

Preliminary Report on the Development of a Coast Redwood Growth Model for Use in
Developing Silvicultural Prescriptions

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INTRODUCTION

The development of thinning prescriptions for intensive forest management requires information on the relationship between the growing space of given height trees and tree and stand growth rates on different sites as well as information on growth responses of trees during the period of release. In vigorous even-aged stands that have not been recently thinned, the growing space of trees largely determines their growth rate and, consequently, the stand growth rate as well. Genetic variation among individuals, and differences between trees of sprout and seed origin in the case of redwood, is the major contributor to variation in the growing space-growth rate relationship for trees of a given height growing on sites of a given quality. Therefore, the growing space per tree rather than basal area or some other stand characteristic is the characteristic that silviculturists need to modify in any thinning operation.

Historically, spacing trials have been used by silviculturists to establish growing space-growth rate relationships. This approach has limitations, however, particularly with a species such as redwood that maintains rapid height growth to a relatively old age. The time and investment required to carry out spacing trials make them impractical. Furthermore, the process of self-thinning makes it impossible to maintain very small growing spaces per tree as trees get taller. As a result, the complete relationship between growing space and tree and stand growth cannot be established for the full range of growing spaces. Although trees in older stands will not grow with a small growing space all the way around their crowns, the crowns of many trees will have a small growing space around at least some portion of their crowns. Consequently, the growth response of trees to small growing spaces needs to be known in developing prescriptions for even relatively tall trees.

More recently, mensurationists have developed stand simulators with density dependent growth models designed specifically for simulating growing space-growth rate relationships. The adequacy of these simulators, however, is in doubt because the correlation between the competition or growing space component of the model and tree growth is relatively low -- typically between .4 and .7. Furthermore, the models always incorporate dbh as an additional variable. Dbh must either be estimated for trees of a given height with different size growing spaces or assumed to be the same regardless of the size growing space. In the latter case, the simulation runs must be started with seedlings. In starting runs with seedlings, however, confidence in the growth predictions will decrease with tree height. For example, once the trees have been "grown" to a height of 60 or 80', the error within the models will have accumulated to a significant level.

Recognizing that spacing trials are impractical and that stand simulators with density dependent growth models have serious limitations, we have developed a new approach to simulating growing space-growth rate relationships. The following syllogism summarizes the conceptual basis of this approach.

If the leaf surface area per tree determines the stemwood volume growth rate of trees of a given height growing on a given site, and

if the growing space per tree determines the leaf surface area per tree,

then the growing space per tree must determine the stemwood volume growth rate of trees of a given height growing on a given site.

By establishing the relationships specified in the two premises of this syllogism, all the requisite information for simulating growing space-growth rate relationships is available.

In the first phase of the model development, we established relationships between the leaf surface area of 140' tall redwoods and their growth rate on two sites and the relationship between growing space per tree and leaf surface area per tree for growing spaces less than 55 square meters or a spacing of 26 feet. Although several trees with larger growing spaces were found on the slope where the initial study was carried out, they were insufficient in number for establishing the growing space-leaf surface area and growing space-growth rate relationship between 55 and 625 square meters of growing space (i.e. 26 - 87' spacing). Consequently, only a portion of each relationships is reported here. Additional trees with larger growing spaces have now been located; and the complete relationship between growing space and leaf surface area, and, therefore, growing space and growth rate, will be reported in a subsequent paper. In it, we will also explain how the growing space-growth rate relationships for equally spaced trees can be used to develop prescriptions for unequally spaced trees which are so common in second growth redwood originating from sprouts. Much to our surprise during our preliminary analysis of the data, we found that trees should not be left appreciably closer together than the spacing needed to obtain maximum stand growth even when they are adjacent to an opening. This is true regardless of whether the trees are equally or unequally spaced.

ESTABLISHMENT OF THE RELATIONSHIP BETWEEN THE LEAF SURFACE AREAS OF 140' COAST REDWOODS AND THEIR VOLUME GROWTH RATES

Methods

Leaf surface area was determined on eighteen trees ranging in height from 126-152 feet and growing on two sites on the Jackson State Forest (Site Index 130-135 and 140-170, with a base age of 100 years -- Lindquist and Palley). Each tree was climbed and limbed up to a six-inch diameter after which it was topped and lowered to the ground to minimize the loss of leaves as they were collected.

Before clipping off all the branchlets $\leq 5/32$ " in diameter on each branch, the leaf surface area on each branch was estimated from a regression relating leaf surface area to the cross-sectional area of the branch at the base of the foliage. For every 2.5m² of leaf surface area estimated on a branch, one sample was taken of leaves attached to branchlets $\leq 1/8$ " in diameter to determine the ratio of leaf surface area to leaf and branchlet dry weight. This ratio was used to convert leaf and branchlet biomass into leaf surface area. Given that a significant amount of the variability in this ratio results from the fact that the needles differ morphologically, the leaves on each branch were classified into one of three leaf types. The leaves at the bottom of a tree's crown tend to be long, flat, and sparse and constitute one class. In contrast, at the top, they tend to be short, thick, and dense and constitute a second class. In the middle, they are intermediate in these characteristics and constitute a third class.

The leaf surface area samples were measured with a Delta-T Devices area meter which converts the leaf surface image projected onto a screen by a video camera into area measurements. Before measuring leaf surface area, the leaves were cut off the branchlets to eliminate overlap. After making the measurements, the leaves and branchlets from which

they were cut were dried and weighted. Then the average leaf surface area to dry weight ratio for each type of leaf was calculated.

To reduce the amount of clipping required to obtain all the biomass of leaves and branchlets $\leq 1/8$ " in diameter on a tree, the branchlets were only clipped down to a diameter of $5/32$ ". Prior to drying the leaves and branchlets $\leq 5/32$ " in diameter, a subsample was taken to determine what proportion of the weight of leaves and branchlets $\leq 5/32$ " was also $\leq 1/8$ ". The dry weight of leaves and branchlets $\leq 5/32$ " was multiplied by this proportion to determine the weight of leaves and branchlets $\leq 1/8$ ". This weight, in turn, was multiplied by the appropriate ratio of leaf surface area to leaf and branchlet dry weight to determine the leaf surface area of each type of needle on each tree. The total leaf surface area of each tree was then determined by summing the leaf surface area of each type of needle.

Since all the leaf surface area on a tree is not equally effective, in that it does not have the same photosynthetic capacity, we collected information on the ratio of leaf surface area to dry leaf weight so that we could weight the leaf surface area according to this capacity and possibly improve the relationship between leaf surface area and volume growth. For a number of species, leaves expanded in a high flux of light, or subsequently receiving a high flux, have a much higher photosynthetic capacity. The chloroplast-containing palisade and spongy mesophyll tissue are much more fully developed. The additional cells in those tissues cause leaves receiving a high flux of light to be heavier per unit of leaf surface area than those receiving a low flux. Consequently, we, like others, used the leaf surface area to dry leaf weight ratio to identify those leaves receiving different light fluxes.

The relative importance of the needles of different leaf surface area to dry leaf weight ratios was estimated by determining the amount of protein per unit of leaf surface area. Protein content was selected because it increases as the number of chloroplasts increase. Protein in the leaf tissue is largely made up of ribulose 1,5-bisphosphatase (the enzyme which initiates carbon fixation by joining carbon dioxide from the atmosphere to the five carbon sugar ribulose) found in the chloroplasts.

To determine volume growth, the trees were felled and bucked into 8'9" sections, where possible, so merchantable parts of the trees could be sold as 8' logs. Logs were cut to shorter lengths, however, where breaks in the bole prevented bucking at the desired location. Following felling and bucking, rounds were cut from the base of each log. They were labelled according to their height up the bole, soaked in water, sealed in plastic bags, and stored at 1°C until growth over the past five and ten years could be traced onto acetate sheets. After being traced onto these sheets, the five and ten-year growth areas were cut out, spray painted black to make them opaque, cut into smaller sections, and measured with the Delta-T Devices area meter. The volume growth of the tree was then estimated by using a combination of volume formulae. The formula for the volume of a paraboloid was used for the top of the trees. Newton's formula was used for all the other sections except for the stump and butt log. The formula for a cylinder was used for the stump and Huber's formula was used for the butt log. Finally, a least squares simple linear regression was calculated to develop the model relating leaf surface area to volume growth.

Results

The relationships between the leaf surface area of 140' coast redwoods and stemwood volume growth on two sites are shown in Figure 1. Given the high precision of these relationships, the first premise of the syllogism can be accepted. As would be expected, less

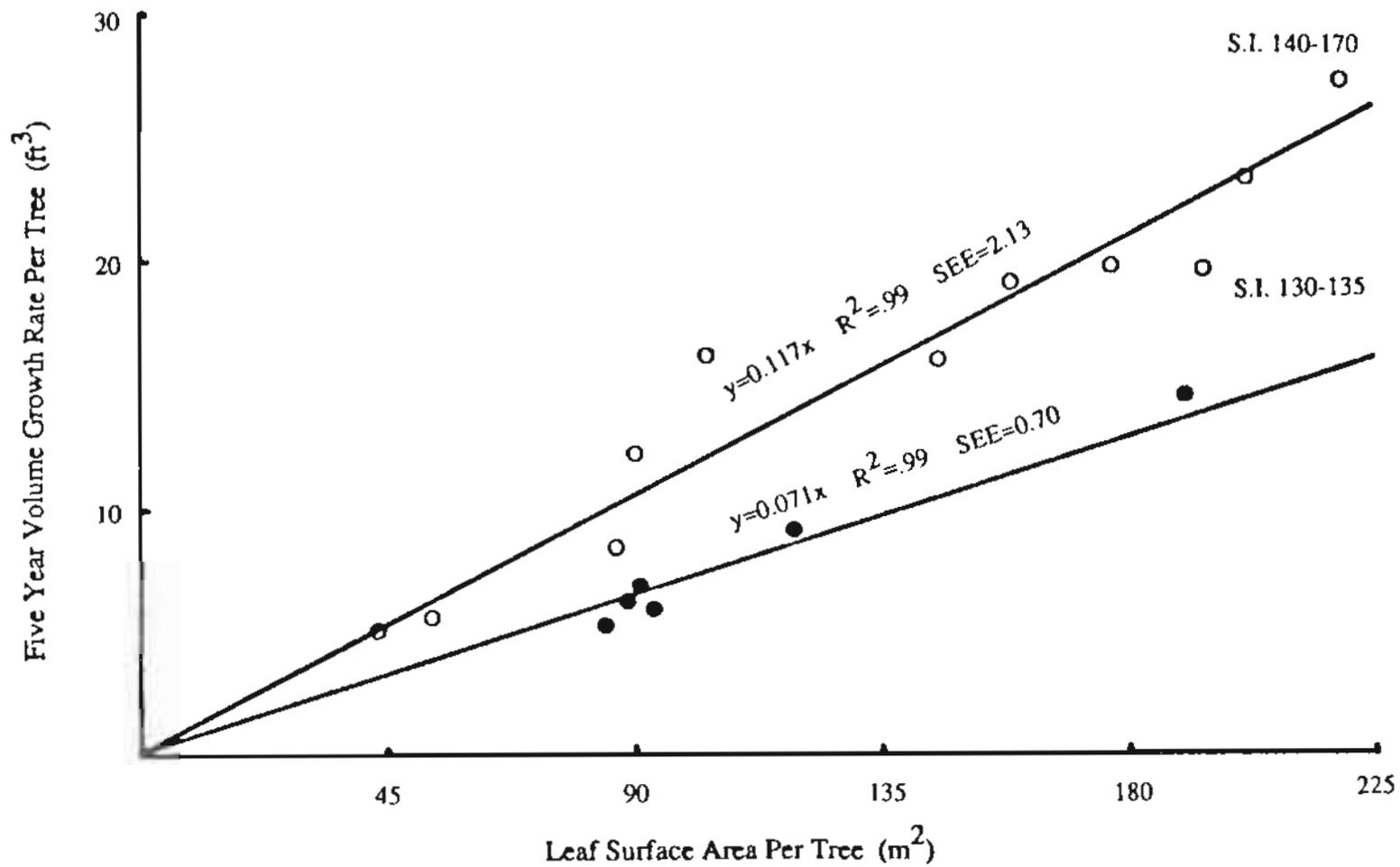


Figure 1. Five year stemwood volume growth per tree as a function of the leaf surface area per tree. Site indexes with a base age of 100 years from Lindquist and Palley .

stemwood volume was produced for a given amount of leaf surface area on the poorer of the two sites.

Adjusting the leaf surface area of the trees on the basis of the photosynthetic capacity of the leaves did not give an appreciably better relationship between leaf surface area and stemwood volume growth. We expect that the variability in the protein content of leaves with a given leaf surface area to dry leaf weight ratio contributed greater variability to the relationship between leaf surface area and growth than it eliminated. Only 70 percent of the variability in protein content was associated with differences in the leaf surface area to dry leaf weight ratio.

DETERMINATION OF THE LEAF SURFACE AREA EXPECTED FOR 140' COAST REDWOODS WITH DIFFERENT SIZE SYMMETRICAL GROWING SPACES

When trees are equidistant, each tree is surrounded by six others and has a symmetrical growing space which is in the shape of a hexagon. Such a growing space can be viewed as being made up of six equilateral triangles each facing one of the adjacent trees or as six equal size trapeziums (Figure 2). One might expect that by chance such configurations could be found in natural stands, but they rarely are. Most of the time "self-thinning" leaves trees in clumps and, thus, they are unequally spaced and have asymmetrical growing spaces. Consequently, to establish the relationship between symmetrical growing space and leaf surface area, we had to stimulate the leaf surface area of trees with different size symmetrical growing spaces. We did so by expanding the leaf surface area measured in a wedge of a tree's crown that had an easily and unequivocally defined growing space to that which a tree would have if the spacing between it and six surrounding trees was the same as the spacing between the trees defining the crown wedge. The wedges were taken on selected trees that were equidistant from at least two other trees which were themselves the same distance apart. In addition, the crowns of these three-tree combinations had to share the intervening growing space equally (Figure 3). Thus, the growing space of the wedge was generally narrower but approached that of one of the trapeziums of a tree's symmetrical growing space. We chose to measure the leaf surface area within a trapezium rather than within an equilateral triangle because less variability could be expected in the leaf surface area for a given size growing space. In this configuration, the same size growing space bordered both sides of the wedge within which we took our measurements.

Methods

While standing against the bole of a selected tree, the boundaries of the definable growing space were determined by taking the compass bearing of each side. When the trees were climbed and topped, the compass bearing of each branch was taken. All branches occurring in the definable growing space were kept separate so that their leaf surface areas could be determined separately from that of the rest of the tree. Thereafter, the leaf surface area in the definable growing space was converted to the leaf surface area that an entire tree would have if it had a symmetrical growing space with the same spacing between trees as in the definable growing space. This was done by multiplying the leaf surface area in the definable growing space by a factor of $360/x$ where x equals the number of degrees in the definable growing space. Finally, a nonlinear regression was calculated to develop the model relating symmetrical growing space to leaf surface area per tree.

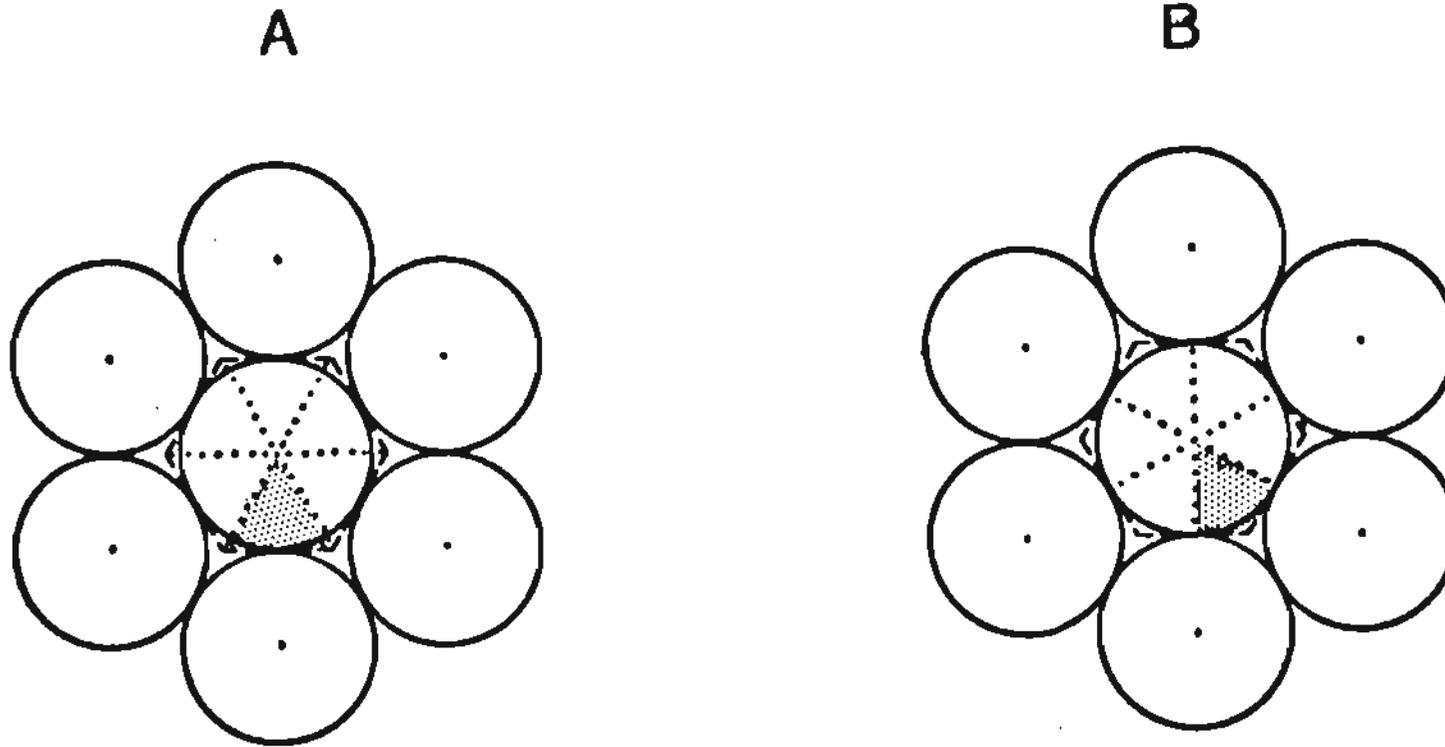


Figure 2. The symmetrical growing space of a tree (dashed lines) is hexagonal when all trees in a stand are equidistant. A: It can be viewed as a composite of six equilateral triangles (dotted lines) with each triangle opposite one of the six trees surrounding a given tree. The distance between trees is twice the height of the equilateral triangles. B: The growing space can also be viewed as a composite of six trapeziums (dotted lines).

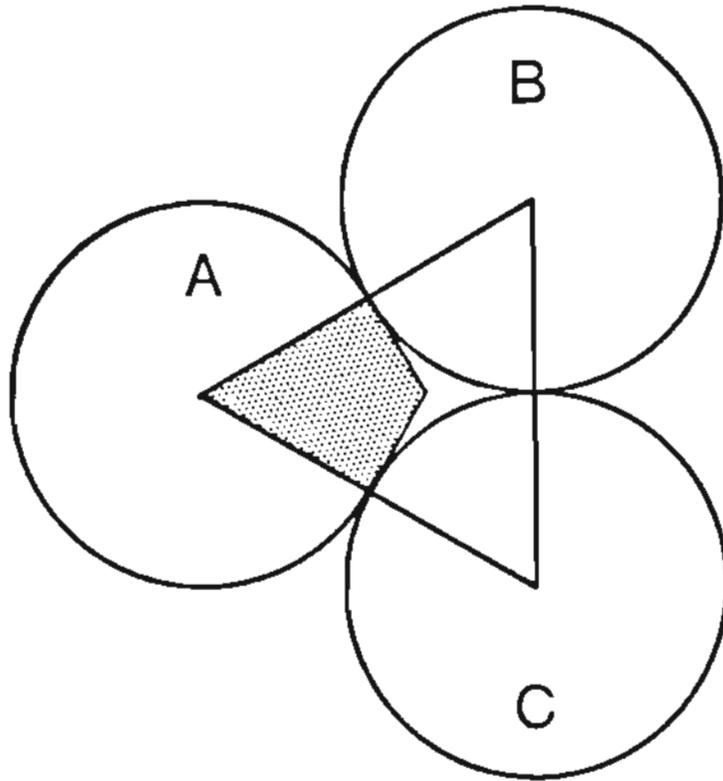


Figure 3. Tree A has an easily definable growing space for a portion of its crown (dotted area) because it is equidistant from trees B and C which are the same distance apart (solid lines) and all three trees share equally the area between their stems. The growing space is equivalent to one of the trapeziums of a tree's symmetrical growing space.

Results

The relationship between symmetrical growing space per tree and the leaf surface area of 140' coast redwoods is shown in Figure 4. Given the scarcity of data points beyond 55 square meters of growing space, a tentative curve beyond that point is shown by a dotted line. The curve will be extended to 625 square meters or 87' spacing once the analysis of the additional data is completed. No site differences could be identified in this relationship. Given the high precision of this relationship at close and intermediate spacings, the second premise of the syllogism can be accepted and the simulation of symmetrical growing space-growth rate relationships is justified.

SIMULATION OF SYMMETRICAL GROWING SPACE-GROWTH RATE RELATIONSHIPS FOR TWO SITES

Methods

The symmetrical growing space-growth rate relationships were simulated by linking the leaf surface area expected for a tree with a given size growing space (Figure 4) with the volume growth expected on a given site for a tree with that leaf surface area (Figure 1).

Results

The simulated symmetrical growing space-growth rate relationships for 140' coast redwoods growing on two sites are shown in Figure 5. Again, the curves beyond 55 square meters of growing space are tentatively shown by a dotted line.

DISCUSSION

To use the symmetrical growing space-growth rate relationships in thinning, a timber management objective must be specified so that the desired symmetrical growing space per tree can be determined. If we assume, for example, that the objective is to maximize productivity (i.e., stand growth), stand growth must be plotted against the symmetrical growing space per tree to determine the target growing space that will produce maximum stand growth. Stand growth is calculated by multiplying the growth expected per individual tree with a given size symmetrical growing space by the number of trees present per acre with that size growing space per tree (Figure 6). With the growing space-growth rate relationship established for 140' coast redwoods and maximizing stand growth as the timber management objective, the desired growing space on both sites is 55 square meters and trees should be separated by 26'. Trees on the higher site should grow at a rate of 25.2 cu. ft. in five years and trees on the lower site at a rate of 15.3 cu.ft. in five years.

In order to obtain the maximum possible stand growth when trees are unequally spaced, the target spacing for equally spaced trees must be modified. To date, silviculturists have had no method for making such an adjustment. We have recently developed a method for making this modification, but need to complete the simulation of the symmetrical growing space-growth rate relationships before presenting it. With the exception of a few details, the prescription will specify that a stand should be thinned so that the residual trees form adjacent triangles or straight lines. The triangles should have sides between x and y feet long and the lines should have end trees between x and y feet apart. As mentioned earlier, the complete details on the development of such thinning prescriptions will be presented in a followup paper.

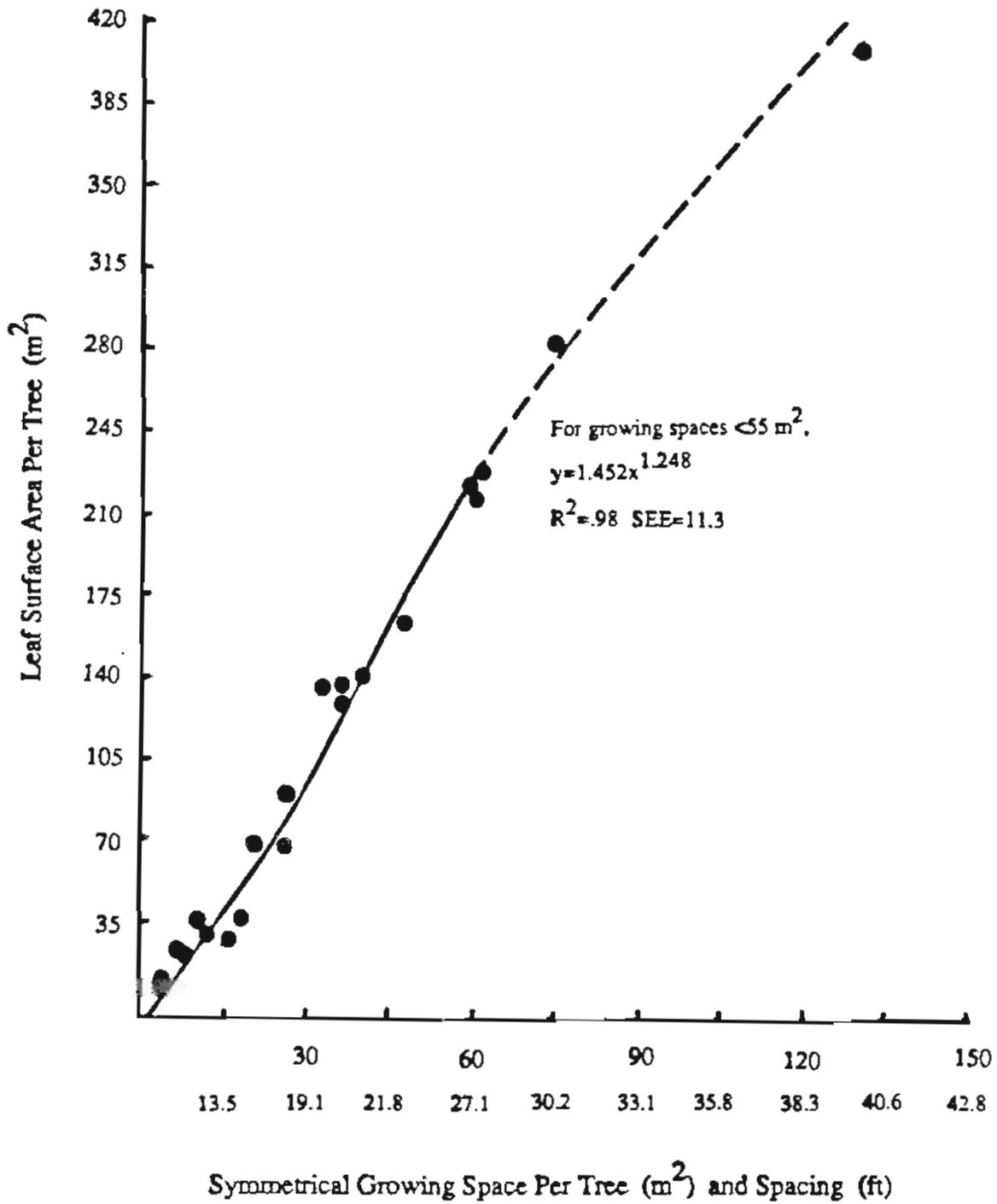


Figure 4. Simulated leaf surface area per tree as a function of the symmetrical growing space per tree. Simulation was based on the leaf surface area measured in crown wedges with different size definable growing spaces.

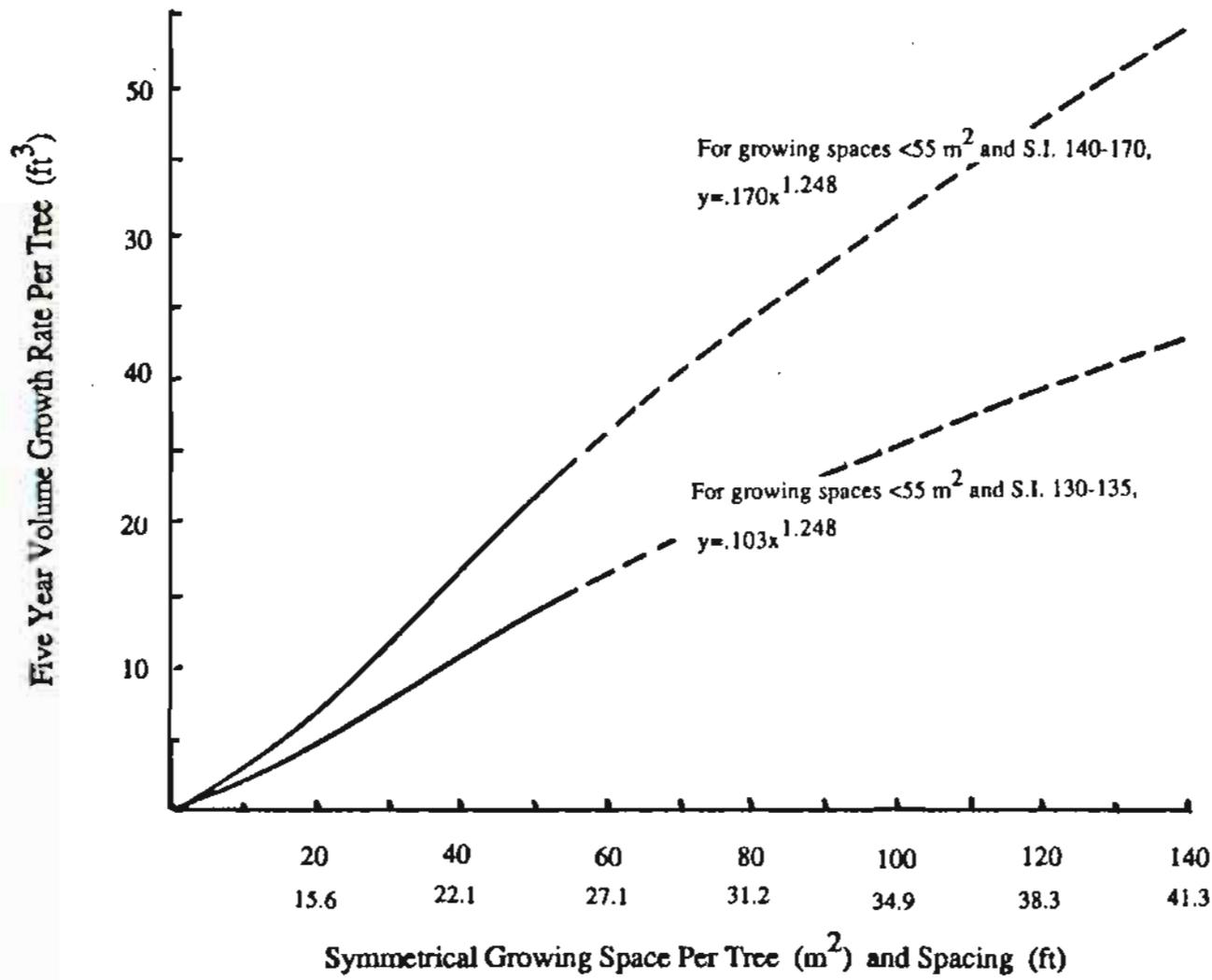


Figure 5. Five year stemwood volume growth per tree as a function of the symmetrical growing space per tree.

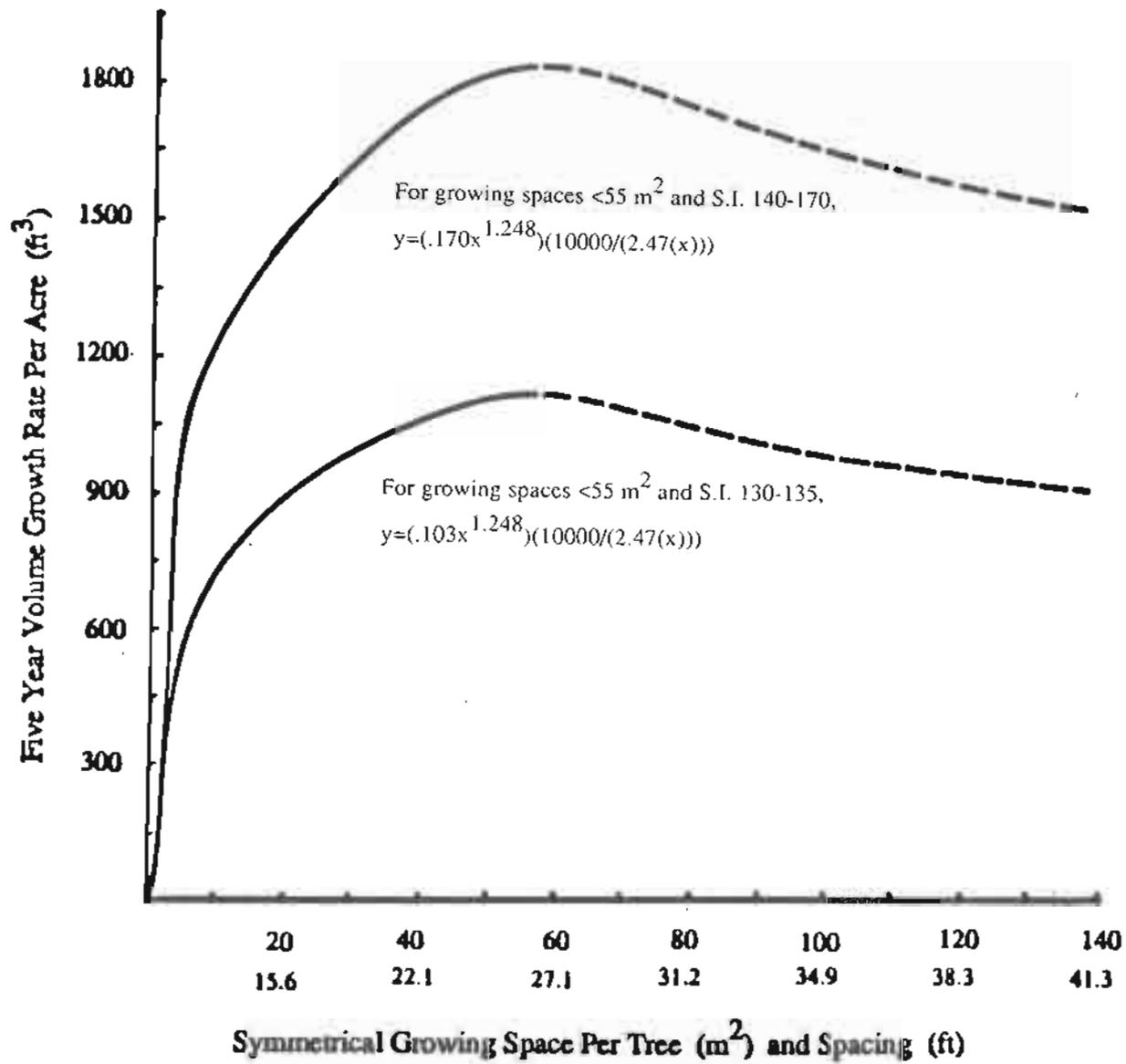


Figure 6. Five-year stand volume growth as a function of the symmetrical growing space per tree.