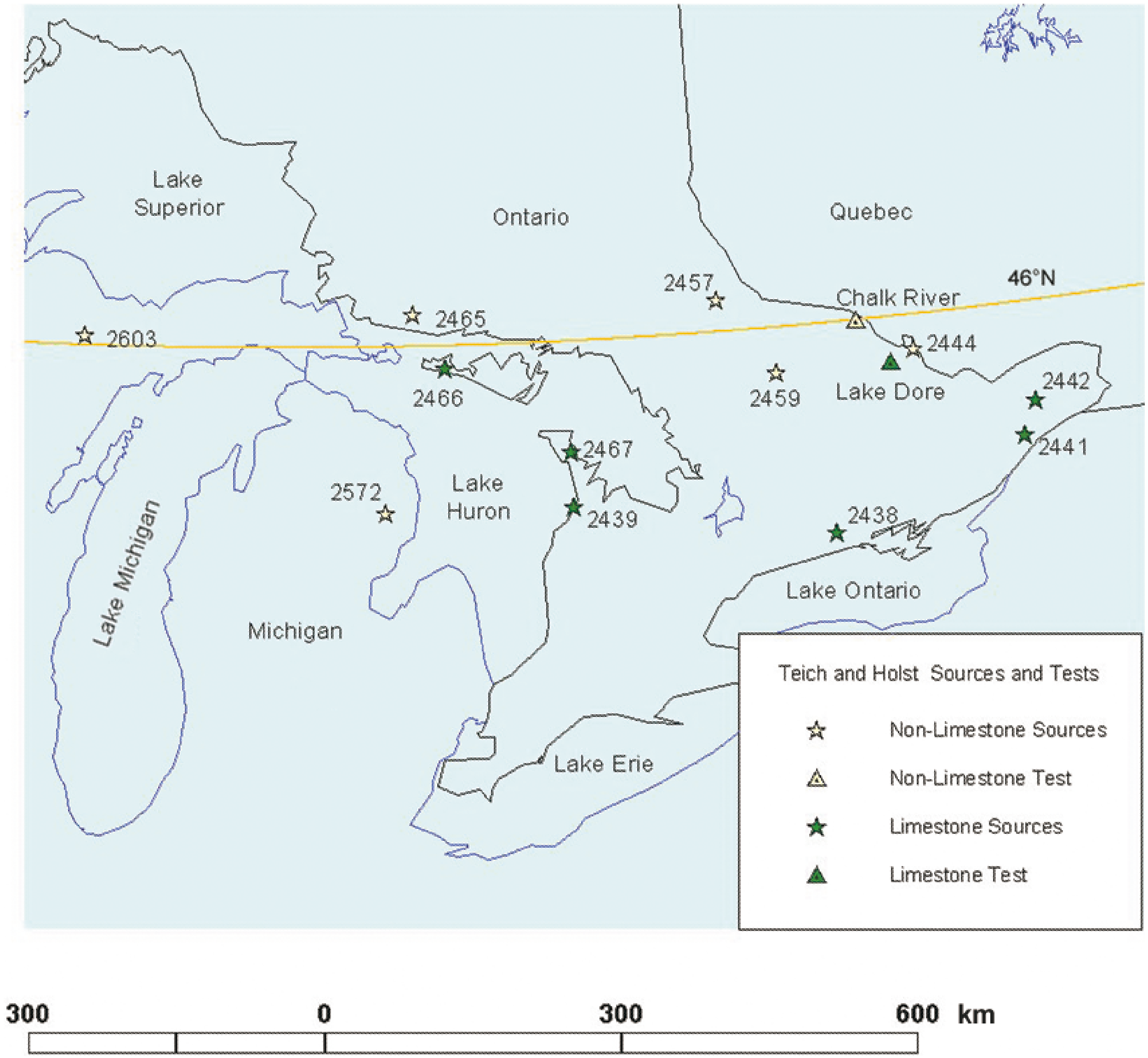
Received 16 June 2003. Accepted 27 November 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 25 May 2004.

M.R. Lesser and W.H. Parker.[1] Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada.
M. Cherry. Pacific Northwest Tree Improvement Research Cooperative, Department of Forest Science, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331-5752, USA.

[1]Corresponding author (e-mail: bill.parker@lakeheadu.ca).

 doi: 10.1139/X03-286

Fig. 1. Location of two test sites and 12 provenances of white spruce of limestone and granitic bedrock origin reported by Teich and Holst (1974).



with limestone parent material and six from soils with granitic parent material, both groups grown at a limestone-origin test site and at a nearby granitic-origin test site (Fig. 1). Although survival did not differ significantly, height growth differences based on soil parent material were significant. Limestone-origin sources consistently grew better then granitic sources on the limestone site, and granitic-origin sources grew better then limestone sources on the granitic site. Overall, both limestone sources and granitic sources performed better on the granitic site, although the authors did not attribute this difference to soil composition.

Other research has suggested or supported the existence of soil-based ecotypic differentiation in white spruce. In a report on chlorosis of white spruce planted at Limestone Lake, Ontario, Timmer and Whitney (1983) suggested that parent material type may have been a factor. Although the source of the planted stock was not known, naturally occurring trees in the plantation were not chlorotic, suggesting a link to soil type. In an experiment consisting of 31 transcontinental provenances planted at a site in Newfoundland, Khalil (1985) noted considerable sensitivity to soil differences, which increased with age. Irving and Skeates (1988) observed differences among 75 provenances planted in the Dryden nursery that may have been connected to ecotypic variation, and they concluded that seed origin should be matched to planting site soil type. As well, Morgenstern and Copis (1999) reported that the 1991 data from the 410 series of provenance tests supported Teich and Holst's (1974) conclusion, although it was not clearly demonstrated because of partial measurements.

In British Columbia, height growth performance in common environment tests for families of interior spruce (*Picea glauca* (Moench) Voss × *P. engelmannii* Parry ex Engelm.) collected from the calcareous soil zone of the East Kootenays was superior to that of samples collected from the acidic soil zone (Xie et al. 1998). Although the authors observed that the differences were not a function of altitude, they concluded that limestone ecotypes had not evolved in this zone of introgression. However, their data and methods paralleled those of Teich and Holst (1974) and revealed racial differences corresponding to the limestone soil – acidic soil difference.

The goal of this study was to further evaluate the existence of white spruce limestone ecotypes in Ontario. The complete remeasurement of the 15 Ontario 410 series of range-wide provenance tests in 2001 provided an opportunity to substantiate the existence of soil-based ecotypic differentiation. Quantified growth differences based on appropriate seed source and planting site selection related to soil parent material type could have impacts on white spruce reforestation efforts. Teich and Holst (1974) estimated that accounting for such variation could lead to approximately 10% gain in growth.

Materials and methods

Study area and provenance selection

A study to detect soil-related ecotypic differentiation in white spruce growth patterns should not confound this type of differentiation with adaptive variation resulting from climate differences. The 2001 measurements of all of the Ontario and immediately adjacent Quebec 410 series of provenances grown at 15 Ontario test sites indicated that the 31 limestone-origin provenances were about 13% greater in height growth than the 136 non-limestone sources (Lesser 2003). However, nearly all of the limestone provenances were from southern Ontario, and it has been repeatedly noted that the southern sources outgrow the northern ones in a common garden situation. Thus, the observed significant difference between limestone- and non-limestone-origin sources in the 2001 data may be largely or entirely the result of adaptation to changing climate conditions associated with latitude. A valid test for soil-related ecotypic differentiation should compare only seed sources from the same latitudinal range and similar climate.

For this study, only provenances and test sites included in the 410 series of range-wide white spruce provenance tests south of 46°N latitude were selected (Fig. 2). The resulting southern subset of test sites and provenances was about equally distributed between bedrock types. Of the four test sites included, two were on limestone bedrock (Owen Sound and Cornwall), and the two remaining ones (Chalk River and Minden) were both on non-limestone bedrock. Although 46 Ontario provenances were located south of 46°N, many were not grown at a site of each bedrock type. On this basis, 23 of the 46 southern provenances were eliminated. The remaining 23 provenances were grown on at least one test site of each bedrock type: 12 were from limestone bedrock sites and 11 from non-limestone bedrock sites (Fig. 2 and Appendix A). Only seven of these were grown at all four of the southern test sites. As the 12 limestone provenances were generally located to the south of the 11 non-limestone ones, the effect of latitude as a primary determinant of height growth for the selected 23 provenances was tested by simple linear regressions of provenance mean heights against latitude for each test site, using the Regression Procedure of SAS (SAS Institute Inc. 2001).

Bedrock geology

Digital geographic information system coverage of the bedrock geology of Ontario was used to classify seed sources as either limestone or non-limestone parent material types. This coverage of the Ontario Geological Survey (OGS 1993) was supplied through the Ontario Ministry of Northern Development and Mines (MNDM 1994). The coverage contained 58 major divisions of bedrock type and a further 56 subdivisions. For the purposes of this study it was necessary to reclassify these divisions and subdivisions into just two categories: limestone and non-limestone.

Based on their similarities in chemical composition, bedrock types classified as containing limestone, dolostone, or marble were included in the limestone grouping. All three of these rock types consist mainly of calcium carbonate and had alkaline pH values (Goudge 1935; Boynton 1966). In all cases, these types of bedrock will result in highly calcareous basic soils, provided that the existing soil is derived from the parent material in situ and not the result of glacial deposition (L. Meyer, Lakehead University, personal communication, 2003).

Data collection and analysis

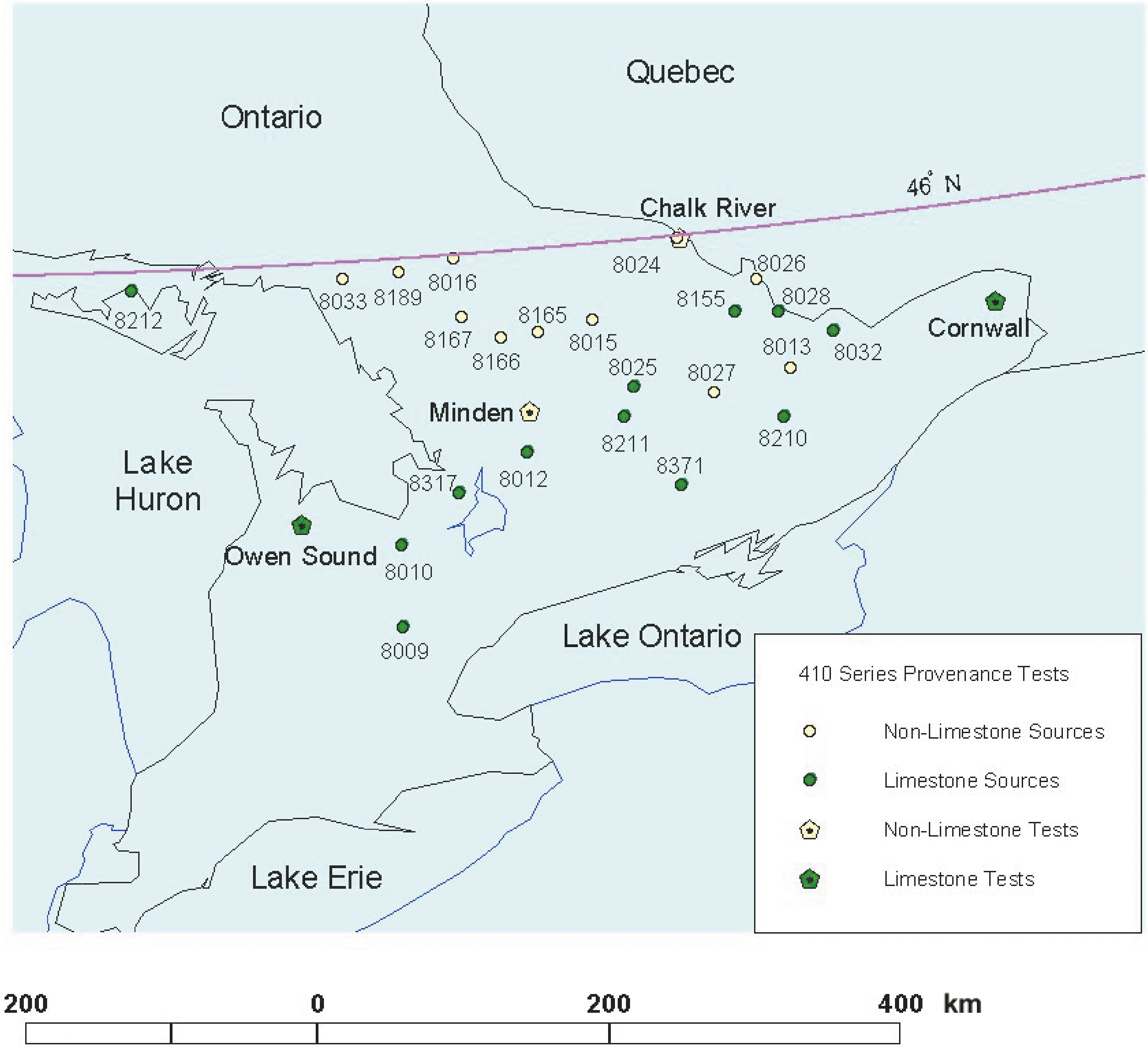
The 410 series of white spruce provenance tests was established as a range-wide experiment to examine genetic variation across the entire range of the species and to assess within-region variability of selected areas (Morgenstern and Copis 1999). Although efforts were made to plant a few provenances representative of the full species range at each test site, no effort was made to replicate sources between test sites. For the Ontario test sites, the primary emphasis was on planting a sampling of Ontario sources that occurred at a latitude similar to that of the test location.

On the basis of the year of planting, the average age of all the Ontario test sites at the time of measurement in 2001 was 19 years. One of the four test sites (Minden) used for this study was planted in 1981, and the other three were planted in 1982. Of the 263 total white spruce seed sources, the number planted at the four test locations in this study varied from 64 at the Cornwall site to 80 at Minden (Morgenstern and Copis 1999).

To allow direct comparison across the four different tests for analysis of variance (ANOVA), heights were adjusted by dividing by the age of the test site since planting and then multiplying by the average age of all the Ontario test sites. With or without this procedure, problems with direct comparisons of provenances across tests or within tests may result if competition slows the early growth of white spruce at some test sites but not others. However, the adjusting procedure seems reasonable in this case for maintained field trials of a similar age in a fairly localized area. Also, substantial interaction terms expected for limestone ecotypes grown on contrasting sites are far less likely to be affected, because they depend on provenance rank shifts or reversals, rather than absolute growth.

ANOVA of adjusted height data was performed considering the effects of the two bedrock test types (designated bedrock), the two tests nested within each bedrock type, the two provenance bedrock origin types (designated origin), the 23 provenances nested within each origin type, and the bedrock × origin, test within bedrock × origin, bedrock × prove-

Fig. 2. Location of four test sites and 23 provenances of white spruce of limestone and non-limestone bedrock origin from the 410 series of range-wide provenance tests.



nance within origin, and test within bedrock × provenance within origin interactions, using the SAS general linear model procedure (SAS Institute Inc. 2001). Bedrock and origin were treated as fixed variables, and all other variables were considered random.

Adjusted height data were not required in the comparison of the relative performance of individual provenances across the four tests; instead, the standardized deviations of individual provenance means were calculated by subtracting the whole-test mean from the provenance means, followed by division by the whole-test SD. These standardized data provided the basis for a series of discriminant function analyses, using the SAS procedure discriminant (SAS Institute Inc. 2002). These analyses served two purposes. First, they would indicate whether the limestone and non-limestone provenance groupings could be distinguished by any components of variation present in any single test data set or combination of two, three, or four test data sets grouped together regardless of bedrock type. Second, the discriminant analyses might indicate consistent provenance misclassifications of bedrock origin, revealing a provenance designated as the wrong bedrock origin type.

In addition, Spearman's rank correlations for the 23 provenances were determined for the six pairwise groupings of the four tests, to uncover any differential performance trends between test sites, particularly differences predicted on the basis of Teich and Holst's (1974) observations.

Results

Simple linear regressions of provenance means against latitude for the four tests showed no relationship ($p > 0.5$), with r^2 values < 0.03. Hence, growth differences detected between the 23 limestone and non-limestone provenances were not simply the result of latitude.

Table 1. ANOVA of adjusted height data classified by bedrock type for 23 white spruce 410 series of provenances.

Source	df	SS	MS	*F* value	*p* >*F*
Bedrock	1	293 486.7	293 486.7	0.1	0.78
Test(bedrock)	2	4 679 224.6	2 339 612.8	109.54	0.01
Origin	1	4 906.4	4 906.4	0.11	0.75
Prov.(origin)	21	657 267.6	31 298.4	3.41	0.00
Bedrock × origin	1	42 350.5	42 350.5	1.83	0.35
Bedrock × prov.(origin)	21	193 805.8	9 228.8	0.91	0.58
Test(bedrock) × origin	2	42 129.1	21 064.5	2.07	0.15
Test(bedrock) × prov.(origin)	21	213 754.9	10 178.8	1.04	0.42

Note: ANOVA, analysis of variance; df, degrees of freedom; MS, mean square; SS, sum of squares; prov., provenance.

The results of ANOVA of height data are presented in Table 1. Highly significant differences ($p < 0.01$) were present only between provenances within origin type and between tests within bedrock type. A significant difference demonstrated between the two bedrock types and (or) a bedrock × origin interaction would provide support for the existence of edaphic ecotypes, but these indications were not present in our data. Neither bedrock type nor origin type was significant; neither was their interaction or any other source of variation.

Table 2 lists the mean adjusted heights for ungrouped and grouped limestone- and non-limestone-origin provenances sorted by bedrock type for each of the four tests. Although there were great differences between tests, probably most of these differences can be attributed to climate, competition, and other sources of between-stand variation, rather than to soil type. The ranking of the four tests was the same for both limestone and non-limestone provenance groupings, with limestone bedrock test sites ranked first and last, regardless of provenance bedrock type. Of greater interest for a study on edaphic ecotypes are the differences between limestone- and non-limestone-origin provenances within each test and the changes in relative performance of provenances between tests of differing bedrock types. For three of the tests, the mean adjusted heights of limestone and non-limestone provenances were nearly the same, with the non-limestone group slightly greater at Minden and the limestone group slightly greater at Chalk River. However, the mean of the limestone provenances at Owen Sound, a limestone test, was 11% greater than that of the non-limestone ones, resulting in the slightly increased significance ($p = 0.15$) of the test within bedrock × origin interaction term. The small fraction of non-limestone provenances tested at Owen Sound (4 of 11) and the poor match of relative performance with the other limestone bedrock test (Cornwall) suggest that this discrepancy may be the result of sampling error.

Table 2 also compares the relative performance of each white spruce provenance across the four tests by means of standardized deviations from the test means. If edaphic differentiation were present, relative differences would be expected when provenances were tested at sites with different bedrock type. No consistent pattern was observed, and the relative performance for 13 of the provenances was fairly constant across all tests, with overall deviations of less than 0.7 SD. The 10 remaining provenances showed an overall range of ≥0.9 SD across the tests; and of these 10, only 2 provenances displayed a pattern consistent with Teich and Holst's (1974) observations. Two limestone-origin provenances (8212 and 8317) each grew more poorly at the one non-limestone test site (Minden) where they were tested. Conversely, two non-limestone-origin provenances (8167 and 8189) showed substantially better growth at the one limestone test site (Cornwall) where they were planted. The other six provenances that showed a deviation of ≥0.9 did not follow a pattern of growth consistent with bedrock type (Table 2). Certain provenances performed well at one of the limestone test sites but poorly at the other; conversely, some provenances showed contrasting performance at the two non-limestone-origin test sites.

Rank comparisons provide another way to compare relative performance between limestone and non-limestone sources at the four test sites. Because the numbers of provenances tested at Owen Sound and Chalk River were about one half of those tested at the other two test sites, it was easier to compare rank quartiles than actual ranks between tests. Generally, relative performance was consistent across test sites. Fifteen of the 23 provenances ranked within two quartiles at all of their test sites (Table 2). Of the remaining eight provenances that varied by three or four quartiles, only one of these (8024) followed a pattern consistent with Teich and Holst's (1974) observations. Provenance 8024 (Chalk River), with a non-limestone source, occurred in the third and fourth quartiles at the two limestone test sites and was the top-ranked provenance overall at its home test site — Chalk River — and in the second quartile at the second non-limestone test site. However, another non-limestone provenance (8026, Beachburg), located a short distance to the south of Chalk River, showed the opposite result, ranking first among the limestone provenances at both the two limestone test sites and in the second and fourth quartile at the two non-limestone test sites. The remaining six provenances all expressed quartile differences within the two test bedrock groupings.

The Spearman rank correlations shown in Table 3 represent quantified similarity coefficients calculated separately for each of the six possible test-pair groupings. If limestone and non-limestone ecotypes were present, one would anticipate that rank comparisons between tests of the same bedrock type would produce higher coefficients than those between dissimilar bedrock types. The rank correlations between pairs of test sites with matching bedrock type were fairly low: 0.06 between Minden and Chalk River and 0.31

Table 2. Comparison of adjusted height means, standardized deviations, and test rank quartiles of 23 limestone- and non-limestone-origin white spruce 410-series provenances.

	Limestone tests						Non-limestone tests					
	Owen Sound			Cornwall			Minden			Chalk River		
Provenances	Adj. ht. (cm)	Dev.[a]	Rank	Adj. ht. (cm)	Dev.[a]	Rank	Adj. ht. (cm)	Dev.[a]	Rank	Adj. ht. (cm)	Dev.[a]	Rank
Limestone												
8009	392.26	0.40	2	705.78	0.20	3	660.52	0.47	3	628.65	0.24	2
8010	324.63	–0.43	4	702.98	0.18	4	517.24	–0.75	4			
8012				798.13	0.96	1	696.18	0.77	2			
8025				751.36	0.57	3	661.52	0.47	3			
8028	374.04	0.18	3	774.27	0.76	2	647.54	0.36	3	620.43	0.16	2
8032	428.31	0.85	2	791.15	0.90	1	696.51	0.77	1			
8155	446.50	1.07	1	781.38	0.82	2	764.02	1.34	1	630.91	0.26	1
8210	447.25	1.08	1	683.71	0.02	4	609.02	0.03	3	605.71	0.01	3
8211				766.74	0.70	2	754.50	1.26	1	583.72	–0.20	4
8212	378.34	0.23	3	673.71	–0.06	4	526.21	–0.67	4			
8317	357.34	–0.02	3	748.00	0.55	3	518.50	–0.74	4			
8371	426.19	0.82	2	783.03	0.83	2				648.78	0.44	1
Mean	395.69			746.71			643.47			619.70		
Non-limestone												
8013	336.60	–0.28	4	816.41	1.11	1	729.55	1.05	1			
8015				770.26	0.73	2	696.72	0.77	1	618.72	0.14	3
8016	323.67	–0.44	4	676.73	–0.04	4	597.00	–0.07	4	589.22	–0.15	4
8024	324.59	–0.43	4	763.11	0.67	3	688.47	0.70	2	649.98	0.45	1
8026	451.49	1.13	1	790.24	0.89	1	680.17	0.63	2	602.06	–0.02	4
8027				686.67	0.04	4	562.30	–0.37	4			
8033				724.18	0.35	3	681.72	0.65	2			
8165				690.27	0.07	4	632.12	0.22	3	607.92	0.04	3
8166				714.76	0.27	3	667.43	0.52	2	587.14	–0.17	4
8167				804.21	1.01	1	584.16	–0.18	4	629.60	0.25	2
8189				778.54	0.80	2	627.44	0.18	3			
Mean	356.50			746.36			650.50			611.56		
Test mean	359.34			681.26			605.64			604.26		
Test SD	81.39			122.19			117.87			101.31		

Note: Adj. ht., adjusted height; dev., deviation from whole-test mean.
[a]Dev. expressed in whole-test standard deviations.

between Owen Sound and Cornwall. The four pairings mismatched by bedrock type were quite variable, ranging from –0.11 for Owen Sound and Chalk River to the highest observed coefficient of 0.59 between Cornwall and Minden.

Table 3 also presents the partial results of discriminant analysis in the form of percentage of provenances that were misclassified when each test-site pairing was considered. Misclassifications ranged from 25% for the 12 provenances tested at Minden (non-limestone) and Owen Sound (limestone) to 91% for the matching of 22 provenances at Minden and Cornwall (limestone), with no consistent pattern. The discriminant analyses of the three combinations of three tests and of all four tests combined showed the same erratic pattern of misclassification (results not shown). Also, there were no individual provenances that stood out as being consistently misclassified.

Table 3. Spearman's rank correlation of height across four test sites for 23 white spruce provenances (below diagonal) and percent provenances misclassified by discriminant analysis (above diagonal).

	Owen Sound	Cornwall	Minden	Chalk River
Owen Sound	———	42% n=13	25% n=12	43% n=7
Cornwall	0.31 n=13	———	91% n=22	76% n=13
Minden	0.32 n=12	0.59 n=22	———	69% n=12
Chalk River	–0.11 n=7	0.40 n=13	0.06 n=12	———

Discussion

The existence of limestone ecotypes of white spruce in southern Ontario has been supported by laboratory studies (Farrar and Nicholson 1967; Cunningham 1971) and a genecological study by Teich and Holst (1974) that included six limestone-origin provenances and six granitic-origin provenances, replicated on a test site of each bedrock type. Teich and Holst observed a strong test × bedrock type interaction associated with rank changes for individual provenances, with most performing better on the matching bedrock type. At age 15 years, limestone provenances achieved 9.7% better height growth than granitic-origin provenances at the limestone test, and height growth of granitic provenances were 8.8% better at the granitic test site. More recent height data from the 194 series of white spruce provenance tests have been published for 10 of the same 12 provenances tested at the same two locations. These newer 21-year height data for Lake Dore (194-D2 test) and 19-year data for Chalk River (194-M test) indicate somewhat reduced differences of 4.4% and 5.2%, respectively (Morgenstern and Copis 1999), but they continue to support the existence of limestone ecotypes.

The 410 series of white spruce provenance tests, which provided the data for this follow-up study, was never intended to test the hypothesis of the existence of white spruce limestone ecotypes. Provenance selection at Ontario test locations focused on range-wide representation, with a primary emphasis on Ontario provenances from similar latitudes. Regardless, provenances from both bedrock types were included in all of the tests, with a greater fraction of limestone sources at the southern tests. Unfortunately, no effort was made to replicate different soil-type origin provenances across tests with different bedrock types.

Despite these shortcomings, the remeasurement of the Ontario 410 series of tests in 2001 provided an opportunity to substantiate the observations of Teich and Holst (1974). Although this data set was not originally intended for studying soil-related adaptation, it provides the best data currently available in Ontario for this purpose. The 410 series offers some desirable features: it doubles the number of tests, to four, and nearly doubles the number of provenances, to 23. Of these, only one test (Chalk River) and one provenance (Beachburg) were duplicated between this study and the earlier one.

Because the existence of clinal variation associated with latitude–climate has been widely reported for white spruce (Nienstaedt and Teich 1972), a field test for edaphic differentiation must be designed to include only seed sources and test sites with similar climates. Otherwise, the superior growth potential of the southern sources would confound the results. The seed sources and test sites of Teich and Holst (1974) are mapped in Fig. 1, and it may be seen that provenances were chosen out of the 194 series of white spruce provenance tests near 46°N latitude and extending south to about 44°N. For the same reason, a subset of southern Ontario 410 series of provenances and test sites was isolated from south of 46°N latitude for this study (Fig. 2). Although the limestone provenances and tests occur in the southern portion of the study areas, owing to the pattern of bedrock geology of southern Ontario, regression indicated that latitude by itself was not a significant factor in the present study.

The results presented here indicate that between-stand variation in growth potential is statistically significant for white spruce in southern Ontario but that this pattern of variation does not correspond to either latitude or bedrock origin of provenances. The results further indicate that the differences in growth between the test sites do not correspond to bedrock origin either.

On the basis of Teich and Holst's (1974) observations, it was expected that the data from the 410 series of provenance trials would support the conclusion that limestone ecotypes exist in white spruce; that is, Teich and Holst's results would be replicated. Either a significant difference would be observed between bedrock types, or a significant interaction between test and bedrock type would be present. This interaction would result in differences in rank associated with test bedrock type owing to the different relative performance of individual provenances that had become adapted to limestone or non-limestone soil types. Surprisingly, the 410-series data offered no support for the limestone ecotype conclusion. Although a difference between limestone and non-limestone provenance group means did exist at one of the four test sites (Owen Sound), this difference was not statistically significant, and the unbalanced composition of the provenances (nine limestone sources and four non-limestone sources) at that site, together with the dissimilar performance of the same four non-limestone sources at the other limestone test site (Cornwall), suggests that these results may not be repeatable. As well, the low mean of the four non-limestone provenances at Owen Sound was anomalous, as it was the only instance out of eight comparisons in which the bedrock group mean was less than the whole-test mean (Table 2). As all 23 provenances were from southern Ontario, they would be expected to perform better, on average, than the entire sample of provenances from throughout the range of the species, regardless of bedrock origin.

Variation in the relative performance of individual provenances corresponding to bedrock type was examined with the use of standardized deviations from test means and rank shifts. Although relative performance and rank did differ across the four tests, there were few instances in which the differences could be interpreted as supporting the limestone ecotype hypothesis. It is notable that non-limestone provenance 8026 (Beachburg), the only provenance common to both this study and Teich and Holst's (1974) study, produced contradictory results in the two studies. In the earlier work this provenance (identified as 2444 in the 194 series of provenance tests) was the best performing of the granitic provenances at the granitic test site (Chalk River) but ranked only fifth of 12 at the limestone site. In the current work the reverse has happened, with this provenance ranking in the first quartile at the two limestone tests and in the second and fourth quartiles at the two non-limestone tests (Table 2). The greatest difference was present at the Chalk River test site, where this provenance was first of 12 in the earlier study but only 10th of 13 in this study. Having slightly different geographic coordinates, the two populations are not derived from the same stand (Morgenstern and Copis 1999). Thus, the contradictory results of this and the earlier study indicate a high level of localized between-stand genetic differentiation in the Beachburg area. However, it is still possible that this pattern of variation corresponds to localized soil differences, owing to a mosaic of bedrock types in that region (OGS 1993).

The results of this study do not corroborate the work of Teich and Holst (1974) and offer little support for the existence of limestone ecotypes in white spruce. But because of the nature of the 410-series test design, these results do not disprove their existence either. Two features of the 410 series tend to weaken the value of the results. First, although the 23 provenances and four test sites were from a smaller section of Ontario than chosen for the Teich and Holst study, the test sites were farther apart, suggesting that climate differences may have played a greater role (Figs. 1 and 2). Second, although 23 provenances were tested on at least one limestone and one non-limestone site, only 7 were tested on all four sites. However, the comparison based on just the two 410 series of provenance tests with the best representation and having almost twice as many provenances as the earlier study (11 provenances of each bedrock type from non-limestone Minden and limestone Cornwall) also provided essentially no indication of edaphic ecotypes (Tables 2 and 3).

A primary assumption of this study is that soils are derived from their underlying bedrock material. Although many soils are formed through the breakdown and degradation of the parent material rock, soils can also be formed through transport processes, including water, gravity, wind, and moving ice (Webber 1985). In Ontario, glacial deposits in the form of till are widespread. Glacial meltwater deposits, such as kames, eskers, and outwash plains, are common throughout the province. Lake basin sediments are also a common source of soil composition (MNDM 1994). As a result of these processes, an unknown number of the provenance classifications performed for this study, based solely on parent material that is bedrock, may not reflect the actual soil composition. Errors of this sort might become evident as consistent misclassifications detected by discriminant analyses of performance at various test groupings, but no consistent provenance misclassifications were observed by this process.

Unfortunately, it is not possible to validate the soil origin designations for the 410 series of provenance seed sources, because the detailed site locations could not be found. There are two requirements for further work on limestone ecotypes of white spruce in southern Ontario. First, the classification as indicated by the OGS (1993) needs to be verified by laboratory testing or at least field tests to determine pH levels; or second, a large enough number of provenances in each category (about 10) is required to avoid misinterpretation due to between-stand variability arising from non-soil-related factors.

Acknowledgements

Funding for this study was provided by the Government of Ontario Interministerial Climate Change Committee, under Project CC-145. We are grateful for the technical assistance of Denny Irving, Ontario Ministry of Natural Resources (MNR), and Joel Symonds and Claire Riddell (Lakehead University). We also thank Paul Gray (MNR) for his continued support; and the Superior Woods Tree Improvement Association for providing financial support for thesis research by the senior author.

References

Boynton, R.S. 1966. Chemistry and technology of lime and limestone. InterScience Publishers, New York.

Cunningham, R.A. 1971. Genotype × environment interactions in white spruce. Ph.D. thesis, University of Wisconsin, Madison, Wis.

Farrar, J.L., and Nicholson, J.J.M. 1967. Response of ten provenances of white spruce seedlings to variable concentration of calcium in the nutrient medium. *In* Proceedings of the 14th Northeastern Forest Tree Improvement Conference, Toronto, Ont., 10–11 August 1966. pp. 39–42.

Goudge, M.F. 1935. Limestones of Canada: their occurrence and characteristics. Part IV: Ontario. Canada Department of Mines and Resources, Mines and Geology Branch, Ottawa, Ont.

Irving, D.E., and Skeates, D.A. 1988. Nursery indications of white spruce provenance variability in northwestern Ontario. Ontario Tree Improvement and Forest Biomass Institute; Queen's Printer for Ontario, Toronto, Ont.

Khalil, M.A.K. 1985. Genetic variation in eastern white spruce (*Picea glauca* (Moench) Voss) populations. Can. J. For. Res. **15**: 444–452.

Lesser, M.R. 2003. White spruce limestone ecotypes from provenance tests. B.Sc. (For.) thesis, Lakehead University, Thunder Bay, Ont.

Morgenstern, E.K., and Copis, P. 1999. Best white spruce provenances in Ontario. Can. For. Serv. Inf. Rep. ST-X-16.

Nienstaedt, H., and Teich, A.H. 1972. The genetics of white spruce. USDA For. Serv. Res. Pap. WO-15.

Nienstaedt, H., and Zasada, J. 1990. *Picea glauca* (Moench Voss.) white spruce. *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654. pp. 204–226.

OGS (Ontario Geological Survey). 1993. Bedrock geology, seamless coverage of the province of Ontario, ERLIS data set 6 [CD-ROM]. OGS, Toronto, Ont.

MNDM (Ontario Ministry of Northern Development and Mines). 1994. Rock Ontario. Queen's Printer for Ontario, Toronto, Ont.

SAS Institute Inc. 2001. SAS system for IRIX64 [computer program]. SAS Institute Inc., Cary, N.C.

Teich, A.H., and Holst, M.J. 1974. White spruce limestone ecotypes. For. Chron. **50**: 110–111.

Timmer, V.R., and Whitney, R.D. 1983. Chlorosis in planted white spruce at Limestone Lake, Ontario. Can. For. Serv. Inf. Rep. O-X-346.

Webber, L.R. 1985. Ontario soils: physical, chemical and biological properties and soil management practices. University of Guelph, Guelph, Ont. Publ. 492.

Xie, C.-Y., Yanchuk, A.D., and Kiss, G.K. 1998. Genetics of interior spruce in British Columbia: performance and variability of open-pollinated families in the East Kootenays. British Columbia Ministry of Forests, Victoria, B.C. Res. Rep. 07.

Appendix A

Appendix appears on the following page.

Table A1. The 410 series of white spruce provenances from below 46°N latitude tested at four Ontario test locations.

Provenance	Location	Origin	Bedrock type[b]	Latitude (°N)	Longitude (°W)	Replications at each test[c]			
						d3	g	f1	f2
8009[a]	Erin Township	Ont.	L	43°44′	80°06′	4	16	6	6
8010	Mulmur Township	Ont.	L	44°14′	80°04′	4		6	6
8012	Digby Township	Ont.	L	44°45′	78°56′	5			6
8013	Poland	Ont.	N	45°07′	76°35′	5		6	6
8015	Whitney	Ont.	N	45°32′	78°16′	4	12		6
8016[a]	Trout Creek	Ont.	N	45°59′	79°27′	5	14	5	6
8024[a]	Petawawa National Forest Institute	Ont.	N	45°59′	77°27′	4	14	6	6
8025	Bancroft	Ont.	L	45°06′	77°58′	4			5
8026[a]	Beachburg–Foresters Falls	Ont.	N	45°41′	76°48′	4	16	5	6
8027	Irvine Lake	Ont.	N	45°01′	77°16′	4			6
8028[a]	Renfrew	Ont.	L	45°28′	76°38′	4	16	6	6
8032	Antrim	Ont.	L	45°19′	76°11′	5		6	6
8033	Mowatt Township	Ont.	N	45°54′	80°26′	5			6
8155[a]	Douglas	Ont.	L	45°30′	77°01′	4	16	6	6
8165	Peck Township	Ont.	N	45°29′	78°45′	4	12		6
8166	Sinclair Township	Ont.	N	45°28′	79°05′	4	16		6
8167	Armour Township	Ont.	N	45°37′	79°25′	4	14		6
8189	East Mills Township	Ont.	N	45°55′	79°56′	5			6
8210[a]	Silver Lake	Ont.	L	44°49′	76°41′	4	16	5	6
8211	Anstruther Township	Ont.	L	44°55′	78°04′	4	16		6
8212	Gore Bay	Ont.	L	45°53′	82°19′	4		6	6
8317	Oro Township	Ont.	L	44°32′	79°33′	4		6	6
8371	Marmora	Ont.	L	44°28′	77°38′		16	5	6

[a]Provenances occurring at all four southern test locations.
[b]L, limestone; N, non-limestone.
[c]d3, Minden test site; g, Chalk River test site; f1, Owen Sound test site; f2, Cornwall test site.