

Discussion

Since an apparent effect of the pedigree errors of the kind studied here was a rise in $\hat{\sigma}_D^2$ and a drop in $\hat{\sigma}_A^2$, any surprisingly high estimate of dominance variance indicates that the results should be viewed with some caution. Even small levels of pedigree errors of the kind simulated here could explain abnormally low heritabilities or $\hat{\sigma}_A^2 / \hat{\sigma}_D^2$ ratios, but it would take moderate levels of errors to deteriorate the genetic gains from selection.

Cases where expected selection response tends to be unusually low may as well indicate identification errors, but this may well be less serious in the sense that selected trees should perform better than their BVs indicate. The important consequence is that, on average, identification errors will cause underestimation of the selection effect. Additionally, the standard errors in table 2 indicate that with some unknown positive error rate one will often obtain BVs that deviate substantially from what should be found with correct tree identification.

Identification errors under testing conditions similar to those in this example should not inflate general genetic parameter estimates, except in the case of $\hat{\sigma}_D^2$. A general average identification error rate below 1% to 2% should not seriously affect the success of a breeding program based on additive genetic effects.

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Cloning Strategy for Chinese-fir (*Cunninghamia lanceolata* (LAMB.) HOOK.) Suggested by Early Test Results

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Abstract

Fifteen cuttings from each of 252 donors, originating from seedlings from a seed-orchard of an appropriate provenance were taken and rooted in spring 1991. The stecklings were planted in Hubei in a randomized complete-block design; seedlings from a local source were used as controls. About 15% of the least-desired clones were rogued from the test plantations in each of the third and sixth years.

It was found that: (1) the height, diameter and volume growth of the stecklings were consistently and significantly higher than those of the seedlings over the years; (2) the absolute growth difference between the seedlings and the stecklings increased with age dramatically; however, the gain as a percentage of current size decreased rapidly; (3) there were significant differences among clones and roguing raised the average performance of the steckling population; (4) early-late correlation coefficients in growth were low.

The results indicated that: (1) clonal selection can be done while timber-production plantations are growing, so that increases in later plantation performance and the development of clonal varieties can be achieved incrementally over time by roguing in the cutting orchard; (2) early selection of a very few clones is likely to be less effective than retaining more clones for later selection approaching or at rotation age; (3) a very few clones that have not been well studied should not be used in operational practice.

Key words: *Cunninghamia lanceolata*, clonal forestry, tree improvement.

Introduction

Chinese-fir (*Cunninghamia lanceolata* (LAMB.) HOOK.) is the most important timber species in southern China. Afforestation and reforestation of Chinese-fir by cuttings has been used for

at least 800 years and was a routine practice before the 1950's (CHEN, 1953; LI, 1995, 1998; LI and RITCHIE, 1999a and b). Unfortunately, in the 1950's and 1960's, Russian plant physiologist LYSENKO's theory affected Chinese forestry. Cutting plantations were replaced by seedlings, so that most of the valuable clones developed during the past 800 years were lost (LI, 1995). In 1986, a two-step cloning strategy similar to one for Norway spruce (KLEINSCHMIT and SCHMIDT, 1978; LIBBY, 1983) was proposed (LI, 1993). In the late 1980's, a special type of cutting orchard was developed, in which shoots from mature trees can be rejuvenated so that trees of various ages can be propagated by cuttings (LI et al., 1990a; LI and SHEN, 1990, 1998; LI and RITCHIE, 1999a and b). Since then, rooting cuttings has become a large-scale operation (LI et al., 1990b). However, controversy about cloning strategy continues in China (LI, 1998). First, poplar and fruit-tree clonal breeding methods were accepted as a national strategy for Chinese-fir cloning. This requires a long testing time and releases very few clones with a consequent narrow genetic base. Then, MA CHANGGEN (MA, 1991) and ZHOU TIANXIAN (ZHOU, 1990) presented an idea that clonal forestry can be achieved by cloning few clones identified in very young test plantations. They provided an example in which only 4 clones were selected, based on their high percentage of gain after only 3-years in a test plantation. The clones were selected in Kaihua, Zhejiang Province but were extended to many other provinces of the species' distribution range. Approximately 560,000 ramets of the clones were used for propagation or planting in 1991 alone. A textbook was published and many training classes were conducted to extend the strategy. Major scientific journals, newspapers and TV stations announced that this is a great achievement in Chinese forestry. Scientific awards have been given to this program (ZHOU, 1990). However, this report challenges that strategy, demonstrates that clonal selection and timber production can be done concurrently, and indicates that deploying only a very few clones is not only relatively inefficient but is both biologically and economically dangerous.

1. Material and Methods

1.1. Source of the clones

Fifteen cuttings from each of 1,000 donors, originating from seedlings from a seed orchard of an appropriate provenance were taken and rooted in spring 1991 in nursery beds in Tondou, Hunan Province. Cuttings of each donor were planted in one row and developed a clone. The original plan was to select 750 clones as a whole for testing. However, because of cattle browsing, a total of only 552 clones were selected. The clones were selected based on their nursery performance, specifically better height, root-collar diameter, sprouting ability, survival rate and resistance to diseases and insects. The 552 selected clones were randomly divided into two groups. One group contained 300 clones and was planted in Hunan, and these have not yet been measured. The second group contained the other 252 clones and was planted in Jingshan, Hubei Province in spring 1992. This paper deals only with the 252 clones in Hubei.

1.2. Field design of the test plantations

Six ramets of each clone were lifted from the nursery beds. One ramet was used to set up a new sprout-orchard for propagation use and the other 5 were used to establish test plantations; two blocks in one location and 3 blocks in a second location. A randomized complete-block design, with single-tree-plots was employed. Rooted cuttings of each block (replication) were planted in 12 rows along the contours and 21 columns up- and down- the slopes. These 5 test blocks were separately

placed within two seedling plantations of the same age. Seedlings in 4 rows on each side of the block that occupied about the same area were measured as controls (Fig. 1). The planting density was higher for ramets than for seedlings, which allowed thinning before crown closing. In 1994 and 1997 a total of 70 poorer performing clones were rogued from the test plantations, based on their 3 and 6 year performance in the plantations, specifically their heights and root-collar (1994) or breast-height (1997) diameters.

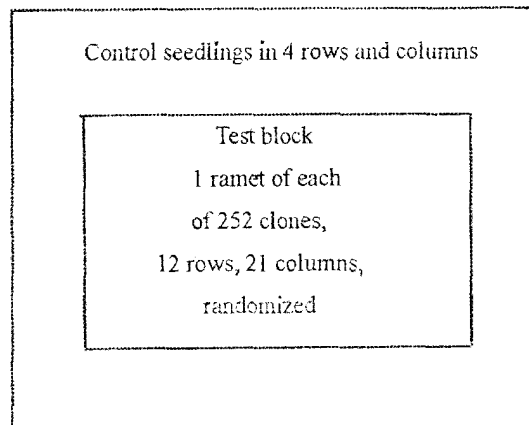


Fig. 1. - Field design of the test block. Each test block was set up within a seedling plantation.

1.3. Correction of soil gradient within block

Variation in height and diameter caused by soil quality within blocks on both up-down and horizontal directions of the slope were corrected by an adjustment based on differences along a gradient as used in agricultural crop testing and that assumes uniform gradients across the plots. The correction was made by following equation:

$$C_{ij} = (A_{ij} / B_{ij}) * B$$

Here, C_{ij} is the corrected height or diameter of the clonal ramet at row i ($i = 1$ to 12) and column j ($j = 1$ to 21).

A_{ij} is the measured height or diameter of the clonal ramet at row i and column j . B_{ij} is the proportional height or diameter of a regression-adjusted "control" at row i and column j . B is the mean value of the stecklings of the block.

1.4. Volume-index calculation

Height and diameter at root collar or DBH of each tree were measured every year. After 1995, the following equation commonly used for Chinese-fir was used for volume calculation:

$$V = (\pi / 4) * D_{1.3}^{2*} (H+3) * 0.41$$

Here V is the volume, $D_{1.3}$ is the diameter at the breast height of 1.3 m and H is the height.

Before 1995, the following equation was used for volume calculation:

$$V = (\pi / 4) * D_0^{2*} (H+3) * 0.41 * 0.482$$

Here D_0 is the diameter at root collar. The figure, 0.482, is a transfer coefficient, by which the volume data calculated in 1995 by both equations are the same.

1.5. Analysis of the data

SAS system for Windows was used to perform statistical analyses. The heights and diameters of the rooted cuttings are usually larger than are those of seedlings. Covariance analysis was used to modify the data when necessary. A paired T test was used to compare the difference between the clones and the controls. GLM procedure was used for variance analysis among blocks and clones.

2. Results and Analysis

2.1. Differences between the clonal mixture and the seedling control

The average height, diameter and volume of the clones and the controls in each block in various years are listed in *table 1*. Block means and the T test results are also given.

From *table 1*, it is clear that the heights, diameters and volumes of the clone mixtures are consistently and significantly higher than the controls over the years.

2.2. Absolute value and its percentage of the differences

The absolute values and percentages of the gain in height, diameter and volume of the clones over seedling controls at different ages are listed in *table 2*. The increment of the gain following roguing out the poorer clones is also given.

From *table 2* we can see that as age increased the absolute value of the difference between the clones and seedlings in height, diameter and volume growth increased, however, the percentage of the difference decreased. It is clear that the percentage of the difference will go down continuously. The reason for this is that the difference between the clones and the control increased much slower than did the total height, diameter and volume of the controls. Therefore, high percentages of difference in early ages can never be viewed as the difference at the rotation time, although in this case the clones have remained superior to the controls.

From *table 2* we can also see that roguing undesired clones in 1994 and 1997 increased both the absolute value and the percentage of the difference. For example, after 38 clones were culled in 1994, the absolute value and its percentage of the height increased from 31 cm to 37 cm and 14.7% to 17.5%, etc. *Figure 2* shows the situation when 32 clones were culled in 1997. The three curves stand for the control, and the clone mixture before and after roguing; X1, X2 and X3 are their corresponding means, respectively. As expected, the shape of the curve of the clones changed and the mean X2 moved forward to X3. However, please note that such roguing should remove only small or modest percentage of the clones. If most clones are rogued early, the process will lead to a mistake as stated later.

2.3. Influence of plant size

With present Chinese-fir nursery practice, the height, diameter and volume of seedlings are usually greater than those of seedlings of the same age when planting. On average, a one-year-old rooted cutting is 8 cm to 10 cm taller than a seedling of similar age. In our experiment, seedlings originating from a seed-orchard located in Huitong, Hunan province, and the control seedlings were of local source. In provenance-test plantations established in 1972 in Hubei, the seed source of Huitong shows superiority to local source. Therefore, the measured differences in height, diameter and volume between the seedlings and the controls when planting and thereafter in *table 2* should be partitioned to seed source and plant size in the nursery (i.e. the planting size), and the allocation can be done by covariance analysis. Height, diameter and volume have the same change pattern, therefore only the volume allocations are shown in *table 3*.

From *table 3*, we can see that as the age increased the absolute value of the difference in both the seed source and planting size components increased, however, the percentage of them decreased. Roguing had a different effect on seed source and planting size. Roguing increased both the absolute and the percentage of the difference allocated to seed source, but decreased the percentage allocated to planting size so dramatically that the percentage of the difference in the seventh year

Table 1. – Growth comparison between the clonal mixture and the control in various years.

Block	1992		1993		1994		1995		1996		1997	
	Clone	CK	Clone	CK	Clone	CK	Clone	CK	Clone	CK	Clone	CK
Height (cm)												
I	59	33	136	97	249	205	413	351	529	468	634	542
II	53	36	130	109	231	207	399	351	480	450	582	541
III	59	32	137	109	252	203	402	352	536	455	646	556
IV	51	37	130	118	243	229	398	352	513	464	596	564
V	52	35	123	112	233	210	380	349	493	458	564	542
Mean	55**	35	131**	109	242**	211	398**	351	510**	459	604*	549
Diameter at root collar (cm) DBH (cm)												
I	1.5	1.0	3.0	2.2	5.6	4.4	6.4	5.1	7.8	6.8	8.6	7.8
II	1.3	1.0	2.8	2.5	4.8	4.4	5.9	5.4	7.2	6.4	8.0	7.6
III	1.5	1.0	3.1	2.4	5.5	4.6	6.2	5.2	7.8	6.7	8.5	7.4
IV	1.2	1.1	2.9	2.7	5.3	4.9	5.9	5.5	7.7	6.8	8.5	7.4
V	1.3	1.1	2.8	2.6	4.9	4.5	5.7	5.2	7.1	6.6	8.7	7.5
Mean	1.36*	1.04	2.92*	2.48	5.22**	4.56	6.02**	5.28	7.52**	6.66	8.46**	7.54
Volume (cm ³)												
I	25	7	232	86	1362	708	5266	2886	11177	7717	15371	12210
II	18	7	208	133	1006	725	4503	2938	8772	6425	13827	11485
III	25	6	231	126	1331	787	4852	2791	11257	7228	16067	11442
IV	15	8	207	167	1216	988	4370	3136	10494	7622	15085	13382
V	16	8	201	151	1031	808	4076	2764	8994	7906	15024	11842
Mean	20**	7	216**	133	1189**	803	4613**	2903	10139**	7380	15075**	12072

*) Significant at 0.05 level **) Significant at 0.01 level

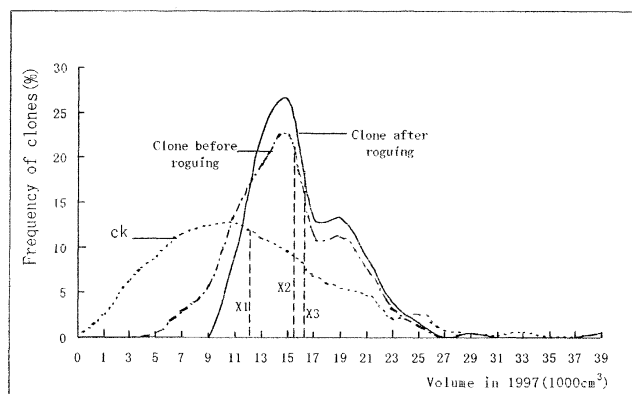


Fig. 2. – Roguing increased the difference in 1997 and changed the shape of the frequency distribution.

Table 2. – Absolute values and percentages (%) of the differences in height, diameter and volume of the clones over seedling controls.

Year and Treatment	Height		Diameter		Volume	
	Abs. (cm)	(%)	Abs. (cm)	(%)	Abs. (cm ³)	(%)
1992	20	57,1	0,32	30,8	13	185,7
1993	22	20,2	0,44	17,7	83	62,4
1994	31	14,7	0,66	14,5	386	48,1
Roguing	37	17,5	0,70	15,4	494	61,5
1995	47	13,4	0,74	14,0	1710	58,9
1996	51	11,1	0,86	12,9	2759	37,4
1997	55	10,0	0,92	12,2	3003	24,9
Roguing	66	12,0	0,96	12,7	4001	33,1

after roguing is close to zero. This meant that planting size affects early competition and growth, but does not much affect the difference in propagule-type performance in later years. For long term research and production, it can be ignored.

2.4. Possibility of selection of the clone mixture

The F and P (probabilities) values obtained from variance analysis by GLM among blocks and clones in height, diameter and volume before and after roguing were listed in table 4.

Table 4 shows that there were significant differences among clones indicating that selection by roguing can be effective.

Table 3. – Absolute value of volume and its percentage difference between the clones and controls allocated by covariance analysis.

Year and Treatment	Absolute (cm ³)			Percentage (%)		
	Total	Seed source	Planting Size	Total	Seed source	Planting Size
1992	13	5	8	185,7	71,4	114,3
1993	86	59	27	62,4	42,9	19,5
1994	386	331	55	48,1	41,2	6,9
Roguing	494	458	36	61,5	57,0	4,5
1995	1710	1588	122	58,9	54,7	4,2
1996	2759	2476	283	37,4	33,6	3,8
1997	3003	2564	439	24,9	21,3	3,6
Roguing	4001	3926	75	33,1	32,5	0,6

2.5. Effect of early selection

Table 5 lists PEARSON (upper right) and SPEARMAN (down left) correlation coefficients for the clones between plant height in 1991 and the volumes, and among volumes, in later years. Both PEARSON and SPEARMAN correlation coefficients of volumes among years are significant at the 0.01 level; however, they decreased with differences in age as usual. It is to be expected that the correlation of early volume with harvest volume will be rather low when plantations reach their rotation age of 25 to 30 years. Because genetic gain is better predicted by the coefficient of determination, r², rather than correlation coefficient, r, itself, the observed pattern of correlation coefficients indicates that the genetic gain from early selection will be small; the earlier, the smaller. The lower correlation coefficients as age differences increased suggest that some of the “best” clones in early years may even be below-average in performance in later years. Figure 3 demonstrates that if the “best” 10 clones were selected based on their 1994 volumes, there will be only 3 of these clones remaining among the best 10 in 1997; if the best 4 clones were selected at the age of 3, not one was among the best 4 at the age 6.

(Each point stands for a clone. After first roguing, 252-38=214 clones remain. The dotted horizontal and vertical delineate the cutoff below the 10 largest-volume clones in 1994 and 1997. This figure is from our real data. We did not do this selection at age of 3. This is a hypothetical selection. We use it to indicate that 4 clones selected at age 3 are not effective.)

It may be noted that there was no significant correlation between plant height in the first year and volumes in later years (Table 5). In this experiment, planting size little affected volume growth in later years.

Table 4. – The F and P values obtained from variance analysis among blocks and clones in height, diameter and volume in 1992, 1994 and 1997.

Item	Degree of freedom	Height		Diameter		Volume	
		F	P	F	P	F	P
1992							
Block	4	23,96	0,0001	39,80	0,0001	35,50	0,0001
Clone	251	1,86	0,0001	1,99	0,0001	2,02	0,0001
1994							
Block	4	9,55	0,0001	14,01	0,0001	11,17	0,0001
Clone	251	1,42	0,0002	1,88	0,0001	1,69	0,0001
1997							
Block	4	20,22	0,0001	19,48	0,0001	13,51	0,0001
Clone	213	1,24	0,0201	1,84	0,0001	1,95	0,0001

Table 5. – PEARSON (upper right) and SPEARMAN (down left) correlation coefficients among height and volumes of the clones.

	H1991	V1992	V1993	V1994	V1995	V1996	V1997
H1991		0.30463**	0.01461	-0.01350	-0.02705	0.00162	-0.00253
V1992	0.24505**		0.45321**	0.43860**	0.43317**	0.39480**	0.34608**
V1993	0.02736	0.57129**		0.59969**	0.59475**	0.53757**	0.48795**
V1994	-0.04935	0.43829**	0.67068**		0.79692**	0.75933**	0.71049**
V1995	-0.09816	0.40007**	0.61974**	0.79985**		0.88699**	0.76680**
V1996	-0.07584	0.38504**	0.53727**	0.73748**	0.88088**		0.89121**
V1997	-0.07671	0.34906**	0.50341**	0.71014**	0.78917**	0.90785**	

(H – height, V – volume) **) Significant at 0.01 level

3. Discussion

3.1.

We already knew that Chinese-fir cutting-orchards provide planting stocks 5 to 6 years earlier than do seed-orchards; that stecklings are larger in height and diameter than seedlings of the same age; and that the cost of the stecklings is 15% to 20% lower than that of the seedlings (LI et al., 1990b; LI and RITCHIE, 1999a and b). It is shown in many species that genetic gain can be greatly increased by clonal selection and vegetative propagation, particularly if the number of clones selected from is large (AHUJA and LIBBY, 1993). Therefore, cutting-orchard based on sound selection procedures provide substantial advantages over seed-orchards, which are limited to obtaining genetic gain from provenance, mass and family selection for tree-improvement of Chinese-fir.

3.2.

Clonal selection and timber production can be done concurrently. The development of clonal varieties and increases in the productivity of plantations can be achieved at the same time by incrementally roguing cutting-orchards as information on clonal performance in plantations becomes available. In this experiment, only 252 clones and 5 replications are small numbers, but serve to demonstrate the principles. To start a moderate tree-improvement program, 1000 to 3000 clones should be obtained from good families in appropriate provenances. This may be done gradually, with groups of a few hundred clones at a time.

3.3.

The 6th, 7th and 8th National-Five-Year Tree Improvement Plan set a rule that traditional fruit and poplar clonal breeding methods has to be used for Chinese-fir cloning. So, it might be that 30 ramets of each of only 200 clones would be tested. Suppose 2% to 3%, or four to six clones, were selected at the age of only 4 or even only 3. These clones can not be put into immediate production. We have to wait until at least one rotation age to thoroughly test these very few clones and this requires 25 to 30 years. Because of their narrow genetic base, poplar and fruit trees can only be planted on flat plains or hillsides and insects and diseases attacks are serious problems. However, Chinese-fir is grown on mountain slopes where the soil condition varies considerably even in a very small area. Because of greater environmental heterogeneity, and the unacceptable financial and environmental costs of chemically controlling pests, the method should not be used for Chinese-fir. Compared to traditional clonal breeding methods for fruit trees and poplars, the strategy we proposed for Chinese-fir takes less time and maintains a broader genetic base. The broader genetic base provides greater and more efficient selection, as well as increasing adaptability, stability and resistance to diseases and insects. Therefore, traditional clonal breeding methods may be good for fruit and poplar trees, but they are not as good for Chinese-fir.

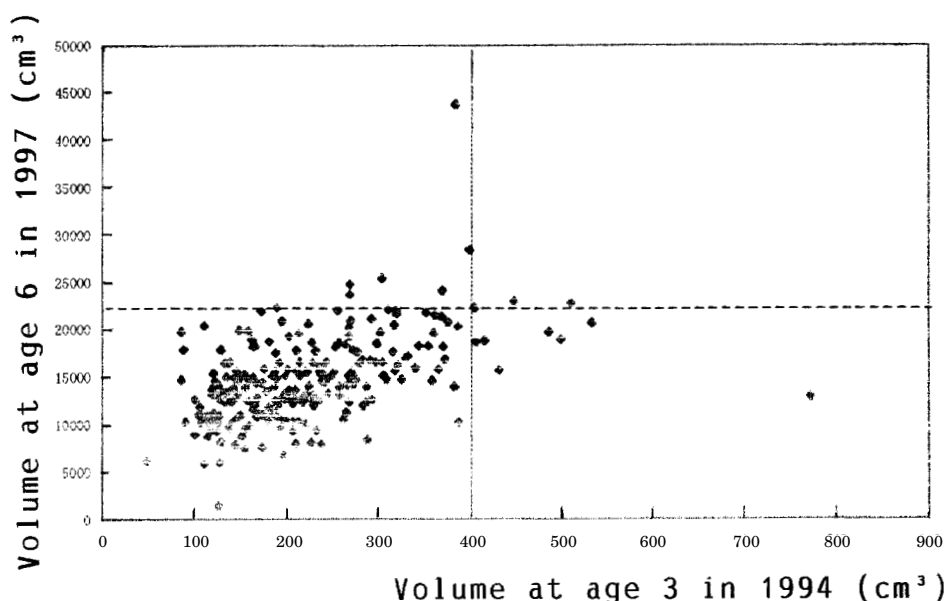


Fig. 3. – Effect of selection in 1994 on volume gain in 1997.

3.4.

In 1986, LI MINGHE presented a two-step cloning strategy for Chinese-fir. The first step is acquiring for tests superior families of appropriate provenance, for which the effective population size should be large owing to the HARDY-WEINBERG Law. The second step is incremental roguing of undesired clones, for a strategy of repeated current evaluation followed by low-intensity roguing (LI, 1993). However, MA CHANGGEN and ZHOU TIANXIANG stated that clonal forestry of Chinese-fir can be achieved by cloning few clones selected from very young test plantations. We have demonstrated in this paper an example where few clones that could have been selected early were soon no longer among the best available. Deploying these few early-selected clones and discarding the rest would have lost opportunity for greater gain and might even be counterproductive. Theoretically, the MA and ZHOU idea is unacceptable for most forest tree species (AHUJA and LIBBY, 1993). The author's arguments are as follows:

a. According to the theory of random genetic drift or sampling error (FALCONER, 1989), selection of a small population is frequently ineffective and the direction of change is unpredictable, which means that the genetic gain of few clones at rotation age may be positive or negative.

b. Because each clone has its own growth rhythm; the correlation of juvenile to harvest growth is low. With rotation age of Chinese-fir ranging from 25 to 30 years, 3-years' testing is too short. The 4 selected clones may appear to be good at present, but they may not be good at the harvest age. An example is that ZHOU TIANXIANG selected his 4 best clones in 1987 based on 3-years' plantation performance, however, when he reported his best 10 clones in 1998, we noticed that none of these early selected 4 remained among the best 10 (ZHOU, 1990 and 1998).

c. If the 4 clones are planted over a broad area, genetic gain may be positive in some places but negative in others because of genotype-site interactions, and the total gain in the country may be zero or worse.

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