Development of size hierarchies prior to the onset of density-dependent mortality in irrigated and fertilized loblolly pine stands

U. Nilsson, T.J. Albaugh, and H.L. Allen

Abstract: Nine years of growth and stand development were investigated in a 2 × 2 nutrient and water factorial experiment with four replications. The study was located on an infertile, excessively drained sandy site in Scotland County, North Carolina, U.S.A. The hypothesis tested was that increased growth following irrigation and fertilization would increase the rate at which size hierarchies develop. The hypothesis was investigated by comparing the coefficient of variation (CV) of stem volume over time and examining the stem volume relative growth rate (RGR) of trees of different initial size in control and irrigated + fertilized stands. Even though there were no statistically significant differences in CV among treatments, there was a tendency for increased CV over time in the control stands, whereas CV initially increased, then decreased, and became constant in the irrigated + fertilized plots. The lack of increase in CV in the irrigated + fertilized plots was explained by unusually low variation in RGR across tree size classes and negative relation of RGR and size. Therefore, the hypothesis that increased growth resulted in a more rapid development of size hierarchies was rejected. The high RGR of small trees in the irrigated + fertilized treatment could not be explained by differences in vertical distribution of needles compared with the control treatment. Small trees in the irrigated + fertilized plots were overtopped by neighboring trees to the same degree as small trees in the control plots.

Résumé : La croissance et le développement d'un peuplement ont été étudiés au bout de 9 ans à l'aide d'un dispositif factoriel comportant deux quantités de nutriments et deux intensités d'irrigation avec quatre répétitions. Le dispositif était situé sur un sol sableux non fertile avec un drainage excessif dans le comté de Scotland en Caroline du Nord, aux États-Unis. L'objectif consistait à tester l'hypothèse selon laquelle une meilleure croissance provoquée par l'irrigation et la fertilisation entraînerait une augmentation du taux de hiérarchisation basée sur la dimension. L'hypothèse a été testée en comparant le coefficient de variation (CV) du volume de la tige dans le temps et en examinant l'accroissement relatif (AR) du volume de la tige chez des arbres de dimension initiale différente dans des peuplements témoins et dans des peuplements irrigués et fertilisés. Bien que le CV ne diffère pas de façon statistiquement significative entre les traitements, il a tendance à augmenter avec le temps dans les peuplements témoins alors qu'il augmente au début puis diminue et se stabilise dans les parcelles irriguées et fertilisées. L'absence d'augmentation du CV dans les parcelles irriguées et fertilisées s'explique par la variation exceptionnellement faible du taux relatif de croissance entre les différentes classes de dimension des arbres et la relation négative entre l'AR et la dimension. Par conséquent, l'hypothèse selon laquelle une augmentation de croissance entraîne le développement plus rapide d'une hiérarchisation des dimensions est rejetée. L'AR élevé des petites tiges dans les parcelles traitées ne peut être expliqué par les différences dans la distribution verticale des aiguilles comparativement aux parcelles témoins. Les petits arbres sont dominés par les arbres voisins autant dans les parcelles témoins que dans les parcelles traitées.

[Traduit par la Rédaction]

Introduction

Conifer stands often undergo a predictable development of stand structure (Mohler et al. 1978; Knox et al. 1989). Soon after planting, variation in seedling size and growth rate is introduced because of differences in genetics, heterogeneous planting spots, seedling quality, damage, planting quality, etc. (Weiner 1985). As the trees grow larger, they begin to compete with each other, the variation in tree size that was introduced in the seedling stage is increased, and size hierarchies develop. Later, as self-thinning begins, stand variation remains constant or decreases as the smallest trees in the stands are removed from the population (Mohler et al. 1978; Weiner and Thomas 1986).

Competition between neighboring trees is a continuum between one- and two-sided competition (Weiner 1990). Two-sided competition means that competition is symmetric, and trees interfere with one another in proportion to their size. In contrast, one-sided competition or resource depletion is asymmetric; large individuals are able to capture a greater share of a limiting resource than would be expected according to their size (Weiner 1990). Thus, in symmetric two-sided competition, there should be no correlation, or a negative correlation, between relative growth rate (RGR) and size

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within a crowded population (Weiner 1990), while RGR should be positively correlated to size in asymmetric, one-sided competition (Stoll et al. 1994).

Size hierarchies are characterized by variation in tree size, typically with many small and few large trees and by large individuals representing a large proportion of stand biomass (Weiner and Solbrig 1984). Several authors have argued that size hierarchies result from one-sided competition for light, because competition for light often involves overtopping; large individuals are able to shade smaller ones, while the shading from small individuals on larger ones is insignificant (Weiner 1990; Nilsson 1994; Newton and Jolliffe 1998). However, it is also possible to envisage one-sided competition below ground, if the soil is heterogeneous and large individuals are proportionately more successful in relation to their size in obtaining pockets of a limiting resource (Thomas and Weiner 1989; Weiner et al. 1997). Conversely, competition above ground for light may be two sided, if small individuals maintain height growth and avoid overtopping (Lieffers and Titus 1989), or in a species with deep crowns, where small trees shade the lower portion of the crowns of large individuals (Weiner et al. 1997).

It has been generally emphasized that fertilizing stands with nutrient limitations will accelerate stand development (Miller 1981). Consequently, fertilized stands will reach the point where individuals start to interfere with one another, and the development of size hierarchies will start earlier (Harper 1977). Weiner (1985) found an increase in size inequality of herbaceous plants after fertilization. Lieffers and Titus (1989) found increased size inequality for shoot, root, and total biomass after fertilization for white spruce, while fertilization only affected inequality of root biomass in lodgepole pine. They concluded that interference from neighbors invoked a plastic response in biomass allocation and that lodgepole pine was more plastic than white spruce. Morris and Myerscough (1991) found that the onset of self-thinning was increased by improved nutrition if time was used as a base but that self-thinning was reduced by increased nutrition if standing biomass was used as a base (i.e., individuals in the fertilized populations could grow larger per ground area before self-thinning began).

The objective of the present study was to examine the effect of irrigation and fertilization on the development of size hierarchies prior to density-dependent mortality in a loblolly pine (*Pinus taeda* L.) stand on an infertile site in the southeastern United States. The hypothesis tested was that increased growth following irrigation and fertilization would accelerate the development of size hierarchies.

Material and methods

Study sites

The study was established in the Sandhills of Scotland County, North Carolina (35°N, 79°W) on a flat, infertile, excessively drained, sandy, siliceous, thermic Psammentic Hapludult soil. Annual precipitation averages 1210 mm (30-year mean). The site was hand planted on a 2 × 3 m spacing with loblolly pine in 1985 after felling of the previous natural longleaf pine (*Pinus palustris* Mill.) stand and application of Velpar™ grid balls (17 kg·ha^{-1}).

Table 1. Mean height, diameter, and length of the living crown and basal area, volume, and coefficient of variation before (December 1991) and after (December 2000) the 9-year study period.

Year	Control	Irrigated	Fertilized	Irrigated + fertilized
Mean height (m)				
1991	3.44*a*	3.31*a*	3.36*a*	3.31*a*
2000	9.10*c*	10.2c	11.9*b*	13.2*a*
Mean diameter (cm)				
1991	4.71*a*	4.47*a*	4.47*a*	4.45*a*
2000	13.8*b*	15.1*b*	18.3*a*	19.5*a*
Basal area ($m^2 \cdot ha^{-1}$)				
1991	2.51*a*	2.26*a*	2.32*a*	2.23*a*
2000	18.5*b*	21.7*b*	32.9*a*	35.3*a*
Volume ($m^3 \cdot ha^{-1}$)				
1991	13.5*a*	13.2*a*	13.5*a*	12.8*a*
2000	88*b*	111*b*	189*a*	224*a*
Mean length of living crown (m)				
1991	3.11*a*	2.96*a*	2.99*a*	2.98*a*
2000	5.53*d*	6.05*c*	6.64*b*	7.10*a*
Coefficient of variation (volume)				
1991	25.7*a*	23.8*a*	26.8*a*	29.2*a*
2000	46.0*a*	42.9*a*	41.4*a*	42.7*a*

Note: Values within a row with the same letter are not significantly different ($p > 0.05$).

Treatments

Sixteen 50 × 50 m treatment plots with 30 × 30 m measurement plots centered in the treatment plot were established in January 1992 in the 8-year-old stand. Stand characteristics at the start of the experiment are given in Table 1. Treatments were installed in a 2 × 2 factorial combination of nutrition and water additions replicated four times in a randomized block design. Thus, the experiment contained four treatments: (*i*) control, (*ii*) irrigation only, (*iii*) fertilization only, and (*iv*) irrigation + fertilization. At the start of the experiment, no statistical significant differences in tree height or diameter were found between plots (Table 1). A 10-m buffer zone separated the treatment plots, and in the case where the buffer was less than 10 m, a 150 cm deep trench between the treatment plots was dug, lined with plastic, and refilled. Complete control of non-pine vegetation in the treatment plots has been maintained since 1992 through a combination of mechanical and chemical (glyphosate) methods.

The nutrition treatments, which began in March 1992, were (*i*) "optimum nutrition" through fertilization or (*ii*) no addition. Optimum nutrition was defined as (*i*) maintaining a foliar nitrogen (N) concentration of 1.3–1.4%; (*ii*) maintaining foliar macronutrient concentration/N concentration ratios of 0.10 for phosphorus (P), 0.35 for potassium (K), 0.12 for calcium (Ca), and 0.06 for magnesium (Mg); and (*iii*) maintaining foliar boron (B) concentration greater than 12 ppm. Foliar nutrient status was monitored monthly, and fertilizers were applied annually to meet the target concentrations.

Water treatments, which began in April 1993, were (*i*) natural precipitation and (*ii*) natural precipitation plus irrigation applied to meet the target soil water content. The target was set as maintaining soil water content greater than 3.0 cm soil

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water content in the upper 50 cm of soil (40% available water content). Irrigation was applied using Rainbird irrigation nozzles positioned on 35 cm risers spaced on a 10 × 10 m grid. For more details on the nutrition and irrigation treatments, see Albaugh et al. (1998).

Measurements

In December of each year from 1991 (prior to treatment) to 2000, measurements of diameter at breast height (D, 1.4 m), height (H), and live crown length (L) were made on all trees in each plot (≈100 trees/plot). Individual stem volume was estimated by (Shelton et al. 1984):

$$V = 0.007\,48 + (0.000\,035\,3 \times D^2 \times H)$$

where V was total outside bark volume in cubic metres.

In April 1999, branch diameters of 25 trees in the control plots and 30 trees in fertilized and irrigated plots were measured. Trees were selected to represent the range in heights for each treatment. Branch diameters of all branches on each tree were measured to the nearest millimetre with a caliper. Measurements were made 2 cm from the stem. Individual branch foliage biomass was estimated by applying these branch measures to the foliage biomass equation:

$$FW = 1.198\,e^{-13.107 + 2.696\ln(Bd) + 4.816\ln(DfT) - 0.537[\ln(DfT)]^2 - 0.0302Age + ADJ}$$

where FM is foliage masss per branch, Bd is branch base diameter, DfT is distance from top, Age is tree age, and ADJ is the treatment adjustment term. ADJ was calculated as

$$\begin{aligned} ADJ = {} & 3.253C - [0.248\ln(Bd)]C + [0.124\ln(DfT)]C - [1.208\ln(DfT)]C + [0.104(\ln(DfT))^2]C - (0.023Age)C \\ & - [0.248\ln(Bd)]I + [0.124\ln(DfT)]I - (0.023Age)I + 3.254F - [1.208\ln(DfT)]F + [0.104(\ln(DfT))^2]F \end{aligned}$$

where Bd, DfT, and Age are as above and C, I, and F are indicator variables for no irrigation or fertilization (control), irrigation, and fertilization treatments, respectively. The indicator variables were assigned values of 1 if the treatment was applied and 0 otherwise.

Analysis of size hierarchy development

Treatment effects on mean height, mean diameter, stem volume, and basal area per hectare and coefficient of variation (CV) before the start of the study and at the end of the study period were examined using analysis of variance. Differences among treatment means were evaluated with Tukey's honestly significant difference (HSD) mean separation test when the treatment effects were significant (p = 0.05) in the analysis of variance. The CV for stem biomass was calculated for each plot, and the mean CV per year was calculated for each treatment. For each plot and year, the yearly rate of change in CV was calculated. A one-sided t test against the null hypothesis of no change was then performed on the yearly rate of change using all appropriate plots. Relative stem biomass growth rate (RGR = $\ln(V_n) - \ln(V_{n-1})$) was calculated for 10 stem-volume classes per treatment, and the effect of initial stem volume on RGR was examined using correlation analysis. Foliage biomass is reported in height layers for the 25% smallest and tallest trees per treatment.

Results

Effects on growth and stand characteristics

During the 9-year study period, height, diameter, basal area, and stem volume growth were increased by the fertilization and irrigation treatments (Table 1). Cumulative differences in stem volume ranged from 88 $m^3 \cdot ha^{-1}$ for controls to 224 $m^3 \cdot ha^{-1}$ for irrigation + fertilization (Table 1). Both fertilization and irrigation + fertilization treatment effects were statistically significant but not the irrigation treatment. In addition, height growth was significantly higher for the irrigation + fertilization treatment than for the fertilization treatment. Mean length of the living crown was significantly increased by all treatments and treatment combinations, while there was no significant differences among CVs at the end of the 9-year study period (Table 1).

Development of stand structure

The stand structure as described by the relationship between CV and standing stem volume varied during the 9 years of the study (Fig. 1). For all treatments, CV increased significantly during 1992 and 1993, the first and second growing season after the start of the experiment (Fig. 1). For the control, CV increased during the whole 9-year period, but the yearly rate of change was not significant in 1999. For the irrigation treatment, CV increased significantly during 1992–1996. After that, the yearly rate of change in CV was not statistically significantly different from zero except for 1997 when a significant positive change was recorded. After the initial increase in CV during 1992 and 1993, change of CV in the fertilization was not significantly different from zero. During the 1994 growing season, the CV in the irrigation + fertilization treatment decreased significantly, whereas it stayed relatively constant (yearly rate of change not significantly different from zero) during the 1995–2000 growing seasons (Fig. 1).

The stem volume RGR was positively correlated with initial stem volume for all treatments during the first 2 years of the study (Table 2), i.e., RGRs were lower for the small tree classes than for larger ones (Fig. 2). However, this correlation decreased over time. For the control plots, RGR was positively correlated with tree size during all years except the 1998 growing season (Fig. 2, Table 1). In the irrigated plots, RGR was positively correlated with stem biomass during the 1992–1995, 1997, and 2000 growing seasons and relatively constant during the other years. In the fertilized

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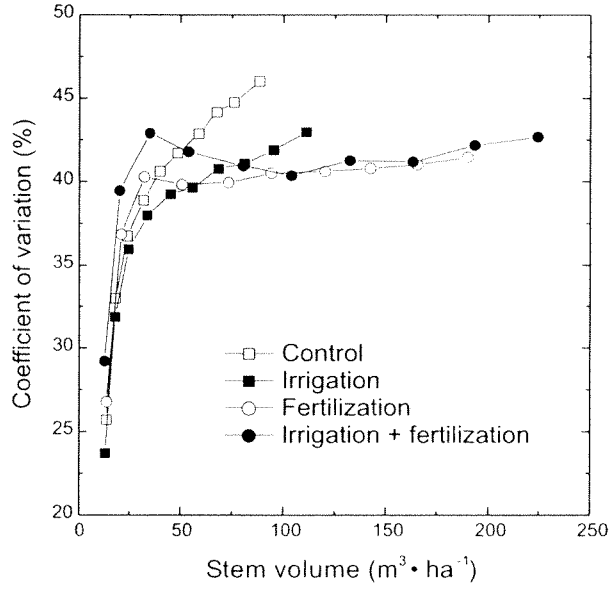
Table 2. Year- and treatment-specific Pearson's correlation coefficients (ρ) for relative stem volume growth rate with stem volume at the beginning of the growing season.

Year	Control	Irrigated	Fertilized	Irrigated + fertilized
1992	0.6142 (0.0001)	0.6232 (0.0001)	0.6098 (0.0001)	0.6117 (0.0001)
1993	0.4617 (0.0001)	0.3973 (0.0001)	0.3883 (0.0001)	0.4034 (0.0056)
1994	0.3603 (0.0001)	0.3167 (0.0001)	0.1070 (0.0001)	–0.0651 (0.1792)
1995	0.2701 (0.0001)	0.2014 (0.0001)	0.0653 (0.1660)	–0.0507 (0.2975)
1996	0.2292 (0.0001)	0.0836 (0.0808)	0.1081 (0.0224)	–0.0391 (0.4242)
1997	0.2839 (0.0001)	0.2285 (0.0001)	0.0811 (0.0887)	0.0987 (0.0434)
1998	0.1187 (0.0187)	0.0126 (0.7953)	–0.0049 (0.9190)	–0.0530 (0.2817)
1999	–0.0001 (0.9999)	0.0303 (0.5531)	0.0904 (0.0591)	–0.0285 (0.5654)
2000	0.1509 (0.0010)	0.1322 (0.0066)	0.1995 (0.0001)	0.0979 (0.0487)

Note: The p values for the test of the null hypothesis (H_0) that $\rho = 0$ are given in parentheses.

Fig. 1. Coefficient of variation (CV) of stem biomass versus standing stem volume ($m^3 \cdot ha^{-1}$) for the various irrigation and fertilization treatments. Measurements were made each December from 1991 to 2000, and treatments began in the 1992 growing season.



treatment, the RGR was positively correlated with stem volume during the 1992–1994, 1996, and 2000 growing season. In the irrigated + fertilized plots, RGR was not correlated with stem volume during the 1994–1996 and 1998–1999 growing seasons, while there were weak positive correlations during the 1997 and 2000 growing seasons (Fig. 2, Table 2).

Relative stem biomass growth rate decreased with time for all treatments. Mean RGR for the irrigated + fertilized treatment reached a maximum in 1993 (0.53 $m^3 \cdot m^{-3} \cdot year^{-1}$) and decreased thereafter to a minimum in 1998 (0.14 $m^3 \cdot m^{-3} \cdot year^{-1}$). The corresponding values for the control treatment were 0.28 and 0.14 $m^3 \cdot m^{-3} \cdot year^{-1}$ (Fig. 2).

For comparison, absolute growth rate of 10 size-classes for the control and irrigated + fertilized are shown in Fig. 3. Mean absolute growth rate per tree varied between 3.9 and 10.6 dm^3 for control and between 5.9 and 28.4 dm^3 for irrigated + fertilized. Absolute growth rates also varied among years. In 1996, the growth rate decreased for irrigated + fertilized as a result of loss of needles in a hurricane in the autumn of 1995. In 1998, growth of irrigated treatments was higher than for not irrigated because of a dry period.

A comparison of the vertical distribution of foliage biomass in spring 1999 for the smallest and tallest trees in the control and irrigated + fertilized treatments showed that the smallest trees were similarly overtopped by larger neighbors in both treatments (Fig. 4). The mean middle of the crown (defined as the height where half of the cumulative foliage biomass for all trees was found below) was at 5.1 and 8.0 m for control and irrigated + fertilized plots, respectively. The smallest trees in the control plots had about the same portion of foliage biomass above the middle of the crown as the smallest trees in irrigated + fertilized plots (18.1 ± 3.9% (mean ± SE) and 18.2 ± 5.4% for control and irrigated + fertilized plots, respectively).

Discussion

The hypothesis that the rate at which size hierarchies develop would be increased by fertilization was not confirmed by this study. In fact, the results suggest that the rate of size hierarchy development was decreased by the fertilization treatment. Typically, size hierarchies are decreased when self-thinning begins, because mortality is often concentrated among the smallest trees in the stand (Knox et al. 1989). However, in this study little mortality was found. On average for all years, mortality was 1.6 and 3.1% for the control and irrigated + fertilized treatments, respectively. Thus, density-dependent mortality cannot be used as an explanation why size hierarchies did not increase in the fertilized plots. Instead, the lack of increase in size hierarchies was explained by unusually low variation in relative growth rate across tree size classes. Generally, the increase in size hierarchies is due to greater relative growth rate of large individuals compared with smaller ones (Weiner 1990). In this study, lower relative growth rate of small trees was only found in the beginning of the study period. However, this reduction in relative growth rate was probably not caused by competition for light between neighboring trees, since the canopies were not closed at that time (see below).

There are several possible explanations as to why the small trees in fertilized plots were able to have about the same or greater relative growth rate as larger ones. First, the smallest trees had about 20% of their needle biomass in the

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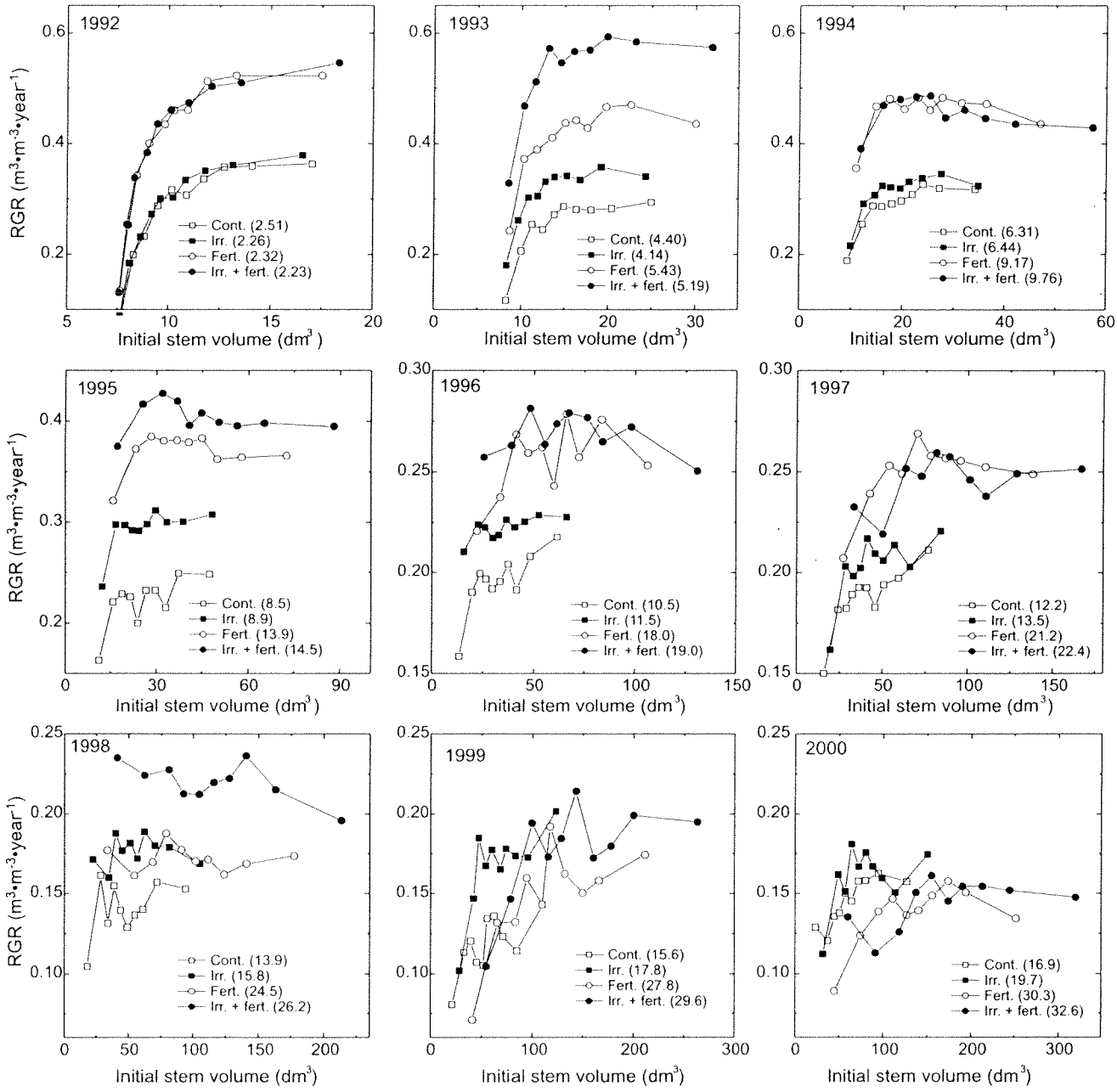
Fig. 2. Relative stem volume growth rate (RGR, $m^3 \cdot m^{-3} \cdot year^{-1}$) for the various fertilization and (or) irrigation treatments during the 1992–2000 growing seasons. RGR was calculated for 10 stem-volume classes based on pre-growing season stem biomass. Basal area ($m^2 \cdot ha^{-1}$) at the beginning of each growing season is shown within parentheses.



upper part of the stand canopy. Therefore, they were not completely overtopped and competition for light may not have been a serious problem, especially since the sun angle is high during a great proportion of the growing season. Second, Nilsson and Albrektson (1993) found that suppressed trees allocated more of their annual aboveground growth to stemwood than dominant trees. Thus, the inequality in total aboveground biomass may have been larger than the inequality in stemwood biomass. Third, allocation to belowground growth is less in crowded stands than in less crowded situations (Pearson et al. 1984; Newton and Cole 1991; Nilsson and Albrektson 1993) indicating that trees may respond to competition for light by allocating more biomass to aboveground growth. In addition, Lieffers and Titus (1989) showed that inequality in root biomass was higher than inequality in aboveground biomass for crowded lodgepole pine seedlings, indicating that small suppressed trees were able to maintain aboveground growth by reducing allocation to roots. Albaugh et al. (1998) developed regression functions for different tree components including stem, branches, and coarse roots for trees that were harvested in 1992 prior to treatment, 1994, and 1996 in the various treat-

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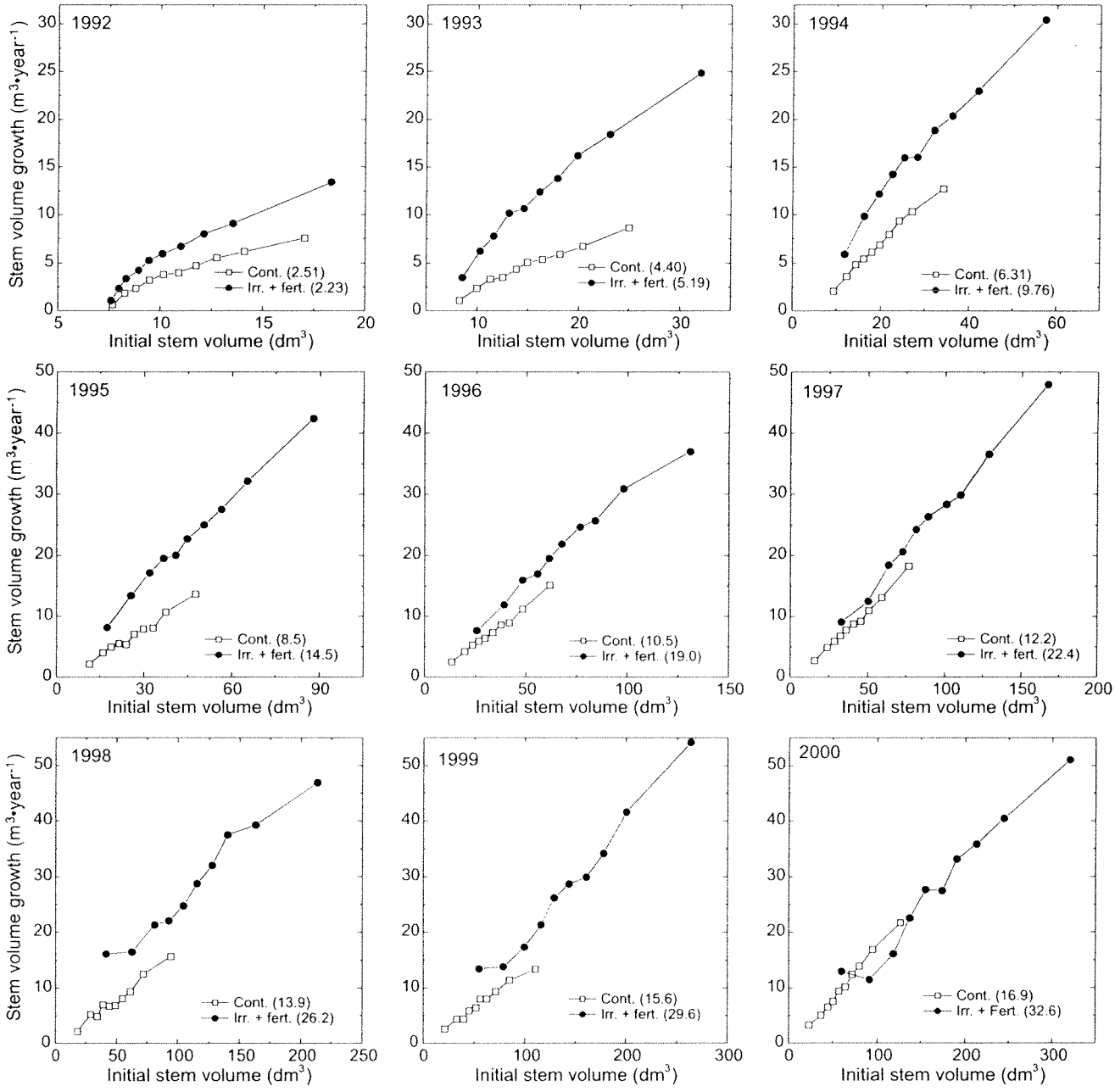
Fig. 3. Stem volume growth ($m^3 \cdot year^{-1}$) for the control and irrigation + fertilization treatments during the 1992–2000 growing seasons. Stem volume growth was calculated for 10 stem-volume classes based on pre-growing season stem biomass. Basal area ($m^2 \cdot ha^{-1}$) at the beginning of each growing season is shown within parentheses.



ments. Estimates from these regression functions indicated less allocation to belowground biomass for small trees than for large trees. Fourth, the fertilization and irrigation treatments probably resulted in a more equal access to the major limiting soil resources among the various tree classes.

The constant or decrease in CV with time and the lack of positive correlation between tree size and relative growth rate suggests that competition between trees in the fertilized and irrigated plots was two sided (Weiner 1990). It has been hypothesised that two-sided competition is the outcome of competition below ground for water and (or) nutrients (Weiner 1990; Nilsson 1994). However, it was not possible to verify that hypothesis in the present study. Competition above ground may be two sided when small trees are slightly overtopped by larger ones as was the case in this study (Lieffers and Titus 1989). Thus, it is likely that the reduction in individual tree relative growth rate for trees of equal initial size observed during the course of the experiment was due to competition for both above- and belowground resources.

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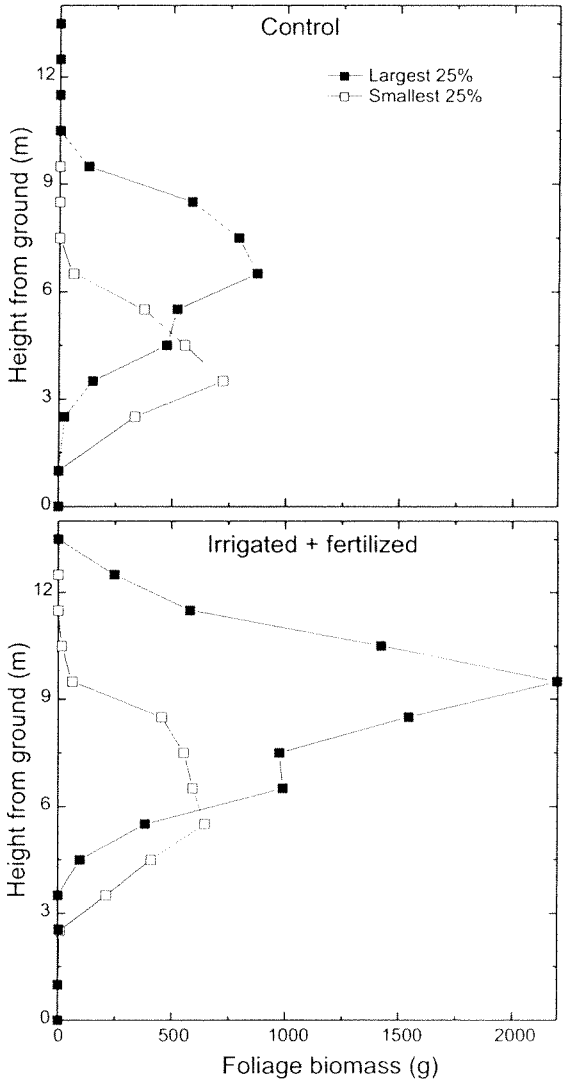
Fig. 4. Mean foliage biomass in spring 1999 for 1-m height classes for the smallest 25% and the largest 25% trees in the control (upper panel) and irrigated + fertilized (lower panel) treatments. Each tree class was represented by six to eight trees.



During the first 2 years after the start of the experiment, the RGR was positively correlated with the size of the tree. We do not think that this was caused by one-sided competition for light between trees, because the trees were too small to shade one another. Also, the relative growth rate became more uniform on control plots with time. If light was an important factor, the RGR–size relationship would have been expected to remain positive. There are several possible alternative explanations for the initial low RGR of the small trees. It has been shown that the trees on this site rely on water taken up from deep soil levels during periods of drought (Ewers et al. 1999). During the first years of the study, the root systems of the small trees may not yet have exploited enough soil volume to meet their water need and, therefore, may have been more negatively affected by drought. Furthermore, small trees are affected by variations in the environment more than large ones, because the root distribution in small trees is less widespread. Thus, microsites with unfavourable conditions may have affected the growth of small trees negatively in the beginning of the experiment, while this effect was less evident later in the study when the root systems of the smallest trees exploited more soil volume. Other possible explanations may be that the smallest trees were still suffering from damage or competition from herbaceous vegetation that had occurred before the start of the experiment, the smallest trees were affected more than large trees by competition from residual vegetation that was not killed immediately by the herbicides, or initial differences in mycorrhizal association between large and small trees.

Competition between trees in a stand begins when the potential use for a limiting resource is greater than the supply. Eventually, competition for limiting resources will lead to self-thinning and maximum mean tree size – density relations can be constructed (DeBell et al. 1989). Some authors hypothesize that this level is fixed, with only the time required to reach some fixed limiting density varying with, for example, site quality (Westoby 1984; Long 1985). However, if belowground resources are limiting stand growth, this may not be true (Westoby 1984; DeBell et al. 1989; Morris and Myerscough 1991). This is supported by the finding that stands on better sites are able to maintain a larger mean tree size at a given density than stands on poor sites (Westoby 1984).

In this study, self-thinning had not begun, but conclusions can be drawn from the observed interactions between trees. Self-thinning is the result of size hierarchies where large individuals take an unproportionally large part of limiting resources. In contrast to our expectations, size hierarchies did not develop at a faster rate in the irrigated + fertilized plots, since the small trees were able to grow at the same or greater relative growth rate as larger ones. Therefore, we hypothesize that self-thinning will be postponed by the fertilization treatment if standing biomass is used as the base for comparison and that carrying capacity will be increased by repeated fertilization.

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