ABSTRACT

Winborne, Ian Christopher. Seasonal Nutrient Dynamics and Vertical Nutrient Distribution in Loblolly Pine (*Pinus taeda*)(Under the direction of H. Lee Allen.)

Nutrient deficient stands may respond favorably to nutrient additions. However, deficient stands must be efficiently identified. Leaf area has been shown to diagnose gross nutrient deficiencies while chemical analysis of foliage can provide more specific nutritional data. Nutrient levels fluctuate throughout the year and vary with crown position. Therefore, it is important to know the proper time and location for foliage sampling.

The effects of nutritional treatments and time on foliar nutrient status were studied at SETRES. SETRES is a 2X2 factorial study of optimum nutrition and water additions in Scotland County, North Carolina, USA. Monthly foliage samples were collected and nutrient concentration and contents were determined for each sample for examination of seasonal variation. Foliage samples were collected in 1994, 1996, and 1998 and nutrient concentration and contents were determined for each sample for examination of vertical distribution patterns.

Fertilization significantly increased the nutrient content of all nutrients added. Copper concentrations increased on fertilized plots even though no Cu was added. Fertilization caused changes in seasonal nutrient dynamics of added nutrients, especially B. Retranslocation efficiencies of N, P, and K decreased with fertilization while retranslocation rates of several micronutrients increased. Concentrations of mobile nutrients increased with crown height while concentrations of immobile nutrients decreased with crown height. Distribution patterns also changed with fertilization. For example, boron concentrations on fertilized plots increased with crown height while concentrations on control plots decreased with crown height.

The ability to detect differences among sites and stability in concentrations are two criteria used to develop appropriate sampling protocols. Greatest sensitivity to detect site difference may occur at the times of year when the largest treatment differences occurred in this study. Unfortunately, concentrations are highly dynamic during those periods making the sampling window so small that it is impractical to use these periods for operational sampling. We recommend that foliage be sampled during the dormant season when nutrient concentrations are stable and there appears to be reasonable opportunity to detect difference among sites as indicated by significant treatment differences in this study. Greatest sensitivity to detect site difference may occur in the upper crown, where the largest treatment differences occurred in this study. Therefore we recommend that foliage be sampled from upper crown positions.

Seasonal Nutrient Dynamics and Vertical Nutrient Distribution in Loblolly Pine (*Pinus taeda*)

By
Ian Christopher Winborne

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APPROVED BY:

Barry Goldfarb	**Marcia Gumpertz**

H. Lee Allen
Chair of Advisory Committee

Biography

Ian Winborne was born in 1972 in North Carolina. He completed undergraduate work in Botany and a Masters of Science in Forestry at NCSU.

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Chapter I: Seasonal Foliar Nutrient Dynamics in Loblolly Pine (*Pinus taeda*)

Summary

The increase in pine productivity in the United States can be partially attributed to fertilization. Nutrient deficient stands may respond favorably to nutrient additions. However, deficient stands must be efficiently identified. Leaf area has been shown to diagnose nutrient deficiencies (Vose and Allen, 1988) while chemical analysis of foliage can provide more specific nutritional data. Nutrient levels fluctuate throughout the year making consistent and accurate sampling difficult.

The effects of nutritional treatments and time on foliar nutrient status were studied at SETRES. SETRES is a 2X2 factorial study of optimum nutrition and water additions in Scotland county, North Carolina, USA. Monthly foliage samples were collected and nutrient concentration and contents were determined for each sample.

Fertilization significantly increased the nutrient contents of all nutrients added. Copper concentrations increased on fertilized plots even though no Cu was added. Fertilization caused changes in seasonal nutrient dynamics of added nutrients, especially B. Retranslocation efficiencies of N, P, and K decreased with fertilization while retranslocation rates of several micronutrients increased. The ability to detect differences among sites and stability in concentrations are two criteria used to develop appropriate sampling protocols. Greatest sensitivity to detect site difference may occur at the times of year when the largest treatment differences occurred in this study. Unfortunately, concentrations are highly dynamic during those periods making the sampling window so small that it is impractical to use these periods for

operational sampling. We recommend that foliage be sampled during the dormant season when nutrient concentrations are stable and there appears to be reasonable opportunity to detect difference among sites as indicated by significant treatment differences in this study.

Introduction

Intensive silviculture has dramatically increased the productivity of pine forests in the southern United States (Allen *et al*, 1998). Gains in yield can be partially attributed to the addition of fertilizers to nutrient deficient stands. In order for fertilization to be a profitable investment, responsive stands must be efficiently identified. Leaf area has been shown to reliably diagnose nutrient deficiencies, especially for nitrogen (N) (Vose and Allen, 1988). However, more specific data can be gained from chemical analysis of foliage. Timing of foliage sampling is problematic due to lack of data on seasonal changes in foliar nutrient levels. Seasonal nutrient dynamics are dependent on the relative mobility of particular nutrients. Alteration of the nutrient status of a stand may also change nutrient levels and retranslocation rates of nutrients.

Fertilization has generally been found to increase the concentrations and contents of nutrients added. Additions of potassium (K) to red pine in New York significantly increased concentrations of K in the foliage (Leaf *et al.*, 1970). Similar patterns were observed for N in Douglas Fir (Brix, 1981) and Monterey pine (*Pinus radiata*) (Crane and Banks, 1992), for N and P in loblolly pine (*Pinus taeda*) (Valentine and Allen, 1990), and for boron (B) (Olykan *et al*., 1995), copper (Cu) (Hopmans and Clerhan, 1991), and zinc (Zn) (Boardman and McGuire, 1990) in Monterey pine.

Addition of water seems to have an indirect effect on foliar nutrient status, causing changes in soil properties or tissue weight. Significantly greater foliar N, P, and K concentrations were found for control plots compared with plots receiving additional water in loblolly and slash pine

(Walker, 1961), white pine (*Pinus strobus*) (Schomaker, 1969) and Monterey pine (Crane and Banks, 1992). Walker (1961) found that fertilization increased foliar N, P, and K concentrations in control and irrigated trees and narrowed the differences between the treatments; however, the addition of fertilizer increased the differences between irrigation treatments in white pine (Schomaker, 1969). Boron deficiencies have been reported in dry regions even when soil B levels seem optimal (Wikner, 1985). Problems with B nutrition were found to be related to low rainfall in New Zealand (Knight *et al*., 1983) and with the previous season's low precipitation (Hopmans and Clerhan, 1991).

Foliar weight gains and increases in nutrient concentrations resulting from water or nutrients additions may substantially change foliar nutrient balances. Nitrogen fertilization decreased the relative amounts of P, K, Ca, and Mg in semi-mature loblolly pine (Adams and Allen, 1985. Zhang and Allen, 1996). However, it was found that adding P alone and N and P in combination increased the proportion of P, K, Ca, and Mg to N (Adams and Allen, 1985). Proper nutrient proportions are essential for proper growth, and altering foliar nutrient balances can limit growth and reduce the effectiveness of nutritional treatments.

Retranslocation patterns of the major nutrients have been studied extensively in conifer species. Recycling of the mobile nutrients N, P, and K to prevent loss during needle senescence is of great importance in maintaining nutrient levels within the tree (Wells and Metz, 1962; Nambiar and Fife, 1987, 1991; Fife and Nambiar, 1984; Zhang and Allen, 1996). Calcium, Mg, and manganese (Mn) are generally regarded as immobile and tend to accumulate in older foliage (Zhang and Allen, 1996; Saur *et al*, 1992; Helmisaari, 1990). Recently, attention has focused on the effects of N, P, and K additions on growth rates and nutrient movement. Studies

of Monterey pine in Australia and loblolly pine in the U.S. have shown that high rates of retranslocation coincide with periods of rapid growth (Nambiar and Fife, 1987, 1991. Zhang and Allen, 1996). Fife and Nambiar (1984) reported that rapidly growing fertilized trees had the highest levels of absolute and relative retranslocation of mobile nutrients compared to non-fertilized treatments. During periods of rapid growth, mobile nutrients were withdrawn from needles of all ages to supply growing tissues. Replenishment of needle nutrient stores occurred during times of low growth and low soil nutrient supply (Nambiar and Fife, 1987), indicating that these trees were dependent upon internal and external nutrient pools. Similarly, Helmisaari (1992) found that fertilization of Scot's pine increased relative retranslocation rates of mobile nutrients. Studies have determined that winter needle nutrient concentrations are relatively stable (Helmisaari, 1990; Chapin and Kedrowski, 1983; Zhang and Allen, 1996).

Mobility levels of the micronutrients are less clear. Boron and Cu mobility may be concentrations dependent (Pendias and Pendias, 1984). Hopmans and Clerhan (1991) demonstrated that B was retranslocated when foliar B concentrations were above 5mg kg^{-1}. Helmisaari (1992) described Zn and B as intermediately mobile. The lack of data in this area, especially in loblolly pine, highlights the need for further work.

Objectives

The objectives of this study were to determine the effects of water and nutrient additions on foliar nutrient status, seasonal foliar nutrient dynamics, and nutrient retranslocation.

Methods

Samples were gathered as part of the SETRES site in Scotland County, NC. SETRES is a 2X2 factorial test of nutrient and water effects on loblolly pine replicated four times (four blocks with four plots each). Fertilization treatments consisted of 1) no addition and 2) optimum nutrition. Optimum nutrition is defined by maintaining foliar N concentrations at 1.3% and maintaining foliar nutrient: N ratios at the following levels: 0.10 P, 0.35 K, 0.12 Ca, and .06 Mg. B concentrations were kept at or above 12 ppm, but no attempt was made to control other micronutrient levels. Nutrients additions were made annually as solid fertilizer to sustain target levels (Table 1.1). Water treatments were 1) natural precipitation and 2) natural precipitation plus irrigation. Water was added to maintain soil water content greater than 3.0cm in the upper 50cm of soil (See table 1.2). Irrigation water contained small amounts of several nutrients (Table 1.2). For complete details on the SETRES study site see Albaugh *et al* (1998).

The first flush from the 1992 (first year of treatment) and 1996 (sixth year of treatment) cohorts were followed. Each foliage cohort was sampled for approximately 15 months. Monthly foliage samples were taken from the mid-upper crown of five representative trees in each treatment plot and bulked (16 samples total per month). Brown foliage on the tree was collected in the fall of 1993 and litter was collected in the fall of 1997.

Foliage samples were dried at 70^{o}C to a constant weight. Fascicle weight was determined by weighing the sample from each plot and dividing by the number of fascicles. Samples were ground and wet digested using a modified Kjeldahl method for N, P, K, Mg, Ca, (Parkinson and Allen, 1975). B, Cu, Zn, Mn, and S were extracted using a nitric acid digestion (Kovacs, *et al*., 1996). N concentration was determined colorimetrically using flow injection analysis

(Lachat QuikChem 8000, Lachat Instruments). P, K, Mg, Ca, B, Cu, Zn, Mn, and S concentrations were determined using an ICP-AES (ICP-2R, Varian Instruments). Nutrient concentrations are expressed on a dry weight basis.

Retranslocation rates were determined in the following manner (Zhang and Allen, 1996):

Retranslocation Before Senescence (RE1) = [(c1-c2)/c1]* 100
Retranslocation During Senescence (RE2) = [(c2-c3)/c1]* 100
Total Retranslocation (RT) =RE1 + RE2
Where
c1 = Maximum nutrient content of a needle
c2 = Nutrient content just before senescence
c3 = Nutrient content of brown needles on the tree or litter

Nutrient content = fascicle weight * nutrient concentration

Needle nutrient content, concentration, retranslocation, and ratios were analyzed as a repeated measures design with nutrition and water treatments serving as whole plot treatments and sampling date serving as repeated subplot treatments. The MIXED procedure was used to incorporate repeated measures errors (SAS Institute, 1996). Errors were assumed to be auto correlated over time within each plot and uncorrelated from one plot to another. The following model was used for each cohort for analysis:

$$Y_{ijkl} = \mu + B_i + F_j + I_k + (F*I)_{jk} + D_l + (D*F)_{lj} + (D*I)_{lk} + (D*F*I)_{ljk} + \varepsilon_{ijkl}$$

Where:
B = Random block effects
F = Fertilization effects
I = Irrigation effects
D = Date effects

Cov ($\varepsilon_{ijkl,}\ \varepsilon_{ijkl}$')=$\sigma^2\rho^d$, where d is the time difference between sampling time *l* and *l*' and ρ is the correlation between one month and the next.

Results

Fascicle Weight

Fascicle weight increased significantly as a result of fertilization for the 1992 and 1996 cohorts, and increased significantly as a result of irrigation for the 1996 cohort (Table 1.3). There was a significant irrigation by sampling date interaction for the 1992 cohort. Foliage development followed similar patterns for both cohorts (Figure 1.1) and not surprisingly was statistically significant (Table 1.3). Developing fascicles gained weight from early June until late in the summer of the following year. After this peak, a slight decreasing trend began and continued until senescence when substantial weight loss occurred.

Nutrient Concentration and Content

The concentrations of N, P, and K in the foliage increased significantly with fertilization (Table 1.3). In contrast, irrigation significantly reduced the P concentrations of the 1996 cohort. Nutrient concentrations among the sampling dates differed significantly, although nutrient dynamics were similar among the treatments for N, P, and K. Initial concentrations were high, but quickly diminished as fascicle weight increased (Figure 1.2). After a low during September and October of the first year, concentrations increased to a winter peak. Foliar concentrations decreased slowly in the second growing season until senescence, when concentrations converged to similar levels for all treatments. Fertilization by sampling date interactions were significant for N and K for both cohorts (Table 1.3). Irrigation by sampling date interactions were significant for N and P for the 1996 cohort. These interactions between sampling date and treatments were due to monthly differences in response to treatments rather than a consistent difference in response over time.

Fertilization with N, P, and K significantly increased the foliar contents of these nutrients while irrigation caused no significant changes (Table 1.4). Nitrogen, P, and K showed similar patterns of seasonal mobility for contents (Figure 1.2). Nutrient contents began low and slowly increased through the summer and fall of the first growing season. Contents were relatively stable during the winter months. A slight increase in contents began early in the second growing season and continued through June. Contents began to decrease in July and continued to decrease through October, with the greatest decrease occurring during senescence. The interaction of fertilization by sampling date was significant for both cohorts and the three nutrients. An irrigation by sampling date interaction was significant for N and P for the 1996 cohort. Treatment differences were low during the early stages of foliage growth and during senescence.

Calcium and Mn concentrations varied in response to treatment, but exhibit similar seasonal patterns. Calcium concentrations showed a significant decrease due to fertilization in the 1992 cohort but not in the 1996 cohort, while Mn concentrations were significantly lower due to fertilization in the 1996 cohort (Table 1.3). Irrigation significantly increased Ca concentrations in the 1992 cohort. Calcium contents increased significantly with fertilization for both cohorts, while Mn contents were higher on fertilized plots in the 1992 cohort and lower in the 1996 cohort (Table 1.4). Calcium and Mn concentrations and contents (Figure 1.3) behaved similarly for both cohorts. Both elements showed low initial concentrations followed by steady increase until senescence. A marked increase in concentrations was seen at senescence while contents decreased slightly at this point. The interaction of fertilization and sampling date was significant for Ca concentrations for the 1992 cohort, for Mn concentrations for the 1992 and 1996

cohorts, and Mn contents for the 1996 cohort. Irrigation had a significant interaction with sampling date for Mn concentrations for the 1992 cohort.

Magnesium, S, B, Cu, and Zn varied in their responses to treatments. Fertilization caused significant increases in S concentrations and contents for the 1992 and 1996 cohorts, while irrigation caused significant concentration increases for the 1996 cohort (Tables 1.3, 1.4). There was a significant interaction between the fertilizer and irrigation treatments for the 1996 cohort for concentrations. Concentrations were relatively stable through the life of the cohort, with a slight decreasing trend (Figure 1.4). There were significant fertilization by sampling date interactions for both cohorts. Sulfur contents steadily increased during the first growing season (Figures 1.4). A period of relative stability followed in the winter with a gradual decline to senescence. The effect of sampling date was significant for both cohorts (Table 1.3). Significant interactions between sampling date and fertilization for concentrations and contents were due to rank changes not related to any discernable pattern.

Foliar B concentrations and contents increased significantly as a result of fertilization (Tables 1.3 and 1.4). Irrigation caused significant reductions in B concentrations for the 1996 cohort and contents for the 1992 cohort. The fertilization by irrigation interaction was significant for concentrations for the 1996 cohort and for contents for the 1992 cohort. Sampling date significantly affected concentrations for both cohorts and the fertilization by sampling date interaction was significant for both cohorts. Non-fertilized plots were stable while concentrations on fertilized plots showed large fluctuation between dates (Figure 1.4). Concentrations on fertilized plots were initially low followed by a period of relative stability. The contents of

fertilized plots began relatively low and increased sharply, reaching a high in the mid-fall of the first growing season and then decreasing until senescence.

Copper concentrations and contents increased significantly on fertilized plots (Tables 1.3, 1.4), although no Cu was added. Copper concentrations began high, around 3-3.5 ppm, and immediately dropped to a low in the fall or early winter of the first year (Figure 1.4). Concentrations remained relatively stable after this period. There were significant fertilization by sampling date and irrigation by sampling date interactions for both cohorts. Foliar Cu contents for the 1992 cohort tended to increase until a peak in December. A stable period extended through the early summer when contents began a downward trend until senescence (Figures 1.4). The 1996 cohort was more stable, but exhibited fluctuations throughout the year.

Magnesium concentrations were significantly reduced for the 1992 cohort while contents increased significantly for the 1996 cohort as a result of fertilization (Tables 1.3, 1.4). There was a significant fertilization by irrigation interaction for Mg contents in 1992. Sampling date and the sampling date by fertilization interaction were significant for both cohorts. For the 1992 cohort, Mg concentrations were initially similar among the treatments (Figure 1.3), however the Cu concentrations for fertilized and unfertilized treatments diverged, with both treatments reaching a relatively stable level in the fall of 1992. Concentrations in the 1996 cohort were relatively stable after a slight decrease in the summer of 1996 (Figure 1.3). Magnesium contents increased steadily through the life of both cohorts, with the 1996 cohort reaching a higher level of contents (Figures 1.3).

Although fertilization significantly decreased Zn concentrations for both the 1992 and 1996 cohorts, Zn contents significantly increased with fertilization for the 1992 cohort due to the large

increase in fascicle weight (Tables 1.3, 1.4). Zinc concentrations and contents increased significantly with irrigation for the 1996 cohort. For the 1992 cohort, Zn concentrations were initially similar for all treatments but diverged with concentrations on fertilized plots remaining relatively stable and unfertilized plots steadily increasing (Figure 1.5). Concentrations in the 1996 cohort fluctuated throughout the life of the cohort with only a short period of stability during the second spring (Figure 1.5). Sampling date and the fertilization by sampling date interaction were significant for Zn concentrations in both cohorts. Initially the 1992 cohort had lower Zn concentrations on fertilized plots than on non-fertilized plots (Figure 1.5), however Zn concentrations steadily converged until the summer of 1993 when the treatment rank changed and concentrations began to decrease. Contents for the 1996 cohort fluctuated dramatically with peaks in the fall of 1996 and summer of 1997 and lows in December 1996 and near the time of senescence (Figure 1.5).

Nutrient Retranslocation

Treatment had no impact on the retranslocation efficiencies of the immobile nutrients Ca, Mn, and Mg (Table 1.5, Figure 1.7). Treatment effects on the more mobile nutrients varied by element and cohort. For the 1992 cohort, only N retranslocation increased significantly with fertilization. However, for the 1996 cohort remobilization was decreased by fertilization for P and K. Phosphorus retranslocation efficiency and pre-senescence N retranslocation efficiency decreased significantly on irrigated plots. However, for the 1996 cohort, B and Zn retranslocation efficiency were increased by fertilization. Zinc and Cu retranslocation efficiencies significantly decreased with irrigation. Irrigation significantly increased P retranslocation.

Total retranslocation efficiencies of several nutrients changed with time. Retranslocation efficiencies of all elements, except P, Zn, and S, decreased significantly from the 1992 cohort to 1996 cohort (Table 1.6). There were significant fertilization by cohort interactions for P and K, with total retranslocation efficiency in fertilized treatments decreasing from 1992 to 1996. Total P retranslocation increased on irrigated plots from 1992 to 1996 and the irrigation by cohort interaction was significant. Sulfur retranslocation efficiency increased significantly over this period, while Zn showed no change.

Changes in pre-senescence efficiency from the 1992 cohort to the 1996 cohort were less pronounced than changes in total retranslocation efficiency. Nitrogen, K, and Ca significantly decreased pre-senescence efficiency, while P and Zn increased significantly. The interaction of fertilization and cohort was significant for N and P, with pre-senescence retranslocation efficiency decreasing over time. Nitrogen, P, and Mn each showed significant interactions between irrigation and cohort, with N and Mn decreasing and P increasing over this period.

Nutrient Ratios

Nutrient ratios for P: N and K: N exhibited the least seasonal stability of the ratios examined and showed significant responses to treatments (Tables 1.7 and 1.6, Figure 1.8). Fertilization caused significant reductions for P:N and K:N for both cohorts. Irrigation reduced the P:N ratio for the 1996 cohort. Seasonal P:N and K:N trends resemble those of the concentrations for P and K, with fluctuations being less dramatic. There were significant fertilization by sampling date interactions in 1996 and 1992 for K:N.

Calcium: N ratios steadily increased through the life of the cohort in a pattern similar to that of Ca contents (Figure 1.8). Fertilization significantly decreased the Ca:N ratio for both cohorts (Tables 1.7 and 1.8). Sampling date and the fertilization by sampling date were significant as Ca:N increased over time and fertilized plots had lower Ca:N during and just before senescence.

Magnesium, S, Cu, and Mn to N ratios were stable (Figures 1.8 and 1.9) up to senescence, when a decrease in this stability occurred as N was retranslocated and the ratios increased. Fertilization significantly decreased the ratios of these elements to N (Tables 1.7 and 1.8). There were significant fertilization by sampling date interactions for these nutrients for both cohorts. The irrigation by sampling date interaction was significant for S:N, B:N, Cu:N, and Mn:N.

Zinc to N ratios were significantly lowered by fertilization and unaffected by irrigation (Tables 1.7 and 1.8). Seasonal patterns differed between treatments for the 1992 cohort(Figure 1.9). The fertilized treatments were very stable throughout the life of the cohort, much like Ca. Treatments not receiving fertilization showed an overall increasing trend, almost doubling before senescence. The 1996 cohort behaved very differently, and fertilization caused little difference in the seasonal patterns (Figure 1.9).

Boron to N ratios increased significantly as a result of fertilization while irrigation caused significant reductions in B:N (Tables 1.7 and 1.8). The dynamics of B:N and B contents were very similar (Figures 1.4 and 1.9). B:N on non-fertilized plots were very stable, fertilized plots tended to vary more through the season and showed greater increases at senescence. There were significant fertilization by sampling date interactions and significant irrigation by sampling date for both cohorts.

Discussion

Nutrient and water additions caused substantial changes in fascicle weight and nutritional status. The 60 % gains in fascicle weight are consistent with increases in leaf area and productivity found on this site by Albaugh, *et al* (1998).

As expected, both concentrations and contents of N, P, and K increased with fertilization. This effect has been reported by Zhang and Allen (1996), and is attributed to increases in soil N, P, and K availability.

Nitrogen, P, and K concentrations changed through the life of each cohort. During periods of rapid new foliage growth, nutrient concentrations typically increased indicating retranslocation to supply new growth. In contrast, concentrations tended to increase when new foliage growth rates slowed. During the dormant season foliar concentrations were high and relatively stable suggesting nutrient storage during dormant periods (Chapin and Kedrowski, 1983).

Nitrogen, P, and K showed high levels of retranslocation efficiency, before and after senescence, as has been widely reported (Zhang and Allen, 1996). Previous studies in loblolly and Monterey pines have reported greater retranslocation efficiency after fertilization, either as a result of high nutrient availability or subsequent accelerated growth (Nambiar and Fife, 1987. Zhang and Allen, 1996). In this study total N retranslocation efficiency increased significantly for the 1992 cohort possibly as the result of accelerated growth (Albaugh, *et al*,1998). In contrast, significant reductions in N, P, and K relative retranslocation efficiency were observed on fertilized plots for the 1996 cohort, despite the fact the annual nutrient sinks were larger. This difference in retranslocation between the two cohorts may be due to changes in the soil supply

relative to the growth rates. Initially, fertilization caused a dramatic increase in growth rates. The size of the nutrient sinks created by this growth may have been large compared to the supply available from soil nutrient pools. By 1996, these two sources had increased due to repeated nutrient additions relative to the size of the internal nutrient sink.

The addition of B increased B levels and substantially changed patterns of seasonal movement of this nutrient. Boron is thought to play a crucial role in cell wall development and structure, and cellular development and mobility maybe hampered below a critical level (Hopmans and Clerhan, 1991). The low B mobility and retranslocation found in non-fertilized plots suggested that concentrations were below this critical level. The addition of fertilizer apparently provided adequate, and possibly storage, levels of B. Boron not incorporated into cellular structure or immediately needed for enzyme function maybe available for remobilization, resulting in changed mobility patterns.

Calcium and Mn were immobile. Concentrations and contents of these nutrients increase steadily over time and retranslocation rates were very low or non-existent. Calcium is an important constituent of cell walls and incorporation into the cellular structure probably accounts for its immobility. The near identical behavior of Mn suggested a similar role. Low retranslocation efficiency rates indicate limited internal nutrient availability (Nambiar and Fife, 1987). However, continued increases in Ca and Mn levels through time indicate adequate soil supply (Zhang and Allen, 1996).

Foliar Mg levels and dynamics differed substantially between cohorts. For the 1992 cohort, Mg concentrations on fertilized plots decreased. This may have been due in part to dilution, however, although Mg was added it may not have reached the foliage. Soil properties or

nutrient interactions may have limited Mg availability as well. Magnesium concentrations increased on fertilized plots for the 1996 cohort. Apparently enough Mg was added by this time to overcome the dilution effects associated with greater foliage development.

Sulfur, Cu, and Zn exhibited intermediate mobility. Fertilization with S did not change the seasonal dynamics or retranslocation efficiency of S. Cu and Zn contents increased after fertilization even though these nutrients were not included in the treatment. This suggests that there were adequate soil supplies of these nutrients.

The effects of irrigation on foliar nutrient behavior were not clear. Fascicle weight increased on irrigated plots for the 1996 cohort, indicating that water availability was limiting growth. Decreases in P, and S concentrations for the 1996 cohort may be due to dilution. Boron contents decreased on irrigated plots for the 1992 cohort. Decreases in foliar B levels may have been due to leaching by irrigation water, the high solubility of boric acid and the coarse texture of the soil. However, increases in Zn concentrations and contents on irrigated plots cannot be explained as easily. The presence of additional water may have facilitated diffusion of Zn, thereby increasing root uptake.

Mean nutrient ratios during the dormant season deviated substantially from target values and other reports (Table 1.6). Proportions deviating from target values may have been due to dilution, soil nutrient supply, or excess fertilization. Zhang and Allen (1996) reported ratios of 100N: 13P: 70K: 11Ca: 10Mg for control trees and 100N: 8P: 47K: 8Ca: 7Mg, where N was the only added nutrient on a clay soil. Decreases in nutrient levels relative to N were attributed to dilution and high N levels. SETRES received a more balanced mix of nutrients in an effort to

maintain a stable nutrient balance, however, the trend toward high N in relation to other nutrients remained.

Several but not all nutrients ratios were quite stable over the cohort life. Phosphorus, K, and Zn seemed least stable and showed dramatic fluctuations through the growing season. Ratios of Ca, Mg, S, Cu, and Mn to N were almost constant through the life of the cohort, although variation between treatments existed. There may be several implications of this stability. Uptake of these nutrients is either related or dependent on the other nutrients or the internal status of these nutrients is regulated in relation to N.

Conclusions

Not surprisingly, fertilization increased the concentrations and contents of the applied nutrients N, P, K, S, and B. However, increases in Cu, a non-added nutrient, concentrations and contents indicated that Cu soil supply and or uptake was enhanced by the addition of another element. Dilution resulting from increased foliage weight decreased concentrations of non-added nutrients.

Retranslocation efficiencies decreased after fertilization for N, P, and K. This contrasts with earlier work demonstrating increased retranslocation efficiencies with increased nutrient availability. Boron mobility and retranslocation efficiency did increase after fertilization, supporting the hypothesis that B mobility is concentrations dependent.

Calcium and Mn contents and concentrations increased with foliage age and these two elements were the least mobile of all the nutrients examined. Steady increases in Mn and Ca foliar levels indicated that the soil supply of these nutrients was adequate.

Nutrient proportions with N generally decreased with fertilization. Proportions of Ca, Mg, S, Cu, and Mn remained remarkably stable over the life of the foliage while P, K, and Zn fluctuated more dramatically.

The ability to detect differences among sites and stability in concentrations are two criteria used to develop appropriate sampling protocols. Greatest sensitivity to detect site difference may occur at the times of year when the largest treatment differences occurred in this study. Unfortunately, concentrations are highly dynamic during those periods making the sampling window so small that it is impractical to use these periods for operational sampling. We recommend that foliage sampling be completed during the dormant season when nutrient concentrations are stable and there appears to be reasonable opportunity to detect difference among sites as indicated by significant treatment differences in this study.

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Table 1.1: Nutrient additions made on fertilized plots at SETRES.

Year	N (kg ha^{-1})	P (kg ha^{-1})	K (kg ha^{-1})	Ca (kg ha^{-1})	Mg (kg ha^{-1})	S (kg ha^{-1})	B (kg ha^{-1})
1992	224	56	112				
1992				134.4	56		
1992							1.6
1993		28					
1993	25.7	22.4	21.2		0.1		
1993			91.8		56	119.8	
1993	56						
1994 Cumulative Total	**305.7**	**106.4**	**225.1**	**134.4**	**112.1**	**119.8**	**1.6**
1994	112						
1995	56	28	56	23.5	33.6	73.9	
1995							1.1
1996	112	11.2	56	10.0		14.5	
1996							1.1
1997	134.4						
Cumulative Total	**720.1**	**145.6**	**337.1**	**168**	**145.7**	**208.3**	**3.9**

Table 1.2: Natural precipitation levels and water added as irrigation and incidental nutrient additions made on irrigated plots at SETRES.

Year	Natural (mm)	Irrigated (mm)	B (kg ha^{-1})	Cu (kg ha^{-1})	K (kg ha^{-1})	Mg (kg ha^{-1})	Zn (kg ha^{-1})	S (kg ha^{-1})	Total N (kg ha^{-1})
1993	735	668			1.4		29.3	3.3	10.0
1994	885	167							2.0
1995	990	601							7.2
1996	922	439							5.3
Cumulative Total	**4398**	**1875**	**0**	**0**	**1.4**	**0**	**29.3**	**3.3**	**24.6**

*Ca, and Mn were below detection limits for all years.

Table 1.3: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), and sampling date (Date) treatment effects and their interactions (F*I, F*Date, I*Date, and F*I*Date) on nutrient concentrations and fascicle weights (FasWt) for the 1992 and 1996 cohorts.

1992 Cohort

Effect	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn	FasWt
F	**0.0001**	**0.006**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0056**	**0.0001**	0.1039	**0.0001**
I	0.3805	0.3295	0.2397	**0.0522**	0.3356	0.8072	0.0719	0.2474	0.789	0.7225	0.9873
F*I	0.1968	0.1987	0.8481	**0.0173**	0.1124	0.7973	0.0702	0.6415	0.2077	0.5376	0.3307
Date	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
F*Date	**0.0001**	0.1034	**0.0001**	**0.0006**	**0.0001**	**0.0005**	**0.0001**	**0.0002**	**0.0001**	**0.005**	**0.0001**
I*Date	**0.0012**	**0.0001**	0.6578	0.4629	0.8286	0.4394	0.6673	**0.0534**	0.5019	**0.0126**	**0.002**
F*I*Date	0.8357	0.9925	**0.0035**	**0.0256**	0.3855	0.3691	0.2285	**0.0115**	0.3122	**0.0001**	0.121

1996 Cohort

Effect	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn	FasWt
F	**0.0001**	**0.0001**	**0.0001**	0.2317	0.7599	**0.0001**	**0.0001**	**0.0153**	**0.0001**	**0.0001**	**0.0001**
I	0.1127	**0.0009**	0.1217	0.7552	0.0724	**0.0008**	**0.0069**	0.8593	**0.0391**	0.739	**0.0133**
F*I	**0.0113**	0.5782	**0.003**	**0.0345**	0.9252	**0.0023**	**0.0097**	**0.0209**	0.967	0.7311	0.116
Date	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
F*Date	**0.0002**	0.0755	**0.0033**	0.4562	**0.0049**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0005**	0.1368
I*Date	0.2199	0.7036	0.9409	0.0817	0.4616	0.1035	0.7862	**0.0001**	0.8061	0.7777	0.8271
F*I*Date	0.6178	0.6988	0.7787	0.3688	0.8944	0.9883	0.4431	0.7877	0.5073	0.9047	0.8429

Table 1.4: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), and sampling date (Date) treatment effects and their interactions (F*I, F*Date, I*Date, and F*I*Date) on nutrient content for the 1992 and 1996 cohort.

1992 Cohort

Effect	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn
F	**0.0001**	**0.0001**	**0.0001**	**0.0214**	0.1394	**0.0001**	**0.0001**	**0.0001**	**0.0561**	**0.0328**
I	0.6149	0.3837	0.3634	0.2682	0.7143	0.675	**0.0527**	0.1382	0.8413	0.6896
F*I	0.8834	0.1465	0.4352	0.1662	0.3715	0.507	**0.0527**	0.567	0.6393	0.6438
Date	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
F*Date	**0.0001**	**0.0001**	**0.0001**	0.21	0.1383	**0.0001**	**0.0001**	**0.0087**	**0.0001**	0.8074
I*Date	**0.0012**	**0.0084**	0.211	0.0605	**0.041**	0.1447	0.6233	0.0943	0.8196	0.8985
F*I*Date	0.3373	0.7281	0.8221	0.5655	0.2046	0.6109	0.6137	**0.0044**	0.6907	**0.0381**

1996 Cohort

Effect	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn
F	**0.0001**	**0.0001**	**0.0001**	**0.0283**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	0.9927	**0.0128**
I	0.2042	0.7994	0.5546	0.2151	0.5604	0.4835	0.2506	0.108	**0.0047**	0.5213
F*I	0.9065	0.1767	0.1685	0.2518	0.4346	0.8314	0.2438	0.6331	0.3954	0.9599
Date	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.001**	**0.0001**	**0.0001**
F*Date	**0.0001**	**0.0001**	**0.0001**	0.8458	0.1719	**0.0016**	**0.0001**	**0.0024**	**0.0001**	**0.0362**
I*Date	0.4265	0.3254	0.9124	0.4179	0.523	0.1112	0.5829	**0.0004**	0.5779	0.2907
F*I*Date	0.7823	0.7904	0.9543	0.5219	0.9657	0.9626	0.392	0.9111	0.4784	0.6851

Table 1.5: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), and their interactions (F*I) on total and pre-senescence retranslocation efficiencies for the 1992 and 1996 cohort.

1992 Cohort

	Effect	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn
Total	**F**	**0.0044**	0.4352	0.1288	0.2044	0.4043	0.2357	0.3719	0.5259	0.0717	0.7588
	I	0.8406	**0.0221**	0.6992	0.1705	0.0856	0.6191	0.9945	0.4902	0.1658	0.3657
	F*I	0.941	0.315	0.573	0.392	0.294	0.243	0.274	0.568	0.497	0.728
Pre-Senescence	**F**	0.456	0.9872	0.3001	0.1805	0.8195	0.4965	0.7353	0.3287	0.2073	0.5005
	I	**0.0285**	0.6878	0.9306	0.177	0.3809	0.1532	0.4591	0.0659	0.4646	0.0763
	F*I	0.36	0.246	0.09	0.357	0.109	0.267	0.788	0.083	0.152	0.476

1996 Cohort

	Effect	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn
Total	**F**	0.7663	**0.0001**	**0.0005**	0.6866	0.9462	0.6822	**0.0001**	0.6953	**0.0017**	0.1453
	I	0.5993	0.1139	0.9674	0.3743	0.4458	0.6788	0.3804	**0.0119**	**0.0425**	0.2311
	F*I	0.17	0.156	0.296	0.63	0.942	0.524	0.255	0.41	0.261	0.326
Pre-Senescence	**F**	**0.0425**	**0.0001**	0.5625	0.6866	0.2904	0.0884	**0.0558**	0.4309	**0.0179**	0.1201
	I	0.1845	**0.0001**	0.9971	0.3743	0.7417	0.9258	0.436	0.8439	0.3036	0.1554
	F*I	0.098	0.292	0.481	0.63	0.499	0.574	0.52	0.248	0.654	0.391

Table 1.6: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), and cohort (C) treatment effects and their interactions (F*I, F*C, I*C, F*I*C) on total and pre-senescence (Pre) retranslocation efficiencies.

	Effect	**N**	**P**	**K**	**Ca**	**Mg**	**S**	**B**	**Cu**	**Zn**	**Mn**
Total	F	0.2356	**0.0001**	**0.0001**	0.1819	0.5149	0.2008	**0.0016**	0.7626	**0.0005**	0.2752
	I	0.5709	0.8139	0.7831	0.4144	0.0718	0.7517	0.6612	0.2771	**0.0167**	0.9254
	F*I	0.1782	0.0788	0.6235	0.5957	0.4755	0.376	0.1276	0.3416	0.2118	0.7947
	C	**0.0221**	0.2105	**0.0001**	**0.0001**	**0.0002**	**0.0001**	**0.0372**	**0.013**	0.0673	**0.0001**
	F*C	0.5347	**0.0001**	**0.0117**	0.3392	0.5782	0.3232	0.0656	0.4515	0.3366	0.5598
	I*C	0.6452	**0.007**	0.8333	0.0978	0.4484	0.5346	0.67	0.0319	0.7872	0.1524
	F*I*C	0.166	0.577	0.236	0.32	0.415	0.179	0.671	0.993	0.848	0.399
Pre-Senescence	F	0.0947	**0.0001**	0.2589	0.1622	0.3327	0.4581	0.0915	0.8394	**0.0076**	0.1235
	I	0.8131	**0.0001**	0.9567	0.4332	0.4033	0.25	0.9658	0.186	0.79	0.5912
	F*I	0.2308	0.7832	0.0934	0.5593	0.11	0.6532	0.5121	0.0367	0.1805	0.2688
	C	**0.0121**	**0.0596**	**0.0004**	**0.0001**	0.037	0.889	0.4032	0.089	**0.0031**	0.0819
	F*C	**0.0254**	**0.0001**	0.8041	0.3105	0.501	0.088	0.2146	0.2054	0.2861	0.6078
	I*C	**0.0292**	**0.0001**	0.9522	0.1016	0.7362	0.3046	0.2776	0.1157	0.2056	**0.0214**
	F*I*C	**0.054**	0.114	0.527	0.292	0.55	0.226	0.779	0.568	0.485	0.994

Table 1.7: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), and sampling date (Date) treatment effects and their interactions (F*I, F*Date, I*Date, and F*I*Date) on nutrient ratios for the 1992 and 1996 cohort.

1992 Cohort

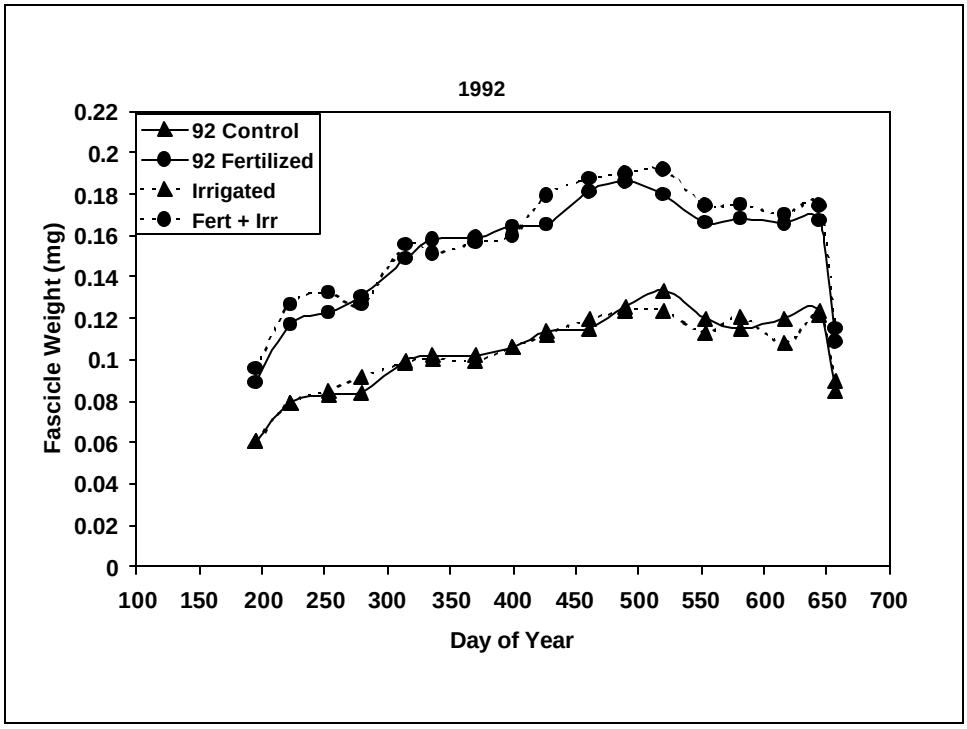
Effect	P:N	K:N	Ca:N	Mg:N	S:N	B:N	Cu:N	Zn:N	Mn:N
F	**0.0001**	**0.089**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0002**
I	0.3205	0.1127	**0.0093**	0.1583	0.3682	**0.064**	0.0961	0.4916	0.7808
F*I	0.1836	0.472	**0.0021**	0.0655	0.64	0.0562	0.8536	0.3031	0.5278
Date	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
F*Date	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0008**	**0.0001**	**0.0017**
I*Date	0.3199	0.4833	0.2939	0.8627	**0.0001**	**0.0001**	**0.0216**	0.4756	**0.0001**
F*I*Date	0.9876	**0.0334**	**0.0001**	0.9635	0.4935	**0.0001**	0.1142	0.1852	0.8492

1996 Cohort

Effect	P:N	K:N	Ca:N	Mg:N	S:N	B:N	Cu:N	Zn:N	Mn:N
F	**0.0001**	**0.0117**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
I	**0.0119**	0.7447	0.7538	0.1271	0.1661	0.1375	0.757	0.1478	0.7942
F*I	**0.0508**	0.1709	**0.0007**	0.0884	0.3656	0.2288	0.6182	0.5244	0.9783
Date	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
F*Date	0.1604	**0.0007**	**0.0001**	**0.0001**	**0.0951**	**0.0001**	**0.0002**	**0.0001**	**0.0001**
I*Date	0.8103	0.9799	0.1775	0.6337	0.7047	0.9598	0.8382	0.9482	0.1755
F*I*Date	0.8936	0.972	0.5021	0.9505	0.699	0.5655	0.3911	0.8006	0.4551

Table 1.8: Mean dormant season foliar nutrient:N ratios for 1992 and 1996 cohorts.

Cohort	Treatment	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn
1992	Control	100	10.58	37.72	20.23	8.38	8.63	0.000841	0.000272	0.004289	0.059049
1992	Irrigated	100	10.54	38.63	22.50	8.79	8.55	0.000815	0.000277	0.004373	0.058652
1992	Fertilized	100	7.73	37.36	12.45	3.99	6.86	0.002295	0.000204	0.002343	0.037806
1992	Fert+Irr	100	8.15	38.80	11.84	4.00	7.03	0.001919	0.000212	0.002261	0.035589
Standard Error			.2274	.4072	.7826	.1715	0.120	130.04	3.530	1288.0	52581
1996	Control	100	10.24	41.23	13.65	8.43	9.81	0.000853	0.000311	0.004955	0.049276
1996	Irrigated	100	9.22	42.22	12.68	7.78	9.53	0.000817	0.000312	0.005105	0.050234
1996	Fertilized	100	8.68	39.90	7.928	5.45	7.57	0.003282	0.00023	0.002605	0.016452
1996	Fert+Irr	100	8.54	38.23	9.043	5.48	7.51	0.00298	0.000226	0.002919	0.01778
Standard Error			.1914	.6191	.2345	.1322	.0843	75.6191	4.8176	1623.08	36407
Target		100	10	35.0	12.0	6.0	na	.0012	na	na	na



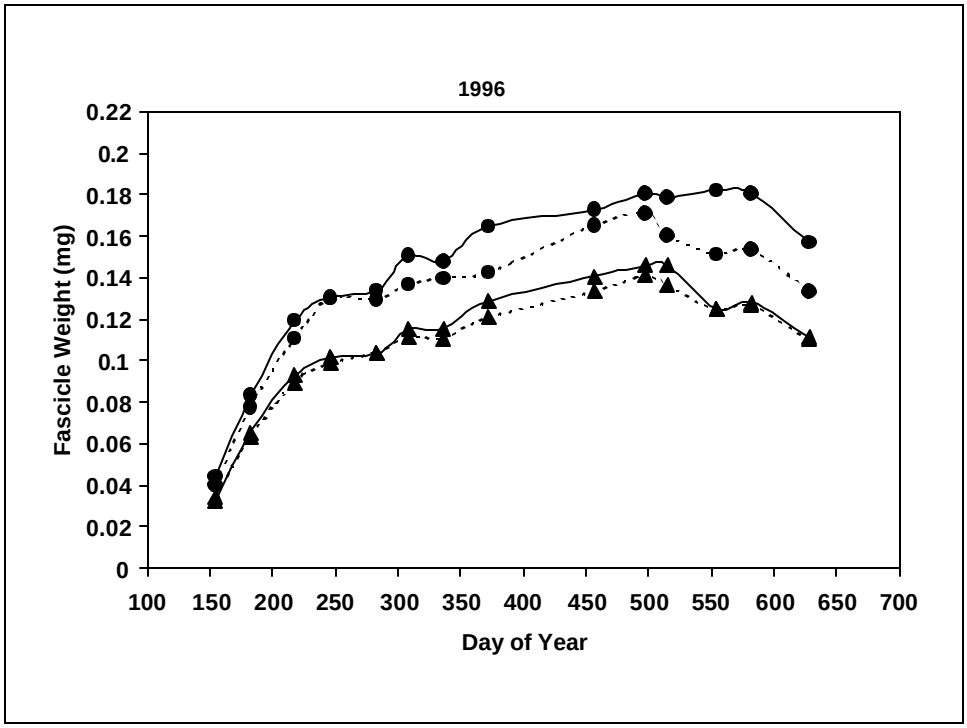


Figure 1.1: Seasonal fascicle weight dynamics for 1992 and 1996. Day of year represents number of days from January 1 of the year of cohort inception. The last point of each sequence represents litter or brown foliage.

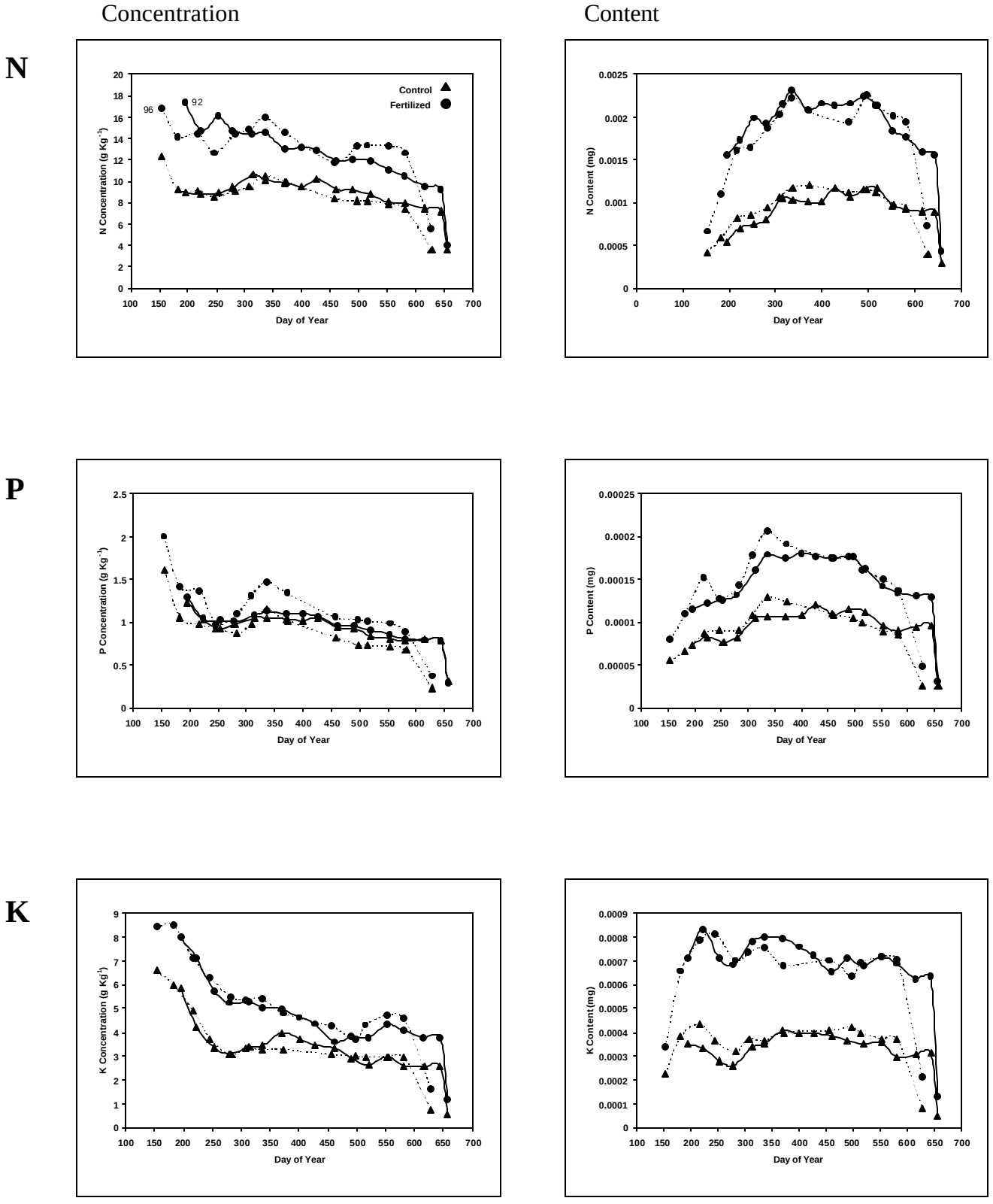


Figure 1.2: Foliar nutrient concentration and content dynamics of fertilized (circles) and control (triangles) plots from the 1992 (solid line) and 1996 (broken line) cohorts. Day of year represents number of days from January 1 of the year of cohort inception. The last point of each sequence represents litter or brown foliage.

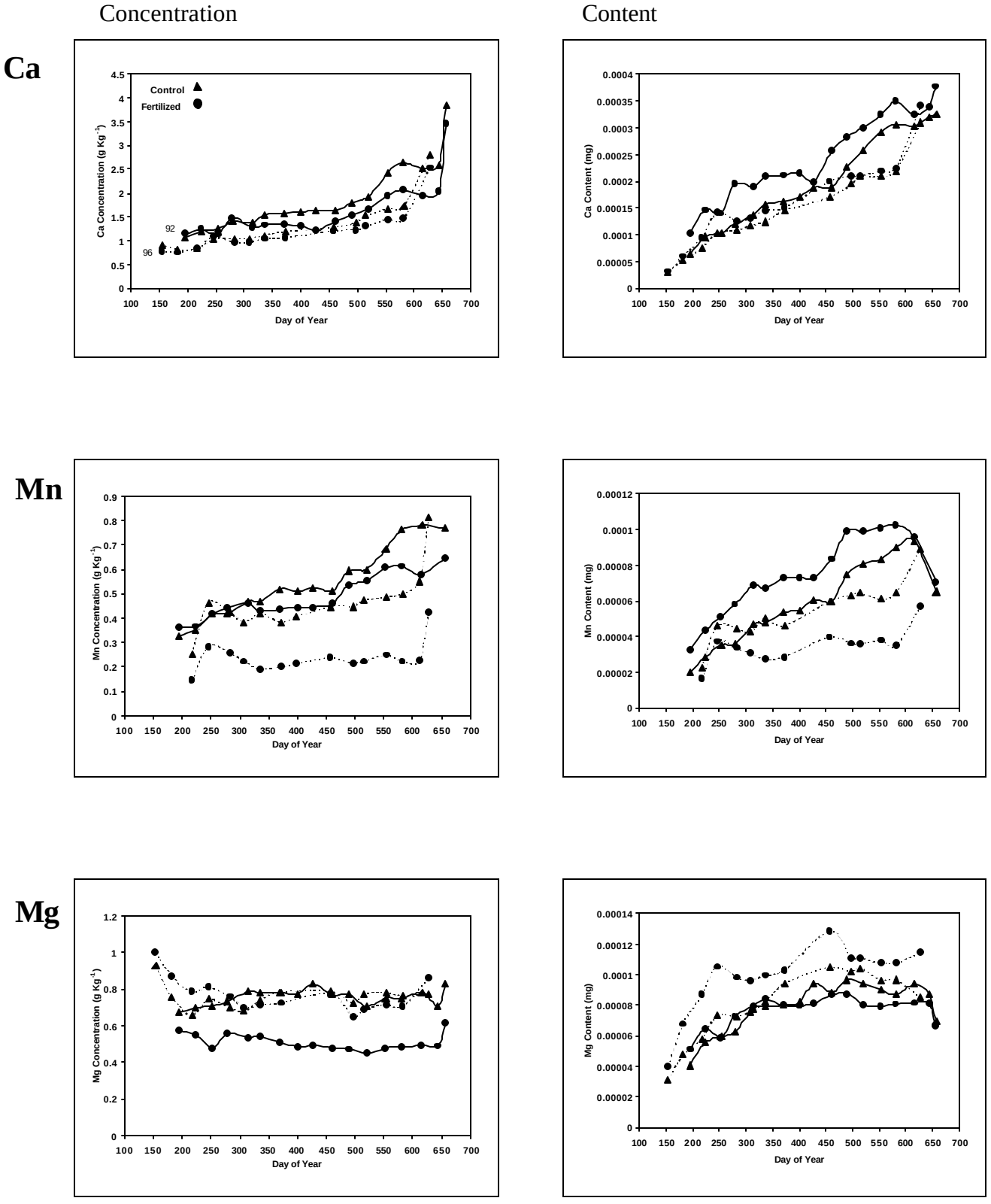
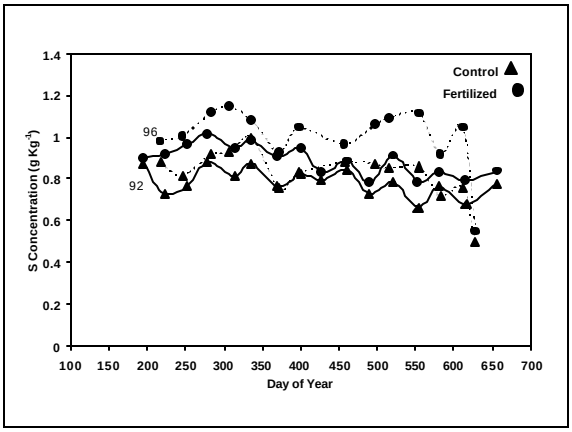


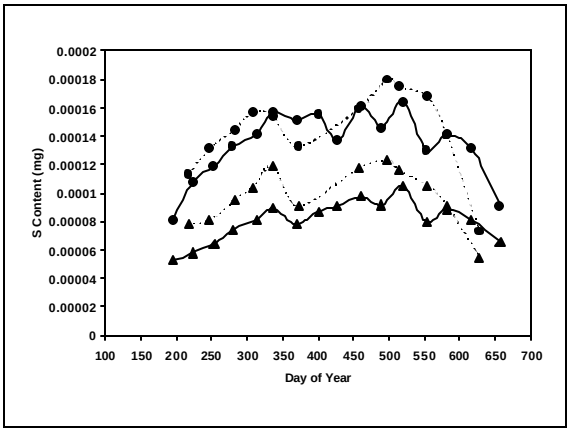
Figure 1.3: Foliar nutrient concentration and content dynamics of fertilized (circles) and control (triangles) plots from the 1992 (solid line) and 1996 (broken line) cohorts. Day of year represents number of days from January 1 of the year of cohort inception. The last point of each sequence represents litter or brown foliage.

Concentration

Content

S





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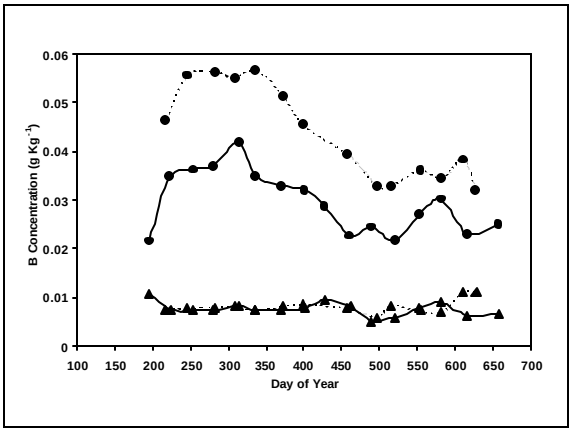
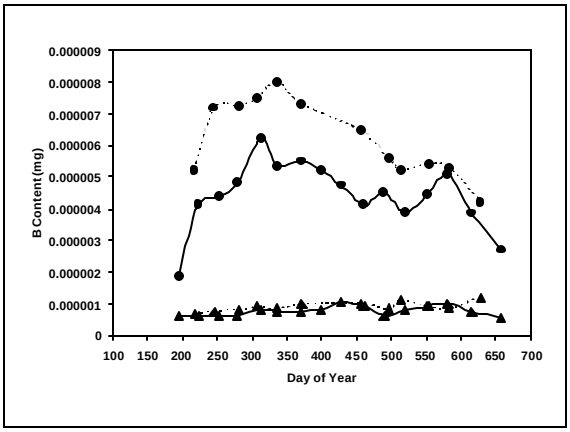
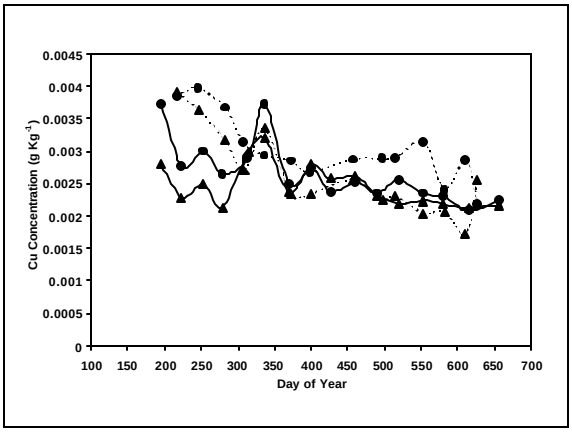




Cu



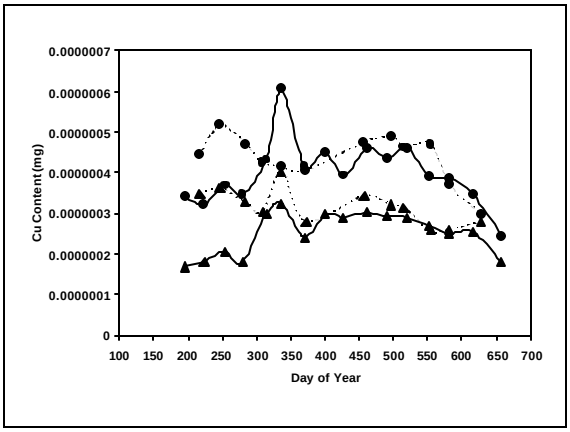
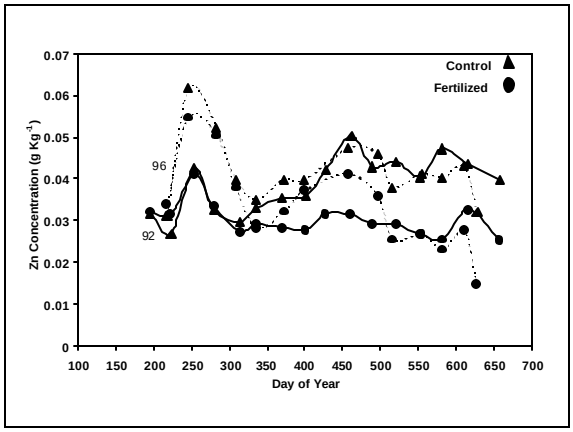


Figure 1.4: Foliar nutrient concentration and content dynamics of fertilized (circles) and control (triangles) plots from the 1992 (solid line) and 1996 (broken line) cohorts. Day of year represents number of days from January 1 of the year of cohort inception. The last point of each sequence represents litter or brown foliage.

Concentration

Content

Zn



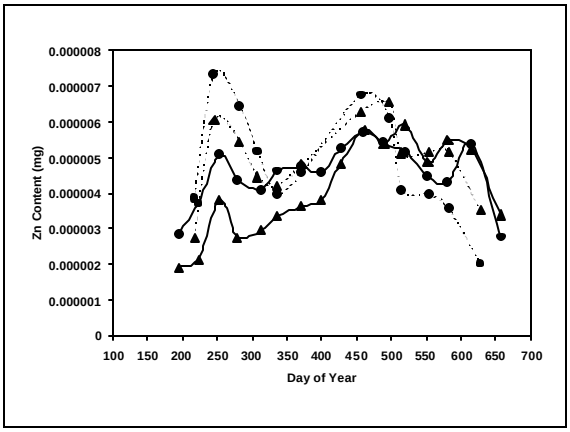
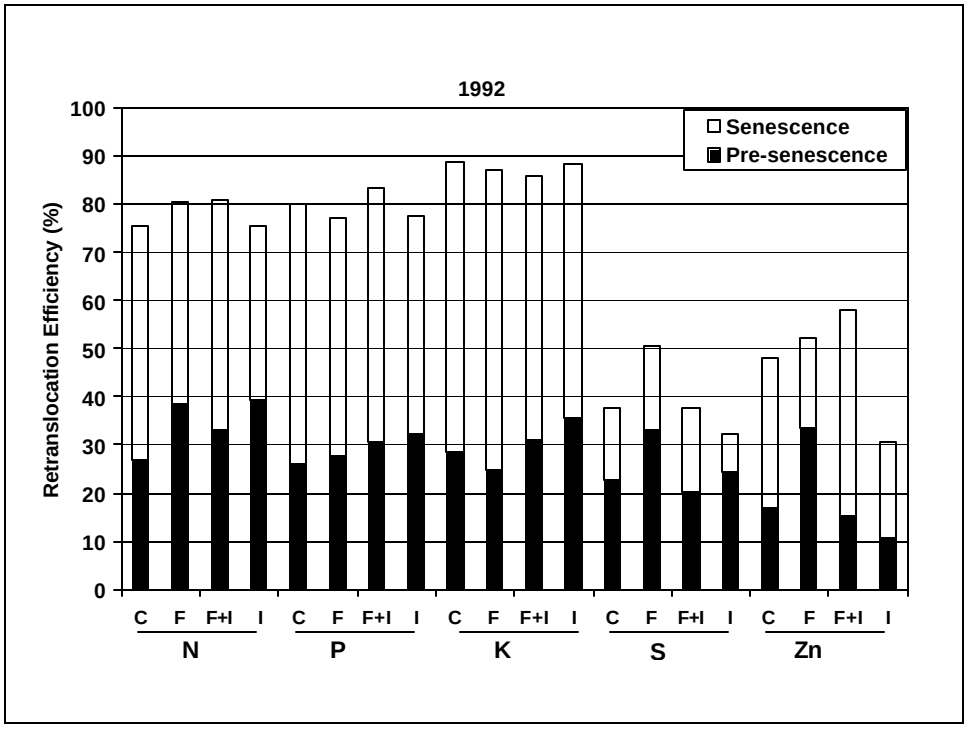


Figure 1.5: Foliar nutrient concentration and content dynamics of fertilized (circles) and control (triangles) plots from the 1992 (solid line) and 1996 (broken line) cohorts. Day of year represents number of days from January 1 of the year of cohort inception. The last point of each sequence represents litter or brown foliage.



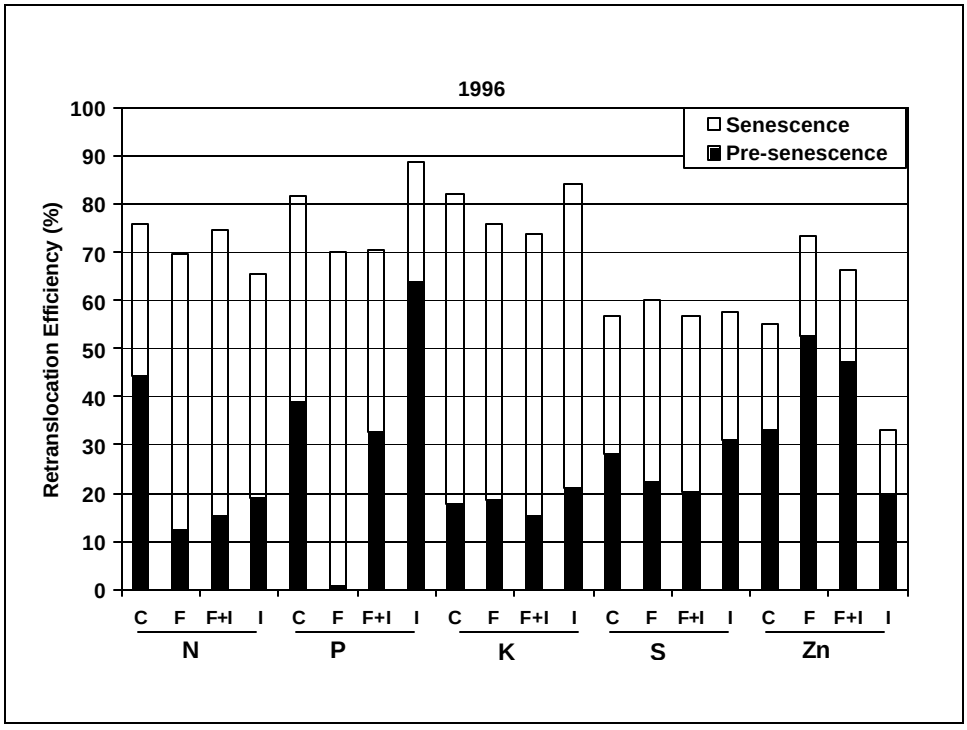
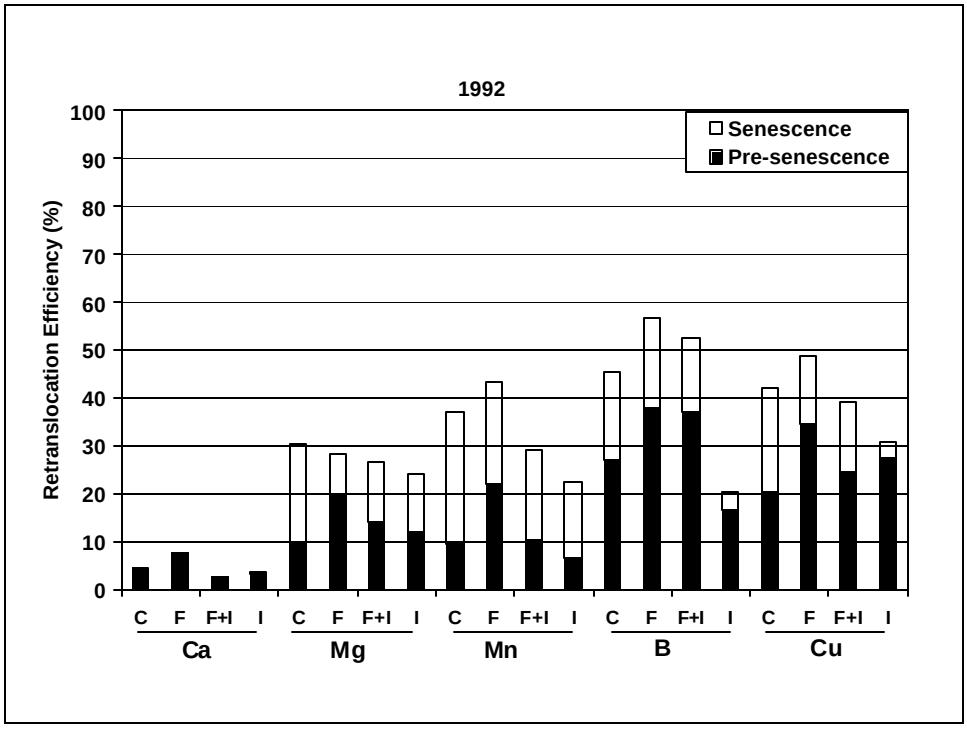


Figure 1.6:Foliar nutrient retranslocation efficiency before (Pre-senescence) and during senescence (Senescence) of mobile nutrients for 1996 and 1992.



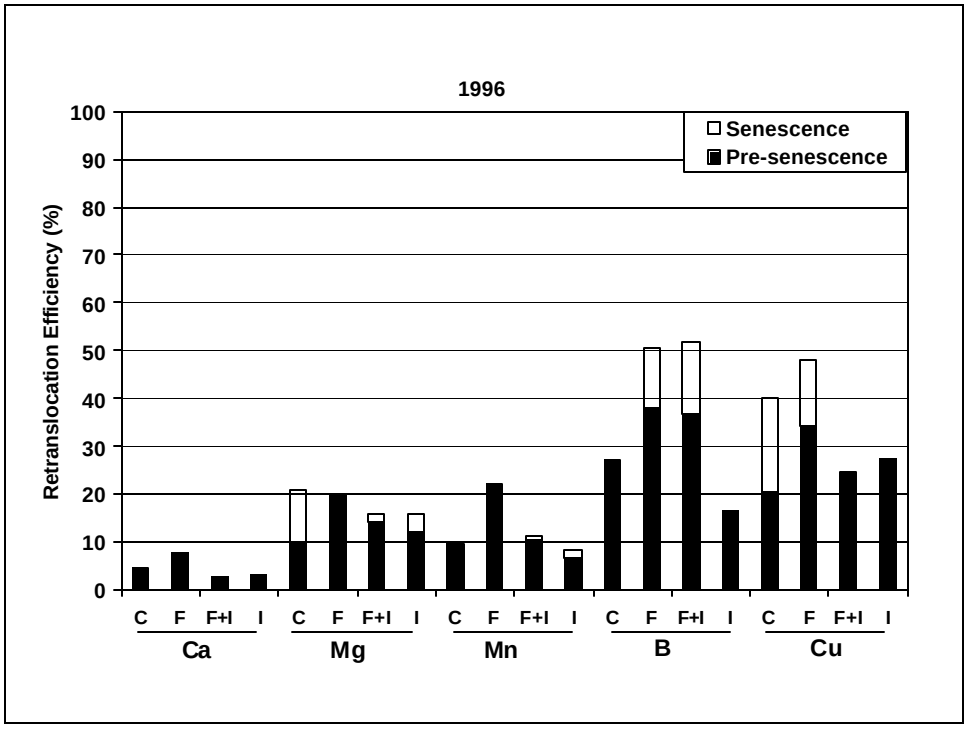


Figure 1.7:Foliar nutrient retranslocation efficiency before (Pre-senescence) and during senescence (Senescence) of less mobile nutrients for 1996 and 1992.

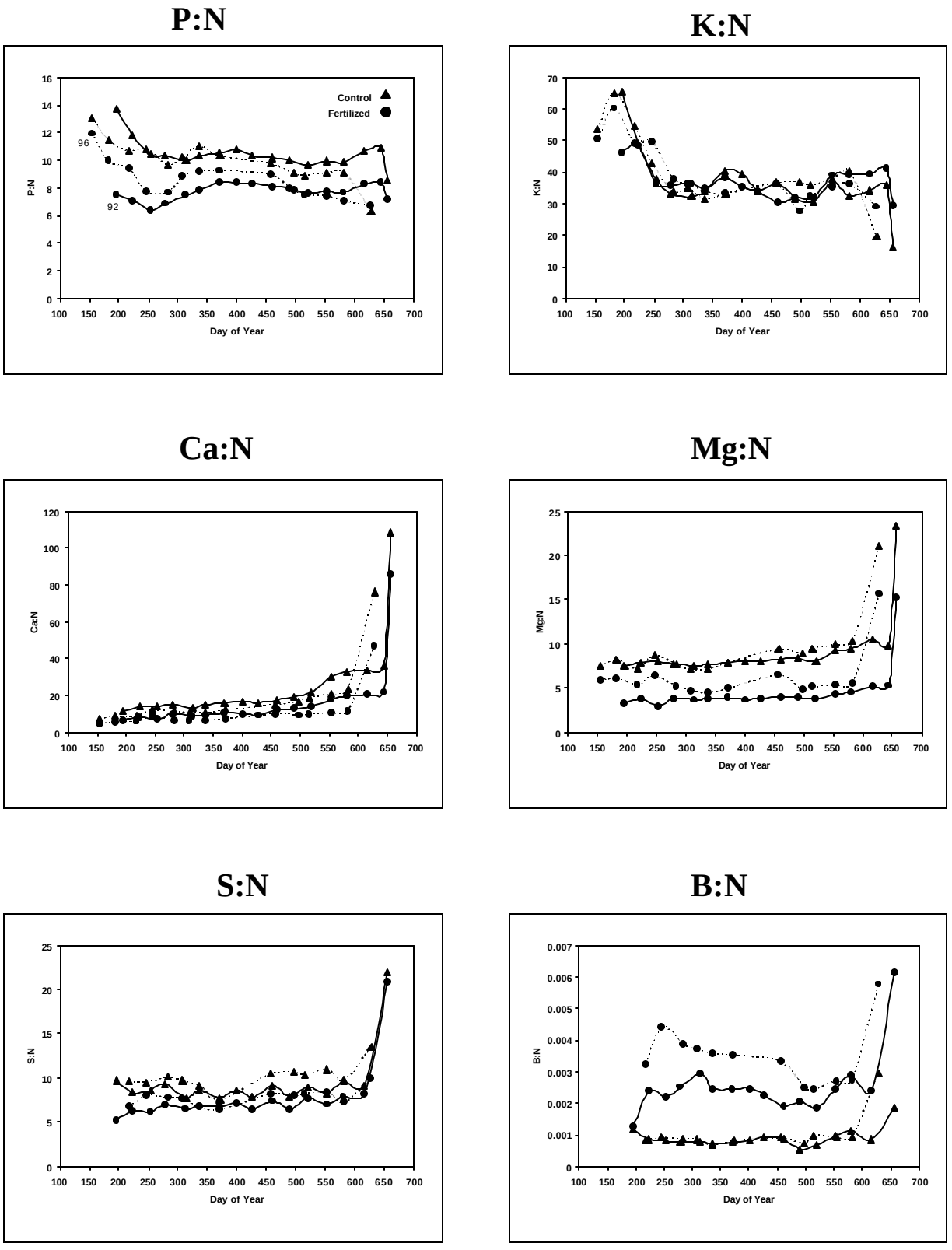


Figure 1.8: Foliar nutrient:N dynamics of of fertilized (circles) and control (triangles) plots from the 1992 (solid line) and 1996 (broken line) cohorts. Day of year represents number of days from January 1 of the year of cohort inception. The last point of each sequence represents litter or brown foliage.

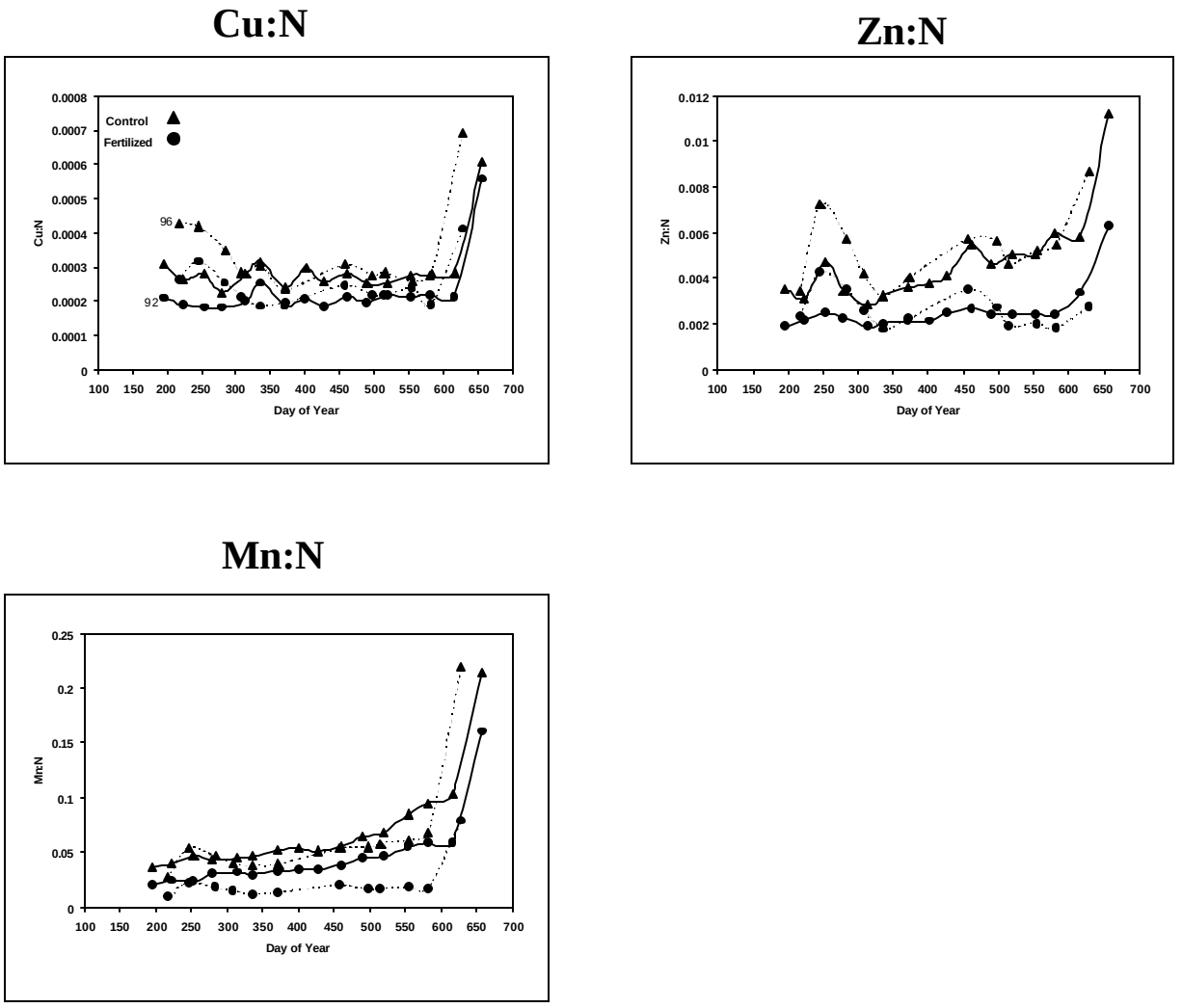


Figure 1.9: Foliar nutrient:N dynamics of of fertilized (circles) and control (triangles) plots from the 1992 (solid line) and 1996 (broken line) cohorts. Day of year represents number of days from January 1 of the year of cohort inception. The last point of each sequence represents litter or brown foliage.

Chapter II: Vertical Foliar Nutrient Distribution in Loblolly Pine (*Pinus taeda*)

Summary

The increase in productivity pine productivity in the United States can be partially attributed to fertilization. Nutrient deficient stands may respond favorably to nutrient additions. However, deficient stands must be efficiently identified. Leaf area has been shown to diagnose gross nutrient deficiencies (Vose and Allen, 1988) while chemical analysis of foliage can provide more specific nutritional data. Nutrients are unevenly distributed throughout the crown (Zhang and Allen, 1996). Therefore it is critical to sample from the crown position that will most accurately reflect the nutrient status of the tree.

The effects of nutritional treatments and crown location on foliar nutrient status were studied at SETRES. SETRES is a 2X2 factorial study of optimum nutrition and water additions in Scotland county, North Carolina, USA. Foliage samples were collected in 1994, 1996, and 1998 and nutrient concentrations and contents were determined for each sample.

Fertilization significantly increased the concentrations of all nutrients added. Copper concentrations increased on fertilized plots even though no Cu was added. Concentrations of mobile nutrients increased with crown height while concentrations of immobile nutrients decreased with crown height. Distribution patterns changed with fertilization. For example, B concentrations on fertilized plots increased with crown height while concentrations on control plots decreased with crown height. The ability to detect differences among sites and stability in concentrations are two criteria used to develop appropriate protocols. Greatest sensitivity to detect site difference may occur in the upper crown, where the largest treatment differences occurred in this study. We recommend that foliage be sampled from upper crown positions

where there appears to be reasonable opportunity to detect difference among sites as indicated by significant treatment differences in this study.

Introduction

Intensive silviculture has dramatically increased the productivity of pine forests in the southern United States. Gains in yield can be partially attributed to the addition of fertilizers to nutrient deficient stands. In order for fertilization to be a profitable investment, responsive stands must be efficiently identified. Samples for nutritional analysis are generally taken from the mid to upper-crown, but this may ignore important differences in distribution patterns (Zhang and Allen, 1996). Additionally, alteration of the nutrient status of a stand may change nutrient distribution patterns.

The distribution of nutrients in foliage is dependent upon the mobility and physiological role of the nutrient. In Monterey pine, K, Ca, and P were found to increase towards the base of the crown (Will, 1957) and N, Ca, and Mg followed the same trend in loblolly pine (Wells and Metz, 1963). However, P and K concentrations increased as crown height increased in loblolly (Wells and Metz, 1963) and White (1954, 1970) found similar patterns for N, K, and P concentrations. More recently, Zhang and Allen (1996) reported that N, P, and K concentrations increased with crown height while Ca and Mg concentrations decreased with crown height. Discrepancies among these studies may be due to species effects, differences in nutrient limitations, or stand density (shading effects).

Objectives

The objectives of this study were to investigate the effects of nutrient and water additions on foliar nutrient concentrations and the distribution of these nutrients within the crown.

Methods

Samples were gathered as part of the SETRES site in Scotland County, NC. SETRES is a 2X2 factorial test of nutrient and water effects on loblolly pine replicated four times (four blocks with four plots each). Fertilization treatments consisted of 1) no addition and 2) optimum nutrition. Optimum nutrition is defined by maintaining foliar N concentrations at 1.3% and maintaining foliar nutrient: N ratios at the following levels: 0.10 P, 0.35 K, 0.12 Ca, and .06 Mg. B concentrations were kept at or above 12 ppm, but no attempt was made to control other micronutrient levels. Nutrients additions were made annually as solid fertilizer to sustain target levels (Table 2.1). Water treatments were 1) natural precipitation and 2) natural precipitation plus irrigation. Water was added to maintain soil water content greater than 3.0cm in the upper 50cm of soil (See table 1.2). Irrigation water contained small amounts of several nutrients (Table 2.2). For complete details on the SETRES study site see Albaugh *et al* (1998).

Trees were destructively sampled in January and February of 1994, 1996, and 1998 to obtain tissue samples. One tree from each block- treatment combination was harvested. Trees were selected to represent the treatment range in height and diameter at the time of sampling (one small, two average, and one large). The height of each branch above the ground was measured. Six branches representing the treatment ranges were selected from one of three

crown positions within each tree. Two small, two medium, and two small branches were selected from the three crown positions, for a total of six branches per tree. Current year foliage from these representative branches was removed for nutrient analysis. See Albaugh *et al* 1998 for complete details on site conditions, treatments, and sampling methods used.

Foliage samples were dried at 70°C to a constant weight. Samples from 1994, 1996, and 1998 were ground and wet digested using a modified Kjeldahl method for N, P, K, Mg, and Ca (Parkinson and Allen, 1975). Micronutrient (S, B, Mn, Cu, Zn) determinations were made only on 1998 samples. Nitric acid digestion (Kovacs, *et al*., 1996) was used to extract B, Cu, Zn, Mn, and S. Nitrogen concentration were determined colorimetrically using flow injection analysis (Lachat QuikChem 8000, Lachat Instruments). Phosphorus, K, Mg, Ca, B, Cu, Zn, Mn, and S concentrations were determined using an ICP-AES (ICP-2R, Varian Instruments). Nutrient concentrations were expressed on a dry weight basis.

The relative branch height within the crown was determined for each foliage sample. Each sample was assigned to a group representing one third of the live crown, with crown position one (1) representing the third nearest the ground and crown position three (3) representing the upper third of the crown.

Data were analyzed using the MIXED procedure to account for correlations among branches within trees and temporal correlations within each plot (SAS Institute, 1996). Macronutrient data from 1994, 1996, and 1998 was analyzed as repeated measures experiment. Errors were assumed to be auto correlated over time within each plot. The following model was used for analysis:

$$Y_{ijklmn} = \mu + B_i + F_j + I_k + (F*I)_{jk} + D_l + (D*F)_{jl} + (D*I)_{kl} + (D*F*I)_{jkl} + P_m + (P*F)_{jm} + (P*I)_{km} + (P*F*I)_{jkm} + (P*D)_{lm} + (P*D*F)_{jlm} + (P*D*I)_{klm} + (P*D*F*I)_{jklm} + \varepsilon_{ijklm}$$

Where:

B = Random block effects

F = Fertilization effects

I = Irrigation effects

D = Date effects

P = Crown position

ε_{ijklm} = Residual error

Cov ($\varepsilon_{ijklm,}$ $\varepsilon_{ijkl'm'}$)=$\sigma^2\rho^d$, where d is the time difference between sampling time *l* and *l'* and ρ is the correlation between one month and the next for observations on the same tree.

Effects of fertilization, irrigation, date, and crown position were tested using Wald-type F-statistics with Sattathwaite's approximation for the degrees of freedom.

Results

Fertilization significantly increased foliar N, P, and K concentrations (tables 2.3 and 2.4, Figures 2.1 and 2.2). Potassium concentrations significantly decreased with irrigation. Generally, N, P, and K concentrations significantly increased as relative crown height increased. Phosphorus and K concentrations on irrigated plots increased to a greater extent than non-irrigated plots in the upper third of the crown resulting in a significant irrigation by crown position interaction. Nitrogen and P concentrations increased significantly with the passage of time and fertilization significantly increased this effect for N.

Calcium and Mn showed similar responses to treatments and crown position. Fertilization significantly decreased Ca concentrations for all years (tables 2.3 and 2.4 figure 2.2) and Mn concentrations in 1998 (table 2.4, figure 2.4). Concentrations of these two nutrients were highest in the lower crown positions and decreased with crown height. Interactions between fertilization and crown position were significant for Ca, with fertilized treatments having a less pronounced gradient. Calcium concentrations decreased with time and the concentration gradient across corn positions became steeper with time.

Fertilization and irrigation did not significantly affect Mg, S, or Zn concentrations (tables 2.3 and 2.4, figures 2.3 and 2.4). Patterns of Mg and Zn concentrations were somewhat variable through the crown and fertilization significantly interacted with crown position for both elements. This was manifested by a pronounced drop in Mg concentrations in the middle third of the crown and either an increase or no change as crown height increased. Foliar Zn concentrations

increased with crown height on fertilized plots. Non-fertilized treatments showed decreasing concentrations with crown height for both Mg and Zn.

Boron and Cu concentrations significantly increased with fertilization (table 2.4, figure 2.4). Crown position was not a significant factor for Cu or B, but there was a significant fertilization by crown position interaction for B. Concentrations of B on fertilized plots remained constant or increased with crown height while B concentrations on non-fertilized plots decreased with crown height.

Fertilization and irrigation interacted to significantly affect the P:N ratio (tables 2.5 and 2.6, figure 2.5) and the P:N ratio significantly increased with crown height. Crown position significantly interacted with irrigation. P:N ratios were higher for upper crown position on irrigated than non-irrigated plots. P:N ratios changed significantly with sampling year, with 1996 having the highest values.

Overall K:N ratios increased significantly with fertilization and crown height and changed significantly with time (tables 2.5 and 2.6, figure 2.5). There was a significant fertilization by crown position interaction in 1998, K:N ratios tend to decrease with crown height on fertilized plots. The crown position by irrigation interaction was significant; generally, irrigated treatments had lower K:N in the lower crown and higher concentrations in the upper crown than the corresponding non-irrigated treatments.

Calcium: N ratios significantly decreased with fertilization for all years (tables 2.5 and 2.6, figure 2.6). Irrigation significantly increased the Ca:N ratios in 1996. The same distribution pattern appeared across treatments, Ca:N ratios decreased with increasing crown height. Ca:N ratio for all treatments tended to converge in the upper crown position, resulting in a significant

interaction between fertilization and crown position. Ca:N ratios changed significantly over time. Ratios on irrigated plots peaked in 1996 while non-irrigated plots decreased with time.

Plots receiving fertilizer had significantly lower Mg: N ratios (tables 2.5 and 2.6, figure 2.6). Crown location significantly affected Mg:N , trending toward decreasing concentration with increasing crown height. There was a significant overall fertilization by crown position interaction, with distribution patterns similar to those of Mg concentrations. Mg:N changed significantly with time as Mg:N peaked in 1996.

Boron to N ratios significantly increased as a result of fertilization (table 2.6, figure 2.7). Crown position significantly affected B:N and there was a significant fertilization by crown position interaction. Non-fertilized plots tended to have B:N ratios that decreased with crown height while fertilized plots showed no consistent gradient.

Sulfur: N, Zn:N, and Mn:N ratios were significantly lowered by the addition of fertilizer (table 2.6, figure 2.7). Lower crown positions had significantly lower Mn:N than upper crown positions. Fertilization by crown position interactions were significant for Zn:N and Cu:N. Fertilized trees had low Cu:N in mid crown positions compared with relatively higher ratios in the upper and lower crown. Lower crown Zn:N ratios on fertilized plots were lower than non-fertilized plots but treatments converged in higher crown positions.

Discussion

Fertilization increased foliar N, P, and K concentrations as expected. However, Ca concentrations generally decreased with fertilization despite the additions of 134, 23, and 10 kg ha^{-1} Ca in 1992, 1995, and 1996, respectively. Similarly, Mg concentrations decreased on fertilized plots in 1994 and 1996 despite additions of 56, 56, and 134 kg ha^{-1} Mg in 1992, 1993, and 1995, respectively. By 1998 concentrations were greater in fertilized plots. The early reductions may be attributed to dilution, resulting from the increase in foliage growth following fertilization (Albaugh, *et al*. 1998). The slow uptake of Mg is in agreement with previous attempts to ameliorate deficiencies in pines (Huetle, 1993).

Decreased P and Ca concentrations on irrigated plots may be attributed to dilution. Water was limiting growth on this site; the addition of water increased growth and reduced P and Ca concentrations.

Nitrogen, P, and K concentrations increased with crown height as has been reported elsewhere (Zhang and Allen, 1996). Upper crown positions receive more sunlight and are therefore favored for foliar growth and have higher photosynthetic and metabolic rates. Nutrient use is high in these physiologically active regions, creating strong nutrient sinks that resulted in high concentrations of mobile nutrients. In addition, the upper crown positions generally showed the greatest differences between fertilized and non-fertilized treatments.

The immobile nutrients Ca and Mn (see chapter one) had low concentrations in the upper crown but concentrations tended to increase and height differences diminish at the lower crown positions. While immobility may not be the cause of accumulation lower crown positions, the

relationship between mobility and crown position is remarkable. One possible explanation for low Ca and Mn concentrations in the upper crown is that these crown positions had larger needles. In a previous study dilution caused reductions concentrations and substantially different patterns of content and concentration distribution (Zhang and Allen, 1996).

High Ca concentrations in lower crown may indicate high Ca availability on this site. Initially, Ca concentrations in the lower crown on control plots were more than 100% greater than Ca concentrations in upper crown positions. By 1998 concentrations in the lower crown were reduced and the difference between the lower and upper crown was less pronounced. Ca concentrations on fertilized plots showed a similar difference in crown position, but this difference diminished more quickly. Apparently, soil Ca supplies were being depleted as indicated by lower overall concentrations over time and diminished difference between lower and upper crown positions

Magnesium distribution in the crown was unique. Concentrations on non-fertilized plots generally decreased with crown height while fertilized plots decreased dramatically in the mid-crown position. This pronounced drop suggested a mild deficiency since no obvious symptoms, such as chlorosis or yellowing, were observed. Mid-crown deficiency symptoms have been reported for Mg in the past (Huetl, 1993). As discussed above, high growth on fertilized plots resulted in dilution and induced Mg deficiency. Why this deficiency was manifested in the mid-crown region remains unclear.

Sulfur was similar to Mg in that large amounts of S were added (208 kg ha^{-1}) as fertilizer but foliar S concentrations changed little. Brockley and Sheran (1994) found only small differences in foliar S concentrations between treatments receiving 50kg ha^{-1} and 100 kg ha^{-1} in lodgepole

pine (*Pinus contorta*). The N:S ratio of 14.6 (S:N = .068) cited by Brockley and Sheran (1994) was very similar to the values found on this study and supports their assertion that this is a constant ratio for conifers.

Copper and Zn concentrations followed similar patterns. Neither Cu nor Zn were added but foliar Cu concentrations increased on fertilized plots and Zn showed no change with fertilization. Site supply was apparently adequate to meet the Cu and Zn needs of fast growing fertilized trees. Because non-fertilized trees did not, or were not able to, fully exploit soil Cu and Zn pools, uptake of these nutrients from the soil was apparently regulated by the plant.

Foliar B concentrations increased more than 10 ppm with fertilization. Low B concentrations on non-fertilized plots suggested that the site was naturally deficient in B. Boron distribution patterns reversed with fertilization, non-fertilized plots decreased with crown height while fertilized plots increased with crown height. Boron distribution on fertilized plots was similar to that of N, P, and K while patterns of B distribution in non-fertilized plots was more similar to that of the immobile nutrients Ca and Mn. Boron has been reported to become mobile above threshold levels (Hopmans and Clerhan, 1991) and increased B mobility on fertilized plots may account for distribution similar to that of mobile nutrients.

Nutrient concentrations changes from 1994 to 1998. Both control and fertilized plots showed overall increases in N and P concentrations over time. Fertilized plots continually received nutrients and nutrient accumulation in the soil and foliage may be expected. However, the increase in nutrient levels in the control plots was not expected. Nutrient pools in untreated trees may have increased because mobile nutrients were continually recycled within the crowns

resulting in increased foliar concentrations. However, the possibility that nutrients from fertilized plots contaminated control plots cannot be excluded.

Target ratios for fertilized plots (100N: 0.10 P, 0.35 K, 0.12 Ca, .06 Mg) were very close to actual ratios for mid crown locations in all three years examined. Nutrient proportions occasionally fell below targets but may still fall within acceptable values (Adams and Allen, 1985).

Conclusions

The ability to detect differences among sites and stability in concentrations are two criteria used to develop appropriate protocols. Greatest sensitivity to detect site difference may occur in the upper crown, where the largest treatment differences occurred in this study. We recommend that foliage be sampled from upper crown positions where there appears to be reasonable opportunity to detect difference among sites as indicated by significant treatment differences in this study.

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Table 2.1: Nutrient Additions made on fertilized plots at SETRES.

Date	N (kg ha^{-1})	P (kg ha^{-1})	K (kg ha^{-1})	Ca (kg ha^{-1})	Mg (kg ha^{-1})	S (kg ha^{-1})	B (kg ha^{-1})
1992	224	56	112	134.4	56		1.6
1993	81.7	50.4	113.1		56.2	119.8	
1993 Cumulative Total	**305.7**	**106.4**	**225.1**	**134.4**	**112.2**	**119.8**	**1.6**
1994	112						
1995	56	28	56	23.5	33.6	73.9	1.1
1995 Cumulative Total	473.7	134.4	281.1	157.9	145.8	193.8	2.8
1996	112	11.2	56	10.1		14.5	1.1
1996 Cumulative Total	**585.7**	**145.6**	**337.1**	**168**	**145. 8**	**208.3**	**3.9**
1997	134.4						
Cumulative Total	**720.1**	**145.6**	**337.1**	**168**	**145.8**	**208.3**	**3.9**

Table 2.2: Natural precipitation levels and water added as irrigation nutrient additions made on irrigated plots at SETRES.

Year	Natural (mm)	Irrigated (mm)	B (kg ha^{-1})	Cu (kg ha^{-1})	K (kg ha^{-1})	Mg (kg ha^{-1})	Zn (kg ha^{-1})	S (kg ha^{-1})	Total N (kg ha^{-1})
1993			1.4		29.3	3.3	10.0	0.6	10.0
1994							2.0	1.1	
Cumulative Total	**0**	**0**	**1.4**	**0**	**29.3**	**3.3**	**12.0**	**1.8**	**10.0**
1995							7.2	4.2	
1996							5.3	3.0	
Cumulative Total	**0**	**0**	**1.4**	**0**	**29.3**	**3.3**	**24.6**	**9.1**	**10.0**
1997							6.9	3.9	
1998	0.4	0.1		1.1	1.1		2.4		12.4
Cumulative Total	**0.4**	**0.1**	**1.4**	**1.1**	**30.4**	**3.3**	**34.0**	**13.1**	**22.4**

*Ca and Mn were below detection limits for all years

Table 2.3: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), crown position (CP), and sampling year (FYR) treatment effects and their interactions (F*I, F*CP, I*CP, F*I*CP, F*FYR, *etc*..) on overall nutrient concentrations.

Effect	N	P	K	Ca	Mg
F	**0.0001**	**0.0001**	**0.0001**	**0.0599**	0.7497
I	0.2554	**0.0257**	0.7064	0.1769	0.8001
F*I	0.4077	0.0872	0.7999	0.4626	0.9307
CP	**0.0001**	**0.0001**	**0.0001**	**0.0001**	**0.0001**
F*CP	0.2167	0.2046	0.0877	**0.004**	**0.0343**
I*CP	0.2967	0.2363	**0.0258**	0.3445	0.5535
F*I*CP	0.5273	**0.0519**	0.1511	0.461	0.2017
FYR	**0.0001**	**0.0001**	0.5888	**0.0035**	0.1023
F*FYR	**0.0215**	0.2422	0.5168	0.1798	0.6527
I*FYR	0.6511	0.2439	0.3242	**0.0289**	0.6808
F*I*FYR	0.605	0.4025	0.5024	0.7391	0.9093
CP*FYR	0.1407	**0.0199**	**0.0001**	**0.0075**	0.7811
F*CP*FYR	0.3444	0.9436	0.0974	0.6943	0.3823
I*CP*FYR	0.1414	0.2975	0.4042	0.522	0.7594
F*I*CP*FYR	0.2143	0.6403	0.9226	0.7559	0.5373

Table 2.4: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), and crown position (CP) treatment effects and their interactions (F*I, F*CP, I*CP, F*I*CP) on 1998 nutrient concentrations.

1998

Effect	N	P	K	Ca	Mg	S	B	Cu	Zn	Mn
F	**0.0001**	**0.0001**	**0.0001**	0.819	0.5324	0.494	**0.0001**	**0.0057**	0.2878	**0.0004**
I	0.6274	0.7416	0.7406	0.1282	0.5209	0.8451	0.2512	0.6812	0.3129	0.9478
F*I	0.5454	0.0989	0.3691	0.8066	0.7863	0.709	0.3935	0.89	0.4464	0.7727
CP	**0.0046**	**0.0048**	**0.0092**	**0.0001**	**0.0002**	0.5514	0.3226	0.3289	**0.022**	**0.0001**
F*CP	**0.0147**	0.6652	0.2783	**0.0401**	0.4675	0.7343	**0.004**	0.1535	**0.0023**	0.1616
I*CP	0.64	**0.0181**	0.3172	0.3337	0.2233	0.2727	0.8631	0.363	0.6295	0.093
F*I*CP	0.7326	0.3556	0.5648	0.842	0.723	0.767	0.8933	0.2738	0.7023	0.6878

Table 2.5: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), crown position (CP), and sampling year (FYR) treatment effects and their interactions (F*I, F*CP, I*CP, F*I*CP, F*FYR, *etc*..) on overall nutrient ratios.

Effect	P:N	K:N	Ca:N	Mg:N
F	0.8314	**0.0001**	**0.0001**	**0.0002**
I	0.2436	0.1574	0.0708	0.5455
F*I	**0.0018**	0.6188	0.7619	0.6427
CP	**0.0001**	**0.0001**	**0.0001**	**0.0001**
F*CP	0.4357	0.5054	**0.0017**	**0.0241**
I*CP	**0.0037**	**0.0119**	0.5338	0.7578
F*I*CP	0.1459	0.3673	0.4449	0.1868
FYR	**0.0001**	**0.0224**	**0.0001**	**0.0007**
F*FYR	0.4894	0.2477	0.3954	0.4625
I*FYR	0.0807	0.1019	**0.045**	0.5933
F*I*FYR	0.9803	0.2024	0.8582	0.9611
CP*FYR	**0.0398**	**0.0003**	**0.0031**	0.3608
F*CP*FYR	0.1077	0.0706	0.702	0.3165
I*CP*FYR	0.7275	0.2152	0.3617	0.3008
F*I*CP*FYR*	0.4813	0.8367	0.8104	0.2878

Table 2.6: Summary of statistical significances (prob>F) of fertilization (F), irrigation (I), and crown position (CP) treatment effects and their interactions (F*I, F*CP, I*CP, F*I*CP) on yearly nutrient ratios.

1998

Effect	P:N	K:N	Ca:N	Mg:N	S:N	B:N	Cu:N	Zn:N	Mn:N
F	0.8993	**0.0145**	**0.002**	0.1216	**0.0028**	**0.0001**	0.1446	**0.0001**	**0.0001**
I	0.7712	0.9964	0.2055	0.6064	0.9412	0.2696	0.8527	0.2308	0.9401
F*I	**0.0001**	0.6246	0.5471	0.993	0.802	0.4861	0.7362	0.3049	0.884
CP	**0.0406**	**0.0042**	**0.0001**	**0.0001**	0.1047	**0.0239**	0.3928	0.0811	**0.0001**
I*CP	**0.0362**	0.3853	0.3069	0.1315	0.3268	0.943	0.319	0.3627	0.1336
F*CP	**0.0048**	**0.0009**	**0.0422**	0.6248	0.3908	**0.0155**	**0.0333**	**0.0159**	0.1864
F*I*CP	**0.0443**	0.3173	0.8711	0.7431	0.7686	0.8294	0.1438	0.4953	0.731

Table 2.7: Mean element: N ratios for 1998, 1996, and 1994. The number 1 represents lower crown positions and the number 3 represents upper crown positions.

1998

TRT	Crown Position	P:N	K:N	Ca:N	Mg:N	S:N	B:N	Cu:N	Zn:N	Mn:N
Control	1	9.06416	27.12794	16.41635	8.10242	9.26653	0.00116	0.00024	0.00329	0.0403
Control	**2**	**8.97054**	**26.75788**	**12.78959**	**7.42387**	**8.69327**	**0.00093**	**0.00023**	**0.00294**	**0.03691**
Control	3	9.22201	31.2272	9.52021	7.21036	8.25543	0.00088	0.00023	0.00315	0.03193
Irrigated	1	8.13324	26.47943	17.07118	8.68016	8.7001	0.00108	0.00021	0.00335	0.04889
Irrigated	**2**	**8.40368**	**30.6277**	**10.3506**	**6.74897**	**8.43793**	**0.00074**	**0.00024**	**0.00308**	**0.03465**
Irrigated	3	8.60654	32.18993	7.26028	6.11256	9.38336	0.0008	0.00023	0.00299	0.02803
Fertilized	1	8.70811	37.96286	11.39537	7.12527	8.41566	0.0025	0.00022	0.00185	0.02182
Fertilized	**2**	**8.3854**	**34.35057**	**9.80191**	**6.07362**	**6.68545**	**0.00245**	**0.00019**	**0.00205**	**0.01966**
Fertilized	3	8.16152	34.5625	8.61507	6.4418	7.17413	0.00265	0.00021	0.00249	0.0159
Fert + Irr	1	9.12794	35.75417	11.33771	7.24027	7.72084	0.00212	0.00023	0.00248	0.02411
Fert + Irr	**2**	**8.66833**	**31.65699**	**9.0543**	**5.62618**	**6.79947**	**0.00201**	**0.0002**	**0.00229**	**0.01739**
Fert + Irr	3	9.31486	34.96806	7.1202	5.52034	7.21572	0.00191	0.00021	0.00272	0.01486

1996

TRT	Crown Position	P:N	K:N	Ca:N	Mg:N
Control	1	11.1579	26.947	25.2716	10.2958
Control	**2**	**10.5341**	**25.9663**	**15.1954**	**9.4978**
Control	3	11.1306	34.6713	10.5306	8.055
Irrigated	1	9.1597	25.3993	30.1882	11.1584
Irrigated	**2**	**9.3135**	**28.8565**	**21.2469**	**9.2187**
Irrigated	3	9.9503	35.7665	14.4194	8.0623
Fertilized	1	10.6228	36.6157	15.3058	9.8761
Fertilized	**2**	**10.5155**	**40.6112**	**11.4006**	**7.6808**
Fertilized	3	10.8219	47.5658	7.9198	6.9231
Fert + Irr	1	9.9869	30.3595	23.2551	10.9918
Fert + Irr	**2**	**10.1152**	**40.3611**	**11.7402**	**7.6483**
Fert + Irr	3	11.3512	49.0106	12.0952	8.0344

Table 2.7 Continued

1994

TRT	Crown Position	P:N	K:N	Ca:N	Mg:N
Control	1	9.5213	30.4702	29.9731	10.8509
Control	**2**	**9.4194**	**32.6093**	**13.1117**	**7.7515**
Control	3	10.1462	37.9752	10.5754	9.1486
Irrigated	1	8.9818	28.2391	29.9668	10.0447
Irrigated	**2**	**9.4237**	**35.8541**	**19.9928**	**10.7437**
Irrigated	3	9.3458	43.9775	9.9855	7.4568
Fertilized	1	8.8113	28.9558	20.2197	8.1949
Fertilized	**2**	**8.6699**	**34.8115**	**10.2064**	**5.5974**
Fertilized	3	9.2476	38.878	11.8066	6.9147
Fert + Irr	1	8.9075	33.1546	21.4815	8.5054
Fert + Irr	**2**	**9.3651**	**41.1133**	**12.0728**	**5.8798**
Fert + Irr	3	10.6771	63.8883	11.0783	8.4274

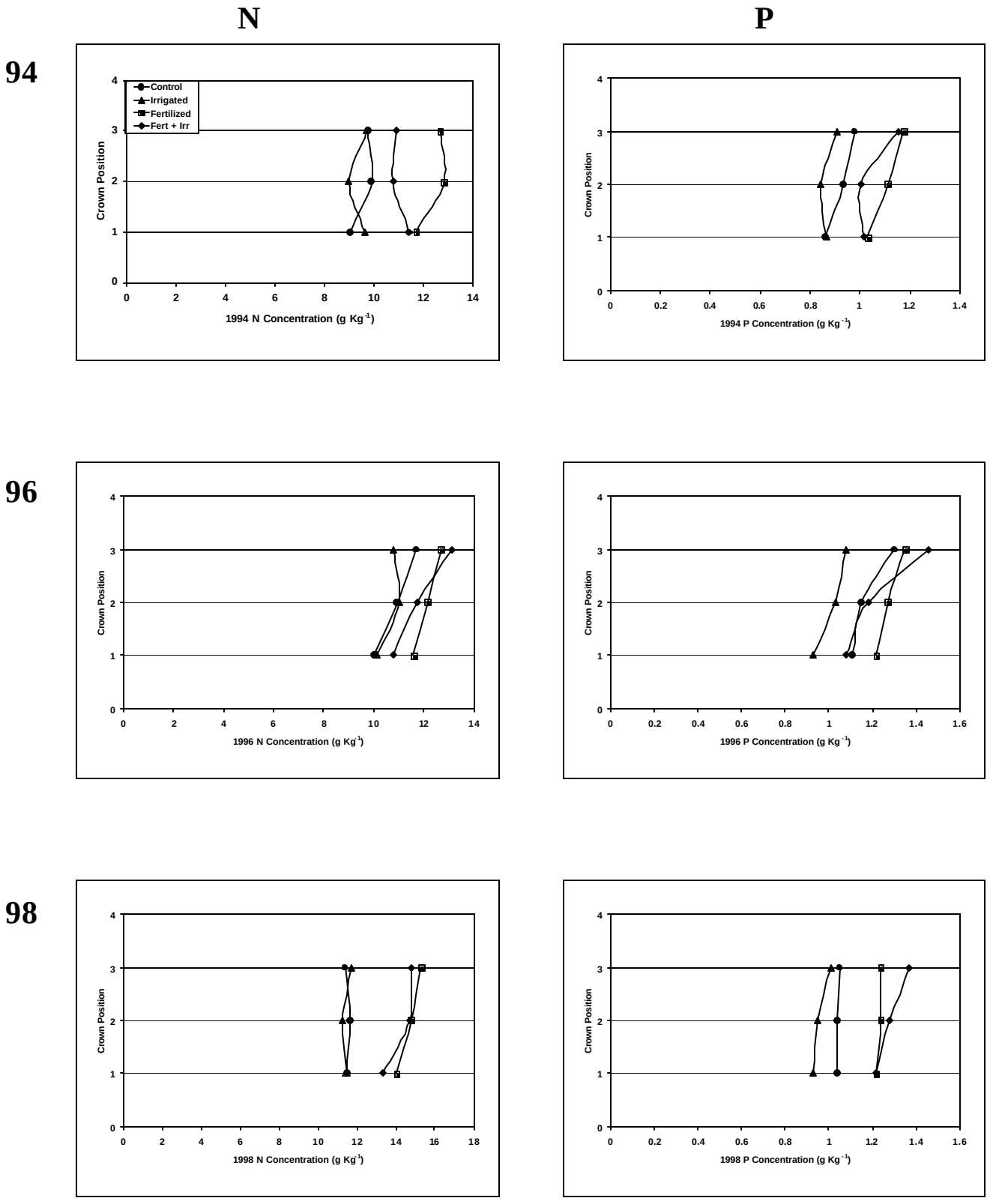

Figure 2.1: Foliar N and P distribution patterns of fertilized (squares), fertilized and irrigated (diamonds), irrigated (triangles), and control (circles) plots for 1994, 1996, and 1998.

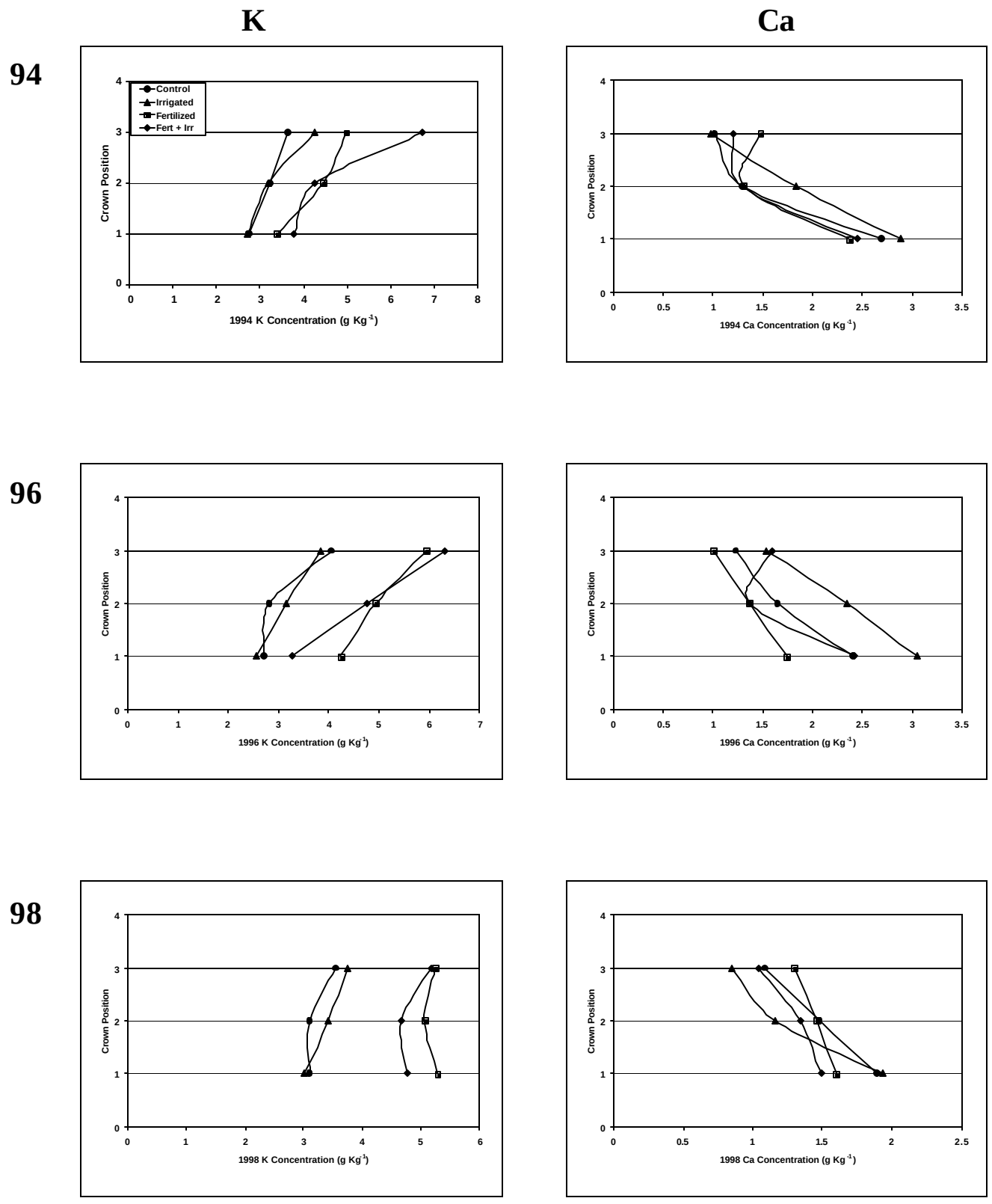

Figure 2.2: Foliar K and Ca distribution patterns of fertilized (squares), fertilized and irrigated (diamonds), irrigated (triangles), and control (circles) plots for 1994, 1996, and 1998.

Mg

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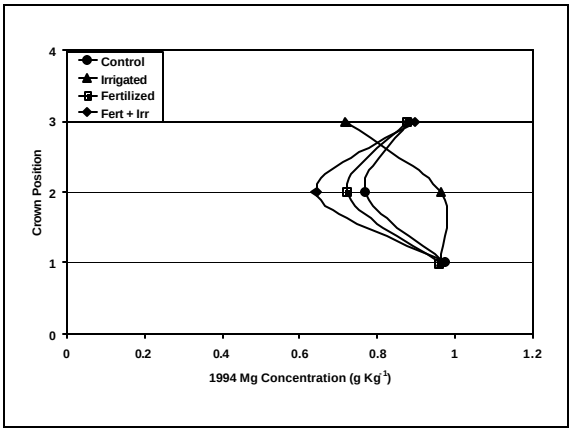
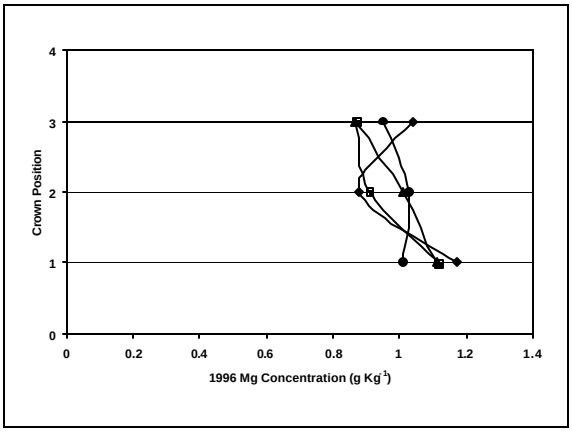


96



98

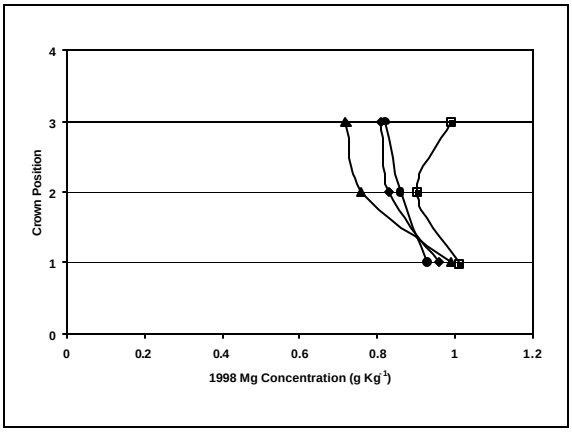


Figure 2.3: Foliar Mg distribution patterns of fertilized (squares), fertilized and irrigated (diamonds), irrigated (triangles), and control (circles) plots for 1994, 1996, and 1998.

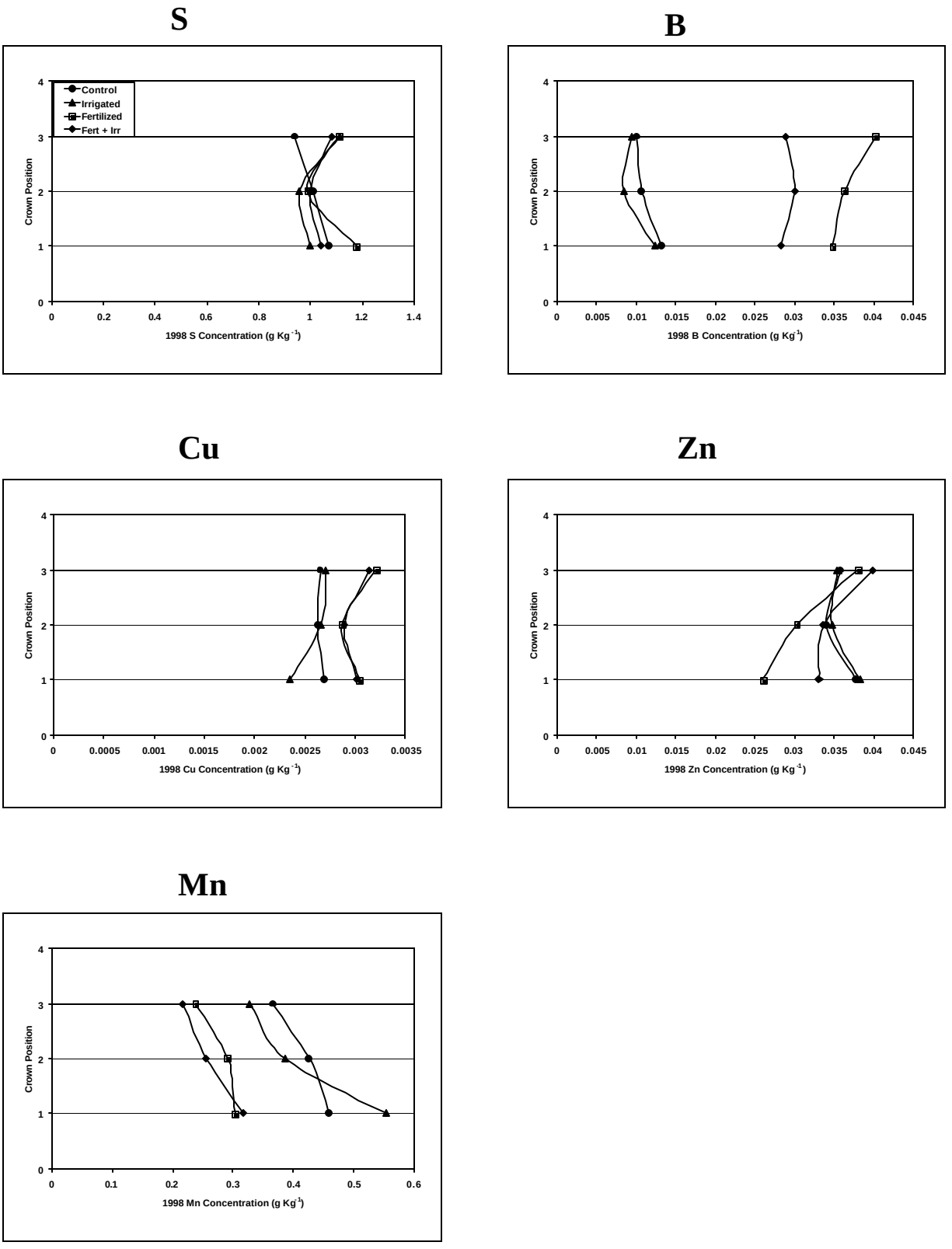


Figure 2.4: Foliar S, B, Cu, Zn, and Mn distribution patterns of fertilized (squares), fertilized and irrigated (diamonds), irrigated (triangles), and control (circles) plots for 1998.

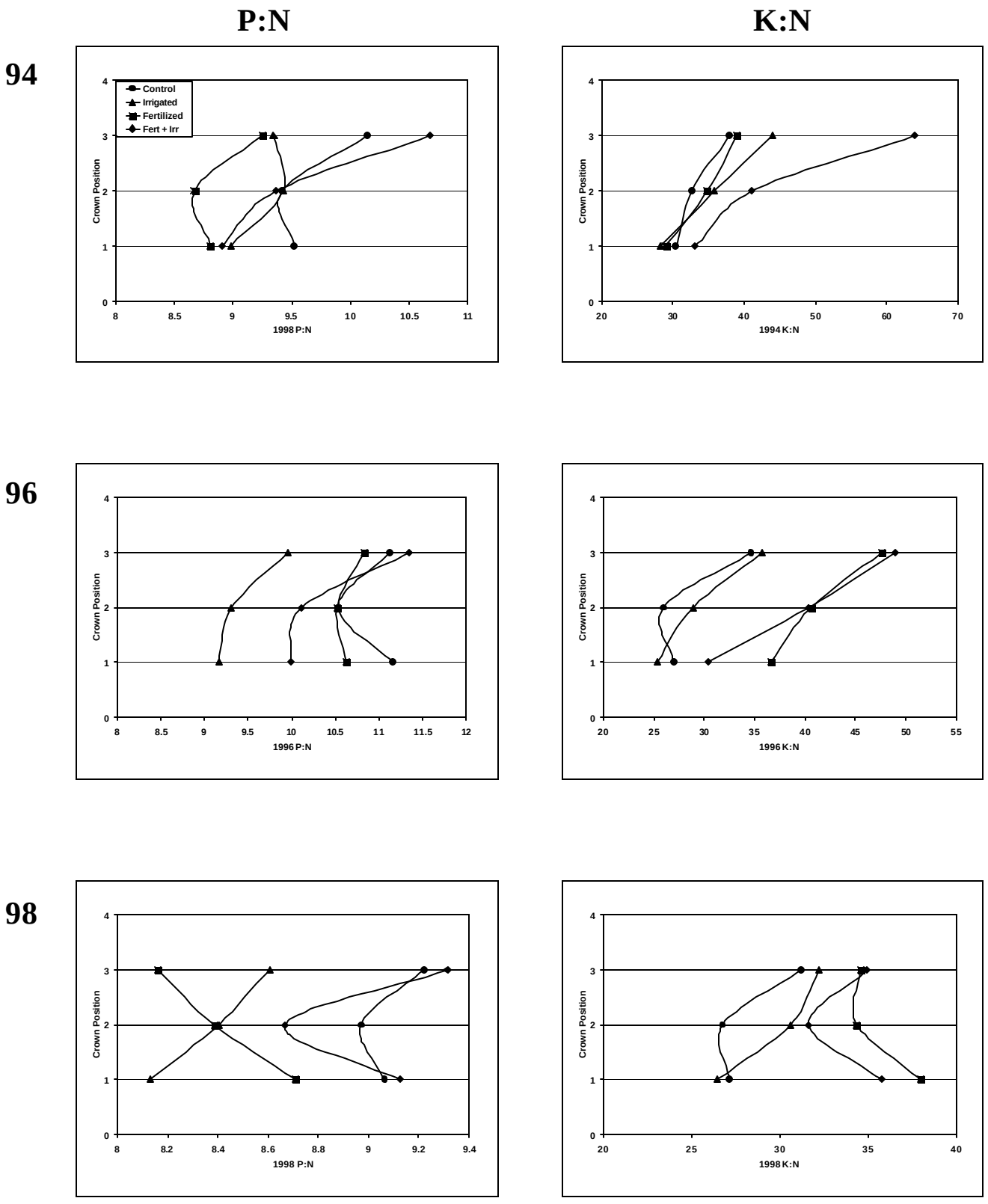


Figure 2.5: Foliar P:N and K:N distribution patterns of fertilized (squares), fertilized and irrigated (diamonds), irrigated (triangles), and control (circles) plots for 1994, 1996, and 1998.

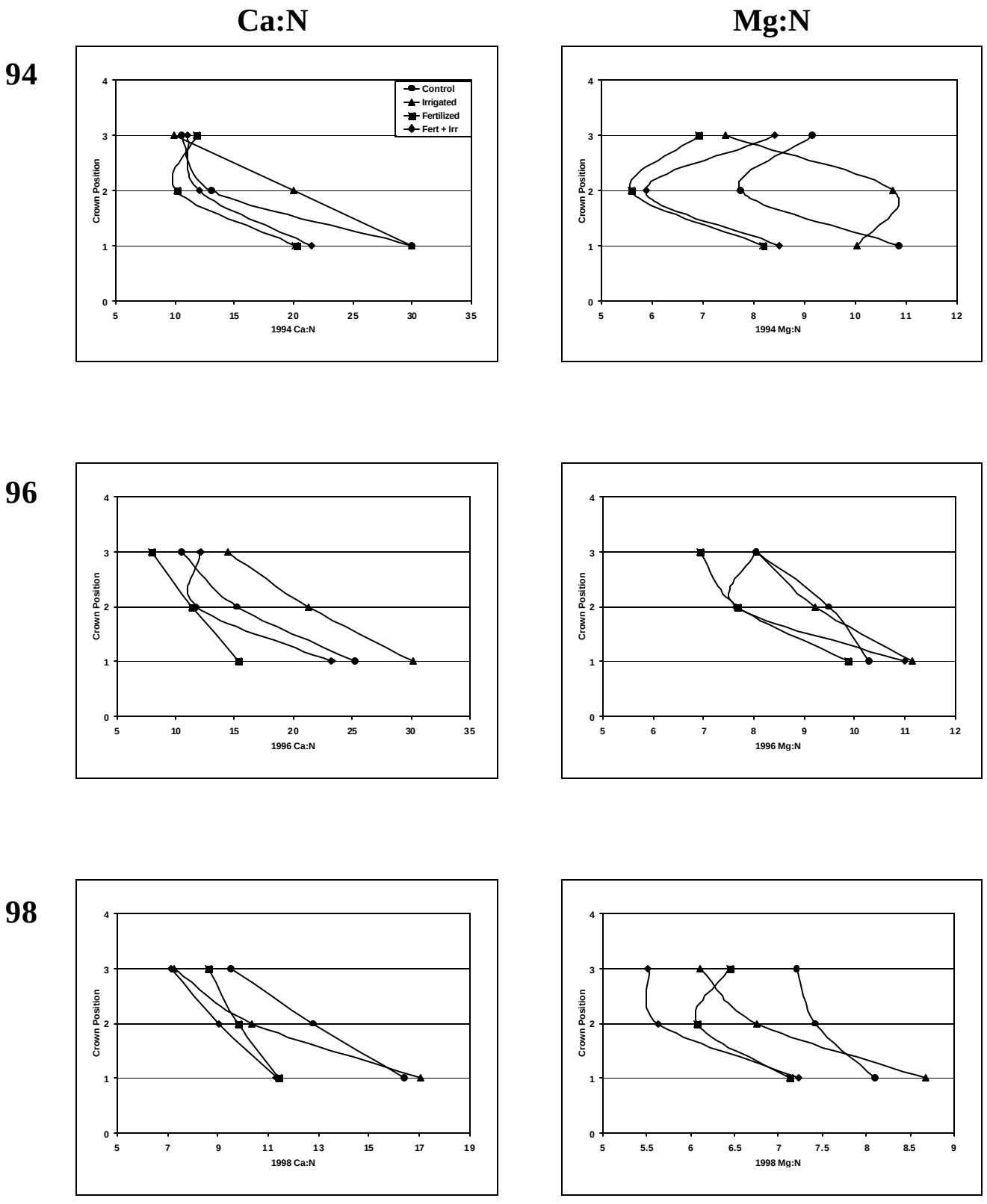


Figure 2.6: Foliar Ca:N and Mg:N distribution patterns of fertilized (squares), fertilized and irrigated (diamonds), irrigated (triangles), and control (circles) plots for 1994, 1996, and 1998.

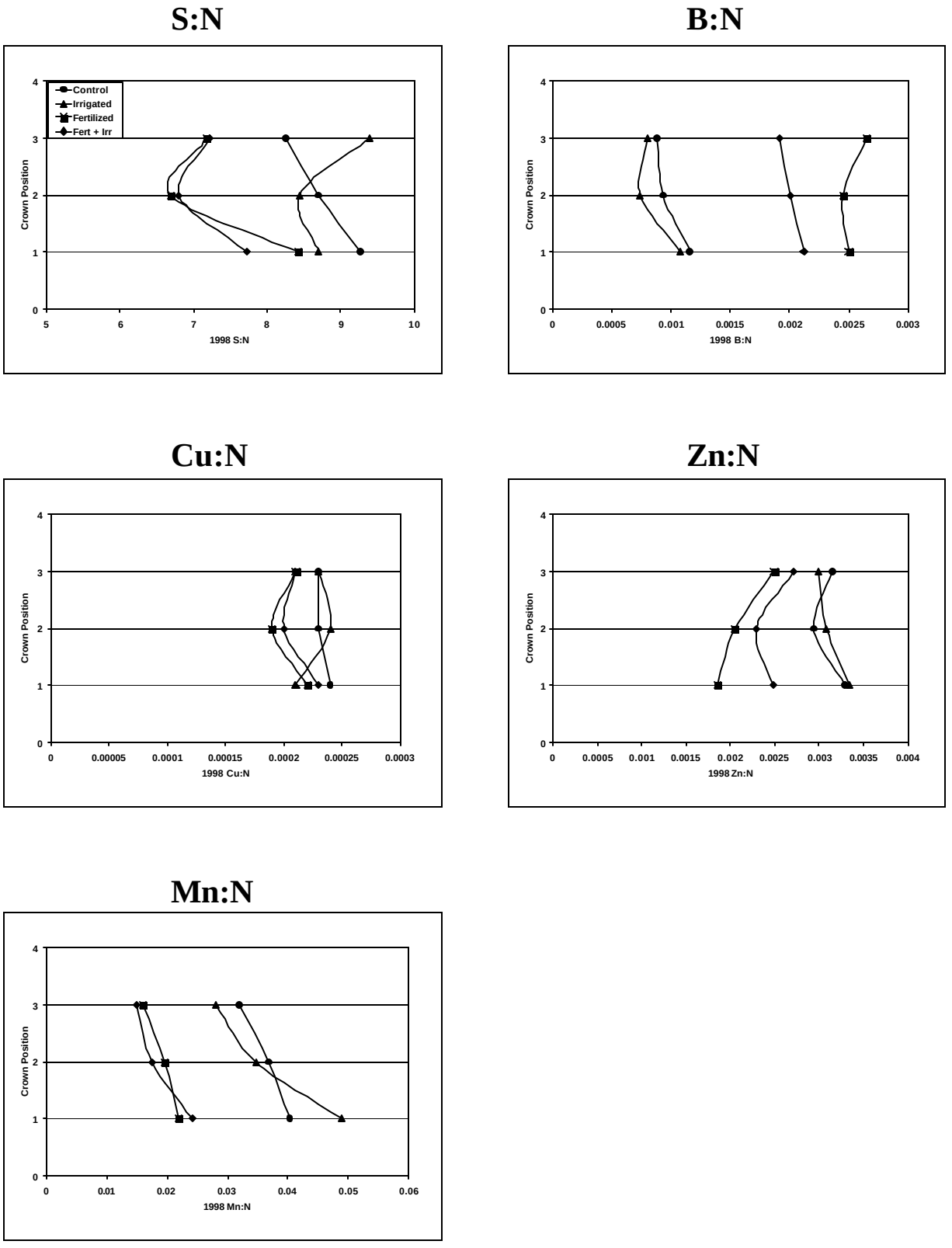


Figure 2.7: Foliar S:N, B:N, Cu:N, Zn:N, and Mn:N distribution patterns of fertilized (squares), fertilized and irrigated (diamonds), irrigated (triangles), and control (circles) plots for 1998.