

Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings

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Abstract. Single and multiple linear regression techniques were used to explain the capacity of initial seedling root volume (Rv) and first-order lateral roots (FOLR) relative to shoot height, diameter, and fresh mass to serve as important indicators of stock quality and predictors of first- and second-year height and diameter on an afforestation site in southern Indiana, USA. This was accomplished for northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), and black cherry (*Prunus serotina* Ehrh) seedlings graded into four Rv categories at establishment. Field survival was high (85–97%) for all species. Initial diameter, height, fresh mass, and Rv provided similar predictive ability of second-year field response for absolute height ($R^2 = 0.59\text{--}0.77$) and diameter ($R^2 = 0.50\text{--}0.73$) for both oak species. Initial seedling Rv was a better predictor of field response than FOLR for both oak species, though not for cherry. Multiple-variable models accounted for a greater proportion of the total variation in seedling field height and diameter than did single-variable equations. The high R^2 (up to 0.95) of regression models suggests field performance of these species can be reliably predicted and confirms the importance of initial seedling morphology in dictating early plantation performance.

Introduction

Many plantations of hardwood species fail to survive or grow satisfactorily after outplanting (Dixon et al. 1984; Jacobs et al. 2004b). These failures are often associated with transplant shock (Struve and Joly 1992), deer browsing (Stange and Shea 1998; Tripler et al. 2002), and competing vegetation (Crow 1988). Additionally, poor soils or nutrient deficiencies (Oak et al. 1991; Demchik and Sharpe 2000) and poor seedling quality (Clark et al. 2000; Ward et al. 2000) may account for the failure of oak plantings. This suggests the need for high-quality seedlings that can survive and grow rapidly after outplanting (Duryea 1985; Mattsson 1997). Hence, identification and quantification of superior seedling morphological and physiological attributes that can be quantitatively linked with improved field response and early plantation success is warranted (Rose et al. 1990).

Several morphological attributes, such as seedling shoot height and diameter are often used as indicators of seedling quality and predictors of field response (Rose et al. 1990; Dey and Parker 1997) because they are relatively simple to measure (Racey 1985; Thompson 1985) and correlate well with field success (Kaczmarek and Pope 1993a; Dey and Parker 1997). Northern red oak (*Quercus rubra* L.) seedlings with root collar diameter > 8 mm and shoot heights > 50 cm were more competitive than smaller stock when planted on a variety of sites (Johnson 1992; Pope 1993). However, initial shoot height has provided inconsistent ability to predict seedling field performance for some species (Chavasse 1977; Thompson and Schultz 1995).

Several authors argue that some measure of root morphology may be important in assessing seedling quality and predicting field success (Rose et al. 1997; Jacobs and Seifert 2004). Various measurements of seedling root system morphology include root mass, root volume (Rv), number of first-order lateral roots ≥ 1 mm in diameter at junction with the tap root (FOLR), root length, and root area index (Ritchie and Dunlap 1980). Many of these measurements are destructive, difficult, laborious, and (or) time consuming, which limits their practical application in operational forestry. Root volume and FOLR, however, are relatively rapid and non-destructive. FOLR provide the structural framework of the root system, contain many sites of new root initiation, and are active in water and nutrient uptake (Thompson and Schultz 1995; Glass 2002). Root volume has been directly correlated with reforestation success for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) in the western USA (Rose et al. 1991a, b, 1997). Carlson (1986) found that larger root volume is associated with higher root growth potential and increased capacity for water uptake prior to new root growth in loblolly pine (*Pinus taeda* L.). This may lead to greater exploitation of soil volume for growth resources (Struve 1990; McMillin and Wagner 1995), which may facilitate field survival and growth.

Despite the demonstrated importance of Rv in coniferous species, the majority of root morphology studies with deciduous tree species of the eastern USA have focused on FOLR. These studies have shown that hardwood seedlings with >5 FOLR perform better in the field than those with fewer FOLR (Thompson and Schultz 1995; Schultz and Thompson 1997; Ponder 2000). Also, strong correlations between FOLR and seedling field response suggest that FOLR is one of the best predictors of field performance and competitive ability of outplanted seedlings (Kormanik et al. 1988; Dey and Parker 1997). Though clearly linked to improved plantation establishment, estimate of FOLR likely does not provide the most accurate characterization of root system size. For instance, the FOLR approach generally does not distinguish between small vs. large FOLR. Furthermore, lateral root length and the quantity of higher-order lateral roots (i.e., root fibrosity) are not accounted for. Also, Ponder (2000) showed that although FOLR was positively

correlated with 4-year height growth in red oak, it was not useful for predicting field success of black walnut (*Juglans nigra* L.) and white oak (*Quercus alba* L.). Root volume may provide a more accurate quantitative assessment of seedling root system size and quality than the commonly used FOLR grading criterion, and may better reflect ability of seedling root systems to exploit soil for growth resources.

Relatively few studies have directly compared the effectiveness of FOLR for predicting seedling field performance to other easily measured morphological variables, such as diameter and shoot height. Moreover, standard morphological indicators of stock quality seldom account for a large proportion of the total variation in growth response in planted red oak (Thompson and Schultz 1995; Dey and Parker 1997). For example, although Dey and Parker (1997) found that initial diameter was the best predictor of field response in red oak seedlings, it accounted for <25% of the total variation in second-year field growth. No single morphological variable has consistently and reliably predicted field performance of red oak seedlings (Dey and Parker 1997), which suggests that a combination of variables may provide better predictive ability than a single indicator to explain variation in field response (Thompson and Schultz 1995; Dey and Parker 1997).

The objectives of this study were to compare FOLR and Rv to initial shoot height, stem diameter, and plant fresh mass as indicators of seedling quality and predictors of year-1 and year-2 field performance for red oak, white oak, and black cherry (*Prunus serotina* Ehrh.) planted in the Central Hardwood Region, USA. Specifically, we tested the following hypotheses: (1) initial seedling Rv is a better predictor of year-1 and year-2 field height and diameter than FOLR, and (2) multiple-trait models have higher predictive capacity and account for a greater proportion of the variability in year-1 and year-2 field height and diameter than single-variable equations.

Materials and methods

Plant material

In February 2002, nursery-grown (1 + 0, undercut) seedlings of northern red oak, white oak, and black cherry were obtained from the Indiana Department of Natural Resources State Tree Nursery near Vallonia, IN, USA (38°85' N, 86°10' W). These species are commonly planted within the 608,647 km² Central Hardwood Region, which harbors the most extensive concentration of deciduous hardwoods in the world. This region is located 'south of the beech-maple forest, east of the Great Plains, and north and west of the southern pine forest of the Coastal Plain and Piedmont' (Hicks 1998). Seedlings were grown and graded in the nursery according to operational bareroot cultural practices.

Seedling sorting and plantation establishment

Approximately 1000 seedlings from each species were washed free of soil, tagged, and measured in a laboratory at Purdue University for shoot height (root collar to base of terminal bud), stem diameter (1 cm above root collar), fresh mass, number of first-order lateral roots (FOLR), and root volume (Rv) by water displacement (Burdett 1979). Seedlings were then grouped into four Rv categories, representative of 25 percentiles within the Rv distribution of each species (Table 1), and stored in bags in a cooler at 2 °C for about 5 months prior to planting. Seedlings from the resulting 12 treatments (three species × four Rv categories) were then outplanted into a replicated experimental design on a field planting site in southern Indiana at Purdue

Table 1. Range, mean, and standard error (SE) of initial northern red oak, white oak, and black cherry seedling characteristics by root volume category which were used as predictors of first and second-year field response (for each mean, $n = 20$).

Characteristic by root volume category	Northern red oak		White oak		Black cherry				
	Range		Mean ^a (SE)		Range		Mean (SE)		
	Min	Max	Min	Max	Min	Max	Min	Max	
Root volume (cm ³)									
RvC1	15	16	15 (0.2)d	14	18	16 (0.4)d	11	13	12 (0.2)d
RvC2	23	25	24 (0.1)c	25	27	26 (0.2)c	23	26	25 (0.3)c
RvC3	33	35	34 (0.2)b	37	39	38 (0.2)b	40	45	42 (0.5)b
RvC4	54	66	59 (1.3)a	56	72	61 (1.5)a	78	117	94 (4.3)a
Fresh mass (g)									
RvC1	20	23	21 (0.3)d	18	24	22 (0.6)d	19	24	22 (0.5)d
RvC2	32	50	33 (0.4)c	35	37	36 (0.2)c	41	49	45 (0.1)c
RvC3	45	50	48 (0.5)b	51	55	53 (0.5)b	69	87	76 (1.9)b
RvC4	79	93	85 (1.5)a	79	104	88 (2.3)a	128	234	174 (12)a
Diameter (mm)									
RvC1	4	5	5 (0.1)c	5	6	5 (0.1)d	4	5	5 (0.1)d
RvC2	5	6	5 (0.1)c	6	6	6 (0.1)c	6	7	6 (0.1)c
RvC3	5	6	6 (0.1)b	6	7	7 (0.1)b	7	9	8 (0.1)b
RvC4	7	8	8 (0.1)a	8	9	9 (0.1)a	10	13	11 (0.3)a
Height (cm)									
RvC1	25	41	34 (1.3)d	18	24	20 (0.5)d	56	71	64 (1.5)d
RvC2	32	54	39 (1.1)c	22	27	24 (0.5)c	72	86	80 (1.7)c
RvC3	43	51	47 (0.9)b	27	30	28 (0.4)b	86	106	97 (2.3)b
RvC4	57	66	62 (1.0)a	36	46	39 (0.9)a	99	137	115 (4)a
FOLR									
RvC1	4	6	4 (0.2)d	2	6	4 (0.3)d	3	8	5 (0.4)d
RvC2	5	8	7 (0.3)c	4	10	7 (0.7)c	6	12	8 (0.5)c
RvC3	7	11	8 (0.4)b	6	15	11 (1.0)b	8	13	11 (0.5)b
RvC4	9	15	12 (0.7)a	11	20	16 (0.9)a	11	17	14 (0.5)a

^aColumn means followed by different letters within root volume categories for each parameter differ significantly according to Duncan's multiple range test at $\alpha = 0.05$.

University's Southeast Purdue Agricultural Center (39°01' N, 85°35' W) in April 2002. Twenty seedlings from each treatment were planted into each of 10 blocks (1.22 m spacing) for a total of 2400 plants in the experiment. An electronic deer fence was installed immediately following planting and maintained throughout the experiment. Weeds were controlled using glyphosate (Roundup[®], 1.68 kg a.i. ha⁻¹), and azafenidin (Milestone[®], 0.39 a.i. ha⁻¹) on 5 May 2002, 15–16 July 2002, and 20–21 April 2003. The objective was to attain maximum weed control to minimize competition for moisture and nutrients from non-crop vegetation. Seedling field survival, total height (ground level to base of last surviving bud), and stem diameter were measured after each growing season.

Statistical analysis

Analysis of variance (ANOVA) was conducted on initial, first, and second-year data to determine if initial seedling characteristics differed among Rv categories, and whether these trends were maintained for 2 years after outplanting. Significant means were ranked according to Duncan's multiple range tests at $\alpha = 0.05$ (SAS 2001). Pearson correlation coefficients (R) were computed to test the strength of linear relationships between initial predictor variables and first- and second-year measured response (seedling total height and diameter). Statistical modeling of the relationships between first- and second-year height and diameter and the explanatory variables (initial height, diameter, FOLR, Rv, and fresh mass) was accomplished using the backward elimination method of variable selection (Neter et al. 1996; Salifu 2002). In this iterative process, the dependents or response variables were each regressed on the full set of the explanatory or predictor variables (full model). Non-significant variables were dropped one after the other until all variables were significant ($p = 0.05$). The selected model was then tested with the full model to ensure that no useful information was left out in the modeling process. Model comparisons were based on the F -test (Neter et al. 1996; Salifu 2002). After variable selection, the model was evaluated for goodness of fit by graphical analysis of residuals. These were assumed to be normally distributed over the range of independent variables, and hence, showed constant variance and no systematic variations. Where assumptions of normality and homoscedasticity were not met, independent variables (initial fresh mass and Rv) were transformed to obtain improved coefficient of determination, standard error of estimate for the models, and desired behavior of residuals. SPSS version 11.0 (Chicago, IL, USA) was used for the regression analysis (SPSS Inc. 2001). Computed coefficient of determination (R^2) illustrates the percentage of variation in the response that is explained statistically by predictor variables as summarized in Table 2.

Table 2. Coefficient of determination (R^2 values) of simple linear regression models of first- and second-year total height and diameter on initial northern red oak, white oak, and black cherry seedling characteristics measured in the laboratory prior to field planting for one and two growing seasons ($n = 38-40$)

Initial laboratory measurement	Coefficient of determination for ^a			
	Year 1		Year 2	
	Height	Diameter	Height	Diameter
Northern red oak				
Height	0.92***	0.79***	0.62***	0.50***
Diameter	0.91***	0.83***	0.66***	0.51***
Root volume	0.91***	0.77***	0.59***	0.53***
First-order lateral roots	0.75***	0.59***	0.45***	0.36***
Fresh mass	0.92***	0.79***	0.60***	0.54***
Height:diameter	0.22***	0.15*	0.11*	0.10
White oak				
Height	0.88***	0.81***	0.77***	0.73***
Diameter	0.78***	0.73***	0.69***	0.65***
Root volume	0.85***	0.78***	0.71***	0.67***
First-order lateral roots	0.61***	0.54***	0.51***	0.47***
Fresh mass	0.84***	0.78***	0.71***	0.66***
Height:diameter	0.48***	0.44***	0.42***	0.42***
Black cherry				
Height	0.57***	0.33***	0.10*	0.12*
Diameter	0.65***	0.47***	0.19**	0.23**
Root volume	0.58***	0.42***	0.15*	0.19**
First-order lateral roots	0.59***	0.48***	0.27**	0.32***
Fresh mass	0.59***	0.41***	0.14*	0.18**
Height:diameter	0.45***	0.53***	0.36***	0.39***

^aRegression significant at *** $p < 0.0001$, ** $p < 0.001$, * $p < 0.05$. All regression slopes were positive linear except height:diameter for cherry, which was negative linear for all.

Results

Initial seedling morphology

Seedlings were sorted into four root volume categories (RvC1–RvC4) as shown in Table 1. Mean root volume differed significantly among categories within species ($p < 0.0001$). Similarly, number of FOLR increased ($p < 0.0001$) with root volume for all species. Generally, initial seedling height, diameter, and fresh mass increased with increasing root volume ($p < 0.0001$) for all species (Table 1).

Seedling survival and growth

Seedling field survival ranged from 94 to 97% for red oak and white oak, and 87 to 95% for black cherry at the end of the second growing season and did not differ among Rv categories. Since percentage survival was very high for all species,

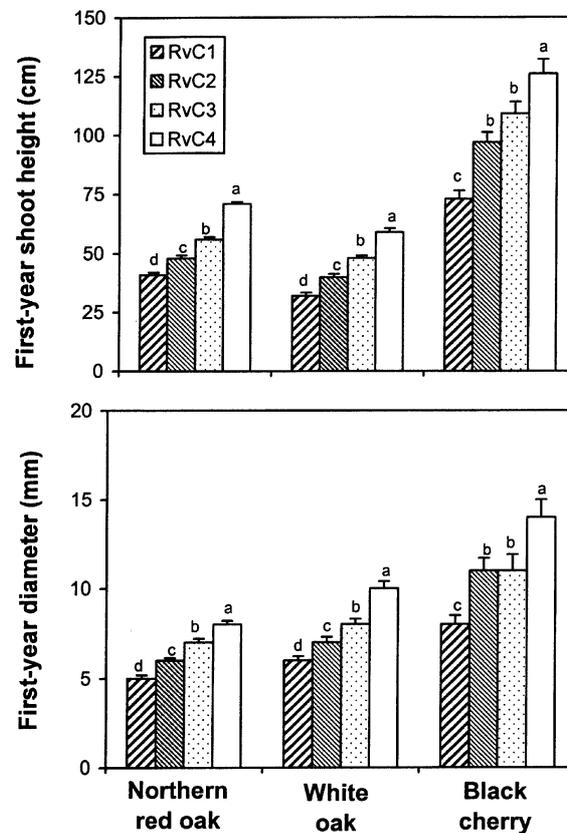


Figure 1. First-year total height and diameter of northern red oak, white oak, and black cherry seedlings sorted into four root volume categories (RvC1–RvC4) and established in the field for two growing seasons. Bars are means and error bars are SEs. Bars marked with similar letters within species are not statistically different according to Duncan's multiple range test at $\alpha = 0.05$.

relationships between survival and initial parameters were not investigated. Seedlings in larger Rv categories had significantly ($p < 0.001$) greater first- and second-year field height and stem diameter (Figures 1 and 2). Relative to RvC1, height of RvC4 was 73% greater in red oak and black cherry and 81% greater in white oak after year-1 (Figure 1). Similarly, first-year stem diameter was 60, 67, and 75% greater in red oak, white oak, and black cherry, respectively. After two growing seasons, height was 61, 109, and 36% greater from RvC1 to RvC4 for red oak, white oak, and black cherry, respectively (Figure 2).

Simple linear regression models

Pearson correlation coefficients (R) indicated that first-year height and diameter were positively and significantly correlated with initial seedling charac-

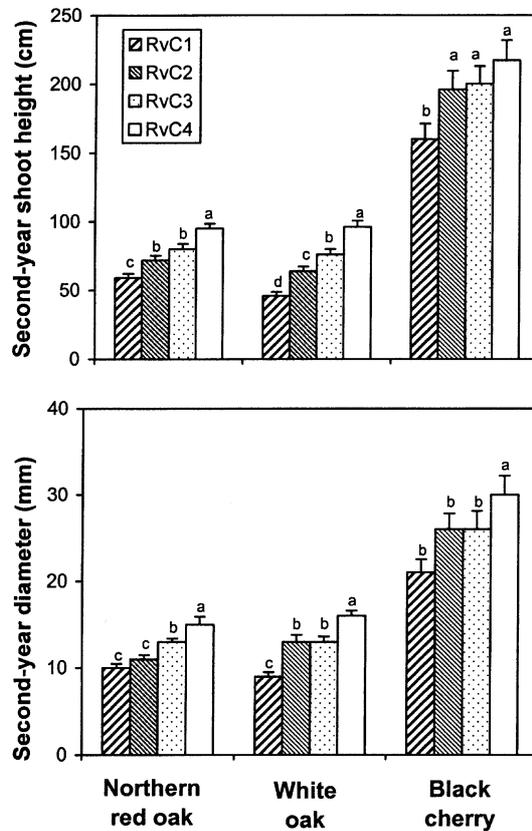


Figure 2. Second-year total height and diameter of northern red oak, white oak, and black cherry seedlings sorted into four root volume categories (RvC1–RvC4) and established in the field for two growing seasons. Bars are means and error bars are SEs. Bars marked with similar letters within species are not statistically different according to Duncan's multiple range test at $\alpha = 0.05$.

teristics for all species which diminished in the second year, especially for black cherry. First-year black cherry seedling height was correlated with initial height ($R = 0.75$, $p = 0.01$) and diameter ($R = 0.80$, $p = 0.01$), which decreased to 0.31 and 0.44, respectively, in year-2. Regression analysis was based on total heights rather than increments since preliminary data analysis suggested growth increments were not useful for model building. For instance, initial height could account for 75% of the variation in black cherry total field height vs. 2% based on height increment (Jacobs and Seifert 2004). Similar comparisons for diameter were 50% vs. 0.1%. For red oak, these comparisons were 91% vs. 1% of explained variation for height, and 82% vs. 3% for diameter.

The least important variable was height: diameter, except for black cherry where it was useful for predicting year-1 diameter and generated the highest R^2 value among variables for year-2 height and diameter (Table 2). Initial Rv,

height, diameter, and fresh mass were equally important in their ability to predict first-year field height ($R^2 = 0.91\text{--}0.92$) and diameter ($R^2 = 0.77\text{--}0.83$) of red oak seedlings. Similarly, year-2 height ($R^2 = 0.59\text{--}0.66$) and diameter ($R^2 = 0.50\text{--}0.54$) of red oak may be adequately predicted from initial height, fresh mass, diameter, and Rv (Table 2). The capacity of initial indicators to predict field height and diameter in white oak were similar to those observed in the red oak models although these had lower coefficients of determination. Except for black cherry, Rv was more important than FOLR in predicting field height and diameter (Table 2). Rv accounted for 91 and 77% of the variation in first-year height and diameter of red oak, compared with 75 and 59% explained by FOLR. Initial indicators of black cherry field response were associated with lower R^2 than the oak species and could not account for a large proportion of the variation in field success, especially in year-2 (Table 2).

Multiple linear regression models

Multiple linear regression models were developed to explore whether a combination of variables accounted for a greater proportion of the variation in field height and diameter than single-variable equations (Table 3). In nearly all cases, multiple linear regression models produced higher R^2 values than single-variable models. For example, four initial variables (height, diameter, root volume, and fresh mass) combined accounted for 95% of the variation in first-year height of red oak seedlings vs. 91–92% for these variables individually (Table 2). Initial diameter alone accounted for 47% of the variation in first-year diameter of black cherry seedlings (Table 2), while addition of other variables to models improved the R^2 to 58% (Table 3). Generally, the coefficient of determination was lower in year-2 compared with year-1 models. For instance, 58% of the variation in diameter of red oak was accounted for by the year-2 predictive equation compared with 87% explained in the first year (Table 3). Similar trends were observed for white oak and black cherry.

Discussion

Seedling survival and growth

Seedling survival was high for all species in this study, which may be explained by adequate weed control and elimination of deer browsing. Tendency for low survival of red oak seedlings, especially on harsh sites (Thompson 1991; Thompson and Schultz 1995), emphasizes the need for adequate weed control for successful early plantation establishment (Dey and Parker 1997; Jacobs et al. 2004b). Seedlings with a greater initial height at planting are better able to out-compete weeds than smaller stock (Cleary et al. 1978), which is particularly important for survival on weed-prone sites. Larger Rv category seedlings with

Table 3. Regression coefficients and related statistics for the best models selected by the backward elimination process of variable selection for prediction of first- and second-year total height and diameter of northern red oak, white oak, and black cherry seedlings.

Model	Regression coefficients ^a											Goodness of fit statistics	
	bo	iht	idia	iRv	iFOLR	iFm	Log (iRv)	Sqr (iRv)	Log (iFm)	Sqr (iFm)	R ²	SE	n
Year 1													
<i>Northern red oak</i>													
HT	9.6 ^b	0.21	0.72	-	-	-	-	-13.26 ^c	-	15.75 ^c	0.95 ^a	2.77	40
Dia	-1.5	-	1.13 ^b	-	-0.20 ^b	-	-4.51	-	5.92	-	0.87 ^a	0.47	40
<i>White oak</i>													
HT	3.4	0.95 ^b	-	-	-	105.80	-	-	-87.79	-	0.90 ^a	3.60	38
Dia	0.3	0.20 ^b	0.36	-	-0.10	-	-	-	-	-	0.82 ^a	0.81	38
<i>Black cherry</i>													
HT	35.4 ^a	-	8.52 ^a	-	-	-	-	-	-	-	0.65 ^a	14.61	40
Dia	3.3	-0.17 ^b	333 ^a	-0.10	-	-	-	-	-	-	0.58 ^a	2.16	40
Year 2													
<i>Northern red oak</i>													
HT	-9.8	-	18.41 ^a	-	-3.04	-	-	-	-	-	0.70 ^a	9.61	40
Dia	2.9 ^c	-	-	-	-0.45	-	-	-	1.85 ^a	-	0.58 ^a	1.74	40
<i>White oak</i>													
Ht	-719 ^c	432 ^b	11.39	-	-	-1.08 ^c	-	-	-	-	0.80 ^a	10.38	38
Dia	-8.7	0.66 ^b	1.72	-	-	-0.18 ^c	-	-	-	-	0.76 ^a	1.55	38
<i>Black cherry</i>													
HT	115.9	-2.42 ^c	34.01	-	3.47	-	79.85	-	-	-14.80	0.39 ^a	37.89	40
Dia	26.2 ^b	-0.51 ^b	4.45	-0.57 ^c	1.49	0.26	-	-	-	-	0.48 ^a	5.17	40

Initial seedling height (iht), dia (idia), root volume (iRv), first order lateral roots (iFOLR), and fresh mass (iFm) were used as predictors of field response.

^aASE, standard error of estimate for the model; bo, intercept. Regression coefficient is significant; ^a $p < 0.0001$, ^b $p < 0.001$, ^c $p < 0.05$.

more FOLR outperformed those in smaller Rv categories with fewer FOLR, which is consistent with published information (Bardon and Countryman 1993; Teclaw and Isebrands 1993; Thompson and Schultz 1995; Dey and Parker 1997; Clark et al. 2000).

Predicting field response using simple linear regression

The relatively low R^2 values generated when examining field height and diameter increments strongly pointed to the need to model based on total parameters. Similarly, Dey and Parker (1997) modeled relationships between initial seedling characteristics of red oak with field response based on absolute height and diameter.

Seedling shoot height, diameter, FOLR, and fresh mass have been used to relate stock quality to future field success of red oak, white oak, and black cherry planted on a variety of field sites (Johnson 1984; Kaczmarek and Pope 1993a, b; Thompson and Schultz 1995; Dey and Parker 1997). We also found a significant, positive correlation between these variables with first and second-year field height and diameter (Table 2). The best predictors of first and second-year red oak seedling height and diameter were initial basal diameter, height, fresh mass, and Rv. The greater field height and diameter observed with increasing Rv (Figures 1 and 2) supports the contention that this variable is an important predictor of field performance (Rose et al. 1997; Jacobs et al. 2004a).

Initial diameter could predict second-year field diameter of red oak seedlings with higher coefficient of determination (51%) in our study, compared with <25% found in the Dey and Parker (1997) study. This difference could be partly associated with the presumably less uniform shelterwood environment compared to the afforestation site in our study, as well as the approach adopted in the model building process; Dey and Parker (1997) used stepwise linear regression compared with the more rigorous backward elimination process adopted in our study. The R^2 values of these simple linear regression models decreased from year-1 to year-2 for all variables, and in some cases could not account for a large proportion of the variation in field height and diameter, especially for cherry in year-2 (Table 2). This suggested that a combination of variables may be more important in predicting seedling field success.

Predicting field response using multiple linear regression

The addition of other variables to models containing diameter improved the ability to predict future response (Table 3). Individually, initial height, diameter, and Rv accounted for 33–47% of the variation in year-1 field height of black cherry compared with 58% when combined, demonstrating significant joint contribution to explain field variance (Table 3). This concurs with the

contention that a combination of some variables may more accurately characterize seedling morphological quality (Kaczmarek and Pope 1993a; Dey and Parker 1997; Jacobs and Seifert 2004). It is also consistent with the target seedling concept, which is based on the premise that numerous seedling traits must work together to produce the desired field response (Rose et al. 1990; Puttonen 1996).

Initial diameter contributed largely to development of multiple regression models (Table 3). The ability of diameter to predict field success may be partly attributed to the strong linear association between initial diameter with R_v and FOLR, as documented in other studies (Johnson 1984; Johnson et al. 1984; Dey and Parker 1997; Jacobs and Seifert 2004). Furthermore, large diameter seedlings have more stored carbohydrates and nutrients (Johnson et al. 2002), which are immediately available following planting to meet sink demand (Salifu and Timmer 2001, 2003) until plants re-establish root–soil contact to exploit resources from the site. Greater diameter also enables seedlings to withstand physical abuse and animal browsing (Cleary et al. 1978), which promotes field success.

Diminished capacity of initial seedling root and shoot morphological parameters to predict field response over time suggests plants are progressively able to exploit the environment and become less dependent on initial attributes (Burdett et al. 1984; Sands 1984; Nambiar and Sands 1993). Also, the inability of our multiple regression models to statistically account for a portion of field variance in both year-1 and year-2 (5–42% and 20–61% unexplained variation, respectively) may be associated with genetics, shoot/root balance, and nutrient or carbohydrate reserves, which were not considered in the models.

FOLR vs. R_v as predictors of seedling field performance

Studies have shown that water deficit is the major contributor to transplanting stress encountered by newly planted seedlings (Kramer and Bullock 1966; Kramer 1986; Blake and Sutton 1987; Haase and Rose 1993). This can result because of confinement of roots to the planting hole, poor root–soil contact, and low root permeability (Burdett 1990; Margolis and Brand 1990; Nambiar and Sands 1993). Increased root growth relative to shoot growth following planting is an adaptive mechanism by plants to avoid drought (Kramer 1986), but root system morphology of planted seedlings likely provides an initial indicator of capacity to exploit soil resources during the establishment phase.

Several authors contend that FOLR could be one of the best predictors of field response and competitive ability of planted seedlings, based on strong correlations between FOLR and seedling growth (Kormanik et al. 1988; Schultz and Thompson 1990; Teclaw and Isebrands 1993; Kormanik et al. 1995). However, Kaczmarek and Pope (1993a, b) were unable to detect a direct relationship between red oak performance and FOLR, but noted that initial

height and diameter were important in predicting future field response. Dey and Parker (1997) also found that FOLR was not as strong a predictor of future performance as diameter or shoot length. With the exception of black cherry, these results are consistent with our observations.

As discussed previously, measurement of Rv likely conveys a more accurate assessment of root system size, and therefore may provide a better indicator of potential field performance than FOLR. This contention was confirmed for the oak species examined in our study, as Rv alone accounted for 91 and 77% of the variation in respective height and diameter of first year red oak seedlings compared with 75 and 59% for FOLR. Similar trends were observed for white oak, though not for black cherry where FOLR explained 48 and 27% of the variation in respective year-1 and year-2 diameter compared with 42 and 15% accounted for by Rv (Table 2).

Root volume provides a simple, accurate, and non-destructive characterization of root system morphology, which has potential for transfer to operational nursery grading. We found that quantitative assessment of Rv can be accomplished at least as rapidly as counting of FOLR, particularly for seedlings with many FOLR. Additionally, Rv better captures the discrepancy between small vs. large diameter roots, short vs. long lateral roots, and few vs. many second and third-order lateral roots. This, combined with our current results, suggests that Rv may provide a more effective quantitative reflection of root system quality than FOLR for some hardwood species.

Conclusions

The following conclusions can be drawn from this study:

- (1) The very high seedling survival found in this study demonstrates the benefits of effective weed control and elimination of deer browse.
- (2) Initial seedling Rv was a better predictor of field response than FOLR for the oak species studied. When using simple linear regression models to predict field success, initial diameter, Rv, fresh mass, and shoot height accounted for similar proportions of variance in field performance for these species.
- (3) Multiple variable models predicted field response with higher R^2 than single variable equations. This suggests that seedling quality assessment should not be based on single indicators.
- (4) The unexplained variation in the models suggests the need to examine potential to integrate physiological indicators into stock quality evaluation programs.
- (5) Replication of this study across different vegetation management regimes and varied site conditions is warranted to identify superior seedling characteristics that can be consistently linked to field success, and to select these variables in stock quality grading programs. This

information may be used to help adjust nursery cultural techniques to improve seedling quality, which will enhance early plantation establishment and development.

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