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A tree survival equation and diameter growth model for loblolly pine based on the self-thinning rule

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Summary

1. A system of equations was developed to describe the reciprocal effects of stand density and quadratic mean diameter through time, by use of data from a loblolly pine (*Pinus taeda*) plantation.

2. These equations were based on the self-thinning rule, which regulates an overcrowded population by imposing a maximum mean tree size for a given stand density.

3. The system explained 98% of the variations in surviving tree number and quadratic mean diameter, and should provide reasonable extrapolation.

Key-words: −3/2 power law, *Pinus taeda*, quadratic mean diameter, stand density.

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Introduction

The self-thinning rule (Yoda *et al.* 1963) established a relationship between mean tree size and stand density in pure even-aged stands. As noted by Zeide (1987), stem diameter is an easy measure of tree size and might be as good as the total tree mass used by Yoda *et al.* (1963) in modelling density-dependent mortality. Quadratic mean diameter (Q) is the diameter of a tree having the average basal area. If quadratic mean diameter is used as a measure of average tree size, the self-thinning curve represents the maximum attainable mean diameter (Q_m) for a given stand density based on the number of surviving trees per unit area (N):

$$Q_m = \alpha N^{\beta} \qquad \text{eqn 1}$$

This rule has been incorporated in recent survival functions and growth models (Smith & Hann 1984, 1986; Lloyd & Harms 1986; Somers & Farrar 1991). Such models should provide reasonable predictions beyond the range of data on which they were built since they were based on the biological relationships between trees growing in a stand. This study aimed at developing a system of equations that described the reciprocal effects of stand density and quadratic mean diameter through time, using data from a loblolly pine (*Pinus taeda* L.) plantation.

Data

Data for this study were obtained from a loblolly pine plantation at the Hill Farm Research Station, Homer, Louisiana, USA. Site index averaged 21 m on a 25-year base. Seedlings were planted in 10 blocks, two each at one of the following spacings; 1·2 × 1·2, 1·8 × 1·8, 1·8 × 2·4, 2·4 × 2·4, and 3·0 × 3·0 m. Four treatments were then applied to each block at age 6:

1. thinned to 988 trees ha^{-1};
2. pruned to 2·4 m or up to one-half total height;
3. thinned and pruned as above;
4. control.

At age 11, all plots except the control plots were randomly thinned to approximately 247, 494, or 741 trees ha^{-1} and all trees in these plots were pruned to 5·2 m. This data set was described in detail by Sprinz, Clason & Bower (1979). There was a total of nine control plots, which were measured at ages 13, 18, 21, 22, 25, 28 and 29; and 26 treated plots measured at ages 11, 12, 13, 14, 15, 16, 21, 28 and 29. Quadratic mean diameter and number of surviving trees ha^{-1} were computed for each plot at each measurement time.

Table 1 shows summary statistics for number of trees ha^{-1}, quadratic mean diameter, and basal area ha^{-1}, by treatment and age. Relationships between mean tree size (quadratic mean diameter) and stand density (trees ha^{-1}) are shown in Fig. 1.

Model development

It is always difficult to constrain a growth model such that it behaves reasonably well even when it extrapolates beyond the range of the data. The self-thinning curve was used in this study to establish a limit on diameter growth, subject to current stand density. As the stand grows older it approaches the self-thinning curve, while its quadratic mean

Table 1. Summary statistics for number of trees ha^{-1}, quadratic mean diameter at breast height (Q) and basal area ha^{-1}, by treatment and stand age

Treatment	Stand age (years)	Number of observations	Trees ha^{-1} Min.	Mean	Max.	Q (cm) Min.	Mean	Max.	Basal area ($m^2 ha^{-1}$) Min.	Mean	Max.
Unthinned	13	9	947	2220	4285	10·7	14·9	19·9	29·0	33·2	38·7
	18	9	947	2220	4285	11·6	16·7	22·8	38·5	41·6	47·0
	21	9	947	2175	4151	12·0	17·3	23·6	41·0	43·8	49·2
	22	9	917	1922	3394	12·6	17·8	23·9	40·8	42·5	45·1
	25	9	888	1811	3081	13·5	18·9	25·0	42·5	45·6	48·2
	28	9	858	1523	2533	14·7	20·4	26·3	36·3	46·3	52·8
	29	9	799	1298	2125	16·3	21·5	27·2	30·5	44·9	54·1
Thinned	11	26	225	474	780	11·1	16·0	20·1	4·9	9·1	17·6
	12	26	225	474	780	11·7	17·1	21·4	5·3	10·4	20·3
	13	26	225	474	780	13·0	18·8	23·8	7·0	12·4	22·2
	14	26	225	474	780	13·4	19·5	25·1	7·8	13·2	22·3
	15	26	225	472	780	15·1	21·4	27·6	9·5	15·8	26·1
	16	26	225	472	780	15·8	22·5	29·1	10·7	17·3	28·2
	21	26	225	471	780	19·0	26·5	35·7	15·4	23·6	36·1
	28	26	205	460	780	22·0	30·7	41·3	21·1	30·6	46·3
	29	25	194	430	717	22·9	31·6	42·2	21·9	30·6	45·9

diameter increases and approaches the maximum attainable mean diameter (Q_m). In other words, the difference between Q_m and Q should decrease over time and can be expressed as

$$Q_{m2} - Q_2 = (Q_{m1} - Q_1)(t_2/t_1)^{\delta-1}e^{\gamma(t_2^{\delta}-t_1^{\delta})} \quad \text{eqn 2}$$

or

$$Q_2 = \alpha N_2^{\beta} - (\alpha N_1^{\beta} - Q_1)(t_2/t_1)^{\delta-1}e^{\gamma(t_2^{\delta}-t_1^{\delta})} \quad \text{eqn 3}$$

where subscripts 1 and 2 correspond to ages t_1 and t_2, respectively, and α, β, γ, and δ are regression coefficients.

Future stand density is limited between two extremes: (a) no mortality, i.e. $N_2 = N_1$, when the stand undergoes little or no competition, and (b) maximum mortality when the stand is near the self-thinning curve. This maximum mortality defined a lower limit, N_{m2}, for survival density:

$$N_{m2} = N_1 e^{\phi(t_2^2-t_1^2)} \quad \text{eqn 4}$$

As a stand grows from age t_1 to t_2, stand density will lie somewhere between these two limits, and can be computed as the weighted average of the two limits. The weighting coefficient (p), which is between 0 and 1, is used here to model this phenomenon as follows

$$N_2 = (1 - p)\, N_1 + pN_1 e^{\phi(t_2^2-t_1^2)} \quad \text{eqn 5}$$

where $p = e^{\psi(\alpha N_1^{\beta}-Q_1)}$, and α, β, ϕ, and ψ are regression coefficients. eqn 6

The advantage of equations 5 and 6 is that $N_2 = N_1$ when $p = 0$, and when p approaches 1 the stand reaches the self-thinning curve. In the latter case, stand mean diameter (Q_1) approaches maximum mean diameter ($Q_m = \alpha N^{\beta}$). When this happens, N_2 reaches the lower limit described in equation 4. Note

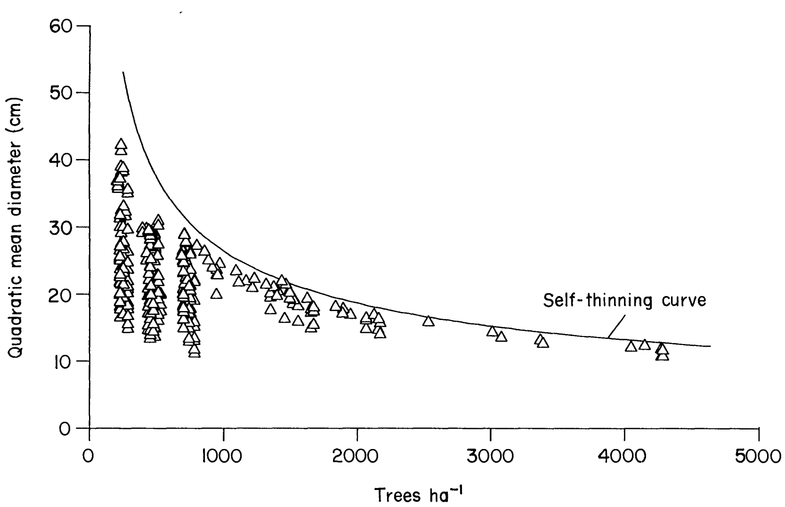

Fig. 1. Relationship between quadratic mean diameter at breast height and stand density in a loblolly pine plantation. The self-thinning curve is given by $Q_m = 835{\cdot}47462\, N^{-0{\cdot}5}$.

that equation 5 is not step-invariant, i.e. predictions from t_1 to t_2 and then from t_2 to t_3 do not give the same results as a one-step prediction from t_1 to t_3. This undesirable property can be overcome by successive annual prediction of stand density. Equations 5 and 6 are then combined and expressed as a difference equation in the form

$$N_{i+1} = N_i \{1 - [1 - e^{\phi(t_{i+1}^2 - t_i^2)}]e^{\psi(\alpha N_i^\beta - Q_i)}\}, \qquad \text{eqn 7}$$

where $t_{i+1} = 1 + t_i$.

Results and discussion

Estimating coefficient β of the self-thinning curve (equation 1) has proved to be a difficult task due to lack of data near the self-thinning region. Lloyd & Harms (1986) decided to fix β at an empirical value of $-0{\cdot}5$, whereas Somers & Farrar (1991) used Reineke's (1933) estimates for both α and β. In the present study, β was fixed at $-0{\cdot}5$. Equation 3 predicts diameter growth for stands of all density levels, and thus its remaining parameters, α and γ, were obtained from all plot data using regression techniques. Observed values of N_2 were used in fitting equation 3. An effort to use predicted values of N_2 instead by estimating simultaneously the parameters of equations 3 and 7 failed to yield acceptable results and was therefore abandoned.

Since the control plots maintained a relatively high number of trees per unit area, these plots were close to or inside the self-thinning zone. Thus, only data near the self-thinning curve from the control plots were used to estimate the regression coefficient ϕ of equation 4, which described tree survival near the self-thinning curve. The next step was to determine parameter ψ of equation 7 from all plots, given the above parameter estimates. Estimation procedures for ψ involved intermediate steps of successive annual predicitions for tree survival until the end of the growth period was reached. Table 2 presents regression coefficients for the diameter growth and tree survival equations.

Since each plot was re-measured several times, the diameter growth and survival equations 3 and 7 were applied to all possible growth pairs in the data to determine the projection ability of these equations. Table 3 shows evaluation statistics for three different density levels: under-stocked (<25% of the maximum density), well-stocked (25–50% of the maximum density), and over-stocked (>50% of the maximum density). These density levels were based on the time when canopy closure occurs and when density-related mortality begins in loblolly pine stands (25 and 50% of the maximum density, respectively, according to Dean & Baldwin 1993).

Overall, accuracy and precision of the projections remained fairly stable for most projection lengths in the evaluation. The system tended to over-estimate

Table 2. Parameter estimates for tree survival and diameter growth equations

Equation*	Parameter	Estimate	Asymptotic Standard Error
3	α	835·47462	30·55409
	β	−0·5	—
	γ	−0·12631	0·02917
	δ	0·56146	0·10838
4	ϕ	−0·00078	0·00014
7	ψ	−0·24273	0·05257

* Equations

$$Q_2 = \alpha N_2^\beta - (\alpha N_1^\beta - Q_1)(t_2/t_1)^{\delta-1} e^{\gamma(t_2^\delta - t_1^\delta)} \qquad \text{eqn 3}$$

Fit Index = 0·984; $s_{y.x}$ = 0·77; n = 262.

$$N_{m2} = N_1 e^{\phi(t_2^2 - t_1^2)} \qquad \text{eqn 4}$$

Fit Index = 0·958; $s_{y.x}$ = 73·32; n = 37.

$$N_{i+1} = N_i \{1 - [1 - e^{\phi(t_{i+1}^2 - t_i^2)}]e^{\psi(\alpha N_i^\beta - Q_i)}\} \qquad \text{eqn 7}$$

Fit Index = 0·981; $s_{y.x}$ = 99·09; n = 262.

where Q_i is quadratic mean diameter (cm) at time i; N_i is number of trees ha^{-1} at time i; N_{m2} is lower limit for number of trees ha^{-1} at time 2; t_i is stand age (years) at time i; and t_{i+1} is $1 + t_i$ (only for equation 7). Fit Index = 1 − (residual SS/corrected SS), SS is the sum of squares, and $s_{y.x}$ is the root mean squared error.

tree density and under-estimate quadratic mean diameter. High over-estimation of stand density (26–28%) was observed in over-stocked cases when projection lengths were 11 and 16 years (ages 18–29, and 13–29, respectively). These values were from control plots that had excessive mortality at age 29.

Survival curves and diameter growth curves were generated for five hypothetical stands having mean diameter of 2 cm and densities ranging from 1000 to 5000 trees ha^{-1} at an initial age of 5 years (Fig. 2). Figure 3 shows the mean diameter-stand density trajectory for these stands from age 5 to age 70. These curves tend to be vertical from the start (i.e. increasing in size with little or no mortality) and then begin to conform to the self-thinning curve after competition sets in.

Application

Table 4 illustrates the use of this system in projecting tree survival and diameter growth of three loblolly pine plots. Successive annual predictions were provided for plot 21 from age 13–29, 18–29 and 22–29, using actual plot measurements as initial stand attributes. For Plots 13 and 42, annual projections were for ages 11–29, 16–29 and 21–29. As an example, consider Plot 21 at age 13 with 2065 trees ha^{-1} and a quadratic mean diameter of 14·77 cm. Projection to age 14 involves first predicting tree survival

$$N_{14} = 2065 \{1 - [1 - e^{-0{\cdot}00078(14^2 - 13^2)}] \times \times e^{-0{\cdot}24273[835{\cdot}47462(2065)^{-0{\cdot}5} - 14{\cdot}77]}\} = 2047 \text{ trees ha}^{-1},$$

Table 3. Evaluation statistics: projection difference* (%) for predictions of tree number ha^{-1} and quadratic mean diameter at breast height (Q)

Projection length (years)	Under-stocked†					Well-stocked†					Over-stocked†				
		Trees ha^{-1}		Q			Trees ha^{-1}		Q			Trees ha^{-1}		Q	
	N	Mean	SD‡	Mean	SD‡	N	Mean	SD‡	Mean	SD‡	N	Mean	SD‡	Mean	SD‡
1	86	−0·03	0·40	7·27	2·71	53	−0·53	2·22	4·17	2·86	35	−7·5	8·84	−1·63	2·89
2	75	−0·08	0·60	7·29	2·07	29	−0·51	1·51	5·75	2·43	—	—	—	—	—
3	59	−0·15	0·82	6·28	2·73	19	−0·58	1·69	5·85	2·57	27	−0·88	8·39	0·96	3·27
4	42	−0·44	1·28	7·35	2·44	10	−0·25	1·56	7·60	2·23	27	−11·22	18·50	−1·63	5·58
5	30	−0·37	1·26	5·42	3·34	21	0·30	1·21	5·09	2·68	10	4·43	1·83	6·08	1·24
6	11	−0·15	0·80	2·27	1·80	15	0·63	1·29	5·57	2·80	9	−7·18	13·81	0·80	5·95
7	16	−0·26	1·08	5·78	2·62	29	−1·88	4·79	3·76	4·97	34	−9·88	21·01	0·38	6·64
8	17	−0·17	1·09	4·53	2·95	28	−4·40	7·19	2·29	5·66	25	−8·68	28·39	1·71	7·68
9	19	−0·51	1·92	5·51	4·19	7	0·55	2·08	8·46	4·29	9	−0·67	4·86	3·19	2·79
10	23	−0·48	1·96	5·36	4·92	3	1·80	0·36	8·07	1·93	9	−11·40	19·28	−0·38	7·28
11	—	—	—	—	—	—	—	—	—	—	9	−27·74	37·21	−3·35	10·92
12	7	−5·79	6·95	−2·16	5·80	18	0·46	4·26	5·61	4·04	10	0·70	7·23	4·88	3·31
13	18	−4·70	6·86	−0·53	5·95	33	−2·17	7·05	4·73	5·07	1	8·36	—	8·14	—
14	27	−3·94	6·62	2·25	6·17	25	−2·52	7·85	5·72	5·92	—	—	—	—	—
15	33	−3·84	6·23	3·12	5·76	19	−3·26	10·08	6·20	6·85	9	−9·54	17·05	2·72	7·71
16	36	−4·01	6·29	3·17	6·23	16	−2·70	10·43	6·48	7·15	9	−25·85	33·88	−0·49	11·37
17	42	−4·45	7·41	3·41	6·90	10	−0·41	8·55	8·08	5·27	—	—	—	—	—
18	23	−6·75	8·46	2·57	7·04	3	3·34	3·40	8·90	2·54	—	—	—	—	—

* Percentage difference, 100 (actual − predicted)/actual.

† Under-stocked, below 25% of maximum density; well-stocked, between 25 and 50% of maximum density; over-stocked, above 50% of maximum density.

‡ SD, standard deviation.

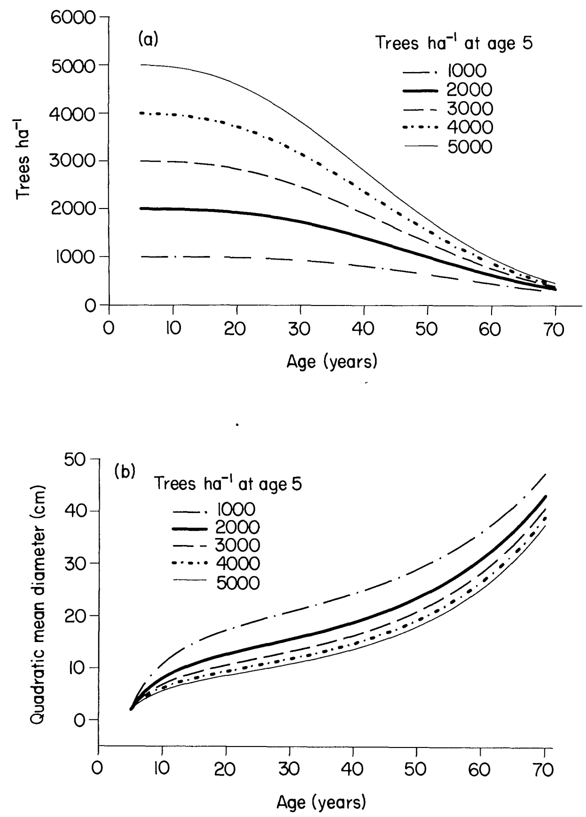

Fig. 2. (a) survival curves and (b) diameter growth curves of loblolly pine stands having quadratic mean diameter at breast height of 2 cm and various densities at an initial age of 5 years. These stands were simulated from age 5 to age 70.

Fig. 3. Mean diameter at breast height–stand density trajectory for loblolly pine plantations having initial mean diameter of 2 cm and initial densities of 1000, 2000, 3000, 4000, and 5000 trees ha^{-1} at age 5. These stands were simulated from age 5 to age 70.

and then computing quadratic mean diameter as

$$
\begin{aligned}
Q_{14} &= 835{\cdot}47462(2047)^{-0{\cdot}5} - \\
&- [835{\cdot}47462 - (2065)^{-0{\cdot}5} - 14{\cdot}77] \times \\
&\times [(14/13)^{0{\cdot}56146^{-1}} e^{-0{\cdot}12631(14^{0{\cdot}56146}-13^{0{\cdot}56146})}] \\
&= 15{\cdot}05 \text{ cm}.
\end{aligned}
$$

The same procedures were then repeated to predict tree survival and diameter growth at subsequent ages.

Conclusion

The system of two equations (3 and 7) presented

Table 4. Projection of tree survival and growth in quadratic mean diameter at breast-height (Q) for three loblolly pine sites

Stand age (years)	Observed		Projected					
	Trees ha^{-1}	Q (cm)	Trees ha^{-1}	Q (cm)	Trees ha^{-1}	Q (cm)	Trees ha^{-1}	Q (cm)
Plot 21								
13	2065	14·77	2065*	14·77				
14			2047	15·05				
15			2027	15·31				
16			2005	15·57				
17			1981	15·83				
18	2065	16·08	1955	16·08	2065	16·08		
19			1927	16·34	2031	16·33		
20			1897	16·60	1996	16·58		
21	2065	16·36	1865	16·87	1958	16·84		
22	1946	16·89	1831	17·14	1919	17·11	1946	16·89
23			1796	17·42	1878	17·39	1905	17·17
24			1759	17·70	1835	17·69	1863	17·46
25	1896	17·83	1720	18·00	1791	17·99	1819	17·76
26			1680	18·31	1745	18·30	1773	18·07
27			1639	18·64	1698	18·63	1727	18·39
28	1625	19·30	1597	18·97	1650	18·98	1679	18·73
29	1405	20·40	1553	19·32	1602	19·34	1630	19·09
Plot 13								
11	780	11·07	780	11·07				
12	780	11·73	780	12·22				
13	780	12·98	780	13·23				
14	780	13·44	780	14·13				
15	780	15·14	779	14·94				
16	780	15·82	779	15·67	780	15·82		
17			778	16·35	780	16·49		
18			777	16·96	779	17·10		
19			776	17·53	778	17·66		
20			775	18·06	777	18·19		
21	780	18·97	774	18·56	775	18·68	780	18·97
22			772	19·03	774	19·14	778	19·43
23			771	19·47	772	19·58	776	19·85
24			768	19·89	770	20·00	774	20·26
25			766	20·30	767	20·40	771	20·65
26			763	20·68	764	20·79	768	21·03
27			760	21·06	761	21·16	765	21·40
28	780	21·97	757	21·42	758	21·52	761	21·76
29	709	22·91	753	21·78	754	21·87	757	22·11
Plot 42								
11	252	19·48	252	19·48				
12	252	21·36	252	21·49				
13	252	23·19	252	23·26				
14	252	23·80	252	24·84				
15	252	26·72	252	26·25				
16	252	27·81	252	27·53	252	27·81		
17			252	28·69	252	28·96		
18			252	29·75	252	30·01		
19			252	30·73	252	30·98		
20			252	31·63	252	31·87		
21	252	33·07	252	32·46	252	32·69	252	33·07
22			252	33·24	252	33·46	252	33·82
23			252	33·96	252	34·18	252	34·53
24			252	34·64	252	34·85	252	35·19
25			252	35·28	252	35·48	252	35·81
26			251	35·88	251	36·08	251	36·39
27			251	36·45	251	36·64	251	36·95
28	252	38·30	251	36·99	251	37·18	251	37·48
29	252	38·81	251	37·51	251	37·69	251	37·98

* Underlined values are actual measurements used as initial stand attributes in the growth projection.

here performed reasonably well in predicting tree survival and diameter growth. Because they are based on the self-thinning rule, these equations seem to be compatible with underlying biological principles and thus should be able to provide reasonable predictions outside the range of the data.

The self-thinning limit should vary little regardless of growth rates. On the other hand, parameters of this system might be sensitive to growth rate in different stands and might need to be estimated for stands with different rates of growth.

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