



Duration of response to nitrogen and phosphorus applications in mid-rotation *Pinus taeda*

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ABSTRACT

We quantified the response duration to one-time applications of 112, 224, and 336 kg ha⁻¹ of elemental nitrogen (112 N, 224 N, and 336 N, respectively) combined with 28 or 56 kg ha⁻¹ of elemental phosphorus in mid-rotation *Pinus taeda* L. stands. Post-application measurements continued for 10 years at 32 sites in the south-eastern United States and one site in Argentina, and we fit a Ricker model to data from each treatment in the event that a zero growth response was not observed in our measured data. The response duration was eight (measured), 14 (modeled), and 16 (modeled) years after treatment for the respective 112 N, 224 N, and 336 N treatments. The corresponding growth response per unit of applied nitrogen estimated from fertilization to when the growth response was not different from zero (whether measured or modeled) was 0.20, 0.16, and 0.13 m³ kg⁻¹ for the 112 N, 224 N, and 336 N treatments, respectively. We hypothesized that the mechanism controlling the response duration was related to the amount of fertilizer nitrogen remaining in the foliage over time after treatment; previous studies found that nitrogen application had large impacts on the foliage amount and foliar nitrogen content. Based on retranslocation rate estimates from the literature of 67% of fertilizer nitrogen per year, our results suggest that a good correlation exists between the growth response and the amount of fertilizer nitrogen remaining in the foliage.

1. Introduction

Forest managers have a wide range of options to effectively manage site resources during a rotation. At one extreme, managers can choose a more extensive approach where the primary tool is species selection by choosing a species that will perform well with few additional inputs (Clark and Saucier 1991, Fox 2004). On the other extreme, an intensive approach could be implemented to reach and maintain high resource availability throughout the rotation. Here, the goal is to eliminate nutrient limitations, as has been done in research trials (Albaugh et al., 2016). An intermediate approach is to take advantage of a Type B (Snowdon and Waring 1984, Morris and Lowery 1988) treatment response and ameliorate a limiting resource. Treatment responses can be grouped into four types (A, B, C, and D) based on the way that resources

are made available to the trees. Type A responses are positive responses that continue through the end of a rotation because the resource that is added previously limited growth and the untreated trees never had access to this resource. A Type B response is a positive response that occurs for a short time and is observed until the added resource is exhausted or is no longer available; the untreated trees never have access to the resource, and the growth gain is maintained after the treated stands return to control conditions and growth rates. Type C responses initially appear similar to Type B, with positive responses after treatment; however, the untreated trees eventually gain access to additional resources and begin to grow better than the treated trees. The final response type, D, results in a detrimental response where treated trees grow less than untreated ones immediately after treatment.

A common example of a Type B response is a one-time application of

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limiting nutrients in a mid-rotation fertilizer application (typically nitrogen and phosphorus) (Snowdon and Waring 1990, Moore et al., 1991, Stegemoeller and Chappell 1991, Fox et al., 2007, Campion 2008). This treatment provides limiting resources at a time when the trees will respond and grow quickly into more commercially valuable size classes. In addition to increasing individual tree size, one-time mid-rotation fertilization treatments result in a permanent increase in growth and effectively increase stand development (Long et al., 2004) and reduce rotation length by ~ 1 year in Monterey pine (*Pinus radiata* D. Don) (Snowdon 2002) and by ~ 1.5 – 3.5 years in loblolly pine (*P. taeda* L.) (Carlson et al., 2008). One-time mid-rotation fertilizer treatments in *P. taeda* commonly combine nitrogen and phosphorus due to the large synergistic response observed when the two elements are added at the same time such that the response to an application of both elements can be two to four times greater than the response to the application of either alone (Fox et al., 2007). The stem volume response to an application of 224 and 28 kg ha⁻¹ of elemental nitrogen and phosphorus, respectively, averages about 3.8 m³ ha⁻¹ yr⁻¹ for eight years (Albaugh et al., 2017; Carlson et al., 2014; Fox et al., 2007; Albaugh et al., 2012b). The eight-year period was the reporting focus because measurements in many of the studies that were used to determine response stopped after eight years. Understanding the longevity of response to a single fertilizer application would be important in guiding plans for future applications and for harvest planning to ensure that all of the benefit from the fertilizer was captured prior to harvest. A one-time fertilizer application response duration has been reported for commercial species including *P. radiata* (McGrath et al., 2003; Mead and Gadgil, 1978; Ramírez Alzate et al., 2016a; Turner et al., 1996), *Pseudotsuga menziesii* (Mirb.) Franco (Miller and Tarrant 1983, Stegemoeller and Chappell 1991), and *P. taeda* (Ballard 1981, Allen 1987).

At the same time, developing insight into the mechanism(s) controlling the response duration may improve our ability to manage stands if this permits the potential to manipulate the mechanism to increase stand productivity from a given application. Fertilizer treatments that include nitrogen and phosphorus typically result in an increase in the leaf area index (foliage amount) (Binkley and Reid 1984, Linder 1987, Vose and Allen 1988, Raison et al., 1992) and nitrogen concentration (and concomitantly, content) in the foliage (Albaugh et al., 2008, Coleman et al., 2014). Prior to foliage senescence and depending on species, 11 to 70% of nitrogen is retranslocated each year (*P. taeda* (Albaugh et al., 2008), *P. radiata*, *Pseudotsuga menziesii*, *Picea abies* (Landsberg and Sands 2011)). The retranslocated nitrogen moves into nearby shoot and foliage tissue and then eventually back out to newly developing foliage in the next growing season (Albaugh et al., 2012a). Over time, added nitrogen in the foliage from fertilization will diminish. Even though some nitrogen is retranslocated, a proportion of it is lost in litterfall annually. The nitrogen remains sequestered in the litterfall until some type of disturbance occurs, usually a thinning operation or a clear-cut (Miller 1981, Piatek and Allen 2001) when it may be released (Carlyle, 1995; Ramírez Alzate et al., 2016b). Consequently, the persistence of fertilizer nitrogen in the foliage may be related to the longevity of the response.

One-time mid-rotation fertilization is used for many commercial species around the world. Indeed, fertilizer applications are most common in *P. taeda* plantations (Albaugh et al., 2007), with more than 200,000 ha yr⁻¹ receiving mid-rotation nitrogen and phosphorus applications in the southeastern United States (SEUS) (Albaugh et al., 2019). *Pinus taeda* is an important contributor to the global wood supply (Carle and Holmgren 2008), and data on retranslocation (Albaugh et al., 2008) and response longevity (Ballard 1981, Allen 1987) have been reported. However, response longevity reports for *P. taeda* may be underestimated (Carter et al., 2021). Response duration reports relied on early study results and may have been underestimated because there were few sites with long response periods (Allen 1987) or because researchers utilized studies where the treatment plot sizes and buffer areas between plots may not have been large enough to prevent confounding

of the control plots, which would reduce the apparent response duration (Ballard 1981). The response duration will also influence the observed growth response per unit of applied nitrogen, where a longer response period will allow for a greater growth response to accumulate per unit of applied material. Whether a given amount of applied nitrogen produces a larger response for a short time or a smaller response but over a longer time will be important information for managers to determine the appropriate amount of nutrients to apply at any given time. The combination of these factors suggests there is benefit in reexamining response longevity in *P. taeda* while including an examination of growth per unit of applied nitrogen and of the factors determining that longevity.

Our interest then was to quantify the duration of response and the growth response per unit of nitrogen that was applied for a range of one-time applications of nitrogen and phosphorus in *P. taeda*. Additionally, we wanted to examine the amount of applied nitrogen found in the foliage as a potential mechanism to explain why the response to fertilization eventually dissipates. We examined two hypotheses: 1) response duration would increase with an increasing amount of applied nitrogen and 2) volume growth response and the estimated amount of fertilizer nitrogen in the foliage would be well correlated over time.

2. Methods

We identified 33 sites where nitrogen and phosphorus were applied in mid-rotation *P. taeda* stands. The criteria for including sites were as follows: (1) Nitrogen was applied with phosphorus one time in a mid-rotation *P. taeda* stand with mid-rotation defined as a stand older than five years. (2) The sites had to have 10 years of measurements after the fertilizer application with data collected every two years to ensure that our population remained constant throughout the study period. (3) Each site was likely nitrogen and phosphorus limited, determined by examining cumulative volume response four years after treatment. If growth responses were positive, the site was likely nitrogen and phosphorus limited and was included in the analysis if all other criteria were met. We calculated response as the treated volume growth minus the control volume growth.

Sites meeting these criteria were from the Forest Productivity Cooperative's Regionwide (RW) 13, 15, 17, and 19 studies that were installed between 1984 and 2010. The RW13 was a factorial combination of four levels of elemental nitrogen (0, 112, 224, and 336 kg ha⁻¹) and three levels of elemental phosphorus (0, 28, and 56 kg ha⁻¹) originally installed at forty-two locations in the SEUS (Fox et al., 2007); 19 of these studies met our criteria for inclusion. The RW15 examined nitrogen, phosphorus, potassium, and micronutrient applications and included a control (no additions) and a treatment where 224 and 56 kg ha⁻¹ of elemental nitrogen and phosphorus, respectively, were applied (Carlson et al., 2014). Two of the 24 RW15 sites met our criteria. The RW17 examined fertilization and competing vegetation control and had a control treatment (no fertilizer and no vegetation control) and a fertilizer-only treatment where 224 and 56 kg ha⁻¹ of elemental nitrogen and phosphorus, respectively, were applied (Albaugh et al., 2012b). Five of the 10 RW17 sites with *P. taeda* met our criteria. The RW19 examined fertilization and thinning and included a control treatment (no thinning and no fertilizer) and a fertilizer-only treatment where 224 and 28 kg ha⁻¹ of elemental nitrogen and phosphorus, respectively, were applied (Albaugh et al., 2017). Seven of the nine RW19 sites met our criteria.

Our population of interest was *P. taeda*, and as such, our sites were distributed across a large geographic area and included a variety of soil types, stand ages, and initial stand conditions. The studies consisted of 2–4 blocks at each site. Prior to fertilizing plots at a given site, we grouped similar plots into blocks to account for differences in stand metrics (stand density, basal area, tree size) so that as the treatments were applied and the stands developed, the blocks accounted for this variation. Consequently, our growth response comparisons used the

treated and control plots within each block at a given site. All studies had approximately 30 trees in each measurement plot. Measurement plots were centered in treatment plots that consisted of two to three rows of trees. Buffers (10 m) typically separated the treatment plots. The combination of a treated area around the measurement trees and the buffer gave confidence that the control plots were not confounded by fertilizer (or other types of treatments in a given study) treatment plots. Fertilizer applications were a combination of urea and diammonium phosphate or urea and triple super phosphate; there were no differences in the response between diammonium phosphate and triple super phosphate as long as the elemental phosphorus rate was the same. Competing vegetation was present and was not controlled in any study; however, all stands used for the experiments would have been considered good operational stands with relatively little competing vegetation present.

Diameter (at 1.37 m, breast height) and height were measured on all trees in each measurement plot in the dormant season immediately before treatment application (0 years since treatment) and every two years after treatment for 10 years for all selected sites. Consequently, there were six measurements for all plots (years 0, 2, 4, 6, 8, and 10), resulting in five increments (0–2, 2–4, 4–6, 6–8, and 8–10). We estimated individual tree stem volume using diameter and height (Tasissa et al., 1997). We calculated volume growth at the individual tree scale as the difference between one measurement period and the next, scaled to an area basis, and then annualized the estimate for each two-year interval (by dividing by two for the two years between measurements). Incremental volume growth response was the area-scaled volume growth for the treated plot minus the corresponding volume growth for the control plot in the same block for each two-year increment. We calculated the four-year cumulative volume response as the sum of the incremental responses for years 0–2 and 2–4 and, as noted, if this response was positive, we concluded that the site was nutrient limited and it was included in our examination.

Phosphorus was applied at either 28 or 56 kg ha⁻¹. We did not differentiate between these phosphorus treatments because there is evidence to suggest that there is little additional mid-rotation growth response when phosphorus application rates are increased from 28 to 56 kg ha⁻¹ (Fox et al., 2007). Retranslocation rates and foliar uptake estimates are available in the literature for nitrogen but not for phosphorus (no similar uptake data were found). Nitrogen and phosphorus are co-limiting in our stands; however, our focus in this analysis is on nitrogen. Consequently, we use the nitrogen application amount (112 N, 224 N, and 336 N) to denote the treatments that were applied here.

In order to determine the response duration, our primary metric was a one-sample *t*-test completed using PROC TTEST (SAS-Institute 2002–2012); we compared the incremental volume growth response averaged across all sites to zero for each measurement period and nitrogen application rate combination. For each time period, the sample number and degrees of freedom were 90 and 89, 146 and 145, and 104 and 103 for the 112 N, 224 N, and 336 N treatments, respectively. The variation in sample number among the treatments occurred because there were multiple blocks at each site and not all treatments were applied at all sites. We used a threshold alpha level of 0.05 to indicate significant differences for all statistical tests. If the *t*-test indicated that there was no difference between zero and the average incremental volume growth response for a given measurement, we concluded that there was no further response at that time and, consequently, duration of response was maintained through the previous measurement. Given that measurements continued for 10 years after treatment, it was possible that the response would continue beyond our measurements. To estimate response duration in this situation, we fit a Ricker curve (Archontoulis and Miguez 2015) for each nitrogen rate using PROC NLIN (SAS-Institute 2002–2012):

$$VR = a_1 * MP * \exp(-a_2 * MP)$$

where VR is the incremental volume response; MP is the

measurement period, where the measurements were conducted in years (0, 2, 4, 6, 8, 10); and a_1 and a_2 are parameters to be estimated. Both a_1 and a_2 control the magnitude (height) of the response and the width of the skewness to the right. There is no direct biological meaning for the parameters relative to our analysis; however, $(a_1/a_2) * e^{-1}$ is the height of the peak (in our case, the maximum incremental volume growth response), and $1/a_2$ is the time since treatment when the peak occurred (Bolker 2008). We selected the Ricker curve because the model form had the same appearance as our data: a hump-shaped pattern similar to a normal distribution curve but skewed to the right. Other models were examined including the beta model but none of the other models converged in PROC NLIN. We used the Ricker curve to project the estimated response, and when the projected response was less than the standard error for year 10 measurements (our last measurement), we concluded that the response was not different from zero and had ended.

We estimated the growth response per unit of nitrogen applied in two ways. First, we used only measured data (i.e., through 10 years after treatment) as long as the measured data were significantly different from zero. Second, we included measured and modeled data when our response estimate continued to be greater than zero through the end of the measured data. In the second method, we determined the response duration had ended when the modeled growth response was less than the standard error for year 10 measurements. The growth response per unit of nitrogen applied was calculated as follows:

$$GRN = \Sigma VR / N$$

where GRN is the growth response per unit of nitrogen applied in m³ kg⁻¹, VR is the incremental volume response in m³ ha⁻¹ yr⁻¹ summed over all years when the incremental response was greater than zero, and N is elemental nitrogen applied in kg ha⁻¹.

To examine a potential mechanism explaining why the response to nutrient additions dissipates over time, we estimated the amount of nitrogen remaining in the foliage after a fertilizer application as follows:

$$FN_{t(n+1)} = 0.67 * FN_{t(n)}$$

where $FN_{t(n+1)}$ is the foliar nitrogen in kg ha⁻¹ remaining in the foliage at time $n + 1$, $FN_{t(n)}$ is the foliar nitrogen in kg ha⁻¹ remaining in the foliage at time n , n is the number of years after nitrogen was applied, and 0.67 is a constant estimating the amount of total foliar nitrogen that is retranslocated prior to foliage senescence each year and is the average of the reported range (0.64–0.71) (Albaugh et al., 2008). All sites were fertilized in the winter prior to forecasted rain, and some sites received urea coated with a urease inhibitor to minimize potential losses attributable to urea volatilization. Raymond et al. (2016) found up to 15% of applied fertilizer nitrogen was retained in the foliage using ¹⁵N-labeled nitrogen, and we used this metric to estimate the initial amount of fertilizer nitrogen in the foliage for our treatments. Consequently, the initial FN_t was 16.8, 33.6, and 50.4 kg ha⁻¹ of fertilizer nitrogen in the foliage for the 112 N, 224 N, and 336 N treatments, respectively. We did not find an estimate of how much applied phosphorus fertilizer is retained in the foliage similar to the nitrogen data in Raymond et al. (2016). However, the reported range for phosphorus retranslocation is 0.68–0.73, which is similar to that for nitrogen retranslocation (Albaugh et al., 2008). Regardless of the initial amount of fertilizer phosphorus that is allocated to the foliage, the loss rate would be similar to that of nitrogen. Consequently, we expect that while we do not show a comparison with phosphorus, the pattern of loss over time of fertilizer phosphorus in the foliage would be similar to that for nitrogen. We examined the relationship of our modeled incremental volume growth response and the estimated amount of fertilizer nitrogen remaining in the foliage over time with a graphical comparison. Additionally, we completed a correlation analysis on the estimates of incremental volume growth response and the amount of fertilizer nitrogen remaining in the foliage using PROC CORR (SAS-Institute 2002–2012). For the correlation analysis, we used data beginning four years after treatment because

this coincided with the beginning of the decline in the incremental volume growth response. Even though the reported range (64–71% (Albaugh et al., 2008)) for nitrogen (and phosphorus) retranslocation is quite narrow across a wide range in stand conditions, we completed a sensitivity analysis. In this analysis we selected the 224 N treatment incremental volume growth response data and calculated FN_t using retranslocation rates of 0.33, 0.67 (the same as in our other analyses), and 0.90 as an example.

3. Results

The 33 sites used for our analysis ranged in age from 6 to 22 years at initiation, in basal area from 5 to 39 $m^2 ha^{-1}$, in stand density from 504 to 1888 trees ha^{-1} , in drainage from well to poorly drained, and in soil texture from fine to coarse texture (Table 1). The sites were located throughout the SEUS, and there was one study in Argentina. In the SEUS, the sites largely covered the native range of *P. taeda*, spanning an east–west distance of 1770 km and a north–south distance of 965 km.

Averaged across all sites, the maximum annual incremental volume growth was 4.15 $m^3 ha^{-1} yr^{-1}$ (in years 1–2), 5.51 $m^3 ha^{-1} yr^{-1}$ (in years 1–2), and 6.30 $m^3 ha^{-1} yr^{-1}$ (in years 3–4) for the 112 N, 224 N, and 336 N treatments, respectively (Table 2). For the 224 N and 336 N treatments, the incremental response for all measurement years was significantly different from zero. However, for the 112 N treatment, the incremental response in years 9–10 (1.08 $m^3 ha^{-1} yr^{-1}$) was not different from zero. Therefore, based on measured data, we concluded that a significant response to 112 N ended in years 7–8.

The Ricker model parameter estimates ranged from 4.4 to 5.8 for a_1 and from 0.31 to 0.41 for a_2 , and none of the 95% confidence intervals

Table 2

Average incremental volume response and *t*-test *P*-value testing if the response was different from zero for three rates of nitrogen application combined with 28 or 56 $kg ha^{-1}$ of elemental phosphorus for measurements through 10 years following treatment. The projected year is the first year when the value that was estimated by the Ricker model was less than the standard error in the last year of measurement (years 9–10).

Elemental nitrogen application rate (kg ha ⁻¹)	Time since treatment initiation (years)	Average incremental volume response		<i>t</i> -test <i>P</i> -value
		Mean	Standard error	
		(m ³ ha ⁻¹ yr ⁻¹)		
112	1–2	4.15	0.26	<0.001
112	3–4	3.16	0.36	<0.001
112	5–6	2.26	0.38	<0.001
112	7–8	1.49	0.49	0.003
112	9–10	1.08	0.60	0.073
Projected	11	0.56		
224	1–2	5.51	0.29	<0.001
224	3–4	5.39	0.32	<0.001
224	5–6	3.38	0.41	<0.001
224	7–8	1.81	0.54	0.001
224	9–10	2.33	0.39	<0.001
Projected	15	0.33		
336	1–2	5.22	0.26	<0.001
336	3–4	6.30	0.35	<0.001
336	5–6	5.37	0.47	<0.001
336	7–8	2.65	0.66	<0.001
336	9–10	2.64	0.51	<0.001
Projected	17	0.47		

Table 1

Sites used to determine the duration of response to nitrogen and phosphorus in mid-rotation *Pinus taeda* stands. State abbreviations for the United States are Alabama (AL), Arkansas (AR), Florida (FL), Georgia (GA), Louisiana (LA), Mississippi (MS), North Carolina (NC), South Carolina (SC), and Tennessee (TN), and CR represents the Argentinian province Corrientes. Phosphorus was added at all sites at 28 or 56 $kg ha^{-1}$.

Site	Latitude	Longitude	County	State	Soil series	Installation year	Stand age	Basal area	Density	Elemental nitrogen application rates
	(decimal degrees)				name		(years)	(m ² ha ⁻¹)	(trees ha ⁻¹)	(kg ha ⁻¹)
1	37.26	−78.09	Amelia	VA	Durham	1987	19	18.6	627	112, 224, 336
2	35.17	−77.19	Craven	NC	Leaf	1984	14	15.3	599	112, 224, 336
3	34.09	−78.39	Brunswick	NC	Goldsboro	1985	14	23.4	1317	112, 224, 336
4	34.07	−78.49	Brunswick	NC	Pantego	1986	15	26.9	947	112, 224, 336
5	32.99	−80.75	Colleton	SC	Lynchburg	1984	12	23.5	1207	112, 224, 336
6	31.30	−87.23	Conecuh	AL	Fuquay	1985	14	22.6	1888	112, 224, 336
7	31.63	−87.13	Conecuh	AL	Orangeburg	1986	13	24.6	1787	112, 224, 336
8	31.20	−86.25	Covington	AL	Dothan	1986	11	17.3	1519	112, 224, 336
9	31.76	−82.07	Wayne	GA	Olustee	1984	14	22.9	1224	112, 224, 336
10	31.76	−82.07	Wayne	GA	Pelham	1984	12	17.1	1189	112, 224, 336
11	31.65	−81.52	MacIntosh	GA	Wahee	1985	12	20.9	1275	112, 224, 336
12	32.40	−81.45	Effingham	GA	Stilson	1986	10	14.5	1552	112, 224, 336
13	36.21	−76.95	Bertie	NC	Leaf	1987	10	19.7	1501	112, 224, 336
14	35.72	−84.77	Rhea	TN	Lonewood	1984	12	21.6	1383	112, 224, 336
15	35.02	−84.84	Bradley	TN	Fullerton	1986	12	24.2	1800	112, 224, 336
16	34.29	−94.35	Polk	AR	Sherwood	1985	11	15.7	854	112, 224, 336
17	30.85	−89.81	Washington	LA	Malbis	1984	14	22.3	1644	112, 224, 336
18	31.32	−89.52	Lamar	MS	Malbis	1985	14	21.7	1422	112, 224, 336
19	34.13	−82.23	Greenwood	SC	Cecil	1987	14	21.0	1434	112, 224, 336
20	35.00	−79.50	Scotland	NC	Wakulla	1994	9	5.4	1096	224
21	31.67	−82.16	Appling	GA	Olustee	1990	15	13.3	1236	224
22	32.96	−86.03	Coosa	AL	Pacolet	1999	12	21.9	1502	224
23	32.88	−85.64	Tallapoosa	AL	Cecil	1996	10	14.2	1489	224
24	36.28	−77.57	Halifax	NC	Lenoir	1999	13	16.5	606	224
25	33.09	−87.26	Bibb	AL	Smithdale	1998	18	16.9	504	224
26	34.69	−81.04	Chester	SC	Appling	1997	22	18.5	509	224
27	31.01	−93.42	Vernon	LA	Otanya	2012	12	22.6	1232	224
28	33.44	−91.73	Drew	AR	Henry	2010	12	35.9	1211	224
29	33.23	−87.23	Tuscaloosa	AL	Sipsey	2007	15	39.0	1211	224
30	31.66	−86.27	Crenshaw	AL	Arundel	2008	16	30.8	1227	224
31	30.67	−81.79	Nassau	FL	Chaires	2014	14	21.9	1236	224
32	−28.04	−56.22	Corrientes	CR	Cuarajbí Yará	2009	6	33.8	1238	224
33	37.43	−78.66	Buckingham	VA	Littlejoe	2009	15	30.3	982	224

Table 3

Ricker model attributes (parameter estimates and their standard errors and upper and lower 95% confidence intervals (CI); maximum incremental volume growth response (maximum); time after treatment when the maximum was achieved (Time of Maximum), model residual mean and standard error) for three elemental nitrogen application rates applied with 28 or 56 kg ha⁻¹ elemental phosphorus in midrotation *Pinus taeda* stands. The Ricker model is a non-linear model of incremental volume growth response versus time since treatment; see text for the model form.

Model attribute	Statistic	Elemental nitrogen rate (kg ha ⁻¹)		
		112	224	336
Parameter a ₁	Estimate	4.4170	5.7607	5.1193
	Standard error	0.6420	0.5241	0.4746
	Lower 95% CI	3.1560	4.7321	4.1873
	Upper 95% CI	5.6781	6.7893	6.0513
Parameter a ₂	Estimate	0.4058	0.3720	0.3070
	Standard error	0.0345	0.0201	0.0179
	Lower 95% CI	0.3381	0.3325	0.2718
	Upper 95% CI	0.4735	0.4115	0.3421
Maximum	m ³ ha ⁻¹ yr ⁻¹	4.004	5.697	6.134
Time of Maximum	years after treatment	2.464	2.688	3.257
Model Residual	Mean	0.045	0.049	-0.022
Model Residual	Standard error	0.162	0.150	0.175

for the parameter estimates included zero (Table 3). For all treatments, the data displayed the same pattern, with a rapid increase in the early years after treatment followed by a slow decline as time since treatment increased (Fig. 1). The model projections indicated that the growth response was not different from zero (i.e., the calculated growth response was less than the measurement year 9–10 standard error for the growth response) in years 11, 15, and 17 after application of the 112 N, 224 N, and 336 N treatments, respectively (Table 2).

The average growth response per unit of applied nitrogen for measured data through year 10 measurements was 0.20, 0.16, and 0.13 m³ kg⁻¹ for the 112 N, 224 N, and 336 N treatments, respectively. The average growth response per unit of applied nitrogen for modeled data where the cessation of the growth response varied by treatment was 0.22, 0.18, and 0.15 m³ kg⁻¹ for the 112 N, 224 N, and 336 N treatments, respectively.

An examination of the modeled growth response and estimated foliar nitrogen revealed that all three treatments had similar patterns, i.e., the growth response increased as foliar nitrogen decreased in the initial years after nitrogen application (Fig. 2). About three to four years following nitrogen application, the pattern changed such that the

growth response decreased as foliar nitrogen decreased. After this time, incremental volume growth response was highly correlated with fertilizer nitrogen remaining in foliage with correlation coefficients of 0.977, 0.959, and 0.916 for the 112 N, 224 N, and 336 N treatments, respectively.

In the nitrogen retranslocation rate sensitivity analysis, with our selected retranslocation rate of 0.67, fertilizer nitrogen in the foliage and incremental volume response dissipated at about the same time (Fig. 2B and 3). With a retranslocation rate of 0.33, the fertilizer nitrogen in the foliage approached zero about five years after treatment when the incremental volume response was still higher than 4 m³ ha⁻¹ yr⁻¹ (Fig. 3). With a retranslocation rate of 0.90, 7 kg ha⁻¹ of fertilizer nitrogen remained in the foliage 15 years after treatment when the incremental volume response was within the standard error of the last measurement.

4. Discussion

We quantified the response duration as eight (measured), 14 (modeled), and 16 (modeled) years after applications of 112, 224, and 336 kg ha⁻¹ of elemental nitrogen, respectively, which was applied with 28 or 56 kg ha⁻¹ of elemental phosphorus in mid-rotation *P. taeda* stands. Our model fit the data well, but as noted in the methods, the metric for estimating the modeled and measured response duration was different, and our modeled response duration estimate for the 112 N treatment was 10 years, two years longer than the measured result (Table 2). Based on this difference, the modeled result for the 224 N and 336 N treatments may be an overestimate of the termination of the response, by up to two years, but the 224 N and 336 N treatments still had a longer response duration than the 112 N treatment. Based on these results, we accepted our first hypothesis that response duration would increase with an increasing amount of applied nitrogen. Previous response duration estimates for *P. taeda* were generally shorter, i.e., five to 10 years (Ballard 1981, Allen 1987, Hynynen et al., 1998, Fox et al., 2007). The earliest report (Ballard 1981) with the lowest estimate (five years) may have suffered from the use of small plots with inadequate buffers where the control trees may have been able to access the applied fertilizers (Carter et al., 2021). This combination would have adversely affected (reduced) the estimated response duration. Hynynen et al. (1998) estimated the response at eight years using a two-parameter Weibull model with eight-year measurement data for 13 of the RW13 sites but included sites that were responsive and non-responsive, so their selection of sites from the RW13 was different from ours. It is possible that we underestimated the response duration given that we did not use dendrochronological methods, which can detect extremely small changes in stem diameter. However, from a practical standpoint, if estimates based on forest mensuration methods suggest no additional response, it is unlikely that the differences detected using dendrochronological methods would be meaningful from a management perspective.

We estimated that the 112 N treatment had the greatest growth per unit nitrogen that was applied but had the shortest response duration, whereas the 336 N treatment had the longest response duration with the lowest growth per unit of applied nitrogen. This information would be useful to forest managers to capture all of the benefit from fertilization by determining how much nitrogen should be added to meet their expectations regarding the time between nitrogen application and the final harvest. If the true response duration for the 224 N and 336 N treatments is somewhat shorter than the modeled estimate as noted above, the growth per unit of nitrogen that was applied would be even less for these treatments given that there would be fewer years to include in the sum of responses whereas the amount that was applied would not change.

There is evidence to suggest that the observed growth response to fertilization is the same provided the cumulative dose applied is the same (Albaugh et al., 2015). For example, two applications of 168 kg ha⁻¹ of elemental nitrogen with phosphorus would yield approximately the same response as one application of 336 kg ha⁻¹ of elemental

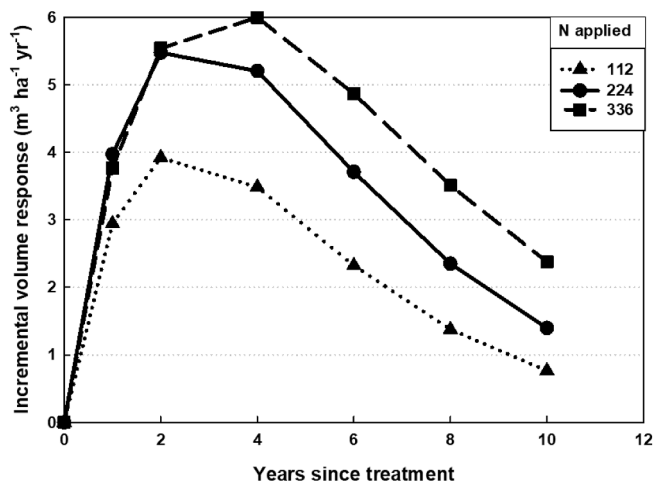
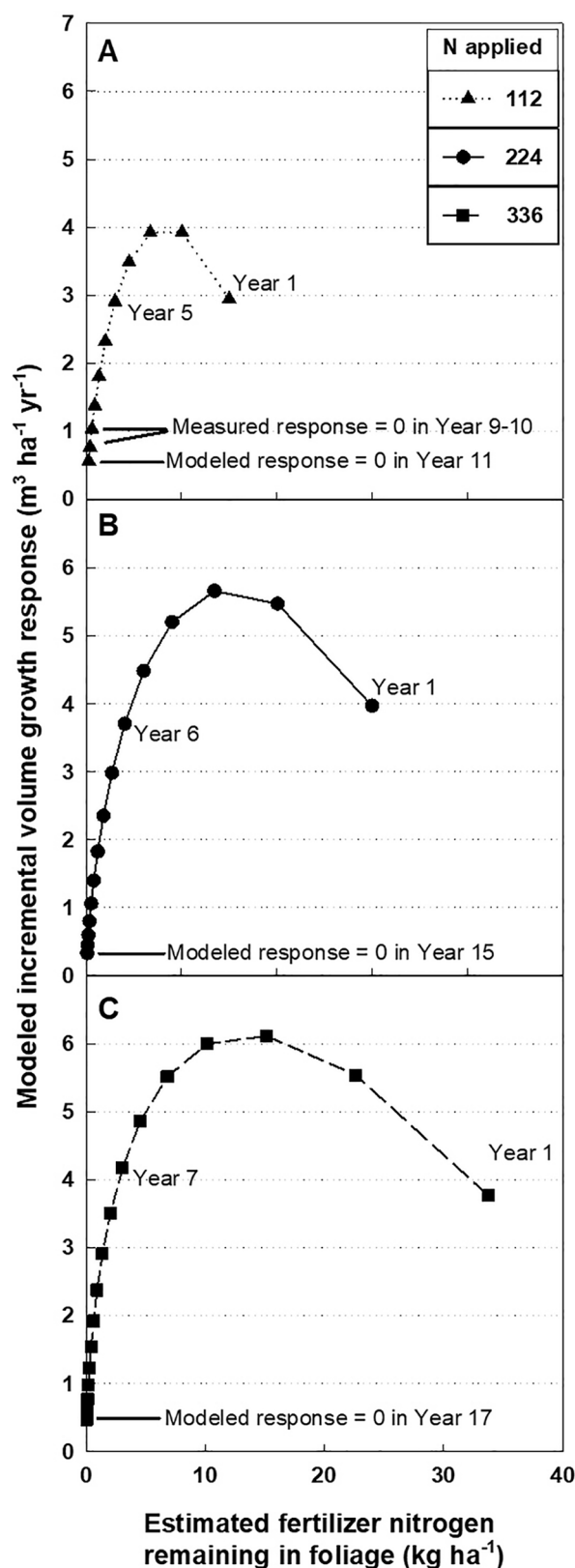


Fig. 1. Incremental volume response over time modeled using a Ricker curve for applications of 112, 224, and 336 kg ha⁻¹ (112, 224, and 336, respectively) of elemental nitrogen, which was applied with 28 or 56 kg ha⁻¹ of elemental phosphorus in mid-rotation *Pinus taeda* stands.



(caption on next column)

Fig. 2. Modeled incremental volume growth response versus estimated amount of nitrogen from fertilization remaining in the foliage for applications of 112 (A), 224 (B), and 336 (C) kg ha^{-1} of elemental nitrogen, which was applied with 28 or 56 kg ha^{-1} of elemental phosphorus in mid-rotation *Pinus taeda* stands. We assumed that 15% of applied nitrogen was allocated to the foliage and that 67% of nitrogen was retranslocated prior to foliage senescence each year. The lines represent data over time, where each point represents one year of measurement. The first year after fertilizer application (Year 1), the subsequent year when the modeled incremental volume growth response was approximately the same as that in Year 1, and the years when the measured (measured response = 0) and modeled (modeled response = 0) growth responses were not different from zero are labeled in each panel.

nitrogen with phosphorus. The use of two applications rather than one would also reduce the length of time over which the investment for the second application would be carried. This would likely be beneficial from an economic perspective given that fertilizer application costs are a function of the amount of material moved, and if the cumulative dose was the sum of the two separate doses, then the material and application cost should be about the same (Albaugh et al., 2019). At the same time, costs related to the time value of money can have large effects on whether a given silvicultural input results in a positive benefit to the landowner (Trlica et al., 2021). However, the scenario of splitting the application would move a forest manager away from a one-time application and would require more active management than a one-time application.

Other studies have reported similar results, where lower nitrogen applications resulted in greater application efficiency, e.g., 157, 314, and 471 kg N ha^{-1} resulted in values of 0.44, 0.36, and 0.28 $\text{m}^3 \text{kg}^{-1}$, respectively, after 15 years for *Pseudotsuga menziesii* (Miller and Tarrant 1983). Miller and Tarrant (1983) indicated that their estimates of growth per unit of applied nitrogen may be underestimated because they continued to observe a growth response 15 years after treatment. The site that was used by Miller and Tarrant (1983) could have had a Type A response (i.e., a continued increase over time relative to the control) rather than a Type B response (i.e., a brief increase relative to the control) that is typically associated with mid-rotation fertilization. Other studies with *Pseudotsuga menziesii* reported response durations between eight and 14 years depending on whether the stand had been thinned, with longer response periods in unthinned stands (Stegemoeller and Chappell 1991).

The response duration appeared to be related to the amount of nitrogen remaining in the foliage over time. Initially (for the first three to four years after nitrogen application), the growth response increased while the amount of nitrogen in the foliage decreased, but then the subsequent reduction in the response and in the amount of nitrogen remaining in the foliage appeared to be well correlated and independent of the nitrogen application (Fig. 2). Based on these results, we accepted our second hypothesis that volume growth response and the estimated amount of fertilizer nitrogen would be well correlated over time when examining data later than four years after treatment (when incremental volume growth response began to decline). All treatments exhibited a similar modeled incremental volume growth response for very different amounts of estimated fertilizer nitrogen remaining in the foliage, i.e., in years 1 versus 5, 1 versus 6, and 1 versus 7 for the 112 N, 224 N, and 336 N treatments, respectively (Fig. 2). However, different patterns of growth occurred at these times. In year 1 for all treatments, the trees increased the amount of foliage and the foliar nitrogen content in response to the added fertilizer. In the later years, (5, 6, and 7 for 112 N, 224 N, and 336 N, respectively), the amount of foliage and the foliar nitrogen content likely decreased because less fertilizer nitrogen was available to the trees, given that some of it was lost in the intervening years as litterfall and became unavailable to the trees. While nitrogen mineralization occurs continuously at the native site level, increases in nitrogen availability after fertilization are relatively short-lived (months to perhaps one year) (Mudano 1986, Carlyle 1998). However, the

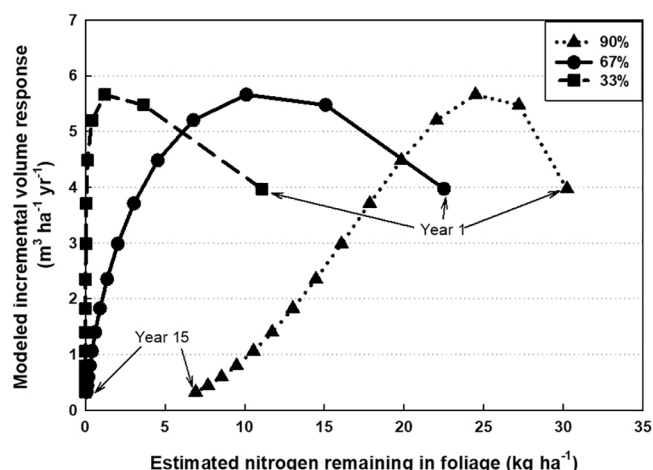


Fig. 3. Retranslocation rate sensitivity analysis with modeled incremental volume growth response versus estimated amount of nitrogen from fertilization remaining in the foliage for an application of 224 kg ha^{-1} of elemental nitrogen that was applied with 28 or 56 kg ha^{-1} of elemental phosphorus in mid-rotation *Pinus taeda* stands. We assumed that 15% of applied nitrogen was allocated to the foliage and that 90, 67, or 33% of nitrogen was retranslocated prior to foliage senescence each year. The lines represent data over time, where each point represents one year of measurement. The first year after fertilizer application (Year 1) and the year (Year 15) when the modeled growth response was not different from zero are labeled.

response clearly carries on for a long time (years) after changes in nitrogen availability as a result of fertilization have diminished. The response of *P. taeda* to nitrogen application is driven by an increase in the amount of foliage (Vose and Allen 1988) and in nitrogen use and uptake, where the newly acquired nitrogen is allocated primarily to foliage (Albaugh et al., 2008). The delay where foliar nitrogen decreased while the growth response increased in the first three to four years after application likely represents the time required for the trees to increase their foliar nitrogen content and leaf area. This lag reflects the model proposed by Fagerström and Lohm (1977), which predicts a one-year delay from fertilizer application to an observed growth response and has been observed across many species including *P. taeda* (e.g., (Albaugh et al., 1998)). As mentioned, the trees retranslocate about 67% of foliar nitrogen prior to foliage senescence, and research suggests that in the absence of disturbances, nitrogen in the litter layer (from senesced foliage over time) remains in the litter (Miller 1981, Piatek and Allen 2001). Litter nitrogen is not available to the trees until there is some type of disturbance in the stand such as a thinning operation or a clear cut. The relatively slow transfer of nitrogen after application through the foliage and then to the litter layer may be the mechanism that controls the response duration in this species. *Pinus taeda* foliage survives for two growing seasons (Kinerson et al., 1974, Albaugh et al., 2010). Species that differ in foliage longevity, e.g., one to four years for *P. radiata* (Rubilar et al., 2013), four years for *P. sylvestris* L. (Fagerström and Lohm 1977), and 3.9 years for *P. menziesii* (Maguire et al., 2011), or exhibit different rates of nutrient retranslocation (Landsberg and Sands 2011) may have different patterns of response duration.

We did not measure the amount of nitrogen in the foliage as a result of fertilization; instead, we based our calculations on data from the literature. The actual amount of fertilizer nitrogen in the foliage could be higher or lower than our estimate. Any differences from the true amount would change the initial amount of fertilizer nitrogen in the foliage but would not affect the pattern of decline that was observed in Fig. 2. For *P. taeda*, measured retranslocation falls within a fairly narrow range for diverse stand conditions (Albaugh et al., 2008), including non-fertilized (64%) and fertilized (67%) stands. This indicates there was likely no difference in retranslocation due to fertilization and suggests that the pattern we observed here well represented what would be observed for

P. taeda across the SEUS. Reported retranslocation rates for other species were lower than that for *P. taeda*, i.e., 11%, 40%, and 61% for *Picea abies*, *P. radiata*, and *Pseudotsuga menziesii*, respectively (Landsberg and Sands 2011). The method used in Albaugh (2008) sampled dead brown senesced foliage that was still attached to the tree, which would provide a robust estimate of retranslocation without needing to make adjustments for mass loss if sampling foliage from litter traps. Foliage may separate from the tree at any time of the year as green foliage during events that include instances when branches rub on other branches or on other trees or when winds from hurricanes and other storms knock foliage from the tree. However, foliage loss in this manner would normally represent a small percentage of a given cohort. Foliage longevity studies for *P. taeda* have shown that the bulk of foliage senescence occurs during a short time in the fall of the second growing season (Stow et al., 1992, Albaugh et al., 2010). This evidence suggests that the 0.67 retranslocation rate used here for the entire cohort is reasonable. Additionally, our sensitivity analysis indicates that higher or lower retranslocation rates would not correspond well with the dissipation of the incremental volume growth response over time. A lower retranslocation rate (0.33) reduced fertilizer nitrogen in the foliage much more rapidly while a higher rate (0.90) resulted in a situation where more fertilizer nitrogen was retained in the foliage after the incremental volume growth response had dissipated. Similarly, for species with a longer foliage lifespan and a given retranslocation rate, the response duration would likely increase because fertilizer nitrogen would be retained in the older foliage. It appears that the net effect of retranslocation and foliage longevity may play a large role in the response duration.

Our focus was on the amount of fertilizer nitrogen in the foliage over time and its relationship with the growth response; however, all sites received 28 or 56 kg ha^{-1} elemental phosphorus with the nitrogen application. We did not find an estimate for the initial amount of fertilizer phosphorus that would be present in the foliage after fertilization similar to the amount reported for nitrogen in Raymond et al. (2016). We did find data on the phosphorus retranslocation rate (68–73%) that was similar to the nitrogen retranslocation rate we used (67%). Even without knowing the initial amount of fertilizer phosphorus in the foliage, if the retranslocation rate was similar, then the pattern of the initial fertilizer phosphorus in the foliage over time would be similar to that of nitrogen and would dissipate in a similar time frame. Phosphorus applications similar to those in our studies can produce long-term responses in *P. taeda*, even with effects that carry over into the next rotation (Everett and Palm-Leis 2009). It is likely then that the amount of phosphorus applied at our sites was sufficient to meet the stand demand for phosphorus during the response period. Consequently, nitrogen was likely the first nutrient to then become limiting in the stand after fertilization following Liebig's Law of the minimum (Landsberg and Sands 2011), suggesting that following fertilizer nitrogen in the foliage would be reasonable to track continued growth responses.

The observed response to mid-rotation fertilization may not follow a Type B response pattern. In a study examining nitrogen dose and application frequency in poorly drained and well-drained sites with a clayey subsoil in the SEUS, the *P. taeda* growth response to nitrogen applications reached an asymptote when the cumulative applied nitrogen amount was $300\text{--}400 \text{ kg ha}^{-1}$ (Albaugh et al., 2015). However, data from the same study showed a linear positive growth response to nitrogen application when the cumulative nitrogen amount reached 800 kg ha^{-1} on poorly to excessively drained soils with spodic horizons or without a clay subsoil. On these site types, the amount of added nitrogen was likely large relative to the site supply and resulted in something closer to a Type A response (Miller 1981, Long et al., 2004). A Type A response may also be observed where nitrogen mineralization rates are reflective of soil organic matter enrichment, which provides a long-term nitrogen supply (Ramírez Alzate et al., 2016b). Similarly, Zhao et al. (2016) found that there is a limit to the response across the landscape in that some sites are inherently more productive than others and respond less to fertilizer additions, which could result in a reduced response

duration or no response at all.

Just as the initial presence or absence of a response to nitrogen addition will be influenced by factors such as other limiting elements and drought, the response duration may also be influenced by these same factors. For example, low levels of potassium, calcium, and micronutrients may limit growth and would reduce the response duration or eliminate any response, if severe enough, to nitrogen applications (Will 1978, Stone 1990, Jokela et al., 1991, Kyle et al., 2005, Vogel and Jokela 2011, Carlson et al., 2014). Low water availability would have a similar result (Sands and Mulligan 1990, Stegemoeller and Chappell 1991). These observed differences across site types indicate that our analysis could be further refined by examining subsoil type, drainage, inherent productivity, water availability, and other factors that were beyond the scope of this analysis to better quantify the response duration.

CRediT authorship contribution statement

Timothy J. Albaugh: Conceptualization, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Janine M. Albaugh:** Formal analysis, Writing – review & editing. **David R. Carter:** Conceptualization, Writing – review & editing, Funding acquisition. **Rachel L. Cook:** Conceptualization, Writing – review & editing, Funding acquisition. **Chris W. Cohrs:** Conceptualization, Writing – review & editing. **Rafael A. Rubilar:** Writing – review & editing, Funding acquisition. **Otávio C. Campoe:** Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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