REMOVAL OF COMPETITION BIAS FROM FOREST GENETICS EXPERIMENTS

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Abstract.--Estimates of genetic gains and of juvenile-mature correlations in small-plot breeding experiments may be inflated because trees that grow rapidly early continue to be the largest trees, and trees that begin slowly usually stay small. A procedure which takes missing trees, relative sizes and distances between competing trees, and the intensity of competition into consideration was used to adjust diameter measurements in small-plot cottonwood clonal breeding experiments. The F ratio of clone to error mean square was increased and predicted genotypic gain was decreased.

Additional keywords: Cottonwood, genotypic gain.

In field experiments of planted trees, there normally are missing trees and trees considerably larger or smaller than their neighbors. As a result, the growing space available to a tree will differ from the space originally allotted. Trees with rapid early growth may appear better and trees with slow initial growth may appear poorer than their inherent potential. It is difficult for trees with poor early growth to catch up since they are suppressed by larger trees. Thus, the breeder may overestimate the genetic variability among experimental genotypes and predict greater genetic gains than are actually attainable. In addition, estimates of genetic correlations between measurements taken at different ages can be inflated, causing the breeder to believe that early selection is more effective than it really is. The problem is particularly serious in cottonwood, where a high incidence of missing and small trees resulting from the use of unrooted cuttings, rapid growth rate, and sensitivity to crowding cause competition bias to become important at an early age.

Partial solutions to the problem include: (1) reducing competition by wide spacing or early thinning, (2) causing competition to be as uniform as possible by testing only clones with similar growth potential (possible in advanced clonal tests) and by planting two or more cuttings per spot and thinning back soon after establishment to the best tree to reduce the number of missing spots and to improve uniformity of early growth, and (3) using data adjustment procedures which compensate for the effects of missing and suppressed trees. A combination of the above procedures should give the best results. This paper describes a data adjustment procedure and its application to diameter data in small-plot cottonwood clonal tests. It illustrates what happens when data are adjusted and may provide a starting point from which better procedures can be developed.

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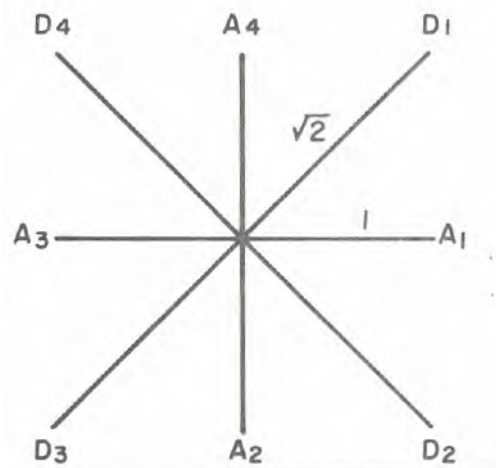
MATERIALS AND METHODS

Missing trees, relative sizes and distances between competing trees, and intensity of competition were taken into consideration in choosing an adjustment procedure which would tend to convert tree diameter to that which would have occurred if the tree utilized no more or less than its allotted space. Only the positions immediately surrounding the measurement tree were considered. It was arbitrarily assumed that the effect of one tree on another could be approximately described as the reciprocal of the square of the distance between them times the difference in their basal areas times a coefficient which would reflect the intensity of competition. Thus, with a square grid arrangement of trees, a diagonal neighbor would have only one-half as much effect as an adjacent neighbor of the same size. The coefficient would be zero if there is no competition among trees or if they compete evenly. It would increase as uneven competition develops. Proper adjustment would depend on an accurate estimate of this coefficient.

The adjustment computation for trees arranged in a square grid pattern was made as follows:



$J = B - CE$

where J = adjusted basal area
B = measured basal area
C = competition coefficient for the experiment
E = adjustment value =

$$\left(\sum_{i=1}^{4}(D_i - B)\right)/12 + \left(\sum_{i=1}^{4}(A_i - B)\right)/6$$

where D_i = measured basal area for the ith diagonal neighbor
A_i = measured basal area for the ith adjacent neighbor

Programs were developed in BASIC for a HP9830A computer[1/] to allow efficient computation of the adjustment. Data were divided into manageable arrays and stored on tape. Data were then converted to basal area per tree and an adjustment value computed for each tree. The unadjusted dbh, unadjusted basal area, and the adjustment value were then printed out. Values from missing and extremely small trees were deleted and identification, unadjusted basal area, and adjustment values were re-entered. Analyses of variance based on plot means and separate analyses of within plot variance were then performed repeatedly with various competition coefficients. The effects of adjustment on within-plot variance, replication x clone variance, clone variance, and F ratio of clone to error mean square for clones were examined.

[1/] The use of trade name is for the information and convenience of the reader. Such use does not constitute an official evaluation, conclusion, recommendation, endorsement, or approval of any product or service to the exclusion of others which may be suitable.

The adjustment routine was applied to four separate cottonwood clonal studies that represented a range of genotypes, plot sizes, planting sites, ages, and competition intensities.

Study 1 consisted of 12 random clones from a single full-sib family. There were 2 replications of 4-tree linear plots at 12 x 12 ft. spacing. Mean dbh was 5.6 in. at age 3 and 7.3 in. at age 5. Crowns were still relatively full at age 5 but it appeared to be time for thinning in order to keep the trees growing rapidly.

Study 2 consisted of from 2 to 4 random clones from each of 16 full-sib families produced by crossing 4 superior female parents with 4 superior male parents. Two replications of two-tree plots at 12 x 12 ft. spacing were used. Mean diameter was 6.2, 6.8, and 7.2 in. at ages 4, 5, and 6 respectively. The general appearance of the crowns indicated that considerable competition was occurring by age 4. Data adjustment procedures were applied and clones not present in both replications were then dropped from further analysis leaving 48 clones.

Study 3 originally consisted of 25 select clones, 4 replications, and 2-tree plots at 10 x 20 ft. spacing. Three cuttings were planted per planting spot and thinned to the one best tree in June of the first growing season. One tree per plot was removed at age 5 leaving the remaining trees at 20 x 20 ft. spacing. The trees averaged 6.5 inches dbh at age 4 and produced a consistent 0.8 in, annual diameter increment for the next 6 years, slowing down to less than 0.4 in. annual increment during the eleventh and twelfth years. The data adjustment procedure was applied to age 12 dbh. Clones missing in one or more replications were excluded from further analysis, leaving 19 clones. Because of wide initial spacing, use of multiple cuttings, early thinning, and inclusion of only good clones in the study, the appropriate coefficient of competition was expected to be small, although mean dbh was 12.0 in. and basal area was 89 sq. ft. per' acre.

Study 4 consisted of a single clone (Stoneville 66) planted at 10 x 10 ft. spacing. Three blocks, each 10 trees by 10 trees, were chosen at random. The trees averaged 3.0 in. dbh at age 3 and 3.6 in. dbh at age 4, but because of insufficient late-season moisture in the Sharkey clay soil at this site, competition was probably already important by age 3. Adjustment values were computed on the interior 8 tree by 8 tree portion of each block. Analyses of variance of adjusted values were computed considering each block as being made up of 1-, 2-, and 4-tree plots.

RESULTS

Within-plot variance was minimized when the competition coefficient was approximately 0.7 to 0.8 for all ages involved in Studies 1, 2, and 4 (Fig. 1). Adjustment removed nearly all of the within-plot variance.

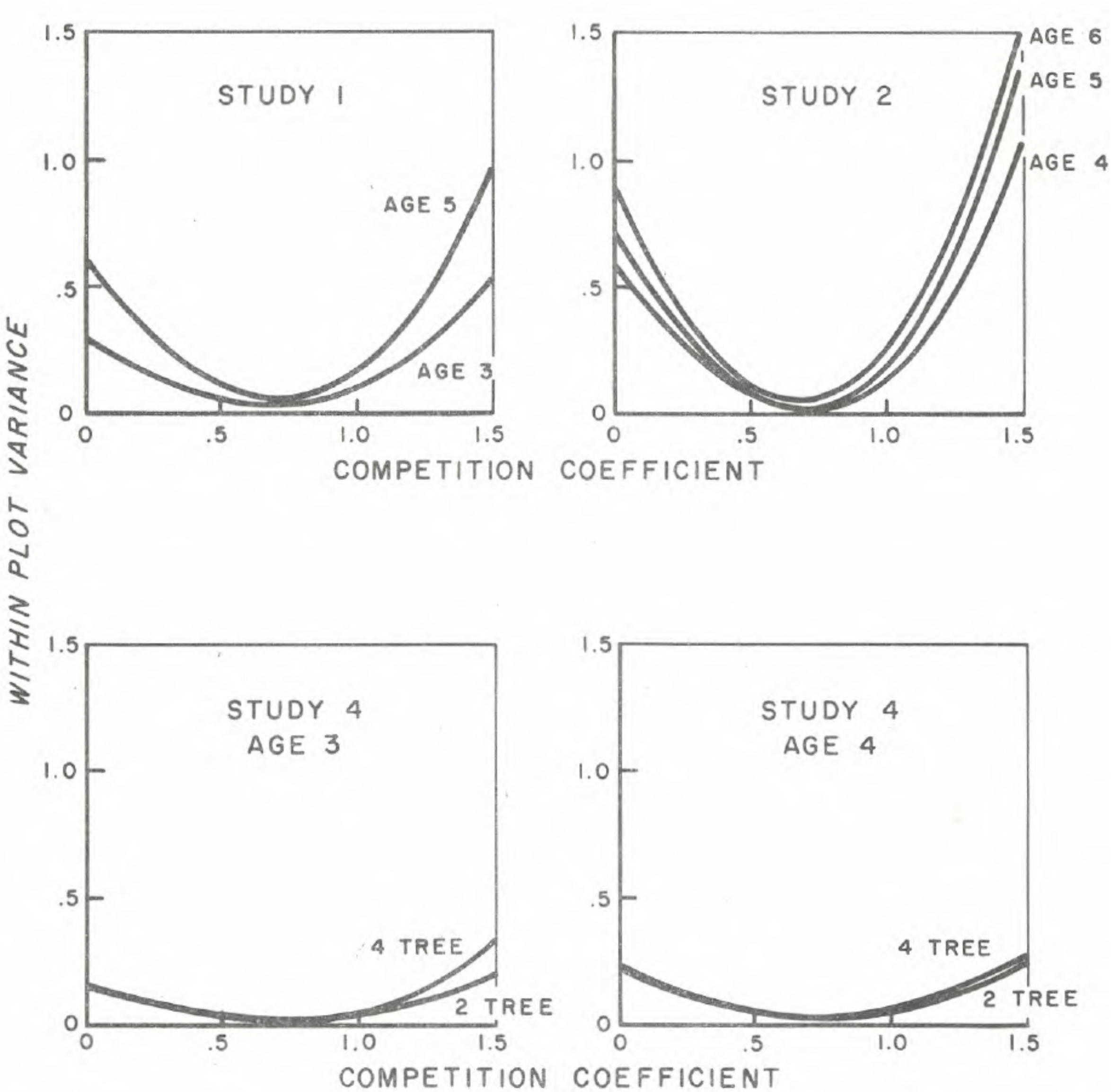


Figure 1.--Differences in within plot variance as competition coefficient is changed for Studies 1, 2, and 4.

Replication x clone variance dropped less rapidly than within-plot variance. Replication x clone variance was minimized when the competition coefficient was 0.4 at age 3 and 0.5 at age 5 in Study 1 (Fig. 2). In Study 2 it was minimized at 0.6, 0.7, and 0.6 for ages 4, 5, and 6 respectively. It was minimized at 0.6 in Study 3. In Study 4 it was minimized at 0.8, 0.7, and 0.6 at age 3 and at 0.7, 0.6, and 0.5 for 1-,2-,and 4-tree plots at ages 3 and 4 respectively.

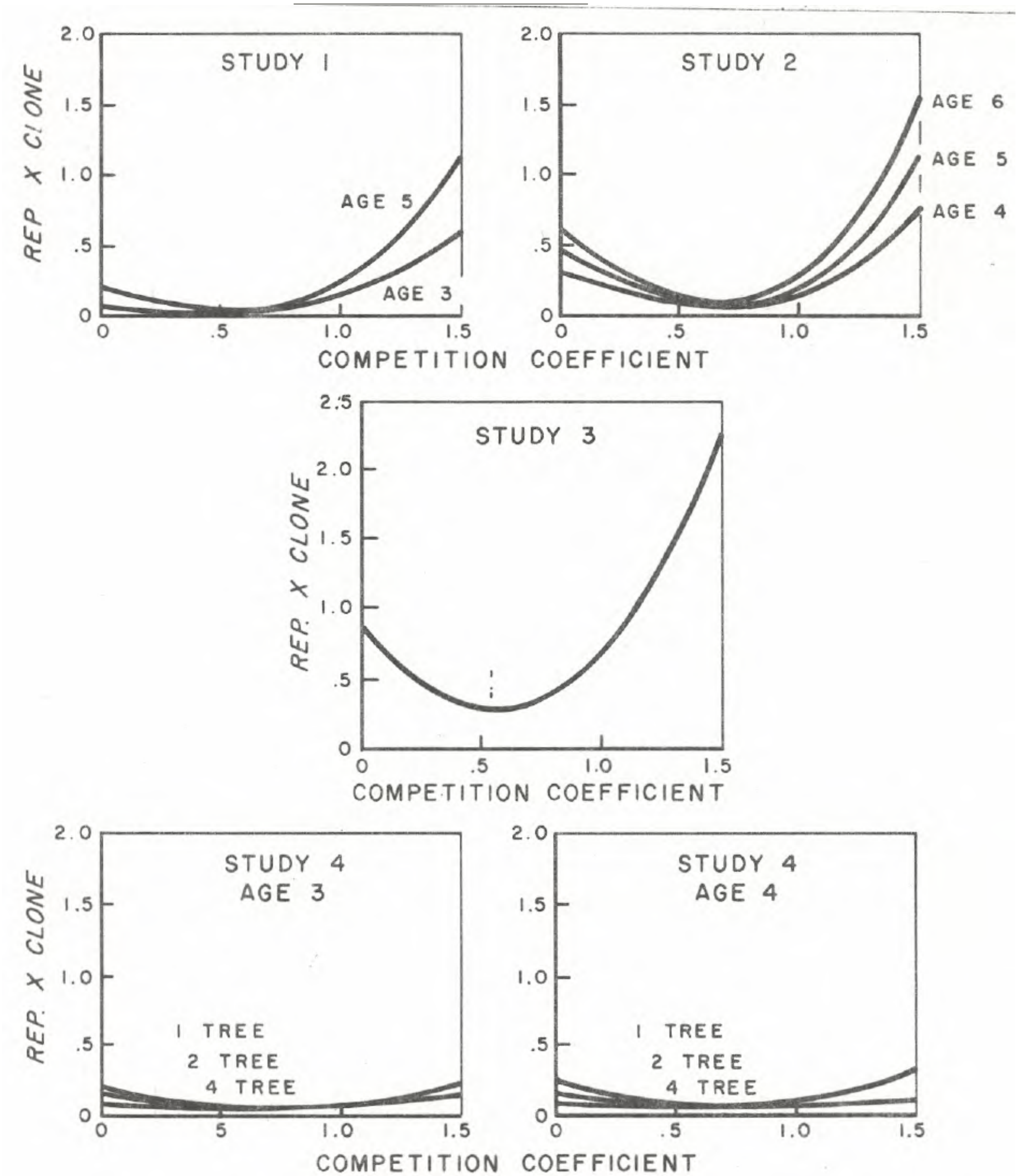


Figure 2.--Differences in replication x clone variance as competition coefficient is changed in Studies 1, 2, 3, and 4.

The pattern of change in the clone component of variance differed considerably among studies. As a result, the patterns of change for genotypic gain and the F ratio of clone to error mean square differed.

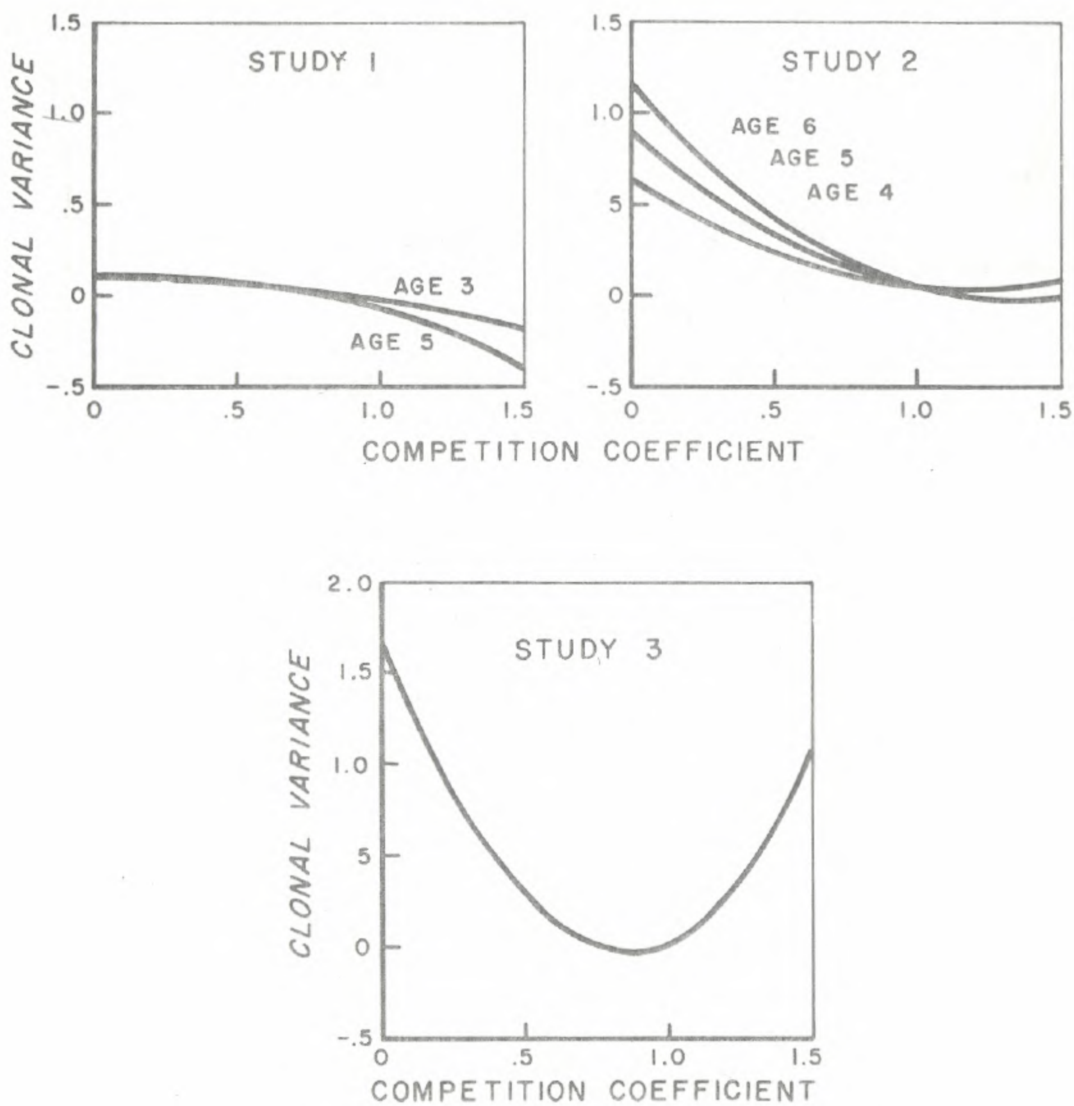


Figure 3.--Differences in clonal variance as competition coefficient changed in Studies 1, 2, and 3.

The F ratio increased initially and then dropped (Fig. 4). The competition coefficient for maximum F in Study 1 was 0.4 at age 3 and increased to 0.5 at age 5. In Study 2, F was maximized when the competition coefficient was 0.5 for ages 4, 5, and 6. F was maximized in Study 3 when the competition coefficient was only 0.1.

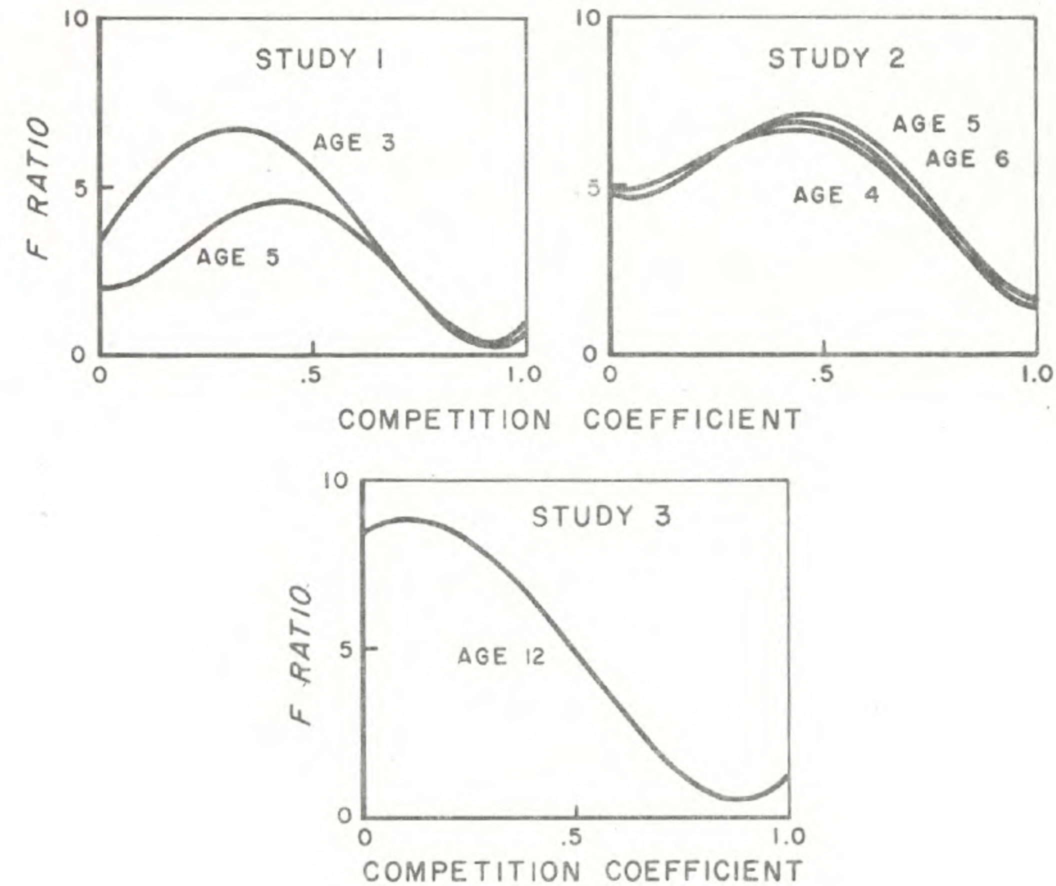


Figure 4.--Differences in F ratio of clone to error mean square as competition coefficient changed in Studies 1, 2, and 3.

The competition coefficient required to maximize the F ratio appeared to correspond with the apparent amount of competition observed in the various studies much better than the competition coefficient required to minimize - within-plot or replication x clone variance. Maximizing F usually decreased predicted gain. In Study 1, predicted gain for data adjusted to maximum F was 89 and 104 percent of that of unadjusted data at age 3 and age 5 respectively. In Study 2, predicted gain for data adjusted to maximum F was approximately 65 percent of that of unadjusted data at each age. In Study 3, predicted gain for data adjusted to maximum F was 88 percent of that for unadjusted data.

DISCUSSION

The adjustment procedure takes missing trees, relative sizes and distances between competing trees, and intensity of competition into consideration to adjust diameters of large trees with little competition downward and diameters of small trees with intense competition upward. It shifts part of the area-related growth to missing positions which then are omitted from further data analysis. Values for trees which fail to take advantage of extra growing space are reduced and values for trees that grow well despite competition are increased. Thus, the results express something slightly different from the ability of the trees to grow in uniform, genotypically pure stands, but the error should favor clones capable of utilizing all available space.

Several improvements could possibly be made in the adjustment procedure. The effect of direction of the various neighbors on tree growth was ignored, which may not be accurate for crown competition but should be acceptable for below-ground competition Trees more than one position removed from the tree for which adjustment was made could be taken into account. The reciprocal of the square of the distances between trees in the adjustment formula was chosen arbitrarily, and a greater increase in the F ratio might occur if a value different than the square was used. The adjustment procedure considered the relative sizes of the trees at a single time and it might be better to use the relative increase in size of the trees during the period just before adjustment.

The adjustment procedure is not suitable for removing microsite or soil gradient differences. It should be valuable on relatively uniform sites with fairly homogeneous material where missing and small trees result in unequal growing space per tree.