Growth efficiency–survivorship relationship and effects of spacing on relative diameter growth rate of Japanese cedars

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Received 5 June 2007; received in revised form 19 November 2007; accepted 27 November 2007

Abstract

Relative growth rate (RGR) is considered to be one of the most sensitive measures of competitive ability. As such, RGR should correlate positively with survivorship. The proposition, however, has not been fully tested with long-term data. Another question that has not been fully addressed is the long-term effect of initial density on the RGRs of survivors. Based on data from a long-term Japanese cedar (*Cryptomeria japonica*) spacing trial (with square spacing of 2, 3, 4, and 5 m), we tested the following two hypotheses: (1) within each spacing, survivors have higher average relative diameter growth rate (RGR_{DBH}) than those trees that did not survive, and (2) the mean RGR_{DBH} of survivors increases with increasing initial spacing. A two-parameter monomolecular model and nonlinear mixed-effects regression were used to model individual tree diameter growth over a 50-year period, with the model's growth-rate parameter as a surrogate measure for RGR_{DBH} . Our results supported both hypotheses conditionally. Survivors were indeed the more efficient ones, but only when competition became intense. Our study suggested that self-thinning likely thins out trees that were inefficient in diameter growth. When young, survivors of the widest spacing did have the highest average RGR_{DBH} . However, after 55 years, all survivors had about the same diameter growth efficiency, regardless of the initial density. In the end, survivors that experienced more intense competition, possibly by making diameter growth a high priority in carbon allocation, achieved the same RGR_{DBH} as did those that experienced less intense competition.

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Keywords: Competition; *Cryptomeria japonica*; Growth efficiency; Relative growth rate

1. Introduction

Relative growth rate (RGR), defined as the rate of size increase per unit of time per unit of size (i.e., $RGR = (d_{size}/d_{time})(1/size)$, Hunt, 1990), plays a prominent role in plant ecology. As a measure of growth efficiency (Blackman, 1919), a higher RGR means that an individual plant, or a species, can grow more efficiently when resources are limited. Thus, the trait has been considered to be a sensitive measure of competitive ability (e.g., Ford, 1975, 1984; Harper, 1977; Grime, 1979; Hara, 1984; Goldberg and Landa, 1991; Larocque and Marshall, 1993), and several competition indices have been developed based on the trait (Weigelt and Jolliffe, 2003). Cannell et al. (1984) suggested that the only way to assess intraspecific competition is to observe the distribution of RGR.

If RGR is indeed a good measure of competitive ability, then the trait should correlate positively with survivorship. Although several studies have examined the relation between RGR and survivorship (e.g., Sletvold, 2005), those studies were based mainly on short-term experiments with annual plants or seedlings of perennial plants as the subjects. For perennials, such as trees, competition is a long and continuing process. It would be desirable to know under what circumstances a higher RGR does ensure long-term survivorship (Question 1). Another gap in plant ecology literature concerns the long-term effect of initial density on survivors' RGR. Will survivors under intense competition (e.g., high density) be as efficient as those that experience less intense competition (Question 2)?

In this study, using a functional growth analysis approach (Hunt, 1982) in conjunction with nonlinear mixed-effects (NLME) modeling, our objective was to answer the two questions based on long-term (1955–2005) data from a Japanese cedar (*Cryptomeria japonica* D. Don) spacing trial. To answer Question 1, we formulated Hypothesis 1: survivors,

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on the average, are more efficient than those trees that did not survive. To test this hypothesis accurately requires the annual growth and survival status information of each tree, which is usually unavailable. The best that we can do, based on periodic inventory data, is to use a retrospective and sequential approach to determine whether trees that are still alive in the i th inventory grew more efficiently between the first and the $(i - 1)$ th inventories than those that died between the $(i - 1)$ th and the i th inventories. To answer Question 2, we formulated Hypothesis 2: since more resources are available, survivors that experience less intense competition are more efficient (Sletvold, 2005), on the average, than those that experience more intense competition (i.e., the mean RGR of survivors increases with increasing initial spacing).

We tested the two hypotheses based on the RGR of diameter at breast height (RGR_{DBH} , with DBH measured over-bark at 1.3 m above the ground). We used relative diameter growth rate (RGR_{DBH}) as a measure of overall growth efficiency. Previous studies have suggested that diameter growth is last in the carbon allocation priority ranking for trees (Waring, 1983; Waring and Pitman, 1985). Therefore, any growth in DBH implies that a tree has acquired enough resources to meet all other demands. RGR_{DBH} should therefore be an effective indication of a tree's overall growth efficiency (Larocque and Marshall, 1993; Larocque, 1998). However, Nilsson and Albrektson (1993) suggested that under intense competition for light, diameter growth becomes a high priority. Despite different views, both arguments suggest that RGR_{DBH} should be a robust measure of a tree's competitive ability.

2. Materials and methods

2.1. Description of the spacing trial

Japanese cedar, native to China and Japan, was introduced to Taiwan during the 1890s. It is one of the fastest growing plantation tree species in Taiwan. The spacing trial is located in the National Taiwan University Experimental Forest, Si-Tou Forest District of central Taiwan ($120^{\circ}47'E$, $23^{\circ}40'N$, elevation 1200 m).

The spacing trial was established in 1950, using 1-year cuttings with square spacings of 1, 2, 3, 4, and 5 m (i.e., initial densities of 10,000, 2500, 1111, 625, and 400 trees/ha, respectively). The experimental design was a completely randomized design with three plots (replicates) for each spacing. The area of each plot was 0.1 ha ($25\text{ m} \times 40\text{ m}$), with a 5-m spacing between plots. The entire spacing trial was established within a 3 ha area. The first inventory was conducted in 1955, with subsequent inventories taken in 1960, 1965, 1980, 1985, 1995, 2000, and 2005. We will refer to the years since establishment as “stand age”. While DBH was measured for all survived trees in every inventory, only a portion of the trees was measured for their heights in the first two inventories. The plots of 1-m spacing were thinned immediately after the 1965 inventory. Data from the thinned plots were excluded from this study.

2.2. Data

To minimize edge effects, only data from trees located approximately within the central 70% area of each plot were used (956 trees in total). As expected, trees grown under wider spacings were larger, on the average, at stand age 55 (Fig. 1), and the overall mortality rate increased with decreasing spacing (Table 1). Within each spacing, the mean growth trends were similar, except for one plot in the 3-m spacing (Fig. 1). For the 2-m and 3-m spacings, self-thinning began between stand ages 15 and 30. For the other two spacings, significant mortality did not occur until after stand age 35 (Fig. 2). However, self-thinning probably was not the only cause of mortality. Density-independent factors, such as typhoons, probably also contributed.

To test the first hypothesis, we began our analysis with the 1980 (fourth) inventory since we needed at least three points in time to fit a nonlinear growth model (described below). In addition, we focused only on spacings with at least five dead trees in a particular inventory. Thirteen data sets were so created—five for the 2-m spacing, four for the 3-m spacing, three for the 4-m spacing, and one for the 5-m spacing (Table 1). For the 3-m spacing at stand age 55, we used only data from one particular plot since all the dead trees were from that plot alone.

We used survivors in every inventory, starting from the 1965 (third) inventory, in order to test the second hypothesis (six data sets in all).

2.3. DBH growth model

Since the mean DBH growth trends over the 50-year period for all plots seemed to follow a simple asymptotic curve (Fig. 1), we adopted a two-parameter monomolecular model (Hunt, 1982; Zeide, 1993) of the form:

$$DBH(t) = \text{Asymp} \cdot [1 - \exp(-rc \cdot t)] \quad (1)$$

Fig. 1. Mean DBH growth trends for each spacing based on the survivors of each inventory. Dashed lines represent the plot-level trends, solid lines represent the spacing-level trends, and the error bars represent the plot-level means $\pm$ 1 S.E.

Table 1
Summary of mortality information for the data used in testing Hypothesis 1

Spacing	Inventory year (stand age)								Total dead trees	Total trees ^a	Mortality ^b
	1955 (5)	1960 (10)	1965 (15)	1980 (30)	1985 (35)	1995 (45)	2000 (50)	2005 (55)			
2-m	0 ^c	17	6	116^d	42	76	9	29	295	470	0.63
3-m	0	5	0	27	10	34	2	8	86	242	0.36
4-m	0	0	0	12	3	16	1	5	37	156	0.24
5-m	0	3	1	4	3	11	1	0	23	88	0.26
Total dead trees	0	25	7	159	58	137	13	42	441		

^a Number of trees tallied in the first inventory.

^b Overall mortality rate.

^c Table entries are the number of dead trees in each inventory.

^d Numbers in boldface indicate the data sets used to test Hypothesis 1.

to model DBH growth trends. In the model, $DBH(t)$ is DBH (cm) at stand age t (years), $Asymp$ is the asymptote (cm) of the model, and rc is the growth-rate coefficient (year^{-1}). This model implies that the rate of DBH growth is proportional to the difference between the ultimate DBH when the time approaches infinity (i.e., $Asymp$) and the current DBH (Erickson, 1976; Hunt, 1982). From Eq. (1), we can derive:

$$RGR_{DBH}(t) (\text{cm cm}^{-1} \text{ year}^{-1}) = \frac{rc \cdot \exp(-rc \cdot t)}{1 - \exp(-rc \cdot t)} \quad (2)$$

as the instantaneous relative DBH growth rate at stand age t (Hunt, 1982; Zeide, 1993). It is clear from Eq. (2) that RGR_{DBH} is independent of tree size and a monotonically decreasing function of rc . Because of the monotonicity, we used rc as a surrogate measure for RGR_{DBH} in this study.

2.4. Statistical analysis

Because the data were longitudinal, we used either a generalized nonlinear least-squares or a NLME modeling approach to analyze the data, depending on whether it was

necessary to treat any of the two parameters in the above monomolecular model as a mixed-effect. In mixed-effects modeling, a fixed effect represents the population average, whereas the associated random effect represents random deviations of individual trees from the fixed effect (Pinheiro and Bates, 2000). In all cases, a two-level modeling approach was used, with plots as the first level and individual trees within each plot as the second level (i.e., trees nested within a plot). Random variations at the plot level might be due to environmental heterogeneities, whereas random variations at the tree level might be due to within-plot heterogeneities or genetic differences (Dijkstra and Lambers, 1989).

Under NLME, let DBH_{ijk} be the observed DBH of the j th tree in the i th plot at the k th inventory, we modeled the DBH growth curve of an individual tree as

$$DBH_{ijk} = (Asymp_{\text{fixed}} + Asymp_i + Asymp_{i,j}) \times \{1 - \exp[-(rc_{\text{fixed}} + rc_i + rc_{i,j}) \cdot t_k]\} + \varepsilon_{ijk},$$

where $Asymp_{\text{fixed}}$, $Asymp_i$, $Asymp_{i,j}$, rc_{fixed} , rc_i , and $rc_{i,j}$ are the fixed-effect, the plot-, and tree-level random effects for the parameters $Asymp$ and rc , respectively, t_k is the stand age at the k th inventory, and ε_{ijk} is the within-group random error. In all of the models, stand age was the continuous covariate, and depending on the hypothesis, either the survival status (Hypothesis 1) or initial spacing (Hypothesis 2) was the discrete fixed-effect covariate.

For all models, we assumed that within-group errors distribute as $N(0, \sigma^2 I)$. For NLME models, we also assumed that: (1) all the random effects were normally distributed; (2) the random effects for different plots were independent; (3) for different trees within the same plot, their random effects were also independent; (4) the random effects and the within-group errors were independent of each other.

All statistical analyses were conducted using R software (R Development Core Team, 2006). We used the NLME package of R (Pinheiro et al., 2006) to fit generalized nonlinear least-squares and NLME models. To satisfy the independence and equal variance assumptions for the within-group errors, we used various options available in the NLME package (Pinheiro et al., 2006) until the residuals met the two assumptions. We used a likelihood ratio testing approach to determine the best random effect variance-covariance structure and to select the best

Fig. 2. The relation between the residual densities (log scale) and the quadratic mean DBH (log scale) for the data used in this study.

Table 2
Summary of the random effect structures for models used to test the two hypotheses

Hypothesis 1		Hypothesis 2	
Data set	Random effect structure	Data set	Random effect structure
2-m 1980	plot ^a = rc ~ 1, tree ^a = rc ~ 1	1965	plot = Asymp ~ 1
2-m 1985	plot = rc ~ 1, tree = Asymp ~ 1	1980	plot = Asymp + rc ~ 1, tree = Asymp ~ 1
2-m 1995	plot = rc ~ 1, tree = Asymp ~ 1	1985	plot = Asymp + rc ~ 1, tree = Asymp ~ 1
2-m 2000	plot = rc ~ 1, tree = Asymp ~ 1	1995	plot = Asymp + rc ~ 1, tree = Asymp ~ 1
2-m 2005	plot = rc ~ 1, tree = Asymp ~ 1		
3-m 1985	plot = pdDiag(Asymp + rc ~ 1), tree = Asymp ~ 1		
3-m 1980	No random-effect, model fitted by generalized nonlinear least-squares		
3-m 1995	plot = pdDiag(Asymp + rc ~ 1), tree = Asymp ~ 1		
3-m 2005	tree = Asymp ~ 1		
4-m 1980	plot = Asymp ~ 1		
4-m 1995	tree = Asymp ~ 1		
4-m 2005	tree = Asymp ~ 1		
5-m 1995	tree = Asymp ~ 1		

^a Plot or tree level random effect; pdDiag denotes that the corresponding random effect variance–covariance matrix is a diagonal one. Notations follow Pinheiro and Bates (2000).

options to account for the within-group variance heterogeneity and serial correlation (Pinheiro and Bates, 2000).

We used graphical methods (e.g., residuals diagnostic plots, the observed trend augmented by the fitted trend plots) and the squared Pearson's correlation coefficient (r^2) between the observed and the fitted means to assess the adequacy and performance of a final fitted model.

3. Results

3.1. Summary of the fitted models

For all data sets, at least one of the two parameters was treated as a mixed-effect, except in one case (Table 2). In almost all of the NLME fitted models, the random component of the parameter rc was present at the plot level, rather than at the tree level.

For NLME fitted models, all of the random effects met the normality assumption. For all of the fitted models, the residuals met the normality assumption, except in four cases. For those cases, departures from normality were mainly due to the presences of influential observations (“outliers”), which were likely caused by measurement or recording errors (e.g., sudden increases in DBH growth, trees were larger in the previous inventory). In those data sets, the distributions of the standardized residuals were symmetric, but heavy tailed. We chose to not delete the outliers or to transform those data, since such residual patterns tend to inflate the estimated within-group error variances. In turn, this leads to more conservative tests (Pinheiro and Bates, 2000).

In most of the cases, the within-group unequal variance was overcome by using a combination of an exponential variance function (varExp in NLME package) with stand age as the variance covariate, and a scaling of the within-group variance estimate for each plot or spacing (varIdent variance function in NLME package). For the majority of the fitted models, we accounted for their serial correlation structure by using either an AR(1), AR(2), ARMA(1,1), or ARMA(2,1) process.

3.2. Results for testing Hypothesis 1

The predicted mean growth trends from the 13 fitted models matched the corresponding observed trends closely (Figs. 3–6).

For the 2-m spacing, the estimated population mean growth-rate coefficients (i.e., the fixed-effect component of the parameter rc, rc_{fixed}) for the survivors were significantly smaller than those for the dead trees, except at stand age 30 (Fig. 7). For the 3-m spacing, we detected a significant difference in rc_{fixed} between the dead and the survived groups only at stand age 55. Compared to the dead trees, survivors at stand age 55 did have a more efficient diameter growth between stand ages 5 and 50. For the 4-m spacing, trees that were dead at either age 45 or 55 had rc_{fixed} values that were significantly higher from stand age 5 up to stand age 35 or 50, respectively, than those of the survivors. For the widest spacing, results from the only data set showed that trees that died between stand ages 35 and 45 had a significantly lower rc_{fixed} between stand ages 5 and 35 than that of the survivors.

As expected, the group with a significantly lower rc_{fixed} leading to the i th inventory also had a greater mean DBH in the $(i - 1)$ th inventory (Figs. 3–6). The dead groups all had higher rc_{fixed} values (except in two cases) and larger standard errors (Fig. 7). The larger standard errors might be due to both the limited numbers of dead trees in the data sets and density-independent factors.

3.3. Results for testing Hypothesis 2

The predicted trends from the six fitted models all matched the corresponding observed trends quite satisfactorily (Fig. 8). As expected, the mean DBHs for the wider spacings were greater than those for the narrower spacings throughout the inventories (Fig. 8).

Between stand ages 5 and 10, rc_{fixed} values for the survivors were about the same, regardless of the initial spacings (Fig. 9). During that period, the survivors of the 2-m spacing actually

Fig. 3. Observed plot-level mean DBH trends augmented with the fitted mean trends for the 2-m spacing data sets used to test Hypothesis 1. In each panel, solid lines represent the observed trends, dashed lines represent the fitted trends, and the error bars represent the observed means $\pm$ 2S.E. For each fitted model, the squared Pearson's correlation coefficient (r^2) between the observed and the fitted plot-level means is also provided.

Fig. 4. Observed plot-level mean DBH trends augmented with the fitted mean trends for the 3-m spacing data sets used to test Hypothesis 1. Refer to Fig. 3 for the legends.

had the lowest rc_{fixed} value and the smallest standard error. At stand age 30, the survivors in the two wider spacings had smaller rc_{fixed} values. However, as the trees aged, only the survivors in the 5-m spacing had a significantly smaller rc_{fixed} than that of the survivors in the other spacings until stand age 50, at which time rc_{fixed} values for all of the survivors were about the same, except for those in the 3-m spacing.

For all spacings, the standard errors for the rc_{fixed} values declined through time, which suggests that the mean diameter growth efficiency for the survivors in each spacing became less variable as trees aged (Fig. 9).

4. Discussion

4.1. Hypothesis 1: survivors are more efficient

Are survived Japanese cedars more efficient? Based on the only data set from the widest spacing, that certainly was not the case. Instead, the opposite was true. For the other spacings,

the survivors were no more efficient in diameter growth prior to the onset of self-thinning. Once self-thinning began, the survivors were more efficient indeed (Figs. 2 and 7).

Thus, our results partially supported this hypothesis. When density is low or competition is weak, a higher RGR_{DBH} does not guarantee survival. Under such circumstances, density-independent factors are likely to be the main cause of mortality. Since Taiwan is in a typhoon-prone area, we suspected that disturbance might be an important cause of mortality. When density was the main cause of mortality, however, Japanese cedars with a lower rc_{fixed} value (i.e., a higher RGR_{DBH}) did have a higher likelihood to survive (Fig. 7). Our findings suggest that self-thinning eliminates Japanese cedars that were less efficient in diameter growth. The findings confirm the assertion made by Ford (1984) and Perry (1985), and provide an answer as to the cause of mortality in self-thinning (Thomas and Weiner, 1989). Previous studies suggested that competition reduces the RGR of small trees relative to that of larger trees (Ford, 1975, 1984; Cannell et al., 1984; Perry, 1985; Larocque

Fig. 5. Observed plot-level mean DBH trends augmented with the fitted mean trends for the 4-m spacing data sets used to test Hypothesis 1. Refer to Fig. 3 for the legends.

Fig. 6. Observed plot-level mean DBH trends augmented with the fitted mean trends for the 5-m spacing data sets used to test Hypothesis 1. Refer to Fig. 3 for the legends.

and Marshall, 1993; Larocque, 1998). Results from the 2-m spacing confirm that assertion, since all dead Japanese cedars after the onset of self-thinning were small trees that had a lower RGR_{DBH} .

In our data, 15 years separated the third and fourth inventories. That was also the period during which heavy self-thinning took place in the higher density plots (about 25% of the trees in the 2-m spacing died during that time). Unfortunately, without data from that period, we could only conclude that, for trees in the higher density plots died during that period, they were as efficient as the survivors were during the first 15 years (Fig. 7).

Results from the 3-m spacing were the exceptions to the general trend presented above. Density-independent factors might be the cause. For that spacing, the plot-level mean DBHs for trees that died between stand ages 30 and 35 or between 35 and 45 all had large standard errors at stand age 30 or 35, respectively (Fig. 4). This indicated that even relatively large Japanese cedars died during the corresponding periods. Since large trees had higher growth efficiencies in general, their

Fig. 7. Estimated population mean growth-rate coefficients, rc_{fixed} , of the survived (●) and dead (○) trees for each spacing in each inventory, with the error bars representing means $\pm$ 2S.E. The number above a set of error bars is the P -value that the estimated rc_{fixed} values of the two groups are equal.

deaths would increase the estimated standard errors in rc_{fixed} . On the other hand, density-dependent mortality was probably more important since the rc_{fixed} values were still higher for the dead trees (Fig. 7).

It is often difficult to weigh the relative importance of density-dependent and density-independent mortalities. If we can assume that the main victims of self-thinning are trees with low growth efficiencies, as this study and others have demonstrated, then by comparing the estimated rc_{fixed} values and the associated standard errors between the dead trees and the survivors, we might be able to determine the relative importance of the two types of mortality. When density-dependent mortality is the main, or only, cause of tree deaths, we expect not only a larger rc_{fixed} for the dead trees, but also a smaller estimated standard error (e.g., 2-m spacing in Fig. 7). In contrast, if random mortality is the main cause of deaths, we expect both the rc_{fixed} values and the standard errors between the survived and the dead trees to be similar (e.g., 5-m spacing in Fig. 7). Based on this reasoning, we concluded that density-dependent mortality was the main cause of deaths over the 50-year period for the spacing trial.

In general, Japanese cedars recorded as dead in a particular inventory had much slower growth trends leading to that inventory (especially the 2-m spacing, Fig. 3). Correspondingly, there was a decreasing trend for both rc_{fixed} values and standard errors for the survivors in each spacing (Fig. 7). This result suggested that Japanese cedars died because they were unable to grow efficiently over an extended period. Otherwise, the average growth trends of the dead and survived trees should match closely, except at the end. This finding supports the competition-induced mortality modeling approach currently

used in several gap models (e.g., Botkin, 1993), in which a tree dies when it fails to meet the minimum required annual diameter increment for several consecutive years.

4.2. Hypothesis 2: survivors' RGR_{DBH} increases with increasing initial spacing

What is the long-term effect of initial spacing on survivors' RGR_{DBH} ? During the first 15 years after stand establishment, when competition was likely to be weak, initial density had no effect on survivors' diameter growth efficiency. It is evident that as time progressed, Japanese cedars that were grown in a less stressful environment had higher efficiencies since more resources were available to them (Fig. 9). However, with the onset of self-thinning, survivors that experienced more intense competition also became efficient in diameter growth. As the stands matured, all survived Japanese cedars had about the same RGR_{DBH} , regardless of the initial spacing. Thus, our results partially supported the second hypothesis. However, it would be incorrect to simply conclude that initial density had little, or no, long-term effect on survivors' RGR_{DBH} .

The rc_{fixed} values of survivors that experienced more intense competition declined (i.e., RGR_{DBH} increased) through time (Fig. 9), likely the result of re-prioritizing carbon allocation to height and diameter growth (Nilsson and Albrektson, 1993). Trees grown under high density must first allocate carbon to height growth in order to survive. In order to grow tall, trees must also allocate carbon to radial growth. The declining trends for both rc_{fixed} and the associated standard errors supported the above statement (Fig. 9). In that respect, intense intraspecific competition likely thins out Japanese cedars that were unable to make such an adjustment. In contrast, the average RGR_{DBH} for survivors in the widest spacing peaked around age 30, and then declined (Fig. 9), probably because of the accumulation of non-productive tissues (Perry, 1985). Thus, two trends in survivors' RGR_{DBH} emerged from our study. Japanese cedars experienced more intense competition gaining diameter growth efficiency through time, whereas those that experienced less intense competition lost diameter growth efficiency through time. These two trends led to the observed results.

4.3. Other considerations

For trees, the best measure of growth efficiency probably is the production efficiency, that is, total biomass increase per unit of leaf area (Reid et al., 2004; Adegbi et al., 2005). However, production efficiency is difficult to measure accurately in practice. Relative height growth rate is also a sensitive measure of competitive ability, as height is critical to tree survival (Cannell et al., 1984). However, for large trees their heights are also difficult to measure accurately. In this study, we adopted RGR_{DBH} as a measure of the overall growth efficiency, based on the assumptions that radial growth is the lowest in carbon allocation priority ranking (Waring, 1983; Waring and Pitman, 1985), and that trees

Fig. 8. Observed mean DBH trends augmented with the fitted mean trends for the six data sets used to test Hypothesis 2. In each panel, dotted lines represent the observed plot-level trends, solid lines represent the observed spacing-level trends, and dashed lines represent the fitted spacing-level trends. For each fitted model, the squared Pearson's correlation coefficient (r^2) between the observed and the fitted spacing-level means is also provided.

experiencing intense competition might make radial growth a high priority (Nilsson and Albrektson, 1993). Both views suggest that RGR_{DBH} should be a sensitive measure of competitive ability, and our results supported the contention,

as the RGR_{DBH} of the survivors in a crowded environment increased as competition intensified.

Among the individuals within a population, variations in RGR could be due to random variations (e.g., due to genetic

Fig. 9. Estimated population mean growth-rate coefficients, rc_{fixed} , trends of each spacing based on the survivors in each inventory, with the error bars representing means $\pm$ 2S.E. At a given stand age, estimated rc_{fixed} values marked by different letters differ significantly ($P < 0.05$).

differences, Dijkstra and Lambers, 1989), competition, or both. Using a mixed-effect modeling approach, we were able to test explicitly whether the parameter rc , hence RGR_{DBH} , should be considered as a random effect at the tree level, and found that, for the majority of the cases, it should not (Table 2). Since the trees planted in the spacing trial were cuttings from a population of Japanese cedar, the result is no surprise. At that level, the “variation” in rc can be explained by either survival status or initial spacing. Thus, our findings supported the assertion that one could assess intraspecific competition by examining the distribution of RGR within a stand (Ford, 1975; Cannell et al., 1984; Wyszomirski et al., 1999). The parameter did vary among the plots in some instances (Table 2), however. This suggests that, even in a small area, environmental heterogeneities could still exist and affect tree growth (Fajardo and McIntire, 2007; Fox et al., 2007a,b). Nevertheless, we suggest that future studies should differentiate among the causes of variations in RGR .

Several plant competition or growth models used the RGR_{DBH} of isolated individuals as the basis on which to derive RGR_{DBH} for individuals in a crowded environment (e.g., Merriam et al., 1995) or to detect the mode of competition (e.g., Hara, 1992), as suggested by Hypothesis 2. However, our study has shown that the hypothesis might not hold, at least in the early and late stages of Japanese cedar stand development. Thus, we might want to consider other approaches in modeling the growth of individuals in a crowded environment.

Acknowledgements

Funding for this study was partially supported by National Science Council of Taiwan (NSC 94-2621-B-002-014). We deeply appreciate NTU Experimental Forest for permission to the use the data and for providing field supports. We also thank two reviewers for their comments.

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