Application of Nelder's Designs in Tree Improvement Research [1] [2]

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Silviculture can be roughly described as the art and science of controlling the competitive use of the resources of the site. Thus, in one sense, site preparation and weed eradication constitute the control of interspecific competition for young trees,

[1] Published. with the approval of the Director of Research, North Carolina Agricultural Experiment Station, as Paper No. 2021 of the Journal Series. It is a contribution of the Genetics Department of N. C. State University at Raleigh and. Southern Forest Experiment Station, Forest Service, U. S. Department of Agriculture.

[2] The computing services in this project were supported. by N.I.H. Grant No. FR-00011, held by the Institute of Statistics, N. C. State University at Raleigh.

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while initial spacing and subsequent thinning regulate intraspecific competition. Spacing is therefore a major environmental variable, and probably the one under most direct silvicultural control. The effects of spacing (or stand density) vary with soil and other physical factors of the environment and also with species (DeWit, 1960; Donald, 1963). It is reasonable, too, to expect that genotypes within species will vary in their responses to density, and therefore that genotypic selection may be affected by the spacing of the test environment. Present practices of testing under single spacing regimes are satisfactory only if there exists little or no genetic variance in response to a reasonable range of densities. In evaluating family performance, therefore, breeders must regard competition as an integral part of the environmental complex.

Evidence for genetic variation in density response exists, but is limited and indirect. For instance, Toda (1956) has reported genetic variation in crown diameter of Cryptomeria. Also, since density response and. growth rate are interdependent variables, and. genetic variance in the latter exists, genetic variance in the former must also be expected. If that variance is assumed to exist, then it is critically important that density response be measured as carefully as growth rate, especially when breeding in speceis for which the silviculture is rapidly developing.

GROWTH RESPONSE

In measurements of growth and competition effects, time or some other factor usually is the independent variable and vegetative growth the dspendsnt variable. Several equations are reviewed by Neldsr (1961), Turnbull (1963), and by Van Slyke (1964a), but the general function of Richards (1959) is apparently flexible enough to encompass any form of vegetative growth likely to be encountered in forest genetics experiments. The equation is:

$$w^{(1-m)} = W^{(1-m)}(1 + be^{-kx})$$

where w = momentary plant or average plant yield (i.e., weight or volume),

W = the ultimate or asymptotic limit of yield, per plant,

k = growth rate constant,

m = constant determining inflexion of the growth curve,

$b = \left[\frac{w_0}{W}\right]^{(1-m)}$, and w at $x = 0$ is w_0,

x = the time or environmental variable.

If x is allowed to be time, and if the relation of $W = \frac{\text{total yield per unit area}}{\text{number of trees per unit area}} = \frac{Y}{\rho}$, is used where ρ = plant density or number of plants per unit area [as in Shinozaki and Kira (1956)], then Bleasdale and Nelder (1960) derive the equation:

$$\frac{1}{w^{\theta}} = \rho^{\theta} A + B \qquad A = y^{(1-m)}(1-e^{-kx})$$

$$\text{where } \theta = m - 1 \qquad B = w_0^{(1-m)} e^{-kx}$$

They also suggest using $w^{-\theta} = \rho^{\phi} \beta + \alpha$ where the constants θ and ϕ differ.

A less general form of the Richards' equation takes m = 2 and it becomes:

$$w = \frac{W}{1 + be^{-kx}} .$$

This is the so-called logistic, or auto-catalytic, or Pearl-Reed function. Using this equation and $W = Y/\rho$ as before, Shinozaki and Kira (1958) derive $w^{-1} = \rho A + B$, when $A = \frac{1-e^{-kx}}{Y}$,

$$\text{and} \quad B = \frac{e^{-kx}}{w_0} ,$$

for the linear equation for density response. The same form has been independently derived by Holliday (1960), among others. Thus, for several possible forms of the density response, the parameters can be estimated for any given time and. their development traced over a time interval. Ways of estimating growth curve parameters have been investigated by Stevens (1951) , Patterson (1956) , Nair (1954), Neld.er (1961) , Day (1963) and Turnbull (1963) , among others, and the reader is referred to them for discussion of estimation techniques.

The response of other traits such as branching pattern will have different forms which must also be estimated, but at possible different levels of density for efficient estimation.

EXPERIMENTAL CONSIDERATIONS

To study the relations between density and parameters of growth, branching, and other traits, it is necessary to sample an adequately wide range of densities in any single field experiment. To efficiently span a given range in densities, it would be best to adjust the sampling points of density to minimize errors in estimating the time-dependent functions, such as the A and B of Shinozaki and Kira's growth equation. If the exact form of the equation is known, maximally efficient estimators can be derived, Nelder (1962) suggests that graphical methods are sufficient when his four-parameter density equation is assumed. With the equation of Shinozaki and Kira (1958), simple linear regression techniques suffice. As conceived by Nelder, the problem is further complicated by effects due to the shape of the area available for individual plant growth. Thus, simple considerations for spacing alone are insufficient, at least for seed. (Fawcett, 1964) and vegetable crops (Nelder, 1962).

If a test is to be made at high and low densities in rectangular spacings, many more trees are required at the high densities to occupy the same area as at the low densities. The result is differential precision of estimate and a great waste in trees. Alternatively, keeping equal numbers of trees per density level confounds density with size of plot and introduces error heterogeneity. With either spacing or number held constant the most serious of all defects probably is the separation of density levels into separate blocks and the inclusion of block variation in errors of estimate for the density response. Unless many density levels are sampled, the error thus introduced may be overwhelming. Also, since it is often desirable to use multiple-tree plots to minimize whthin-plot error (Conkle,1963) and avoid. intergenotypic competition, the rectangular designs become excessively large. Single-tree plots, however, are economical of space and, often also of trees, and should be seriously considered. for density tests. The land areas (exclusive of borders) required. for single-tree and. three-tree plots are given in Table 1.

In order to sample a range of spacings independently of the shape of the individual plant's growing space, Nelder developed, a set of systematic planting designs that deserve the close attention of foresters in silvicultural research and tree breeding. These designs are well described, by Nelder (1962) and, have been excellently reviewed by Van Slyke (1964) for their application to forest trees. The Continental Can Company, which is participating in the N. C. State University Hardwood Research Program, has installed two studies with Nelder's designs. International Paper Company, at its Southlands Experiment Forest, has put in studies with slash pine and Freeman (1962) reports the establishment of these designs with cocoa.

Table 1. Areas required for plots in rectangular designs without border trees. Values are sums of areas required for one replication of one family.

Number of densities sampled	Single-tree plots	Three-tree plots
	Density span = 20 — 2,020 trees per acre	
	Acre	Acre
3	.0515	.152
4	.0527	.158
5	.0541	.162
6	.0565	.170
7	.0571	.171
8	.0587	.176
9	.0604	.181
10	.0622	.187
11	.0639	.192
12	.0657	.197
13	.0676	.203
	Density span = 50 — 1,250 trees per acre	
3	.0223	.067
4	.0242	.073
5	.0263	.079
6	.0284	.085
7	.0307	.092
8	.0330	.099
9	.0354	.106
10	.0378	.113
11	.0402	.121
12	.0420	.126
13	.0452	.136

Briefly, Nelder suggested five designs, four based on polar coordinates and one on a rectangular logarithmic grid. All may be made suitable to silvicultural experiments, but only two can be adapted for small family or genotypic plots of interest to tree breeders. Of these two, design la varies plant spacing while the other varies shape of the growing space.

The components of design la are angles of arc turned by successive spokes of an imaginary wheel which intersect successive rims or circumferences at specified radial distances. The intersections of spokes and radial distances are the planting point locations. A circular block of 100 trees could be laid, out on 10 spokes at successive angles of 36^{0}, with 10 trees planted. along each spoke. By specifying that the shape of the growing space available for each plant is to be the same throughout the whole circular plot, and. that plants at different spokes but at the same radius shall have equal spacing, Nelder derives the relations:

$$r_n = r_o \alpha^n, \text{ and} \tag{1}$$

$$\theta = \text{constant}$$

where r_n is the radial distance of the n^{th} plant in the spoke, radial distance of the n^{th} circumference,

r_o is the radial distance of the starting plant in each spoke,

α is the constant determining the rate of change in growing space, and

θ is the angle between adjacent spokes.

The other three circular designs alternatively specify that:

lb) Growing space is constant, shape changes with radius;
lc) Space changes on a rectangular grid, shape changes with spoke;
ld) Space changes with spoke, shape changes on a rectangular grid.

The fifth design (2) is on a rectangular grid on which spacing and shape are varied by making each axis logarithmic. Designs lc, ld., and 2 can be used to estimate both spacing and shape parameters but require many plants and large plots. Therefore, they are most suitable for studies in which genetic and environmental effects can be confounded (as is mostly done in silvicultural work) or in which few genetic entries are used. Design lb is useful for studying the effects of growing space shape -- a factor that may be of critical importance when trees are to be planted and harvested in rows. However, if interest lies primarily in spacing and restrictions are placed. on plant numbers and plot size, only design la is suitable. Further discussion will be limited to it.

For laying out the planting areas, Nelder suggests marking two planting wires at the appropriate intervals for within-spoke spacing and attaching these to a center post. The first planting point of each wire corresponds to the inner border row, the second point marks the first and. most densely crowded experimental planting location, the third marks the next most dense. If the two wires are joined. by a length of wire equal to [2 (router border) sine (θ/2)1 at their outer ends and the three wires pulled taut, the angles between the spokes will be 9 and the planting points along the spokes easily marked. By leap-frogging one wire over the other, the successive spokes of the circular plot can be turned and the planting spots marked. A segment of a plot is shown in Fig. 1. It may be easier, however, to make the layout with a transit, since tree plots are quite large.

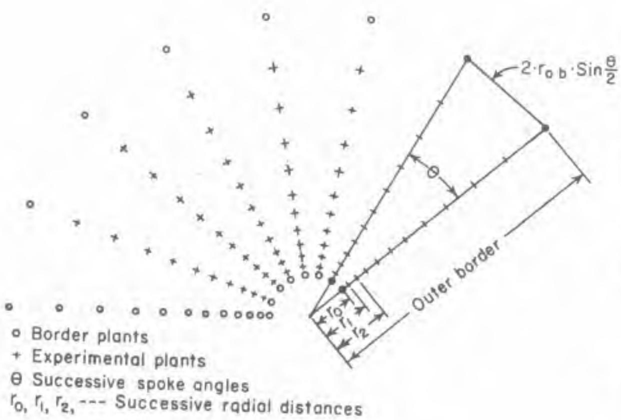

Figure 1 -- Segment of a variable-density plot.

SPECIFYING DESIGN PARAMETERS

The design parameters are easily computed if the growing space of the most and least crowded experimental plants and the number of plants per "spoke-plot" (N) can be specified. If the plot shape is also specified by the desired ratio (β) of within-spoke spacing to between-spoke spacing α, θ, and r_o can be found by using the equations:

$$\log \alpha = (\mathrm{Log}\ A_n - \mathrm{Log}\ A_1) \;/\; (2N - 2), \qquad (2)$$

$$2 \tan(\theta/2) = (\alpha - \alpha^{-1}), \qquad (3)$$

$$r_o = \sqrt{4A \;/\; [\tan(\theta/2) \cdot f(\alpha)]}, \qquad (4)$$

$$\text{where } f(\alpha) = \alpha^2 [(1 + \alpha)^2 - (1 + \alpha^{-1})^2],$$

where A is the area of the n^{th} or first plot and all other symbols are as given by Nelder.

It is simple then to compute r_1, r_2, etc. by formula (1). Formulae 3 and 4 differ from Nelder's and are discussed in Appendix A.

If lengths of spoke-plots are uniform, planting genotypes or families one to a spoke, or in three adjacent spokes, will achieve freedom from intergenotypic competition. The larger angles become awkward to handle physically and. stretch the concepts of linear intra-specific competition. If the number of spokes is less than that required for a full circle, guard spokes of the sector borders are required. Since the minimum number of spokes per center is 3, any number between 3 and 360/θ can be used, and successive centers can be located for as many sets of plots as desired. Some possible arrangements are shown in Figure 2. I would suggest that border spokes be maintained to enclose the test spokes and, that they be made up of "controls" so that soil trends within plots may be adjusted for Also, the numbers of spokes per center may be varied in order to "turn" the plot sequence in any desired. direction. A great deal of freedom is thus obtained in replication shape and arrangement of genotypes, and one may construct randomizedblock or any partially balanced incomplete block design.

It may be specifically desired to test the response of genotypes to particular competitors or to isolate genotypes from other specific competitors. In such cases, the use of the same or different "center-hubs" is indicated. For instance, in studies involving families of different provenances in which interprovenance competition is undesirable, separate provenance circles or sectors could be established and the spokes within each could be allocated. to the genotypes within each provenance.

In general, two conflicting restrictions are imposed by the nature of tree breeding, particularly in hardwoods. These are lack of knowledge of the size and form of genetic variability in density response and the desirability of distributing the usually small numbers of seeds among several environments. The first factor forces the experimenter to span a wide range in density levels and the latter restricts the number of levels he may sample in any one plot. If he wishes to estimate early density responses, close spacings are required; as many as 2,000 trees per acre may be needed, for species with slow early growth. In order to sample among the light or late density responses such as occur at the

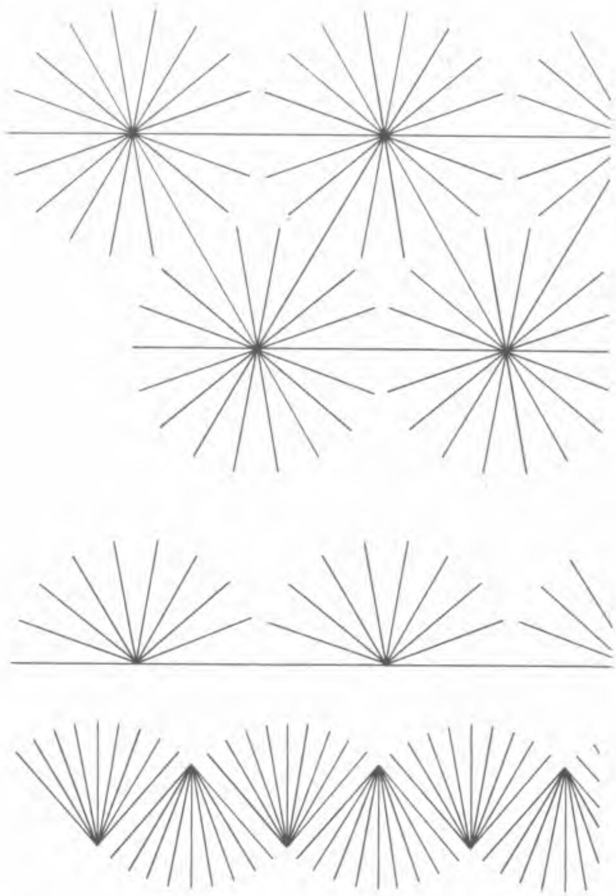

Figure 2 -- Alternative spoke arrangements.

lower limit of competition with mature trees, as few as 20 trees per acre may be required. In fast-growing, short-lived. species, the span may be cut to approximately 50-1,250 trees per acre or less. Much smaller intervals will often be desired, but these two are chosen as examples to illustrate the difficulties encountered. at the extreme levels of testing.

For these spans, a minimum of four and a maximum of 13 trees would normally be available for each plot for each family. The minimum of four is required for precision in estimation and, a miximum of 12 or 13 per replication will rarely be exceeded. Several optional planting regimes may be followed. These are given in Table 2, according to span of densities (either 2,000 or 1,200), and for roughly square and roughly rectangular growing-space shapes. For each plot size of 4 through 13 plus two border trees, the table shows planting point distance from the center hub and the density represented by the space available. The area, number of spokes, angle 9, and a are given for each plot size. The departure of the plants from the center of the space is given as a percentage of the growing space length. If there are more test families than spokes, more centers are required and analysis for incomplete blocks may be followed. The two shapes chosen in Table 2 include one in which within-spoke spacing equals that between spokes at any planting spot which would be suitable if intergenotypic competition were desired or if border rows were used. The other shape has within-spoke spacing at half that of between-spokes. This forces the earliest competition to be within genotypic families and delays intergenotypic competition. It also forces the rhomboid shape of the growing space into greater deviation from circular than for the first case.

In no case does the plant occur at the center of the space available to it, but since the angle between successive spokes is constant, the only dimension of concern is the non-central location of the plant between its two neighbors on the same spoke. Nelder suggests that a departure of less than 5% from the intraspoke distance of the theoretical growing space may be acceptable for vegetable crops. Small deviations require slow increases in spacing. For a maximum non-centrality of 5%, α must be less than 1.1. Otherwise, there will be bias if intergenotypic differences occur in response to shape variations. Because trees have more time to make appropriate growth adjustments, non-centrality and non-regularity of the growing space perimeter probably affect them less than annual crops. It would be reasonable at least to assume that such effects would rapidly diminish with age and that in testing for many traits considerable latitude can be afforded at the wider spacings.

ALTERNATIVE RADIAL SEQUENCES

Nelder's designs allow spacings to vary systematically but keep the plots in reasonable proximity. They require relatively few guard plants and are economical of experimental plants or area. However, several difficulties exist in the direct application of design la to forest genetics. Primary among these is the excessive sampling of low densities, with consequent waste of land area. For example, when a plot size of six spans the 50-1,250 interval, all but one tree are at the lower half of the density range. One alternative is to establish two series of tests, one for the upper, and one for the lower densities. This course will introduce plot errors into the response curve and may only lightly sample the middle range of densities, which is likely to be of greatest practical importance.

Another alternative is to relax the requirement for constant shape of growing space and. to allow variation in shape to be confounded with density. Nelder suggests that one of his

Table 2. Planting Points for Nelder's Design 1a.

Density Span 20 - 2020

Growing Space Shape 1 : 1

Plot Size 4	$\theta = 45.92^{o}$	$\alpha = 2.1580$		β(max.) = 18%		No. of experimental spokes = 6				Area per plot = .147 acres						
	Plant. Pts.	2.36	5.09	11.00	23.74	51.24	110.58									
	Density		2020	434	93	20										
Plot Size 5	$\theta = 33.89^{o}$	$\alpha = 1.7800$		β(max.) = 14%		No. of experimental spokes = 9				Area per plot = .137 acres						
	Plant. Pts.	4.10	7.31	13.02	23.18	41.28	73.49	130.86								
	Density		2020	637	201	63	20									
Plot Size 6	$\theta = 26.88^{o}$	$\alpha = 1.5864$		β(max.) = 11%		No. of experimental spokes = 11				Area per plot = .149 acres						
	Plant. Pts.	5.96	9.46	15.00	23.81	37.77	59.92	95.07	150.83							
	Density		2020	803	319	127	50	20								
Plot Size 7	$\theta = 22.29^{o}$	$\alpha = 1.4690$		β(max.) = 10%		No. of experimental spokes = 15				Area per plot = .140 acres						
	Plant. Pts.	7.87	11.56	16.99	24.96	36.67	53.86	79.13	116.24	170.77						
	Density		2020	936	433	201	93	43	20							
Plot Size 8	$\theta = 19.05^{o}$	$\alpha = 1.3904$		β(max.) = 8%		No. of experimental spokes = 17				Area per plot = .154 acres						
	Plant. Pts.	9.81	13.64	18.97	26.38	36.69	51.02	70.94	98.65	137.17	190.73					
	Density		2020	1045	540	279	145	75	39	20						
Plot Size 9	$\theta = 16.63^{o}$	$\alpha = 1.3343$		β(max.) = 7%		No. of experimental spokes = 20				Area per plot = .160 acres						
	Plant. Pts.	11.77	15.71	20.96	27.97	37.33	49.81	66.47	88.69	118.35	157.92	210.73				
	Density		2020	1135	637	358	201	113	63	36	20					
Plot Size 10	$\theta = 14.76^{o}$	$\alpha = 1.2922$		β(max.) = 6%		No. of experimental spokes = 23				Area per plot = .167 acres						
	Plant. Pts.	13.74	17.76	22.96	29.67	38.34	49.55	64.03	82.74	106.93	138.18	178.57	230.76			
	Density		2020	1210	724	434	260	156	93	56	33	20				
Plot Size 11	$\theta = 13.27$	$\alpha = 1.2595$		β(max.) = 6%		No. of experimental spokes = 26				Area per plot = .174 acres						
	Plant. Pts.	15.73	19.81	24.95	31.43	39.59	49.87	62.81	79.11	99.65	125.51	158.09	199.13	250.81		
	Density		2020	1273	803	506	319	201	127	80	50	32	20			
Plot Size 12	$\theta = 12.06^{o}$	$\alpha = 1.2334$		β(max.) = 5%		No. of experimental spokes = 28				Area per plot = .189 acres						
	Plant. Pts.	17.71	21.85	26.95	33.24	41.00	50.57	62.38	76.94	94.90	117.05	144.37	178.07	219.63	270.89	
	Density		2020	1328	872	573	377	248	163	107	70	46	30	20		
Plot Size 13	$\theta = 11.05^{o}$	$\alpha = 1.2120$		β(max.) = 5%		No. of experimental spokes = 31				Area per plot = .197 acres						
	Plant. Pts.	19.71	23.89	28.95	35.09	42.53	51.55	62.48	75.73	91.79	111.25	134.84	163.43	198.09	240.09	291.00
	Density		2020	1375	936	637	434	295	201	137	93	63	43	29	20	

Table 2 (continued).

Density Span 20 - 2020

Growing Space Shape 1 : 2

Plot Size 4	$\theta = 80.54^\circ$	α = 2.1580		β(max.) = 18%		No. of experimental spokes = 3				Area per plot = .147 acres						
	Plant. Pts.	1.67	3.60	7.78	16.79	36.23	78.19									
	Density		2020	434	93	20										
Plot Size 5	$\theta = 62.71^\circ$	α = 1.7804		β(max.) = 14%		No. of experimental spokes = 4				Area per plot = .154 acres						
	Plant. Pts.	2.90	5.17	9.20	16.39	29.18	51.97	92.53								
	Density		2020	637	201	63	20									
Plot Size 6	$\theta = 51.10^\circ$	α = 1.5864		β(max.) = 11%		No. of experimental spokes = 6				Area per plot = .137 acres						
	Plant. Pts.	4.21	6.68	10.61	16.83	26.71	42.37	67.22	106.65							
	Density		2020	803	319	127	50	20								
Plot Size 7	$\theta = 43.02^\circ$	α = 1.4690		β(max.) = 9%		No. of experimental spokes = 7				Area per plot = .150 acres						
	Plant. Pts.	5.56	8.17	12.01	17.65	25.92	38.09	55.95	82.20	120.75						
	Density		2020	936	434	201	93	43	20							
Plot Size 8	$\theta = 37.10^\circ$	α = 1.3904		β(max.) = 8%		No. of experimental spokes = 8				Area per plot = .164 acres						
	Plant. Pts.	6.94	9.65	13.42	18.66	25.94	36.07	50.16	69.75	96.99	134.86					
	Density		2020	1045	540	279	145	75	39	20						
Plot Size 9	$\theta = 32.60^\circ$	α = 1.3343		β(max.) = 7%		No. of experimental spokes = 10				Area per plot = .160 acres						
	Plant. Pts.	8.32	11.11	14.82	19.78	26.39	35.22	47.00	62.71	83.69	111.67	149.00				
	Density		2020	1135	637	358	201	113	63	36	20					
Plot Size 10	$\theta = 29.06^\circ$	α = 1.2922		β(max.) = 6%		No. of experimental spokes = 11				Area per plot = .175 acres						
	Plant. Pts.	9.72	12.56	16.23	20.98	27.11	35.03	45.27	58.51	75.61	97.71	126.26	163.17			
	Density		2020	1210	724	434	260	156	93	56	33	20				
Plot Size 11	$\theta = 26.21^\circ$	α = 1.2595		β(max.) = 6%		No. of experimental spokes = 12				Area per plot = .189 acres						
	Plant. Pts.	11.12	14.01	7.64	22.22	27.99	35.26	44.41	55.94	70.46	88.75	111.79	140.80	177.35		
	Density		2020	1273	803	506	319	201	127	80	50	32	20			
Plot Size 12	$\theta = 23.86^\circ$	α = 1.2334		β(max.) = 5%		No. of experimental spokes = 14				Area per plot = .189 acres						
	Plant. Pts.	12.52	15.45	19.06	23.50	28.99	35.76	44.11	54.40	67.10	82.76	102.08	125.91	155.30	191.55	
	Density		2020	1328	873	574	377	248	163	107	70	46	30	20		
Plot Size 13	$\theta = 21.90^\circ$	α = 1.2120		β(max.) = 5%		No. of experimental spokes = 15				Area per plot = .204 acres						
	Plant. Pts.	13.93	16.89	20.47	24.81	30.07	36.45	44.18	53.55	64.90	78.67	95.35	115.56	140.07	169.77	205.76
	Density		2020	1375	936	637	434	295	201	137	93	63	43	29	20	

Table 2 (continued).

Density Span 50 - 1250

Growing Space Shape 1 : 1

Plot Size 4	$\theta = 31.42^\circ$	$\alpha = 1.7099$		β(max.) = 13%		No. of experimental spokes = 10				Area per plot = .054 acres						
	Plant. Pts.	5.92	10.12	17.31	29.61	50.63	86.58									
	Density		1250	427	147	50										
Plot Size 5	$\theta = 23.35^\circ$	$\alpha = 1.4953$		β(max.) = 10%		No. of experimental spokes = 14				Area per plot = .056 acres						
	Plant. Pts.	9.36	13.99	20.93	31.30	46.80	69.99	104.66								
	Density		1250	559	250	112	50									
Plot Size 6	$\theta = 19.59^\circ$	$\alpha = 1.3797$		β(max.) = 8%		No. of experimental spokes = 17				Area per plot = .064 acres						
	Plant. Pts.	12.89	17.79	24.55	33.87	46.74	64.48	88.97	122.76							
	Density		1250	657	345	181	95	50								
Plot Size 7	$\theta = 15.45^\circ$	$\alpha = 1.3076$		β(max.) = 7%		No. of experimental spokes = 22				Area per plot = .065 acres						
	Plant. Pts.	16.48	21.55	28.18	36.85	48.19	63.01	82.40	107.75	140.90						
	Density		1250	731	427	250	146	85	50							
Plot Size 8	$\theta = 13.23^\circ$	$\alpha = 1.2584$		β(max.) = 6%		No. of experimental spokes = 26				Area per plot = .070 acres						
	Plant. Pts.	20.08	25.28	31.81	40.04	50.39	63.42	79.81	100.44	126.41	159.09					
	Density		1250	789	498	315	199	125	79	50						
Plot Size 9	$\theta = 11.56^\circ$	$\alpha = 1.2228$		β(max.) = 5%		No. of experimental spokes = 30				Area per plot = .076 acres						
	Plant. Pts.	23.71	28.99	35.46	43.36	53.02	64.84	79.29	96.96	118.57	144.99	177.30				
	Density		1250	836	559	374	250	167	112	75	50					
Plot Size 10	$\theta = 10.27^\circ$	$\alpha = 1.1958$		β(max.) = 4%		No. of experimental spokes = 34				Area per plot = .081 acres						
	Plant. Pts.	27.34	32.70	39.10	46.76	55.92	66.87	79.97	95.62	114.35	136.74	163.52	195.54			
	Density		1250	874	611	427	299	209	146	102	71	50				
Plot Size 11	$\theta = 9.24^\circ$	$\alpha = 1.1746$		β(max.) = 4%		No. of experimental spokes = 37				Area per plot = .089 acres						
	Plant. Pts.	30.99	36.40	42.75	50.22	58.99	69.29	81.39	95.61	112.30	131.92	154.95	182.01	213.79		
	Density		1250	906	657	476	345	250	181	131	95	69	50			
Plot Size 12	$\theta = 8.39^\circ$	$\alpha = 1.1575$		β(max.) = 4%		No. of experimental spokes = 41				Area per plot = .095 acres						
	Plant. Pts.	34.63	40.09	46.41	53.72	62.19	71.98	83.33	96.46	111.65	129.25	149.61	173.19	200.47	232.06	
	Density		1250	933	696	520	388	289	216	161	120	90	67	50		
Plot Size 13	$\theta = 7.69^\circ$	$\alpha = 1.1435$		β(max.) = 3%		No. of experimental spokes = 45				Area per plot = .100 acres						
	Plant. Pts.	38.28	43.78	50.06	57.25	65.47	74.87	85.61	97.90	111.95	128.02	146.40	167.41	191.44	218.92	250.34
	Density		1250	956	731	559	428	327	250	191	146	112	85	65	50	

Table 2 (continued).

Density Span 50 - 1250

Growing Space Shape 1 : 2

Plot Size 4	$\theta = 58.72^{o}$	$\alpha = 1.7099$		β(max.) = 13%		No. of experimental spokes = 5			Area per plot = .054 acres							
	Plant. Pts.	4.18	7.16	12.24	20.93	35.80	61.22									
	Density		1250	427	146	50										
Plot Size 5	$\theta = 44.91^{o}$	$\alpha = 1.4953$		β(max.) = 10%		No. of experimental spokes = 7			Area per plot = .056 acres							
	Plant. Pts.	6.61	9.89	14.80	22.13	33.09	49.49	74.00								
	Density		1250	549	250	112	50									
Plot Size 6	$\theta = 36.26^{o}$	$\alpha = 1.3797$		β(max.) = 8%		No. of experimental spokes = 8			Area per plot = .070 acres							
	Plant. Pts.	9.12	12.58	17.36	23.95	33.05	45.60	62.91	86.80							
	Density		1250	657	345	181	95	50								
Plot Size 7	$\theta = 30.37^{o}$	$\alpha = 1.3076$		β(max.) = 7%		No. of experimental spokes = 10			Area per plot = .072 acres							
	Plant. Pts.	11.65	15.23	19.92	26.05	34.07	44.55	58.26	76.19	99.63						
	Density		1250	731	427	250	146	85	50							
Plot Size 8	$\theta = 26.11^{o}$	$\alpha = 1.2584$		β(max.) = 6%		No. of experimental spokes = 12			Area per plot = .076 acres							
	Plant. Pts.	14.20	17.87	22.49	28.31	35.63	44.84	56.43	71.02	89.38	112.44					
	Density		1250	789	498	315	199	125	79	50						
Plot Size 9	$\theta = 22.89$	$\alpha = 1.2228$		β(max.) = 5%		No. of experimental spokes = 14			Area per plot = .081 acres							
	Plant. Pts.	16.76	20.50	25.07	30.66	37.49	45.85	56.06	68.56	83.84	102.52	125.37				
	Density		1250	836	559	374	250	167	112	75	50					
Plot Size 10	$\theta = 20.38^{o}$	$\alpha = 1.1958$		β(max.) = 4%		No. of experimental spokes = 16			Area per plot = .086 acres							
	Plant. Pts.	19.33	23.12	27.65	33.06	39.54	47.28	56.54	67.62	80.86	96.69	115.62	138.27			
	Density		1250	874	611	427	299	209	147	102	71	50				
Plot Size 11	$\theta = 18.36^{o}$	$\alpha = 1.1746$		β(max.) = 4%		No. of experimental spokes = 18			Area per plot = .092 acres							
	Plant. Pts.	21.91	25.74	30.23	35.51	41.71	49.00	57.55	67.60	79.41	93.28	109.57	128.70	151.17		
	Density		1250	906	657	476	345	250	181	131	95	69	50			
Plot Size 12	$\theta = 16.70^{o}$	$\alpha = 1.1575$		β(max.) = 4%		No. of experimental spokes = 20			Area per plot = .097 acres							
	Plant. Pts.	24.49	28.35	32.81	37.98	43.97	50.90	58.92	68.20	78.95	91.39	105.79	122.46	141.75	164.09	
	Density		1250	933	696	520	388	289	216	161	120	90	67	50		
Plot Size 13	$\theta = 15.32^{o}$	$\alpha = 1.1435$		β(max.) = 3%		No. of experimental spokes = 22			Area per plot = .103 acres							
	Plant. Pts.	27.07	30.96	35.40	40.48	46.29	52.94	60.53	69.22	79.16	90.52	103.52	118.38	135.37	154.80	177.01
	Density		1250	956	731	559	427	327	250	191	146	112	85	65	50	

Table 3. Planting Plans for Constant Density Increments.

Density Span 20 - 2020

Plot Size 10 $\theta = 24^{o}$ Growing Space Shape 1:4 through 1:4.3 up to 1:1 No. of exp. spokes = 15 Plot area = .137

Plant. Pts.	19.79	22.09	24.39	26.92	29.63	32.85	36.71	42.18	52.19	78.59	104.44	168.50
Length/Width		.25	.23	.23	.24	.25	.30	.43	.82	.78	1.01	
β		0%	2%	2%	4%	5%	9%	15%	23%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 30^{o}$ Growing Space Shape 1:4 through 1:4.8 up to 1:1.2 No. of exp. spokes = 12 Plot area = .135

Plant. Pts.	15.35	17.63	19.91	22.33	24.93	27.92	31.53	36.54	45.68	69.49	92.60	149.87
Length/Width		.24	.22	.21	.21	.22	.26	.36	.67	.63	.81	
β		0%	1%	2%	3%	5%	8%	15%	22%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 26^{o}$ Growing Space Shape 1:2 through 1:3.2 up to 1:1 No. of exp. spokes = 12 Plot area = .156

Plant. Pts.	11.17	14.41	17.65	20.60	23.94	27.37	31.73	37.32	47.75	73.85	99.02	161.03
Length/Width		.49	.38	.33	.31	.31	.34	.46	.83	.75	.95	
β		0%	2%	3%	1%	6%	6%	15%	21%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 30^{o}$ Growing Space Shape 1:2 through 1:3.6 up to 1:1.2 No. of exp. spokes = 12 Plot area = .134

Plant. Pts.	9.24	12.47	15.69	18.48	21.73	24.92	29.09	34.29	44.10	68.36	91.81	149.38
Length/Width		.48	.36	.30	.28	.28	.30	.41	.72	.65	.82	
β		0%	4%	4%	0%	7%	6%	15%	21%	0%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 24^{o}$ Growing Space Shape 1:1 through 1:2.7 up to 1:1 No. of exp. spokes = 15 Plot area = .124

Plant. Pts.	5.60	10.19	14.77	17.76	21.98	25.22	30.35	35.71	46.95	72.97	98.72	160.55
Length/Width		.97	.55	.44	.37	.36	.37	.50	.86	.77	.96	
β		0%	10%	9%	7%	11%	1%	18%	20%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 30^{o}$ Growing Space Shape 1:1 through 1:3.1 up to 1:1.2 No. of exp. spokes = 12 Plot area = .133

Plant. Pts.	4.25	8.81	13.38	16.09	20.21	23.10	28.05	32.91	43.54	67.58	91.65	148.92
Length/Width		.97	.50	.40	.32	.32	.33	.44	.74	.66	.83	
β		0%	13%	11%	9%	13%	5%	19%	19%	1%	20%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Density Span 50 - 1250

Plot Size 7 $\theta = 18^{o}$ Growing Space Shape 1:4 up to 1:1 No. of exp. spokes = 20 Plot area = .055

Plant. Pts.	34.57	37.51	40.44	44.20	48.50	54.80	65.47	94.11	123.76
Length/Width		.25	.26	.29	.34	.49	.95	.98	
β		0%	6%	3%	9%	13%	23%	1%	
Density		1250	1010	770	530	290	100	50	

Plot Size 7 $\theta = 20^{o}$ Growing Space Shape 1:2 through 1:2.3 up to 1:1 No. of exp. spokes = 18 Plot area = .052

Plant. Pts.	19.71	23.85	28.00	32.56	37.80	44.75	56.35	85.44	114.24
Length/Width		.49	.44	.43	.46	.59	1.02	.96	
β		0%	2%	3%	9%	13%	21%	1%	
Density		1250	1010	770	530	290	100	50	

Plot Size 7 $\theta = 22^{o}$ Growing Space Shape 1:1 through 1:1.9 up to 1:1 No. of exp. spokes = 15 Plot area = .056

Plant. Pts.	9.48	15.32	21.17	25.94	32.23	39.01	51.36	79.53	107.72
Length/Width		.98	.64	.55	.53	.63	1.01	.91	
β		0%	5%	7%	2%	15%	20%	1%	
Density		1250	1010	770	530	290	100	50	

Plot Size 10 $\theta = 16^{o}$ Growing Space Shape 1:4 up to 1:1 No. of exp. spokes = 21 Plot area = .070

Plant. Pts.	39.28	42.21	45.15	48.44	51.88	55.89	60.39	66.10	73.70	86.75	108.55	142.33
Length/Width		.25	.25	.25	.26	.27	.30	.36	.50	.71	.91	
β		0%	3%	1%	4%	3%	6%	7%	13%	13%	11%	
Density		1250	1100	950	800	650	500	350	200	100	50	

Plot Size 10 $\theta = 16^{o}$ Growing Space Shape 1:2 through 1:2.6 up to 1:1 No. of exp. spokes = 21 Plot area = .067

Plant. Pts.	25.69	29.85	34.00	38.14	42.54	47.23	52.60	58.96	67.49	81.47	104.51	139.19
Length/Width		.50	.43	.40	.38	.38	.40	.45	.59	.81	.98	
β		0%	0%	2%	2%	3%	4%	7%	12%	12%	10%	
Density		1250	1100	950	800	650	500	350	200	100	50	

Plot Size 10 $\theta = 18^{o}$ Growing Space Shape 1:1 through 1:2.4 up to 1:1 No. of exp. spokes = 20 Plot area = .060

Plant. Pts.	12.88	18.75	24.62	29.06	34.50	39.08	45.22	51.26	60.33	73.66	96.50	129.24
Length/Width		.99	.66	.54	.46	.43	.42	.47	.59	.78	.91	
β		0%	7%	5%	4%	7%	4%	10%	10%	13%	9%	
Density		1250	1100	950	800	650	500	350	200	100	50	

Plot Size 6 $\theta = 20^{o}$ Growing Space Shape 1:4 up to 1:1 No. of exp. spokes = 18 Plot area = .047

Plant. Pts.	30.81	33.74	36.67	40.77	45.93	55.76	85.26	113.87
Length/Width		.25	.28	.33	.47	1.01	.98	
β		0%	8%	6%	16%	25%	1%	
Density		1250	950	650	350	103.5	50	

Plot Size 6 $\theta = 28^{o}$ Growing Space Shape 1:2 through 1:2.4 up to 1:1 No. of exp. spokes = 11 Plot area = .056

Plant. Pts.	12.88	16.99	21.11	25.66	31.46	41.06	69.61	92.34
Length/Width		.50	.42	.42	.51	.96	.76	
β		0%	2%	6%	12%	25%	6%	
Density		1250	950	650	350	103.5	50	

Plot Size 6 $\theta = 30^{o}$ Growing Space Shape 1:1 through 1:2 up to 1:1.1 No. of exp. spokes = 12 Plot area = .047

Plant. Pts.	5.40	11.21	17.01	21.47	28.34	37.53	65.10	88.33
Length/Width		1.00	.58	.51	.55	.95	.75	
β		0%	7%	11%	7%	25%	4%	
Density		1250	950	650	350	105.0	50	

density-response parameters (β) does vary with space shape in vegetable crops. For forest trees, there is meagre evidence on this aspect of growth. One may guess that the effect of non-isometric spacing, if any, would occur most predominantly with young plants, on traits sensitive to crown form, and at extremes of rectangularity. Therefore, it is reasonable to allow some freedom in this restriction in order for the other variables to be adequately studied. It remains highly desirable to test the effects of rectangularity with trees, as for instance with Neldor's design lb. Also, some freedom as regards non-centrality may be allowable for trees. It is for the individual experimenter to decide what liberties to take.

To provide guides for constructing plots with variable spacing, it was assumed, that a planting system with equal intervals of density is usually easiest and most economical to establish. Therefore, two series of possible planting layouts were computed, one to span the range in densities from 20 to 2,020; and, the other to go from 50 to 1,250. Each series was tested in intervals of two degrees from 2° to 40° for the angle between spokes and for plot sizes (exclusive of borders) of 4 to 13. At these density intervals and plot sizes, the ratios of within-spoke to between-spoke spacing generally decreased, then increased, with the distance from the hub. Therefore, a series of ratios for the innermost experimental tree was established for each plot size and angle series. The analytical steps are given in Appendix B. It became necessary to depart from perfect regularity of density intervals in order to keep the non-central location of the plant within the growing space within reasonable bounds. If only the plants at the widest spacings are allowed to depart very much from centrality and these only to a maximum of 25 percent, then an extra plant or two at the wider spacings will provide sufficient control. Methods for using these extra plants were examined, and a computer program was written to give the planting points for the most acceptable designs, examples of which are given in Table 3. In this table, the shape index is taken as the ratio of Within-spoke to between-spoke spacing, and, is allowed to vary in three ways:

1:4 up to 1:1,
1:2 up to 1:1,
and. 1:1 through 1:2, up to 1:1.

Non-centrality is allowed to vary up to 25% at the wider spacings. Within these limits, other plot sizes and angles can be successfully used. These are listed in Table 4.

Table 4. Plot Sizes and Angles with Acceptable Growing Space Shape and Centrality.

Density Span = 20 - 2020

Plot Shape	1:5 up to 1:1	Plot Shape	1·3 up to 1:1	Plot Shape	1:2 up to 1:1
N = 10	$\theta \geq 24^{o}$	N = 10	$\theta \geq 26^{o}$	N = 8	$\theta \geq 38^{o}$
N = 11	$\theta \geq 24^{o}$	N = 11	$\theta \geq 24^{o}$	N = 10	$\theta \geq 26^{o}$
N = 12	$\theta \geq 24^{o}$	N = 12	$\theta \geq 24^{o}$	N = 11	$\theta \geq 26^{o}$
N = 13	$\theta \geq 22^{o}$	N = 13	$\theta \geq 24^{o}$	N = 12	$\theta \geq 26^{o}$
				N = 13	$\theta \geq 26^{o}$

Density Span = 50 - 1250

Plot Shape	1:5 up to 1:1	Plot Shape	1:3 up to 1:1	Plot Shape	1:2 up to 1:1
N = 5	$\theta \geq 26^{o}$	N = 5	$\theta \geq 28^{o}$	N = 5	$\theta \geq 38^{o}$
N = 6	$\theta \geq 20^{o}$	N = 6	$\theta \geq 28^{o}$	N = 6	$\theta \geq 30^{o}$
N = 7	$\theta \geq 18^{o}$	N = 7	$\theta \geq 20^{o}$	N = 7	$\theta \geq 20^{o}$
N = 8	$\theta \geq 18^{o}$	N = 8	$\theta \geq 18^{o}$	N = 8	$\theta \geq 20^{o}$
N = 9	$\theta \geq 16^{o}$	N = 9	$\theta \geq 18^{o}$	N = 9	$\theta \geq 20^{o}$
N = 10	$\theta \geq 16^{o}$	N = 10	$\theta \geq 16^{o}$	N = 10	$\theta \geq 18^{o}$
N = 11	$\theta \geq 14^{o}$	N = 11	$\theta \geq 16^{o}$	N = 11	$\theta \geq 16^{o}$
N = 12	$\theta \geq 14^{o}$	N = 12	$\theta \geq 14^{o}$	N = 12	$\theta \geq 16^{o}$

One may wish to establish some other function for the sequence of densities. This may easily be done by formulating the function of radial distance sequences, solving for the initial radius', and sequentially solving for the remaining distances.

DISCUSSION AND CONCLUSIONS

Anyone desirous of examining density-time responses may choose among several possible plot designs, arrange his plot sequences and border plots to fit his planting area, and analyze his results on a single-plant basis or on parameters of plot-response variables. Non-linear responses to density would suggest that Bleasdale and Nelder's equation is more appropriate than the logistic growth relations. In any case, estimates of the rate constant can be obtained over a series of years and environments.

The desirability of including density as an important variable of the cultural environment seems clear, especially for species with non-standardized spacings.

The circular plots developed, by Nelder make it possible to avoid the difficulties of the rectangular plots and still study density response over a wide range. For instance, densities of 50 to 1,250 can be samples with six-tree plots occupying only .064 (for 1:1 spacing) or .070 (for 1:2 spacing) acres per plot including border trees. Rectangular three-tree plots sampling six densities would require .085 acres per family even without border rows.

The alternative sequences developed. in this paper allow limited. variabilit y to exist for various shape parameters but improve the sampling of densities and. are even more economical of space than Nelder's designs. A six-tree plot constructed as for the above designs requires only .047 acre including all borders.

Circular plots have the serious disadvantage of not being amenable to easy mechanical planting, cultivation, and. maintenance. If the differences in size of plots or areas are of no concern, intergenotypic competition is desired or can be ignored, and single-tree plots are otherwise acceptable, the traditional rectangular planting is more efficient. In many cases when density responses are desired, however, circular plots will be found to be the most economical design.

APPENDIX A

Nelder (1962) uses the relations:

$$r_n = r_o \alpha^n$$

and $r_{n+1/2} = r_o \alpha^{n+1/2}$,

for his developments. Instead, assume that

$$r_{n+1/2} = 1/2(r_n + r_{n+1}). \quad \text{Then,}$$

$$r_{n+1/2} = r_o \alpha^n (1+\alpha)/2.$$

Also, if we assume that the growing space border approaches a straight line more closely than a curve, the length of the border between adjacent plants of the same spoke is 2 [tan $(\theta/2)$] . The following equations for Nelder's design la would then be appropriate:

$$A_n = \tan(\theta/2) \left[r^2_{n+1/2} - r^2_{n-1/2} \right]$$

$$= \tan(\theta/2) \left[\frac{r^2_n}{4} \cdot f(\alpha) \right],$$

where $f(\alpha) = (1+\alpha)^2 - (1+\alpha^{-1})^2$,

$$= 2 \tan(\theta/2) \,/\, (\alpha - \alpha^{-1}),$$

$$A_1 = 1/4 \tan(\theta/2) \left[r_o^2 \alpha^2 \cdot f(\alpha) \right],$$

$$A_N = 1/4 \tan(\theta/2) \left[r_o^2 \alpha^{2N} \cdot f(\alpha) \right],$$

$$(2N - 2) \log \alpha = \log A_N - \log A_1,$$

$$r_o = \sqrt{4A_1 \,/\, \left[\tan(\theta/2)(\alpha^2 \cdot f(\alpha) \right]}$$

APPENDIX B

Using the relationships

$$\text{Area}_n = \tan(\theta/2)\alpha \,(r^2_{n+1/2} - r^2_{n-1/2})$$

and Density = 43560 / Area,

and specifying any form for the distribution of densities, one may sequentially solve for the location of the growing spaces.

Since interplant spacing between spokes is $2r \cdot \sin(\theta/2)$, the shape of the space may be taken as

$$(r_{n+1/2} - r_{n-1/2}) : (r_{n+1/2} + r_{n-1/2}) \sin(\theta/2).$$

Therefore: $r^2_{n-1/2} = \dfrac{r^2_{n+1/2} - r^2_{n-1/2}}{f(\theta)}$, where $f(\theta) = \left(\dfrac{1 + k \sin(\theta/2)}{1 - k \sin(\theta/2)}\right) - 1$,

and k = the shape fraction. Then, for any given angle (θ), sequence of densities and therefore a sequence of $(r^2_{n+1/2} - r^2_{n-1/2})$, and initial or final shape fraction, the remaining borders to the growing spaces may be calculated. In order to place the maximum non-centrality at the wide spacings and to minimize it at the close spacings, the initial planting point was located at the center of its growing space. Other methods for locating the planting points are being investigated. The remaining planting points are those located according to:

$$r_n = 2r_{n-1/2} - r_{n-1}$$

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