MODELLING THE EFFECTS OF HERBICIDE RELEASE ON EARLY GROWTH AND SURVIVAL OF *PICEA MARIANA*

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ABSTRACT

A modelling approach was used to evaluate the effects of weed control on the growth and survival of *Picea mariana* (Mill.) B.S.P. (black spruce) up to 11 years after planting. The data were generated from a split-plot experimental design with a completely randomised arrangement of whole-plot treatments (2 herbicides × 3 replicates). There were six split-plot treatments distinguished by stock type (0.4-, 0.6-, and 1.5-g paperpots, and 1.5/1.5 bareroot transplants) and planting season (spring and summer). The two weed-control treatments were an untreated control and glyphosate applied at 70 ℓ/ha with a spinning disc applicator at 2.14 kg a.e./ha. The experiment was located in north-eastern Ontario, Canada, on an upland mixed-wood herb-rich site in the boreal forest region.

Of the models tested, the exponential and linear-exponential, respectively, provided the best fits to the seedling growth and survival data. An interpolation procedure was developed to augment the diameter observations with additional estimates for years when only seedling height (and survival) were recorded. Because of the serial correlation over time in the data, model parameter estimates were used as primary data in multivariate analyses to test for treatment effects.

Reduction of weed competition almost always accelerated the growth of the black spruce outplants. Eight growing seasons after weeding, the trees on the weeded plots were up to almost three growing seasons ahead of their counterparts on the non-weeded plots. By the end of the experiment, the growth advantage for trees in weeded plots relative to those on non-weeded plots was increasing with respect to volume at about 1.5 times its rate with respect to height. Tree survival was not significantly affected by weed control, planting season, or stock type. Planting season and stock type did affect tree growth, however. The relative rates of volume growth of the spring-planted stock exceeded that of the corresponding summer-planted stock by 10–14%. The bareroot stock was initially taller and increased in volume at a relative rate which was 4–22% faster than stock in the 0.4-g paperpots in the same weed control and planting season regimes. This superiority of the bareroot stock over the paperpot stock was 3–5% greater when planted in the summer than in the spring.

Keywords: weed control; seedling growth and survival; bareroot stock; container-grown stock; long-term study; glyphosate; vegetation management; *Picea mariana*.

INTRODUCTION

About 474 000 ha of Canada's forest land goes out of production annually due to unsatisfactory restocking of commercial tree species (Honer *et al.* 1991). The boreal upland black spruce site type can be particularly difficult to regenerate (Weetman 1989). This type, the white spruce (*Picea glauca* (Moench) Voss) mixed woods, and the pure white spruce types in western Canada, include a very large portion of failed cutovers, or cutovers converted from conifers to hardwoods and even to grass.

On most cutover sites in the boreal forest, vegetation management is needed to successfully regenerate spruce and jack pine (*Pinus banksiana* Lamb.) stands (Hearnden *et al.* 1992). Interest in vegetation management in Ontario has increased dramatically since the mid 1980s, partly as a result of the steady expansion of the provincial planting programme from about 50 million trees in the mid 1970s to 171 million in 1988. Much of this expansion was directed toward black spruce (Kuhnke 1989). Since competition for site resources is a widely recognised constraint on conifer establishment (Burton 1993), there has also been a rapid increase in the area treated with herbicides—from 30 100 ha in 1980–81 to 93 800 ha 9 years later (Deloitte & Touche 1992). Glyphosate was often the herbicide of choice (Campbell 1990).

Currently, vegetation management in Ontario, in particular, and Canada in general, suffers from a lack of objective criteria for making decisions on the release of plantations from vegetative competition. Such criteria are required to respond to both the increasing public pressure to reduce herbicide application rates and the goal of forest managers to make vegetation management decisions more cost-effective (Hearnden *et al.* 1992). Although the short-term benefits of weed control in Ontario's black spruce plantations are well documented (Hearnden *et al.* 1992; Weetman 1989), the longer term (i.e., ≥10 years since planting) effects are unknown.

To develop longer-term criteria, individual black spruce outplants were sampled up to 11 years after planting as part of a vegetation management and stock comparison experiment in Kenogaming, north-eastern Ontario (Wood & Mitchell 1995). Static descriptive statistics of crop-response data by themselves, however, are of only limited value for plantation management, although such data may be useful from a scientific perspective. It is when such data are synthesised in the form of dynamic time-dependent models, especially in a decision-support context, that they can usually achieve their potential in helping forest managers make cost-effective and environmentally considerate vegetation management decisions (Richardson 1991). In this study, quantitative dynamic models were fitted to the Kenogaming data to reveal the effects of stock type, planting season, and weed control on changes in tree height, volume, and survival up to 11 years after planting.

There are many reports of such models in the biological sciences. Many of them can be related back to Bertalanffy's (1957) deduction of a theoretical growth function for animals. A number of authors have built upon this work for specific applications in forest growth and yield research (e.g., Ek 1971; Golden *et al.* 1981; Martin & Ek 1984; Murphy 1983; Payandeh & Wang 1995). Although the various curve shapes produced by this family of growth functions lend themselves to biological or physiological interpretation (Pienaar & Turnbull 1973), the functions themselves have not been derived from detailed considerations of the fundamental physiological processes of growth, and hence are open to some of the potential drawbacks of empirical models in general (cf. Korzukhin *et al.* 1996).

The experiment described in this paper can be considered a longitudinal-type study *sensu* Koch *et al.* (1988) in which each experimental unit is randomly allocated to a particular treatment regime and afterwards the same response variables are observed repeatedly. Typically, the goal is to determine how the different treatments affect the response over time and, because time is a quantitative variable, a regression-based approach is preferred to the use of univariate or multivariate analyses which ignore this fact (Mize & Schultz 1985). The problem is that since the **same** experimental units are observed repeatedly, all observations are not independent, and this violates a fundamental assumption of regression (Draper & Smith 1981). Hence, direct comparison of the parameter estimates of regression equations fitted to the response curve data from different treatments could produce misleading results. To circumvent this difficulty, regressions were fitted to the data from each experimental unit and the resulting parameter estimates were then compared indirectly by using them as primary data for multivariate analysis. As Meredith & Stehman (1991) explained, this allows one to use the preferred regression-based approach without foundering on the serial correlation in the observations.

METHODS AND MATERIALS

Site and Site Preparation

The experiment was conducted in Kenogaming Township (at 48°10'N, 82°00'W) in the Missinaibi-Cabonga Forest Sections of the Boreal Forest Region (Rowe 1972). The site was productive and well drained with silty to loamy sand soils—Hardwood Mixedwood - Coarse Soil site type (McCarthy *et al.* 1994). The forest cover before harvest (which occurred in 1979–80) consisted of black spruce, white spruce, trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), and white birch (*Betula papyrifera* Marsh.).

Bladed strips 5 to 6 m wide were cut, and 3 to 8 m of logging debris and standing deciduous and cedar (*Thuja occidentalis* L.) trees were left between strips. The summer site preparation was quite severe and this resulted in considerable exposure of the mineral soil. To decrease the likelihood of frost heave, patches of exposed mineral soil were avoided when planting the seedlings.

Planting Stock

Three-year-old bareroot transplant stock (1.5 + 1.5) and two sizes of containerised paperpot stock were grown for both the spring and summer plantings. The "spring-planted" paperpot stock was 0.4 and 1.5 g; the "summer-planted" paperpot stock was 0.4 and 0.6 g. The "summer-planted" transplant stock was fresh-lifted prior to completing its third growing season in the nursery. Spring and summer plantings occurred from 14 to 28 May and 7 to 15 July 1982, respectively.

Experimental Design

The underlying experiment was organised as a split-plot, with a completely randomised arrangement of whole-plot treatments (two herbicides (fixed effects), three whole-plots nested within herbicides). The two herbicide treatments were an untreated control and glyphosate formulated as the isopropylamine salt (Roundup® 356 g a.e./ℓ) at 2.1 kg a.e./ha. A spinning disc hand-held sprayer* designed for low-volume herbicide applications was calibrated to deliver a volume rate of 70 ℓ/ha with a swath width of 1.75 m. On 30 August 1984 the herbicide was applied as a broadcast band over the top of the crop seedlings; areas between the bladed strips were not treated.

There were six split-plot planting treatments (fixed effects) which were distinguished by stock type (bareroot transplant or one of three sizes of paperpot) and planting season (May or July 1982). A random selection of 50 seedlings from each stock type × planting season combination was destructively measured for basal diameter and height immediately before planting. Thereafter, each of the six plots comprised six subplots (bladed strips), and each subplot, which represented a single experimental unit, comprised 50 planted trees. The height and vitality of each of these trees were evaluated non-destructively after the 1982, 1983, 1984, 1986, and 1992 growing seasons. After the 1986 and 1992 growing seasons, the diameter of each stem was measured 5 cm above ground level; the basal diameter was estimated as $D = \{H/(H-5)\} \times$ (measured diameter). The expression, $V = \pi D^2H/1.2$, was used to estimate total stem volume in cubic centimetres given the basal diameter, D, in centimetres and the height, H, in decimetres. Wood & Mitchell (1995) have provided additional details about the experimental site, experimental design, and planting stock.

Interpolation of Basal Diameter

Since the planted trees were measured for basal diameter only twice (in 1986 and 1992), diameters for the early years (1982–84) were interpolated to provide additional data for modelling volume growth over time. The observations from the initial definitive sampling in 1982 were combined with corresponding observations from 1986 to make a single dataset for each of the six planting treatments. Whether the data for interpolation came from the weeded or non-weeded plots, the treatment-related differences between the resulting volume estimates for 1982–84 were so small compared to the corresponding differences in the observations for 1986 and 1992 that the observations alone were the source of all treatment effects on volume.

For each of these six datasets, scatter plots of diameter against height on arithmetic and logarithmic scales, suggested that the polynomial

$$D = a + a_TT + (b + b_TT)H + (c + c_TT)H^2 \qquad (1)$$

could provide accurate interpolations. Here, a, a_T, b, b_T, c, and c_T are parameters to be estimated; H represents tree height (dm); D represents basal diameter (cm); and T is the time in number of growing seasons experienced since planting. This equation was fitted to each dataset and the resulting parameter estimates were substituted back into the equation to produce a unique interpolating polynomial for each planting treatment. These polynomials were then used to estimate the basal diameter as a function of height for each planted tree at the end of the 1982, 1983, and 1984 growing seasons. These estimates were combined with the measured basal diameters in 1986 and 1992 to construct a comprehensive dataset of tree basal diameter and volume estimates.

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* Herbi by Micron Sprayers Ltd, Three Mills, Bromyard, Herefordshire, England

Model Specification

In the search for appropriate models, scatterplots of mean seedling height (H) and volume (V) against time (T) were produced for each treatment. These scatterplots suggested two possible general models: the exponential-type model which can be written

$$Y = (s + 1) \exp(r\ T^{(a+1)})$$

and the power function (Hastings & Peacock 1975) which can be written

$$Y = (s + 1) ([a+1] + T^{(r + 1)}).$$

In preliminary attempts to fit both of these equations to data from the five growing seasons for which seedling growth was observed, parameter "a" was not significantly different from zero. Hence, the exponential model was reduced to

$$Y = (s + 1) \exp(r\ T) \tag{2}$$

and the power function was reduced to

$$Y = (s + 1) \{1 + T^{(r + 1)}\} \tag{3}$$

In these equations, Y is the independent variable (i.e., either height (H) in decimetres, or volume (V) in cubic centimetres); s and r are parameters to be estimated; and T is the time in years since August 1982 when the first subplot measurements were taken. When T=0, these equations reduce to Y= s+1, so we refer to parameter s as the "initial conditions" parameter. Since parameter r has units of 1/time in the exponential model, it is referred to as the "relative growth rate" parameter in that model. To compare the suitability of these equations for describing and interpreting tree growth in each planting treatment, the equations were fitted to the 15 sample means (from five growing seasons of observations in each of three replicate subplots).

To identify a family of models for describing survival, the mean proportion of seedlings surviving (log scale) was plotted against time (T) for each treatment. The models were required to be flexible enough to describe a range of possible survival curves and to be derivable from basic considerations of an ageing property, a death process, or a biological failure (Johnson & Kotz 1970; Keyfitz 1982; Bain & Engelhardt 1991). The search resulted in three possible models for describing seedling survival as a function of time:

the Weibull, $$S = \exp(-[r\ T]^{(1+s)}) \tag{4}$$

the linear-exponential, $$S = \exp(-r\ T - s\ T^2) \tag{5}$$

and the Gompertz, $$S = \exp\{(s + 1)[1 - \exp(r\ T)]\} \tag{6}$$

In these models, s and r are parameters to be estimated, S is seedling survival, and T is the time in years since planting. Although the Weibull and Gompertz are commonly used to describe growth, the analysis of survival with such models is not new to forest science (e.g., Fleming & Piene 1992a,b). For each planting treatment, the best general model of Equations (4)–(6) was determined by comparing the fits provided to the seedling survival data.

Statistical Analysis of the Models

Time-dependent nonlinear regression models were used to project the effects of the imposed management regimes on tree volume, height, and survival. Because each subplot of 50 trees constituted a single experimental unit, these models were fitted to the means for each subplot. Technically, the process was one of recursive model building using a pseudo

Gauss-Newton algorithm for nonlinear least squares estimation (Ralston 1983). Parameters with estimates not significantly different from zero ($p < 0.05$) according to the partial F-test (Draper & Smith 1981) were removed and these reduced models were refitted. This procedure was continued until only parameters with statistically significant estimates remained for each subplot. Residual distributions and residuals plotted against predictions were examined to verify that the regression assumptions were adequately satisfied.

To circumvent problems associated with serial correlation in the data, the parameter estimates resulting from these nonlinear regressions were entered as primary data in a multivariate analysis (MANOVA) and tested for statistically significant effects of weed control (the whole-plot factor) and the six split-plot planting treatments (Meredith & Stehman 1991). Various *a priori* hypotheses were tested using contrasts and when the MANOVA indicated significant effects, univariate analyses (ANOVA) were examined to find the source of these effects. Weed control effects were tested over the whole-plot residual (i.e., 4 df in ANOVA); split-plot effects were tested with the overall model residual (i.e., 20 df in ANOVA).

To display the overall results, data were pooled among treatments in the absence of statistically significant differences, and nonlinear regression was then used to estimate the parameters of the previously specified model for the response curve. Reported fit statistics include the SEE (standard error of the estimate), R^2 (coefficient of determination as recommended by Kvalseth 1985), and the ESS (error sum of squares). The SE (standard error) is reported for most parameter estimates. Where nonlinear approximation methods are required to fit the models (Ralston 1983), the reported statistics should be viewed as asymptotic approximations (Gallant 1975). The doubling time, $DT = \ln(2) / r$, where ln represents the natural logarithm and r is the relative growth rate, is provided for the exponential model.

RESULTS

Interpolation of Basal Diameters

The relationship observed between basal diameter and height in young trees from each planting treatment in the weeded plots is described in Table 1. The statistical significance of at least one parameter subscripted by T for all treatments indicates that the diameter-height relationship was not static. The 1986 trees tended to have a larger diameter than 1982 trees of comparable height. This tendency was evident for the shorter trees (Fig.1). It may be a consequence of the age difference in the trees or it may be a realisation of the view (e.g., Weiner & Thomas 1992) that "crowded" plants usually have smaller diameter/height ratios than less "crowded" plants. Because herbicide was applied to these plots in 1984, the 1986 trees presumably represent the less crowded situation. That such patterns, which are implicit in the interpolation equations, are corroborated by earlier work adds some credence to the interpolation procedure. Given the amount of pure error evident in the scatter plots (e.g., Fig. 1), the fit statistics (Table 1) are also encouraging.

Model Specification

Both the exponential model, Equation (2), and the adapted power function, Equation (3), generally provided reasonable fits to the ($n=15$) subplot means of seedling height and volume

TABLE 1–Sample sizes (n), parameter estimates (standard errors), and fit statistics for regressions of the interpolating polynomial Equation (1), on the observed relationships in the weeded plots between basal diameter (cm) and tree height (dm) at planting in July 1982 and later in August 1986.

Planting treatment		n	Statistically significant parameter estimates (SE)		R^2	SEE
Season	Stock					
Spring	1.5-g paperpot	192	a = 0.219 (0.0264)	b_T = 0.0309 (0.00069)	0.915	0.201
Spring	0.4-g paperpot	180	a = 0.183 (0.0245)	b_T = 0.0307 (0.00068)	0.920	0.190
Spring	Bareroot	186	a_T = 0.0843 (0.0153)	b = 0.217 (0.0169)	0.868	0.299
			b_T = –0.0139 (0.00367)			
Summer	0.6-g paperpot	173	a_T = 0.163 (0.0067)	c = 0.0365 (0.08436)	0.885	0.148
			c_T = –0.00686 (0.00110)			
Summer	0.4-g paperpot	152	a_T = 0.0742 (0.00899)	b = 0.112 (0.0057)	0.914	0.131
Summer	Bareroot	172	a = 0.483 (0.0279)	b_T = 0.0296 (0.00252)	0.811	0.218
			c = 0.00268 (0.00111)			

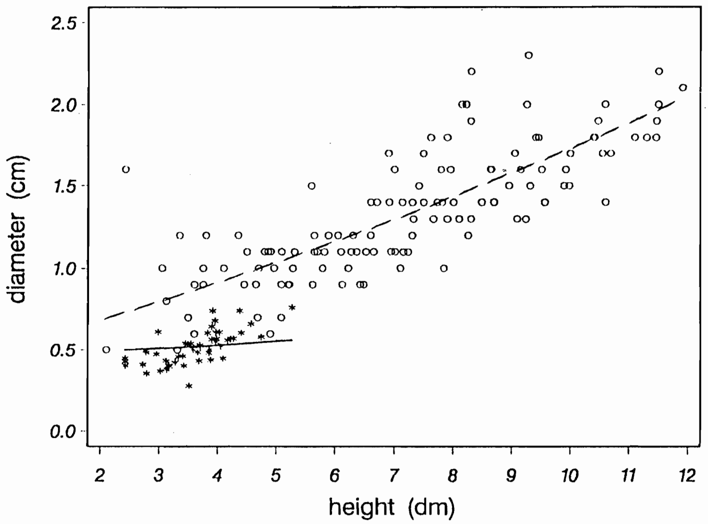

FIG. 1—Diameter-height relationships of individual trees for summer-planted bareroot stock at planting in July 1982 (asterisks, n=50), and later on the weeded plots in August 1986 (circles, n=122). Herbicide was applied in August 1984. The solid and dashed curves illustrate the combined fit of the single interpolating equation (Table 1) to the 1982 and 1986 data, respectively.

against time in each of the 12 planting treatment × weed control combinations. For each equation, all but two of the resulting 24 fits explained over 90% of the variance in the relevant growth variable. The lower R^2 values occurred with volume in the non-weeded plots. The R^2 values were identical for both equations: 0.713 for the 1.5-g (spring-planted) paperpots and 0.775 for the 0.6-g (summer-planted) paperpots. Overall, these results and separate residual examinations suggested that both Equations (2) and (3) provided acceptable fits. Since its parameters lend themselves more easily to biological interpretation, the exponential was selected as the general model for describing seedling growth.

The relationship between mean survival and time (years since planting) for each treatment was fitted reasonably well by the Weibull model Equation (4), the linear-exponential model Equation (5), and the Gompertz model Equation (6). For planting treatments with and without weed control, however, the linear-exponential was the only one of the three models to consistently explain over 90% of the variance (minimum $R^2 = 0.938$). The minimum R^2 values for the Weibull and the Gompertz models, 0.789 and 0.697 respectively, were considerably less. Hence the linear-exponential model Equation (5) was chosen as the basis for describing the observed decline in black spruce survival over time.

Response of Tree Height

Multivariate analyses and related contrasts identified similarities and differences in height growth (Table 2). Weed control ($p = 0.001$) and the split-plot treatments ($p = 0.0001$) had highly significant effects on height growth. Both stock type ($p = 0.0001$) and planting season ($p = 0.0001$) contributed to the treatment effect, but their interaction ($p = 0.4$) did not. Three specific contrasts were also examined. Differences between the summer-planted 0.4- and 0.6-g paperpots were not significant so the data from these treatments were pooled.

TABLE 2–P-values for multivariate (MANOVA) and univariate analyses of the parameter estimates of the exponential model Equation (2), derived from fits to the data in each subplot of mean seedling height (dm) against time (years).

Source of variation	MANOVA P-value	Univariate P-values r	s
Weed control (whole plot)	0.0012	0.0001	0.0193
Planting treatments (split plot)	0.0001	0.0947	0.0001
Planting treatments × weed control	0.153		
Contrasts:			
Stock (0.4-g paperpot *v.* bareroot)	0.0001	0.278	0.0001
Season (spring *v.* summer)*	0.0001	0.0996	0.0001
Interaction (season × stock)	0.428		
0.4-g paperpot *v.* 0.6-g paperpot, summer	0.734		
0.4-g paperpot *v.* 1.5-g paperpot, spring	0.0103	0.133	0.0022
1.5-g paperpot *v.* bareroot, spring	0.0001	0.807	0.0001

* Averaged over weeded and non-weeded, but only for the bareroot and 0.4-g paperpot stock.

Comparisons among the spring-planted stock revealed significant differences between the 1.5-g paperpots and both the 0.4-g paperpots (p = 0.01) and the bareroot (p = 0.0001) stock.

The univariate analyses showed that the relative rate of height growth, r, responded at a statistically significant level to only weed control. On the other hand, the planting treatments, and to a much lesser extent weed control, both had significant effects on s, the parameter describing the initial conditions. This indicates that the significant effects of the split-plot planting treatments in the MANOVA were due to their influence on s, and not on r. This view is supported by the parallelism between the results of the contrasts for parameter s in the univariate and the MANOVA results, and gains further support from the results of fitting the exponential model to the data for each statistically unique treatment (Table 3). Within the weeded and within the non-weeded plots there was overlap of the approximate 95% confidence intervals (estimate ± 2 × SE) for all relative height growth rates, r, but not for estimates of parameter s.

Only weed control (average r = 0.185, SE = 0.0042 on non-weeded subplots; average r = 0.221, SE = 0.0025 on weeded subplots), and not stock type nor planting season, affected the relative rate of height growth, r, of the exponential model. In contrast, parameter s, which in theory ought to describe the height at time T=0 (i.e., in August 1982), was apparently affected by all these factors. Stock type differences relate to size at planting, and since the T=0 measurements occurred within 4 months of planting, it is not surprising that stock type should significantly affect parameter s. Thus, within a given planting season, the s-estimates (Table 3) went from lowest to highest according to stock type in the order: small (0.4–0.6 g) paperpot, large (1.5 g) paperpot, and bareroot stock. This order held when the results from the weeded and non-weeded plots were pooled; it reflected the average heights at planting (1.72, 2.74, and 3.04 dm for the small paperpot, large paperpot, and bareroot stock, respectively).

The planting season effect on s may be because the spring-planted stock experienced a season of growth before the T=0 measurements, while the summer-planted stock did not. This interpretation is supported by the fact that, for common stock types, the s-estimates for the spring-planted subplots exceed those of the summer planted subplots (regardless of weeding).

TABLE 3–Sample sizes (n), parameter estimates (with standard errors), and fit statistics for non-linear regressions of the exponential model Equation (2) on the tree height (dm) : time (years since 1982) data from each planting treatment. Data for treatments not significantly different (MANOVA) have been pooled. DT is the estimated doubling time (years) for tree height.

Planting treatment: Season	Stock	n	r	(SE)	s	(SE)	R^2	SEE	DT
Not weeded									
Spring	1.5-g paperpot	15	0.167	(0.0162)	2.66	(0.528)	0.912	1.98	4.15
Spring	0.4-g paperpot	15	0.186	(0.0110)	2.20	(0.323)	0.969	1.26	3.73
Spring	Bareroot	15	0.187	(0.0082)	3.49	(0.336)	0.983	1.31	3.71
Summer	0.4- & 0.6-g paperpot	30	0.189	(0.0095)	1.41	(0.209)	0.955	1.16	3.67
Summer	Bareroot	15	0.198	(0.0062)	2.34	(0.191)	0.992	0.765	3.50
Weeded									
Spring	1.5-g paperpot	15	0.217	(0.0057)	2.49	(0.189)	0.995	0.786	3.19
Spring	0.4-g paperpot	15	0.220	(0.0095)	2.08	(0.278)	0.987	1.17	3.15
Spring	Bareroot	15	0.210	(0.0084)	3.01	(0.316)	0.988	1.30	3.30
Summer	0.4- & 0.6-g paperpot	30	0.234	(0.0095)	1.10	(0.191)	0.978	1.17	2.96
Summer	Bareroot	15	0.214	(0.0049)	1.94	(0.135)	0.996	0.556	3.24

There is no immediately apparent biological reason why weeding should affect s in our experimental design. This effect may be merely an artifact of the fitting (*see* Fig. 2). The plot was typical of the regressions of the exponential model on tree height which led to the results in Table 3 and indicated some lack of fit at T=0 and T=4. At T=0 there was a tendency for the model to over-estimate the mean observed height in both the weeded and non-weeded plots. This bias was slightly greater for the non-weeded curve than for the weeded one. Although this differential bias was small (mean difference = 0.299 dm), it was consistent (SE = 0.118 dm), and it is probably this consistency that resulted in a statistically significant effect of weed control on s, the parameter describing the initial conditions.

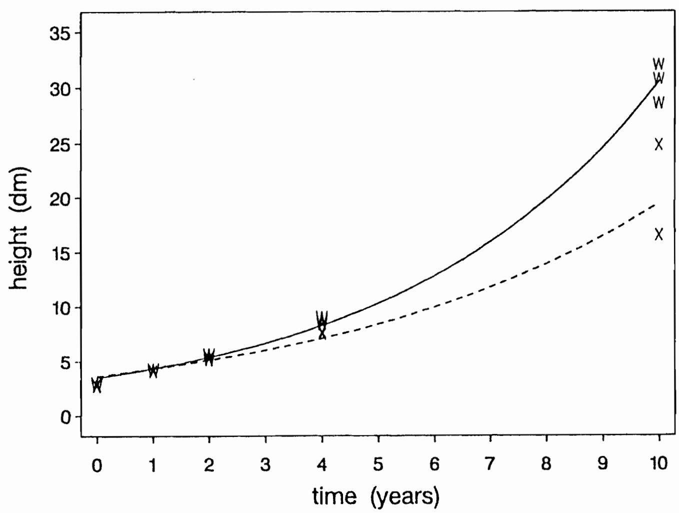

FIG. 2–Fits of the exponential model Equation (2) to the relationships between tree height (dm) and time (years after 1982) for the spring-planted 1.5-g paperpot stock. The solid and dashed curves represent the model predictions (Table 3) for the weeded and non-weeded plots, respectively. The "Ws" and "Xs" distinguish the average seedling heights observed in the weeded and non-weeded subplots, respectively, at each measurement. Weed control occurred just after the data collection at T=2 (i.e., in August 1984).

Response of Tree Volume

The responses of volume growth to weed control and the planting treatments were compared using multivariate analyses and related contrasts (Table 4). Weed control ($p = 0.02$) and planting treatment ($p = 0.0001$) had significant effects. The MANOVA showed that stock type ($p = 0.0001$), planting season ($p = 0.0001$), and their interaction ($p = 0.0002$) contributed to the planting treatment effects. Three specific contrasts were also examined. Neither the differences between the summer-planted 0.4- and 0.6-g paperpots nor the differences between the spring-planted 0.4- and 1.5-g paperpots were significant, and so the data from these treatments were pooled. In contrast, comparisons among the spring-planted 1.5-g paperpots and the bareroot stock revealed highly significant differences ($p = 0.0001$).

The univariate analyses in Table 4 showed that the "initial conditions" parameter, s, responded at a statistically significant level only to planting treatment ($p = 0.0001$), and not

TABLE 4–P-values for multivariate (MANOVA) and univariate analyses of the parameter estimates of the exponential model Equation (2), derived from fits to the data in each subplot of mean seedling volume (cm^3) against time (years).

Source of variation	MANOVA P-value	Univariate P-values r	Univariate P-values s
Weed control (whole plot)	0.0185	0.0092	0.503
Planting treatments (split plot)	0.0001	0.0027	0.0001
Planting treatments × weed control	0.145		
Contrasts:			
Stock (0.4-g paperpot *v.* bareroot)	0.0001	0.0040	0.0001
Season (spring *v.* summer)*	0.0001	0.0026	0.0001
Interaction (season × stock)	0.0002	0.0001	0.143
0.4-g paperpot *v.* 0.6-g paperpot, summer	0.784		
0.4-g paperpot *v.* 1.5-g paperpot, spring	0.733		
1.5-g paperpot *v.* bareroot, spring	0.0001	0.0120	0.0001

* Averaged over weeded and non-weeded, but only for the bareroot and 0.4-g paperpot stock.

to weed control, nor to the planting treatment × weed control interaction. On the other hand, the planting treatments ($p = 0.003$), and to a lesser extent weed control ($p = 0.01$), both had significant effects on the relative rate of volume growth, r. This indicates that weed control produced significant volume effects in the MANOVA through its influence on parameter r, but not on s.

This interpretation is supported by the results of fitting the exponential model to the volume data for each statistically unique planting treatment identified by the MANOVA (Table 5). Of immediate interest in Table 5 is the lack of any statistically significant s-parameter estimates for volume response. This suggests that the statistically significant effects revealed by the univariate analyses on parameter s (Table 4), although real, were so small as to be biologically unimportant. The sole function of parameter s in the exponential model Equation (2), is to determine the intercept, and the volume growth curves were so steep that the effects of any differences in the intercepts were lost by the tenth year (Fig. 3). (The contention made earlier that any interpolation errors in deriving volume estimates for T=0–2 are trivial compared to the treatment differences among the observations, particularly at T=10, is also supported in Fig. 3). Since the effects on parameter s are not biologically important, we focused solely on the rate parameter, r, to accommodate the results of the MANOVA on estimated tree volumes. This follows easily from Table 4 due to the close correspondence between the results of the contrasts for r in the univariate analysis and the MANOVA. Underlying reasons for the significant effects revealed in Table 4 are indicated in Table 5. The weed control effect was due to the greater volume growth rates of trees in the weeded plots than of trees in the non-weeded plots which were of the same stock type and were planted in the same season. The planting season effect can be explained by the stock, season, and stock × season interaction (Table 4), and these in turn can be explained using Table 5. The average relative rate of volume growth of the bareroot stock (0.731) exceeded that of the paperpot stock (0.653), and the average relative rates of the spring plantings (0.720) exceeded those of the summer plantings (0.638). The stock × season interaction was because the mean difference between the summer-planted (bareroot and 0.4-g paperpot) stock, 0.085, exceeded that of the same stock types when spring-planted, 0.071.

TABLE 5–Sample sizes (n), parameter estimates (with standard errors), and fit statistics for non-linear regressions of the exponential model Equation (2) on the tree volume (cm^3) : time (years since 1982) data from each planting treatment. Data for treatments not significantly different (MANOVA) have been pooled. DT is the estimated doubling time (years) for volume growth.

Planting treatment Season	Stock	n	r	(SE)	s	(SE)	R^2	SEE	DT
Not weeded									
Spring	0.4- & 1.5-g paperpot	30	0.637	(0.0075)	–	–	0.825	107.5	1.088
Spring	Bareroot	15	0.749	(0.0068)	–	–	0.921	211.7	0.925
Summer	0.4- & 0.6-g paperpot	30	0.557	(0.0062)	–	–	0.875	39.9	1.244
Summer	Bareroot	15	0.682	(0.0025)	–	–	0.989	38.9	1.016
Weeded									
Spring	0.4- & 1.5-g paperpot	30	0.755	(0.0038)	–	–	0.948	179.3	0.918
Spring	Bareroot	15	0.784	(0.0031)	–	–	0.982	138.1	0.884
Summer	0.4- & 0.6-g paperpot	30	0.663	(0.0045)	–	–	0.932	82.6	1.045
Summer	Bareroot	15	0.709	(0.0044)	–	–	0.967	91.2	0.978

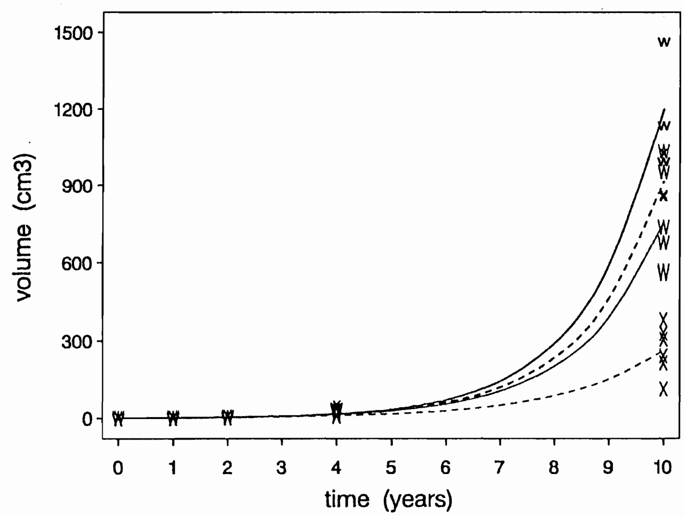

FIG. 3–Fits of the exponential model Equation (2) to the relationships between tree volume (cm^3) and time (years after 1982) for the summer-planted stock. The solid and dashed curves represent the model predictions (Table 5) for the weeded and non-weeded plots, respectively. The "Ws" and "Xs" distinguish the average seedling heights observed in the weeded and non-weeded subplots, respectively, at each measurement. The thicker lines and lower-case bolded letters distinguish the bareroot stock from the (pooled) paperpot stock (thinner lines, upper-case letters). Weed control occurred just after the data collection at T=2 (i.e., in August 1984).

Seedling Survival

Tree survival was exceptionally low on one of the weeded subplots of the summer-planted 0.4-g paperpot stock (Fig. 4). Since there was no obvious reason for eliminating this outlier, the analysis was performed both with and without its influence. To maintain the balanced design while omitting the effect of the outlier's parameter estimates, averages were calculated from the two other replicates of the same planting treatment × weed control combination. Both these sets of parameter estimates for the linear-exponential model Equation (5) were subjected to MANOVA to identify significant effects on survival but none were found in either dataset. This implies that neither weed control, nor planting treatment, nor their interaction, made any significant difference to seedling survival. For the original set of parameter estimates (i.e., including the outlier's), the two lowest probability-values in the MANOVA were for the effects of weed control ($p=0.116$) and season ($p=0.110$). The corresponding differences in the sample means (± SE) hinted that significantly higher survival might be developing on weeded plots (0.789 ± 0.0293) than on the non-weeded plots (0.758 ± 0.0289) and in spring-planted subplots (0.829 ± 0.0240) than on the summer-planted subplots (0.718 ± 0.0280). Nonetheless, all that can be concluded is that even 10 years after planting and 8 years after weed control, seedling survival showed no significant responses to planting treatment or weed control. The rather weak fit ($R^2 = 0.463$, SEE = 0.0829) of the linear-exponential model to the n = 216 observations pooled from all planting treatments × weed control combinations is illustrated in Fig. 4. The estimate for the s parameter was not significantly different from zero, that of the mortality rate parameter was ($r = 0.0286$, SE =

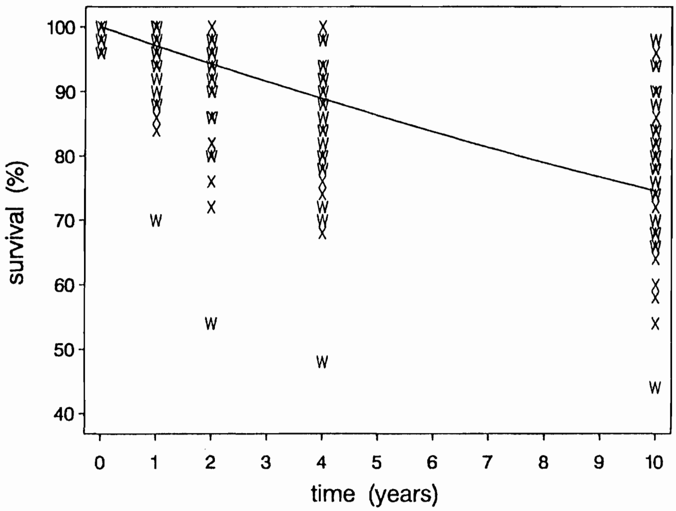

FIG. 4—The fit of the linear-exponential model Equation (5) to the relationship between tree survival (%) and time (in years since planting). Data from all planting treatments have been pooled: the "Ws" and "Xs" distinguish the average seedling survival observed in the weeded and non-weeded plots, respectively, at each measurement. Weed control occurred just after the data collection at T=2 (i.e., in August 1984).

0.00156). One-quarter of the experimental trees had died after 10 years, and if this rate of tree mortality continues half will be dead in about 24 years.

DISCUSSION

The modelling approach employed above has a couple of advantages over the more usual practice of relying entirely on hypothesis testing for data analysis and interpretation of results. In this study the effects of weed control and various planting trearments on longer-term crop growth and survival were measured by differences in parameter estimates derived from fitting time-dependent models to the data. This approach is both dynamic and integrative in that it distinguishes temporal trends and combines the results from all years of observation.

There are reasons for caution, however, in employing these models for forecasting more than 10 years since planting. First, it is not clear when asymptotic behavior may begin to limit growth rates. Second, the precision of the estimates and the goodness of fit are probably exaggerated to some degree in Tables 3 and 5. Two factors may be contributing to this exaggeration. First, 3 years of data were recorded when seedling size hardly changed at all ($0 \leq T \leq 2$) (Fig. 2 and 3). Therefore, it was effectively only the data from T=2 and T=4 that determined the shape of the lower asymptote in these trends. Thus, in effect, the first 2 years of data inflated the R^2 values without really testing the models. In this respect, it is useful to compare the R^2 values in Tables 3 and 5 with those for the survival curve ($R^2 = 0.463$) because changes in survival are relatively consistent over time.

Serial correlation may also be causing some exaggeration of the estimates of precision in Tables 3 and 5 because the measurements in successive time intervals (Fig. 2 and 3) were made on the same set of subplots and hence are not independent as required by regression theory. In addition, the population variance of the response variable may vary depending on the value of the independent variable (Fig. 2–4). This also violates an assumption of regression theory. Hence, the fit statistics and SEs for these final response curve regressions should be viewed as approximations which may over-estimate the precision. This, however, should not prevent the use of the parameter estimates as indicators of the mean response over time up to 10 growing seasons after planting.

Weed Control

Weed control led to increased growth of the black spruce container-grown and bareroot stock. The average relative rates of height growth were $r = 0.185$ (SE = 0.0042) on the 18 non-weeded subplots, and $r = 0.221$ (SE = 0.0025) on the 18 weeded subplots. The corresponding average relative rates of volume growth on the non-weeded and weeded plots were $r = 0.637$ (SE = 0.0302) and $r = 0.722$ (SE = 0.0209), respectively. These rates imply that, on average, tree height and volume doubled on the weeded plots in about 85% of the time it took them to double on the non-weeded plots.

The widening gaps between the curves fitted to the weeded and non-weeded data over time (Fig. 2 and 3) show that the benefits of weed control in terms of absolute growth were continuing to increase 8 years after weed control was applied. This is an example of the general observation (e.g., Wagner & Radosevich 1991) that size is a key determinant of tree growth; in general, the larger a growing tree's present size, the faster its absolute rate of growth, and the larger its future size. The advantages of weed control can also be considered in terms of time. For instance, the trees in the weeded and non-weeded plots in these figures started at approximately the same size. Eight growing seasons after weeding, however, trees in the non-weeded plots needed an average of 2.7, and 0.4–1.9 additional growing seasons, respectively, at present growth rates to reach the current heights (Fig. 2) and volumes (Fig. 3) of corresponding trees on the weeded plots.

The relative rate at which the gaps in tree size are widening (Fig. 2 and 3) can be estimated from the ratio of the slopes of the appropriate independent variables at T=10. Given that the initial conditions parameter, s, is little affected by weeding, it follows from Equation (2) that this ratio can be approximated as

$$(dY_W / dY_{NW})_{T=10} = (r_W / r_{NW}) \exp\{10(r_W - r_{NW})\} \tag{7}$$

Here Y represents height or volume and the subscripts distinguish the non-weeded (NW) curve from its corresponding weeded (W) curve. For height and volume these ratios are 1.71 and 2.64, respectively. These values suggest that 8 years after herbicide application, the rate of increase in volume's relative response to weed control is about 1.5 times that of height. This difference corroborates earlier work (e.g., Brand 1991; Lautenschlager 1991; MacDonald & Weetman 1993; Richardson 1991) in which it was found that reducing competing vegetation for black spruce and certain other conifers produced a greater response in basal diameter (and hence volume) than in height growth.

Weed control had no statistically significant impact on survival. Hence, in this study, it can be concluded that volume (diameter) growth followed by height growth were the most sensitive indicators of competitive pressure. This is consistent with the notion (e.g., Lanner 1985; Zutter *et al.* 1986) that crop trees often respond to interspecific competition by sacrificing diameter (and hence volume) growth in order to maintain height growth and thus keep their crowns in the canopy as long as possible. According to this hypothesis, it is only after the trees become over-topped by competitors and even height growth slows, that survival starts to fall.

Planting Season

Where planting season had an effect, the spring-planted stock performed a little better than the summer-planted stock. With respect to height growth, the effect of planting season was to confer an initial height advantage on the spring-planted stock. Relative height growth was similar for spring- and summer-planted stock thereafter, but planting season did influence the relative rates of volume growth. Spring plantings grew between 10% and 14% faster than summer plantings of the same stock type (Table 5). The response of volume, but not height, growth rates to planting season may be another indication that volume (diameter) has greater sensitivity than height to competing vegetation or other factors in the growing environment. Although there were no statistically significant effects of planting season on the parameters of the fitted survival function Equation (5), there were indications that the spring-planted stock (83% ± 2% survival at T=10) might outlive the summer-planted stock (72% ± 3% at T=10).

Stock Type

There were significant effects of stock type on growth, but not on survival. Where stock type affected growth, the bareroot stock grew better than the paperpot stock. With respect to height growth, stock type had no effect on the rate, but it did affect the initial-conditions parameter which was closely correlated with the original heights at planting. Stock type also had a strong influence on the relative rates of volume growth. The rates for bareroot stock were between 4% and 22% greater than those of paperpot stock in similar regimes of planting season and weed control, and this superiority of the bareroot stock was 3–5% greater when planted in the summer than in the spring. The lack of a significant planting season × weed control interaction (Table 4) does not support the common recommendation (e.g., Howard & Newton 1984; Lautenschlager 1991; Long & Carrier 1993; MacDonald & Weetman 1993; Newton *et al.* 1993) to plant larger stock where vegetative competition is high. However, there are indications that weeding might significantly reduce the volume growth rate advantage for the bareroot stock in the future. On non-weeded plots the relative rates of volume growth for bareroot stock were between 18% and 22% greater than those of paperpot stock; on weeded plots the advantage of bareroot stock fell to 4–7% (Table 5). This is consistent with findings by Newton *et al.* (1993) that competition had a greater effect on shorter trees than on taller trees and that this effect was related inversely to the initial height of the stock. In addition, the fact that volume but not height growth rates responded to stock type is another indication that volume (diameter) is a more sensitive measure of competing vegetation than height.

CONCLUSIONS

Black spruce outplants grew more quickly in the weeded than in the non-weeded plots and the difference in size increased over time. Eight growing seasons after weeding, the trees on the weeded plots were up to almost three growing seasons ahead of their counterparts on the non-weeded plots. By the tenth and final growing season of observation, the growth advantage for trees in weeded plots relative to those on non-weeded plots was increasing with respect to volume (diameter) at about 1.5 times its rate with respect to height. Because of its relatively slow growth rates compared to volume, height may not be as sensitive to competitive pressure shortly after release as volume. Nonetheless, by the end of the experiment, tree height was showing a highly significant ($p = 0.001$) response to weed control. Tree survival was not significantly affected by weed control.

Spring plantings generally grew more quickly than summer plantings of the same stock type. In essence, the spring-planted stock experienced a growing season in the field before the initial measurements were taken and so it was taller than the summer-planted stock when field measurements began. Thereafter the volume growth of spring plantings exceeded that of the corresponding summer plantings by 10–14%. There were no significant planting-season effects on survival.

Stock type affected tree growth but not survival. The bareroot stock was initially taller and increased in volume at a relative rate which was 4–22% faster than that of the 0.4-g paperpots in the same weed control and planting season regimes. This superiority of the bareroot stock over the paperpot stock was 3–5% greater when planted in the summer than when planted in the spring. Although the planting treatment × weed control interaction was non-significant, there were indications that weeding might significantly reduce the volume growth rate advantage for the bareroot stock over the paperpot stock in the future.

There are at least two avenues for future research. Perhaps the most obvious is to continue to observe the treatments with tree size and survival measurements taken after the thirteenth and fifteenth growing seasons as a start. (The recommended increase in measurement frequency is because of the accelerating differences in tree size already observed). The beginnings of asymptotic growth in tree volume and the establishment of weed control and planting season effects on survival could be expected. The establishment of weed control × planting treatment interactions in both height and volume growth could also be anticipated. A second avenue for future research is largely theoretical. It involves the development of algebraic growth models derived from simplistic botanical assumptions so that the simple models fitted to tree growth data may have a stronger botanical underpinning.

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