Effectiveness of Nearest-neighbor Data Adjustment in a Clonal Test of Redwood

By T. S. ANEKONDA[1]) and W. J. LIBBY

Dept. of Forestry and Resource Management, University of California, Berkeley 94720, USA

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Abstract

Tree-to-tree environmental correlations were estimated for various traits in a clonal experiment with coast redwood (*Sequoia sempervirens* (D. DON) ENDL.). A nearest-neighbor adjustment was performed to reduce the effects on individual-tree data of environmental gradients and patchiness within the test site. The size of the environmental correlation proved reliable as a predictor of the usefulness of neighbor adjustment.

Some results of the neighbor adjustments were: (a) clonal means and rankings for metric traits were changed, in some cases substantially so; (b) for traits with neighbor-tree correlations greater than 0.15, estimates of within-clone components of variance were substantially decreased; (c) estimates of among-clone components of variance were moderately but consistently increased; (d) broad-sense heritabilities and predicted genetic gains were thus increased. Estimates of among-stand components of variance were little changed.

Key words: analysis of variance, correlation, environmental heterogeneity, field-test design, heritability, selection efficiency, test power.

FDC: 232.13; 165.3; 165.441; 174.7 *Sequoia sempervirens.*

Introduction

Heterogeneous environmental variation is often substantial on sites used for field tests of forest trees. Such variation may be random, patchy, or produce gradients in the plantation site. In all three cases, the precision of estimating entry means and genetic parameters, and the power of statistical tests run on them, are adversely affected by large amounts of environmental variation within the test site. Adjustments of individual-tree data based on performance of its neighbors may improve the accuracy of the experiment in "patchy" or "gradient" cases.

One such procedure, suggested by WRIGHT (1978), is referred to as a "moving average" method. Several other methods have been proposed to account for and statistically remove the effects of environmental heterogeneity by analyzing and then utilizing covariances among neighbors (reviewed by MAGNUSSEN, 1990). These methods are effective when the size of a patch or extent of a gradient is larger than the plot occupied by an entry.

LOO-DINKINS (1992) suggested a preliminary analysis of the data, namely a calculation of average environmental correlations (r) between pairs of nearby and adjacent trees. Note that if genetic entries in a field layout are random, then correlations among neighboring entries are environmental correlations. As a suggested rule of thumb, if the estimated environmental correlation is larger than 0.15, it indicates the existence of patches or gradients large enough for neighbor adjustments to be effectively employed to reduce this variation.

We followed the lead of WRIGHT and the suggestion of LOO-DINKINS, in an effort to improve the quality of field data collected in a redwood experiment on an irregularly heterogeneous site. We present our results as an example of the effectiveness of such procedures, and also to focus on some questions raised while gaining this experience.

Materials and Methods

Range-wide collections and plantation establishment

The work reported below analyzed unadjusted and adjusted field data for 172 redwood clones planted at the Russell Reservation site of a provenance test (KUSER et al., 1984). It includes samples from 81 "stands" (i.e. from 81 populations systematically sampled from throughout redwood's native range) with (usually) 2 clones sampled per stand (map and details are presented in ANEKONDA's 1992 PhD dissertation: A Genetic Architecture Study of Coast Redwood. Unpublished, available from the University of California, Berkeley, Library). In some of these stands, 1 or 2 additional clones were sampled from substantially different elevations within the stand. The field design also included a bulked set of seedling controls (California seed zone 91-1.0), plus 20 additional clones that were not randomly selected from the 81 stands (some of these 20 clones are from mature ortets, at least partially rejuvenated by tissue-culture procedures; others are from juvenile ortets). The means and neighboring-tree observations of these seedlings and 20 non-random clones were used to provide neighbor data for adjustment of the 172 clones' data, but their data were not further analyzed for the purposes of this paper.

The stecklings (field-plantable rooted cuttings) and seedlings had been grown at Simpson Timber Company's Korbel Nursery. In general, they were rooted in trays of containers, and thus ramets of each clone were in contiguous locations during rooting. The stecklings were, with a few minor exceptions, orthotropic, and their vigorous growth following planting indicated that both seedlings and stecklings were in appropriately good physiological condition at planting.

The Russell Reservation planting site is located 15 km inland from San Francisco Bay, in central California. It is transected by a powerline and 2 roads. Two border rows, arranged as (usually) 12-tree contiguous demonstration plots of available clones, surrounded each of the 4 areas comprising the site. It was clear at the time of site preparation that parts of the planting site differed from each other in aspect, fertility and/or other elements of site quality. The westernmost 2 areas, flanking the powerline, have approximately a 5% south-facing slope. The central (largest) area is level and the most fertile, as judged by redwood growth and by the intensity and height of weed growth before and after plantation establishment. The easternmost (smallest) area has a slight west-facing slope and it proved to be, on average, the poorest part of the site. All plants in the experiment were protected from browsing by perimeter fences.

[1]) Present Addresses: Section of Molecular and Cellular Biology, Univ. of California, Davis, CA, 95616; and Forest Products Laboratory, University of California, Berkeley, CA, 94720, USA

These available planting areas were not of equal size, and patches within them that seemed likely to differ in site quality were too small or ill-defined for effective or accurate blocking. Therefore, the 6 ramets of each of the 192 clones, plus 28 seedling controls, were randomly deployed as single-tree (i.e. non-contiguous) plots over the entire site without regard to area or to patches and gradients differing in site quality within the 4 available areas.

The seedlings and stecklings were planted in winter 1988 to 1989 at 3-meter hexagonal spacing. During the first 2 years following planting, weeds were controlled by mowing and water was periodically delivered to each tree by drip irrigation, as needed.

As seemed likely at the time of site preparation, redwood growth varied in a non-random manner. Irregular patches of a few (4 or 5) to many (about 20) trees soon exhibited growth rates and crown color indicating similar site quality, and these graded into adjacent patches whose growth and crown color indicated different site quality.

Field data collection

Data were collected at the end of the first (1989) and second (1990) growing seasons after outplanting. Crown closure had barely begun in the most fertile patches at the time of the second-season measurements; thus these analyses are likely to be essentially free of effects of competition between neighboring trees.

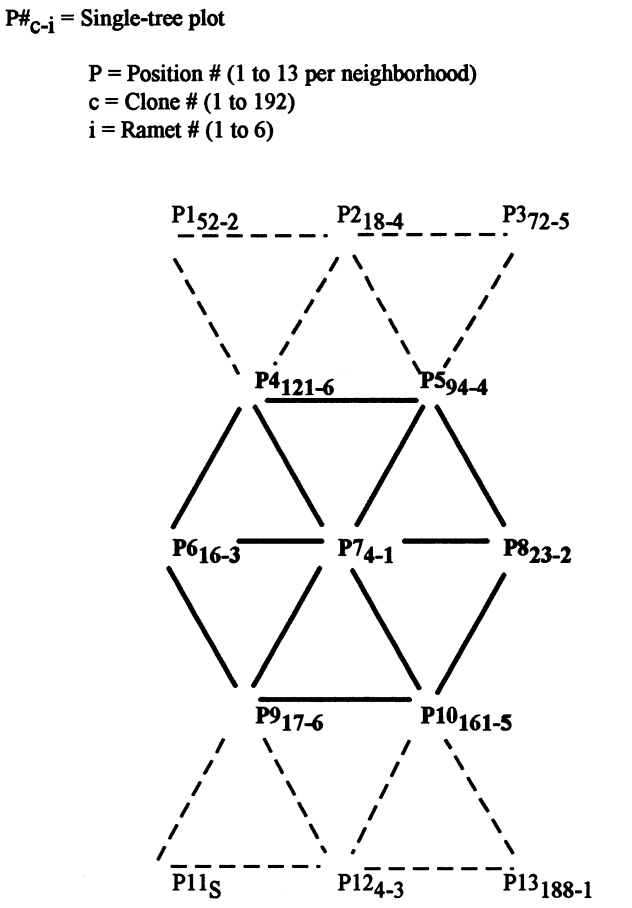

Figure 1. – A 13-tree neighborhood. A single-tree plot ($P\#_{c\text{-}i} = P7_{4\text{-}1}$) is surrounded by 6 other single-tree plots in the highlighted hexagon; it is the first (ith) ramet (single-tree plot) of the fourth (cth) clone occupying the seventh (Pth) position in the neighborhood. Note that P11 is occupied by a seedling, S, and that P7 and P12 are occupied by random ramets (1 and 3) of clone 4.

It is not a purpose of this paper to report detailed data on the traits measured. Rather, it reports the effects of neighbor adjustment on such traits. Details on measurement technique and full analyses of the 14 traits were included in ANEKONDA's dissertation (Unpublished). We intend to report them more fully in other manuscripts in preparation.

Having completed the analyses, we found these 14 traits could be divided into groups that were similarly affected by neighbor adjustment. This grouping could be based on the environmental correlations for each trait. Before listing the traits by group, we present the method of calculating these environmental correlations.

Paired-tree correlation analyses

A SAS program routine was presented and used by LOO-DINKINS (1992) to calculate average environmental correlations between all possible pairs of trees in a so-called "moving neighborhood" of 13 trees. For example, it would take paired data on the trees in positions P1 and P2 (*Figure 1*), then P1 and P3, etc. through P1 and P13, then P2 and P3 through P2 and P13, until it completed P12 and P13. It would then shift this configuration over 1 position and repeat the process. The correlations for each of these paired positions in all possible neighborhoods (i.e., a different neighborhood centered on each research tree in the experiment) were calculated by the SAS program.

In our analyses of the full sets of 13-tree neighborhoods for all 14 studied traits, we found that correlations of all configurations of contiguous pairs (i.e., nearest neighbors) were of similar magnitudes for each trait, although of different magnitudes for different traits. Furthermore, as expected, within each trait the correlations were smaller for more distantly separated (non-contiguous) pairs, for example, P1 and P5 (and even smaller for P1 and P13), than they were for contiguous pairs (for example P1 and P2, P5 and P8, P12 and P13). MAGNUSSEN (1990) reviewed similar analyses, and found that using data from plots more distant than those immediately adjacent to the plot to be adjusted added little to the accuracy of the adjusted data.

We therefore used only the nearest-neighbor data from the 6 (or fewer) trees contiguous to each studied tree. But first, we characterized each of the 14 traits by its average correlation of the 12 contiguous pairs in this neighborhood (shown in *bold face* with solid connecting lines in *Figure 1*, and listed in the left column of *Table 1)*.

Table 1. – Observed and average PEARSON correlation coefficients[1]) between the central contiguous paired positions throughout the experiment for each of 4 traits.

Position pairs[2]	Branch size	Crown diameter	Stem volume	Height
P4-P5	0.11	0.30	0.39	0.38
P4-P6	0.10	0.29	0.32	0.37
P4-P7	0.05	0.24	0.24	0.33
P5-P7	0.12	0.25	0.31	0.37
P5-P8	0.13	0.26	0.32	0.33
P6-P7	0.10	0.27	0.32	0.41
P6-P9	0.10	0.25	0.27	0.36
P7-P8	0.08	0.34	0.42	0.47
P7-P9	0.10	0.27	0.35	0.41
P7-P10	0.12	0.24	0.29	0.36
P8-P10	0.13	0.23	0.30	0.40
P9-P10	0.08	0.34	0.38	0.46
Max	0.13	0.34	0.42	0.47
Min	0.05	0.23	0.24	0.33
Avg	0.10	0.27	0.33	0.39

[1]) Correlations (r) > 0.08 are signifcant at $p < 0.01$, > 0.05 are significant at $p < 0.05$.
[2]) See *figure 1.*

Table 1 lists the observed and average correlations, as examples, for 4 of the 14 traits analyzed. Note that there is no consistency as to which particular pairs have the larger or smaller correlations, a generalization that holds up in the analyses of all the 14 traits (ANEKONDA's dissertation, unpublished). Thus, it seems that no pair orientation was particularly likely to share common environmental factors, and thus that all contiguous-pair orientations could be weighted equally.

Neighbor adjustments

In the adjusted-data analyses presented below, each ramet of the 172 clones of interest had its data adjusted by data from the 6 trees occupying its immediately surrounding hexagon (hereafter called "nearest neighbors", *Figure 1*). For each trait, the difference between the value for each nearest-neighbor tree and its clonal mean (seedlings mean if neighbor a seedling) was calculated. These 6 (fewer if nearest-neighbor trees were missing or disqualified) values were then averaged. If positive (an above-average neighborhood), the central tree's value was adjusted down by that average amount. If negative, it was adjusted up. If patch sizes are small or irregular, the 6 nearest trees should be better for adjustment than larger numbers (where more trees would be outside the patch or across a gradient inflection). However, if patch sizes are large or gradients extensively uniform, then >6 would probably be better. It seems the former situation is the common one in our redwood experiment.

Note that in this study, adjusted values for all derived traits (ratios, periodic growth, volume index) were re-derived from their adjusted component values, rather than using average derived-trait values of neighboring trees. We did not investigate this latter alternative.

Analyses

Genetic and environmental components of variance were estimated using the analysis of variance model (*Table 2*) provided by VARCOMP procedures for unbalanced nested classifications (SAS, 1989). After testing for normality, branch-size and stem-volume data were transformed to base 10 logarithms for analysis and subsequent presentation, while crown-diameter and height data were analyzed and are presented in their original centimeter units.

Table 2. – Analysis of variance model for variance-component estimation.

Sources of variation	D.F.	Expected Mean Squares
Stands (S)	80	$V_E + 5.33\ V_{C(S)} + 11.14\ V_S$
Clones (C) in S	91	$V_E + 5.19\ V_{C(S)}$
Ramets (R) in C in S, or Error	732	V_E

The total phenotypic variance for each of the traits was partitioned into an environmental/error component (within-clone, V_E) and 2 genetic components (among-stands, V_S; and among-clones-within-stands, $V_{C(S)}$). Stands and clones were treated as random effects in the model. Within-stand heritabilities for clone means within stands (BECKER, 1992) were calculated as follows:

Heritability of clone means (within stands) =
$h^2_{\bar{C}(S)} = V_{C(S)} / [V_{C(S)} + (V_E/k)]$
where, k = harmonic mean for number of ramets per clone.

A predicted genetic gain for each of the 4 selected traits was estimated using the following equation:

Predicted genetic gain, $\Delta G = i\ (\sigma_{\bar{C}(S)})\ (h^2_{\bar{C}(S)})$
where selection differential, i = 1.755 with an assumption that 1/10 of the clones are selected, and $\sigma_{\bar{C}(S)}$ is the standard error of clone means and is the $\sqrt{[\text{variance of clone means}]} = \sqrt{[V_{C(S)} + (V_E/k)]}$.

Presentation of results

Having completed the analyses, we found that the 14 traits we studied could be divided into 4 groups with similar effects of neighbor adjustments, based on similarity of nearest-neighbor correlations (r). Those are:

(i) r = 0.04 to 0.16: Second-year crown shape, *second-year relative mid-crown branch size*, first-to-second-year crown-diameter growth.

(ii) r = 0.26 and 0.27: *Second-year crown diameter,* second-year mid-crown-branch diameter, first-to-second-year basal-bole diameter growth.

(iii) r = 0.32 and 0.33: first-year tree height, first-year basal bole diameter, first-year crown diameter, *second-year stem-volume index.*

(iv) r = 0.38 to 0.41: second-year quarter-height-bole diameter, *second-year height,* second-year basal-bole diameter, first-to-second-year height growth.

For purposes of space and clarity in this paper, we present only 1 trait (*italicized*) from each of these 4 groups, hereafter called "branch size", "crown diameter", "stem volume" and "height". Applying the LOO-DINKINS criterion (r exceeds 0.15), neighbor adjustments would be expected to be useful for the latter three traits (groups ii, iii and iv), but perhaps not for branch size (group i).

Results

The effects of neighbor adjustment on the following parameters were as follows.

Plantation phenotypic data

For all traits, comparing adjusted to unadjusted data, the plantation mean was essentially unchanged. The standard deviation was moderately smaller (*Table 3*), except for branch size (group i), and individual-tree data-points were more frequent closer to the trait's mean value (not shown here, but presented in ANEKONDA's unpublished dissertation).

Table 3. – Plantation means and standard deviations for 4 traits before and after neighbor analyses.

Trait	# of clones	Mean	Std. Dev.
Before neighbor adjustments			
Branch size (log mm)	172	1.13	0.115
Crown diameter (cm)	172	65.0	17.4
Stem volume (log cm^3)	172	5.31	0.655
Height (cm)	172	107.7	22.9
After neighbor adjustments			
Branch size (log mm)	172	1.13	0.136
Crown diameter (cm)	172	65.2	16.8
Stem volume (log cm^3)	172	5.37	0.646
Height (cm)	172	107.6	20.8

Clone means

Data adjustments of the type reviewed by MAGNUSSEN (1990) are expected to change the estimated means of the entries, and by so doing increase the accuracy of most of the estimates and of their ranking. With our neighbor-adjusted values, changes in the estimates of clone means were of different degrees for different traits.

Figure 2 presents percentage change in clonal means for the 4 traits, grouped in percentage-change intervals of 10%. Branch size was the least affected of the 4 traits. Among the 172 studied clones, branch-size means changed 10% or less in 139 of them, and they changed more than 30% in only 4 of them (*Fig. 2a*). In strong contrast, stem-volume means were the most affected of the four representative traits, with only 47 clonal means being changed 10% or less and 54 being changed 30% or more (*Fig. 2c*).

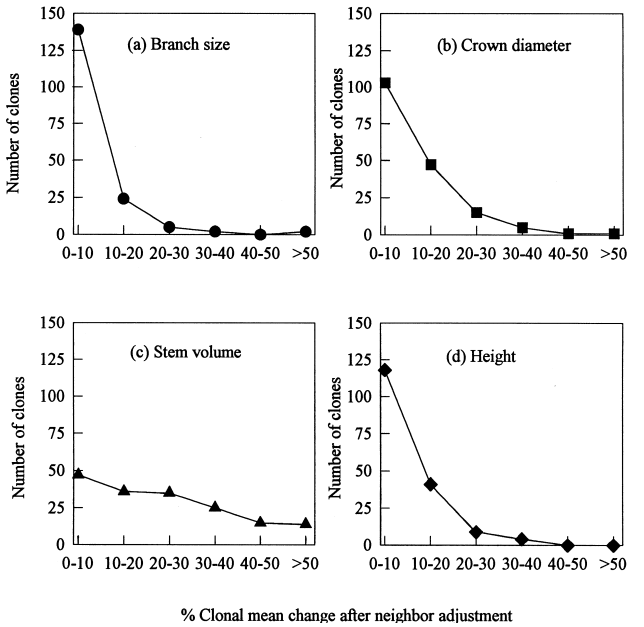

Figure 2. – Distribution of clones by percent change (10% interval) in clonal means after neighbor adjustments of 4 traits: (a) branch size, (b) crown diameter, (c) stem volume, and (d) height.

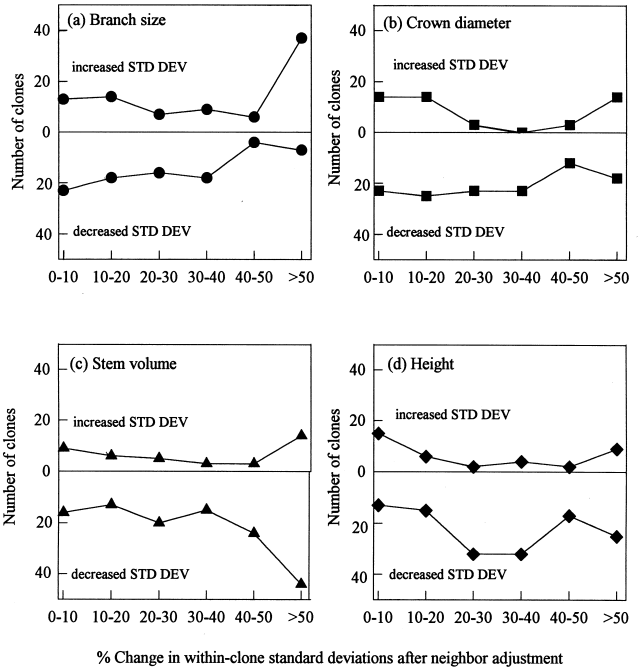

Figure 3. – Distribution of clones by percent change (10% interval) in clonal standard deviations (upper graphs indicate clones whose STD DEV increased and lower graphs indicate clones whose STD DEV decreased) for each of the 4 traits: (a) branch size, (b) crown diameter, (c) stem volume, and (d) height.

Within-clone standard deviations

Neighbor adjustment, if effective, should reduce data variation within individual clones. A comparison is made between clones that increased (upper part of each graph) or decreased (lower part of each graph) within-clone standard deviations for all 4 traits in *figure 3a* to *d*. The results indicate that the majority of the studied clones (about 70%, the exact percentage varying among traits) showed smaller adjusted-data within-clone standard deviations, compared to their unadjusted data. Note also in *figure 3* that the reductions (lower part of each graph) in clonal standard deviations are greatest for stem volume and least for branch size. In other words, for each trait some clones show increased within-clone standard deviations, but most show decreased within-clone standard deviations.

Components of variance, heritabilities, and predicted genetic gains

Variance components, heritabilities of clone means and predicted gains for the 4 representative traits are presented in *table 4*, with estimated values given before and after neighbor adjustments.

Table 4. – Variance-component estimates[1]), estimated variance components as percentage of total variance[2]), estimated clonal heritabilities[3]), and the amount and percentage of predicted genetic gains[4]) for 4 traits, based on measurements and adjustments of 172 redwood clones.

	Variance components			Percentage of total			Herita-bility	Predicted Genetic gain	
Trait[5]	V_S	$V_{C(S)}$	V_E	V_S	$V_{C(S)}$	V_E	$h^2_{\bar{C}(S)}$	ΔG	G%
Before neighbor adjustments									
Branch size	0.010	0.005	0.602	2^{ns}	1^{ns}	98	0.04	0.008	1
Crown diameter	41	79	919	4^{ns}	8^{*}	88	0.31	8.64	13
Stem volume	0.084	0.108	1.180	6^{*}	8^{**}	86	0.32	0.328	6
Height	120	112	1464	7^{**}	7^{**}	86	0.28	9.89	9
After neighbor adjustments									
Branch size	0.006	0.020	0.775	1^{ns}	2^{ns}	97	0.12	0.027	2
Crown diameter	41	109	671	5^{ns}	13^{***}	82	0.46	12.4	19
Stem volume	0.054	0.185	0.835	5^{ns}	17^{***}	78	0.53	0.550	10
Height	71	195	815	7*	18^{***}	75	0.55	18.2	17

[1]) Components of variance:
- V_S Among stands.
- $V_{(C)S}$ Among clones within stands.
- V_E Among ramets within clones = environmental or error.

[2]) Statistical significances indicated for the V_S and $V_{(C)S}$ percentages are for the associated variance components.
- ns Not significant
- * $0.05 > P > 0.01$
- ** $0.01 < P < 0.001$
- *** $P < 0.001$

[3]) Clonal heritabilities presented are estimates of within-stand heritability of clone means, $h^2_{\bar{C}(S)} = V_{C(S)}/[V_{C(S)}+(V_E)/k]$. Where, k = harmonic mean of ramets/clone = 5.19.

[4]) Genetic gains are predicted using an equation, $\Delta G = i\ (\sigma_{\bar{C}(S)})\ (h^2_{\bar{C}(S)})$, where selection differential, i = 1.755 based on 1/10 clones being selected. Percent gains are based on the mean values of 172 clones listed in *table 3*.

[5]) See *table 3* for measurement units.

(1) V_E, the error and/or environmental component, measured as the variance among ramets within clones

V_E was modestly increased for branch size, from 0.602 to 0.775, but it was decreased substantially for crown diameter, stem volume and height. The percentage of total variance accounted for by V_E was reduced for all the 4 traits.

(2) $V_{C(S)}$, the clones-in-stands component

Both the absolute and the percentage values of $V_{C(S)}$ were increased by neighbor adjustment for all 4 traits. The statisti-

cal significance of this component was increased for crown diameter, stem volume and height, but remained non-significant for branch size.

(3) V_S, the among-stands component

For all 14 traits (ANEKONDA, unpublished), the absolute values of (V_S) were not consistent in their changes following neighbor adjustment. For our 4 presented traits, V_S remained similar for crown diameter, while it decreased for the other 3 and lost statistical significance for stem volume and height. The percentage of total variance for V_S changed little for all 4 traits.

(4) Heritabilities

Increases in $h^2_{\bar{C}(S)}$ estimates occurred for all 4 traits. Standard errors (not presented) of the heritabilities were little changed; thus, for all 4 traits, the standard errors were a smaller percentage of the heritability estimate with the adjusted data.

(5) Predicted genetic gains

As an example, gain was predicted using a mild (10%) selection intensity. In all 4 traits, the predicted gains were substantially greater using adjusted data.

Discussion

Effects of adjustments on clone means

In his seminal paper, WRIGHT (1978) found small (less than 8%) changes in the family means in 75 of the 83 seedlots he studied, and no mean changes exceeded 16%. In contrast, our adjustment procedure has caused adjusted mean values of many clones to differ by more than 16% from unadjusted, particularly in the important stem volume trait, with 8% of the clones exhibiting changes of more than 50% (*Figure 2*). For purposes of selection, such changes in clonal means are clearly important. Whether the adjusted or raw data provide the more accurate basis for selection is still to be shown, but it seems likely that the adjusted data would be better. The increases in estimated heritabilities (*Table 4*) would predict greater accuracy and greater genetic gains if these increases were wholly due to decreases in the within-clone (V_E) variation (however, see below).

Within-clone standard deviations

A decrease in within-clone standard deviation, expected from WRIGHT's moving-average method, was clearly shown for the majority of clones following nearest-neighbor adjustments (*Figure 3a* to *d*). However, there is an interesting group of 10-to-40 clones whose within-clone standard deviations were increased by over 50%, particularly evident for branch size *(Figure 3a)*. This latter appears to be due to neighbor adjustments having occasionally created non-equivalent changes in the 2 variables that were used to calculate the relative mid-crown branch-size ratio.

Components of variance and heritabilities

Neighbor adjustment, if effective, should mostly reduce the "within-clone" variance component. Since this is done by reducing some effects of local environmental covariation, it is also expected that neighbor adjustment would not result in large or consistent changes in the "stand" or "among clone" components of variance. This should lead to a greater accuracy in estimating average performances of different genotypes, reflected by increases in estimated heritabilities of clone means.

However, LOO-DINKINS noted that estimates of the lowest-order genetic component of variance are often increased by neighbor adjustment, not only relatively but absolutely. Our data support LOO-DINKINS' observations; our lowest-order genetic component (*Table 4*, $V_{C(S)}$ estimate column) was increased by neighbor adjustment. Neither she (personal communication to w.j.l. July and August 1992) nor we have been able to offer a confident explanation for this.

LOO-DINKINS' simulation work indicated that the raw data estimates the (known) genetic variances more accurately, and the adjusted data generally overestimates them. This remains an interesting and important problem with respect to confident use of neighbor-adjustment procedures.

The less-consistent changes in the higher-order "stands" component of genetic variance may be an artifact of changes in the clones-in-stands component, and we remain unsure whether the adjusted or raw data provides the better estimate of the values of this component.

The increases in estimated heritabilities and predicted genetic gains that we observed are expected and desired if they reflect only a decrease in the environmental component of variance. In such case, they would accurately index the proportion of genetic causation of variability in the neighbor-adjusted data. But some of the observed increases in $h^2_{\bar{C}(S)}$ and predicted gains are also due to increased estimates of the absolute components of lowest-order genetic variation, creating a likely upward bias in such $h^2_{\bar{C}(S)}$ and gain estimates. Until this is better understood, it seems prudent to expect that the increases in estimated heritabilities accompanied by neighbor adjustments will overestimate the increases in gain likely by this procedure.

Field design

If neighbor adjustment of data is to be used, there seem to be substantial advantages to single-tree or non-contiguous plots, compared to contiguous plots of any shape. In an early paper on non-contiguous plots (LIBBY and COCKERHAM, 1980), it was suggested that row or block demonstration plots could be used in border rows without damage to assumptions concerning random neighbors for the interior trees. Such contiguous plots are unlikely to be efficient for neighbor adjustment because the members of such entries, used for estimating whether and how much these trees are above or below average, are not distributed throughout the plantation for which the average is relevant. A contiguous-plot demonstration can be placed next to one or more of the borders, but it should not be included in the borders.

We now recommend that the border be composed of randomized trees installed as single-tree plots, and the border should be composed of the same entries that are randomized over the entire experiment. Alternatively, because borders often require more trees than are available in all entries being studied, a subset of the entries in the experiment or a different set of entries similar to those in the experiment, can be used in the border. Since border trees are experiencing an "edge" environment, their values may be better compared to other border trees of their entry, rather than to entry averages from the whole experiment. In either case, the border trees should be non-contiguous (single-tree-plot) entries.

A hexagonal layout may be better than a square layout because it creates six rather than four nearest neighbors. This advantage is probably reduced if more-distant neighbors are also used.

Computing

The computer programs used for making neighbor adjustments in this study are fairly efficient and flexible. Thus, it is

feasible to define a larger, smaller or different-shaped neighborhood than the adjacent hexagon we used. Also, many traits can be adjusted independently for neighborhood effect. Once the required data and programs were in the computer in a standard format, we were able to adjust each additional trait's data in about 2 minutes on an IBM 286 Personal Computer (and in much less time on the newer 486 and Pentium CPUs).

A Fortran program written by A. STRANGENBERGER (based on an earlier program in BASIC by J. BERTENSHAW) was used to accomplish the data adjustments reported above. It can be used with either square or hexagonal layouts. Copies of this program are available on disc upon request. Write to Dr. AL STRANGENBERGER, ESPM Department, Forestry Program, University of California, Berkeley, CA 94720, USA.

Why was our adjustment more effective than WRIGHT's?

There could be several reasons for the differences between WRIGHT's results and ours. Those that are likely to be important include:

(i) WRIGHT used a field design with contiguous 4-tree row plots in contrast to the non-contiguous (single-tree) plots of this study. The number and shape of the neighbor plots used per entry (clone or seedlot) clearly influence the effectiveness of the adjustment. WRIGHT used only the four nearest and next-nearest plots, sampling environments on the lengthwise sides of the adjusted row-plot. Our design provided up to 6 equally-spaced independent neighbors, closely sampling the environments on all 6 sides of the subject tree.

(ii) Clones probably reflect the environmental differences that exist in the plantation more accurately than did the open-pollinated families in WRIGHT's experiment.

(iii) WRIGHT measured 15-year-old trees, compared to 2-year-old trees in this study. Between-tree competition probably reduced the precision of environmental adjustments in WRIGHT's experiment. In addition, differential sensitivities to environmental variability are not uncommon in developmental stages of forest trees. (For example, we noted that neighbor adjustments were more effective on our second-growing-season data.).

Alternative adjustment protocols

The program that we used in this study includes data from the contiguous neighboring trees in the calculation of their respective clonal means. Inclusion of this data incorporates bias in the calculation, because the contiguous neighbors share the environment of the neighborhood. Thus, this procedure contains an environmental covariance and incompletely removes the effects of a gradient or patch.

We investigated three alternative adjustment protocols. In one, data from the neighbors contiguous to the central tree (*Figure 1*) were excluded from their respective clonal means. In the other 2, we used proportional rather than absolute adjustments, 1 with contiguous-tree data included, the other with it excluded. Each of these further improved the overall data fit to a normal distribution (the best being the proportional adjustment based on contiguous-tree data excluded from its entry mean). However, none of these 3 alternatives substantially or consistently improved the power of the test more than did the data-adjustment procedure reported in the presentation, above.

Furthermore, all 4 adjustment protocols estimated larger absolute values for the clonal component of variance ($V_{C(S)}$) than did the raw-data analysis, with inconsistent trends among the traits analyzed (i.e., no one adjustment protocol consistently estimated larger, smaller, or intermediate absolute values of the clonal component among the four values estimated by these 4 protocols). The spline procedure suggested by BONGARTEN and DOWD (1987) does not inflate the estimate of the lowest-order genetic entry (personal communication, Prof. B. BONGARTEN, University of Georgia, February 1995), and in favorable cases may be a more effective data adjustment than the neighbor adjustments we have investigated.

The estimates of the among-stands component (V_S) were similar with all 5 protocols that we investigated, and no consistent trends were apparent.

We thus conclude that all 4 neighbor-adjustment protocols that we investigated were effective in reducing patchy or clinal environmental variation in our field experiment, but that no one of them was consistently better across all traits investigated. We therefore presented the simplest of the 4 in some detail as an example of the use, effectiveness and possible problems of neighbor-adjustment of field data.

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