The Effects of Fertilization and Release on Growth, Physiology, Nutrition, and Sapwood Quality of Young Yellow-Poplar

by

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(ABSTRACT)

The effects of crop tree release and fertilization of young yellow-poplar on low and medium quality Southern Appalachian sites were compared. In June of 1989, 96 individual 10 year-old yellow-poplar crop stems were treated in factorial combinations. The crop trees were either released, using a 4% triclopyr ester in kerosene basal spray, fertilized with 224, 291 and 243 kg/ha of N, P, and K; released and fertilized, or left untreated. These treatments were repeated in June of 1992. In 1992, treatments were slightly different. Crop trees were released mechanically, and only nitrogen was applied at 224 kg/ha. After five years, only release resulted in significant growth responses. Released trees responded positively to increased sunlight and horizontal space by increasing their uptake of nitrogen and iron - elements essential for photosynthesis. This led to an increase in foliage production, and presumably, an increase in total photosynthesis. Released trees reacted to the increased growing space by filling in the space created by release. Released trees increased both diameter and crown volume growth; unfortunately, they did so at the expense of height growth, which was decreased by crop tree release. Current stemwood volume, was therefore not increased.

Crop tree release also significantly increased the specific gravity of the stem from ground line to 4 meters, and numerically from 4 to 6 meters. This may be the result of

a greater proportion of latewood production near the base of the tree, or changes in the anatomical structure of the wood. At greater heights, juvenile wood negated the increase in mean stem specific gravity. The lower bole specific gravity increase also resulted in an increased dry mass for the entire stem.

Although phosphorus and potassium availabilities were increased by fertilization, and phosphorus uptake was increased, the yellow-poplar were unresponsive to fertilization. This suggests that phosphorus and potassium were not limiting to growth. Nitrogen availability, however, was not increased. This implies that the soil was not responsive to additions of nitrogen. Unfortunately, as additional nitrogen was either not mineralized, or it was sequestered elsewhere in the system, we can not know whether tree growth was limited by nitrogen deficiencies .

At the whole tree level, only iron content was increased by release. Fertilization did not affect nutrient content. Although foliage accounted for only 6 % of the whole tree dry mass, an average of 31% of the seven elements assessed in this study were found in the foliage. Assuming zero translocation - we can expect an average of 31% nutrient conservation if harvesting is done during the dormant season.

Nutrient conservation is even more hampered in whole tree harvesting. While stemwood only, or stem only harvests remove 71 and 82% of the whole tree dry mass, they only remove an average of 28 and 51% of the nutrients of the entire tree. When the crown is also harvested, a gain of only 18% dry mass is recognized, while an additional 49% of the tree nutrients are removed.

In general, if the objective of growing yellow-poplar on low to medium quality sites is short-rotation pulpwood production, crop tree release may be beneficial, as

diameter growth and stem yield are increased. Although release resulted in increased diameter and crown volume growth, and higher first log specific gravity, the reduced height growth will make the maintenance of these increases problematic. As released trees become overtopped by competitors, it is likely that diameter growth will also decrease. Therefore, if production objectives are to grow full rotation saw logs, crop tree release, like fertilization, is likely not a worthwhile investment.

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CHAPTER ONE: Introduction and Justification

Yellow-poplar (*Liriodendron tulipifera* L.), because of its availability, rapid growth, excellent form, clear bole, and good working properties, has long been one of the outstanding hardwood timber species in the eastern United States. Yellow-poplar is widely distributed, and comprises over 13 percent of the hardwood growing stock in the Appalachian Mountains (Beck and Della-Bianca, 1981) Its growth exceeds removal more than five-fold (Tansey, 1988). On moderate sites, yellow-poplar may be outcompeted by its associated species, but on site indices greater than 95 (base age 50), it will outgrow all of its competitors (Doolittle, 1958). When grown on high-quality sites, it has a very tall, straight trunk, and because it is an excellent self-pruner, its lower bole is usually free of branches (Beck, 1990). In addition, its foliage is not a preferred food of the gypsy moth (*Lymantria dispar* L.), an extremely destructive pest in the eastern United States (Gansner *et al.*, 1987).

The principal uses of yellow-poplar include furniture and fixtures, boxes and shook, millwork, core stock for veneer panels, dimension stock, and miscellaneous piece products. Most yellow-poplar veneer goes into plywood, while pulpwood is converted mostly into wrapping paper and printing paper (Koch, 1985). There have also been recent efforts to educate the forest products industry of the potential of yellow-poplar as a construction lumber (Muench, 1989).

Since 1984, there has been increased interest in the commercial use of yellow-poplar (Frame, 1989). Foresters have become more interested in intensive management practices, such as fertilization, crop tree release, and thinning, to improve

the competitive position of yellow-poplar on sites where less desirable species compete strongly with it, and to increase growth on sites where yellow-poplar has a competitive edge.

While silvicultural inputs may result in increased yield of yellow-poplar, these inputs may also affect the amount of nutrients that can be recycled throughout the forest ecosystem. While nutrient oversaturation or toxicity rarely occurs, nutrient deficiencies are possible if faster growth results in a greater number of harvests over time, or if increased fiber demand results in a greater proportion of tree removal during harvests.

Whereas forest managers are primarily concerned with the inputs and outputs of a stand, the forest products industry is principally concerned with the properties of the raw material. Since the end product reflects both growth history and chemical and physical properties, the relationship between these factors needs to be understood. Specifically, we need to know the effect of silvicultural treatments on (*i*) growth - as it pertains to the physiological status of the tree, the nutrient distribution within the tree, and the physical wood properties; (*ii*) nutrient distribution - and its relationship to silvicultural inputs and outputs; and (*iii*) physical wood properties. Numerous studies have addressed single silvicultural treatments, and combinations of treatments - some of which related treatment to wood density (Ike, 1962; Schomaker and Rudolph, 1964; Finn and White, 1966; Madgwick, 1971; Shipman, 1977; Ross *et al.*, 1979; Groton and Buckner, 1985; Loftis, 1985; Lamson and Smith, 1989; Rathfon *et al.*, 1991; Bollig *et al.,* 1993), but none addressed the combined treatment of fertilization and

crop tree release on low to medium quality sites, and its effect on growth, physiology, nutrient partitioning, and physical properties of the wood. Specifically, no studies have profiled whole tree and partitioned storage of nutrients.

Objectives

The specific objectives of this project were to:

(1) determine the effect of fertilization and crop tree release on yellow-poplar growth, physiology, nutrition, and wood properties; and

(2) develop biomass regression equations for various tree components based on easily measured dimensional variables.

CHAPTER TWO: Literature Review

Silvics of Yellow-Poplar

The natural range of yellow-poplar encompasses almost the entire eastern United States. The species occurs from southern Massachusetts to northern Florida, and from the northern coastal plain to Lake Michigan in the north, and from the southern coastal plain to Louisiana in the south (Beck and Della-Bianca, 1981). Within its range, yellow-poplar is not evenly distributed. Boyce and McClure (1975) divided the species' growing stock into physiographic provinces and found that nearly 75 percent of the growing stock was in the Piedmont and Mountain provinces, 16 percent in the Coastal Plain, 8 percent in the Interior, and the remaining 3 percent was scattered elsewhere within its range.

Yellow-poplar expresses its greatest development where rainfall is well distributed over a long growing season (USDA Forest Service, 1990). Due to its broad geographic distribution, rainfall and temperature vary considerably. At its northern limit, yellow-poplar is usually found in valleys and stream bottoms at elevations below 300 m (1000 ft). In the southern Appalachians, it can be found on a variety of sites, including stream bottoms, coves, and moist northern slopes up to an elevation of about 1370 m (4,500 ft) (Beck and Della-Bianca, 1981). Yellow-poplar grows well on soil types with various physical and chemical properties, and parent materials. Its best growth has been observed on alluvial soils bordering streams, on loam soils of mountain coves, on talus slopes below cliffs and bluffs, and on well watered, gravelly soils (McCarthy, 1933).

For good growth, yellow-poplar is exacting in soil and moisture requirements. The variables most often associated with site quality for yellow-poplar include soil depth, porosity, permeability, moisture, aspect and slope position (Mack, 1968). Where it occurs naturally and grows well, the soils are moderately moist, well drained, and loose textured. It seldom grows well in very wet or very dry situations (Koch, 1985). Several researchers have isolated A_1 horizon depth as being an important determinant in yellow-poplar growth. Others have noted that a yellow-poplar overstory improves upper layer soil conditions due to the nutrient content of freshly fallen leaves, and the incorporation of organic matter into the soil which increases water holding capacity and improves soil structure (Lutz and Chandler, 1946; Lane and Witcher, 1967). Clark (1964) found that reduced soil porosity in old-fields was detrimental to the growth of yellow-poplar, as it reduced soil aeration and available water holding capacity. Hebb (1961) concluded that topographic position, aspect, and soil depth were important factors. He found that lower north-facing slopes with deep soils were the most conducive to good yellow-poplar growth. Hay *et al.* (1987) found that rooting depth was a function of soil morphology and nutrient availability. They found that the deepest soils allowed for the greatest rooting volume and growth. They also determined that rooting volume, soil moisture, and overall soil structure were adversely affected by clay subsoils that bound soil moisture, and fragipans that tended to inhibit root growth and access to deep water.

In addition to being site sensitive, yellow-poplar is known to be shade-intolerant. Although the species produces copious seed (Whipple, 1968) and is a

prolific stump sprouter (Wendel, 1975), its growth is severely retarded when overtopped by competing species (Williams, 1976). However, Loftis (1983) and O'Hara (1986) have demonstrated that in Appalachian mixed hardwood stands, yellow-poplar dominated the understory of shelterwood and released stands for 13 and 80 years, respectively. Although intolerant, this dominance may be maintained because yellow-poplar seedlings reach maximum or near maximum photosynthetic efficiency at relatively low light intensities (Olson, 1969). This in turn may be the result of comparatively higher leaf enzymatic activity (Dietrich and Rose, 1974) which can lead to greater carbon assimilation. Williams (1976) suggests that as long as yellow-poplar maintains vigor, it should respond well to release.

Following a regeneration harvest, yellow-poplar generally colonizes a site rapidly, producing large amounts of seedlings and sprouts. At this point, since light is not limiting, site quality determines the dominating species of the future stand. Although classified as intolerant, yellow-poplar can overcome most competition simply because it grows so fast. In addition to being photosynthetically efficient (see above), some researchers have suggested that yellow-poplar's fast growth may be related to good internal water management (Miller, 1974). This allows for comparatively lower transpiration rates (Kochenderfer and Lee, 1973) and continuous terminal growth throughout the entire growing season (Zahner, 1968). These factors are either directly or indirectly affected by available soil moisture, soil structure, and exposure, and thus - site quality.

When site conditions are favorable, yellow-poplar is the largest broad-leaved

species in North America (Harlow *et al.* 1979). It commonly attains heights of 30-46 m (100-150 ft) with diameters between 0.6-1.5 m (2-5 ft). Old-growth trees on good sites may reach 61 m (200 ft) and have diameters between 2.4-3.7 m (8-12 ft) (USDA Forest Service, 1990). Once established on good sites, yellow-poplar may grow in excess of 1.5 m (5 ft) per year (McCarthy, 1933). When the stand closes, at about 20-30 years, the pole-size trees slow their annual growth to about 1.0 m (3 ft) (Beck, 1962).

Most of the sites where yellow-poplar occurs, however, are not favorable for its best growth. In the upland hardwood region of Virgina alone, 69 percent of the timberlands are of site indices less than 80 feet at 50 years (Bechtold *et al.*, 1987). The relative competitiveness of yellow-poplar then becomes important to its survival in the stand. Doolittle (1958) has shown that in the southern Appalachians, on site indices 95 and above (base age 50), yellow-poplar outcompetes all associated species. On site indices from 71-94, only Eastern white pine (*Pinus strobus* L.) will outgrow it, and below a site index of 71, most of its associated species will overtop it (Table 2.1). Olson and Della-Bianca (1959), and Nelson and Beaufait (1957) showed similar trends in the North Carolina and Georgia Piedmonts, respectively.

Yellow-poplar is often a pioneer on abandoned old-fields and clearcut lands, and may form almost pure stands on very good sites. More commonly, it regenerates as a mixed type with other species, and will commonly persist in climax stands as scattered individuals (USDA Forest Service, 1990). In either case, when grown in a forest situation, yellow-poplar exhibits excellent morphological form. The tall

Table 2.1. Height comparisons based on site indices (base age 50) for yellow-poplar and selected competitor species inthe Southern Appalachian upland hardwood region. (Adapted from Doolittle, 1958)

Site Index	65	80	95
	<----------(feet)---------->		
Yellow-Poplar	65	80	95
White Pine	76	86	95
Virginia Pine	68	78	86
White Oak	60	68	77
Black, Chestnut and Scarlet Oak	66	75	84

excurrent stem is almost arrow-straight and terminates far above in a small, rather open, oblong crown (Harlow *et al.*, 1979). The species is an extremely effective self-pruner, and a clear bole of 18.3-30.5 m (60-100 ft) is not uncommon (Little *et al.*, 1962). Because of these traits, yellow-poplar can develop and produce considerable quantities of high quality, high value logs and products (USDA Forest Service, 1990).

Fertilization

As mentioned in the preceding section, soil physical properties and moisture conditions determine the distribution and growth of yellow-poplar. However, many researchers have found that low levels of soil nutrients - most frequently nitrogen, but also phosphorus and potassium - have occasionally been linked to slow growth of yellow-poplar (Beck and Della-Bianca, 1981). The importance of these three macronutrients are well documented in the literature. Nitrogen forms a part of every

living cell within a tree, serving as a major constituent of chlorophyll and proteins, with many of the latter serving as enzymes. Phosphorus is again a constituent of every living cell, occurring in the protoplasm. This element plays an indispensable role as an energy source for all biochemical work in living cells. Potassium is essential in cell metabolic processes and apparently influences the uptake of other elements, and affects respiration and transpiration. It also encourages the synthesis and translocation of carbohydrates, which encourages cell wall thickening and stem strength (Fitzpatrick, 1986).

A number of micronutrients have also been shown to affect photosynthesis, and thus growth, in woody plants. Iron, occurring in ferredoxin and cytochromes, has been shown to inhibit photosynthesis by inducing chlorosis and affecting enzymatic activity when deficient. Manganese, essential for the release of oxygen, may influence photosynthesis if present in too large or too small amounts by reducing CO_2 uptake. Calcium, a large component of cell walls, serves also as an activator of several enzymes and is involved in nitrogen metabolism. Deficiencies often result in meristematic injury. Magnesium, although a constituent of the chlorophyll molecule and an activator of several enzyme systems, has rarely been linked to reduced photosynthesis or slower growth (Kramer and Kozlowski, 1979).

Effects on Growth

Yellow-poplar has shown a growth response to fertilization in numerous studies. Growth response to additions of nitrogen have been the most consistent, with additional response when phosphorus is added to the nitrogen fertilizer (Beck and

Della-Bianca, 1981). On an area basis, Finn and White (1966) found that in a slow-growing stand of yellow-poplar in Michigan, N-P-K fertilization increased height growth 100 percent, diameter growth 85 percent, and lasted in some degree for five years. Van der Werken and Warmbrod (1969) reported that trees receiving heavy applications of N (a total of 960 lbs/acre over 8 years) were 7.4 m (24.4 ft) tall and 13.5 cm (5.4 in) in diameter after eight years, compared to 4.4 m (14.3 ft) and 5.5 cm (2.2 in) for controls. However, more does not always mean better, as Madgwick (1971) showed that there was an optimum concentration of nitrogen depending on site, with slower growth rates above and below the optimum. In general, growth effects have lasted from 3-5 years; however, Groton and Buckner (1985) have reported continued growth effects 18 years after application.

Irrespective of the type or amount of fertilizer applied, the growth response of yellow-poplar is dependent on site, as the greatest response occurs on the poorest sites (Baker and Blackmon, 1977; Francis, 1977; Beck and Della-Bianca, 1981; Stone, 1986). On a good old-field site, Buckner and Maki (1977) reported that height of fertilized seedlings was 90 percent greater than that of controls after seven years, but on a better site, an identical application yielded only 42 percent greater height growth over controls. More recently, Rathfon *et al.* (1991) revealed that on a slope site (poor), diameter growth was 38 percent greater and height growth was 25 percent greater on fertilized vs. unfertilized plots after two years. Fertilization on a cove site (good) resulted in no growth response.

Whether the site is good or poor, growth response to fertilization cannot be

considered exclusively dependent on increased soil nutrients, as the factors that affect metabolism, and thereby the availability of respiratory energy, will directly affect nutrient uptake (Foth, 1978). These factors include the supply of respiratory substrate, available soil moisture, soil temperature, and soil oxygen supply, or alternately - the physical properties of the soil.

Physiological Response

Physiologically, stimulation of growth of fertilized trees reflects increased photosynthetic efficiency (Kozlowski *et al.*, 1991), and increases in the leaf area and leaf area index (LAI). Gower *et al.* (1992) showed a 24 percent increase in LAI and a 20 percent increase in the amount of foliage two years after applying nitrogen to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) study plots in New Mexico. Brix (1983) showed that 37 percent of the increased growth of a fertilized Douglas-fir plot was attributable to increased photosynthetic efficiency, and the remainder to greater leaf area. He determined that the increase in photosynthetic efficiency lasted only 3-4 years, after which increased leaf area became more important. Also, the photosynthetic capacity of leaves may be influenced by their mineral nutrition, and thus fertilization, because stomatal opening and closing are slowed in mineral deficient trees (Davies and Kozlowski, 1974). This is supported by Brix and Mitchell (1986) who found that water use efficiency (WUE) was improved by fertilization.

Crop Tree Release and Thinning

Because yellow-poplar stands are usually reproduced naturally, the stands are

often greatly overstocked. This results in severe inter- and intraspecific competition for water and minerals when very young, and water, minerals and light at the pole stage (Kozlowski *et al.*, 1991). The purpose of release or thinning operations is to increase the amount of growing space for the crown and roots of residual trees, thereby redirecting these limited resources to selected trees. Usually, the rates of vegetative and reproductive growth of the trees left standing is increased (Kozlowski *et al.*, 1991). Although the ultimate goal of redirecting resources to selected trees is common to both crop tree release and thinning, their methodologies differ. Crop tree release involves the selection of future crop trees, and then the elimination of overtopping trees, or trees that interfere with the crown of selected trees. In crop tree release, only the vegetation that directly interferes with the desired trees is killed or removed. Elimination of competing vegetation can be accomplished mechanically or chemically. Thinning, on the other hand, generally implies some form of spacing control - although there are several methods of thinning (Smith, 1986). Thus, in "geometric" or "mechanical" thinning, the trees to be cut or retained are chosen on the basis of some predetermined spacing, with little regard for their position in the crown canopy.

Response to release or thinning varies greatly depending upon the condition of the released tree. Successful operations result in increased diameter growth, and may or may not increase height growth. However, results may not be apparent for several years, because of the time required for crown expansion, or because of problems associated with sudden exposure to the elements. This is known as "thinning shock"

(Kozlowski *et al.*, 1991).

Whether the treatment is a crop tree release or a thinning, a stand can only support a given amount of phytomass, which varies by site. Beck and Della-Bianca (1981) suggest that no more than 200 trees per acre (494/ha) suitable in vigor and crown class to consider as future crop trees, can be carried to the pole stage. If more are carried, competition and mortality among released trees will result. If the objective of the landowner is to maximize the production of the highest value saw logs or veneer bolts, between 109-200 well spaced trees per acre (269-494/ha) should be retained at the sapling stage (Roach and Gingrich, 1968; Lamson and Smith, 1978). When grapevines are established in young stands, Trimble and Tryon (1976) recommend cutting all grapevines in the stand at ground level. This should be done when the stands are 8-10 years old (Beck and Della-Bianca, 1981), which is also the best age to thin or perform a crop tree release on sapling stands (Trimble, 1973).

Effects on Growth

Past studies of release and thinning in yellow-poplar have shown mixed results. It appears that the major determinant of response to release is crown class (Beck and Della-Bianca, 1981). Releasing dominant and codominant trees has resulted in slight diameter growth increase, but often causes a reduction in height growth compared to unreleased trees (Allen and Marquis, 1970; Lamson and Smith, 1978). This in turn makes the maintenance of these crown classes problematic (Lamson and Smith, 1978). Lamson (1983) reported that five years after releasing dominant or codominant stump sprouts, diameter growth of released trees was 3.0 in (7.5 cm) compared to 2.2 in (5.5

cm) for the control trees. Height growth was unaffected by treatment. Beck and McGee (1974) and Williams (1976) have shown that release of overtopped intermediates with good vigor resulted in increased diameter and height growth compared to unreleased trees. Della-Bianca (1971) reports that more than one release operation will probably be needed, as the effect will only last 6-8 years and will be obscured over the course of a rotation if not repeated.

Thinning of young yellow-poplar stands has shown more consistently positive results. In West Virginia, Carvell (1964) found that after 11 years, thinning resulted in 2.9 in (7.3 cm) diameter growth compared to 2.1 in (5.3 cm) in unthinned stands. In New Jersey, Tepper and Bamford (1959) found that thinning an 18 year old stand to a residual basal area of 35 ft^2 per acre resulted in 39 percent diameter growth increase over unthinned stands after 15 years. Beck and Della-Bianca (1975) concluded that yellow-poplar responds well to thinning over a wide range of site quality, stand age and tree sizes.

Site has also been shown to have an influence on response to crop tree release and thinning. Trimble (1971) determined that response to thinning was greater on site indices over 70, and ultimately favored yellow-poplar. Below a site index of 70, however, the response was poor, and oaks (*Quercus spp.*) and maples (*Acer spp.*) were favored. Rathfon *et al.* (1991) concluded that released cove site trees responded positively in stem diameter growth and crown volume, but slope sites elicited no growth response, or possibly even a negative response after two years.

Physiological Response

Following thinning or release, released trees usually respond to the greater availability of resources by increasing crown width, leaf growth, and branch survival and size (Kramer and Kozlowski, 1979). The greater leaf area is accompanied by increased photosynthesis and general physiological activity of the crown. This is often brought on by higher xylem water potentials and improved water relations within the tree (Donner and Running, 1986). It should be noted, however, that thinning may or may not increase the amounts of available water. In general, though, Hibbert (1967) reported that the results of 30 studies indicate that a reduction in forest cover resulted in increased water availability.

With greater leaf area and less competition-induced shading as a result of thinning, Waring *et al.* (1981) contend that growth efficiency is improved as released trees intercept more sunlight, produce more carbohydrates, and allocate proportionally more assimilates to stemwood than trees in shaded canopies. Ginn *et al.* (1991) also determined that increased growth following thinning may be due in part to the physiological ability of newly exposed lower crown foliage to take advantage of increased light. However, greater assimilation due to newly exposed lower foliage may only be apparent in species with a more "plastic" shade-leaf response to increased light.

The effects of temperature on photosynthesis, and thus carbon assimilation, can also be as important as the effects of the major limiting resources on tree growth. Higher temperatures brought on by greater exposure of released trees, may in some

instances, have an antagonistic effect on growth as high temperatures often increase transpiration, causing water deficits. This can close stomata and reduce the supply of CO_2 available for photosynthesis (Kramer and Kozlowski, 1979).

Nutrient Distribution

Information on nutrient profiles within trees can be helpful in assessing relationships between nutrient distribution and growth, soil/site relationships, nutrient uptake and cycling, nutrient deficiencies, and the impact of whole tree harvesting (Koch, 1985). To date, a fair amount of research has been done on foliar nutrient analysis, but very little has been done on nutrient distribution within the bole and crown, and none has assessed the impact of silvicultural treatments on total above-ground nutrient distribution in yellow-poplar.

Comparative data are scarce, but it seems likely that tree species differ in their relationships between growth and foliar chemical contents (Koch, 1985). For white oak (*Quercus alba* L.), Finn (1953) found highly significant correlation between nitrogen content of leaves and site index. For yellow-poplar, Gilmore *et al.* (1968) found that height of 18 year old trees had a significant positive correlation with foliar calcium, phosphorus, magnesium and nitrogen. White and Finn (1964) concluded that foliar potassium had a negative correlation to frost damage.

Chandler (1941) found yellow-poplar foliar nutrient concentrations to be 0.51 percent N, 0.11 percent P, 0.95 percent K, 2.56 percent Ca, and 0.01 percent Mg. However, Auchmoody (1974) and Auchmoody and Hammock (1975) found significant variations in nutrient concentrations in different locations within the crown. These

researchers found that nitrogen and phosphorus concentrations were higher in blades than in petioles, and that concentrations of potassium and calcium were generally higher in the lower portions of the crown. This supports White (1954), who concluded that lower canopy leaves often have higher nutrient concentrations because of little "nutrient dilution" due to low photosynthesis rates. Also, Smalley (1976) found that foliar nutrient concentration varied considerably over the course of the growing season. He found that nitrogen concentration decreased during the season, phosphorus concentration was relatively stable, potassium and magnesium gradually increased, and calcium concentration increased rapidly in early summer, decreased in mid-September, and peaked before leaf abscission.

Rathfon *et al.* (1991) assessed yellow-poplar foliar N, P and K concentrations on varying sites and under various silvicultural treatments. They found than on slope sites, fertilization significantly increased foliar concentrations of N, P and K, and crop tree release decreased K concentration. They found no nutrient concentration differences on cove sites, which would indicate that soil nutrients were not limiting and uptake was not increased. Cole and Newton (1986) found that thinning increased the availability of mineral nutrients such that both foliar N and P concentrations were higher in widely spaced Douglas-fir trees than in closely spaced trees.

Some researchers have found an antagonistic interaction between elements, where a change in the concentration of one element is accompanied by a change in the concentration of another or other elements. Cain (1959) found that an increase in N supply generally decreases foliar P and K concentrations, but may increase Mg

concentration. Other researchers have found similar results.

While quantities rarely exceed one percent of dry weight of stemwood, nutrient concentrations within the bole may be important, as mineral components (especially nitrogenous compounds) play an important role in biogenesis, determining cell wall thickness, cell length, cell type distribution, sap transport, and enzyme activity (Koch, 1985). In an unpublished report (Koch, 1985), Manwiller reported that in yellow-poplar growing on southern pine sites, nutrient concentrations within the stem were as follows: 1,182 ppm calcium, 517 ppm potassium, 108 ppm phosphorus, and 265 ppm magnesium - nitrogen concentrations were not available. Branchwood contents were generally very similar, but stembark and branchbark contents were much higher. In Tennessee, Johnson (1983) found mature stem nutrient concentrations of 0.18 percent N, 0.13 percent P, 0.03 percent K, and 0.27 percent Ca. Stump sprout concentrations were much higher. Although Grozdits and Ifju (1969, 1973) and Panshin and de Zeeuw (1980) submit that nitrogen concentration will be highest in the cambial zone and decrease sharply throughout the current annual increment and towards the pith due to nutrient dilution following xylem differentiation, very little is known about the silvicultural effect of stemwood nutrient concentrations and contents with and without bark, and within different partitions of the tree.

The Concept of Wood Quality

In attempting to examine how silvicultural practices affect wood quality, it is necessary to first explain the concept of quality. Haygreen and Bowyer (1989) define wood quality as a measure of the characteristics of wood that influence properties of

products made from it. Briggs and Smith (1986) say, "wood quality is a measure of the aptness of wood for a given use." A set of prescribed measurements for assessing wood quality may be elusive, however, as the various wood product industries perceive wood quality in different manners. For producers of structural lumber and other solid wood products, quality may be measured in terms of density; uniformity of growth rings; percent juvenile wood; location, number and size of defects; and percent knot-free wood (Haygreen and Bowyer, 1989). Pulp and paper manufacturers, on the other hand, may measure wood quality in terms of cellulose yield, fiber-to-vessel ratio, and proportion of juvenile wood (Thomas and Kellison, 1990).

Larson (1969) summed up the matter of wood quality fairly well when he wrote: "During wood formation, numerous factors both inside and outside the tree lead to variation in the type, number, size, shape, physical structure, and chemical composition of wood elements. Wood quality is the arbitrary classification of these variations in the wood elements when they are counted, measured, weighed, analyzed, or evaluated for some specific purpose. Wood quality is therefore a concept...."

Measures of Wood Quality

Although the concept of wood quality differs within the various wood product industries, several factors influence the suitability of wood for a variety of uses. However, cellular and anatomical features vary by species, therefore, some measurements may be valuable in assessing wood quality concerns for one species, but not for another. Only factors considered important for evaluating wood quality for diffuse-porous species, such as yellow-poplar, are addressed in this project. Review of

the literature indicates that the singular most important factor most often used to determine the effects of silvicultural treatments on wood quality in hardwoods is specific gravity (Haygreen and Bowyer, 1989).

Specific Gravity

The specific gravity of wood is its single most important characteristic. It is closely correlated to the mechanical strength of wood, amount of shrinkage and surface hardness; and largely determines pulp yield from a given volume of wood (Koch, 1985). Sluder (1972) found specific gravities of yellow-poplar in the southern Appalachians ranging from 0.32 to 0.55 with a mean of 0.41. A number of other researchers have also found variability of specific gravity within the species. Kellison (1967) found significant geographic variation in specific gravity in North Carolina. He found mean specific gravity values of 0.43 in the Piedmont, 0.42 on the Coastal Plain, and 0.41 in the Mountain Region. Sluder (1972) concluded that specific gravity decreased with increasing elevation, more northerly latitudes, and increasing site index.

Other researchers have found within-tree variation also. Clark *et al.* (1974) and Clark and Schroeder (1977) found increasing specific gravity with increasing height in the tree. In another study, Koch *et al.* (1968) found that specific gravity was highest near the bottom of the tree, decreased rapidly to about 10 ft (3.0 m), remained stable until about 28 ft (8.5 m), and then increased to 34 ft (10.4 m) before once again levelling off. Thorbjorsen (1961) and Taylor (1964) found that radial variation in specific gravity follows a relationship with interactions between height in stem and number of rings from the pith. They found that at breast height, least dense wood is

near the pith, and specific gravity increases with increasing number of rings from the pith to a height of about 60 ft (18.3 m) where the trend reverses itself.

Growth Effects on Wood Properties

The primary economic objective of silvicultural treatments, in regard to timber production, is to increase the growing space (to include light, moisture, nutrients and physical space) of desired trees so that growth can be maximized and rotation length minimized. If value is a function of both quantity and quality, though, what are the effects of accelerated growth on the qualitative properties of wood?

The effect of accelerated growth on wood properties varies with species, but in general, negative effects are more pronounced in conifers than in hardwoods. This is largely due to the effects of accelerated growth on the relative proportions of earlywood and latewood in the individual growth rings (Paul, 1963). Bendsten (1978) and others, have since challenged these findings, citing an age effect as the primary determinant of specific gravity. For the more uniform, diffuse-porous species such as yellow-poplar, anatomical differences in early and latewood are not as overt.

In regard to density, studies involving yellow-poplar have shown mixed results. Paul (1963) concluded that specific gravity was 8 percent greater in faster-grown trees. Paul and Norton (1936) found that yellow-poplar grown to more than 5 rings per inch showed no important variation in specific gravity. More recently, Thor and Core (1977) found that 30 percent accelerated growth induced by fertilization and irrigation had no effect on specific gravity or fiber length. Fukazawa (1984) reported that growth rate had no effect on specific gravity, but rather specific gravity was related to

age, while Koch and Stenglein (1986) again confirmed no relationship between growth and density. On the other hand, Wooten *et al.* (1973) showed that radial growth increases resulting from crop tree release caused a slight (but significant) increase in specific gravity, and had no effect on fiber length. In another study, Ross *et al.* (1979) reported small but significant decreases in specific gravity due to fertilizer induced growth. In general, the effect of growth stimulation on specific gravity appears to be small. Noted benefits of accelerated growth include greater within-ring uniformity (Zobel and Talbert, 1984), and reduced occurrence of spiral grain (Boyd, 1968; Brazier, 1977).

Wood degrade as a result of epicormic branching following thinning or crop tree release has not been shown to be a problem in yellow-poplar. Following thinning, epicormic branches are confined mostly to the upper bole, and those that do form on the lower bole portions will likely not persist past canopy closure (Smith, 1965; Della-Bianca, 1972).

The most serious problem associated with accelerated growth is an enlarged juvenile core. Juvenile wood is characterized by low specific gravity, short, thin-walled tracheids, and increased amounts of compression wood compared to mature trees (Bendsten, 1978). The principal concern regarding juvenile wood, is that it usually has inferior structural properties and lower product yields than mature wood (Kellison and Zobel, 1978). This problem is particularly important where solid wood products are concerned (Panshin and de Zeeuw, 1980). It is sufficiently serious that delays in treatments that stimulate growth may be warranted until the end of the

juvenile phase (Haygreen and Bowyer, 1989). It should be noted, however, that increased growth may have little impact on wood properties in the juvenile stage (Gladstone and Gray, 1973), which may not affect some pulpwood qualities (Haygreen and Bowyer, 1989). Mitchell (1972) suggests that fast-grown yellow-poplar should be just as suitable for solid wood products, and be as good or better, for pulp and paper products, as slower growing trees.

CHAPTER THREE: Methods

Study Area

Two adjacent study stands were selected approximately 10 km (6 miles) southwest of Blacksburg, VA, on Cassidy's Ridge in the Fishburn Experimental Forest (latitude 37° 12' N, longitude 80° 29' W, elevation approximately 630 m (2070 ft)). Stand one was located in a slight cove-like depression immediately north of the ridgetop. This site had a very slight slope and no detectable aspect. Stand two was located on a side slope above a minor drainage on a northerly aspect. The two stands were chosen such that a range of low to medium quality sites that support yellow-poplar would be represented. Due to the age of the stands, only yellow-poplar site index classes (to base age 50 - SI_{50}) could be determined in these stands (Beck and Della-Bianca, 1981). Stand one's SI_{50} class was 22.9-25.9 m (75-85 ft), and stand two's SI_{50} class was 18.3-21.3 m (60-70 ft) (MacCarthy, 1933).

Soil pits were dug in each stand to characterize the physical properties of the soils. The soil supporting stand one was a fine-loamy mixed mesic Typic Hapludult of the Clymer series. Soils of the Clymer series formed in residuum of sandstone, siltstone and shale, and are generally deep and well drained. The soil supporting stand two was a loamy-skeletal mixed mesic Typic Dystrochrept of the Berks series. Soils of the Berks series formed in residuum of shale, siltstone and sandstone, and are eroded and fairly shallow soils (Creggar *et al.*, 1985) (Table 3.1).

The area's climate is typically moderate with very few extremes (Table 3.2). Fifty-four percent of the annual precipitation occurs during the growing season

between the months of April and September, while 97 percent of the snow falls in the dormant season (October-March). October 10th and April 29th are generally the first and last freeze dates, respectively, allowing for an average 155 day growing season. The average relative humidity in midafternoon is about 66 percent. Humidity at night is higher, and the average at dawn is about 81 percent (Creggar *et al.*, 1985).

Table 3.1. Pretreatment comparisons of stand and site characteristics of the yellow-poplar crop tree release and fertilization study. (from Rathfon *et al.*, 1991)

Site	Mean DBH (cm)	Mean Tree Height (m)	Total Basal Area (m^2/ha)	Litter Depth (cm)	Depth to C Horizon (cm)	Depth to Bedrock (cm)	Soil Series
Stand One	8.1	9.7	17.9	8	79	140+	Clymer
Stand Two	5.4	7.6	15.2	3	48	79	Berks

Table 3.2. Temperature and precipitation recorded during the period 1953-1991 at Blacksburg, Virginia.

Category[1]	Growing (Apr.- Sept.)	Dormant (Oct.- March)	Yearly
Mean Monthly Precip. (cm)	9.2	7.8	101.8
Mean Monthly Snowfall (cm)	0.3	8.8	57.2
Mean Min. Daily Temp. (°C)	10.9	-2.4	4.2
Mean Max. Daily Temp. (°C)	24.3	10.3	17.3
Mean Daily Temp. (°C)	17.6	4.0	10.8

[1]Source: National Climatic Data Center Asheville, North Carolina.

Prior to the establishment of the present stands, the area supported a mature mixed-oak stand with some yellow-poplar present. The current stand was created in 1979 when the area was clearcut, removing all existing stems. The sites regenerated naturally, with most of the yellow-poplar stems being of seed origin while other species such as maples and oaks were of sprout and seed origin.

Prior to treatment, stand basal areas were 15 and 18 m^2/ha for stands one and two, respectively. Mean crop tree size differences were also evident (Table 3.1). Yellow-poplar accounted for 51 percent of the total basal area in stand one, while chestnut oak (*Quercus prinus* L.) comprised 18 percent. The remainder of the stand was composed of Virginia pine (*Pinus virginiana* Mill.) and a mixture of Appalachian hardwood species, none of which accounted for more than 10 percent of the total basal area. In stand two, yellow-poplar and chestnut oak each comprised 15 percent of the total basal areas. The remainder was made up of a mixture of Appalachian hardwood species, none of which accounted for more than 12 percent of total basal area (Rathfon *et al.*, 1991).

Field Methods

Treatments

In June of 1989, release and fertilization treatments were randomly applied in factorial combinations to 48 individual crop trees on each of the two sites. To be considered for selection, prospective crop trees had to be of seed origin, and show no evidence of mechanical or pathogen related damage, including crooks and sweeps. Because third year analysis indicated that treatment effects were beginning to level-off,

treatments were reapplied in early June of 1992. Each tree recieved the same treatment in 1992 as it did in 1989. Prior to both treatments, dbh, total height, height-to-live crown, and crown radius measurements were made on all trees.

Release and fertilization treatments were applied in factorial combinations to the 48 individual crop trees in both stands in June of 1989 and 1992. The treatments included: (1) control; (2) release; (3) fertilize; and (4) release plus fertilize. Each treatment was replicated 12 times on each site.

The 1989 release treatment was applied using a basal application of a four-percent solution of triclopyr ester in diesel oil to all trees within a *two* meter radius of the crop tree. Only competing yellow-poplar were released with a hand ax to preclude translocation of herbicide through root grafts. The 1992 release treatment was accomplished mechanically using a hand axe and a chainsaw. In addition to removing all competing stems within a *three* meter radius of the crop tree, a crown touching method of release was employed. Using this method, all crowns that either touched or interfered with the crown of the crop tree were removed.

The 1989 fertilizer application was broadcast in a two meter radius band around the crop tree. A complete fertilizer was used to apply 224, 291, and 243 kg/ha of elemental nitrogen, phosphorus and potassium, respectively. The second fertilizer treatment was also broadcast in a 2 meter radius band around the crop tree. However, because the levels of phosphorus and potassium in the soil of fertilized trees were significantly higher than unfertilized trees at the end of three years (Bollig *et al.*, 1993), only urea (46-0-0) was applied at the rate of 224 kg/ha of N.

Measurements of Response

Physiology

In order to characterize the three major limiting factors of plant growth (water, light, nutrients), measurements of photosynthetically active radiation (PAR), xylem water potential, available soil nutrients, and tissue nutrient concentrations were assessed. PAR measurements were made in mid-August 1993 using a LI-185B portable quantum photometer (LI-COR, Inc., Lincoln NB). Six randomly selected trees of each treatment were sampled on both sites. Measurements were made every 0.4 m to a distance of 2.0 m in all four cardinal directions, for a total of 20 measurements per sampling unit. Measurements were conducted under clear skies, and expressed as a percentage of ambient light..

Mid-day xylem water potentials were recorded monthly from July to September, 1993. Twig and foliage samples were taken from the upper-crown (sun leaves) between the hours of 1000 and 1400, and measured with a pressure chamber (PMS Instrument Corp., Corvallis, OR) within two minutes of being clipped from the tree. To avoid water potential differences due to changing ambient conditions, a rotating method of twig collection was employed. Using this method, a twig was collected and measured from like treatments on both sites, before moving on to another treatment. Thus, one rotation of all four treatments was collected and measured from both sites before moving on to the next rotation. Six randomly selected trees of each treatment were sampled on both sites, thus, there were six rotations.

Soil nutrients, pH and organic carbon were assessed prior to treatment, and again during the growing season of 1993. The upper 10 cm of soil was sampled adjacent to each tree with a soil probe. A total of eight soil cores were removed from the base of each tree - two in each cardinal direction, at both 0.5 m and 1.0 m from the base of the tree. All eight cores were composited into a single sample and taken to the lab for drying and analysis.

To assess levels of foliar nutrients, the upper crown foliage of six randomly selected trees of each treatment on both sites was sampled in mid-August of 1993. Samples were stored in plastic bags in a cooler and taken to the lab for drying and analysis.

Growth

Tree measurements were made three times during the course of this study: (1) prior to the first treatment (1989); (2) prior to the second treatment (1992); and (3) at the end of the fifth growing season (1993). Measurements included dbh, total height, height-to-live crown, and crown radius. Crown volumes were calculated using the following formula:

$$CV = \pi r^2 H/2$$

where: CV = crown volume in cubic meters
r = crown radius in meters
H = length of crown = total height - height-to-live crown in meters.

Whole-Tree and Partitioned Dry Mass and Volume

At the end of the fifth growing season (1993), six randomly selected trees from each treatment on both sites were harvested at ground level. To assess the dry mass of the various components of the tree, the tree was partitioned into the following components: foliage, current year's branches, all other branches, and bole. The bole was sectioned into 2 m vertical segments starting at the base of the tree and culminating at the terminal bud. Each component of the tree was weighed in the field (wet mass), and a minimum five percent subsample of crown components was selected, weighed, and reweighed after drying (dry mass). A 3 cm radial slice (cookie) at the upper and lower end of each bole segment was also taken , weighed and reweighed after drying. Prior to drying, the bark of all the cookies was removed and the diameters of all cookies were measured. The inside bark volumes of each bole segment were calculated using the following formula:

$$V_c = [(B_s+B_l)/2](L)$$

where: V_c = cubic meter volume inside bark
B_s = cross-sectional area at small end of log in square meters
B_l = cross-sectional area at large end of log in square meters
L = length of log in meters.

Woody samples were then placed in a 103 °C oven (65 °C for foliage samples) and dried for a minimum of three days. After complete drying, samples were reweighed and the masses of these subsamples were expanded to include the full sample mass.

Laboratory Methods

Soil Analysis

Soil samples were air-dried and ground to pass a 2 mm sieve. Ground samples were tested for anaerobically-mineralizable nitrogen using the techniques set forth by Keeney (1982), and analyzed on a Technicon Auto Analyzer II (Technicon Instruments Corp., Tarrytown, NY) using the indophenol colorimetric technique. Soil samples were also analyzed for available phosphorus, potassium, calcium, magnesium, manganese and iron using the dilute double-acid extraction method (Olsen and Sommers, 1982). Subsequent analysis was performed using an Inductively Coupled Plasma Emission Spectrophotometer (ICP). Total organic carbon in the soil samples was measured using the LECO Carbon Determinator CR12 (LECO Corp., St. Joseph, MI), and soil pH was determined with a Chemtrix Type 40 pH meter (Chemtrix, Inc., Hillsboro, OR).

Nutrient Analysis

Foliage was oven-dried (65 °C) for 72 hours, ground in a Wiley mill to pass a 1 mm sieve, and analyzed for total nitrogen, phosphorus, potassium, calcium, magnesium, manganese and iron. Total Kjeldahl nitrogen (TKN) was determined by block digestion (Bremner and Mulvaney, 1982) and subsequent analysis was performed using the ammonia salicylate colorimetric technique on a Technicon Auto Analyzer II. Samples analyzed for the remaining elements were ashed at 500 °C for 16 hours then extracted with 6 M HCl. The extracts from this procedure were analyzed using the ICP.

This analysis yielded the amount of each element per unit dry weight of foliage (nutrient concentration). Foliar nutrient concentrations were then expanded to include the total amount of each element in the entire foliar mass (nutrient content).

Wood Nutrient Analysis

Wood, branch and bark samples were oven-dried (103 °C) for 72 hours. The samples were then ground in a Wiley mill to pass a 2 mm sieve, and analyzed for TKN, phosphorus, potassium, calcium, magnesium, manganese and iron using the same methods as outlined in the Foliar Analysis section above.

Wood Properties Analysis

Wood samples were oven-dried (103 °C) for 72 hours, and oven-dried weights were measured and recorded to the nearest 0.001 gram. The samples were then immersed in liquid paraffin, and then in a tared beaker of water. The weight of displacement was recorded to the nearest 0.001 gram. The paraffin dip was employed to prevent water from entering the exposed lumens, which can result in erroneously low volume determinations. The specific gravity of the samples was then calculated using the following formula:

$$\frac{\text{Oven-dry mass/volume}}{\text{Density of water}}$$

where: Density of water = 1.0 g/cm^3 (Haygreen and Bowyer, 1989).

Data Analysis

The experiment was designed as two separate completely randomized designs

with two factor, factorial treatments. However, because initial analysis using a randomized complete block design revealed that stand (block) response was not significant, the two stands were combined and analyzed as a completely randomized design. This experimental design was chosen to allow a valid estimation of σ^2 as well as a test for treatment interactions. The general response model was:

$$x_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk}$$

		df
where:	μ = overall mean	1
	α = treatment - release	1
	β = treatment - fertilize	1
	$\alpha\beta$ = release * fertilize	1
	ε = random error	92
		96

Statistical Procedures

Experiment One

Purpose: Experiment One examined the effect of factorial combinations of fertilization and release on low to medium quality southern Appalachian sites on relative growth, tree physiology, nutrient distribution, and wood properties. The experiment was designed as a completely randomized experimental design with a two factor, factorial treatment. Each individual tree was considered an experimental unit.

The following null hypotheses were tested:

$H_0$1: Treatment had no effect on bolewood, bark, branchwood or foliar nutrient concentrations or contents.

$H_0$2: Treatment had no effect on soil nutrient levels, xylem water potentials or PAR levels.

$H_0$3: Treatment had no effect on bolewood, bark, branchwood, or foliar

phytomass, or on bolewood volume.

$H_0$4: Treatment had no effect on relative height, diameter, or crown volume growth.

$H_0$5: Treatment had no effect on specific gravity, either vertically within the bole, or on the mean bole specific gravity.

As differential growth may have occurred as a result of the relative sizes (ie - crown positions) of the trees prior to treatment, two factor analysis of covariance (ANCOVA) was used for phytomass and volume comparisons using pretreatment diameter and/or height as the covariate(s). This in effect, removed any main factor mass and volume variation due to differential growth caused by different pretreatment tree dimensions. As pretreatment tree dimensions were available, relative growth, rather than absolute growth, was employed to normalize growth as per ANCOVA, and to allow the results of this study to be comparable to other growth studies. Relative growth (height, diameter, crown volume) was calculated using the following formula:

$$RG = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where:

RG = relative growth

$\ln W_2$ = the natural log of the measured variable (height, diameter, crown volume) at the end of the 1993 growing season

$\ln W_1$ = the natural log of the measured variable prior to treatment

t_2 = the number of growing seasons since treatment (t_2 = 5)

t_1 = the number of growing seasons to be considered in this analysis prior to treatment (t_1 = 0).

Two factor analysis of variance (ANOVA) was used for all other comparisons.

Experiment Two

Purpose: The purpose of experiment two was to develop predictive dry mass models based on easily measured dimensional variables and silvicultural treatment regimes. Dummy variables (for release and fertilization) were employed along with an all possible regression procedure to assess treatment effect and look for significant model terms. Adjusted R^2, and Error Mean Square were employed to determine the best model fit. The C_p statistic as compared to p was used to determine the best predictive model.

CHAPTER FOUR: Results and Discussion

Relative Growth and Bolewood Volume

The primary objective of timber-oriented silvicultural operations, including crop tree release and fertilization, is to increase the quality, growth and yield of desired trees. The primary assessment of any cultural input, therefore, is its effect on the intermediate growth, and final yield of those trees. Although increased intermediate growth does not always result in increased final yield, if the rotation length of a stand can be reduced such that the present net value of a manipulated stand is greater than that of an untreated stand, the treatment is likely worth the cost (Smith, 1986). Intermediate growth and volume comparisons are therefore helpful in assessing the potential rotation length, and/or final yield of a stand or tree.

The following section will examine the effect of crop tree release and fertilization on the relative diameter, height, and crown volume growth, and stemwood volume of yellow-poplar five years after treatment. Relative growth will be based on all 96 trees, while stemwood volume will be based on the 48 harvested trees.

Diameter Growth

Crop tree release elicited a positive basal height diameter growth response averaged over five years (Figure 4.1). Release *x* fertilization interactions were not apparent. This positive response has been observed in a number of yellow-poplar studies (Beck and McGee, 1974; Williams, 1976; Lamson and Smith, 1978; Lamson 1983), however most of these were accomplished using a more geometric type of

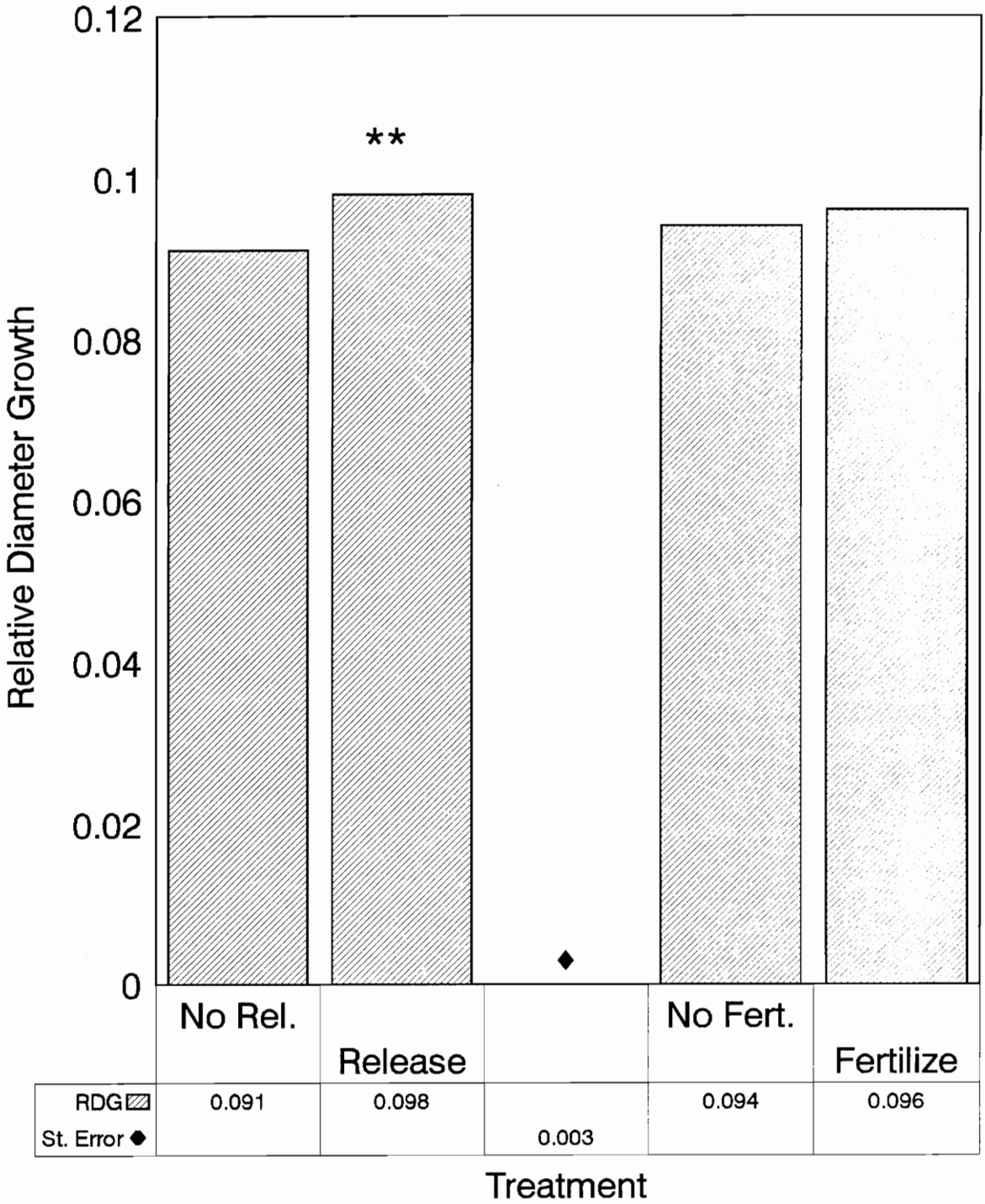


Figure 4.1. Mean relative diameter growth and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites. ** Different at p = 0.10.

thinning. Fertilization had no effect on diameter growth (Figure 4.1).

Height Growth

Unlike diameter growth, release did not result in increased height growth after five years. In fact, release decreased the height growth of yellow-poplar on these low to medium quality sites (Figure 4.2). A negative height growth response to thinning by yellow-poplar has been confirmed in past studies also (Allen and Marquis, 1970; Lamson and Smith, 1978; Rathfon *et al.,* 1991), and has generally been attributed to a reallocation of growth. Fertilization, again, did not effect height growth (Figure 4.2).

Crown Volume Growth

Crop tree release significantly increased the crown volume growth of the released trees (Figure 4.3). However, this effect may be misleading, as whole crown dry mass was not increased (See Figure 4.11). This suggests one of two possibilities: (*i*) the specific gravity of released branches is reduced by treatment, or (*ii*) crown morphology is changed. Since only the last five years of branch growth, and therefore only a portion of the branchwood, could be changed by release, it is unlikely that the overall crown specific gravity could be altered to such an extent. It is more likely, that in order to occupy the space created by release, branch elongation and crown length expansion were greater for released trees, while unreleased crowns grew mainly by putting radial growth on older branches. However, crown elongation was not greater for released trees (Figure 4.4), therefore, the equivalent crown dry masses between released and unreleased trees must be attributed to lateral branch expansion.

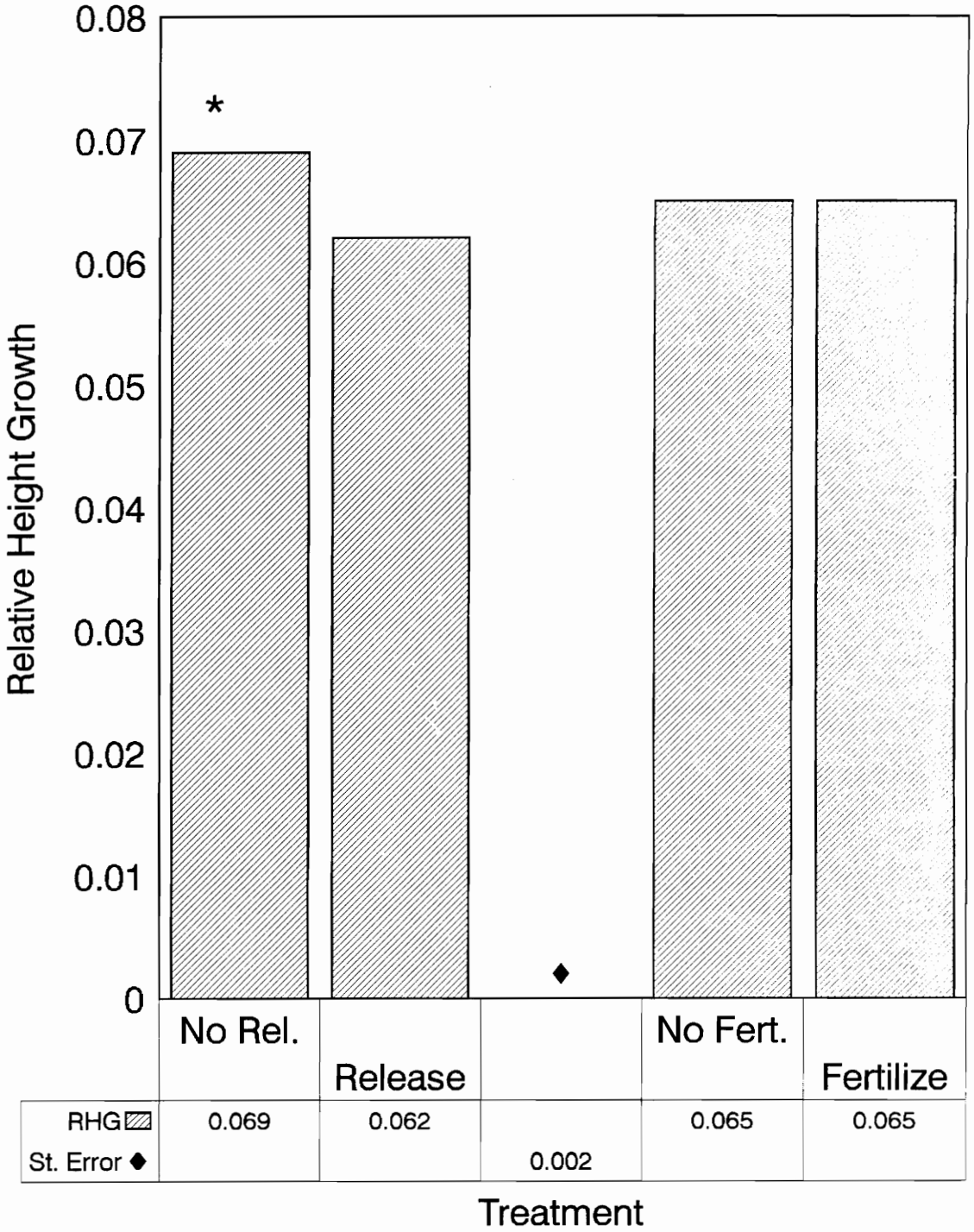


Figure 4.2. Mean height growth and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites. * Different at p = 0.05

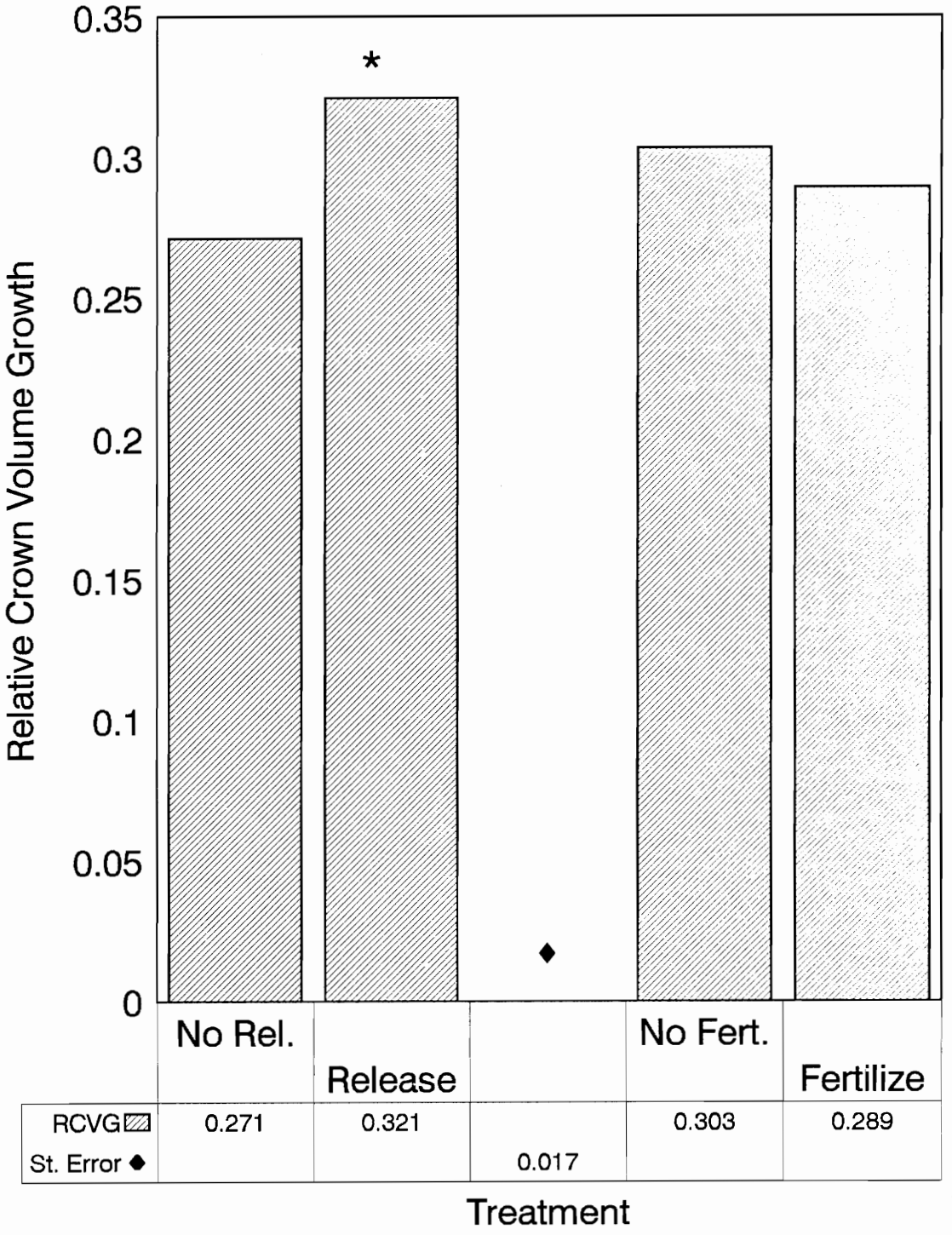


Figure 4.3. Mean relative crown volume growth and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites. * Different at p = 0.05

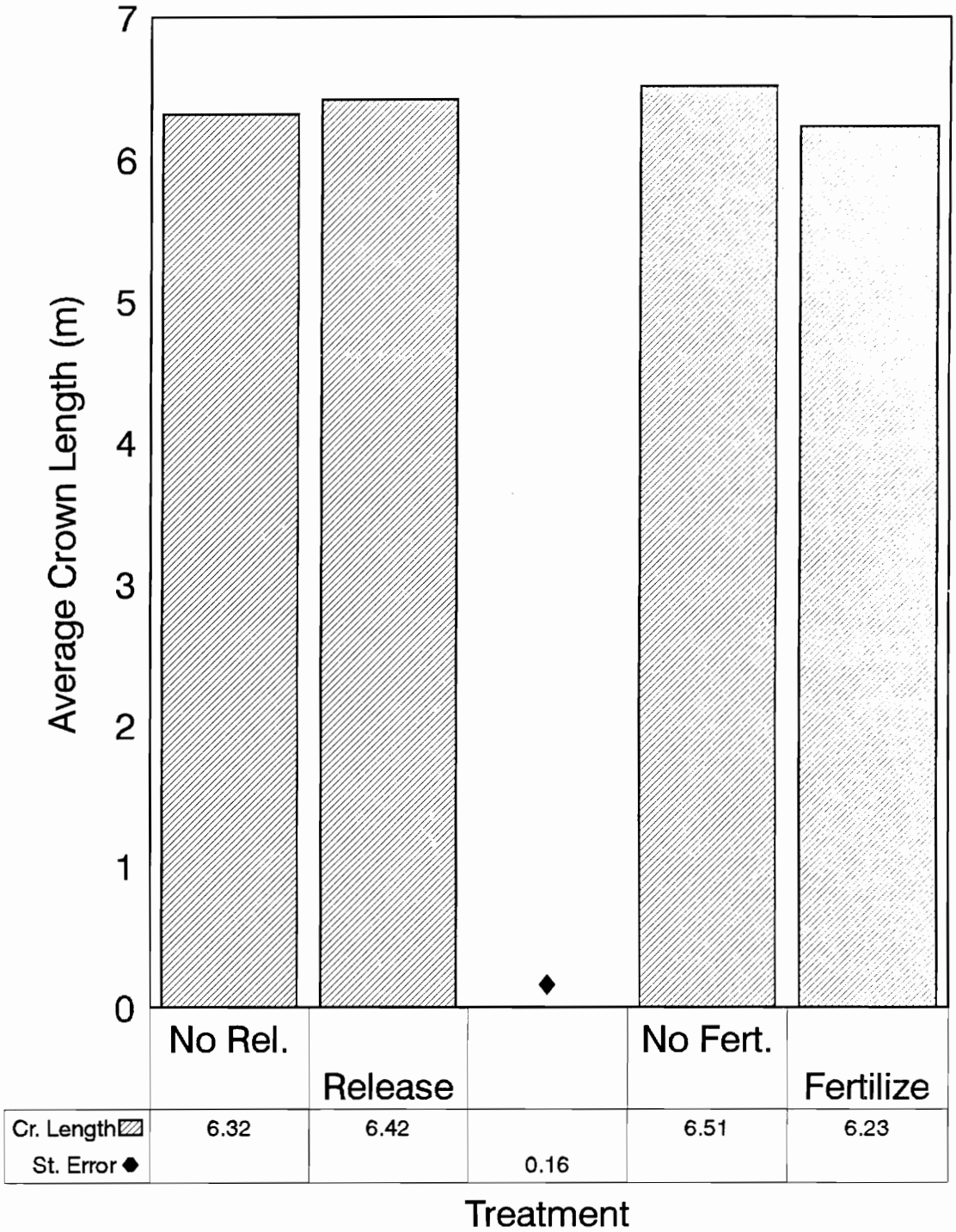


Figure 4.4. Mean crown length and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Because new branch growth is less massive than older woody branches, the total crown dry mass of released trees did not increase. Once again, fertilization did not affect crown volume growth (Figure 4.3).

Stemwood Volume

Neither release nor fertilization resulted in an increased inside bark stemwood volume (Figure 4.5). This is not surprising for fertilization, as no other dimensional variable was affected by treatment. For release, it appears that increased diameter growth (Figure 4.1) and decreased height growth (Figure 4.2) cancel each other when stemwood volume is considered.

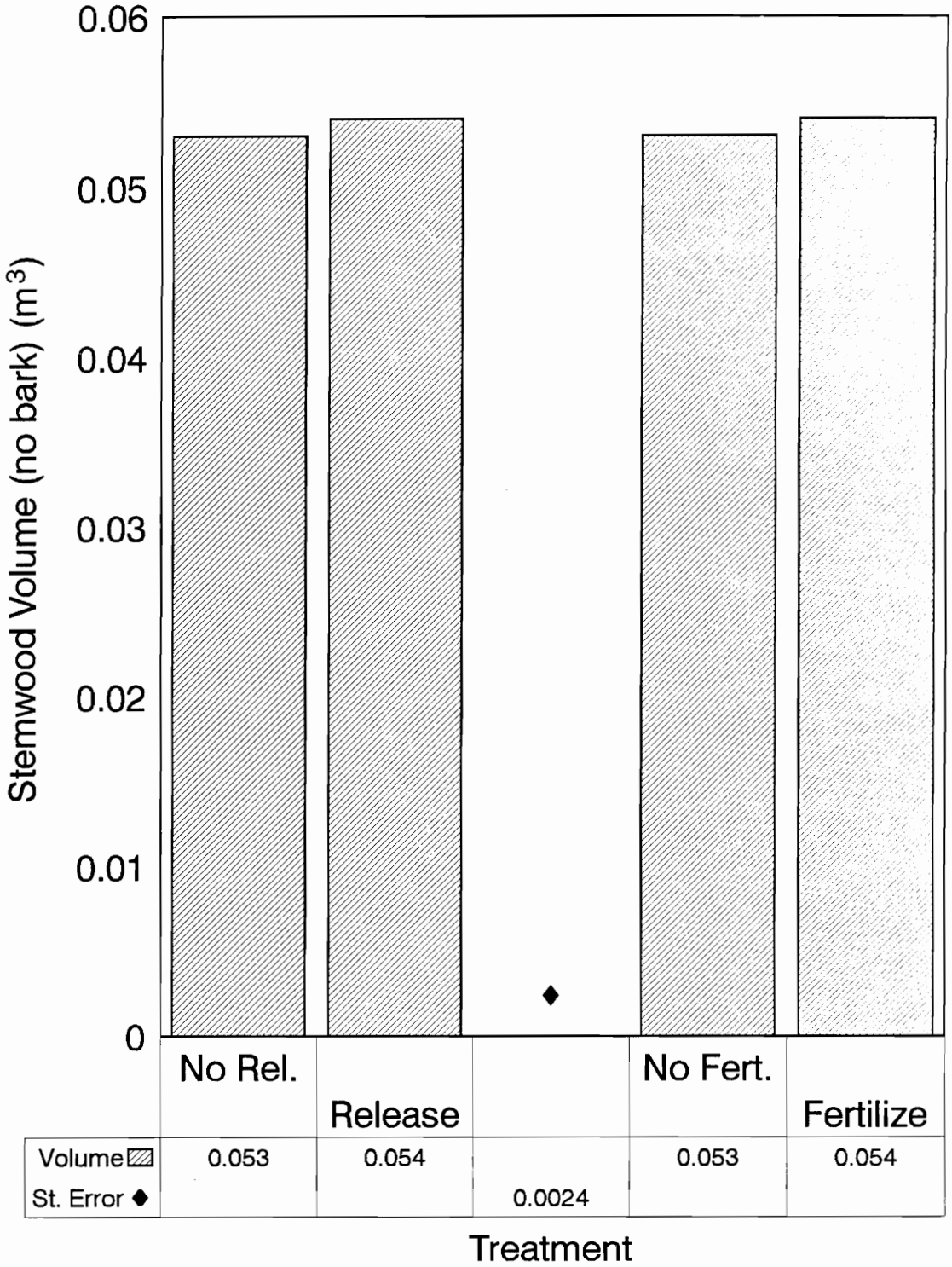


Figure 4.5. Mean inside bark volume and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Physiological Effects

Factors that most commonly limit tree growth, including available sunlight, and available water - are often collectively termed as *growing space* (Oliver and Larson, 1990). Light energy is an essential element of the photosynthetic reaction. When other factors are not limiting, trees generally photosynthesize increasingly faster in bright sunlight - up to full sunlight (Kimmins, 1987). Quantitative measures of photosynthetically active radiation (PAR) can therefore be useful in assessing potential tree growth. Water is also an essential component of photosynthesis, cell turgor, and other biochemical reactions within a tree (Kramer, 1983). Measures of water stress or water availability can prove useful in determining potential tree growth. Ritchie and Hinkley (1975) have described the use of the pressure chamber, a method of quantifying water stress and availability by measuring xylem water potential (a measure of negative pressure in the cells of trees).

In general, trees growing in suitable climates will increase growth until one or more factors necessary for growth are no longer available. While oversimplifications abound regarding limitations to growth, the interactions between limiting factors are often very complex (Oliver and Larson, 1990). As most silvicultural operations, including crop tree release and fertilization, are aimed at increasing the growing space of desired individuals, it is essential that we understand the interactions between silviculturally altered growing space, and growth itself.

The following section will describe the effects of crop tree release and fertilization on growing space. To assess treatment effect on available sunlight, PAR

will be compared between treatments, and available water will be examined by comparing xylem water potentials between treatments. Observed treatment growth differences, with respect to growing space, will also be discussed.

Photosynthetically Active Radiation

PAR, as expected was drastically increased by the release treatment (Figure 4.6). Release resulted in a 300% increase in PAR - from 1.6% of full sunlight, to 4.6% of full sunlight. This is in large part responsible for the increased diameter and crown volume growth of released trees (Figures 4.1 and 4.3). As horizontal growing space was created by the release, the crop trees reacted by radially filling the new space. As light (competition from above) was no longer the limiting factor to growth, the released trees reduced their allocation of carbohydrates to vertical elongation, and redistributed it to diameter and crown growth. Consequently, height growth was reduced (Figure 4.2). As the horizontal growing space created by release becomes occupied by the crop trees and their competitors, it is likely that vertical competition and height growth of released trees will once again increase.

Interestingly, PAR is also significantly increased by fertilization (Figure 4.6). This is largely the result of a release *x* fertilization interaction. It appears that release + fertilization may induce a morphological change in either the size, quantity, or density of the foliage of the yellow-poplar in this study, as these trees were not able to expand their crown and utilize the increased growing space created by the combined treatment.

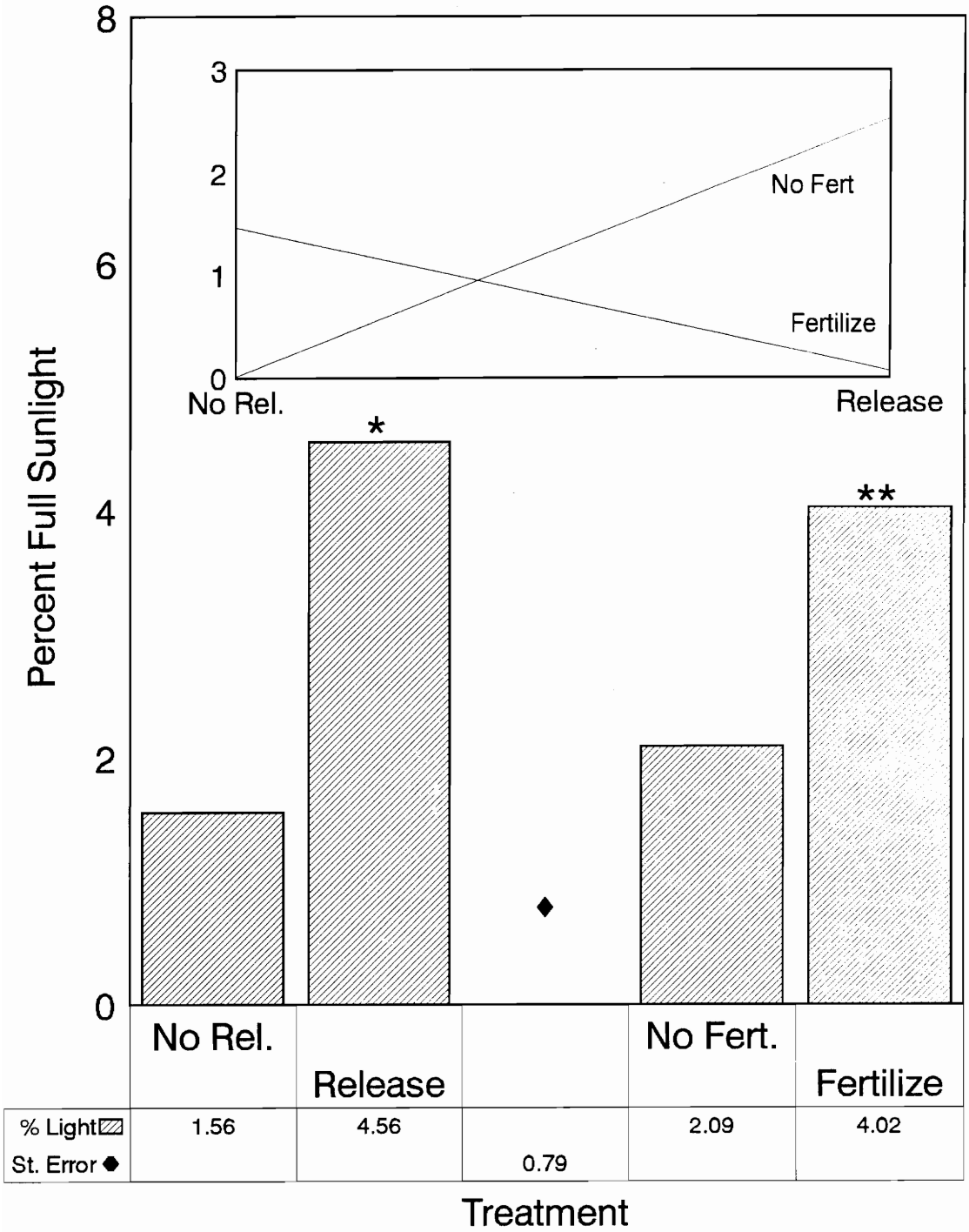
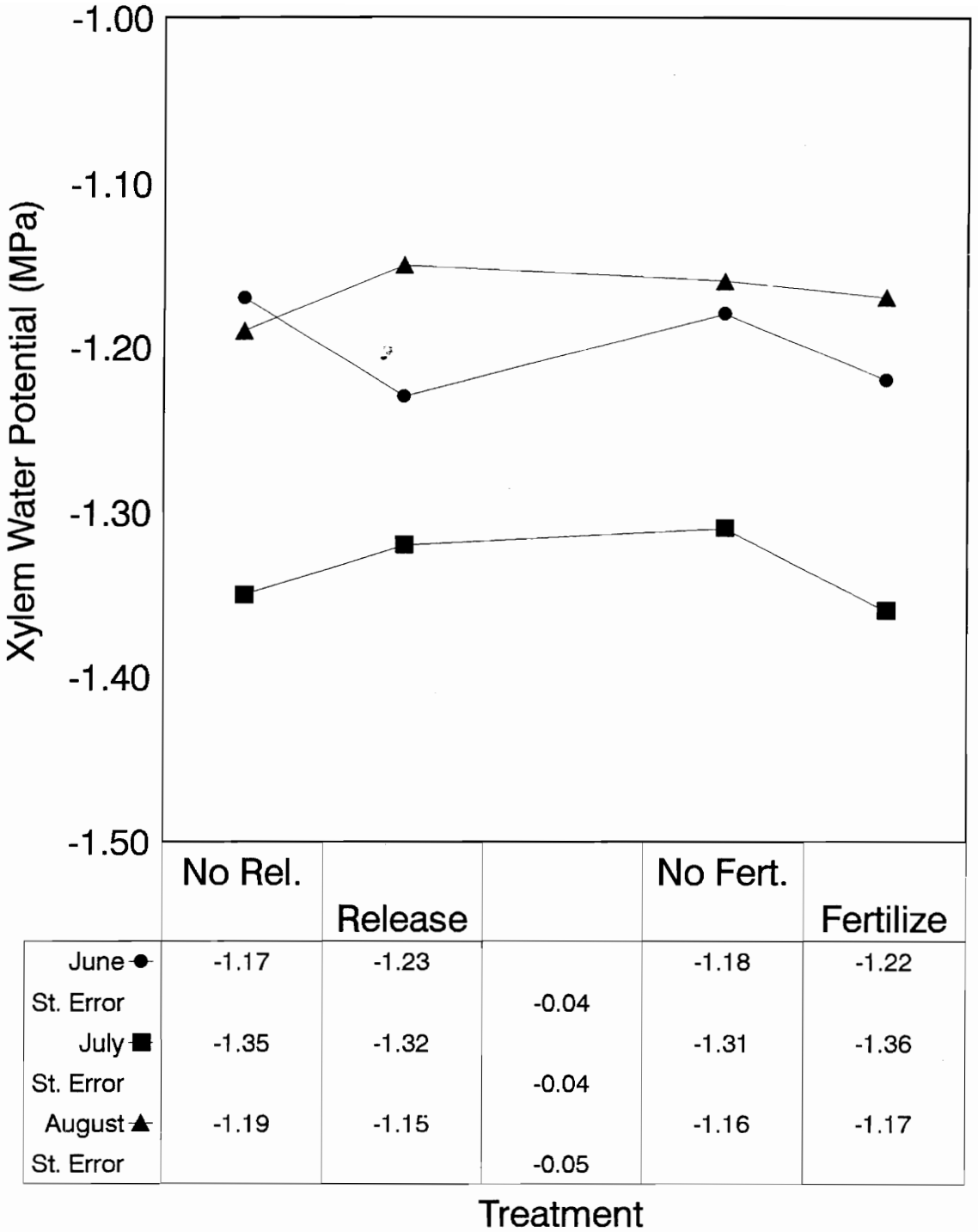


Figure 4.6. Mean and release x fertilization interaction percent full sunlight and standard error 1.5 m from the ground at the base of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

*** Different at p = 0.05 ** Different at p = 0.10**

Xylem Water Potential

Neither release nor fertilization resulted in xylem water potential differences during the three measurement dates (Figure 4.7). Treatment interactions were also not apparent. As expected, there were different degrees of water stress for the different measurement times, however, this effect was constant over all treatments. This lack of water potential effect suggests that either water was not the limiting factor to growth, or water availability was not affected by any treatment combination. Unfortunately, we are not able to distinguish between these two possibilities.



	No Rel.	Release		No Fert.	Fertilize
June ●	-1.17	-1.23		-1.18	-1.22
St. Error			-0.04		
July ■	-1.35	-1.32		-1.31	-1.36
St. Error			-0.04		
August ▲	-1.19	-1.15		-1.16	-1.17
St. Error			-0.05		

Figure 4.7. Mean xylem water potentials and standard errors taken three times during the 1993 growing season on released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Effects on Nutrition and Dry Mass

Nutrient availability is also a component in the collective concept of growing space (Oliver and Larson, 1990). Once in the tree, nutrients are either converted to molecules essential for photosynthesis, or are used as catalysts for the many biochemical reactions inside the tree (Pritchett and Fisher, 1987). Most nutrients are concentrated in the foliage, crown and bark (this section), however, the essential elements for metabolism and growth, excluding carbon and oxygen, need to first be taken up from the soil through the roots. Therefore, quantifying mineral concentrations in the soil can be quite useful in assessing nutrient availability.

Nutrient concentrations, especially those of foliage and soil, have long been used to assess the overall nutritional status of trees, and what its effect may be on the growth and carbon allocation of the tree (Kolb *et al.*, 1990, Johnson *et al.,* 1991). Often, higher concentrations of nutrients in the foliage and soil, especially phloem-mobile nutrients, result in greater growth, or increased above-ground carbon allocation.

Nutrient content, although useful in assessing the nutritional status of the tree, is more useful in examining the nutrient budgets of a particular system (Everett and Thran 1992), and the effect of phytomass removal (fire, harvest, *etc.*) or addition on these nutrient budgets. As additions of nutrients (fertilization), or culturally-induced reallocation of carbon (crop tree release), may affect the overall dry mass and distribution of nutrients in the system, it is important to understand the relationship between silvicultural treatments and nutrient partitioning.

The following section will examine the effect of crop tree release and

fertilization on soil nutrient availability, tree component dry mass, and nutrient contents and concentrations of nitrogen, phosphorus, potassium, calcium, iron, magnesium and manganese in the various above-ground components of the tree. Nutrient availability will be appraised by examining the nutrient concentrations of anaerobically available nitrogen, and available phosphorus, potassium, calcium, iron, magnesium and manganese in the upper rooting zone (top 10 cm) of the individual tree's soil. Since the pH of the soil can effect nutrient availability, and because the amount of organic carbon in the soil plays a large part in future nutrient availability and soil water holding capacity (Pritchett and Fisher, 1987), the soil pH and organic carbon will also be examined. Observed growth differences, with respect to tree nutrition, will be discussed.

Nutrient Availability

Surprisingly, fertilization did not result in increased anaerobically available nitrogen (Table 4.1). Although leaching is a possible explanation for the lack of nitrogen response, it is unlikely, as the mineralization --> nitrification process of urea in acidic soils is quite slow (Pritchett and Fisher, 1987). Another possiblility is volatilization. Nommick (1973) has shown that losses due to volatilization of urea derived ammonium, when applied as small pellets in the summer season, can be as high as 20 to 40 percent. However, a more likely explanation is a simple nonresponsiveness of the system to additions of nitrogen. The anaerobic mineralization index used for these soils is a qualitative index that detects only that nitrogen that is quickly mineralized to ammonium. It assesses the biological potential

Table 4.1. Soil nutrient concentrations of the upper 10 cm of soil in a 2 meter diameter circle on released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites as compared to pretreatment concentrations.

Treatment	Anaerobic NH_4	P	K	Ca	Fe	Mg	Mn
	<----------μg/g---------->						
Pre-treatment	45.7	2.390	58.00	168.00	--	25.50	--
Post-treatment							
No Release	58.7	1.407	15.37	94.19	7.913	11.44	12.90
Release	64.3	2.128*	15.68	124.5	6.848	13.26	14.81
No Fertilization	57.4	0.155	14.12	103.2	7.670	11.73	13.63
Fertilize	59.9	3.380*	16.94*	115.4	7.091	12.96	14.07
Standard Error	8.07	0.210	0.762	14.35	0.70	1.23	1.35

* Main effect mean nutrient difference at $\alpha = 0.05$

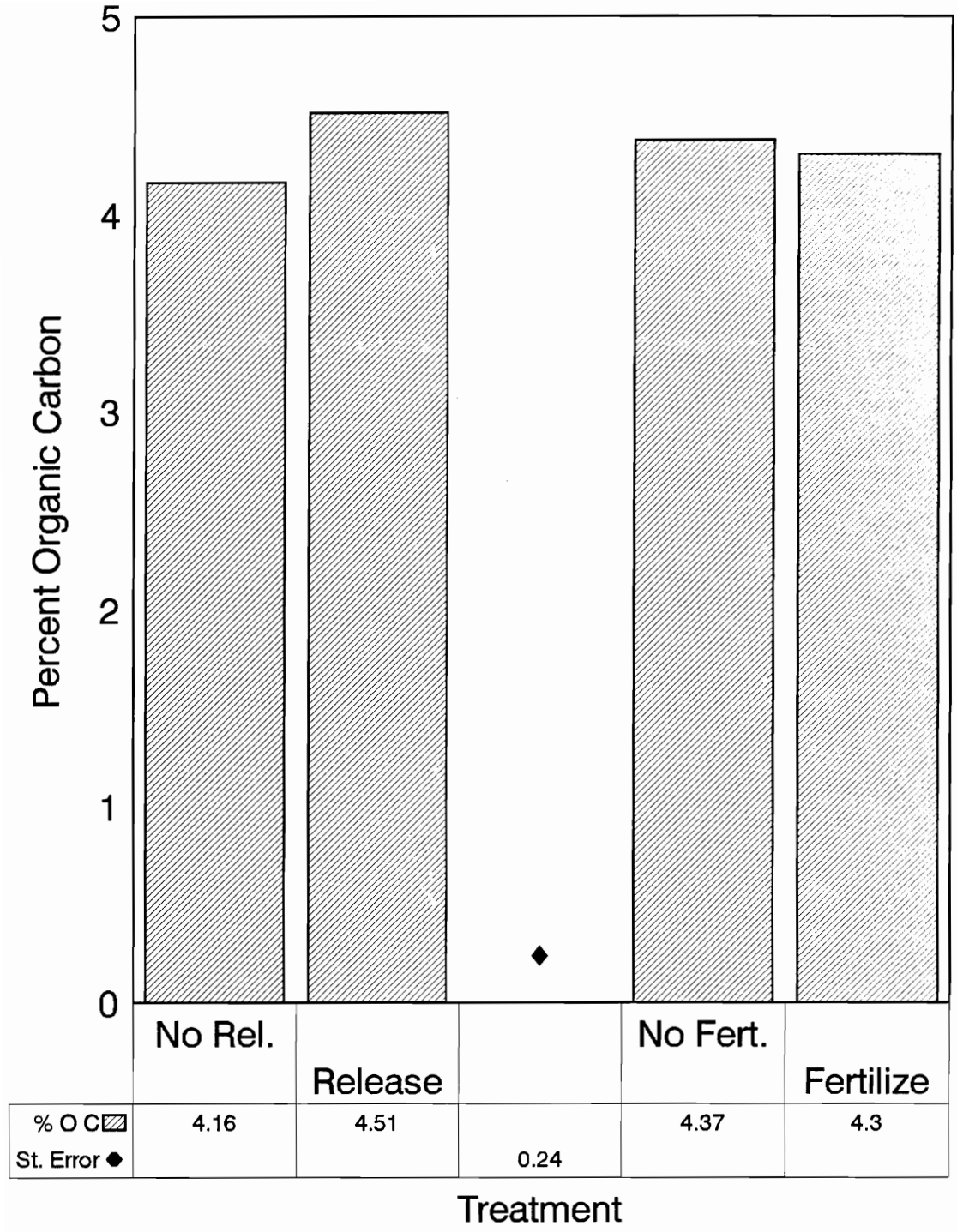


Figure 4.8. Mean organic carbon and standard error of the upper 10 cm of the soil of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

of a soil to mineralize nitrogen into a form that can be taken up by trees, however, it is not a quantitative measure of total nitrogen in the soil (Keeney, 1982). It is probable, therefore, that the additional nitrogen was either absorbed quickly and stored in crop tree yellow-poplar roots (or in other plants outside the crop tree system), or *mineralized* nitrogen was not increased by urea input; but, *total* nitrogen (available plus immobilized) was increased. This theory of nonresponsiveness of the yellow-poplar system to additions of nitrogen is well supported by the complete lack of growth stimulation due to fertilization, and the nonresponsive nitrogen distribution results discussed in the following pages.

It is not too surprising that fertilization did increase the concentrations of both phosphorus and potassium. Phosphorus is considered relatively immobile, especially in acidic soils, as it forms very stable bonds with iron and aluminum (Fitzpatrick, 1986). However, its greater abundance also proportionally increased its availability to be taken up by the trees. Phosphorus concentration was also greater under the released trees. As organic matter is the principal source of phosphorus in many forest soils (Pritchett and Fisher, 1987), the increased availability is likely a result of the greater foliar mass (See Figure 4.10) of released trees. However, percent organic carbon was numerically, but not significantly increased by release (Figure 4.8). This failure to statistically differentiate organic carbon percentage is likely due to the random nature of where foliage lands following abscission. Fertilization resulted in a higher potassium concentration because potassium is rapidly and efficiently cycled in forest stands, and little leaches out of the rooting zone (Pritchett and Fisher, 1987).

No treatment effect could be found with respect to soil pH (Figure 4.9). Although the soils supporting these poplar stands were not extremely acidic, there pH's may have been sufficiently low to slow the rate of ammonification in the fertilized stands, which would help explain the nonresponsive nature of the system to nitrogen additions. This, however, is unlikely, as pH's well below 4.0 are generally required to slow ammonification to such a degree.

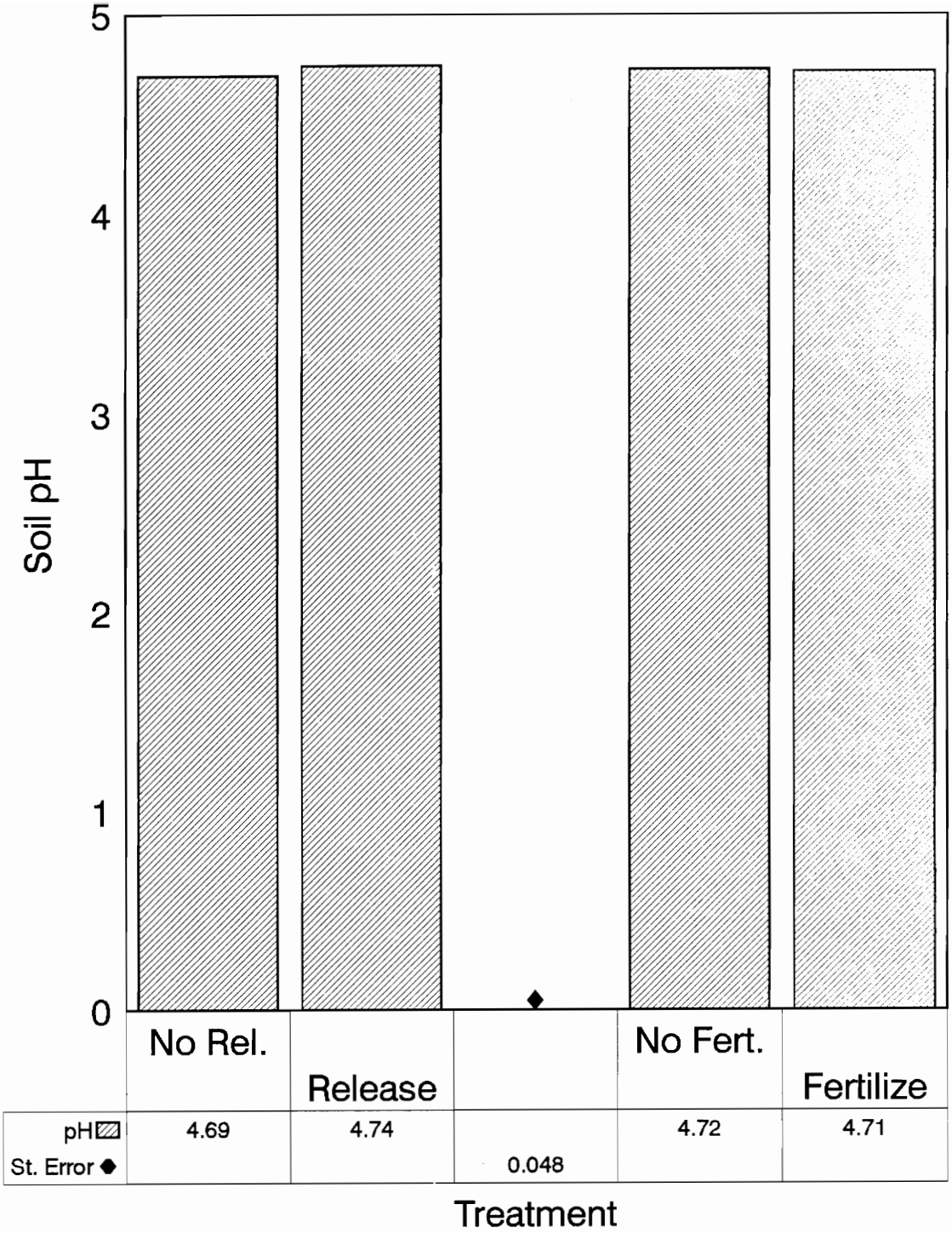


Figure 4.9. Mean pH and standard error of the upper 10 cm of the soil of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Foliage

Crop tree release increased the foliar content of nitrogen, calcium and iron, but had no effect on phosphurus, potassium, magnesium or manganese (Table 4.2). This increased content can be attributed to a greater foliar mass (Figure 4.10), as foliar concentrations of these elements were not greater than those of unreleased trees. Although not significant, the concentrations of these elements tended to be lower than those of unreleased trees. In addition, the foliar concentrations of potassium and magnesium were significantly greater in unreleased individuals, suggesting a release-induced nutrient dilution of these elements.

Release also resulted in increased foliar mass (Figure 4.10). Because sunlight was no longer the limiting factor to growth (Figure 4.6), released trees increased their uptake of nitrogen, calcium and iron (Table 4.2) - elements essential for photosynthesis - and allocated more carbohydrates to the production of foliage and radial growth (Figure 4.2) (Farrar, 1961). Released trees produced larger crowns (Figure 4.3), which usually results in an increase of gross and/or net photosynthesis (Ginn *et al.,* 1991). However, photosynthesis was not measured in this study. As total above ground dry weight of released trees, and thus above ground net primary production, had a large numerical (but not significant) increase (See Figure 4.14), it is likely that photosynthesis did increase.

Fertilization did not elicit a foliar content response for any of the seven elements (Table 4.2). It did, however, increase the foliar phosphorus concentration. This response suggests that (*i*) only phosphorus was limiting, and therefore uptake of

Table 4.2. Mean foliar nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	N	P	K	Ca	Fe	Mg	Mn
	<----------grams/tree---------->						
No Release	148	0.046	0.318	0.596	0.0003	0.131	0.050
Release	201*	0.061	0.403	0.992*	0.0005**	0.173	0.058
No Fertilization	201	0.056	0.378	0.892	0.0004	0.152	0.057
Fertilize	180	0.051	0.344	0.696	0.0004	0.152	0.051
Standard Error	29.8	0.008	0.047	0.130	0.00007	0.021	0.009
	<----------grams/kilogram---------->						
No Release	89	0.028*	0.192	0.376	0.0002	0.084**	0.030
Release	91	0.025	0.182	0.373	0.0002	0.074	0.026
No Fertilization	90	0.025	0.186	0.387	0.0002	0.075	0.028
Fertilize	91	0.028**	0.189	0.362	0.0002	0.082	0.028
Standard Error	2.2	0.001	0.009	0.022	0.000006	0.004	0.003

* Main effect mean nutrient difference at $\alpha = 0.05$
** Main effect mean nutrient difference at $\alpha = 0.10$

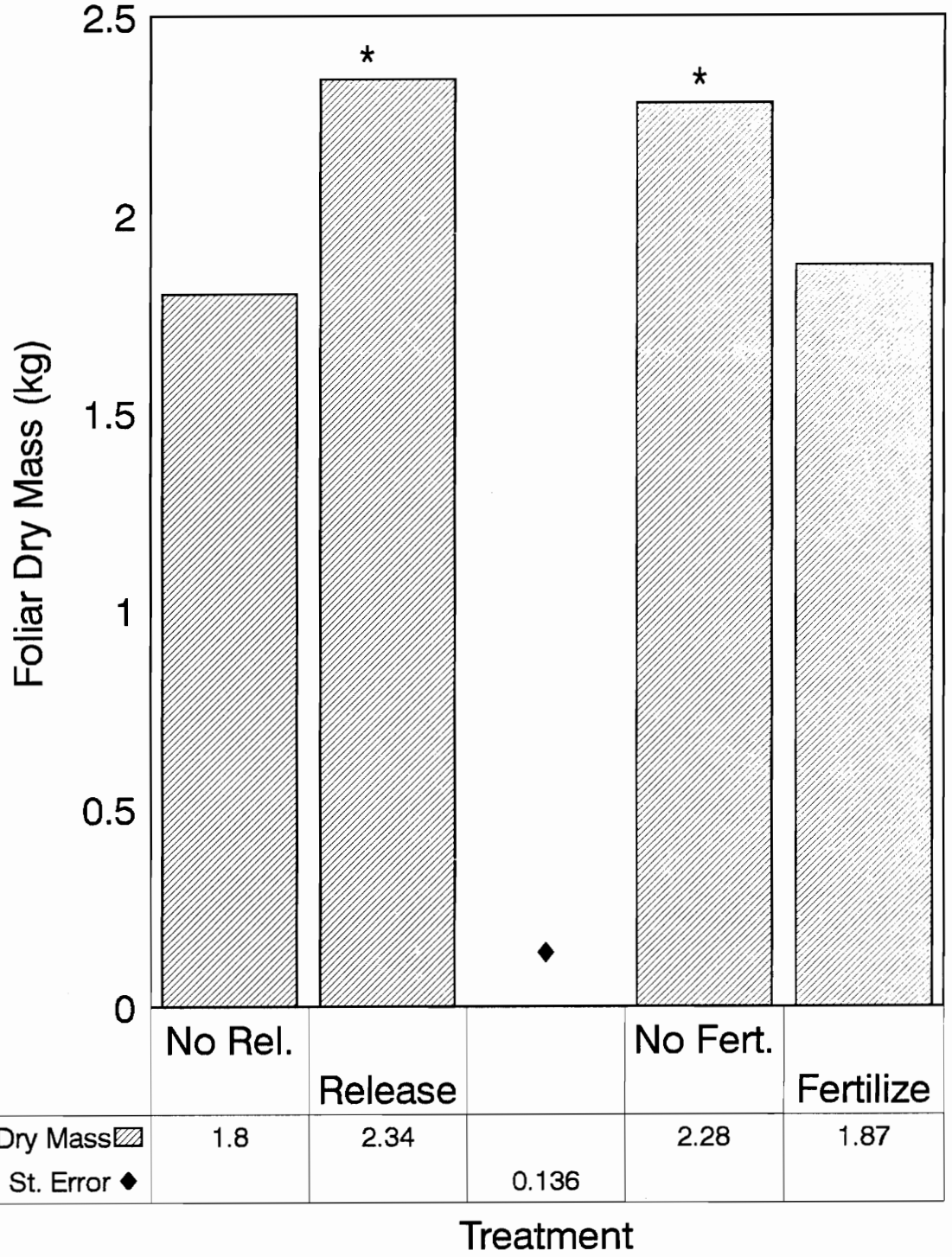


Figure 4.10. Mean foliar dry mass and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites. * Different at p = 0.05

only phosphorus was increased, or (*ii*) by year five, fertilization did not result in an increased availability of nutrients. Either because all the nutrients (except the relatively immobile phosphorus which did have greater availability - Table 4.1), were sequestered somewhere else in the system, or they were lost to the sytem *via* leaching. Because fertilized trees did not show positive growth responses (Figures 4.1-4.3), it is unlikely that phosphorus was limiting to growth.

Interestingly, fertilization resulted in decreased foliar dry mass (Figure 4.10). It is likely that any increased foliage building nutrients available for uptake, were better utilized by the trees surrounding the crop tree itself. Treatment interactions, however, were not significant.

The nutrient distribution results suggest that disturbances that remove foliage from the site (*ie.* litter raking, strong winds, intense fires and whole tree harvesting) may have a greater impact on the nitrogen, calcium and iron budgets of areas that have undergone a crop tree release.

Current Year Branches

Neither release nor fertilization influenced the nutrient content of any of the seven elements in the current year's branches (Table 4.3). Fertilization did, however, increase phosphorus and magnesium concentrations. Because buds were included in the nutrient analysis of this partition, these results suggest that the current year's branches of fertilized trees (probably the buds) may serve as a more effective sink for phosphorus and magnesium than the current year's branches of unfertilized trees. As these elements are major constituents of chlorophyll, this may be an important factor

Table 4.3. Mean current year branch and bud dry mass, nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	Dry Mass	N	P	K	Ca	Fe	Mg	Mn
	kg	<----------grams/tree---------->						
No Release	0.45	11.3	0.006	0.032	0.043	0.00003	0.008	0.002
Release	0.49	13.6	0.007	0.038	0.054	0.00004	0.009	0.002
No Fertilization	0.46	11.2	0.006	0.032	0.046	0.00003	0.007	0.002
Fertilize	0.48	13.7	0.007	0.039	0.051	0.00003	0.010	0.002
Standard Error		2.64	0.001	0.006	0.012	0.000008	0.002	0.0003
		<----------grams/kilogram---------->						
No Release		25.2	0.013	0.078	0.093	0.00006	0.018	0.005
Release		25.3	0.014	0.074	0.096	0.00006	0.018	0.005
No Fertilization		25.0	0.012	0.074	0.099	0.00006	0.016	0.004
Fertilize		25.5	0.014*	0.078	0.090	0.00006	0.019*	0.005
Standard Error		0.72	0.0004	0.002	0.004	0.0000039	0.0009	0.0005

* Main effect mean nutrient difference at $\alpha = 0.05$ in the manufacture of chlorophyll for the next year's foliage - potentially affecting photosynthesis or photosynthetic efficiency.

Older Branches

Like the current year's branches, neither release nor fertilization affected the nutrient content of any of the seven elements in the older branches (Table 4.4). However, just as in the current year's branches, phosphorus concentration was increased by fertilization. Again, this may be due to a greater sink strength in branches of fertilized trees, but because older branches have comparatively few cells that have differentiated to form lateral leaf buds, it is more likely a result of increased uptake, stimulated by an increased availability of phosphorus (Table 4.1).

Whole Crown

Although phosphorus concentrations are still slightly higher in fertilized trees when the whole crown is considered, neither release nor fertilization had a significant effect on the nutrient content of the entire crown (Table 4.5). Arithmetically, release appears to increase the nutrient content of all seven elements, however, variability was such that statistical differences could not be found. Release treatments did not result in nutrient concentration differences. This may arouse suspicion that the whole crown mass of released trees must be greater than those of unreleased trees. This, however, did not prove to be true (Figure 4.11). Therefore, the apparent differences can only be attributed to random variation.

Although released trees increased their foliage production (Figure 4.10), it is interesting to note that when the whole crown is considered, there is no increase in crown mass for the release treatments. This is especially interesting given that relative crown volume growth was greater for released trees (See Figure 4.3). This suggests

Table 4.4. Mean old branch (not current year) dry mass, nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	Dry Mass	N	P	K	Ca	Fe	Mg	Mn
	kg	<----------grams/tree---------->						
No Release	3.9	61.2	0.040	0.215	0.341	0.00024	0.050	0.017
Release	4.4	65.5	0.046	0.258	0.413	0.00031	0.051	0.022
No Fertilization	3.7	56.4	0.036	0.209	0.345	0.00023	0.040	0.019
Fertilize	4.5	70.4	0.051	0.264	0.409	0.00032	0.060	0.020
Standard Error		19.0	0.014	0.074	0.101	0.000080	0.017	0.0040
		<----------grams/kilogram---------->						
No Release		14.1	0.009	0.051	0.085	0.00006	0.012	0.005
Release		15.0	0.009	0.054	0.088	0.00006	0.012	0.006
No Fertilization		14.9	0.009	0.054	0.089	0.00006	0.011	0.005
Fertilize		14.2	0.010**	0.051	0.083	0.00006	0.012	0.006
Standard Error		0.51	0.0005	0.003	0.003	0.0000041	0.0005	0.0005

** Main effect mean nutrient difference at $\alpha = 0.10$

Table 4.5. Mean whole crown (branches and foliage) nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	N	P	K	Ca	Fe	Mg	Mn
	<----------grams/tree---------->						
No Release	221	0.092	0.565	0.980	0.00058	0.189	0.070
Release	312	0.114	0.700	1.459	0.00081	0.233	0.083
No Fertilization	269	0.097	0.618	1.283	0.00069	0.199	0.079
Fertilize	265	0.109	0.647	1.156	0.00070	0.222	0.074
Standard Error	46.9	0.022	0.117	0.219	0.000144	0.037	0.0132
	<----------grams/kilogram---------->						
No Release	40.5	0.016	0.101	0.184	0.00010	0.036	0.013
Release	43.4	0.015	0.104	0.190	0.00011	0.035	0.013
No Fertilization	42.5	0.015	0.104	0.196	0.00011	0.034	0.013
Fertilize	41.2	0.016**	0.101	0.178	0.00010	0.036	0.012
Standard Error	1.40	0.0006	0.0049	0.0095	0.0000037	0.0019	0.0014

** Main effect mean nutrient difference at $\alpha = 0.10$

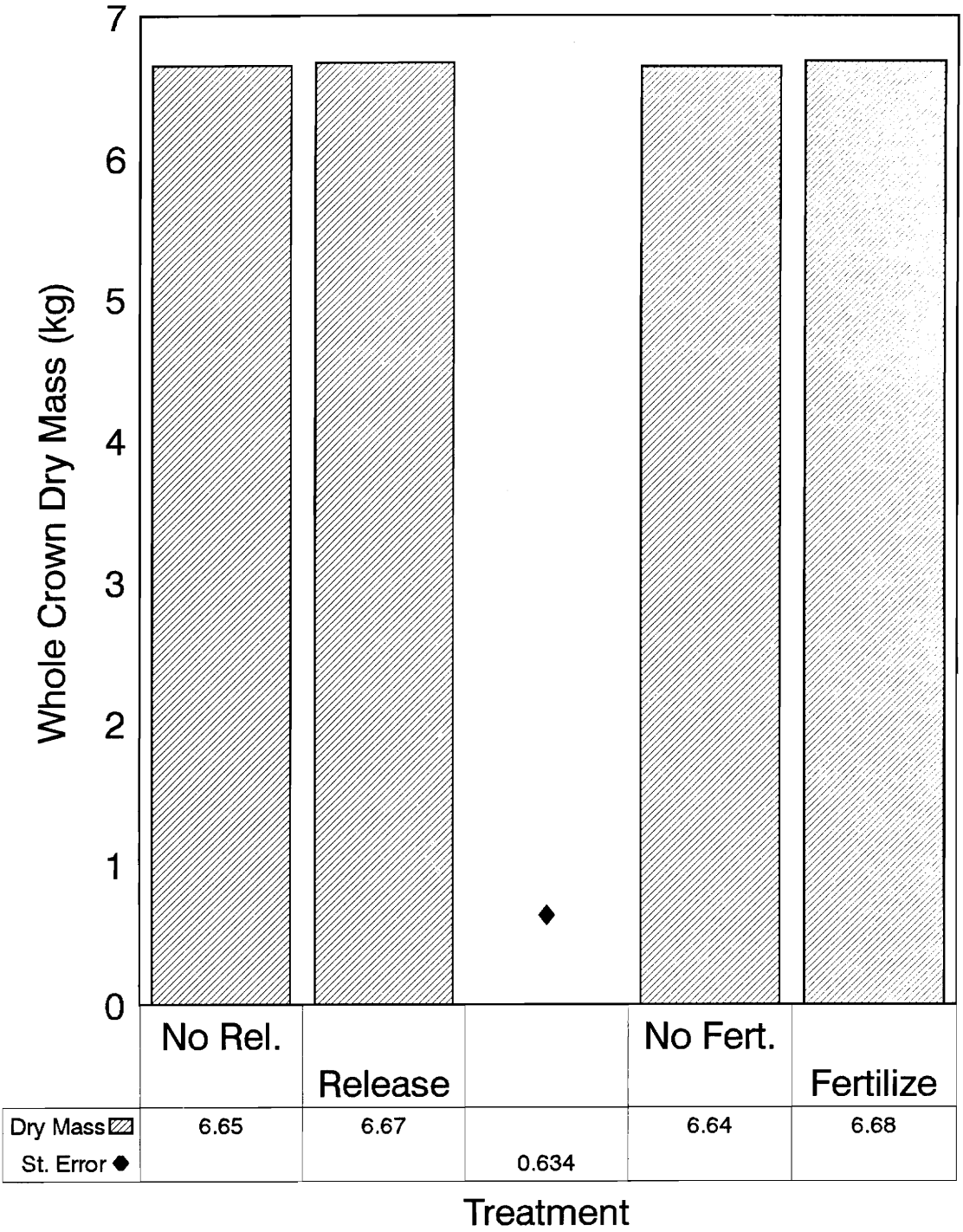


Figure 4.11. Mean whole crown dry mass and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

that branches of released trees are less massive than those of unreleased trees (See discussion on Relative Crown Volume Growth).

Bolewood (Without Bark)

Stemwood nutrient content does not appear to be influenced by either release or fertilization (Table 4.6). Although arithmetic differences are again apparent for release treatments, neither nutrient concentrations nor stemwood dry mass differ significantly (Figure 4.12). Therefore, these apparent differences must be attributed to random variability. Phosphorus stemwood concentrations are increased by fertilization, and must be ascribed to greater phosphorus availability (Table 4.1).

Bolebark

Release significantly increased the bark content of both phosphorus and iron, and arithmetically increased the content of all other elements (Table 4.7). This effect, however, must be ascribed to a greater bark mass in the released trees, as elemental concentrations in the bark were not greater in the released trees. Because only nitrogen, phosphorus and potassium were added to the system, this effect would suggest that the nutrient sink strength, at least in the bark, is a function directly related to mass, rather than treatment or physiological activity.

Bolebark (including the phloem) calcium concentrations were greater for both unreleased and unfertilized treatments. As calcium is an activator of alpha and beta amylase (the enzymes involved in the degradation of complex carbohydrates to simple glucose) (Kozlowski et al., 1991), a calcium dilution in the phloem, brought on by

Table 4.6. Mean stemwood (without bark) nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	N	P	K	Ca	Fe	Mg	Mn
	<----------grams/tree---------->						
No Release	111	0.056	0.396	0.344	0.00095	0.077	0.021
Release	150	0.071	0.481	0.433	0.00158	0.092	0.025
No Fertilization	125	0.058	0.434	0.374	0.00129	0.078	0.022
Fertilize	135	0.069	0.443	0.403	0.00125	0.091	0.024
Standard Error	22.2	0.010	0.072	0.060	0.000283	0.001	0.0003
	<----------grams/kilogram---------->						
No Release	4.69	0.002	0.017	0.015	0.00004	0.004	0.001
Release	4.84	0.002	0.016	0.015	0.00005	0.003	0.001
No Fertilization	4.72	0.002	0.017	0.015	0.00005	0.003	0.001
Fertilize	4.81	0.003*	0.017	0.015	0.00005	0.004	0.001
Standard Error	0.18	0.00008	0.0009	0.0007	0.0000068	0.0001	0.0001

* Main effect mean nutrient difference at $\alpha = 0.05$

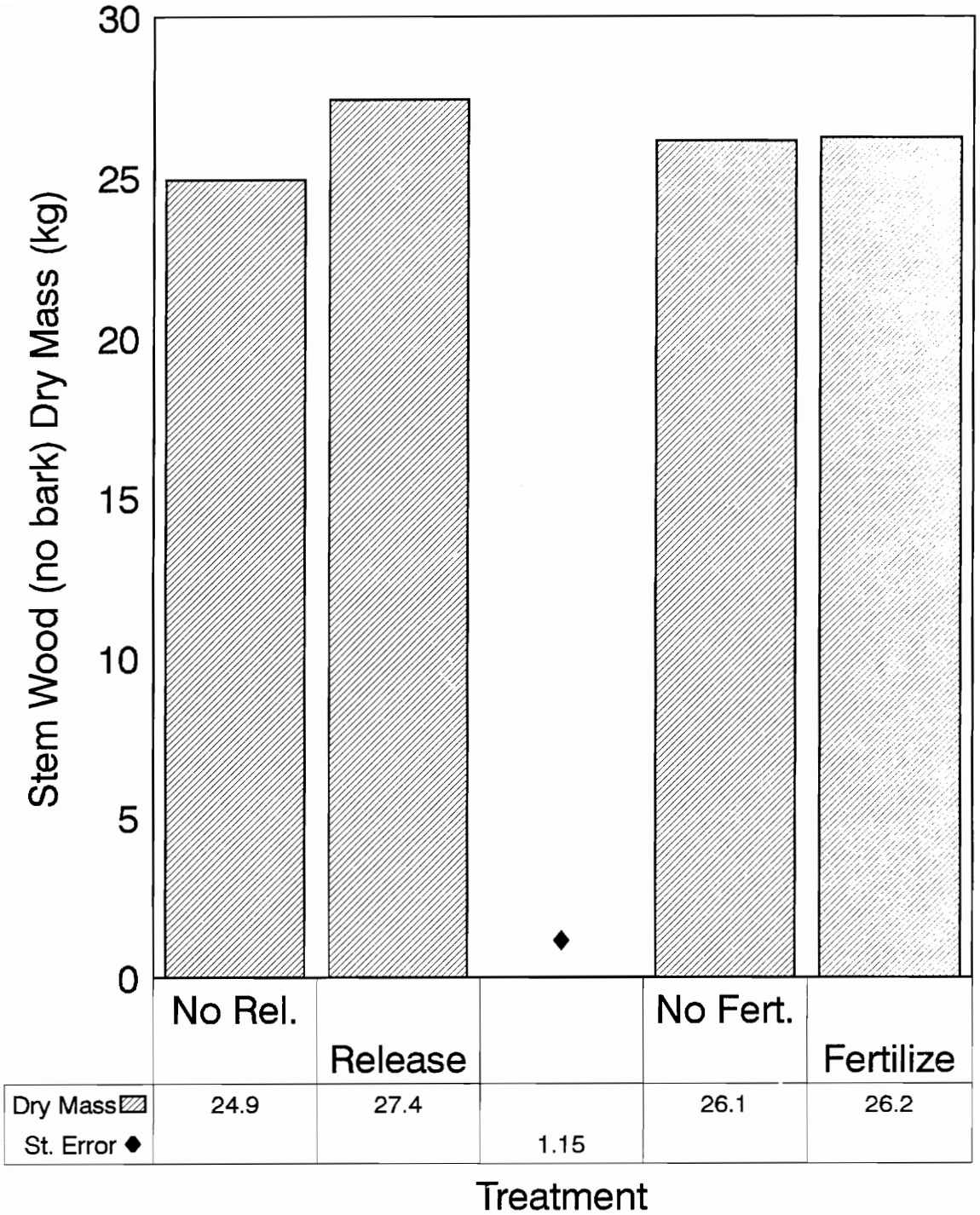


Figure 4.12. Mean stemwood (no bark) dry mass and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites

Table 4.7. Mean bolebark (not wood) dry mass, nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	Dry Mass	N	P	K	Ca	Fe	Mg	Mn
	kg	<----------grams/tree---------->						
No Release	3.6	72	0.037	0.288	0.673	0.00035	0.084	0.028
Release	4.8	101	0.054**	0.387	0.855	0.00053*	0.115	0.037
No Fertilization	4.4	89	0.042	0.335	0.818	0.00049	0.096	0.034
Fertilize	4.1	84	0.049	0.341	0.710	0.00040	0.102	0.032
Standard Error		13.9	0.007	0.053	0.113	0.000067	0.014	0.0051
		<----------grams/kilogram---------->						
No Release		20	0.011	0.085	0.194*	0.00011	0.025	0.009
Release		20	0.013	0.079	0.174	0.00011	0.025	0.009
No Fertilization		20	0.010	0.079	0.194*	0.00012	0.024	0.008
Fertilize		20	0.014	0.085	0.174	0.00010	0.026	0.009
Standard Error		0.52	0.0017	0.0030	0.0049	0.0000111	0.0011	0.0008

* Main effect mean nutrient difference at $\alpha = 0.05$
** Main effect mean nutrient difference at $\alpha = 0.10$

release and fertilization, may negatively affect carbon assimilation over the entire tree. In addition, calcium occurs in considerable quantities as calcium pectate in cell walls, a molecule that apparently influences cell wall elasticity (Kramer and Kozlowski, 1979). A deficiency of calcium, which often results in meristematic damage, may be in part responsible for increased terminal damage often observed in trees that have undergone silvicultural treatments.

Stem (Wood and Bark)

Release significantly increased the stem content of iron, and arithmetically increased the content of all other elements (Table. 4.8). As elemental concentrations in the stem were not greater for released trees, this effect must be attributed to the greater mass of released tree stems (Figure 4.13). The greater mass of released tree stems can not be ascribed entirely to an increase in bark mass, however. Although significant bolewood dry mass differences were not evident (Figure 4.12), they were sufficiently greater, such that when the numerically greater bark mass was added to it (Table 4.7), the entire stem dry mass of released trees became significantly greater than unreleased trees.

Phosphorus concentration of fertilized trees was greater than that of unfertilized trees. This effect can likely be attributed to increased phosphorus availability (Table 4.1). Calcium concentrations in the stems of unfertilized trees were also greater. This is presumably a carry-over effect of the higher bark concentrations (Table 4.7).

Table 4.8. Mean stem (wood and bark) nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	N	P	K	Ca	Fe	Mg	Mn
	<----------grams/tree---------->						
No Release	182	0.094	0.685	1.017	0.00131	0.161	0.049
Release	251	0.125	0.868	1.288	0.00211**	0.207	0.063
No Fertilization	214	0.100	0.769	1.192	0.00178	0.175	0.056
Fertilize	220	0.118	0.784	1.113	0.00164	0.194	0.056
Standard Error	35.3	0.016	0.118	0.168	0.000328	0.025	0.0077
	<----------grams/kilogram---------->						
No Release	6.7	0.004	0.026	0.040	0.00005	0.006	0.002
Release	7.2	0.004	0.026	0.039	0.00006	0.007	0.002
No Fertilization	6.9	0.003	0.026	0.042*	0.00006	0.006	0.002
Fertilize	6.9	0.004*	0.026	0.037	0.00005	0.007	0.002
Standard Error	0.22	0.0002	0.0011	0.0013	0.0000056	0.0003	0.0002

* Main effect mean nutrient difference at $\alpha = 0.05$
** Main effect mean nutrient difference at $\alpha = 0.10$

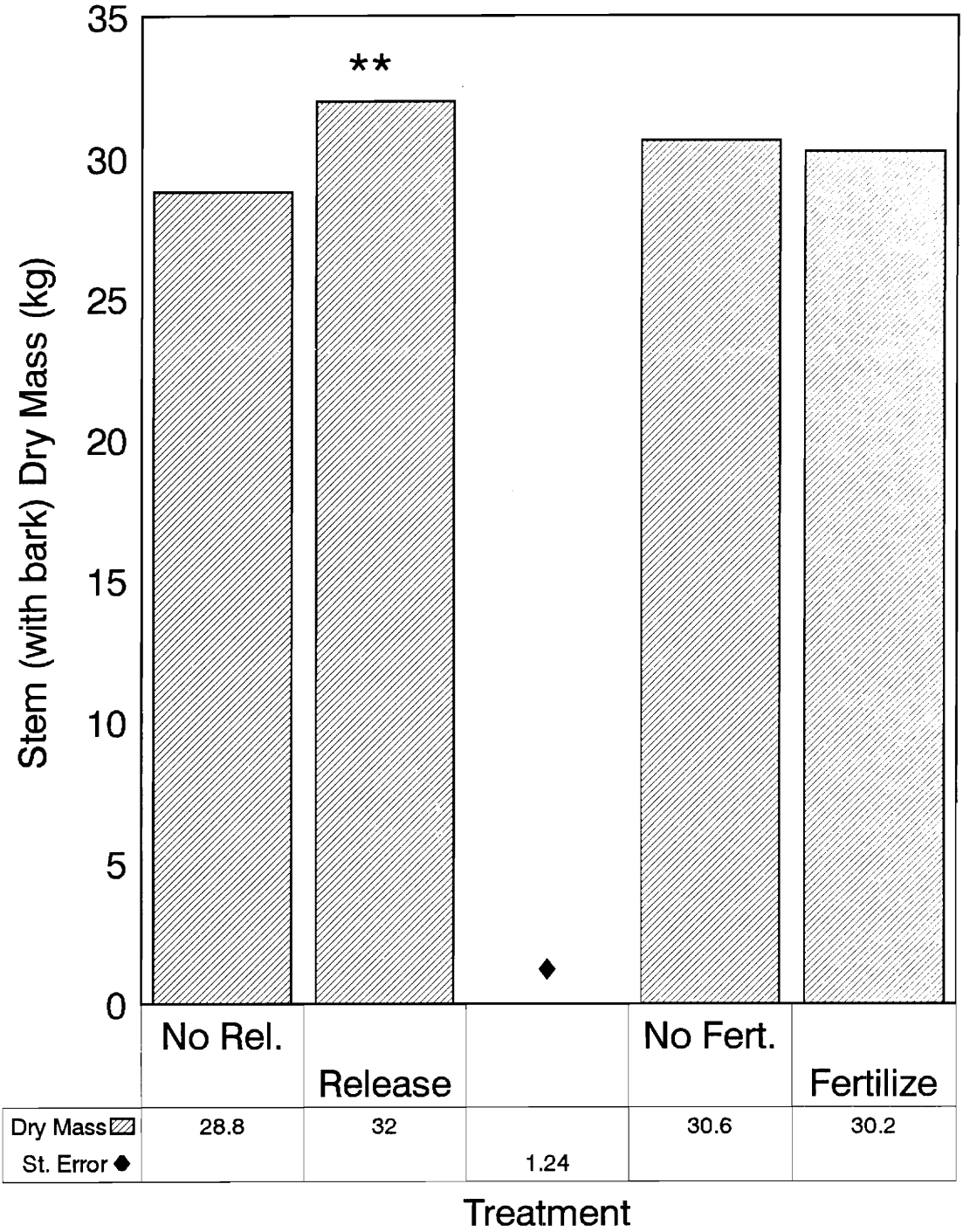


Figure 4.13. Mean stem (bolewood and bark) dry mass and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.
**** Different at p = 0.10**

Whole Tree

Release resulted in an increased iron content and concentration over that of unreleased trees (Table 4.9). No other nutrient content differences were apparent. Because ironconcentrations were also positively affected by release, increased iron content can not be attributed to greater tree mass. This may be important, as past research has shown iron content to be closely related to chlorophyll content and photosynthesis in poplar (Keller and Koch, 1964). This may be in part responsible for the greater diameter and crown volume growth of released trees (Figures 4.1 and 4.3).

Release also resulted in increased whole tree nitrogen concentration. However, the nonsignificantly increased whole tree mass (See Figure 4.14), masked the nitrogen content effect. Notwithstanding, higher concentrations of nitrogen in released trees - along with higher iron levels - may increase photosynthesis or photosynthetic efficiency, resulting in increased growth of released trees.

Whole tree phosphorus concentrations were higher for fertilized trees. Again, this can be attributed to increased phosphorus availability (Table 4.1). Because increased phosphorus concentration and availability (due to fertilization) did not result in increased growth (Figures 4.1-4.3), we can assume that phosphorus was not limiting in this study.

Calcium concentrations were also higher in the unfertilized trees. This is likely a carry-over effect from the bark; however, it may still affect starch conversion and/or meristematic structure at the whole tree level.

Table 4.9. Mean whole tree nutrient contents and concentrations of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Treatment	N	P	K	Ca	Fe	Mg	Mn
	<----------grams/tree---------->						
No Release	403	0.186	1.250	1.997	0.00189	0.350	0.119
Release	564	0.239	1.568	2.747	0.00293**	0.440	0.145
No Fertilization	482	0.197	1.387	2.475	0.00247	0.374	0.135
Fertilize	485	0.228	1.430	2.269	0.00235	0.416	0.129
Standard Error	80.4	0.036	0.224	0.379	0.000442	0.060	0.0201
	<----------grams/kilogram---------->						
No Release	12.2	0.006	0.039	0.063	0.00006	0.011	0.004
Release	13.7*	0.006	0.040	0.066	0.00007**	0.012	0.004
No Fertilization	13.1	0.005	0.040	0.069*	0.00006	0.011	0.004
Fertilize	12.7	0.006*	0.039	0.060	0.00006	0.012	0.004
Standard Error	0.36	0.0002	0.0014	0.0023	0.0000045	0.0005	0.0004

* Main effect mean nutrient difference at $\alpha = 0.05$
** Main effect mean nutrient difference at $\alpha = 0.10$

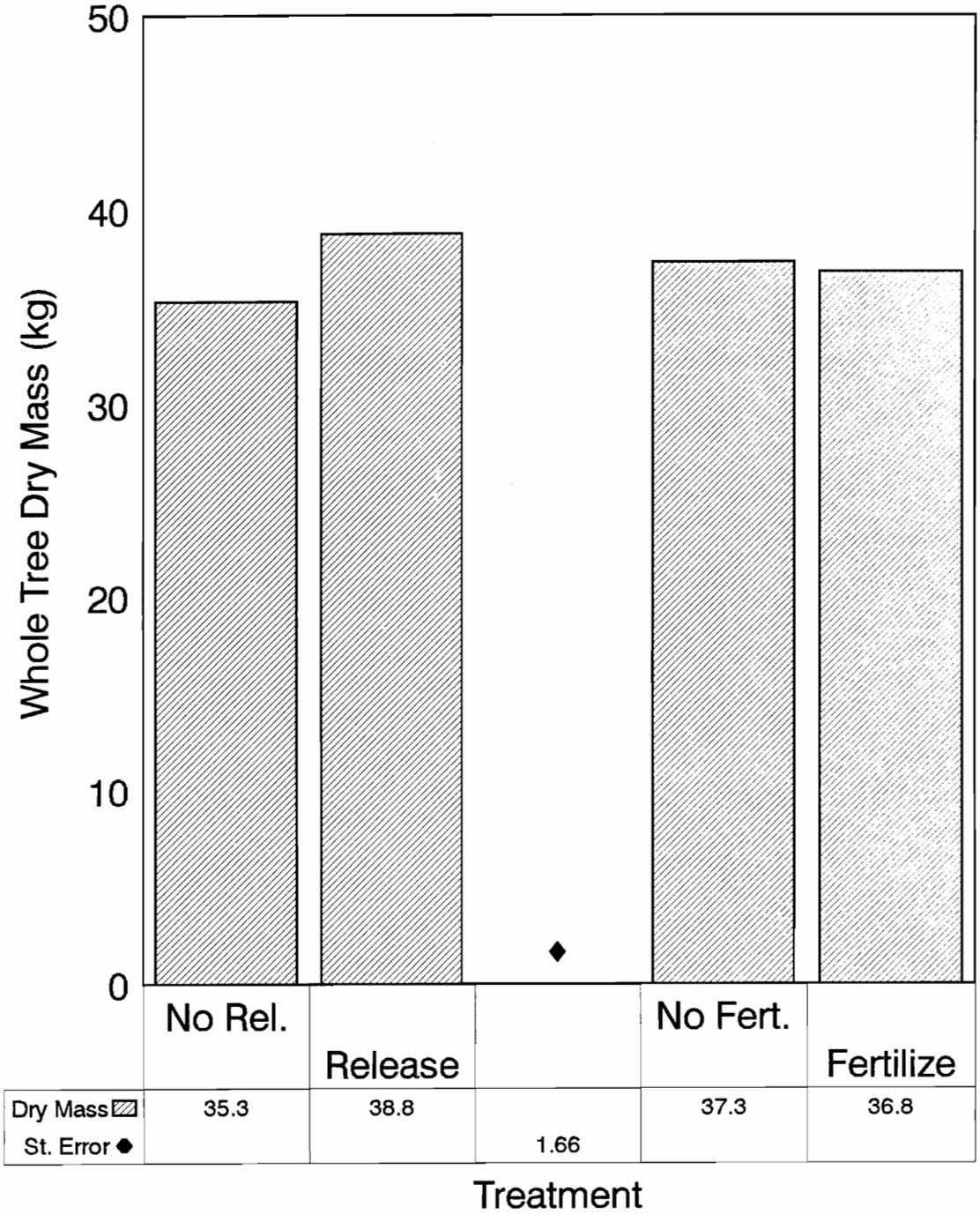


Figure 4.14. Mean whole tree dry mass and standard error of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Percent Dry Mass and Nutrient Content in Tree Partitions

Although foliage only accounts for six percent of the whole tree dry mass, an average of 31 percent of the seven essential elements assessed in this study are found within this partition (Figure 4.15). This has relevance to whole tree harvesting when the operation is performed prior to leaf fall, and foliage is chipped along with branches. Although nutrient translocation does occur in various proportions prior to leaf fall (depending on the element), assuming zero translocation - we can expect an average of 31 percent nutrient conservation if harvesting is done during the dormant season.

Nutrient conservation is even more hampered when the entire crown is harvested and removed from the site. While stemwood only (field debarking), or stem only harvests remove 71 and 82 percent of the whole tree dry mass, respectively, they only remove an average of 28 and 51 percent of the nutrients of the entire tree (Figure 4.15). When the crown is also harvested, a gain of only 18 percent dry mass is recognized (most of which is bark, reaction wood and foliage), while an additional 49 percent of the entire tree nutrients are removed (Figure 4.16).

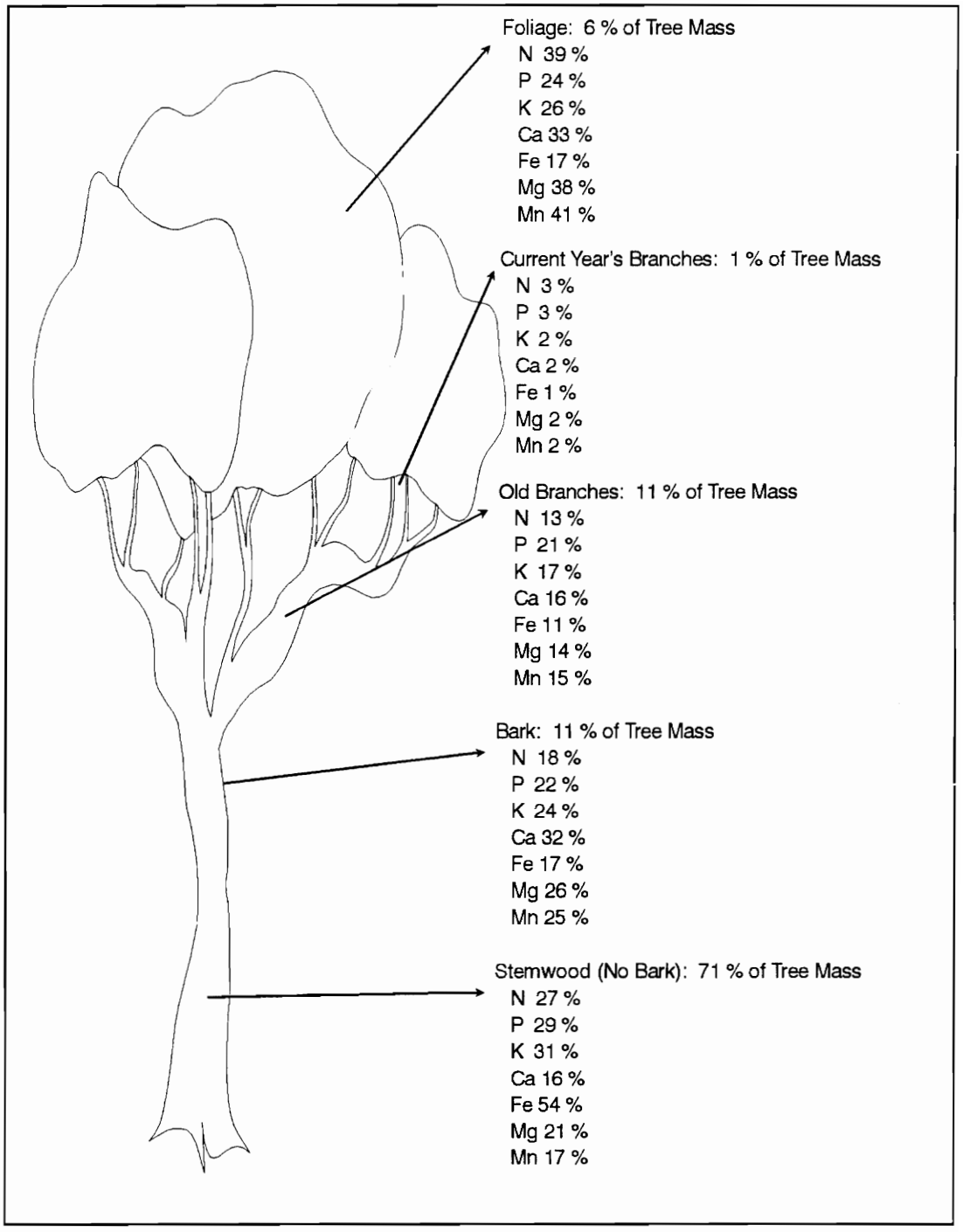


Figure 4.15. Above ground percent dry mass and percent above ground total tree nutrients in the various tree partions of 15 year-old yellow-poplar. Values are the mean of 48 trees.

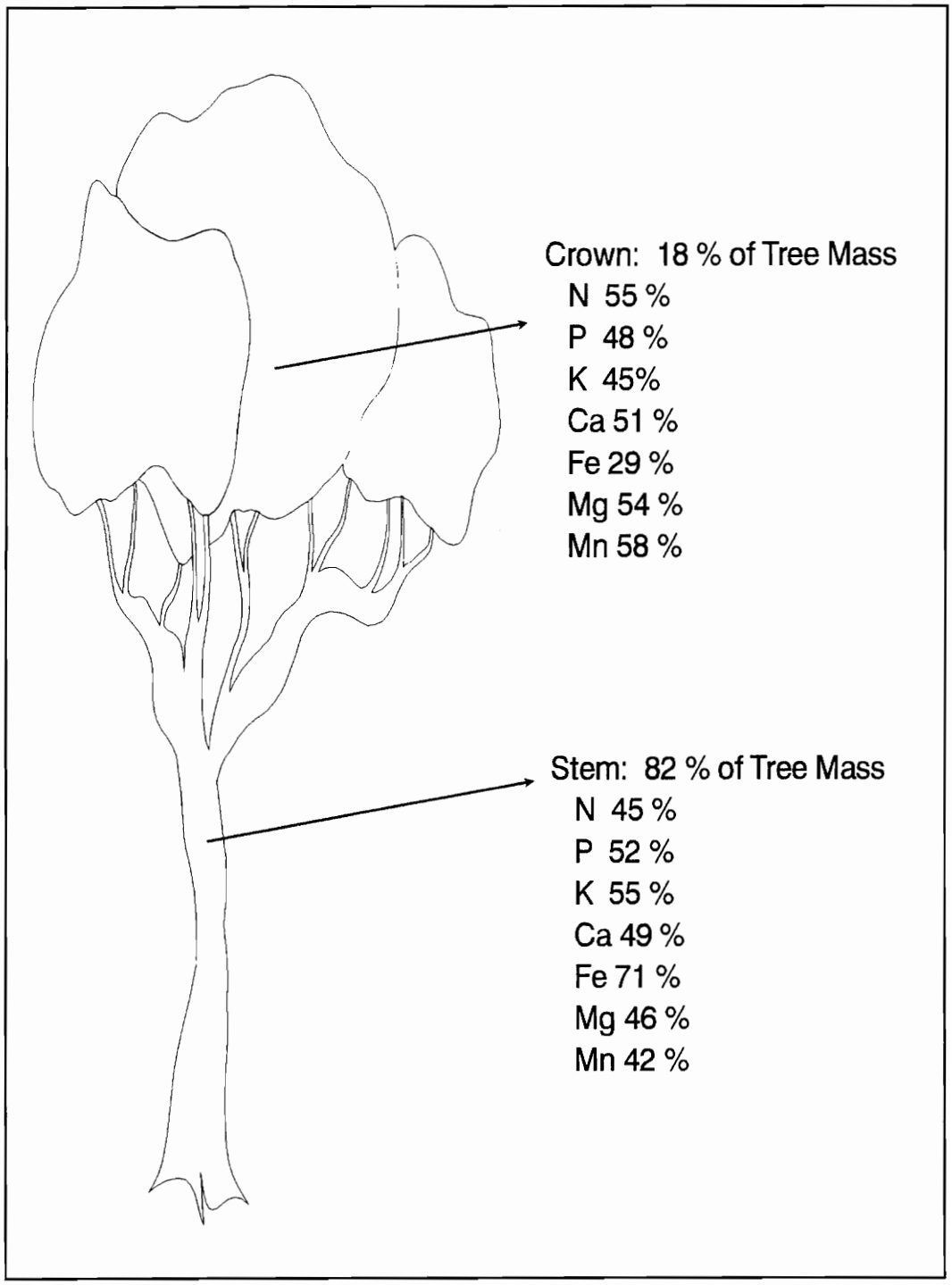


Figure 4.16. Above ground percent dry mass and percent above ground total tree nutrients in the crown and stem of 15 year-old yellow-poplar. Values are the mean of 48 trees.

Wood Quality

As discussed in Chapter 3, overall wood quality can be affected by changes in the growth rate of a tree. As many wood product industries are interested in the strength or yield properties of harvested wood, silviculturists need to understand the effect of cultural treatments, not only on growth, but on the physical properties of the wood.

While there is no perfect single measurement of wood quality, the specific gravity of the wood is the most commonly measured variable, and has the widest application to the various forest product industries. Specific gravity is highly correlated to the mechanical strength of wood, amount of shrinkage and surface hardness; and largely determines the cellulose yield from a given volume of wood (Koch, 1985). To gain a better understanding of the effect of crop tree release and fertilization on the specific gravity of yellow-poplar, the following section will examine the effect of these two treatments on specific gravity vertically within the bole, and on the mean bole specific gravity.

To maintain α-values of 0.05, sectional stemwood data were not compared between the various two meter segments. Rather, they were analyzed using a *two x two* factorial within the two meter segment only. Mean specific gravity was compared over the entire stem.

Specific Gravity

Stemwood specific gravity from ground line to 2 m, and from 2 to 4 m was significantly increased by crop tree release (Figure 4.17). It is numerically greater

from 4 to 6 m, at which point the trend reverses itself. From 6 to 10 m, specific gravity is numerically less in released trees, from 10 to 14 m it is numerically greater, and from 14 to 16 m, released trees once again have significantly greater specific gravity. Treatment interactions were not significant.

The lower bole specific gravity increase was not entirely unexpected. Farrar (1961) showed that proportionally more wood was allocated to the lower stems of thinned trees during the first years after thinning. This additional lower bole wood is generally more dense than it is in unthinned stands, and may be attributed to any one, or a combination, of various factors. These factors include thicker fibers; smaller vessels; decreased production of vessels; or a prolonged growth growing season that in non-diffuse porous species, has been shown to increase the proportion of denser latewood (Kozlowski *et al.*, 1991). The numerically decreased specific gravity in the stem's midsection is likely due to a slight decrease in the wood production in the middle of the bole (Farrar, 1961), and increased juvenile wood proportion within the crown portion of the bole (Koch, 1985). The increased specific gravity near the top of released trees is presumably a result of decreased height growth (Figure 4.2), which resulted in more compact radial growth. As yellow-poplar did not respond to fertilization, specific gravity was not affected by the fertilization treatment.

Mean bole specific gravity was not affected by either release or fertilization (Figure 4.18). However, this is likely due to a release *x* fertilization masking effect. Mean specific gravity is constant within fertilized trees, but untreated trees have much

	Stem of Tree	
No Release 0.310 Release 0.467 **	14 - 16 m	No Fertilization 0.410 Fertilize 0.366
No Release 0.414 Release 0.466	12 - 14 m	No Fertilization 0.456 Fertilize 0.425
No Release 0.387 Release 0.442	10 - 12 m	No Fertilization 0.424 Fertilize 0.406
No Release 0.487 Release 0.457	8 - 10 m	No Fertilization 0.470 Fertilize 0.474
No Release 0.469 Release 0.446	6 - 8 m	No Fertilization 0.458 Fertilize 0.457
No Release 0.462 Release 0.481	4 - 6 m	No Fertilization 0.472 Fertilize 0.469
No Release 0.450 Release 0.473 **	2 - 4 m	No Fertilization 0.457 Fertilize 0.464
No Release 0.415 Release 0.466 *	0 - 2 m	No Fertilization 0.441 Fertilize 0.441

Figure 4.17. Vertically separated stemwood specific gravity of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.
*** Different at p = 0.05**
**** Different at p = 0.10**

lower mean specific gravity than trees that were released only. It appears that fertilization buffers the increase inmean stem specific gravity due to release, while at the same time slightly increases mean specific gravity over trees that are not treated at all. However, this buffering capacity of fertilization is only active at the whole-stem level, as release *x* fertilization interactions were not apparent in the various two meter bole segments (Figure 4.17). This loss of treatment effect is also confirmed by the lack of release response on stemwood dry mass (Figure 4.12) and stemwood volume (Figure 4.5). The same holds true for the lack of fertilization effect.

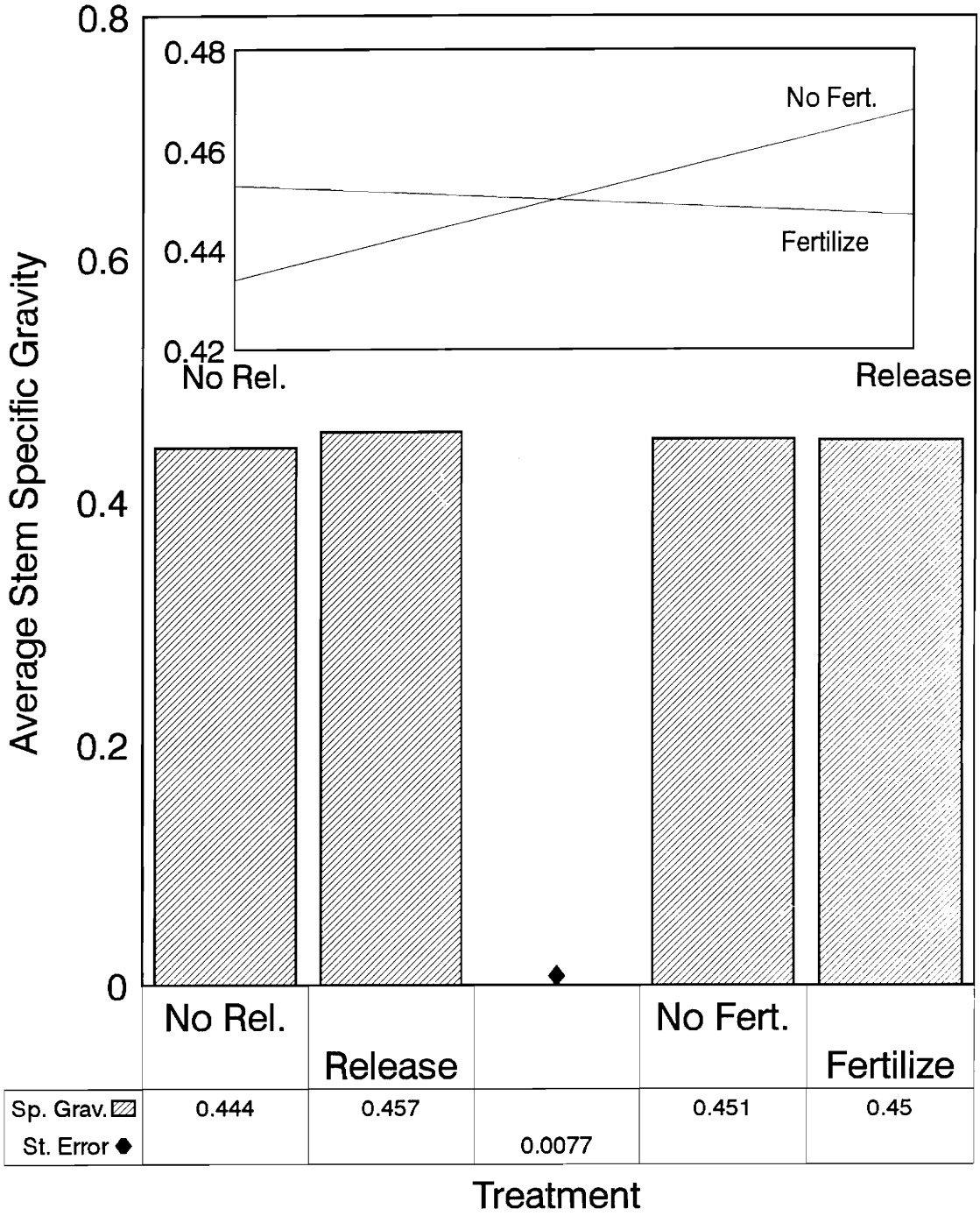


Figure 4.18. Mean and release x fertilization interaction stemwood specific gravity of released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Biomass Equations

As yellow-poplar is an important commercial species in the pulp and paper industry, reliable estimates of whole tree and stemwood biomass are essential for projecting pulp yields from young yellow-poplar trees and stands. This is especially true as foresters attempt to apply more intensive management to yellow-poplar - including crop tree release and fertilization. It is also important in plantation management, where young poplar are harvested to make room for selected crop trees. In addition, reliable partitioned biomass estimates have utility in assessing tree nutrition, system nutrient budgets, and expected gain from whole tree harvesting.

In this section, empirically derived biomass equations for the whole tree and partitioned segments of young yellow-poplar grown on low to medium quality sites will be presented. Where crop tree release or fertilization affects the slope or intercept of the model, (as determined by the significance of "dummy" variables) alternate models will be given. The biological implications of model terms will also be discussed where applicable.

Foliar biomass equations were the only tree partition equations that were affected by crop tree release or fertilization (Table 4.10 and Figure 4.19). This is logical, as foliar dry mass was also significantly affected by both treatments (Figure 4.10). Not only did the release and fertilization biomass equations differ, but untreated tree foliar biomass also was estimated with a separate equation. In all three equations, the only significant predictive variable was the commonly-used combined variable d^2h. The combined variable, d^2h, is closely related to stem volume, hence, the high

Table 4.10. Equations, fit and predictive measures for predicting dry mass components (in kilograms) of untreated, thinned or released 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites.

Model	Adjusted R^2	Mean Square Error	C_p	p
Whole Tree (N=48)				
$y = 0.2182 + 0.0185(d^2h)^{a} + 1.4213(cd)^{b}$	0.99	8.67	3.09	3
Stem - with bark (N=48)				
$y = -5.0148 + 0.0163(d^2h) + 3.9899(cd) - 0.0571(cv)^{c}$	0.99	5.87	2.37	4
Stem - no bark (N=48)				
$y = -4.7115 + 0.0143(d^2h) + 3.4772(cd) - 0.0516(cv)$	0.99	3.59	3.97	4
Crown - with foliage (N=48)				
$y = 4.9689 + 0.0038(d^2h) - 0.9152(hlc)^{d}$	0.88	2.57	2.30	3
Foliage - no fertilization or release (N=12)				
$y = 0.0188 + 0.0014(d^2h)$	0.95	0.06	0.93	2
Foliage - fertilized trees (N=24)				
$y = 0.5480 + 0.00075(d^2h)$	0.76	0.45	4.33	2
Foliage - released trees (N=24)				
$y = 0.6776 + 0.00094(d^2h)$	0.83	0.47	4.00	2

[a] Square of the diameter (at 1.37 meters) measured in centimeters multiplied by the total tree height measured in meters
[b] Average diameter of the crown measured in meters
[c] Crown volume calculated as a cone measured in $meters^3$
[d] Height to live crown (lowest live branch) measured in meters

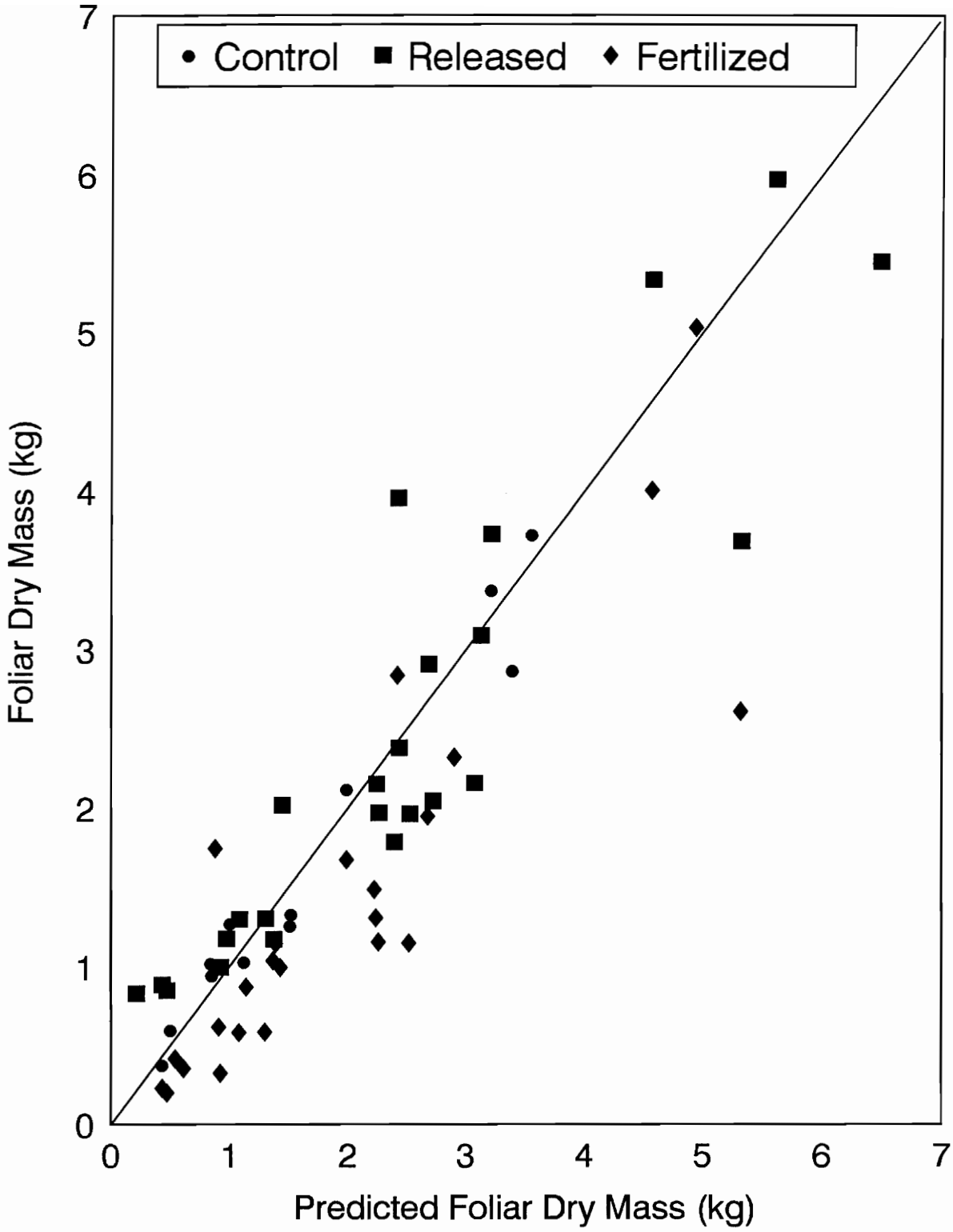


Figure 4.19. Predicted versus actual foliar dry mass of untreated, released and fertilized 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites. Solid line represents a 1:1 relationship.

correlation between foliar biomass and d^2h. However, as the slopes and intercepts of the equations were different for the various treatments, treatment also plays an important role in the mass of young yellow-poplar foliage. It should be noted, however, that when release or fertilization is applied to young yellow-poplar, the fit and predictive ability of foliar biomass equations are reduced (Table 4.10). This was largely due to a few higher influence outliers at the heavier foliar masses (Figure 4.19)

Whole tree, stemwood, and stem biomass equations had both excellent fit and excellent predictive ability (Table 4.10 and Figure 4.20). Outliers were virtually nonexistent, and higher influence points were in line with the mean. As expected, d^2h was a significant predictive variable in all equations. However, various crown dimensions improved the fit and predictive ability of all three equations. Although the particular crown dimension variable(s) included in the equations are slightly different, their inclusion is understandable in biological and physical terms. As biomass is directly related to specific gravity, variables that effect specific gravity affect biomass. Previous discussion has shown that specific gravity is influenced by the vertical height within the stem (Figure 4.17). This height trend is largely influenced by the lower specific gravity associated with the juvenile wood that predominates throughout the length of the crown (Koch, 1985). Therefore, variables that characterize the amount of juvenile wood (ie - crown dimensions) are important in the prediction of biomass in these tree partitions. In addition, because crown dimensions differed by treatment, the crown variables serve as surrogates for treatment.

The whole crown biomass equation had good fit and excellent predictive ability

(Table 4.10 and Figure 4.20). It seems as though one outlier was the basis of the less than excellent fit. Like whole tree, stemwood and stem biomass equations, crown dimensions also proved important. Again, d^2h was a significant predictive variable in the equation. However, the addition of height to live crown was also significant, but was not associated with juvenile wood. Rather, it simply described the dimension of the crown, whose mass the equation was to predict.

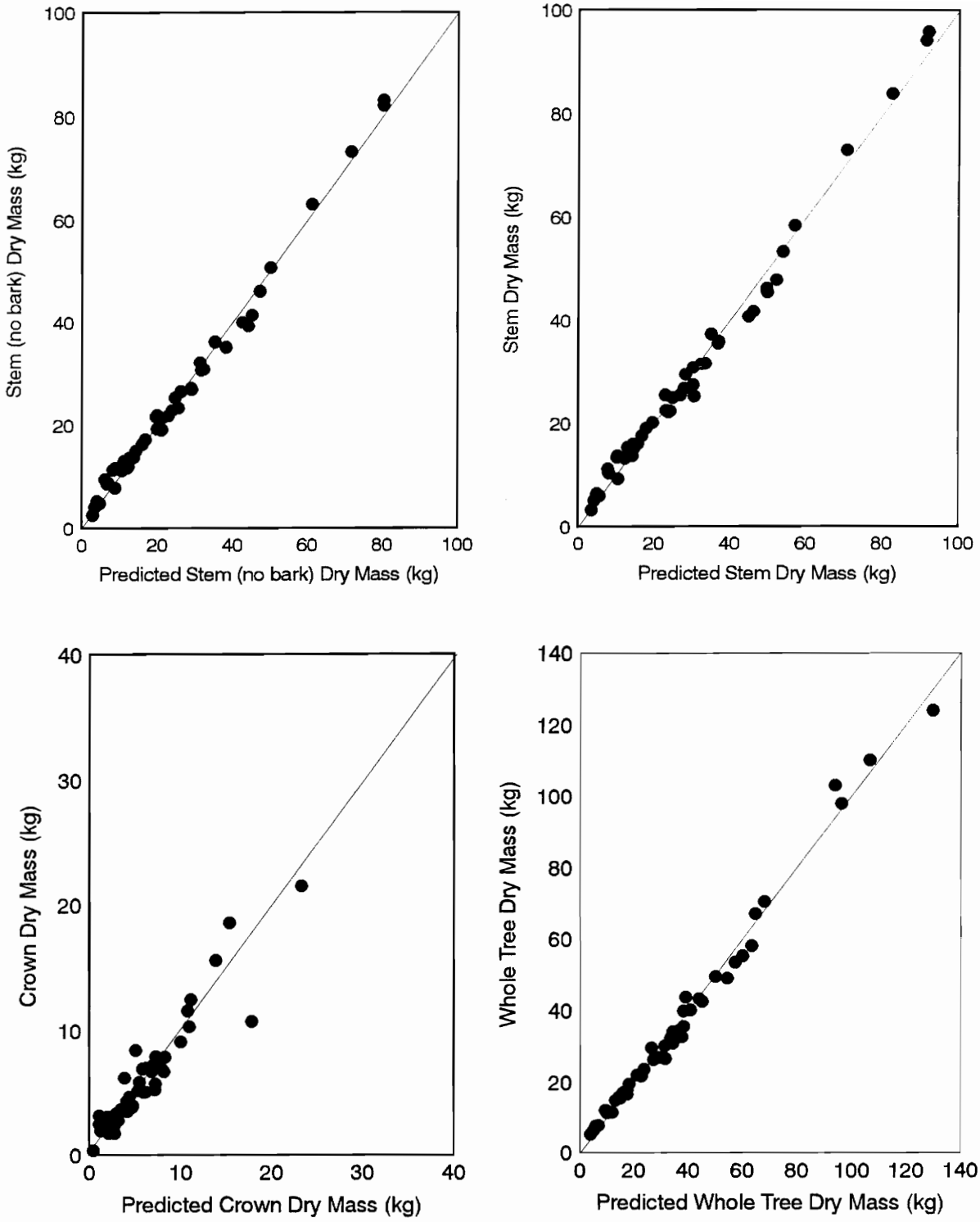


Figure 4.20. Predicted versus actual stemwood, stem, crown, and whole tree dry masses of 15 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites. Solid lines represent 1:1 relationships.

CHAPTER FIVE: Summary and Conclusions

Five years after applying factorial combinations of crop tree release and fertilization to 10 year-old yellow-poplar grown on low to medium quality Southern Appalachian sites, only release resulted in significant growth responses. Released trees responded positively to increased sunlight and horizontal space by increasing their uptake of nitrogen and iron - elements essential for photosynthesis. This led to an increase in foliage production, and presumably, an increase in total photosynthesis. Released trees reacted to the increased growing space by filling in the space created by release. Released trees increased both diameter and crown volume growth; unfortunately, they did so at the expense of height growth, which was decreased by crop tree release. Current stemwood volume was therefore not increased.

Crop tree release also significantly increased the specific gravity of the stem from ground line to 4 meters, and numerically from 4 to 6 meters. This may be the result of a greater proportion of latewood production near the base of the tree, or changes in the anatomical structure of the wood. More research is needed in this area. At greater heights, juvenile wood negated the increase in stem specific gravity. The lower bole specific gravity increase also resulted in an increased dry mass for the entire stem.

Although phosphorus and potassium availabilities were increased by fertilization, and phosphorus uptake was increased, the yellow-poplar were unresponsive to fertilization. This suggests that phosphorus and potassium were not limiting to growth. Nitrogen availability, however, was not increased. This implies

that the soil was not responsive to additions of nitrogen. Unfortunately, as additional nitrogen was either not mineralized, or it was sequestered elsewhere in the system, we can not know whether tree growth was limited by nitrogen deficiencies .

At the whole tree level, only iron content was increased by release. Fertilization did not affect nutrient content. Although foliage accounted for only 6 % of the whole tree dry mass, an average of 31 % of the seven elements assessed in this study were found in the foliage. Assuming zero translocation - we can expect an average of 31 % nutrient conservation if harvesting is done during the dormant season.

Nutrient conservation is even more hampered in whole tree harvesting. While stemwood only, or stem only harvests remove 71 and 82 % of the whole tree dry mass, they only remove an average of 28 and 51 % of the nutrients of the entire tree. When the crown is also harvested, a gain of only 18 % dry mass is recognized, while an additional 49 % of the tree nutrients are removed.

In general, if the objective of growing yellow-poplar on low to medium quality sites is short-rotation pulpwood production, crop tree release may be beneficial, as diameter growth and stem yield are increased. Although release resulted in increased diameter and crown volume growth, and higher first log specific gravity, the reduced height growth will make the maintenance of these increases problematic. As released trees become overtopped by competitors, it is likely that diameter growth will also decrease. However, this is only speculation, and longer-term research is necessary in this arena. Therefore, if production objectives are to grow full rotation saw logs, crop

tree release, like fertilization, is likely not a worthwhile investment.

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APPENDICES

A: One Way Analysis of Variance Tables for all Variables (All units as previously reported).

Variable	Control	Fert.	Release	Fert. + Release	Standard Error
Rel DBH Growth	0.091	0.092	0.097	0.100	0.00418
Rel Hgt Growth	0.070	0.068	0.061	0.063	0.00312
Rel CV Growth	0.282	0.260	0.324	0.318	0.02148
Cr Length	6.424	6.215	6.595	6.250	0.22848
Stem Volume	0.053	0.052	0.053	0.055	0.00334
Percent PAR	1.643	1.474	2.534	6.576	1.12000
XWP June	-11.29	-12.13	-12.21	-12.33	-0.53333
XWP July	-13.38	-13.67	-12.88	-13.50	-0.53352
XWP August	-11.63	-12.17	-12.17	-11.62	-0.74868
Soil N	49.68	56.40	65.20	63.46	11.4096
Soil P	0.110	2.704	0.200	4.056	0.29643
Soil K	13.58	17.16	14.65	16.71	1.07839

Variable	Control	Fert.	Release	Fert. + Release	Standard Error
Soil Ca	79.48	108.9	127.0	121.9	20.3022
Soil Fe	8.176	7.651	7.165	6.531	0.99405
Soil Mg	10.62	12.26	12.85	13.67	1.74390
Soil Mn	12.58	13.22	14.69	14.92	1.90336
Soil pH	4.649	4.727	4.790	4.690	0.06846
Soil % Org Carb	4.283	4.036	4.466	4.556	0.33449
Foliar Mass	2.066	1.541	2.492	2.190	0.19234
Foliar N - cont	151.3	145.7	250.8	215.4	42.1347
conc	90.36	88.27	88.74	93.01	3.16307
Foliar P - cont	0.047	0.045	0.064	0.057	0.01132
conc	0.026	0.029	0.024	0.026	0.00143
Foliar K - cont	0.331	0.305	0.424	0.383	0.06581
conc	0.199	0.186	0.173	0.191	0.01262
Foliar Ca - cont	0.659	0.534	1.125	0.858	0.18427
conc	0.396	0.357	0.378	0.368	0.03175
Foliar Fe - cont	0.00032	0.00031	0.00054	0.00040	0.0000927
conc	0.00019	0.00019	0.00018	0.00018	0.0000083

Variable		Control	Fert.	Release	Fert. + Release	Standard Error
Foliar Mg -	cont	0.120	0.142	0.184	0.163	0.03003
	conc	0.081	0.087	0.070	0.077	0.00607
Foliar Mn -	cont	0.045	0.055	0.069	0.047	0.01335
	conc	0.029	0.031	0.027	0.025	0.00450
New Branch Mass		0.431	0.473	0.490	0.486	0.06662
N Bran N -	cont	7.804	14.97	14.70	12.52	3.72947
	conc	24.33	26.08	25.72	24.91	1.02319
N Bran P -	cont	0.004	0.008	0.007	0.007	0.00161
	conc	0.012	0.015	0.013	0.014	0.00062
N Bran K -	cont	0.025	0.040	0.039	0.037	0.00818
	conc	0.076	0.079	0.071	0.077	0.00341
N Bran Ca -	cont	0.030	0.056	0.063	0.046	0.01633
	conc	0.096	0.089	0.101	0.091	0.00564
N Bran Fe -	cont	0.00002	0.00003	0.00004	0.00003	0.0000112
	conc	0.00006	0.00006	0.00007	0.00006	0.0000055
N Bran Mg -	cont	0.006	0.010	0.009	0.009	0.00226
	conc	0.017	0.019	0.016	0.020	0.00121
N Bran Mn -	cont	0.001	0.002	0.002	0.002	0.00048
	conc	0.005	0.005	0.004	0.005	0.00072

Variable	Control	Fert.	Release	Fert. + Release	Standard Error
Old Branch Mass	4.009	4.777	3.797	3.883	0.74895
O Bran N - cont	36.70	85.79	76.05	55.03	26.9070
conc	14.27	13.94	15.62	14.36	0.72464
O Bran P - cont	0.020	0.060	0.051	0.041	0.02017
conc	0.008	0.010	0.009	0.010	0.00076
O Bran K - cont	0.122	0.308	0.295	0.220	0.10493
conc	0.051	0.052	0.058	0.050	0.00398
O Bran Ca - cont	0.215	0.466	0.474	0.352	0.14285
conc	0.086	0.083	0.093	0.083	0.00488
O Bran Fe - cont	0.00014	0.00034	0.00033	0.00029	0.0001137
conc	0.00006	0.00006	0.00006	0.00006	0.0000057
O Bran Mg - cont	0.026	0.074	0.055	0.046	0.02337
conc	0.011	0.012	0.011	0.012	0.00074
O Bran Mn - cont	0.012	0.022	0.026	0.018	0.00559
conc	0.005	0.006	0.006	0.005	0.00077
Crown Mass	6.508	6.792	6.775	6.560	0.89591
Crown N - cont	195.8	246.4	341.5	282.9	66.2993
conc	43.18	37.53	41.88	44.82	1.97648
Crown P - cont	0.071	0.113	0.123	0.105	0.03047

Variable		Control	Fert.	Release	Fert. + Release	Standard Error
	conc	0.015	0.016	0.015	0.016	0.00091
Crown K -	cont	0.478	0.653	0.759	0.640	0.16612
	conc	0.107	0.095	0.100	0.107	0.00687
Crown Ca -	cont	0.904	1.056	1.662	1.257	0.30911
	conc	0.202	0.166	0.190	0.190	0.01347
Crown Fe -	cont	0.00048	0.00069	0.00091	0.00072	0.0002047
	conc	0.00011	0.00010	0.00010	0.00011	0.0000052
Crown Mg -	cont	0.151	0.226	0.248	0.218	0.05235
	conc	0.037	0.035	0.032	0.038	0.00271
Crown Mn -	cont	0.059	0.080	0.098	0.067	0.01864
	conc	0.014	0.013	0.013	0.013	0.00201
Stem (no bark) Mass		25.14	24.76	27.05	27.72	1.62019
St n B N -	cont	88.34	132.9	162.2	138.0	31.4440
	conc	4.565	4.815	4.870	4.813	0.25405
St n B P -	cont	0.043	0.070	0.073	0.068	0.01406
	conc	0.002	0.003	0.002	0.002	0.00012
St n B K -	cont	0.348	0.447	0.524	0.439	0.10202
	conc	0.017	0.017	0.016	0.017	0.00134
St n B Ca -	cont	0.284	0.404	0.464	0.402	0.08408

Variable		Control	Fert.	Release	Fert. + Release	Standard Error
	conc	0.016	0.015	0.015	0.014	0.00093
St n B Fe -	cont	0.00097	0.00094	0.00161	0.00155	0.0004004
	conc	0.00004	0.00004	0.00005	0.00006	0.0000096
St n B Mg -	cont	0.064	0.091	0.093	0.092	0.01629
	conc	0.004	0.004	0.003	0.004	0.00019
St n B Mn -	cont	0.002	0.002	0.003	0.002	0.00420
	conc	0.001	0.001	0.001	0.001	0.00015
Bark Mass		4.157	3.591	4.897	4.296	0.40237
Bark N -	cont	63.83	79.43	113.2	89.45	19.6813
	conc	19.15	20.20	20.00	20.32	0.73134
Bark P -	cont	0.031	0.043	0.053	0.056	0.00977
	conc	0.010	0.012	0.010	0.016	0.00242
Bark K -	cont	0.260	0.317	0.410	0.364	0.07519
	conc	0.082	0.088	0.076	0.082	0.00417
Bark Ca -	cont	0.648	0.698	0.987	0.722	0.15997
	conc	0.204	0.185	0.185	0.164	0.00689
Bark Fe -	cont	0.00028	0.00042	0.00070	0.00037	0.0000947
	conc	0.00010	0.00011	0.00014	0.00008	0.0000156

Variable		Control	Fert.	Release	Fert. + Release	Standard Error
Bark	Mg - cont	0.074	0.094	0.119	0.111	0.02048
	conc	0.024	0.026	0.023	0.026	0.00158
Bark	Mn - cont	0.025	0.032	0.043	0.031	0.00721
	conc	0.008	0.009	0.008	0.009	0.00117
Stem (w/bark)	Mass	29.29	28.35	31.95	32.02	1.74921
Stem	N - cont	152.2	212.3	275.5	227.5	49.9459
	conc	6.575	6.822	7.288	7.031	0.31120
Stem	P - cont	0.074	0.113	0.126	0.124	0.02257
	conc	0.003	0.004	0.003	0.004	0.00031
Stem	K - cont	0.604	0.765	0.934	0.803	0.16718
	conc	0.026	0.026	0.026	0.026	0.00149
Stem	Ca - cont	0.932	1.102	1.452	1.124	0.23793
	conc	0.042	0.037	0.042	0.036	0.00188
Stem	Fe - cont	0.00125	0.00136	0.00231	0.00192	0.0004642
	conc	0.00005	0.00005	0.00006	0.00006	0.0000080
Stem	Mg - cont	0.137	0.184	0.212	0.202	0.03602
	conc	0.006	0.007	0.006	0.007	0.00037
Stem	Mn - cont	0.042	0.056	0.071	0.055	0.01087
	conc	0.002	0.002	0.002	0.002	0.00034

Variable	Control	Fert.	Release	Fert. + Release	Standard Error
Whole Tree Mass	35.52	35.10	39.14	38.48	2.35319
Tree N - cont	347.9	458.7	617.0	510.4	113.758
conc	12.58	11.81	13.69	13.66	0.51011
Tree P - cont	0.146	0.226	0.249	0.229	0.05086
conc	0.005	0.006	0.006	0.006	0.00033
Tree K - cont	1.082	1.418	1.693	1.443	0.31642
conc	0.040	0.038	0.040	0.041	0.00199
Tree Ca - cont	1.837	2.157	3.114	2.381	0.53620
conc	0.068	0.058	0.070	0.062	0.00332
Tree Fe - cont	0.00173	0.00205	0.00321	0.00264	0.0006253
conc	0.00006	0.00005	0.00007	0.00007	0.0000063
Tree Mg - cont	0.288	0.411	0.460	0.421	0.08518
conc	0.011	0.011	0.011	0.012	0.00075
Tree Mn - cont	0.101	0.136	0.169	0.122	0.02836
conc	0.004	0.004	0.004	0.004	0.00063
Spec Grav 0-2 m	0.4117	0.4202	0.4705	0.4608	0.02238
Spec Grav 2-4 m	0.4396	0.4597	0.4760	0.4694	0.01280
Spec Grav 4-6 m	0.4612	0.4623	0.4838	0.4774	0.01382

Variable	Control	Fert.	Release	Fert. + Release	Standard Error
Spec Grav 6-8 m	0.4627	0.4758	0.4546	0.4391	0.01830
Spec Grav 8-10 m	0.4672	0.5080	0.4743	0.4408	0.02644
Stem Spec Grav	0.4350	0.4531	0.4681	0.4471	0.01096
Yearly DBH Grow cm	0.7581	0.7668	0.8577	0.8483	0.04027
Yearly Hgt Grow m	0.7140	0.6944	0.6030	0.6093	0.03152
Yearly CV Grow m^3	4.489	4.202	7.355	5.277	0.76324

B: Absolute Growth Values (From ANCOVA using pretreatment diameter as the covariate)

	Diameter	Height	Cr. Volume
	cm/yr	m/yr	m^3/yr
No Release	0.762	0.704*	4.346
Release	0.853*	0.606	6.316*
No Fertilize	0.808	0.659	5.922
Fertilize	0.808	0.652	4.740
St. Error	0.040	0.032	0.763

* Main factor differences significant at $\alpha = 0.05$.

C: Whole Tree Dry Mass Tables Based on Diameter, Height, and Crown Dimensions

1. Crown Diameter = 3 meters

Total Height (m)	6	8	10	12	14	16	18
DBH (cm)	Kilograms						
6	8.45	9.78	11.12	12.45	13.78	15.11	16.44
9	13.46	16.44	19.44	22.44	25.43	28.43	31.43
12	20.44	25.77	31.10	36.42	41.75	47.08	52.41
15	29.43	37.76	46.08	54.41	62.73	71.06	79.38
18	40.42	52.41	64.40	76.38	88.37	100.36	112.35
21	53.41	69.72	86.04	102.36	118.67	134.99	151.31
24	68.39	89.70	111.20	132.33	153.64	174.95	196.26

2. Crown Diameter = 5 meters

Total Height (m)	6	8	10	12	14	16	18
DBH (cm)	Kilograms						
6	11.28	12.61	13.94	15.27	16.60	17.94	19.27
9	16.27	19.27	22.26	25.26	28.26	31.26	34.25
12	23.26	28.59	33.92	39.25	44.58	49.90	55.23
15	32.25	40.58	48.90	57.23	65.55	73.88	82.20
18	43.24	55.23	67.22	79.21	91.20	103.18	115.17
21	56.23	72.55	88.86	105.18	121.50	137.82	154.13
24	71.22	92.53	113.84	135.15	156.46	177.78	199.09

3. Crown Diameter = 7 meters

Total Height (m)	6	8	10	12	14	16	18
DBH (cm)	Kilograms						
6	14.10	15.43	16.76	18.10	19.43	20.76	22.09
9	19.10	22.09	25.09	28.09	31.08	34.08	37.08
12	26.09	31.42	36.74	42.07	47.40	52.73	58.06
15	35.08	43.40	51.73	60.05	68.38	76.70	85.03
18	46.07	58.06	70.04	82.03	94.02	106.01	118.00
21	59.06	75.37	91.69	108.01	124.32	140.64	156.96
24	74.04	95.35	116.66	137.98	159.29	180.60	201.91

Vita

of

John Joseph Bollig

PERSONAL

Date of Birth:	March 18, 1967
Place of Birth:	Tacoma, Washington
Parents:	Henry and Rita Ann Bollig, Henderson, Nevada
Wife:	Robynne Ann Crockett
Children:	Ainsley Helen and Nicole Olivia Bollig
Work Service:	Forestry Research Specialist in Chemical Silviculture and Synecology, Department of Forestry, VPI & SU, Blacksburg, VA (9 publications from 1992-1994)

EDUCATION

M.S. - 1994	Virginia Polytechnic Institute & State University, Blacksburg, VA. Major: Forest Biology
B.S. - 1991	University of Washington, Seattle, WA Major: Forest Resource Management
H.S. Diploma - 1985	Spanaway Lake High School, Spanaway WA