Variation in Photosynthesis and Respiration Among Loblolly Pine Progenies

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Photosynthesis and respiration are of overwhelming importance to the production and accumulation of dry matter by plants. Unfortunately, the range of variability and the importance of the genetic control of these two aspects of metabolism, photosynthesis and respiration, has not been adequately measured in natural populations.

This report is based on a sample of families from the North Carolina State University and International Paper Company cooperative study of heritability in a natural population of loblolly pine (Pinus taeda L.) (Stonecypher, 1966). The objectives were to 1) determine whether variation in net and total photosynthesis, respiration, and P/R ratio exists within the population, 2) estimate components of variance and heritabilities for photosynthesis 3) estimate whether the major mode of inheritance of photosynthesis is of the additive or the dominance type, and 4) compare the rate of photosynthesis of the progeny of a cross between select trees from the North Carolina State University-Industry Tree Improvement Program with photosynthesis in the progeny of random crosses.

LITERATURE REVIEW

Though many estimates of heritability in forest trees are becoming available, little information pertinent to the estimation of genetic variance has been published on photosynthesis and respiration. With a total of 90 families from a stand of Douglas-fir,Campbell and Rediske (1966) measured photosynthesis and seedling dry-weight traits. They used a design 1 mating scheme in which each of a number of males is crossed to a different series of females. Their determinations extended over four months. Plants were held under a regime designed to keep them dormant. Dominance variance was found to be greater than additive variance.

Reines (1962) and Robertson and Reines (1965) investigated net photosynthesis and respiration in eight half-sib loblolly pine families and five half-sib slash pine families. Though they reported variation in photosynthesis among families the samples were small and heritabilities were not estimated. No variation in respiration was observed on a per unit weight basis.

Differences in photosynthesis were found between 16 poplar clones by Huber and Polster (1955), and the differences were related to variation in yield. However, variation in relative leaf area explained a greater proportion of the differences in yield than did photosynthetic rate. The poplar clones represented species and their hybrids and therefore this study does not indicate the degree of genetic variation found in natural populations.

MATERIAL AND METHODS

Material. Three experiments are reported which compare the photosynthetic and respiration rates of a sample of seedling progenies from crosses within a population of loblolly pine from southern Georgia. Two sets of trials were made with full-sib mating schemes and one with design 1. For the first full-sib trial, seed was germinated and seedlings were grown in pots under an open-sided polyethylene shelter until measurement in early October. For the second full-sib and the design 1 experiments, seedlings were placed in a greenhouse in mid-October and a supplemental photo-period was provided; measurements were made in mid-November.

Conditions of Measurement. Using a Beckman infrared gas analyzer, photosynthesis was measured as rate of CO_2 assimilation in a closed system with a flow rate of 750 cc. per minute. After the photosynthetic determination, the plant was covered with a dark-cloth and respiration measured as rato of‘CO_2 evolved in the dark.

Though it is desirable to measure photosynthesis under a variety of light intensities, temperatures,

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and seasons, this increases the difficulty of making a large numberof comparisons among genotypes. Our experimental technique restricted the measurement to ci maximum of two plants per hour. In addition, preliminary experiments indicated that replicates which extend over more than one day have high error due to large day-to-day variation. Because of these restrictions, comparisons could not be made over a range of light and temperature and conditions were employed which were representative of the Southeast in summer. A light intensity of 3000 ft. candles had been shown by Bormann (1956) to be near light saturation for loblolly pine seedlings with juvenile needles, and a temperature of 27°C (80.F) is common in the summer and near optimum for loblolly pine.

After the gas exchange measurements, the seedlings were disected into needles, stems, and roots and weighed to the nearest milligram. The resultant data were used to express photosynthesis and respiration on a dry weight basis.

Expression of Results. Net photosynthesis and respiration in mg of CO2/hr are transformations of the time to ken to change the CO2 concentration of a given volume of air from 320 ppm to 270 ppm by volume. For comparison of genotypes, these rates must be divided by some measure of the photosynthetic surface or mass and the respiring mass, respectively. A per seedling basis is unsatisfactory because variation in leaf area or mass is greater than variation in photosynthetic rate. With fascicled needles (Kozlowski and Schumacher, 1943; Smith, 1967) or the leaves of hardwoods (Kramer, 1937; Kramer and Kozlowski, 1960), it is not difficult to estimate surface area, thus providing a common base for photosynthetic rates. Due to the lack of analogy with simple geometric figures, it is difficult to estimate leaf area for juvenile needles of pine. In addition, efficiency (production per unit cost) in terms of chemical energy production is more closely related to the mass of material required to produce a unit input than its surface area. Therefore, net photosynthesis was based on mg needle, and respiration on mg shoot, shoot being the dry weight of needles plus stem. The P/R ratio, cited as an efficiency index (e. g. Huber, 1964; Bordeau, 1958), is net photosynthesis in mg CO_2 'hr divided by respiration in mg 'CO2 /hr.

Total photosynthesis was calculated as net photosynthesis plus respiration, both in mg CO2 /hr, divided by mg needles. The assumption involved in the estimation of total photosynthesis, i.e. that respiration in the dark equals that in the light, is probably incorrect. In many plants dark respiration is not the same as light respiration (**e.g.** Moss, 1966; Zelitch, 1958, 1965; Decker, 1955; Tregunna et al., 1961, 1964).

Experimental Design. All trials of photosynthetic and respiration measurements were randomized complete blocks with days as the block. In the first experiment, using progenies having full-sib relationships in the group, five repliCations and seventeen families were used. In the second set of trials, also with five replications, sixteen of the same families were compared. A combined analysis was performed, allowing measurement of genotype-environment interaction through the family times experiment component. The progeny of a cross between select trees of the North Carolina State University-Industry Tree Improvement Program was also :ncluded in each trial.

For the design 1 experiment, there were fourteen families consisting of seven male groups with two females in each, replicated six times. There were two replicates in each of three days. One of the male groups was represented by the progenies from controlled crosses between select trees.

FULL-SIB COMPARISONS

Components of variance attributable to differences among full-sibs may be interpreted as one-half the additive plus one-quarter of the dominance variance (Falconer, 1960). A heritability calculated on the basis of individual plants is considered a strict heritability. For full-sibs, the value lies between broad and narrow sense estimates. Narrow sense heritability is the ratio of the additive genetic variance to the total variance, so estimates based on the variance attributable to differences among full-sib families are upper limits of narrow sense heritability.

To interpret the families component of variation as one-half of the additive genetic variance for a trait plus one-quarter of the dominance variance requires the following familiar assumptions: 1) regular diploid and Mendelian inheritance, 2) population in linkage equilibrium, 3) relatives random members of a non-inbred population, 4) parents mated at random to produce progeny, 5) no epistasis, and 6) no maternal effects. Stonecypher (1966) discussed these assumptions for this population. Those assumptions concerning the relationships of members of progenies and parents might offer the most trouble in a natural stand where the degree of inbreeding and relatedness of individuals is unknown.

For the present investigation the assumption of no maternal effect deserves additional consideration. Correns in 1909 gave the now classic example of maternal effect in connection with cytoplasmic inheritance and his illustration may be directly applicable here. He found that the color of F1 progeny of **Mirabilis jalopa** crosses was due to differences in chloroplasts and depended only on the phenotype of the female parent. In most plants the chloroplast is contributed to the embryo (probably in the form of proplastids) mainly through the maternal gamete. In **Pinus,** the cytoplasmic material carried by the pollen, including mitochondria and proplastids, disintegrates after segregating in one region of the fertilized oosphere and does not contribute to the embryo (Jinks, 1964). The light reaction in photosynthesis is localized in the chloroplast and therefore, differences in photosynthetic rate might be due to a genetically unalterable organization of the plastid. The result of differences in chloroplast structure would be variation attributable to maternal effect.

Results and Discussion

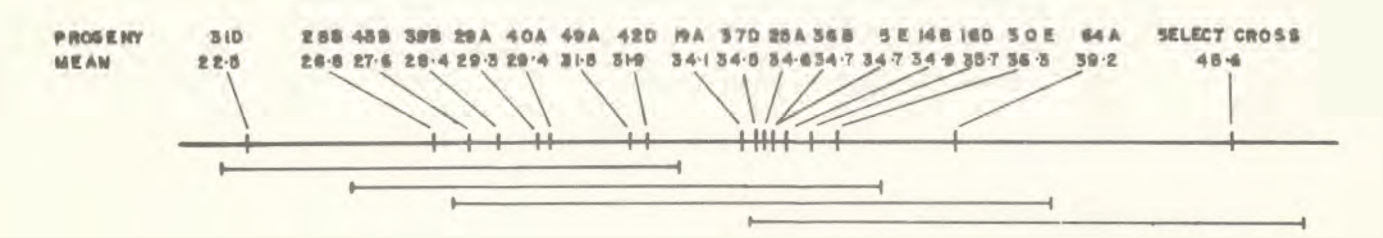
Full-Sib Experiment 1. The progeny of the select tree cross was superior in photosynthetic rate to the other progenies (table 1, Duncan's test). It had a rate of total photosynthesis of 51.8 mg CO2/hr/mg needle which was 6.4 mg CO_2/hr/mg needle, or one-third of the entire range, above the progeny with the next highest rate of photosynthesis. Such a difference could account for a large divergence in growth between select seedlings and control seedlings in a matter of months if other factors contributing to dry matter production were equal. A t-test was valid in this case and indicated that the photosynthetic rate of the select tree progeny is significantly greater than that of the other families. Since the select tree progeny is a cross between wide geographic races, the observed superiority may be a result of hybrid vigor rather than selection.

This comparison of a select tree progeny with those from natural stands is the only one reported which can be interpreted on the basis of photosynthesis per unit needle weight.Wyatt and Beers (1964) compared the CO_2 assimilation of select tree progeny to control progeny over two years, using a nullpoint compensating system monitored by a gas chromatograph. Their results could only be applied on a per-seedling basis. Though it was true that their plus trees had a high capacity to assimilate CO2, it was equally obvious that the plus trees were larger and had more leaf mass than the control seedlings.

The results of the analyses of variance (table 2) supply information on the quantitative inheritance of photosynthetic and respiration rates and seedling dry weight. While family differences in netand total photosynthesis and total dry weight were obvious, there are apparently no differences in respiration rate or P/R ratio. The difference among days of replication was important for all gas exchange measurements.

The genetic coefficients of variation for photosynthesis and for total dry weight are 0.09 and 0.22 respectively. Heritabilities are 0.28 and 0.34 for net and total photosynthesis, and 0.86 for total dry weight. The estimates indicate a fair amount of genetic variation in photosynthesis with much more variation in seedling dry weight. For photosynthesis, standard errors of the family components of variation are greater than half the size of the component and for to to l

TABLE I DUNCAN'S NEW MULTIPLE RANGE TEST OF NET PHOTOSYNTHESIS IN UG CO_2 /HR/MG NEEDLE FOR FULL - SIB EXPERIMENT NO 1



MEANS UNDERSCORED BY THE SAME LINE ARE NOT SIGNIFICANTLY DIFFERENT ON THE 5 PERCENT LEVEL OF PROBABILITY

Table 2. Mean squares and F-ratios for analyses of variance of net and total photosynthesis, respiration, P/R ratio, and total dry weight for full-sib experiment no. 1

		Net Photosynthesis		Total Photosynthesis		Respiration		P/R Ratio		Total Dry Weight	
Source	d.f.	mean	F	mean .u. -		mean		mean		mean	
Days	4	876.4791	17.81***	1061.6123	20.27***	8.6255	7.38***	14.6130	6.42***	25,571.6	3.13***
Families	16	90.0794	1.84**	106.8242	2.04**	1.2911	1.10 ns	1.6912	0.743 ns	39,089.8	4.78**
Residual	64	49.2022		52.3752		1.1695		2.2771		8,170.1	

ns non-significant

** significant on the 0.05 level

*** significant on the 0.01 level

dry weight they are less than half the component.

Phenotypic correlations of -0.288 (5% level) were found for both net and for total photosynthesis on total dry weight. However, a priori reasoning suggests that seedlings with higher photosynthetic rates should accumulate more rather than less dry matter. Negative correlations of photosynthesis and plant size may be due to 1) greater mutual shading of the needles in larger seedlings (Kramer and Clark, 1947) or 2) a decline in needle efficiency during the development of the seedling (Clark, 1961).

Zobel (1965) found strong negative correlations between apparent photosynthesis per dm2 I ea f surface on the one hand and leaf area per seedling on the other in sweetgum (**Liquidambar styraciflua L.**). Such a situation not only confuses any possible tendency of high photosynthetic rates to result in larger seedlings but may actually result in decreasing the rate of divergence in growth between seedlings with high and low photosynthetic rates respectively.

Full-Sib Experiment 2. There were many noticeable differences between Experiment 1 in which seedlings were conditioned out-of-doors and Experiment 2 in which pre-conditioning occurred in a greenhouse. Though net and total photosynthesis again varied among families, there were also differences in P/R ratio (table 3). This can be explained by the partial dependence of the ratio on photosynthetic rates which

Table 3. Mean squares and F-ratios for analyses of variance of net and total photosynthesis, respiration, P/R ratio, and total dry weight for full-sib experiment no. 2

		Net Photosynthesis		Total Photosynthesis		Respiration		P/R Ratio		Total Dry Weight	
Source	d.f.	mean square		mean square	F	mean square	F	mean square	F	mean square	F
Days	4	23.1834	2.83**	26.6452	2.96**	0.4237	1.96 ns	5.6230	2.75**	145,879.8	1.04 ns
Families	15	21.4780	2.62***	23.2112	2.58***	0.3616	1.67*	4.0806	1.99**	735,953.3	5.25-"*
Residual	60	8.1875		9.0094		0.2162		2.0484		140,260.5	

ns non-significant

significant on the 0.10 level

significant on the 0.05 level

significant on the 0.01 level

varied greatly.

Average photosynthetic rate was only two-thirds of that in the preceding experiment. Bormann (1956, 1958) has shown that loblolly pine seedlings having only juvenile needles, photosynthesize at a more rapid rate than seedlings with fascicled needles (presumably due to more self-shading in the latter).

The effect he observed was especially pronounced at the light intensity used in this study. Seedlings in Experiment 2 had mainly fascicled needles while those in Experiment 1 were almost entirely juvenile, perhaps accounting for the decrease in photosynthesis in the second experiment.

The progeny of the select tree cross had an average rate of photosynthesis. Racial variation makes the comparison between the select trees and those from the natural population inappropriate in this case. The parents of the cross between select trees were from the North Carolina piedmont and southwestern South Carolina provenances. The progeny were observed to be in a different physiological state than the southern Georgia material at the time of measurement and did not respond as vigorously to the conditions in the greenhouse. The reaction of piedmont loblolly is typical of northern races.

Heritabilities for net and total photosynthesis were 0.50 and 0.48, respectively. The relative increase in precision and apparent increase in heritability between this and the preceding experiment is due to a great decrease in total variation and in particular to the error variance. Probably the buffering of the environment by the controlled temperature and photoperiod in the greenhouse is responsible for reducing the variation. Variation among days in photosynthesis and respiration was obvious, however.

Phenotypic correlations between both net and total photosynthesis on the one hand and total dry weight on the other were not statistically significant.

Combined Analysis. The results of the combined analysis using the 16 families common to both experiments are summarized in terms of components of variance and heritabilities in table 4 along with the statistics for each experiment separately. In the combined analysis, the families component of variance is small and heritabilities for net and total photosynthesis are 0.07 and 0.08.

Table 4. Estimates of means, variance components, standard error of the genetic component, genetic coefficient of variation, and heritability for net and total photosynthesis and total dry weight for each experiment separately and for both experiments combined.

PARAMETER'	NET PHOTOSYNTHESIS (pgm CO_2/hr/mgm needle)			TOTAL PHOTOSYNTHESIS (ugm CO_2/hr/mgm needle)			TOTAL DRY WEIGHT (mgm)		
ESTIMATED	Expt. no. 1	Expt. no. 2	Combined	Expt. no. 1	Expt. no. 2	Combined	Expt. no. 1	Expt. no. 2	Combined
p	32.87	23.61	27.97	38.81	27.15	32.72	362	1645	990
$a^{t}e$	49.202	8.188	29.986	52.375	9.009	32.324	8,170	140,260	74,254
$a^{2}gxe$			4.272			5.461			54,410
$a^{2}g$	8.175	2.658	1.213	10.890	2.840	1.398	6,184	119,139	8,230
$0_{(o^{2}g)}$	6.245	1.502	5.653	7.351	1.625	6,551	2,621	50,737	37,846
ag/p	0.09	0.07	0.04	0.09	0.06	0.04	0.22	0.21	0.09
h^{2}	0.28	0.50	0.07	0.34	0.48	0.08	0.86	0.92	0.11

[a] Oe^{2} = variance due to random error

$a^{2}gxa$ = variance due to the interaction of families in experiments

$a^{2}g$ = variance due to differences among families

$a_{(a^{2}g)}$ = standard error of estimate of the component of variance due to differences among families

ag/p = genetic coefficient of variation

h^{2} = heritability computed as $2a^{2} / (a_{e}^{2} + a^{2})$ for each experiment and $2o_{g}^{2}/(o_{e}^{2} + o2_{gxe} + a^{2})$ for both experiments combined

This reflects the relatively large interaction component between families and experiment, i.e. between families and the conditions under which they were grown and the time of measurement. There is no other data in the literature on the magnitude of genotype-environment interactions of 'photosynthetic rate on the population level. The present experiment does not identify the source of the interactions found but suggests that they are of overriding importance. It is likely that the genes functioning under one set of conditions may not be the same as those operating under other circumstances.

As a manifestation of the interaction there was almost no correlation between the performance of progenies in the two trials. It is interesting to speculate on the outcome of Campbell an d Rediske's (1966) experiment repeated when the seedlings are not held dormant. The knowledge provided by this study indicates that there may be little relationihip between the ranks of progenies in photosynthesis under different preconditioning. The estimates of heritability obtained by these authors, 0.21 and 0.53 based respectively on a variance attributable to all plots and a variance within plots, are close to those reported here.

The difficulty in investigating photosynthesis and respiration as genetic traits occurs because both traits are far from gene action. The manifold effects of the environment in modifying photosynthesis suggests that feedback from many interacting metabolic pathways is involved. Gas exchange, i.e. uptake of CO_2 in the light for net photosynthesis and release of CO_2 in the dark for respiration, is an end result of the processes of the entire metabolic system. Still, if yield is a suitable trait for breeders, then photosynthesis may also be, for the observed dry weight of a plant almost entirely represents the balance in organic carbon between CO_2 assimilated and that respired again as CO_2. However, it is presumptuous to expect that measurement of photosynthesis and respiration under one set of conditions can be related to the summation of these processes, the final plant weight.

DESIGN 1 EXPERIMENT

Design 1,developed by Comstock and Robinson. (1948, 1952) can be used to divide genetic variation into additive and dominance components. This design mates each of a series of male parents to a different sample of female parents. Half-sib components are estimated from the males mean square and represent one-quarter of the additive variance and none of the dominance. The females-in-males component is a measure of the variance among full-sib families minus the variance among half-sibs and estimates one-quarter of the additive plus one-quarter of the dominance variance. Therefore, any difference between the males and the females component should indicate the presence of dominance deviation. The assumptions discussed above for the full-sib case apply to the estimation of components from the females-in-males mean square in this experiment.

Results and Discussion

In the experiment using design 1 the female-in-male mean square is larger than that of the males for both net and total photosynthesis (table 5). The relative importance of the female-in-male **source** of

TABLE 5.•-Mean squares and F-ratios for analyses of variance of net and total photosynthesis, respiration, and P/R ratio for a design 1 experiment

		Net Photosynthesis		Total Photosynthesis		Respiration		P/R Ratio	
Source	d.f.	mean square	F	mean square	F	mean square		mean square	
Days	2	71.2248	2.106 ns	52.7783	1.571 ns	9.3523	10.106 ***[a]	83.1 520	5.064 ***[a]
Reps/Days	3	33.8138	3.143 ***	33.5983	2.496 *	0.4560	0.481 ns	0.7229	0.128 ns
Males	6	31.8920	0.294 ns	44.1359	0.339 ns	1.0808	0.592 ns	1.0709	0.102 ns
Females/Males	7	108.4409	10.079 ***	130.1963	9.671 ***	1.8246	1.926 *	10.4693	1.851 *
Residual	65	60.7587		13.4623		0.9474		5.6564	

ns non-significant

ns non-significant

significant on the 0.10 level

** Significant on the 0.05 level

*** significant on the 0.01 level

a based on the pooled mean square of times-days plus residual variation compared to the male source suggests that much of the genetic variation in photosynthetic rate may be of the dominance or dominance-epistatic types predominantly. However, a smaller and inadequate preliminary experiment had indicated that all variation was associated with the males or additive component. (Ledig, 1967). Dominance variati on for net photosynthesis was 1.7 times greater than additive genetic variance in the study of Campbell and Rediske (1966) on seedling Douglas-fir. Thus there may be some significance to the results of the present experiment which indicate a high female-in-male component. The relative importance of maternal effect has not been assessed, however, and designs using reciprocal crosses are necessary to clarify this situation. The use of paternal half-sib families would permit estimation of genetic constants by avoiding the problem of maternal effect but the production of large numbers of paternal half-sib progenies is not practical with forest trees.

SUMMARY AND CONCLUSIONS

For net photosynthesis, the two estimates of heritability, 0.28 and 0.50, based on individuals from full-sib families are of moderate size. These must be considered somewhat larger than narrow-sense heritabilities since besides the additive variance they presumably contain half the dominance variance. They are the only estimates available of her itabili ty for photosynthetic rate in loblolly pine.

From the combined analysis of these two experiments, it was obvious that a progeny's performance when grown under one set of conditions may have no correlation with its performance when grown under other environments. Genotype-environment interaction seems to be of overriding importance, and day to day variation is also an important variable in photosynthetic measurements. Photosynthesis, as measured by gas exchange, in seedlings preconditioned by one environment may not be the -same process as that measured when preconditioning occurs under other environments. Likewise, photosynthesis under one set of light, temperature, and moisture conditions may not be the same trait as photosynthesis under a different set of measurement conditions because the functioning genes may be different.

Because of the many environmental effects on photosynthesis and the inability to ascribe variation in gas exchange to one process, overly-simplified genetic experiments will be unprofitable. Studies which determine the reaction of the genotype to the range of environmental modifiers of photosynthetic rate are required.

Design 1 experiments of the size reported are too small for estimation of variance components. However, this experiment suggests that genetic variation in photosynthesis may be predominantly of the dominance or dominance-epistatic types. At least one other explanation of these results exists: maternal effect. High female components may indicate that in addition to dominance variance there are differences in chloroplasts which are apparently inherited entirely through the seed parent in Pinus. Designs utilizing reciprocal crosses are recommended to clarify the significance of high "dominance" variance.

When progeny of a cross between select trees was compared near the seasonal peak of photosynthesis to progenies from random matings, the select tree progeny was greatly superior in photosynthesis in *ikg* CO2/hr/mg needle. This is the first time such a comparison has been reported and may indicate that the intensive selection practices of the cooperative Tree Improvement Program have resulted in selection of photosynthetically superior trees. The alternative hypothesis is that the progeny of the select tree cross exhibited hybrid vigor because it is a wide cross between geographic areas.

No correlation, or very weak negative correlations, were seen between photosynthetic rate and seedling dry weight in this investigation. Because the rank of progenies in photosynthetic rate may change with environmental variation, prediction of dry matter production can only be made by integration of the photosynthetic response over the diurnal and seasonal cycles, eliminating the possibilities of making selections by a simple method. Model systems and growth chambers are **required.** Such an approach to the problem has begun.

Decker (cited by Campbell rind Rediske, 1966), Kramer (1958), and Bourdeau (1958) have all suggested the possibility of using the infra-red gas analyzer to select trees. This approach may still have merit. However, the high sampling error from branch to branch when photosynthesis is measured on excised or attached twigs would seem to preclude such selection as a practical method among mature trees. Measuring photosynthesis in second year shoots from grafted ramets may offer attractive possibilities for the early testing of clones in grafted seed production orchards.

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