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H.X. Wu · C.C. Ying

Variation on reaction norm in lodgepole pine natural populations

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Abstract Variations on the norm of reaction among ten natural lodgepole pine populations sampled from three lodgepole pine subspecies (*Pinus contorta* ssp. *contorta*, ssp. *latifolia* and ssp. *murrayana*) were studied by using 20 year heights measured in 57 provenance test sites across interior British Columbia (B.C.). There were significant population by site interactions. Concurrent joint regression and the AMMI model were used to dissect these population by environmental interactions. Joint regression analysis indicated that three populations (from the northwest) had a negative linear regression coefficient with environmental deviation, three (from central and southeast sites) had a positive regression coefficient and four (from the southwest) had a zero regression coefficient. The AMMI model revealed a similar pattern of reaction norm among the ten populations. But the three significant IPCA axes, which captured twice as much of the G × E sum of squares than joint regression, were more effective in separating the ten populations and associating their performance with the climate of test sites and their origin. The variation patterns of reaction norm in lodgepole pine populations demonstrated that adaptation of lodgepole pine natural populations to the various physical environments, at sub-species as well as at population level, was due largely to a balance between selection for high growth potential in less severe environments and selection for high cold hardiness in severe environments.

Keywords Norm of reaction · G × E interaction · Adaptation · Lodgepole pine · AMMI · Provenance variation

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H.X. Wu (✉)
CSIRO Forestry and Forest Products, P.O. Box E4008, Canberra, ACT 2604, Australia
e-mail: Harry.wu@ffp.csiro.au

C.C. Ying
Research Branch, British Columbia Ministry of Forests,
P.O. Box 9519, Stn. Prov. Govt., Victoria V8W 9C2, B.C., Canada

Introduction

Lodgepole pine (*Pinus contorta* Douglas) is the most wide-ranging and one of the most variable of pines in North America (Critchfield 1980). This species is notable for its adaptation to a wide range of environments, from low elevation, coastal bogs to alpine conditions, and occurs naturally in 12 out of the total 14 biogeoclimatic zones in British Columbia (B.C.) (Pojar 1985; Ying et al. 1985). Genetic variation among its populations in the subspecies *latifolia* has been extensively studied. The subspecies *latifolia* is the most-widely distributed and commercially the most valuable of the four geographic races of lodgepole pine (Critchfield 1980; Koch 1996). Both short-term (in a semi-controlled environment both in greenhouse and nursery) and long-term (in a forest environment) trials revealed large population variation in growth (Lindgren 1993; Ying et al. 1989; Xie and Ying 1996), pest tolerance (Wu et al. 1996; Wu and Ying 1997; 1998), phenological cycle and hardiness (Rehfeldt 1980, 1983, 1985, 1987). Populations in the central and northern range in Canada and the Yukon, a region of dissected plateaus, are arranged along gentle clines that follow climatic gradients across 18° of latitude from the Yukon to southern British Columbia. In the mountainous region of Idaho and Utah, population differentiation occurs along steep elevational clines that parallel the environmental changes associated with elevation (Rehfeldt 1987). Lodgepole pine is regarded as a specialist species because of its clinal mode of population response to environmental gradients (Rehfeldt 1984).

This causal interpretation of micro-evolution (specialist evolution) implies a process from the observed patterns; that is, populations genetically track environmental changes and the local population is adaptively optimal (Heslop-Harrison 1964; Bradshaw 1965). Adaptation means genetic adjustments (of structures and functions) on the part of individuals or populations resulting in a better fit to their environments (Antonovics 1971; Lewontin 1978). Populations occupying different ecological niches, e.g. central vs marginal populations, may evolve differently in terms of genetic adjustment (Rehfeldt et al. 1999). Analysis of the norm of reaction – a profile of phenotypes produced by a population across environments (Schmalhausen 1949; Gomulkiewicz and Kirkpatrick 1992) – in the context of population by environment interaction (G × E) seems to be conceptually attractive to depict the differential fitness of populations in heterogeneous environments, which fits with the definition of population adaptation of Wright (1976) and Lewontin (1978) mentioned above. Formation of the landscape pattern of reaction norm tends to be more revealing in its mechanistic correlation with evolutionary forces (e.g. natural selection, gene flow, etc.) (Wright 1951).

This report is based on growth data generated from large-scale long-term provenance testing in British Colombia (B.C.) (Ying and Illingworth 1986). We analyzed the response of ten geographically separated populations, across a wide-range of forest environments in interior B.C. represented by 57 test sites. Our main objective is to evaluate population variation in the norm of reaction in the broad context of G × E and to compare the efficiency of joint regression (Finlay and Wilkinson 1963) and AMMI (Additive Main effect and Multiplication Interaction model, Gauch 1992) in elucidating the regional pattern of the norm of reaction represented by ten natural populations originating from a broad geographic origin and a different climate.

Materials and methods

The adaptation analysis reported in this paper is based on growth data from the long-term provenance testing of lodgepole pine in interior B.C. The testing originally involved a total of 140 provenance samples throughout the species natural range, which were tested at 60 sites across the forest environments in interior B.C. (Fig. 1, where only 57 sites still existing are shown) and where lodgepole pine is a major timber species. Details of the testing are described in Illingworth (1969), Ying et al. (1985) and Wu et al. (1996). The 60 provenance tests were planted in spring 1974 with 2+1+1 seedlings which were raised at the B.C. Ministry of Forests research nursery at Red Rock, Prince George. The 60 sites span approximately 11° of latitude (49°05′ to 59°47′), 15° of longitude (from 114°41′ to 129°08′) and 1,450 m of elevation (from 380 to 1,830 m).

A subset of 60 out of the 140 provenance samples were tested at each site in two completely randomized blocks with a 3 by 3-tree square plot of nine trees, with trees spaced every 2.5 m. Ten of the 140 provenances were tested at all 57 sites (see Fig. 1). The ten standard provenances include provenance 119 (P119, Zig Zag) of ssp. *murrayana,* provenance 95 (P95, Petersburg) of ssp. *contorta*, and eight provenances of ssp. *latifolia*. Height was measured at 57 sites in the fall of 1994, 20 years after planting. Our analysis of population adaptation was based on the 20 year height of the ten standard provenances at the 57 sites. The provenance designates the geographic origin of seedling progeny samples of a particular population; provenance and population are used as synonyms in this report.

Analysis of adaptive variation is, in its broad context, an analysis of G × E. Statistical methods commonly applied to G × E are: (1) analysis of variances (ANOVA), (2) principal components analysis (PCA), and (3) linear regression. These methods are not always adequate to dissect a complex interaction structure (Zobel et al. 1988). ANOVA can only test the significance of G × E, and can not provide any insight about its patterns; PCA only considers the multiplicative effects of G × E. The linear regression method combines additive and multiplicative components, but it has inherent statistical rigidity; even minor deviation can lead to misinterpretation, e.g. the confounding of interaction and main effects (Wright 1971) and misrepresenting non-linear genotype response to environments or non-linear genotype by environment interaction (Nachit et al. 1992). To circumvent these problems, an additive main effect and multiplicative interaction (AMMI) model was proposed (Gollob 1968). The AMMI model incorporates both additive and multiplicative components into an integrated least square analysis and it has been suggested that it provides more insight into the nature of the genotype by environment interaction, particularly when the interactions are non-linear (Mandel 1971; Freeman 1985; Gauch 1992). In forestry, multiple regression is commonly used to detect a relationship between population variation and environmental gradients for inferring adaptive variation (Campbell 1978; Rehfeldt 1987), in which local adaptive optimality and minimal G × E are implicitly assumed. Because of the large number of test sites across wide diverse environments (Fig. 1), B.C.'s lodgepole pine provenance trials offer the opportunity to analyze population adaptation in the context of G × E explicitly, focusing on the concept of the norm of reaction (Gregorius and Namkoong 1986; Baker 1987).

We used the following three models to analyse adaptation patterns of the ten lodgepole pine provenances across the 57 test sites in interior British Columbia: analysis of variances, concurrence or joint linear regression (Tukey 1949; Finlay and Wilkinson 1963), and the additive main effects and multiplicative interaction (AMMI) model (Gauch 1992).

The analysis of variance model (ANOVA) is

$$Y_{per} = \mu + \alpha_p + \beta_e + \theta_{pe} + \varepsilon_{per}\,, \qquad (1)$$

the linear regression model (LR) is

$$Y_{per} = \mu + \alpha_p + \beta_e + \xi_p \beta_e + \phi_e \alpha_p + \kappa\alpha_p \beta_e + \rho_{pe} + \varepsilon_{per}\,, \qquad (2)$$

and the AMMI model is

$$Y_{per} = \mu + \alpha_p + \beta_e + \sum_{n=1}^{N} \lambda_n \zeta_{pn} \eta_{en} + \rho_{pe} + \varepsilon_{per}\,, \qquad (3)$$

where Y_{per} is the tree height of the p-th provenance (p from 1 to 10) in the e-th environment (e from 1 to 57), μ is the grand mean, α_p is the provenance mean deviation, and β_e is the environment mean deviation. In the ANOVA model (Eq. 1), θ_{pe} is the provenance by environment interaction (G × E) component. In the LR model (Eq. 2), κ is the Tukey's concurrence constant, ξ_p is the provenance slope on the environmental deviations, and ϕ_e is the environment slope on the provenance deviations. The LR technique partitioned the provenance by environment interaction (θ_{pe}) into joint ($\kappa\alpha_p\beta_e$), provenance ($\xi_p \beta_e$), environmental regression ($\phi_e \alpha_p$) and a residual term (ρ_{pe}).

In the AMMI model (Eq. 3), λ_n is the square root of the eigenvalue of the n-th principal component axis (PCA), ζ_{pn} and η_{en} are the provenance and environment PCA values, respectively for the n-th axis, N is the number of PCA axes retained in the model and ρ_{pe} is the residual. The ζ and η eigenvector values for each PCA axis are scaled to unit vectors such that ($\sum\zeta^2 = \sum\eta^2 = 1$). The eigenvalue for a given PCA axis is the sum of squares (SS) accounted for by that axis, and it equals λ^2 (Gauch 1992).

For an AMMI model, the sum of the eigenvalues ($\sum\lambda^2$) for N axes and the residual SS (ρ_{pe}) for a reduced model is equal to the provenance by environment interaction SS. The condensation for most of the provenance by environment interactions in a few interaction principal component (IPCA) axes [n < min(P-1, E-1)] results in a reduced AMMI model with a residual term (ρ_{pe}); therefore, ρ_{pe} is different for each of these different models. For a replicated experiment such as the lodgepole pine provenance trials in British Columbia, there is an error term ε_{per} for all the models: $Y_{per} = Y_{pe} + \varepsilon_{per}$. This error term is used for significance testing for all other terms in the models. The degrees of freedom (*df*) for the IPCA axes and an *F*-test (F_{GH2}) for each PCA axis are calculated according to Mandel's method (1971). The provenance by environment interaction is modeled by the multiplication of a provenance IPCA score ($\lambda_n^{0.5}\, \zeta_{pn}$) with an environment IPCA score ($\lambda_n^{0.5}\, \eta_{en}$). All statistical analyses were performed by SAS software (SAS Inc. 1990).

Fig. 1 Location of ten provenances and 57 field trials of lodgepole pine

Table 1 Location, predicted climatic parameters and average height for ten standard provenances and 57 environments in British Columbia[a]

Provenance		Latitude	Longitude	Elevation	Height	MAT[b]	MAP	NFFD
No.	Name							
P1	Trapping	49.35	119.01	1,005	758.0	4.77	496.5	156.7
P13	Horne	51.46	124.44	915	575.9	3.62	887.0	161.0
P30	Lower	59.59	128.33	640	617.3	–2.01	295.9	112.8
P44	Marl	51.31	117.11	945	777.5	3.85	514.5	155.5
P61	Purden	53.52	121.44	840	742.0	2.30	509.2	151.8
P71	Flyhills	50.43	119.27	1,525	738.9	1.39	626.6	127.5
P95	Petersburg	56.47	132.58	23	455.3	5.47	2057.9	233.3
P100	Nina	55.48	124.48	760	728.4	0.96	505.4	143.5
P104	Nechako	54.01	124.31	730	742.9	2.79	591.8	159.7
P119	ZigZag	45.23	121.52	550	556.1	7.55	831.1	250.7
Site								
Region	Name							
1	WUHO	49.45	115.95	1,340	812.5	3.17	415.1	130.3
1	LAMB	49.32	115.90	1,250	815.8	3.75	429.1	135.4
1	ELKC	50.25	115.48	1,190	734.8	3.51	527.9	140.9
1	LUSS	49.80	115.50	1,650	564.6	1.34	521.9	120.7
1	FREE	49.08	115.85	1,520	706.4	2.44	463.3	119.8
2	RODY	50.08	118.57	1,460	701.0	2.08	477.0	127.5
2	BISN	50.03	118.57	1,130	673.7	3.85	401.0	145.4
2	LASI	49.62	118.92	1,370	733.9	2.76	513.6	130.6
2	MCLA	49.35	114.68	1,550	747.2	2.07	470.8	120.2
3	CHUW	50.58	120.62	1,430	513.7	1.85	633.2	130.3
3	COMM	50.92	120.07	1,370	736.0	2.04	578.2	132.8
3	PETI	49.25	120.20	1,520	542.4	1.96	959.8	123.9
3	HADO	50.08	119.10	1,340	768.2	2.68	466.3	132.9
3	EQUI	50.37	119.62	1,370	699.7	2.35	511.4	132.1
4	WIGW	50.82	117.98	790	715.8	5.11	422.6	171.1
4	SUEB	51.57	117.40	1,550	470.6	0.99	922.7	131.8
4	SUEF	51.57	117.35	1,190	815.4	2.67	605.2	141.4
4	SUEM	51.58	117.32	950	833.3	3.77	513.0	155.0
4	BEAV	51.03	116.33	1,370	577.7	2.18	678.1	134.2
5	NIQU	52.45	121.32	950	716.4	3.03	510.6	152.0
5	TIMY	51.90	120.28	1,280	606.9	1.89	650.1	136.4
5	BOSS	51.98	120.80	1,190	728.8	2.25	600.8	140.0
5	BOSK	52.18	120.80	1,100	694.1	2.54	557.9	144.0
5	TUYA	51.45	120.35	1,250	787.6	2.32	571.5	137.9
6	MI70	51.28	121.33	1,070	449.5	3.27	534.8	148.5
6	HOLD	51.62	121.52	1,160	606.0	2.60	592.1	142.2
6	MONS	51.67	123.00	1,280	484.0	1.89	811.9	136.7
6	CUIS	52.50	122.38	850	705.4	3.46	535.0	159.4
6	KLOK	51.67	123.50	1,520	406.8	0.62	1105.9	128.9
7	BATE	53.88	121.98	730	797.2	2.77	480.1	159.3
7	GOAT	53.50	120.58	700	1044.6	3.22	465.4	163.8
7	HOLM	53.35	119.83	910	750.8	2.45	539.0	150.6
7	VALE	52.78	119.32	1,100	747.5	2.12	635.1	143.2
7	DAVE	52.75	119.08	980	877.5	2.67	553.5	149.3
8	ATIS	52.97	121.92	1,220	643.9	1.45	743.2	137.3
8	BAKR	53.05	122.23	910	769.8	2.72	540.3	151.9
8	CMP4	53.70	122.42	1,000	726.3	1.76	616.2	143.4
8	NECK	53.25	122.33	950	732.0	2.37	566.7	148.3
8	WHIT	53.33	122.58	670	606.9	3.59	512.0	168.6
9	DECK	54.37	125.82	930	634.1	1.61	730.9	143.6
9	FRAS	53.95	124.78	850	799.2	2.30	641.7	151.3
9	OTSA	53.77	126.83	1,040	671.1	1.60	967.3	141.4
9	TZEN	52.65	122.72	1,220	562.3	1.56	772.3	137.0
9	BART	53.50	123.42	790	638.1	2.92	556.0	158.1
10	BLAC	55.53	123.55	730	570.1	1.24	477.6	147.3
10	CARP	54.60	122.92	790	829.1	1.86	507.8	150.3
10	DOGC	54.27	124.40	950	768.4	1.53	657.1	142.9
10	WEST	55.83	123.70	670	804.4	1.19	455.3	148.8
10	SAMN	54.85	123.92	950	652.3	0.98	632.0	139.5
11	MCBR	54.07	127.30	850	608.4	2.34	882.8	152.4

Table 1 (continued)

Site		Latitude	Longitude	Elevation	Height	MAT[b]	MAP	NFFD
Region	Name							
11	CHAP	54.92	126.68	790	716.8	1.85	684.2	149.4
11	SUSK	55.32	127.27	640	776.2	2.27	679.2	158.5
11	NILK	55.32	126.67	760	752.9	1.62	630.9	148.2
11	TELK	54.62	127.32	760	767.0	2.33	779.7	154.9
12	M451	58.83	125.72	1,100	223.2	–3.23	961.2	111.1
12	M559	59.75	127.38	610	147.6	–1.88	300.8	116.8
12	BLUE	59.78	129.13	730	179.3	–2.14	323.1	109.6

[a] Height – cm; latitude (degree); longitude (degree), elevation (meter); MAT-mean annual temperature; MAP-mean annual precipitation; NFFD-number of frost-free days

[b] MAT, MAP, and NFFD were estimated from the climatic model developed by Dr. Jerry Rehfeldt in the Intermountains Research Station, USDA Forest Service, except for the Zig Zag site (provenance P119), where climatic data were estimated by the closest weather station of Appleton, 45°82′, 121°27′, 712 m)

Table 2 Analysis of variance, linear regression, and AMMI for lodgepole pine height of ten standard provenance in 57 British Columbia environments

Source	*df*	Sum of squares	Mean squares	*F* values	*Pr*
ANOVA					
Treatments	564	40,330,735	71,508	14.24	0.0001
Site	56	24,495,390	437,418	87.11	0.0001
Provenance	9	11,963,316	1,329,257	264.72	0.0001
Site × provenance	499	3,872,029	7,760	1.55	0.0001
Error	557	2,796,859	5,021		
Total	1121	43,127,593			
Linear regression					
Treatments	564	40,330,735	71,508	14,24	0.0001
Site	56	24,495,390	437,418	87.11	0.0001
Provenance	9	11,963,316	1,329,257	264.72	0.0001
Site × provenance	499	3,872,029	7,760	1.55	0.0001
Joint reg.	1	173,917	173,917	34.64	0.0001
Prov. reg.	8	553,368	69,171	13.78	0.0001
Site reg.	55	570,892	10,380	2.07	0.0001
Residual	440	2,573,851	5,850	1.17	0.0426
Error	557	2,796,859	5,021		
Total	1121	43,127,593			
AMMI analysis					
Treatments	564	40,330,735	71,508	14.24	0.0001
Site	56	24,495,390	437,418	87.11	0.0001
Provenance	9	11,963,316	1,329,257	264.72	0.0001
Site × provenance	499	3,872,029	7,760	1.55	0.0001
PCA1	102	1,324,759	20,699	2.70	0.0001
PCA2	93.6	616,453	9,943	1.34	0.0251
PCA3	88.3	564,314	9,405	1.87	0.0523
PCA4	81.7	404,638	6,977	1.39	0.5316
Residual	255	961,865	3,772	0.75	0.9962
Error	557	2,796,859	5,021		
Total	1121	43,127,593			

Results

Both provenances and sites had considerable variation in productivity (height) at age 20 (Table 1). Height varied from 455.3 cm for P95 (ssp. *contorta*), to 777.5 cm for P44. P119, which belongs to ssp. *murrayana*, was the second lowest with average height of 556.1 cm. P13 (a mixture of ssp. *contorta* and *latifolia* from the coast-interior transition) and P30 (from northern B.C.) also grew poorly. All the other six provenances, from interior B.C. (ssp. *latifolia*), had a high growth rate with tree height above 728 cm. A comparison between growth and climatic data reveals that provenances from regions with high rainfall (coast, i.e. P95) and high temperature (far

Fig. 2 Significant linear relationship between environmental deviation and interaction for six lodgepole pine provenances tested in 57 British Columbia sites

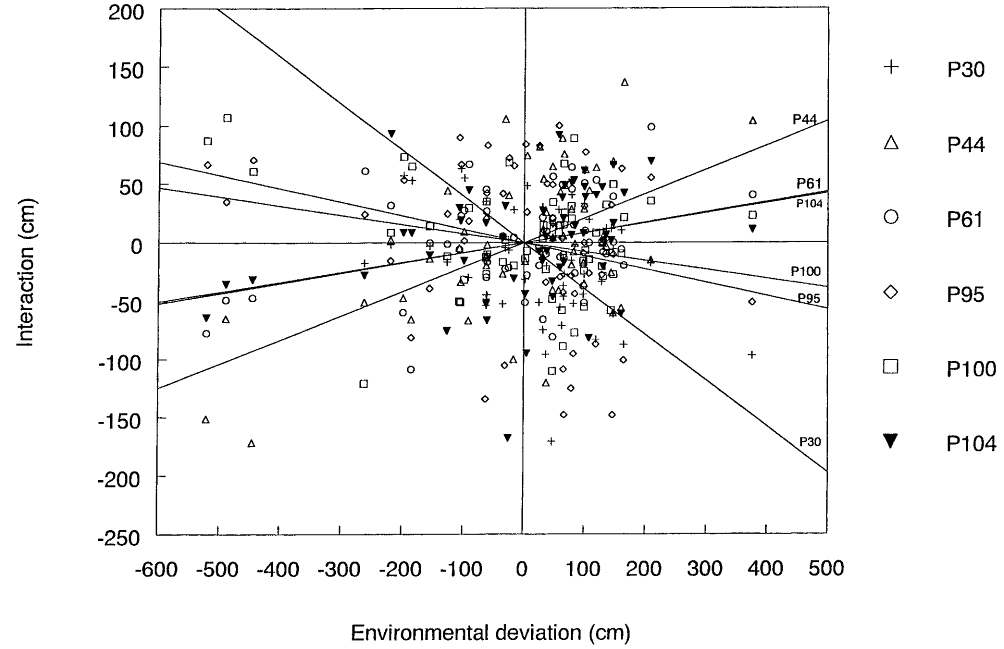
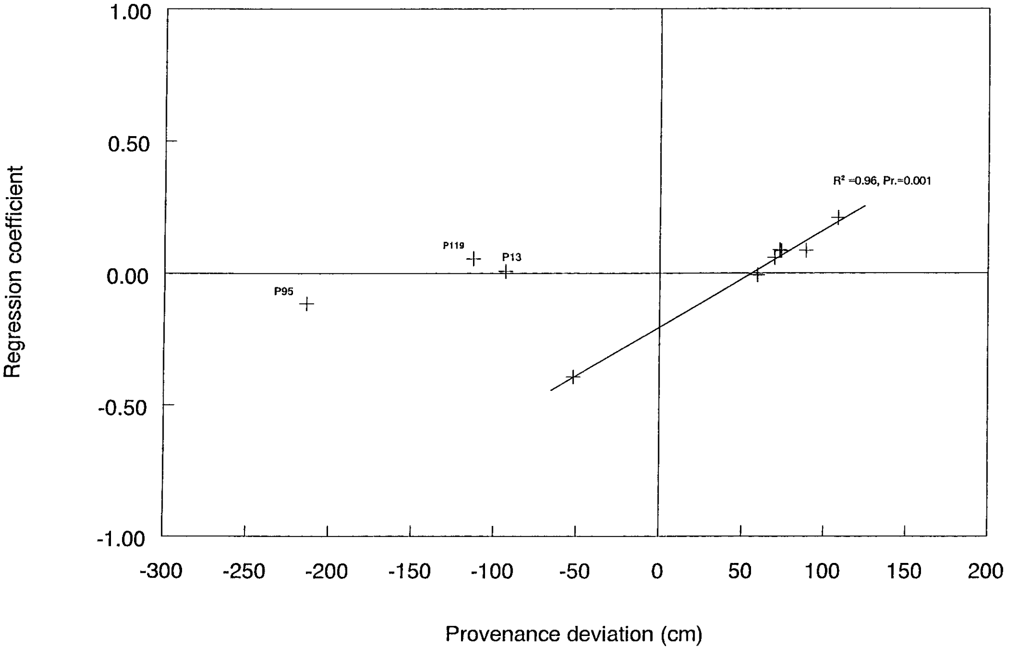


Fig. 3 Relationship between provenance deviation and regression coefficient for ten standard provenances (also showing regression when excluding P95-contorta, P119-murrayana, and P13-transition)



south, i.e. P119) or low temperature (far north, i.e. P30) were not well-adapted to the growth environment in interior B.C., relative to native populations (Table 1).

The three most-northern sites (M451, M559 and BLUE) had the lowest average height (223.2 cm, 147.6 cm and 179.3 cm, respectively) while the site at Goat River (a low elevation site) had the highest growth (1,044.6 cm). Trees grew poorly at high elevation sites, e.g., SUEB, MONS, KLOK. A comparison between growth and climatic data for the 57 sites again indicates that sites with high rainfall (above 700 cm, except for site TELK) and low temperature (mean annual temperature <1.5°) had poor growth in interior B.C. (Table 1).

Analysis of variance showed that the mean squares of sites, provenances, and provenance by site interaction were highly significant (Table 2) and accounted for 60.7%, 29.7%, and 9.6%, respectively, of the treatment (site plus provenance) combination SS. Although the ANOVA indicated significant interaction between provenances and sites, the nature of this interaction was not revealed.

Linear regression analysis demonstrated that the joint provenance and site regressions were highly significant (Table 2) and accounted for 4.5%, 14.3%, and 14.7% of the interaction SS, respectively. Six provenances had a significant linear relationship between their site by provenance interactions and environmental effects (Fig. 2).

Table 3 Deviation (α_p β_e), Linear regression models (Slope R^2, SE^a, Prob), and AMMI models (IPCA1, IPCA2, IPCA3, IPCA4) for lodgepole pine height of ten standard provenances in 57 British Columbia environments

Item		Deviation	Slope	R^2	SE^a	Prob.	IPCA1	IPCA2	IPCA3	IPCA4
Provenance										
No.	Name									
P1	Trapping	88.8	0.085	0.066	0.043	0.054	–7.41	–1.62	2.68	–8.68
P13	Horne	–93.4	0.008	0.001	0.056	0.883	–0.25	21.92	–2.18	0.93
P30	Lower	–52.0	–0.394	0.533	0.049	0.000	21.78	–2.80	–5.67	–0.63
P44	Marl	108.3	0.208	0.306	0.042	0.000	–12.04	–2.47	–3.77	–0.94
P61	Purden	72.7	0.087	0.119	0.031	0.008	–4.35	–3.75	–1.12	–4.96
P71	Flyhills	69.6	0.058	0.040	0.038	0.137	–3.35	2.45	–2.63	7.09
P95	Petersburg	–214.0	–0.114	0.080	0.052	0.032	7.84	0.82	15.73	–7.45
P100	Nina	59.2	–0.077	0.070	0.037	0.046	4.81	–4.69	–6.56	5.54
P104	Nechako	73.7	0.084	0.079	0.038	0.034	–3.75	–4.64	–7.41	–4.65
P119	ZigZag	–113.1	0.055	0.023	0.048	0.262	–3.28	–4.60	10.92	13.77
Site										
Region	Name									
1	WUHO	143.2	–0.109	0.065	0.147	0.478	0.01	–3.24	3.87	0.66
1	LAMB	146.6	–0.152	0.128	0.139	0.309	–1.27	3.08	1.76	2.87
1	ELKC	65.6	0.296	0.332	0.148	0.081	–3.10	–2.00	–2.64	4.88
1	LUSS	–104.6	–0.092	0.046	0.148	0.551	2.56	–1.44	0.82	–2.78
1	FREE	37.2	–0.340	0.267	0.199	0.126	1.83	–1.08	4.46	6.18
2	RODY	31.8	0.120	0.049	0.187	0.539	–3.06	–4.24	2.09	2.41
2	BISN	4.5	–0.017	0.001	0.218	0.938	0.27	–4.62	3.43	–0.04
2	LASI	64.6	–0.058	0.013	0.176	0.750	–2.68	2.42	1.69	0.23
2	MCLA	78.0	0.231	0.540	0.075	0.015	–1.00	–1.59	–2.49	–1.19
3	CHUW	–155.5	0.053	0.019	0.133	0.702	–0.60	–3.28	0.93	4.00
3	COMM	66.8	0.368	0.443	0.145	0.035	–2.80	1.15	–6.18	3.14
3	PETI	–126.8	–0.083	0.069	0.107	0.462	–0.83	0.59	2.55	0.05
3	HADO	99.0	0.127	0.109	0.129	0.253	–1.48	–3.04	–0.52	–0.09
3	EQUI	30.5	–0.001	0.000	0.069	0.991	1.00	–2.03	0.49	–0.03
4	WIGW	46.6	–0.197	0.059	0.277	0.497	–5.78	1.39	7.04	0.58
4	SUEB	–198.7	–0.112	0.049	0.173	0.538	3.93	–1.33	–0.71	1.54
4	SUEF	146.1	0.412	0.320	0.212	0.088	–2.41	–5.30	–5.22	6.17
4	SUEM	164.1	0.432	0.438	0.172	0.037	–5.54	–3.36	–2.90	3.38
4	BEAV	–91.6	0.168	0.106	0.172	0.358	0.10	0.44	–2.27	–4.55
5	NIQU	47.2	–0.166	0.112	0.164	0.344	–0.56	–0.54	4.04	–1.52
5	TIMY	–62.3	–0.167	0.201	0.118	0.193	–1.30	2.97	3.12	2.55
5	BOSS	59.6	0.093	0.044	0.152	0.561	–1.89	4.34	–2.26	1.28
5	BOSK	24.9	–0.004	0.000	0.183	0.981	–1.37	1.90	0.83	–5.33
5	TUYA	118.4	0.386	0.567	0.119	0.012	–4.81	–1.70	–2.44	–1.41
6	MI70	–219.7	0.145	0.124	0.136	0.319	–0.04	0.26	–3.71	–2.97
6	HOLD	–63.2	0.356	0.429	0.145	0.039	–0.74	1.50	–6.10	0.60
6	MONS	–185.3	0.004	0.000	0.213	0.985	1.88	1.81	–2.49	2.36
6	CUIS	–262.4	–0.096	0.030	0.190	0.629	–1.28	2.09	3.53	–3.71
6	KLOK	36.2	0.110	0.052	0.166	0.525	–3.62	4.88	–1.13	–0.10
7	BATE	128.0	0.143	0.323	0.073	0.086	–1.75	0.71	–1.42	–1.59
7	GOAT	375.4	0.352	0.340	0.173	0.076	–4.32	2.71	–4.26	–1.66
7	HOLM	81.6	0.359	0.345	0.175	0.074	–2.26	–5.06	–3.06	4.89
7	VALE	78.3	0.361	0.405	0.154	0.047	–0.39	0.08	–6.03	–2.78
7	DAVE	208.3	0.108	0.022	0.252	0.679	–0.20	–7.26	1.52	–5.72
8	ATIS	–25.3	0.328	0.217	0.220	0.175	1.56	0.46	4.65	5.95
8	BAKR	100.6	–0.120	0.065	0.160	0.478	0.14	0.57	0.59	–3.46
8	CMP4	57.1	–0.049	0.004	0.265	0.857	1.93	–8.63	3.02	–2.93
8	NECK	62.8	0.403	0.395	0.176	0.051	–4.36	–2.82	–1.22	–4.43
8	WHIT	–62.3	0.057	0.016	0.158	0.730	–0.97	–3.12	2.94	–1.33
9	DECK	–35.1	–0.037	0.019	0.093	0.705	–1.16	–0.39	2.41	–0.66
9	FRAS	130.0	–0.069	0.053	0.103	0.524	–0.67	–0.17	2.19	–0.74
9	OTSA	1.9	–0.227	0.248	0.139	0.143	–0.00	1.75	4.45	–2.53
9	TZEN	–106.9	–0.221	0.284	0.123	0.112	1.77	1.15	1.52	–1.72
9	BART	–31.1	0.292	0.276	0.167	0.119	–2.79	0.18	–3.95	–0.92
10	BLAC	–99.1	0.067	0.053	0.100	0.522	0.98	–1.04	–0.64	–2.84
10	CARP	159.9	–0.297	0.570	0.091	0.011	2.11	3.82	2.51	0.24
10	DOGC	99.2	0.221	0.305	0.118	0.098	1.76	3.30	0.26	–0.34
10	WEST	135.2	–0.022	0.003	0.146	0.882	1.23	3.92	–2.62	–2.18

Table 3 (continued)

Item		Deviation	Slope	R^2	SE[a]	Prob.	IPCA1	IPCA2	IPCA3	IPCA4
Site										
Region	Name									
10	SAMN	–16.9	–0.398	0.619	0.110	0.006	3.25	3.47	2.82	1.98
11	MCBR	–60.8	–0.332	0.492	0.119	0.023	0.32	4.56	3.65	1.12
11	CHAP	47.5	–0.038	0.008	0.152	0.807	1.06	3.10	–0.55	–1.29
11	SUSK	107.0	0.019	0.003	0.121	0.877	–0.16	1.79	–0.42	1.92
11	NILK	83.7	0.058	0.013	0.178	0.754	–1.10	5.52	–2.25	–1.09
11	TELK	97.8	–0.124	0.133	0.112	0.299	–1.04	3.56	0.86	1.93
12	M451	–446.0	–0.574	0.275	0.329	0.119	12.20	2.75	–1.45	1.57
12	M559	–521.6	–0.652	0.205	0.453	0.188	16.29	–0.34	–2.17	1.57
12	BLUE	–489.9	–0.218	0.039	0.380	0.582	11.14	–4.59	–2.95	–2.13

[a] SE – standard error of the slope

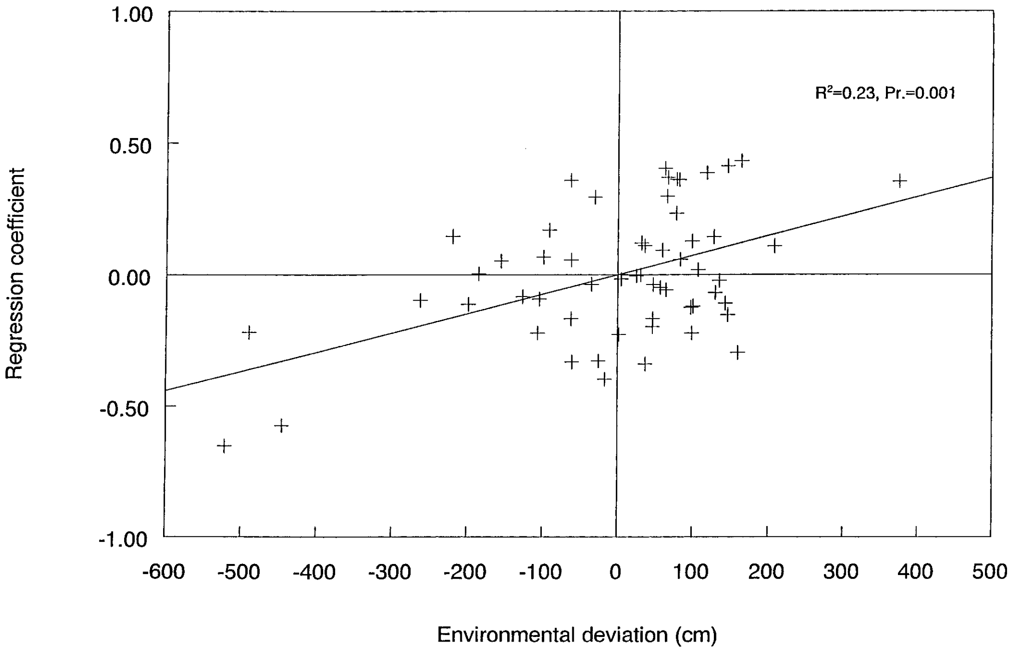


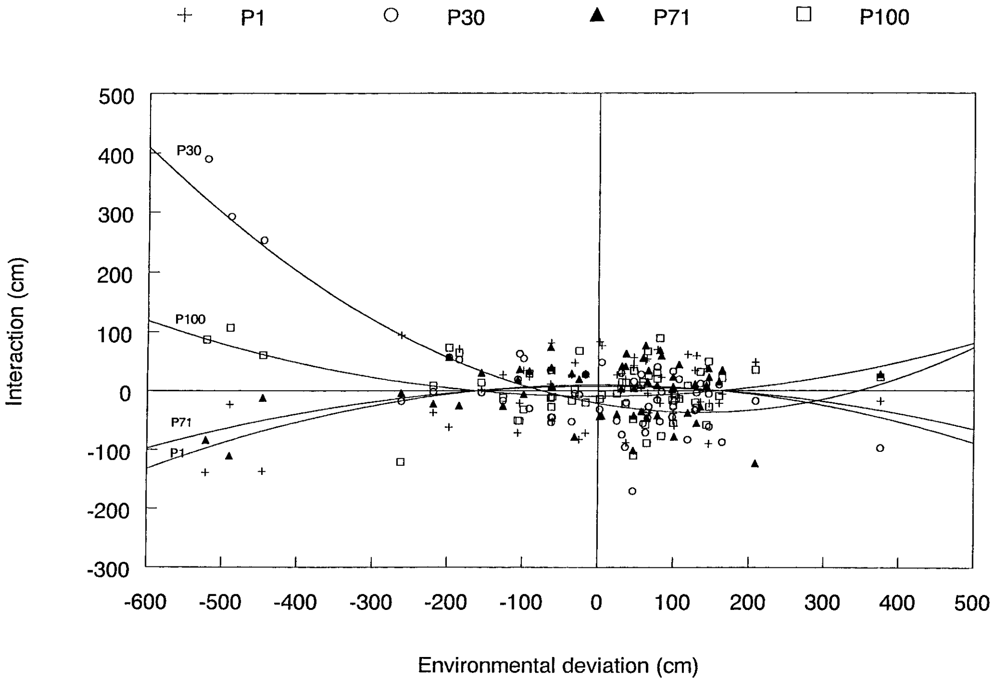
Fig. 4 Relationship between environmental deviation and regression coefficient for 57 lodgpole pine provenance tests in British Columbia

Three provenances (P44, P61 and P104) had positive regression coefficients (the interaction increases as the environmental effect increases), indicating that these provenances perform better in the more-productive sites than expected from the average linear regression, but worse than expected in the lower-productive site. The other three (P30, P95 and P100) had negative regression coefficients. There was no significant relationship between interactions and environmental effects for the remaining four provenances (P1, P13, P71 and P119). Three provenances (P95, P119 and P13) (Fig. 3) significantly influenced the outcome of regression analysis. Excluding these three provenances (i.e. an analysis based on the seven interior B.C. provenances) resulted in a much improved correlation between provenance effects and their regression coefficients (r = 0.98, *Pr.* = 0.001). This further reinforces the observation that productive provenances were better adapted to productive sites, whereas less-productive provenances performed better at poor sites (e.g. P30 at sites M451, M559 and BLUE).

Among the 57 sites (environments), only ten had a significant linear regression at the 5% probability level. Another five sites were significant at the 10% probability level (Table 3). This may be because of the small number of provenances (few degrees of freedom). Regardless of this, a significant positive relationship between site productivity (site effects) and the regression coefficient (*r* = 0.483, *Pr.* = 0.001) supports the results of population regression analyses which indicate that productive sites favour productive provenances, and vice versa with poor sites (Fig. 4). However, this relationship was not statistically significant if the three most northern sites (M449, M559, BLUE) were excluded.

Although both provenance and site regressions accounted for a highly significant portion of the provenance by site interaction SS, the residual after accounting for regressions was still significant and accounted for 66.5% of the G × E SS. This significant residual suggests that the interactions between provenance and site were

Fig. 5 Significant non-linear relationship between environmental deviation and inter action for four lodgepole pine provenances tested in 57 British Columbia sites



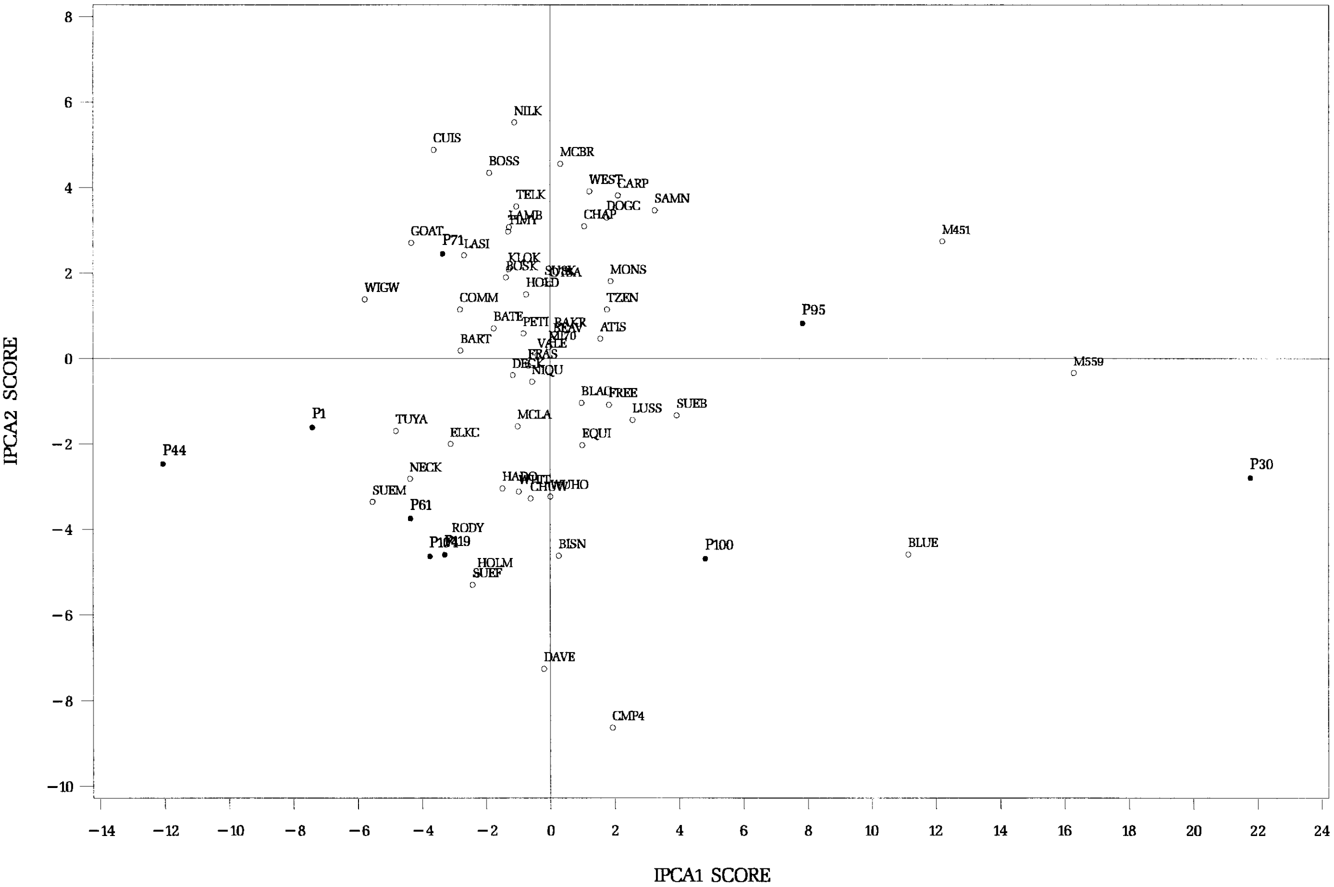


Fig. 6 B-plot of G*E interaction for ten lodgepole pine provenances (●) and 57 test sites (○) in British Columbia. P13 with IPCA1 = –0.25 and IPCA2 = 21.92 is out of the figure

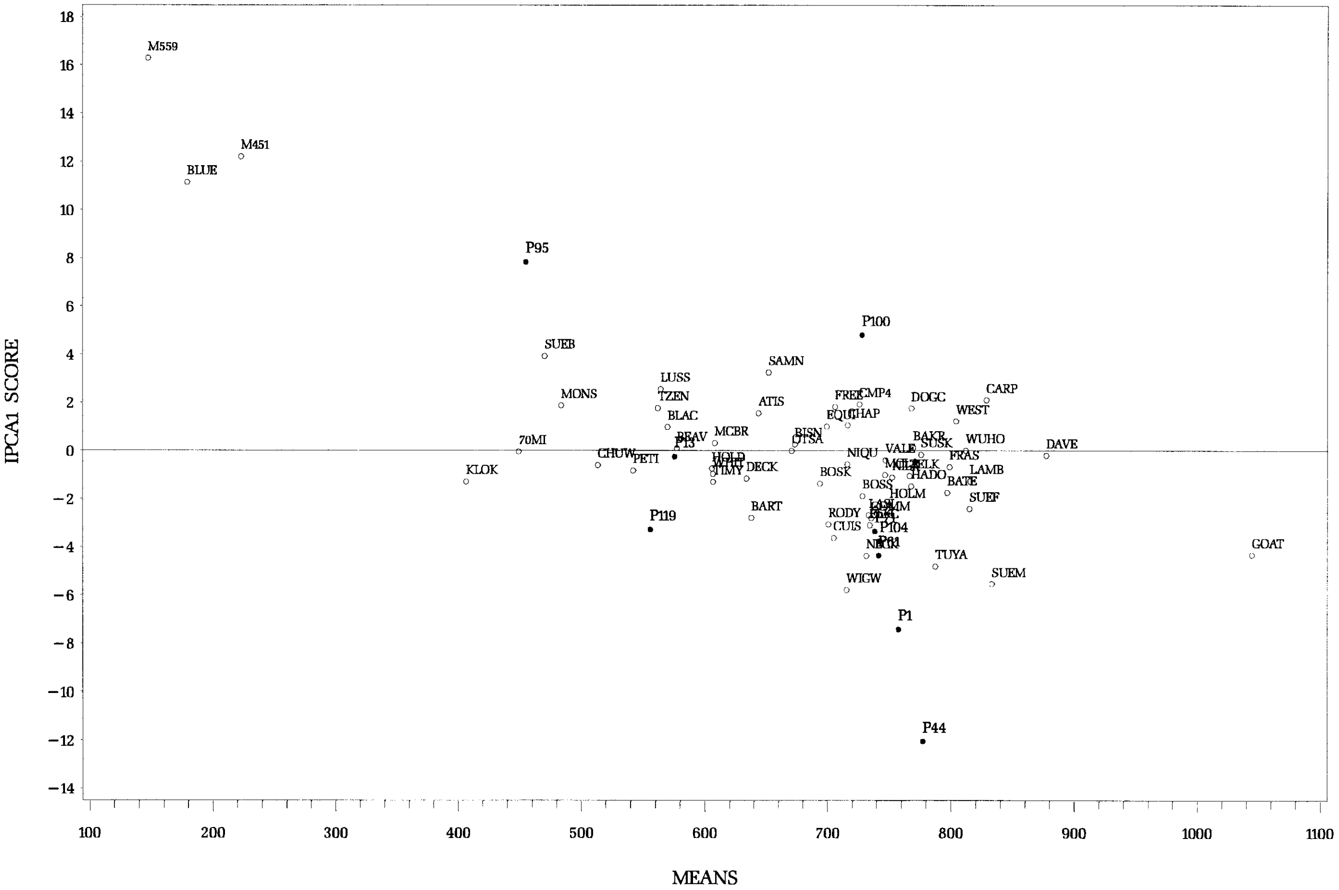


Fig. 7 Relationship between IPCA1 score and mean for ten lodgepole pine provenances (●) and 57 test sites (○) in British Columbia. P30 with mean height = 617 and IPCA1 = 21.78 is out of the figure

not always linear. Further analysis, indeed, showed that there were significant non-linear relationships between provenance by site interactions, with environmental effects for four provenances (Fig. 5). P30 and P100 had a positive quadratic relationship with environment effects whereas P1 and P71 had a negative quadratic relationship with environment effects. Fitting a quadratic regression accounted for an additional SS of 32%, 146%, 147% and 163% over that of linear regressions for P30, P100, P1 and P71, respectively (Table 3). The quadratic response to an environmental gradient indicates that populations from the northern region (e.g. P30, P100) or from high elevation (e.g. P1, P71) are sensitive to transfer outside their native habitats.

Since the residuals after fitting linear regression for both provenance and site were still significant, we proceeded to use the AMMI model to further examine the patterns of provenance by site interactions. The AMMI model partitioned the provenance by site interactions into four significant interaction principal component axes (IPCA, Table 2). The three significant IPCA axes accounted for 64.7% of the provenance by site interaction SS, compared with 33.5% accounted for by linear regressions. Of the three significant IPCA axes, IPCA1 accounted for 34.2% of the provenance by site interaction SS in 20.4% of the interaction degrees of freedom, and IPCA2 15.9% in 18.8% of the degrees of freedom. IPCA 3 captured 14.6% the G × E SS in 17.7% of the degrees of freedom.

The first IPCA axis alone accounted for more G × E SS than the three regression components combined in the joint regression analysis (34.2 vs 33.5%). The first three significant IPCA axes accounted for twice as much G ×E SS than the three linear regressions. These results demonstrate the effectiveness of the AMMI model in capturing and partitioning the SS of provenance by site interaction in comparison to the joint linear regression techniques.

Figure 6 shows a biplot between the IPCA1 and IPCA2 scores. This figure captured 50.1% of the SS of the interaction. The distribution pattern of provenances on the plot reflects their respective geographic origin except for P119 and P44 (Fig. 1). P30 is located to the far right on the plot (equivalent to far north, Fig. 1). P95 and P100 from the northwest are together on the right side of the plot. P13 from the west (Fig. 1) is far up on the plot (outside the figure to avoid clutter). P104 and P61 from the central region, and P71 and P1 from the southern interior are close to each other relative to their geographic distributions. The plot also shows that sites from a particular geographic region tend to cluster together, such that sites from regions 7, 8 and 9 are clustered in the upper right corner of the plot (the area above zero for

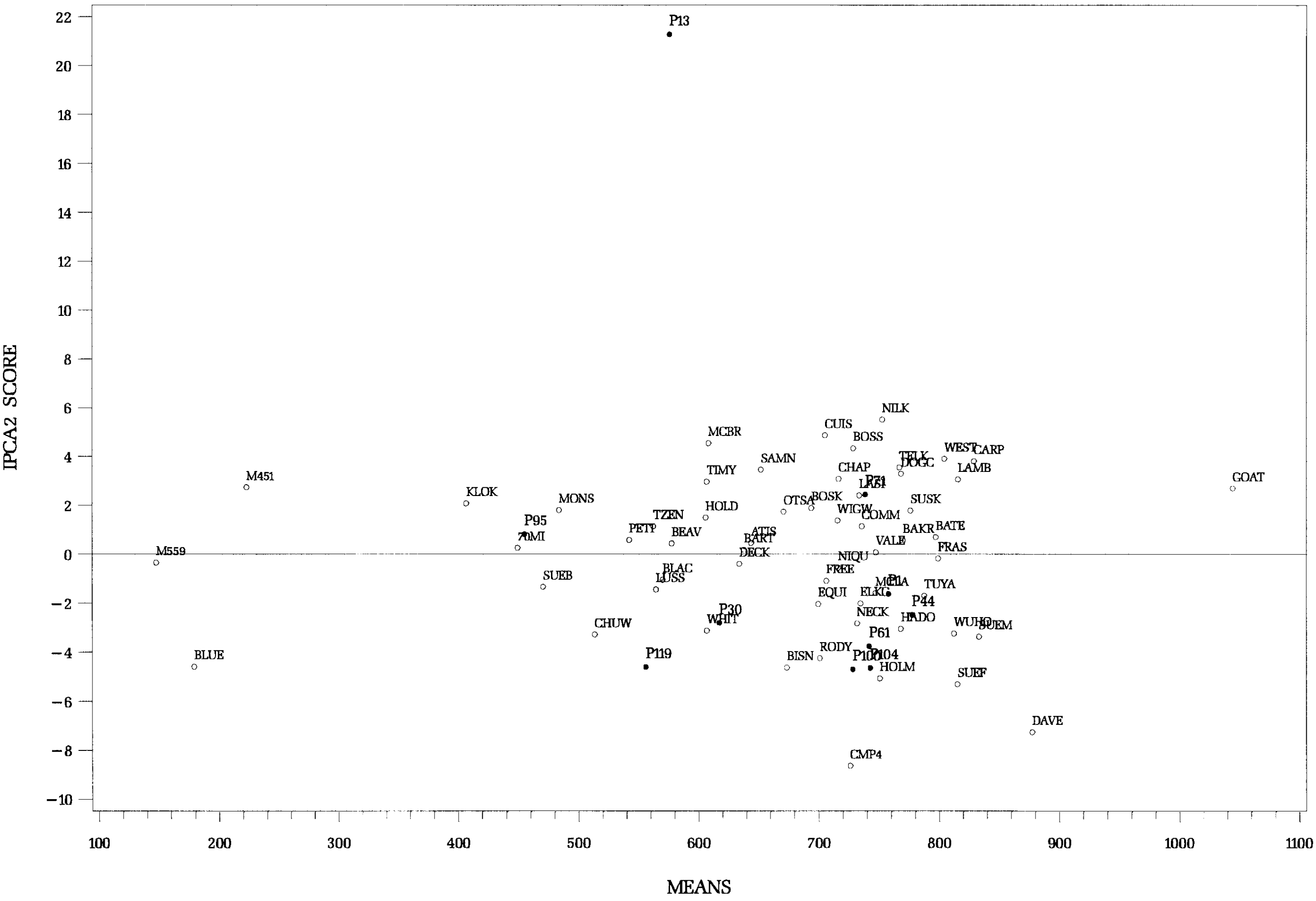


Fig. 8 Relationship between IPCA2 score and mean for ten lodgepole pine provenances (●) and 57 test sites (○) in British Columbia

IPCA2 and close or above zero for IPCA1). The three most-northern sites (M451, M559 and BLUE) are mapped to the far right of the plot (equivalent to the north in Fig. 1). This demonstrates that the interactions have a geographic pattern which Fig. 6 well captures. In addition, Fig. 6 reveals that provenances P13, P30 and P44 contributed far more interaction than other individual provenances. Furthermore, the provenances are more spread than the sites in the plot, indicating that provenances had more interactions than sites. This coincided with the fact that the locations of the ten provenance samples are more spread than the locations of the 57 test sites.

The relationship of provenance and site main effects with IPCA1 scores was plotted in Fig. 7. Figure 7 counts for 93.7% of the treatment SS and is very informative. For example, P119 and P71 differ only in main effects, not in interaction; P100 and P71 are similar in main effect, but differ in interaction; while P71, P104 and P61 are all rather similar with respect to both main and interaction effects on the IPCA axis. P30 (outside the figure to avoid clutter) and P44 had the most interactions, but in the opposite direction. P13 has no interaction on the IPCA1 axis. On the other hand, site differences reflect largely on the main effect, with small interaction components on the IPCA axis except for the three most-northern sites (M451, M559 and BLUE). The latter were the poorest in yield, but showed the largest interaction components on the IPCA1 axis. According to the AMMI model, provenances and environments with large IPCA scores of the same sign (an indication of the affinity of provenance adaptation to site environments) are expected to have a high yield, above the combination of the grand mean, provenance and site effects, whereas large scores of opposite sign (poor adaptation) indicate low yields, below the expected value of the combination. For example, AMMI predicted the 20 year height of provenance P30 at the three most-northern sites M451, M559 and BLUE, respectively, as 445 cm ($677-446-52+21.78 \times 12.2 = 445$), 458 cm and 378 cm, while for provenance P44 the predictions were 192 cm, 67 cm, and 161 cm, respectively. On the other hand, at Goat River (the most productive site), the predicted 20 year height of provenance P44 was 1,212 cm, compared to the 905 cm of provenance P30. The interactive relationship of other provenances with sites can be similarly examined, though they are not as obvious. Figure 7 generally indicates that provenances from the southern and central B.C. interior (e.g. P19, P44, P1, P71, P61, P104 and P71) were well-adapted to the southern and low-elevation sites (e.g. WIGW, CUIS, NECK, TUYA, SUEM, GOAT, et al.), since they all had a negative IPCA1 score

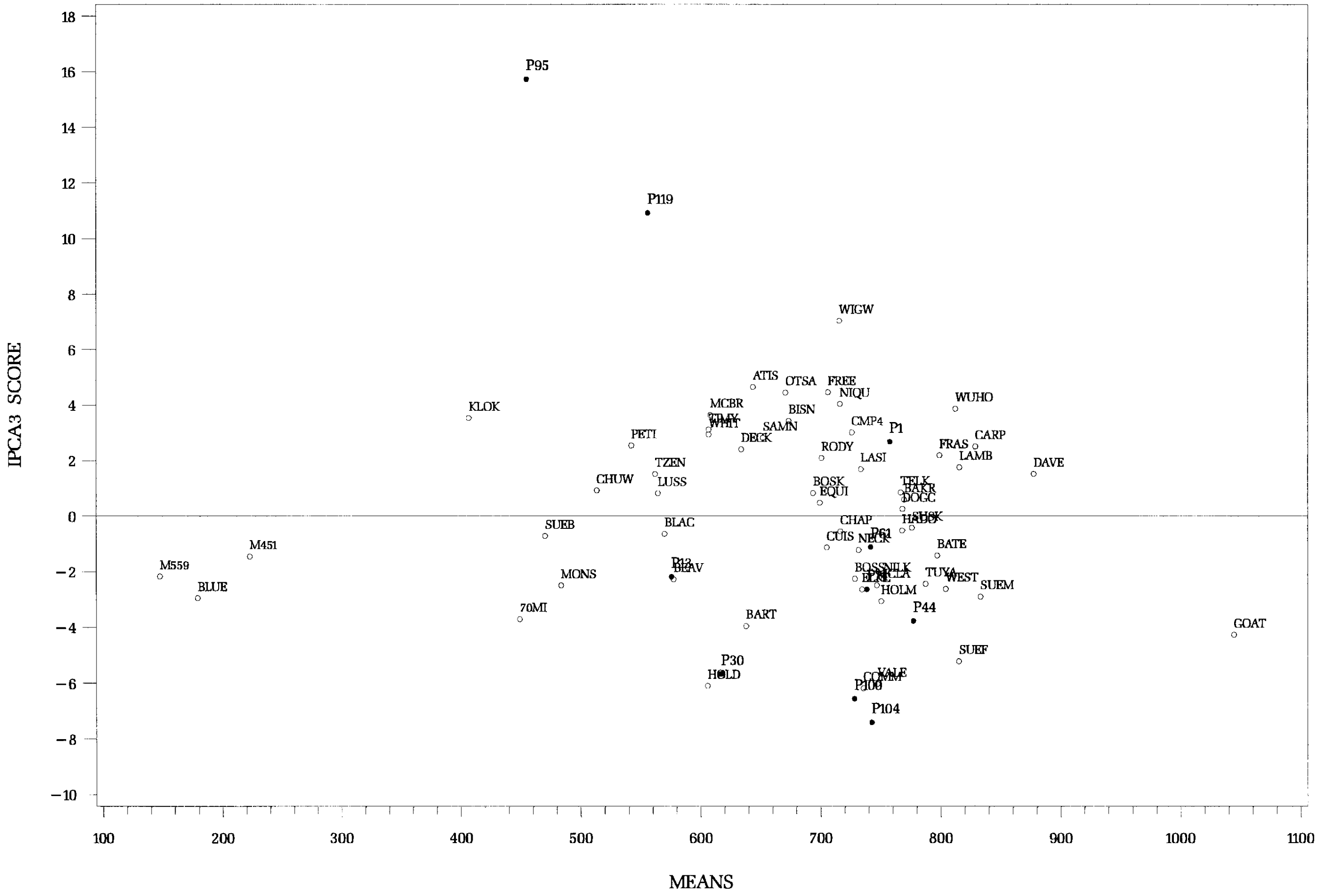


Fig. 9 Relationship between IPCA3 score and mean for ten lodgepole pine provenances (●) and 57 test sites (○) in British Columbia

at these sites. Similarly, the more-northern provenances (P30, P95 and P100) had positive IPCA1 scores at the northern (e.g., SAMN, CARP, WEST, DOGC, CAMP4, ATIS, et al.) and higher elevation (e.g., SUEB, MONS, KLOK, LUSS, TZEN, PETI and CHUW, Figs. 1 and 7) sites, indicating their adaptive affinity. Thus, IPCA1 seems to represent interactions caused by the temperature variation among provenance and site. Indeed, we observed a significant correlation between mean annual temperature and environmental IPCA1 ($r = -0.846$, $Pr. = 0.001$) and provenance IPCA1 ($r = -0.602$, $Pr. = 0.048$).

Figure 8 shows the relationship between main effects and the IPCA2 scores and accounts for 91.9% of the treatment SS. P13 had a high IPCA2 score, but showed no close affinity with any of the test sites. Environmental IPCA2 scores had a significant correlation with mean annual precipitation ($r = 0.311$, $Pr. = 0.018$). P13, which originated from a climate transitional from wet (coast) to dry (interior), is perhaps not fully adapted to the dry interior. Figure 8 simply reveals that none of the 57 sites provides the site environment which is optimal for growth in terms of the interactive effect of precipitation. The IPCA3 axis together with main effects of site and provenance captured 91.8% of the treatment SS, and seems to have effectively separated P95 and P119 from the others (Fig. 9). Like P13, they showed no close affinity with any test sites. P95 was from the high-precipitation northern coast and P119 from the relative warm, moist west slope of Cascade (Fig. 1), and provenance IPCA3 scores were closely correlated with mean annual precipitation($r = 0.844$, $Pr. = 0.002$), mean annual temperature ($r = 0.735$, $Pr. = 0.015$) and the number of frost-free days ($r = 0.873$, $Pr. = 0.001$) of provenance origin. Again, IPCA3 may represent an off-site effect of provenances which were not fully adapted to the dry, cold interior environment.

Discussion

The AMMI model has certain statistical advantages over the joint regression approach in dissecting genotype by environment interactions. Removal of the additive parameter β_e from the multiplicative component in the AMMI model (eq. 3) overcomes one major statistical deficiency, that is the dependency of the site and population indicators encountered in joint regression (eq. 2) (Freeman 1973; Gauch 1992). Second, linear regression provides only a single parameter for each genotype or environment, with no opportunity to describe a complex interaction structure beyond a linear mode (Freeman

1985). The AMMI model has been recommended to analyse complex genotype by environmental interaction and has been shown to be able to reveal the nature of interaction, particularly if an AMMI model captures more interaction SS than joint regression (Crossa et al. 1991; Nachit at al. 1992; Cornelius 1993).

The AMMI model identified three significant IPCA axes in our lodgepole pine data and captured 64.7% of the provenance by site interaction SS, almost twice of the SS captured by the joint regression analysis (33.5%). The first IPCA axis alone captured 34.2% of the interaction SS, more than the joint regression analysis. The performance patterns of ten provenances in Fig. 2 could be revealed when only the first IPCA axis was examined (Figs. 6 and 7).

The difference in adaptation among provenances P13, P1, P71 and P119 was clearly revealed by a very high IPCA2 score for P13 (Figs. 6 and 7), though not by the regression coefficient (insignificant, Fig. 2 and Table 3). In addition, the difference between P95 and P119 was only revealed by IPCA3 (Fig. 9) while joint regression analysis only indicated a small difference. The AMMI model had the most-revealing insight to the three most-northern sites (M451, M559 and BLUE). Linear regressions were not significant for these three sites or for the other 44 sites (Table 3). Therefore, the three northern sites are not distinguishable from the 44 sites by the regression method. But in the AMMI1 model, these three sites were separated by IPCA1 scores, along with P30. This is because P30 had an unusual interaction on these three sites, which had made the joint regression insignificant for the three northern sites. But on IPCA1, the effects of the three northern sites and P30 were separable (e.g. P30 is more adaptive than any other provenance in these three sites): AMMI is quite effective to describe the interaction in this lodgepole pine data.

Differential responses of ten lodgepole pine populations from a broad geographic area reflect their adaptation to natural environments. P95, which is a subspecies *contorta* from the Alaska coastal region, and P119, which is a subspecies *murrayana* from the Cascade Mountains of Oregon, behaved poorly in interior B.C., having the lowest growth rate at all sites with high scores on the IPCA3 axis (Fig. 9). The Alaska coastal region occupies a variety of extreme habitats at low elevation with high rainfall and a relative warm winter, which are not very favourable conditions for the growth of lodgepole pine. The northwest Oregon Cascades Mountains has usually poorly drained, highly organic soil, but warmer temperature relative to interior B.C. (Stephens 1966). Lodgepole pine populations in the Alaska coast and Oregon Cascades Mountains may have evolved to be suitable only to those high-humidity and relatively warm regions, respectively, but to be maladapted to the more heterogeneous and severe environments (colder and less rainfall) in interior B.C.

P13 also had poor growth in 57 sites, but its interactions are paralleled with environmental deviation (regression coefficient not significantly different from 0), and had an unusually high score in IPCA2 (Fig. 8). The region where P13 was from has a profound maritime component with a relatively high annual rainfall (887 mm). In addition, an influence of the coastal *contorta* gene pool was proposed in this population based on tree morphology and less hardiness (Ying and Illingworth 1986; Ying *et al.* 1989). This study shows that populations adapted to relatively mild semi-maritime environments (transition from coastal to interior) are not particularly well adapted to more severe interior B.C. environments.

P30 is from the most-extreme climate: e.g. the coldest (-2.01 MAT) and with a very low rainfall (296 mm MAP). Overall, it has unfavourable growth on sites in central and south interior B.C., but it's interaction had a large negative linear regression with environmental deviation (Fig. 2), and showed a nonlinear trend (Fig. 5) and a very high IPCA1 score (Fig. 7). P30 grows much better than all other provenances in the northern region of B.C. (e.g. M451, M559 and BLUE) although its growth is poorer than other B.C. interior provenances in the other more-southern sites. This shows that P30 is specifically adapted to the most-severe environments in this series of trials and developed extreme cold hardiness in its local environment. This adaptation to physical environments in northern B.C. may be viewed as a balance between selection for cold hardiness and growth.

The three most-northern sites (M451, M559 and BLUE) had the largest influence on the responses of provenances to environments. They were not only the poorest growing sites due to the extreme environment (coldness and long days), but also had the largest effects on the slopes of regression (Fig. 4), the non-linearity of regressions (Fig. 5) and the IPCA scores (Figs. 6, 7, 8 and 9). The geographic variation for the most-northern sites was also observed to be much different from the other sites. For example, the elevation was not significant in the regression and response surface model (Ying and Illingworth 1986; Ying 1991; Wu and Ying 1998). This behaviour of the local populations near Yukon coincided with the peculiar geographic variation patterns observed in other studies of growth and hardiness (Hagner 1970; Lindgren 1983; Fries and Lindgren 1986) and isozyme variation (Weeler and Guries 1982b). The non-significant elevation effect was also suspected to be due to the narrow elevational distribution of lodgepole pine in the species' northern ranges (Ying 1991; Koch 1996). Surveys of enzyme loci provided the most-conclusive evidence for the genetic distinctness of those northern interior populations (Yeh and Layton 1979; Wheeler and Guries 1982a,b). From a cluster analysis based on genetic distance using 42 isozyme loci, Wheeler and Guries (1982a) found that eight populations in the Yukon and extreme northern British Columbia (including P30) tended to cohere in a group distinct from the interior B.C. populations farther south. With the help of evidence for the distinctive distribution of rare alleles among northern and southern populations, Wheeler and Guries (1982a) concluded that northern interior populations originated from refugia in the unglaciated part of west-central Yukon. It was proposed that interior lodgepole pine, that survived in Yukon refugia at the last glacial age (10,000 and 14,000 years ago), re-colonized its present range in the Yukon and northern B.C. about a few hundred kilometers across the border, where it was met by those pines moving north from their refugia in the United States (Weeler and Guries 1982a). The unique variation patterns from northern populations observed in this study may confirm this proposal.

All the other six provenances (P1, P44, P61, P71, P100 and P104) were from the Rocky Mountains and the Inter-Mountains range in central and southern interior B.C.; although these provenances behaved more similarly compared with four more-marginal provenances (P13, P30, P95 and P119). However, there are differences in their norm of reaction. P100, the most-northern population with the poorest growth and highest IPCA1 score among interior B.C. populations, had a negative linear regression with environmental deviation, while others had a positive or zero correlation with environmental deviation, indicating that P100 is not as well-adapted to the more-productive sites of interior B.C. as its southern counterparts. By contrast, P44, the most-eastern and the highest productive population with the lowest IPCA1 score among the interior B.C. populations, had the highest positive linear regression. Thus, within interior B.C., local differentiation of environmental responses exists among populations. This demonstrates that adaptation of lodgepole pine to the various physical environments at the subspecies level, as well as within interior B.C., may be due to a balance between selection for high growth-potential in less-severe environments and selection for high cold-hardiness in severe environments. Therefore, populations well adapted in less-severe environment are not as well adapted as local populations in severe environments. The implication of this adaptive landscape of the native lodgepole pine population is obvious to tree breeding. Since populations are environmental-specific, successful re-forestation requires adaptive traits to be precisely matched to the environments of the planting sites. Successful re-forestation and breeding programs for natural populations demand that seed transfer be restricted on the basis of patterns of adaptive variation.

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