Genetic Variation in Height and Volume of Loblolly Pine Open-Pollinated Families During Canopy Closure

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Abstract

Heritabilities and age-age genetic correlations for heights and volumes were estimated for 12 open-pollinated families of loblolly pine planted in 100-tree plots on a lower coastal plain site in North Carolina from age 4 to 11 years. Families differed significantly in cumulative height for all ages, but no family effects were present for diameter at breast height. Family differences in individual tree volume were not present until after age 8 and in stand volume after age 10. Heritabilities showed the same pattern over ages, having the highest family and individual heritabilities for height (h^2_F=0.65 to 0.84, h^2_I=0.15 to 0.27), moderate to none for tree volume (h^2_F=0.43 to 0.61, h^2_I=0.06 to 0.05) and stand volume (h^2_F=0.32 to 0.53). Genetic correlations between early height and height at 11 years were high (around 0.95) and did not change from age 4 to 10. Similar high correlations were found for height and tree volume (0.9) and height and stand volume (>0.95). The stability in rank among families and high correlation suggests that selection for height would be efficient at age 4.

The increased difference in volume production between families with time even after canopy closure indicated that families differed in the efficiency by which they utilized the site's resources for stemwood growth. A superior family will maintain a higher growth rate even after the stand has closed. This could be due to higher light interception and/or more stemwood produced per unit light intercepted.

Key words: Pinus taeda L., juvenile-mature correlation, mid-rotation, stand volume, family block plots.

Introduction

The assessment of genetic parameters in tree breeding programs is important for estimating future gains and developing breeding strategies. Early evaluation of progeny trials will increase the gain per unit time and thus the economic return of tree improvement activities (e.g., Squillace and Gansel, 1974; Lambeth, 1980; McKeand, 1988). The problem with early estimation of mature performance in juvenile material is the uncertainty associated with the correlated response of the selected trait with the performance at rotation. For many programs, the best early predictor and selection trait for volume yield at rotation has been height due to its higher heritability and juvenile-mature correlation (Nance and Welles, 1981; Lambeth *et al.*, 1983; Foster, 1986). Other studies have indicated that diameter or stem volume would be more efficient for early selection (Li *et al.,* 1996). The study of correlation components such as phenotypic, family mean or genetic correlations has resulted in varying optimum selection ages for loblolly pine; e.g. 6 to 8 years (Lambeth, 1980; McKeand, 1988), 7 to 10 years (Balocchi *et al.*, 1994), ≤ 6 years (Li *et al.*, 1996) or half the rotation (Franklin, 1979) depending on genetic material and methods. Most studies have used conventional genetic tests with family row plots, and only a few used family block plots (Foster, 1986). Questions have been raised about the behavior of genetic variance versus environmental variance at the time of stand closure when inter-tree competition increases (Franklin, 1979). The use of small-tree plots in genetic trials may inflate estimates as differences in size will tend to be augmented due to competition effects (Williams *et al.*, 1983; Foster, 1989; Magnussen, 1995). If genetic stocks are to be deployed as plantings of a single family, the assessment of family performance and genetic parameters may be better done in family block plots (Duzan and Williams, 1988; Williams *et al.,* 1983). Family block plots are also suitable for estimation of stand level performance such as production per hectare and leaf area index.

Although, selection for quality and increased yield has been successful, the reasons why a genotype exhibits outstanding performance is still not clear and may vary between environments and genotypes (Li *et al.*, 1991; van den Driessche and El-Kassaby, 1991; Albrektsson *et al.,* 1995; McKeand and Svensson, 1997). Silvicultural studies have shown that growth is an expression of the ability to acquire and utilize site resources such as; nutrients, water and light (Linder, 1987; Allen *et al.,* 1990; Albaugh *et al.,* 1998). Differences in stemwood yield then reflect how well genotypes utilize available resources for stemwood growth (cf. Cannell, 1989).

The objectives with this study were to determine: 1) if family differences in production would be expressed early in stand development, and 2) the magnitude of heritabilities and genetic correlations of heights before stand closure and volume at age 11. The design with family block plots also allowed for estimations on a per hectare basis.

Material and Methods

Description of the trial

The study was carried out in a field trial planted in the spring of 1985 with seedlings from 12 open-pollinated families of loblolly pine from the coastal plain of North Carolina and South Carolina, United States *(Table 1).* The trial was located on Weyerhaeuser Company land in Jones County on the lower coastal plain of North Carolina (35°08' N, 77°21' W). The soil was very poorly drained and classified as a fine-loamy, siliceous, thermic, umbric paleaquult of the Pantego series. Site preparation before planting consisted of burning, bedding and application of phosphorus fertilizer (40 kg P ha^{-1}). The trees were planted in family plots of 100 trees at 2 m x 3 m spacing and replicated 4 times in a randomized complete block design.

Stem-wood biomass

At the end of 1988 and from 1990 to 1995, total height of the trees were measured and from 1990 to 1995, diameter at breast

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Table 1. – List of the 12 families (mother trees) and their geographic origin in the progeny trial.

Family:	Origin:	Family:	Origin:
8-01	Beaufort Co., NC	11-106	Georgetown Co., SC
8-103	Onslow Co., NC	7-1037	Georgetown Co., SC
8-1082	Bertie Co., NC	8-1005	Onslow Co., NC
8-1086	Craven Co., NC	8-1056	Onslow Co., NC
8-59	Hertford Co., NC	8-68	Craven Co., NC
8-61	Bertie Co., NC	8-74	Jones Co., NC

height (1.4 m) was measured. Height measurements up to 1994 were done with height poles. In 1995 height measurements were done on a sample of 20 trees per plot using a clinometer and heights for the remaining trees were estimated using regressions on previous year's height and height growth and diameter growth. Total tree volume outside bark was estimated using an equation for loblolly pine in cutover and site prepared plantations (AMATEIS and BURKHART, 1987).

Stand volume (m^3ha^{-1}) was estimated for each plot by summing tree volumes and dividing by plot area. Annual production was determined by the difference in total volume from the previous year volume. Mortality rate was low (<10% at age 11) and had no major impact on productivity estimates.

Statistical analyses

All analyses of variance were done using the PROC GLM procedure and estimates of variance components and their variances using PROC MIXED and the restricted maximum likelihood method of the statistical software package from SAS® Institute Inc., Cary, NC (SAS, 1988, 1992). Family effects were considered significant if prob.>F was equal or less than 0.05.

Analyses of variances and estimates of individual and family tree heritabilities for tree height (m), diameter (cm) and volume (dm^3) were performed on observations of individual trees using equations 1 to 3.

$$Y_{ijk} = \mu + B_i + F_j + BF_{ij} + e_{ijk} \qquad \textbf{(formula \#1)}$$

μ: overall Mean, B_i: block df=3, F_j: family df=11, BF_{ij}: block x family df=33; e_{ijk}: within plot df≈3800

$$h_I^2 = 4 \times \sigma_F^2/(\sigma_w^2 + \sigma_{BF}^2 + \sigma_F^2) \qquad \textbf{(formula \#2)}$$

(formula #3)

$$h_F^2 = \sigma_F^2 / (\sigma_w^2/k_1 + k_2/k_1\, \sigma_{BF}^2 + \sigma_F^2)$$

σ_w^2, σ_{BF}^2, σ_F^2 = variance components for within plot, block x family, and family.

k_1, k_2 = coefficients (adjusted number of observations for family and plot) obtained from the type III expected mean squares for an unbalanced design due to differences in number of trees per plot.

Analysis of variance was also applied to plot means of stand volume (m^3ha^{-1}), and volume production for each sampling year ($m^3ha^{-1}yr^{-1}$) using the model:

$$Y_{ij} = \mu + B_i + F_j + e_{ij} \qquad \textbf{(formula \#4)}$$

B_i: block df=3, F_j: family df=11, e_{ij}: error (block x family) df=33

Family heritabilities were then estimated from variance components:

(formula #5)

$$h_F^2 = \sigma_F^2 / (\sigma_w^2/r + \sigma_F^2) \qquad r{=}4 \text{ (number of entries per family)}$$

Juvenile-mature correlations, mature being the tree height, volume or stand volume at age 11, were estimated using covariates. Subscript (J) was used for the juvenile trait and (11) for the trait at age 11. The variance of the sum of the juvenile trait and the trait at age 11 ($\sigma_{F\,(J+11)}^2$) includes the variances for each trait ($\sigma_{F\,(J)}^2$, $\sigma_{F\,(11)}^2$) and twice their covariance ($\sigma_{F(J,\,11)}$) thus:

(formula #6)

$$\sigma_{F(J,11)} = (\sigma_{F\,(J+11)}^2 - \sigma_{F\,(J)}^2 - \sigma_{F\,(11)}^2) / 2$$

and the genetic correlation coefficients were calculated as:

$$r_{g(J,11)} = \sigma_{F(J,11)} / (\sigma_{F(J)}\, \sigma_{F(11)}) \qquad \textbf{(formula \#7)}$$

Standard errors of heritability estimates from individual tree data were estimated using a TAYLOR's series approximation of a function of variances (BULMER, 1985; DIETERS *et al.*, 1995).

(formula #8)

$$\begin{aligned} Var(h^2) \approx\ & Var(\sigma_F^2)\cdot\left[\frac{dh^2}{d\sigma_F^2}\right]^2 + Var(\sigma_F^2)\cdot\left[\frac{dh^2}{d\sigma_{BF}^2}\right]^2 + Var(\sigma_F^2)\cdot\left[\frac{dh^2}{d\sigma_W^2}\right]^2 + \\ & +2\cdot Cov(\sigma_W^2,\sigma_{BF}^2)\cdot\left[\frac{dh^2}{d\sigma_W^2}\right]\cdot\left[\frac{dh^2}{d\sigma_{BF}^2}\right] + 2\cdot Cov(\sigma_W^2,\sigma_F^2)\cdot\left[\frac{dh^2}{d\sigma_W^2}\right]\cdot\left[\frac{dh^2}{d\sigma_F^2}\right] + \\ & +2\cdot Cov(\sigma_{BF}^2,\sigma_F^2)\cdot\left[\frac{dh^2}{d\sigma_{BF}^2}\right]\cdot\left[\frac{dh^2}{d\sigma_F^2}\right] \end{aligned}$$

Standard errors for estimates of genetic correlations were estimated also by approximation using a formula where precision is dependent on the estimates of heritabilities (FALCONER, 1989; BECKER, 1992).

$$\sigma_{(r_A)} \approx \frac{1-r_A^2}{\sqrt{2}} \cdot \sqrt{\left[\frac{\sigma_{h_X^2} \cdot \sigma_{h_Y^2}}{h_X^2 \cdot h_Y^2}\right]} \qquad \textbf{(formula \#9)}$$

Results

Family differences

The family mean heights showed a pattern of increasing differences with time with family 8-103 being the tallest and 8-1086 the shortest; the overall mean height at age 11 was almost 12 meters *(Figure 1)*. Only half of the families in the study are displayed, but they represent the range in heights. Heights did show highly significant family effects for all years *(Table 2)*, and family heritabilities increased to $h_F^2 = 0.84$ by age 9 *(Table 3)*. Heritabilities for individual trees showed similar increase but were lower and stayed around $h_I^2 = 0.25$. Standard errors for heritabilities were generally high primarily due to the small number of families in the study *(Table 3)*.

Although rankings appeared different for diameters compared to heights *(Figure 2)*, no significant family effects on diameter were detected. Family differences for diameter at breast height were not as great as family difference for heights *(Table 2)*. Thus, heritability estimates were extremely low and not significantly different from zero *(Table 3)*.

Tree stem volumes showed increases in the differences between the top and bottom ranked families with age *(Figure 3)*. Families with the greatest tree volumes were 8-103 and 8-61, and least volumes were 8-1082 and 8-1086. Family differences increased in significance with age from being non-significant at ages 6 to 8 ($p = 0.13$ to 0.08) to significant at ages 9 to 11 ($p = 0.03$ to 0.02) *(Table 2)*. Individual tree heritabilities did not show any change with time *(Table 3)*, but family heritabilities increased with age (0.43 to 0.61). Both heritabilities had large standard errors, but the standard errors for individual tree heritability tended to decrease with age *(Table 3)*.

Stand volumes were high with a mean volume at age 11 of 195 m^3ha^{-1} and a range of family means from 176 m^3ha^{-1} to 214 m^3ha^{-1} *(Figure 4)*. Family means diverged with time as for individual stem volumes. Family effects were initially non-significant but became significant with age ($p=0.21$ to 0.05) *(Table 2)*. The trend of family mean heritabilities was to increase with time while standard errors, although large, did not increase at the same rate *(Table 3)*. Current annual volume increments were high, with family means ranging between 32 $m^3ha^{-1}yr^{-1}$ and 40 $m^3ha^{-1}yr^{-1}$ at the end of the study *(Figure 5)*. However family differences were only significant for age 9 and 11 *(Table 2)*. Family mean heritabilities were around 0.6 for ages 9 and 11. At 10 years, differences in current annual increment between families were not present and family variance components and heritability were zero *(Table 3)*. The large difference between current annual volume increment at age 10 and 11 are suspected to be due to an underestimate of stem volume at age 10 resulting in a low volume increment and subsequently and overestimate of volume increment at age 11.

Age-age correlations

The genetic correlations of juvenile heights with height at age 11 were generally high and stable for the ages in this study *(Table 4)*. Height at age 4 was highly correlated with height at age 11 ($r_g > 0.97$) and selection efficiency would not increase with later selection. The same was true for the correlation of height with stem volume at age 11. Correlation of height at age 4 with stem volume at age 11 was 0.92 and stayed around 0.90 for all ages *(Table 4)*. The genetic correlations based on plot means of height and stand volume were higher and near 1 for all ages *(Table 4)* confirming the stability of ranks among the families. Similar correlations were found for tree volume and volume at age 11 *(Table 4)*. Since no significant genetic variances were found for juvenile volumes, correlations of juvenile volumes with mature traits were not calculated.

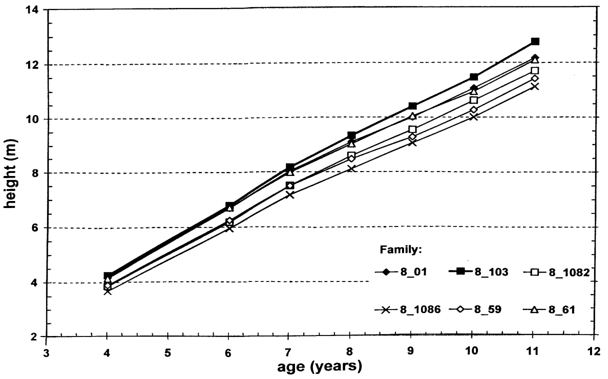

Figure 1. – Family means of tree height from age 4 to 11, (years 1988 to 1995). Six families that represent the range of all 12 families are displayed.

Table 2. – P values of F ratios of family effects for different traits at different ages.

	Age						
	4	6	7	8	9	10	11
height	0.009	0.005	0.002	0.000	0.000	0.000	0.000
DBH		0.304	0.252	0.305	0.293	0.279	0.148
tree volume		0.135	0.103	0.080	0.034	0.027	0.017
stand volume		0.212	0.193	0.188	0.120	0.101	0.048
vol. increment			0.220	0.200	0.012	0.520	0.006

Table 3. – Individual and familiy mean heritabilities with standard errors (S.E.) of the estimates.

		4 years	6 years	7 years	8 years	9 years	10 years	11 years
		est. (S.E.)	est. (S.E).	est. (S.E.)	est. (S.E.)	est. (S.E.)	est. (S.E.)	est. (S.E.)
height	h_I^2	0.154 (0.099)	0.208 (0.122)	0.224 (0.126)	0.248 (0.128)	0.277 (0.132)	0.244 (0.117)	0.271 (0.129)
	h_F^2	0.654 (0.170)	0.701 (0.146)	0.731 (0.131)	0.786 (0.104)	0.840 (0.079)	0.843 (0.077)	0.841 (0.078)
DBH	h_I^2		0.020 (0.040)	0.018 (0.033)	0.010 (0.025)	0.009 (0.020)	0.007 (0.016)	0.012 (0.015)
	h_F^2		0.228 (0.376)	0.250 (0.369)	0.190 (0.399)	0.202 (0.393)	0.214 (0.386)	0.367 (0.312)
tree volume	h_i^2		0.064 (0.067)	0.059 (0.060)	0.054 (0.051)	0.058 (0.045)	0.047 (0.036)	0.046 (0.033)
	h_F^2		0.427 (0.279)	0.433 (0.279)	0.468 (0.262)	0.560 (0.217)	0.577 (0.208)	0.612 (0.191)
stand volume	h_F^2		0.325 (0.329)	0.316 (0.337)	0.322 (0.334)	0.408 (0.291)	0.435 (0.278)	0.526 (0.233)
vol. increment	h_F^2			0.284 (0.352)	0.307 (0.341)	0.635 (0.180)	0.000 0.000	0.674 (0.161)

Discussion

The family ranks for volume production did not change substantially from ages 6 to 11 years. The continued increase in differences in mean height and stand volume *(Figures 1* and *4)* were due to families maintaining differences in growth rate. We refer to this as a Type "A" response, where growth curves continue to diverge over time (e.g. MORRIS and LOWERY, 1988)[5]. A Type "B" response is exemplified by the diameter growth *(Figure 2)* which did not show the same divergence over time. The differences in diameter are obtained early and maintained with approximately a year difference in development between families with the greatest and the smallest mean diameter.

Higher growth rates of families such as 8-103 and 8-61 could be due to higher light interception or more efficient use of intercepted light for stemwood production. This in turn could be the result from differences in phenology (CANNELL, 1989), higher uptake rate or more efficient use of nutrients and water (VOSE and ALLEN, 1989; LI *et al.,* 1991), and/or greater carbon allocation to stemwood (VAN BUIJTENEN, 1978; BONGARTEN and TESKEY, 1987). If these factors show genetic variation, then superior families may differ in the causes for their high yields. In this study, light interception differed between family 8-103 and 8-61 in that 8-103 had lower light interception and thus higher growth efficiency (SVENSSON *et al.,* 1999b, in review). Although family differences in light-saturated photosynthesis, and foliar contents of phosphorus were found, they did not

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[5] Type A, B and C responses were first described by HUGHES, J. H., R. G. CAMPBELL, H. W. DUZAN, Sr. and C.S. DUDLEY, 1979. Site Indices Adjustments for Intensive Management Treatments at North Carolina. Forestry Research Technical Report. Weyerhaeuser Co., New Bern, NC.

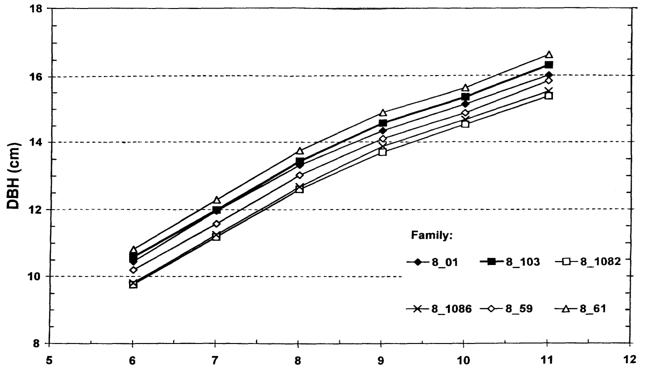

Figure 2. – Family means of tree diameter at breast height (1.4 m) from age 6 to 11. Six families that represent the range of all 12 families are displayed.

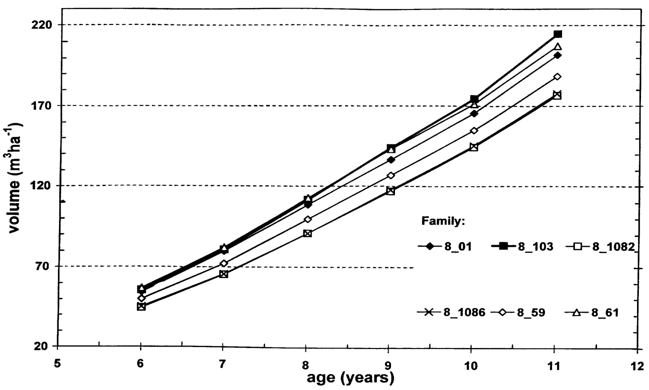

Figure 4. – Family means of stand volumes from age 6 to 11. Six families that represent the range of all 12 families are displayed.

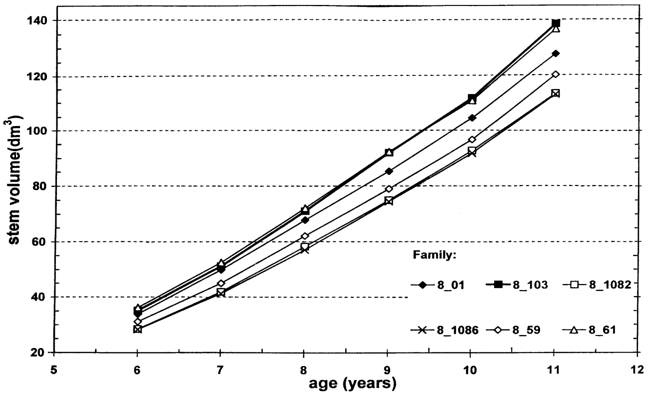

Figure 3. – Family means of tree stem volume from age 6 to 11. Six families that represent the range of all 12 families are displayed.

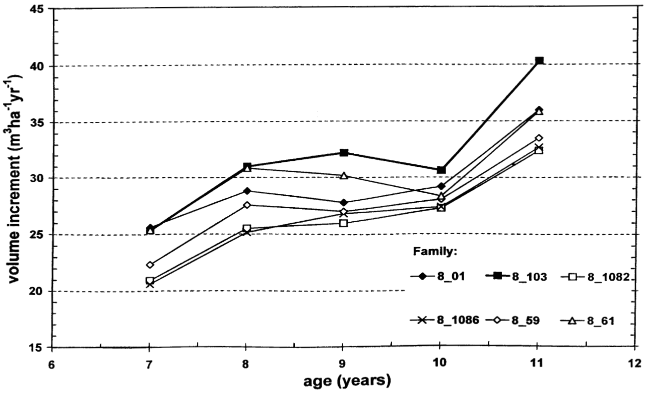

Figure 5. – Family means of annual production from age 7 to 11. Six families that represent the range of all 12 families are displayed.

Table 4. – Genetic correlations with standard errors in parentheses of juvenile height with height, tree and stand volumes at age 11 years.

Age correlations: heights and volumes	Age 4 to 11	Age 6 to 11	Age 7 to 11	Age 8 to 11	Age 9 to 11	Age 10 to 11	Age 11 to 11
ht,ht(11)	0,974(0,020)	0,919(0,058)	0,946(0,039)	0,954(0,031)	0,972(0,018)	0,954(0,031)	1,000(0)
ht,tree vo.(11)	0,922(0,071)	0,899(0,087)	0.880(0.100)	0,875(0,100)	0,922(0,061)	0,887(0,088)	0.901(0,077)
ht, stand vo.(11)	1,048(-)	0,994(0,004)	0,955(0,031)	0,946(0,035)	0,978(0,014)	0,942(0,037)	0,968(0,020)

explain the differences in growth rates (Svensson *et al.*, 1999a, in review). Differences in leaf area, light interception, photosynthesis and nutrition could still contribute to growth differences, but their usefulness for selection is questioned as they are difficult to assess and change with environmental conditions. The high juvenile-mature correlations and heritabilities for height growth confirms that past performance is a good predictor of future performance for a particular site and genotype.

Higher heritabilities for height as compared to diameter and volume have been reported in other studies and indicate that genetic expression in height is less affected by environmental variation (Nance and Welles, 1981; Foster, 1986; Balocchi *et al.,* 1993). Some studies have advocated the use of diameter or stem volume to predict rotation-age volume (Li *et al.,* 1996), but in this study the genetic variance in these traits was very low. The design with family block plots will elliminate the inter-family competition effects, and therefore inter-family competition would not affect differences in diameters. If the design would have been small family plots, as is typical in most genetic tests, competition could have exagerated family differences in diameters.

The high genetic correlations of heights at age 4 with stem and stand volumes at age 11 are very promising for early evaluation and selection of families and progenies. At least for the type of conditions that these 12 families have been growing under, selection for height at age 4 can be used for evaluation of the best families for use in regeneration programs.

Conclusions

Family differences in cumulative height during age 4 to 11 were highly significant and cumulative volume production showed a trend that family differences will be even more significant in later years. The increase in family differences in volume production with age indicated that some families differed in their utilization of site resources for stemwood production. Height had the highest heritabilities and together with its high genetic correlation, is the best early predictor for future performance.

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