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THE USE OF TERBACIL AS A TOOL TO ESTABLISH A PHOTOSYNTHETIC THRESHOLD IN APLLES

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THE USE OF TERBACIL AS A TOOL TO ESTABLISH A PHOTOSYNTHETIC THRESHOLD IN APPLES

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ABSTRACT

THE USE OF TERBACIL AS A TOOL TO ESTABLISH A PHOTOSYNTHETIC THRESHOLD IN APPLES

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Ten-year-old apple trees (Malus domestica Borkh.) cv. Redchief 'Delicious' carrying either heavy or light fruit loads were sprayed with terbacil, [5-chloro-3-(1,1-dimethylethyl)-6-methyl-2,4(1H,3H)-pyrimidinedione)], a photosynthetic inhibitor at 63 ppm + surfactant X-77 (1.25 ml. l^{-1}) at: 15, 30, 60, 80, 100, and 145 days after full bloom (DAFB) and compared with a control.

Inhibition of photosynthesis (Pn) at 15 and 30 DAFB induced fruit abscission, which was markedly higher for trees having a high crop load. Both treatments significantly reduced yield by reducing fruit number. Pn inhibition at 30, 60, 80, and 100 DAFB reduced return bloom. Terbacil at 63 ppm plus surfactant caused a 50-60% reduction in Pn, but Pn recovered 13 days after application. Pn and the ratio variable fluorescence to maximal fluorescence (Fv/Fm) were significantly correlated ($r = 0.7$, $Y = 3.21 \times (10.24)^{x}$). No differences were found in total terminal shoot growth, cold hardiness, soluble solid concentration (SSC), fruit firmness, density of the fruit or fruit color.

DEDICATION

To my parents. To Maryflor and Coqui for all their support while I was studying at MSU. To Ing. Agr. Alberto C. Ferreri (1919 - 1987) who introduced me to the world of the viticulture.

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A	Net carbon dioxide assimilation (molar units)
BCSA	Branch cross-sectional area
CHES	Clarksville Horticultural Experiment Station
Chl	Chlorophyll
Chl a	Chlorophyll a
Chl b	Chlorophyll b
DAFB	Days after full bloom
FS	Full sunlight
Fv/Fm	Variable fluorescence/maximum fluorescence
HTRC	Horticultural Teaching and Research Center
PAR	Photosynthetically active radiation
PSII	Photosystem II
PSG	Plant and Soil Greenhouses
Pmax	Maximum leaf photosynthesis
Pn	Net photosynthesis (mass units)
PPFD	Photosynthetic photon flux density
ppm	Parts per million
r	Correlation coefficient
SSC	Soluble solids concentration
SLW	Specific leaf weight
TCSA	Trunk cross-sectional area
T_{50}	Temperature required to kill 50% of samples

LITERATURE REVIEW

LITERATURE REVIEW

The importance of photosynthesis to plant productivity is evident, for 90-95% of the dry weight of plants is derived from photosynthetically fixed carbon (Flore and Lakso, 1989). As much as 70% of a fruit tree's annual assimilation of carbohydrate is often partitioned into fruit. Yet the tree must have sufficient carbohydrate for maintenance respiration, to form shoots and roots, to initiate and develop flower buds for the next season, and to provide energy to survive the cold stress of winter. Additional physiological activities such as transpiration and respiration must also be considered as carbohydrate demanding processes (Faust, 1989).

Fruit tree productivity is dependent on the efficiency of photosynthesis and the allocation of photosynthates to economic end products (DeJong, 1986).

The flow of carbon during early growth of apple trees is dependent on both stored reserves and currently produced photosynthates (Johnson and Lakso, 1986). The relative importance of these two components on the early growth of different organs is still not well understood. The leaf area of trees develops rapidly during the spring (greater than 50% within 30 DAFB) up to a maximum value, then becomes stable during midseason and finally decreases when leaves start to fall during autumn (Faust, 1989). Leaf area development is dependent upon degree day accumulation, and begins before

flower buds open. Spur leaves are the first to develop after bud break and comprise the majority of the tree canopy until a few weeks after bloom. A high degree of spur formation is desirable in apple to increase productivity. The leaf area is relatively high in this species as compared with others that develop leaves only on shoots (Faust, 1989).

Johnson and Lakso (1986) developed a computer model simulating the carbon balance of a growing 'Jonamac' apple shoot in order to estimate the time of first net carbohydrate export from the shoot. That model was based on measurements of net photosynthesis, dark respiration, and dry weight of the different components of the shoot. The model showed that a shoot growing to a final length of 50 cm became a net exporter of carbohydrates 19 days after budbreak, when the shoot was 4 cm long with 10 unfolded leaves. A shoot with a final length of 2 cm starts exporting at 15 days after budbreak. According to this model, short shoots export more carbohydrates than do long shoots until 36 days after budbreak, indicating that short shoots supply greater amounts of carbohydrates to the rest of the plant during this early period. The model estimated a total import of carbohydrates from reserves of about 165 mg for the long shoot and 80 mg for the short shoot. In each instance, these reserves only accounted for about 20% of the total carbohydrates used by the shoot up to that point. The remainder was supplied by current photosynthesis.

Watson and Landsberg (1979) have concluded that apple spur leaves become net exporters of carbohydrates when they reach 5% of their final size. In other species, such as tomato and cucurbits, export begins at about 35% of final size. Watson and Landsberg (cited by Lakso, 1984) estimated that under English growing conditions spur leaves began to export carbohydrates within 10 days of beginning growth. In contrast, extension shoots do not exhibit net carbohydrate export to the tree until they reach 12-15 unfolded leaves about; 3-4 weeks after full bloom (Lakso, 1984).

Factors affecting Pn potential

Variables under field condition which affect maximum Pn potential of apple are: leaf age and position, leaf exposure to light, temperature, and environmental or biological stress.

Genetic variation in carbon assimilation (A) due to scion, cultivar, or rootstock does not seem to be great in apple, although it is difficult to compare rates between studies (Flore and Lakso, 1989). Flore and Lakso (1989) reported a maximum photosynthetic rate for apple in the order of 15.7 ± 5.6 μmol CO_2 m^{-2} s^{-1}. This value is influenced by the environment, stage of development, fruit load, and time of determination and equipment used.

- Light levels to net photosynthesis (Pn).

Palmer (1986) found a linear relationship between light

interception and both total dry matter production and fruit weight in apple. This observation agree with those of Monteith (1977) and Gallagher and Biscoe (1978; cited by Ort and Baker, 1988), who reported a strong correlation between total dry matter production and the total amount of light interception in barley, potato, sugar beet and wheat.

Both by experimentation and definition light is obviously the most important environmental factor in photosynthesis of fruit trees (Lakso, 1986; Flore, 1994). The response of Pn to increasing irradiance is a hyperbolic response characteristic of C_3 plants. In general, photosynthesis saturates between 400 and 600 uE m^{-2} s^{-1} for individual apple leaves (Faust, 1989). In peach, cherry and other fruit trees this value is slightly higher and may range between 400 and 700 μE m^{-2} s^{-1}.

Single-leaf photosynthesis is saturated approximately at 20-40% of full sunlight, but the saturation of a full tree canopy is considerably higher due to the variety of leaf exposures and inherent differences between sun and shade leaves (Lakso, 1986; Lakso and Seeley, 1978).

Marini and Marini (1983) reported that apple leaves developing 0.5 m from the tree periphery had lower Pn potential, dark respiration and SLW than peripheral leaves. Kappel and Flore (1983) reported that peach leaves under shade became light-saturated between 400 and 600 μE m^{-2} s^{-1}, while full-sun leaves became light-saturated at 700-900 μE m^{-2} s^{-1}.

However, Lakso and Barnes (1978) demonstrated that interior leaves could be relatively efficient, or at least instantaneously respond to incoming light when a sunfleck strikes them. They found that apple leaf photosynthesis was more efficient under short term fluctuating light than under continuous light. The authors reported an 85% higher photosynthetic rate in apple leaves exposed to alternating light than in those exposed to continuous high light.

Ort and Baker (1988) mentioned that the majority of the photosynthesis occurring under field conditions occurs at non-saturating light levels. In their opinion, plants have evolved numerous photosynthetic mechanisms and chloroplast features to ensure efficient photosynthesis at low light levels.

- Light thresholds for maximum Pn

According to Heinicke and Childers (1937) and confirmed by others (Flore and Lakso, 1989), 25 to 30% of full sun intensity is considered to be the minimum for the maximum photosynthetic rate in apple. These authors in also noted that areas that received less than 30% of full sunlight were unproductive. Therefore, this level of light is considered as a minimum threshold for light.

According to Rom (1990), approximately 30-50% of full sunlight (600 - 1000 μmoles photon flux, 400-700 nm) is required for maximum Pn rates. Shading apple shoots to levels

between 50 to 100% ambient sunlight caused only a 10-50% reduction in Pn. However, shoots grown in 25% sunlight had Pn rates of 30-40% of full sunlight. Thus, 30% full sunlight is a critical threshold value for maximum photosynthetic activity and carbohydrate production.

Ninety percent shading reduced dry matter production of potted apple rootstocks to 6 to 12% of that of controls (Priestley, 1969). Similar results were reported by Barden (1977) where reducing the irradiance by 80% caused a 50% reduction in dry matter in apple trees.

- Effect of crop load (sink strength)

Carbohydrate sinks are either reproductive or vegetative (Flore and Lakso, 1989). Sink strength is defined as sink activity times sink size, and varies with season, depending on the stage of fruit and vegetative development, and with the life cycle of the tree.

Carbohydrates are preferentially partitioned to the fruit. Therefore, heavy fruit loads in apple trees result in reduced leaf area as compared with trees having light loads. Total dry matter is generally the same or higher in fruiting trees (Faust, 1989). For example, Maggs (1960) found that cropping apple trees produced more total dry matter per unit

area than did non-cropping trees. The presence of fruits leads to higher rates of Pn (Hansen, 1967; DeJong, 1986; Flore and Lakso, 1989; Sams and Flore, 1983).

Fruits also affect translocation and distribution of photosynthates. The growth in diameter of branches and of the trunk is depressed when a large amount of fruit is produced (Hansen, 1967). Maggs (1963) reported that increased fruit production occurred at the expense of root growth. The author hypothesized that the assimilates produced in the leaves were diverted to the fruit rather than moving down the stem to the roots. Translocation studies conducted with $^{14}CO_2$ by Hansen (1967) to shoots with and without fruits, have demonstrated that nearly 90% of the ^{14}C assimilated by the leaves can be transferred to the fruits close by. The majority of the ^{14}C-label was transferred during the first 4 to 5 days. Leaf ^{14}C was reduced more rapidly in shoots with fruits than in those without. The uptake of $^{14}CO_2$ per cm^2 of leaf area was 1.5 greater in fruit-bearing shoots than in those not containing fruits. These data imply that fruit removal should reduce Pn in adjacent leaves.

Avery (1969) reported that in the apple cv. 'Worcester Pearmain' fruiting suppressed the total dry weight increment produced, but that the leaf efficiency (calculated as g dry matter produced per dm^2 of leaf surface) was greater on fruiting trees. The same author concluded that "trees of high fruitfulness produced as much, or even more, than deblossomed

trees because of increased photosynthetic efficiency". He reported values of 0.81 and 0.60 Kg m^{-2} for bearing versus non-bearing apple trees for the growing season up to harvest. These results are close to those of Proctor et al. (1976) who found values of 1.07 and 0.62 Kg m^{-2} for fruiting and de-fruited trees, respectively.

Proctor et al. (1976) reported that fruit removal had no effect on the Pn of the adjacent leaves during intervals of up to 0.5 hr. The discrepancy in the results obtained may be due to the different time periods involved. For example, Hansen's data were obtained after several days of the application of labelled carbon; whereas in the experiments of Proctor et al., 0.5 hr may be insufficient to reflect the adjustment in "source-sink" balance to cause reduced Pn. These results agree with that found by Rom and Ferree (1986), who observed that the Pn of intact spur leaves of 'Golden Delicious' apple trees were similar, regardless of the fruiting condition of the spur.

Roper et al. (1988) reported no difference in Pn in fruiting vs. non-fruiting cherry plants on either a seasonal or a diurnal basis. They suggested that Pn rates in sweet cherry in the fields were primarily affected by ontogeny and environment and not by sink strength.

Gucci and Flore (1990) observed different responses on Pn of plum trees depending on the time of the season that fruits were removed. Defruiting at pit-hardening stage decreased CO_2

assimilation by 25% within 24 hours, whereas removing mature fruits did not affect it. There is evidence from other studies with apple that the fruit is dominant over other sinks in the plant and may exert significant control over leaf activity. In various experiments to manipulate the balance between fruit and leaf area, reducing the fruit load resulted in accumulation of leaf sugar and starch and, conversely, reducing leaf area with constant fruit load resulted in smaller concentrations of leaf sugar (Treharne, 1986). Priestley (unpublished, cited by Treharne, 1986) has demonstrated that the leaf responds to change in sink demand by a rapid change in rate of assimilate export; in apple this is mainly reflected in the sorbitol component.

Seasonal changes in photosynthesis

Heinicke and Childers (1935, cited by Faust, 1989) determined the total photosynthesis of a young bearing apple tree through the year. Their investigation showed that early in the season as the leaf area expands, the net photosynthesis increases, reaches a maximum and then declines as the leaves senesce. Throughout the season the most important factor governing this process was light level (irradiance) and the total amount of light intercepted by the tree canopy.

Light interception and distribution are not only dependent on the tree size, spacing, row orientation, canopy

shape, and training system, but in the seasonal development of the foliage. Several studies have concluded that apple leaf photosynthesis reaches a maximum just before or at the time of full expansion. A different response was observed for fruiting and non-fruiting shoots (Palmer, 1986b). According to Ghosh (1973) the maximum assimilation rates in apple occurred in his studies, at the end of June and the minimum rates at the end of July for leaves of fruiting shoots. Toward the end of the vegetative period Ghosh (1973) found that the leaves of fruit-bearing shoots showed a slightly higher rate of photosynthesis, whereas leaves of shoots without fruits showed the opposite trend. Kennedy and Fuji (1986) found that as apple leaves enlarged, the rate of photosynthesis increased rapidly to a maximum of 40 to 43 mg CO_2 dm^{-2} hr^{-1}. Thereafter, photosynthetic rates remained constant (30 mg CO_2 dm^{-2} hr^{-1}) for several weeks before declining toward the beginning of senescence.

In orchard studies, Kennedy and Fuji (1986) observed two periods during the growing season when the rate of photosynthesis in leaves of flowering or fruiting spurs was 10-20% higher than the leaves on non-flowering or non-fruiting spurs. The first period was during flowering, and the second during fruit maturation. Palmer (1986b) observed a different pattern of Pn according to the type of leaf (spur vs shoot leaves). In his study spur leaf Pn declined from early June to late October. During August, Pn rate varied considerably

between spurs of different ages. Pn in extension shoot leaves showed a later maximum, and during August and September Pn rate was three times greater than for spur leaves. The rate of decline in photosynthesis after a maximum in both types of leaves was associated with a decline in stomatal and mesophyll conductances.

Rom (1990) studied the seasonal variation of carbon balance in spur leaves in apple. When "supply" (Pn on a daily per spur basis) and "demand" (fruit relative growth rate) curves were plotted against time, demand equalled supply at bloom, after which supply exceeded demand for approximately a 40 day period.

Effect of Pn on productivity

- Relationship between photosynthesis and yield

Evidence for a direct relationship between improved photosynthesis and productivity has been elusive. In most cases, there appears to be no direct association between maximum leaf photosynthetic rates (Pmax) and yield in perennial tree crops (Charles-Edwards, 1978; Ozbun, 1978; Nelson, 1988; cited by DeJong, 1990). DeJong (1990) pointed out that the lack of correlation between Pmax and productivity reflects the fact that leaf Pmax is not an appropriate indicator of total carbon assimilation by plant canopies.

According to Lakso (1980) four factors determine the production of apple fruits: 1) light interception by the canopy leaves, 2) potential photosynthetic capability of the leaves, 3) internal and external factors that determine actual photosynthesis and 4) distribution of the photosynthetically fixed carbon to the developing organs of the tree. Nevertheless, a canopy of high light interception, high photosynthetic potential and high actual photosynthesis does not guarantee a high yield of quality fruit. Therefore, the distribution of the photosynthetic products to the various organs in the tree is critical.

Flore and Sams (1989), suggested that the carbon must not only be produced, but be partitioned efficiently to fruit for the current year's crop and to flowers for the next year's crop. The lack of a relationship between Pmax and yield emphasizes the importance of sink strength in determining yield. This, coupled with evidence for feedback effects on Pmax suggest, that sink strength rather than Pn is the primary factor limiting yield in many crops (Chalmers, 1975).

Circumstantial evidence exists to support the hypothesis that there is a direct relationship between yield and Pn (Seely, 1978). Some of this has been reviewed by Moss (1976) and Zelich (1971). This evidence includes decreased crop yields in shaded conditions, the yield reduction resulting from defoliation, enhancement of growth and productivity by atmospheric CO_2 enrichment, and faster crop growth rates in

photosynthetically efficient species.

Flore and Sams (1986) have demonstrated, based on sour cherry studies, that photosynthesis may limit cropping in this species. They proposed that, when considering whether photosynthesis is limiting yield, a distinction should be made between photosynthetic rate (CO_2 fixed per unit area) and total carbon fixed, which also takes into account the leaf area and leaf area duration. According to the authors, photosynthesis could limit growth of the crop during stage three of fruit growth in sour cherry, if severe defoliation occurs due to insect attack or disease, if environmental conditions are not conducive for optimum photosynthesis, or if the leaf to fruit ratio is less than 2. They also pointed out that in most cases photosynthetic capacity is large enough in cherries to provide carbohydrates even for relatively large crops, but photosynthesis could limit yield when fruit crop loads are high and/or when stresses occur during stage three of fruit development. In some cases overcropping can limit carbohydrate storage and vegetative growth to the extent that cropping or plant health might be adversely affected (Flore and Lakso, 1989; Flore and Howell, 1987).

Chang et al. (1987) pointed out the importance of the effects of Pn on components of tree yield. Two major components are important in determining fruit tree productivity: fruit number and fruit weight. Both components are obviously influenced by Pn. Fruit weight is dependent on

the leaf area and leaf number/fruit, whereas fruit number is usually determined not only by current photosynthesis that ensures a high degree of fruit set but also by the previous year's photosynthesis.

Hansen (1977) found a positive curvilinear relationship between fruit growth/m^2 of leaf area and crop load. The same relationship was reported by Beers et al. (1987) who found a curvilinear relationship between mean fruit weight and leaf fruit ratio (LFR) in apples.

Carbohydrate levels must be high enough that, in addition to supporting fruit and tree growth, the tree can develop sufficient flower buds and reserves in the wood. During the spring reserves are needed for a high fruit set, and therefore high yield. In sour cherry Pn is limited when the leaf-fruit ratio is less than 2.0 (Flore and Sam, 1986). Carbohydrate shortage in apple has been reported for leaf-fruit ratios less than 15 leaves per fruit (Faust, 1989).

Flore (1986) stated that the Pn potential in fruit crops is under two forms of control: 1) the environment, which directly influences the immediate physical and biochemical reactions and indirectly, through light exposure, affects the morphological development of the leaf, and 2) through sink demand and some type of feedback signal from the sink itself. He emphasized that the Pn potential is seldom reached in fruit trees. Thus, when improvement of crop is considered, photosynthesis may be only one of the many important factors.

Studies of the effect of photon flux density (PFD) on yield show a direct relationship between light intensity, over a certain threshold, and yield affected through its different components. Experiments with spinach (Jackson et al., 1991) and lettuce (Sanchez et al., 1989) showed that a decrease in PFD substantially reduced crop yield in these species. In lettuce, shading, regardless of the degree, reduced growth and yield during the heading stage of development. Similar results were found in tomato grown under different light conditions. McAvoy et al. (1989) observed a strong correlation (r=0.947) between the total yield of tomato plants and total photosynthetic photon flux (PPF) received in the period from anthesis to harvest.

Bravdo (1986) reported that a 25% reduction in PFD in apple trees, cv. 'Granny Smith', by the use of net covering, increased leaf photosynthesis and fruit yield.
In the experiments conducted the number and size of fruits were significantly higher in the shaded trees. The author attributed this increase to an increase in water potential observed in the shaded trees. Reduced atmospheric stress and increased water potential during bloom and various stages of fruit growth can reduce fruit drop and also increase fruit size (Assaf et al., 1982).

Any factor that affects Pn, such as altered light levels, injury to the leaf, defoliation of trees, markedly affects fruit set, flower bud formation, fruit size, fruit color and

quality, carbohydrate distribution, specific leaf weight (SLW), and wood hardiness.

Effects of light on fruit production and quality

- Light levels and flower bud formation

The contribution of leaves to flower bud initiation has been established in most plants, including mangos, apple, olives and oranges (Monselise and Goldschmidt, 1982).
The strongly negative effect of shade on flower bud initiation has been known for a long time (Auchter et al., 1926; Paddock and Charles, 1928). In apple trees several years of shading have a cumulative negative effect on the initiation of flower buds (Jackson and Palmer, 1977).

Recently investigators have attempted to evaluate the light effect on flower bud initiation quantitatively. An increase in radiation from 32.3% to only 37.5% of full sunlight increased the percentage of flowering spurs in the center of the apple tree from 13.6 to 43.8%. 30% of full sunlight or 27% of photosynthetically active radiation (PAR) are regarded as threshold values for flower bud formation (Gur, 1985). A hyperbolic regression of the number of flowering apple spurs on the "fisheye perc, sky value" in late May, in the year preceding the counting of the flowering spurs, has also been established (Lakso, 1980).

The negative effect of shade on flower bud initiation explains the negative effects results of densely spaced hedgerows on flowering (Jacyna and Soczek, 1980).

Finally, Jackson and Palmer (1977) pointed out that in some experiments they found a marked interaction between shading and crop load in their influence, not only on flower bud formation, but also on fruit set and size. This suggests that the effect of shading in one year may partially pre-adapt the tree for such conditions in the following year.

- Light levels and fruit set

The importance of photosynthesis as the major factor governing yield can be established by analyzing the effects of low light levels and leaf injury/defoliation on the different components of crop yield.

Reducing light level within the canopy 20% at bloom and 10-20% the remainder of the season by over-tree shade, reduced fruit set 62% in 'Delicious' apple trees (Doud and Ferree, 1980). These results agree with those found by Jackson and Palmer (1977). 'Cox's Orange Pippin' apple trees were shaded so as to receive 37, 25 or 11% of full sunlight during the post-bloom growing season, and their flowering and fruit development and yield was compared with those of non-shaded control plants. Shading reduced fruitlet retention and fruit size and percentage dry matter in the year of shading. The

number of fruit per 100 flower clusters was reduced 25% by heavy and medium shading. Moreover, trees shaded heavily during two consecutive years produced only one-third as many fruits per 100 flower clusters in the second year as did the controls. Similar effects of shading on apple fruit set were reported by Auchter et al. (1926) and Heinicke (1977).

Conclusive studies about the effect of shading apple trees at different times on fruit set came from the studies of Byers et al. (1990a). Shading (92%) of Redchief 'Delicious' apple trees for 10 day periods at different times after full bloom showed that 10 to 30 DAFB, when fruits were 8 to 33 mm in diameter, was the most sensitive period for inducing fruit abscission. Similar results were obtained by Byers et al. (1990b) with spur 'Delicious' apples. Shading trees for 4 days at FB + 17 days with 92% shade reduced fruit set 50%.

Byers et al. (1984) reported that abscission can be induced in nectarines when trees are shaded 45 to 58 DAFB. Peaches most sensitive to shade at 31 to 41 DAFB.

Early removal of spur leaves similarly reduces fruit set. Ferree and Palmer (1982) demonstrated the importance of spur leaves on fruit set and development. Removal of 50% 'Golden Delicious' spur leaves at full pink reduced final fruit set. The combination of spur ringing and removal of all leaves resulted in a complete loss of fruit. Comparable results were reported by Arthey and Wilkinson (1964), Llewelyn (1966) and Lakso (1984). Lakso (1984), reported that defoliation of spur

leaves prior to fruit set caused severe reductions in fruit set while defoliation of shoot leaves had relatively little effect. Neither removal of spur leaves later in the season (after 30-50 DAFB) or shading spur leaves after bloom affected fruit size. On the other hand, Rom and Ferree, 1986 reported that later in the season, shoot leaves contribute to continued fruit growth. All these results pointed out the importance of photosynthesis in fruit set.

However, partial defoliation below a certain threshold may be overcome photosynthetic compensation (Flore and Irwin, (1983); Layne and Flore, (1992), see below).

On the other hand, Darnell and Martin (1988) found no correlation between ^{14}C accumulation in strawberry flower receptacles and fruit set or initial fruit growth. ^{14}C-labeled photosynthate was not the source for the observed dry weight increases. From their study they concluded that fruit set and initial fruit growth in strawberry is not limited by the capacity of receptacles either to mobilize current sources of assimilates or to accumulate carbohydrates.

- Light levels and fruit size

Light penetration into trees and the relationship of this to fruit size and color was studied by Heinicke (1966) who found that both size and color of 'McIntosh' and Red 'Delicious' apples were correlated with degree of exposure to

sunlight. A linear relationship was found between light interception and fruit dry weight (Palmer, 1986); and between yield and leaf area/light interception (Barritt et al., 1991). Fourty-five percent shade of 'Cox's Orange Pippin' apple trees resulted in the production of high numbers of small fruits (Jackson, 1968). Shading reduced fruit size and especially fruit weight. Sixty-two percent shade did not affect fruit size, but fruit color. Jackson et al. (1977) reported that shading to 34% or 13% of full sunlight caused a decrease in fruit size by reducing both cell size and cell number. Fruits grown under shade had less dry matter and starch per unit fresh weight than those grown under full sunlight. In a study of fruit characteristics at different positions within the tree canopy, Barritt et al. (1987) observed that apple fruit weight and size were greater at the top than at the bottom. Size was correlated with the percentage of full sunlight received by each area of the tree. The top of the trees (3m) received 48% of full sunlight, whereas at the bottom the percentage was 9%.

- Light levels and fruit quality

In general the better colored apple fruits occur on the more exposed portion of the trees. Fruits from the tops, where photosynthetic photon flux density (PPFD) is greatest, are redder and have higher soluble solid concentration (SSC) than

fruits harvested with similar ground color from the tree interiors (Marini, 1985).

Several studies have shown the importance of light on fruit color and content of soluble solids. All of them revealed a positive correlation between high light levels and fruit color and sugar content (Jackson et al., 1977; Barritt et al. 1987). Heinicke (1966) reported that color development of Red 'Delicious' and 'McIntosh' apple was directly related to light exposure, with best color in fruit exposed to more than 70% of full sunlight (FS). Fruits exposed to 40-70% of FS were adequately color; those receiving less than 40% FS were very poorly color. Seeley et al. (1980) showed that apple fruit size, red color, and soluble solids concentration (SSC) increased linearly with PPFD for on shaded 'Delicious' limbs. Morgan et al. (1984) found similar relationships for 'Gala' fruit developing at various canopy positions.

Izso and Rom (1989) observed that fruit epidermal chlorophyll content exhibited a quadratic response, with maximum apparent greenness between 30% and 60% of full sun and decreases at irradiances above 60% of full sun.

Campbell and Marini (1992) determined a PPFD threshold for apple color intensity and SSC. The authors found a threshold level of 250 μmol m^{-2} s^{-1} for all fruit quality characteristics. On the other hand, Saks et al. (1990) demonstrated that development of red pigmentation had a threshold PPFD level of 150 umol m^{-2} s^{-1}, whereas SSC should

presumably have a higher threshold due to its dependence on photosynthesis.

- Light levels and specific leaf weight

The structure of the apple leaf varies with the light conditions under which it develops and functions (Jackson, 1980). Specific leaf weight (SLW) is highly correlated with net photosynthesis in apple (Barden, 1977; Marini and Marini, 1983). Barden suggested that SLW might be a useful index of the light environment previously experienced by the leaf and of its Pn potential. Palisade cell development is responsible for the difference in SLW of apple leaves grown under different PPFD (Warrington et al. 1990). Studies of peach and apple canopies have indicated that leaves in areas of the tree receiving less than 36-40% PAR have a lower SLW than peripheral or non-shaded leaves (Kappel and Flore, 1983; Marini and Marini, 1983).

Effects of defoliation by diseases and insects. Damage thresholds.

Injury to the leaf caused by diseases or insects, as well as defoliation, can decrease Pn rate and cause economic loss. Ferree (1978) and Ferree et al. (1986) summarized the effects of diseases on Pn. The authors reported that powdery mildew

(Podosphaera leucotricha) caused a 75% decrease in Pn 35 days after infection. Apple scab (Venturia inaequalis) reduced Pn 20%. However, the loss of foliage induced by apple scab may cause much more severe damage, especially when defoliation occurs at the time of flower initiation. Pn was not reduced until visible lesions were present and leaves did not recover photosynthetic capacity when the disease was inactivated by fungicides.

Ferree et al. (1986) observed that mite infestation decreased Pn in apple trees. As the population of two-spotted spider mites (Tetranychus urticae) increased, Pn decreased and the reductions appeared to permanently destroy the photosynthetic capacity of the leaf. A population of 60 mites per leaf caused a significant reduction in apple Pn three days after placement on the leaf. Nine days after infection, 15 mites per leaf reduced Pn by 26%, 30 mites per leaf by 30%, and 60 mites per leaf by 43% below the value observed in uninfested controls. Similar results were reported by Campbell et al. (1990) using greenhouse trees. Working with two-spotted spider mite (Tetranychus urticae Koch) on infested Imperial 'Delicious' apple, they found that accumulation of 1200 mite days per leaf (MD) reduced Pn by 40%. Field experiments showed that 3056 MD reduced Pn only 17%.

Mites can also reduce yield in citrus. Hare et al. (1992), using 'Navel' orange (Citrus sinensi L.) reported that when populations of Panonichus citri (McGregor) reached

densities of 2.2, 7.1 and 9.7 adult females per leaf, yield was reduced 6.6, 9.0, and 11.4%, respectively.

The simultaneous impact of European red mite and spotted tentiform leafminer on 'McIntosh' apple yield and quality was studied over a three year period by Nyrop et al. (1993). Cumulative mite days up to 500 per leaf and leaf miner densities of 2 per leaf independently or jointly did not affect yield or quality. However, reductions in whole tree photosynthesis were observed. These reductions were correlated with cumulative mite days and fruit growth, indicating that reduction in fruit size was a good integrator of foliar damage by spider mite.

Nyrop et al. (1993) proposed the following empirical damage threshold densities for different insects: European red mite - 400 mite days; spotted tentiform leafminer - 2 mines per leaf; white apple leafhopper - 50 hopper days.

Jones (1993) studied the effect of different population densities of two spotted spider mites in order to establish damage levels on tart cherry. The population densities were 0, 185, 470 and 750 mite-days per leaf. Levels of over 470 mite-days reduced photosynthesis approximately 33%. The author suggested that preliminary economic thresholds be set at 185 mite-days per leaf.

Reaction to mite infestation varies among cultivars. Among eight cultivars tested , Pn reduction ranged from 0 to 20%. Mites caused greater decreases in Pn of 'Delicious',

'Gallia Beauty', 'Jonathan', and 'Melrose' than in the other cultivars tested (Ferree et al., 1986)

Studies of simulated defoliation have shown that removal of part of the leaf blade does not affect Pn until more than 7.5% of the leaf is removed (Ferree et al. 1986). More than 15% has to be removed before the photosynthetic capacity on the remaining tissue is reduced. Greater reduction in Pn occurs when main lateral veins are severed as part of leaf removal compared to removal of only intervenal tissue. Reduction in Pn due to leaf injury was closely related to the amount of cut surface exposed. Similar results have been observed in experiments with defoliating arthropods and artificial defoliation on peanut canopies (Boote et el., 1980). Removal of 25% of the total leaf area of peanuts re*^T $^{14}CO_2$ uptake by 30% and canopy C exchange rate (CER) by 35%. In a second experiment, severe leafspot damage reduced LAI by 80%, $^{14}CO_2$ uptake by 85%, and canopy CER by 93%.

Proctor et al. (1982) found that at 20 mines per leaf, spotted tentiform leafminer (Phyllonorycter blancardella) injured 33% of the apple leaf, but assimilation was decreased by only 23%. In this study, at maximum irradiance, 10 mines (17% leaf area loss) were needed before Pn fall below that of the control plants. Flore and Irwin (1983) reported similar response to mechanical injury and tentiform leafminer for 'Golden Delicious' apple. Photosynthesis was reduced when 20% of the leaf area was removed. When one-year-old trees were

defoliated to 90, 80 and 70 % of the control at weekly intervals, total tree growth was not affected at 10 or 20% defoliation, which indicated a degree of compensation to the leaf loss by the remaining tissue on the plant.

Sylvertsen et al. (1986) found that in citrus leaves infested with six-spotted and spider mite Pn was depressed in relation to the percentage of damage. However, citrus leaves exhibited some recovery, and apparently they compensate for mite damage, showing little loss of net gas exchange potential at low damage levels. Similar results were reported by Layne and Flore (1992) for sour cherry. They observed that when defoliation does not exceed 20% the plant is capable of compensating by increasing its photosynthetic rate. This compensation was accounted for by a higher estimated carboxylation efficiency and ribulose-1,5-bisphophate (RuBP) regeneration capacity of the remaining leaves.

Studies on leaf photosynthetic responses to injury by insects indicated that gross tissue removal did not alter photosynthetic rates in remaining, uninjured tissue in soybean, apple, or sunflower (Higley, 1992). In early reproductive stages, soybean canopies with defoliation of over 70% exhibited no significant reduction in canopy photosynthesis as compared to the non-defoliated control. Delayed leaf senescence in defoliated plants was responsible for this compensation.

Starck and Stahl (1986) found that partial defoliation

did not retard fruit growth in tomato. Partial defoliation did not affect the final fruit dry matter, but reduced accumulation of substances in the leaf blades. Measurements of assimilation of $^{14}CO_2$ and partitioning of ^{14}C-substances in tomato plants with modified source-sink relationships (defruited and/or defoliated) showed that fruit growth was not limited by photosynthetic production, but by the sink capacity.

According to Flore and Lakso (1989), compensation may occur because the remaining leaves are relieved from constrains, i.e., carbohydrate accumulation, feedback inhibition from sugar or starch buildup, the loss of some inhibitory phytohormone, or increased allocation of resources remaining leaf area.

Effect of Pn on cold hardiness

Any factor that affects photosynthesis and thus carbohydrate accumulation, has an effect on cold hardiness. Early leaf loss in tart cherry trees causes delayed acclimation in the fall and more rapid deacclimation in the spring (Howell and Stackhouse, 1973) resulting in reduced bud survival and decreased fruit set. The effects of early defoliation carried over into the second season.

Two possible roles of carbohydrates in hardiness have been suggested (Howell and Stackhouse, 1973). Some investigators suggest that sugars prevent protein denaturation

(Faust, 1989). Some others take a more general view of the role of carbohydrates and suggest that acclimation, deacclimation, and reacclimation are all energy-requiring phenomena and the role of carbohydrates is to provide that energy.

The effects of time of leaf removal.

- Removal of spur leaves vs. shoot leaves.

Carbohydrate supply throughout the growing season is important for fruit growth and production. Early in their development apple fruits depend on the Pn provided by spur leaves; the availability of carbohydrates during the first stage of fruit growth is crucial for fruit retention. Inhibiting photosynthesis at that time is an effective way of thinning peaches and apples (see below). Previous studies have indicated that removal of spur leaves early in the season reduces fruit set, fruit growth and fruit calcium content (Rom, 1990). Removal of spur leaves 55-117 days after petal fall has no effect on eventual fruit size (Faust, 1989). Rom (1990) reported that removing spur leaves after 30-50 DAFB or shading them after 60 DAFB did not affect fruit size. Ryugo (1986) observed that when spur apple leaves were removed at weekly intervals after full bloom, no flower buds formed on spurs that were defoliated 6 to 10 weeks after full bloom. Shoot leaves early in the season have no effect on fruit size.

However, shading or removing of shoot leaves later in the season reduces the size of the fruit (Rom and Ferree, 1986). The authors conducted an experiment on Starkrimson 'Delicious' apple trees. Shading shoots from 60 DAFB until maturity, reduced fruit growth and delayed maturity, but shading spurs had no effect on either. This is further corroborated by ringing experiments that prevented carbohydrate transport from the shoot leaves, but not from the spur leaves, to the fruit (Faust, 1989). Ringing bourse shoots decreased fruit size (Ferree and Palmer, 1982). The authors found that although early in the season the presence of bourse shoot on 'Golden Delicious' apple was detrimental for fruit set, later in the season shoot leaves provide the carbohydrates needed for fruit growth and thus, high yield.

Photosynthetic inhibition

- Selective inhibitors of photosynthesis

Several herbicides are photosynthetic inhibitors, such as the ureas (1951), the triazines (1955) and the bipridiniums (1960) (Van Rensen, 1989). About 50% of all commercially available herbicides are inhibitors of photosynthesis (Trebst, 1981). Among this class of herbicides, terbacil (3-tert-butyl-5-chloro-6-methyluracil) is classified as an organic herbicide of the uracil group (Ashton and Crafts, 1977). It is used to

control many annual weeds, and some perennial weeds, in deciduous tree fruit orchards, blueberries, citrus, alfalfa, mint, and sugarcane. It is a soilborne toxicant absorbed by the roots and translocated apoplastically to the leaves. However, it may also be taken up by the leaves directly, especially with the aid of surfactant materials (Izawa and Good, 1965). Leaf chlorosis followed by necrosis is a common response of plants following terbacil application. Ultrastructural examination of these leaves usually reveals abnormal and degenerating chloroplasts as well as deteriorating membranes.

Mechanism of action of photosynthetic inhibitors

The studies of Cooke (1956) and Wessels and Van der Veen (1956) demonstrated that photosynthetic inhibitors interfered with the Hill reaction, which occurs in the chloroplasts. The Hill reaction is defined as the evolution of oxygen by a suspension of isolated chloroplasts when illuminated in the presence of an artificial electron acceptor (Moreland, 1980). The Hill reaction is associated with ATP formation. Therefore, the mechanism of herbicide action involves an inhibition of energy production. This concept was maintained as the primary explanation of the herbicide action of herbicides for convenience and because herbicide action was evaluated under nonphosphorylating conditions.

In recent years, more sophisticated studies have been conducted with herbicides and more is known about their differential action. Moreland (1967, cited by Moreland, 1980) separated herbicidal inhibitors of the photochemically induced reactions into electron transport inhibitors and inhibitory uncouplers. Electron transport is inhibited when one or more of the intermediate electron transport carriers is removed or inactivated. The site of action of most herbicidal electron transport inhibitors studied is closely associated with photosystem II (PS II). Most of the herbicides are inhibitors of electron flow at the functional site between the primary and secondary electron acceptors of PS II (plastoquinone Q and B). Inhibitory uncouplers are those electron flow inhibitors that also have an uncoupling property on the photophosphorylation system (Trebst, 1981).

Mechanism of action of uracils

Uracils are herbicides that block both the Hill reaction and photosystem II in the photosynthetic pathway (Ashton and Crafts, 1973). D1 protein of the PSII reaction centre is the "herbicide binding protein" (Dodge , 1991). Hoffmann (1971) proposed that the mechanism of action of uracils is very similar to, if not identical with, that of the urea-type herbicides. They have no effect on bacteria, fungi and non-photosynthetic organisms except at concentrations one or two

times greater than those that affect photosynthesis. Foliar chlorosis is the first symptom following application of the uracil herbicides; root and shoot growth are also inhibited. Ashton et al. (1977) studied the effect of uracils on growth, anatomy, morphology and cytology of oat plants. Bromacil at 10^{-3} M was marginally inhibitory of root growth, with effect been restricted to 0.5 mm segment immediately behind the meristem. Chloroplast grana development was inhibited; normal growth in the number of loculi per granum and normal increase in width of grana was prevented. However, the length of the grana was increased. The authors concluded that these effects appear to be associated with loss of integrity of membranes. Loss of membrane integrity has been reported to occur within 2 to 4 hr following treatment with herbicidal Hill inhibitors (Moreland, 1980). In contrast Sieber et al. (1973) reported that Lenacil (uracil herbicide) had no effect on ultrastructure of chloroplasts of sugar beet or Capsella Bursa Pastoris. In Phaseolus vulgaris, Citrus sinensis L. and Citrus jambhiri L., Herhodt (1968) reported a similar degree of inhibition of the Hill reaction in isolated chloroplasts of both species. Beans were more susceptible to terbacil, so he concluded that the difference in susceptibility between the two species was due to differential accumulation and transport.

Schiver and Bingham (1973) found that following foliar absorption, Bromacil moved acropetally in Kentucky bluegrass

and orchardgrass, and these patterns are typical of apoplastic translocation. They suggested that Bromacil diffused predominantly along cell walls, entered the xylem, and did not readily enter the phloem. The same patterns of translocation of terbacil following root absorption has been found in peppermint. Adjuvants increase herbicidal activity by increasing cuticle retention, penetration, absorption, and possible translocation (Kirkwood, 1991). The importance of the leaf cuticle as a barrier to penetration of herbicides is well documented. Among a range of factors, the physicochemical characteristics of the epicuticular waxes may be of particular significance since they can affect the retention and distribution of the active ingredient. The incorporation of surfactants may be required to achieve spreading or activation.

Metabolism of uracil herbicides

A characteristic of many uracil herbicides is the reversibility of their effects (Van Rensen, 1989). Van Rensen and Van Steekelenburg (1965) found that the inhibition of oxygen evolution in algae by some urea-type herbicides could be removed easily by washing. Izawa and Good (1965) showed that diuron was reversibly bound to chloroplasts. This implies that only weak bonds were involved in the interaction of this herbicide and the receptor molecule in the thylakoid membrane.

Cyclization reactions appear to be important in the metabolism of terbacil in alfalfa tissues, which are capable of metabolizing terbacil through a cyclization pathway yielding a heterocyclic oxazolo ring formed from the cyclization of the carbonyl group (C=0) at the 2-position and of the tert-butyl group [$-C(CH_3)_3$] at the 3-position of the molecule (Rhodes, 1979).

Herholdt (1968) reported extensive degradation of terbacil in citrus and beans following root uptake, but he did not characterize its metabolites. Terbacil was degraded more in susceptible species such as beans than in tolerant ones such as citrus. On the other hand, Barrentine and Warren (1970) found that terbacil was metabolized at a higher rate in tolerant species (e.g., peppermint) than in susceptibles (e.g., Ipomoea sp.) with both leaf and root treatments.

Determination of herbicide inhibition by fluorescence

In recent years, chlorophyll a fluorescence has been increasingly applied to various fields of plant physiology. The technique of measuring chlorophyll fluorescence has been used to determine photosynthetic activity, and to provide detailed information about the photosynthetic system (Krause and Weis, 1984). Measurement of chlorophyll fluorescence at 685 nm indicates the energy state of the P 680 reaction centres of photosystem II (PSII) and its associated pigments.

Fluorescence reflects the rate of electron transport from PSII to chemical acceptors, and the coupling between ATP and electron transport (krause and Weis, 1984).

In the leaf, the yield of fluorescence is influenced in a very complex manner to events that are directly or indirectly related to photosynthesis. A part of the light absorbed by green plants is reemitted in the form of chlorophyll fluorescence. When photosynthetic electron transport is blocked, an increased proportion of the absorbed excitation energy is reemitted as fluorescence. Pannels et al. (1987) reported an inverse relationship between assimilation and photosynthesis after the application of electron transport herbicides. Miles and Daniels (1973) detected changes in leaf fluorescence resulting from the inhibition of photosynthetic electron transport by several inhibitors, including the herbicides simazine and diuron. Schreiber et al. (1977) quantitatively demonstrated the effects on the fast phase of chlorophyll fluorescence following vacuum infiltration of spinach leaves with diuron and following exposure of bean leaves to ozone. In the latter study, ozone-induced injury was detected by fluorescence assay 20 hr before any visible signs of leaf injury. Richard et al. (1983) used the technique of Chl fluorescence measurement for detecting herbicide inhibition in studies using intact soybean leaves. They concluded that this kind of technique can be used quantitatively measure the effects of photosynthetic electron

transport inhibiting herbicides in intact plants, prior to visual symptoms. Increases in terminal levels of fluorescence (F_T) were detected in plants 0.5 and 1 hr, following the foliar application of atrazine or diuron, respectively. Panneels et al. (1987) observed that in barley and weed species treated with DCMU and S-triazine there was a linear relationship between the increase of the variable fluorescence/maximal fluorescence (Fv/Fm or photochemical efficiency of PSII) and the log of herbicide concentration used. Similar results were reported by Voss et al. (1984). When analyzing the Chl fluorescence from leaves of different species treated with photosynthetic inhibitors, they found that the decrease in the ratio Fv/Fm provided a good estimative of the changes in the photosynthetic capacity of the leaves after the herbicide treatment.

The use of terbacil as a fruit thinning agent on fruit trees.

It has been demonstrated in a series of experiments, that terbacil can induce fruit abscission in peaches and apples through its action as a photosynthetic inhibitor. Byers et al. (1985) observed that terbacil at 400 ppm applied to Starkrimson 'Delicious' apple limbs at 6 and 16 days after full bloom (DAFB) significantly reduced fruit set, but applications 26 and 36 days AFB were ineffective. Similar results were found by the same authors with terbacil

application on peaches. Terbacil, applied to peach cv. Biscoe limbs at 400 ppm thinned fruits 35 and 40 DAFB. Byers et al. (1990) reported similar results of terbacil applied to Redchief 'Delicious'. Application at 50 ppm plus surfactant at 5, 10 or 15 DAFB reduced fruit set and increased fruit size, but did not affect shoot growth. All these findings suggest that different species, as well as different cultivars within a species, vary in their responses to terbacil. Inhibition of Pn caused by natural conditions may affect the response of plants differently depending on the time at which the inhibition occurs, and also depending upon the period when the plant or parts of the plants, e.g., fruit, are more sensitive. Responses to chemical inhibitors can be expected to rang in a similar way.

In all the above studies, photosynthesis was reduced to 60 to 90% within the three days following the application. Inhibition was maintained for several days, and recovered to normal levels approximately 10 days after the treatment. Higher doses of terbacil caused leaf yellowing, but the symptoms disappeared a few days after treatment. Other photosynthetic inhibitors tested have shown good performance as thinning agents but they cause irreversible damage to the foliage at the effective dose required to be active for thinning.

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INTRODUCTION

INTRODUCTION

The significance of photosynthesis to crop production is widely accepted. Although increasing the rate of photosynthesis could increase yield, there is no direct evidence to support this relationship. Similarly, a reduction in photosynthetic capacity does not always result in a yield reduction. Previous studies have not clearly identified the period during the growing season when a reduction in carbon assimilation reduces the current season's and/or the next year's fruit production. Circumstantial evidence for the contention that photosynthesis limits yield includes: enhancement of growth and productivity by atmospheric CO_2 enrichment (Baker, 1965; Collins, 1976; Wittwer, 1970; Heinicke, 1963, 1966; Landsberg et al., 1975; Monteith, 1976); decreased crop yields following shading, through reduced fruit set and size (Boardman, 1977; Heinicke, 1963; Moreshet et al., 1975; Hansen, 1977; Beers et al., 1987; Flore and Sam, 1986; Sanchez et al., 1989; Jackson et al., 1991, McAvoy et al., 1989; Doud and Ferree, 1980; Jackson and Palmer, 1977; Byers et al., 1984, 1990a, 1990b); and the effect of leaf injury and early defoliation on fruit set, fruit size and fruit quality (Ferree, 1978; Ferree et al., 1986; Campbell et al., 1990; Hare et al., 1992; Nyrop et al., 1993; Jones, 1993). Likewise, any factor that inhibits Pn may affect flower bud formation for the next season (Autchter et al., 1926; Paddock and Charles, 1928; Jackson and Palmer, 1977; Monselise and

Goldschmidt, 1982; Gur, 1985).

The purpose of this study was to establish the relationship between leaf Pn and yield in apple. Two main objectives were proposed:

1. To determine if a reduction in Pn over a certain threshold in trees carrying heavy vs. light crop loads could cause a decrease in current and future crop yield and;

2. If a reduction in yield occurs, when during the season an inhibition of Pn may limit current or future crop production.

Parallel and supportive experiments were conducted to find the appropriated terbacil dose that caused a 50-60% inhibition of Pn during a 15-20 day period and the time required for recovery of the leaves' photosynthetic potential. The relationship between Pn and Chlorophyll a fluorescence was determined, on trees grown under greenhouse conditions.

MATERIALS AND METHODS

This research was conducted in 1993-1994. During this period a main field experiment was conducted in conjunction with supportive experiments.

Field experiments

The main field experiment was at the Clarksville Horticultural Experiment Station, Clarksville, Michigan.

Plant material. Ten-year-old apple trees (Malus domestica Borkh.) cv. Redchief 'Delicious' on MM106, planted in north-south rows and spaced 3.0 x 6.0 m grown in a Bixby sandy loam soil were used for the field study. The trees were pruned prior to initiation of the experiment, and not summer pruned again until the last evaluation was performed.

Trees were blocked into two categories: heavy and light crop load. Crop load was considered heavy when a tree bore an average of 3 to 4 fruits per cluster on 80-90% of its spurs. The light crop load was 40 to 50% smaller than the heavy load, i.e., an average of 2 fruits per cluster.

Hand thinning was performed on June 17, 1993 only on trees carrying an excessive number of fruits and on the high fruit load postharvest treatment. Trees were hand-thinned 5 to 6 weeks after full bloom. Pesticides, fertilizer, and irrigation were applied according to commercial recommendations (Mich. Ext. Bul. E-154, Fruit Pesticide Handbook) and were standard practices for apples grown in the West Central part of Michigan.

Treatments. Heavy and light crop load trees were sprayed at selected times during the growing season with the photosynthetic inhibitor terbacil [(5-chloro-3-(1,1-dimethylethyl)-6-methyl-2,4(1H,3H)-pyrimidinedione)]. Terbacil at 63 ppm plus X-77 at 1.25 ml l^{-1} was applied to trees bearing both high and low crop loads at the following times: 1) June

2 (15 DAFB), 2) June 17 (30 DAFB), 3) July 15 (60 DAFB), 4) August 4 (80 DAFB), 5) August 25 (100 DAFB), 6) October 8 (145 DAFB - post harvest). Trees were sprayed to the drip point using a high pressure 150 L sprayer. Terbacil was applied as an aqueous (dilute) high volume spray. In order to obtain full coverage, trees received an average of 8 L of solution/tree at the beginning of the season (first treatment), increasing to 14 L/tree by the third application. All the treatments were compared with both a non thinned and a hand thinned control. The post harvest treatment (145 DAFB) was hand thinned on June 17, 1993 (30 DAFB). Full bloom occurred on May 17, 1994. The experimental design was a randomized complete block. Each treatment was applied to whole, single-tree plots with four replications (blocks).

Evaluations.

Inhibition of photosynthesis was corroborated after each treatment by measuring leaf chlorophyll fluorescence the day following application and again one week later. A Morgan CF-1000 chlorophyll fluorescence measurement system (P.K. Morgan Instruments, Inc., Andover, MA) was used. Leaves were dark acclimated for 15 min using acclimation cuvettes, then irradiated with 1000 μmol m^{-2} s^{-1} PPFD actinic light. Chlorophyll kinetics were then recorded over a 60 s period. Data are reported as the ratio of Fv (variable fluorescence)/Fm (maximum fluorescence), which can be directly

related to quantum efficiency.

Reproductive and vegetative growth. Trunk circumference and trunk cross-sectional area (TCSA) 15 cm above the graft union were determined for all the trees with a vernier caliper. Change in TCSA were determined for the period of study.

At the time of each terbacil treatment, 10 current season shoots on both the east and west sides of each tree were selected and tagged. Shoot growth was measured at 7-10 day intervals. Final shoot growth was determined on July 28, 1993, after terminal all buds had set. In the year following treatment (June 27, 1994) trees were summer pruned and the fresh weight of one-year-old watersprouts (or suckers) were determined. The average value/cm^2 TCSA was compared among treatments.

Flower density [(number of flower clusters/cross-sectional area of the branch (BCSA)] was evaluated in 1994 for all trees to determine the effect of the previous year's terbacil treatments on return bloom.

Fruit growth was determined by selecting 20 fruit per tree and measuring fruit diameter at 7-10 day intervals from 15 DAFB until fruit maturity. Diameters were measured at the equatorial zone of each fruit in an east-west orientation, with a precision caliper.

Fruit set was determined as the number of fruit per cm^2 area (BCSA) at the base of two branches on opposite sides of

the tree in both 1993 and 1994. In 1993, fruit drop was calculated by counting the number of fruit that abscised. This number was also related to the number of fruit at harvest to calculate the percentages of fruit set and fruit drop for each treatment.

Trees were harvested at fruit maturity on October 7, 1993. Fruit from counted, weighed and graded and average fruit weight was calculated. Six size categories according to the commercial standards for fruit diameter as follows: Cat I > 8.9 cm; Cat II < 8.9 cm to > 8.3 cm; Cat III < 8.3 cm to > 7.6 cm; Cat IV < 7.6 cm > 7.0 cm; Cat V < 7.0 cm to > 6.4 cm; Cat VI < 6.4 cm. Fruit less than 6.4 cm were consider as "cull" fruits. Crop density (CD = number of fruits/TCSA) was calculated for each treatment.

A random sample of ten fruits in the 3rd size category (< 8.3 cm to > 7.6 cm) from each tree were visually rated for percentage and degree of red color. The intensity of red pigmentation was rated on a scale of 1 to 4, where 1 = light and 4 = dark red. Percent soluble solids was determined for each fruit using a portable refractometer. Flesh firmness was measured on three sides of each fruit with a hand presiometer. Fruit density was estimated by measuring the volume of a sample of ten fruits per tree. Each sample was weighed and then placed into a plastic net with a weight attached to prevent the apples from floating. The water displacement was measured as a measure of sample volume. Density was determined

according to the formula: density = weight/volume.

Cold hardiness.

Deep winter hardiness was evaluated for current season shoots from all the trees that were sampled every month from harvest time until budbreak the next year (from Oct. 15, 1993 to Mar. 01, 1994). Samples were evaluated according to methods of Bittenbender and Howell (1974). Three shoots from the medium position of each tree were randomly selected from all treatments and replications. Shoots were cut into two inch sections and then subjected to a controlled temperature reduction (3^0 C/hr) in a freezing chamber. Samples were exposed to temperatures ranging from -13 to -53 ^{0}C and then visually evaluated for cambium browning 7 days after keeping the samples at room temperature. T_{50} values, or the temperature (^{0}C) required to kill half of the samples, were determined for each treatment.

Terbacil concentration experiment.

In 1993, two separate supportive experiments, one in the field and other in the greenhouse, were performed. The first experiment was conducted at the Horticultural Teaching and Research Center at Michigan State University, East Lansing, MI.

Five shoots from five 12-years-old Red 'Delicious' on Malling-Merton 106 (MM106) trees in south-north oriented rows at approximate spacing of 7.0 m x 2.80 m were selected at random, blocked, tagged and sprayed with different concentrations of terbacil plus surfactant (X-77 at 1.25 ml L^{-1}). Each shoot was considered as a replication. A hand pump sprayer was used for the applications. Shoots were sprayed with Sinbar (terbacil) plus surfactant at the following concentrations: 1) 0 ppm (control), 2) 12.5 ppm, 3) 25.0 ppm, 4) 50 ppm, 5) 100 ppm, 6) 200 ppm, 7) 400 ppm, and 8) 800 ppm. Control shoots were sprayed with water plus surfactant at 1.25 ml L^{-1}. A randomized complete block experimental design with five replications was used. Shoots were sprayed to the point of drip on May 19, 1993.

Chlorophyll fluorescence was measured at regular intervals following treatment as described previously. The photosynthetic inhibition caused by terbacil was determined over a 22-day period. Visual symptoms of leaf injury for the different herbicide concentrations were recorded.

Greenhouse experiment

The greenhouse experiment was performed in the Plant and Soil Science Greenhouses at Michigan State University, East Lansing.

Dormant one-year-old apple trees, [(Malus domestica Borkh.] cv. 'Golden Delicious' on M9 rootstock were planted in 8 L

plastic pots with a soil mix (7 field soil : 1 sand : 1 organic matter). All trees were cut 10 cm above the graft union and placed in an environmentally controlled greenhouse (day and night means 18 and 13^{0}C, respectively). Peter's soluble 20N-20P-20K fertilizer (500 μg/L) was applied every three weeks and trees were watered every two days. Pesticides were applied as necessary.

Following six weeks of active growth when shoots had 15-20 expanded leaves, 15 trees were selected for each treatment and one leaf in the median position of each tree was tagged and dipped in a solution of terbacil containing X-77 surfactant at 1.25 m.L^{-1}. Concentrations were 1) 0 ppm (water plus surfactant control); 2) 50 ppm; and 3) 100 ppm. At daily intervals for a 12 day period gas exchange and chl fluorescence were measured for each of the treated leaves. Chlorophyll fluorescence was evaluated as described previously. Photosynthesis (A) was determined using an ADC LCA-2 portable photosynthesis system (Analytical Development Company, Hoddesdon, UK) under the following conditions: flow rate = 0.4 L/min, leaf temperature range 27 to 30^{0}C, inlet relative humidity 23%, ambient CO_2 330-340 μl L^{-1} and PAR > 1000 μmol m^{-2} s^{-1}. Leaf photosynthesis was calculated as previously described (Moon and Flore, 1986).

A randomized complete block experimental design with 15 replications (trees) was used. Correlations between gas exchange and chlorophyll fluorescence measurements were

calculated.

A third field experiment was conducted in 1994 at the Horticultural Teaching and Research Center at Michigan State University, East Lansing, to determine the possible effect of terbacil on leaf chlorophyll content. Five shoots of Redchief 'Delicious' trees on MM106 spaced approximately 4.50 m x 3.0 m, were selected, tagged and sprayed to the point of drip with terbacil at 63 ppm plus X-77 at 1.25 ml L^{-1} using a hand pump sprayer. Every day for a period of 15 days A and chlorophyll fluorescence (both measured as described above) were evaluated and compared with control leaves which had received water plus X-77 alone at the same dose as treated. The measurements were conducted on leaves near the middle of the shoot. One leaf per shoot was collected at each time of Pn and chlorophyll fluorescence measurement. Chlorophyll content was determined according to the method of Moran (1982). Two discs (0.328 cm diameter) were punched from the lamina of each leaf using a paper holepunch, and were pooled as one sample. Chl was extracted in 7 ml N,N-dimethylformamide in darkness at 5^0C for 36 hours. Absorbance of extracts was read at 664, 647, and 625 nm on a Hitachi U-3110 UV/Vis spectrophotometer (Hitachi Ltd., Tokyo). Calculations for chl a, chl b and P chl were made according to Moran (1982).

Statistical calculations.

All data were subjected to analysis of variance (ANOVA). When necessary, data were transformed by x + 0.5 for the statistical analysis. The relationship between Pn (Y) and Fv/Fm (X) was analyzed by simple regression analysis.

RESULTS

Effect of terbacil on the rate of photosynthesis.

Concentration response curve. Quantum efficiency as determined by chlorophyll fluorescence was inhibited by terbacil, the degree and length of inhibition being directly related to the concentration applied (Figure 1). The reduction in quantum efficiency (Fv/Fm) that resulted from dosages of 50 ppm and higher was approximately 60% for all treatments during the 5 days following application. The effect of terbacil at 12.5 ppm was not significantly different from the control 10 days after its application or thereafter. Doses of 100 ppm and higher reduced photosynthesis significantly for 15 days, whereas twenty-two days after treatment only 400 and 800 ppm caused a significant reduction in Fv/Fm. Phytotoxicity symptoms in leaves appeared 10 days after treatment with 50 ppm or higher, but disappeared in the 50 ppm treatment 20 to 25 days after application. Necrosis was noticed in those leaves that received 100 ppm or higher. In these, symptoms were irreversible and persisted until fall.

When terbacil at 63 ppm plus surfactant was sprayed on apple shoots under field conditions A and Fv/Fm was inhibited for 12 days (figure 2).

Three days after treatment leaves showed a reduction of 68% and 63% in Pn and Fv/Fm, respectively.

Figure 1. Effect of terbacil concentration on Fv/Fm (% of control) 1 to 22 days after treatment, Red 'Delicious', HTRC.
Mean separation within dates by DMRT P<0.05.

Figure 1.

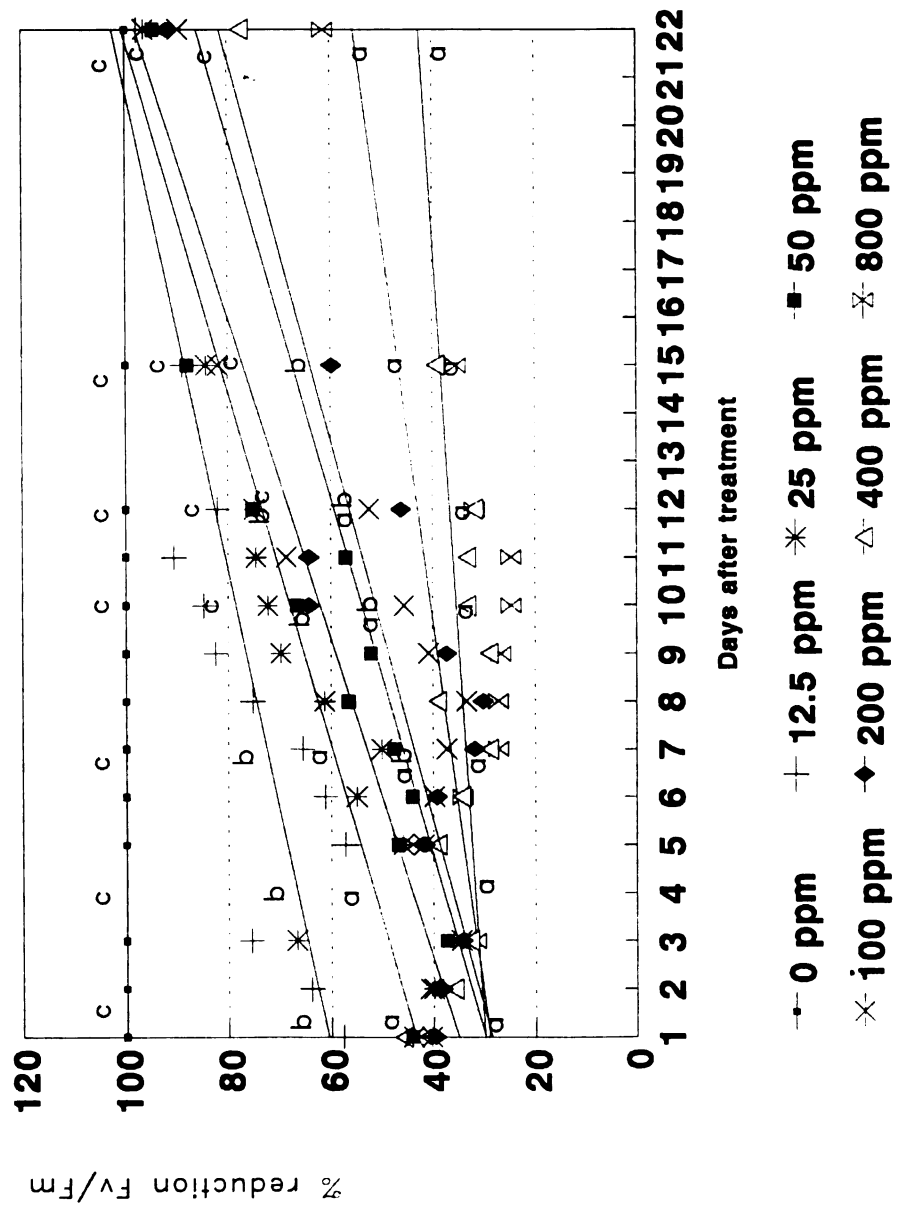
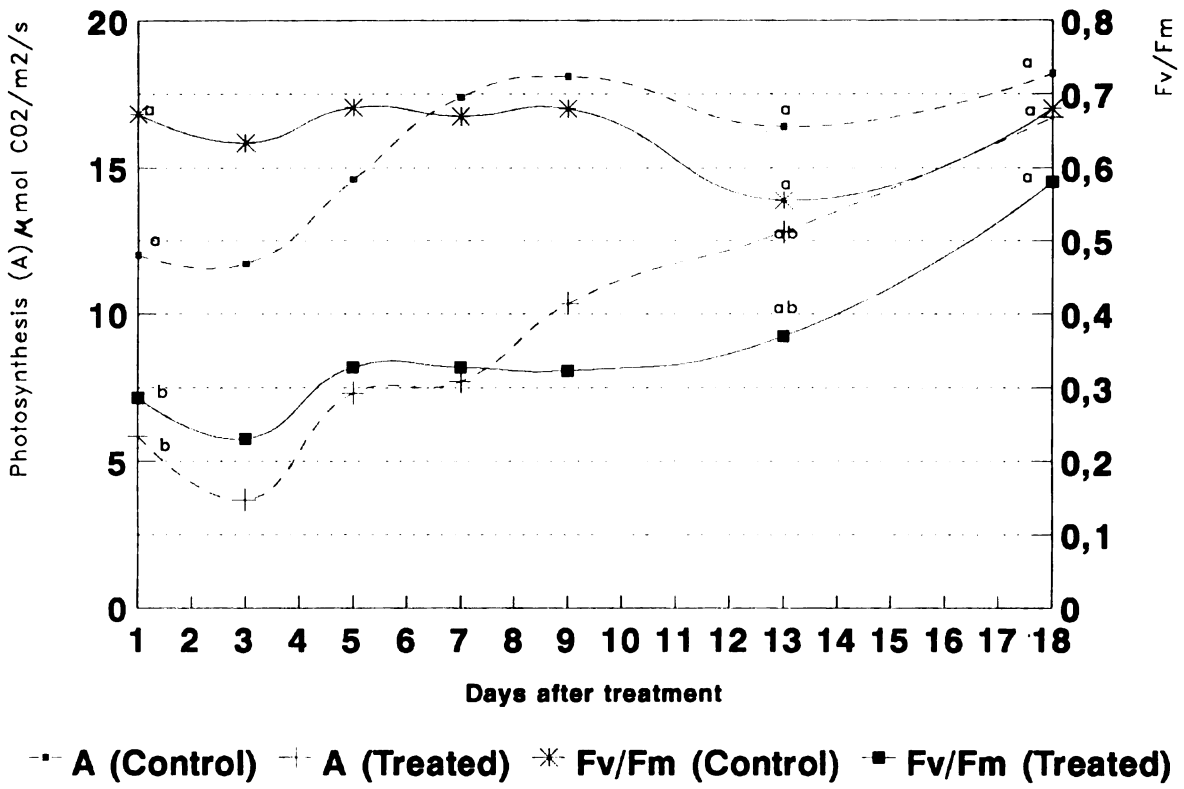

% reduction Fv/Fm
120
100
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
Days after treatment
0 ppm
12.5 ppm
25 ppm
50 ppm
100 ppm
200 ppm
400 ppm
800 ppm

Figure 2. Effect of terbacil (63 ppm) on Fv/Fm and A of Redchief 'Delicious' at HTRC.

Figure 2.



Values followed by the same letter are not significantly different at P<0.05 (Student's t-test).

Leaves gradually recovered following terbacil application. Thirteen days after treatment the reductions were 3.7 % and 34.3 % for A and Fv/Fm, respectively. Eighteen days after treatment, the leaves regained their photosynthetic capacity.

When Pn and Fv/Fm were measured in 'Golden Delicious' apple leaves (PSG) both parameters were significant correlated ($r = 0.689$) on an exponential scale ($Y= 3.21 \times (10.24)^X$) (Figure 3).

Main experiment

The reduction in Fv/Fm by terbacil (63 ppm) on the main field experiment at Clarksville was approximately 50% 1 day after its application on the first date of application, and 30-40% 1 week later. However, the percentage reduction was lower when treatment was applied 100 or 145 DAFB (Table 1). Phytotoxicity symptoms were observed only in leaves treated 30 DAFB (field experiment). Intervenal leaf yellowing appeared in young leaves 8 to 10 days after treatment, and symptoms disappeared 10 to 15 days later.

Chlorophyll content. Terbacil reduced chl a and total leaf chl content, but altered neither P chl (Table 2) or the chl a to b ratio (data not shown). Chl a and total leaf chl returned to control levels within 13 days.

Figure 3. Relationship between Pn (Y) and Fv/Fm (X) during the 12 days following application of terbacil at concentrations of 50 and 100 ppm to 'Golden Delicious' at PSG.

Figure 3.

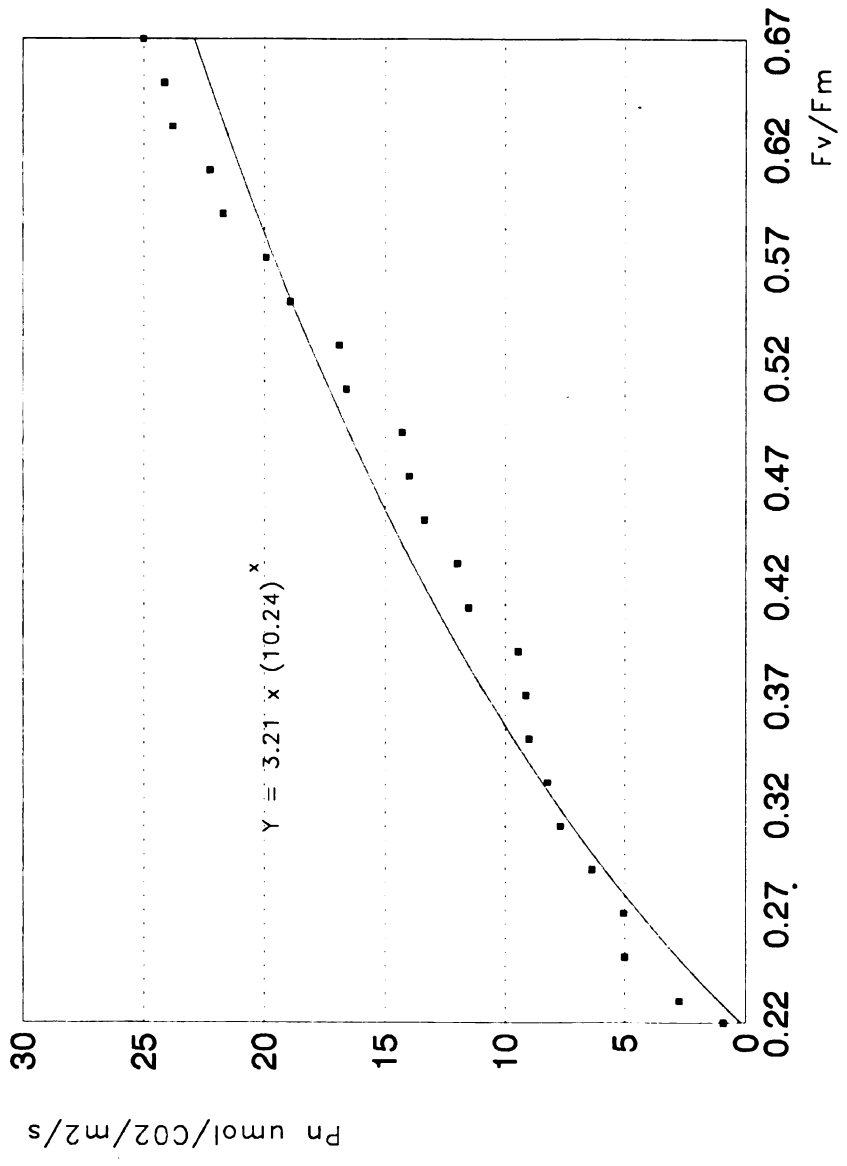

Pn umol/CO2/m2/s
30
25
20
15
10
5
0
0.22
0.27
0.32
0.37
0.42
0.47
0.52
0.57
0.62
0.67
Fv/Fm
Y = 3.21 x (10.24)^x

Table 1. Effect of terbacil (63 ppm) treatment on Fv/Fm values and percentage of photosynthetic efficiency reduction with respect to the controls 1 and 7 days after each Terbacil treatment Redchief 'Delicious' at CHES.

	15 DAFB		30 DAFB		60 DAFB		80 DAFB		100 DAFB		145 DAFB	
	1 day	7 days	1 day	7 days	1 day	7 days	1 day	7 days	1 day	7 days	1 day	7 days
TREATED	0.372b	0.381b	0.209 b	0.384 b	0.327 b	0.386 b	0.370 b	0.452 b	0.373 b	0.422 b	0.435 b	—
CONTROL	0.702 a	0.609 a	0.678 a	0.642 a	0.657 a	0.623 a	0.683 a	0.674 a	0.633 a	0.601 a	0.643 a	—
% REDUCTION	47.0	37.4	69.2	40.2	50.2	38.0	46.2	33.0	41.0	29.8	32.4	—

Means followed by the same letter within each column are not significantly different at P< 0.05 (Student's t-test)

Table 2. The effect of Terbacil treatment (63 ppm) on Redchief 'Delicious"leaf chl a, b, P chl, and total chl content over time at HTRC.

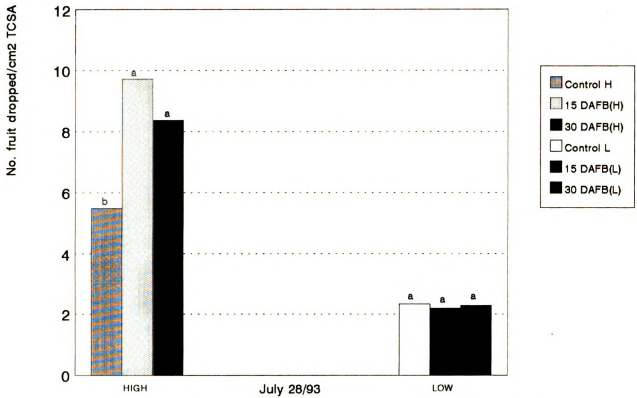
	Time following treatment (days)					
(Days)	1	3	5	7	9	13
			Chl a content ($\mu g\ cm^{-2}$)			
Untreated (control)	52.3a	53.8a	54.1a	52.3a	52.7a	53.4a
Treated	48.3b	49.8b	49.0b	48.3b	48.8b	58.8a
			Chl b content ($\mu g\ cm^{-2}$)			
Untreated (control)	12.2a	13.2a	12.8a	13.9a	13.7a	13.6a
Treated	12.7a	14.0a	12.1a	14.0a	14.0a	13.9a
			P chl content ($\mu g\ cm^{-2}$)			
Untreated (control)	12.2a	13.9a	12.8a	9.8a	9.1a	8.0a
Treated	12.7a	14.8a	12.1a	10.0a	8.0a	8.1a
			Total chl content ($\mu g\ cm^{-2}$)			
Untreated (control)	76.7a	80.9a	79.7a	76.0a	75.5a	75.0a
Treated	73.7b	78.6b	73.2b	72.3b	71.8b	74.8a

Means are average of 5 replicates. Mean separation within columns and parameters by Student's t-test, $P<0.05$.

Fruit set. Fruit abscission was induced by terbacil (63 ppm) applied 15 and 30 DAFB to heavily cropping trees, as indicated by the number of fruits dropped/cm^2 of trunk cross sectional area (TCSA), the percentage of fruit dropped (Figure 4, Figure 5), and by the number of fruits/cm^2 branch cross sectional area (BCSA) retained (Figure 6). Fruit diameter 15 and 30 DAFB was 9.8 ± 1.1 mm and 24.5 ± 1.4 mm, respectively. Fruit trees sprayed 15 DAFB abscised earlier than did control fruits; June drop began on June 23 in the latter, on June 15 in the former. Terbacil treatment 60 DAFB (fruit diameter 45 ± 0.78 mm) had increased fruit drop on trees with a heavy fruit load as of July 28, one week after treatment (data not shown). However, response was much less than that observed for earlier applications. Although terbacil application for the first and second treatments resulted in a reduction of fruits/cm2 BCSA, response in trees having a low crop load was much less than in those with a high crop load, and fruit retention was the only parameter to be significantly affected by treatment (Figure 7, Figure 8). Just prior to harvest (129 DAFB - Sep. 23), the number of fruits/cm^2 BCSA was significantly lower for low crop than for high crop treated 15, 30 and 60 DAFB, and as well as for low crop trees treated with terbacil was applied 15 and 30 DAFB (Figure 9). Treatment after 30 (low crop) or 60 days (high crop trees) did not reduce cropload. Hand thinning 30 DAFB reduced final cropload in both sets of trees.

Figure 4. Effects of timing of terbacil application and cropload on fruit drop of Redchief 'Delicious' at CHES, as of 28 July 1993 (72 DAFB).

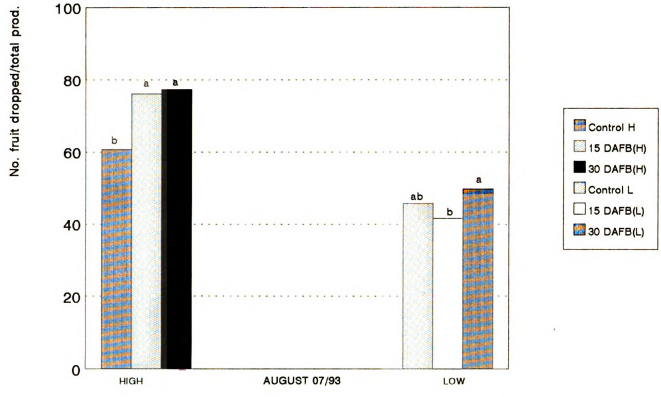
Figure 4.



Means followed by the same letter are not significantly different (Duncan's test $P<0.05$)
Data from high and low loaded treatments were analyzed separetely.

Figure 5. Total fruit dropped as percentage of total number of fruit produced (dropped + harvested), Redchief 'Delicious', CHES.

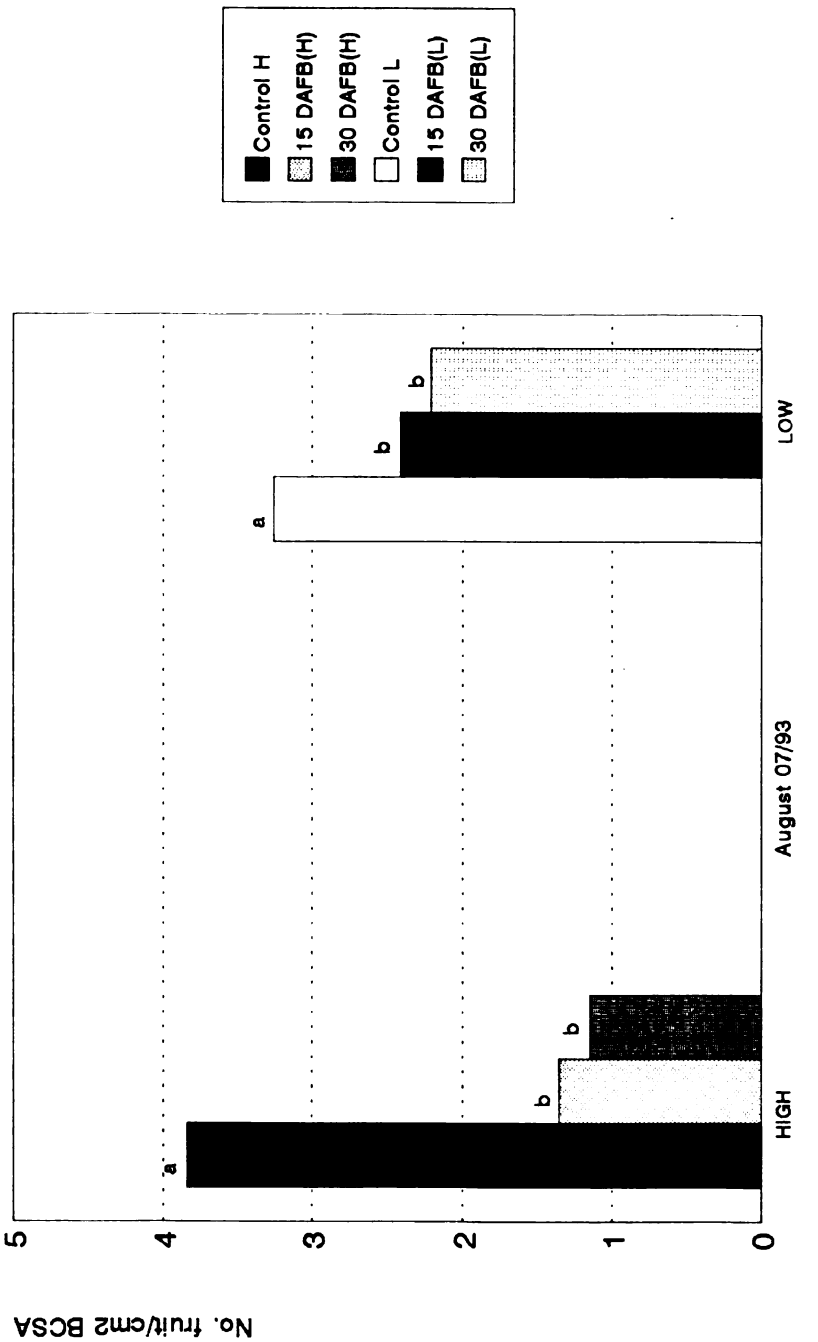
Figure 5.



Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).
Data for high and low loaded treatments were analyzed separetelly.

Figure 6. Effect of terbacil (63 ppm) treatment and timing on fruit set (number of fruit/cm^2 BCSA), 'Redchief Delicious', CHES.

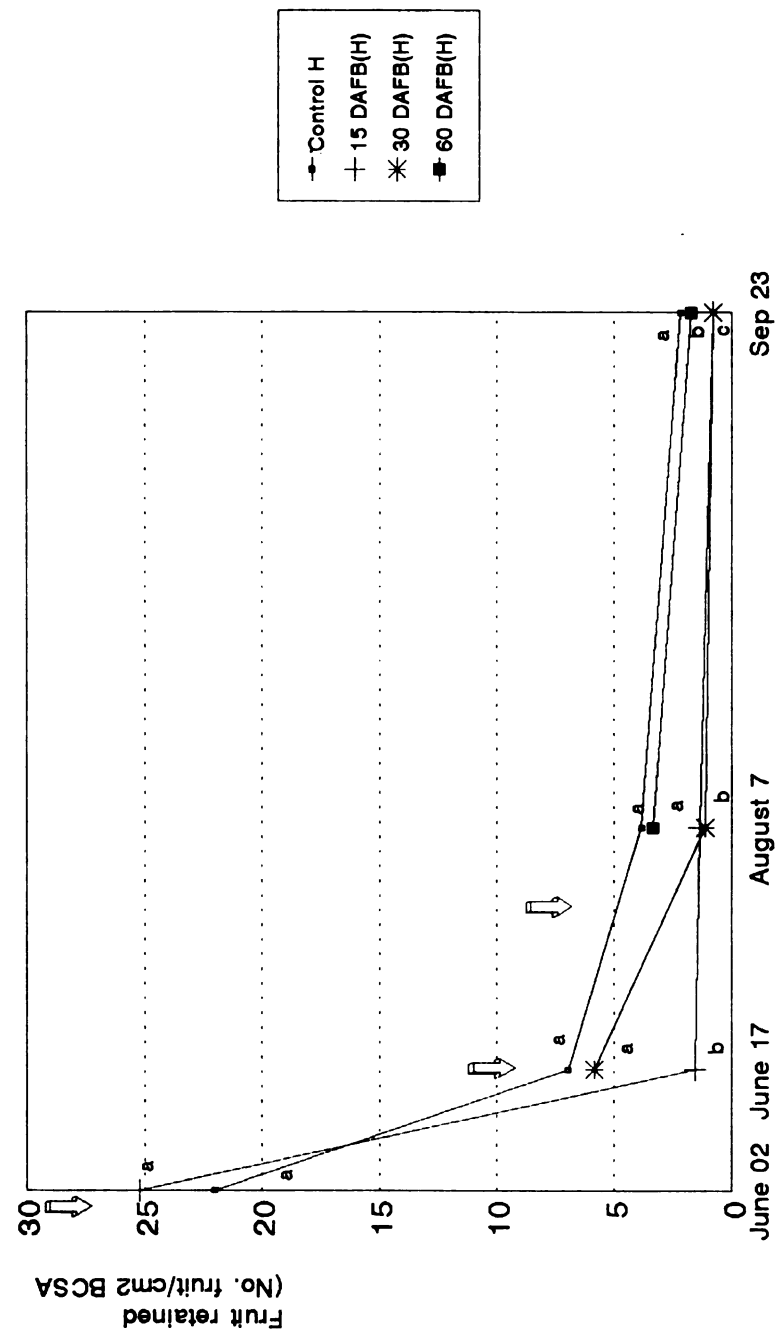
Figure 6.



High and loaded treatments were analyzed separately.
Means followed by the same letter are not significatively different (Duncan's test $P<0.05$).

Figure 7. Effect of terbacil on fruit retained. Number of fruit/cm^2 BCSA through the season (1993) for high crop load Redchief 'Delicious' at CHES.

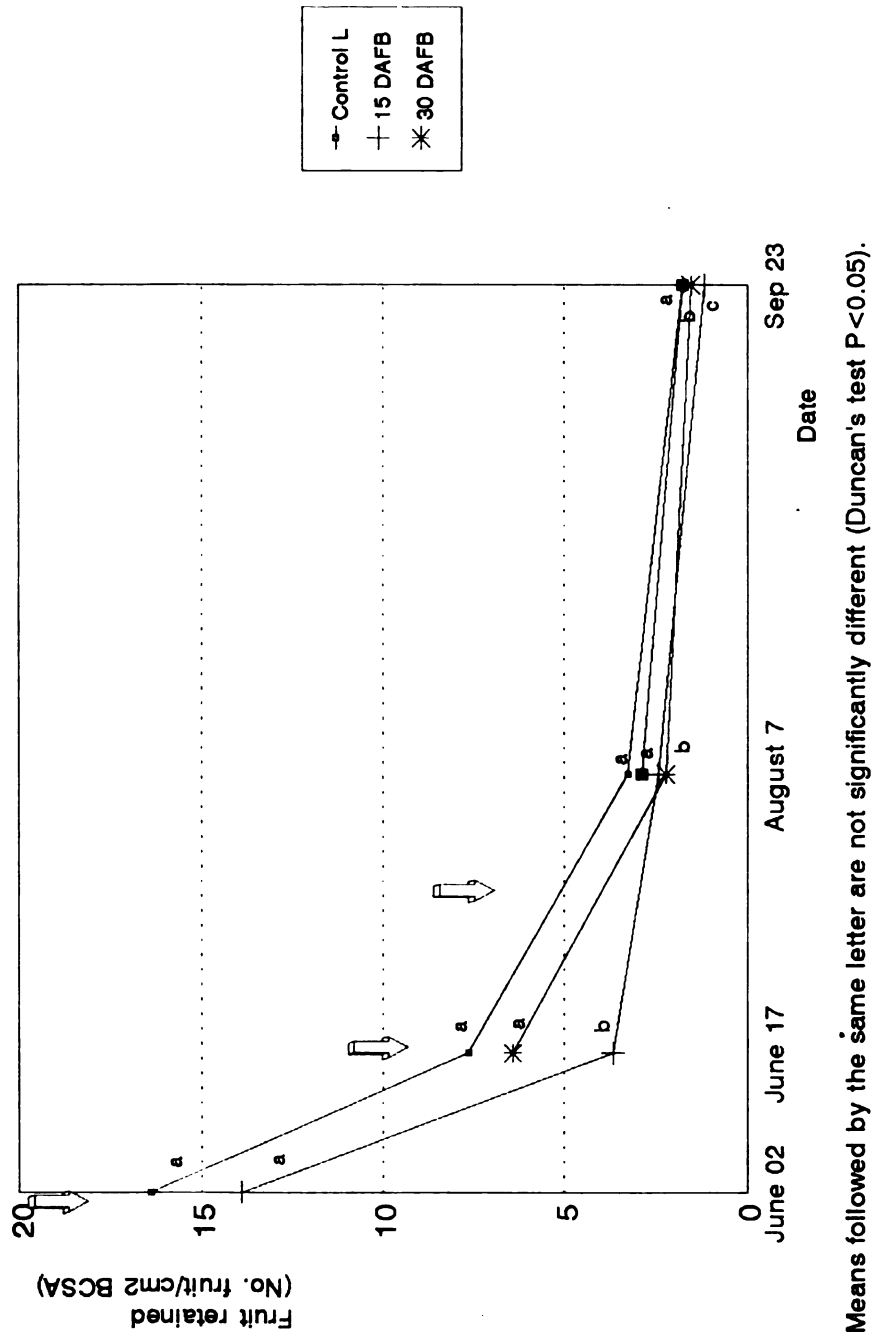
Figure 7.



Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).
Arrows indicate the time of each treatment.

Figure 8. Effect of terbacil (63 ppm) on fruit retained. Number of fruit/cm^2 BCSA through the season (1993) for low crop load Redchief 'Delicious' at CHES.

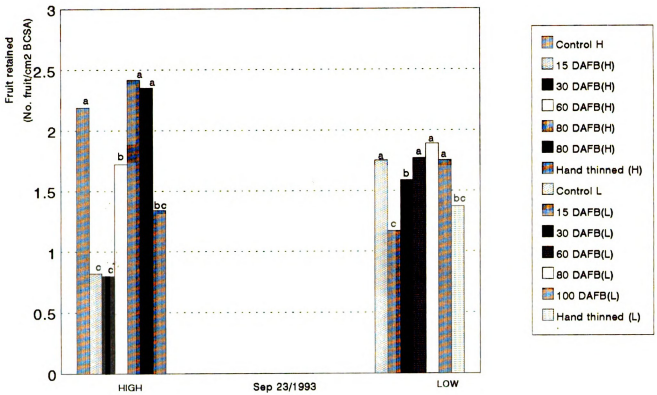
Figure 8.



Means followed by the same letter are not significantly different (Duncan's test P<0.05).
Arrows indicate the time of each treatment.

Figure 9. Effect of crop load and terbacil (63 ppm) applied 15 to 100 days after full bloom (DAFB) on fruit retention on September 23, 1993, Redchief 'Delicious' at CHES.

Figure 9.



Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).
Data for high and low loaded treatments were analyzed separetelly.

Fruit growth-size. Regardless of the crop load, the final fruit size of the king fruit was not affected by terbacil treatments (Figures 10, 11). Fruit growth followed a sigmoidal curve characteristic of pome fruits. However, terbacil inhibited normal fruit growth for the following week only when applied 15 DAFB (June 1) in low crop load trees or 30 DAFB (June 17) in the heavy crop load trees (Figure 11, Table 3). From June 17 to June 23, the percent increase in size of fruits treated 30 DAFB on trees carrying a heavy crop was 9.73%, whereas in control plants it was 20.5%. During this period, fruits from plants treated 15 DAFB increased in diameter 48.3%. Inhibition of growth was observed only when terbacil was applied 15 DAFB on the low crop trees (Figures 12, 13, Table 3). However, that inhibition was of a lower magnitude than the observed 30 DAFB in fruits of heavy loaded trees.

Although final fruit size of the tagged king fruits was not significantly affected by terbacil treatments (figure 13), higher percentage of large fruits (Cat I) were harvested from trees of high load crop treated with terbacil 15 DAFB. Likewise, a greater proportion of small fruits (Cat VI) was observed when terbacil was applied 30 and 60 DAFB (Figure 14, Table 4). Terbacil applied 100 DAFB did not increase the percentage of small fruit produced (Cat VI), and increased the number of medium sized fruit (Cat IV) (Figure 14, Table 4). No significant trend for large sized fruit distribution was found

on the trees with a low crop load (Figure 15, Table 5), although all terbacil treatments reduced the percentage of fruits in the largest size category. This also can be observed when analyzing the average fruit weight at harvest and the percentage of fruits larger than 8.3 cm in diameter (Cat I + Cat II). Regardless of the crop load, those trees who received terbacil 60, 80 and 100 DAFB had the lower percentage of larger fruits (Table 6).

Fruit yield. Terbacil applied 15 and 30 DAFB significantly reduced yield. Crop density (number of fruits/cm^2 of TCSA) and harvested yield efficiency (kg of fruit produced/cm^2 TCSA) were greatly decreased by the first two treatments, especially when crop load was high (Figures 16, 17, Tables 7, 8). Later applications of terbacil became progressively less effective in reducing fruit number and total weight, and the applications at 100 DAFB and after were completely ineffective (Figures 16, 17). Although reductions were significant regardless of crop load the effect was more pronounced when crop load was high (Tables 7, 8).

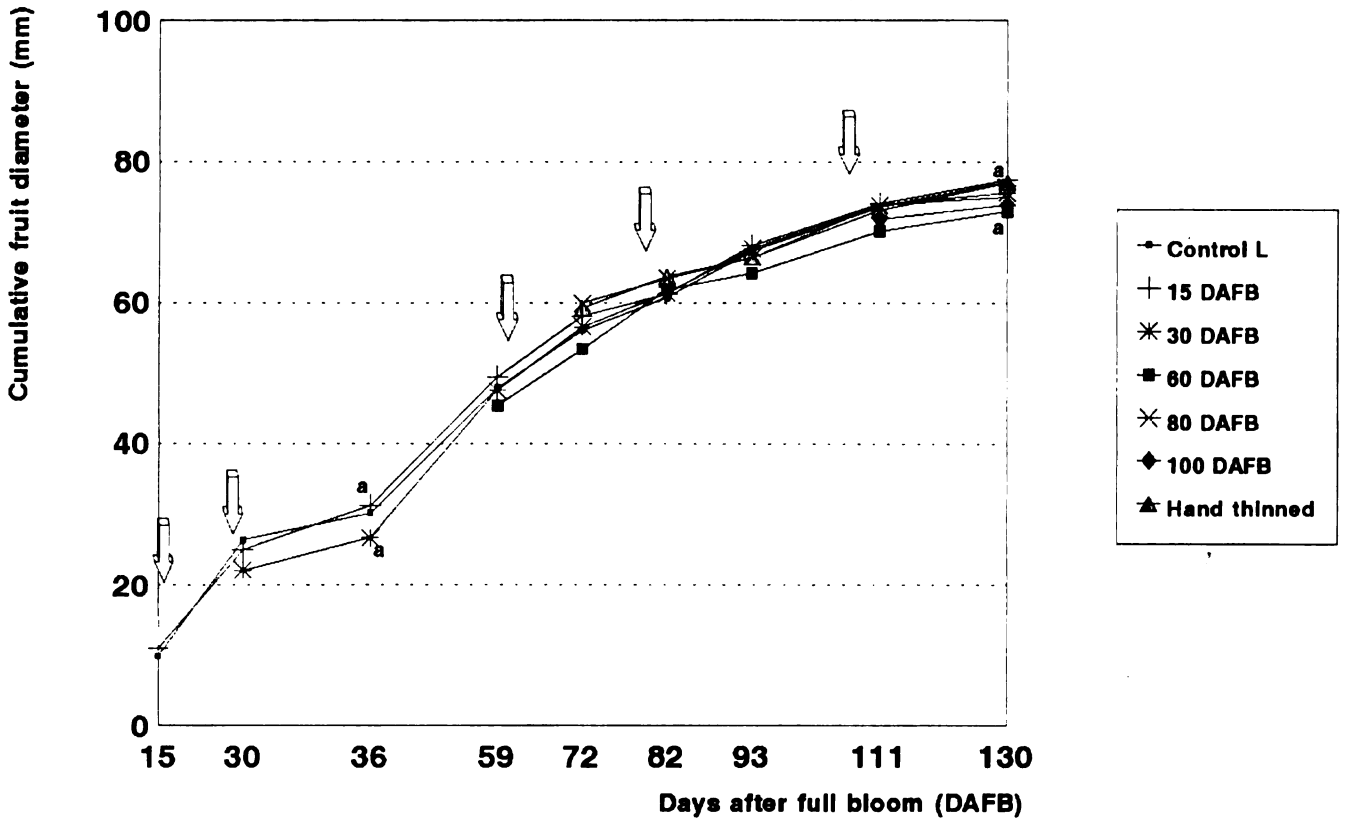
Fruit quality. Neither fruit soluble solids nor fruit firmness was affected by any terbacil treatment regardless of the crop load (Figures 18, 19). No differences were found in fruit specific gravity (Figure 20) or in fruit color (data not shown). Percent of red surface color and color intensity were similar for all treatments. Red surface color intensity averaged 3.5 (4.0 = dark red) (data not shown) for all the

treatments.

Vegetative growth. Terbacil treatment did not affect total shoot terminal length significantly (Figure 21). Shoot growth was slightly greater for the low crop trees (26.23 cm ± 1.027), including control plants, than for the heavy crop trees (23.94 cm ± 1.08). No differences in the final shoot length/cm^2 of TCSA was found among treatments (data not shown). Terbacil applied 30 DAFB almost completely inhibited shoot growth on the heavy crop loaded trees for one week (Figure 23, Table 9), and was similar to the inhibition observed in fruit growth. During the week following treatment shoot growth rate averaged 0.08 mm/day vs. 1.80 mm/day in control plants. Both heavy and low crop loaded treatments showed an earlier cessation of shoot growth (July 15) when terbacil was applied 15 and 30 DAFB. Following later treatment shoots continued growing for almost two more weeks until July 28 (Figure 22, Figure 23). The final number of leaves per shoot was not significantly affected by treatment. Trees carrying heavy crop load had an average of 21.6 ± 0.9 unfolded leaves, while light crop loaded plants had 21.7 ± 0.6. In all treatments spur shoots stopped growing on July 6, when they had an average of 6.83 ± 0.808 mature leaves. Whereas total shoot growth was similar for all the treatments, total weight of watersprouts (kg/cm^2 TCSA) was significantly higher than the control for all heavy crop trees in which thinning was significant (terbacil at 15, 30 DAFB; hand thinned 30 DAFB).

Figure 10. Cumulative fruit diameter (mm) for Redchief 'Delicious' king fruit in low crop trees treated with terbacil (63) ppm at different times during the season.

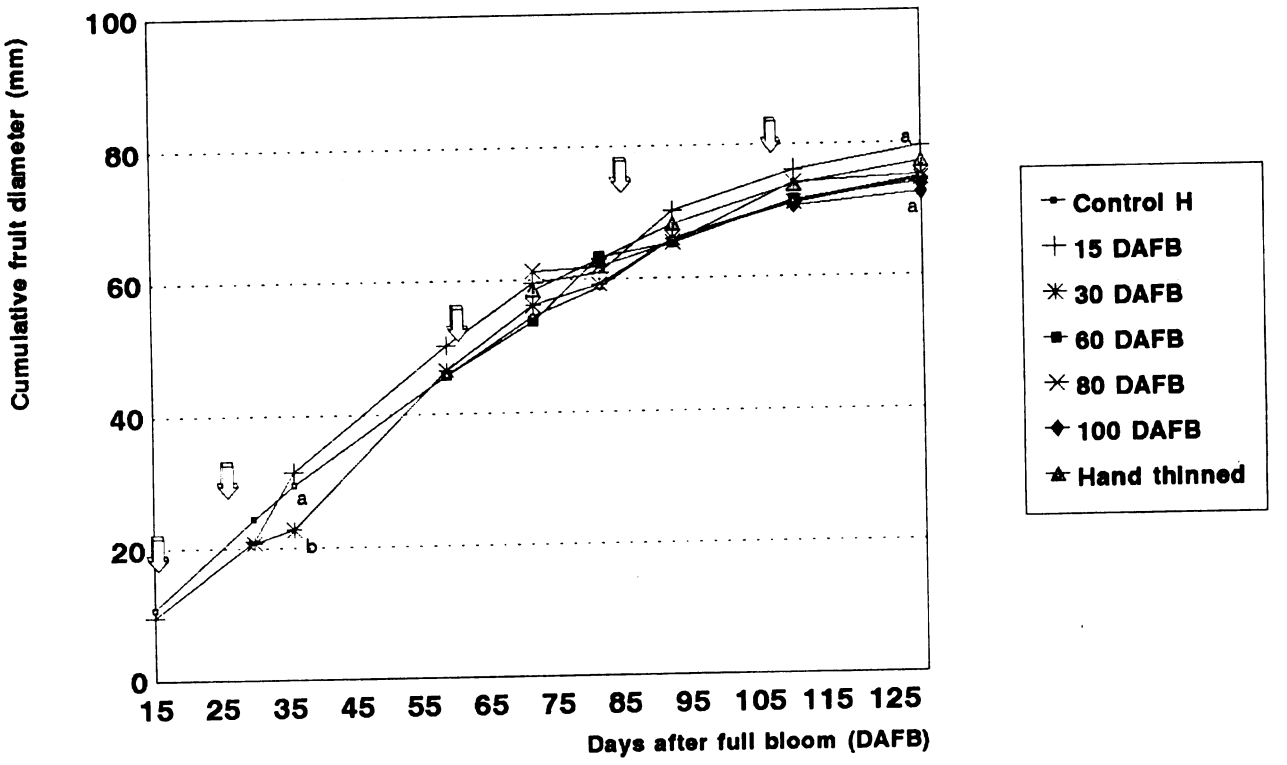
Figure 10.



Means followed by the same letter are not significantly different (Duncan's test P<0.05).
Arrows indicate the time of each treatment.

Figure 11. Cumulative fruit diameter (mm) for Redchief 'Delicious' king fruit on high crop trees treated with terbacil at 63 ppm at different times during the season.

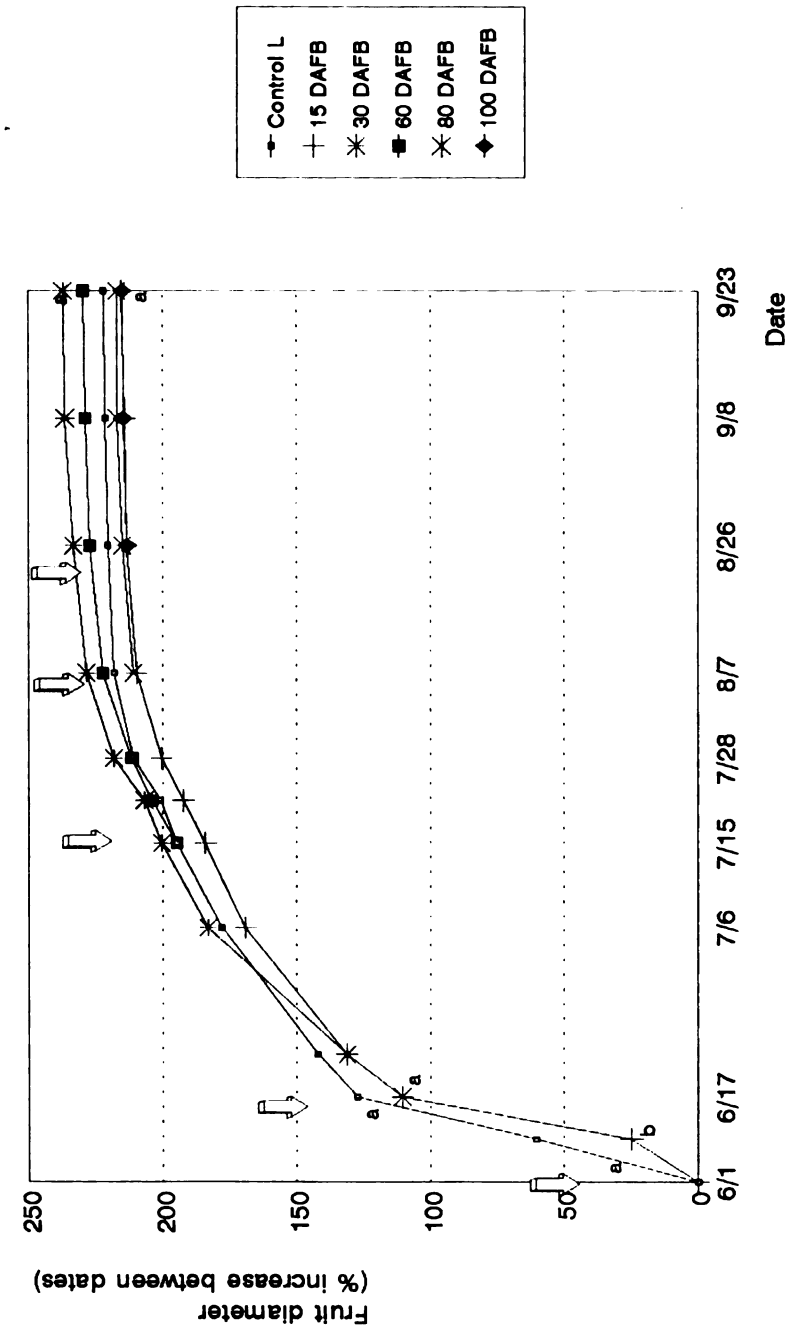
Figure 11.



Means followed by the same letter are not significantly different (Duncan's test P<0.05).
Arrows indicate the time of each treatment.

Figure 12. Absolute fruit growth (percentage of fruit diameter increment between dates) of Redchief 'Delicious' king fruit on low crop trees treated with terbacil (63 ppm) at different times during the season.

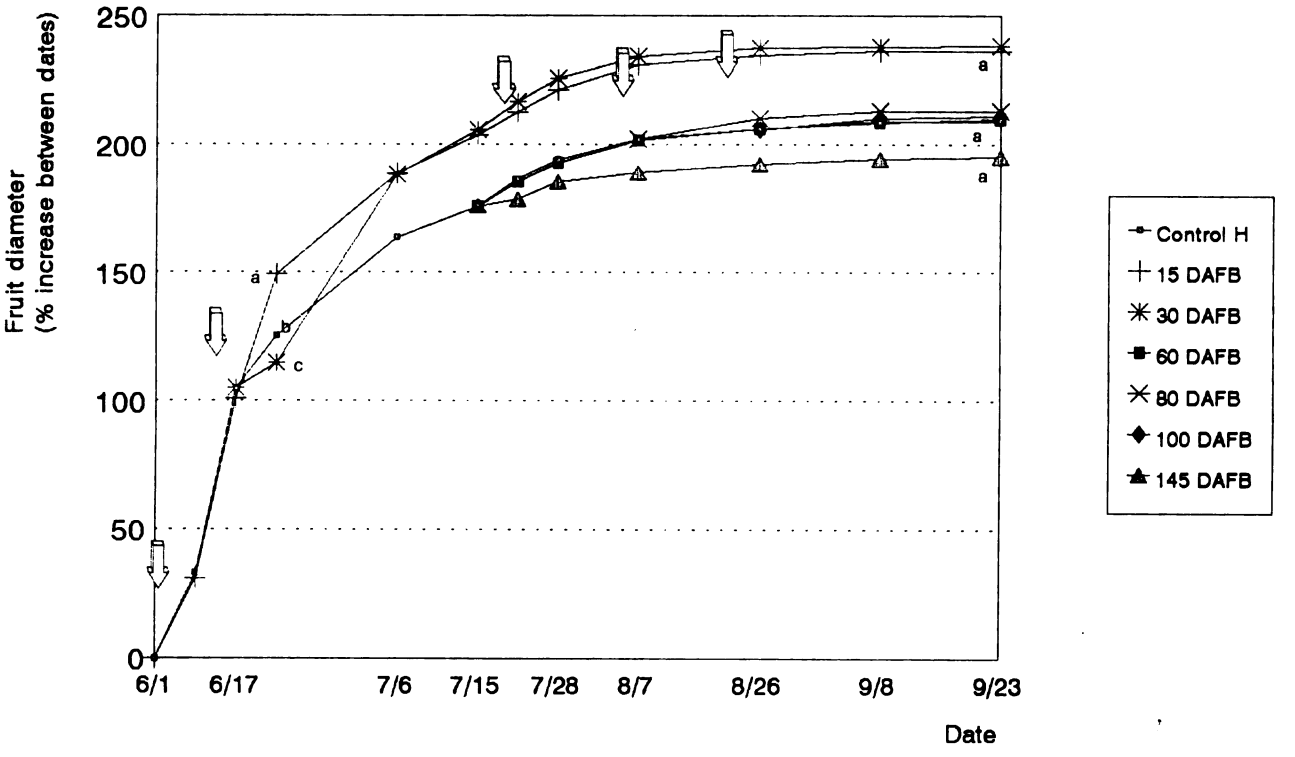
Figure 12.



Means followed by the same letter are not significantly different (Duncan's test P<0.05)
Arrows indicate the time of each treatment.

Figure 13. Absolute fruit growth (percentage of fruit diameter increment between dates) of Redchief 'Delicious' king fruit on high crop trees treated with terbacil (63 ppm) at different times during the season.

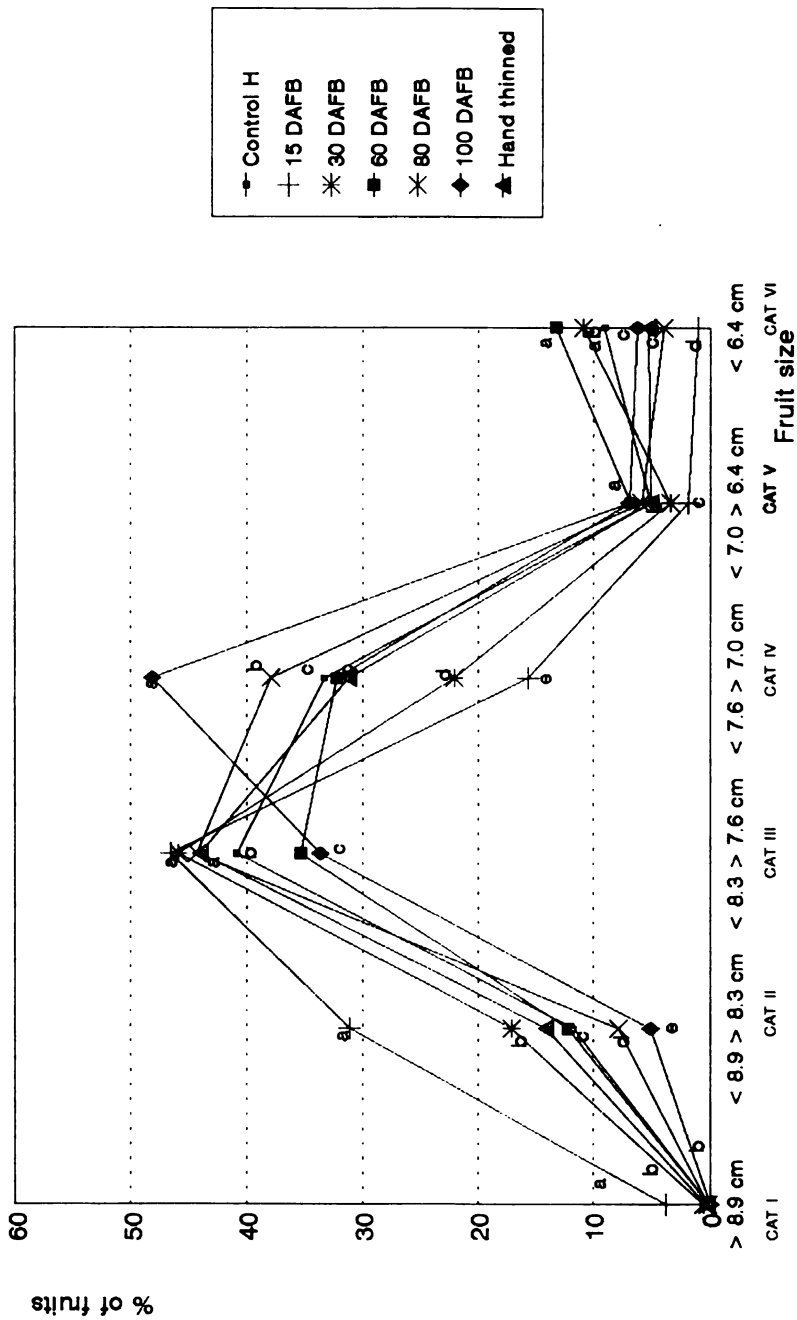
Figure 13.



Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).
Arrows indicate the time of each treatment.

Figure 14. The effect of terbacil (63 ppm) applied to Redchief 'Delicious' at different times during the growing season on percentage of fruit in six categories on trees with a high initial crop load.

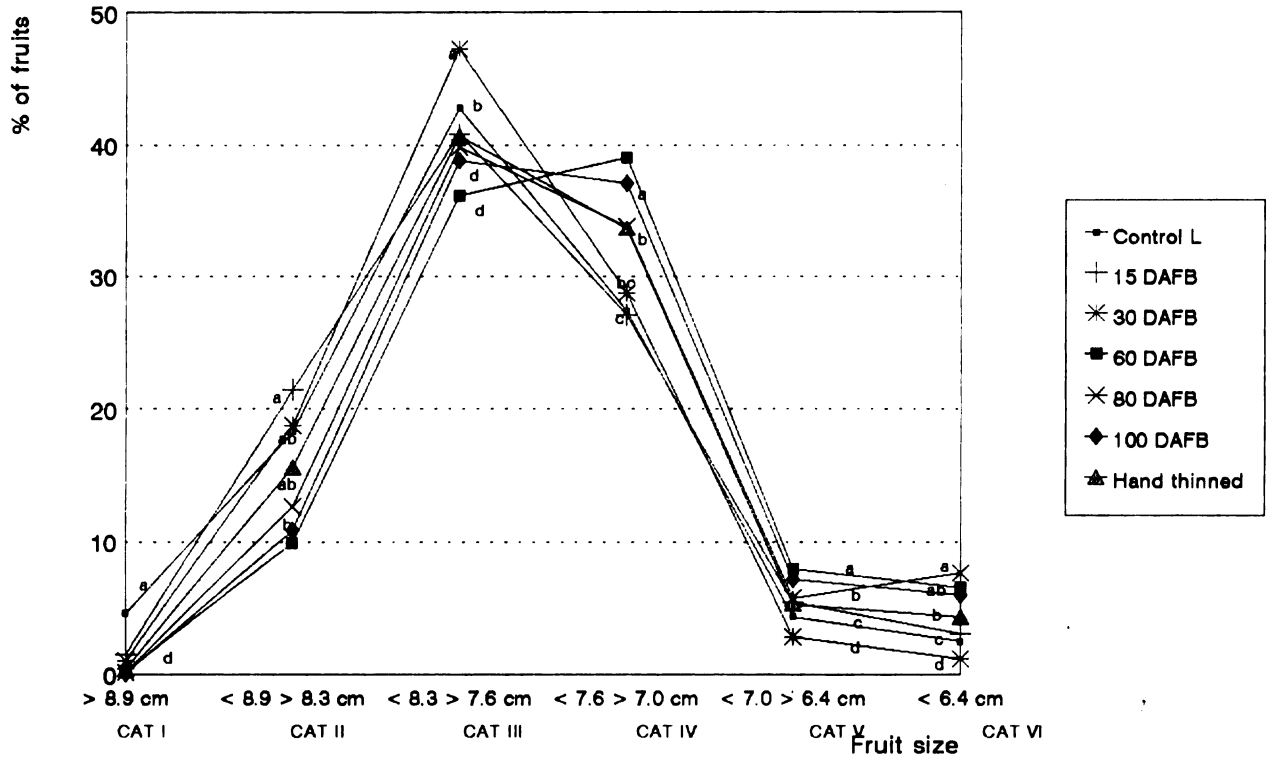
Figure 14.



Means followed by the same letter are not significantly different (Duncan's test P<0.05).

Figure 15. The effect of terbacil (63 ppm) applied to Redchief 'Delicious' at different times during the growing season on percentage of fruit in six categories on trees with a low initial crop load.

Figure 15.



Means followed by the same letter are not significantly different (Duncan's test P<0.05).

Table 3. Fruit growth rate (mm/day) of king fruit for the period 7-10 days after treatment with terbacil (63 ppm), Redchief 'Delicious', CHES, 1993.

APPLICATION DATE	CROP LOAD LOW		HIGH	
	Control	Treated	Control	Treated
15 DAFB	0.85 a	0.40 b	0.51 a	0.48 a
30 DAFB	0.87 a	0.91 a	1.00 a	0.40 b
60 DAFB	0.80 a	0.85 a	0.97 a	0.90 a
80 DAFB	1.04 a	0.99 a	1.15 a	1.15 a
100 DAFB	0.07 a	0.09 a	0.21 a	0.26 a

Values were compared within dates and crop loads. Means followed by the same letter within rows are not significantly different at P<0.05 (Student's t-test).

Table 4 . The effect of Terbacil (63 ppm) applied to Redchief 'Delicious' at different times during the growing season on percentage of fruit by size on trees with a high initial crop load at CHES.

Treatment	CAT I	CAT II	CAT III	CAT IV	CAT V	CAT VI	TOTAL Fruit (Kg/tree)
Control H	0.09 b	11.7 c	40.8 c	33.3 c	5.1 b	9.1b	71.3 bc
15 DAFB	3.73 a	31.1 a	46.5 a	15.7 e	1.9 d	1.0 d	46.4 d
30 DAFB	0.58 b	17.1 b	45.9 a	22.1 d	3.4 c	10.9 ab	40.3 d
60 DAFB	0.13 b	12.2 b	33.4 d	32.3 c	6.8 a	13.2 a	69.08 c
80 DAFB	0.18 b	7.8 d	44.3 b	37.8 b	5.9 ab	4.0 c	71.53 b
100 DAFB	0.01 c	5.1 e	33.7 e	48.2 a	6.9 a	6.2 c	71.37 b
Hand-thinned	0.34 b	14.1 c	44.1 b	31.2 c	5.1 b	5.3 c	87.09 a

Within columns means followed by the same letter not significantly different at $P< 0.05$ (Duncan's NMR test). For the statistical analysis data were transformed by $x + 0.5$.

Table 5. The effect of Terbacil (63 ppm) applied to Redchief 'Delicious' at different times during the growing season on percentage of fruit by size on trees with a low initial crop load at CHES.

Treatment	CAT I	CAT II	CAT III	CAT IV	CAT V	CAT VI	TOTAL Fruit (Kg/tree)
Control L	4.6 a	18.3 ab	42.8 ab	27.4 e	4.3 c	2.5 de	69.87 a
15 DAFB	1.5 b	21.4 a	40.8 ab	27.1 e	5.4 b	3.1 cd	60.56 c
30 DAFB	1.0 bc	18.8 ab	47.3 a	28.7 d	2.9 d	1.21 e	62.03 b
60 DAFB	0.26 cd	9.9 b	36.1 b	39.0 a	7.9 a	6.5 ab	62.43 b
80 DAFB	0.19 cd	12.6 ab	39.9 ab	33.7 c	5.8 b	7.6 a	56.60 d
100 DAFB	0.10 d	10.8 b	38.8 b	37.1 b	7.2 a	6.0 b	67.71 a
Hand - thinned	0.40 cd	15.7 ab	40.7ab	33.7 c	5.3 b	4.3 c	60.40 c

Within columns means followed by the same letter are not significantly different at $P< 0.05$ (Duncan's NRM test). For the statistical analysis data were transformed by $x + 0.5$.

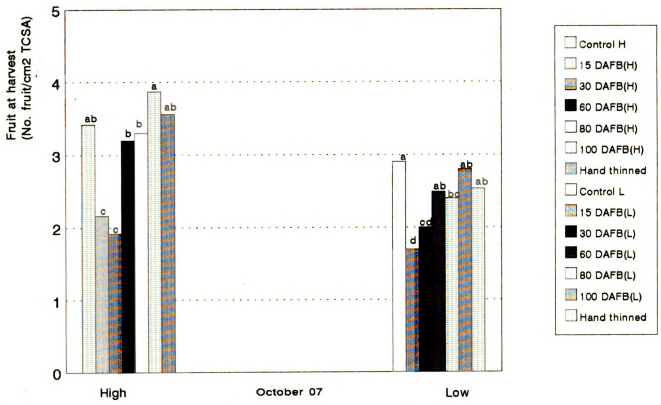
Table 6. Effect of terbacil (63 ppm) on fruit weight and percentage of large fruits (> 8.3 cm) at harvest on Redchief 'Delicious' at CHES.

APPLICATION DATE	CROP LOAD			
	LOW		HIGH	
	Avg. fruit Wt (g)	% fruit>8.3cm (Cat I + II)	Avg. fruit Wt (g)	% fruit >8.3cm (Cat I + II)
CONTROL	204 b	11.79 b	199 b	22.90 a
15 DAFB	231 a	34.80 a	265 a	22.90 a
30 DAFB	219 b	17.78 b	210 b	19.80 a
60 DAFB	197 c	12.33 b	190 c	10.60 c
80 DAFB	197 c	7.98 c	205 b	12.79 c
100 DAFB	190 c	5.10 c	191 c	10.90 c
HAND-THINNED	212 b	14.40 b	203 b	16.10 b

Values were compared within dates and crop loads. Means followed by the same letter within columns are not significantly different at $P<0.05$ (Duncan's NMR test)

Figure 16. The effect of terbacil (63 ppm) application at different times of the season on the number of fruit (fruit/cm^2 TCSA) at harvest for Redchief 'Delicious' at CHES.

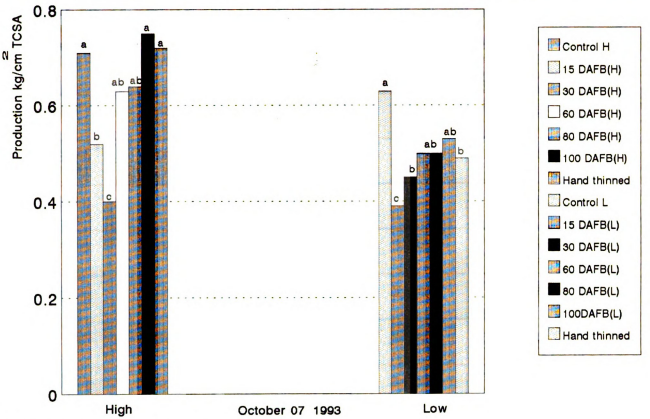
Figure 16.



Data were analyzed separately for high and low loaded treatments.
Means followed by the same letter for each crop load are not significantly different (Duncan's test $P<0.05$).

Figure 17. The effect of terbacil (63 ppm) application at different times during the season on final yield (Kg/cm^2 TCSA) of Redchief 'Delicious' at CHES.

Figure 17.



Data were analyzed separatelly for high and low loaded treatments.
Means followed by the same letter for each crop load are not significantly different (Duncan's test $P<0.05$).

Table 7. The effect of terbacil (63 ppm) on the total number of fruits, total production per tree, fruit number and production per cm^2 trunk cross section area (TCSA) at harvest (10/07/93) for trees with heavy crop load, Redchief 'Delicious', CHES.

Treatment	Total No. Fruit	Total prod Kg	No. fruit/ cm^2 TCSA	Prod Kg/cm^2 TCSA
Control H	348.7 d	71.3 bc	3.5 ab	0.71 a
15 DAFB(H)	200.3 e	46.4 d	2.2 c	0.52 b
30 DAFB(H)	183.7 e	40.3 d	1.9 c	0.40 c
60 DAFB(H)	368.7 c	69.08 c	3.2 b	0.63 ab
80 DAFB(H)	361.3 d	71.53 b	3.3 b	0.64 ab
100 DAFB(H)	374.3 b	71.37 b	4.0 a	0.75 a
Hand thinned	409.3 a	87.09 a	3.4 ab	0.72 a

Within columns means followed by the same letter are not significantly different at $P< 0.05$ (Duncan's NMR test). For the statistical analysis data were transformed by $x + 0.5$.

Table 8. The effect of terbacil (63 ppm) on the total number of fruits, total production per tree, fruit number and production per cm^2 trunk section area (TCSA) at harvest (10/07/93) for trees with low crop load, Redchief 'Delicious', CHES.

Treatment	Total No. fruit	Total prod Kg	No. fruit/ cm^2 TCSA	Prod/cm^2TCSA
Control L	350.0 a	69.87 a	2.9 a	0.63 a
15 DAFB(L)	228.3 e	60.56 c	1.7 d	0.39 c
30 DAFB(L)	295.2 c	62.03 b	2.0 cd	0.45 b
60 DAFB(L)	328.0 ab	62.43 b	2.5 ab	0.50 ab
80 DAFB(L)	276.0 d	56.60 d	2.4 bc	0.50 ab
100 DAFB(L)	354.0 a	67.71 a	2.8 a	0.53 ab
Hand thinned	296.3 c	60.40 c	2.5 ab	0.49 ab

Within columns means followed by the same letter are not significantly different at $P < 0.05$ (Duncan's NMR test). For the statistical analysis data were transformed by $x + 0.5$.

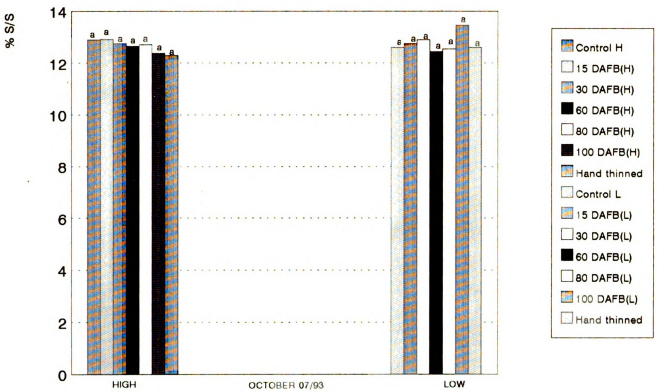
Table 9. Shoot growth rate (mm/day) for the period 7-10 days after treatment with terbacil (63 ppm), Redchief 'Delicious', CHES, 1993.

APPLICATION DATE	CROP LOAD LOW		HIGH	
	Control	Treated	Control	Treated
15 DAFB	2.50 a	3.30 a	3.40 a	4.10 a
30 DAFB	3.60 a	4.90 a	1.80 a	0.08 b
60 DAFB	0.52 a	0.43 a	0.04 a	0.07 a

Values were compared for each date. Low and high crop treatments were analyzed separately. Means followed by the same letter within rows are not significantly different at P<0.05 (Student's t-test). Shoot growth rate for 80 DAFB and latter are not included. Shoots stopped growing on July 28/93 (72 DAFB).

Figure 18. The effect of crop load and terbacil (63 ppm) application at different times during the season on fruit soluble solid content at harvest for 'Redchief Delicious' at CHES.

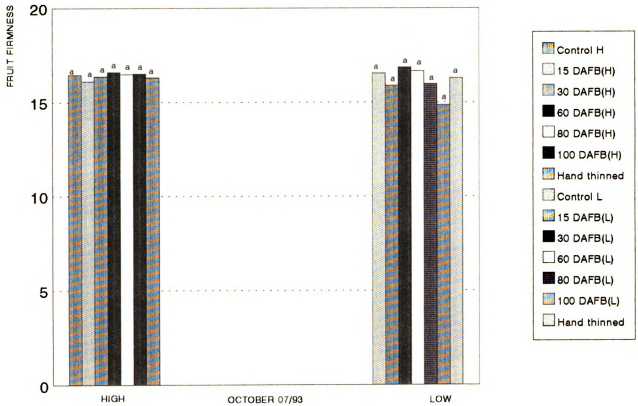
Figure 18.



Data were analyzed separatelly for high and low loaded treatments.
Means followed by the same letter for each crop load are not significantly different (Duncan's test $P<0.05$).

Figure 19. The effect of terbacil (63 ppm) application at different times during the season on fruit firmness at harvest for high and low loaded trees of Redchief 'Delicious' at CHES.

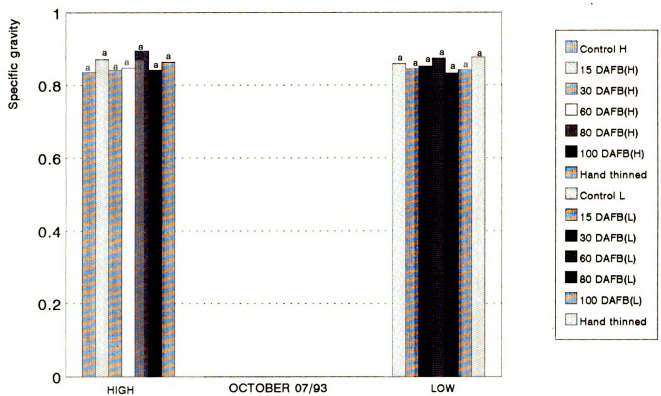
Figure 19.



Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).

Figure 20. The effect of terbacil (63 ppm) application at different times during the season on fruit density at harvest for high and low loaded trees of Redchief 'Delicious' at CHES.

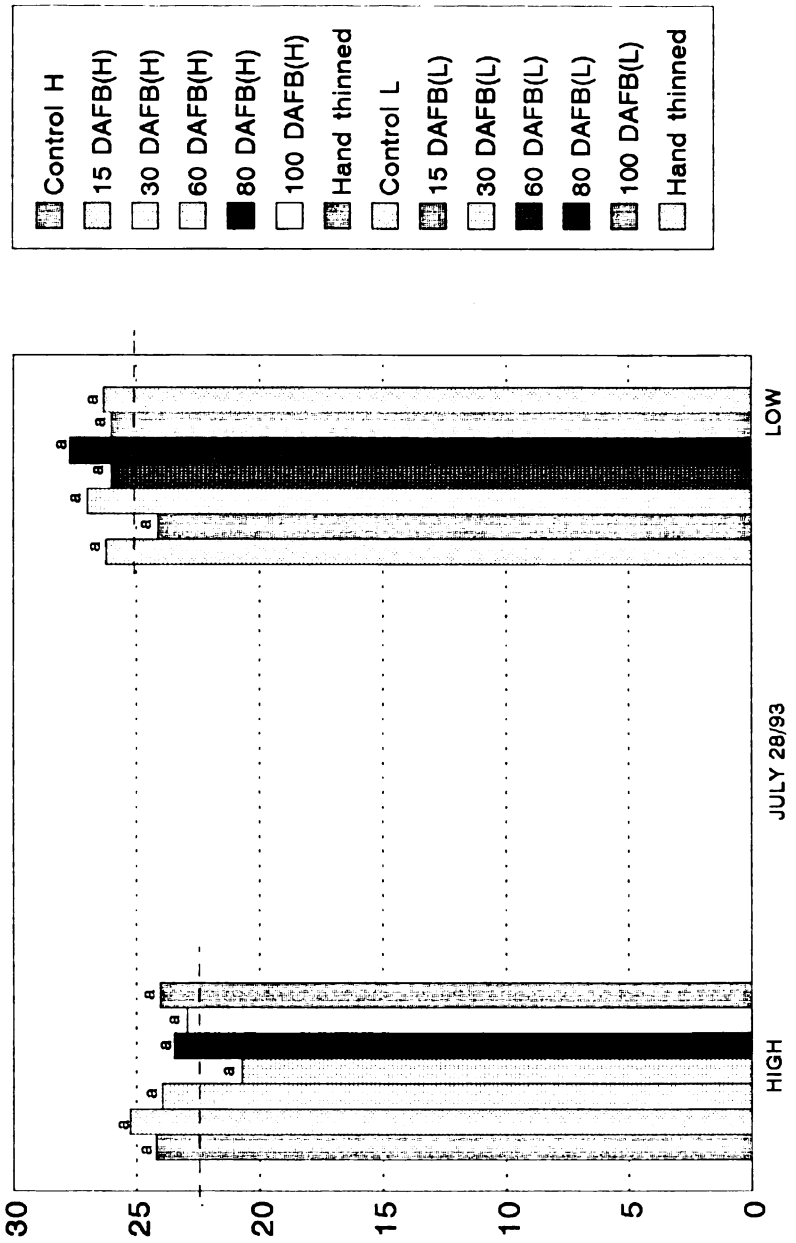
Figure 20.



Data for high and low loaded treatments were analyzed separately.
Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).

Figure 21. The effect of terbacil (63 ppm) application at different times during the season on final shoot length on high and low crop loaded trees of Redchief 'Delicious' at CHES.

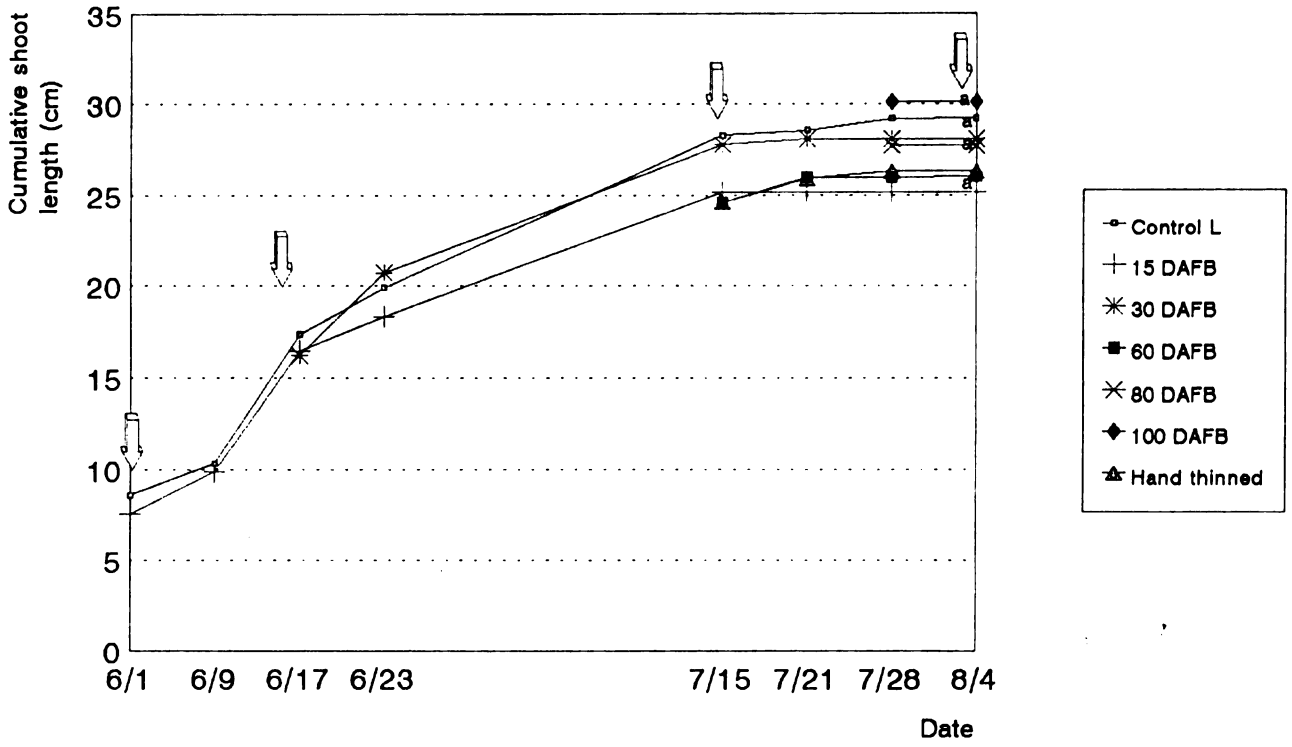
Figure 21.



Data for high and low loaded treatments were analyzed separately
Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).

Figure 22. The effect of terbacil (63 ppm) application at different times of the season on shoot growth of Redchief 'Delicious', CHES, on trees with a low crop load.

Figure 22.

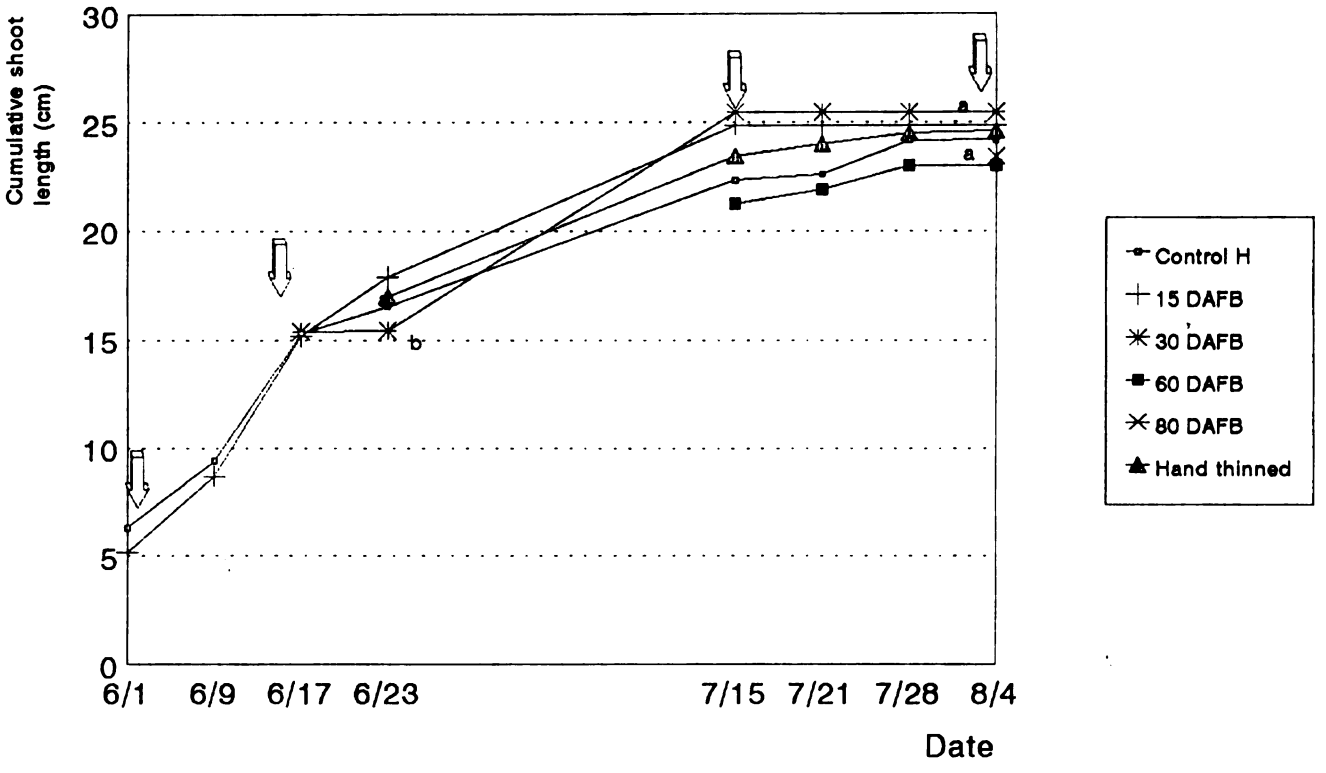


Values represent average shoot growth. Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).

Arrows indicate the time of each treatment.

Figure 23. The effect of terbacil (63 ppm) application at different times during the season on shoot growth of Redchief 'Delicious', CHES, on trees with a high crop load.

Figure 23.



Values represent average shoot growth. Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).

Arrows indicate the time of each treatment.

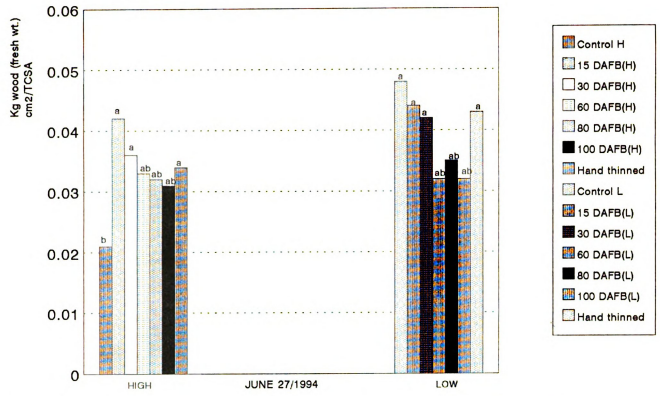
Likewise, the degree of watersprout formation decreased progressively as treatment was delayed (Figure 24). No greater tendency was observed for watersprout production in the low cropped trees. However, in those trees that received terbacil earlier in the season (15 and 30 DAFB) and in the hand-thinned control the production of watersprouts was higher.

Cold hardiness. No differences were observed in the T_{50} among treatments between November 1993 and April 1994 (Table 10).

Return bloom-fruit set. Terbacil applied at 30, 60, 80 and 100 DAFB significantly inhibited return bloom the following season (1994) as indicated by the number of flower clusters/cm^2 of BCSA whereas the 15 DAFB treatment promoted flowering (Figure 25). In the light-cropping trees only 2 treatments significantly affected flowering. Terbacil applications at 30 and 145 DAFB (hand thinned 30 DAFB) promoted flowering (Figure 25). Final fruit set, measured on July 20, 1994 was higher in trees treated with terbacil 15 DAFB and in those hand thinned and treated with terbacil 145 DAFB. In contrast terbacil treatments 30 and 60 DAFB inhibited flowering (Figure 26). In low crop trees, the only treatment that affected fruit set in 1994 was application of terbacil 30 DAFB in 1993. This reduced set significantly.

Figure 24. The effect of terbacil (63 ppm) application at different times during the season on water sprout production of Redchief 'Delicious' at CHES.

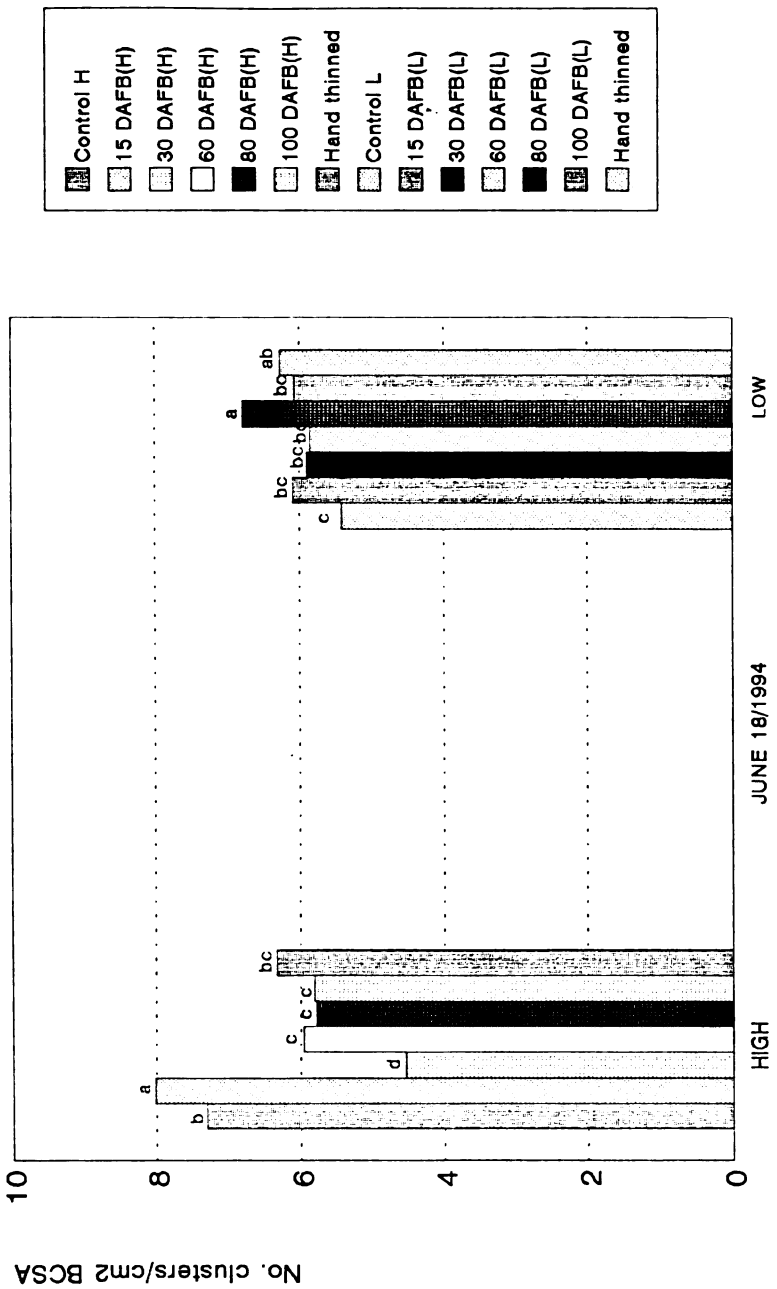
Figure 24.



Low and high crop treatments were analyzed separatelly. Means followed by the same letter for each crop load are not significantly different (Duncan's test $P<0.05$).

Figure 25. The effect of terbacil (63 ppm) application at different times during the season on return to bloom (cluster flowers/ cm^2 BCSA) the following year (1994) on low and heavy crop load trees of Redchief 'Delicious' at CHES.

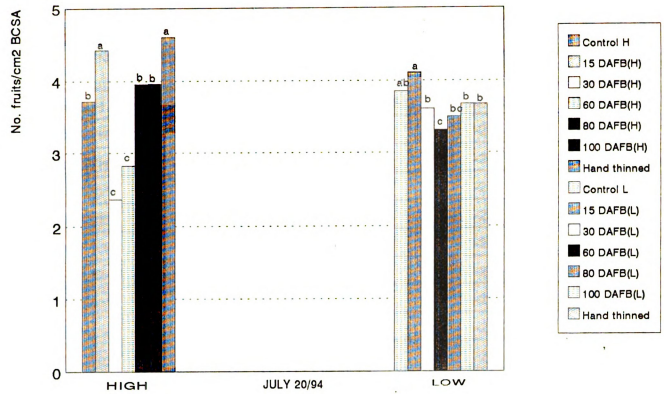
Figure 25.



Data from low and high loaded treatment were analyzed separately.
Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).

Figure 26. The effect of terbacil (63 ppm) application at different times during the season on final fruit set (number of fruit/cm^2 BCSA) the following year (1994) on low and high crop load trees of Redchief 'Delicious' at CHES.

Figure 26.



Data of high and low loaded treatments were analyzed separately.
Means followed by the same letter are not significantly different (Duncan's test $P<0.05$).

Table 10 . The effect of crop load and terbacil (63 ppm) application at different times during the season on cold hardiness (T_{50}) of new shoots during the dormant period of Redchief 'Delicious' at CHES.

TREATMENT	NOV 8/93	DEC 18/93	JAN 26/94	FEB 26/94	APR 21/94
Control H	-31 NS	-41 NS	-41 NS	-27 NS	-25 NS
15 DAFB(H)	-31	-41	-41	-27	-25
30 DAFB(H)	-31	-41	-41	-27	-25
60 DAFB(H)	-31	-41	-41	-27	-25
80 DAFB(H)	-31	-41	-41	-27	-25
100 DAFB(H)	-31	-41	-41	-27	-25
145 DAFB(H)*	-31	-41	-41	-27	-25
Control L	-31	-41	-41	-27	-25
15 DAFB(L)	-31	-41	-41	-27	-25
30 DAFB(L)	-31	-41	-41	-27	-25
60 DAFB(L)	-31	-41	-41	-27	-25
80 DAFB(L)	-31	-41	-41	-27	-25
100 DAFB(L)	-31	-41	-41	-27	-25
145 DAFB(L)*	-31	-41	-41	-27	-25

Values were compared for each date. NS- Not significantly different (Duncan's test P< 0.05).
* Hand-thinned 30 DAFB.

DISCUSSION

Several experiments have shown the effectiveness of terbacil as a photosynthetic inhibitor on fruit crops. Photosynthesis in a variety of different fruit trees was inhibited for varying lengths of time by concentrations from 50 to 2000 ppm (Byers et al., 1984, 1895; DelValle et al., 1985). However, the degree of plant responses in terms of 1) magnitude of inhibition, 2) foliar damage and 3) time of recovery varied. Environmental factors, as well as stage of development of the different organs of the plant, play a very important role in the response obtained. The same dose applied to the same species, and sometimes to the same varieties, may have different effects (Byers et. al, 1984, 1990a, 1990b).

The environment prior to application can have a profound effect on cuticle development, in particular epicuticular wax deposition, chemistry and fine structure, which influence the retention and penetration of foliar applied sprays (Baker, 1974). In the main field experiment, the late treatments (100 and 145 DAFB) caused less Fv/Fm reduction (Table 1) than did earlier applications. The cuticle of older leaves is less permeable and thicker, and herbicide absorption is decreased (Kirkwood, 1983; Unrath, 1981; Bukovac et al., 1979). In addition, wax deposition and cuticle thickness increase with leaf age. Therefore it is not surprising that the degree of inhibition in this study was not constant; the second

treatment had the greater effect in reducing Fv/Fm. This treatment was the only one in which phytotoxicity was observed. The environmental conditions at the time of treatment may have been responsible for this response. The day terbacil was applied (June 15) the relative humidity and temperature were high (Appendix, Figure 1), and it was cloudy. An important factor that influences the effect of dose is the 'duration of exposure' (Streibig, 1992). The time of exposure of this treatment was longer than for the others; furthermore the herbicide did not dry rapidly, which could cause greater uptake. Slower drying time usually results in greater activity attributed to both extended wetting time and increased chemical activity on the leaf surface (Unrath, 1981).

Symptoms of herbicide injury disappeared approximately 20 days after application. Many of the uracils produce symptoms that dissipate after a short period of time (Van Rensen, 1989). Some of them are either weakly bound to the receptor molecule in the thylakoid membrane (Izawa and Good, 1965), or metabolized by the plants (Herholdt, 1968).

As expected inhibition of photosynthesis was extended as concentration increased (dose response curve, Figure 1). Leaves treated with 12.5, 25 and 50 ppm recovered their photosynthetic capacity 15 days after the herbicide application. The data also reveal different degrees of inhibition according to the concentration applied. This

differential response could be observed after 5 days of treatment. At that time, the leaves that received the lower concentrations began to recover their photosynthetic capacity, while those that received 100 ppm or higher amounts had a value 40% of that of the control.

An analysis of leaf tissue from the second experiment in which terbacil was applied at 63 ppm indicated that the herbicide degraded chl a (Table 2), whereas chlorophyll a content remained similar to that of the control leaves 13 days after treatment. This was coincident with the increase in Pn observed (Figure 2). Photosynthetic inhibition was almost nil 18 days after terbacil application. However, after 13 days the Pn of treated leaves was only 3.7% less than the control, while Fv/Fm was 34.3% lower than untreated leaves. Similar effects of terbacil (78 ppm) were found by Hubbard, et al.(1994, unpublished data) on photosynthesis in tart cherry. This difference observed may have resulted from the high sensitivity of the fluorimetric detection in revealing the photochemical efficiency of PSII (Gleiter and Renger, 1993). This method also detects the level of metabolism-detoxification of the herbicide by the photosystem. Measurement of chlorophyll a fluorescence has been reported to be an accurate method for evaluating PSII (Krause and Weiss, 1984; Pannels et al., 1987; Miles and Daniels, 1973; Schreiber et al, 1977; Richard et al., 1983; Gleiter and Renger, 1993; Voss et al., 1984). Fv/Fm has provided excellent results for

the investigations of inhibitors that act at the acceptor site of photosystem II in sugar beet, soya, dwarf bean and cotton (Voss et al., 1984). On the basis of my data, I can infer that chlorophyll a fluorescence is an accurate method for the measurement of photosynthetic status of the leaf. Pn and Fv/Fm were significantly correlated (Figure 3). Interestingly, full PSII integrity does not seem to be necessary for maximum or near maximum Pn, implying that excess electron transport is occurring. This might be a useful tool as an early detection method for inhibition of Pn by biotic or abiotic stress.

The importance of Pn on fruit set is well documented. Studies in which light levels were reduced within the canopies - with the consequent reduction in Pn during bloom and shortly after - indicate the importance of photosynthate supply for fruit retention (Doud and Ferree, 1980; Jackson and Palmer, 1977; Auchter et al., 1926; Byers et al., 1990a, 1984, 1990b, Flore and Sams, 1986). Similar effects have been found following 1) early defoliation of spur leaves (Ferree and Palmer, 1982; Arthley and Wilkinson, 1964; Lewelyn, 1966; Lakso, 1984), and 2) application of photosynthetic inhibitors (Byers et al. 1984, 1985, 1990a, 1990b, Del Valle et al. 1985). Moreover, a possible mechanism for apple fruit abscission during June drop is the competition for essential metabolites among individual fruitlets and between fruitlets and vegetative shoots (Abbott, 1960; Quinlan and Preston,

1971; Wardlaw, 1968). Early development of apple flower clusters after budbreak also utilizes stored reserves of carbohydrates and nutrients (Hansen, 1971; Hansen and Grauslund, 1973).

Our results showed a high dependence of fruitlets and growing fruits on substrate produced by the leaves. High fruit drop was induced by terbacil application. Although all references known support inhibition of fruit development by photosynthetic inhibition soon after bloom, some discrepancies exist as to the effect of later treatments. Variable results have been reported in reference to fruit diameter and abscission. Byers et al. (1990a), and Byers et al.(1986) demonstrated thinning of fruits of 8 to 33 mm in diameter when plants were shaded 10 to 30 DAFB, or terbacil was applied soon after full bloom. We found that tree with heavy crop loads were thinned by low concentration of terbacil until 60 DAFB, when diameter was approximately 45 mm (Figures 7, 8 and 9). Greatest effect on fruit abscission were caused by the first and second treatment (15 and 30 DAFB).

In our study an interaction of crop load was observed. In trees carrying low numbers of fruits, fruit abscission was lower than in high crop trees. However, when comparing the time of abscission of fruit between heavy and light crop trees, we observed that fruit abscission continued at a low rate until September 23 (time of the last evaluation)(Figures 7, 8).

In plants treated 15 DAFB, fruit drop followed the same pattern as in the controls (see slope of graph in Figure 8). This is evident if we compare the number of fruits/cm^2 BCSA on August 7 and September 23. Fruits from trees treated 15 DAFB continued abscising at a higher rate than those from trees treated 30 DAFB. On September 23 the number of fruits/ cm^2 BCSA of light crop trees treated 15 DAFB was almost 40% higher than that of heavy loaded plants treated at the same time (Figure 9). More extreme was the difference observed with the second treatment. Fruit number/cm^2 of BCSA of low loaded trees treated 30 DAFB was approximately double than in heavy loaded ones (Figure 9). Obviously fruits were more dependent on photosynthates during the early stage (until 30 DAFB); but when availability was decreased in two different situations, high and low demand, the trees' response was different in regulating the number of fruits it was capable of supporting. The effect was more marked in plants carrying high numbers of fruits, where demand exceeded supply. In other words, when photosynthesis was inhibited, carbohydrate supply was not enough to maintain a heavy demand. In addition, fruit and shoot growth rate was markedly reduced on heavy cropping trees treated 30 DAFB (Table 3, Table 9). During the early phase fruit growth depends on the carbohydrates transported from spur leaves near them. Shoot leaves do not exhibit net carbohydrate export to the tree until 3-4 weeks AFB (Lakso, 1984).

Terbacil applied 15 DAFB inhibited fruit growth the week following treatment only in low crop trees (Table 3, Figures 10 and 11), whereas the same treatment 30 DAFB inhibited fruit growth only in high crop trees (Table 3, Figures 11 and 13). Unsprayed fruits on heavy cropping trees grew in diameter an average of 1.0 mm/day, while fruits treated 30 DAFB, grew only 0.40 mm/day. This can be observed in the slopes of the fruit growth curves (Figures 11, 13).

The different response caused by the treatments 15 and 30 DAFB on fruits in heavy loaded trees was unexpected. A possible explanation is that fruits have the greatest demand (sinks) for current photosynthate in mid-June (Hansen, 1977), when we inhibited photosynthesis was inhibited by terbacil. Grochowska (1973) and Priestley (1969) reported a dramatic fall in starch levels in fruit-bearing apple spurs in the 5th - 6th week AFB (end of June - beginning of July).

Natural fruit drop did not begin in control plants until June 23 (36 DAFB). At that time, an adequate carbohydrate supply was required not only for fruit and vegetative growth, but also for flower induction-initiation (Westwood, 1978; Buban and Faust, 1982; Faust, 1989). Additional energy was required by the leaves to repair the damage caused to the photosynthetic apparatus. This metabolic activity may have affected the rate of carbohydrate consumption.

The different response observed in low loaded trees, where terbacil applied 15 DAFB was the only treatment that

inhibited fruit growth (Table 3), may reflect an effect of the previous tree history. At the early stages of fruit development, when growth was dependent on both current and stored carbohydrate, a shortage in the latter accomplished to an inhibition in Pn, could have resulted in a decrease in fruit growth rate.

When terbacil was applied 30 DAFB, the effect on shoot elongation was greater than on fruit growth. In heavy loaded trees shoot growth increment during the week following terbacil treatment was 0.45 %, while in untreated trees was 8.13 %. That corresponded to growth rates of 1.80 mm/day and 0.08 mm/day for treated and control plants, respectively (Table 9). Although reproductive and vegetative growth were influenced by the Pn inhibition, fruits were evidently a stronger sink for carbohydrates than shoots (Avery, 1969; Hansen, 1971; Faust, 1989). According to Daie (1985), absolute growth rate of apple fruits reflects the daily rate of carbohydrate accumulation, and can be considered as representative of the 'sink strength'.

Fruit growth in apple is divided into two main periods: cell division and cell enlargement. Both processes are involved in determining the rate of growth and final potential for fruit size. The cell division occurs during the first 4 to 6 weeks following fertilization (Hulme, 1971).

The effect of Pn on fruit size is well known. Direct evidence

comes from the results of several shading experiments (Jackson, 1968; Jackson and Palmer, 1977; Marini et al., 1991). The dependence of fruit size on light penetration into the trees was assessed by Heinicke (1966) who found a direct correlation between fruit size and degree of light exposure.

Most of the studies indicate directly or indirectly that competition for carbohydrates among sinks affects fruit size mainly during the cell division period (Westwood 1968, Faust, 1989, Lakso et al. 1989). Early fruit thinning results in larger fruit size supporting this hypothesis (Preston and Quinlan, 1968; Quinlan and Preston, 1968; Abbott, 1965; Cobianchi, 1973; Knight and Spencer, 1987). Although total cell number is considered to be the primary factor determining fruit size at harvest, but this relationship is not always evident. Clearly supply of photosynthates is necessary during cell enlargement for maximum fruit size, as the bulk of dry weight accumulation occurs during the post cell division period, after June drop (Archbold, 1992). My data suggest that carbohydrates are important in the achievement of large fruit size in both early and late stages of fruit development. Heavy cropping trees treated with terbacil 15 DAFB had a higher proportion of fruits in Cat I (> 8.9 cm) (Fig. 14, Table 4). Although fruit cell count was not recorded the higher percentage of large fruits probably reflects a higher cell division following fruit thinning. Similar results were not observed in the hand-thinned control, probably because the

fruit were thinned too late to affect size. Similar results were obtained by Cook (1985) on Red 'Delicious'. Nevertheless, my results also suggest that fruit size is reduced when photosynthesis or carbohydrate supply is decreased, as indicated by the following: 1) All low loaded trees to which terbacil was applied had a low percentage of fruits in the largest category (Fig. 15, Table 5).

2) Low crop loaded plants that were substantially thinned by terbacil at 15 DAFB would be expected to bear a high percentage of Cat I (> 8.9 cm) fruits. However, these trees had significantly lower number of these fruits than the control. Likewise, the percentage of larger fruits observed (> 8.3 cm) was similar to the control (Table 6). The inhibition of fruit growth observed may account for this result.

3) Independently of crop load a higher number of 'cull' fruits were found when terbacil was applied from 30 to 100 DAFB. The higher number observed in the heavy cropping controls may indicate high fruit competition for carbohydrate supply.

My data supports previous observations (Byers et al 1990a, 1990b; Knight, 1981) that terbacil applied early promoted fruit thinning but did not increased fruit diameter in some experiments. Moreover, Byers et al. (1986) reported that shading apples 20-30 DAFB did not cause fruit thinning, but reduced fruit size. Rom and Ferree (1986) demonstrated that shoot leaves supply the photosynthate needed for late fruit enlargement. They found that shading apple shoots from

60 DAFB until maturity reduced fruit growth and resulted in small size at harvest. Severe red mite infestation in July also reduces apple fruit size (Beers et al., 1987).

Terbacil applied 15 and 30 DAFB significantly reduced the number of fruits and total weight produced per TCSA at harvest on both heavy and light crop trees (Figures 16 and 17, Table 7 and 8). Since terbacil treatments had no effect on fruit size on the low crop trees, and only a slight influence on the heavy cropped trees, it appears that fruit number was more responsible for the difference in total production than was size. Similar results were reported by Knight (1981) and Byers et al. (1990a, 1990b). This can also be observed when comparing the production of heavy cropping trees treated with the herbicide 30 DAFB vs. 60 and 80 DAFB (Table 7). Although these three treatments increased the percentage of fruits in the small categories (Cat V and VI) (Table 4), the 60 and 80 DAFB treatments did not differ significantly from the control in fruit number and total production per TCSA. These treatments did not thin.

Fruit quality was not greatly affected by terbacil treatment. Generally, fruit color has not been influenced directly by terbacil application (Byers et al., 1984; 1990b). Several studies indicate that color is affected by environmental factors, being light exposure one of the most important. Erez and Flore (1986) reported that color

development in peach fruits was a function of exposure to solar radiation. Direct light to the fruit is needed in apples for anthocyanin synthesis and, therefore, red color development (Marini, 1985; Jackson et al., 1977; Barritt et al., 1987; Jackson, 1968; Heinicke, 1966; Seeley et al.,1980; Morgan et al., 1984; Izso and Rom, 1989; Campbell and Marini, 1992, Saks et al., 1990). Experiments in which fruits were exposed to different light levels support this observation (Proctor and Creasy, 1971; Greene and Lord, 1975). My data did not show an extreme effect of inhibition of photosynthesis at different times on color formation. Tselas et al. (1979) reported a complete independence from photosynthesis in the development of anthocyanin in maize roots. According to Westwood (1978), a high level of carbohydrates in the fruit during the preharvest period tends to increase the content of anthocyanins. Walter (1967) pointed out that chromogen (anthocyanin precursor) synthesis depends on a supply of carbohydrates from green leaves. However, Redchief is a highly colored variety (Brooks and Olmo, 1972). Most, if not all, Redchief 'Delicious' strains do not present coloration problems. In general, they start coloring earlier than many other 'Delicious' strains and develop strong red color in different environments (Mercier, 1976).

Fruit SSC (soluble solids concentration) are strongly influenced by light exposure of leaves in the immediate area

of the fruit (Jackson et al., 1977; et al., 1983), implying the importance of photosynthesis, and therefore of carbohydrate supply, on this parameter. Numerous experiments in which shade was applied from 45-60 DAFB until maturity revealed a positive correlation between light (PPFD) and SSC in fruits (Marini, 1985; Jackson et al., 1977; Jackson, 1968; Seeley et al., 1980; Morgan et al., 1984; Campbell and Marini, 1992; et al., 1983). However, Barritt et al. (1987) did not find such a correlation. Marini et al. (1991) reported that the SSC of peach fruits was only related to PPFD during the first half of stage III of fruit growth. I observed no difference among treatments in their effects on sugar concentration. This may imply that a short period of Pn inhibition is not sufficient to influence SSC. However, one would have expected sugar concentration to be negatively correlated with crop load.

Similarly, neither fruit firmness nor density was affected by treatment. If the increase in size observed in fruits from plants treated with terbacil 15 DAFB resulted from a higher number of cells, a difference in both parameters should have been observed. The fact that the comparisons among treatments were among fruits of the same size (CAT III) may have concealed such differences. A composite sample including fruits from all size categories would have been more appropriate. Early fruit thinning usually leads to an increase in vegetative growth (Murneek, 1924). Photosynthetic

inhibition at different times of the season did no affect final shoot length, regardless of crop load (Figures 21, 22 and 23). As was expected, shoot growth was greater in low crop than in heavy crop trees. However, one would have expected a greater mean shoot length in those trees in which terbacil increased fruit drop. However, shoot growth ceased earlier in both low and heavy loaded trees with terbacil 15 and 30 DAFB (Figures 22 and 23). Quinlan and Preston (1968) found that thinning did not affect shoot length in 'Sunset' apple, but increased the number of shoots per tree. Although we did not count the number of shoots produced, early terbacil treatment increased watersprout production (more evident in heavy loaded trees) (Fig. 24). Watersprouts were apparently stronger sinks for carbohydrate allocation than were shoots. The latter, as mentioned above, stopped growing 2 weeks earlier than shoots on control and other treated trees.

Jackson (1968) mentions that upright-growing shoots (watersprouts) can compete successfully with other sinks, including fruits. Tymoszuk et al. (1986) found that carbohydrates produced from watersprouts were not translocated to apple fruitlets situated on neighboring spurs, but were used by the apices of the watersprouts and eventually incorporated into the bark and wood of the main limbs near the place of their production. No clear explanation emerged from the analysis of watersprouts in those trees which carried low crop.

The importance of carbohydrate storage in woody tissues and its effects on winter hardiness has been extensively investigated. Acclimation is an active metabolic process that requires a product of photosynthesis (Chandler, 1954). Several reports have indicated that some correlation exists between the levels of soluble sugars and starch in fruit trees and their winter hardiness. Positive correlations have been observed in apple (Williams and Raese, 1974), peach (Malcolm, 1975), and citrus (Mizuno et al., 1968). Fuchigami et al. (1971) observed that dogwood plants did not acclimate when depleted of reserves.

Early leaf loss has been reported as a detrimental factor in tart cherry, causing delayed acclimation and more rapid deacclimation, resulting in reduced bud survival (Howell and Stackhouse, 1973). Similarly, foliage should be in good condition in late fall to produce the maximum photosynthate possible. Any practice that extends growth into fall decreases the hardiness of tissues. My experiment did not show any difference in cold hardiness in any of the treatments (Figure 10). The T_{50} was similar for all of them.

Inhibition of photosynthesis early in the season following terbacil treatments (15 and 30 DAFB) could not have reduced hardiness due to the early thinning of fruits which reduced the total carbohydrate for fruit and increased cold resistance (Edgerton, 1966). This was accomplished by an earlier cessation of shoot growth. Lack of effect of the

treatments on cold hardiness may indicate that: 1) the inhibition of Pn capacity for 14-20 day periods did not reduce carbohydrate storage; 2) the acclimation was preordained by the genetic constitution of the tree and the normal environment the tree responds (Proebsting, 1978) or; 3) sugars and starch do not influence cold hardiness response, as was observed in some peach cultivars (Lasheen and Chaplin, 1977). Although we did not analyze stored carbohydrates in our experiment the first hypothesis appears to be more feasible.

The contribution of leaves, and hence of Pn, to flower bud initiation has been established in most plants (Monselise and Goldschmidt, 1982). According to some researchers, the flower induction-initiation process is governed by hormonal balance (Buban and Faust, 1982); others believe that it is the result of changes in the distribution of nutrients inside the apical meristem (Kraus and Kraybill's C/N theory, 1918; Sach's nutrient diversion theory, 1977). Bernier et al. (1981) considered a high C/N ratio to be essential for flowering. The inhibiting effect of fruiting on flower-bud formation has been associated with the presence of seeds (Chan and Cain, 1967), which are a source of hormones (Luckwill and Silva, 1969; Sinska et al., 1973) that may be transported to the spurs and inhibit flower bud formation. Early fruit thinning increases return bloom the following year (Faust, 1989; Ryugo, 1986). However, several observers have pointed out the importance of

leaves and high photosynthetic levels in this process. The negative effect of early defoliation or shading, has demonstrated that a certain photosynthetic threshold is necessary at the time of flower formation (Ryugo, 1986; Auchter et al., 1926; Paddock and Charles, 1928; Jackson and Palmer, 1977; Gur, 1985; Lakso, 1980).

A reduction in Pn 30 DAFB, at the beginning of the flower initiation period (Westwood, 1978), strongly reduced return bloom the following year in heavy cropping trees (Figure 25). Conversely, inhibition of Pn 15 DAFB, with reduced fruit set, promoted flower formation in heavy-cropping trees. However, flowering was lower in trees that received terbacil 30 DAFB than in those hand-thinned at the same time. This agrees with the results of Worley (1979) and Davis and Sparks (1974) in pecans. They reported that a shortage in carbohydrate at the time of flower initiation inhibited flower formation in this species. On the other hand, Goldschmidt and Golomb (1982) suggested that flower initiation was not energy intensive and high levels of carbohydrates at this time were not highly demanded in citrus. Grochowska (1973) found that a high demand in starch supply occurs in the 5^{th} or 6^{th} week after full bloom in apple, and that time was coincident with our second terbacil treatment. Although little information is available about the sink-strength of flower initials, my data suggest that during this period fruits are stronger sinks than potential flower buds; and a decrease in carbohydrate supply

decreases flower bud initiation.

Sink strength, defined as sink activity times sink size (Flore and Lakso, 1989), could have a marked effect on plants carrying large numbers of fruits. Comparison of return bloom and final fruit set the following year (Figure 26), indicates that although terbacil inhibited flowering less when applied 60, rather than 30 DAFB these flowers were less capable of setting fruits. In general, well formed buds are required to obtain good fruit set (Faust, 1989). The fact that no difference was observed in winter hardiness among treatments suggests that carbohydrate shortage reduced flower initiation rather than cold hardiness.

The hypothesis that time of leaf abscission or reduced competition for carbohydrates late in the season (Nyeki, 1980) can reduce flower 'quality' and fruit set the following season is not supported by my data.

Terbacil appears to be an useful tool to inhibit photosynthesis and to investigate damage thresholds in fruit crops. Among the advantages of its use we could mention:

1. Once the decrease in Pn caused by any insect or disease is known, terbacil can be applied at any time during the season to simulate their effects, avoiding the difficulties of insect or disease infestation, leaf removal, etc.

2. The degree and duration of inhibition can be regulated

by choosing the dosage to be applied.

3. Terbacil usage is easy to apply and is also an inexpensive tool requiring no sophisticated equipment for its application.

SUMMARY AND CONCLUSIONS

Although photosynthesis is recognized as the source of energy and carbon for plant growth, in most cases there appears to be no direct association between maximum leaf photosynthesis and yield.

This study was an attempt to determine if a reduction in Pn over a certain threshold, in trees carrying heavy vs. low crops, can reduce current and/or future crop yield in apple.

The following general conclusions concerning the role of Pn in plant growth-production were drawn:

1. A decrease in photosynthetic efficiency (47-69%) during the first stages of plant growth (15 and 30 DAFB) provoked a marked reduction in total yield regardless of initial fruit load.

2. The reduction in yield resulted from a decrease in fruit number that was not compensated for larger fruit size. Although the treatment 15 DAFB treatment in heavy loaded trees resulted in an increase in fruit size, the great decrease in fruit set reduced total production.

3. Fruit and shoot growth may be compromised when Pn is reduced 60 % , for a 20 days period, from mid-June to mid-July in trees carrying a heavy crop. At this time of high demand, stored carbohydrates are insufficient for both reproductive and vegetative growth; these are therefore dependent on

current photosynthate.

4. An inhibition of Pn during the first phase of the cell enlargement period may lead to the production of a high number of 'cull' fruits.

5. No effect of Pn reduction on fruit quality (red color, SSC and firmness) was found.

6. A decrease in Pn for 20 days during mid June - mid July (30-60 DAFB) strongly reduced flower induction-initiation, and therefore fruit production the following year.

7. Reductions of Pn for 20 day periods at different times in the season did not alter wood carbohydrate storage; hence, the trees' winter hardiness was not affected.

8. Fruits are stronger sinks for carbohydrates than are new shoots, or buds.

9. The supportive experiments showed that photosynthetic efficiency (Fv/Fm) is a good indicator of the leaves' photosynthetic capacity. Fv/Fm and Pn were significantly correlated.

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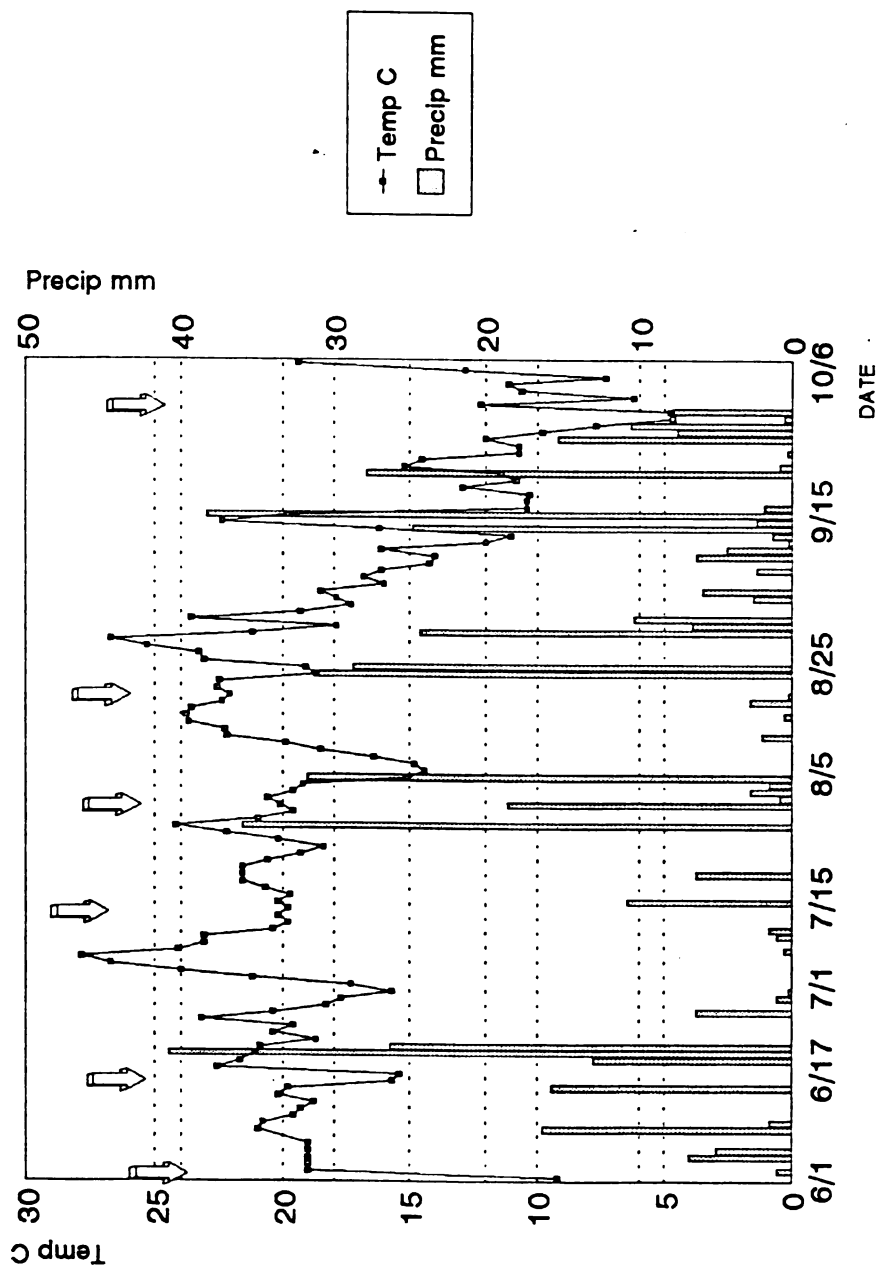
Appendix

Figure 1. Temperature (^{0}C) and precipitation (mm) at CHES during the growing season 1993.


Temp C
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Precip mm
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10/6
DATE

Figure 1.