DYNAMICS OF DENSE DIRECT-SEEDED STANDS OF SOUTHERN PINES

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Abstract—Direct seeding of southern pines is an effective method of artificial regeneration, producing extremely dense stands when survival exceeds expectations. Long-term studies of dense direct-seeded stands provide ideal data for exploring development of stands as they approach the limit of maximum stand density. I present data from seven studies with ages of stands ranging from 11 to 42 years. Reineke's relationship serves as the paradigm of stand density. A weighted regression estimated the limiting density line for loblolly (*Pinus taeda* L.) and longleaf pines (*Pinus palustris* Mill.). The slope was common for both species, but the intercept varied, providing a maximum stand density index for loblolly pine that was roughly 9 percent greater than that for longleaf pine. I fit simple response surfaces for mortality, growth of basal area, volume, and weight to explore how these processes changed with stand density. Stand density did not affect mortality of longleaf pine, allowing stand stagnation as diameter growth decreased greatly. However, dynamics of loblolly pine included significant density-dependent mortality when stand density was > 50 percent of maximum. For basal area growth, both species had maximal growth at or below 50 percent of maximum stand density. For volume growth of loblolly pine, maximal growth occurred near 50 percent of maximum stand density. For volume growth of longleaf pine and weight growth of both species, maximal growth occurred at or near maximal stand density.

INTRODUCTION

As plantations of trees develop over time, trees initially grow unimpeded by competition. As the trees become larger, crowns and roots of neighboring trees begin to interfere with each other. As the interference increases, growth in diameter of the individual trees will decrease relative to trees experiencing less competition. As growth reduces, so will vigor of the trees, making them more likely to die. This density-dependent mortality, termed natural thinning, will progress towards some limiting density relationship (Harper 1977).

If the natural thinning relationship appears on axes of trees per acre and quadratic mean diameter (typically on log-log scale), this limiting density relationship is the Reineke (1933) relationship. This relationship is $N = bD^c$, where N is number of trees per acre, D is quadratic mean diameter, and b and c are parameters. The c parameter was initially -1.605, but subsequent investigators have allowed c to vary. Cao and others (2000) suggest that the limiting density line does not have a constant c for direct-seeded slash pine stands, but that it is curvilinear in log-log scale. If the natural thinning relationship appears on axes of trees per unit area and mean plant weight, this is the -3/2 power law (Yoda and others 1963). It may be represented as $V = bN^c$, where V is average volume or weight, and c was initially believed to be equal to -3/2. Given a relationship of volume proportional to diameter at breast height (d.b.h.)$^{2.4}$, the -3/2 thinning law is mathematically equivalent to Reineke's relationship (Bredenkamp and Burkhart 1990). Thus the choice between exploring the Reineke or -3/2 thinning relationship is rather arbitrary. Foresters have long used the Reineke relationship, which precedes identification of the -3/2 power law by plant population biologists. Frothingham (1914) seems to have used the Reineke relationship in constructing yield tables for white pine. I present stand dynamics on the axes of the Reineke relationship. Zeide (2004) provides a recent discussion of alternative perspectives on quantifying stand density.

Although direct-seeding is an effective method of regenerating southern pines, foresters seldom use this method currently. Planting seedlings, rather than seed, produces stands that are more uniform and less wasteful of improved seed. Direct-seeding remains a viable option only where maximizing timber production is irrelevant to management objectives, or where planting seedlings is impractical. Direct-seeding often produces stands with many more trees per acre than plantations of seedlings. High rates of seeding come from the presumption of high variability of direct seeding and as a hedge against low establishment rates, which may occur in suboptimal conditions. With data of direct seeding with high establishment rates, I hope to explore the dynamics of pine stands as they approach the limiting density line.

MATERIAL AND METHODS

Studies

This analysis used data from seven studies of precommercial thinning of direct seeded stands (table 1). Both the seeding procedure (broadcast or strip) and thinning treatment (selective or strip, or a combination) varied among the studies. The age of precommercial thinning varied from 5 to 20 years; only study 312 was thinned later than age 7 years. Concerned with long-term stand dynamics of dense pine stands, I ignored the specific management practices that produced these dense stands. Six of the seven studies are located in central or west-central Louisiana; one is from southeast Mississippi. The species are appropriate for the sites that were seeded.

Fitting the Limiting Density Line

The objective is to fit a straight line on axes of the natural log of trees per acre and the natural log of quadratic mean diameter that describes the limiting density relationship.

$$\ln(N) = b_0 + b_1 \bullet \ln(D_q) \tag{1}$$

Equation (1) would pass through the middle of the data, rather than represent a limiting relationship, if it were fit to the data

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Table 1—Datasets included in this analysis

Study	Pine species	Plots	Plot size	Range of treatments[a]	Age[b]
		no.	acres		
307	Loblolly	33	0.10	750 – 4,350/acre, unthinned	16 – 34
315	Loblolly	18	0.119	908 – 5,445/acre	14 – 22
318	Loblolly	27	0.10	750 – 4,350/acre, unthinned	14 – 29
325	Loblolly	28	0.053	908 – 5,445/acre	11 – 21
312	Longleaf	21	0.4	40 – 140 ft^2/acre, unthinned	25 – 40
320	Longleaf	24	0.10	500 – 3,000/acre	32 – 42
331	Longleaf	15	0.10	500 – 3,000/acre	18 – 36

[a] Treatments are defined as residual stand at time of study establishment (age 3 to 20 years).
[b] Age represents age at time of measurement.

by least squares. Thus, rather than least squares, I fit the line by weighted least squares by minimizing the following loss function:

$$loss = \sum \left(r^2 \right) w \qquad (2)$$

where r is the residual and w is the weight. The distance of the observation from the maximum stand density index (proportional to $N\left(D_q\right)^{b_1}$) determines the weight.

$$w = \left(\frac{\left(N\left(D_q\right)^{b_i^*} - \min\left(N\left(D_q\right)^{b_i^*}\right) \right)}{\left(\max\left(N\left(D_q\right)^{b_i^*}\right) - \min\left(N\left(D_q\right)^{b_i^*}\right) \right)} \right)^{32} \qquad (3)$$

This weighting function is equal to one for the observation of maximum stand density index and to zero for the observation of minimum stand density index. I arbitrarily set the exponent of 32 so that the line was very near the limit of the data, although some observations were above the line. As the data are measured with error, the fitted line should not represent a true limit to the data. While the error associated with measuring d.b.h. may be small, there is also the generally unrecognized variability in measuring trees per acre. At first blush, one might only expect error in trees per acre if a tree was included in a plot when it should have been excluded or a tree excluded when it should have been included. However, functionally "trees per acre" is not pertinent, but "area per tree" is. For a given plot placement, the plot may exclude some trees that use resources on the plot, and some trees on the plot may use resources off the plot. This is practically unavoidable. Bi (2001) also presents a method to estimate the self-thinning line that allows data points to occur above the line.

Note that the b_1 parameter in equation (3) may not vary as the nonlinear regression procedure estimated equation (1), thus it is designated as b_1^*. From past experience (Leduc and Goelz 2004), allowing variation of the b_1 parameter in equation (3) yields undesirable consequences. Basically, the weighting function will drive the estimate of b_1, rather than the actual relationship I am trying to estimate, equation (1). Thus, there were two iteration procedures. I fit equation (1) using a preliminary estimate of b_1 in equation (3). Then I put the new estimate of b_1 into equation (3) and iterated until the parameter value of b_1 didn't change to the fourth significant digit.

Rather than fit equation (1) independently to the two species, I fit the lines in one procedure by using a dummy variable [actually, I fit equation (1) independently to get starting values for the parameters]. Expanding equation (1) yields:

$$\ln(N) = b_{01} + b_{02}(I) + \left(b_{11} + b_{12}(I)\right)\ln\left(D_q\right) \qquad (4)$$

where I is an indicator variable that is zero if the species is longleaf pine and one if the species is loblolly pine. I deleted parameters b_{02} and b_{12} if they were not significantly different from zero ($\alpha = 0.05$).

Fitting Response Trends for Growth and Mortality

To explore dynamics as stands approached the limiting density line, I produced response surfaces for mortality, basal area growth, total cubic foot volume growth, and total green weight growth on the axes of trees per acre and quadratic mean diameter. I calculated volume and green weights of individual trees with the equations of Baldwin and Saucier (1983) for longleaf pine and Baldwin and Feduccia (1987) for loblolly pine. I based the periodic (current) annual growth on a linear assumption (periodic growth divided by years) between measurements taken at approximately 5-year increments. I based the periodic annual mortality on an assumption of constant mortality, thus equal to 1 minus survival raised to the (1/year) power. The response surface was a simple second-order polynomial of trees per acre and quadratic mean diameter and their interactions.

$$Y = b_o + b_1\ln(N) + b_2(\ln(N))^2 + b_3\ln(D_q) + b_4(\ln(D_q))^2 + b_5\ln(N)\ln(D_q) + b_6(\ln(N))^2\ln(D_q) + b_7\ln(N)(\ln(D_q))^2 + b_8(\ln(N))^2(\ln(D_q))^2 \qquad (5)$$

where Y represents current annual mortality, basal area growth, volume growth, or weight growth. This equation was not meant to represent growth in any functional way but merely to fit a simple response surface to the data to facilitate discussion of dynamics as stands approach the limiting density line. Thus, I did not include age and site quality, two variables known to affect stand dynamics, in the equation. Not all of the terms of equation (5) are significant. After I fit all possible models, the final model had the highest r^2 among those for which all parameters were significant. I estimated the response surfaces independently for longleaf and loblolly pine. By differentiating equation (5) with respect to ln(N) or

ln(D_q) and setting equal to zero, I obtained the extrema (minima or maxima); as they are partial derivatives, they could be plotted as a line. I included extrema when present within the range of the graph of the response surface.

I also plotted directional fields of actual data. Plotting the entire trend for all stands produced graphs that were difficult to interpret because of the many overlapping lines. Thus, I made directional fields by creating line segments where one end was the initial observation and the other end was the sum of the initial observation plus 1 year of change (annualized from growth intervals that were typically 5 years).

RESULTS AND DISCUSSION
In the results and discussion, I use the term "density" to be stand density index, or percent of maximum stand density. Although the figures will not have stand density as an axis, stand density may be a proportion of maximum stand density, which would represent lines that are parallel to the maximum density line. I provide only the maximum and 50 percent of maximum lines. Fit statistics for the response surfaces appear in table 2.

Limiting Density Relationships
The slope of the limiting density relationship is common between species, but the intercept varies (thus, parameter b_{12} is set to zero). The values (and asymptotic standard errors) of the parameters of equation (4) are b_{01}: 10.025 (0.013), b_{02}: 0.0877 (0.0074), b_{11}: -1.775 (0.006). As b_{02} is positive, this indicates that loblolly pine may maintain a greater density than longleaf pine. This finding corroborates Reineke's (1933) initial observation that the maximum stand density index of loblolly pine, 450, is greater than maximum stand density index of

longleaf pine, 400; stand density index is relative to a quadratic mean diameter of 10 inches, and represents the trees per acre at that diameter. However, the parameter estimates correspond to a maximum stand density index of 379 for longleaf and 414 for loblolly pine. The values are lower than Reineke, but the proportions of longleaf to loblolly are similar. Note that I calculate the stand density index as $N(D_q/10)^{1.775}$ for both species. The b_{11} parameter is significantly different from the -1.605 assumption of Reineke; it is a common finding for the slope from real data to vary up or down from Reineke's assumption (Cao and others 2000). For loblolly pine, MacKinney and Chaiken (1935) found a slope of -1.707, Harms (1981) found a slope of -1.696, and Williams (1994, 1996) found a slope of -1.505. In figure 1, the limiting density lines for longleaf and loblolly pines are plotted, along with lines representing 50 percent of maximum and basal area of 50, 100, 150, and 200 square feet per acre. If b_{11} was equal to -2, the limiting density lines would parallel the lines of constant basal area. As the magnitude is < 2, the limiting density line reflects about 150 square feet per acre of basal area at a quadratic mean diameter of 2 inches, and about 200 square feet per acre at quadratic mean diameter of 9 inches. This result is typical for measures of stand density: At a constant stand density, basal area increases with increases in quadratic mean diameter.

Stand Dynamics
Loblolly pine mortality—The response surface for annual mortality appears in figure 2. The 50 percent density line represents a fairly good estimate of where density-dependent mortality begins to increase, although the increase is continuous as density nears the limiting density line, rather than representing an abrupt increase near 50 percent of maximum

Table 2—Parameter estimates (and standard errors), and R^2 and root mean squared error for response surface functions

| Variable	Longleaf				Loblolly			
	Mortality	Basal area growth	Volume growth	Weight growth	Mortality	Basal area growth	Volume growth	Weight growth
Intercept		-162.95 (57.00)	76.322 (14.530)	1.019 (0.216)	5.508 (1.210)	-150.74 (47.33)	-1,083.0 (413.4)	-3.495 (1.289)
ln(tpa)		39.930 (13.615)				34.807 (11.451)	141.78 (49.41)	0.575 (0.149)
ln(D_q)		40.117 (14.889)			210.69 (30.36)	49.567 (10.611)		1.422 (0.222)
ln(tpa)^2	0.137 (0.023)	-2.345 (0.818)				-1.815 (0.700)		
ln(D_q)^2	1.481 (0.220)				-35.777 (6.072)	-9.016 (1.976)	-140.52 (52.10)	
ln(tpa)ln(D_q)		-4.475 (1.673)			-59.220 (7.841)		219.22 (79.00)	
ln(tpa)^{2}ln(D_q)	-0.102 (0.022)				3.929 (0.479)	-0.715 (0.134)	-23.006 (8.777)	
ln(tpa)ln(D_q)^2		-0.706 (0.241)	-21.356 (2.060)	-0.317 (0.031)	6.132 (0.968)			
ln(tpa)^{2}ln(D_q)^2			3.896 (0.360)	0.059 (0.005)				
R^2	0.67	0.42	0.39	0.40	0.85	0.26	0.05	0.10
RMSE	2.616	1.846	57.143	0.848	2.145	4.543	109.71	1.347

RMSE = root mean squared error.
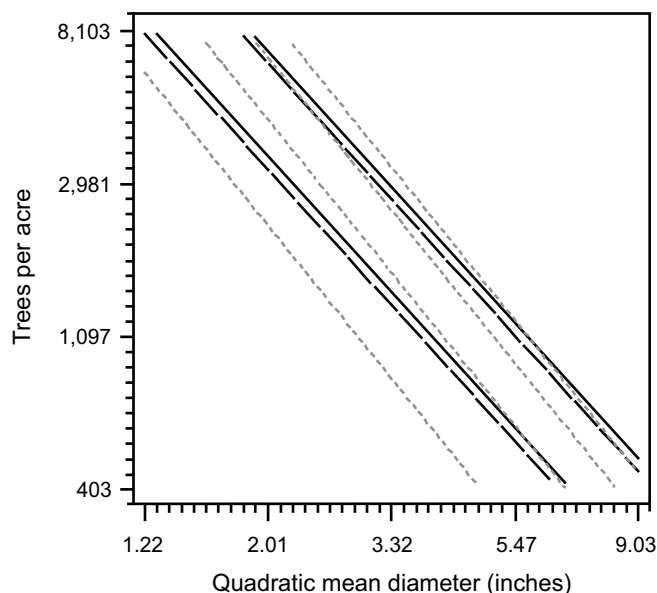
Figure 1—The limiting density function for loblolly pine (dark solid line farthest to right) and longleaf pine (dark dashed line farthest to the right). The lines represent 50 percent of maximum (dark lines to left of the limiting density line) and lines of constant basal area of 50, 100, 150, and 200 square feet per acre (gray dotted lines, with basal area increasing from left to right).
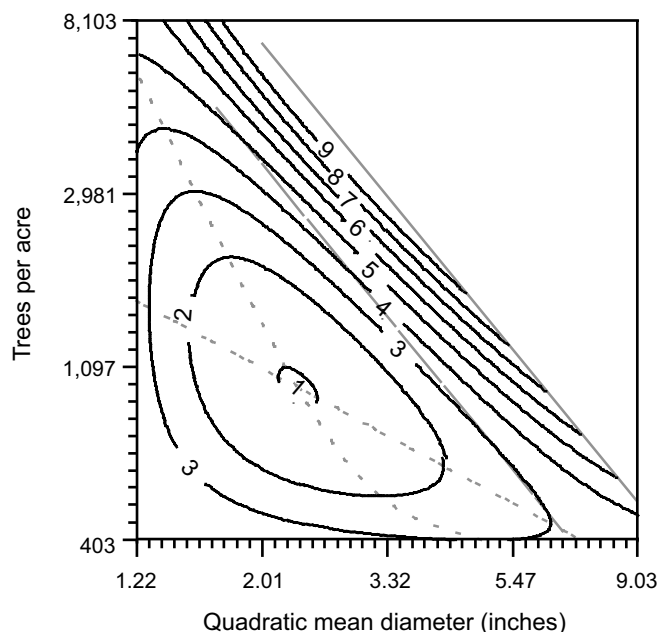

Figure 2—The response surface for annual mortality rate (in percent) for loblolly pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density. The single-dotted line represents minima obtained by taking partial derivatives with respect to diameter. The triplet-dotted line represents minima obtained by taking partial derivatives with respect to trees per acre.

density. At a given level of stand density index (proportional, i.e. parallel, to the maximum density line), mortality is higher where trees are smaller. The extrema, which here are minima, suggest mortality is least at low, but not lowest, stand density.

Loblolly pine growth—The response surface for loblolly pine basal area growth appears in figure 3. At a given level of stand density index, growth is greater for stands of smaller quadratic mean diameter. Growth is greatest at stand density indices that are considerably less than maximum, generally < 25 percent of maximum, although the maxima lines are not exactly parallel to the limiting density relationship and thus are not a constant proportion of maximum density. Generally, somewhat greater stand densities are appropriate for stands of smaller quadratic mean diameter.

Figure 4 plots the response surface for annual total cubic foot volume growth. The maxima, while curving, are generally between 50 and 100 percent of maximum stand density. As density increases from the lower left corner of the graph towards the upper right of the graph, volume growth increases, but the distance between contours increases, suggesting the response surface is getting progressively more flat. The 50 percent of maximum density represents a level that would nearly maximize net volume growth.

Figure 5 plots the response surface for annual net growth in tons per acre. The greater the density, the greater the growth, and at the same density, the greater the quadratic mean diameter, the greater the growth.

Loblolly pine directional field—Figure 6 depicts annual dynamics in trees per acre and quadratic mean diameter.
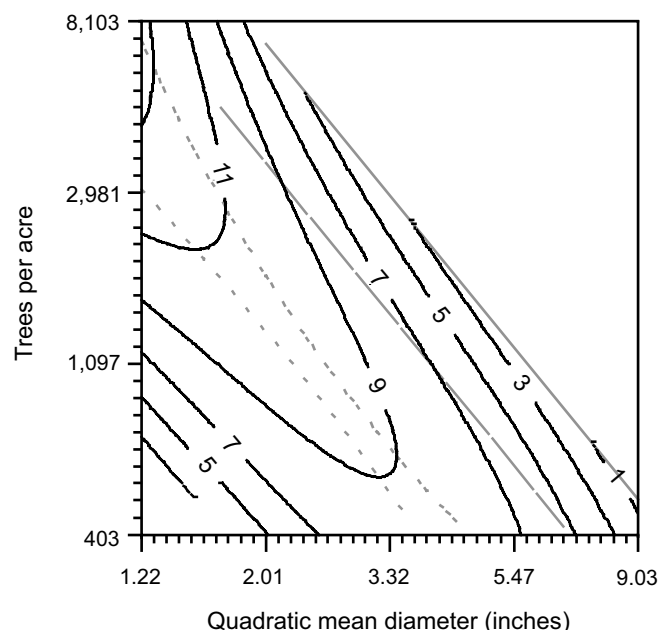

Figure 3—The response surface of annual basal area growth (square feet per acre per year) for loblolly pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density. The single-dotted line represents maxima obtained by taking partial derivatives with respect to diameter. The triplet-dotted line represents maxima obtained by taking partial derivatives with respect to trees per acre.
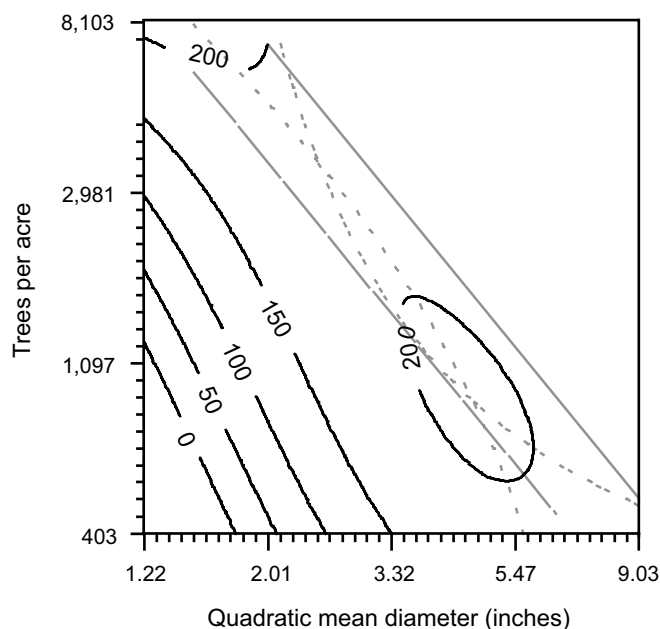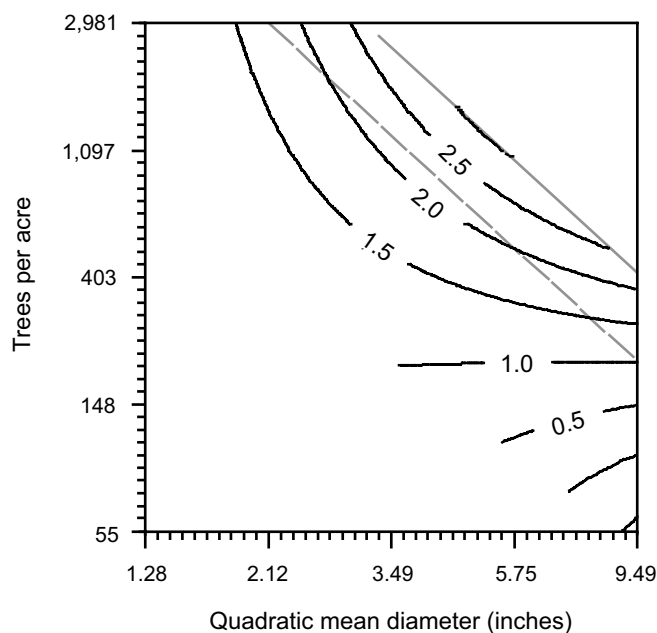
Figure 4—The response surface of annual total cubic foot volume growth, outside bark (cubic feet per acre per year) for loblolly pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density. The single-dotted line represents maxima obtained by taking partial derivatives with respect to diameter. The triplet-dotted line represents maxima obtained by taking partial derivatives with respect to trees per acre.

Figure 5—The response surface of annual total bole dry weight growth outside bark (cubic feet per acre per year) for loblolly pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density.

Horizontal line segments suggest plots where there was no mortality. While there is some mortality before plots cross the line of 50 percent of maximum, there are few or no plots beyond that line that avoid mortality. Therefore, for loblolly pine, the 50 percent of maximum density line is a reasonable threshold for the initiation of density-dependent mortality. Line segments are shorter as the maximum density line is approached; increases in stand density decrease growth of individual trees.

Longleaf pine mortality—Contrary to reason, mortality is not well-related to stand density for longleaf pine (fig. 7). The contours of mortality range from 3 to 6 percent per year, but root mean squared error for the response surface function is 2.6. I will explore mortality more fully below in the section on the directional field.

Longleaf pine growth—The maxima for net longleaf pine basal area growth per year are very near the 50 percent of maximum density line (fig. 8). At a given level of stand density, growth is greater when quadratic mean diameter is smaller. The contours of negative basal area growth are slightly beyond the range of the data. The greatest net volume growth occurs near the maximum density line (fig. 9). For much of the range of data, at the same stand density, volume growth is greater at smaller quadratic mean diameters. The contours for weight growth (fig. 10) are very similar in shape to the contours of volume growth. Three tons per acre per year are predicted when trees per acre are around 1,500 and Dq is around 4.5 inches.

Longleaf pine directional field—Contrary to loblolly pine where mortality is very responsive to stand density, mortality does not determine longleaf pine dynamics with response to density (fig. 11). Rather, density greatly decreases individual tree growth rather than increasing mortality. Note that many
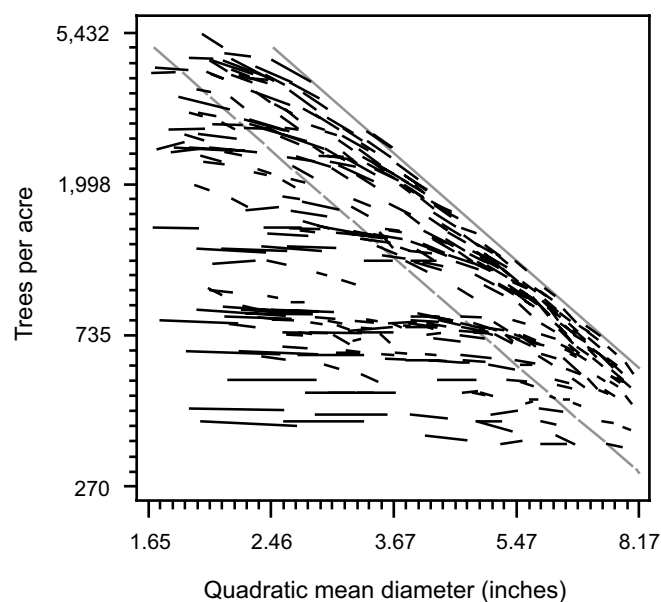

Figure 6—The directional field for stand dynamics of loblolly pine direct-seeded stands. The line segments represent 1 year of change in trees per acre and quadratic mean diameter. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density.
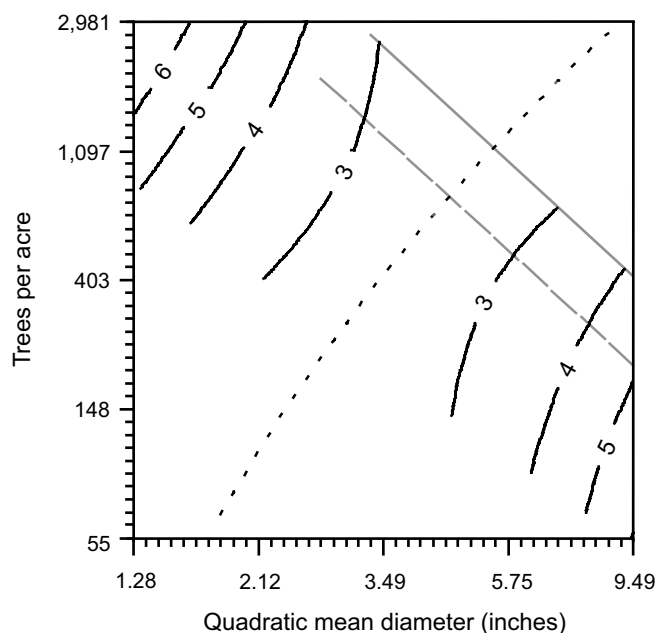
Figure 7—The response surface for annual mortality rate (in percent) for longleaf pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density. The dotted line represents minima obtained by taking partial derivatives with respect to diameter.
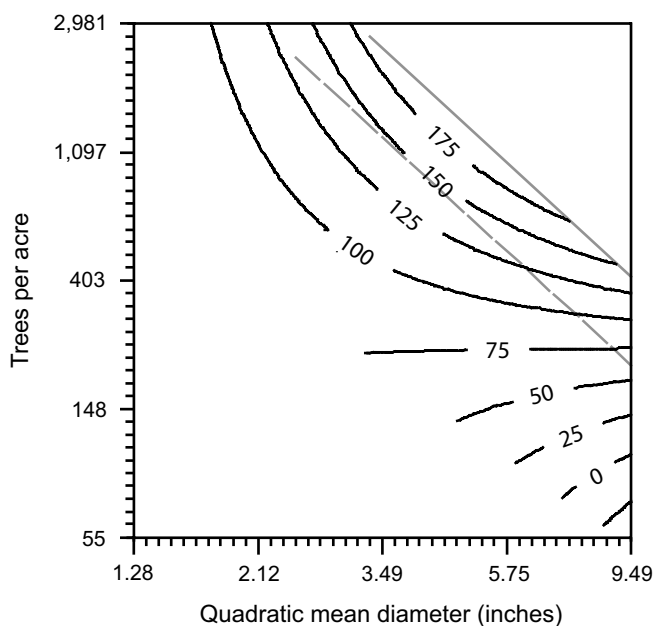

Figure 9—The response surface of annual total cubic foot volume growth, outside bark (cubic feet per acre per year) for longleaf pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density.
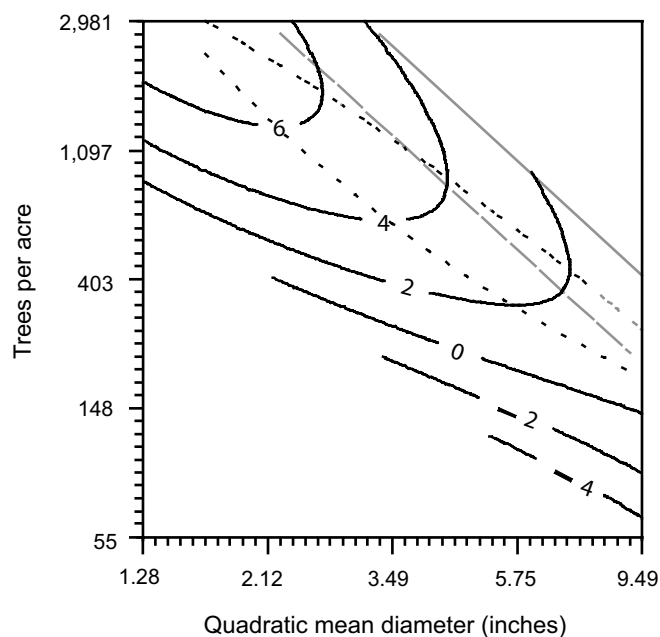

Figure 8—The response surface of annual basal area growth (square feet per acre per year) for longleaf pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density. The single-dotted line represents maxima obtained by taking partial derivatives with respect to diameter. The triplet-dotted line represents maxima obtained by taking partial derivatives with respect to trees per acre.
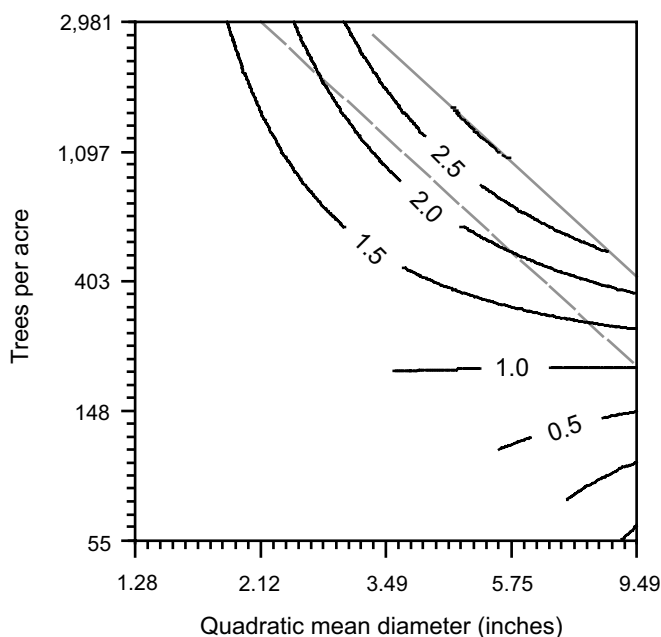

Figure 10—The response surface of annual total bole dry weight growth outside bark (tons per acre per year) for longleaf pine direct-seeded stands. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density.
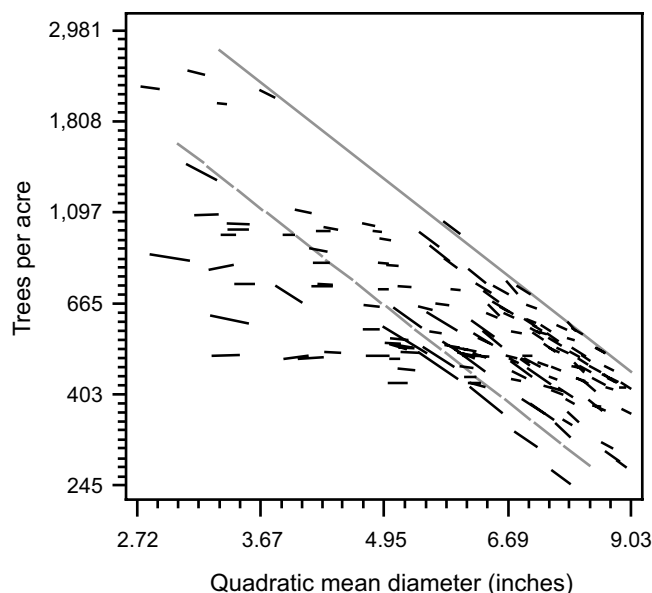
Figure 11—The directional field for stand dynamics of longleaf pine direct-seeded stands. The line segments represent 1 year of change in trees per acre and quadratic mean diameter. The solid gray line represents the maximum density function, and the dashed gray line represents 50 percent of the maximum density.

plots have little or no mortality even though they are greater than the 50 percent of maximum density line. Thus, for longleaf pine, the 50 percent of maximum density line is not a satisfactory threshold for the initiation of density-dependent mortality. In fact, mortality is almost non-density-dependent. Goelz and Leduc (2002) found that intermediate crown class longleaf pine could persist for many years in an inferior crown class, which is atypical for shade-intolerant species. This finding does suggest that longleaf pine stands could be maintained at relatively high densities without high losses to mortality. However, our data do not address whether these near-stagnating conditions permanently reduce vigor and thus potential to respond to subsequent thinning.

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