The cumulative growth of a plant is the result of interrelated processes, and response to selection for changes in the annual growth curve requires many physiological adjustments. Selection to modify the entire annual growth curve may therefore not be as effective as linear models may predict. Periodic growth of a population of *Nicotiana tabacum* L. was estimated to have heritabilities increasing from 7% up to 31% for successive heights, with positive genetic and phenotypic correlations among all periods. Two selection experiments on this population indicate the difficulties of using simple index selection to raise the entire growth curve. A selection index of eight periodic heights resulted in a gain in all periods for the first cycle of selection but mixed losses and gains in subsequent cycles for a small net gain after four cycles of selection. A selection index of three parameters of a nonlinear height growth function resulted in a consistent change in the growth curves over the four cycles of selection but a net loss in early growth and a large net gain in late-season growth.

Annual growth is a complicated function of the plant’s allocation of energies into roots, shoots, leaves, and reproductive organs during the year (Erickson 1959). Genetic changes in the form of the annual growth curve induced by selective breeding obviously require many physiological adjustments. However, for any trait with multiple components, response to selection can generally be expected and depends on heritabilities and intercorrelations among the components as well as on the heritability of the composite trait.

The form of the growth curve as a composite trait has not previously been subjected to genetic analyses in tobacco. Genetic variance components have been estimated for terminal height of tobacco, and selection on total plant height has proven effective (Matzinger, unpublished). Selection to change the entire growth function has been suggested as a general procedure for many organisms by Tallis (1968) and for study of mouse growth (Laird and Howard 1967; Eisen, Lang and Legates 1969).

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1 Joint contribution of the Department of Genetics, North Carolina Agricultural Experiment Station, Raleigh, and the Southeastern Forest Experiment Station. Paper No. 4245 of the Journal Series.
2 Geneticist and Professor of Genetics, respectively, Forest Service, USDA, and North Carolina State University, Raleigh.

Several methods of selection can be developed, and in this study two are compared for efficiency in moving the entire population growth curve. The conceptually most traditional method is to consider the heights of the plants at particular points in time to be from a multivariate normal distribution and to select for the simultaneous change at those points using a selection index. Presumably, these discrete variates would produce plants with smooth curves in which the intermediate time periods would produce a smooth intermediate growth function. With a sufficient number of measurement points, the presumptions should be valid. On the other hand, with very many such variates to measure, the estimation problems increase.

Since there was no a priori reason for defining an ideal growth curve form other than to increase plant size for the whole period, we determined that selection should be directed toward increasing size in proportion to the average size present in the base population. For discrete periodic size variates, this decision implies a desire for unrestricted growth in proportion to the original heights. Therefore, we chose "economic weights" for each periodic height in proportion to the base population size at each measurement time. This is comparable to an unrestricted selection and with many growth periods, should approach a continuous-function solution.

Alternatives to the discrete variate solution include restricted selection functions (Tallis 1968) and fitted functions in a discrete variate selection index where the parameters of the fitted function serve as the variates. The latter option was chosen because it provides for selective change in a continuous function, while Tallis' functions could only be approximated by discrete measurements in our tobacco fields. Since an unrestricted increase in the height curve in proportion to the base population was desired at each measurement point, average changes to achieve the parameters of the desired curve were determined for the economic weights, and a selection index was constructed to change the curve parameters.

MATERIALS AND METHODS

A single base population was established from flue-cured tobacco, *Nicotiana tabacum* L., of eight varieties described by Matzinger, Mann and Cockerham (1962). The varieties were crossed into an eight-line hybrid, and this population was advanced for six additional generations by randomly mating 100 pairs of plants in each generation. The source material for the present study was the sixth generation of random mating, and was planted in two separate locations for the estimation experiment.

Genetic variances were estimated from a diallel analysis of the eight parental varieties (Matzinger, Mann and Cockerham 1962). Plant heights were measured weekly, but only final heights have been reported. Further diallel analyses of the eight weekly plant heights showed that heritability increased from 7% to 31% with successive heights when heritability was expressed on a plot mean basis of 20 plants per plot. The plants used for estimating genetic variances and those used for the base selection population are from different generations of inbreeding. The genetic variances in the two populations would therefore differ due to the combined effects of linkage disequilibrium, dominance, and epistasis. However, a generation mean analysis of the same original lines, single and double crosses among them, and among five generations of random mating indicated that such biases are of little importance (Humphrey, Matzinger and Cockerham 1969).
Two experimental populations were established from this common base population, and each was carried through four cycles of mass selection. One was selected on the basis of an estimated index of eight weekly heights corresponding to the period between 3 weeks after transplanting and cessation of vegetative growth. The other was selected on the basis of an estimated index on three parameters of a fitted nonlinear growth curve. These indices were estimated from data derived from the diallel intermating of the eight inbred lines used to establish the base population. For the selection experiment on the eight weekly height components (hereafter referred to as experiment A), the economic weights \( a \) were proportional to the mean heights at each weekly period. The phenotypic covariance matrix \( (P) \) was estimated by the sum of genetic and experimental error components of variance and covariance, and the genetic covariance matrix \( (G) \) was taken as twice the general combining ability component covariance matrix. The coefficients for the single unrestricted selection index were estimated by the standard formula, \( PXGa \), for the eight heights and were \(-1.043, 4.7984, 4.9820, -2.7688, -0.0394, -0.8471, 0.4896, -0.7540\). The predominance of negative signs for weighing the later heights was unexpected since all genetic and phenotypic covariances were positive. However, the estimate of a linear weighting function is the best we have for achieving an overall proportionate increase in the total curve. Some points are obviously of greater importance to increase than others, at least as judged by the index method.

Selection for the continuous growth curve first required fitting individual plant growth curves to an approximating function with low residual variances and without systematic errors. Several functions with less than five variable parameters were tested for those properties on data from a sample of 100 individual plants using the algorithm of Marquardt (1966). The curves tested were the Gompertz, Logistic, and Richard's generalized function (Richard's 1959), a generalized logistic (Nelder 1961 and 1962), von Bertalanffy's (1957) generalized function, and a fifth degree polynomial as suggested by Grizzle and Allen (1968). In these tests, Richard's generalized function fitted the data with smaller residual variances and fewer indications of systemic errors than any others tested, and was therefore used for all subsequent analyses. This curve is

\[
y_i = A(1+be^{ct_i})^{1/(1-m)}, \quad m > 1
\]

where

- \( y_i \) = measurement at time \( t_i \)
- \( A \) = upper asymptote
- \( c \) = a rate-of-growth parameter
- \( m \) = a shape-of-curve parameter
- \( b \) = a coefficient for fitting initial values
- \( e \) = the base of natural logarithms.

The time derivative function is perhaps more amenable to interpretation:

\[
\frac{dy}{dt} = cy\frac{[(A/\gamma)^{1-m} - 1]}{1-m}
\]

Growth rate is proportional to \( c \), and goes to zero as \( y \) approaches \( A \). The effect of \( m \) is on the earliness of those effects, and the rate generally decreases as \( m \) increases, but the derivative is a nonlinear function of \( m \). Selection was directed to raise the entire curve by changing all three coefficients simultaneously.

To construct a selection index, the \( F_1 \) data from the eight-line diallel were used, and each of 7,680 plants were fitted for estimates of \( A, c, \) and \( m \). Analyses of covariance on the three variables \( A, c, \) and \( m \) provided the \( P \) and \( G \) matrices \((3 \times 3)\) as for experiment A. In this experiment (designated B), the purpose was to change the continuous function. The economic weights were determined by the changes required in the parameters to proportionately increase the growth over the whole season. The weights were proportional to the differences in the \( A, c, \) and \( m \) parameters between the average of those parameters in the base population and the parameters of a curve which was twice as high as that at all points of the base curve. The index was estimated from the standard unrestricted index formula, \( P^{-1}Ga \). The three index values are: 0.0081, \(-1.5362, -0.0322\), for \( A, c, \) and \( m \), respectively.
For the first cycle of selection in both experiments, three plants out of a 20-plant row were selected in each of 20 rows; selection proportion, therefore, was 15%, and the selected population was 60 plants. Within each of the experiments, the 60 selected plants were randomly pair-mated, forming 30 mutually exclusive pairs, and the seeds mixed in equal portions for the next cycle. The populations were thereafter maintained completely independently, each grown in 20 rows of 23 plants each. In each cycle of mass selection three plants per row were selected, all selected plants then randomly pair-mated, the resulting seeds mixed in equal portions to reconstitute the next population cycle. Remnant seeds from each cycle from each experiment were saved.

After four cycles of selection the remnant seeds from all cycles in both experiments were planted, and 30 pairs were randomly crossed within each cycle to prepare seed of equal age for an evaluation of selection response. These were grown in row plots of 20 plants in six replications of a randomized complete block design, and the analyses were made on the plot means. Each selection method was represented by five cycles (the base population plus four selection cycles). These plants, all grown in the same year, constitute the data for comparison of selection efficiency.

RESULTS

*Experiment A:* The index estimated for this experiment was unexpected in that it gave a mixture of positive and negative weights to various growth points. The realized net selection differential tended to increase early growth and depress late growth. Estimates of covariances in the base population indicated positive genetic and phenotypic correlations among all growth stages and the economic weights gave proportionate positive weight to all stages. In addition, the heritabilities are high for late growth and would be expected to reinforce a positive index weighting for late growth.

Nevertheless, the index is appropriately estimated for a linear function for the combined effects of the economic weighting and the heritabilities and correlations observed, and was therefore applied in each cycle. It was noticed that large phenotypic variations in growth curves existed throughout the experiment. While the tallest plants early in the season were rarely the shortest plants late in the season, actual selection differentials did follow the direction of the index values. After four selection cycles the net effect on plant height at the end of the season was only a 1.9% gain, whereas the gain in experiment B was 18.7%.

The first cycle of selection gave a population curve change much as desired; the mean of all weekly heights increased (Figure 1), and the terminal height gain was 1 cm. (Table 1). It can be noted, however, that the derivative curve of the fitted function (Figure 2) shows that the growth rate at any size up to 120 cm. was actually slower for plants in the first selection cycle than for the initial population, indicating that the larger size of the plants at the time of transplanting and first field measure was responsible for their early superiority in size. It was only after 120 cm was reached that the plants in the first selection cycle continued to grow at a faster rate than the initial population at the same relative size, and thereafter continued to grow faster at larger sizes.

Subsequent cycles of selection, however, not only failed to improve size, but gave growths generally intermediate between the base and the first selection
### TABLE 1

*Means and F-tests of results of selection cycles*

<table>
<thead>
<tr>
<th>Breeding cycle</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>Estimates of parameters of Richards’ curve</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>EXP. A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>A</td>
</tr>
<tr>
<td>0</td>
<td>14.42</td>
<td>28.16</td>
<td>45.09</td>
<td>85.81</td>
<td>132.16</td>
<td>166.85</td>
<td>172.09</td>
<td>172.59</td>
<td>174.70</td>
</tr>
<tr>
<td>1</td>
<td>16.87</td>
<td>30.96</td>
<td>49.08</td>
<td>91.79</td>
<td>141.73</td>
<td>178.95</td>
<td>185.41</td>
<td>185.84</td>
<td>187.37</td>
</tr>
<tr>
<td>2</td>
<td>14.93</td>
<td>27.83</td>
<td>46.97</td>
<td>89.16</td>
<td>136.79</td>
<td>174.61</td>
<td>179.53</td>
<td>179.79</td>
<td>181.25</td>
</tr>
<tr>
<td>3</td>
<td>14.93</td>
<td>28.44</td>
<td>47.12</td>
<td>89.46</td>
<td>139.18</td>
<td>176.73</td>
<td>181.41</td>
<td>181.92</td>
<td>183.79</td>
</tr>
<tr>
<td>4</td>
<td>15.22</td>
<td>29.63</td>
<td>49.22</td>
<td>91.30</td>
<td>140.46</td>
<td>173.74</td>
<td>175.83</td>
<td>175.79</td>
<td>177.82</td>
</tr>
<tr>
<td>F-test of cycle diff.</td>
<td>1.115</td>
<td>0.637</td>
<td>0.505</td>
<td>0.524</td>
<td>0.973</td>
<td>6.019**</td>
<td>6.730**</td>
<td>7.600**</td>
<td>6.90**</td>
</tr>
<tr>
<td>EXP. B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>183.09</td>
</tr>
<tr>
<td>0</td>
<td>13.34</td>
<td>24.79</td>
<td>40.51</td>
<td>80.51</td>
<td>126.91</td>
<td>169.22</td>
<td>180.17</td>
<td>180.52</td>
<td>193.03</td>
</tr>
<tr>
<td>1</td>
<td>12.94</td>
<td>25.43</td>
<td>42.87</td>
<td>82.27</td>
<td>125.54</td>
<td>173.69</td>
<td>190.27</td>
<td>191.10</td>
<td>202.09</td>
</tr>
<tr>
<td>2</td>
<td>13.21</td>
<td>25.80</td>
<td>42.15</td>
<td>81.46</td>
<td>123.48</td>
<td>174.87</td>
<td>196.28</td>
<td>199.67</td>
<td>209.87</td>
</tr>
<tr>
<td>3</td>
<td>12.79</td>
<td>25.86</td>
<td>43.46</td>
<td>81.47</td>
<td>121.44</td>
<td>178.14</td>
<td>205.22</td>
<td>207.27</td>
<td>218.06</td>
</tr>
<tr>
<td>4</td>
<td>12.17</td>
<td>23.95</td>
<td>39.05</td>
<td>75.12</td>
<td>112.04</td>
<td>168.50</td>
<td>206.88</td>
<td>214.27</td>
<td>218.06</td>
</tr>
<tr>
<td>F-test of cycle diff.</td>
<td>0.958</td>
<td>0.745</td>
<td>1.280</td>
<td>1.916</td>
<td>5.839**</td>
<td>3.328*</td>
<td>24.959**</td>
<td>39.364**</td>
<td>51.36**</td>
</tr>
</tbody>
</table>

* Significant at 0.05 level of significance.
** Significant at 0.01 level of significance.
cycle populations (Figures 1, 2; Table 1). In the analysis of variance, differences among cycles were not statistically significant for the first 7 weeks after field growth started, but differences were highly significant after that time and relative rankings were maintained. Results of the Student-Newman-Keul's multiple range test on means for cycles at the end of growth period eight were:

<table>
<thead>
<tr>
<th>Growth</th>
<th>Cycle 0</th>
<th>Cycle 4</th>
<th>Cycle 2</th>
<th>Cycle 3</th>
<th>Cycle 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>172.59</td>
<td>175.79</td>
<td>179.79</td>
<td>181.92</td>
<td>185.84</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter A</th>
<th>Cycle 0</th>
<th>Cycle 4</th>
<th>Cycle 2</th>
<th>Cycle 3</th>
<th>Cycle 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>174.70</td>
<td>177.82</td>
<td>181.25</td>
<td>183.79</td>
<td>187.37</td>
</tr>
</tbody>
</table>

An underline indicates the lack of significant differences of the included cycles at the .01 ($\alpha = .01$) level of significance. After four cycles of selection, a small net increase in average size at all growth periods was achieved (Table 1) but the sequence of results indicates an essentially random fluctuation of heights around a mean of 179.19 cms.

**Experiment B:** The index on the three curve parameters was positive for $A$ and negative for $m$, as might be expected from inspection of the $dy/dt$ function. However, the index also gave negative weights for the rate constant $c$. When applied to the selection populations, there was a slightly negative net selection differential to depress early size and a strongly positive differential to increase later sizes. Additional error in estimating and applying this index is caused by
The fitting errors which inevitably exist. The populations responded to this solution with almost no change in mean height for the first six periods of growth after field planting. But they make steady, substantial gains in subsequent periods. Only the final population cycle displayed any depression of growth in the early periods before compensating with a continued high growth rate in the late periods (Figure 1). The population mean for the fourth cycle was small in the fifth period, made compensatory gains to reduce differences in the sixth, and increased greatly in the seventh and eighth periods. There was a complete reversal of cycle ranking between the fifth and seventh periods. The level of significance of the F test was 0.005 for period five, 0.05 for period six, and even lower than 0.005 following period six (Table 1). Results of the Student-Newman-Keuls multiple range test ($a = .01$) on means for cycles at the end of growth period eight were:

<table>
<thead>
<tr>
<th>Growth</th>
<th>Cycle 0</th>
<th>Cycle 1</th>
<th>Cycle 2</th>
<th>Cycle 3</th>
<th>Cycle 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>180.52</td>
<td>191.10</td>
<td>199.67</td>
<td>207.27</td>
<td>214.27</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter $A$</th>
<th>Cycle 0</th>
<th>Cycle 1</th>
<th>Cycle 2</th>
<th>Cycle 3</th>
<th>Cycle 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>183.09</td>
<td>193.03</td>
<td>202.09</td>
<td>209.87</td>
<td>218.06</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Parameter $c$</th>
<th>Cycle 0</th>
<th>Cycle 1</th>
<th>Cycle 2</th>
<th>Cycle 3</th>
<th>Cycle 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>0.5056</td>
<td>0.4396</td>
<td>0.4061</td>
<td>0.3913</td>
<td>0.3742</td>
</tr>
</tbody>
</table>

The response to selection was also proportionate to the index weights on the parameters with increases in $A$ and with decreases in $c$ and $m$ (Table 1). The growth response pattern in terms of the derivative (Figure 2) also indicates that growth rate of plants shorter than 140 cm declined steadily as selection proceeded. Thus, a large size at outplanting is highly important to compensate for slow growth.
growth right after outplanting. Selection was for plants with high growth rates late in the season by large plants. The maximum growth rates do not differ appreciably among cycles, but the selected populations attain that maximum rate at larger sizes and sustain it later in the growing season. The selection toward a slower growth rate for a given size in the early periods has evidently moved so far by the fourth cycle of selection that it has actually reduced the size of the population mean at those early time periods below that of the base population. The longer duration of the growth at larger sizes, however, does advance the later sizes well over all previous cycles.

DISCUSSION

Neither of the experiments could be considered an unequivocal success in the application of a selection index to simultaneously increase performance of all measurement periods. Experiment B, however, consistently moved parameters in the direction of the net effective selection differential. The small decreases in height up to period five were insignificant until the fourth cycle of selection, indicating that it is possible to achieve late growth without sacrificing early size. Several factors could have influenced this response pattern, including physiological limitations which force otherwise unexpected responses. It appears likely that a reestimation of the genetic and phenotypic variances and possible reevaluation of the $G$ and $P$ matrices as well as the economic weighting vector $(a)$ after the second or third cycle of selection could have prevented the loss of early growth in the fourth cycle. With traits such as the growth curve parameters, which are clearly nonlinearly related, a frequent reestimation of index coefficients is desirable. It is also possible that growth curve parameters are especially susceptible to poor estimation due to genotype-by-environment interactions and that we required additional environmental replication in the estimation experiment.

Nevertheless, the major persistent effect of experiment B selections was to increase the duration of vigorous vegetation growth. A correlated response was observed in the lateness at which vegetative growth ceased and flowering began. The increase in average terminal height over the cycles of selection was, therefore, mostly a matter of delaying the change from vegetative to reproductive growth.

In contrast, experiment A surprisingly achieved no consistent results over the four cycles, and only cycle one achieved much gain in the desired direction. The results of cycles zero and one of experiment A with all five cycles of experiment B as tested in a Student-Newman-Keul’s multiple range test of total height at the eighth period of the growing season gave the following results, at the 0.01 level of significance:

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Mean of Period 8</td>
<td>172.59</td>
<td>180.52</td>
<td>185.84</td>
<td>191.10</td>
<td>199.67</td>
<td>207.27</td>
</tr>
</tbody>
</table>
Thus, the populations of cycles 0 and 1 for the two experiments were similar in selection gain. Thereafter, however, experiment A never again achieved the sizes of cycle 1, while experiment B continued to significantly increase terminal height. A regression of period eight height on the cycles was estimated to be 0.023 for experiment A and 0.712 for experiment B. These estimates are taken only for period eight and do not reflect the changes of the whole growth curve. Experiment A does advance mean growth at all eight periods, though the differences are insignificantly small after four selection cycles.

Since heritabilities for single-period heights are substantial and size can be improved by selection, the failure of the combined selection on the index of periodic heights to achieve significantly estimable gains from cycle 0 to cycle 4 in any of the measured periods was unexpected. It is possible that some physiological limit exists which prevents the simultaneous increase of all heights. However, more likely sources of error lie in the index approach itself. The index weights were derived from estimates of \(8 \times 8\) genetic and \(8 \times 8\) phenotypic covariance matrices and, therefore, involve high errors of estimation (Patel, Cockerham and Rawlings 1969). In addition to any initial errors in estimating the index, changes in some of the variances or covariances due to the selection process could make the initial index relatively impotent to cumulatively induce the desired growth curve changes. In particular, the environment of the several stages may have changed from that of the initial populations such that the index weights became even less useful. With many parameters which may have been poorly estimated, the eight-element index may, therefore, have been rendered even less effective after the initial selection cycle. In any case, selection on the three-parameter curve index proved far more effective for increasing at least terminal height in spite of curve fitting errors and the nonlinearity of the relationship among parameters. It is possible, that simple \textit{ad hoc} index weightings would have proven at least as effective over several cycles of selection, but critical growth periods or other parameterizations may be identifiable for more efficient selection.

**CONCLUSIONS**

The complexities of regulating growth curves by mass selection are apparently such that simple index selection is not completely satisfactory. Response to selection is clearly achievable, but the efficiency of several methods is also clearly variable. The use of many growth periods as discrete variables is conceptually simple and should approach the more elegant continuous curve selection method of Tallis (1968) for unrestricted increase in the total curve. However, because of estimation problems or changes in the covariances as selection progressed, the efficiency of this method is highly suspect. Apparently, some curve parameterizations which can approximate the realized growth curves of individual plants can be useful despite fitting problems. The nonlinear relationships of the parameters, however, would require frequent reestimation of any index weights estimated for those parameters. Perhaps other growth functions would require fewer reestimations than the one used in our case.
LITERATURE CITED


Corresponding editor: R. W. ALLARD