ship between crown diameter and branch angle promise that these characters can be combined in a breeding program to develop narrow crowned strains of black pine with a wide branch angle.

Conclusions

From the study of 16 growth and branching characters in a 5-years-old clonal seed orchard of black pine comprising 52 clones the conclusions are:

- There are significant differences among clones in all character studied.
- Branch angle is not a stable character and increases with the age of the whorl, while the number of branches per whorl decreases.
- Repeatability values for branch length and branch thickness increase with the age of the whorl and are always higher for branch length.
- Growth and branching characters are genetically less controlled than the morphological and anatomical features of the needles reported in a previous study in the same population.
- Branch angle and crown diameter are loosely negatively correlated characters indicating that they can be combined in a breeding program to develop a narrow crowned strain of black pine with wide angle branches.

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Geographic Variation in Pinus armandii Franch.

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Abstract

The natural range of *Pinus armandii* Franch. covers a large area from about 23°30' N to 36°30' N and 88°50' E to 113°00' E, whithin which the ecological gradient is considerable. The genetic differentiations of the species are obvious. Although most of the characteristics of *P. armandii* varied clinally with latitude, our research revealed that all provenances may be divided into two geographic groups that are obviously different from each other in growth vigour, cold resistance as well as in many morphological characters. The provenances from Yun-Guei Plateau (come from the Yunnan, Gueizhou Provinces and southwestern part of Sichuan Province, namely southern provenances), though fastgrowing, but all died from winter frost and desication when planted in northern portion of range. The more northern were the provenances introduced in the south of range the worse they grew. Gradually they lost production value all of them.

Key words: *Pinus armandii* Franch., provenance trial, height growth, hardiness, geographic variation, clinal pattern.

Introduction

A provenance test of a tree species, is to reveal the pattern of geographic variation of the main features of the species so as to provide the necessary scientific basis for reasonable transfer of seeds and for the strategy of genetic improvement. Thus many countries around the world have started provenance trials of their main reforestation tree species (Wright, 1976).

Pinus armandii Franch. is one of the important reforestation tree species in sub-alpine regions in our country. The species is seldom found below 1000 m elevation and most common at elevations from 1300 m to 2300 m (Zheng, 1978).

Since its natural range spreads over a large area from the south subtropical region to the northern grasslands, climate is very diverse within the natural range. Most of the populations have been isolated in high mountains, thus many specialized populations have formed since gene exchanges between populations have been limited. To recognize the genetic variation of this species and to identify best seed sources adapted to different ecological regions according to a unified program, we started a series of provenance trials in 1980 in cooperation with forest farms in ten Provinces. After seven years of investigation, we priliminarily analysed the pattern of the geographic variation for many traits of *Pinus armandii* FRANCH. This report deals with the early results in the nurseries and fields in five southern test locations since tree grew slowly in the northern plantations.

Material and Methods

Collection of seed

Methods used in this research program followed the provenance trial criteria currently in use around the world. Seed collecting points and test sites were selected according to geographic coordinates and the distribution status of regional populations (*Fig. 1*), Because of difficulties in collecting seeds in the Chuan-Zang Plateau (Xizang and west sichuan), we got only 30 bulked seedlots from eleven provinces including Yunnan, Sichuan, Gueizhou, Xizang, Hunan, Hubei, Gansu, Shaanxi, Ningxia, Henan and Shanxi within the range centrated in the Yun-Guei plateau (Yunnan, Gueizhou and south Sichuan) and Qinling-Daba mountain regions (North Sichuan, Shanxi, Henan, Ningxia and Gansu) (*Table 1*). The tests were carried out simultaneously at ten locations in ten provinces according to a unified program. In 1982 we again organized experiments involving only a part of the distribution areas (Qinling-Daba mountain regions) in the north because all the seedlings of southern provenances (Yun-Guei plateau) died from winter frost when planted in the northern part of China. Since the seedling grew differently at every test site, one-year, two-year or three-year seedlings were used for the planting in different trails.

The experimental design

Nursery

The bulked seed of 30 provenances obtained from of whole range was sown in the spring of 1980. A randomized complete block design with four replications and three-row per plot were used for seedling cultivation. The spacing was 20 cm between rows and 3—5 cm within rows.

Plantation establishment

Each plantation was laid out as a randomized complete block design with six replications and 16 seedling square plots. Spacing was 2 m × 2 m. The locations of provenance trial presented in *Figure 1.*

Observations and assessments

The weight of 1000 seeds and germination % were determined and the seed coat colour were recorded per provenance. After the first vegetation period the following traits have been evaluated: number and length of cotyledons, length of hypocotyl, shoot and root length for a random sample of 30 plants per provenance. Fresh weight and dry weight, water content and relative dry matter content were evaluated from the 20 seedlings per provenance. Date of terminal bud set, proportion of seedlings with terminal buds in the autumn and occurrence of winter injury were recorded. After planting in filed mean height was measured annually. Needle length, their number on a 10 cm

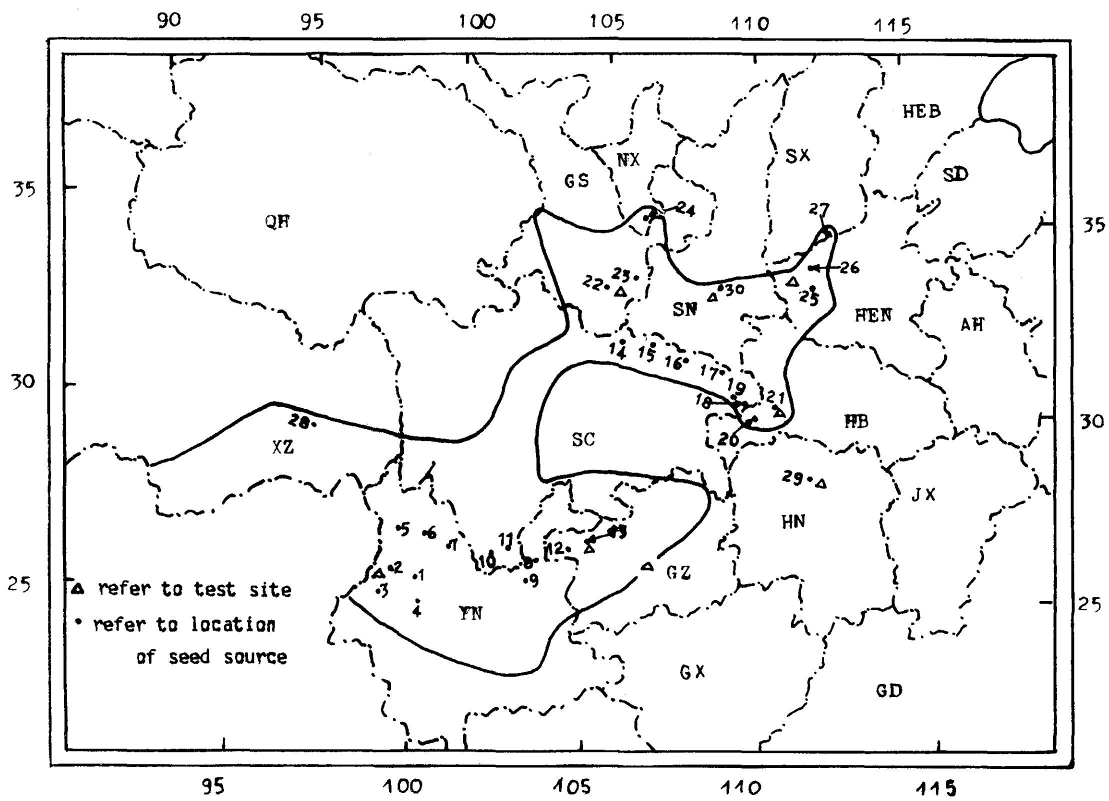

Figure 1. — Natural range, locations of seed sources and test sites.

Table 1. — The meteorological factors and the geographic positions of *Pinus armandii* Franch. provenances.

region and province	County name	Prov. no.	Latitude (°N)	Longitude (°E)	mean annual temperature (°C)	maximum temperature (°C)	minimum temperature (°C)	Relative humidity (%)	Rainfall (mm)
Yun-Guei plateau									
Yunnan	Baoshan	1	25.13	99.15	15.5	23.3	-3.5	75	966.4
"	Tengchong	2	25.07	98.29	14.8	30.5	-4.2	79	1463.8
"	Lianghe	3	24.48	98.18	18.3	33.8	-1.7	79	1357.1
"	Changning	4	24.55	99.37	14.9	31.2	-3.6	81	1251.0
"	Weixi	5	27.13	99.31	11.3	29.6	-5.5	70	951.6
"	Lijiang	6	26.57	100.18	12.7	30.6	-7.0		952.9
"	Yongsheng	7	26.41	100.45	13.5	31.0	-5.9	69	925.8
"	Hueize	8	26.20	103.13	12.7	31.4	-16.2	71	817.7
"	Dongchuan	9	26.11	103.04	13.1	30.7	-9.7	67	831.7
Sichuan	Hueili	10	26.41	102.15	15.1	34.7	-5.8	69	1130.9
"	Hueidong	11	26.37	102.42	16.1	35.6	-5.0	66	1056.0
Gueizhou	Weining	12	26.52	104.17	10.5	32.3	-15.3	80	950.9
"	Hezhang	13	27.07	104.44	13.4	35.7	-10.7	79	854.1
Hunan	Anhua	29	28.25	100.18	12.7	30.6	-7.0		952.9
Daba mountain region									
Sichuan	GuangYuen	14	32.26	105.48	16.1	38.9	-8.1	69	973.3
"	Wangcang	15	32.13	106.19	16.2	38.7	-7.2	74	1142.2
"	Tongjiang	16	31.56	107.14	16.7	40.4	-6.2	75	1088.7
"	Chengkou	17	31.56	108.47	13.8	38.9	-13.2	78	1261.2
"	Wushan	18	31.07	109.50	18.4	41.8	-6.9	67	1049.4
"	Fengjie	19	31.04	109.29	16.5	39.8	-9.2	69	1107.3
Hubei	Badong	20	31.09	110.39	7.4	29	16.1	83	1800.0
"	Xingshan	21	31.14	110.47	17.1	39.9	-5.9	74	984.1
Qinling mountain region									
Gansu	Xihe	22	34.00	105.18	8.4	33.5	-24.0	74	533.0
"	Qingshuei	32	34.45	106.09	8.8	36.0	-23.2	70	574.8
Ningxia	Jingyuen	24	35.30	106.21	5.7	30.0	-26.3	64	637.7
Henan	Luanchuan	25	33.47	111.38	12.2	40.2	-20.2	68	880.0
"	Luoning	26	34.23	111.41	13.7	40.0	-21.3	67	606.1
Shanxi	Yangcheng	27	35.0	112.24	11.7	40.2	-19.7	61	627.4
Xizang	Bomi	28	29.50	95.46	8.5	31.0	-20.3	71	876.9
Shaanxi	Changan	30	34.10	108.55	13.3	43.0	-17.5	73	687.4

section of terminal shoot and the number of branches in a whorl were recorded at 3 years after planting. The growth rhythm and phenological phase were recorded periodically during the 4th growing season after planting.

The analysis of data

The following statistical analysis were conducted. At each site an analysis of variance was computed for each character with an equal number of observations per plot. Simple correlations between the characters and the geographic and climatic data on the place of origins have also been evaluated. Regression analysis of several characters against latitude of seed origin and principal component analysis were conducted also. The growth data used in this report were obtained from the southern test plantations since the trees growing in the north were still rather young.

Results and Discussion

A. Geographic variation and its pattern

1. Seeds

(1) Weight of 1000 seeds

While higly significant differences exist among provenances the mean value ranged from 251 g to 405 g; no pattern of variation with geographic data for this character was found in our experiments. There are significant difference between several neighbouring counties. For example, the 1000 seeds weight was 322 g in Weining county and only 238 g in Hezhang, Gueizhou. The latter was 35.3% less, even though they are two neighbouring counties. The correlation coefficient between 1000-seed weight and the latitude of origin is $r = -0.22$, while with longitude of origin it is only $r = -0.0784$. It appears therefore that the variation of seed weight was random.

(2) Shape and colour of seed coat

In general, the seed collected from the southern portion of natural range are obovoid with grey-dark colour, and those from the northern part are obovate with brown or light brown colour. Shape and colour of seed coat seem useful features for distinguishing southern and northern provenances.

2. Germination and seedling Characters

(1) Rate and response to temperature

Seed germination was carried out under a constant 25° C temperature in a growth chamber with a 16 hours photoperiod, under a 15° C to 25° C alternating temperature in a green-house with natural photoperiod and of 30° C in a thermostat without light. In order to test the response to below zero temperatures some seeds of each provenance were chilled in a soil pit 2 m in depth in January for 20 days. The chilled seeds were puted into a growth chamber to examine the germination rate. As a result the southern provenances germinated at 25° C five days earlier than those from the northern. And the whole germinating process was significantly shorter than those of the northern origins. The duration of germination of southern origins was 27 to 32 days, while the process of germination of northern origins was 60 days. The 30° C temperature was unfavourable to every provenance. At 30° C the seeds from the north germinated only 0% to 13%. The rate of germination of chilled seeds from northern origins increased 1.4 to 3.5 times compare to the control. On the other hand, the rate of germination of southern provenances droped 48 to 90 per cent. This indicanted that seeds of different origin exhibit different response to chill.

(2) Length of hypocotyl

As soon as the seed coat was dropped during germination, the length of hypocotyl was measured for two years. The differences among origins was very highly significant. Provenance mean ranged from 2.9 cm to 6.9 cm. The hypocotyls of southern provenances were twice as long as those of the northern provenances. There was a clear clinal pattern in this trait, with a very long hypocotyl for the Yunnan provenances and the shortest one for the Ningxia provenance. The correlation coefficient between hypocotyl length and latitude of origin was $r = -0.8236^{**}$.

(3) Characteristics of cotyledons

The southern provenances had a greater number of cotyledons than northern provenance (11 VS 10) as well as longer cotyledons than the latter (6.1 cm vs 4.7 cm). The correlation coefficient of between length of cotyledons and latitudes of origin was $r = -0.8236^{**}$, and with longitudes $r = -0.6959^{**}$. The correlation coefficient of between the number of cotyledons and latitudes of origin was only $r = -0.4514^{*}$, and for longitudes $r = -0.3032$. There was a clear clinal pattern in cotyledon length.

3. Bud set and frost injury in winter

The percentage of bud setting seedlings was recorded for each provenance in late autumn in the nursery at Beijing. We found that the proportion of seedlings with a terminal bud before winter was less than 50 per cent for provenances from the Yun-Guei plateau. And at same time, seedlings of northern provenances, such as from Ningxia, Shanxi, Henan, Gansu, Hubei and northern part of Sichuan provinces, had a 100% setting of terminal buds. The same situation could be seen in other experiments. The correlation coefficient of between bud set percentage and the latitudes of origin was $r = 0.8894^{**}$ with a clear clinal pattern just as with western Hemlock (KUSER and CHING, 1980).

Differences among provenances in frost damage were also highly significant. All seedlings from southern provenances were killed after the winter, while the seedlings from northern provenances appeared normal except those from Daba Mountain provenances which had slightly injuried needles during the winter. The correlation coefficient of seedling mortality due to winter low temperatures with latitude of origin was $r = -0.9698^{**}$ and with longitude $r = -0.8117^{**}$. It is clear that seedling mortality was obviously related to the rate of bud set before winter with a correlation coefficient $r = -0.9119^{**}$. The damage from winter frost occurred not only in nurseries located in the Yellow River basin, but was also observed in test plantations in the Yangze basin. For instance, in the experimental forest of Anhua county, north Hunan, the increment of southern provenances exceeded those of northern provenance in normal years. The net increment of southern provenances was 62.5 per cent greater than the average increment of the northern provenances in Anhua county, Hunan in 1984. But after the severe winter in 1984 to 1985, the needles of the southern provenances got a red-

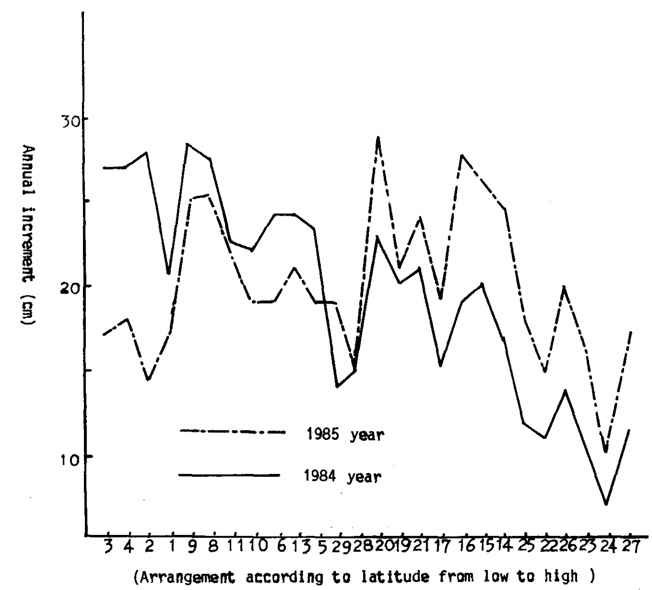

Figure 2. — Response of individual provenance to winter frost (Plantation located in Anhua County, Hunan.).

dening. It made the increment drop by two-thirds in 1985 compared with that of 1984. This situation led to the result that net increment of the southern provenances in 1985 was only 20.6 per cen higher than that of northern provenances. The decrease of net increment corresponded to the degree of the frost-injury suffered by each provenance. The decrease for southern provenances ranged from 1.4% to 48.4% as compared with that of last year. Trees of provenances from Baoshan region in western Yunnan decreased most sharply being 33.3 to 48.4 per cent. The decrease of provenances from southern region in Sichuan was comparatively less. On the contrary, the average annual net increment in 1985 for provenances from the Daba Mountain area increased 33.5 per cent as compared with those of last year. The minimum increase was 5.5 per cent and the maximum was 49.1 per cent corresponding to seed sources. *Figure 2* used the curve of net increament in 1984 and 1985 to show the response to winter injury of *Pinus armandii* from different provenances. As we can see from the diagram, the provenances from lower latitudes (to the south of 28° N) are more sensitive to frosts.

The climate of the test site in Tianshuei, Gansu, (located at west Qinling Mountain, 34°15' N. and 105°40' E.) was a little warmer than normal during the winter of 1980 to 1981. There was no significant difference in survival rates between northern and southern provenances. But there was a severe cold spring in 1982 and almost all seedlings of provenances from western Yunnan were killed by the frosts. The survival rate was only 0.7 to 7.8 per cent. The provenances from the bordering areas of Yunnan, Gueizhou and Sichuan have better cold-resistance compared with provenances from western Yunnan, The survival rate of the seedlings was 10.9 to 40.9 per cent. At the same time, the survival rate of the northern provenances (to the north of 28° N) was 75.7 to 100 per cent. After winter injury the correlation coefficient between seedling survival from various provenances and the latitude of their origin is $r = 0.8976^{**}$.

4. Biomass of seedlings

Determination of biomass of two-year seedlings shows that there were significant difference among different provenances in this respect. For instance, measuring in the Anhua test station, the shoot weight per seedling of the southern provenances was 18.7 g, while that of the northern provenance was only 8.3 g. The aboveground fresh weight (including stem and needles) was 258.3 per cent of the under-ground weight for southern provenances, and for northern provenances only 153 per cent. Obviously a larger part of the photosynthetic products of the northern provenance are used for the forming of the root systems. The correlation coefficient of total biomass (dry weight) for a provenance with latitude of origin is $r = -0.735^{**}$. This value is lower than that between seedling height and latitude. This is due to the difference in relative root volume among provenances.

5. Variation in relative length of roots (root/shoot ratio)

As a criterion of adaptability to soil and climate, we had counted the root/shoot ratio of different provenances in three test sites (*Table 2*). The figures in Table shows that the taproot absolute length of northern provenances decreased compared to southern ones. However the relative length (root/shoot ratio) increased gradually with increasing latitude of seed source. The difference of relative root length between the southern and northern provenances in the northern test site is greater than those in the southern test site. The provenance from the northern end of range such as most northern provenance from Yangcheng, Shanxi, exhibit the longest relative root length at all of the three test sites. It was clear that the relative root length was controlled strongly by genetic factors and that there is a strong clinal pattern with latitudes of origin. The correlation coefficient between relative root length and latitudes of origin was $r = 0.8182^{**}$ and for longitudes $r = 0.6708^{**}$.

6. The water content of above-ground and under-ground parts

In view of the fact that the water holding capacity of tissus is one of the important characteristics of organisms, the variation of water content of shoots and roots was evaluated seperatly during biomass determination. Provenances differed greatly in this respect. For instance, the mean value of the root water content ranged between 68.7% and 166.7%. The above ground water content rate of the southern provenances was much higher than that of the northern provenances. The average of former was 136.6 per cent and of the latter 112.4 per cent. On the contrary, the root water content of the northern provenances was slightly higher than that of the southern provenances, the former was 127.6, and the latter 112.1 per cent.

7. The length of needles

Determination of one-year needle length on two-year old seedlings and of two-year old needles on five-year old trees shows that there are great differences among provenances in this respect. For instance, assessments conducted in 1985 indicated that the average length of two-year old needles of the southern provenances was 11.4 cm with extreme values 9.4 cm to 12.4 cm while the average needle length of all the northern provenances was 5.4 cm with the longest 6.9 cm and the shortest 3.1 cm. The needles of the longest-needle provenance is four times as long as that of the shortest needle provenance. The correlation coefficient of needle length and latitude of origin was $r = 0.7301^{**}$, and for longitude $r = 0.7462^{**}$. These data indicate that mean length of needles exhibited a clinal variation in association with the major geographic gradients.

Table 2. — Root/shoot ratio (%) in three test sites.

seed source	Tengchong			Pingba			Anhua		
	mean	max.	min.	mean	max.	min.	mean	max.	min.
southern (13)	116.5	129.0	89.0	141.0	175.6	93.0	243.1	277.8	191.1
northern (15)	140.0	153.0	128.0	367.8	484.3	219.1	362.0	438.3	288.5

The figures in parentheses are total number of provenances studied.

8. The number of lateral branches in a whorl

The number of the lateral branches in a whorl was usually 6 to 7 for southern provenances and 3 to 4 branches for northern provenances. The correlation coefficient between branch number in a whorl and latitude of origin was r = −0.8685**, and for longitude r = −0.7301**.

9. The duration of the dormant period

To study the dormancy feature and time of occurrence of winter injury, from 1st December of 1981 to 1st March of 1982, monthly we moved several containers with seedlings into the greenhouse to observe the rate of green-turning of needles, the mortality, flushing and shoot elongation for each provenance. Everytime we moved 5 containers with 20 to 25 seedlings per provenance. The needles of Yunnan and Gueizhou provenances turned green rapidly (7 to 10 days) after moving indoor on 1st December and 40 to 80 per cent of sedlings flushed from the top and grew normally without frost-injury in needles. After 15 days in green-house, the needles of Daba-mountain provenances turned green from brown and only 11.1% to 53.3% seedlings started flushing. The rest of the seedlings did not flush even by March of 1982. The needles of Qinling mountain provenances were both late in turning green and flushing and 44.4% to 77.8% of the seedlings grew slowly during the spring. Shoots mostly occured from lateral buds or fascicules of needles instead of the shooting from the terminal bud. The seedlings of southern provenances that were moved indoor in the 1st of January not only had frost-injury symptoms on their needles, but also half of them had dieback. The provenances which come from western region, Hubei, also got winter injury in their needles. The rest of the provenances performed at normally. The Quinling provenances emerged shoots without needles. When the seedlings were moved indoor in February the seedlings from southern provenances were all killed and those of the Qinling provenances grew new shoots quickly and normally. In one month the new shoots were full of newly growing needles. In seedlings of Daba-Mountain provenances new shoots grew abnormally. The flushing rate was still rather low. From that we may conclude that Pinus armandii of all provenances needs a certain amount of low temperatures to become released from dormancy, and to flush and normally grow, but lettle was needed for provenances come from the Yunnan and Gueizhou provinces and the cold spell in November in Beijing was quite enough for most of them to grow normally. The low temperature which occured in January was too low for them to live, and it would certainly kill them. Thus, the longest low temperature period was needed by provenances from neighboring regions of Sichuan and Hubei provinces and the low temperature spell from December to January was not at all enough to release them from dormancy. The 40 to 50 days of low temperature would be all right for Qinling provenances to release from dormancy, and the following growth would be quite normal if they got the favourable conditions. In short, the seedlings of provenances from bordland of Sichuan and Hubei provinces required the longest dormancy.

10. Phenological phase and growth rhythm

Every five days height growth assessments were carried out throughout the growing season in 1985 at the Tengchong test plantation in Yunnan province. Growth measurements were began from the flushing of the terminal bud (the beginning of March) and continued until two consecutive measurements showed no further growth (the end of May). After cessation of height growth the 5-daily increments were computed and expressed as percentage of the total height increment (namely periodical relative increment) for the growing season in question, thus allowing comparison of growth patterns for individual or geographic groups of provenance to be made. The growing season was considered to be the period between the date of flushing of terminal bud of a sampled young tree and date when no further height growth occurred at two consecutive measurements. The results showed that the length of the growing season is about 90 days without notable differences among provenances and all of provenances started flushing within a few days. There were small differences between provenances in flushing date, though the provenances coming from Yun-Guei plateau flushed slightly later than those from Qinling and Dabashan mountain regions. The periodical measurement shows that there are great differences in the timing of the growth peak among provenances. The period of maximum height growth of Yunnan and Gueizhou provenances appeared one month earlier than that for northern provenances. The net increment of southern provenances in April was 40% of the total height increment and for northern provenances this was only 30%. On the other hand, in May the monthly increment of southern provenances decreased sharply to only 26% of the total increment and the net increment of northern provenances increased to 35.9% of the total height increment.

11. Variation in height growth

For a better comparison among provenances as well as for comparison of plantations the absolute mean height for each provenance and each plantation in 1986 are listed in *Table 3*. Analysis of variance showed that differences among provenances were highly significant at the 1% level at all test sites, although an interaction was noted between provenances and test environments. Differences of height among geographic groups of origins were significant and variation of individual seed origins within regional groups might considered as minor. Within any single plantation, the mean height of southern origins (No. 1 to 13) was consistently greater than the mean height of northern provenances (No, 14 to 27). The data in *Table 3* shows that the farther the test site located in the south the greater the difference between the two geographic groups. For example, as compared with northern provenances, in Tengchong plantation, the most southern test site, southern trees grew more than five times as fast as those from northern provenances. In Yichang plantation, the most northern test site among the five southern plantations, difference in mean height between the trees from two geographic groups decreased sharply. The height of southern provenances is 1.4 times greater than that of the northern provenances. Variation in growth characters of *Pinus armandii* was found to follow an obvious clinal pattern from south to north on all test sites. The correlation coefficient between the mean height of the 6-year trees and latitude of the origin was r = −0.9615** in Tengchong, Yunnan; r = −0.952** in Pingba, Gueizhou; r = −0.770** in Anhua, Hunan. From the above mentioned it sems obvious that the pattern of geographic variation of *Pinus armandii* is very similar to the pattern in *Pinus taeda* (Well *et al.*, 1975), *Pinus ponderosa* (Wang and Patee, 1976), *Picea sitchensis* (Pederick, 1978), *Abies grandis* and *Abies concolor*

Table 3. — Mean tree height in Cm at age 7-year of individual provenance on five plantations (cm).

County	Marked No	Locations of provenance trial				
		Tengchong	Pingba	Anhua	Hezhang	Yichang
Southern origins	(1-13)	203	148	116	94	8 8
Baoshan	1	224	207	93	96	85
Tengchong	2	238	220	105	89	80
Lianghe	3	229	200	118	119	79
Changning	4	226	213	113	89	83
Weixi	5	158	141	108	82	51
Lijiang	6	170	191	108		
Yungsheng	7	205	181			74
Hueize	8	216	228	137	93	102
Dongchuan	9	219	253	132	96	96
Hueili	10	205	197	113	88	110
Hueidong	11	191	170	131	96	95
Weining	12	180	159			103
Hezhang	13	176	215	116	91	96
Northern origins	(14-28)	38	76	88	54	62
Guangyuan	14	50	102	103	57	75
Wangcang	15	48	93	113	57	93
Tongjiang	16	44	89	115		76
Chengkou	17	35	79	82	50	73
Wushan	18	48				64
Fengjie	19	43	105	103		
Badong	20	51		122		57
Xingshan	21	50		113		
Xihe	22	25	52	62	47	56
Qingshuei	23	25	60	67	51	43
Jingyuan	24	20		42		37
Luanchuan	25	27	73	73	55	61
Luoning	26	36	52	82	68	62
Yangcheng	27	29	52	67	51	50
Bomi	28	83		72		

(Steinhoff, 1978) and *Populus deltoides* (Jokela and Mohn, 1976).

B. The ecological basis for the geographic variation of P. armandii

Noticing all the geographic variations of the characteristics presented above, it is suggested that identical variation exists between individual seed sources. Furthermore the variation obviously followed the geographic pattern, with a close relation to the latitude of origin. Most assessments also show an obvious correlation with longitude, however since the distribution of *Pinus armandii* is from northeast to southwest, and the changes of meterological factors in China are greater in the latitudinal direction than with longitude, the variation of characteristics of *Pinus armandii* are mostly affected by latitude. The correlations between the main features of *Pinus armandii* and the geographic coordinates of each origin are listed in *Table 4*.

The materials in *Table 4* shows clearly that the geographic variations of most characteristics in *Pinus armandii* have a stronger relationship with latitude than with longitude, so the pattern of the geographic variation of this species can be summerized as primary by a latitudinal cline. Six regression equations and linear diagrams of the main characteristics are shown in *Figure 3* for illustration of the clinal pattern with latitude.

The correlation coefficients of characteristics with meteorological factors of the place of origin are given in *Ta-*

Table 4. — The correlation coefficients between the main characteristics and the geographic coordinates of the origin.

Characteristics	Latitude	Longitude
Hypocotyl length	-0.8236**	-0.8316**
Cotyledon length	-0.8236**	-0.6959**
Ratio root/shoot	0.8182**	0.6708**
Needle length	-0.7301**	-0.7462**
Height growth of six-year trees	-0.9615**	-0.7617**
Number of branches in a whorl	-0.8685**	-0.7301**
Rate of bud setting of one-year seedling	-0.8894**	0.5062**
Dieback rate	-0.9686**	-0.8117**

ble 5. The data in *Table 5* show that the relationship between individual characteristics and both the maximum and minimum temperatures at location of origin were stronger than those with mean annual temperature, rainfall and relative humidity. It is clearly suggested that the critical factors causing different selection pressure between southern and northern portions of the range are extreme temperatures. In fact, in the southern part of range the extreme low temperature was only −3.5° C to −7.5° C, and extreme high temperature was 22.7° C to 35.7° C, which in the northern part of range it was −5.9° C to −26.3° C and 29.0° C to 43.3° C, respectively.

C. Division into regional groups

An ordination using the Principal Component Analysis with 7 characteristics was made, as this provided a means of representing the among-provenance similarities graphically in lesser dimensions than the variate space. Two dimensions were judged to be adequate. The result of PCA is shown in *Figure 4.* The southern provenances (to the south of 28° N) are clearly separated from the northern provenances (to the north of 28° N). There is no evidence for any interlinks between those two geographic groups. This apparent inconformity with clinal pattern of main characteristics as mentioned above probabily results from physiography in the central portion of species range. The central part of the range is a narrow strip (*Fig. 1*). In this zone there are high massive mountains and deep canyons. The *Pinus armandii* occurs usually in mixed stands in association with several spruces and larch. Occasionally they scattered among various trees of associates. Generally, the populations in central portion of range are discontinous and some of the isolated small and rare populations grow separately on cliffs and steep mountain slops forming an impressive barrier to exchange of pollens and seeds in long distance among the disjunctive stands. In fact, there is one major gap between southern and northern parts of the range. The gene flow has been inhibited by extensive mountains and saw-cuts. The genetic distance among the populations of the southern and northern parts of the range is so obvious that seeds or seedlings in a mixture sample can be immediately recognized as belonging to one or the other. Of coures, it is possible that those two distinct groups are parts of a cline, but the continuity of variation is not apparent in our study. The lack of continuity in two dimensions of PAC could be a consequence of particularly inadequate sampling from central portion of the range because abrupt topography exists and seed collection was unavailable.

Conclusion

From those early assessments of *Pinus armandii* provenance trials in China, we can make following preliminary conclusions.

1. There are significant differences among provenances in height growth, cold-resistance, seed coat colour and shape of seed, length of hypocotyl and needles, relative length of root, rhythm of annual growth, etc.

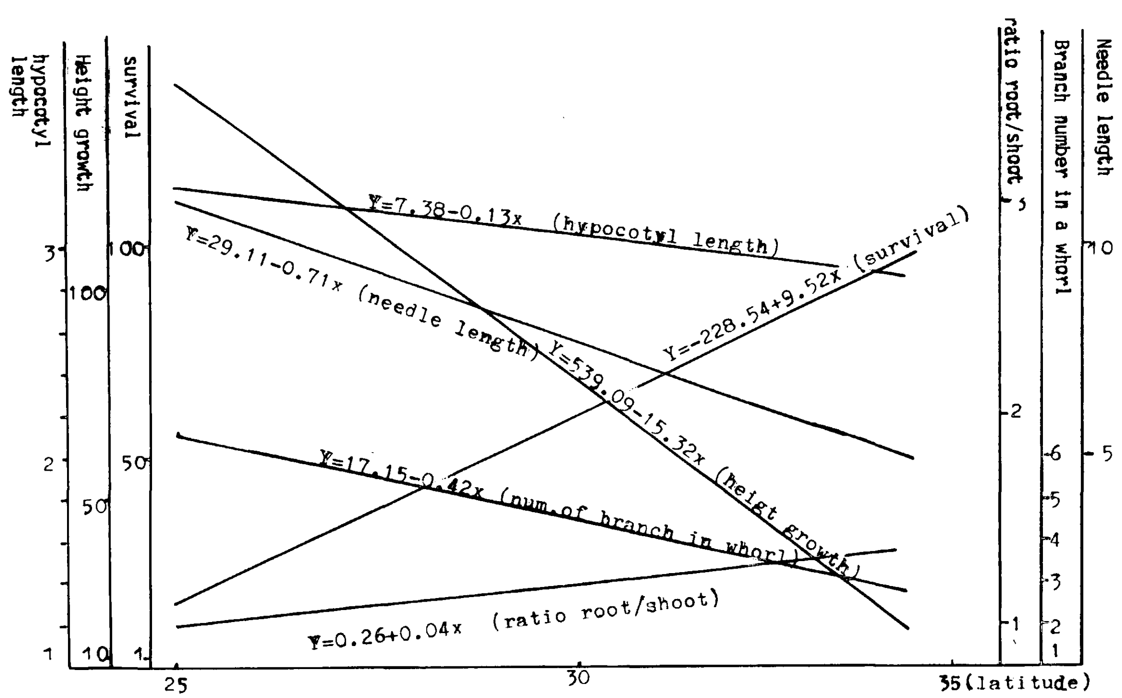

Figure 3. — Regression between six major characteristics and the latitude of origin.

Table 5. — The correlation coefficient (r) between the characteristics and climate variables of seed source.

trait	mean annual temperature (°C)	Maximum temperature (°C)	Minimum temperature (°C)	Relative humidity (%)	rainfall (mm)
hypocotyl length	0.388*	-0.4255**	0.6443**	0.3349	0.2145
ratio root shoot	-0.3736	0.4882**	-0.6160**	-0.1775	-0.1747
num. of branch per whorl	0.1669	-0.5121**	0.5121**	0.1810	0.2808
height of 6-year tree	0.2731	-0.5924**	0.6165**	0.2729	0.250
survival rate	-0.2352	0.7216**	-0.625**	-0.4322**	-0.2805

2. Most characteristics studied in our experiments exhibited clinal variation associated with geographical gradients, in particular with the latitude of seed origin.

3. The provenances studied here tended to divide into two distinct regional groups. They are so different in heredity that they can be considered as two variaties with their own natural ranges, and might be named the southern (Yun-Guei plateau) ecotype and northern (Qinling-Dabashan mountains) ecotype.

4. According to seed coat colour and shape of seed in laboratory as well as hypocotyl length during the germination stage, it is possible to identify easily those two ecotypes.

5. It is safe to say that the southern provenances, such as those from the Yun-Guei plateau grew much better than the northern provenances. However, they are very susceptible to winter cold and desiccation, and therefore, unsuitable for planting in Yellow River valley. They should be used only on sites where winter frosts are not severe. In a similar way. transfer of seeds from the north to south for afforestation will bring unsatisfactory results. In the Yangtze River valley the best performers in term of both height growth and hardiness appear to be found along the bordering region between the southern and northern parts of the range, namely along the Jinsa River.

6. This study has shown for the first time that Pinus armandii can be dividied into two main groups. This finding will be of help to tree breeder seeking improvement, introduction and seed transfer of *P. armandii.*

Acknowledgements

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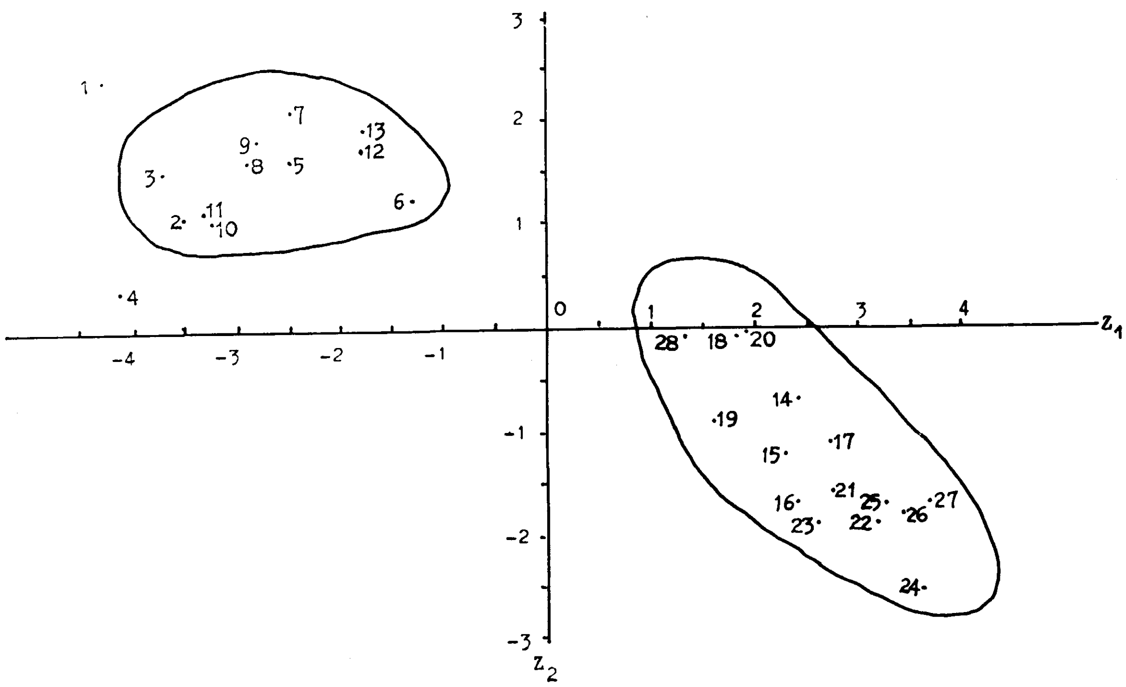

Figure 4. — Distribution of provenances on the basis of two principal components of PCA.

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Inheritance of Partial Resistance to two Races of Leaf Rust, Melampsora medusae in Eastern Cottonwood, Populus deltoides

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Summary

The F_1 progenies of a cross of eastern cottonwood, *Populus deltoides* (BARTR.) were analysed for inheritance of partial resistance (three traits-latent period, uredial infection frequency and sporulation capacity) to two Australien races of leaf rust, *Melampsora medusae* (THÜM.), employing leaf disks excised from the plants. All three traits appeared to be under polygenic control (continuous distribution was observed) and both additive and non-additive interactions were detected. Considerable transgressive segregation and racespecificity was observed for all three traits. Based on the direction of skewness, higher resistance appeared to be partially recessive to lower resistance. We conclude that, although it is possible to select for trees with high partial resistance combined with a hypersensitive-type resistance against specific races of the pathogen, the apparent race-specificity of the partial- resistance traits suggest that this type of resistance may also be vulnerable to pathogen adaptation. These results are discussed in terms of their relevance to the management of the poplar-leaf rust pathosystem.

Key words: Disease Resistance, Genetics, Host-parasite interaction, inheritance, leaf rust, *Melampsora medusae*, partial resistance, poplars, *Populus deltoides*, slow rusting.

1. Introduction

Host resistance is the most popular approach to managing a plant disease because it is economical, efficient and environmentally benign. Thus breeding for resistance to diseases assumes high priority in most tree breeding programs (ZOBEL, 1982; HEYBROEK *et al.*, 1982), as diseases cause considerable reduction in growth and in harvestable wood volume. Various resistance patterns may be observed in plants but complete resistance, characterized by a hypersensitive reaction, is the type of resistance preferred by most breeders as a defense against many foliar pathogens (in both annual and perennial plants) (DAY, 1974; BARRETT, 1985). This is understandable as hypersensitive resistance is easily recognizable in the plant population, is usually under simple genetic control (DAY, 1974) and, hence is easier to incorporate into breeding programs.

However, at the population level complete resistance has an aspect of vulnerability. It is relatively easy for most pathogens to negate the effects of a resistance gene by a simple mutation from avirulence to virulence (PRAKASH and HEATHER, 1986a). The short life cycle and large population size of most pathogens also ensures rapid selection of rare but virulent alleles (PERSON *et al.*, 1976). Several authors have suggested employing partial resistance (also called rate-reducing or incomplete resistance) which is characterized by slower disease progress, reduced infection frequency and restricted sporulation, as a safer alternative to complete resistance in annual crops (PARLEVLIET, 1979; WILCOXSON, 1981; ESKES, 1983). The rationale is that partial resistance may be race-non-specific and, as it allows a limited development of the disease, it may not exert strong selection pressure on the pathogen population. Stable or durable resistance is highly desirable in tree crops as forest systems are composed of relatively static host genotypes maintained exclusively over space and time, and they are thus more volnerable to large-scale shifts in the pathogen population.

Leaf rust caused by *Melampsora medusae* (THÜM.) is a serious disease of eastern cottonwood, *Populus deltoides* (BARTR. ex MARSH.) in Australia and United States, where active breeding programs strive to maintain disease incidence below the economic threshold (JOKELA and MOHN, 1977; PRYOR and WILLING, 1982; HEATHER and CHANDRASHEKAR, 1982; THIELGES, 1985; PRAKASH and THIELGES, 1987).

In an earlier paper (PRAKASH and HEATHER, 1986b), we reported that complete, hypersensitive-type resistance in cv. T-173 of *P. deltoides* to five races of *M. medusae* was simply inherited and mostly under single gene control. Further studies showed that this cultivar was susceptible, at reduced levels, to some races of the leaf rust pathogen (PRAKASH and HEATHER, 1986c). In this study, we report the analysis of inheritance for three partial resistance traits in this cultivar to two virulent, compatible races of *M. medusae* and also examine the usefulness of partial-resistance in the management of leaf rust disease of poplars. An assessment of race specificity of partial resistance and of the association between complete and partial resistance

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