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I am submitting herewith a dissertation written by Christopher G. Milne entitled "The Morphological and Physiological Effects of Paclobutrazol on Apple and Peach Trees." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Plant and Soil Science.

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THE MORPHOLOGICAL AND PHYSIOLOGICAL EFFECTS OF PACLOBUTRAZOL ON APPLE AND PEACH TREES

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Christopher G. Milne

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DEDICATION

To my parents, George and Mary Jo Milne, my son David, and the God who gave me each, I dedicate this dissertation.

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If you think you are beaten you are

If you think you dare not you don't

If you like to win but think you can't

It's almost a cinch you won't

If you think you'll loose your lost

For out in the world we find

Success begins with a fellows will

It's all in a state of mind

If you think you're outclassed you are

You've got to think high to rise

You've got to be sure of yourself before

You can ever win the prize

Life's battles don't always go

To the stronger or faster man

But sooner or later the man who wins

Is the fellow who thinks he can

It's all in a state of mind

Walter D. Wintle

ABSTRACT

Paclobutrazol ((2RS, 3RS)-1-(4-chlorophenyl)-4, 4-dimethyl-2-1, 2, (4-triazol-1-yl) pentane-3-ol) was applied in single or multiple foliar applications to 'Golden Delicious' apple trees in 1985. The growth regulator had little effect on shoot growth in that growing season. The highest rate of paclobutrazol (2.67 $kg \cdot ha^{-1}$) applied as a single or multiple application inhibited overall shoot growth by 89% the following growing season. No differences in shoot growth were observed between single and multiple applications in either 1985 or 1986. A significant negative linear relationship was found between paclobutrazol concentration and shoot growth for both single and multiple applications resulting in increased light penetration into the canopy as measured by Fisheye photography. No significant differences in growth reduction were found between horizontal and vertical shoots. Leaf area was decreased by up to 48% in a significant linear relationship with increasing application rates. Fruit length and the length:diameter ratio were reduced by as much as 15% and 8%, respectively, by paclobutrazol.

Rates of 0, 300, 600, 1200 or 2400 ppm of paclobutrazol were applied as a foliar spray to potted 'Golden Delicious' apple and 'Redhaven' peach trees in 1985. Paclobutrazol had no effect on stomatal conductance of either young or old leaves of apple or peach trees in the year of application. During the year following application, the 2400 ppm paclobutrazol treatment resulted in higher

stomatal conductance levels of both old and young apple leaves. No significant differences in the photosynthetic rates of peach leaves were found in the year of application. In the year following application the 2400 ppm application tended to result in higher photosynthetic rates than the control for both young and old apple leaves.

As paclobutrazol concentrations increased, leader growth of apple trees was significantly reduced by 31 to 47% compared to the untreated controls in 1985. Paclobutrazol decreased total shoot growth by 31 to 48% for apples in 1985 over all application rates. Leader growth, total branch length, and total growth of peach trees were reduced by 5 to 16%, 18 to 55%, and 13 to 35%, respectively, in 1985. In the year following application, paclobutrazol caused a significant linear reduction in total shoot growth ranging from 2 to 28% for 'Golden Delicious' apple trees. A significant reduction of 10 to 38% in total branch length was also found for apple. Reductions in total branch length, total shoot growth, and leader length of peach trees by 6, 10, and 11%, respectively, were found with the highest application rate for the year following treatment.

Paclobutrazol rates of 0, 300, 600, 1200 and 2400 ppm were applied as a foliar spray to potted 'Golden Delicious' apple trees in 1986. Net photosynthesis (Pn) and stomatal conductance readings began with the initial soil moisture at field capacity. Trees treated with the 1200 ppm application rate maintained a significantly higher Pn rate than the control trees under adequate soil moisture conditions. The 2400 ppm application rate maintained significantly higher net

photosynthesis levels for apple leaves at soil moisture values between 2.3% (295 MPa) and 5.8% by volume (2.5 MPa). At 5.8% soil moisture by volume, trees treated with 2400 ppm rate had a net photosynthesis rate 10% above the control. This rate maintained net photosynthesis at 95% above the control at 2.3% soil moisture by volume level.

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CHAPTER I

A. Introduction

Both apples (Malus domestica Borkh.) and peaches (Prunus persica L.) have been grown for consumption for many centuries. Fruit growing was relatively simple back in the early 1900's in comparison to today. Sixty years ago there were very few, if any, chemical sprays used. Today there may be as many as 12 to 15 spray applications consisting of many different chemicals during the course of the year. The increase in spray applications has resulted in the evolution of more tolerant and specific pests and diseases requiring more knowledge from the grower in order to control them. Tree size and canopy density can be extreme limitations to applying pesticides. Better penetration into the canopy may provide increased pest control. Increasing the penetration into the canopy by altering the canopy itself should increase light penetration. This increase in light penetration should increase carbohydrate movement and fruit quality. Paclobutrazol has been shown to reduce shoot growth and increase light penetration into the canopy.

Fruit growers have always been interested in obtaining a good quality crop. A quality crop depends on many variables including fruit color, size, shape, firmness, and sugar content. Many of these indices can be influenced with certain cultural practices. Pruning increases light penetration and spray penetration which allows for better color development and pest management. Within the last 15

years several new chemicals have been introduced to help alter some of the quality parameters (17). Alar was introduced as a growth retardant. It also enhanced earlier and more flowering the year following application. Ethrel has been used to enhance fruit color and hasten maturity, enabling the grower to better schedule harvesting (17).

As interest and demand for better ways of improving growth characteristics increased, growers became more and more concerned with controlling the size of the fruit tree while maintaining maximum yield. Dwarfing rootstocks, which were introduced into this country in the late 1950's, are used to improve the yield and fruiting capabilities, but each rootstock has unique problems that make the correct scion/rootstock choice difficult. The attention and interest in various training systems have allowed the grower to see the potential yield benefits of controlling tree size.

Some of the early research dealing with the chemical control of fruit tree growth began approximately 25 years ago in Wenatchee Washington at the Tree Fruit Research Laboratory (17). Research on apples has advanced to cover many classes of compounds including the triazols. Within this class there are currently five structurally similar compounds being reviewed as potential growth retardants (23). They are Bayleton (Mobay Chemical Corporation), RSW0411 (triapenthenol) (Mobay Chemical Corporation), LAB 150 978 (BASF Corporation), XE1019 (Chevron Chemical Company), and paclobutrazol (ICI) (Appendix A) (23).

Chemical control of the vegetative growth of fruit trees may

lead to a reduction in pruning and the use of dwarfing rootstocks to control the size of fruit trees. Being able affecting certain processes that enhance tree growth characteristics, fruit quality, or the ability to tolerate stress conditions could lead to enhanced yields and quality for fruit growers. The objectives of this dissertation were to determine 1) the effects of varying foliar application regimes of paclobutrazol on season-long vegetative growth control of bearing age 'Golden Delicious' apple trees, 2) the effects of foliar applications of paclobutrazol on photosynthesis, stomatal conductance, and growth of potted 'Golden Delicious' apple and 'Redhaven' peach trees, 3) the effects of foliar applications of paclobutrazol on photosynthesis and stomatal conductance of potted 'Golden Delicious' apple and 'Redhaven' peach trees during water stress, 4) the effects of varying foliar applications of paclobutrazol on fruit maturity and quality, of bearing age 'Smoothee' apple trees, and 5) the effects of foliar applications of paclobutrazol on the epicuticular wax production of apple and peach leaves.

CHAPTER II

LITERATURE REVIEW

A. Historical Review of Paclobutrazol

Paclobutrazol (PP333) (2RS, 3RS)-1-(4-chlorophenyl)-4, 4-dimethyl-2-1, 2, 4-triazol-1-yl) pentane-3-ol is a relatively new plant growth retardant that has been developed by the ICI America Corporation. The chemical formula of paclobutrazol is $C_{15}H_{20}ClN_3O$ (59), and the trade name is Cultar. Paclobutrazol is a broad spectrum growth retardant with a wide range of uses. It has been reported that paclobutrazol inhibits gibberellin biosynthesis by blocking kaurene oxidase between the ent-kaurene to ent-kaurenoic acid step (25, 44, 60). Research dealing with compounds in the triazole class of chemistry show that diclobutrazol, which is very similar to paclobutrazol, inhibited a specific cytochrome P-450 in fungi (7, 106, 105). It was also found to alter fatty acid content and sterol composition. Henery and Sisler (56) reported that miconazole inhibited sterol 14-dimethylation, which is mediated by a cytochrome, P-450, enzyme. At high concentrations miconazole disrupted the membrane phospholipid interaction with the P-450 enzyme, which in turn, resulted in a non-specific allosteric type inhibition.

Paclobutrazol is active on a wide range of crops including over 100 species of both mono- and dicotyledons (25). Paclobutrazol has

been found to shorten and strengthen the internodes of flowering stems of graminaceous crops. Higher rates reduced foliage growth without affecting reproductive organs. Dalziel et al. (25) noted that the retardant's activity was not accompanied by scorch or phytotoxicity when applied at high rates.

B. Absorption and Translocation

Paclobutrazol has been found to be readily absorbed by the roots, stems and foliage. Its primary means of transport is through the xylem. Lack of phloem transport causes foliar applied paclobutrazol to accumulate in the leaves of crops (25). Because of this, little is transported to the meristematic areas (where cell division and expansion occur) which are the primary sites of action for most growth retardants (25). It was found that paclobutrazol applied to a young internode is present in the stem and leaves above that internode with the greatest portion of material present in the adjacent leaf. It was also found that the lower on the stem the applications were made the less material was absorbed by the plant (59). Bausher et al. (10) studied the uptake and translocation by roots of ^{14}C-paclobutrazol in citrus. They found that with controlled soil applications paclobutrazol apparently had slow acropetal movement with most of the compound being found in the root. They suspected that the lack of movement was due to a lack of carriers and/or decreased availability due to site-binding. Mauk et al. (76) using 200 ppm applications applied 7 times to 'Starkrimson

Delicious' apple trees, found that the morphological effects were due to the foliar application and not due to root uptake of foliar runoff. Work by Early and Martin (30) suggested that paclobutrazol is readily taken up by the roots of peach seedlings and translocated passively by the xylem up into the leaves. Once paclobutrazol was in the leaves there was little or no export. Using radiolabeled paclobutrazol they found that within 9 days the amount remaining in the radiolabeled form was 72% in the roots, 41 to 68% in the stem and 7 to 12% in the leaves. They also found paclobutrazol to be degraded more rapidly in the leaves as compared to other parts of the plant. Within 9 days after treatment roughly 90% of the paclobutrazol in the leaves was broken down. Sterrett (90) found paclobutrazol to be relatively stable in apples with only 10% to 15% breakdown 27 days after injection. Shearing (83) also reported stability of paclobutrazol after extended periods of time. The differences in stability between apple and peach may be due to genus, application rate, and method of application. Also, the biochemical activity of paclobutrazol could differ between apple and peach trees.

C. Effect on Leaf and Cell Development

In 1984 Bayless (11) studied the effects of paclobutrazol at the cellular level. He found that when paclobutrazol was added to suspension cultures of 'Pauls Scarlet Rose' it prevented cell number increase after a time and the extent of inhibition was dependent upon

the concentration of the inhibitor. The inhibited cultures had greatly enlarged cells accompanied by an increase in cell volume and dry weight. Jaggard (60) found that paclobutrazol not only increased the thickness and chlorophyll per unit area of leaves of sugar beets at the 12 leaf stage, but it also reduced the leaf area. The increase in thickness was due to elongation of the mesophyll cells, especially those of the palisade mesophyll. These effects were achieved with a 4000 ppm spray of paclobutrazol at the four leaf stage of development. Despite finding an increase in cell volume of sugar beet leaves, Jaggard found no increase in the number of chloroplasts per cell. Lawrence (67) found that paclobutrazol treated sugar beet leaves reached carbon dioxide saturation at lower CO_2 concentrations than the untreated controls. However, he found rates of photosynthesis similar for leaves when expressed per unit of chlorophyll or leaf volume. DeJong and Doyle (27) found no consistent differences in leaf CO_2 assimilation rate, mesophyll conductance or leaf conductance. However, they found consistent differences in water vapor between paclobutrazol treated and untreated nectarines. In late September, the treated trees had a significantly higher CO_2 assimilation rate than non-treated trees. Wang (100) in 1985 reported an increase in chlorophyll of cucumber and Zucchini squash leaves with applications of 1, 5 and 10 mg/l applied as a soil drench. No mention was made of the effects on photosynthesis. Steffins and Wang (88), found that relative chlorophyll content of apple leaves on a leaf area basis increased in paclobutrazol treated trees. The 0.1 mM applications reduced the

weight and area of new shoots and increased the weight, diameter and length of fiberous roots. They also found increases in carbohydrate concentrations in the upper most leaves, stem and fiberous roots. Steffins et al. (89) in 1985 found increases, though not significant, in chlorophyll content of 'Spartan' leaves treated with 1.0 g a.i./tree in 3.7 liters of water. Wieland and Wample (104) found no increase in transpiration rates or chlorophyll content of apple trees treated with paclobutrazol as a soil drench at rates of 25, 50 or 150 mg ai/1.5 l. The fact that Steffins et al. used a foliar spray would account for their noticing increases in chlorophyll content. Paclobutrazol is not phloem mobile and thus tends to remain in the leaf tissue. Wieland's and Wamples' application of paclobutrazol by soil drench would result in movement of the compound throughout the tree via the xylem. Paclobutrazol concentration in the leaves resulting from a soil application would be less than that from foliar sprays.

D. Effect on Photosynthesis and Transpiration

In 1978 Barden reported that many researchers had found net photosynthetic rates (Pn) for apples to be between 10 and 35 mg CO_2 $dm^{-2}hr^{-1}$ (9). Kappel and Flore (63) reported rates of 18.8 mg CO_2 $dm^{-2}hr^{-1}$ for 1 year old peach leaves in full sun. Marini reported photosynthetic rates for peach leaves of 28.7 and 31.2 mg CO_2 $dm^{-2}hr^{-1}$ for a progeny labeled 8370 and 23.8 and 21.4 mg CO_2 dm^{-2} hr^{-1} for a progeny labeled H7141049 (72). It is important to understand the

normal Pn rates of apple and peach leaves in order to determine if an observed effect of paclobutrazol applications increases Pn rates above the normal range or if it maintains Pn rates within the normal range. Paclobutrazol has been shown to increase photosynthetic rates of sugar beets (per unit leaf area), at varying light intensities (60). Various researchers have found alterations in the photosynthetic rate of apples and peaches due to various pesticides including diazinon (5, 40), benomyl (39), and dikar (5, 40). Alterations in photosynthetic rates and growth responses have been reported following applications of (2-chloroethyl) phosphonic acid (28, 29). The effects of varying concentrations of paclobutrazol on photosynthetic rates of apples was studied by Wieland and Wample (104) in 1983. Treatments of 0, 25, 50 or 150 mg ai were either painted on the stem in a (1:1/v:v) dimethylsulfoxide and regulade mixture or applied as a 1.5 L/tree soil drench. Paclobutrazol was found to have no effect on photosynthetic rates, transpiration rates, or chlorophyll content. Total photosynthetic rates, calculated over a 10 day period, were less for the soil treated plants than for painted plants. This could have been due more to a mobility factor than to a physiological factor. Other researchers have reported foliar sprays to alter Pn. Paclobutrazol applied to the leaf basically does not move. Paclobutrazol in trunk paints has to move to the leaves and may not be translocated in high enough concentrations to alter Pn. Swietlik and Miller (93) reported that 0.2 ppm paclobutrazol applied in solution to 11 month old apple seedlings reduced Ca and K uptake. They found this reduction to

precede a reduction in transpiration. Steffens and Wang (88) reported increases in carbohydrates, as well as, other physiological changes. Phlorizin is the major phenolic compound found in apples and has been shown to increase shoot growth as well as to enhance root initiation in apples when used in combination with auxins (61, 62). Since paclobutrazol inhibits gibberellic acid, which is the primary growth promoting hormone, researchers wanted to see paclobutrazol's effect on phlorizin since it also promotes growth. Buta et al. (13) found no differences in phlorizin content of new fiberous roots of paclobutrazol treated seedlings as compared to a control.

E. Effect on Drought Tolerance

Water stress alters the normal growth characteristics and physiological processes of plants. Tan and Buttery (95) reported that as leaf water potentials declined due to increasing water stress, stomatal conductance, Pn, and transpiration of peach seedlings also declined. They also found that transpiration was reduced due to stomatal closure. Harrison and Daniel (54) reported that stress inducing treatments which caused water potentials ranging from -0.9 to -2.5 mPa were directly correlated with decreasing photosynthetic rates. Similar results were also reported by Hand et al. (51).

Simon and Marcelle (84) looked at the effects of various fungicides on water stress. Stomatal conductance is directly

correlated to resistance of water movement during water stress. Net photosynthesis was used to measure water stress since Pn is dependent on stomatal conductance. They found that resistance to developing water stress could be influenced by pre-treatment with fungicides. Swietlik and Miller (92) studied the effects of paclobutrazol on growth and response to water stress of apple seedlings. They found that the addition of .05 or .20 ppm paclobutrazol to nutrient solutions reduced growth and increased root to leaf ratios. Plants pretreated with 20 ppm of paclobutrazol did not show reductions in transpiration due to water stress induced with Polyethylene glycol (PEG). The transpiration rate of untreated trees decreased in response to PEG at -0.5 and -0.75 mPa. Seedlings pretreated with 0.20 ppm paclobutrazol had a greater adaptability to water stress than those pretreated with 0 or .05 ppm paclobutrazol. Atkinson and Crisp (3) reported that 'Colt' cherry trees treated with a soil application of paclobutrazol had reduced transpiration and water use levels one day after treatment. He found stomatal resistance to be lower in treated trees than non-treated trees following ten days of drought.

Swietlik and coworkers in 1983 studied the inhibition of photosynthesis in water stressed apple seedlings (94). Apple seedlings were grown in solution culture using PEG to induce water stress. Stress was gradually applied by modifying the nutrient solutions. Using -8.0 bars (-.08 MPa) as the low point they found that solutions of -6.0 bars (-.06 MPa) or less decreased both net and gross photosynthesis. The ratio of gross/net photosynthesis was

not affected. Swietlik felt that both stomatal and non-stomatal factors were responsible and stated that water stress limits photosynthesis by inducing stomatal closure, thus decreasing the photosynthetic capacity. Improved responses of apple seedlings to water stress reported by Swietlik and Miller (92) with applications of .20 ppm were due to the treated seedlings having a higher water potential than the untreated trees. Hewitt (57) noticed that paclobutrazol treated soybeans had a reduced level of water use.

F. Growth Retarding Activity

In 1984 Quinlan and Richardson (80) studied the effect of paclobutrazol on apple shoot growth. They performed orchard and greenhouse experiments using 200 ppm and 500 ppm, respectively. They found that the effect of paclobutrazol on shoot elongation was influenced by the treatment site. Application to the shoot stem or tip caused a greater reduction in shoot growth than applications to unrolled leaves or older woody stems. Marini and Wefelmeyer (78) reported that terminal shoot growth suppression of peaches increased with increasing concentrations (750, 1500, 3000, 6000 ppm) of foliar applied paclobutrazol. Significant reductions in plant height of five cultivars of Freesia hybrida were obtained with paclobutrazol applied as a 250 mg/l corm soak (43). Flowering was found to be delayed by the corm soak treatment also. Stang and Weis (87) in 1984 reported that rates as low as .58 kg ai/ha applied as a foliar spray significantly suppressed plant growth of 'Bad gerbelle' strawberries.

Greene (47, 48) and Tukey (98) have also shown growth retardation effects on 'Delicious' apple trees.

Researchers have examined the effects of soil applications of paclobutrazol on growth and compared the differences between soil and foliar applications. Andersen and Aldrich (2) reported good growth reduction on 'Cheyene' pecans both in the year of application and the year after application by applying paclobutrazol at 0.05 to 2.60 g a.i./cm^2 trunk cross-sectional area as a soil drench. Quinlan (80) reported that soil applications of paclobutrazol to 'Cox' apple trees soon after harvest had no significant effect on that season's shoot growth. He also found that a foliar application at the same time as the soil application was more effective than just a soil application by itself. Wieland and Wample (104) applied treatments to apples of 25, 50 or 150 mg ai/1.5 L as a soil drench or painted on the stem in a mixture of Dimethysulfoxide and Regulade. They found the stem application reduced growth by 35% and soil drench reduced both root surface area and leaf area. Quinlan (80) reported that long term effects of paclobutrazol on shoot growth had been noted in the years following the foliar applications. However, there were no noticeable effects from similar levels of soil applications which indicated that the long term effect on shoot growth was most likely due to the retention of the compound in the perennial framework of the tree rather than by continual uptake of the chemical from the soil. This suggests that the compound remains in the upper portion of the tree and is not transported else where is responsible for the growth reductions. Ebrahem and Campbell (32) found greater reductions in

shoot growth of 'Golden Delicious' and 'Red Delicious' apple trees with foliar applications than with ground injections. Unrath and El-Khoreiby (99) also received better results with foliar applications than with to soil applications. Williams (107) noted that a single treatment of paclobutrazol (1000-2000 ppm) to the soil controlled the terminal shoot growth of both 'Delicious' and 'Golden Delicious' apple trees for several years. Williams and Edgerton (106) had similar findings as Williams who in earlier work showed a reduction of shoot growth of apple and pear trees with both foliar and soil applications. They found that applications of 1000-2000 ppm as a foliar spray caused a 10-20% reduction in growth the year of application and an 80-90% reduction in growth the year following application. They noted that a soil application seemed to be more effective than a foliar application. Williams et al. (106) compared several methods of applying paclobutrazol to apple trees; foliar, soil surface sprays, trunk drenches, lower trunk sprays and soil injection in narrow bands. They found that the foliar and soil surface sprays provided an effective control of growth but that much of the chemical was dispersed throughout the orchard. Paclobutrazol became partially bound in the upper organic layer from which it was slowly leached into the root zone and absorbed by the roots. The last three methods provided the most desirable amount of growth reduction with a minimum of chemical reaching the orchard floor. The injection method into the soil provided a unique control of both root and shoot.

Paclobutrazol has also been shown to have promising results on

peaches. Erez (37) found that paclobutrazol applications inhibited shoot growth when applied in a foliar spray or to the soil. He found a strong inhibition in shoot growth was found the following year. He also found that summer applications reduced the following spring flush and enhanced fruit development. Ha found autumn applications to increase bloom, and retard the next year's growth. Liyembani and Taylor (69) found that both single and multiple applications reduced growth on 'Early Loring' peach trees. Their highest application rate of 3400 ppm reduced shoot growth by 75%. Root and shoot dry weights were reduced up to 33%. Since shoot growth was reduced more than dry weight, the majority of the growth reduction probably came from a decrease in cell expansion rather than a decrease in cell number.

G. Effects on Fruiting and Fruit Quality

Paclobutrazol has been shown to affect the quality of fruit in many ways. Curry and Williams (24) reported that foliar applications of .5 g to 1.5 g ai. of paclobutrazol per inch trunk diameter caused reduced shoot extension, hastened fruit color development, and slightly lowered fruit acidity. Light penetration was increased on 25 year old 'Top Red' on seedling rootstocks which led to larger and better colored fruit. The size increase may have been due to an increase in carbohydrate movement. This is questionable though, because paclobutrazol inhibits gibberellin biosynthesis. The increase in fruit color is understandable considering the increased

light penetration. 'D'Anjou' Pears treated with similar applications and stored for 6 months at 0°C had significantly greater firmness values than the untreated controls. They also noted that the acidity of treated fruit was consistently lower than that of untreated fruit. Similar results were found by Greene in 1984 (48). In previous work, Curry and Williams (24) also reported that paclobutrazol applied as a ground application at a rate of 20 g/9.5 m^2/tree to 'Delicious' apples resulted in smaller, flatter fruit with shorter pedicels. A large increase in fruit set was also noted by Curry and Williams on the trees receiving the high rate of paclobutrazol. Other parameters such as firmness, soluble solids and color were comparable to fruit from untreated trees. They found significant increases in fruit sorbitol and starch with increasing paclobutrazol applications. Steffins et al. (89) reported that soil drench treatments of paclobutrazol at 1 or 2 g ai/tree had no effect on the levels of soluble carbohydrate fractions in apple flesh at any of the sampling dates during harvest. No significant changes were noticed in the mineral composition of leaves, fruit flesh or fruit peel. Similar results were found by Elfving and Chu (33) who studied both the effects of soil and foliar applications of paclobutrazol on fruit quality parameters. They found significant reductions in fruit diameter and length at the final sampling but no effect on firmness or soluble solids. Ebreham and Campbell (32) found that neither foliar nor soil applied paclobutrazol affected fruit weight or soluble solids after 3 months of storage. However, they did find

firmness of 'Golden Delicious' fruit to be significantly increased after 3 months of storage.

Increases in fruit length and average fruit weight of 'Clapps' Favorite' pear were reported by Embree et al. (36) following soil applications of 6.0 g ai. per tree of paclobutrazol. No effects on firmness, soluble solids or yields were noticed. Williams (108) found no effect on fruit size while fruit color and yield were increased. Storage quality of 'Spartan' apples was found to be increased with soil drench applications of 1.0 and 2.0 g ai./tree (101). Results with similar findings were reported by Elfving et al. (34), using 1000 and 2000 $mg \cdot l^{-1}$ paclobutrazol applied as a foliar spray. Erez (36) noted that paclobutrazol applications to peach trees in late spring led to marked increases in fruit weight as well as in sugar content. He found that autumn applications improved fruit size and color the following year. Knowles et al. (64) using 1, 0.5, and 0.25 g/inch trunk diameter increased fruit bud size of 'Loring' and 'Rubired' peaches. They found no effect on fruit color, soluble solids, percent split-pits, yield or fruit size of 'Redskin' peach in the year of treatment.

H. Effects on Cold Hardiness

Paclobutrazol has been shown in field trials to increase cold hardiness. The reason for the increased tolerance to cold is not yet known but could be due to morphological changes. It is also thought that observed changes in fatty acid saturation and total fatty acid

level may play some role in this phenomena. Holubowicz (58) found that applications of 1000 ppm paclobutrazol resulted in an acceleration of cold acclimatization and an increase in the hardiness in late autumn. He found that one year old peach shoots taken in the middle of November and sprayed with 1000 ppm paclobutrazol survived exposure of -15 to -17°C while untreated shoots only tolerated temperatures down to -12°C. By mid December the shoots from all the treatments were able to tolerate -22°C. By the middle of February the frost resistance decreased to around -17°C which remained unchanged until the middle of March. Proebsting and Mills (77) reported in 1985 that soil applications of 15 g/tree of paclobutrazol applied in late August was not effective in increasing cold hardiness. They found increased cold damage on the treated trees in comparison to the non-treated trees.

I. Factors Influencing Photosynthesis

Many morphological and environmental factors are known to affect the photosynthetic rate of fruit trees. Cultivar, rootstock, leaf structure and age are some of the morphological factors affecting photosynthesis. Environmental factors affecting photosynthesis include light, temperature, carbon dioxide, diurnal trends and water.

Some differences in photosynthetic rate between cultivars have been reported. Understanding how various cultivars respond to different environmental conditions is necessary in this research. This enables a researcher to hopefully separate the effect a chemical

has on a tree from the tree's natural responses to the environment. Looney (70) researched the differences between spur and non-spur strains of 'Delicious' and 'Golden Delicious' apple trees. He found that the spur type trees had Pn rates about 12% higher than the non-spur trees. Other researchers have also found differing net photosynthesis (Pn) rates among various cultivars (14, 15). Ferree and Barden, however, found no significant differences in Pn rates between spur and non-spur 'Delicious' apple trees although the spur type tended to be higher (38). Explanations for the differences have been suggested to be due to physiological differences among cultivars and strains (6, 14).

Rootstocks are known to influence apple tree growth and productivity. The exact influence on physiological processes such as photosynthesis is not yet fully understood. It was found that the Pn rates of leaves from seedling rootstocks were always lower than the Pn rates of leaves from the other rootstocks (97). Svihra (91) and coworkers found that various varieties grown on the M rootstocks produced less dry matter per unit chlorophyll than did the same cultivars grown on the MM series. Ferree and Barden (38) reported that leaves of 2 strains of 'Delicious' had slightly lower Pn rates when grown on either M 7A or seedling rootstocks than when grown on MM106 rootstocks. Curry and Williams reported enhanced Pn effects of paclobutrazol on apple trees grown on dwarfing rootstocks (22). Some researchers have implied a positive correlation between specific leaf weight (SLW) and Pn. Barden (9) reported a high correlation (r=.92) between Pn and SLW of apple leaves. In a similar study Wooge and

Barden found SLW to vary during the season (110). They found SLW, leaf thickness, and palisade depth to be lower from May to October for newly expanded interior canopy leaves than for middle or peripheral leaves.

Leaf structure and age are both factors that influence leaf Pn. Understanding how various physiological processes differ among different leaf structures and leaf ages is required for thorough understanding of how paclobutrazol affects the physiological processes in leaves of differing structures and ages. Ghosh (45) found that spur leaves had shorter palisade parenchyma cells, fewer layers of palisade parenchyma, lower Pn rates, less chlorophyll, and lower SLW than spur leaves. These differences were attributed to light restrictions on interior spur leaves. Cowart (19) also reported differences in internal leaf structure associated with their position on the shoot or spur. Slack (85) reported that maximum Pn could not occur early in the life of an apple leaf due to immature stomates. Barden (9) reported that the maximum Pn rate of apple leaves rose rapidly during expansion and peaked after the leaf was fully expanded. Sams and Flore (81) reported that the maximum Pn rates for sour cherry leaves occurred when the leaves were greater than 80% expanded. After this stage in growth the Pn rates were found to decline.

The presence of fruit on a tree could influence the Pn rate. Avery reported an increase in Pn rates of apple leaves in the presence of fruit (6). Hansen reported that fruit occurrence not only increased leaf Pn rates but increased the translocation of

photosynthates from the leaves (53). Chambers et al. (15) found that photosynthesis of peach leaves increased as fruit growth increased and that there was a decrease in photosynthesis of peach leaves after harvest.

It is obvious that photosynthesis can not occur without light. For each species of plant there is an optimum photosynthetically active radiation (PAR) range in which that plant will reach maximum photosynthetic potential. It is within this range that research measurements should be made. When light levels are below the accepted range or below saturation level, light becomes a limiting factor for photosynthesis. Proctor et al. (78) reported the photosynthetic light saturation point for apples to be between 300 to 400 Wm^{-2} of total solar radiation. Kappel and Flore (63) reported that the shade leaves of peach reached saturation between 400 and 600 uE s^{-1} m^{-2} and leaves receiving full sun saturated between 700 and 900 uE s^{-1} m^{-2}. With this in mind it is understood that shade, cloud cover or other changes in light quality adversely affect the Pn rate of leaves. Lakso and Sealey (65) have shown that apple leaves are photosynthetically efficient under changing light conditions. They found that leaves exposed to alternating high and low light at 1.0 second intervals maintained 85% to 90% of the Pn rates of leaves in continuous high light. Leaves exposed to major changes in light concentration fully responded to the changes within 5 to 15 seconds. A light saturation point of 12 Wm^{-2} was reported by Proctor for apple leaves in full sun (85). Kappel and Flore (63) reported a light compensation point of 46 uE s^{-1} m^{-2} for peach leaves in full sun

while Chambers et al. reported 1 $mW \cdot cm^{-2}$ of photosynthetically active radiation (PAR) (16).

Temperature is known to influence all biochemical reactions. If temperatures are too high or too low most reactions will stop. Chemical reactions are temperature dependent and have optimum operating ranges. Tan and Buttery (96) reported maximum Pn for peaches at temperatures between 20^0 to 26^0 C with PAR at 444 uE s^{-1} m^{-2}. Apple leaves have been reported to have maximum Pn between 20 and 30^o C under saturating light conditions (77) while leaves of sour cherry have maximum Pn at temperature ranges of 15 to 30^o C (80). Net photosynthesis rates were found to decline in cherry above 30 to 35^o C. Net photosynthesis of apple leaves will also decline with temperatures below optimum ranges of 20 to 30^o C (9). Leaf optimum temperatures will not only vary from leaf to leaf within a canopy but will vary among species. The severity of different stress conditions will also affect how the photosynthetic process functions within its optimum range for a leaf.

Watson et al. (102) reported that apple leaf photosynthesis showed a positive response to increasing CO_2 concentrations with a compensation point at 20 ul/liter. Photosynthesis usually changes in a diurnal fashion. It would be logical to assume that diurnal changes in Pn would follow changes in light and be at their peak during mid-day. This, however, is not the case. Heinicke and Childers (55), Lakso (66), and Barden (9) have reported the maximum Pn rate of apple leaves to occur in the morning with rates being less in mid-day and afternoon under equivalent PAR conditions. During

mid-day, temperatures may increase to the point where they exceed the optimum ranges for the leaves causing stomates to begin to close.

J. Instrumentation

Equipment has been developed over the years to aid researchers in the measurement of various physiological processes in plants. Some measurements of photosynthesis are based upon CO_2 utilization by the plant. Early photosynthetic measurements used potassium hydroxide (KOH) as an absorption medium through which the gas samples were passed (55, 83). The amount of CO_2 in the gas sample could be calculated following the addition of an indicator and a titration process. Since these early procedures, more accurate CO_2 analysis processes have been developed. Two of the most widely used instruments for measuring Pn are gas chromatography (GC) and infra-red gas analysis (IRGA) systems.

Some gas chromatographs, such as the Shimadzu model GC-8A, measure CO_2 based on thermal conductivity. As a carrier gas (N_2) passes over a heated wire, the wire cools and it's resistance changes. Since a carrier gas is relatively pure the rate of cooling of the wire should be constant. When no change in resistance occurs the instrument is set at zero. When a new gas sample containing CO_2 is injected into the system and passes over the wire, it will cool the wire at a different rate. This will be recorded as a change in resistance as compared to the carrier gas. This change is interpreted by the instrument and output as CO_2 concentration.

Infra-red gas analyzers such as the Anarad Inc. AR-600 series coupled with an Anarad model APPA-1 panel mount CO_2/H_2O photosynthesis analyzer measures CO_2 on the principle that different gas molecules absorb infra-red light at different wavelengths. Heteratomic gas molecules, i.e. molecules consisting of more than one type of atom, normally absorb radiation at specific infra-red wavelengths (18, 82). Molecules that consist of two identical atoms such as O_2 and N_2 do not absorb in the infra-red spectrum. This property of gases not only allows for accurate measurement of CO_2 but it also allows for the measurement of H_2O, CO, NO, SO_2, and other structurally similar gases.

For the most part, GC's and the IRGA's are used in conjunction with measurement systems having a closed static chamber, measuring gas samples that are removed periodically from the chamber. These apparatus' can be incorporated into a flow through system which constantly measure changes in concentration of the gas in the chamber. Both portable and stationary systems have been designed to measure plant gas exchange. The Analytical Development Corporation (ADC) model LCA-2 portable CO_2 analysis system is a portable unit that includes a leaf chamber, IRGA, microprocessor and pumping system. This instrument enables the user to measure CO_2 gas exchange from individual leaves with relative ease. Along with CO_2 data, the user is able to obtain leaf temperature, relative humidity, and PAR data. A data logger system is built into the system which allows stored data to be transferred to a computer.

Stomatal conductance and transpiration are also gas exchange

processes. Diffusion porometry measures the rate of water vapor loss from a portion of a leaf or entire leaf that is enclosed in a porometer chamber. Either the rate of increase in humidity due to transpiration or the rate at which dry air is added to the system to balance the increase in humidity is measured (18, 82). The Li-Cor model LI-1600 steady state porometer is an instrument designed to measure stomatal conductance on individual leaves. Photosynthetically active radiation (PAR) was measured with a LI-190S-1 quantum sensor and displayed in $uE \cdot m^{-2} \cdot s^{-1}$. Stomatal conductance ($cm \cdot s^{-1}$) and transpiration ($ug \cdot cm^{-2} s^{-1}$) were calculated by an internal microprocessor. Leaf temperature was also measured with this instrument. A difficulty with this instrument is that the transpiration rates obtained may not reflect true rates due to the lowering of the boundary layer around the leaf by the instrument. It also measures relative humidity.

Leaf water potential can be measured using a pressure chamber such as the PMS model 650. Compressed air in the chamber applies pressure to the leaf and forces the water in the leaf to return to conditions prior to removal from the plant. This pressure is equal and opposite to the tension that is present in the xylem of the intact plant (18, 86). Soil moisture can be measured in many ways. One method is to use a Neutron probe such as the Troxler 3220 series depth moisture gauge. This instrument uses americium-241:beryllium neutron sources (4, 8). When the probe is lowered into the soil it will release 'fast' neutrons. When these neutrons collide with particles similar in size (water molecules) they lose some of their

kinetic energy and become 'slow' neutrons. The probe has a slow neutron detector which will monitor the rate of return of slow neutrons over a given time period. The amount of slow neutrons detected is in direct relationship to water present in the soil. Soil moisture values determined with the neutron probe are expressed on a volume to volume basis. A gravimetric soil moisture analysis performed at the same time neutron probe readings are taken allows determination of a calibration curve comparing the soil moisture on a v/v basis to the same soil on a w/w basis. Further information can be obtained from the data by running a soil moisture release curve on the soil used. This would allow the conversion of soil moisture on a w/w basis to bars or MPa.

CHAPTER III

THE EFFECTS OF VARYING FOLIAR APPLICATION REGIMES OF PACLOBUTRAZOL ON SEASON-LONG VEGETATIVE GROWTH CONTROL OF BEARING AGE 'GOLDEN DELICIOUS' APPLE TREES

A. Introduction

Research results have indicated that paclobutrazol can be an effective growth retardant of fruit trees (48, 108). Benefits from these growth-controlling aspects include a decreased need for size controlling rootstocks, as well as increased spray and light penetration (24) and improved fruit quality (33, 89). Paclobutrazol may provide varying degrees of size control depending on the application regime. Defining an optimum rate, time and frequency of application will allow more accurate recommendations to be made for season long vegetative growth control. The objective of this experiment was to determine the effects of single and multiple foliar applications of paclobutrazol on season-long vegetative growth of 'Smoothee' apple trees.

B. Materials and Methods

Applications of paclobutrazol were made in 1985 to 6 year old 'Smoothee' apple trees on MM106 rootstocks. The application regimes

consisted of a control plus 3 levels of single applications and 4 levels of multiple applications (Table 3.1). The single applications and the initial application of the multiple sets were made 25 days from full bloom with subsequent applications at 2 week intervals. The applications were made with a CO^2 backpack sprayer until runoff. In an attempt to reduce or prevent any absorption of the compound by the roots the soil under each tree was covered with plastic during each application. Growth measurements were taken 4 times during the growing seasons of 1985 and 1986 on 8 horizontal and 8 vertical shoots per tree. Two horizontal and 2 vertical shoots were selected from each quadrant of the tree. One hundred leaves were randomly sampled from each tree on Sept. 15-16, 1986 following the procedure described by Lockwood (71). Leaf area measurements were taken using a Li-cor model Li-3000 portable area meter.

Fisheye photography has been used as a method to describe apple tree canopies and light penetration (65). Fisheye photographs were taken on September 8, 1986 as a means of measuring light penetration. The photographs were taken approximately 3 ft above the ground, just above the first set of scaffolds. Pictures were taken on both the east and west side of the tree. The sky percentage was measured by using an aerial point count method (20). Area measurements used to analyze overhead transparencies from pictures were taken by using a Decagon Area Measurement system.

Table 3.1. Paclobutrazol application regime for 1985 treatments.

Tmt #	Rates ($kg \cdot ha^{-1}$)			Total	
	Init.[Z]	Seq.[Y]	No. Seq.[X]	($kg \cdot ha^{-1}$)	(g ai/tree)
1	0.00	----	---	0.00	0.00
2	0.66[W]	----	---	0.66	3.11
3	0.33	0.16	4	1.00	4.66
4	0.33	0.16	5	1.16	5.44
5	1.33	----	---	1.33	6.23
6	0.33	0.33	4	1.67	7.77
7	0.33	0.33	5	2.67	12.46
8	2.67	----	---	2.67	12.46

ZInit=Initial treatment level.
YSeq=Sequentila treatment levels.
XNo.Seq=Number of sequential treatments.
WInitial rate of 0.66=3.11 g ai/tree=972 ppm.

C. Results and Discussion

No differences in horizontal, vertical or mean shoot growth due to treatment were observed in 1985 (Table 3.2). This supports other research showing little response to paclobutrazol the year of treatment (80, 106). Analysis of the 1986 growth data revealed significant differences in shoot growth due to treatment. Significant linear relationships were found to exist between paclobutrazol concentrations and shoot growth for both single and multiple applications. To measure the differences between single and multiple applications, the points on the regression line for the multiple applications were compared with their estimates on the regression line for the single applications. Within the range of data studied, using estimable functions, no evidence was found that multiple applications had an effect any different than that of the single applications when total dose was held constant. This is in contrast with Quinlan and Richardson (79) who reported better vegetative growth control with sequential foliar sprays applied early in the growing season than with a single foliar application applied at the same time as the first sequential spray. Since no differences were found between single and multiple applications they were grouped together for regression analysis. The highest application (2.67 $kg \cdot ha^{-1}$) of paclobutrazol decreased mean shoot growth by 89% during the 1986 season (Figure 3.1). This supports findings by Williams and Edgerton (106) who reported that foliar applications of 1000-2000 ppm reduced vegetative growth by 80-90% the year following application.

Table 3.2. The effect of paclobutrazol on shoot growth of bearing age 'Smoothee' apple trees in 1985, Knoxville, TN.

Rate ($kg \cdot ha^{-1}$)	Shoot Growth		Mean Growth (cm)
	Horizontal (cm)	Vertical (cm)	
0.00	1.49	2.00	1.74
0.66	0.41	0.53	1.92
1.00*	1.17	0.54	0.65
1.16*	1.18	2.67	0.86
1.33	0.37	1.39	1.88
1.67*	2.56	1.21	1.84
2.67*	0.78	0.51	1.57
2.67	1.84	1.84	0.94
F test	NS	NS	NS

NS Not significant at the 5% level by F test.
*Sum of the multiple applications.

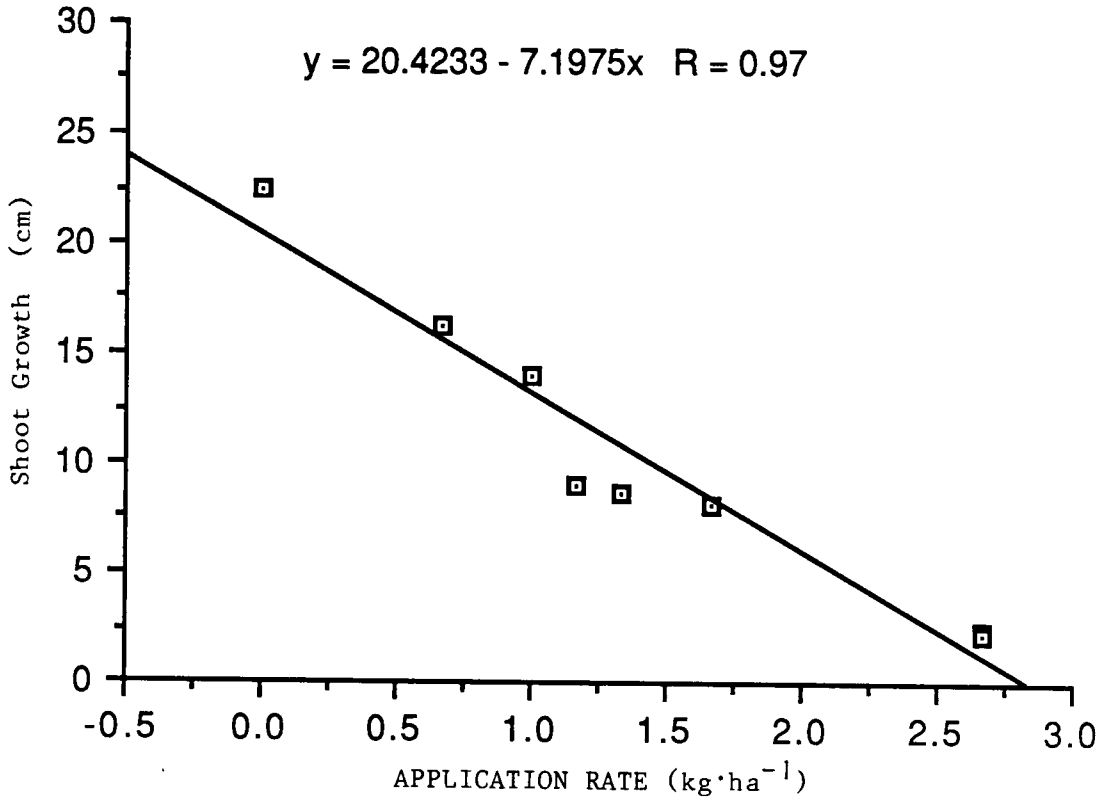


Figure 3.1. The effect of paclobutrazol on mean shoot growth of 'Smoothee' apple trees, 1986.

Equivalent growth reductions were obtained with much lower application rates in this study.

It has been suggested that paclobutrazol may have differing effects on horizontal versus vertical shoot growth. However, a significant negative linear relationship was found for both horizontal and vertical shoot growth in 1986 (Figures 3.2, 3.3). The slope for the vertical shoot growth was -8.0 in comparison to -6.3 for the horizontal growth. This suggests that the vertical shoot growth is reduced slightly more than the horizontal shoot growth but the difference was not statistically significant. No differences were found between single and multiple applications when analyzing the horizontal and vertical growth data. Paclobutrazol applications were found to significantly decrease mean leaf size in a linear fashion with all applications being 16% to 48% smaller than the control (Figure 3.4). No differences in leaf area reduction were found between single and multiple applications.

Based on fisheye photographs, a 20% increase in light penetration was found with the highest concentration (2.67 $kg \cdot ha^{-1}$) of paclobutrazol (Table 3.3). There was a quadratic relationship between paclobutrazol applications and light penetration which might suggest a saturation level for paclobutrazol. Beyond the 1.33 $kg \cdot ha^{-1}$ application rate paclobutrazol may not have as strong an effect as below that concentration. Both the point count method and the overhead transparency method proved sufficient for measuring area from fisheye photographs. No statistical differences were found between the 2 methods.

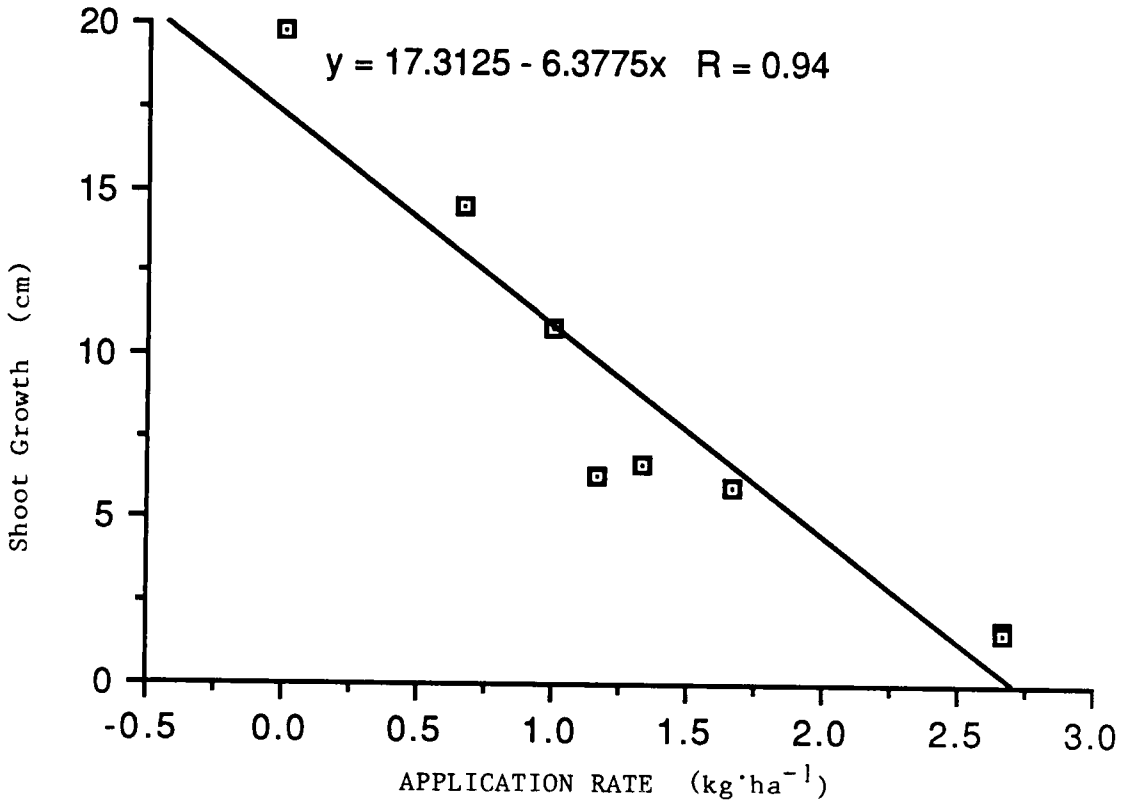


Figure 3.2. The effect of paclobutrazol on horizontal shoot growth of 'Smoothee' apple trees, 1986.

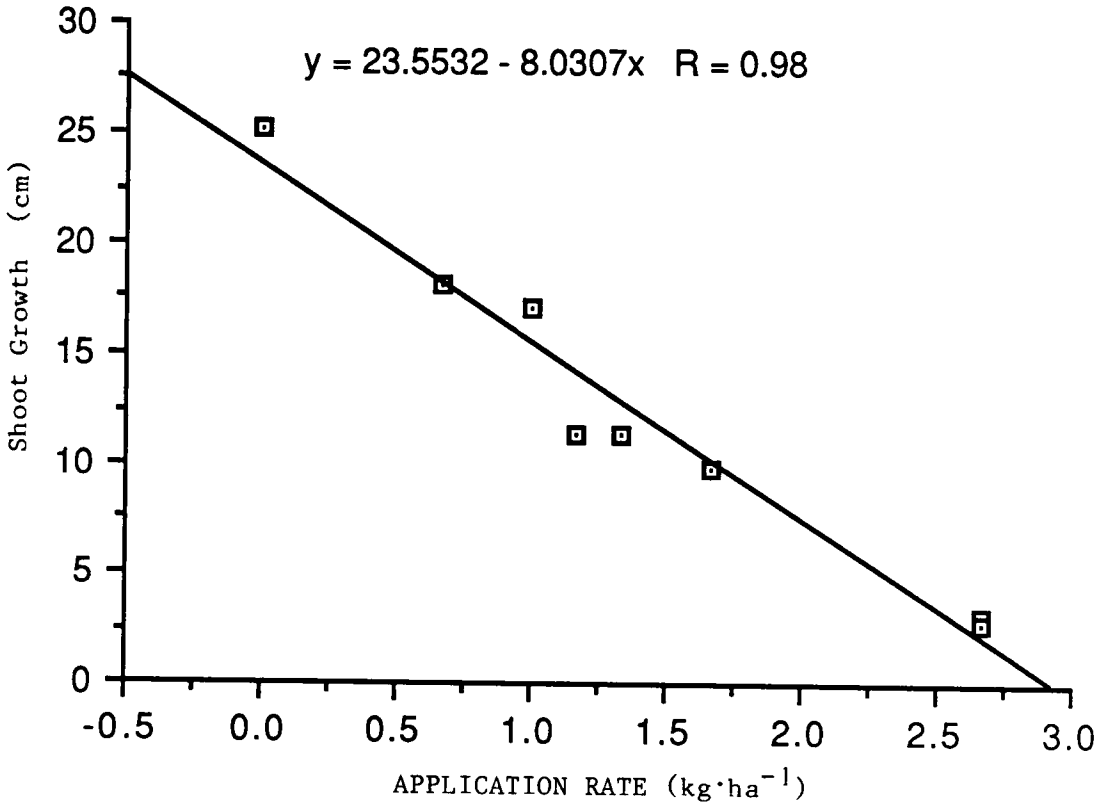


Figure 3.3. The effect of paclobutrazol on vertical shoot growth of 'Smoothee' apple trees, 1986.

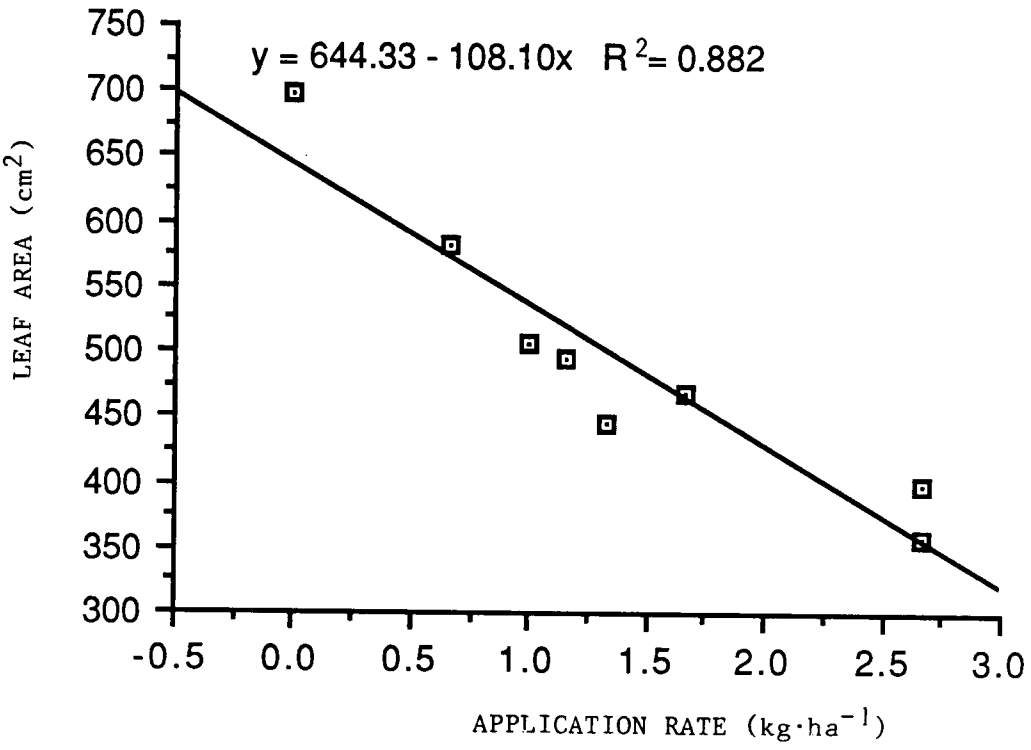


Figure 3.4. The effects of paclobutrazol on leaf area (cm^2) of bearing age 'Smoothee' apple trees the year following application.

Table 3.3. Whole tree area analysis using fisheye photography in 1986.

Total Rate ($kg \cdot ha^{-1}$)	Percent sky	
	Point Count	Area Meter
0.00	25.0	27.3
0.66	23.1	24.3
1.00*	33.5	32.2
1.16*	25.0	25.3
1.33	28.0	26.1
1.67*	32.1	30.3
2.67*	31.4	34.0
2.67	31.6	30.0
L	NS	NS
Q	**	**
C	NS	NS

*Designates multiple applications.

D. Conclusion

Paclobutrazol applications had little effect on shoot growth of apple trees in 1985. The highest application (2.67 $kg \cdot ha^{-1}$) inhibited shoot growth by 89% in 1986. A negative linear relationship was found between shoot growth and paclobutrazol concentrations within the range of 0 to 2.67 $kg \cdot ha^{-1}$. No differences were found between single and multiple applications nor between horizontal and vertical shoot growth reduction either year. The highest application of paclobutrazol was found to increase light penetration by 20% in 1986 as measured by fisheye photography.

CHAPTER IV

THE INFLUENCE OF PACLOBUTRAZOL ON PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, AND GROWTH OF POTTED APPLE AND PEACH TREES

A. Introduction

Many researchers have reported the morphological effects of paclobutrazol on both apple (Malus domestica Borkh.) and peach (Prunis persica L.) trees but little is known about the physiological effects of this compound. It has been reported that paclobutrazol treated sugarbeet leaves had higher photosynthetic rates under several light intensities than untreated controls (67). However, it has also been reported that paclobutrazol painted on the trunk of the tree had no effect on the photosynthetic rates of apple leaves (104). Because of paclobutrazols mobility it is understandable that a foliar application to the leaves would have a greater effect than a trunk paint.

Paclobutrazol has been reported to be an effective growth retardant of apple and peach trees. Potential benefits from these growth controlling aspects include a decreased need for size controlling rootstocks, increased light and spray penetration, and improved fruit quality. More research is needed to determine optimum concentrations to cause the desired degree of growth reduction. The objectives of this experiment were to study the effects of varying

rates of paclobutrazol on photosynthesis, stomatal conductance, vegetative growth and dry matter partitioning of 'Golden Delicious' apple and 'Redhaven' peach trees.

B. Materials and Methods

'Golden Delicious' apple on MM106 rootstocks and 'Redhaven' peach on 'Lovell' rootstocks were planted in 18.9 liter black plastic pots in mid May 1985. Each tree was pruned to 21 cm above the graft union at the time of planting and then to 1 leader approximately 2 weeks prior to treatment. Treatments of paclobutrazol at 0, 300, 600, 1200 or 2400 ppm (0, 3.4, 6.8, 13.6, or 27.2 g ai/11.3 L water) were applied until runoff with a backpack sprayer when terminal growth was approximately 10 cm in length. The surface of each pot was covered with plastic during application to prevent chemical runoff onto the soil. Due to paclobutrazols reported soil residual only the foliar effect was of interest in this study. A randomized complete block (RCB) design with 8 replications consisting of two one tree pots of 5 treatments was used. All trees received approximately 5.6 L of water each day, over a 2.5 to 3 hour period, through an automatic drip irrigation system. Fertilization was maintained at approximately 2 week intervals with each pot receiving 236 ml of a 300 ppm solution of 10-10-10 fertilizer.

Whole tree photosynthesis was evaluated the year of application. The experimental design was a randomized complete block with 5 replications each containing 5 two tree treatments. Treatments from

one replication were measured each day following the diurnal blocking pattern shown in Appendix B. To ensure adequate CO_2 utilization within the chamber, both trees for each treatment within a replication were placed inside the chamber at the same time. Apple measurements began on August 21, 1985 and continued daily until August 25, 1985. Whole tree photosynthesis measurements on the peach trees were taken on August 26 through August 30 in the same manner as with the apple trees.

The whole tree measurements were taken using a closed static system with a 3 X 3 X 3.5 ft assimilation chamber. The chamber was set up with a temperature controlled cooling system and a fan to thoroughly mix the air. The trees were moved into the greenhouse the day before the readings began to allow for equilibration. To allow for adjustment to changing light intensities the trees were placed under the lights outside the chamber for 1 hour prior to being moved inside the chamber. When the trees were placed in the chamber an initial internal and external 60 cc gas sample was taken. At 10 minute intervals thereafter 60 cc gas samples were removed from the chamber with a syringe. Careful attention was paid to proper mixing of the gas with the syringe, removal of the sample and replacement of the lost air. Initial gas analysis was done using an Anarad Inc. AR-600 series infra-red gas analyzer coupled with an Anarad model APPA-1 panel mount CO_2/H_2O photosynthesis analyzer. This system became inoperable and a Shimadzu model GC-8A CO_2 specific gas chromatograph was used. Due to the time required for each sample to be run, the

diurnal blocking schedule had to be revised when work began on this instrument (Appendix C).

The study was repeated in 1986 to reevaluate the first year effects of paclobutrazol. In the repeated experiment an RCB design with 5 replications each containing 5 treatments in single tree plots was used. No whole tree photosynthesis was measured in the repeated experiment or on the second year effect studies.

Net photosynthesis (Pn) and stomatal conductance were measured 4 times across the 1986 season at approximate 2 week intervals beginning May 30 both the 1 year and 2 year old trees. The photosynthesis measurements were taken using an ADC model LCA-2 portable CO_2 analysis system. Stomatal conductance readings were taken using a Li-Cor model LI-1600 steady state porometer. The same pattern was used beginning June 12 in 1987 on the 2 year old trees only. Readings were taken on a leaf tagged at approximately the eighth node and on the newest fully expanded leaf on each of the four reading dates. Growth measurements consisting of height, diameter, total growth, as well as other parameters were taken at the beginning and end of the 1985, 1986, 1987 growing seasons. At the end of the 1986 season half of the trees from the 1985 planting (both apple and peach) were dried and partitioned into stems, branches, and leaves, for additional dry weight analyses. In 1987, all trees planted in 1986 were also dried and partitioned. The study utilized only one and two year old trees. Analysis of the physiological data was done with General Linear Models (GLM), regression analysis, and linear contrasts (LC), performed with the Statistical Analysis System (SAS)

on mean values averaged for the four reading dates. Analysis of the growth and partitioning data was done in the same manner.

C. Results and Discussion

The highest application rate of paclobutrazol (2400 ppm) significantly increased the photosynthetic rate of old apple leaves at the 1% level by F test 64 days after treatment (DAT) in the year of application (Figure 4.1). By 70 DAT old leaves receiving the 2400 ppm application rate were still higher than the other treatments though the difference was not significant. No differences were found prior to 64 DAT although the old leaves receiving the 2400 ppm rate had the highest Pn at 49 DAT. The differences in the plants reaction to paclobutrazol before and after 50 DAT could be due to a delay effect. It could be taking that long for paclobutrazol to have any visible effects. Paclobutrazol has been reported to be stable with only 15% breakdown at 27 DAT (90). Others have reported finding a 90% breakdown of paclobutrazol in leaves at 9 DAT (30). If this is true then an effect that does not show up until 50 DAT may be due to a byproduct from the breakdown process. No significant differences in Pn were found for young leaves the year of application (Figure 4.1). Those leaves receiving the 2400 ppm application rate tended to have greater Pn rates than the control 49 and 70 DAT. The increases in Pn were similar to results with paclobutrazol treatments on pecans reported by Wood (109). However, Wieland and Wample (104) reported that rates of 0, 25, 50, or 150 mg ai per tree applied either as a

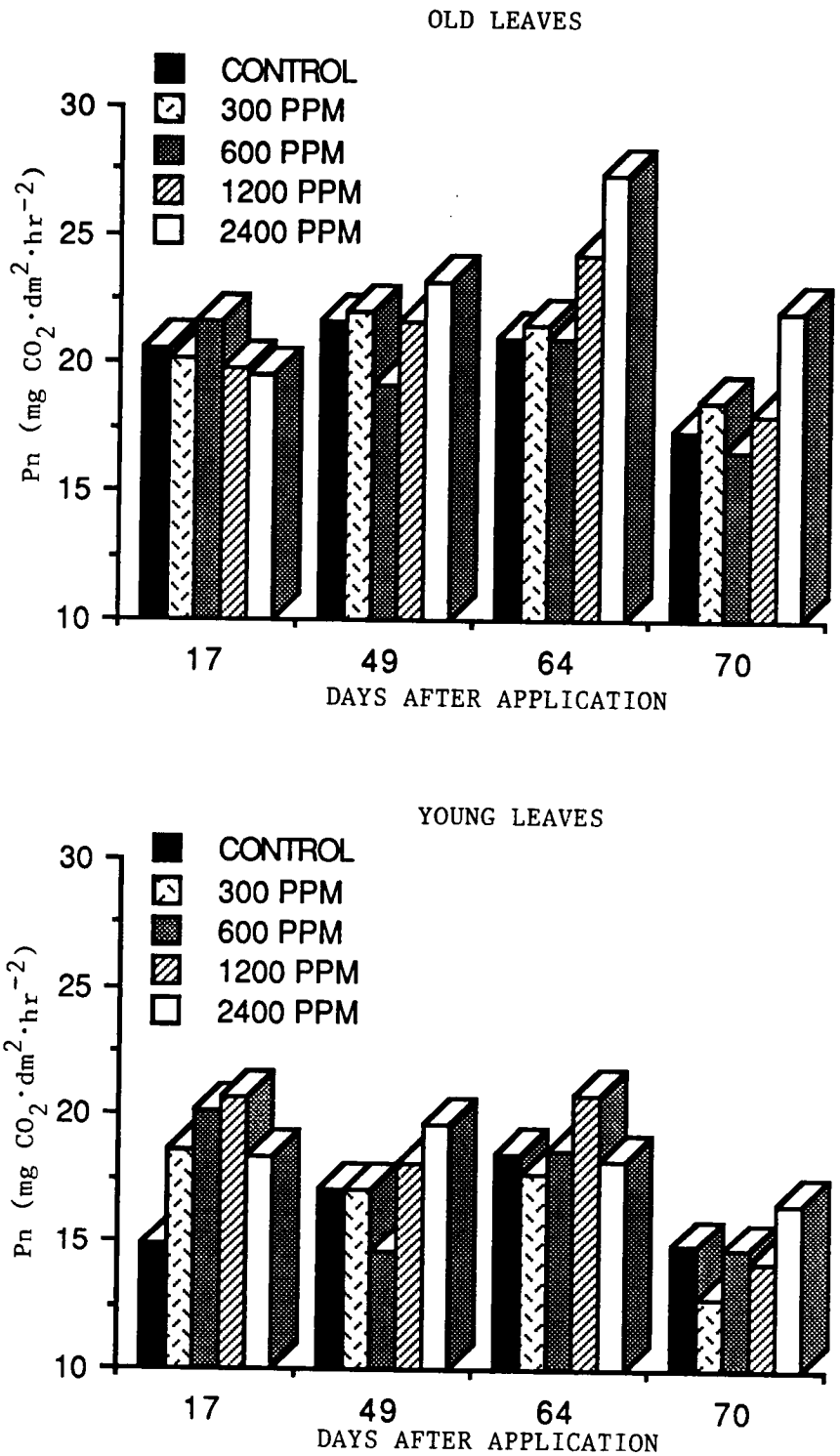


Figure 4.1. The effects of paclobutrazol on photosynthesis of old and young leaves of potted 'Golden Delicious' apple trees the year of application.

trunk paint or soil drench had no effect on the photosynthetic rate of 'Spartan' apple trees. No significant differences or trends in stomatal conductance of old or young leaves were found in the year of application (Figure 4.2). This may have been due in part to the time of year the readings were taken. Differences in photosynthetic levels appeared around 49 DAT and continued thereafter. Here again this indicates paclobutrazols effect is not noticeable until roughly 50 DAT. Due to constraints on instrument usage no stomatal readings were able to be taken on the same day as the photosynthesis readings or beyond 46 DAT.

In the second growing season there was a highly significant positive linear relationship at the 1% level for old leaves, with Pn and paclobutrazol concentration at the first reading date (Figure 4.3). On Julian date 238 there was a significant linear relationship between Pn and paclobutrazol concentration at the 5% level. No significant differences were found after this date. No significant differences were found for young leaf Pn in the second growing season although Pn of plants receiving the 2400 ppm application were higher than the control on both Julian dates 197 and 267 (Figure 4.3). All applications had stomatal conductance rates significantly higher than the control for old leaves on Julian date 162 (Figure 4.4). No significant differences were found after Julian date 162 although on Julian date 197 and 267 the 2400 ppm rate tended to be the highest. Paclobutrazol has had greater effects on Pn and stomatal conductance the year following application. This could relate back to the fact that little or no effect was observed until after 50 DAT. By the

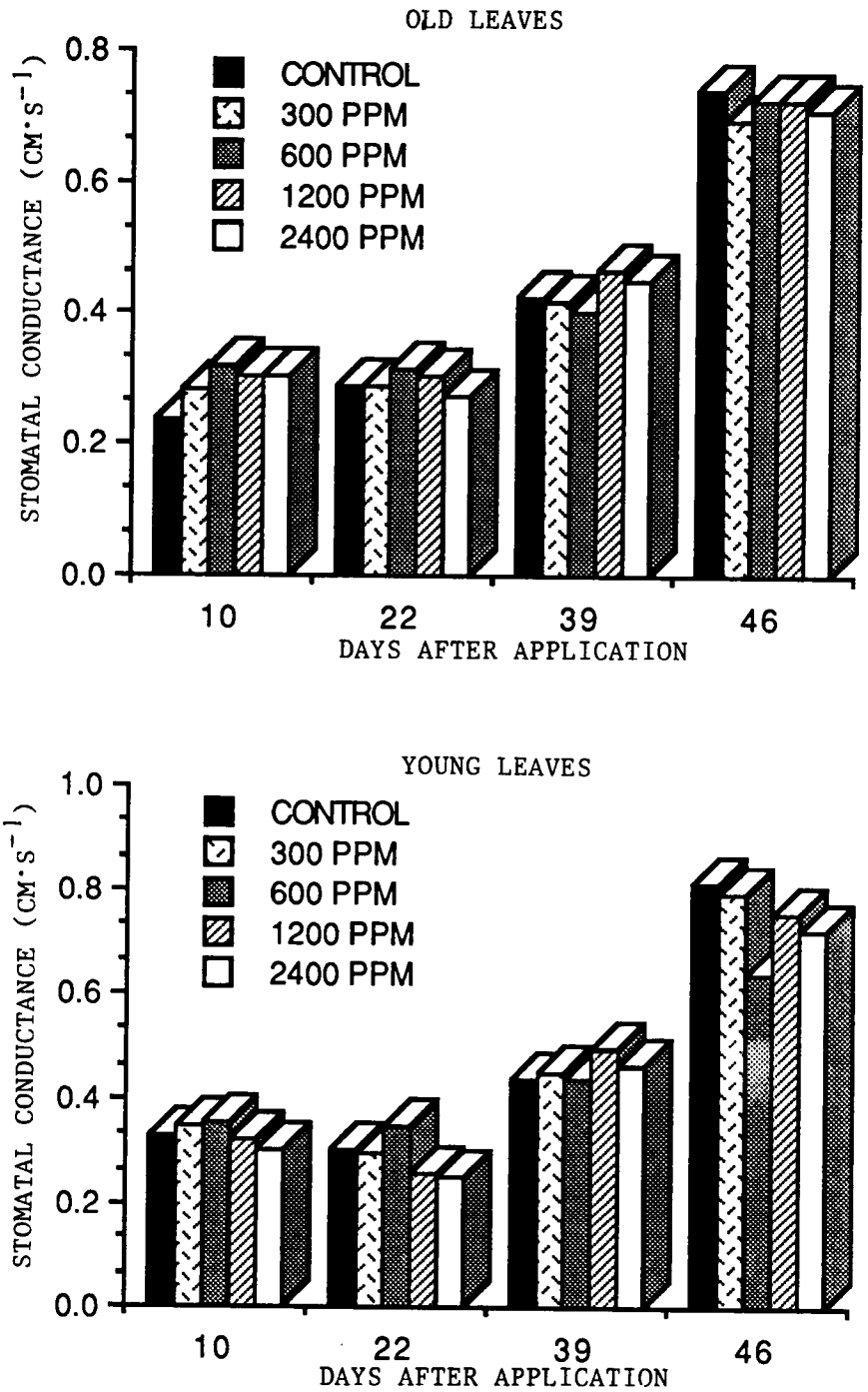


Figure 4.2. The effects of paclobutrazol on stomatal conductance of old and young leaves of potted 'Golden Delicious' apple trees the year of application.

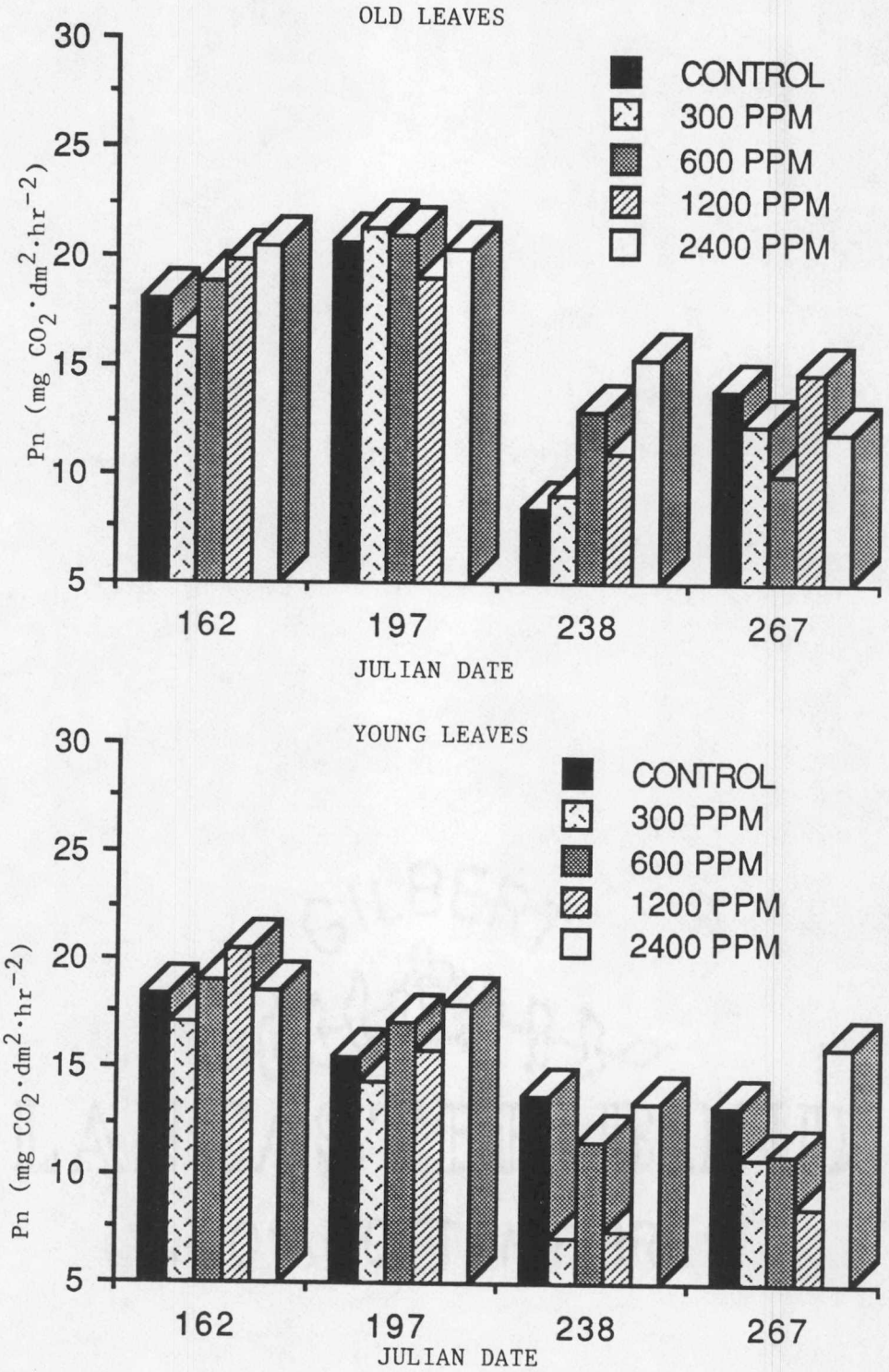


Figure 4.3. The effects of paclobutrazol on photosynthesis of old and young leaves of potted 'Golden Delicious' apple trees the year after application.

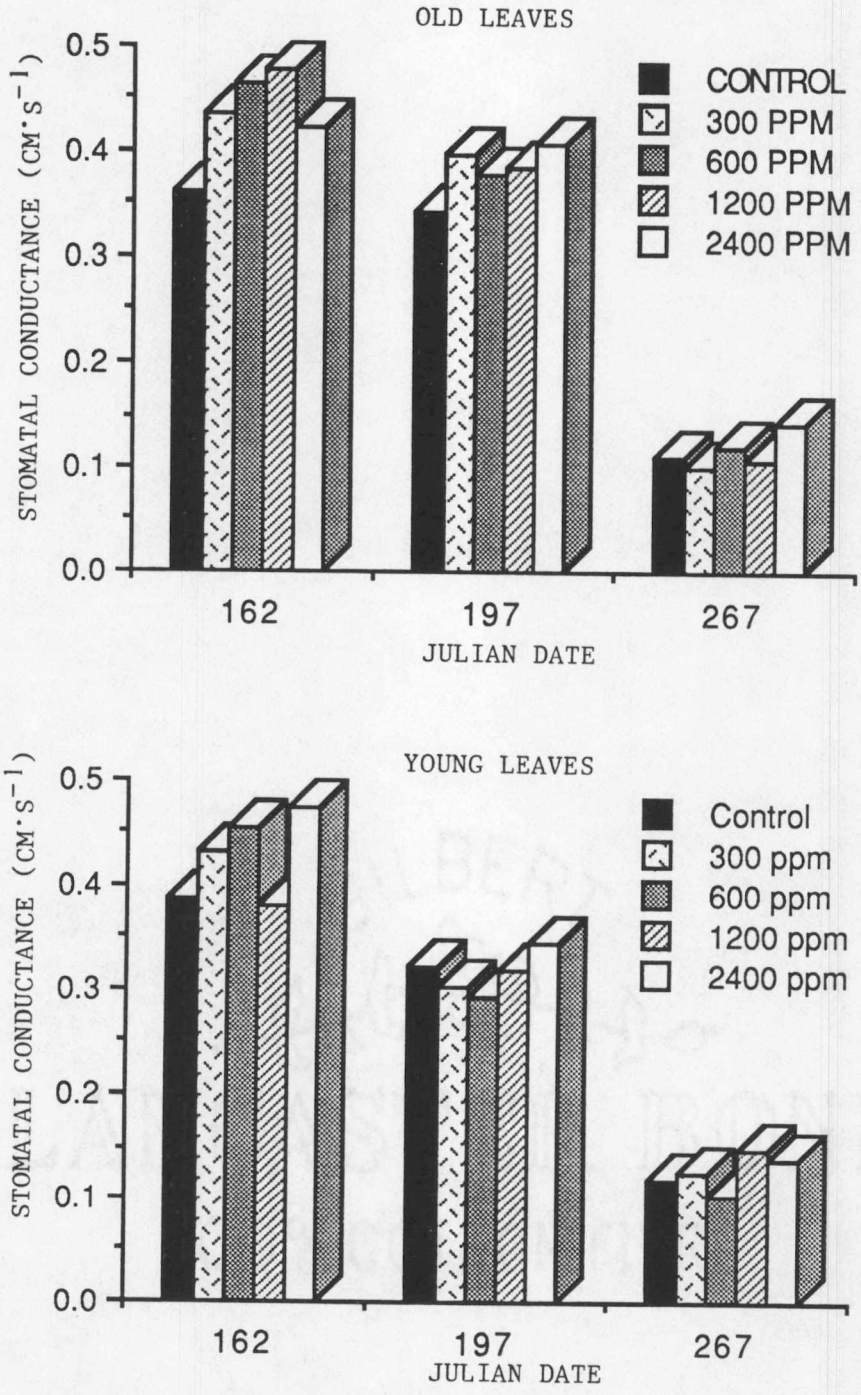


Figure 4.4. The effects of paclobutrazol on stomatal conductance of old and young leaves of potted 'Golden Delicious' apple trees the year after application.

second growing season more than enough time had elapsed to allow for an effect to become noticeable. As mentioned earlier, paclobutrazol is reported to breakdown by between 90 to 15% within 9 to 27 DAT, respectively. If this is the case then the second years effect could be due to a metabolic breakdown product and not paclobutrazol itself. No differences were found for young leaf stomatal conductance the year following application (Figure 4.4).

Paclobutrazol had no significant effect on old leaf Pn of 'Redhaven" peach trees the year of application (Figure 4.5). The Pn levels for all application rates tended to be higher than the control at both 48 an 62 DAT for old leaves. Except for the 300 ppm application rate early in the season, all young peach leaves of all treatments had Pn rates higher than the control on all reading dates the year of application (Figure 4.5). Paclobutrazol significantly increased young peach leaf Pn in a linear fashion with all application rates being significantly higher than the control 48 DAT. All Pn rates for both old and young leaves of 'Redhaven' peach trees were within previously reported ranges (62, 73). Paclobutrazol did not have an effect on the stomatal conductance levels of either old or young peach leaves 9 DAT (Figure 4.6). By 23 DAT all paclobutrazol treated leaves had stomatal conductance rates of old leaves significantly higher than the control. No differences were found 38 or 44 DAT although old leaves at all applications tended to be higher than the control for old leaves. No significant differences in stomatal conductance were found for treated young leaves the year of application. No Pn or stomatal conductance

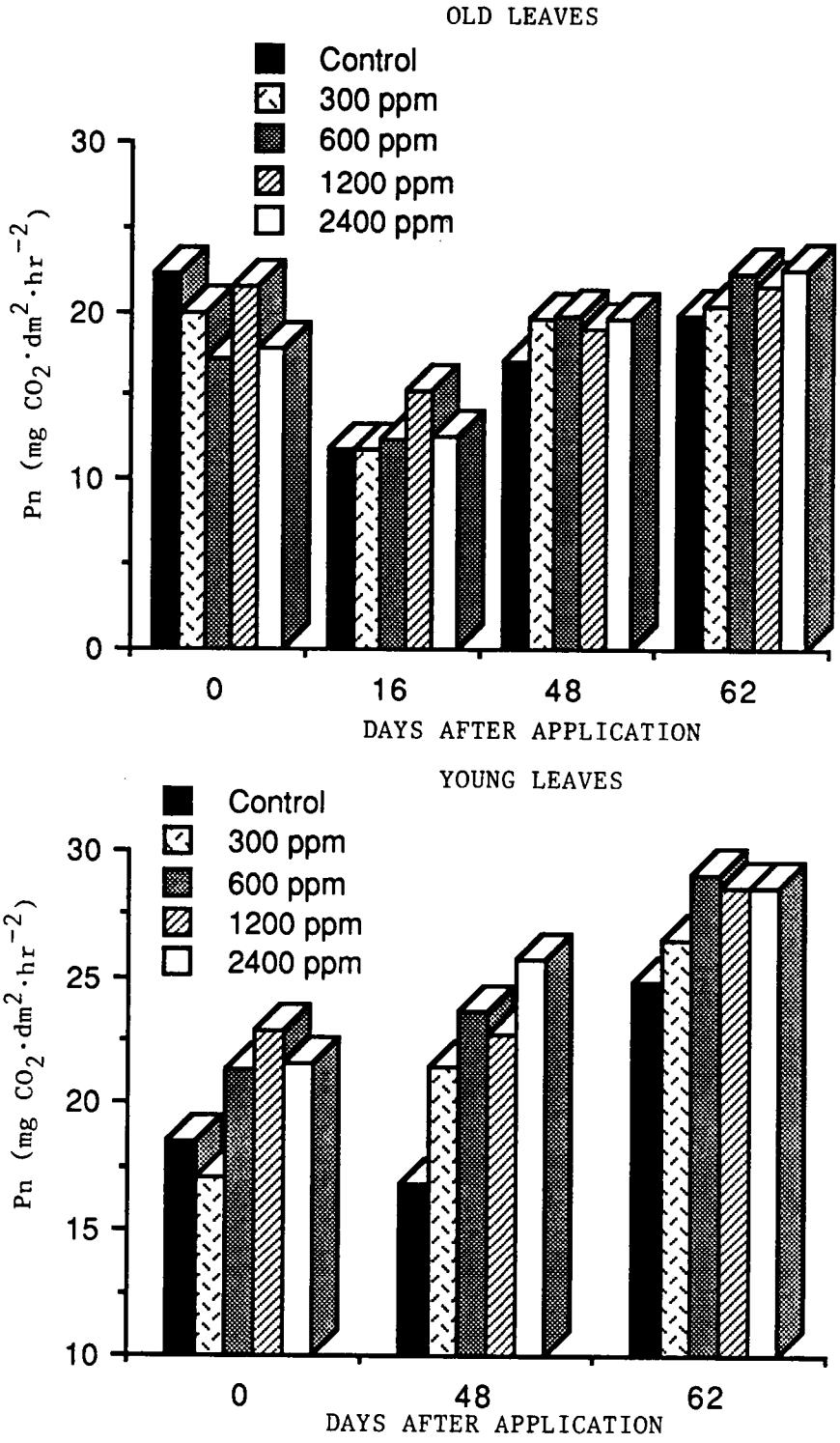


Figure 4.5. The effects of paclobutrazol on photosynthesis of old and young leaves of potted 'Redhaven' peach trees the year of application.

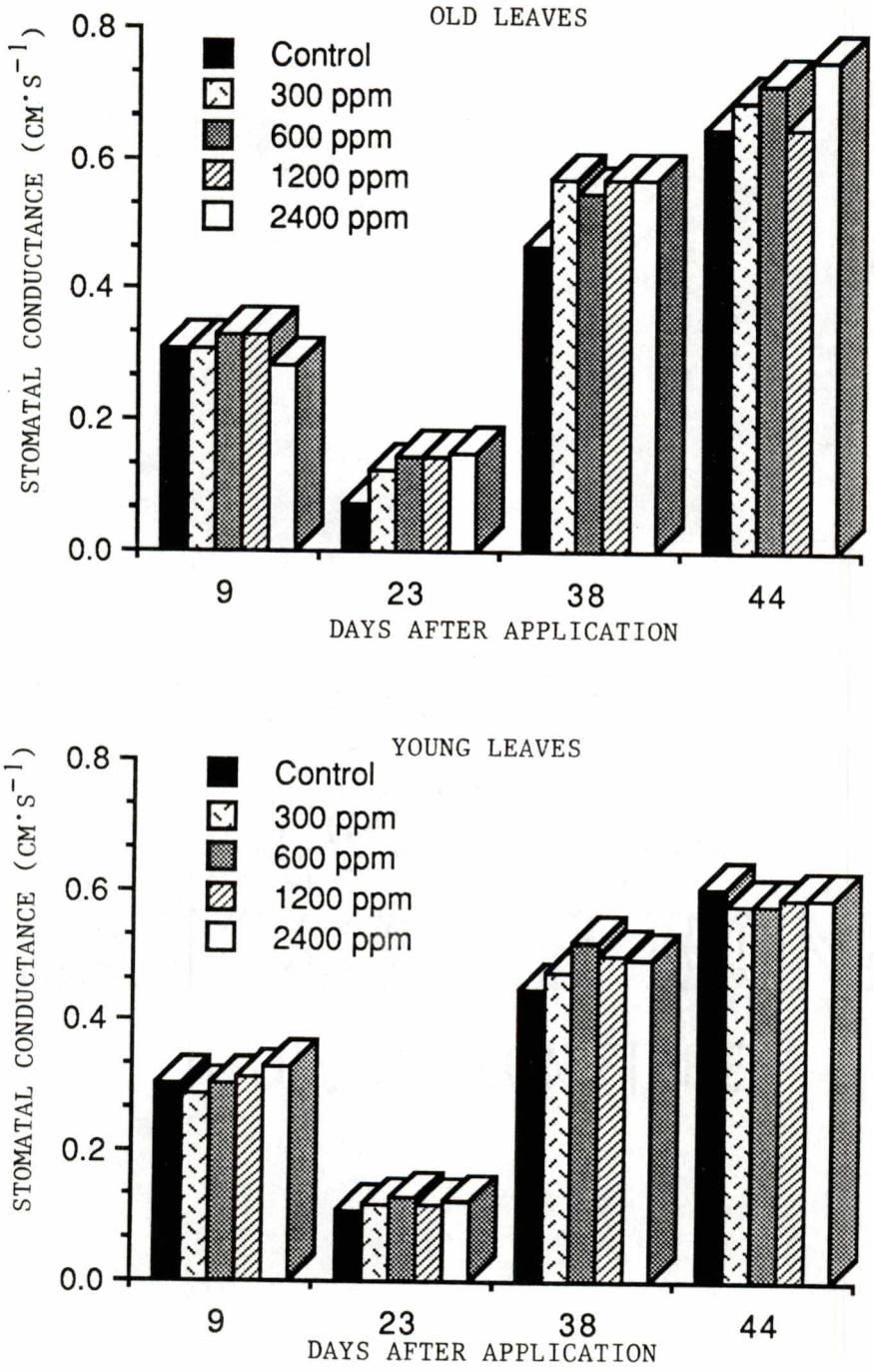


Figure 4.6. The effects of paclobutrazol on stomatal conductance of old and young leaves of potted 'Redhaven' peach trees the year after application.

readings were taken on peaches in the year following application due to severe bacterial spot (Xanthomonas campestris pv. pruni) damage.

Preliminary whole tree photosynthesis data collected 37 and 42 DAT on apple and peach trees, respectively, revealed no significant differences among treatments due to paclobutrazol. This corresponds with the previous findings of no differences early in the season.

The foliar applications of paclobutrazol to 'Golden Delicious' apple trees effectively retarded shoot elongation both in the year of application and in the year after application as reported by other researchers (79, 85, 106) (Figures 4.7, 4.8). Leader growth of 'Golden Delicious' apple trees was significantly reduced by 31 to 47% with increasing concentrations of paclobutrazol in the year of treatment (Table 4.1). Wieland and Wample obtained a 35% reduction in stem length while using lower rates of paclobutrazol that were applied as stem paints (104). Total nodes per leader were significantly reduced by 21 to 35%. Significant reductions of 31 to 48% in total shoot growth per plant were also found. No differences or trends were found in the number of branches per plant in the year of application. Total branch length was reduced slightly but not significantly by paclobutrazol applications (data not shown). During the year following application, both total shoot growth and number of branches of the 'Golden Delicious' apple trees were reduced significantly in a linear fashion (Table 4.1). These reductions were lower than the 80 to 90% reductions in total growth the year following application obtained by Williams and Edgerton (106). This



Figure 4.7. The growth retarding effects of paclobutrazol on 'Golden Delicious' apple trees in the year of application.



Figure 4.8. The growth retarding effects of paclobutrazol on 'Golden Delicious' apple trees in the year following application.

Table 4.1. The effects of paclobutrazol on growth parameters of potted 'Golden Delicious' apple trees during the year of and after application.

	1985				1986			
	Leader		Number of	Total Shoot	Leader		Number of	Total Shoot
Rate (ppm)	Length (cm/ldr)	Nodes (no./ldr)	Branches (no./plt)	Growth (cm/plt)	Length (cm/ldr)	Nodes (no./ldr)	Branches (no./plt)	Growth (cm/plt)
0	632.1	40.6	0.25	672.7	132.4	88.7	13.7	427.2
300	435.4	32.0	0.53	466.6	138.3	84.6	13.8	420.5
600	414.7	33.6	0.28	425.2	139.4	103.0	11.2	361.5
1200	361.2	27.6	0.40	372.5	131.6	99.7	13.0	336.6
2400	339.0	26.2	0.18	344.9	129.6	105.0	8.0	307.5
F test	**	**	NS	**	NS	NS	NS	*
L	**	**	NS	**	NS	NS	*	*
Q	**	**	NS	*	NS	NS	NS	NS
C	*	NS	NS	NS	NS	NS	NS	NS

NSNon Significant.
*Significant at the 5% level.
**Highly significant at the 1% level.

could have been due to varying tree ages and differing rates of paclobutrazol used in the two experiments. Paclobutrazol did not significantly affect leader length, number of nodes, or niternode length. This could have been partly due to severe heat stress during the summer of 1986. This could also be due to a delay effect as related to breakdown products of paclobutrazol as previously mentioned.

Growth reduction of 'Redhaven' peach trees was not as pronounced the year of treatment as for apple trees (Table 4.2). Reductions in leader length ranged from 10 to 16%. and were similar to those previously reported (63, 74). The highest application rate (2400 ppm) significantly reduced total branch length by 54% and number of nodes on the leader by 9%. Total shoot growth was significantly reduced in a linear fashion by 13 to 35%. This reduction in total shoot growth is less than the 75% reduction in peach growth the year after treatment reported by Liyembani and Taylor (69). This difference is probably due to the higher rates used by Liyembani and to the severe water stress these peach trees encountered in 1986. During the year after application, leader growth, number of branches and total shoot growth were reduced by 6, 13, and 9%, respectively, with the 2400 ppm application rate. The number of nodes on the leader were reduced, but no trend was evident.

No dry matter partitioning data was taken in the year of application on either the 'Golden Delicious' apple or 'Redhaven' peach trees. The year following application, paclobutrazol caused

Table 4.2. The effects of paclobutrazol on growth parameters of potted 'Redhaven' peach trees during the year of and after application.

	1985				1986			
	Leader		Number of	Total Shoot	Leader		Number of	Total Shoot
Rate (ppm)	Length (cm/ldr)	Nodes (no./ldr)	Branches (no./plt)	Growth (cm/plt)	Length (cm/ldr)	Nodes (no./ldr)	Branches (no./plt)	Growth (cm/plt)
0	41.5	22.8	3.8	84.1	74.4	46.5	16.3	583.7
300	38.1	23.5	3.0	73.0	66.6	39.7	14.0	465.4
600	39.7	23.9	3.7	70.5	67.2	32.5	16.7	594.6
1200	38.6	22.8	3.2	62.9	66.7	38.2	16.5	564.5
2400	34.8	20.7	2.5	54.1	70.2	46.2	14.1	528.5
F test	*	*	*	*	NS	*	NS	NS
L	NS	*	NS	*	NS	NS	NS	NS
Q	NS	NS	NS	NS	NS	*	NS	NS
C	NS	NS	NS	NS	NS	NS	NS	NS

NSNon Significant.
*Significant at the 5% level.

apple leader dry weight reductions of 34 to 59% (Table 4.3). This reduction in leader dry weight would parallel the reductions in leader length that were found. No significant alterations in total branch dry weight, root dry weight, total shoot dry weight, total plant dry weight or shoot to root ratio were found. Wood (109) reported a decrease in root dry weight of pecans, however, these data showed a 20% increase in root dry weight of peaches with the highest application rate (2400 ppm). This difference may be due in part to tree type and the varying ages of the apple and pecan trees in the two studies. No differences were found in the root:shoot ratio due to paclobutrazol treatments.

Similar results for the dry matter partitioning were found with the 'Redhaven' peach trees (Table 4.4). Paclobutrazol caused a significant reduction in leader dry weight of 21 to 43%. No significant reductions in dry weight were found for any of the other components measured. Since there were few significant reductions in growth this would be expected. Reductions in peach root and shoot dry weight were found by Liyembani and Taylor but they were using much higher rates of paclobutrazol (69). Paclobutrazol has caused little to no changes in Pn or stomatal conductance prior to 49 DAT in the year of application. The year following application the changes in Pn and stomatal conductance were more prevalent than the first year. A similar of trend was found with the growth data. This leads to the conclusion that paclobutrazol was more active the second

Table 4.3. The effects of paclobutrazol on dry weight partitioning of potted 'Golden Delicious' apple trees during the year following application.

Rate (ppm)	Dry Weight					Shoot/ Root Ratio
	Leader (g/ldr)	Total Branch (g/plt)	Root (g/plt)	Total Shoot (g/plt)	Total Plant (g/plt)	
0	80.4	71.2	333.6	151.7	485.3	0.46
300	47.3	38.3	327.1	78.2	405.3	0.24
600	53.2	64.4	294.7	117.6	412.3	0.52
1200	33.0	145.6	327.1	158.7	485.8	0.55
2400	50.5	97.0	419.5	147.5	567.0	0.37
F test	*	NS	*	NS	NS	NS
L	NS	NS	NS	NS	NS	NS
Q	**	NS	NS	NS	NS	NS
C	NS	NS	NS	NS	NS	NS

NS Non Significant.
*Significant at the 5% level.

Table 4.4. The effects of paclobutrazol on dry weight partitioning of potted 'Redhaven' peach trees during the year following application.

Rate (ppm)	Dry Weight: Leader (g/ldr)	Total Branch (g/plt)	Root (g/plt)	Total Shoot (g/plt)	Total Plant (g/plt)	Shoot/ Root Ratio
0	25.2	47.5	241.8	72.7	314.5	0.29
300	19.8	48.8	199.5	68.3	267.8	0.61
600	17.7	41.4	167.8	59.1	226.9	0.43
1200	14.4	39.7	163.2	54.1	217.3	0.40
2400	19.1	27.1	207.8	46.2	254.0	0.26
F test	*	NS	NS	NS	NS	NS
L	NS	NS	NS	*	NS	NS
Q	NS	NS	NS	NS	NS	NS
C	NS	NS	NS	NS	NS	NS

NS Non Significant.
*Significant at the 5% level.

year than the first which supports other reports. By the end of the second year of this study, paclobutrazol treated apple trees had less growth and dry matter production, but with somewhat elevated Pn and stomatal conductance rates. This supports findings in the field study on bearing age trees showing decreased leaf area and decreased shoot growth from paclobutrazol. No Pn data was obtained from the bearing age trees so that aspect could not be compared. If elevated Pn and stomatal conductance rate had been found in the field then it would increase the benefits received from the light penetration and growth aspect. A tree with reduced growth, increased Pn and stomatal conductance levels, and increased light penetration into the canopy would have better potential to develop carbohydrate reserves and subsequently the capability to produce better quality fruit.

CHAPTER V.

THE INFLUENCE OF PACLOBUTRAZOL ON PHOTOSYNTHESIS AND STOMATAL CONDUCTANCE OF GREENHOUSE GROWN APPLE AND PEACH TREES DURING WATER STRESS

A. Introduction

Net photosynthetic rates for apples have been reported to be as high as 35 mg $CO_2 \cdot dm^2 \cdot hr^{-1}$ (96) and for peaches as high as 31.2 mg $CO_2 \cdot dm^2 \cdot hr^{-1}$ (63, 73). Alterations in the photosynthetic rates of apples and peaches have been reported following applications of various pesticides (28, 29). Stomatal closure during water stress has been shown to reduce CO_2 assimilation (94, 95). Stomatal closure has been postulated as the rate limiting factor in photosynthesis in both apple and peach seedlings in response to water stress (94).

Past studies concerning the effects of soil moisture stress on photosynthetic rates in apples have demonstrated that an apple leaf can maintain reasonable photosynthetic levels during a period of considerable stress (9). It has been reported that the photosynthetic rate of an apple leaf was not markedly decreased until more than 80% of the available soil water had been used. At the point of visible wilting, the photosynthetic rate was about 10% of the controls photosynthetic rate (1). Recent research has shown

paclobutrazol to influence photosynthetic levels of apples under water stress conditions (91, 92). Wieland and Wample (104), reported that paclobutrazol had no effect on the photosynthetic rates of apples when painted on the stem. Their study was not a water stress study. Hand et al. (52) reported decreases in net photosynthesis of peaches due to water stress. The decrease they found was dependent on an increase in stomatal resistance in response to the applied stress. Tan and Buttery (95) reported that stomatal conductance, transpiration and photosynthesis of peach leaves declined with decreasing leaf water potential due to induced water stress. It is well known that water stress influences photosynthesis and stomatal conductance. The purpose of this study was to determine if paclobutrazol would alter the physiological responses of photosynthesis and stomatal conductance, of apple and peach trees under water stress.

B. Materials and Methods

First Year Effect

One year old 'Golden Delicious' apples and 'Redhaven' peaches were planted in 66 L pots the first week of June 1986 and treated with paclobutrazol on July 9, 1986. The experimental design was a randomized complete block with 4 replications of two tree plots each receiving 5 treatments. Treatment rates were 0, 300, 600, 1200 or 2400 ppm (0, 3.4, 6.8, 13.6, or 27.2 g ai/11.3 L water) paclobutrazol. Treatments were applied with a backpack sprayer until

runoff. The soil surface of the pots was covered with plastic to prevent root absorption of the compound. The potted trees were saturated for 3 days prior to inducing water stress which was accomplished by withholding water. All measurements on the peaches began September 4, 1986 and were taken every other day until severe stress was encountered and then continued daily until October 10, 1986 at which point severe stress had been encountered for 3 to 5 successive days. Measurements on the apples began October 10, and followed the same pattern as with the peaches until November 10, 1986. Relative humidity (%), CO_2 (vpm), temperature (^oC) and PAR were measured using an Analytical Development Corporation (ADC) model LCA-2 portable CO_2 analysis system. Readings were taken on leaves starting mid way up the trunk of the tree. Each time a reading was taken, the leaf measured was one node higher up the trunk than the previously measured leaf. Access tubes were placed in the soil of each pot at the time the trees were planted and soil moisture was measured on a volume basis with a Troxler 3220 series Neutron probe depth moisture gauge. Data for the neutron probe were correlated with values to gravimetric values on a weight basis shown in Figure 5.1. Stomatal conductance and transpiration levels of the leaves were measured with a Li-Cor model Li-1600 steady state porometer. Entire plants of both the peaches and apples were harvested and partitioned into leaves, shoot, and branches on October 13 and November 14, respectively. Dry weights and linear growth data were taken on the main shoot, branches, leaves and roots.

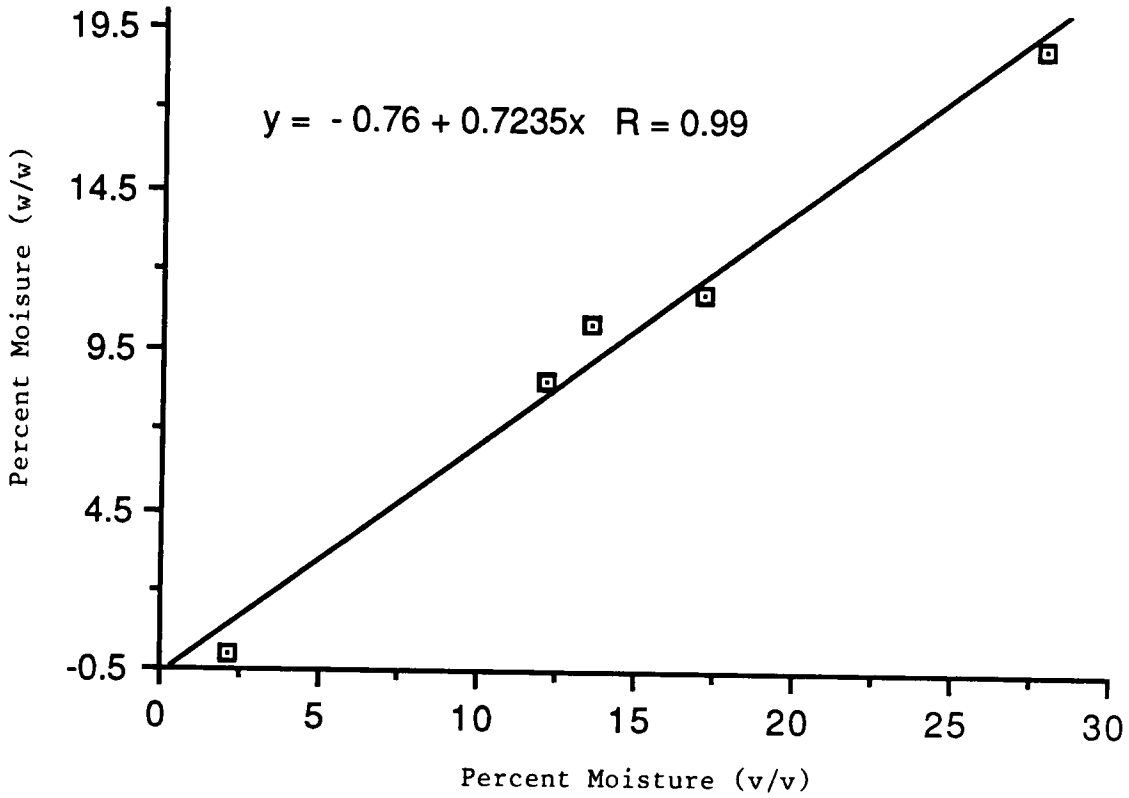


Figure 5.1. Relationship of neutron probe soil moisture levels (v/v) to gravimetric moisture (w/w) determinations the year of application.

Second Year Effect

Trees used for the second year study were planted in 22 L pots the last week of June and treated on July 19, 1986 at the same stage of development and in the same way as those in the first year effect study. These trees were then taken to the Plant Science Field Laboratory to grow until 1987. Only apple trees were used the second year. The experimental design for the second year study was a randomized complete block with 8 replications each containing 6 treatments. An additional treatment (watered control) was added in 1987 to be used as a base line for comparisons. The water controlled data could be subtracted from the stressed trees date to remove variation induced by light and temperature. The apples were transplanted into 66 L pots in late March 1987 and moved into the greenhouse. All pots were saturated in the same manner as those in the first year study and all measurements began on June 15, 1987 and continued every other day until severe stress was encountered. At this point measurements were taken daily until July 4, at which time all treatments were resaturated. Three additional measurements were taken until July 9, to monitor the trees' recovery from the stress. Net photosynthesis, stomatal conductance, and soil moisture measurements were taken in 1987 in the same way as those in 1986 with the addition of leaf water potential measurements on the measured leaves. Leaf water potential readings were taken with a PMS model 650 pressure chamber. Correlation data for the neutron probe from a volume basis to a gravimetric basis as shown in Figure 5.2 and a soil moisture release curve for the soil used is shown in Figure 5.3.

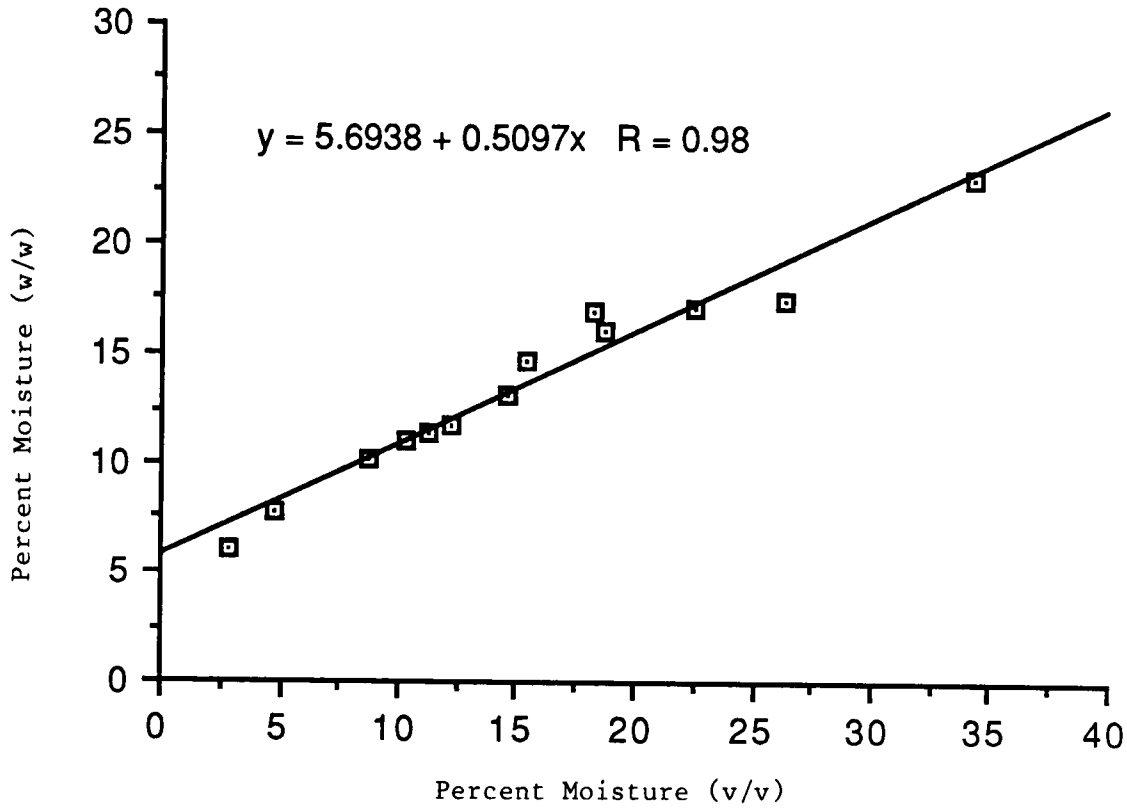


Figure 5.2. Relationship of neutron probe soil moisture levels (v/v) to gravimetric moisture (w/w) determinations the year following application.

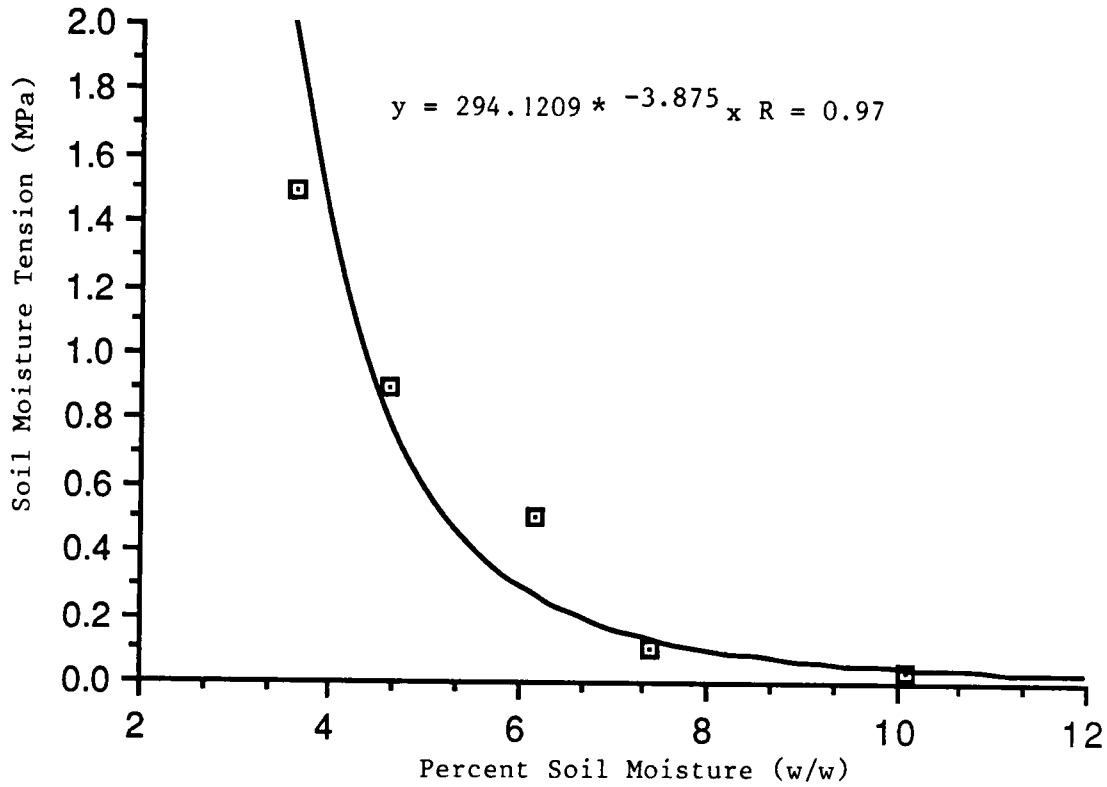


Figure 5.3. Soil moisture release curve for the potting soil used in the second year study.

Growth measurements were taken in September and the trees were partitioned in the same manner as in 1986.

Analysis of the data for both year effects was performed using general linear models (GLM) and linear contrasts (LC). The analysis of the Pn data for the second year effect was done comparing three procedures, (1) asymptotic (2) quadratic and (3) subtraction from the watered control. Asymptotic and quadratic analyses were performed to evaluate the best fit equations and differences between treatments. The watered control was subtracted from the individual treatments within a replication to remove background variation and then an asymptotic analysis was performed. The programing and relationships for these 3 methods of analysis are shown in Appendices (D through I).

C. Results and Discussion

First Year Effect

In 1986 the apple trees receiving the 1200 ppm application rate maintained a significantly higher net photosynthetic rate (Pn) when soil moisture was above 5 % by volume (8.2 % moisture (w/w)) (Figure 5.4). The Pn rate for the 1200 ppm application rate began to decrease at a significantly higher soil moisture level than the other treatments when moisture stress was encountered. The soil moisture level for the 1200 ppm treatment at the Pn rate 95% of the maximum was 11.1. This was 60% higher than the next closest treatment. The reason Pn from the 1200 ppm application rate was above the 2400 ppm

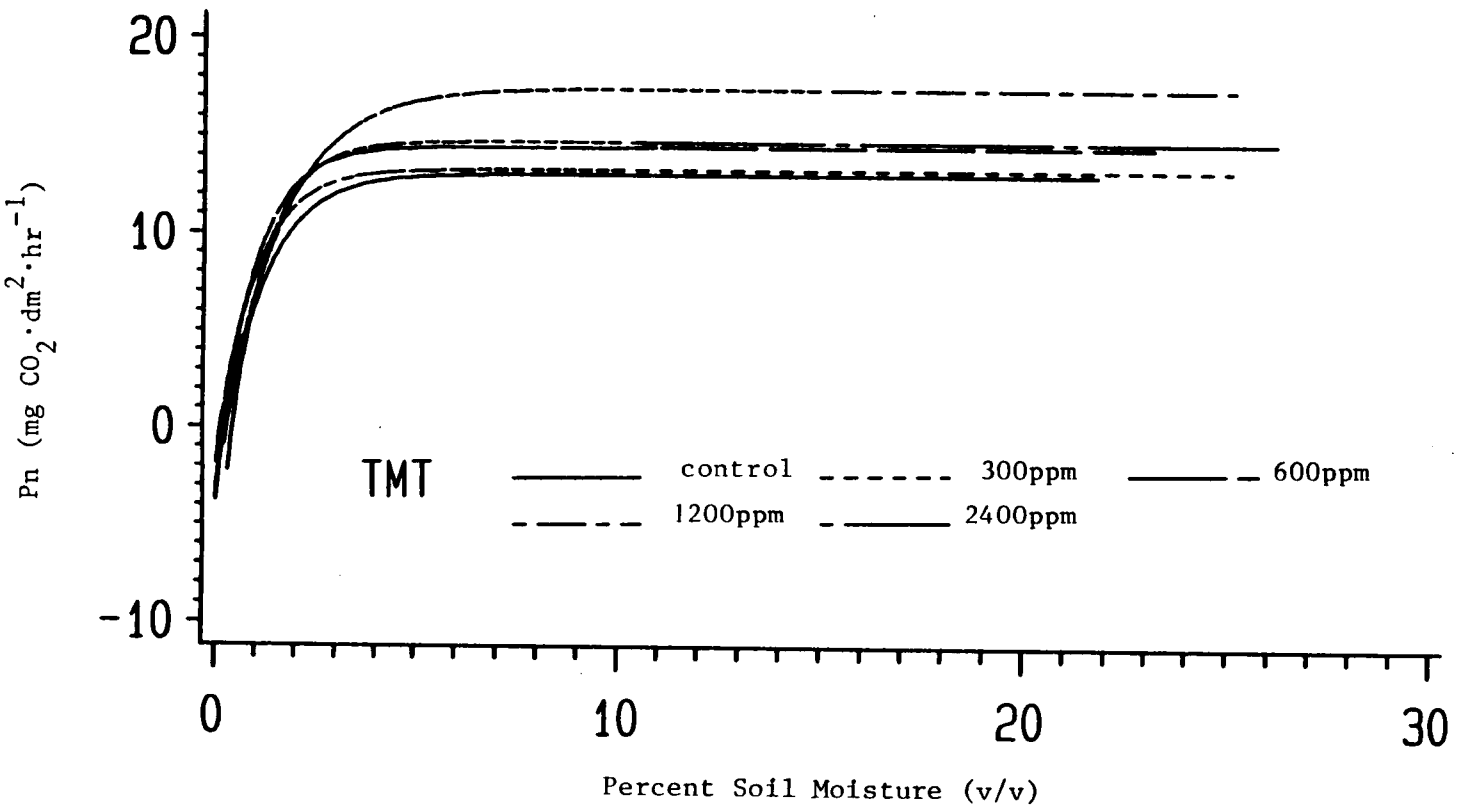


Figure 5.4. The effects of paclobutrazol on the relationship between Pn and soil moisture of potted 'Golden Delicious' apple trees the year of application.

rate is not understood. Since this seemed to be an isolated incident it could have been due to instrumentation error. Paclobutrazol applications did not affect the relationship between Pn and stomatal conductance the year of application (Figure 5.5). Here again as in the other studies, the first year's results were less pronounced than the second years. At soil moisture levels above 10% all application rates had higher peach Pn levels than the 2400 ppm rate in the year of application for peach trees (Figure 5.6). The 2400 ppm application rate maintained a constant Pn rate longer than the other applications. At soil moisture levels between 6% (8.7 % moisture (w/w)) and 1% (6.7 % moisture (w/w)) the 2400 ppm application rate maintained higher Pn levels than the other applications. No significant differences were found for the relationship between Pn and stomatal conductance of peach leaves in the year of application (Figure 5.7). This is similar to responses obtained in the field potted study previously mentioned.

Applications of paclobutrazol were found to significantly decrease both the height and number of branches of apple seedlings in a linear fashion in the year of application (Table 5.1). This corresponds to other research indicating decreased growth with increasing paclobutrazol applications. Overall tree height and number of branches were reduced by 4 to 24%, and 25 to 75%, respectively. The

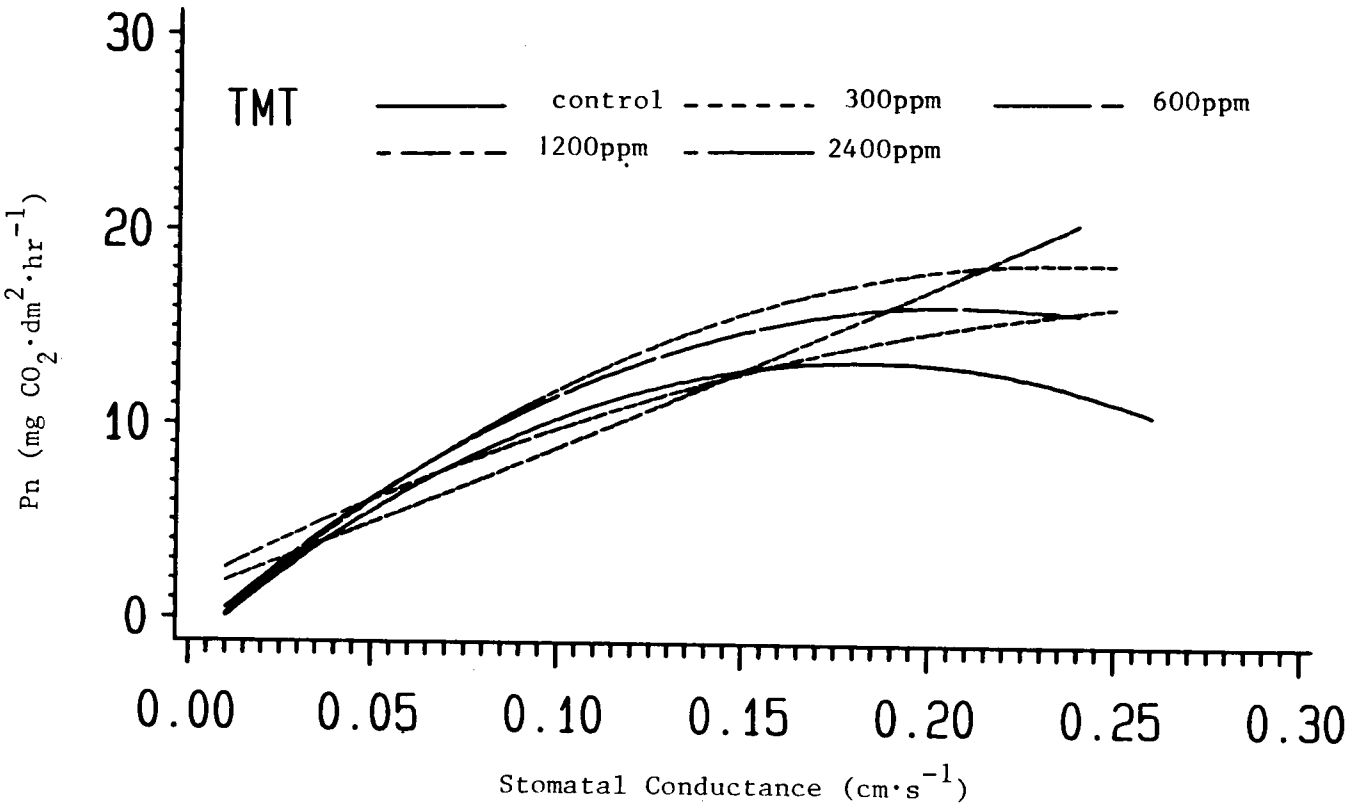


Figure 5.5. The effects of paclobutrazol on the relationship between Pn and stomatal conductance of potted 'Golden Delicious' apple trees the year of application.

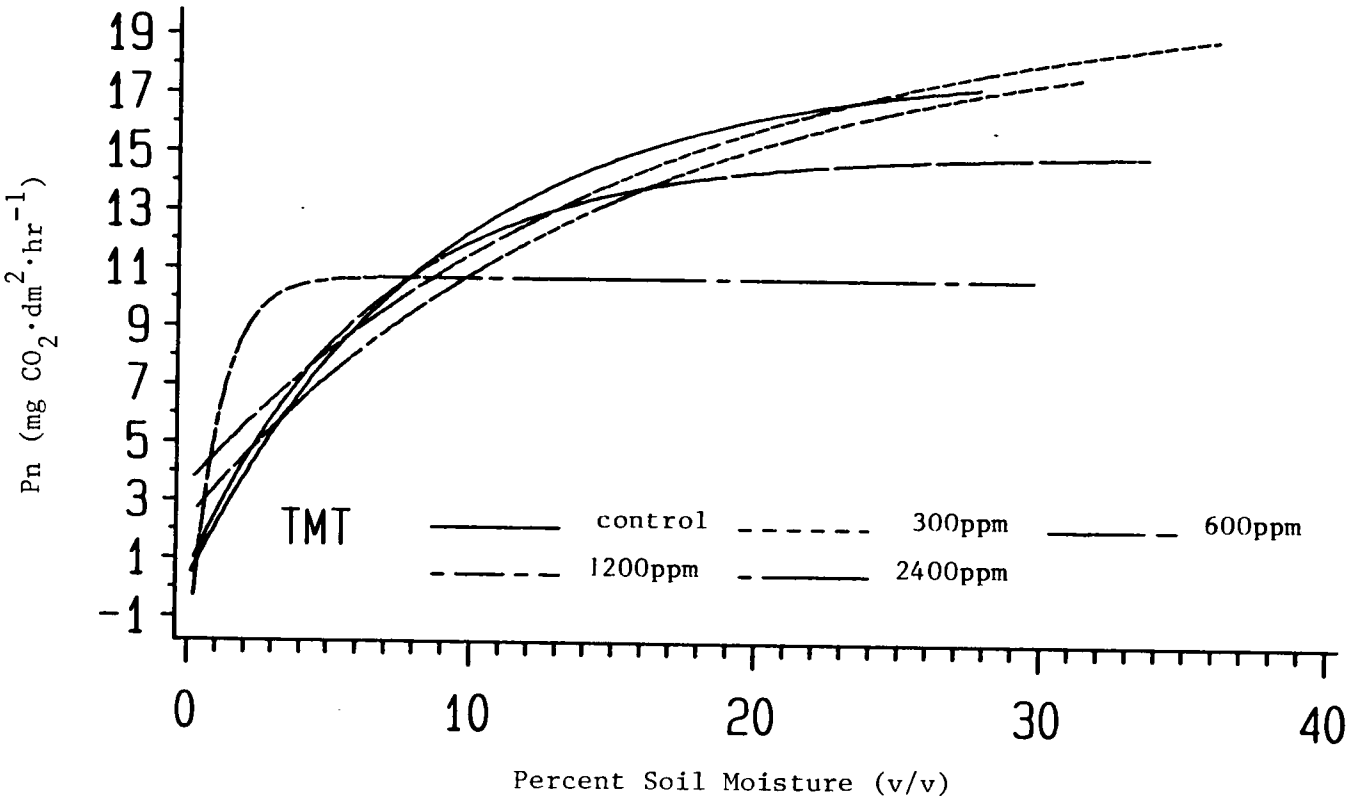


Figure 5.6. The effects of paclobutrazol on the relationship between Pn and soil moisture of potted 'Redhaven' peach trees the year of application.

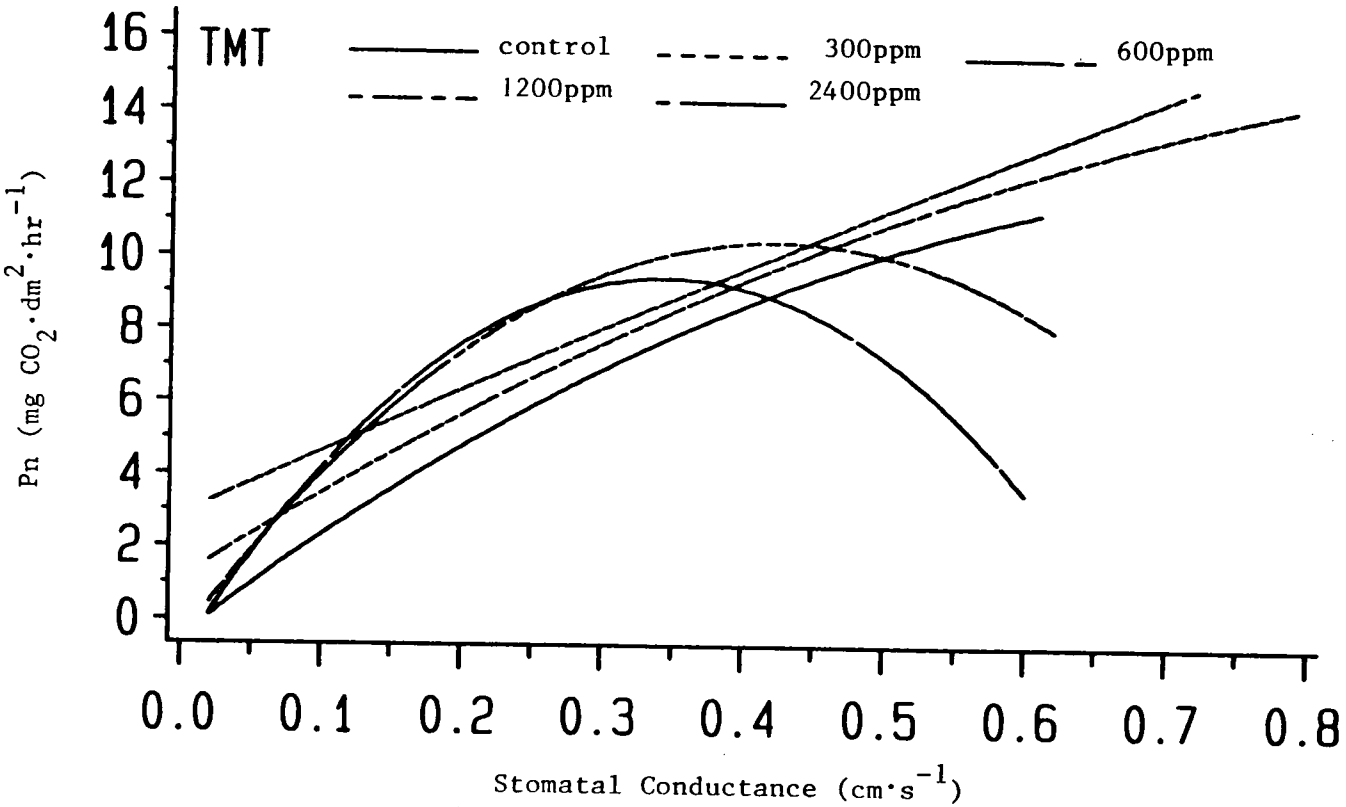


Figure 5.7. The effects of paclobutrazol on the relationship between Pn and stomatal conductance of potted 'Redhaven' peach trees the year of application.

Table 5.1. Growth measurement analysis of paclobutrazol treated potted water stressed 'Golden Delicious' apple trees in 1986.

Rate (ppm)	Length of Leader (cm)	Branches (no.plt)	Total Branch Length (cm)	Leaves (no./plt)	Average Leaf Area (cm^2/leaf)	Total Leaf Area (cm^2/plt)
0	114.5	1.00	36.6	74.7	58.7	469.6
300	110.7	0.25	0.20	65.0	64.5	516.0
600	106.7	0.50	0.40	66.0	58.2	465.6
1200	102.5	0.25	0.85	65.2	64.8	518.4
2400	87.2	0.75	0.77	60.5	64.2	513.6
L	*	*	NS	NS	NS	NS
Q	NS	NS	*	NS	NS	NS
C	NS	NS	NS	NS	NS	NS

NS Not significant.
*Significant at the 5% level by F test.

number of leaves tended to be reduced by 12 to 19%. Similar growth reductions due to paclobutrazol treatments were reported by Swietlik and Miller (92). No differences were found in the average leaf area the year of application. This also agrees with previously reported data. Total branch length was significantly reduced in a quadratic fashion with all treatments being greater than 95% below the control (Table 5.1).

All treatments tended to decrease the height of the water stressed peach trees by 14 to 20% in 1986 although these reductions were not significant (Table 5.2). This again supports the growth reductions obtained in the field. The number of branches on the trees were significantly reduced by 22 to 53%. Total branch length was significantly reduced 31 to 65% although no differences in the average branch length were found. Paclobutrazol treatments also reduced the number of leaves on the trees by 15 to 25% but not significantly. The nonsignificance with a 25% difference could be due to having a coeffient of variation (CV) of 30. Similar results concerning the effects of paclobutrazol on peaches were reported by Daniell and Harrison (26) and Knowles and Dozier (64).

Leaf and total dry weight of apple trees were significantly reduced in a linear fashion in the year of application (Table 5.3). Leaf dry weight was reduced up to 14% with the 2400 ppm application while total plant dry weight was reduced by 10 to 24%. Root dry weight was significantly reduced by 15-28% due to treatment with paclobutrazol. Analysis of the partitioned peach tree dry weights revealed between a 38 to 49% reduction in the weight of the main

Table 5.2. Growth measurement analysis of paclobutrazol treated potted water stressed 'Redhaven' peach trees in 1986.

Rate (ppm)	Length of Leader (cm)	Branches (no./plt)	Average Branch Length (cm)	Total Branch Length (cm)	Leaves (no./plt)	Leaf Area (cm^2/leaf)	Leaf Area (cm^2/plt)
0	107.2	11.8	27.0	313.2	234.5	22.4	448.9
300	94.4	9.2	11.9	111.9	198.5	32.4	648.2
600	85.2	9.2	23.8	214.5	216.5	25.7	515.0
1200	93.8	6.3	18.8	107.8	176.3	30.4	609.5
2400	91.8	5.5	21.5	119.2	189.5	29.3	586.1
L	NS	*	NS	*	NS	NS	*
Q	NS	NS	NS	*	NS	NS	NS
C	NS	NS	NS	NS	NS	NS	NS

NSNot significant.

*Significant at the 5% level by F test.

Table 5.3. Partition measurement analysis of paclobutrazol treated potted water stressed 'Golden Delicious' apple trees in 1986.

Rate (ppm)	Dry Weight			Total Dry Weight (g)	Average Dry Wt. Leaves (g)	Root Dry Weight (g)
	Leader (g)	Branches (g)	Leaves (g)			
0	21.8	3.570	22.5	47.8	0.31	84.9
300	21.2	0.005	21.5	42.8	0.33	60.7
600	20.1	0.015	20.8	41.0	0.31	61.0
1200	20.5	0.037	21.6	42.2	0.33	64.6
2400	16.4	0.017	19.3	36.0	0.31	72.5
L	NS	NS	*	*	NS	NS
Q	NS	NS	NS	NS	NS	*
C	NS	NS	NS	NS	NS	NS

NSNot significant.
*Significant at the 5% level by F test.

shoot and a reduction of between 20 to 32% in total dry weight due to treatment (Table 5.4). These reductions are similar to reductions in growth and dry weight due to paclobutrazol reported by Wieland and Wample (104).

Second Year Effect

Paclobutrazol applications did not significantly affect the relationship between leaf water potential and soil moisture in the year following application (Figure 5.8). However, the leaf water potential level for the 2400 ppm rate was less negative by 12% under moderate (.59 MPa) to no stress (.01 MPa) conditions as compared to the control. The less negative water potential kept water from being a limiting factor in photosynthesis under water stress conditions. This might explain why Pn was maintained at higher levels. Swietlik and Miller felt that the responses of the apple seedlings treated with 0.2 ppm paclobutrazol was due to an increased water potential (92). The highest application rate (2400 ppm) did affect the relationship between stomatal conductance and leaf water potential (Figure 5.9). The slope for the 2400 ppm application rate (-.00049) was significantly lower than the slope for the control (-.00097) as measured by F test. This means that as the water potential within the plant was becoming more negative due to water stress, the stomatal conductance rate of the 2400 ppm treated leaves was decreasing at a slower rate than that of leaves of the control tree. At a water potential of 4.1 MPa the stomatal conductance rate of leaves from the 2400 ppm application were maintained at a

Table 5.4. Partition measurement analysis of paclobutrazol treated potted water stressed 'Redhaven' peach trees in 1986.

Rate (ppm)	Dry Weight Leader (g)	Average Dry wt. Branches (g)	Average Dry wt. Leaves (g)	Total Dry Weight (g)	Root Dry Weight (g)
0	19.9	0.69	0.08	47.8	55.9
300	11.7	0.29	0.09	33.1	58.4
600	12.2	0.65	0.09	38.4	65.0
1200	10.8	0.57	0.10	32.4	52.7
2400	10.2	0.62	0.10	32.8	58.0
L	**	NS	*	*	NS
Q	*	NS	NS	*	NS
C	*	NS	NS	NS	NS

NS Not significant.
* Significant at the 5% level by F test.

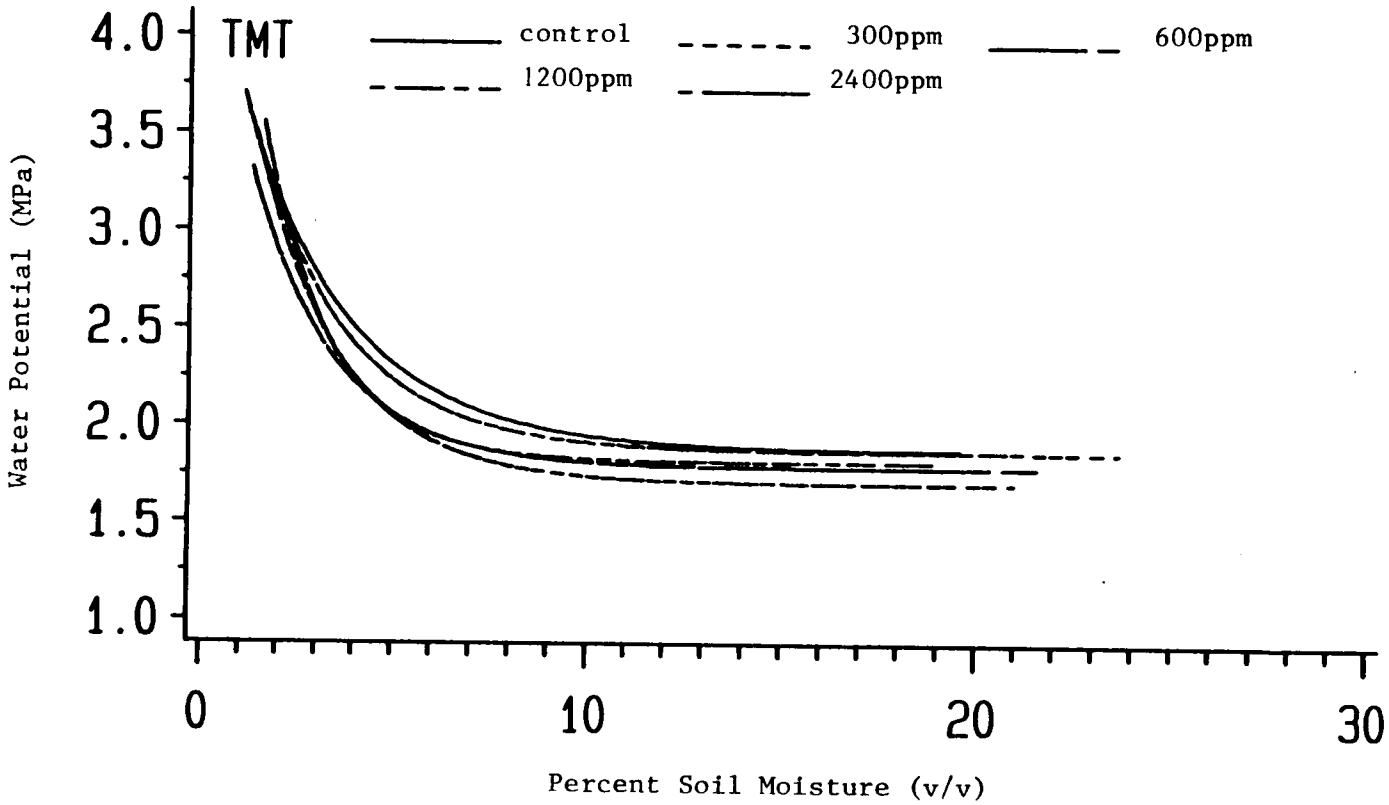


Figure 5.8. The effects of paclobutrazol on the relationship between water potential and soil moisture of potted 'Golden Delicious' apple trees the year following application.

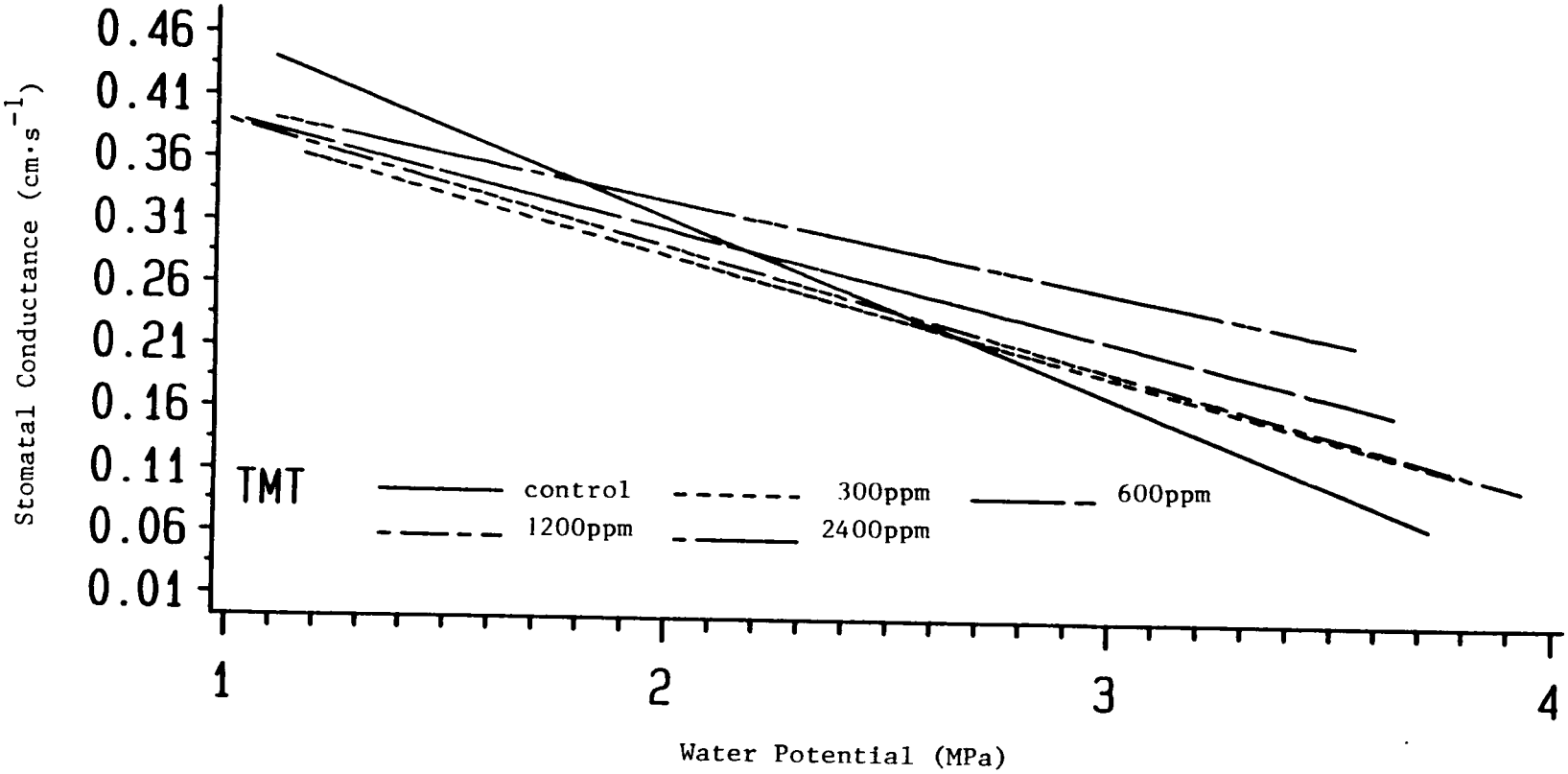


Figure 5.9. The effects of paclobutrazol on the relationship between stomatal conductance and water potential of potted 'Golden Delicious' apple trees the year following application.

significantly less negative level than leaves from the control trees tested at the 10% level by linear contrast (LC). This could be due in part to the fact that leaves from the 2400 ppm rate had water potentials that were less negative than leaves from the control under moderate stress conditions. These results are similar to Atkinson and Crisp (3) who found a reduction in stomatal resistance in fruit trees treated with paclobutrazol as compared to nontreated trees, following a drought period. Swietlik and Miller (92) had similar responses dealing with transpiration. They found that apple seedlings pretreated with 0.20 ppm paclobutrazol withstood water stress better than those pretreated with 0 or 0.05 ppm paclobutrazol. Leaves treated with the 2400 ppm application rate had a significantly higher Pn value by LC between 5.8 (2.5 MPa) and 2.3% soil moisture (295 MPa) than leaves from all other treatments (Figure 10). At the 5.8% soil moisture (v/v), the 2400 ppm application rate had a Pn rate 10% higher than the control while at the 2.3% soil moisture the Pn rate was 95% higher than the control. No significant differences in soil moisture were found between application rates at the 95% of maximum Pn value. The maintenance of Pn levels is felt to result from the trees' ability to maintain a higher stomatal conductance and stomatal opening. This could be attributed to the less negative water potentials found. The combination of these factors apparently kept water and/or CO_2 from being limiting factors during water stress. The year following application paclobutrazol did not significantly alter the Pn level of apple leaves under either saturated or extreme stress conditions. Under the stress conditions

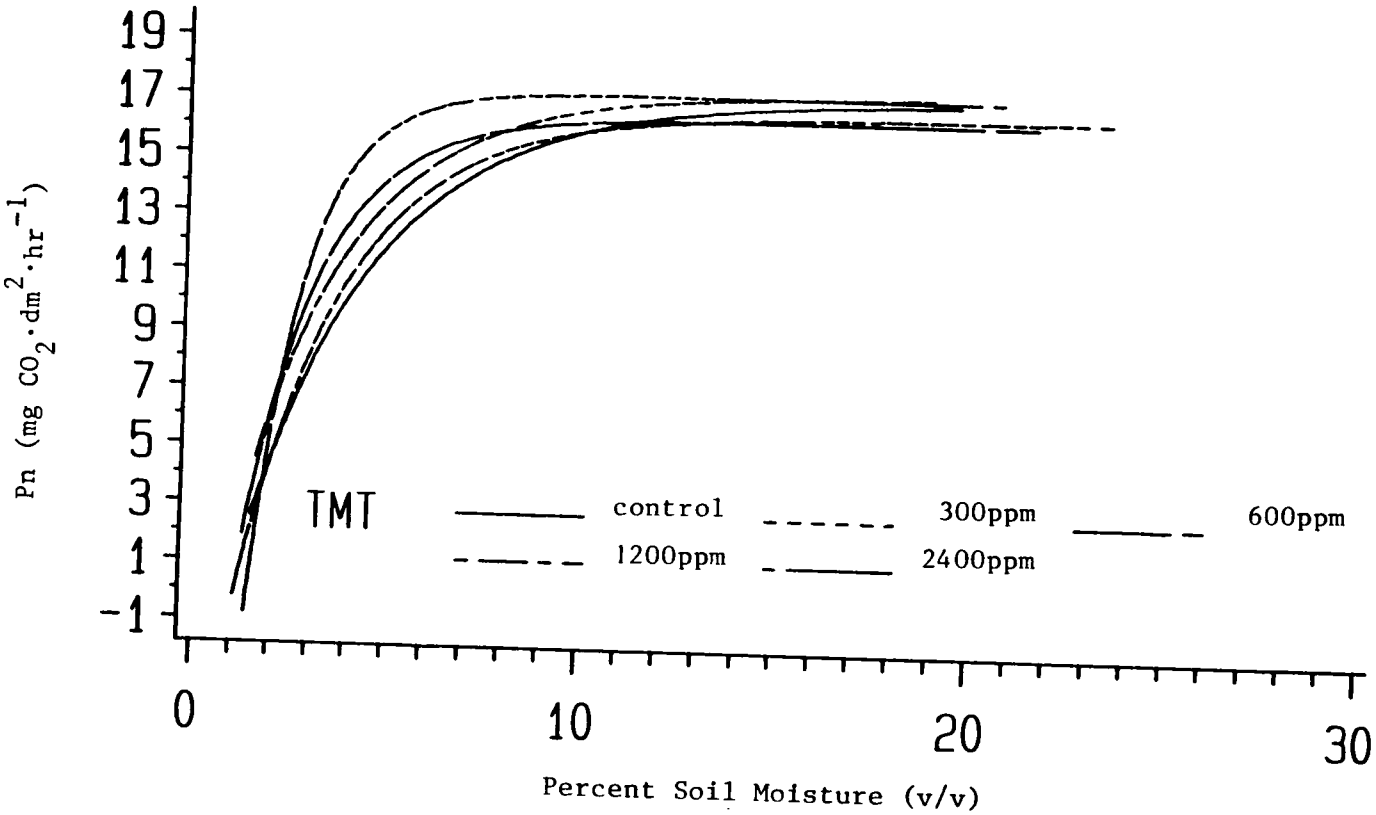


Figure 5.10. The effects of paclobutrazol on the relationship between Pn and soil moisture of potted 'Golden Delicious' apple trees the year following application.

of 2.3 to 5.8% soil moisture (v/v), lower water potentials and maintenance of acceptable stomatal conductance levels were probably major contributing factors to the differences found in photosynthetic rates. Swietlik and Miller (94) also reported that solutions of PEG at -6.0 bars (-0.6 MPa) decreased both net and gross Pn of apple seedlings. The relationship between Pn and stomatal conductance was not affected the year following application, (Figure 5.11), indicating that the changes in Pn are due to water potential rather than stomatal conductance.

The year after application no significant differences in apple growth reduction were found for any of the size related growth parameters measured (Table 5.5). The 2400 ppm application rate tended to reduce leader length, number of branches, and total growth by 10%, 13%, and 17%, respectively. Total branch length was decreased by between 25 to 28% in the year following application. Average leaf area tended to be reduced by between 7 to 15%. Paclobutrazol significantly reduced total weight and leaf dry weight in a linear fashion by up to 31% and 17%, respectively, in the year following application (Table 5.6). Branch dry weight was also significantly reduced in a quadratic fashion. No significant differences were found for any of the other parameters measured. These reductions in dry weight due to paclobutrazol were greater than those found in the field study. This indicates that water stress increased the reduction in dry weight resulting from increasing rates of paclobutrazol. Since paclobutrazol maintained Pn and stomatal conductance levels longer than the control, it might have been

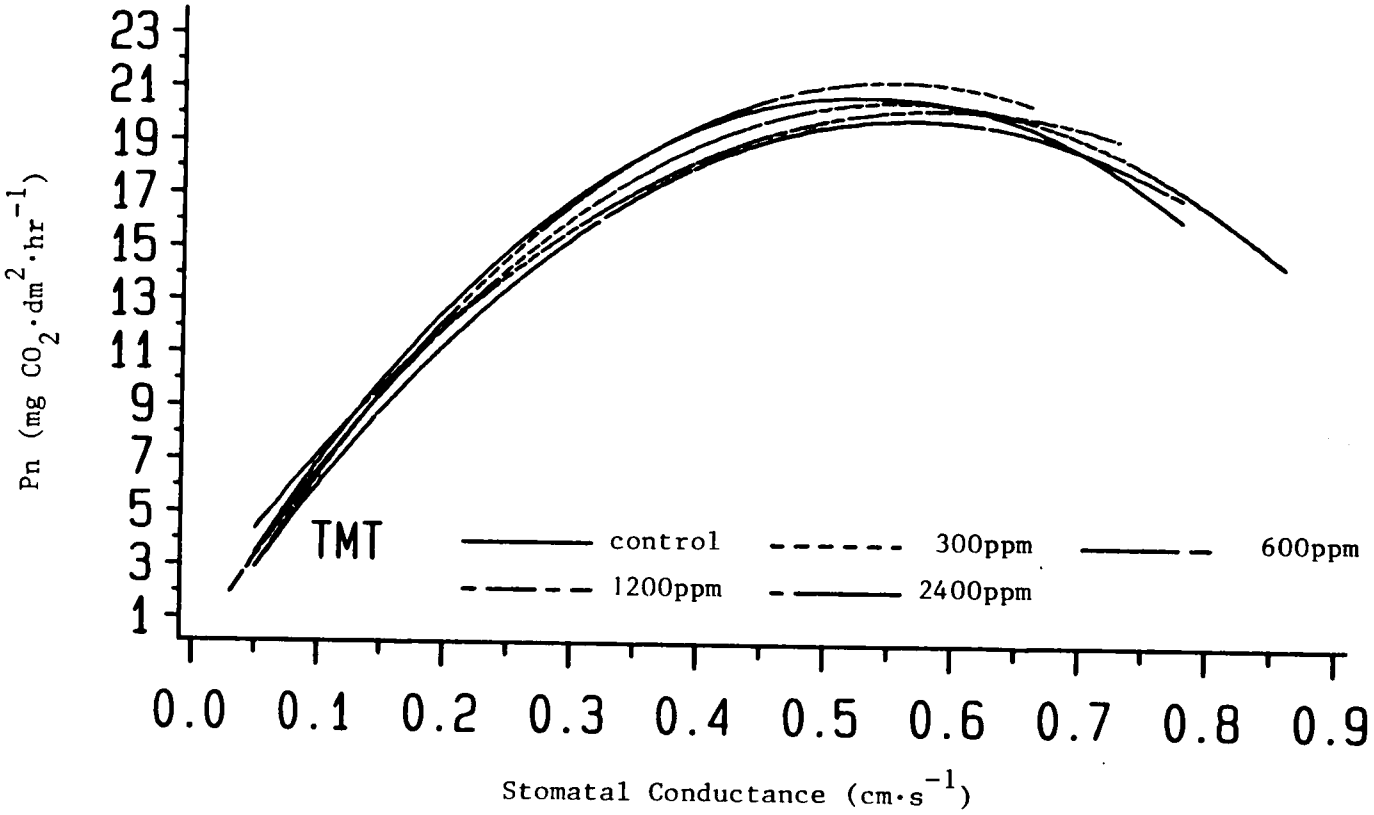


Figure 5.11. The effects of paclobutrazol on the relationship between Pn and stomatal conductance of potted 'Golden Delicious' apple trees the year following application.

Table 5.5. The second year effects of Paclobutrazol on growth parameters of potted 'Golden Delicious' apple trees in 1987.

Rate (ppm)	Length of Leader (cm)	Leaf Area (cm2)	Branches (no./plt)	Total Branch Length (cm)	Leaves (no.plt)	Average Leaf Area (cm2)	Average Branch Length (cm)	Total Growth (cm)
0a[z]	147.7	3202.3	6.0	146.4	178.0	18.2	21.3	294.1
0b[y]	148.6	3024.9	7.5	153.8	202.5	14.9	21.3	302.5
300	163.2	3101.3	7.0	111.6	205.2	15.4	17.3	274.9
600	145.4	3015.4	4.2	104.7	188.1	16.3	29.3	250.1
1200	143.4	3032.5	5.3	111.8	182.6	16.9	31.4	255.2
2400	132.5	2983.1	5.2	110.2	187.5	16.1	23.3	242.8
L	NS	NS	NS	NS	NS	NS	NS	NS
Q	NS	NS	NS	NS	NS	NS	NS	NS
C	NS	NS	NS	NS	NS	NS	NS	NS

[NS]Not significant.
[z]Watered control.
[y]Stressed control.

Table 5.6. The effects of paclobutrazol on dry matter partitioning of potted water stressed 'Golden Delicious' apple trees the year following application.

Rate (ppm)	Dry Weight					Average Leaf Weight (g)	Average Branch Weight (g)	Shoot/ Root Ratio	Leaf/ Root Ratio
	Leader (g)	Branches (g)	Roots (g)	Leaves (g)	Total (g)				
0a[z]	33.7	21.6	170.0	32.4	55.4	.172	3.79	.291	.197
0b[y]	26.6	16.3	192.7	30.5	42.9	.143	2.34	.264	.146
300	34.4	10.6	167.2	32.8	45.1	.186	1.77	.260	.199
600	30.4	10.9	141.7	32.5	41.3	.170	3.20	.292	.230
1200	30.1	10.5	144.5	31.8	40.6	.123	3.22	.283	.232
2400	26.5	11.9	141.7	34.3	38.4	.184	2.07	.287	.235
L	NS	NS	*	NS	**	NS	NS	NS	NS
Q	NS	*	NS	NS	NS	NS	NS	NS	NS
C	NS	NS	NS	NS	NS	NS	NS	NS	NS

[z]Watered control.
[y]Stressed control.
[NS]Not significant.
[*]Significant at the 5% level by F test.
[**]Highly significant at the 1% level by F test.

expected that the highest rate would have more dry weight accumulation. This however was not the case. Since the stress in this study was far more severe than could be expected under field conditions, the benefits from this response from paclobutrazol may be limited to the laboratory or greenhouse research. This research dealing with stress may benefit crops grown in a more susceptible climate.

CHAPTER VI

THE EFFECTS OF VARYING FOLIAR APPLICATION REGIMES OF PACLOBUTRAZOL ON FRUIT MATURITY OF 'GOLDEN DELICIOUS' APPLE TREES

A. Introduction

Commercial fruit growers use various indices such as, fruit color, percent soluble solids, and fruit firmness for determining when their crop is mature and ready for harvest (50). Fruit color, however, has been found to be an unreliable index for predicting fruit maturity (49, 50). The color of fruit depends on many variables that do not remain constant year after year. The soluble solid content of a fruit is an indicator of the amount of starch that has been converted into sugars. Researchers in Washington state have set a minimum level of 12% soluble solids for the earliest possible harvest of 'Golden Delicious' apples while researchers in Virginia uses 11% (50). Fruit firmness is a good indicator of the storage potential of fruits. Researchers in North Carolina have determined 17.0 lbs (7.7 kg) to be the minimum firmness level for 'Golden Delicious' fruit while Washington allows 18.5 lbs (8.4 kg) (50). Values for both soluble solids and firmness vary depending on variety (49, 75). Commercial growers currently use certain plant growth regulators to aid in developing good quality fruit. Alar is used extensively as a vegetative growth retardant, flower initiation

promoter, and to delay preharvest drop (17). This compound is currently under investigation by the Environmental Protection Agency and may be removed from the market. This would lower the quality of fruit produced by growers currently using Alar. As a growth retardant, paclobutrazol could potentially replace Alar.

Research results have indicated that paclobutrazol can not only effectively retard the growth of fruit trees (23, 37, 75), but can also alter fruit quality (33, 47, 64). Paclobutrazol may provide varying degrees of size control depending on the application regime. Based on this, varying rates of paclobutrazol may also have varying effects on the quality of the fruit. Defining an optimum rate, time and frequency of application for paclobutrazol will not only allow more accurate recommendations to be made for season long vegetative growth control but may also beneficially alter the maturity and quality of the fruit. The objective of this experiment was to determine the effects of varying foliar applications of paclobutrazol on fruit quality and maturity indices of 'Smoothee' apple trees.

B. Materials and Methods

Applications of paclobutrazol were made in 1985 to 5 year old 'Smoothee' trees on MM106 rootstocks. The application regimes consisted of a control plus 3 single applications and 4 multiple applications (Table 6.1). The single applications and the initial application of the multiple sets were made 25 days after full bloom with subsequent applications at 2 week intervals. The applications

Table 6.1. Paclobutrazol application regime for 1985 treatments.

Tmt #	Rates ($kg \cdot ha^{-1}$) Init.[Z]	Seq.[Y]	No. Seq.[X]	Total ($kg \cdot ha^{-1}$)	Total (g ai/tree)
1	0.00	-----	---	0.00	0.00
2	0.66[W]	-----	---	0.66	3.11
3	0.33	0.16	4	1.00	4.66
4	0.33	0.16	5	1.16	5.44
5	1.33	-----	---	1.33	6.23
6	0.33	0.33	4	2.80	7.77
7	0.33	0.33	5	2.67	12.46
8	2.67	-----	---	2.67	12.46

[Z]Init=Initial treatment level.
[Y]Seq=Sequential levels of treatment.
[X]No.Seq=Number of sequential treatments.
[W]Initial rate of 0.66=3.11 g ai/tree=972 ppm.

were made with a CO^2 backpack sprayer with the total volume of 3179 ml was sprayed until runoff. Since the desired response of paclobutrazol is in the canopy of the tree only foliar applications were of interest. In an attempt to reduce or prevent any absorption of the compound by the roots the soil under each tree was covered with plastic during each application. Fruit were harvested on 8/14, 8/21, 8/27, and 9/3 in 1985 and on 9/18 in 1986. Measurements of fruit soluble solids, firmness, color, weight, length, diameter, ethylene and CO_2 were taken in 1985. Firmness was tested on opposite sides of each fruit using a Penetrometer model FT 327 fruit pressure tester mounted on a drill stand. Fruit color of the 'Smoothee' fruit was measured with color chart for 'Golden Delicious' fruit developed by Pennsylvania State University. Two wedges were cut from opposite sides of each fruit and the juice from each was tested for percent soluble solids using an Atago hand held refractometer.

In 1986, 5 fruit were sampled from external branches in each quadrant of the tree. Fruit color, soluble solids, firmness, length, diameter, and weight were taken in 1986 in the same way as in 1985.

Statistical analysis was performed using Statistical Analysis System (SAS). Procedures used were general linear models (GLM), regression analysis and linear contrast (LC).

C. Results and Discussion

The number and weight of the fruit were significantly different among treatments with paclobutrazol for the year of application

(Table 6.2). The significance of these results is questionable because the fruit had already been set when the applications were made and because the trees were not thinned evenly that year. An uneven crop load may have biased the data or altered any first year effect of the compound. Fruit soluble solids, color and firmness were not altered in 1985 either (Table 6.2).

Both fruit length and the length/diameter ratio (LDR) were significantly reduced in a linear fashion with increasing paclobutrazol concentrations the year following application (Figures 6.1 and 6.2). Here again, the trees were not thinned to an even number of fruit so crop load must be taken into consideration. These results are understandable since paclobutrazol is a gibberellin (GA) biosynthesis inhibitor. Fruit development depends on cell elongation which is dependent on GA. By blocking GA production a decrease in the amount of cell elongation would occur. These results were similar to those by Curry and Williams (21) who reported shorter and flatter fruit following soil applications of paclobutrazol at 20g/9.5m^2/tree. Elfving and Chu (34) also found reductions in fruit length as well as reductions in fruit diameter and firmness which were not evident in this study. Fruit firmness increased in a significant linear fashion with increasing paclobutrazol concentrations the year after application (Figure 6.3). Since the fruit were shorter and cell elongation was inhibited somewhat, it is understandable that fruit firmness would increase. The cells would be more compact in a small, short fruit than in one that had expanded more by cell elongation. Various researchers have

Table 6.2. The effects of paclobutrazol on various quality parameters of 'Golden Delicious' apple fruit in 1985.

Rate ($kg.ha^{-1}$)	Fruit (no./plt)	Fruit Weight (g)	Soluble Solids (%)	Color	Firmness (kg)
0.00	187.5	47.0	14.3	2.6	7.6
0.66	186.7	54.2	14.4	2.6	7.5
1.00	327.2	84.7	-----	---	---
1.16	169.0	48.0	14.5	2.6	7.6
1.33	102.0	26.1	14.5	2.7	7.7
1.67	240.7	70.7	-----	---	---
2.67	329.2	78.2	-----	---	---
2.67	208.0	51.4	14.8	2.7	7.5
F test	*	*	NS	NS	NS

*Significant at the 5% level by F test.
NSNot significant.

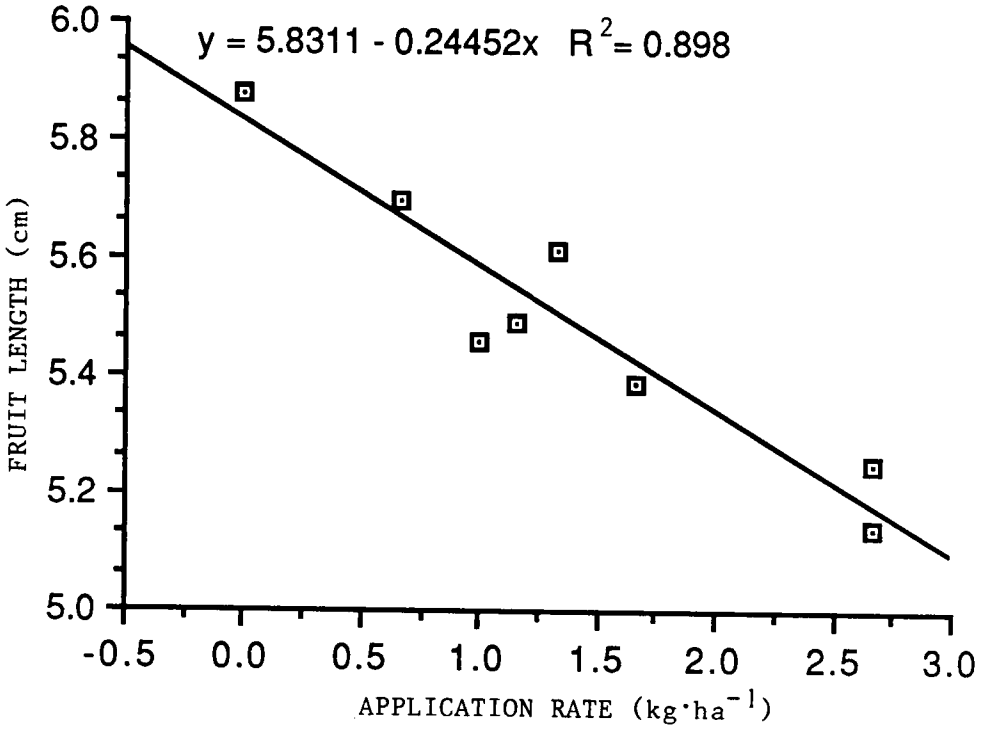


Figure 6.1. The effects of paclobutrazol on fruit length of bearing age 'Smoothee' apple trees the year following application.

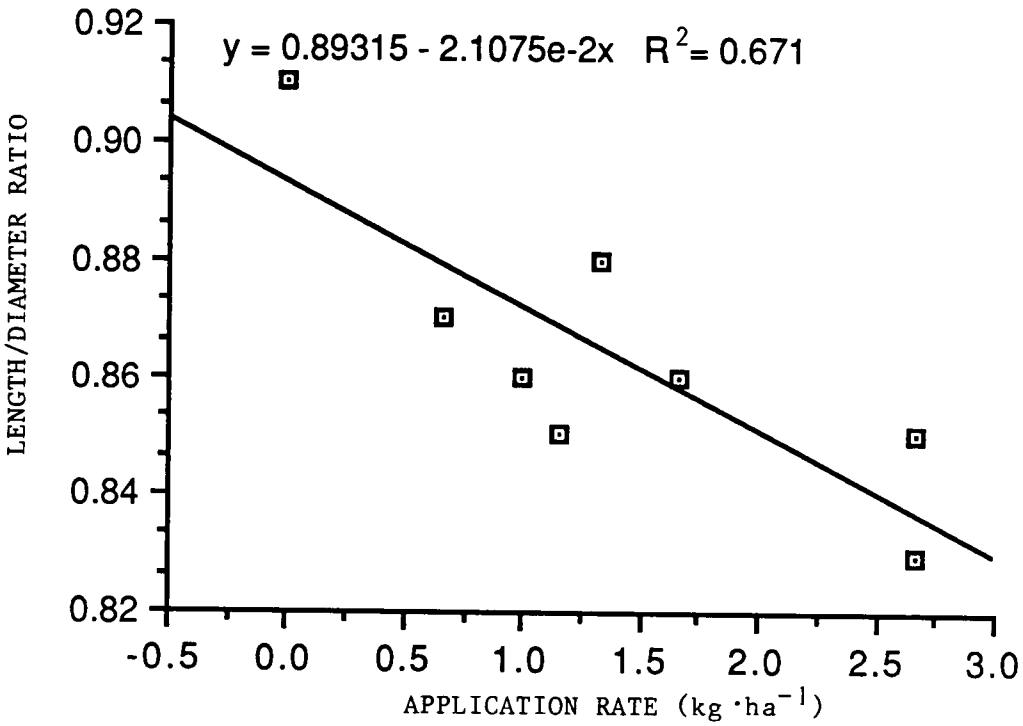


Figure 6.2. The effects of paclobutrazol on the fruit length/diameter ratio of bearing age 'Smoothee' apple trees the year following application.

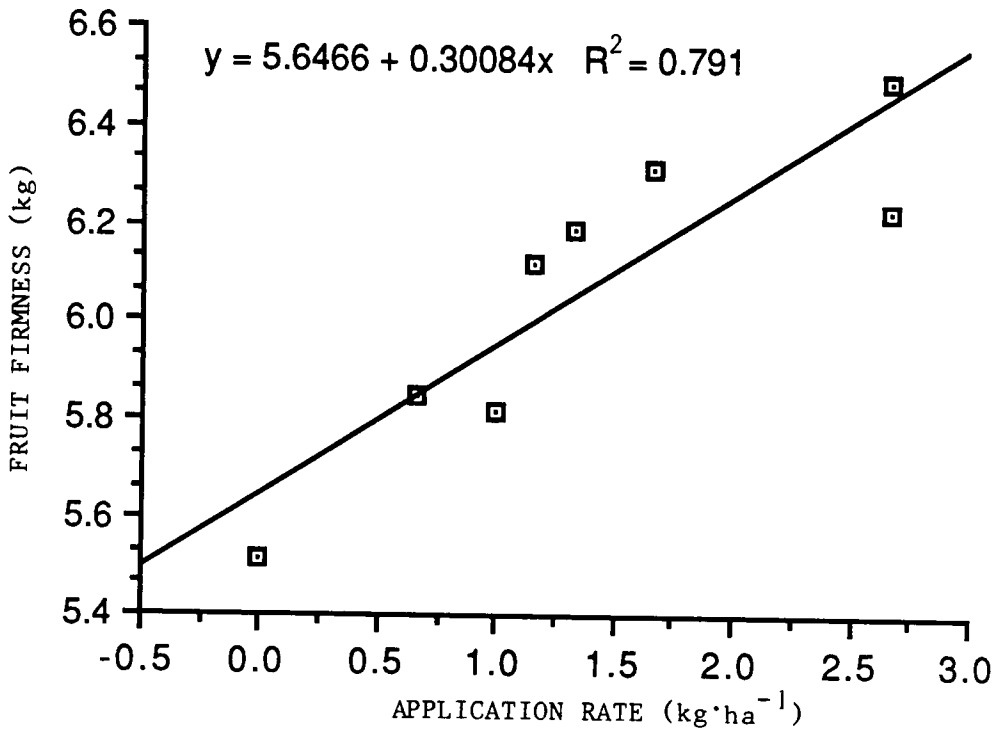


Figure 6.3. The effects of paclobutrazol on fruit firmness of bearing age 'Smoothee' apple trees the year following application.

reported no effect of paclobutrazol on fruit firmness of apples (22, 34, 36). Ebreham and Campbell, however, reported significant increases in apple firmness 3 months after storage with foliar applications of 1500 ppm paclobutrazol (32). Fruit weight, diameter and percent soluble solid were not affected the year after application (Table 6.3). The uneven crop load could have altered or masked any effect from paclobutrazol that year.

Table 6.3. The effects of paclobutrazol on various quality parameters of 'Golden Delicious' apple fruit in 1986.

Rate ($kg \cdot ha^{-1}$)	Fruit Diameter (cm)	Fruit Weight (g)	Soluble Solids (%)
0.00	6.44	120.4	16.7
0.66	6.51	118.3	15.5
1.00	6.32	108.8	15.5
1.16	6.46	114.9	17.1
1.33	6.34	113.7	16.8
1.67	6.23	107.4	16.2
2.67	6.16	101.8	15.8
2.67	6.15	98.6	15.2
F test	NS	NS	NS

*Significant at the 5% level by F test.
NSNot significant.

CHAPTER VII

THE EFFECTS OF PACLOBUTRAZOL ON EPICUTICULAR WAX PRODUCTION OF APPLE AND PEACH LEAVES

A. Introduction

The outermost surface of a leaf is covered with epicuticular wax. The cuticular membrane is composed of a matrix of cutin embedded with cuticular wax, with epicutular wax deposited on the outer surface. This epicuticular wax contains mixtures of free long-chain fatty acids and hydroxy fatty acids, esters of fatty acids, long chain alcohols, long chain alkanes, and long chain ketones (46). This layer of wax helps prevent the excessive passage of water either into or out of the leaf. The structure and composition of epicuticular wax on the surface of the cuticle may influence wettability and permeability of the leaf surface. A plant having an altered cuticular layer may alter the effects of pesticides and influence responses to environmental changes.

Various pesticides such as thiocarbamates, 2,4-D, and some surfactants have been shown to alter the formation and deposition of cuticular layers in expanding leaves (41). El-Otmani and Coggins reported that applications of GA_3 significantly reduced the levels of wax production on naval orange fruit (37). Paclobutrazol has been shown to alter fatty acids (25), as well as inhibit GA production

(25, 68). The effect of paclobutrazol on the cuticular wax or cutin components remains unknown.

Since the cuticle and epicuticular wax deposits are the major protective covering for the plants, any pesticide-induced change in either the formation or composition of this epicuticular wax layer and/or cuticle could have drastic effects on cuticle permeability and leaf water functions. Whether these effects would be beneficial or detrimental to the leaf is unknown. The purpose of this study was to evaluate paclobutrazols effects on the production of epicuticular wax by apple and peach leaves.

B. Materials and Methods

Colorimetric Method

Wax for use as standards was collected in the field from bearing age 'Smoothee' apple and 'Redhaven' peach trees by washing leaves in 400 ml of redistilled chloroform. The chloroform was evaporated off in a hot water bath and the wax from the leaves was collected. A standard curve was drawn based on 0, 0.5, 1, 2, 3, 4, and 5 mg of leaf wax versus the wax's absorbance at 590 nm. This method is based upon a color change that occurs from a reaction between wax and acidic potassium dichromate ($K_2Cr_2O_7$) (12). A randomized complete block design (RCB) with 8 replications each having 5 treatments was used. Applications with concentrations of 0, 300, 600, 1200, or 2400 ppm (0, 3.4, 6.8, 13.6, or 27.2 g ai/11.3 L water) paclobutrazol were sprayed until runoff on one year old potted

apple and peach trees. Two leaves from the lowest 8 nodes and 2 of the newest fully expanded leaves were collected from each tree and labeled as old and young leaves. The procedure described by Ebercon et al. (31) was used to extract and evaluate the wax from the leaves with the exception that ten, 8 mm discs were used in the extraction.

First Gravimetric Method

A randomized complete block design with 8 replications containing 5 treatments was used. Treatments consisted of a control, 300, 600, 1200, or 2400 ppm (0, 3.4, 6.8, 13.6, or 27.2 g ai/11.3 L water) paclobutrazol applied until runoff with a backpack sprayer to one year old potted apple and peach trees. Two leaves were sampled from each tree within each replication in the same way as for the colorimetric analysis. Leaf discs (8mm) were punched from the two leaves and mixed together for a uniform sample. Twenty discs were placed into test tubes and chloroform was added. Three 5ml HPLC grade chloroform washings with agitation were done for approximately 10 seconds each. The washings were filtered into pre-weighed test tubes and evaporated off at 60° C using a Meyer N-EVAP analytical evaporator. The tubes were then oven dried at 40°C and allowed to come to room temperature before final weighing. The difference between the final weight and the pre weight was the amount of wax removed. Statistical analyses with general linear models and linear contrast were performed.

Second Gravimetric Method

The experimental design for this study was an RCB with 8 replications each containing 5 treatments. Applications of 0, 300, 600, 1200, or 2400 ppm (0, 3.4, 6.8, 13.6, or 27.2 g ai/11.3 L water) paclobutrazol were applied to one year old potted apple and peach trees. Leaves were removed from individual trees for analysis one replication at a time. They were separated into 2 sets of 25 and leaf area was measured using a portable area meter. The leaves were allowed to wilt to allow for stomatal closure. Wax extraction followed the procedure described by Flore and Bukovac (41, 42) with the exception that each leaf was dipped in each of 4 successive 200 ml portions of redistilled chloroform for 10 seconds each. Each 200 ml portion was dried with 5 gm of sodium sulfite (anhydrous) for approximately 3 minutes. All portions were filtered into a 1000 ml rotary evaporator flask and reduced to approximately 200 ml. This extract was then transferred and rinsed into 250 ml erlenmeyer flasks for storage. Samples were then filtered into a pre-weighed 250 ml rotary evaporator flasks and all chloroform was removed. The flasks were then dried to a constant weight at 40°C and reweighed. The amount of wax was determined by subtraction.

C. Results and Discussion

Colorimetric Method

Significant differences in total wax on both old and young apple leaves were found in the year of application (Table 7.1). A

Table 7.1. The first year effects of paclobutrazol on old and young apple leaf wax production.

Application Rate (ppm)	Old Leaf Wax ($mg \cdot cm^2$)	Young Leaf Wax ($mg \cdot cm^2$)
0	0.118	0.098
300	0.099	0.112
600	0.139	0.116
1200	0.099	0.115
2400	0.106	0.085
F test	*	*

*Significant at the 5% level by F test.

quadratic trend with increasing paclobutrazol concentrations was apparent with both old and young leaves but these were not statistically significant.

First Gravimetric Method

No significant differences in total wax weight were found for either old or young peach leaves the year of application (Table 7.2). As with the growth and Pn data this could be due to the time of application, the time the leaves were sampled or the breakdown period as previously mentioned. The old leaves receiving no application tended to be higher than the treated leaves, but not significantly. No trends were noticed with the young leaves following this procedure. Leaves from the greenhouse water stress study were also analyzed for wax production the year of application. No significant differences were found for either the apple or the peach leaves (Table 7.3). In both cases however, the controls tended to have the lowest wax production in comparison to the other treatments. The year after application no significant differences were found in wax production on apple leaves, while on the peaches the controls were found to be significantly lower than all other treatments by linear contrast (Table 7.4). This could be one reason the plants were more stress tolerant. If the wax layer was thicker on the treated leaves then they would have a higher stomatal resistance thus lose less water from cuticular transpiration.

Table 7.2. The first year effects of paclobutrazol on old and young peach leaf wax production.

Application Rate (ppm)	Old Leaf Wax ($mg \cdot cm^2$)	Young Leaf Wax ($mg \cdot cm^2$)
0	0.012	0.013
300	0.008	0.008
600	0.010	0.029
1200	0.007	0.007
2400	0.011	0.008
F test	NS	NS

NS Not significant by F test.

Table 7.3. The first year effects of paclobutrazol on potted apple and peach leaf wax production under water stress conditions.

Application Rate (ppm)	Apple Leaf Wax ($mg \cdot cm^2$)	Peach Leaf Wax ($mg \cdot cm^2$)
0	0.54	0.37
300	0.53	0.50
600	0.55	0.45
1200	0.63	0.48
2400	0.54	0.48
F test	NS	NS

NS Not significant by F test.

Table 7.4. The second year effects of paclobutrazol on potted apple and peach leaf wax production.

Application Rate (ppm)	Apple Leaf Wax ($mg \cdot cm^2$)	Peach Leaf Wax ($mg \cdot cm^2$)
0	1.2	0.25
300	1.3	0.54
600	1.1	0.45
1200	1.3	0.58
2400	1.4	0.57
F test	NS	*

NS Not significant by F test.
*Significant at the 5% level by F test.

Second Gravimetric Method

The year following application leaves from the greenhouse water stress were analyzed for wax production. No significant differences in wax production were found among any of the treatments (Table 7.5). The leaves from the control plants tended to have less wax than any of the other treatments but this was not significant. No other trends were evident this year. The amount of wax obtained using this procedure was more than in the others due to the increased leaf area sampled.

D. Conclusion

It is obvious that if any determination is to be made concerning the effect paclobutrazol has on wax production, much more work is needed. Different amounts of wax were found depending on the procedure used. Determining the effect of paclobutrazol on wax production may help explain some of the compounds various effects on water relations previously discussed in this dissertation.

Table 7.5. The second year effects of paclobutrazol on potted apple leaf wax production under water stress conditions.

Application Rate (ppm)	Apple Leaf Wax ($mg \cdot cm^2$)
0	0.12
300	0.29
600	0.19
1200	0.13
2400	0.16
F test	NS

[NS]Not significant by F test.

CHAPTER VIII

GENERAL SUMMARY

The objectives of this dissertation were to determine 1) the effects of varying foliar application regimes of paclobutrazol on season-long vegetative growth control of bearing age 'Golden Delicious' apple trees, 2) the effects of foliar applications of paclobutrazol on photosynthesis, stomatal conductance, and growth of potted 'Golden Delicious' apple and 'Redhaven' peach trees, 3) the effects of foliar applications of paclobutrazol on photosynthesis and stomatal conductance of potted 'Golden Delicious' apple and 'Redhaven' peach trees during water stress, 4) the effects of varying foliar applications of paclobutrazol on fruit maturity and quality, of bearing age 'Smoothee' apple trees, and 5) the effects of foliar applications of paclobutrazol on the epicuticular wax production of apple and peach leaves.

Paclobutrazol decreased the shoot growth of bearing age 'Golden Delicious' apple trees by as much as 89% and increased light penetration into the canopy by 21%. These results could benefit commercial growers. The decreased shoot growth should reduce pruning time and possibly pruning costs. The increased light penetration should lead to improved ripening and coloring of fruit. Increased spray penetration would probably be associated with the decreased growth resulting in improved pest control and possibly reduced spray costs. Fruit length and fruit length/diameter ratio were decreased.

These are not favorable attributes of the compound but further research may uncover acceptable alternatives.

Shoot growth of potted trees was reduced in both the field studies and the greenhouse water stress study. The benefits from this have already been mentioned. Paclobutrazol did not consistently increase photosynthetic levels of the apple or peach trees in the field study. The number of measurements during the growing season may account for this. The significant differences showed up after 50 days after treatment. Better results may be obtained by taking measurements more often and for a longer period of time after treatment.

Paclobutrazol treated trees maintained acceptable Pn levels longer than the non treated trees under water stress conditions. Water potentials were found to be higher in the treated trees also. The levels of water stress that the apple trees were subjected to in the greenhouse were far more severe than would be encountered in the field. The fact that paclobutrazol treated trees were more stress tolerant is still of importance. It may be beneficial to use paclobutrazol on either more stress suceptible susceptible crops or on crops grown in more stressful climates.

Paclobutrazol produced smaller trees with less growth. Some of the trees had elevated Pn and stomatal conductance levels and under stress conditions being more tolerant than the nontreated trees. The benefits from the growth controlling aspects seem obvious but more research is needed to specifically identify what physiological processes paclobutrazol may be altering within the plant.

LITERATURE CITED

1. Allmendinger, D. F., A. L. Kenworthy and E. L. Overholser. 1943. The carbon dioxide intake of apple leaves as affected by reducing the available water to different levels. Proc. Amer. Soc. Hort. Sci. 42:133-140.

2. Andersen, P. C. and J. H. Aldrich. 1987. Effect of soil-applied paclobutrazol on 'Cheyene' pecans. HortScience 22(1):79-82.

3. Atkinson, D., and C. Crisp. 1983. The effect of a number of plant growth regulators on fruit tree root growth and mineral nutrition. J. Sci. Food Agri. 34(3):265.

4. Anonymous. 1980. 3221/3222/3223 and irrigation models 3225/3226/3227 depth moisture gauges. Troxler Electronic Laboratories Inc.

5. Ayers, J. C. and J. A. Barden. 1975. Net photosynthesis and dark respiration of apple leaves as affected by pesticides. J. Amer. Soc. Hort. Sci. 100(1):24-28.

6. Avery, D. J. 1969. Comparisons of fruiting and deblossomed maiden apple trees, and non-fruiting trees on a dwarfing and an invigorating rootstock. New Phytol. 68:323-336.

7. Baldwin, B. C., and T. E. Wiggins. 1984. Action of fungicidal triazoles of the Diclobutrazol series on Ustilago myadis. Pestic. Sci. 15:156-166.

8. Banks, P. A., T. N. Tripp, J. W. Wells and J. E. Hammer. 1985. Effects of tillage on sicklepod (Cassia obtusifolia) interference with soybeans (Glycine max) and soil water use. Weed Science 34:143-149.

9. Barden, J. A. 1978. Apple leaves, their morphology and photosynthetic potential. HortScience 13(6):644-646.

10. Bausher, M. G., G. Ylenosky and C. S. Mauk. 1985. Uptake by roots and translocation of ^{14}C-Paclobutrazol in citrus. HortScience 20(3):595. (Abstr.)

11. Bayliss, M. W. 1984. Regulation of the cell division cycle in cultured plant cells. In: The cell division cycle in plants. Society of Experimental Botany Seminar Series.

12. Bragdon, J. 1951. Colorimetric determination of blood lipids. J. Biol. Chem. 190:513-517.

13. Buta, J. G., S. Y. Wang and G. L. Steffens. 1986. Phenolics in roots of apple seedlings after paclobutrazol treatment. Pro. Plant Gro. Reg. Soc. Amer.

14. Buttner, R., G. Friedrich, and J. Salzer. 1977. Comparison of the leaf area and net photosynthesis of various apple varieties. Archiv. fur Gartenbau 24:159-165. [Hort. Abstr. 47:1168; 1977.]

15. Cervenka, K. 1972. Varietal differences in CO_2 assimilation by apple trees. Vedecke Prace Ovoencirske 4:157-160. [Hort. Absrt. 43:3412; 1973.]

16. Chambers, D. L., R. L. Canterfold, P. H. Jerie, T. R. Jones and T. D. Ugalde. 1975. Photosynthesis in relation to growth and distribution of fruit in peach trees. Aust. J. Plant Physiol. 2:635-645.

17. Childers, N. F. 1976. Modern Fruit Science. Horticultural Publications. Rutgers University, N.J.

18. Coombs, J., and D. O. Hall. 1985. Techniques in bioproductivity and photosynthesis. Pergamon Press. New York, Toronto, Paris.

19. Cowart, F. F. 1936. Apple leaf structure as related to position of the leaf upon the shoot and to type of growth. Proc. Amer. Soc. Hort. Sci. 33:145-148.

20. Cullen, W. C. and T. P. McDonald. 1986. Comparison of stereologic techniques for the quantification of macrokaryotic size and number. Exp. Hematol. 14:782-788.

21. Curry, E. A. and M. W. Williams. 1983. Promalin or GA_3 increase pedicel and fruit length and leaf size of 'Delicious' apples treated with paclobutrazol. HortScience 18(2):214-215.

22. Curry, E. A., M. W. Williams. 1986. Influence of rootstock on intensity of response od 'Delicious' and 'Golden Delicious' apple treated with paclobutrazol. HortScience 21(3):731 (Abstr.)

23. Curry, E. A., M. W. Williams, and A. N. Reed. 1987. Triazol bioregulators to control growth of fruit trees: An update. Plant Growth Regulator Bul. 15:1,2.

24. Curry, E. A. and M. W. Williams. 1985. Quality evaluation of apples and pears from trees treated with Paclobutrazol. HortScience 19(3):529. (Abstr.)

25. Dalziel, J. and D. D. Lawrence. 1984. Biochemical and biological effects of kaurene oxidase inhibitors such as paclobutrazol. British Plant Growth Regulator, Monograph II.

26. Daniell, J. W., and R. D. Harrison. 1986. Effect of paclobutrazol and PPG 1721 on vegetative growth, physiological responses, and yields of peach trees. HortScience. 21(4):938. (Abstr.)

27. DeJong, T. M. and J. F. Doyle. 1984. Leaf gas exchange and growth response of mature 'Fantasia' nectarine trees to paclobutrazol. J. Amer. Soc. Hort. Sci. 109(6):878-882.

28. Dozier, W. A., Jr., and J. A. Barden. 1971. Net photosynthesis and respiration of apple leaves influenced by (2-chloroethyl) phosphonic acid. J. Amer. Soc. Hort. Sci. 96:789-790.

29. Dozier, W. A., Jr. and J. A. Barden. 1973. Influence of (2-chloroethyl) phosphonic acid on growth and abscision of young apple trees. J. Amer. Soc. Hort. Sci. 98:239-243.

30. Early, J. D., and G. C. Martin. 1986. Transport and metabolism of paclobutrazol in peach seedlings. HortScience 21(3):779 (Abstr.)

31. Ebercon, A., A. Blum and W. R. Jordan. 1977. A rapid colorimetric method for epicuticular wax content of sorghum leaves. Crop Science. 17:179-180.

32. Ebraham, K. S. and R. W. Campbell. 1986. Effect of paclobutrazol (PP333) and flurprimidol (EL500) on vegetative growth, fruit characteristics, and storage of 'Golden Delicious' and 'Red Delicious' apple. HortScience. 21(3):730. (Abstr.)

33. Elfving, D. C. and C. L. Chu. 1984. Effect of foliar- and soil-applied Paclobutrazol (PP333) on apple fruit quality parameters. HortScience. 19(3):577. (Abstr.)

34. Elfving, D. C., C. L. Chu, E. C. Lougheed and R. A. Cline. 1987. Effects of Daminozide and Paclobutrazol treatments on fruit ripening and storage behavior of 'McIntosh' apple. J. Amer. Soc. Hort. Sci. 112(6):910-915.

35. El-Otmani, M. and C. W. Coggins Jr. 1985. Fruit age and growth regulator effects on the quantity and structure of the epicuticular wax of 'Washington' navel orange fruit. J. Amer. Soc. Hort. Sci. 110(3):371-378.

36. Embree, C. G., W. E. Craig and F. R. Forsyth. 1987. Effect of Daminozide, Chlormequat, and Paclobutrazol on growth and fruiting of 'Clapp's Favorite' pears. HortScience 22(1):55-56.

37. Erez, A. 1984. Dwarfing peaches by pruning and by paclobutrazol. Acta Horticulturae 146:235-241.

38. Ferree, M. E. and J. A. Barden. 1971. The influence of strains and rootstocks on photosynthesis, respiration, and morphology of 'Delicious' apple trees. J. Amer. Soc. Hort. Sci. 96:453-457.

39. Ferree, D. C. and F. R. Hall. 1975. Influence of Benomyl and Oil on photosynthesis of apple leaves. HortScience 10(2):128-129.

40. Ferree, D. C. and F. R. Hall. 1978. Effects of growth regulators and multiple applications of pesticides on net photosynthesis and transpiration of greenhouse-grown apple trees. J. Amer Soc. Hort. Sci. 103(1):61-64.

41. Flore, J. A. and M. J. Bukovac. 1974. Pesticide effects on the plant cuticle: I. Responses of Brassica oleraceae L. to EPTC as indexed by epicuticular wax production. J. Amer. Soc. Hort. Sci. 99(1):34-37.

42. Flore, J. A. and M. J. Bukovac. 1974. Pesticide effects on the plant cuticle: II. EPTC effects on leaf cuticle morphology and composition in Brassica oleraceae L. J. Amer. Soc. Hort. Sci. 101(5):586-590.

43. Gianfagna, T. and G. Wulster. 1985. Height control of Freesia hybrida utilizing Ancymidol and paclobutrazol. HortScience 20(3):527. (Abstr.)

44. Goldsmith, I. R., K. A. Hood and J. MacMillan. 1983. Inhibition of Gibberellin biosynthesis in Gibberellin fujikuroi by PP333. Paper presented at an SCI symposium on Ergosterol Biosynthesis Inhibitors, Reading, UK. 20-24 March.

45. Ghosh, S. P. 1973. Internal structure and photosynthetic activity of different leaves of apple. J. Hort. Sci. 48:1-9.

46. Goodwin, T. W., and E. I. Mercer. 1983. Introduction to plant biochemistry. Pergamon Press, Oxford, New York, Toronto.

47. Greene, D. W. 1983. Effect of PP333 and its analogues on vegetative growth and fruit quality of 'Delicious' apples. HortScience 17:474. (Abstr.)

48. Greene, D. W. 1984. Effects of paclobutrazol (PP333) on growth and fruit quality of delicious apples. HortScience 19(3):578. (Abstr.)

49. Haller, M. H. and E. Smith. 1950. Evaluation of indexes for maturity for apples. Tech. Bull. 1003, U. S. Dept. of Agri., Washington.

50. Hammett, L. K. 1980. Evaluation of fresh market and storage quality of North Carolina apples. Tech. Bull. No. 262., North Carolina Agri. Res. Ser.

51. Hand, J. M., E. Young and A. C. Vasconcelos. 1982. Leaf water potential, stomatal resistance, and photosynthetic response to water stress in peach seedlings. Plant Physio. 69:1051-1054.

52. Hansen, P. 1967. ^{14}C-studies on apple trees. I. The effect of the fruit on the translocation and distribution of photosynthates. Physiol. Plant. 20:382-391.

53. Hansen, P. 1970. ^{14}C-studies on apple trees. V. Translocation of labelled compounds from leaves to fruit and their conversion within the fruit. Physiol. Plant. 23:564-573.

54. Harrison, R. and J. Daniell. 1986. Water stress and other factors affecting photosynthesis in peach seedlings. HortScience 21(4):948 (Abstr.)

55. Heinicke, A. J., and N. F. Childers. 1937. The daily rate of photosynthesis, during the growing season of 1935, of a young apple tree of bearing age. Memoir 201. Cornell University Agricultural Experiment Station.

56. Henery, M. J., and H. D. Sisler. 1984. Effects of sterol biosynthesis-inhibiting fungicides on cytochrome-P450 oxygenations in fungi. Pestic. Biochem. Physiol. 22:262-275.

57. Hewitt, H. G., J. F. Garrod, L. G. Copping and D. Greenwood. 1982. The effect of BTS 44584, a ternary sulphonium growth retardant, on net photosynthesis and yield of soybeans. In: Chemical Manipulation of Crop Growth and Development. Butterworths.

58. Holubowicz, T. 1983. The possibilities of changing the frost resistance of fruit trees by dodecyl ether of polyethylene glycol (DEPEG) and PP333 sprays. Acta Horticulturae 137:117-124.

59. ICI Technical Information Sheet. 1985.

60. Jaggard, K. W., P. V. Biscoe and D. K. Lawrence. 1982. An understanding of crop physiology in accessing a plant growth regulator on sugar beet. In: Chemical Manipulation of Crop Growth Development. Butterworths.

61. Jones, O. P. 1976. Effect of phloridzin and phloroglucinol on apple shoots. Nature. 262:392-393.

62. Jones, O. P. and S. G. S. Hatfield. 1976. Root initiation in apple shoots cultured in vitro with auxins and phenolic compounds. J. Hort. Sci. 51:495-499.

63. Kappel, F. and J. A. Flore. 1983. Effect of shade on photosynthesis, specific leaf weight, leaf chlorophyll content and morphology of young peach trees. J. Amer. Soc. Hort. Sci. 108(4):541-544.

64. Knowles, J. W. and W. A. Dozier Jr. 1986. Effects of Cultar (paclobutrazol) on vegetative growth and fruit quality and yield of peaches. HortScience. 21(4):938. (Abstr.)

65. Lakso, A. N. 1976. Characterizing apple tree canopies by fisheye photography. HortScience 11(4):404-405.

66. Lakso, A. N., and E. J. Seely. 1978. Environmentally induced responses of apple tree photosynthesis. HortScience. 13(6):646-650.

67. Lawrence, D. K. 1984. Effects of paclobutrazol, a new growth retardant on photosynthetic parameters in sugar beet. In: Proceedings of the Sixth International Congress of Photosynthesis.

68. Lever, B. G., S. J. Shearing and J. J. Batch. 1982. PP333 - A new broad spectrum growth retardant. Proceedings 1982 British Crop Protection Conference. Weeds 3:10.

69. Liyembani, S., and B. H. Taylor. 1985. Growth control of peach with paclobutrazol and XE1019. HortScience 20(3):595 (Abstr.)

70. Looney, N. E. 1968. Comparison of photosynthetic efficiency of two apple cultivars with their compact mutants. Proc. Amer. Soc. Hort. Sci. 92:34-36.

71. Lockwood, D. W. 1983. Foliar analysis. The University of Tennessee, Ag. Ext. Ser. Fruit Facts No. 3.

72. MacKinney, G. 1941. Absorption of light chlorophyll solutions. J. Biol. Chem. 140:315-322.

73. Marini, R. P. 1986. Do net gas exchange rates of green and red peach leaves differ. HortScience 21(1):118-120.

74. Marini, R. and E. L. Wefelmeyer. 1985. Growth of peach seedlings as affected by paclobutrazol and flurprimidol. HortScience 20(3):546. (Abstr.)

75. Mattus, G. E. 1966. Maturity standards for Red Delicious. Amer. Fruit Grower 86:16.

76. Mauk, C. S. , L. J. Lehman, S. M. Blankenship and C. R. Unrath. 1987. Uptake and translocation of exogenously applied paclobutrazol in 'Starkrimson Delicious' apple trees. HortScience 22(5):167. (Abstr.)

77. Proebsting, E. L. and H. H. Mills. 1985. Cold response in peach, apricot and cherry as influenced by applications of PP333. HortScience 20(1):88-90.

78. Proctor, J. T. A., W. J. Kyle, and J. A. Davies. 1975. The penetration of global solar radiation into apple trees. J. Amer. Soc. Hort. Sci. 100:40-44.

79. Quinlan, J. D. 1981. New chemical approaches to the control of fruit tree form and size. Acta Horticulturae. 120:95-106.

80. Quinlan, J. D. and P. J. Richardson. 1984. Effect of paclobutrazol (PP333) on apple shoot growth. Acta Horticulturae 146:105-111.

81. Sams, C. E., and J. A. Flore. 1982. The influence of age, position, and environmental variables on net photosynthetic rate of sour cherry leaves. J. Amer. Soc. Hort. Sci. 107(2):339-342.

82. Sestak, Z., J. Catsky, and P. G. Jarvis. 1971. Plant photosynthetic production. Manual of Methods. The Hauge.

83. Shearing, S. J. 1985. ICI experiences in West Europe on apples and pears. Paper presented at FEP Cultar Conf., New Zealand, 29 Apr-3 May 1985.

84. Simon, P., and R. Marcelle. 1983. Net photosynthesis and water stress of apple seedlings under developing drought conditions: effects of fungicide pre-treatment. IN: Effects of Stress on Photosynthesis. 133-139. Martinus Nijhoff/Dr. W. Junk. Boston, London.

85. Slack, E. M. 1974. Studies of stomatal distribution on the leaves of four apple varieties. J. Hort. Sci. 49:95-103.

86. Slavik, B. 1974. Methods of studying plant water relations. Chapman and Hall, London.

87. Stang, E. L. and G. G. Weis. 1984. Influence of Paclobutrazol plant growth regulator on strawberry plant growth, fruiting and runner suppression. HortScience 19(5):643-645.

88. Steffins, G. L. and S. Y. Wang. 1984. Physiological changes induced by paclobutrazol (PP333) in apple. Acta Horticulturae 146:135-142.

89. Steffins, G. L., S. Y. Wang, M. Faust and J. K. Byun. 1985. Growth, carbohydrate, and mineral element status of shoot and spur leaves and fruit of 'Spartan' apple trees treated with Paclobutrazol. J. Amer. Soc. Hort. Sci. 110(6):850-855.

90. Sterrett, J. P. 1983. Translocation and metabolism of injected ^{14}C-PP333 by young apple trees. Proc. Plant Growth Reg. Soc. Amer. 10:69.

91. Svihra, J., V. Mlada, J. Novotnak, and Z. Damsovicova. 1974. Photosynthetic differences in the leaves of certain rootstocks and the apple cultivars Red Delicious, Winter Golden Pearmain, and Summer Transparent. Rostlinna Vyroba 20:185-192 [Hort. Abstr. 45:2105; 1975.]

92. Swietlik, D. and S. S. Miller. 1983. The effect of paclobutrazol on growth and response to water stress of apple seedlings. J. Amer. Soc. Hort. Sci. 108(6):1076-1080.

93. Swietlik, D. and S. S. Miller. 1984. The effect of paclobutrazol on the growth and uptake of Ca and K by apple seedlings. Journal of Plant Nutrition. 7(11):1555-1565.

94. Swietlik, D., R. F. Korcak and M. Faust. 1983. Stomatal and nonstomatal inhibition of photosynthesis in water stressed apple seedlings. J. Amer. Soc. Hort. Sci. 108(1):54-57.

95. Tan, C. S. and B. R. Buttery. 1982. Response of stomatal conductance, transpiration, photosynthesis and leaf water potential in peach seedlings to different watering regimes. HortScience 17(2):222-223.

96. Tan, C. S. and B. R. Buttery. 1986. Photosynthesis, stomatal conductance, and leaf water potential in response to temperature and light in peach. HortScience 21(5):1180-1182.

97. Titova, N. V. and G. V. Shiskanv. 1976. Photosynthesis and pigment content in apple trees on different rootstocks. In: Fotosintez Yabloni i Vinograda Razlichn. Vsloviyahk Proizrastaniya. 13-32. [Hort. Abstr. 47:4283; 1977.]

98. Tukey, L. D. 1983. Exploring the use of PP333, a new growth regulator for apple trees. Pa. Fruit News. 62:64-66.

99. Unrath, C. R., and A. M. El-Khoreiby. 1986. A comparison of paclobutrazol foliar and soil drench applications on vegetative growth and fruit quality of apples. HortScience. 21(3):178.

100. Wang, C. Y. 1985. Reduction of chilling injury in seedlings of cucumber and zucchini squash by paclobutrazol HortScience 20(3):526. (Abstr.)

101. Wang, C. Y. and G. L. Steffens. 1987. Postharvest response of 'Spartan' apples to preharvest paclobutrazol treatment. HortScience 22(2):276-278.

102. Watson, R. L., J. J. Landsberg, and M. R. Thorpe. 1978. Photosynthetic characteristics of the leaves of 'Golden Delicious' apple. Plant Cell Environ. 1:51-58.

103. Westwood, M. N. and Q. B. Zielinski. 1966. Comparative growth habit and leaf composition of a compact mutant and standard Delicious apple. Proc. Amer. Soc. Hort. Sci. 88:9-13.

104. Wieland, W. F. and R. L. Wample. 1985. Effects of paclobutrazol on shoot growth, photosynthesis and root growth in apple. HortScience 19(3):529. (Abstr.)

105. Wiggins, T. E., and B. C. Baldwin. 1984. Binding of azole fungicides related to diclobutrazol to cytrochrome P-450. Pestic. Sci. 15:206-209.

106. Williams, M. W. and L. J. Edgerton. 1983. Vegetative growth control of apple and pear trees with ICI PP333 (paclobutrazol). A chemical analog of Bayleton. Acta Horticulturae 137:111-116.

107. Williams, M. W. 1984. Improve fruiting efficiency. Acta Horticulturae 146:97-104.

108. Williams, M. W., E. A. Curry and D. B. Visser. 1984. Methods of application of paclobutrazol on deciduous fruit trees. HortScience 19(3):577. (Abstr.)

109. Wood, B. W. 1984. Influence of paclobutrazol on selected growth and chemical characteristics of young pecan seedlings. HortScience 19(6):837-239.

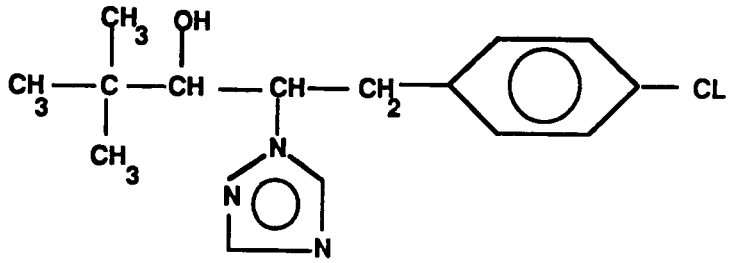
110. Wooge, J. D. and J. A. Barden. 1987. Seasonal changes in specific leaf weight and leaf anatomy of apple. HortScience 22(2): 292-294.

APPENDICES

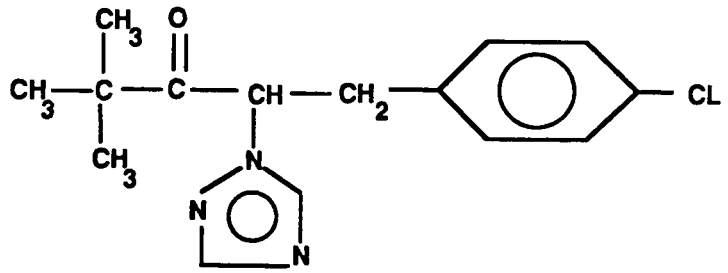
APPENDIX A

CHEMICAL STRUCTURES OF PACLOBUTRAZOL (a), BAYLETON (b), XE1019 (c), RSW0411 (d), AND LAB 150 978 (e).

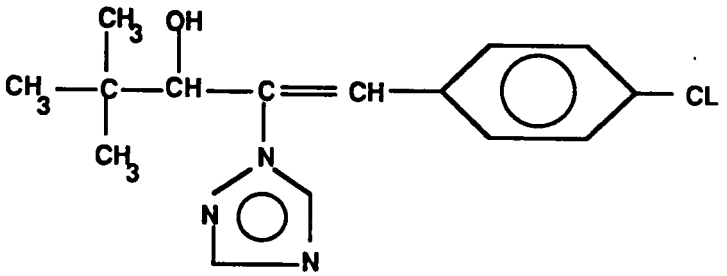
a.



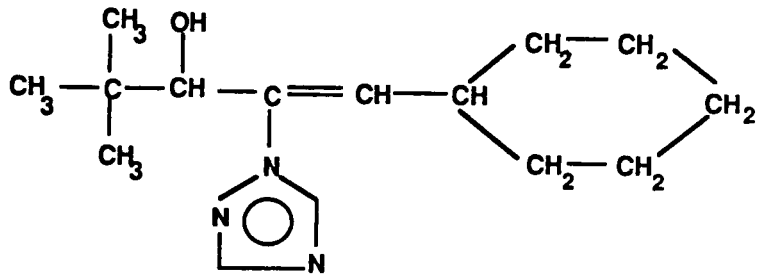
b.



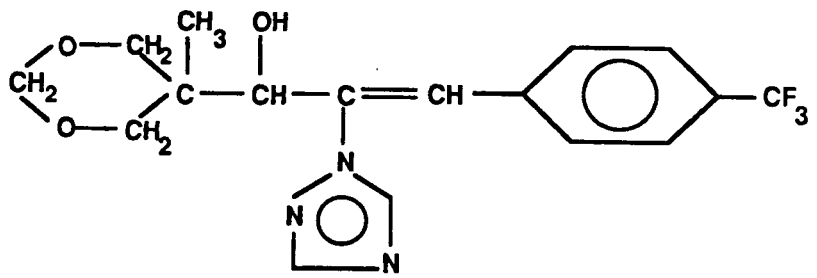
c.



d.



e.

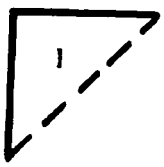


APPENDIX B

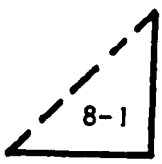
INITIAL DIURNAL BLOCKING SCHEME FOR WHOLE TREE PHOTOSYNTHESIS

DAY

TIME	M	T	W	TH	F
10:00	1 / 8-1	1 / 7-2	1 / 6-3	1 / 5-4	1 / 4-5
11:00	2 / 8-2	2 / 7-2	2 / 6-4	2 / 5-5	2 / 4-1
12:00	3 / 8-3	3 / 7-4	3 / 6-5	3 / 5-1	3 / 4-2
1:00	4 / 8-4	4 / 7-5	4 / 6-1	4 / 5-2	4 / 4-3
2:00	5 / 8-5	5 / 7-1	5 / 6-2	5 / 5-3	5 / 4-4



Block Number



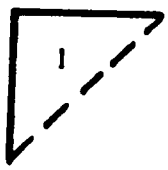
Rep - TMT Numbers

APPENDIX C

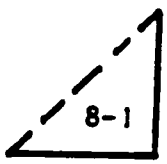
SECOND DIURNAL BLOCKING SCHEME FOR WHOLE TREE PHOTOSYNTHESIS

DAY

TIME	M	T	W	TH	F
7:30	1 / 8-1	1 / 7-2	1 / 6-3	1 / 5-4	1 / 4-5
8:30	2 / 8-2	2 / 7-2	2 / 6-4	2 / 5-5	2 / 4-1
9:30	3 / 8-3	3 / 7-4	3 / 6-5	3 / 5-1	3 / 4-2
4:15	4 / 8-4	4 / 7-5	4 / 6-1	4 / 5-2	4 / 4-3
5:15	5 / 8-5	5 / 7-1	5 / 6-2	5 / 5-3	5 / 4-4



Block Number



Rep - TMT Numbers

APPENDIX D

STATISTICAL ANALYSIS SYSTEM PROGRAM FOR THE ANALYSIS OF WATER STRESS PHOTOSYNTHESIS DATA WITH THE BEST FIT ASYMPTOTIC LINE

```
OPTIONS LS=72;
DATA WS;
TITLE ' ';
**TITLE1 '1987 APPLE WATER STRESS STUDY';
**TITLE2 'SECOND YEAR EFFECTS';
**TITLE3 'CORRECTED PN RATES';
INPUT EXP 1 REP 2 TMT 3 LEAF 4-5 LT 6-8 1 HUM 9-11 1 QUAN 12-15
      RES 16-17 2 TRANS 18-21 2 CO 22-23 RH 24-25 DGC 26-28 1
      PAR 29-32 DATE 33-35 PSI 36-38 STCT 39-41 VOL 42-44 1;
F=CO*.1000599/((DGC+273.15)*140087.5);
PN=F*360000000;
MGPA=(PSI*6.895)/1000;

**IF DATE> 166 AND DATE< 180 THEN DELETE;
**IF DATE> 181 AND DATE< 185 THEN DELETE;
**IF DATE> 185 AND DATE< 190 THEN DELETE;
** DATE=183 THEN DELETE;
** DATE=176 THEN DELETE;
IF TMT=1 THEN L=0;
IF TMT=2 THEN L=300;
IF TMT=3 THEN L=600;
IF TMT=4 THEN L=1200;
IF TMT=5 THEN L=2400;
L=L+1;
IF REP=3 AND TMT=1 THEN TMT=6;
IF REP=4 AND TMT=1 THEN TMT=6;
IF REP=5 AND TMT=1 THEN TMT=6;
IF REP=7 AND TMT=1 THEN TMT=6;
  IF TMT=6 THEN DELETE;

CARDS;
91201265268053030053015263130400166250889192
```

The data set for the program should be placed here.

```
RUN;
DATA WS;
  SET WS;
  IF TMT = 6 THEN DELETE;
RUN;

PROC SORT; BY TMT VOL;

PROC NLIN; BY TMT;
PARAMETERS A=250 B=350 K=.05, .1, .2;
MODEL PN=A-B*(EXP(-K*VOL));
OUTPUT OUT= NEW P=YHAT;
RUN;
```

This section calculates the iterations to determine the best fit line.

```
PROC GPLOT UNIFORM;
  PLOT YHAT*VOL PN*VOL/OVERLAY;
  SYMBOL1 I=SPLINE V=NONE C=BLACK;
  SYMBOL2 I=NONE V=STAR C=BLACK;
  BY TMT;
RUN;

PROC GPLOT UNIFORM;
  PLOT YHAT*VOL=TMT;
  SYMBOL1 I=SPLINE V=NONE C=BLACK L=1;
  SYMBOL2 I=SPLINE V=NONE C=BLACK L=2;
  SYMBOL3 I=SPLINE V=NONE C=BLACK L=5;
  SYMBOL4 I=SPLINE V=NONE C=BLACK L=8;
  SYMBOL5 I=SPLINE V=NONE C=BLACK L=10;

RUN;
DATA DERR;
  DO TMT = 1 TO 5;
    DO VOL = 0 TO 25;
      IF TMT = 1 THEN DO;
         A = 17.4612;
         B = 30.7239;
         K = 0.4488;
       END;
       IF TMT = 2 THEN DO;
         A = 17.2885;
         B = 32.1684;
         K = 0.4664;
       END;
       IF TMT = 3 THEN DO;
         A = 17.2901;
         B = 37.3500;
         K = 0.6429;
       END;
      IF TMT = 4 THEN DO;
         A = 18.1547;
         B = 33.5905;
         K = .4916;
      END;
      IF TMT = 5 THEN DO;
         A = 17.9674;
         B = 53.7518;
         K = .7224;
      END;
      YPRIME = A - B*EXP(-K*VOL);
      VOL1 = 25 - VOL;
      OUTPUT;
    END;
  END;
RUN;
```

This section plots each treatment and its data points.

This section plots all of the treatment lines on the same graph.

This section calculates the derivative of the treatment line.

```
PROC GPLOT UNIFORM;
  PLOT YPRIME*VOL1=TMT;
  SYMBOL1 I=SPLINE V=NONE C=BLACK L=1;
  SYMBOL2 I=SPLINE V=NONE C=BLACK L=2;
  SYMBOL3 I=SPLINE V=NONE C=BLACK L=5;
  SYMBOL4 I=SPLINE V=NONE C=BLACK L=8;
  SYMBOL5 I=SPLINE V=NONE C=BLACK L=10;
RUN;
```

This section plots all the derivative lines on the same graph.

APPENDIX E

GRAPHS OF INDIVIDUAL TREATMENT LINES OF THE WATER STRESS PHOTOSYNTHESIS DATA WITH THE BEST FIT ASYMPTOTIC LINE

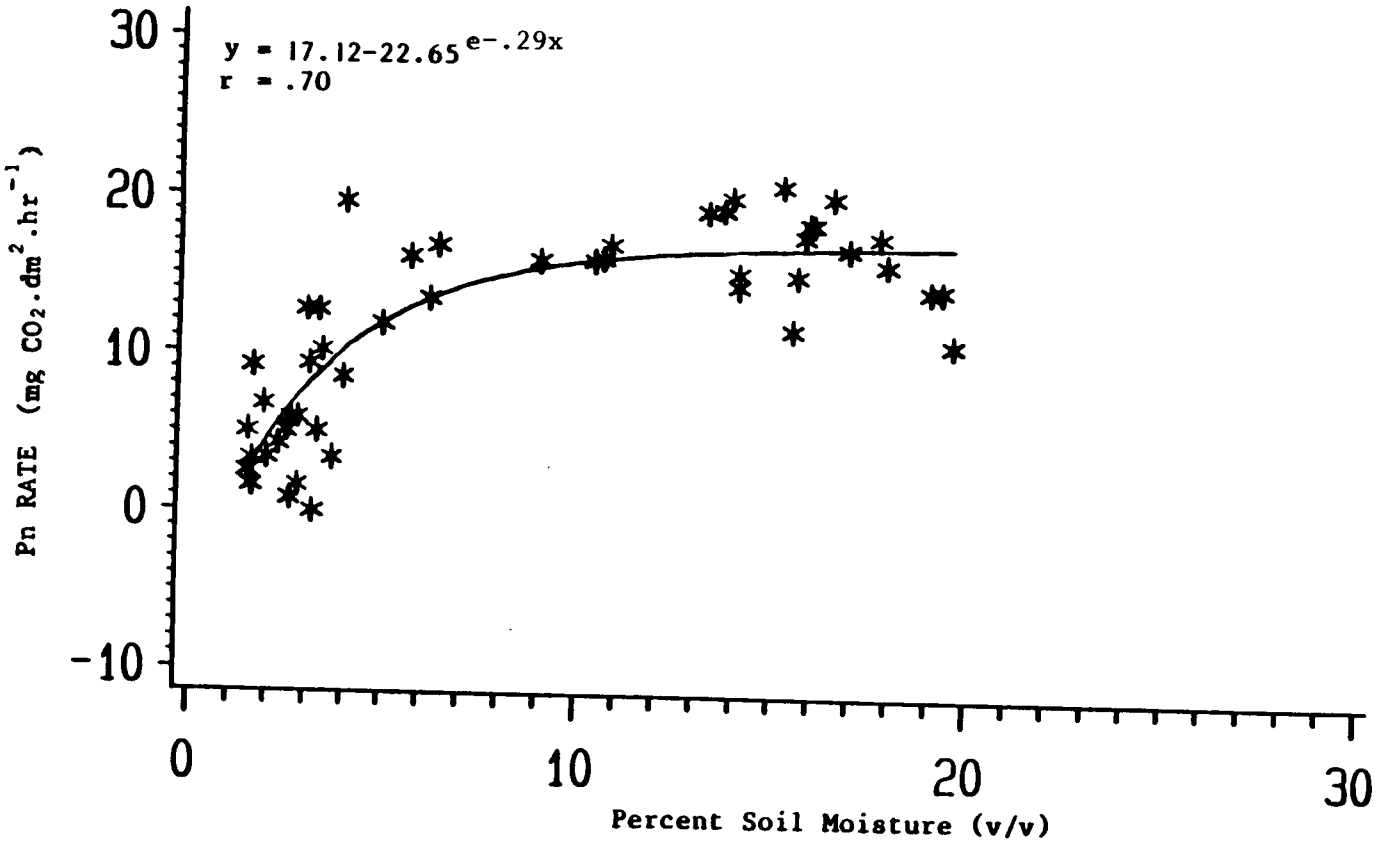


Figure E.1. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture.

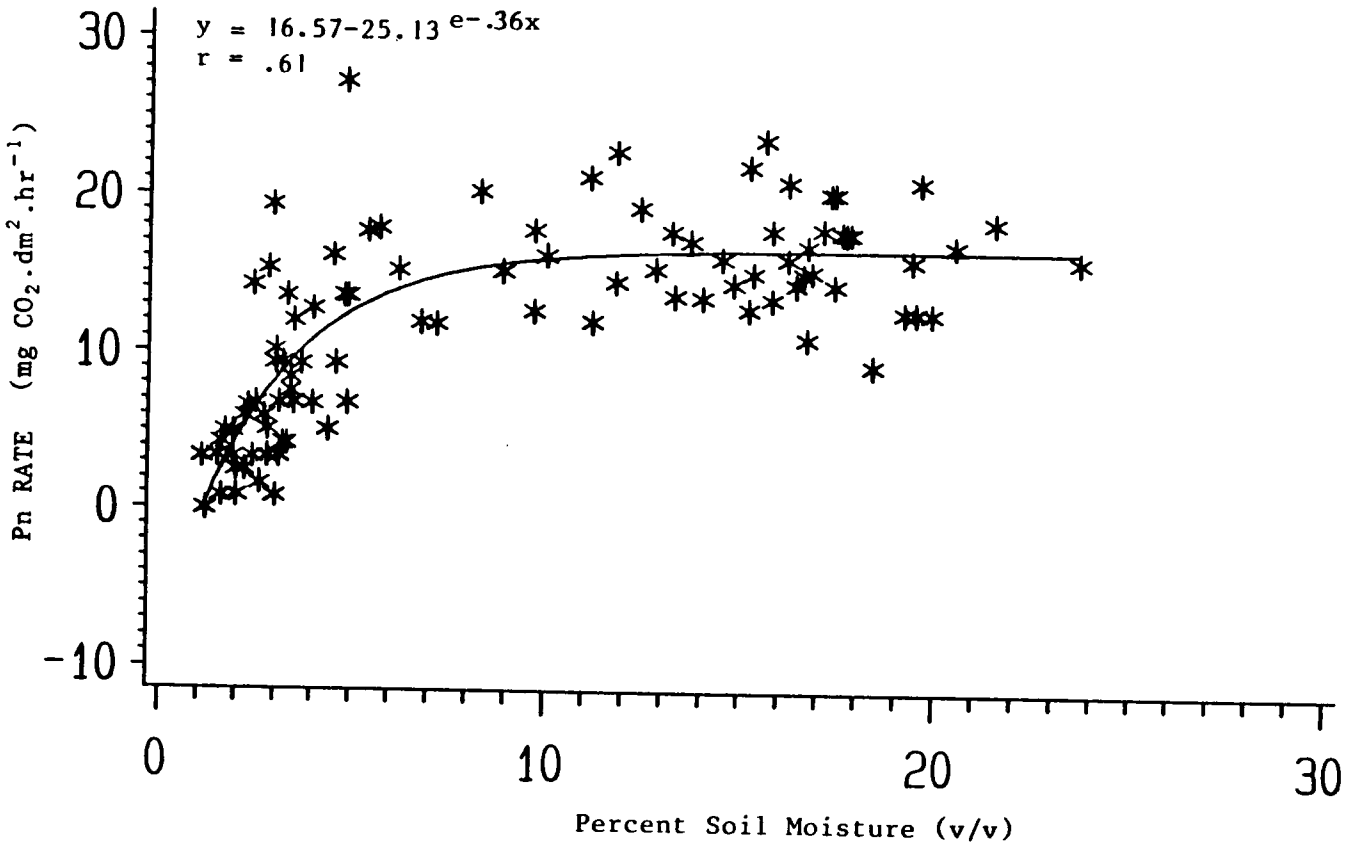


Figure E.2. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 300 ppm paclobutrazol

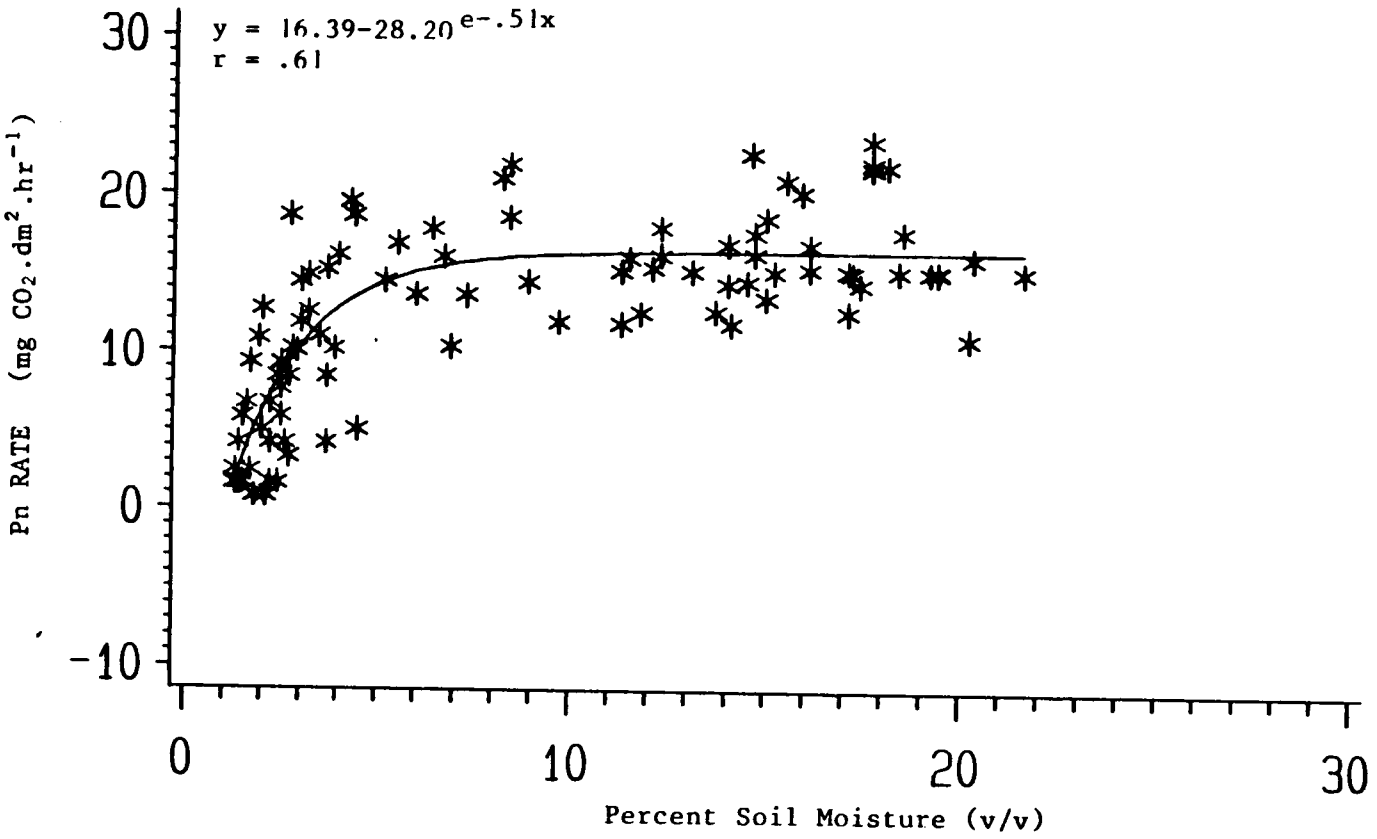


Figure E.3. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 600 ppm paclobutrazol.

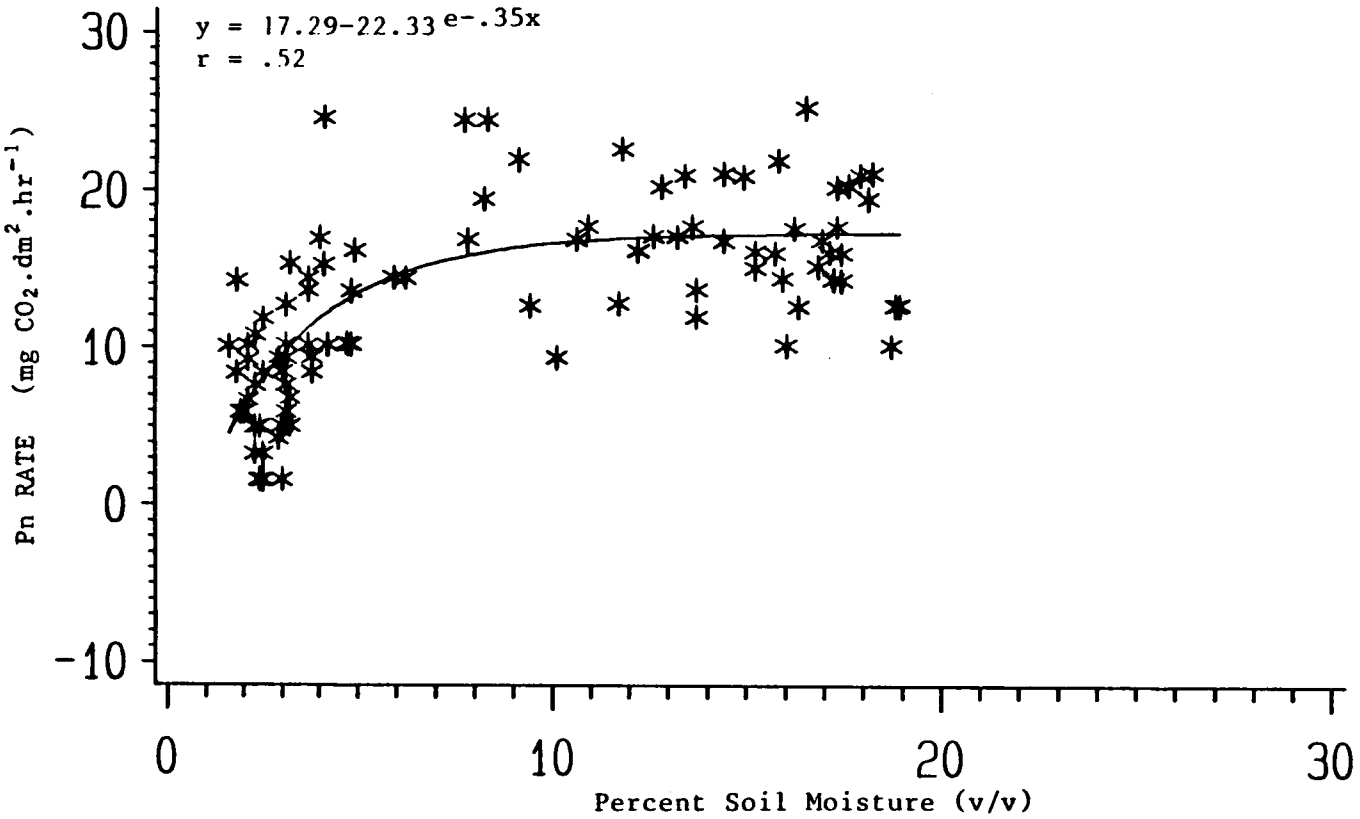


Figure E.4. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 1200 ppm paclobutrazol.

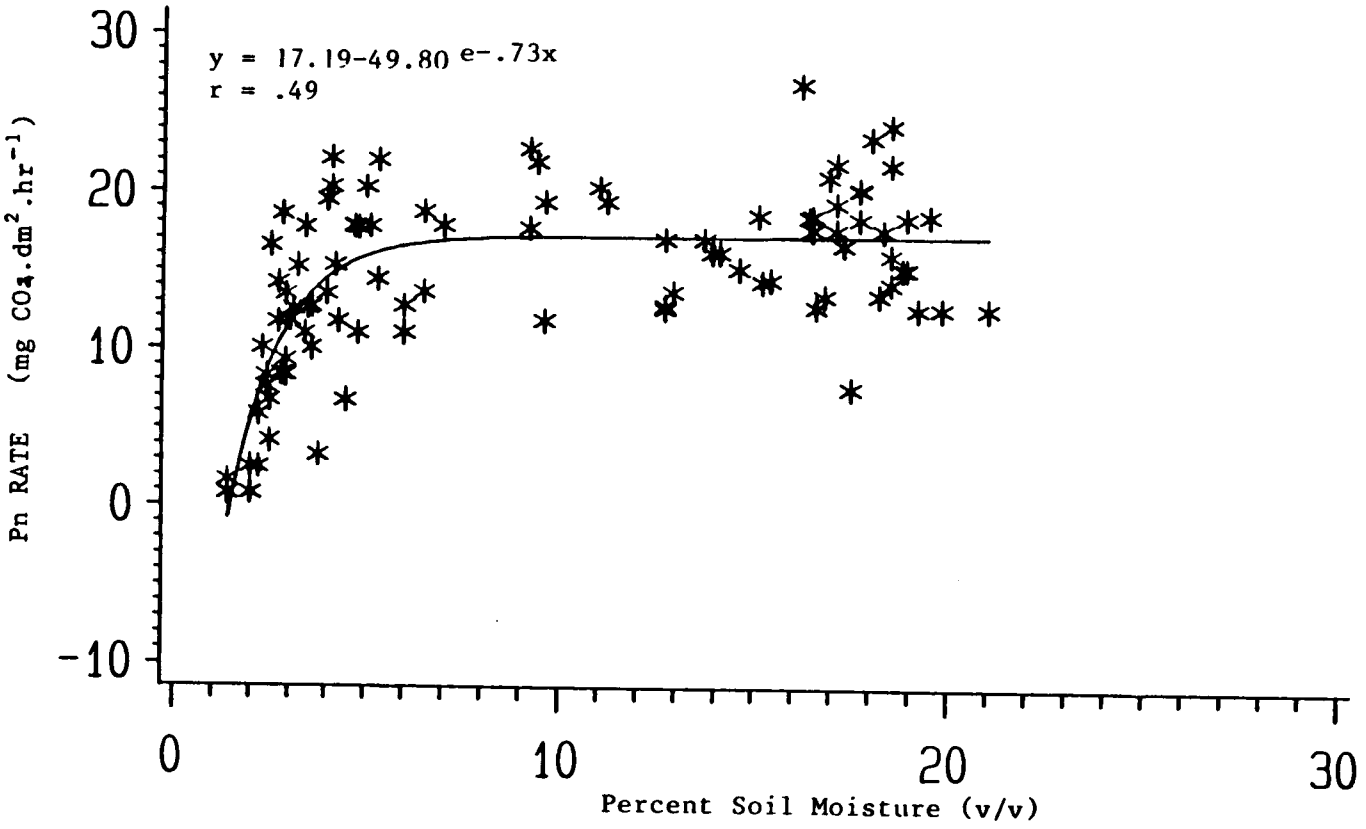


Figure E.5. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 2400 ppm paclobutrazol.

APPENDIX F

STASTICAL ANALYSIS SYSTEM PROGRAM FOR THE ANALYSIS OF WATER STRESS PHOTOSYNTHESIS DATA WITH THE BEST FIT BROKEN REGRESSION LINE

```
OPTIONS LS=72;
DATA WS;
**TITLE1 '1987 APPLE WATER STRESS STUDY';
**TITLE2 'SECOND YEAR EFFECTS';
**TITLE3 'CORRECTED PN RATES';
TITLE '  ';
INPUT EXP 1 REP 2 TMT 3 LEAF 4-5 LT 6-8 1 HUM 9-11 1 QUAN 12-15
      RES 16-17 2 TRANS 18-21 2 CO 22-23 RH 24-25 DGC 26-28 1
      PAR 29-32 DATE 33-35 PSI 36-38 STCT 39-41 VOL 42-44 1;
F=CO*.1000599/((DGC+273.15)*140087.5);
PN=F*360000000;

IF DATE=183 THEN DELETE;
IF DATE=176 THEN DELETE;

IF TMT=1 THEN L=0;
IF TMT=2 THEN L=300;
IF TMT=3 THEN L=600;
IF TMT=4 THEN L=1200;
IF TMT=5 THEN L=2400;
L=L+1;
IF REP=3 AND TMT=1 THEN TMT=6;
IF REP=4 AND TMT=1 THEN TMT=6;
IF REP=5 AND TMT=1 THEN TMT=6;
IF REP=7 AND TMT=1 THEN TMT=6;
IF TMT=6 THEN DELETE;


CARDS;
91201265268053030053015263130400166250889192
```

The data set for the program should be placed here.

```
RUN;
DATA WS;
  SET WS;
  IF TMT = 6 THEN DELETE;
RUN;

PROC SORT;
  BY TMT VOL;
RUN;
```

```
PROC NLIN;
  BY TMT;
  PARAMETERS   A        =  -5
               B1       =  0.08
               B2       =  0.0025
               X1       =  5;
  BOUNDS 3 < X1 < 15;

  U1 = (VOL <= X1);
  U2 = (X1 < VOL);

  Z1 = VOL;
  Z2 = VOL - X1;

  MODEL PN = U1*(A + B1*Z1)
           + U2*(A+(B1*X1)+ B2*Z2);
  OUTPUT OUT=NEW P=PN_HAT PARMS=A B1 B2 X1;
RUN;

PROC GPLOT DATA=NEW UNIFORM;
  BY TMT;
  PLOT PN_HAT*VOL  PN*VOL PN_HAT*X1/OVERLAY;

  SYMBOL1 V = NONE I = SPLINE C=BLACK;
  SYMBOL2 V = STAR I = NONE C = BLACK;
  SYMBOL3 V = NONE I = JOIN C = BLACK;
  LABEL PN_HAT = 'PN RATE';
  LABEL VOL = 'SOIL MOISTURE (% VOL)';
```

This section calculates the 2 best fit lines for the data.

This section plots the individual lines and data points along with the vertical line.

APPENDIX G

GRAPHS OF INDIVIDUAL TREATMENT LINES OF THE WATER STRESS PHOTOSYNTHESIS DATA WITH THE BEST FIT BROKEN REGRESSION LINE

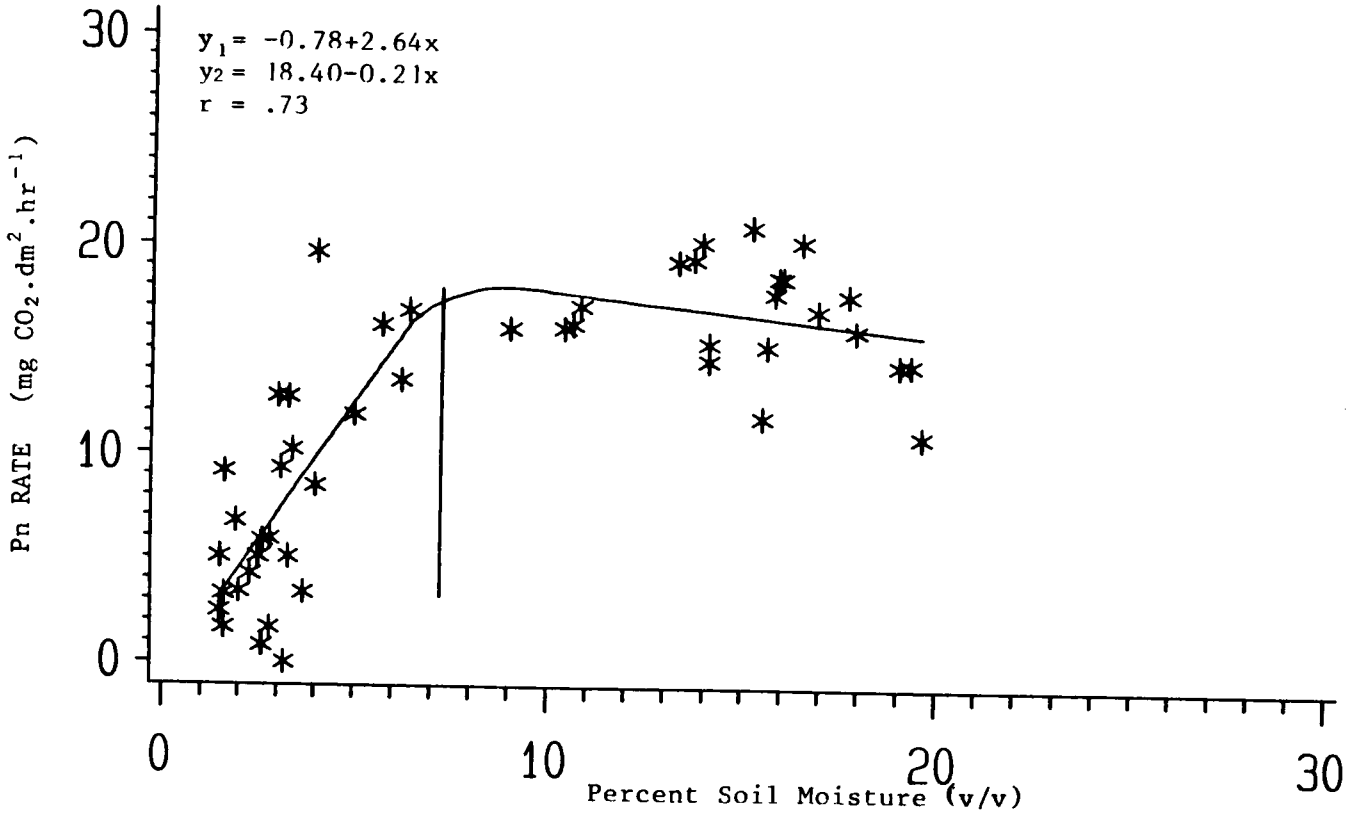


Figure G.1. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture.

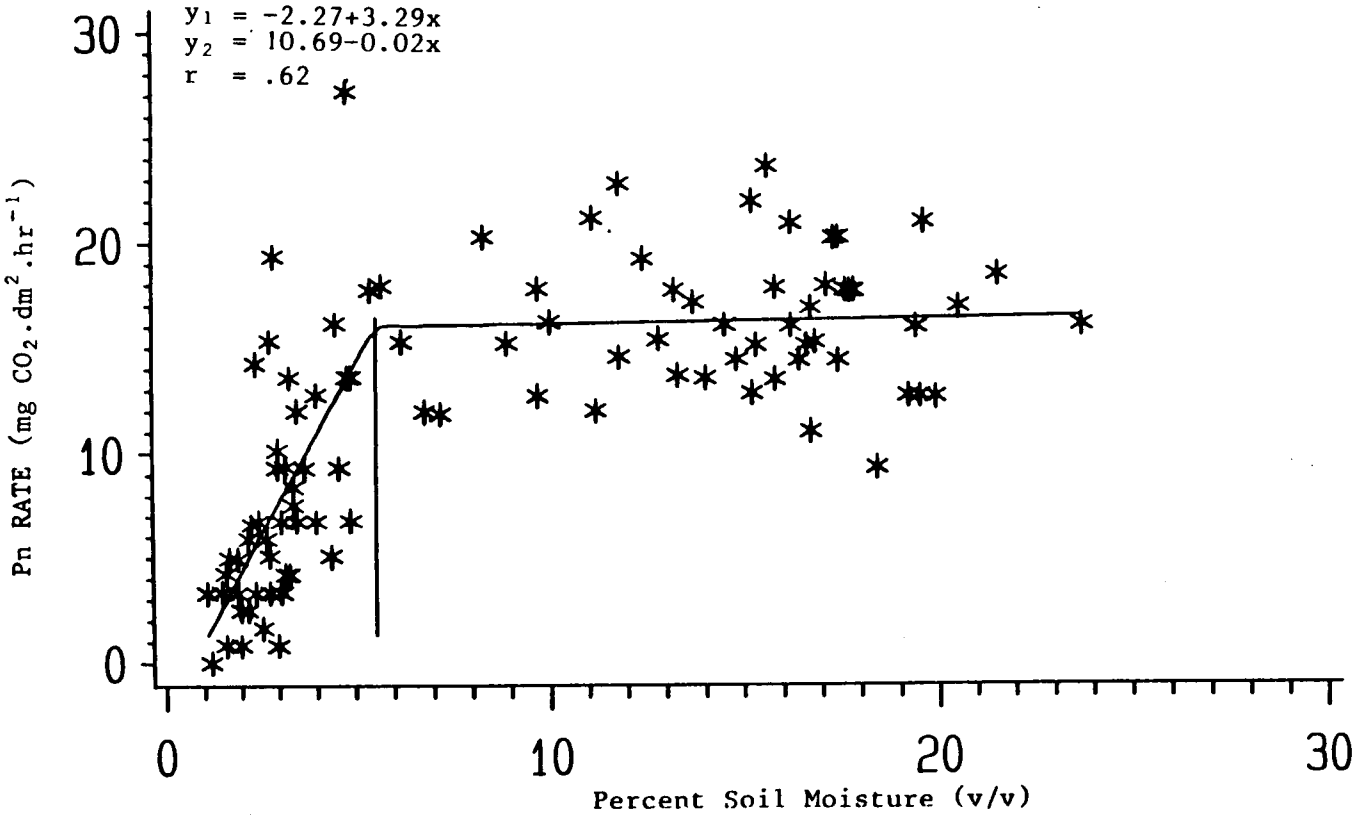


Figure G.2. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 300 ppm paclobutrazol.

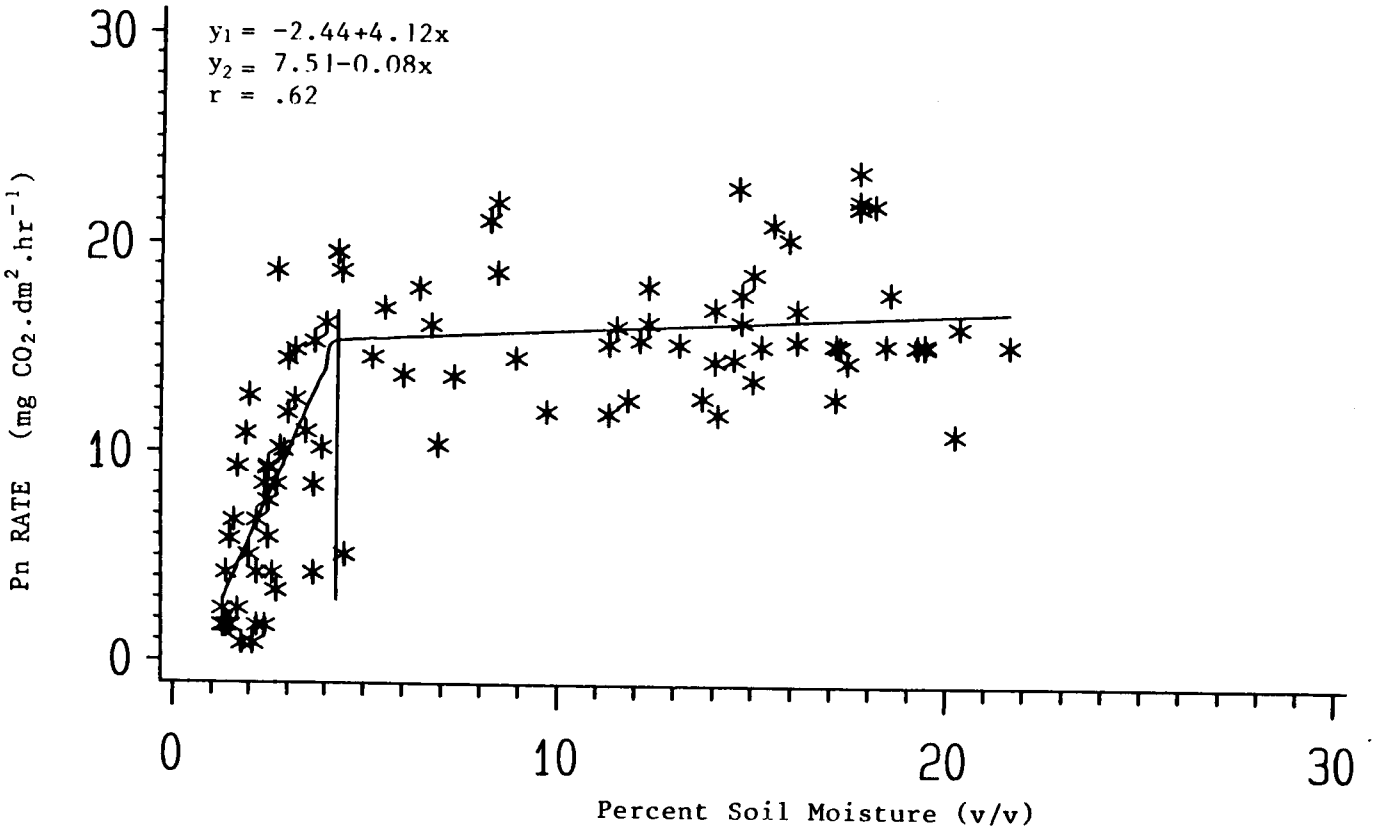


Figure G.3. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 600 ppm paclobutrazol.

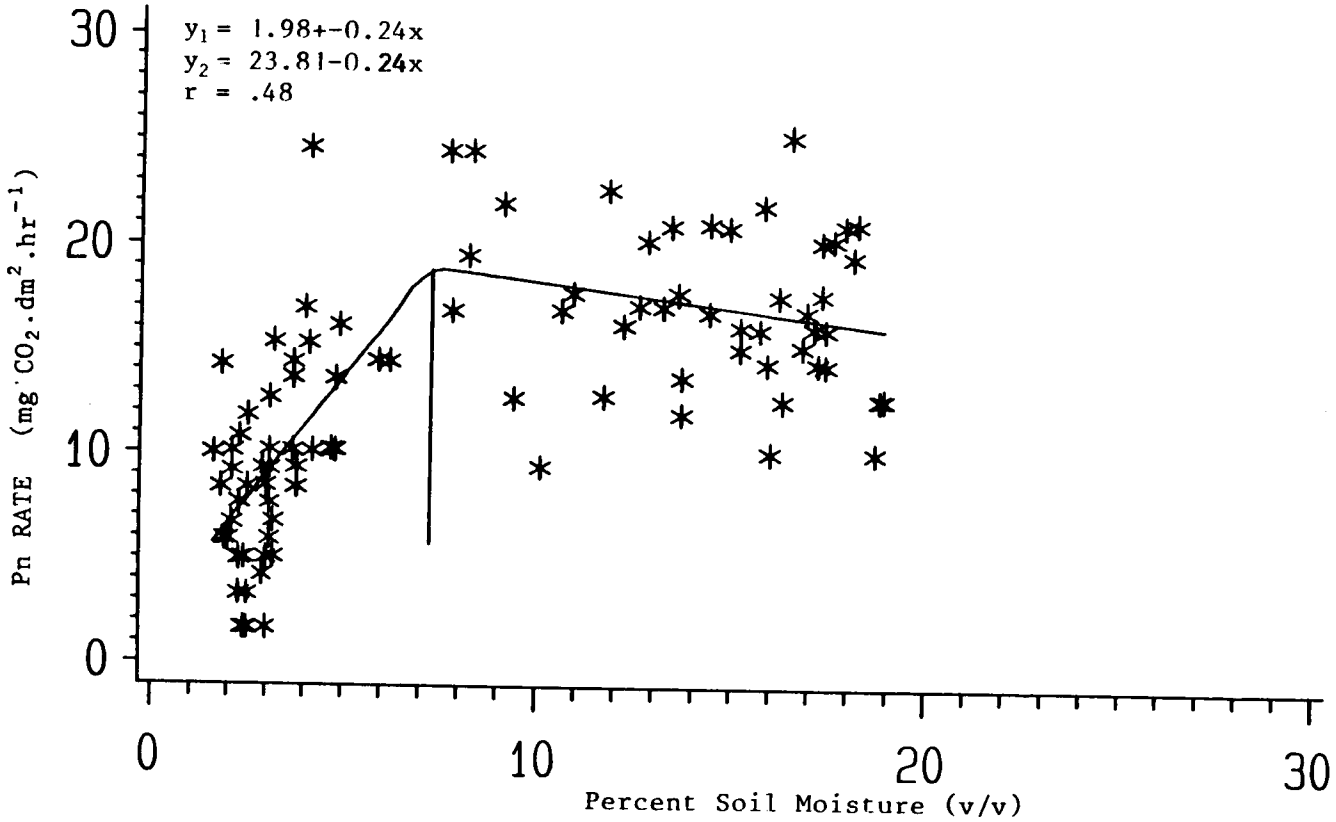


Figure G.4. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 1200 ppm paclobutrazol.

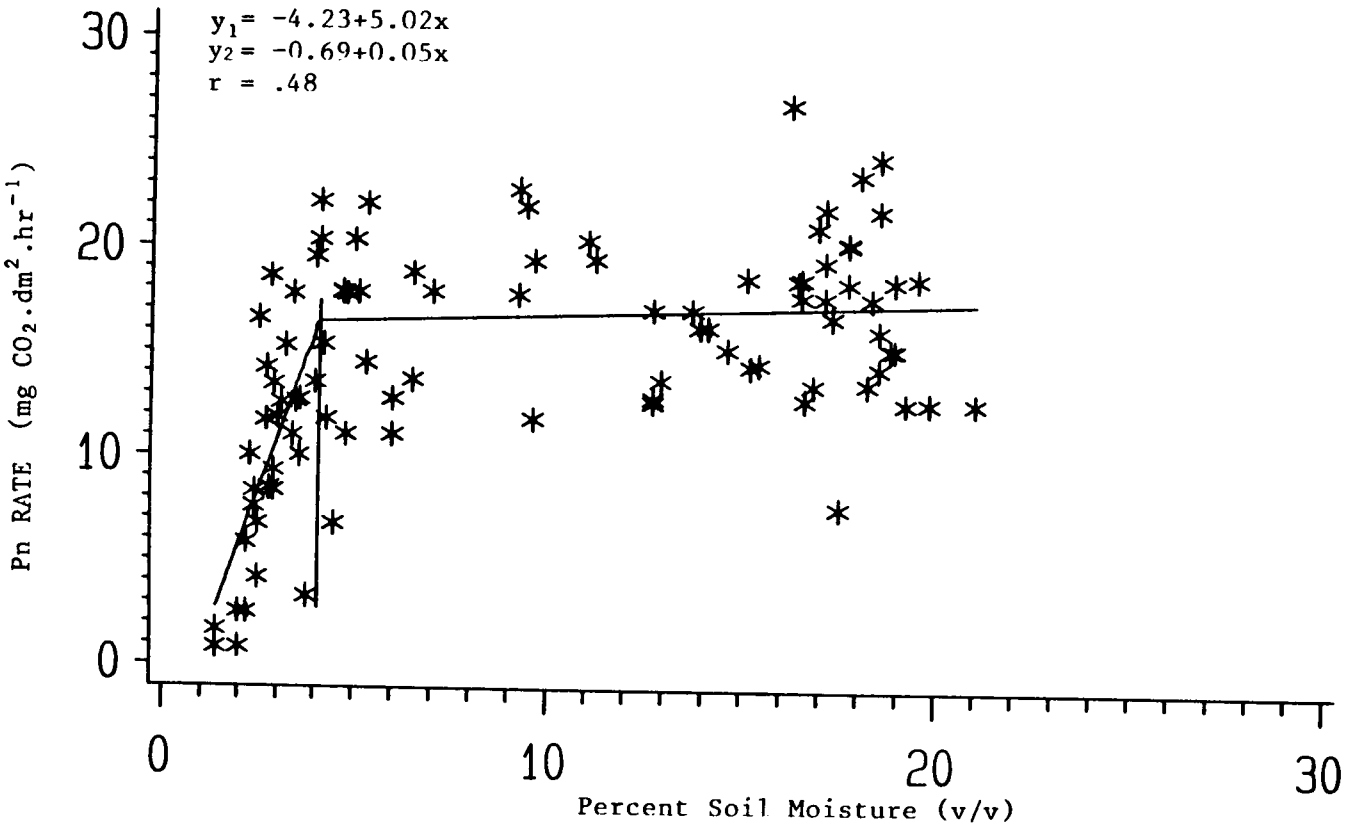


Figure G.5. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 2400 ppm paclobutrazol.

APPENDIX H

STATISTICAL ANALYSIS SYSTEM PROGRAM FOR THE ANALYSIS OF WATER STRESS PHOTOSYNTHESIS DATA WITH THE BEST FIT QUADRATIC LINE

```
OPTIONS LS=72;
DATA WS;
**TITLE1 '1987 APPLE WATER STRESS STUDY';
**TITLE2 'SECOND YEAR EFFECTS';
**TITLE3 'CORRECTED PN RATES';
TITLE '   ';
INPUT EXP 1 REP 2 TMT 3 LEAF 4-5 LT 6-8 1 HUM 9-11 1 QUAN 12-15
      RES 16-17 2 TRANS 18-21 2 CO 22-23 RH 24-25 DGC 26-28 1
      PAR 29-32 DATE 33-35 PSI 36-38 STCT 39-41 VOL 42-44 1;
F=CO*.1000599/((DGC+273.15)*140087.5);
PN=F*360000000;
**IF DATE> 166 AND DATE< 180 THEN DELETE;
**IF DATE> 181 AND DATE< 185 THEN DELETE;
**IF DATE> 185 AND DATE< 190 THEN DELETE;
IF DATE=183 THEN DELETE;
IF DATE=176 THEN DELETE;
IF TMT=1 THEN L=0;
IF TMT=2 THEN L=300;
IF TMT=3 THEN L=600;
IF TMT=4 THEN L=1200;
IF TMT=5 THEN L=2400;
L=L+1;
IF REP=3 AND TMT=1 THEN TMT=6;
IF REP=4 AND TMT=1 THEN TMT=6;
IF REP=5 AND TMT=1 THEN TMT=6;
IF REP=7 AND TMT=1 THEN TMT=6;
**IF TMT=6 THEN DELETE;

IF DATE=166 THEN PC=(14.3543-PN);
IF DATE=170 THEN PC=(15.3520-PN);
IF DATE=174 THEN PC=(18.5634-PN);
IF DATE=176 THEN PC=(26.8424-PN);
IF DATE=178 THEN PC=(16.1604-PN);
IF DATE=180 THEN PC=(22.5098-PN);
IF DATE=181 THEN PC=(18.8049-PN);
IF DATE=182 THEN PC=(13.4792-PN);
IF DATE=183 THEN PC=(11.9371-PN);
IF DATE=184 THEN PC=(20.0151-PN);
IF DATE=185 THEN PC=(19.2296-PN);
IF DATE=187 THEN PC=(21.2150-PN);
IF DATE=189 THEN PC=(20.9762-PN);
IF DATE=190 THEN PC=(18.0437-PN);


CARDS;
```

This section calculates the subtractions from the watered control.

The data set for the program should be placed here.

```
RUN;
```

```
DATA WS;
  SET WS;
  IF TMT = 6 THEN DELETE;
  IF TMT=. THEN DELETE;
RUN;

PROC SORT; BY TMT VOL;

PROC NLIN;BY TMT;
PARAMETERS A=3 B=20 K=.05,.1,.2;
MODEL PC= A-B*(EXP(-K*VOL));
OUTPUT OUT= NEW P=YHAT;
RUN;

PROC GPLOT UNIFORM;
  PLOT YHAT*VOL PC*VOL/OVERLAY;
  SYMBOL1 I=SPLINE V=NONE C=BLACK;
  SYMBOL2 I=NONE V=STAR C=BLACK;
  BY TMT;
RUN;

PROC GPLOT;
  PLOT YHAT*VOL=TMT;
  SYMBOL1 I=SPLINE V=NONE C=BLACK L=1;
  SYMBOL2 I=SPLINE V=NONE C=BLACK L=2;
  SYMBOL3 I=SPLINE V=NONE C=BLACK L=5;
  SYMBOL4 I=SPLINE V=NONE C=BLACK L=8;
  SYMBOL5 I=SPLINE V=NONE C=BLACK L=10;
RUN;


DATA DER;
  DO TMT = 1 TO 5;
    DO VOL=0 TO 25;
      IF TMT = 1 THEN DO;
         A = .9870;
         B = -25.5091;
         K = .3500;
      END;
      IF TMT = 2 THEN DO;
         A = 1.411;
         B = -28.3856;
         K = .4068;
      END;
      IF TMT = 3 THEN DO;
         A = 1.512;
         B = -30.4860;
         K = .5308;
      END;
```

This section performs the iterations around the data to get the best fit asymptotic line.

This section plots each treatment with its data points.

This section plots all of the treatment lines on the same graph.

This section calculates the derivative of the treatment lines

```
      IF TMT = 4 THEN DO;
         A = .5692;
         B = -26.8185;
         K = .4049;
      END;
      IF TMT = 5 THEN DO;
         A = .9394;
         B = -54.3446;
         K = .7478;
      END;
      YPRIME = A - B*EXP(-K*VOL);
      VOL1 = 25 - VOL;
      OUTPUT;
    END;
  END;
RUN;

PROC GPLOT;
  PLOT YPRIME*VOL1=TMT;
  SYMBOL1 I=SPLINE V=NONE C=BLACK L=1;
  SYMBOL2 I=SPLINE V=NONE C=BLACK L=2;
  SYMBOL3 I=SPLINE V=NONE C=BLACK L=5;
  SYMBOL4 I=SPLINE V=NONE C=BLACK L=8;
  SYMBOL5 I=SPLINE V=NONE C=BLACK L=10;
RUN;
```

This section plots all the derivative lines on the same graph.

APPENDIX I

GRAPHS OF INDIVIDUAL TREATMENT LINES OF THE WATER STRESS PHOTOSYNTHESIS DATA WITH THE BEST FIT ASYMPTOTIC LINE FOR THE SUBTRACTION METHOD

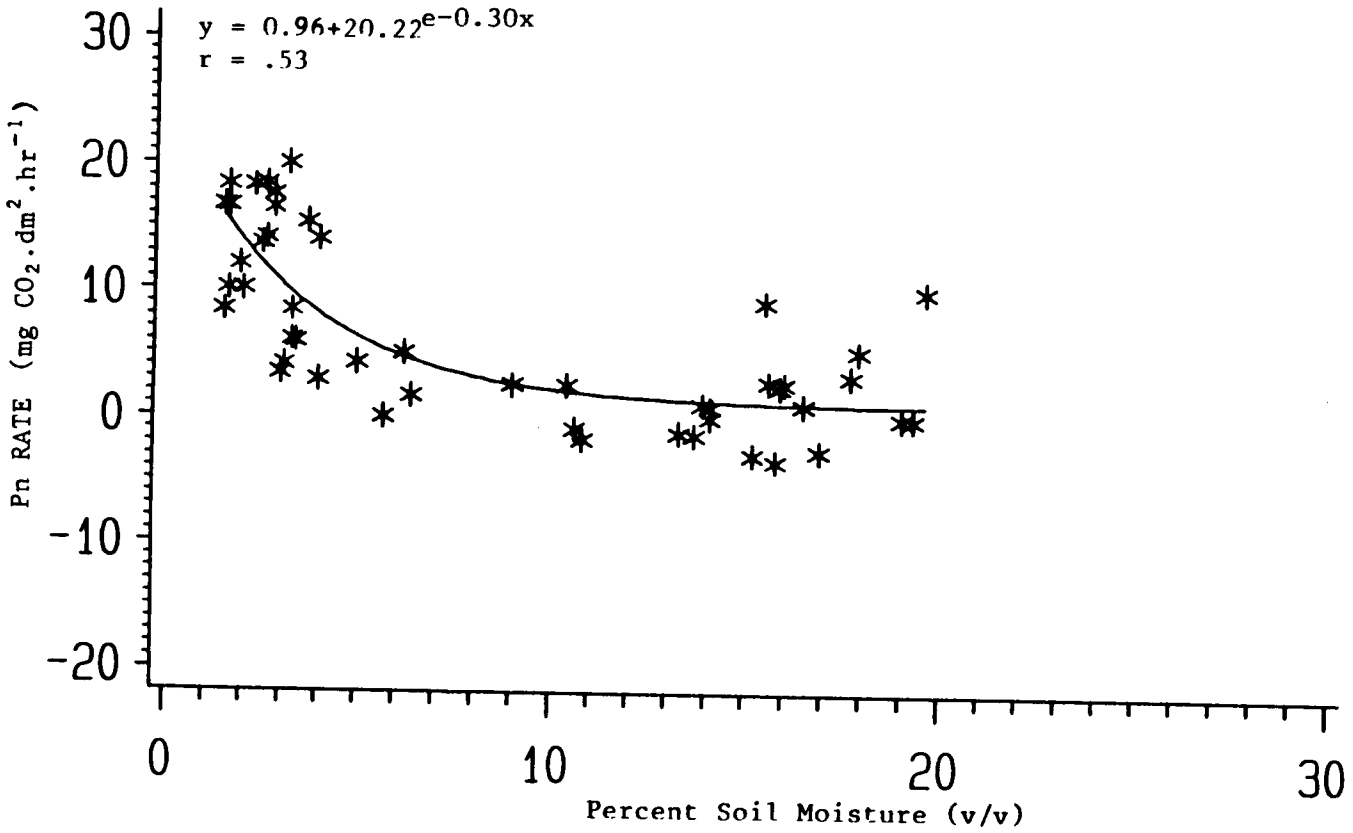


Figure I.1. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture.

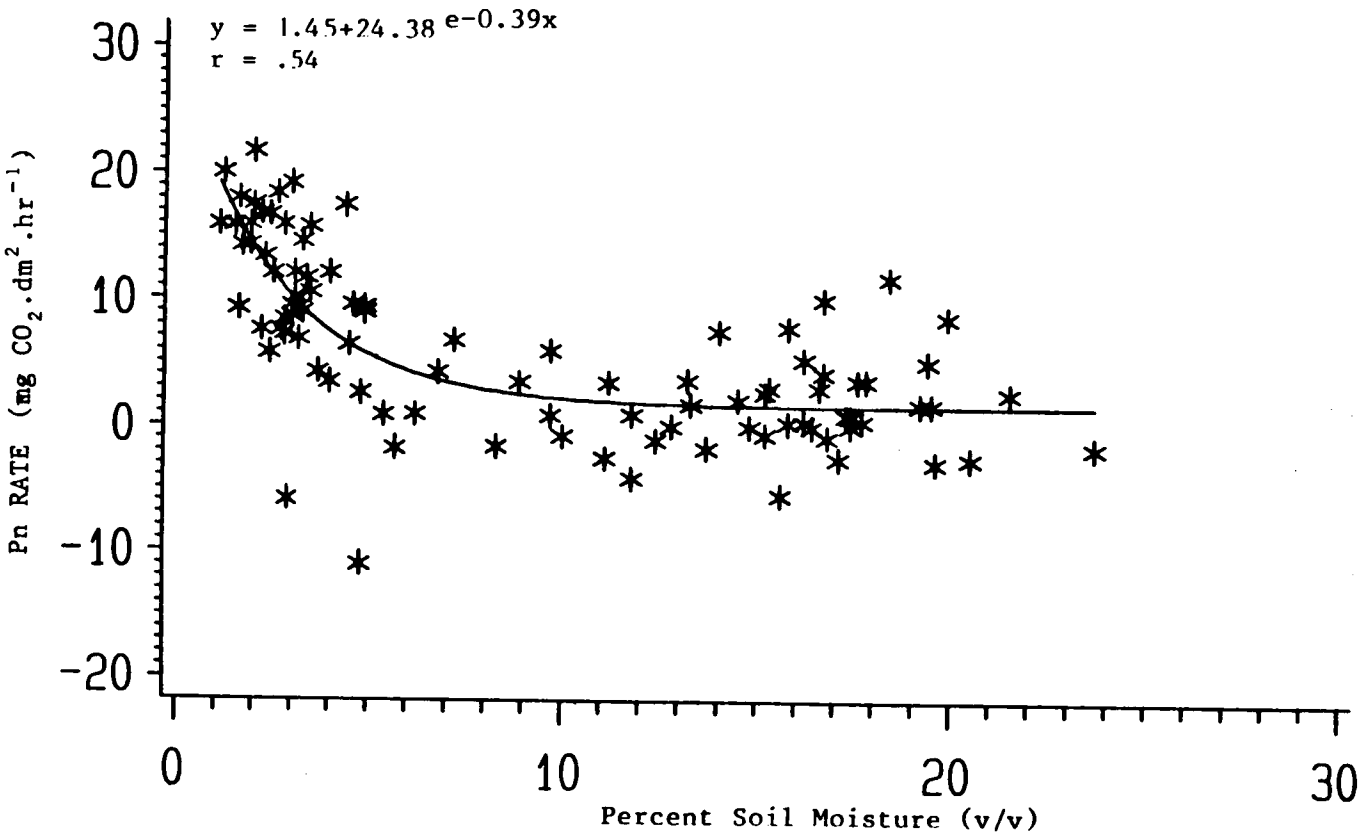


Figure I.2. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 300 ppm paclobutrazol.

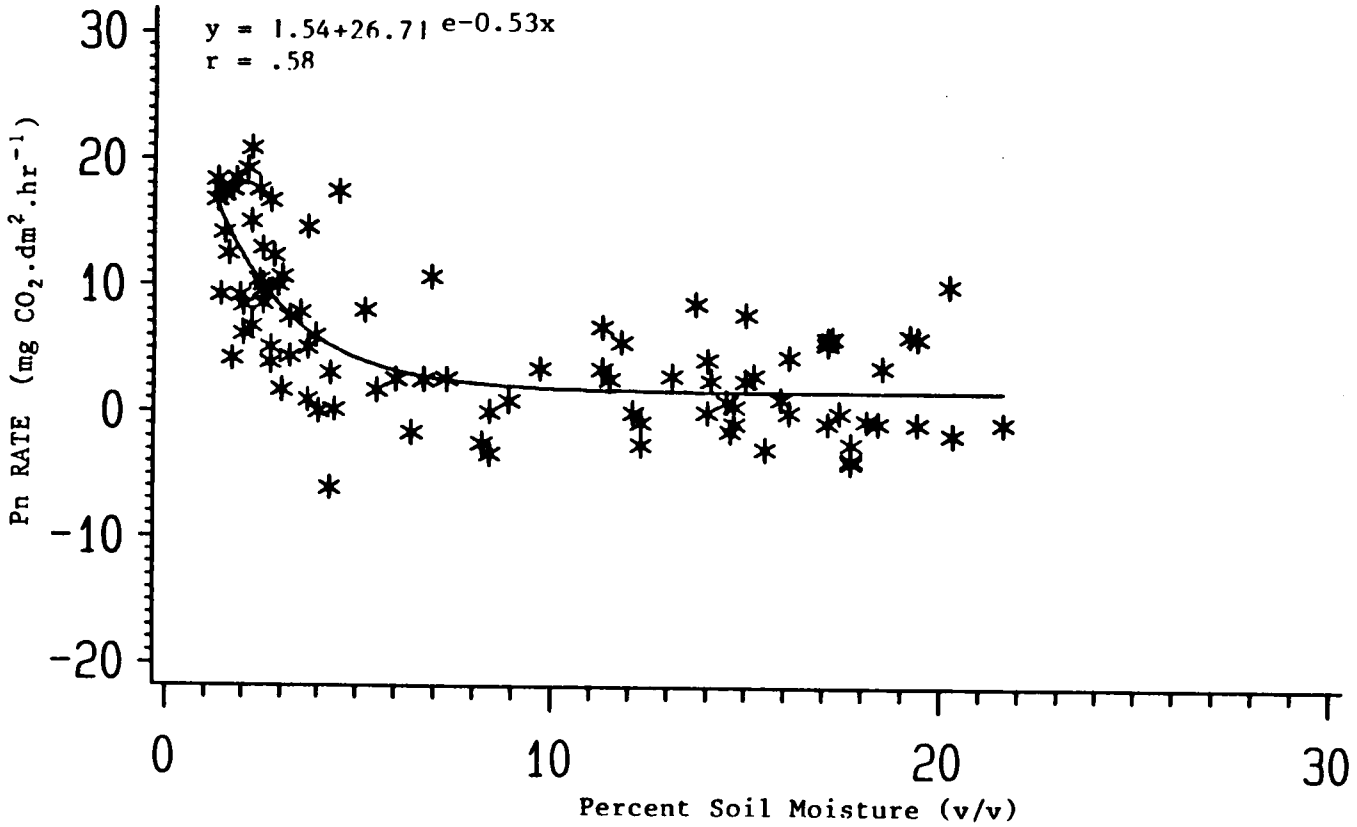


Figure I.3. Net photosynthesis (Pn) of 'Golden Delicious apple leaves at various levels of soil moisture from trees treated with 600 ppm paclobutrazol.

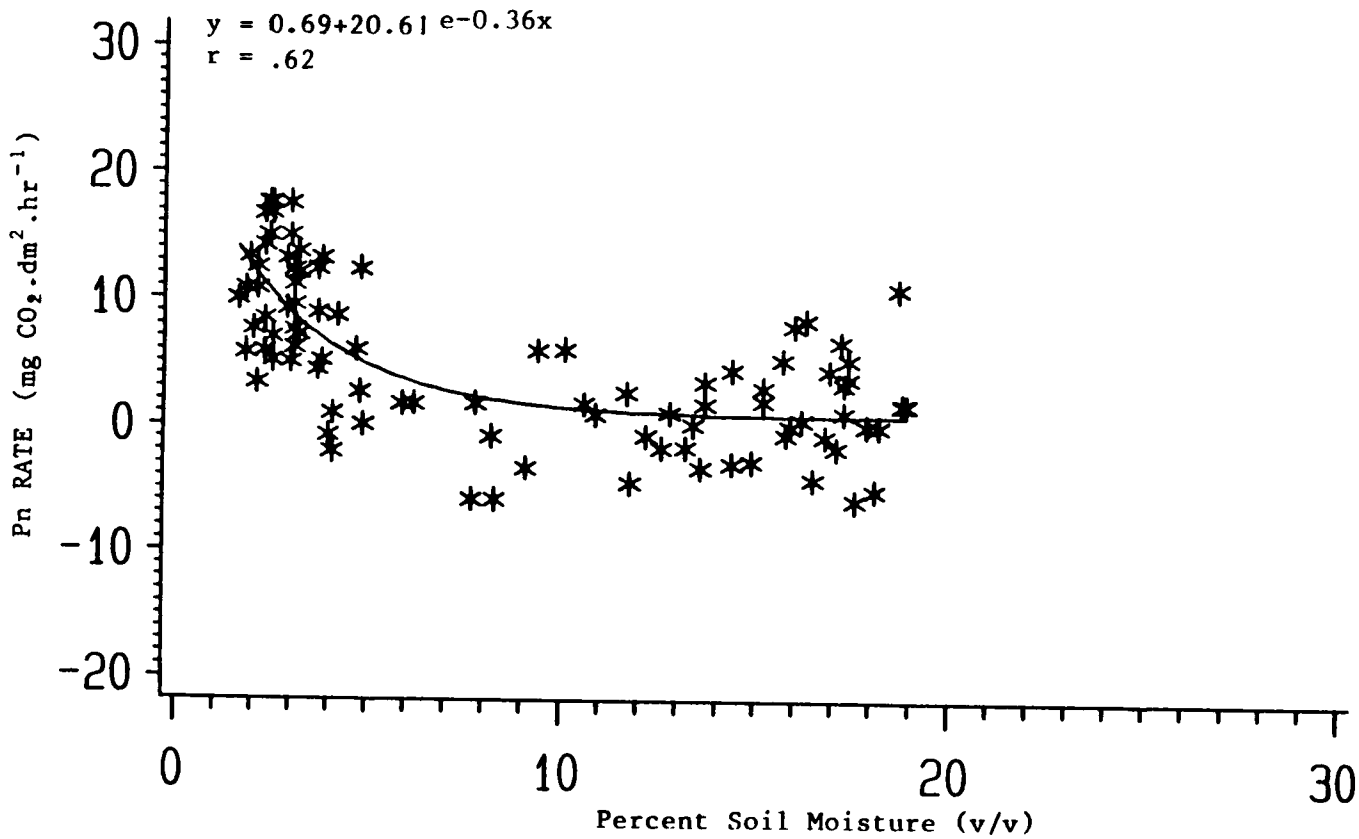


Figure I.4. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 1200 ppm paclobutrazol.

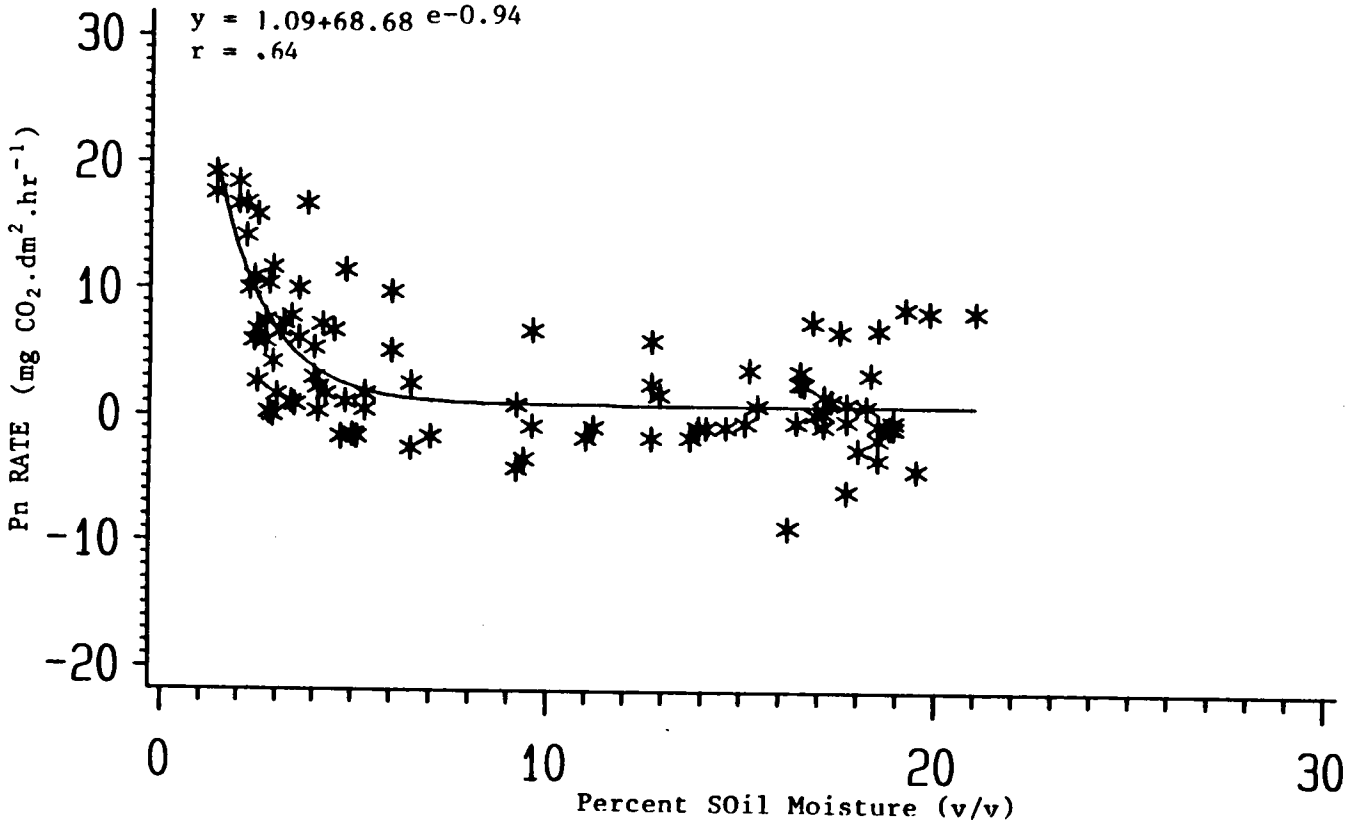


Figure I.5. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 2400 ppm paclobutrazol.

APPENDIX J

THE INDIVIDUAL TREATMENT LINES FOR NET PHOTOSYNTHESIS VERSUS SOIL MOISTURE OF POTTED 'GOLDEN' DELICIOUS' APPLE TREES THE YEAR OF APPLICATION

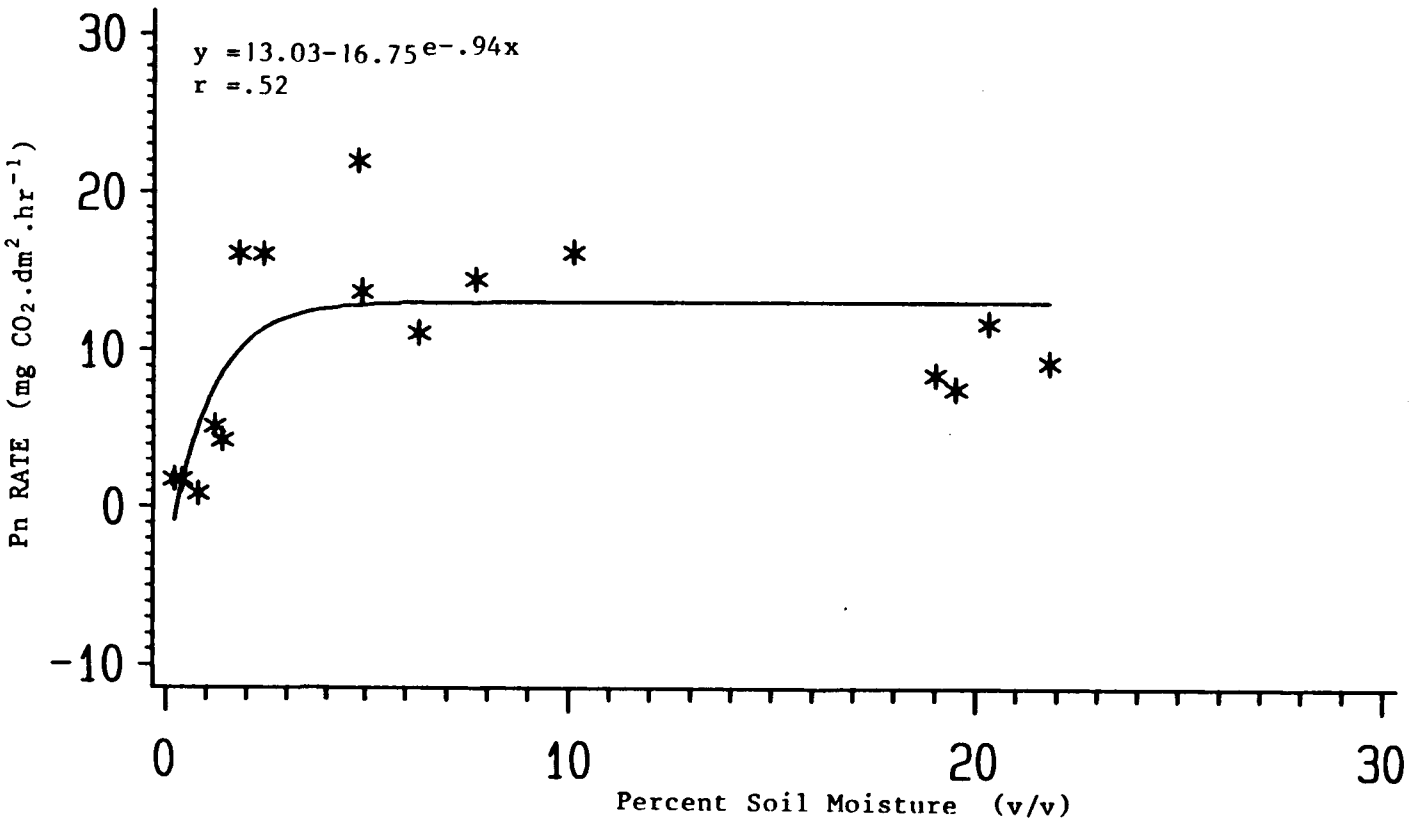


Figure J.1. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture.

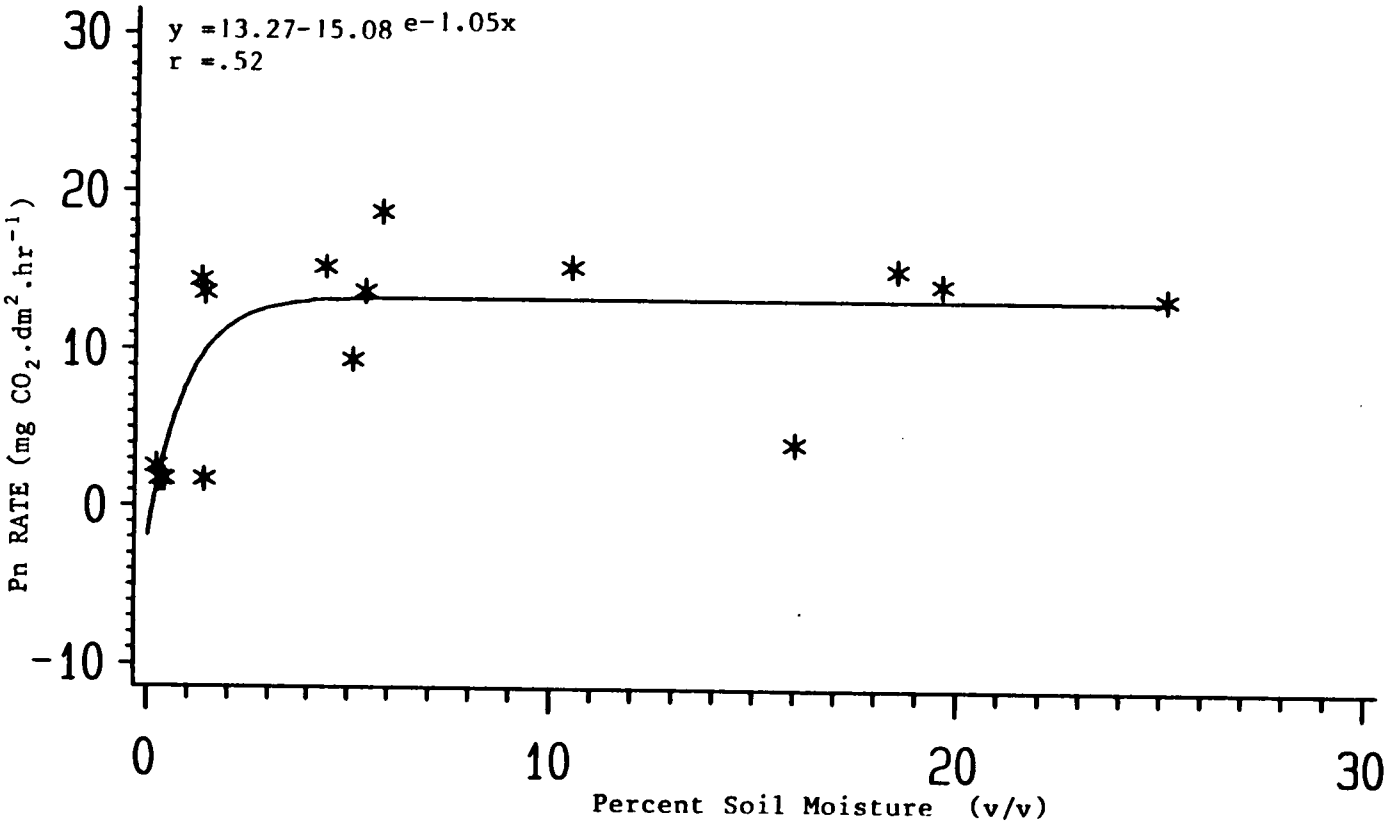


Figure J.2. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 300 ppm paclobutrazol.

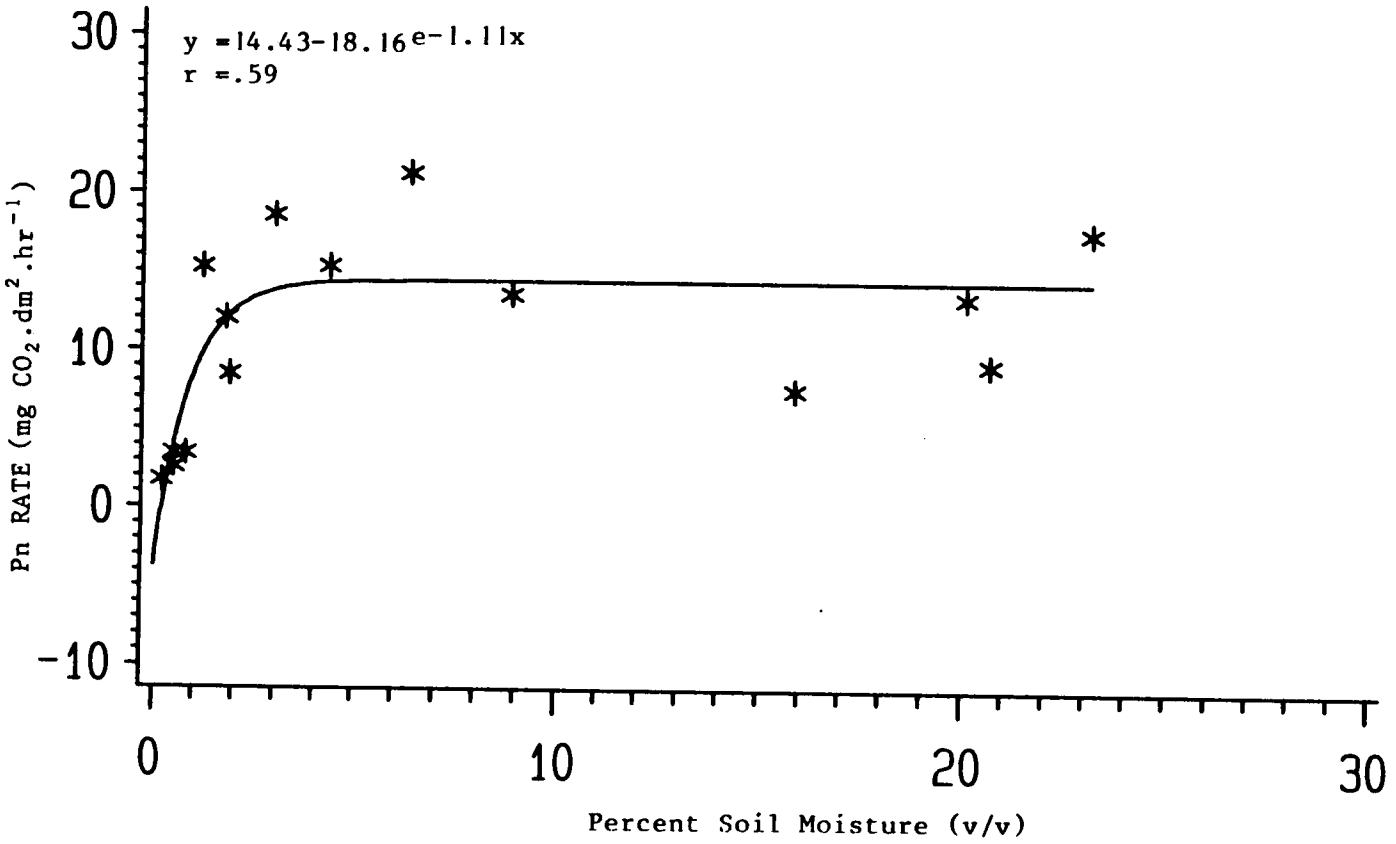


Figure J.3. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 600 ppm paclobutrazol.

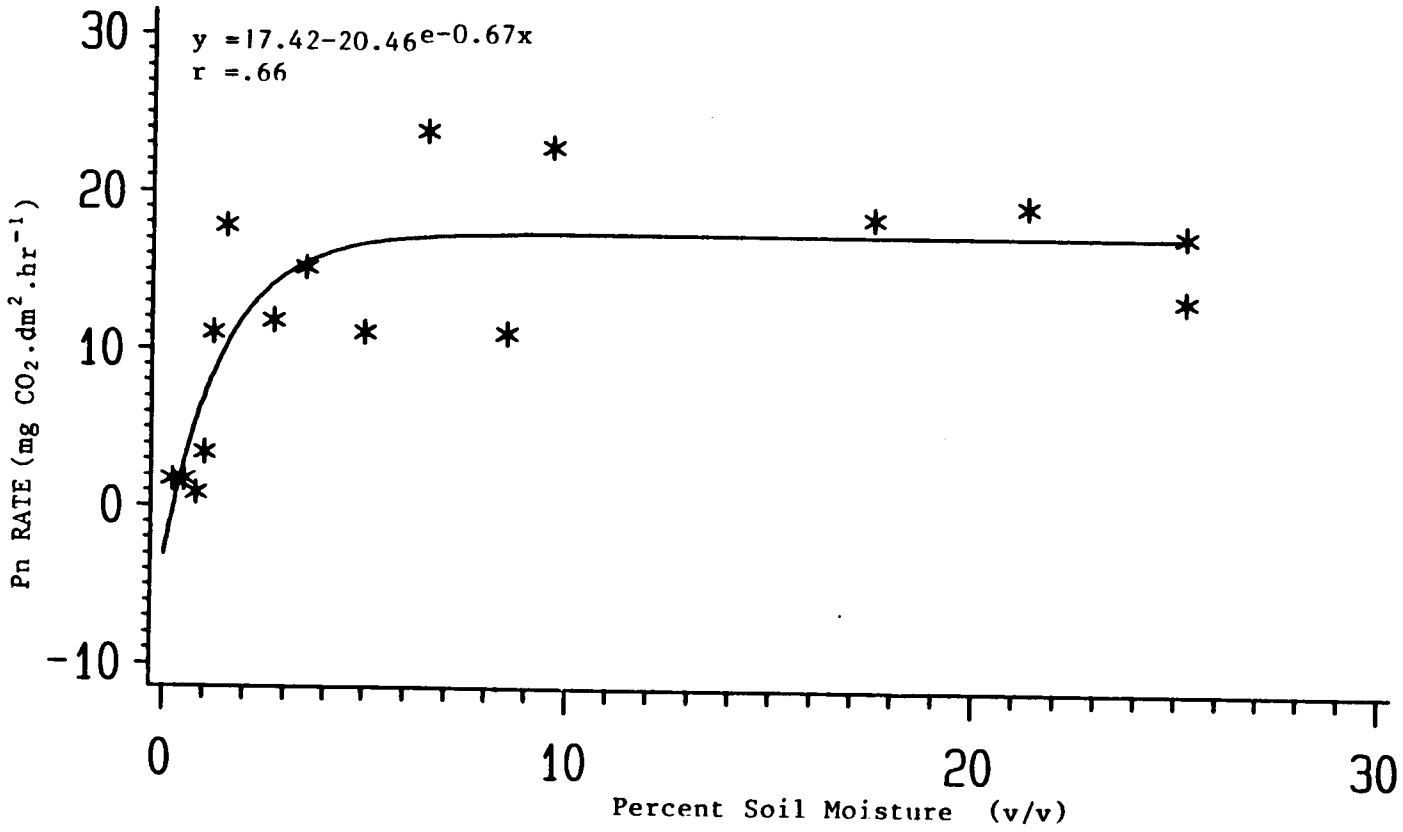


Figure J.4. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 1200 ppm paclobutrazol.

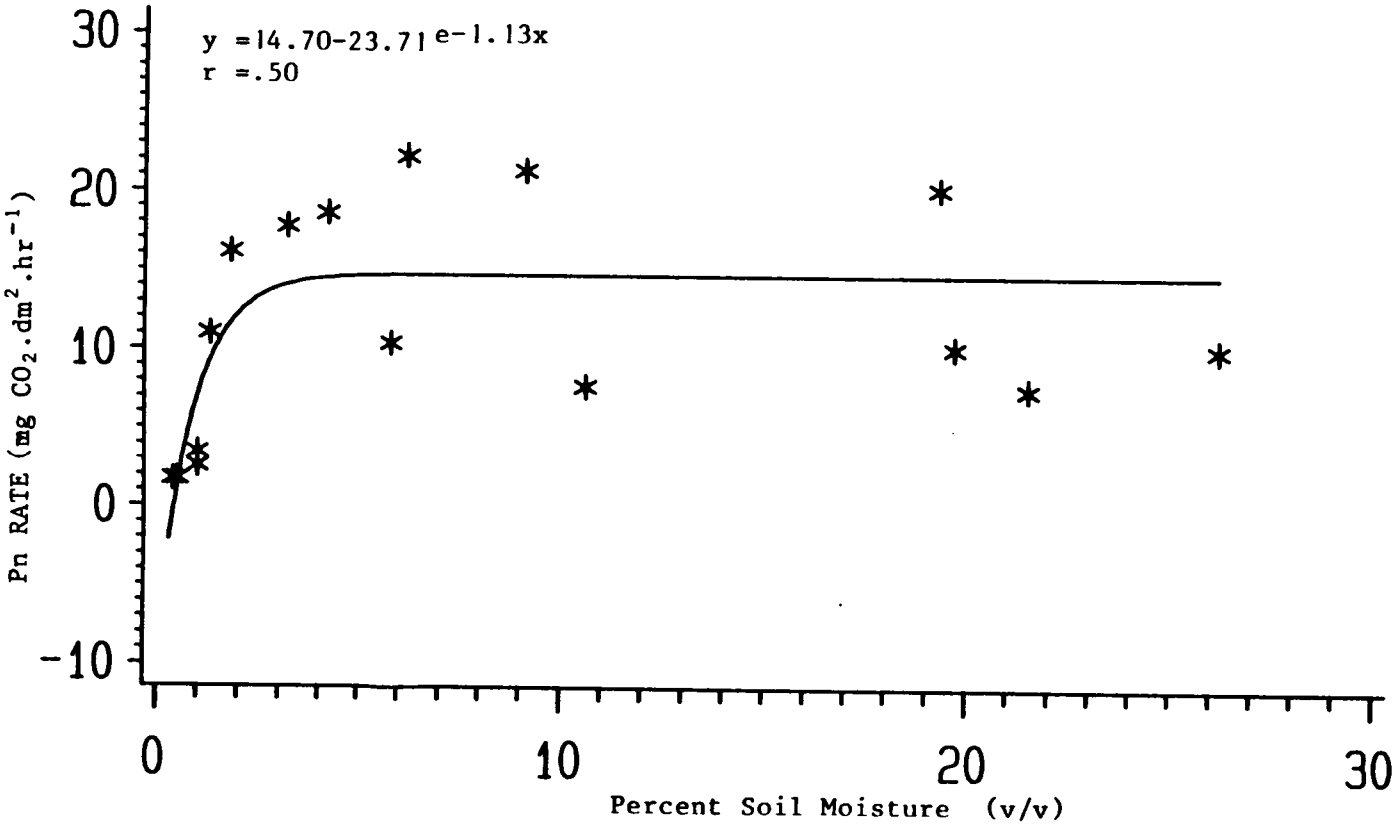


Figure J.5. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 2400 ppm paclobutrazol.

APPENDIX K

THE INDIVIDUAL TREATMENT LINES FOR NET PHOTOSYNTHESIS VERSUS STOMATAL CONDUCTANCE OF POTTED 'GOLDEN DELICIOUS' APPLE TREES THE YEAR OF APPLICATION

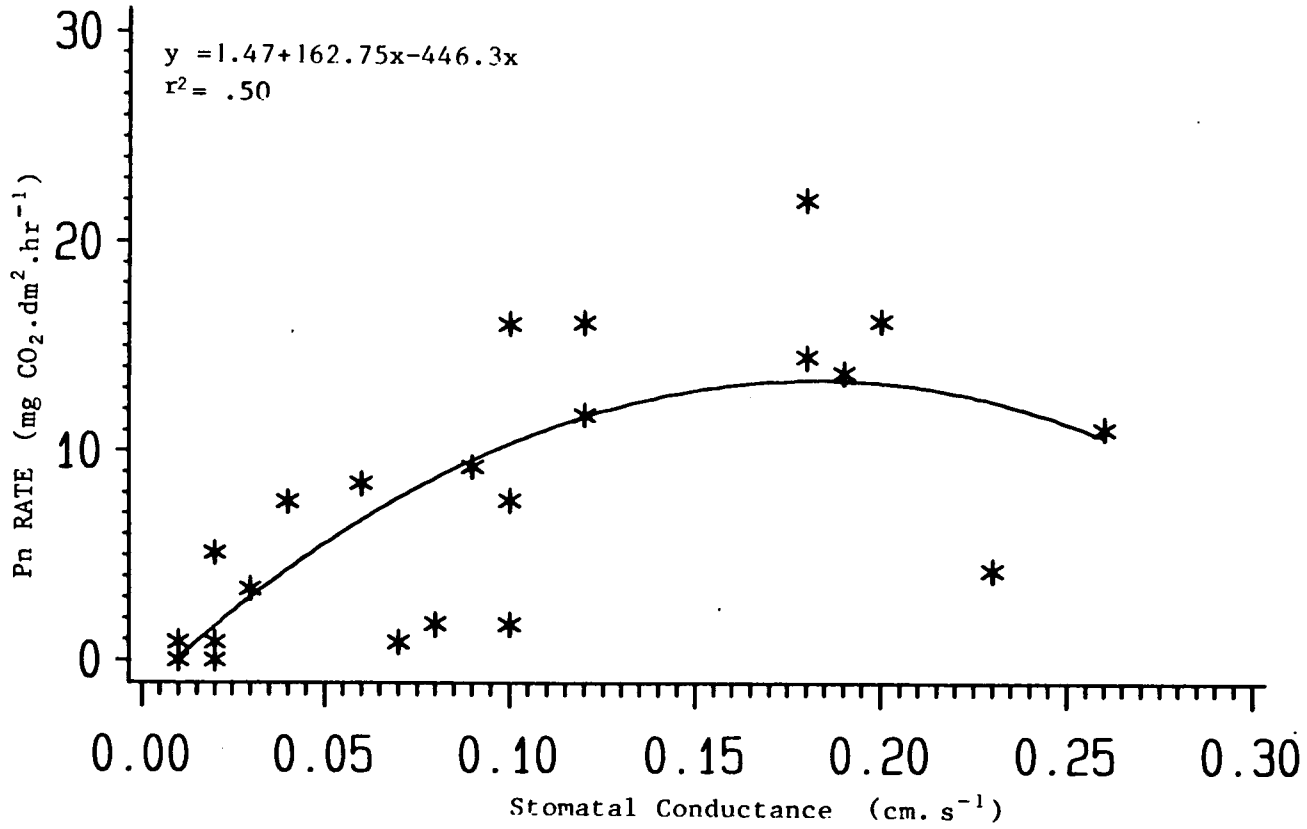


Figure K.1. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates.

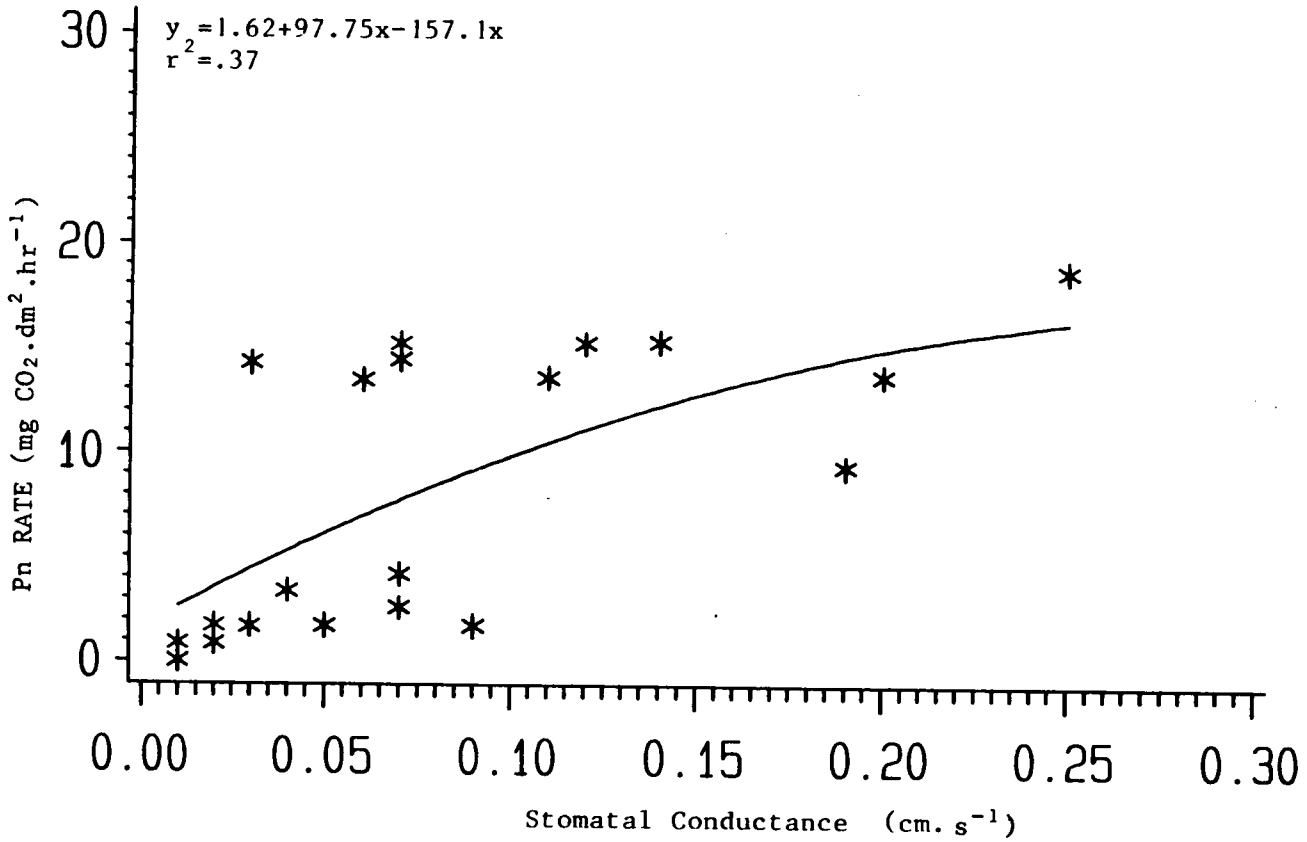


Figure K.2. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates from trees treated with 300 ppm paclobutrazol.

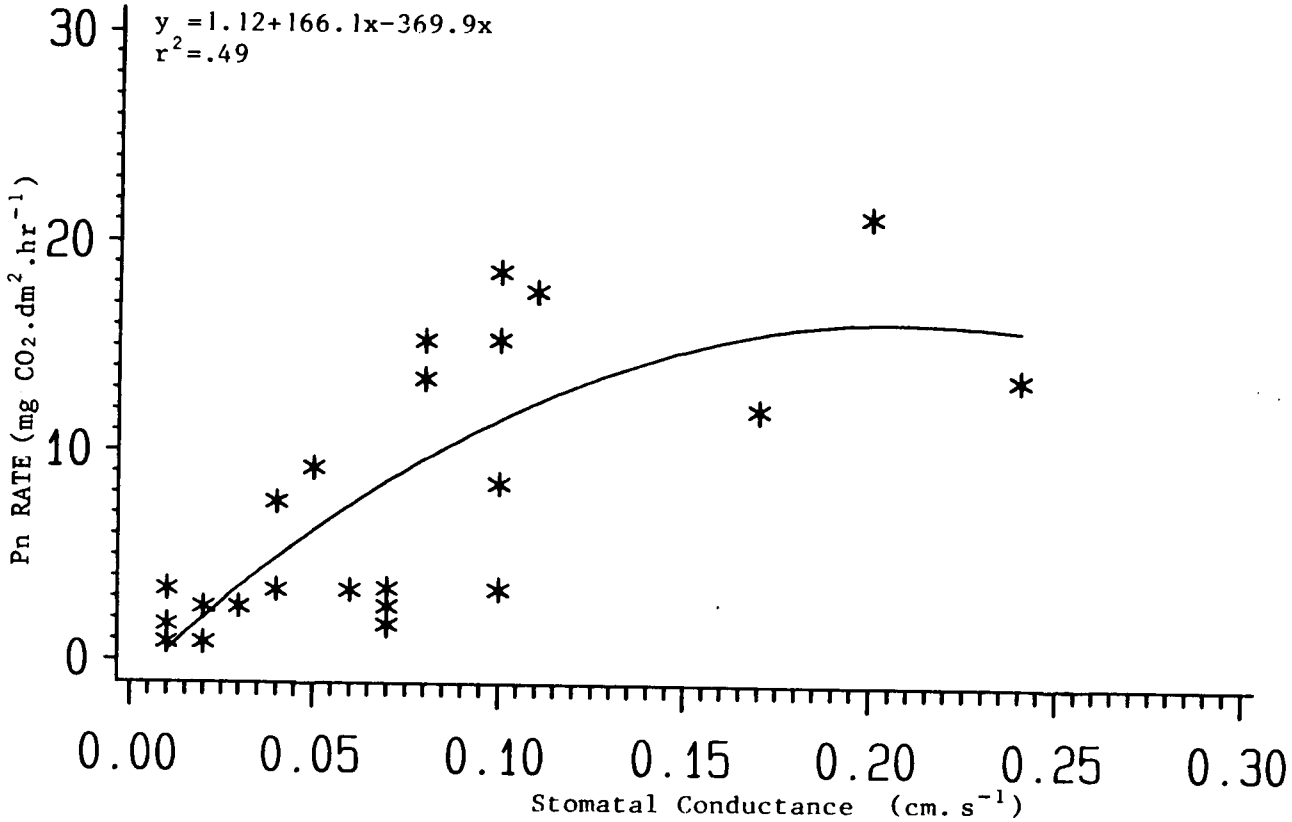


Figure K.3. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates from trees treated with 600 ppm paclobutrazol.

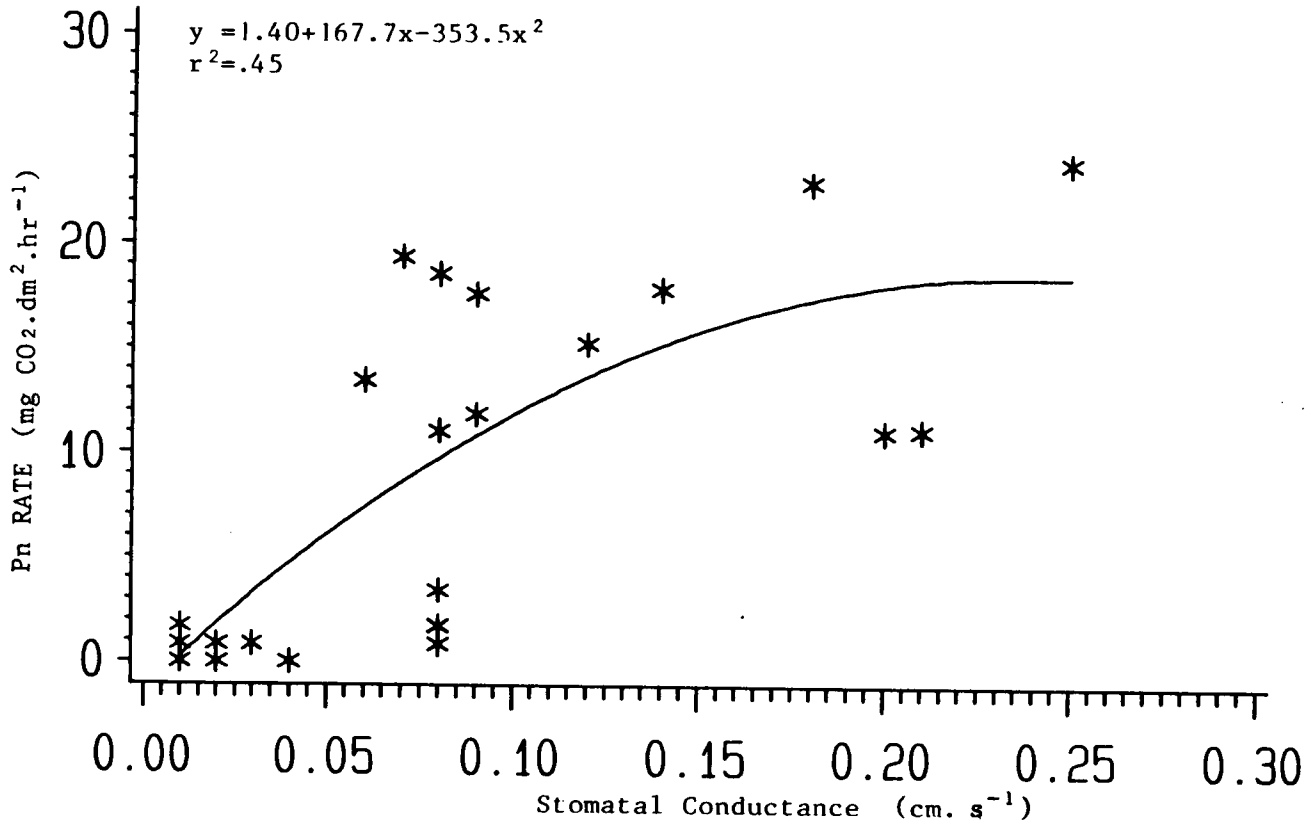


Figure K.4. Net photoysnthesis (Pn) of 'Golden Delicious apple leaves at various stomatal conductance rates from trees treated with 1200 ppm paclobutrazol.

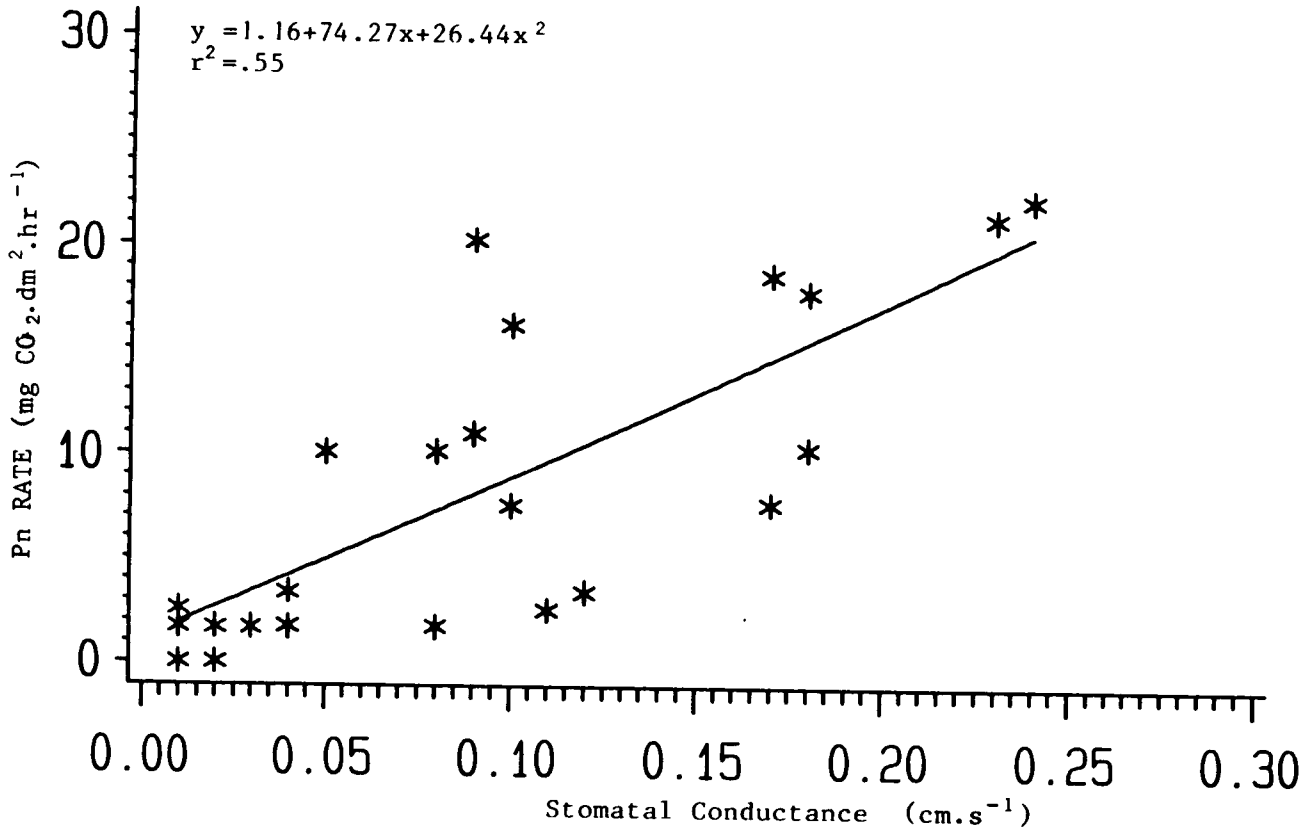


Figure K.5. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates from trees treated with 2400 ppm paclobutrazol.

APPENDIX L

THE INDIVIDUAL TREATMENT LINES FOR NET PHOTOSYNTHESIS VERSUS SOIL MOISTURE OF POTTED 'REDHAVEN' PEACH TREES THE YEAR OF APPLICATION

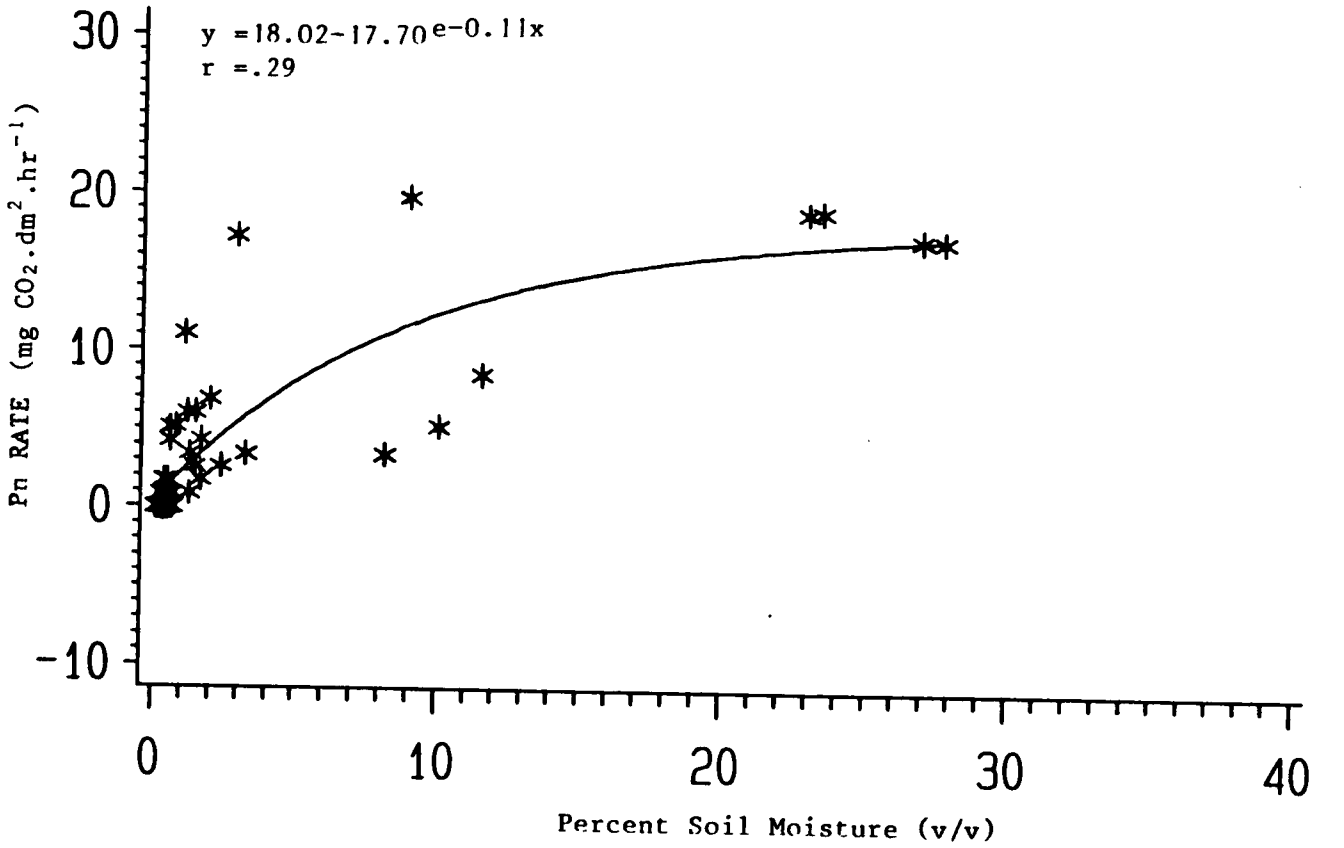


Figure L.1. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various levels of soil moisture.

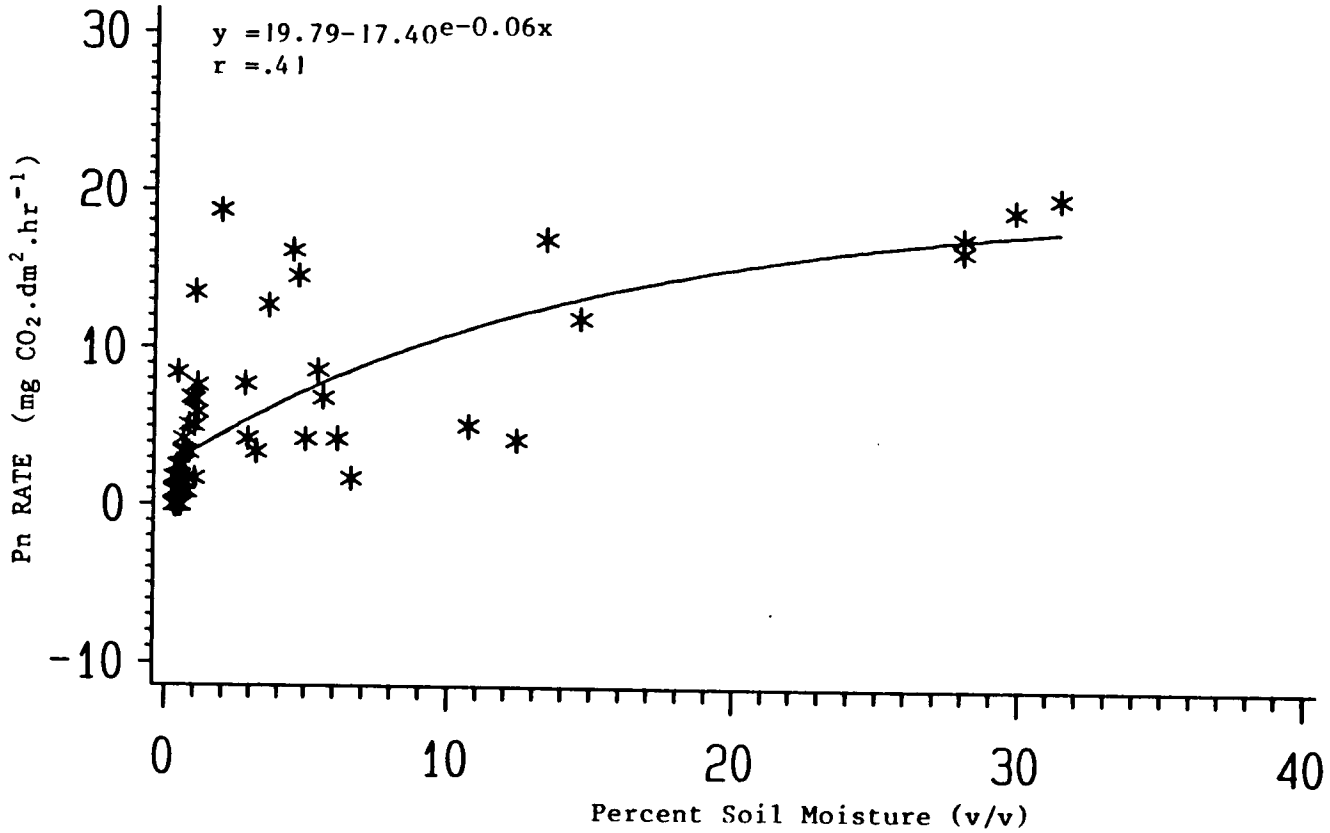


Figure L.2. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various levels of soil moisture from trees treated with 300 ppm paclobutrazol.

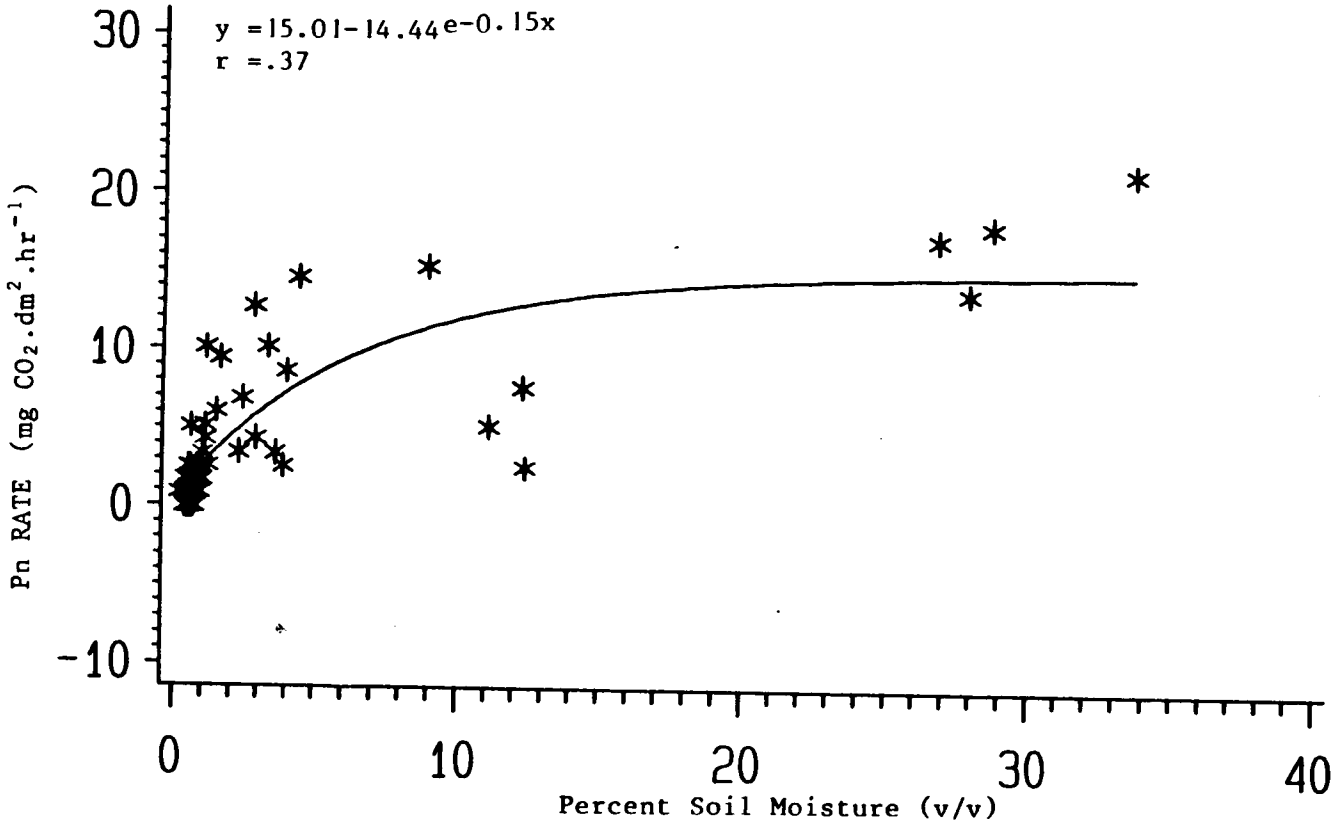


Figure L.3. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various levels of soil moisture from trees treated with 600 ppm paclobutrazol.

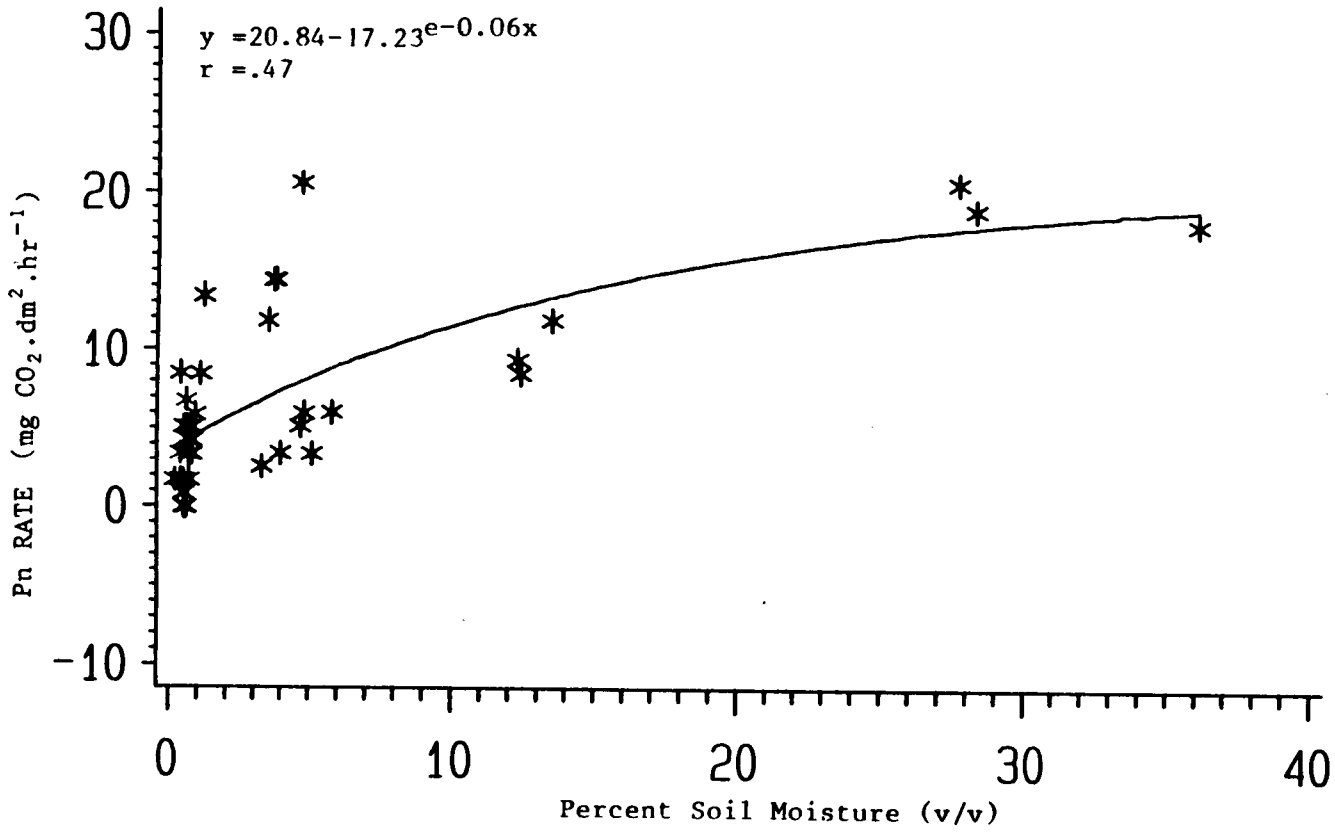


Figure L.4. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various levels of soil moisture from trees treated with 1200 ppm paclobutrazol.

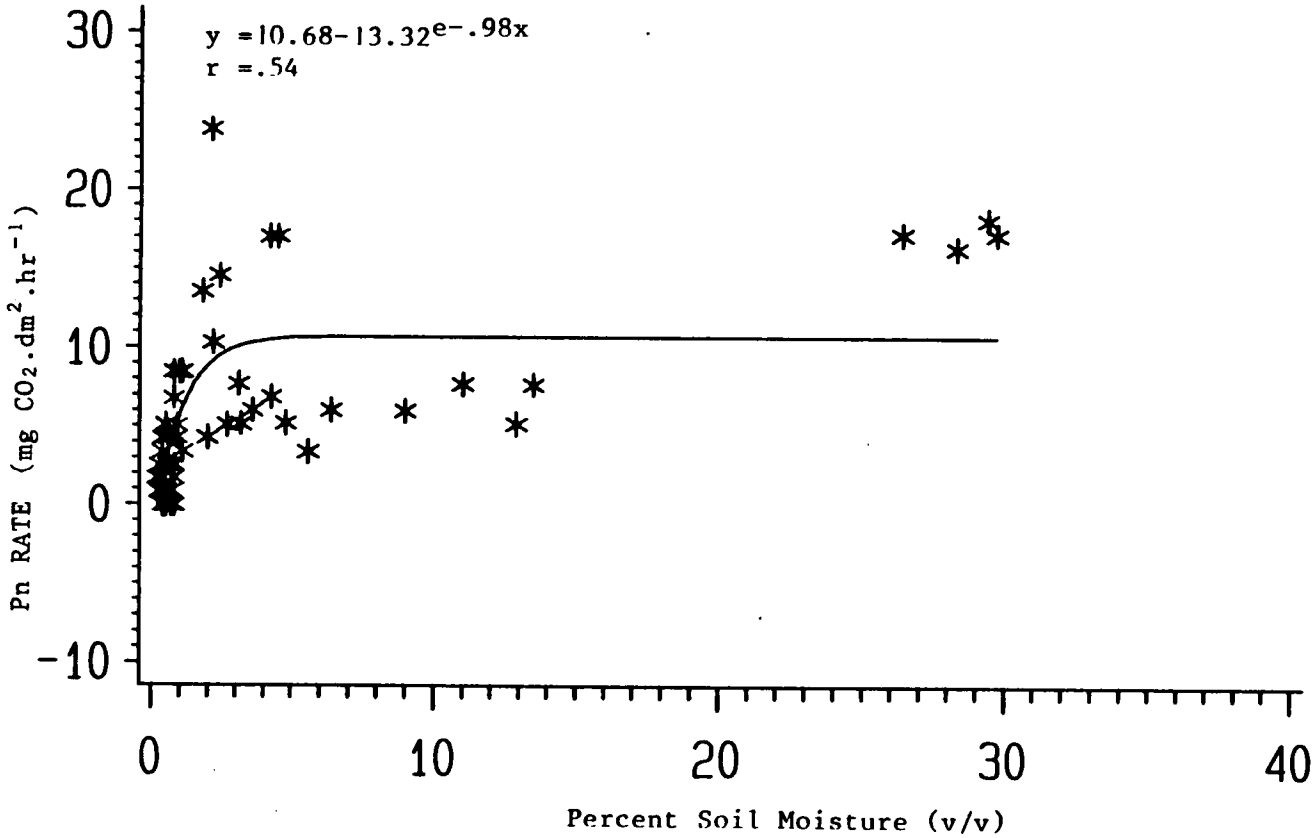


Figure L.5. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various levels of soil moisture from trees treated with 2400 ppm paclobutrazol.

APPENDIX M

THE INDIVIDUAL TREATMENT LINES FOR NET PHOTOSYNTHESIS VERSUS STOMATAL CONDUCTANCE OF POTTED 'REDHAVEN' PEACH TREES THE YEAR OF APPLICATION

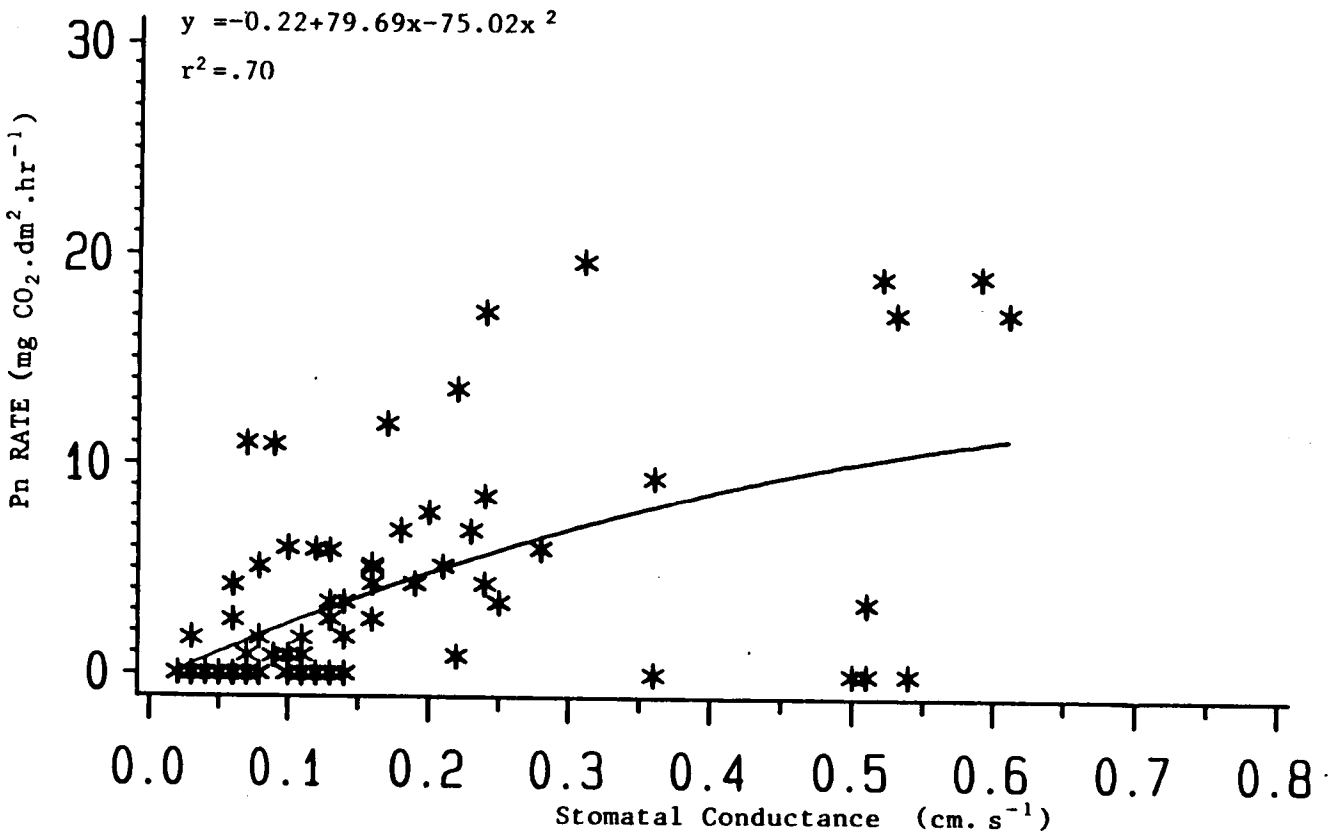


Figure M.1. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various stomatal conductance rates.

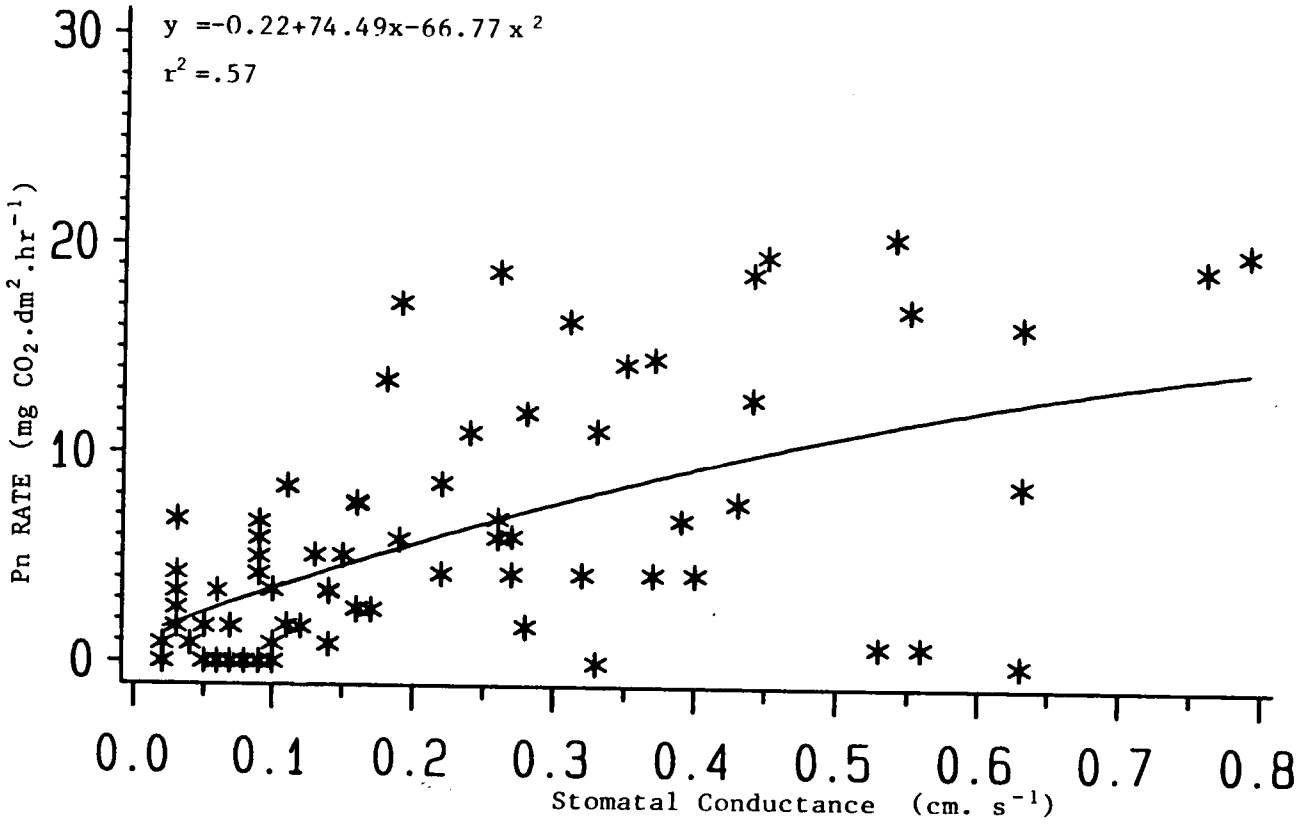


Figure M.2. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various stomatal conductance rates from trees treated with 300 ppm paclobutrazol.

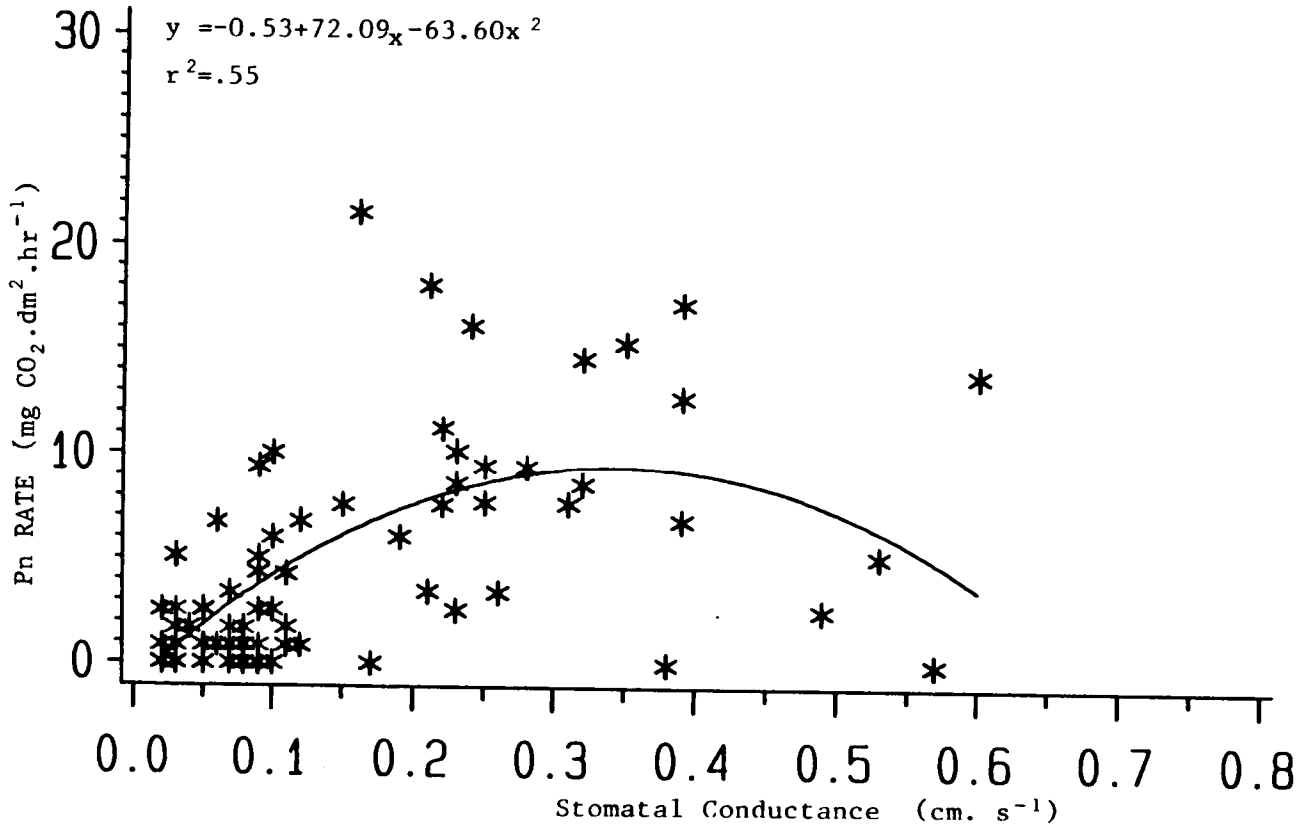


Figure M.3. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various stomatal conductance rates from trees treated with 600 ppm paclobutrazol.

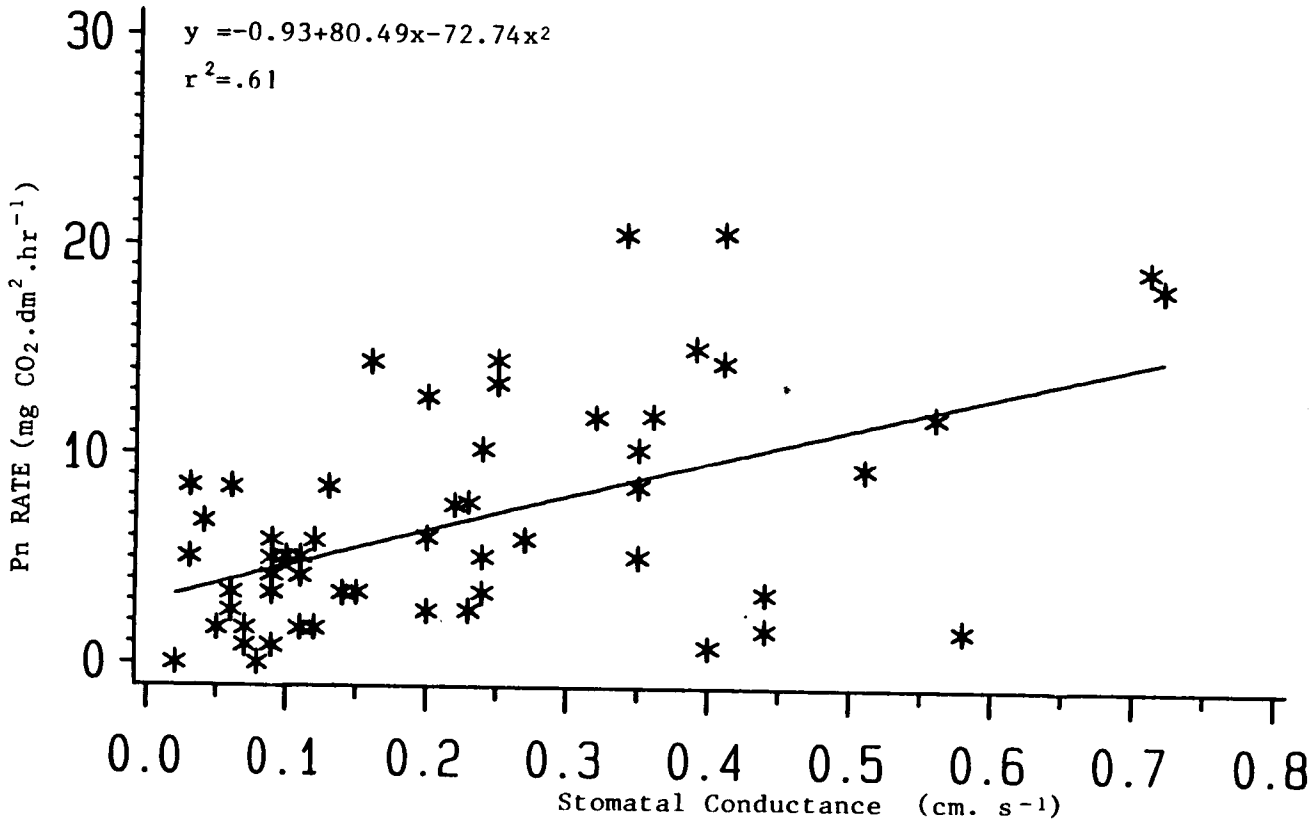


Figure M.4. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various stomatal conductance rates from trees treated with 1200 paclobutrazol.

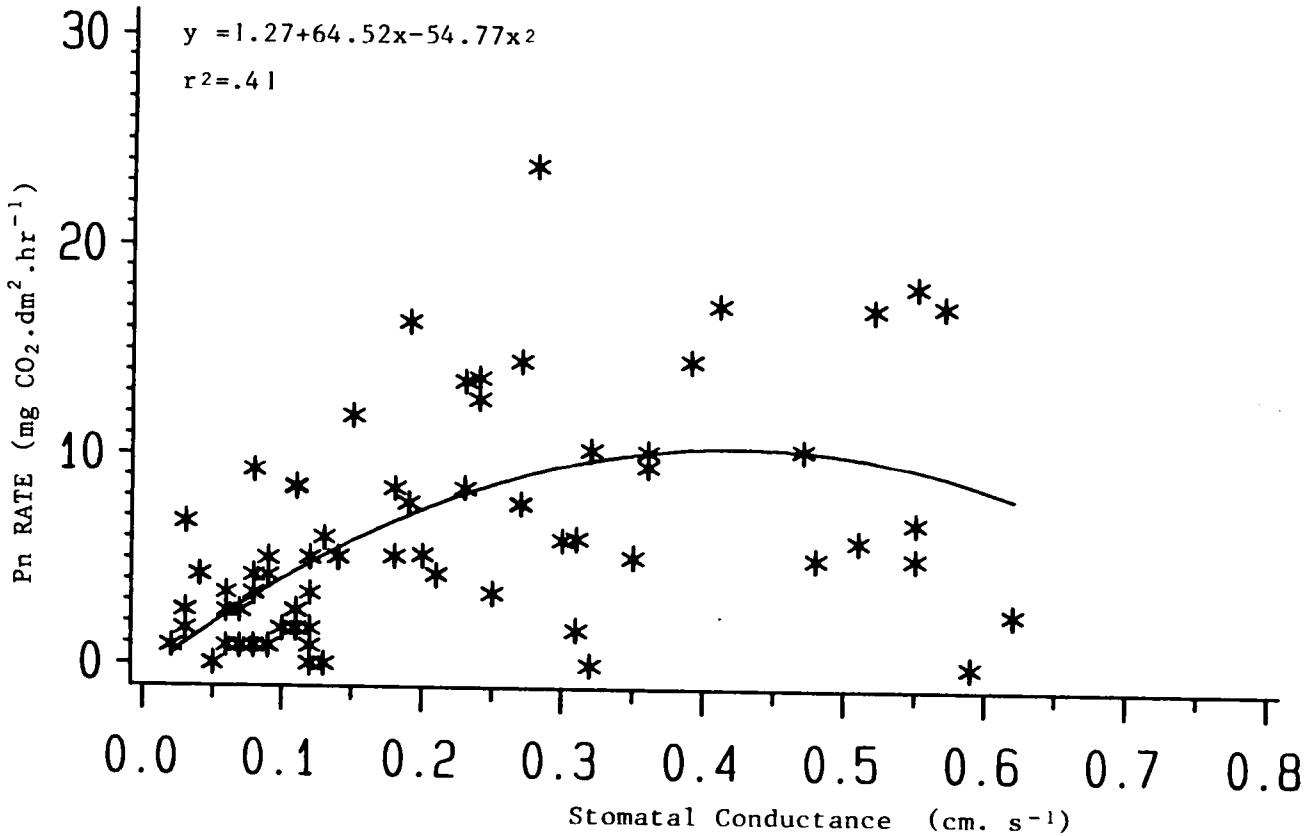


Figure M.5. Net photosynthesis (Pn) of 'Redhaven' peach leaves at various stomatal conductance rates from trees treated with 2400 ppm paclobutrazol.

APPENDIX N

THE INDIVIDUAL TREATMENT LINES FOR WATER POTENTIAL VERSUS SOIL MOISTURE OF POTTED 'GOLDEN DELICIOUS' APPLE TREES THE YEAR FOLLOWING APPLICATION

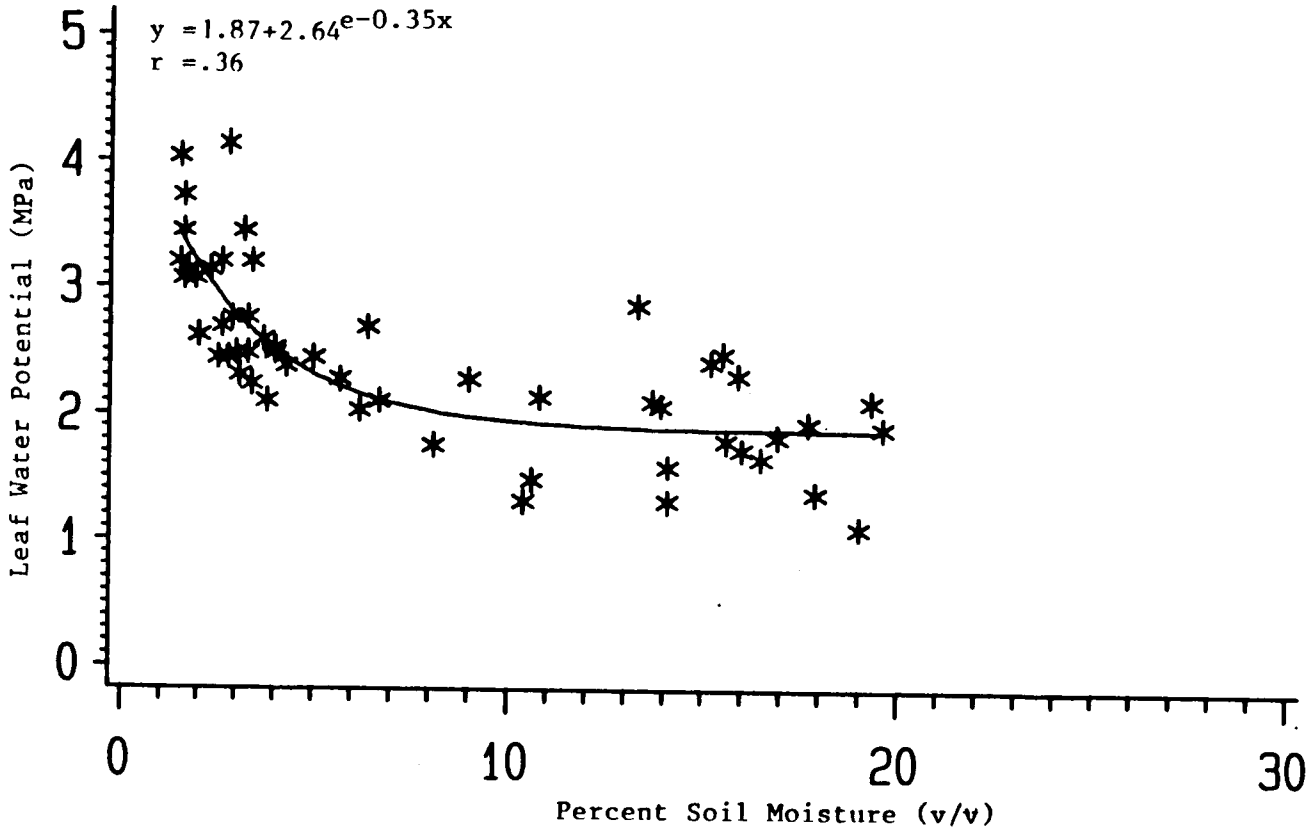


Figure N.1. Water potential of 'Golden Delicious' apple leaves at various levels of soil moisture.

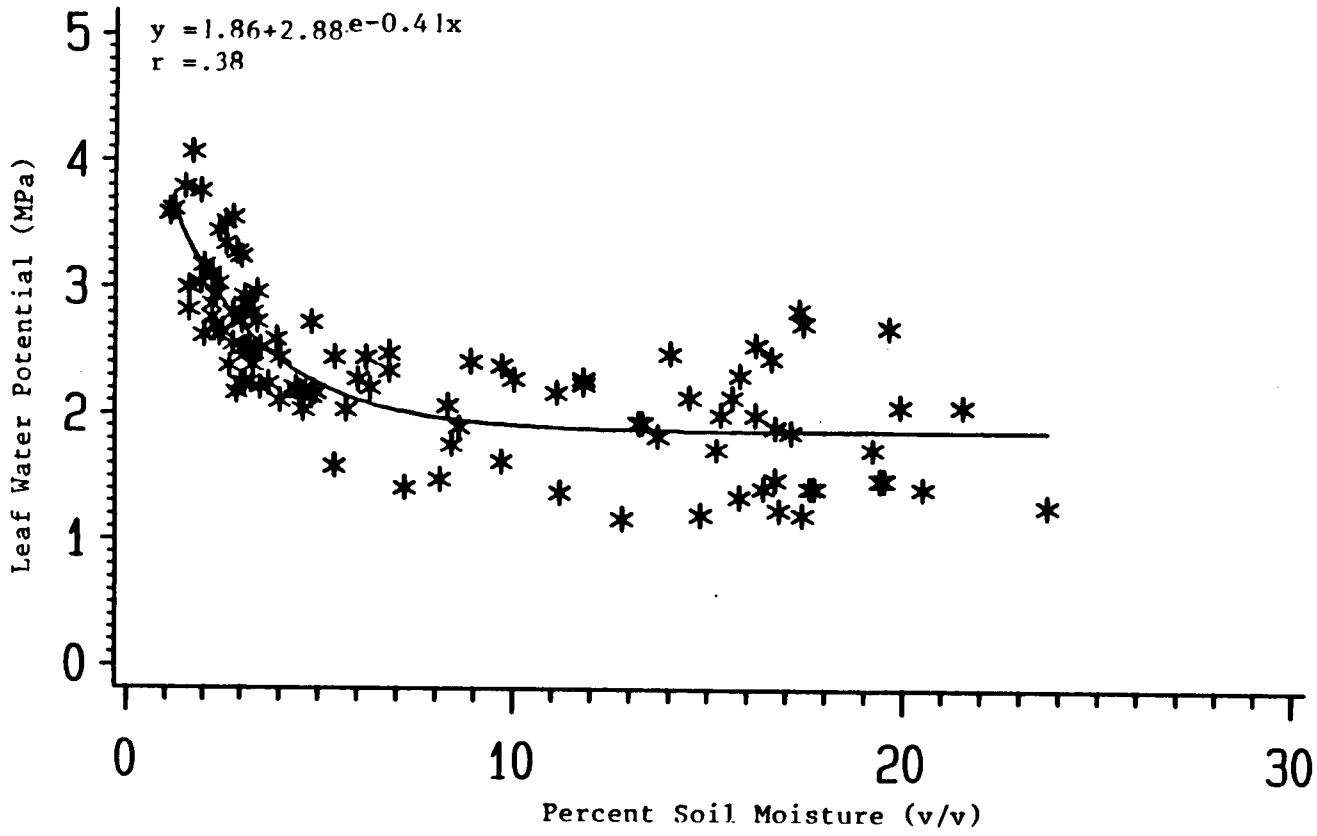


Figure N.2. Water potential of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 300 ppm paclobutrazol.

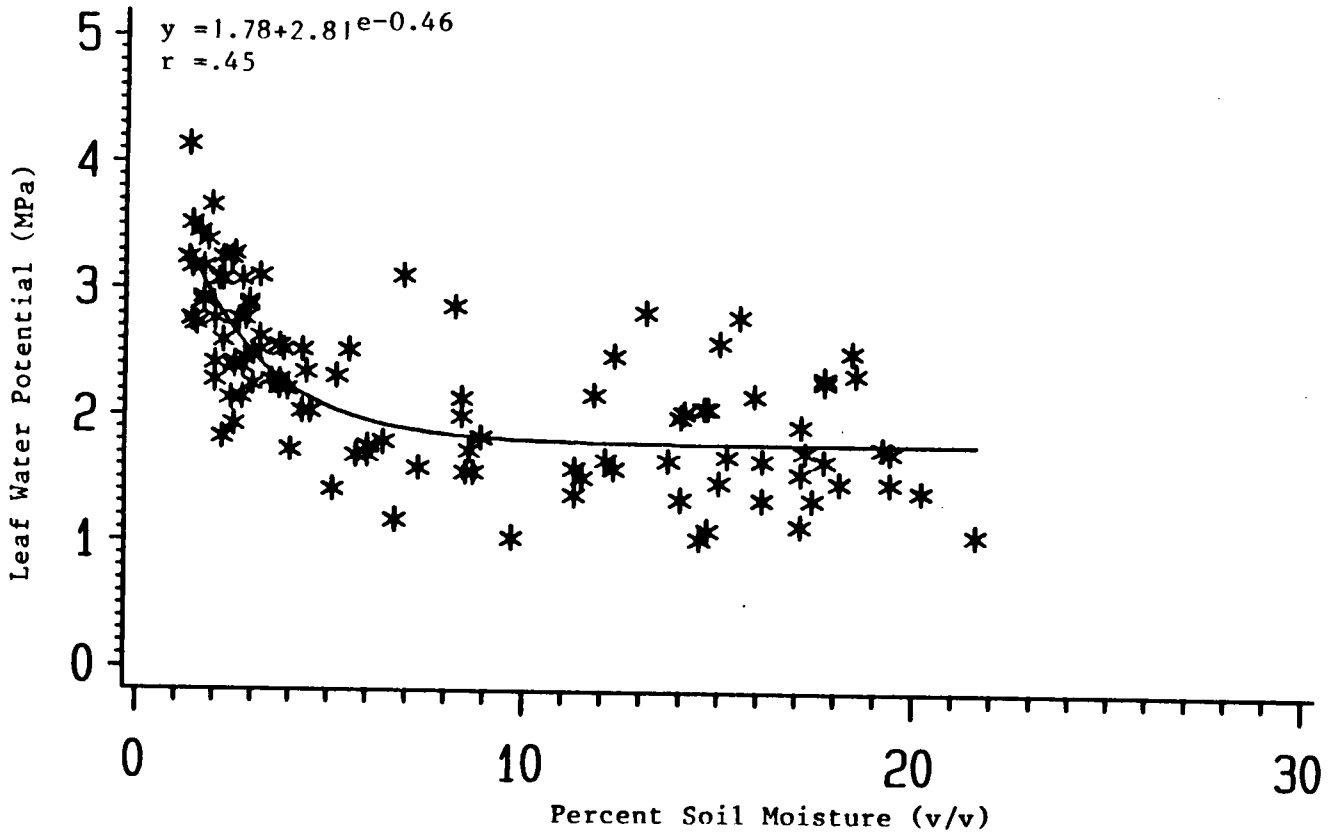


Figure N.3. Water potential of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 600 ppm paclobutrazol.

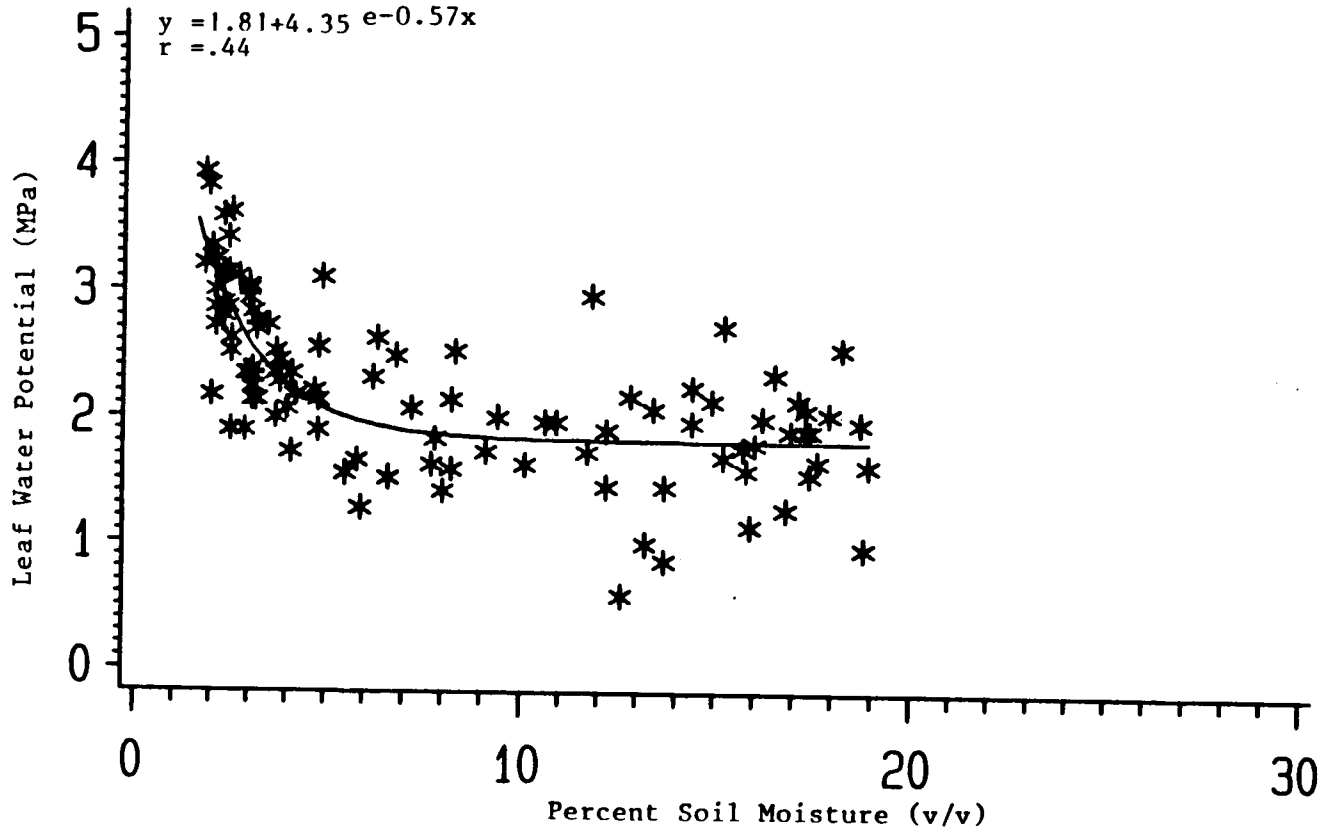


Figure N.4. Water potential of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 1200 ppm paclobutrazol.

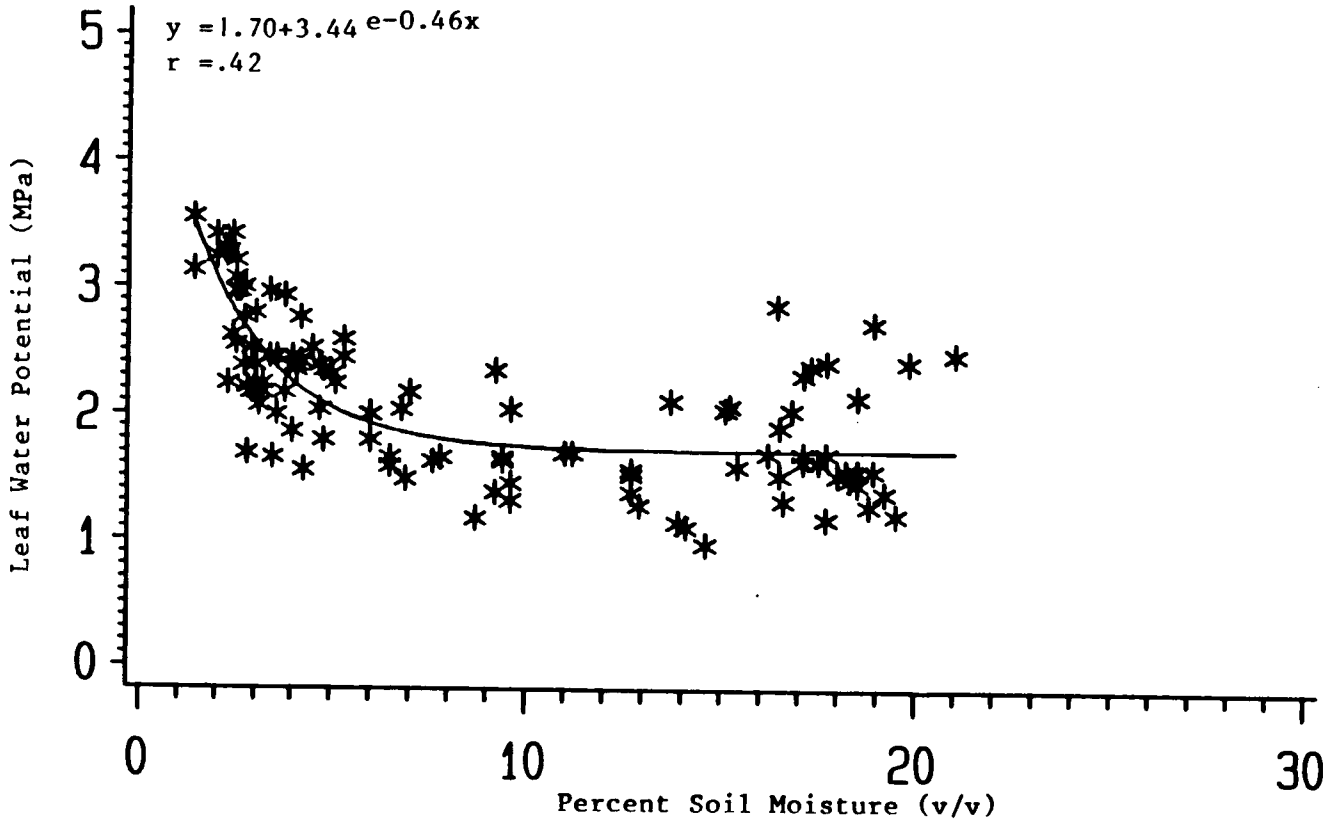


Figure N.5. Water potential of 'Golden Delicious' apple leaves at various levels of soil moisture from trees treated with 2400 ppm paclobutrazol.

APPENDIX O

THE INDIVIDUAL TREATMENT LINES FOR STOMATAL CONDUCTANCE VERSUS WATER POTENTIAL OF POTTED 'GOLDEN DELICIOUS' APPLE TREES THE YEAR FOLLOWING APPLICATION

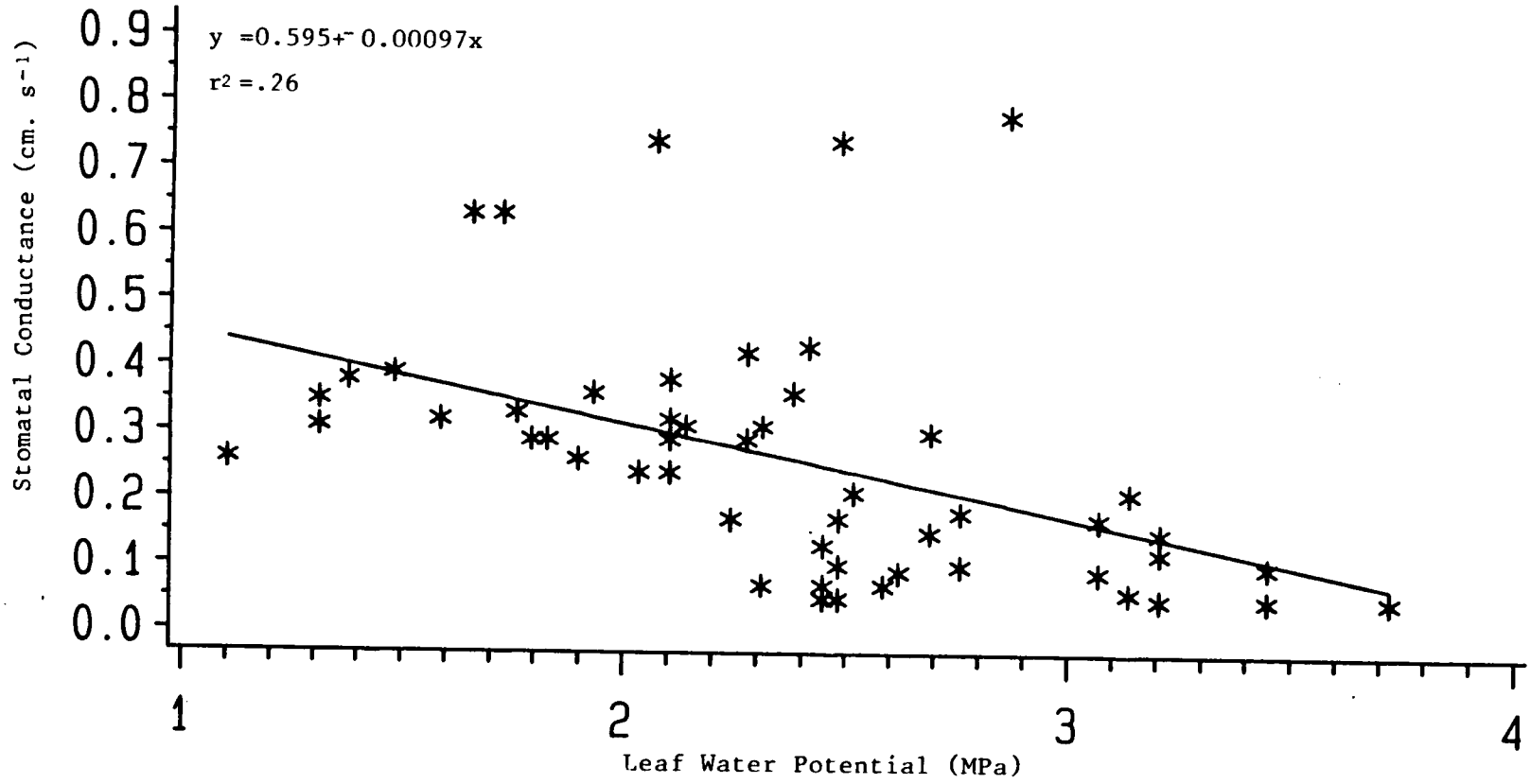


Figure 0.1. Stomatal conductance rates of 'Golden Delicious' apple leaves at various leaf water potentials.

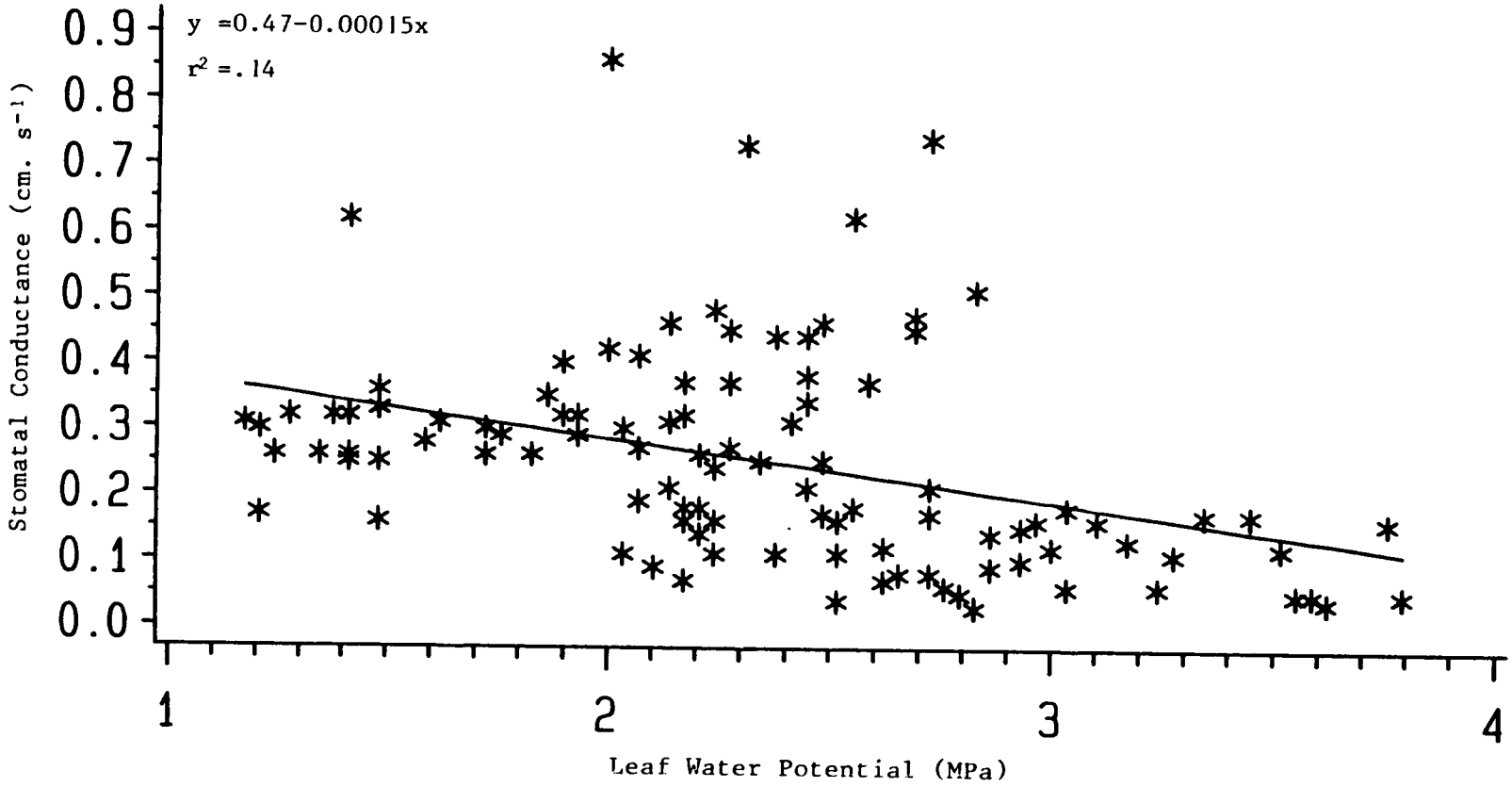


Figure 0.2. Stomatal conductance rates of 'Golden Delicious' apple leaves at various leaf water potentials from trees treated with 300 ppm paclobutrazol.

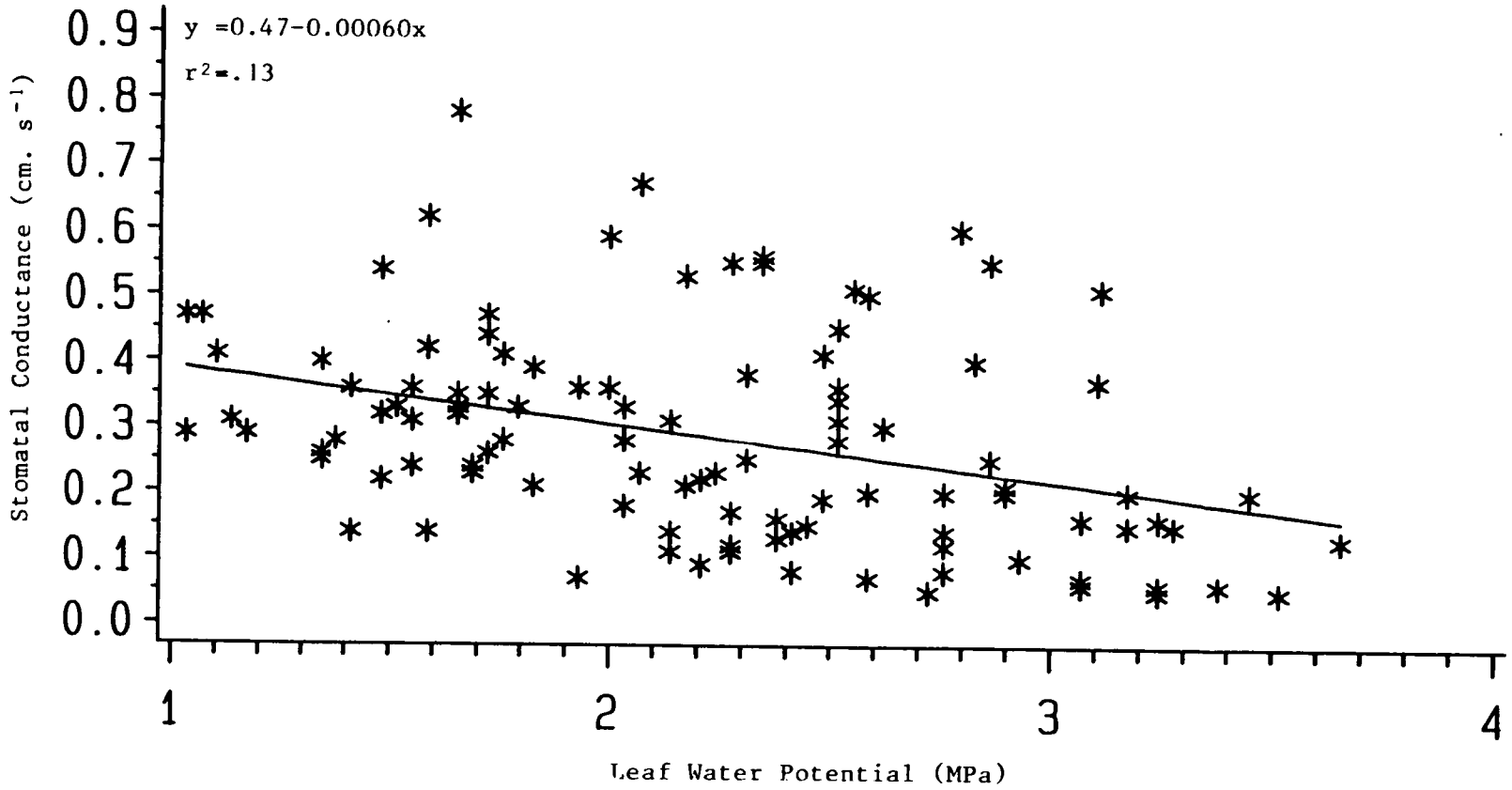


Figure 0.3. Stomatal conductance rates of 'Golden Delicious' apple leaves at various leaf water potentials from trees treated with 600 ppm paclobutrazol.

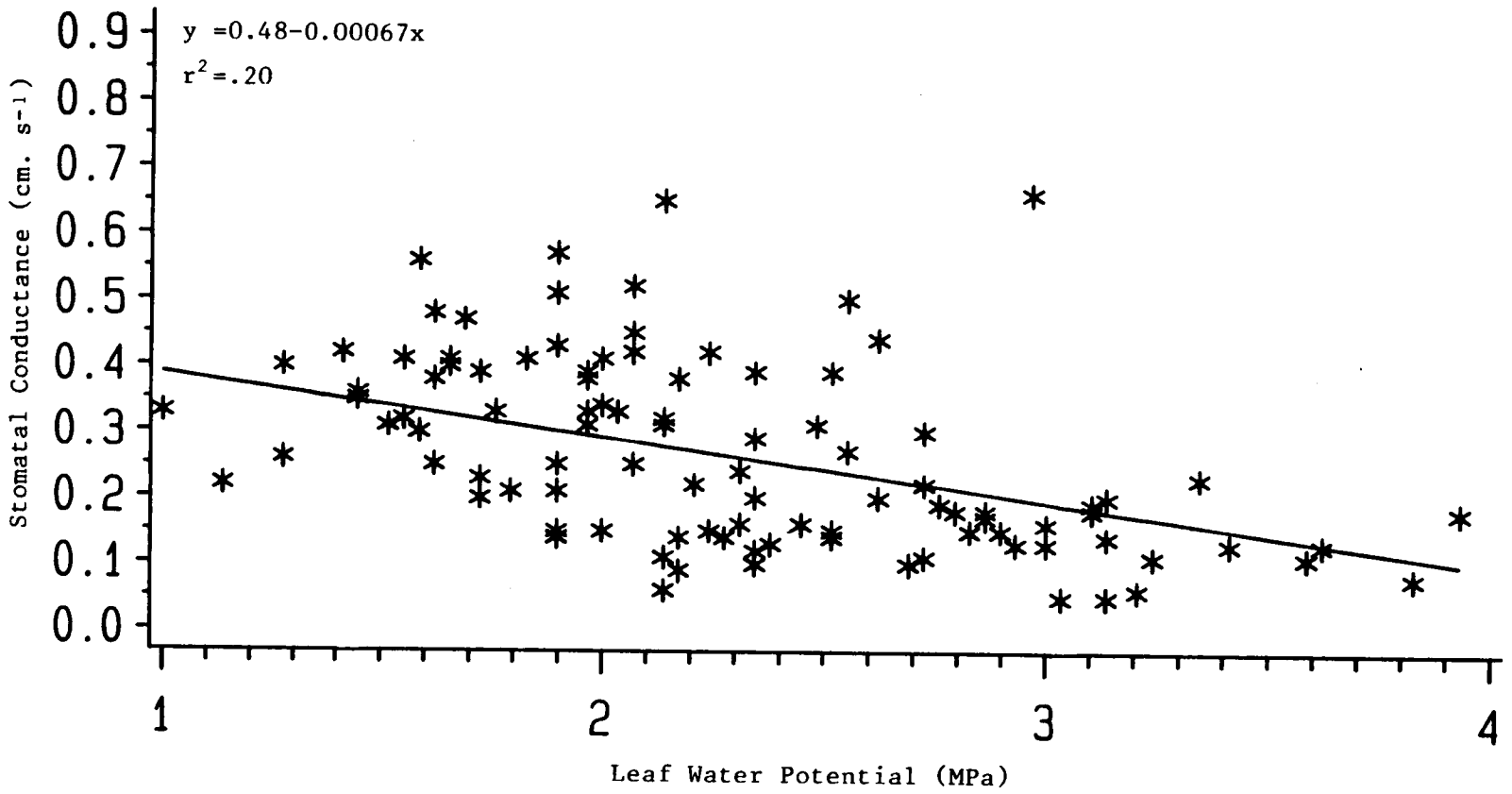


Figure 0.4. Stomatal conductance rates of 'Golden Delicious' apple leaves at various leaf water potentials from trees treated with 1200 ppm paclobutrazol.

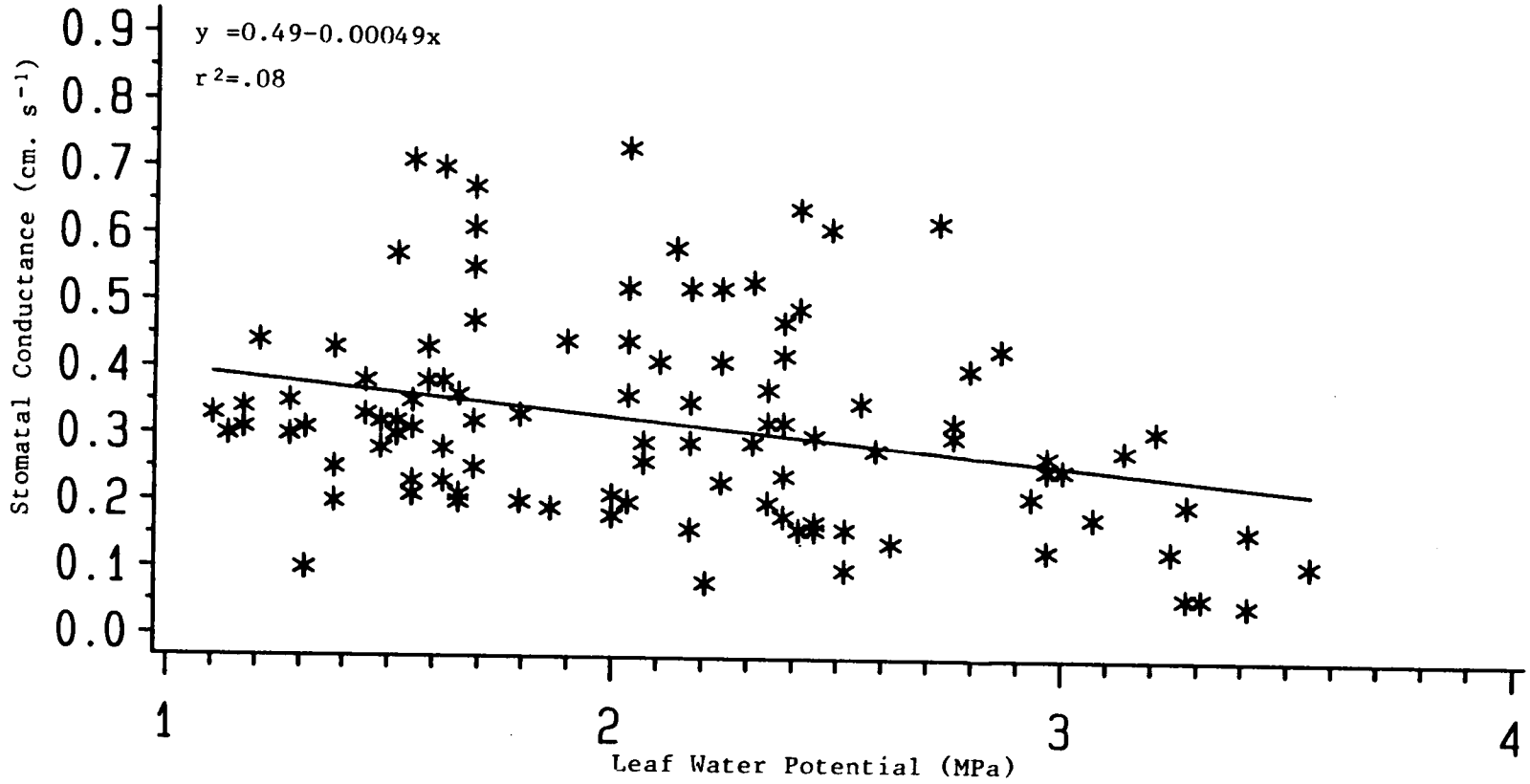


Figure 0.5. Stomatal conductance rates of 'Golden Delicious' apple leaves at various leaf water potentials from trees treated with 2400 ppm paclobutrazol.

APPENDIX P

THE INDIVIDUAL TREATMENT LINES FOR NET PHOTOSYNTHESIS VERSUS STOMATAL CONDUCTANCE OF POTTED 'GOLDEN DELICIOUS' APPLE TREES THE YEAR FOLLOWING APPLICATION

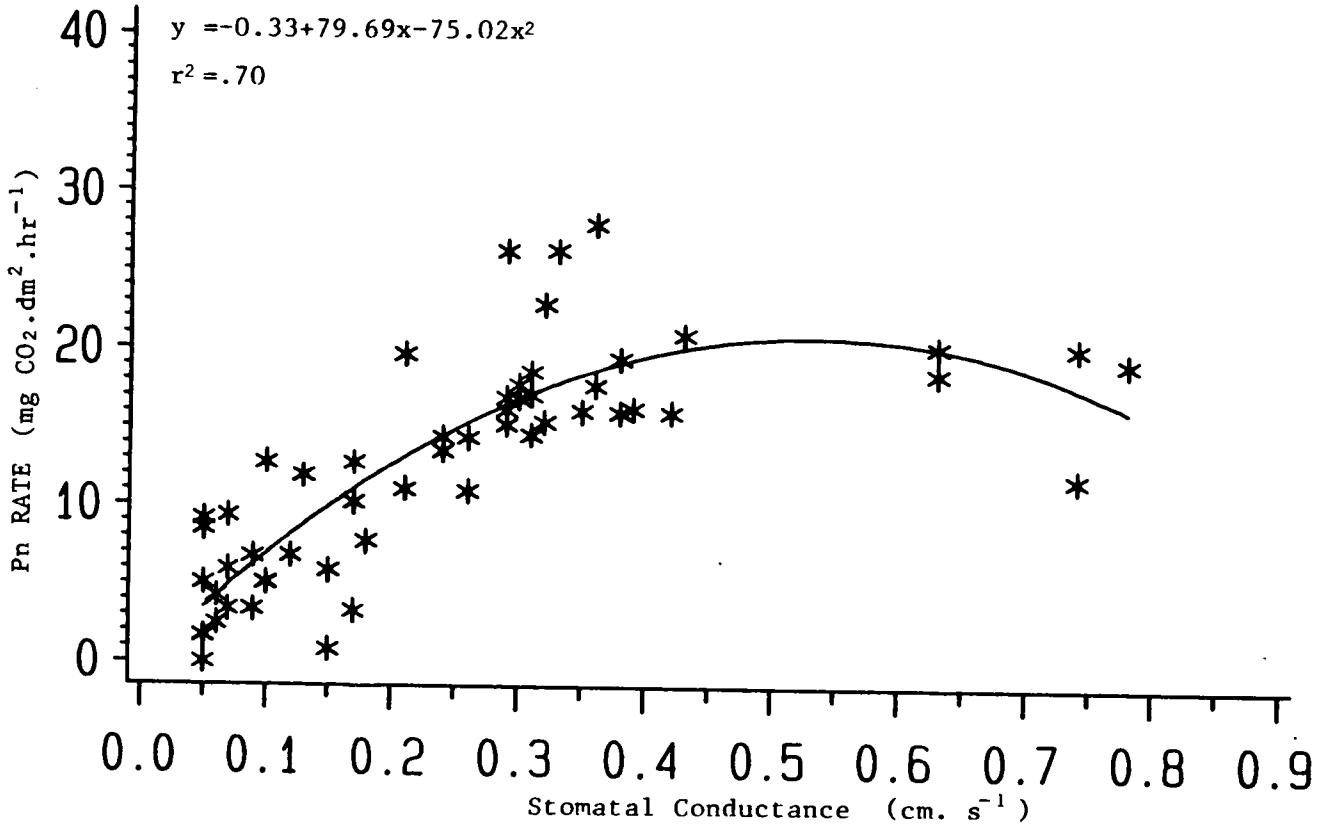


Figure P.1. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates.

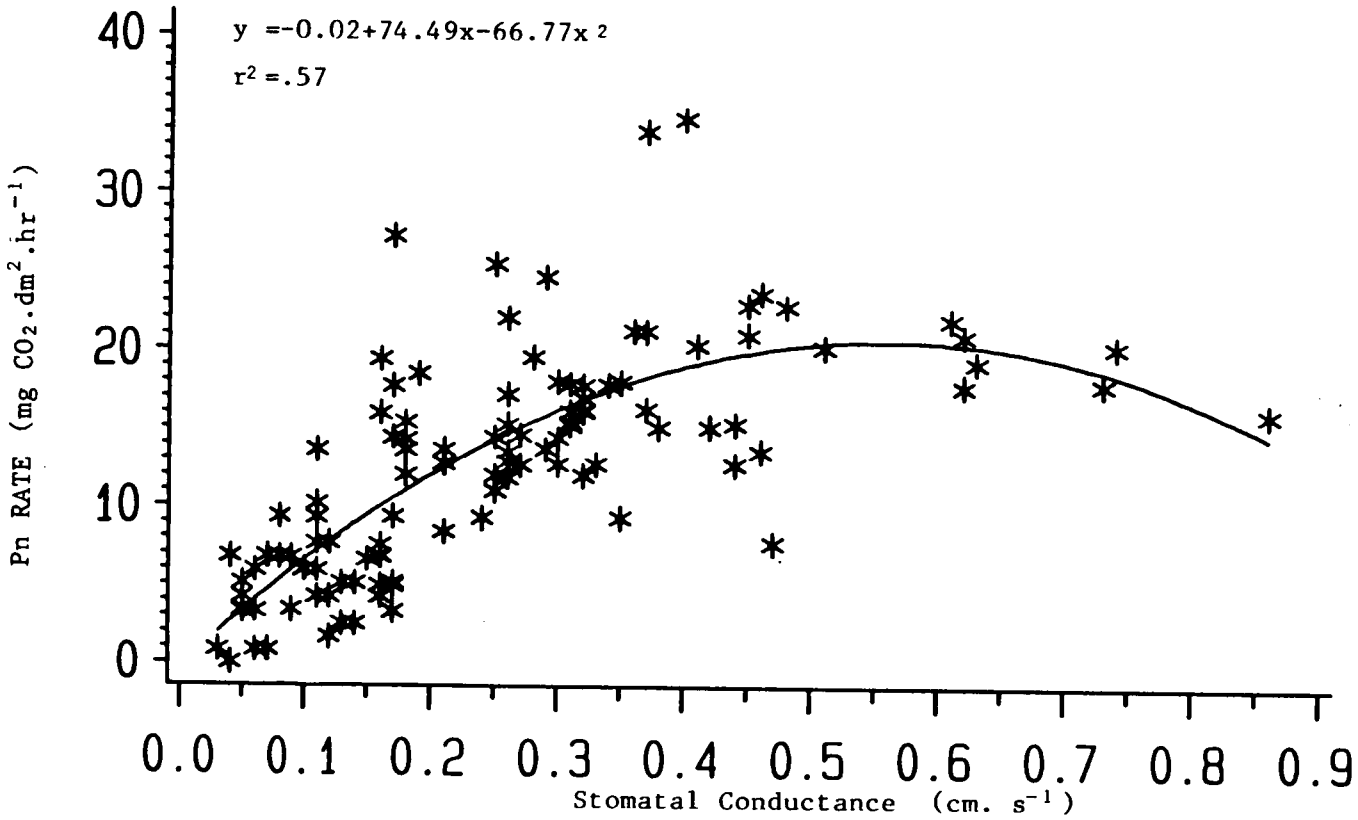


Figure P.2. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates from trees treated with 300 ppm paclobutrazol.

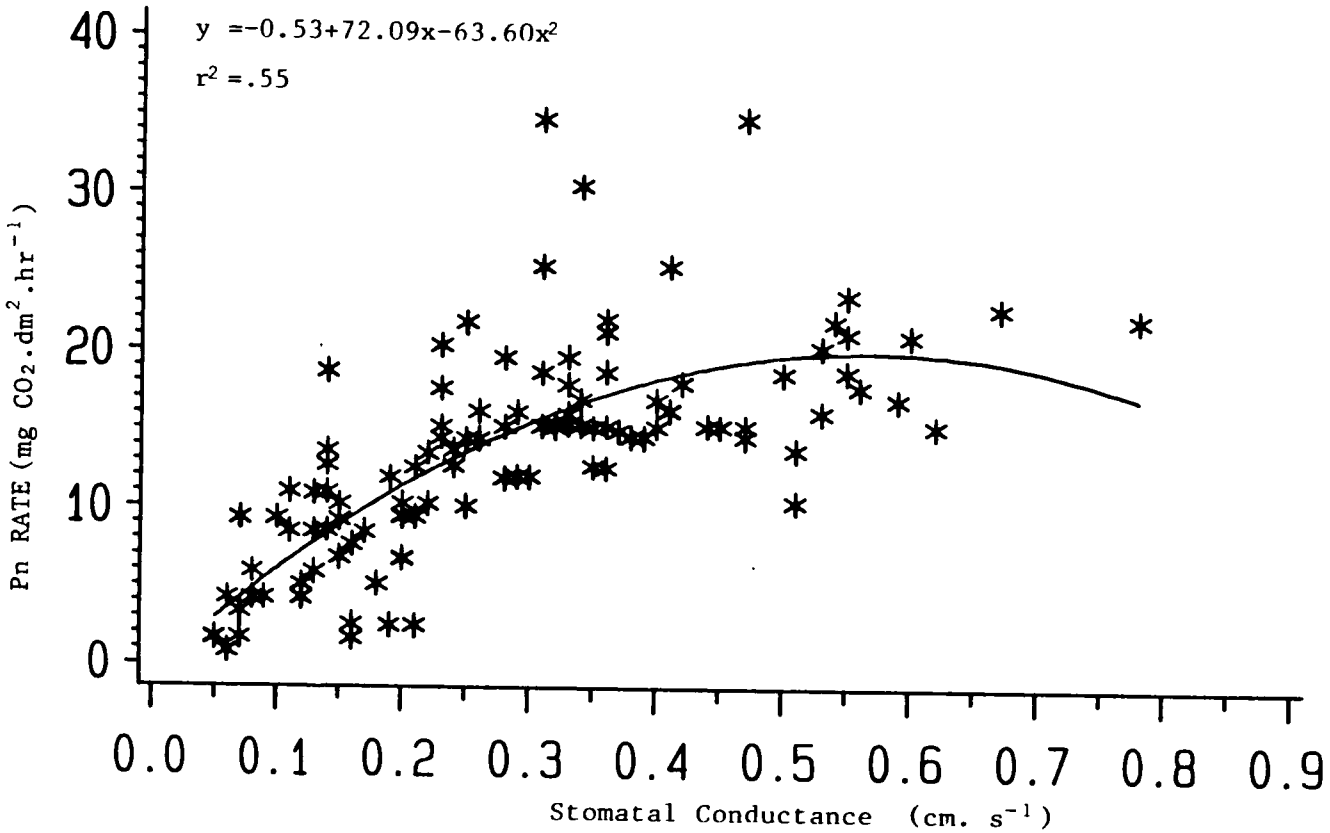


Figure P.3. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates from trees treated with 600 ppm paclobutrazol.

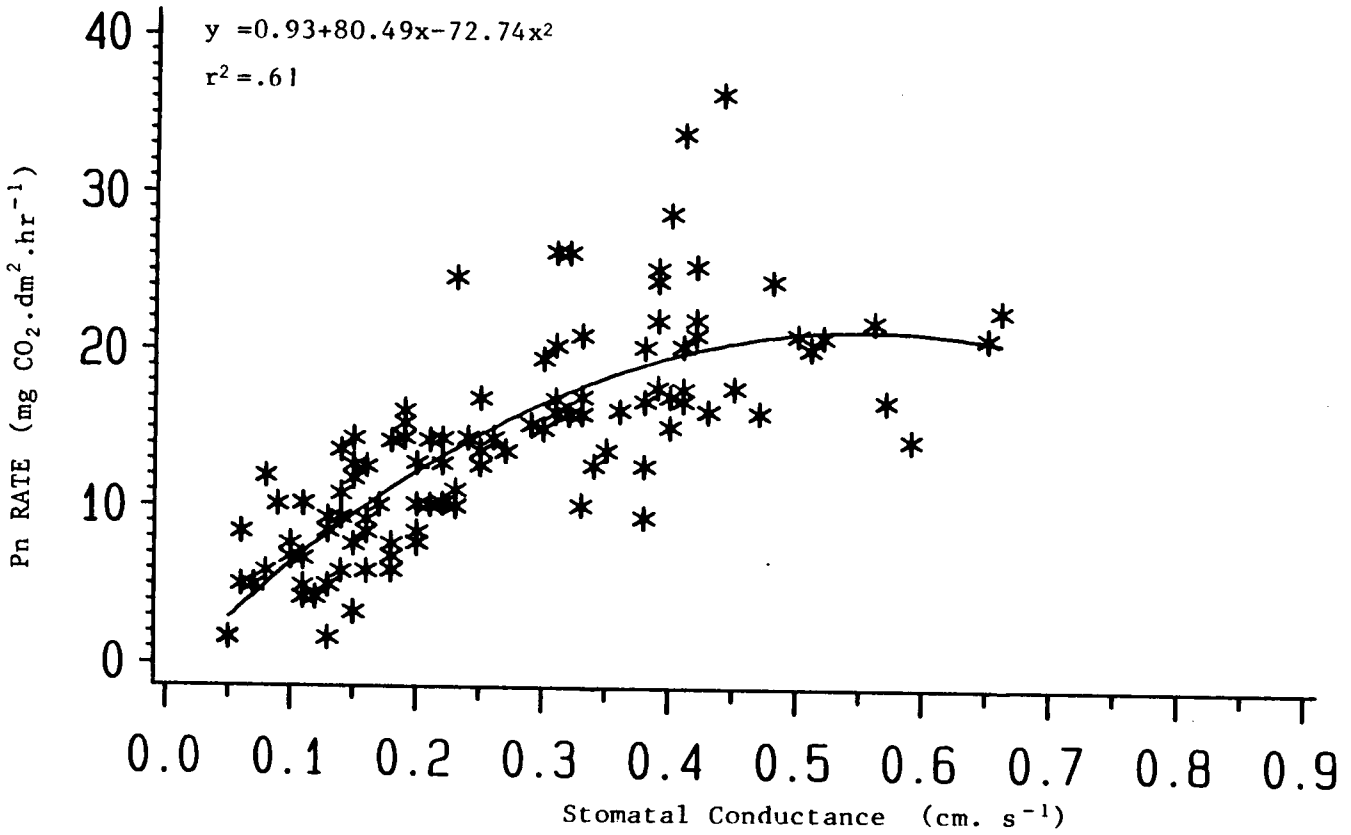


Figure P.4. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates from trees treated with 1200 ppm paclobutrazol.

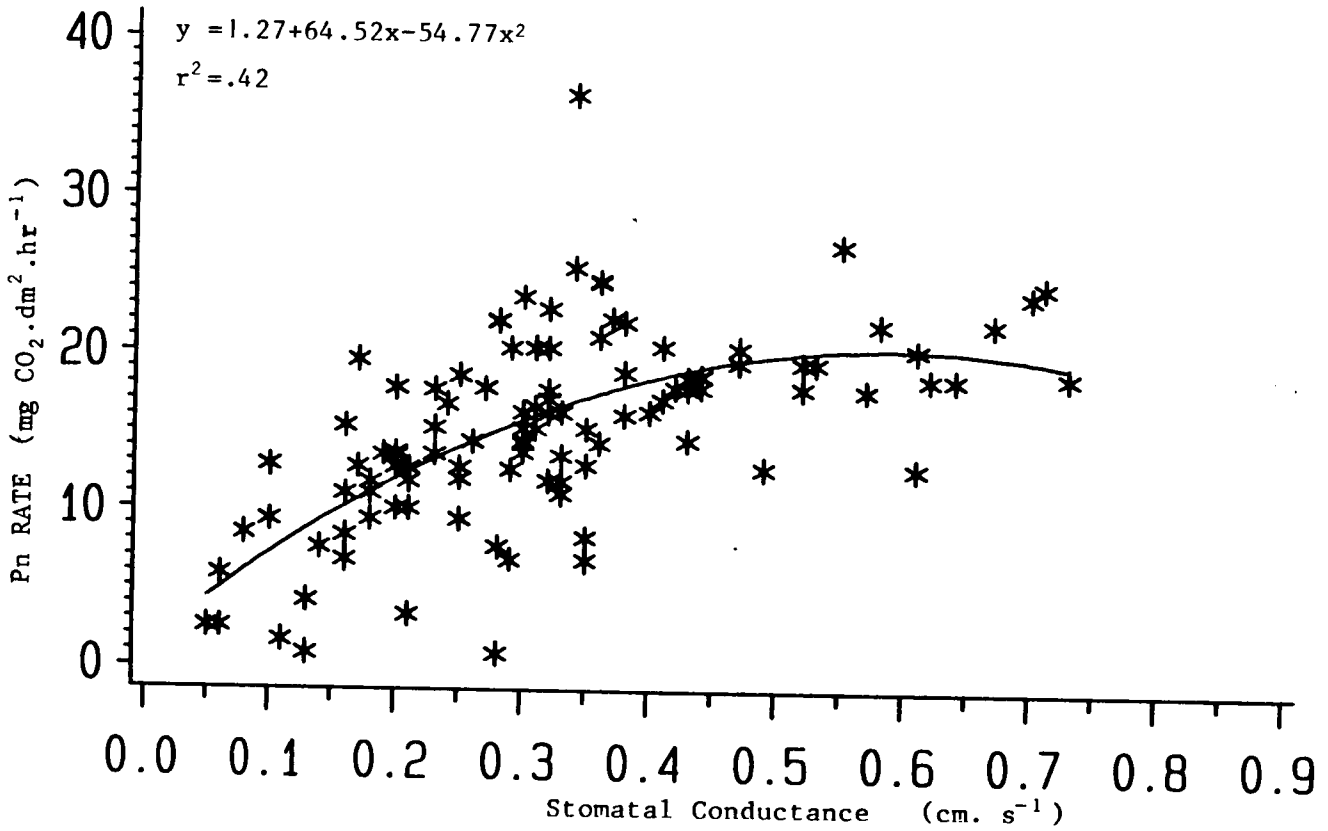


Figure P.5. Net photosynthesis (Pn) of 'Golden Delicious' apple leaves at various stomatal conductance rates from trees treated with 2400 ppm paclobutrazol.

VITA

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