FLOODING TOLERANCE OF SOUR CHERRIES

By

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ABSTRACT

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The effect of soil flooding on growth, leaf gas exchange characteristics and survival of sour cherries (Prunus cerasus L. 'Montmorency' on P. mahaleb L.) was studied utilizing 1 year-old containerized trees.

In one experiment, actively growing sour cherry trees were subjected to soil flooding for 2, 4, 8, 16 or 32 days under greenhouse conditions (total treatment/recovery period of 48 days). In all flooding treatments longer than 2 days, net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l) and shoot extension rates fell to ca. zero within 8 and 12 days, respectively, after initiation of flooding treatment. Gas exchange rates and shoot extension eventually returned to control levels only for the 2 and 4 day flooding treatments, doing so by day 24 and 40 respectively. Chlorophyll content declined for trees flooded longer than 8 days; falling to zero by day 40. Flooding for longer than 2 days resulted in significant defoliation of trees by the end of the 48 day treatment and recovery period. Survival of trees through a second growth period following chilling was inversely related to flooding duration, with an estimated LD_{50} of 6 days.

In a second experiment conducted within a growth chamber, CO_2 and light response curves of sour cherry trees were determined during a five day flooding regime. Soil flooding significantly reduced A within 24 hr after onset of flooding. Net CO_2 assimilation of flooded trees declined to 32% that of controls after 5 days of flooding. Residual conductance

to CO_2 (g_r') responded in a similar manner. Intercellular CO_2 (Ci) and stomatal conductance to CO_2 (g_l) were initially depressed by soil flooding. However, as flooding continued, g_l became markedly depressed while C_i eventually rose above that of control trees. Apparent quantum efficiency was reduced after 24 hrs of flooding and continued to decline throughout the flooding period. Dark respiration increased within 24 hrs after flooding. Results were interpreted within the framework of recent models of leaf gas exchange and indicate that the various stomatal and nonstomatal factors limiting A in sour cherries change in their relative importance as flooding persists.

The relative flooding tolerance of various cherry rootstocks was studied in a separate greenhouse experiment in which trees were flooded for 5 days and then allowed to recover for 10 days. Rootstocks tested included Mahaleb, Mazzard, Montmorency, Colt, MxM clones 2, 39 and 60, and Giessen clones (GC) 148/1, 148/9, 195/1, 195/2 and 196/4 (all grafted with Montmorency). Nonflooded control trees displayed significant rootstock effects on A, g_l and shoot extension rate when averaged over the 15 day experimental period. However, there was no apparent correlation of A, g_l or shoot extension with relative dwarfing ability of the various rootstocks. When compared on the basis of net carbon assimilation rate at end of recovery period and net shoot extension during treatment/recovery period several rootstocks stood out. Montmorency on MxM 2 was the most tolerant to flooding while Montmorency on MxM 39 was the least tolerant. As a group, tested rootstocks displayed a smaller range of tolerance and a more rapid onset of injury than has been reported for rootstocks of other temperate deciduous tree fruit species, e.g. apples and pear.

To all those who don't know enough to quit while they're ahead.

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I hope you all got even somehow because its too late now!

Guidance Committee: -

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LIST OF ABBREVIATIONS

A	net CO_2 assimilation
A/Ci	CO_2 assimilation response curve to internal CO_2
A/Ca	CO_2 assimilation response curve to ambient CO_2
C_a	ambient CO_2 concentration
C_i	intercellular CO_2 concentration
E	transpiration
g_l	stomatal conductance to CO_2
g_r'	residual mesophyll conductance to CO_2
K	hydraulic conductivity
l	stomatal limitation to photosynthesis
LD_{50}	lethal dose for 50% of population
ODR	oxygen diffusion rate
LWP	leaf water potential
PPF	photosynthetic photon flux
Pi	inorganic phosphate
p_s	leaf vapor pressure
R_d	dark respiration
RH	relative humidity
RuBP	ribulose bisphosphate
Rubisco	ribulose bisphosphate carboxylase/oxygenase
SWP	stem water potential
S/R	shoot to root ratio
VPD	vapor pressure deficit

INTRODUCTION

Soil flooding has negative effects on most growth and physiological processes of woody plants. Growers, aware of the potential for damage, will rarely deliberately plant trees on sites likely to flood during the growing season. Nevertheless, locally restrictive soils that are prone to rootzone flooding when subjected to heavy rainfall and/or irrigation are not uncommon in glacial soils typically utilized for agricultural purposes in the Great Lakes region.

Many sour cherry growers have experienced reduced longevity of orchards and trees in Michigan in recent years. Researchers at MSU have addressed this issue in attempting to identify the causal factor(s). While a number of biotic (root rots, insects, diseases, nematodes) and abiotic (soil drainage, winter damage, mechanical harvesting damage) factors apparently involved, researchers have generally observed affected trees in conjunction with locally restrictive soils, i.e. heavy subsoils, plow pans, etc., that are conducive to rootzone flooding when subjected to heavy rainfall and/or irrigation,

Temperate tree fruit species vary widely in their tolerance to soil waterlogging. Within a given species a considerable range of tolerance can often be found among available rootstocks. The two most common cherry rootstocks, seedlings of Prunus mahaleb L. and P. avium L. (Mazzard), have consistently been found to be extremely sensitive to waterlogging. Observations of field performance over the years have

generally noted P. cerasus cv. Stockton Morello to be considerably more tolerant to soil flooding than Mazzard, and Mazzard to be only slightly more tolerant to excess soil moisture than Mahaleb.

Recently, a number of prospective cherry rootstocks have been subjected to limited commercial trials, i.e. MxM clones (presumed natural hybrids of P. mahaleb and P. avium), P. cerasus cv. Montmorency and Colt. Neither these nor new advanced releases from breeding programs have been extensively evaluated for tolerance to waterlogging.

Detailed information concerning the effects of waterlogging on fruit trees is limited, especially for cherries. Herbaceous and woody plants subjected to soil flooding generally display reduced stomatal conductance (g_s), often in conjunction with reduced CO_2 assimilation (A). Decline in g_s is not usually accompanied by a drop in leaf water potential, however, there are some reports of an opposite effect. Recent investigations have shown that soil flooding may cause a reduction in A of various fruit species through a combination of stomatal and nonstomatal limitations. Models of leaf gas exchange have been developed which allow critical evaluation of the presence and relative contribution of some of these proposed mechanisms to limitation of A in stressed plants.

The primary objectives of this series of experiments were:

1. Observe and determine differences in symptom development of sour cherry scions during both long and short term soil flooding.
2. Determine LD_{50}, i.e. lethal "dose", of flooding.
3. Survey available cherry rootstocks and determine their relative sensitivity to soil flooding.
4. Determine physiological causes of plant injury during soil flooding.

Section I

EFFECTS OF FLOODING OF VARYING DURATION ON GROWTH, GAS EXCHANGE CHARACTERISTICS AND SURVIVAL OF CONTAINERIZED SOUR CHERRY TREES (MONTMORENCY/MAHALEB).

ABSTRACT

Soil flooding of containerized one year-old sour cherry trees (Prunus cerasus cv. Montmorency on P. mahaleb) produced a marked reduction in net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l) and stem water potential (SWP) within 24 hours following imposition of treatment. Over a 4 day flooding period A and g_l declined to 6% and 12% of controls, respectively. Stem water potential was significantly more negative in flooded trees the morning after flooding and continued to be more negative for the duration of the treatment period.

In a second experiment, actively growing containerized sour cherry trees (Montmorency/Mahaleb) were subjected to soil flooding for 2, 4, 8, 16 or 32 days under greenhouse conditions (total treatment/recovery period of 48 days). In all flooding treatments longer than 2 days, gas exchange characteristics and shoot extension rates fell to ca. zero within 8 and 12 days, respectively, after flooding. Leaf gas exchange characteristics eventually returned to control levels only for the 2 and 4 day flooding treatments, doing so by ca. day 20 and 32 respectively. Chlorophyll content declined in leaves of trees flooded longer than 8 days; falling to zero by day 40. Flooding for longer than 2 days resulted in significant defoliation of trees by the end of the 48 day treatment and recovery period. Survival of trees through a second growth period following chilling was inversely related to flooding duration, with an LD_{50} (number of days of flooding required to kill 50% of material) of 6 days.

In a third experiment in which containerized, dormant tart cherry rootstocks (Mahaleb on its own roots) were flooded for 4, 8, 16 or 32 days while in storage at 2 ^{o}C, no effects were noted on gas exchange

characteristics during a follow-up growth cycle in the greenhouse, although net shoot growth during this period was inversely related to duration of previous flooding treatment.

In a fourth experiment, a fourteen day treatment regime consisting of 2 days flooding followed by a 12 day recovery period was repeated 4 times over an 8 week period during active growth. Net CO_2 assimilation and stomatal conductance of containerized tart cherry trees (Montmorency/Mahaleb) declined significantly only during the second and third cycles but eventually returned to control levels in all cycles. Shoot growth declined significantly below controls during the second cycle; eventually falling to zero by the end of the fourth cycle. At conclusion of experiment, Phytophthora could not be isolated from any plots.

INTRODUCTION

Soil flooding has negative effects on most growth and physiological processes of woody plants (Kozlowski, 1984; Kozlowski and Pallardy, 1984; Pereira and Kozlowski, 1977). Most growers, aware of the potential for damage will not deliberately plant trees on sites likely to flood during the growing season. Nevertheless, locally restrictive soils, i.e. clay subsoils, plowpans, etc., that are prone to rootzone flooding when subjected to heavy rainfall and/or irrigation are not uncommon in glacial soils typically utilized for agricultural purposes in the Great Lakes region (Whiteside et al, 1963).

Soil flooding results in low soil oxygen levels due to the displacement of soil air and subsequent deplietion of the remaining oxygen by root tissues and aerobic soil microorganisms. Additionally, the low solubility and diffusion rate of oxygen in water compared to air slows the movement of oxygen to plant roots. Investigators have reported the depletion of oxygen in waterlogged soils within one day (Patrick and Mahapatra, 1968; Turner and Patrick, 1968) or even a few hours (Van't Woudt and Hagen, 1957). Shoot growth and root initiation, growth and survival of apples have been shown to reduced by low oxygen levels (Boyton, 1940; Boyton and Reuther, 1938; Boyton and Compton, 1943). In general, however, oxygen concentration alone has been weakly correlated with plant response (Letey and Stolzy, 1964).

In contrast, oxygen diffusion rate (ODR) has proven to be a reliable indicator of oxygen availability (Glinski and Stepniewski, 1985; Stolzy and Letey, 1964) presumably because this measurement technique mimics oxygen use by roots; responding to not only the oxygen concentration gradient between the soil and root but also the diffusion

path resistance (Letey and Stolzy, 1964). Generally, ODR's below 0.3-0.4 micrograms O_2 cm^{-2} min^{-1} impair root function and ODR's below 0.2 result in root death (Stolzy and Letey, 1964). Levels below 0.2 have been correlated with reduced root hydraulic conductivity and/or growth in pear and peach (Andersen et al., 1984a), blueberry (Crane and Davies, 1988) and apple (Olien, 1987).

Stomatal conductance decreases significantly within 4-5 days after onset of flooding in sour orange (Syvertsen et al, 1983), rabbiteye and highbush blueberries (Davies and Flore, 1986a), and peach (Andersen et al, 1984a). Smith and Ager (1988) observed a significant reduction after only 1 day of flooding in pecan. However, some species of Pyrus and selections of Cydonia appear to be tolerant for 20 or more days (Andersen et al, 1984a). Net carbon assimilation generally follows a similar pattern, decreasing rapidly after imposition of flooding in citrus (Phung and Knipling, 1976), rabbiteye and highbush blueberries (Davies and Flore, 1986a), pecan (Smith and Ager, 1988) and apple (Childers and White, 1942).

Reductions in A and g_l have been accompanied by reductions in leaf water potential (more negative) in beans (Wadman-van Schravendijk and van Andel, 1986) and tobacco (Kramer and Jackson, 1954) suggesting that stomatal closure in response to leaf water stress limits A. However, stomatal closure during soil flooding has been observed without concurrent reductions in leaf water potential in Pyrus (Andersen et al, 1984b), peas (Jackson and Hall, 1987) and hardwood species (Pereira and Kozlowski, 1977; Tang and Kozlowski, 1982) indicating that stomatal closure is not necessarily due to water stress. Additionally, reductions in A during soil flooding have been observed without stomatal

closure in sunflowers (Wample and Thornton, 1984) and Euphorbia (Sivakumaran and Hall, 1977) indicating a limitation of A at a more fundamental level. Stomatal and nonstomatal limitation of A during soil flooding has been observed in blueberries (Davies and Flore, 1986a and 1986b), tomato (Bradford, 1983a), beans (Moldau, 1973) and pecan (Smith and Ager, 1988).

Shoot growth is typically reduced during soil flooding of pears and peaches (Andersen et al, 1984a) and apples (Olien, 1987) and many hardwood species (Kozlowski, 1984). In contrast, Dickson, et al (1965) observed that height growth of the flooding tolerant Nyssa aquatica increased during soil flooding. Significant reductions in shoot growth of peach were observed after flooding treatments as short as 3 days during active shoot growth (Rom and Brown, 1979). However, effect was dependent on time of application; flooding just as buds broke in early spring actually improved growth of trees, if treatment was less than 5 days in duration, otherwise a reduction in subsequent growth was observed. Flooding during dormancy has generally not reduced subsequent shoot growth in apple (Heinicke, 1932; Rom and Brown, 1979) and Broadfoot (1967) observed that dormant season flooding actually improved subsequent growth of some hardwood species.

Tree survival is dependent upon duration and season of flooding. Fruit species are more likely to survive prolonged periods of waterlogging if it occurs when trees are not actively growing (Crane and Davies, 1988; Heinicke, 1932; Kongsgrud, 1969; Olien, 1987; Rom and Brown, 1979). A number of hypotheses have been postulated to explain this increased sensitivity during active growth. Flooding typically reduces the hydraulic conductivity of the root system, i.e. reduces

capacity of the root system to supply water to the canopy (Andersen et al, 1984b; Syvertsen et al, 1983). Clearly, this will be more of a problem during the growing season when the tree carries maximum leaf area. Alternatively, soil temperatures will be lower during the dormant season thus reducing root system respiration and hence demand for oxygen. Interestingly, some materials, i.e. some Pyrus and Cydonia species, are able to survive prolonged flooding even when imposed during active growth (Andersen et al, 1984a).

A number of plant growth regulators have been implicated in plant responses to soil flooding. Bradford and Yang (1980) demonstrated in tomato that flooding promoted the synthesis of ACC, an ethylene precursor, in the root system. Subsequent transport to shoots in the transpiration stream and conversion to ethylene resulted in petiole epinasty. However, Bradford (1983b) demonstrated that ethylene had no effect on stomatal conductance or photosynthesis of nonflooded tomato plants although exposure to ethylene resulted in typical petiole epinasty. Nevertheless, stomatal (Pallas and Kays, 1982) and nonstomatal (Govindarajan and Poovaiah, 1982) inhibition of photosynthesis has been reported in the literature.

Abscisic acid (ABA) has been shown to accumulate in the leaves of flooded plants (Hiron and Wright, 1973; Jackson and Hall, 1987; Shaybany and Martin, 1977). Bradford (1983b) demonstrated that although applications of ABA to nonflooded tomato plants caused stomatal closure similar to that of flooded plants, it did not produce a similar reduction in photosynthetic capacity. Raschke (1982), however, has reported nonstomatal inhibition of photosynthesis by ABA in a variety of species.

Burrows and Carr (1969) have reported a marked reduction in cytokinin content of xylem sap of flooded sunflowers. Cytokinins are known to delay senescence of detached leaves (Richmond and Lang, 1957), maintain photosynthetic rates in senescencing leaves (Adedipe, et al, 1971), promote synthesis of photosynthetic enzymes and components of the electron transport chain (Feierabend and de Boer, 1978) and maintain stomatal aperature in stressed plants (Bengston, et al, 1979; Kirkham, et al, 1974). This suggests that cytokinins may be involved in the altered leaf gas exchange characteristics typically observed in flooded plants. Bradford (1983b) reported that applications of benzyladenine maintained both stomatal aperature and photosynthetic capacity in flooded tomato plants.

Reid, et al (1969) and Reid and Crozier (1971) have reported that gibberellin levels drop markedly in tissues and xylem sap in flooded plants. They have also shown that applications of GA_3 produced a relatively greater improvement in shoot growth of flooded tomato plants than in nonflooded tomato plants. Increased auxin has been implicated in causing leaf epinasty. Phillips (1964a), observed that waterlogging induced leaf epinasty in sunflower was relieved by shoot decapitation. Application of IAA to the cut surface restored the epinasty. Phillips (1964b) later reported markedly greater amounts of auxin in shoots of flooded sunflowers than in controls.

Soil flooding and the concurrent reduction in redox potential, oxygen concentration and diffusion rate (ODR) lead to complex changes in both soil chemistry and root metabolism. Under anaerobic conditions a number of potentially toxic compounds are synthesized, several of which have been the subject of research efforts. Hydrogen sulphide evolution

in anaerobic soils has been studied extensively in relation to Citrus response to soil flooding. Culbert and Ford (1972) demonstrated that oxygen deficiency was not damaging in itself during short term flooding but if accompanied by 2-3 ppm of hydrogen sulphide severe root damage occurred. Additionally, they demonstrated that rough lemon, a flooding tolerant citrus rootstock (Hayashi and Wakiska, 1956), was less sensitive to hydrogen sulphide than other flooding sensitive citrus rootstocks.

Under waterlogged conditions root tissue metabolism shifts from aerobic to anaerobic pathways resulting in the formation of ethanol and acetaldehyde, with ethanol formation being favored the more limited the oxygen supply (Rowe, 1966). Although ethanol has been detected in xylem exudate of flooded tomato plants (Fulton and Erickson, 1964) and its production correlated with flooding sensitivity in Senecio (McMannon and Crawford, 1971), conclusive proof that observed amounts are indeed toxic to plant tissues is lacking. Additionally, Phung and Knipling (1976) was unable to detect any difference in ethanol concentrations in tissues of flooded vs non flooded citrus rootstocks.

Cyanogenic glycosides are common in tissues of Prunus spp. (Seigler, 1975). Rowe (1966) observed that under anaerobic stress detached roots of these species evolved phytotoxic amounts of hydrogen cyanide. Additionally, Rowe and Catlin (1971) have demonstrated that the differential sensitivity of peach, apricot and plum to soil flooding was correlated with the cyanogenic glycoside content of their root tissue.

Detailed information concerning the effects of waterlogging on fruit trees is limited, especially for cherries. Sour cherries (Prunus

cerasus, cv. Montmorency) are typically propagated on P. mahaleb (Perry, 1987), a rootstock, characterized as very sensitive to soil flooding (Saunier, 1966). The purpose of this series of experiments was to characterize the response of this particular scion/rootstock combination to flooding stress under a ranged of controlled conditions and regimes.

MATERIALS AND METHODS

Experiment 1: Four day diurnal study. On May 29, 1986, 8 maiden trees of P. cerasus cv. Montmorency grafted on P. mahaleb were pruned to a single, unbranched stem ca. 80 cm tall and planted in 7 liter plastic containers filled with a steam sterilized mineral soil mix (ca. 50% sandy loam, 30% spaghnum peat and 20% sand v/v). Trees were ca. 1.3 cm caliper (measured ca. 2.5 cm above graft union) at time of planting. Trees were moved to a shaded greenhouse (ca. 50% full sun) at the Pesticide Research Center, MSU and set in wooden racks (ca. 60 cm off the floor). Racks were then covered with aluminum foil to prevent direct solar heating of the containers. Plants were fertilized at planting and again 3 weeks later with a soluble fertilizer (20-20-20 NPK) diluted to 200 ppm N, otherwise trees were watered to saturation as needed with tap water. Three unbranched shoots were allowed to develop on each plant; all others were removed as they appeared. Pests and diseases were controlled as needed according to commercial recommendations (Mich. Ext. Bul. E154, Fruit Pesticide Handbook). Mean minimum/maximum air temperatures during pretreatment period were 18± 3/33±5 °C.

At 1100 hr, July 9th, flooding treatments were imposed on one half of the trees by placing each tree container in an 11 liter container

lined with a plastic bag and filled with tap water adequate to cover the soil surface. The experiment was concluded 4 days later after afternoon data was collected. During the treatment period A and g_l were determined in the morning (1000–1100 hr) and afternoon (1800–1900 hr) with a portable system consisting of an Analytical Development Co. (Hoddeston, England) Infrared CO_2 Gas Analyzer (LCA-2), Regulated Air Supply Unit (ASU) and Parkinson leaf Chamber (PLC-B). A single measurement was made on a randomly selected fully expanded mid-shoot leaf on each shoot (3 per tree). Readings typically equilibrated within 1 minute after sealing chamber on leaf. Measurements were made at ambient daytime temperatures and CO_2 concentrations (typically 340–360 ppm). Supplemental light was provided with a 400 W high pressure sodium vapor lamp whenever ambient light levels fell below saturation for photosynthesis, i.e. 1000 micromols m^{-2} s^{-1} PPF (Sams and Flore,1982). Gas exchange parameters were calculated as previously described (Moon and Flore, 1986) with the exception that leaf vapor pressure was estimated in the manner by Richards (1971) and that sample and ambient vapor pressures were calculated as:

$$p = (RH / 100) * p_s,$$

where p equals sample or ambient vapor pressure (with or without leaf within cuvette, respectively) at cuvette temperature, p_s equals leaf vapor pressure at cuvette temperature (presumed to equal the saturation vapor pressure of water) and RH is the appropriate percent relative humidity measured within the cuvette.

Stem water potential (SWP) was measured each morning (800 hr) with the use of a portable pressure bomb (PMS Instrument Co., Corvallis, Oregon). Samples were processed in manner described by Turner and Long

(1980) whereby the leaf was enclosed the evening before by slipping a plastic bag over a single basal leaf and sealing with a wire tie wrapped around the petiole. This allows leaf to equilibrate more rapidly and completely with stem water and gave a better estimate of plant water status.

Chlorophyll content was determined throughout the treatment period by collecting 5 leaf disks (0.32 cm^2 each) from a single randomly selected basal fully expanded leaf on each plant. This leaf was reused for subsequent chlorophyll samplings only. Samples were collected after gas exchange measurements in the afternoon of each day. Chlorophyll was extracted in 5 mls of N,N-Dimethylformamide and the content determined in the manner described by Moran (1980 and 1982).

Controls were watered whenever soil moisture tension exceeded -20 KPa, as measured with a Soil Moisture Equipment Corp. "Quick-Draw" soil moisture probe (Model 2900F), inserted ca. 10 cm into the soil midway between center of pot and rim. Mean minimum/maximum air temperatures during flooding treatments were 19±1/34±7 °C.

A randomized complete block (blocked on the basis of baseline net CO_2 assimilation rates) with 4 replications of two treatments (flooded vs check) was used.

Experiment 2: Flooding during active growth. On February 6, 1987, 20 budded cherry rootstocks of P mahaleb grafted with P. cerasus cv. Montmorency (pruned ca. 1 cm above chip bud and mean fw of 69 gm) were planted in 7 liter plastic containers filled with the steam sterilized mineral soil mix described in Experiment 1. Before filling, a single 2.5 cm diameter aquarium aerator (Krislin, Lansing, MI, Model 062380) connected to ca. 20 cm of plastic tubing was placed in the bottom center

of each pot; with the free end of the tubing exiting through a drainage hole. Trees were placed in a greenhouse at the Pesticide Research Center, MSU and watered regularly with a soluble fertilizer (Peter's 20-20-20 NPK) diluted to 200 ppm N. Trees were trained to a single unbranched stem. Mean minimum/maximum air temperatures during the pretreatment period were 20±1/31±4 °C. In order to complete experimental design, 4 additional trees were brought from a neighboring greenhouse 4 weeks before start of treatments, trees had been planted in identical soil mix, grown under similar regime and were similar in appearance and size to other trees utilized in this experiment. However, the eleven liter containers these trees had been planted in could not be accomodated by the methodology used to impose flooding treatments, therefore, these trees were used as controls.

On the evening of day zero (April 23), flooding was imposed as described in Experiment 1. Flooding was relieved in the evening 2, 4, 8, 16 or 32 days later. Pots were first allowed to gravity drain for 30 minutes after which a vacuum pump was attached via rubber hose and a collection flask to the buried aquarium aerator. Pumping for 10 minutes (typically generating a vacuum of 25-30 KPa in collection flask) allowed the removal of an additional 300-500 mls of water from each pot and the imposition of a soil moisture tension of ca. -3 KPa. During treatment/recovery period trees were watered to saturation whenever soil moisture tension exceeded -40 KPa and mean minimum/maximum air temperatures were 19±2/29±4 °C.

Data collections were made on day 0, 2, 4, 8, 12, 16, 20, 24, 28, 32, 40 and 48 of treatment/recovey period. Shoot length was measured from graft union to middle of shoot apex. Leaf gas exchange

characteristics (A and g_l) were determined on 2 randomly selected, recently fully expanded, mid-shoot leaves on each tree as described in Experiment 1. Chlorophyll content was determined as described in Experiment 1.

Forty-eight days after initiation of the flooding treatments all trees were pruned ca. 10 cm above graft union, defoliated and placed in a refrigerated storage at ca. 2 °C. Trees were watered to saturation once with tap water during storage. Seven weeks later all plants were returned to the greenhouse for a regrowth period (all trees trained to a single unbranched stem). Mean minimum/maximum air temperatures during regrowth period were 20±1/29±4 °C. Trees were watered as needed with tap water. After 60 days, percent survival was noted for each treatment and experiment concluded. Pests and diseases were controlled as needed according to commercial recommendations (Mich. Ext. Bul. E154, Fruit Pesticide Handbook).

A modified Spearman-Karber Method (Bittenbender and Howell, 1974) was used to calculate an LD_{50}, i.e. number of days of flooding required to kill 50% of trees:

$$LD_{50} = [(P_{i+1} - P_i) * (x_{i+1} + x_i) / 2],$$

where $P_i = b_i / n_i$ (mortality index of i^{th} treatment) and x_i=time value of i^{th} treatment.

A randomized complete block (blocked on baseline CO_2 assimilation rates) with 4 replications of 6 treatments (0, 2, 4, 8, 16, or 32 days of flooding) was used.

Experiment 3: Flooding during dormancy. On June 11, 1987, twenty-five rootstocks of P. mahaleb (pruned ca. 10 cm. above nursery ground level, mean fw of 64 gm) were planted in 7 liter plastic containers as

described in Experiment 1. Trees were watered and placed in total darkness in a refrigerated storage (2 °C). In the evening of June 20th, flooding was imposed as described in Experiment 1. Flooding was relieved in the evening 4, 8, 16 or 32 days later as described in Experiment 2.

Eighteen days after relief of last flooding treatment (32 day), all plants were moved from the cooler to a shaded greenhouse (ca 50% full sun) at the Pesticide Research Center, MSU. During this growth period all trees were trained with two unbranched stems (Mahaleb shoots arising from latent buds) and watered as needed with a soluble fertilizer (Peter's 20-20-20 NPK) diluted to 200 ppm N. Mean minimum/maximum air temperatures were 20±1/28±4 °C. After 60 days, shoot length and leaf gas exchange characteristics were determined as described in Experiment 1. Percent survival for each treatment was noted and experiment concluded. Pests and diseases were controlled as needed according to commercial recommendations (Mich. Ext. Bul. E154, Fruit Pesticide Handbook). A randomized complete block (blocked on initial fresh weight) with 5 replications of 5 treatments (0, 4, 8, 16, or 32 days of flooding) was used.

Experiment 4: Repeated short term flooding. On April 12, 1987, 10 P. mahaleb rootstocks budded with P. cerasus cv. Montmorency (pruned ca. 1 cm above chip bud and ca. 65 gm fw) were planted in 7 liter plastic containers as described in Experiment 2. Trees were placed in an unshaded greenhouse at the Pesticide Research Center, MSU and watered once per week with a soluble fertilizer (Peter's 20-20-20 NPK) diluted to 200 ppm N, otherwise with tap water as needed. Trees were trained to a single unbranched stem. Mean minimum/maximum air temperatures during

the 50 day pretreatment period were 19±2/30±5 °C. Shading (ca. 50% full sun) was applied to the greenhouse glass 22 days post-planting.

On the evening of day zero (June 2), flooding treatments were imposed on half of the plots as described in Experiment 1. Flooding was relieved in the evening 2 days later as described in Experiment 2. After a twelve day recovery period, flooding was reimposed on the same trees as described above. This 2 week treatment regime was repeated 3 more times for a total of 4 cycles, after which the experiment was terminated.

Mean minimum/maximum air temperatures during the 8 week treatment period were 21±1/32±4 °C and trees were watered with tap water whenever soil moisture tension exceeded -20 KPa. Pests and diseases were controlled as needed according to commercial recommendations (Mich. Ext. Bul. E154, Fruit Pesticide Handbook).

Every 2 days during experiment, shoot length was measured from graft union to middle of shoot apex. On days 0, 2, 6, 10, and 14 of each 2 week cycle, leaf gas exchange characteristics (A, g_l) were determined. Data was collected from 2 randomly selected, recently fully expanded, mid-shoot leaves of each tree as described in Experiment 1. Leaf chlorophyll content of a fully expanded leaf in the lower third of each shoot was determined at start of flooding treatment as described in Experiment 2. Whenever possible, this leaf was reused for subsequent chlorophyll determinations only which were made every 7 days through the end of the experiment.

At the conclusion of experiment, percent defoliation was estimated as length of shoot defoliated divided by total length of shoot (x100). Trees were removed from pots and their root systems washed clean of soil

by gentle agitation in water filled bucket. Root systems were visually rated for % of tissue rotted and samples collected for isolation of Phytophthora spp. (performed in the manner described by Harris, 1986). Trees were then partitioned into root system, stem (separated at graft union) and leaves. All samples were oven dried for 2 weeks at 90 °C before weighing.

A randomized complete block (blocked on baseline CO_2 assimilation rates) with 5 replications of 2 treatments (check vs flooded) was used.

Experiment 5: Measurement of ODR. Soil oxygen diffusion rates were measure in a separate experiment. Nine actively growing sour cherry trees (Montmorency/Mahaleb), ca. 75 cm tall, planted in same manner as described in Experiment 2 were utilized. Six plants were flooded on day 0. Flooding was relieved after 1 day on three plants and after 10 days on the remaining three. Flooding was imposed and relieved in the manner described in Experiment 2. Mean minimum/maximum air temperature during the 16 day flooding/recovery period was 20±1/26±4 °C. Soil oxygen diffusion rates were measured periodically during this experiment with an oxygen diffusion ratemeter (manufacturer unknown) equipped with a $Ag^+/AgCl$ reference electrode. Five 25 gauge platinum electrodes were inserted ca. 10 cm into the soil midway between the pot rim and its center on each sampling date. ODR measurements were taken after a 3 minute equilibration period at an applied voltage of 0.65 V (Lemon and Erickson, 1952; Stolzy and Letey, 1964).

Statistical analyses were performed with MSTAT Microcomputer Statistical Program (Michigan State University, E. Lansing, MI). Regression analyses and figures were prepared with Plotit Interactive Graphics and Statistics Package (Scientific Programming Enterprises, Haslett, MI).

RESULTS

Experiment1: Four day diurnal study. Effects of flooding over a 4 day period on net CO_2 assimilation (A), stomatal conductance to CO_2 (g_1) intercellular CO_2 (Ci), stem water potential (SWP) and leaf chlorophyll content are shown in Table 1. Flooding produced a significant reduction in net CO_2 assimilation the morning after imposition (21 hours later). Net photosynthesis of flooded plants dropped to near zero in 3 days. Carbon assimilation rates were generally lower in the afternoon than morning for both treatments, declining an average of 27% and 37% for control and flooded trees, respectively.

Effects on stomatal conductance displayed a similar pattern in that a significant depression was evident in the flooded trees the morning after imposition of treatment. Afternoon measurements were uniformly lower than those collected in the morning of each day, declining an average of 38% and 41% through the day for control and flooded trees respectively.

Intercellular CO_2 in flooded plants did not differ significantly from controls throughout experimental period. Stem water potential was significantly more negative the morning following imposition of flooding (21 hours) and was invariably more negative for flooded trees throughout the treatment period. Leaf chlorophyll content did not differ significantly from controls throughout experimental period.

Experiment 2: Flooding during active growth. Flooding exhibited marked effects on net CO_2 assimilation (Figure 1). Within 4 days after imposition of flooding treatments all trees displayed a significant reduction in A compared to controls. Flooding treatments of 4-32 days all dropped to ca. 0 net assimilation within 8 days after initiation of

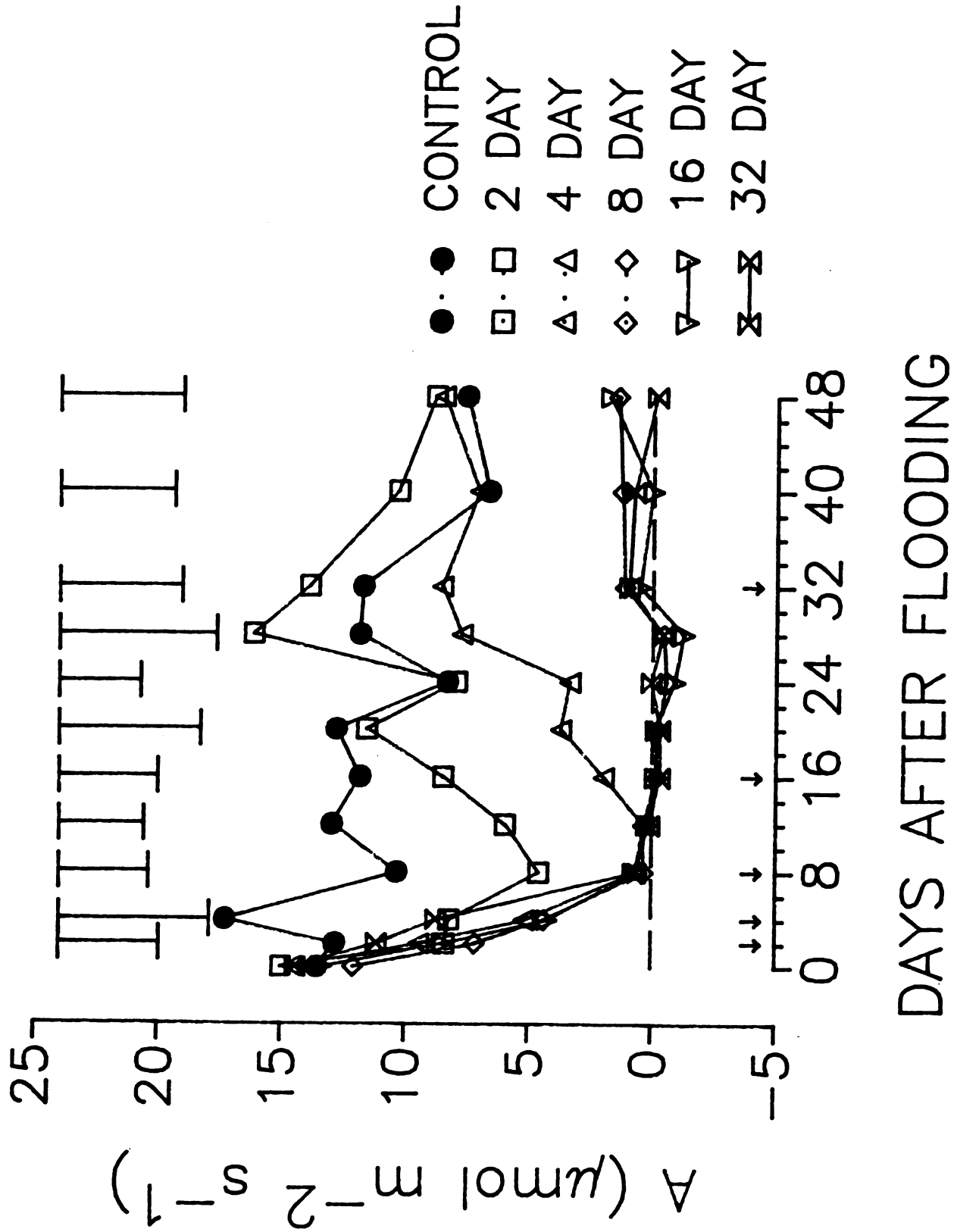
Table 1. Effects of 1-4 days of flooding[z] on net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l), intercellular CO_2 (Ci), stem water potential (SWP) and leaf chlorophyll content (Chlor) of sour cherry trees (Montmorency/Mahaleb).

Parameter	Trt	Day 0		Day 1		Day 2		Day 3		Day 4	
		am[y]	pm	am	pm	am	pm	am	pm	am	pm
A	Control	13.6[x]	6.8	8.8a	7.9a	12.5a	10.0a	13.5a	10.7a	14.3a	9.7a
(micromol m^{-2} s^{-1})	Flooded	12.6	5.9	4.4b	5.9b	5.6b	4.2b	0.6b	0.3b	1.6b	0.6b
g_l	Control	185	87	120a	75a	127a	75a	230a	205a	220a	97a
(mmol m^{-2} s^{-1})	Flooded	217	77	87b	57b	47b	22b	47b	35b	17b	12b
Ci	Control	192	125	179	166	179	200	210	222	210	199
(micromol mol^{-1})	Flooded	202	107	172	161	193	211	292	293	256	281
SWP	Control	-6.0	-	-9.2a	-	-5.0	-	-9.6a	-	-9.8	-
(MPa)	Flooded	-6.2	-	-13.4b	-	-7.2	-	-12.5b	-	-17.1	-
Chlor	Control	-	5.77	-	5.96	-	5.76	-	4.02	-	5.55
(mg dm^{-2})	Flooded	-	5.50	-	5.58	-	5.37	-	3.82	-	5.24

[z] Flooding imposed after morning data collection (1100 hr) on day 0.
[y] Morning and afternoon data collections for A and g_l typically 1000-1100 hr and 1200-1300 hr respectively; morning data collection for SWP typically 8 am.
[x] Values in same column for each parameter followed by different letter significantly different at the 5% level, F test. Each value is the mean of 4 observations.

Figure 1. Effects of 2-32 days of flooding on net CO_2 assimilation (A) of containerized sour cherry trees (Montmorency/Mahaleb). Arrows indicate day flooding relieved for various treatments. Bars represent $LSD_{.05}$ at each sampling date.

FIGURE 1


CONTROL
2 DAY
4 DAY
8 DAY
16 DAY
32 DAY
A (μmol m⁻² s⁻¹)
25
20
15
10
5
0
-5
0
8
16
24
32
40
48
DAYS AFTER FLOODING

flooding. In contrast, the 2 day flooding treatment was still fixing CO_2 at 44% of control levels at that point and slowly recovered to control levels by day 16. The 4 day flooding treatment was the only other treatment to eventually recover, returning to control levels by day 28.

Effects on stomatal conductance to CO_2 (g_l) were equally marked and similar in pattern (Figure 2). Within 4 days after imposition of flooding treatments all trees displayed a significant reduction in g_l compared to controls. Flooding treatments of 4 to 32 days declined rapidly to near zero within 8 days of onset of flooding while the 2 day treatment still retained 33% of control levels at that point and eventually recovered to control levels by day 20. The 4 day flooding treatment also recovered to control levels by day 40. All other treatments showed no apparent recovery even by day 48.

Within 6 days after imposition of flooding all trees displayed a significant reduction in shoot extension rate compared to controls (Figure 3). Flooding treatments of 4 to 32 days all dropped to near zero levels by day 12 while the 2 day flooding treatment dropped more slowly, falling to near zero levels only by day 28. Shoot extension of control treatment dropped gradually near the end of the experiment, as a result, by day 28 differences between control and any flooded treatments were not significant.

Chlorophyll content of the 16 and 32 day flooding treatments declined significantly below that of control trees by day 24, eventually falling to near zero levels by day 40 and 32, respectively (Figure 4). Chlorosis and abscission of the most basal leaves of flooded treatments was first observed on ca. day 6 and day 12, respectively, and proceeded

Figure 2. Effects of 2-32 days of flooding on stomatal conductance to CO_2 (g_1) of containerized sour cherry trees (Montmorency/Mahaleb). Arrows indicate day flooding relieved for various treatments. Bars represent $LSD_{.05}$ at each sampling date.

FIGURE 2

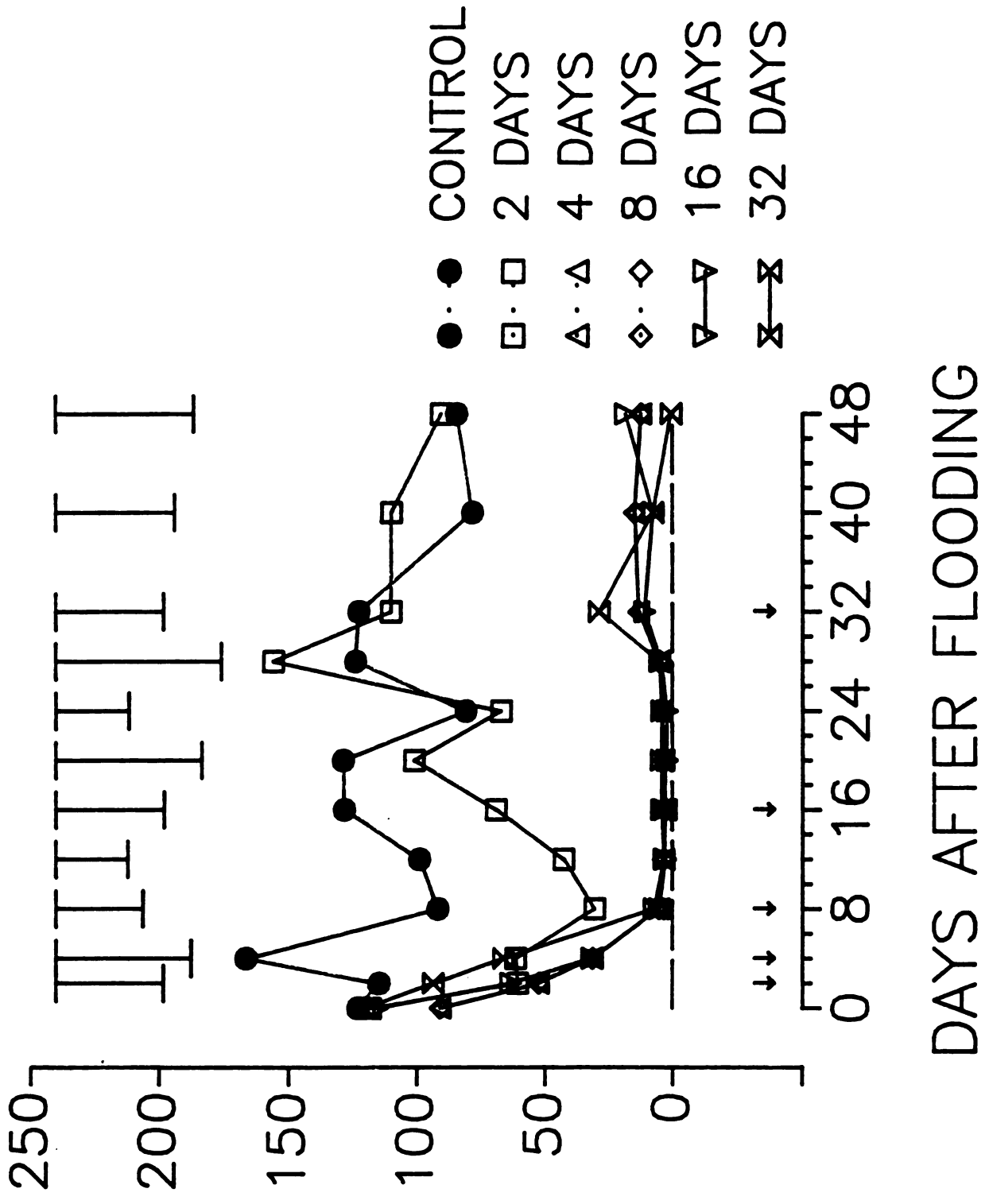

gl (mmol m⁻² s⁻¹)
250
200
150
100
50
0
0 8 16 24 32 40 48
DAYS AFTER FLOODING
CONTROL
2 DAYS
4 DAYS
8 DAYS
16 DAYS
32 DAYS

Figure 3. Effects of 2-32 days of flooding on shoot extension rate of containerized sour cherry trees (Montmorency/Mahaleb). Arrows indicate day flooding relieved for various treatments. Bars represent $LSD_{.05}$ at each sampling date.

FIGURE 3

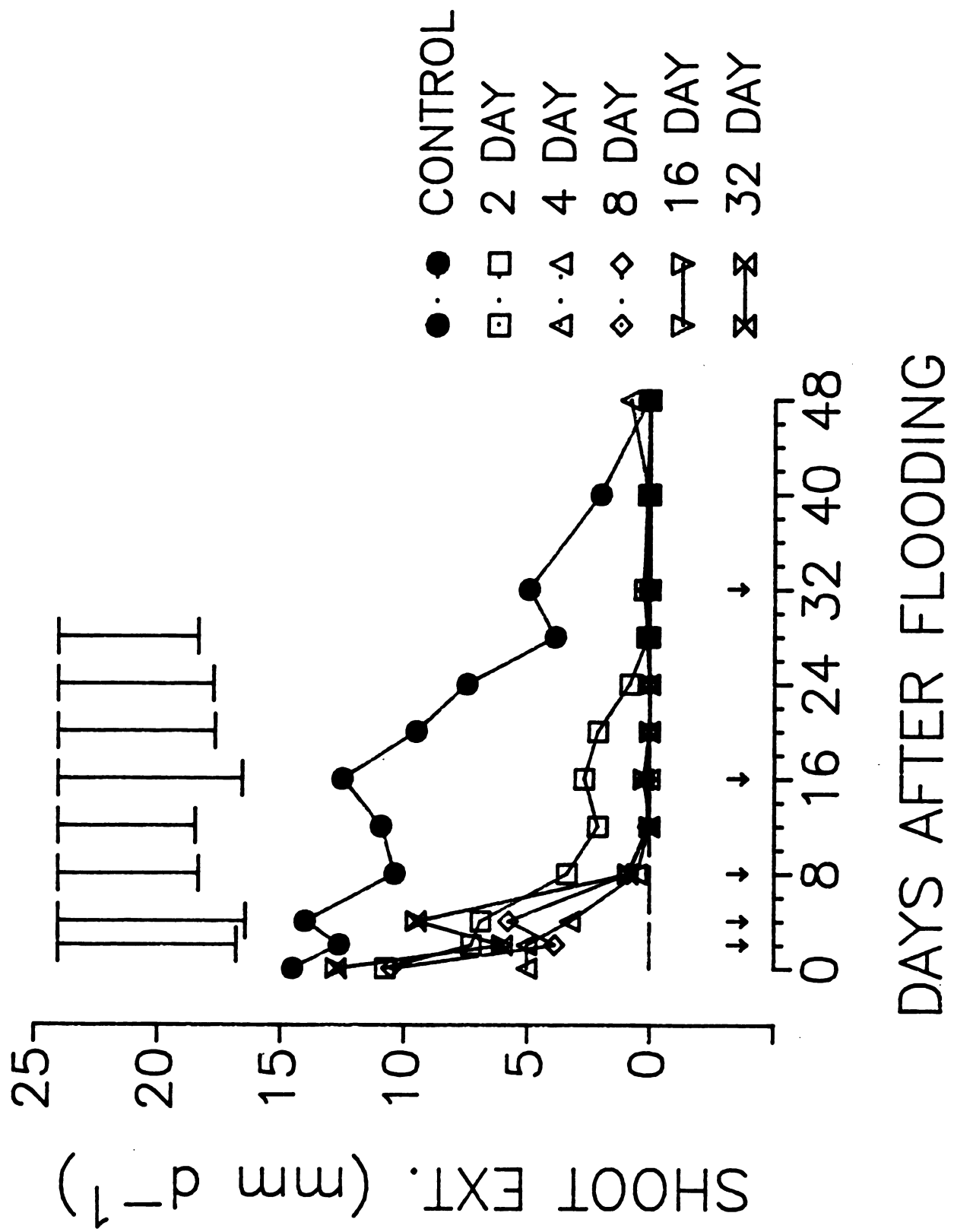
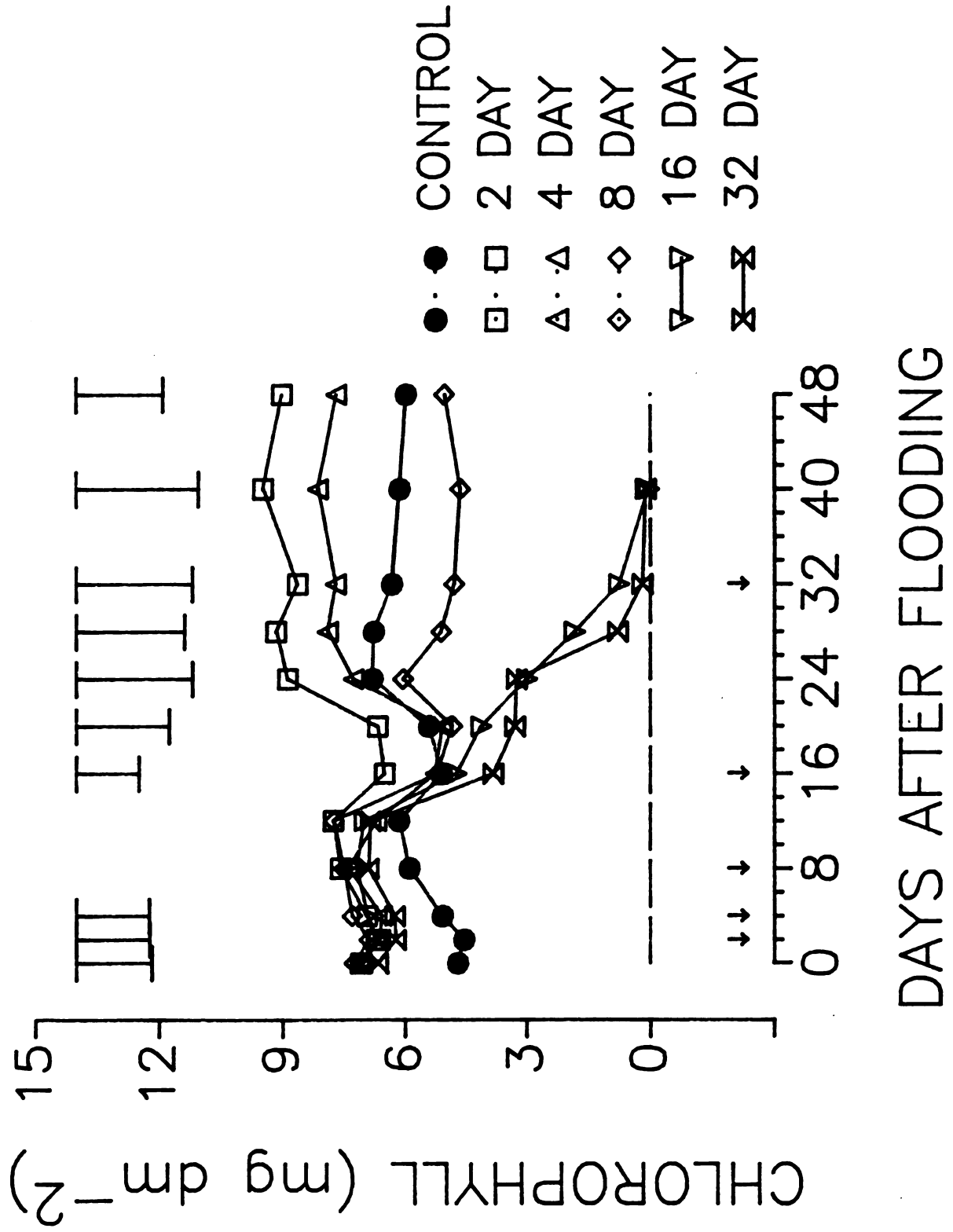

SHOOT EXT. (mm d⁻¹)
25
20
15
10
5
0
0 8 16 24 32 40 48
DAYS AFTER FLOODING
CONTROL
2 DAY
4 DAY
8 DAY
16 DAY
32 DAY

Figure 4. Effects of 2-32 days of flooding on total leaf chlorophyll content of containerized sour cherry trees (Montmorency/Mahaleb). Arrows indicate day flooding relieved for various treatments. Bars represent $LSD_{.05}$ at each sampling date.

FIGURE 4



chlorophyll

ooding relieve
at each

acropetally.

Percent defoliation at end of 48 day treatment/recovery period is noted in Table 2. Flooding for any period longer than 2 days resulted in significant canopy loss compared to controls. Percent survival declined markedly with more than 2 days of flooding (Table 2). Most trees that ultimately died made no growth during regrowth period. However, one tree in each of the 4, 8 and 16 day flooding treatments made some growth initially (<2 cm) but died by the end of the 60 day regrowth period. In dead trees all tissues appeared to be necrotic; brown cambium, with dessicated leaves (if any) and roots. Shoot growth and gas exchange characteristics were similar to controls in those trees that survived.

The regression analysis of percent survival vs number of days flooding (significant at the 0.7% level) predicted an LD_{50} (number of days required to kill 50% of trees) of ca. 4 days of flooding (Figure 5). An LD_{50} of ca. 6 days was calculated with a modified Spearman-Karber Method.

Experiment 3: Flooding during dormancy. At the end of the 60 day regrowth period there was a gradual reduction in subsequent shoot growth as flooding treatments were lengthened and no marked long term effects on leaf gas exchange characteristics (Table 3). Total shoot regrowth was negatively correlated with previous floodig treatment duration as shown in Figure 6. With the "worst case" assumption that no trees would have survived 64 days of flooding, an LD_{50} of 42 days was calculated with a modified Spearman-Karber method.

Experiment 4: Repeated short term flooding. Flooding effects on gas exchange parameters and shoot extension are shown in Table 4. Net

Table 2. Effects of flooding for 2-32 days during active shoot growth of sour cherry trees (Montmorency/Mahaleb) on defoliation[z] (DEF) at end of 48 day treatment/recovery period and on survival (S), net carbon assimilation (A), stomatal conductance to CO_2 (g_l), total new shoot length (SHOOT) and total leaf chlorophyll (CHLOR) at the end of 60 day regrowth period following dormancy.

DAYS FLOODED	DEF (%)	S (%)	A (μmol m^{-2} s^{-1})	g_l (mmol m^{-2} s^{-1})	SHOOT (cm)	CHLOR (mg/dm^2)
0	0.0 d[y]	100	11.4 ± 2.4	119.0 ± 34.5	75.6 ± 24.3	5.57 ± 0.85
2	2.1 d	100	11.3 ± 1.5	114.3 ± 26.3	93.3 ± 9.7	6.10 ± 1.53
4	45.6 c	50	11.7 ± 1.0	124.0 ± 12.8	91.7 ± 13.6	7.28 ± 1.43
8	68.0 bc	25	9.4	78.8	40.2	8.45
16	95.4 a	0	–	–	–	–
32	92.0 ab	0	–	–	–	–

[z] Calculated as length of shoot defoliated divided by total shoot length (x100).
[y] Values followed by same letter not significantly different at 5% level, DMR Test.

Figure 5. Percent survival vs. number of days flooding for containerized sour cherry trees (Montmorency/Mahaleb).

FIGURE 5

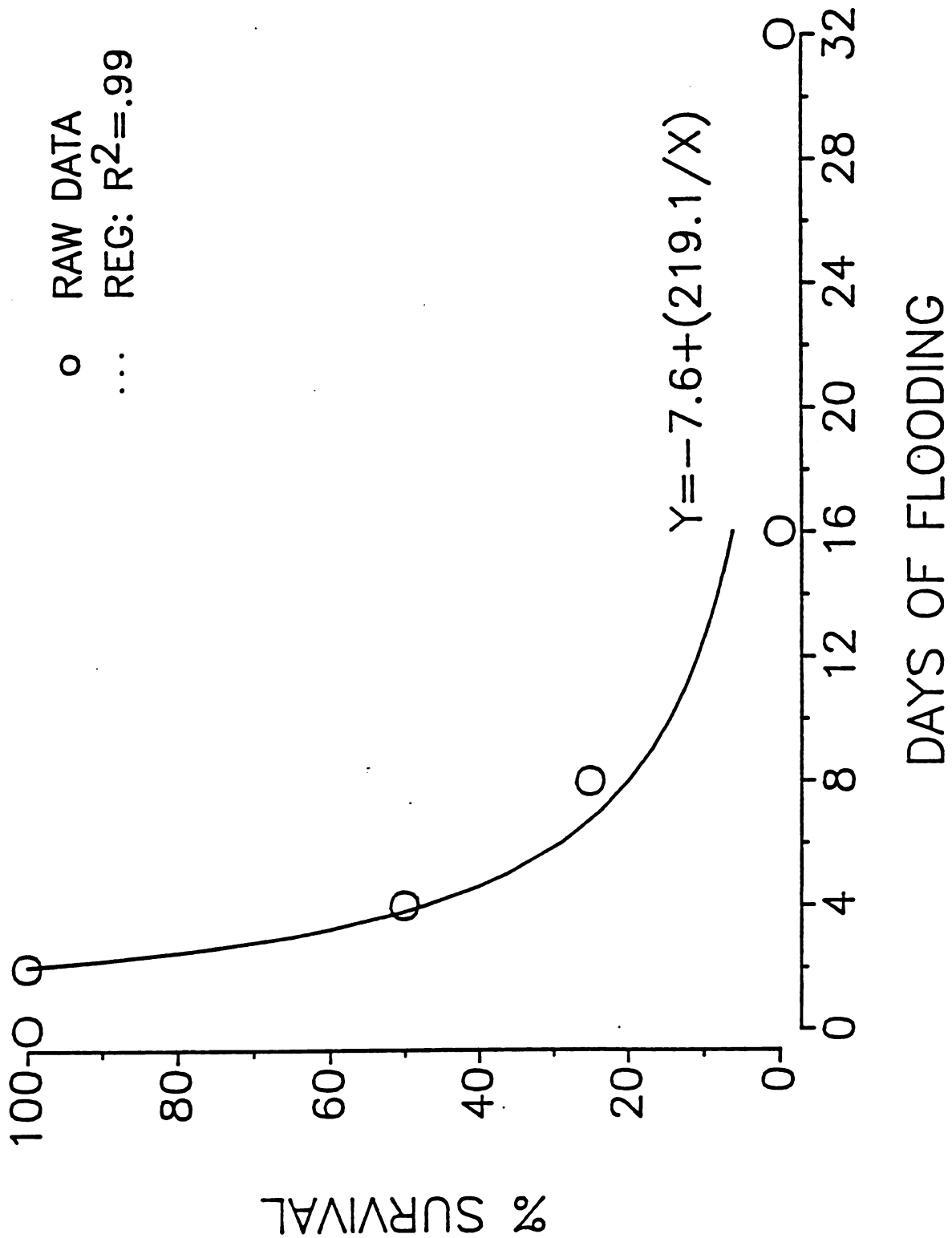

o RAW DATA
... REG: R^2=.99
Y=−7.6+(219.1/X)
% SURVIVAL
100
80
60
40
20
0
0
4
8
12
16
20
24
28
32
DAYS OF FLOODING

Table 3. Effects of flooding for 4-32 days during dormancy of P. mahaleb on survival (S), net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l) and total new shoot length (SHOOT) at end of 60 day regrowth period.

DAYS FLOODED	S (%)	A ($\mu mol\ m^{-2}\ s^{-1}$)	g_l ($mmol\ m^{-2}\ s^{-1}$)	SHOOT (cm)
0	100	11.5 ± 2.8	133.0 ± 38.5	79.7 ± 5.6
4	80	12.6 ± 1.4	143.5 ± 6.8	80.2 ± 4.7
8	100	11.7 ± 3.5	121.5 ± 39.2	71.1 ± 5.0
16	100	11.2 ± 0.6	135.3 ± 11.3	67.5 ± 11.1
32	80	11.6 ± 1.6	138.3 ± 22.3	61.8 ± 17.2

Figure 6. Relationship of total shoot growth (during 60 day regrowth period) and previous flooding treatment for unbudded Mahaleb rootstocks. Each point represents mean of 5 trees per treatment (2 shoot per tree) ± sd (except 4 and 32 flooding treatments, mean of 4 trees each), $r^2 = 0.88$ ($P < 0.02$).

FIGURE 6

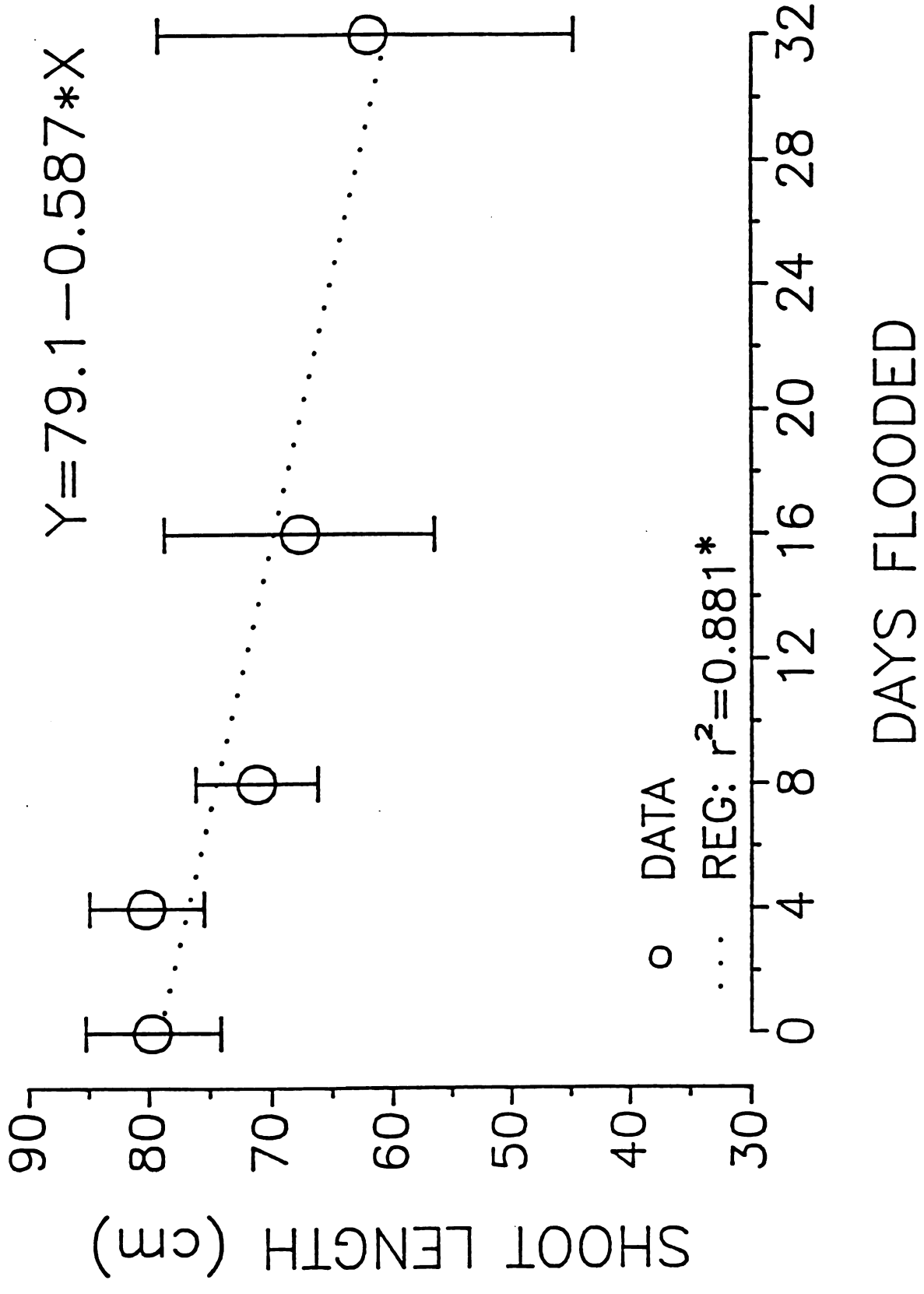

Y=79.1−0.587*X
o DATA
... REG: r²=0.881*
SHOOT LENGTH (cm)
DAYS FLOODED
90
80
70
60
50
40
30
0
4
8
12
16
20
24
28
32

Table 4. Effects of repeated short term flooding on relative change (% of control) of net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l) and shoot extension rate of sour cherry trees (Mont/Mahaleb).

		Day					
Parameter[z]	Cycle[y]	0	2	6	10	14	Mean Control Rate
A (micromol m^{-2} s^{-1})	1	88	104	85	88	93	10.4 ± 1.1
	2	–	67*[x]	82	83	109	10.8 ± 1.9
	3	–	80*	78	96	89	9.8 ± 2.1
	4	–	98	80	79	93	10.5 ± 2.8
g_l (mmol m^{-2} s^{-1})	1	82	112	83	118	89	111.5 ± 23.8
	2	–	63*	72**	74*	100	121.5 ± 37.3
	3	–	79*	72	82	80	116.0 ± 32,8
	4	–	99	86	82	95	120.8 ± 25.5
Shoot Extension (mm d^{-1})	1	104	89	96	76	83	12.0 ± 1.6
	2	–	62**	43**	42*	42	9.0 ± 2.5
	3	–	23*	15*	12*	2*	9.9 ± 2.3
	4	–	2*	4*	0*	0*	8.4 ± 2.0

[z] Expressed as percent of control mean.
[y] 14 day cycle consisted of 2 day flooding treatment followed by 12 day recovery period.
[x] Significance of difference between control and flooded treatments within each cycle at each date indicated at 5% (*) or 1% (**) level, otherwise nonsignificant, F Test.

CO_2 assimilation of flooded trees fell significantly below controls only on day 2 of the second and third cycles. Effects on stomatal conductance were similar; flooded trees dropped significantly below controls during cycle 2 from day 2 to 10 and again during cycle 3 on day 2. Invariably, both parameters returned to ca. control levels by the end of each 14 day cycle.

During cycle 1, shoot extension of flooded trees initially declined but returned near to control levels by the end of the 12 recovery period. During cycles 2 and 3, however, shoot extension declined steadily and eventually dropped to zero by the end of cycle 4.

Chlorophyll content of flooded trees generally declined throughout the experiment, becoming significantly different from control trees midway through cycle 3 and again from the midpoint of cycle 4 to the end of the experiment (Table 5).

Flooding effects on final component dry weights, percent defoliation and percent root system rotted are shown in Table 6. Flooding treatments produced a significant reduction in total leaf dry weight (dw) and non-significant reductions in stem dw and total dw. Root dw was greater for flooded trees than controls, though not significantly. Shoot/root ratio for controls was more than twice that for flooded trees, though difference was not significant. At end of the experiment flooded trees had suffered slightly more leaf abscission and root rot than controls, though neither difference was significant. All Phytophthora cultures were negative (data not shown).

Experiment 5: ODR Measurements. Oxygen diffusion rates during 1-10 days of soi flooding are shown in Figure 7. ODR falls below 0.3 micrograms O_2 cm^{-2} min^{-1} within minutes of flooding, eventually falling

Table 5. Effects of repeated short term flooding on total leaf chlorophyll[z] of sour cherry trees (Montmorency/Mahaleb).

Cycle[y]	Day 0	Day 7	Day 14	Mean Control Content (mg/dm^2)
1	109.0	103.1	99.6	6.60 ± 0.82
2	-	101.4	90.6[+x]	6.47 ± 1.79
3	-	81.7[+]	85.1[+]	8.25 ± 0.98
4	-	74.0	66.4	8.19 ± 1.60

[z] Expressed as % of control.
[y] 14 day cycle consisted of 2 day flooding treatment followed by 12 day recovery period.
[x] Significance of difference between control and flooded treatment within each cycle at each date indicated at 10% (+) level, otherwise not significantly different from control, F Test.

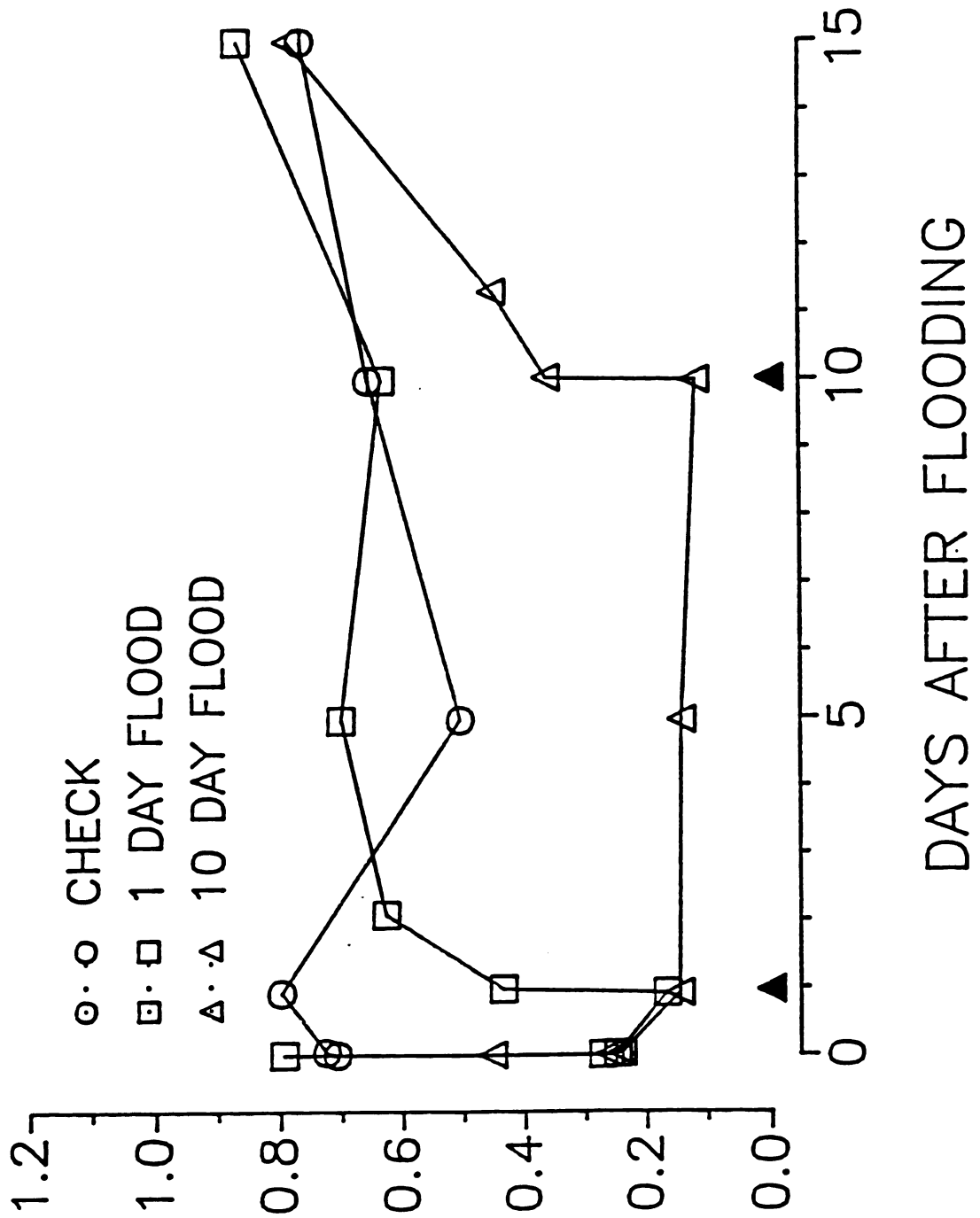
Table 6. Effects of repeated short term flooding on final component dry weights (gm), shoot/root ratio (S/R), percent defoliation (DEF) and percent root rot (ROT) of sour cherry trees (Montmorency/Mahaleb).

Treatment	Leaf	Stem	Root	Total	S/R	% Def	% Rot
Control	15.7a[z]	16.1	33.5	65.4	1.00	3.9	3.4
Flooded	9.3b	10.2	42.0	61.5	0.46	5.5	5.4

[z] Values in same column followed by different letter significantly different at 5% level, otherwise nonsignificant, F Test.

Figure 7. Effect of 1 or 10 days of flooding on oxygen diffusion rate (ODR) of containerized sour cherry trees (Mont/Mahaleb). Flooding relieved at times indicated by filled triangles. Each point represents mean of 3 trees per sampling time (5 determinations per tree).

FIGURE 7


OXYGEN DIFFUSION RATE
(μg O2 cm-2 min-1)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
CHECK
1 DAY FLOOD
10 DAY FLOOD
0
5
10
15
DAYS AFTER FLOODING

below 0.2 within 24 hours. ODR rose above 0.4 immidiately following relief of the 1 day flooding treatment, while recovery was slower after 10 days of flooding. ODR of both flooding treatments recovered to near control levels (0.6) within a few days after relief of flooding.

DISCUSSION

The simultaneous drop in both A and g_l following imposition of soil flooding observed in this series of experiments is similar to results obtained with a number of temperate species (Davies and Flore, 1986a and 1986b; Smith and Ager, 1988). This apparent correlation of net photosynthesis and stomatal conductance indicates that A may be limited by stomatal closure in flooded plants. The initial drop in stomatal conductance could be the result of an increased internal water deficit as indicated by the significantly more negative stem water potential observed in flooded trees the morning after imposition of flooding in Experiment 1. This in turn might be the result of a decrease in hydraulic conductivity of the root system. We have attempted to document changes in hydraulic conductivity during soil flooding of cherry trees but results have been inconclusive due to extreme variability in data (Beckman, unpublished).

If stomatal limitations were the sole cause of the drop in A, then intercellular CO_2 (Ci) should also decrease in flooded plants. Such an effect has been noted in blueberries (Davies and Flore, 1986a and 1986b). In Experiment 1, differences in Ci of control and flooded plants were not statistically significant, however, trends are interesting. C_i was lower in flooded plants only during pm measurements on day 0, although, A of flooded tress was not significantly different from

controls at this time (ca. 7 hours after flooding). Differences in Ci were minimal between control and flooded trees during day 1, while from day 2 through day 4, Ci was invariably higher in flooded plants even though A and g_l was markedly reduced in flooded plants, indicating some impairment of CO_2 assimilation capacity relative to controls as flooding stress continues.

Overall pattern of A, g_l, Ci and SWP suggests that initial reductions in growth and gas exchange parameters of sour cherries following imposition soil flooding may be caused by a decrease in stem water potential possibly due to reduced hydraulic conductivity of flooded root system. If flooding stress persists, carbon assimilation capacity is lost which supplants stomatal limitation of A. A combination of stomatal and nonstomatal limitations to A have been observed during soil flooding of blueberries (Davies and Flore, 1984a and 1984b), beans (Moldau, 1973) and citrus (Phung and Knipling, 1976). In contrast, loss of CO_2 assimilation capacity alone seems responsible for depression of A during soil flooding of apples (Childers, 1942), pecans (Smith and Ager, 1988) and sunflowers (Guy and Wample, 1984).

In experiment 2, chlorophyll content of controls and trees flooded for 2, 4 and 8 days were similar throughout the treatment and recovery period. Net CO_2 assimilation rates of trees flooded for 2 or 4 days eventually recovered to control levels, while A of trees flooded for 8 days had not recovered by the end of the experiment. Thus, it seem unlikely that loss of chlorophyll is a significant factor limiting A during short term flooding of sour cherry.

Typically, the time required for recovery of gas exchange parameters following relief of flooding increases as the flooding period

is lengthened (Kozolowski and Pallardy, 1979; Smith and Ager, 1988). Similarly, we observed in experiment 2 that if flooding treatment was short (i.e. 2-4 days) that A and g_l eventually returned to control levels. Full recovery required a period ca. 7-8 times the length of the initial flooding stress.

In experiment 4 (Repeated short term flooding), flooding effects on gas exchange parameters were exhibited only while shoots were still actively growing and ceased during the third and fourth cycles when shoot growth slowed considerably and eventually dropped to zero. Shoot growth might be related to gas exchange through internal water deficits. Cessation of shoot growth limits total canopy area and thus total transpiration which must be supported by water absorption and transport by the root system. Internal water deficits would presumably ease if the root system was not totally and permanently damaged by anaerobiosis and could accommodate limited demands placed on it by a stable canopy area. This in turn would allow stomata to reopen and A to increase. This mechanism might be lost gradually as flooding duration is increased and permanent injury spreads in the root system.

Some support for this hypothesis can be seen in the shoot/root ratios measured at the termination of this experiment. Most species have displayed an increased shoot/root ratio in response to soil flooding (Kongsgrud, 1969; Kozlowski, 1984; Olien, 1987; Tang and Kozlowski, 1982). However, we observed a reduced shoot/root ratio in flooded plants at the end of this experiment reflecting relatively greater root than shoot growth during the short treatment period. Cripps (1971) noted a similar response in apple trees subjected to soil flooding. This might be the result of compensatory root growth at the

expense of shoot growth following the short flooding treatment used. Roth and Gruppe (1985) reported substantially greater root growth in flooded cherry trees compared to controls after relief of flooding. Although final shoot/root ratios were not reported in their experiment, inspection of shoot and root incremental growth data reported seems to indicate at least a similar, if not reduced, shoot/root ratio in flooded plants compared to controls.

During experiments 2 and 4 shoot growth of all flooded trees never recovered to control levels. A number of temperate fruit species display a similar sensitivity (Andersen et al, 1984a; Olien, 1987; Rom and Brown, 1979). In contrast, shoot extension rates are maintained during even prolonged flooding in some flood tolerant bottomland species (Dickson et al, 1965) and Populus deltoides (Regehr et al, 1975).

Significant defoliation of trees in experiment 2 flooded longer than 2 days is similar to response of other flooding intolerant species (Kozolowski and Pallardy, 1984). Andersen et al (1984a) observed that peaches were completely defoliated after 8 days of flooding. In contrast, Pereira and Kozlowski (1977) noted that some flooding tolerant species retained foliage during flooding treatments as long as 37 days. Howell and Stackhouse (1973) demonstrated that early defoliation by cherry leaf spot reduced winter hardiness. Subsequent mortality of trees following chilling paralleled % defoliation observed at end of treatment period. However, it seems unlikely that hardiness of these trees could have been reduced to such a level as to cause them to succumb to the very mild chilling temperatures employed (ca. 2 ^{o}C). Nevertheless, Howell and Stackhouse's research certainly suggests that mortality might have been significantly higher had these trees been

subjected to the harsher winter conditions normally encountered in the field.

Mortality was markedly greater for trees flooded during active shoot growth than those flooded during dormancy as can be seen by comparing LD_{50}'s, e.g. 4-6 days vs a "worst case" estimate of 43 days respectively. Several authors have observed that trees subjected to flooding during active summer growth vs other times in the yearly growth cycle generally display more severe injury and mortality (Crane and Davies, 1988; Heinicke, 1932; Kozlowski, 1984; Rom and Brown, 1979). Increased sensitivity during active summer growth has been attributed to a number of possible causes including reduced CO_2 assimilation (Crane and Davies, 1988; Davies and Flore, 1986b), increased respiration of either shoot or root tissues (Rom and Brown, 1979; Davies and Flore, 1986b) and increased damage due to root rot (Crane and Davies, 1988) associated with higher air and soil temperatures or increased demand for water by the shoot system (Heinicke, 1932) during active growth.

Rowe and Catlin (1971) have demonstrated in plum, peach and apricot that production of cyanide during soil flooding through hydrolysis of cyanogenic glucosides, typically found in Prunus species (Seigler, 1975), was markedly reduced at lower soil temperatures. This reduced production of cyanide was correlated with improved survival. Alternatively, a number of toxins are produced by endogenous and exogenous sources during soil flooding, i.e. ethanol, ethylene, acetaldehyde, hydrogen sulfide, etc. (Rowe and Beardsell, 1973). Production of these materials might also be limited at low soil temperatures. Clearly more research will be required to identify the precise basis of differential sensitivity to soil flooding at different

times of the year.

Trees which survived dormant season flooding subsequently displayed A and g_l similar to controls. However, shoot growth appeared to be inversely related to duration of dormant season flooding. This is in contrast to Broadfoot (1967) observations that dormant season flooding actually improved subsequent growth of some hardwood species. Very few trees survived extended periods of flooding during active shoot growth. However, lone surviving tree of the 8 day flooding treatment displayed A and g_l similar to controls but reduced shoot growth. Whether reductions in shoot growth flollowing prolonged flooding are the result of subtle root injury, accumulation of toxins or some other mechanism will require further research.

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SECTION II

RELATIVE TOLERANCE OF VARIOUS CHERRY ROOTSTOCKS TO WATERLOGGING AND ROOTSTOCK EFFECTS ON NET CARBON ASSIMILATION, STOMATAL CONDUCTANCE AND SHOOT EXTENSION RATES OF MONTMORENCY SCIONS.

ABSTRACT

Maiden, containerized trees of Montmorency grafted onto 12 different rootstocks were flooded for 5 days during active growth and then allowed a 10 day recovery period before termination of the experiment. Rootstocks tested included Mahaleb, Mazzard, Montmorency, Colt, MxM clones 2, 39 and 60, and Giessen clones (GC) 148/1, 148/9, 195/1, 195/2 and 196/4. Nonflooded control trees displayed significant rootstock effects on net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l) and shoot extension rate when averaged over the 15 day experimental period. When compared to nonflooded controls, flooded trees displayed reductions in most growth and leaf gas exchange parameters measured including new shoot dry weight (dw), new leaf dw, shoot extension rate, leaf expansion rate, A and g_l. When compared on the basis of leaf gas exchange characteristics and shoot extension, Montmorency on MxM 2, and GC 148/1 were the most tolerant to flooding while trees on MxM 39 were the least tolerant. As a group, the rootstocks displayed a smaller range of tolerance and a more rapid onset of injury than has been reported for rootstocks of other temperate deciduous tree fruit species, e.g. apples and pears.

INTRODUCTION

Many sour cherry growers have experienced reduced longevity of orchards and trees in Michigan in recent years. Researchers at MSU have addressed this issue in attempting to identify the causal factor(s). While a number of biotic (root rots, insects, diseases, nematodes) and abiotic (soil drainage, winter damage, mechanical harvesting damage) are apparently involved, they have generally observed affected trees in conjunction with locally restrictive soils, i.e. heavy subsoils, plow pans, etc., that are prone to rootzone flooding when subjected to heavy rainfall and/or irrigation (Perry, 1982).

Temperate tree fruit species vary widely in their tolerance to soil waterlogging. Rowe and Beardsell (1973) ranked species in order of decreasing tolerance to flooding as quince > pear > apple > plum > cherry > apricot = peach = almond. Within a given species a considerable range of tolerance can often be found among available rootstocks. In a survey of apple rootstocks, Remy and Bidabe (1962) found Northern Spy to be extremely sensitive to waterlogging; M2, and M104 very sensitive; M9, and M26 moderately sensitive and M7 fairly resistant.

The two most common cherry rootstocks, seedlings of Prunus mahaleb L. and P. avium L. (Mazzard), were found by Saunier (1966) to be extremely sensitive to waterlogging. Gruppe (1982) reported that Giessen clones (GC) 172/9 (P. fruticosa x avium) and GC 173/9 (P. fruticosa x cerasus) to be more tolerant than Colt (P. avium x pseudocerasus) or Mazzard F12/1 which in turn were more tolerant than Mahaleb SL64. Observations of field performance over the years have generally noted P. cerasus cv. Stockton Morello to be considerably more

tolerant to soil flooding than Mazzard, and Mazzard to be only slightly more tolerant to excess soil moisture than Mahaleb (Coe, 1945; Day 1951; Hutchinson, 1969).

Recently, a number of relatively new rootstocks have been subjected to limited commercial trials, i.e. MxM clones (presumed natural hybrids of P. mahaleb and P. avium), P. cerasus cv. Montmorency and Colt. Neither these nor new advanced releases from breeding programs have been evaluated for tolerance to waterlogging. The purpose of this research was to evaluate the relative flooding tolerance of a number of rootstocks (Table 1.) under controlled conditions.

MATERIALS AND METHODS

On July 24, 1985, 96 maiden, tart cherry trees, (8 each of Montmorency on 12 different rootstocks) were cut back to a single unbranched stem ca. 50 cm tall and planted in 7 liter plastic containers filled with a steam sterilized soil mix (ca. 50% sandy loam, 30% sphagnum peat and 20% sand v/v). Trees were ca. 1.3 cm caliper (measured ca. 2.5 cm above graft union) and a mean fresh weight of 156 gm (after pruning). Plants were set in wooden racks (ca. 60 cm off floor) in an unshaded greenhouse at the Pesticide Research Center, MSU. Racks were then covered with aluminum foil to prevent direct solar heating of the containers. Three or four unbranched shoots were allowed to grow on each plant (all other growing points were removed as they appeared). Plants were watered regularly with a soluble fertilizer (Peters, 20-20-20 NPK) diluted to 200 ppm N until the start of flooding treatments. Pests and diseases were controlled as needed according to commercial recommendations (Mich. Ext. Bul. E154, Fruit Pesticide Handbook).

On August 12th, half the trees of each rootstock combination were flooded by placing each tree container in an 11 liter container lined with a plastic bag and filled with tap water adequate to cover the soil surface. Flooding was relieved 5 days later by allowing pots to first gravity drain for ca. 1 hour, then a vacuum pump was attached via rubber hose and a collection flask to a 2.4 cm diameter aquarium aerator that had been buried in the bottom center of each pot at planting. The pump was activated for ca. 10 minutes (typically generating a vacuum of 25–30 KPa in collection flask) which allowed the collection of an additional 300–500 ml of water and imposed a soil moisture tension of ca. 2 KPa (as measured with a Soil Moisture Equipment Corp. "Quick Draw" soil moisture probe, Model 2900F). During 5 day flooding treatment, all controls were watered to saturation as needed with tap water (ca. 1 liter) as were all treatments during 10 day recovery period which followed. Mean minimum/maximum air temperature during the treatment and recovery period was 15.6±2.3/28.0±3.7 °C.

Leaf gas exchange data was collected periodically from a randomly selected, fully expanded mid-shoot leaf on the uppermost shoot of each tree. Measurements were made with Analytical Development Co. (Hoddeston, England) portable photosynthesis equipment consisting of an Infrared CO_2 Gas Analyzer (LCA-2), Regulated Air Supply (ASU) and a Parkinson Leaf Chamber (PLC-B). Measurements were made between 1200 and 1400 hours; cuvette temperature range of ca. 25–30 °C and CO_2 concentration (ca. 350 micromol mol^{-1}). Supplemental light was provided as needed with a 400 W high pressure sodium vapor lamp to bring light levels above 1000 micromols m^{-2} s^{-1} PPF during measurements. This level of light has been shown to be above light saturation for sour cherry

Table 1. Sour cherry rootstocks[z] utilized in study.

Seedling Stocks:	Virus Free Status
Prunus mahaleb (Mahaleb)	presumed
P. avium (Mazzard)	presumed
Clonal Stocks:	
P. cerasus (Montmorency)	certified
P. avium x pseudocerasus (Colt)	certified
P. avium x mahaleb (MxM2, 39 and 60)[y]	presumed
P. cerasus x canescens (148/1 and 148/9)[x]	certified
P. canescens x cerasus (195/1 and 195/2)[x]	certified
P. canescens x avium (196/4)[x]	certified

[z] Supplied by Hilltop Corp., Hartford, MI. All grafted with P. cerasus cv. Montmorency except own-rooted Montmorency.
[y] Presumed natural hybrids
[x] Advanced selections from Giessen, W. Germany Breeding Program

(Sams and Flore, 1982). Carbon assimilation and stomatal conductance values were calculated as previously described (Moon and Flore, 1986) with the exception that leaf vapor pressure was estimated in the manner described by Richards (1971) and that sample and ambient vapor pressures were calculated as:

$$p = (RH/100) * p_s,$$

where p equals sample or ambient vapor pressure (with or without leaf within cuvette, respectively) at cuvette temperature, p_s equals leaf vapor pressure at cuvette temperature (presumed to equal saturating vapor pressure of water) and RH is the appropriate relative humidity measured within the cuvette.

Shoot length was measured on the uppermost shoot of each tree from point of origin on trunk to mid-apex. Leaf area was estimated in the manner described by Kappes (1985):

$$\text{Area} = \text{length} * \text{width} * 0.65,$$

where length is measured along midrib of expanding leaf from base of blade to tip, width is measured at the widest part of the blade and 0.65 is a correction factor for sour cherry derived by Kappes (r^2=0.998**). A single leaf (between 20 and 60 mm length) was measured per plant.

On August 29th, 10 days after relief of flooding treatments, the experiment was concluded. Trees were then separated at the graft union and partitioned into root system, trunk, new shoots and leaves. Materials were oven dried for at least 1 week at 90 ^{o}C.

A randomized complete block design was used (blocked on basis of initial fresh weight) with 4 replications of each treatment. Rootstock effects on growth and leaf gas exchange characteristics were determined by performing an analysis of variance (ANOVA) on data collected from non

flooded trees (data combined for each tree over all sampling dates during treatment/recovery period). An ANOVA was also performed for flooding treatment effects within each rootstock. In order to facilitate the comparison of the various rootstocks, in spite of obvious inherent differences in growth rates, data was standardized by expressing each flooded rootstock's performance as a percentage of it's control within each block, i.e. all controls were set to 100%. An ANOVA was then performed for rootstock effect. Statistical analysis was performed with MSTAT Microcomputer Statistical Program (Michigan State University, East Lansing, MI). Regression analyses and figures were prepared with Plotit Interactive Graphics and Statistics Package (Scientific Programming Enterprises, Haslett, MI).

RESULTS

Rootstock effects on non flooded trees. Rootstock had a marked effect on mean net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l) and shoot extension rate of Montmorency scions during this experiment (Table 2). Trees on GC 195/2 and Colt displayed the highest A, while trees on GC 148/9 and 148/1 displayed the lowest A. Pattern was similar for g_l and shoot extension. There was no apparent correlation between A, g_l or shoot extension with relative dwarfing ability of the various rootstocks; all $r^2 < .002$, ns. (data not shown).

Flooding effects. Wilting occurred on recently emerged leaves of flooded trees within 2-3 days after imposition of flooding. Symptoms often disappeared overnight and recurred whenever conditions likely to promote high vapor pressure deficits prevailed. New leaves on flooded trees were typically smaller and cupped with a dull finish compared to

Table 2. Rootstock effects on mean net CO_2 assimilation (A), stomatal conductance to CO_2 (g_l) and shoot extension rate of Montmorency scions (nonflooded trees) during treatment/recovery period.

Rootstock	Relative Size[z] (% of Mazzard Sdlg)	A (micromol m^{-2} s^{-1})	g_l (mmol m^{-2} s^{-1})	Shoot Extension (mm d^{-1})
196/4	120	9.49 abc[y]	72.7 abc	12.0 ab
195/1	110	9.09 abc	60.8 bc	8.4 bc
195/2	110	11.06 a	74.6 ab	12.2 ab
Mazzard	100	10.63 abc	72.7 abc	12.0 ab
MxM 2	100	9.25 abc	62.8 bc	9.0 bc
148/1	100	8.56 c	55.1 c	7.0 c
Colt	95	11.00 ab	81.6 a	14.9 a
MxM 60	95	9.83 abc	69.2 abc	11.4 abc
Montmorency	90	8.89 bc	63.1 bc	9.1 bc
148/9	85	8.88 bc	62.1 bc	9.6 bc
Mahaleb	80	10.32 abc	68.9 abc	10.1 bc
MxM 39	80	9.45 abc	63.6 abc	12.1 ab

[z] Compiled from Perry (1987).
[y] Values in same column followed by same letter not significantly different at 5% level, DMR test.

nonflooded controls. At end of 10 day recovery period, visible chlorosis was evident in basal leaves of flooded trees, although very little leaf abscission had occurred by that time.

Flooded trees of Montmorency on MxM 2, MxM 39 and Giessen clone (GC) 195/2 and 196/4 produced significantly less total new stem and leaf dw when compared to their respective controls (Table 3). Total, root and trunk dw was generally higher for control trees compared with their flooded counterparts although differences were not significant for any of the rootstocks tested (Table 4).

Shoot extension of flooded treatments slowed markedly within a few days after imposition of flooding (Table 5). At end of 5 day flooding treatment, shoot extension rates of most rootstocks had fallen significantly below that of their respective controls. Ten days later (after relief of flooding treatments), only those trees on MxM 2, GC 148/1, Mazzard and MxM 60 were growing at rates not significantly different from their respective controls.

Leaf expansion rates of flooded treatments slowed gradually after imposition of flooding (Table 6). By the end of the 5 day flooding treatment, only trees on Mahaleb and MxM 60 had fallen significantly below that of their respective controls. However, ten days later (after relief of flooding treatments), only those trees on GC 148/9, MxM 2, Mahaleb, MxM 60 and GC 195/1 displayed leaf expansion rates not significantly different from their respective controls.

Stomatal conductance to CO_2 and net CO_2 assimilation of flooded trees generally declined slowly over the first 2-3 days of flooding and then dropped rapidly on most rootstocks (Tables 7 and 8, respectively). At end of 10 day recovery period, flooding had significantly reduced g_l

Table 3. Flooding effects on total new shoot and leaf dry weight (at end of treatment/recovery period) of Montmorency on various rootstocks.

	Shoot dw (g)			Leaf dw (g)		
Rootstock	Control	Flooded	% of Control	Control	Flooded	% of Control
Mahaleb	1.73	1.68	97	5.75	5.31	92
Mazzard	2.50	1.38	55	6.34	4.30	68
Montmorency	1.39	1.22	88	4.49	3.96	88
Colt	3.06	1.68	55	8.46	6.24	74
MxM 2	1.32	0.74	56*[z]	3.94	2.67	68*
MxM 39	1.67	0.83	50*	4.82	2.72	56*
MxM 60	2.76	1.29	47	6.87	3.91	57
148/1	1.20	0.86	72	4.18	3.51	84
148/9	1.41	1.10	78	4.43	3.96	89
195/1	1.42	1.10	70	4.43	3.96	73
195/2	2.10	1.02	49**	5.65	3.66	65*
196/4	1.71	0.86	50**	5.67	3.42	60**

[z] Significance of difference between control and flooded treatments within each rootstock and component dw indicated at the 5% (*) or 1% (**) levels, otherwise nonsignificant, F test.

Table 4. Flooding effects on root, trunk and total[z] dry weight of sour cherry trees (Montmorency grafted onto various rootstocks).

	Root dw (g)		Trunk dw (g)		Total dw (g)	
Rootstock	Control	Flooded	Control	Flooded	Control	Flooded
Mahaleb	65.7	62.8	19.3	17.8	92.5	87.5
Mazzard	51.4	48.3	22.5	22.8	82.7	76.8
Montmorency	50.8	51.4	21.2	22.1	77.8	78.7
Colt	62.5	61.7	28.3	18.0	102.4	87.6
MxM 2	35.1	51.2	14.2	20.3	54.6	74.9
MxM 39	36.7	34.5	19.9	15.4	63.1	53.5
MxM 60	91.6	83.4	38.9	49.6	140.2	138.3
148/1	50.1	52.7	41.1	35.8	96.5	92.8
148/9	30.5	27.2	15.1	17.4	52.1	49.6
195/1	33.5	29.7	14.3	15.4	54.1	49.6
195/2	41.5	43.9	19.5	18.1	68.8	66.7
196/4	54.6	50.7	16.8	22.8	78.7	77.7

[z] Calculated as total=root+trunk+shoot+leaf

Table 5. Flooding effects on shoot extension rate[z] of Montmorency scions on various rootstocks.

Rootstock	Days after start of flooding[y] 1	2	3	4	5	15	Mean Rate of Control[x] (cm/day ±sd)
Mahaleb	150	112	72*[w]	32*	44	42**	1.01 ± 0.43
Mazzard	126	84	69	40**	25**	40	1.20 ± 0.39
Montmorency	114	102	81	48*	25**	34**	0.91 ± 0.41
Colt	56	61	50	34**	43*	37*	1.49 ± 0.56
MxM 2	107	69	55	51	69	80	0.90 ± 0.36
MxM 39	100	32*	30*	12**	14*	9**	1.21 ± 0.41
MxM 60	89	67	42	23*	21**	33	1.14 ± 0.42
148/1	115	119	117	80	85	78	0.70 ± 0.49
148/9	166	52	56	31	31	18*	0.96 ± 0.48
195/1	85	121	60	24*	37	3*	0.84 ± 0.38
195/2	98	56	70	39	31**	5**	1.22 ± 0.46
196/4	92	82	57	42*	50*	19**	1.34 ± 1.25

[z] Expressed here as % of mean control rate on each date.
[y] Flooding imposed on evening of day 0, relieved on evening of day 5; experiment terminated on day 15.
[x] Mean of 36 measurements: 4 reps each on day 0,1,2,3,4,5,8,11 and 15 of experiment.
[w] Significance of difference between control and flooded treatments within each rootstock indicated at 5% (*) and 1% (**) levels, otherwise nonsignificant, F test.

Table 6. Flooding effects on leaf expansion rate[z] of Montmorency scions on various rootstocks.

Rootstock	Days after start of flooding[y] 1	2	3	4	5	15	Mean Rate of Control[x] (cm^2/day ±sd)
Mahaleb	77	74	74	32*[w]	25*	44	2.30 ± 1.07
Mazzard	55*	81	63	44	55	35**	2.62 ± 1.24
Montmorency	102	60	59*	38**	39	20*	1.81 ± 1.03
Colt	57	57	53	84	60	54*	2.99 ± 1.46
MxM 2	46	56	79	66	56	66	1.75 ± 0.93
MxM 39	44	63	40	31	69	3**	2.07 ± 0.81
MxM 60	96	57	81	18*	17**	30	2.18 ± 1.03
148/1	184	65	65	25	33	0**	1.45 ± 0.73
148/9	128	107	100	45	43	90	1.83 ± 1.21
195/1	82	60	68	61	71	36	1.56 ± 0.80
195/2	90	66	70	44	88	21*	2.05 ± 0.75
196/4	114	65	52	30*	52	14*	2.16 ± 0.98

[z] Calculated as Area=length*width*0.65 (r^2=.998**, Kappes, 1985), expressed here as % of mean control rate on each date.

[y] Flooding imposed on evening of day 0, relieved on evening of day 5; experiment terminated on day 15.

[x] Mean of 28 measurements: 4 reps each on day 0,1,2,3,4,5 and 15 of experiment.

[w] Significance of difference between control and flooded treatments within each rootstock indicated at 5% (*) and 1% (**) levels, otherwise nonsignificant, F test.

Table 7. Reduction of stomatal conductance[z] (g_l) in leaves of Montmorency scions on various rootstocks during five days of flooding and 10 days after relief.

Rootstock	Days after start of flooding[y] 1	2	3	4	5	15	Mean control g_l[x] (mmol m^{-2} s^{-1} ±sd)
Mahaleb	104	89	80	49	29*[w]	66*	68.9 ± 22.3
Mazzard	106	114	124	86	53	44**	72.7 ± 20.3
Montmorency	108	86	85	69	69	46	63.1 ± 19.8
Colt	100	83	107	36*	37*	60*	81.6 ± 19.8
MxM 2	105	93	70*	110	40**	65	62.8 ± 27.5
MxM 39	72	70	73**	60	59	19*	63.6 ± 22.0
MxM 60	99	108	95	90	34*	26*	69.2 ± 20.5
148/1	67	75	84	73	46*	68	55.1 ± 17.5
148/9	103	92	88	48	11*	25*	62.1 ± 26.3
195/1	87	77	87	55*	58	16**	60.8 ± 19.3
195/2	91	87	77*	60	42	15*	74.6 ± 23.5
196/4	79	65	99	54	62	18*	65.6 ± 15.0

[z] Expressed here as % of mean control rate on each date.
[y] Flooding imposed on evening of day 0, relieved on evening of day 5; experiment terminated on day 15.
[x] Mean of 36 measurements: 4 reps each on day 0,1,2,3,4,5,8,11 and 15 of experiment.
[w] Significance of difference between control and flooded treatments within each rootstock indicated at 5% (*) and 1% (**) levels, otherwise nonsignificant, F test.

Table 8. Reduction of net CO_2 assimilation[z] (A) in leaves of Montmorency on various rootstock during five days of flooding and 10 days after relief.

Rootstock	Days after start of flooding[y] 1	2	3	4	5	15	Mean control A[x] (micromol m^{-2} s^{-1} ±sd)
Mahaleb	99	90	71	59*[w]	28*	73	9.49 ± 2.87
Mazzard	111	109	103	84	52*	56**	10.63 ± 2.06
Montmorency	105	110	97	65	43**	31*	8.89 ± 2.82
Colt	100	92	94	39**	20**	61	11.00 ± 2.02
MxM 2	94	86	82*	49	48	71	9.80 ± 2.99
MxM 39	84	76	75	57**	33**	18*	9.45 ± 3.38
MxM 60	99	104	94	73	37**	32**	9.83 ± 2.37
148/1	92	92	95	57*	51*	52*	8.56 ± 3.27
148/9	103	95	110	48	24*	21*	8.88 ± 3.24
195/1	97	83	89	42**	25**	19**	9.09 ± 2.42
195/2	95	85	90	39*	21*	19*	11.06 ± 2.87
196/4	94	79	93	46*	31**	12**	9.49 ± 2.17

[z] Expressed here as % of mean control rate on each date.
[y] Flooding imposed on evening of day 0, relieved on evening of day 5; experiment terminated on day 15.
[x] Mean of 36 measurements: 4 reps each on day 0,1,2,3,4,5,8,11 and 15 of experiment.
[w] Significance of difference between control and flooded treatments within each rootstock indicated at 5% (*) and 1% (**) levels, otherwise nonsignificant, F test.

of Montmorency on all rootstocks except MxM 2, GC 148/1 and Montmorency; while A was significantly depressed on all rootstocks except MxM 2, Mahaleb and Colt. Net CO_2 assimilation was correlated with g_l throughout experiment for flooded and control trees (Figure 1), r^2=0.862** and 0.615**, respectively (slopes significantly different at 1% level, t test). Net CO_2 assimilation was also correlated with shoot extension rate (Figure 2), r^2=0.590** and 0.131** for flooded and control trees, respectively (slopes significantly different at 1% level, t test).

When A and net shoot extension data was analyzed as percent of control response several rootstocks stood out (Table 9). Flooded trees of Montmorency on MxM 2 fixed CO_2 significantly more like their control counterparts than did trees on MxM 39, GC 195/1 or GC 196/4. Net shoot extension (during the treatment/recovery period) of flooded trees on MxM 2 and GC 148/1 was significantly more like that of their control counterparts than it was for flooded trees on MxM 39.

Discussion

Very few reports of rootstock effects on photosynthetic rates of scion leaves have appeared in the literature. Ferree and Barden (1971) observed higher A in 'Delicious' strains grafted to seedling apple rootstocks vs dwarfing. However, Marro and Cerghini (1976) observed higher A of 'Richared Delicious' scions grafted on M9 vs seedling, and Titova and Shiskanu (1976) reported higher rates in leaves of dwarfing apple rootstocks vs those of seedlings. In contrast, Barden and Ferree (1979) reported no difference in A of 'Delicious' trees on seedling and dwarfing rootstocks. In this study we observed significant differences

Figure 1. Relationship between A and g_1 of flooded and nonflooded sour cherry trees (Montmorency on 12 different rootstocks). Each point represents mean of 4 replications of each rootstock for each flooding treatment and date of sampling.

FIGURE 1

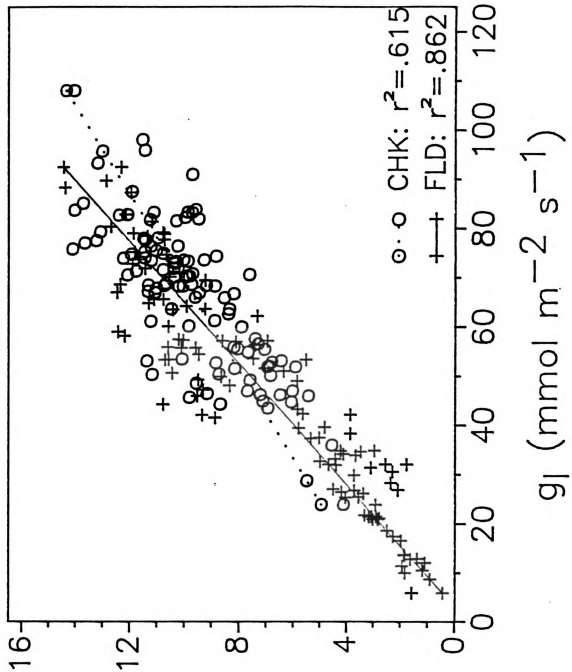
A (μmol m⁻² s⁻¹)
gl (mmol m⁻² s⁻¹)
o·o CHK: r²=.615
+—+ FLD: r²=.862
0
4
8
12
16
0
20
40
60
80
100
120

Figure 2. Relationship between A and shoot extension rate of flooded and nonflooded sour cherry trees (Montmorency on 12 different rootstocks). Each point represents mean of 4 replications of each rootstock for each flooding treatment and date of sampling.

FIGURE 2

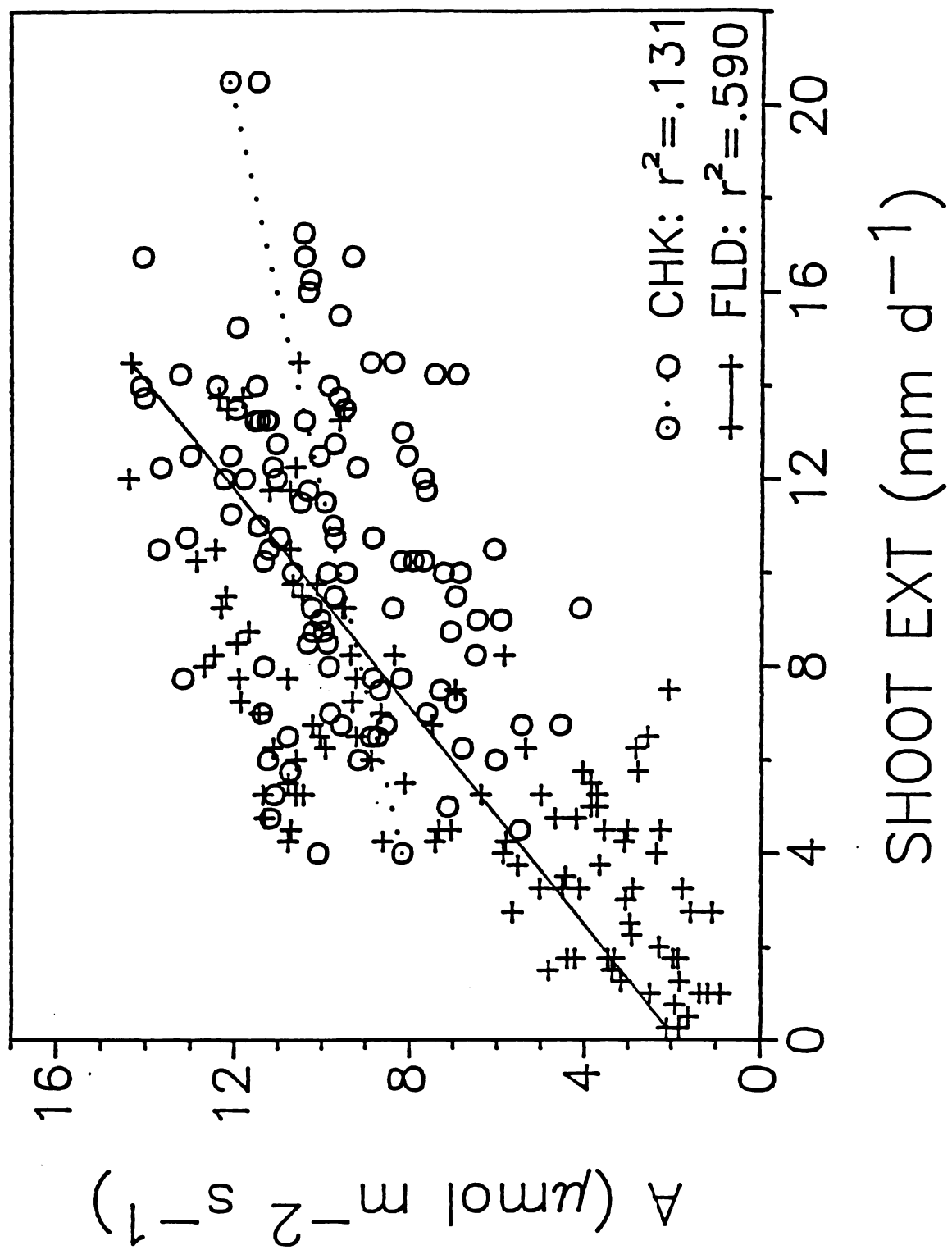
A (μmol m⁻² s⁻¹)
16
12
8
4
0
0
4
8
12
16
20
SHOOT EXT (mm d⁻¹)
o o CHK: r²=.131
+—+ FLD: r²=.590

Table 9. Rootstock effects[z] on net CO_2 assimilation 10 days after relief of flooding and net shoot extension during 15 day flooding/recovery period.

Rootstock	Net CO_2 Assimilation (% of Control)	Net Shoot Extension (% of Control)
MxM 2	75 a[y]	60 a
Mahaleb	68 ab	55 ab
Colt	62 abc	41 abc
148/1	52 abcd	60 a
Mazzard	49 abcd	49 ab
Montmorency	33 abcd	36 abc
MxM 60	27 bcd	34 abc
148/9	23 cd	35 abc
195/2	21 cd	31 abc
195/1	17 d	33 abc
196/4	15 d	31 abc
MxM 39	15 d	21 bc

[z] ANOVA performed on flooded treatment response expressed as % of respective control within each block.

[y] Values in same column followed by same letter not significantly different at the 5% level, DMR test.

in A of 'Montmorency' scions grafted onto a number of cherry rootstocks differing substantially in dwarfing ability. However, there was no apparent correlation between A and reported relative dwarfing ability of these rootstocks.

Lack of any correlation between shoot extension rates and relative tree size at maturity is not surprising in light of reports by Hutchinson and Upshall (1964) and Westwood (1978) that young cherry trees on Mahaleb often grow more vigorously than on Mazzard even though final tree size is usually larger on Mazzard. Additionally, in rootstock tests in Washington (Webster, 1980) and Michigan (Perry, unpublished) trees on Colt have grown as vigorously as trees on other rootstocks generally regarded as more vigorous than Colt. Evidently growth rate of each scion/rootstock combination adjusts differentially as trees mature and cropping begins.

Overall visual impressions of tree response to flooding were similar to those reported by other researchers working with temperate fruit species (Andersen et al, 1984a; Childers and White, 1942 and 1950; Crane and Davies, 1988; Heinicke, 1932, Rom and Brown, 1979). Wilting symptoms suggest an increased internal water deficit which could be caused by a reduction in water conduction by the root system. One possible explanation is loss of root surface due to attack by soil pathogens encouraged by soil flooding, i.e. Phytophthora root rot. We did not test for presence of Phytophthora spp. in this experiment, however, in a similar study in which sour cherry trees (Montmorency/Mahaleb) were subjected to repeated short term flooding we were unable to isolate Phytophthora from any plot (Beckman, in preparation).

Alternatively, the inability of the root system to supply water to the shoot might be due to a decrease in root hydraulic conductivity after imposition of anaerobic conditions. Although not measured in this experiment, we have verified that oxygen diffusion rates (ODR) typically fall below 0.2 within a few hours after imposition of soil flooding in the soil mix used in this experiment. ODR rises to nearly 0.4 immediately following drainage and pumping; ultimately returning to control levels (ca. 0.6) within 2-3 days (Beckman, in preparation). Levels below 0.2 have been correlated with reduced hydraulic conductivity and/or growth in pear and peach (Andersen et al, 1984a); blueberry (Crane and Davies, 1988); and apple (Olien, 1987).

Although treatment/recovery period represented ca. 80% of total time period for shoot growth, reductions in total new shoot and leaf dw due to flooding were small on most rootstocks, including Mahaleb, a rootstock generally regarded as very sensitive to flooding. Flooded trees on Mahaleb displayed a significant reduction in shoot extension rate throughout most of the experimental period and one would expect a reduction in shoot and leaf dw as a consequence. Lack of a correlative reduction in shoot and leaf dw might be a result of variability in shoot growth rate within a tree, i.e. shoot extension rate was measured on only the uppermost shoot in each tree, and suggests the necessity of either training experimental trees to a single shoot or measuring shoot extension on all shoots.

Shoot extension and leaf expansion data displayed essentially the same trends in response to flooding. However, significant differences detected in shoot extension did not always coincide with those detected in leaf expansion perhaps because leaf expansion was measured on a

lateral shoot rather than the uppermost shoot utilized for shoot extension and, thus, may reflect differential growth rates of the various plant parts.

Higher correlation coefficient and steeper slope of the A vs g_l regression line for flooded vs control trees during this experiment suggests the possibility that stomatal closure limits photosynthesis during soil flooding. However, in other experiments we have estimated stomatal limitations from CO_2 response curve and found very similar limitations in both control and flooded trees of Montmorency/Mahaleb throughout a five day flooding treatment (Beckman, in preparation). Perhaps this correlation indicates not so much a stomatal limitation to photosynthesis as a photosynthetic regulation of stomatal aperture. A number of possible mechanisms for this have been discussed by Farquhar and Sharkey (1982) and Smith and Ager (1987).

We might speculate that the higher correlation and steeper slope of the A vs shoot extension regression line for flooded trees may be the result of different source-sink relationships in the two treatments. Although not measured in this experiment, we would expect distinctly root growth rates in the two treatments. Stolzy and Letey (1964) have demonstrated that root function ceases at O_2 diffusion rates (ODR) below 0.3 micrograms O_2 cm^{-2} min^{-1} and that root death occurs at ODR's below 0.2; levels which we presume to have attained in this experiment (Beckman, in preparation) . Thus, if virtually all root growth has ceased in the flooded treatments then shoot growth becomes the primary sink for photosynthates. Conversely, in control trees, it seems reasonable to assume that both shoots and roots serve as important sinks for photosynthates. Therefore, one would expect a better correlation

between A and shoot growth in flooded trees where shoot growth represents a relatively better estimate of total sink strength than in control trees where we have not taken into account the possibly strong sink strength of the roots.

Flooding tolerant woody species generally maintain growth and stomatal aperture during flooding better than intolerant species. This has been observed in Pyrus and Cydonia species (Andersen et al, 1984a); Salix and Eucalyptus species (Pereira and Kozlowski, 1977); Citrus species (Phung and Knipling, 1976) and Populus deltoides (Regehr et al, 1975). MxM 2 and GC 148/1 were the only rootstocks for which shoot extension rates did not fall significantly below their respective controls throughout the course of this experiment. No rootstock included in this study maintained both stomatal conductance and net CO_2 assimilation near control levels at all sample dates. However, differences were statistically significant on fewer occasions for trees on MxM 2, GC 148/1 and Montmorency.

During the growing season, flooding is likely to be of relatively short duration in most orchards since growers will typically avoid extremely poorly drained sites for cherries. Therefore, ability to recover from temporary waterlogging should be a more useful criteria for selecting superior rootstocks than ability to survive long periods of flooding. With this consideration in mind and the data summarized in Table 9 we have tentatively ranked the twelve rootstocks included in this study for relative flooding tolerance (Table 10). We have some limited field experience with MxM 2 indicating that it may provide superior performance compared to Mahaleb or Mazzard on sites with heavy soils prone to transient soil flooding (Perry, unpublished).

Table 10. Relative flooding tolerance of various containerized sour cherry rootstocks under greenhouse conditions.

Moderately Tolerant	Sensitive	Very Sensitive
MxM 2	Mahaleb	196/4
	148/1	MxM 39
	Colt	
	Mazzard	
	Montmorency	
	MxM 60	
	148/9	
	195/1	
	195/2	

We must caution, however, that in this ranking considerable overlap occurs from one class to the next. Moreover, the range of tolerance exhibited in these rootstocks does not appear to be nearly as wide as that observed in other temperate fruit species, most notably pears in which some rootstock species can maintain shoot growth and stomatal conductance near control levels for up to 30 days of flooding (Andersen et al, 1984a and 1984b). Additionally, our rankings fail to differentiate between Mahaleb and Mazzard in flooding tolerance which is contrary to observations of field performance through the years (Coe, 1945; Day, 1951; Hutchinson, 1969). This might be due to the age of the trees utilized in this study. Older trees generally tolerant flooding much better than young trees of the same species (Kozlowski, 1984) suggesting that differences between these species may be too small at one year of age to be detected in our experiment.

Alternatively, field grown trees may have available to them mechanisms for tolerating or "escaping" flooding that cannot be expressed when the entire root system is flooded as in this experiment. Mazzard's root system is typically more horizontal and spreading than Mahaleb's (Coe, 1945; Day, 1951). Therefore, a perched water would typically inundate a relatively smaller portion of a Mazzard root system than a deep rooted Mahaleb root system. Work by Roth and Gruppe (1985) and ourselves (Beckman, unpublished) in which the entire rootzone was never completely flooded (or flooded for only a part of each day), has demonstrated that cherry rootstocks are considerably more tolerant in terms of both growth and survival than when subjected to treatments like those used in this experiment. This response may be due to some escape mechanism, i.e. compensatory root growth, or perhaps increased water

conduction, growth regulator production or detoxification of anaerobic products by the nonflooded portion of the plant's root system.

Some support for compensatory root growth as an escape mechanism can be found in the literature. In an experiment in which half of a cherry tree's root system was continuously flooded and the other half flooded only 12 hours each day Roth and Gruppe (1985) observed a marked increase in root growth in the intermittently flooded portion of the root system compared to nonflooded controls. At the same time, root growth dropped to near zero in the continuously flooded portion of the root system. Following relief of the flooding regime, root growth of the entire root system increased markedly compared to controls. This response was more pronounced in Mazzard F12/1 and Colt than Mahaleb SL64, especially when flooding regime was imposed late in the season. Mendoga (1987) observed a differential response in root and shoot growth of Montmorency on seedling Mazzard and Mahaleb rootstocks subjected to an interposed high bulk density soil layer in a containerized study. Both rootstocks produced similar shoot dw and displayed a similar rooting pattern when the interposed layer was the same bulk density as the remaining soil volume (ca. 1.0 gm/cc). However, when a high bulk density layer (ca. 1.7 gm/cc) was interposed, the response of the two rootstocks was markedly different. Shoot dw was significantly reduced on both rootstocks, but markedly more so on Mahaleb than Mazzard. The total number of roots was reduced by more than 50% on Mahaleb and by only 10% on Mazzard. Furthermore, ca. 10% of Mazzard's roots successfully penetrated the barrier layer while all of Mahaleb's were confined to the upper layer. In another study, Beckman (1984) demonstrated Mazzard's superiority over Mahaleb in regenerating roots

lost through root pruning. This effect was evident only during active shoot growth and disappeared at other times of the year. These observations indicate Mazzard's advantages over Mahaleb in exploiting the available soil volume favorable for root growth when confronted with a soil stress and correlate well with observed field performance of these two rootstocks in heavy soils (Coe, 1945; Day, 1951; Hutchinson, 1969). This area is clearly deserving of more research.

There appears to be no consistent relationship between flooding tolerance and parentage exhibited by the rootstocks examined in this survey. For example, rootstocks with P. avium parentage, i.e. Mazzard, Colt, MxM clones and GC 196/4, are present in each of the four classifications even though P. avium (Mazzard) is generally regarded as moderately tolerant of flooding. An analogous point can be made for those rootstocks with P. mahaleb or P. cerasus parentage. However, with the exception of GC 148/1, those rootstocks with P. canescens parentage, i.e. GC 148/8, 195/1, 195/2 and 196/4, generally fell into the bottom two rankings, which is in agreement with the observation by Gruppe (personal communication, cited in Perry, 1987) that hybrid rootstocks with P. canescens parentage are generally very sensitive to flooding.

In summary, all rootstocks were affected negatively by the short flooding treatment utilized in this experiment, however, MxM 2 was generally the least sensitive and clearly superior to MxM 39 in most parameters. Due to its simplicity and the short time required to generate significant flooding effects, the methodology employed in this experiment may prove useful as an initial screen for flooding tolerance.

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SECTION III

SHORT-TERM FLOODING EFFECTS ON GAS EXCHANGE CHARACTERISTICS OF SOUR CHERRY TREES (*PRUNUS CERASUS* L. CV. MONTMORENCY/*P. MAHALEB* L.)

ABSTRACT

Soil flooding of containerized sour cherry trees (Prunus cerasus L. cv. Montmorency/P. mahaleb L.) significantly reduced net carbon assimilation (A) within 24 hr of flooding although differences were not uniformly significant through day 2 of flooding. Net CO_2 assimilation (A) of flooded trees declined to 32% that of controls after 5 days of flooding. Residual conductance to CO_2 (g_r') responded in a manner very similar to A. Stomatal conductance to CO_2 (g_1) gradually declined in flooded trees but differences were never significant during the 5 day treatment period. Intercellular CO_2 (Ci) was initially depressed slightly in flooded trees. As flooding continued, Ci of flooded trees gradually rose above that of controls, however differences were never significant. Apparent quantum efficiency was reduced after 24 hrs of flooding and continued to decline throughout the flooding period to 52% that of controls. Dark respiration of flooded trees increased significantly within 24 hrs to 166% that of controls. Dark respiration of flooded trees remained greater than that of controls from day 2-5 but differences were not significant. In a second experiment, CO_2 response curves were interpreted within the framework of recent models of leaf gas exchange and indicated that the various stomatal and nonstomatal factors limiting A in flooded sour cherries changed in their relative importance as flooding persists.

INTRODUCTION

Herbaceous and woody plants subjected to soil flooding generally display reduced stomatal conductance, often in conjunction with reduced CO_2 assimilation (Bradford, 1983a; Davies and Flore, 1986a; Phung and Knipling; 1976). Decline in g_s is not usually accompanied by a drop in leaf water potential (Bradford and Hsiao; 1982; Jackson et al., 1978; Pereira and Kozlowski, 1977; Tang and Kozlowski, 1982), however, there are some reports of an opposite effect (Kramer and Jackson, 1954; Wadman-van Schrovendijk and van Andel, 1986). Reductions in A have variously been shown to be due to stomatal and/or mesophyll limitations (Davies and Flore; 1986a, 1986b and 1986c; Moldau, 1973; Phung and Knipling, 1976, Smith and Ager, 1988).

Our recent investigations (Beckman et al., in preparation) have shown that soil flooding may cause a reduction in A of sour cherry scions through a combination of stomatal and nonstomatal limitations, and that the relative importance of each seems to change as flooding persists.

Models of leaf gas exchange have been developed which allow critical evaluation of the presence and relative contribution of some of these proposed mechanisms to limitation of A in stressed plants (Blackman, 1905; Farquhar and Sharkey, 1982; Farquhar and von Caemmerer, 1982; Farquhar et al., 1980; Gaastra, 1959; Jones, 1973; von Caemmerer and Farquhar; 1981). The purpose of this series of experiments was to characterize the effects of soil flooding on sour cherries under controlled conditions and determine the extent to which some of these mechanisms operate in this species.

MATERIALS AND METHODS

Plant Materials. On September 24th, 1987, dormant budded sour cherry trees (Montmorency/Mahaleb) were planted in 7 liter plastic containers filled with a steam sterilized mineral soil mix (ca. 50% sandy loam, 30% spaghnum peat and 20% sand v/v). Trees were placed in a shaded greenhouse (ca. 60% full sun) at the Pesticide Research Center, MSU and watered every other week with a soluble fertilizer (Peters 20-20-20 NPK) diluted to 200 ppm N, otherwise as needed with tap water. Trees were trained to a single unbranched stem. Mean minimum/maximum temperatures during the pretreatment period were 20±1/26±2 °C. Pests and diseases were controlled as needed according to commercial recommendations (Mich. Ext. Bul. E154, Fruit Pesticide Handbook).

Experiment 1: Diurnal response. Selected trees were brought from the greenhouse to the lab January 5th; the evening before the start of experiment. All plants had ceased active shoot growth several weeks before (mean height ca. 70 cm). Plants were placed in a walk-in growth chamber (Conviron Model PGV36) set on a 12 hour photoperiod (800-2000 hr; light provided by bank of cool white fluorescent and incandescent bulbs suspended above plants), day/night temperature of 25/20 °C, and relative humidity of ca. 50%.

A randomly selected, fully expanded leaf (ca. 5-6 weeks old) in the upper half of each tree was sealed in an environmentally controlled plexiglass chamber (Sams and Flore, 1982). Gas exchange measurements were made every 2 hours (from 900 to 1700 hr) using an open gas-exchange system with an Analytical Development Co. (Hoddeston, England) infrared (IR) gas analyzer (Model 225-MK3) and 2 General Eastern (Watertown, MS) dew point hygrometers (Model 1100). Air flow and gas composition

through individual leaf chambers was controlled with a Matheson (Joliet, IL) Multiple Dyna Blender (Model 8219) equipped with mass flow controllers. Air entering leaf chambers was preconditioned for humidity control by saturating the chamber air stream with water at a set temperature, lower than the temperature of the leaf chamber heat exchanger.

Gas exchange measurements were made within optimum environmental conditions for sour cherries (Sams and Flore, 1982): photosynthetic photon flux (PPF), 1000 micromols m^{-2} s^{-1}; leaf temperature, 25 °C; ambient CO_2, 340-360 micromol mol^{-1} and leaf to air vapor pressure deficit (VPD) of 1.0-1.5 kPa. Flow rate through individual chamber was ca. 3 liter min^{-1}. Carbon assimilation and conductance values were calculated as described previously (Moon and Flore, 1986).

Plants were flooded at hour 2300 of day 0 (January 6) by placing 7 liter tree containers inside a 12 liter bucket which was then filled slowly with 20-22 °C tap water sufficient to cover the soil surface ca. 2 cm deep. Oxygen diffusion rates (ODR) were not measured in this experiment but we have previously verified that ODR typically falls to ca. 0.25 micrograms O_2 cm^{-2} s^{-1} within a few hours after flooding in the media used (Beckman et al., in preparation). Throughout experiment, control trees were watered with tap water whenever soil moisture tension exceeded -20 KPa as measured with a Soil Moisture Equipment Corp. "Quick-Draw" soil moisture probe (Model 2900F), inserted ca. 10 cm into the soil midway between center of pot and rim.

Apparent quantum yield was calculated from light response curves (data collected between 1500 and 1700 hours on day 0, between 1100 and 1300 hours on day 1 and between 1700 and 1900 hours on day 2-5). Light

levels were adjusted in 6 steps from 1000 to 0 micromols m^{-2} s^{-1}. Light levels between 1000 and 200 micromols m^{-2} s^{-1} were obtained by either adjusting height of light bank above plants or turning off sets of fluorescent and incandescent lights (in equal proportions). Levels below 200 micromols m^{-2} s^{-1} were then attained by placing various neutral density filters over chambers. Dark respiration was measured by turning off all lights in the chamber. Leaves were allowed to equilibrate for 10-15 minutes at each light level prior to gas exchange readings. Quantum yields were estimated by differentiating the fitted light response curves (dA/dPPF) and evaluating the resulting equations at 100 micromol m^{-2} s^{-1} PPF. Since light levels were measured as incident light upon the leaf and not as absorbed this was reported as "apparent" quantum yield. Light compensations points were estimated by solving the fitted light response curves for PPF at A=0 micromols CO_2 m^{-2} s^{-1}.

Experiment 2: CO_2 Response. In a second experiment, selected sour cherry trees were brought from the greenhouse to the lab on January 17th and placed under 400W high pressure sodium vapor lamps in a hood (mean temp 23 °C, relative humidity 20-30%, photosynthetic photon flux (PPF) at mid-shoot ca. 900 micromols m^{-2} s^{-1} (12 hour photoperiod, 800-2000 hr). Flooding was imposed the evening of day 0 (January 17) as described above and CO_2 response determined 2 and 5 days later by placing plants in walk-in growth chamber (ca. 900 hr) under conditions described in Experiment 1 except for CO_2 concentration and VPD imposed within individual leaf chambers.

Plants were allowed to equilibrate for 1-2 hours at ca. 350 micromol mol^{-1} CO_2 and VPD of 2.0 KPa. CO_2 concentration was adjusted

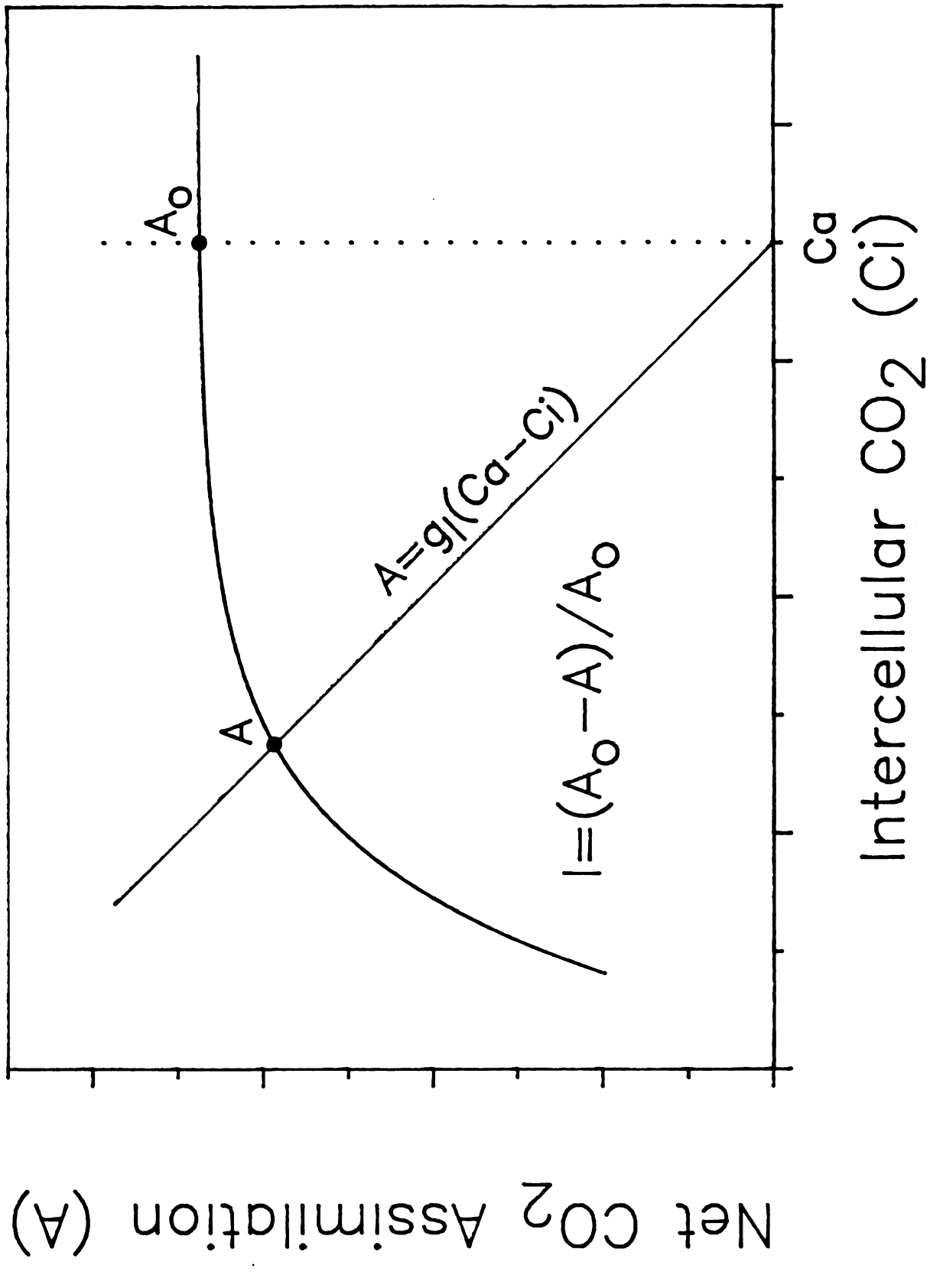
by adding CO_2 from a standard tank (5%) to air stream that had been scrubbed of CO_2 using soda lime (Sams and Flore, 1982). Proportions of each component were controlled by a Matheson (Joliet, IL) Multiple Dyna Blender, Model 8219, equipped with mass flow controllers. CO_2 concentration was increased in 6 steps from ca. 70-625 micromol mol^{-1} and was monitored on the reference side of the system using a portable Analytical Development Co. (Hoddeston, England) IR gas analyzer (Model LCA-2). CO_2 depletions rates were allowed to stabilize 15-30 minutes at each CO_2 concentration before data collection. CO_2 response curves were determined between 1030-1230 hr on day 1 and between 1100-1330 on day 5. CO_2 compensation points were estimated from fitted CO_2 response curves (i.e. curves were extrapolated and solved for ambient CO_2 concentration at A=0 micromol CO_2 m^{-2} s^{-1}).

Stomatal limitations to A were estimated from A vs Ci data in the manner suggested by Farquhar and Sharkey (1982). Supply curves (solid line in Figure 1) for flooded and control trees were calculated as $A=g_l(Ca-Ci)$; where A=net CO_2 assimilation rate, g_l=stomatal conductance to CO_2 (estimated by evaluating g_l vs Ca regression equations at Ca=363 and 348 micromol mol^{-1} for day 2 and 5, respectively), and Ca and Ci=volume fractions of CO_2 in air (ambient CO_2) and inside leaf (intercellular CO_2), respectively. Stomatal limitations were then estimated as $l=(A_o-A)/A_o$; where A_o=assimilation rate that would occur if resistance to CO_2 diffusion were zero, i.e. intersection of vertical dotted line at Ci=Ca with fitted A vs Ci curve, A=actual assimilation rate at Ca, i.e. intersection of supply curve with fitted A/Ci curve.

Experiment 3: Vapor Pressure Deficit Response. In a third experiment, selected sour cherry trees were brought to the lab on

Figure 1. Typical relationship of net CO_2 assimilation (A) and intercellular CO_2 (Ci). Curve represents "demand function" in a leaf. Solid line represents "supply function". Dotted vertical line represents the "supply function" if resistance to CO_2 diffusion were zero. Point A_o on figure represents assimilation rate that would occur if there were no stomatal limitation to CO_2 diffusion, while point A represents actual assimilation rate. Stomatal limitation to net CO_2 assimilation is calculated by the formula indicated (after Farquhar and Sharkey, 1982).

FIGURE 1


Net CO_2 Assimilation (A)
Intercellular CO_2 (Ci)
A_o
Ca
A
$A=g_l(Ca-Ci)$
$l=(A_o-A)/A_o$

January 23rd and placed in a hood as described for Experiment 2. Flooding was imposed in the evening of day 0 (January 23) and VPD response determined 2 and 5 days later by placing plants in walk-in growth chamber under conditions described in Experiment 1 except for VPD, flow rate and leaf temperature imposed within individual leaf chambers. Plants were initially allowed to stabilize for 1 hour at 1 kPa VPD (Flow rate of 3.0 liter min^{-1} and leaf temp of 27 ^{o}C). VPD was calculated as:

$$VPD=p_l-p_s,$$

where p_l equals leaf vapor pressure at cuvette temperature (presumed to equal the saturation vapor pressure of water) and p_s equals vapor pressure of air exiting leaf chamber. All vapor pressures were calculated in the manner of Goff and Gratch (1946). Vapor pressure deficit was varied from ca. 0.7 to 3.0 kPa by changing either the dew point of air entering chamber or by adjusting the flow through individual chambers (or a combination of both). VPD's above 2.5 kPa were attained by raising leaf temperature to ca. 29 ^{o}C. Leaves were allowed to stabilize at each setting for ca. 15-20 minutes before data collection.

A completely randomized design was used in all experiments with two replications of the two treatments: flooded and unflooded trees. Fitted curves were calculated with Plotit Interactive Graphics and Statistics Package (Scientific Programming Enterprises, Haslett, MI). Mean separations were accomplished with t tests.

RESULTS AND DISCUSSION

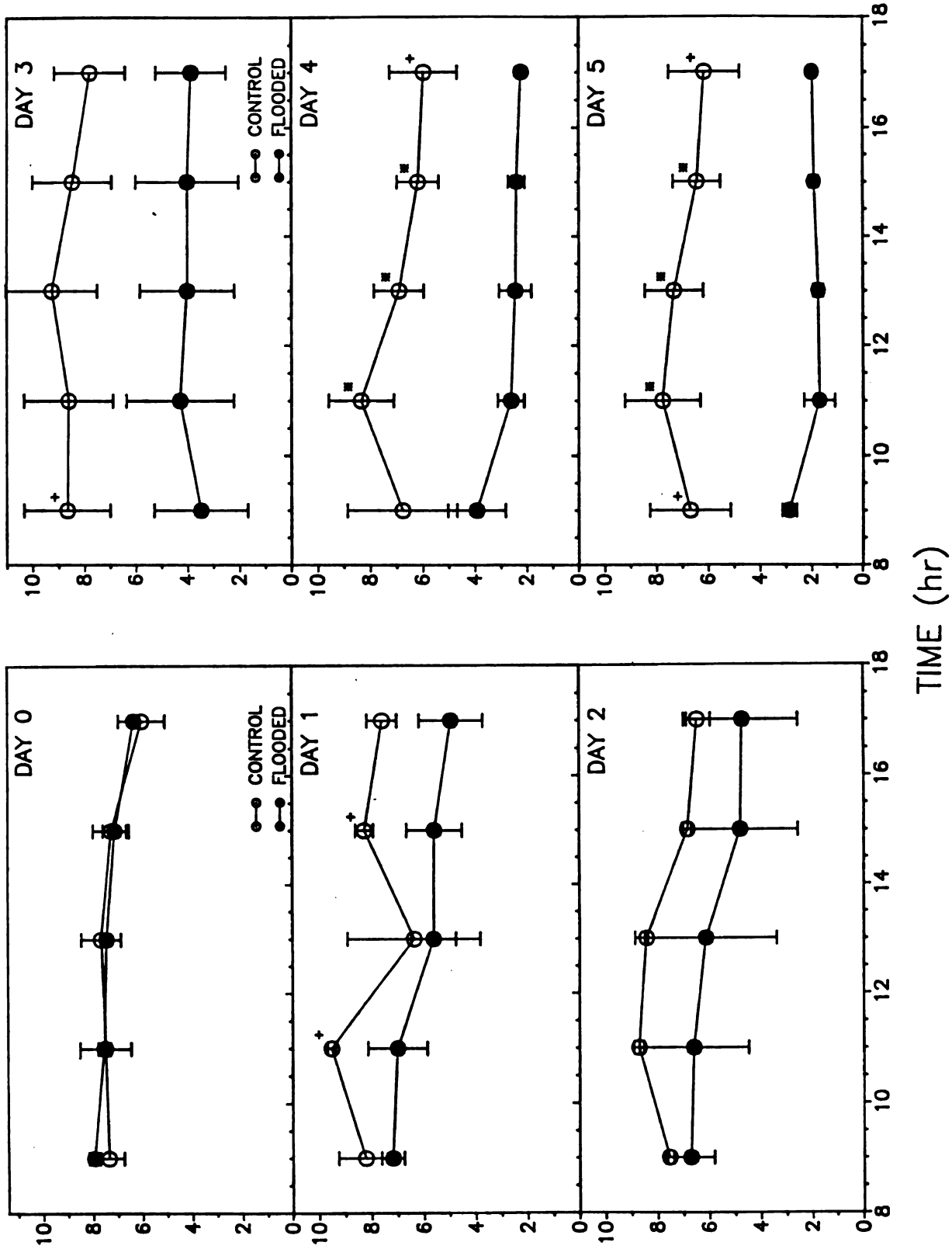
There were no apparent differences in the physical appearance of controls and flooded trees during the course of these experiments. No wilting was observed unlike similar experiments performed in greenhouse environments (Beckman et al., in preparation). This is most likely due to the relatively low temperature and high humidity maintained in the growth chamber and hood during the experimental period compared to the harsher conditions often encountered on sunny days in the greenhouse. Additionally, the age of leaves utilized in this experiment (several weeks older than those typically utilized in greenhouse experiments) may have influenced development of wilting symptoms.

Net CO_2 assimilation (A) of flooded trees decreased significantly compared to controls during only a portion of the first day of flooding (Figure 2). Sharp drop in A of controls at 1300 hr measurement may have been in response to the handling and transient changes in leaf illumination experienced during collection of light response data from 1100-1300 hr. Hence, all light response data was collected from 1700-1900 hours. On day 2, A of flooded trees was uniformly lower than controls although differences were not significant. On day 3, differences in A of flooded and control trees increased but were significant only at 900 hr. On day 4 from 1100 hour on, A of flooded trees was significantly lower than controls. After 5 days of flooding, A of flooded trees was only 32% that of controls.

Carbon assimilation of control trees generally reached a maximum between 1100 and 1300 hr each day and slowly declined through remainder of day. Flooded trees displayed a pattern similar to controls through day 3. However, on day 4 and 5, flooded trees displayed maximum A at

Figure 2. Effects of 1-5 days of flooding on net CO_2 assimilation (A) of sour cherry trees (Montmorency/Mahaleb). Data points are means of 2 plants/time ± sd. Significance of difference between 2 treatments at each time indicated at the 10% (+) or 5% (*) level, otherwise ns, t test.

FIGURE 2


DAY 0
DAY 1
DAY 2
DAY 3
DAY 4
DAY 5
CONTROL
FLOODED
A (μmol m⁻² s⁻¹)
TIME (hr)

900 hr each day and declined through the rest of the day. Values of A for controls were lower than those previously reported for sour cherry (Sams and Flore, 1982) possibly due to leaf age.

Stomatal conductance to CO_2 (g_l) in flooded plants dropped slightly below that of controls on day one, differences increased during day 2 and remained relatively stable through end of experiment, however, differences were not significant at any time (Figure 3). Residual conductance to CO_2 (g_r') of flooded plants dropped significantly below that of controls after three days of flooding and remained significantly depressed through end of experiment (Figure 4).

Intercellular CO_2 (Ci) fell slightly in flooded plants during the morning of the first day of flooding, however, they rose slightly above controls during the afternoon. From the second day on, differences in Ci of flooded and control trees generally increased but were not significant at any time (Figure 5).

Initial decline of A in flooded plants closely parallels changes in residual conductance during day 1 of flooding. Stomatal conductance and Ci also dropped in flooded plants during the same time frame, but declines were relatively small. This suggests that initial decline of A in flooded plants is primarily through a loss of CO_2 assimilation capacity and secondarily by stomatal closure. As flooding continues, differences in A of flooded and control plants become more pronounced, again paralleled by similar changes in their respective residual conductances. However, differences in stomatal conductance were relatively stable from day 2 onward, while differences in Ci increased somewhat suggesting a gradual increase in nonstomatal limitations to A as flooding persists.

Figure 3. Effects of 1-5 days of flooding on stomatal conductance to CO_2 (g_l) of sour cherry trees (Montmorency/Mahaleb). Data points are means of 2 plants/time ± sd. Significance of difference between 2 treatments at each time indicated at the 10% (+) or 5% (*) level, otherwise ns, t test.

FIGURE 3

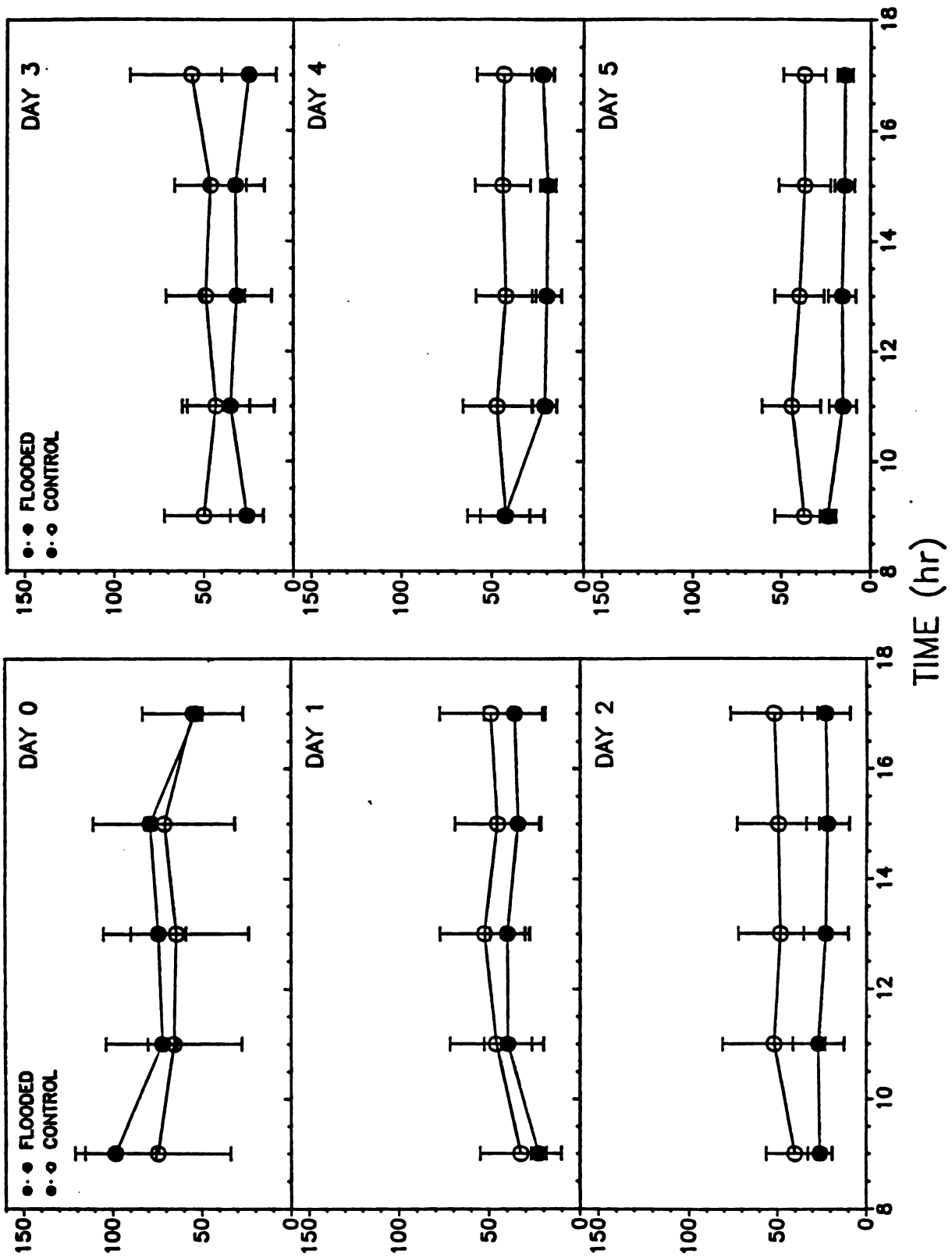

DAY 0
DAY 1
DAY 2
DAY 3
DAY 4
DAY 5
●-● FLOODED
●-○ CONTROL
g_L (mmol m^{-2} s^{-1})
TIME (hr)
0
50
100
150
8
10
12
14
16
18

Figure 4. Effects of 1-5 days of flooding on residual conductance to CO_2 (g_r') of sour cherry trees (Montmorency/Mahaleb). Data points are means of 2 plants/time ± sd. Significance of difference between 2 treatments at each time indicated at the 10% (+) or 5% (*) level, otherwise ns, t test.

FIGURE 4

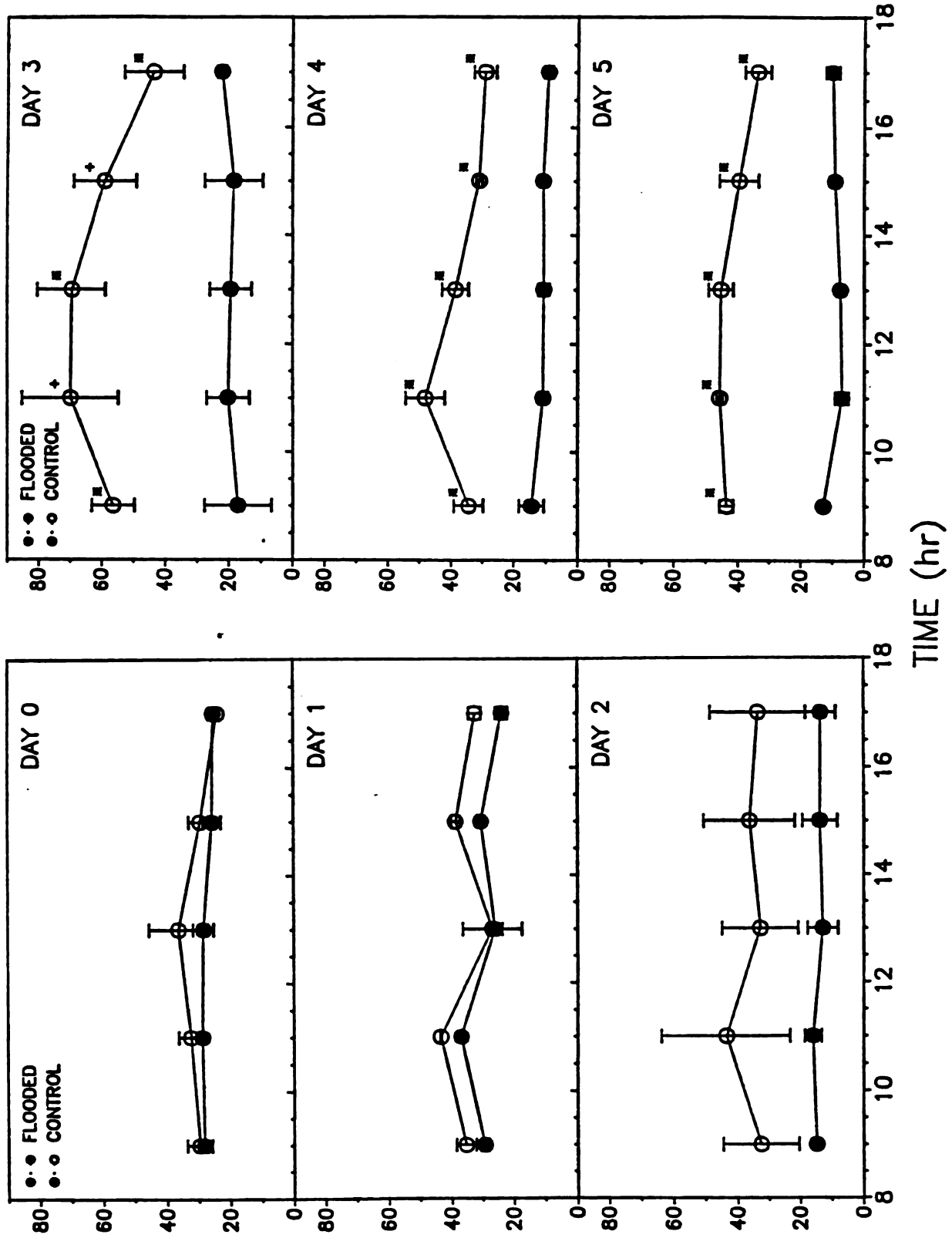
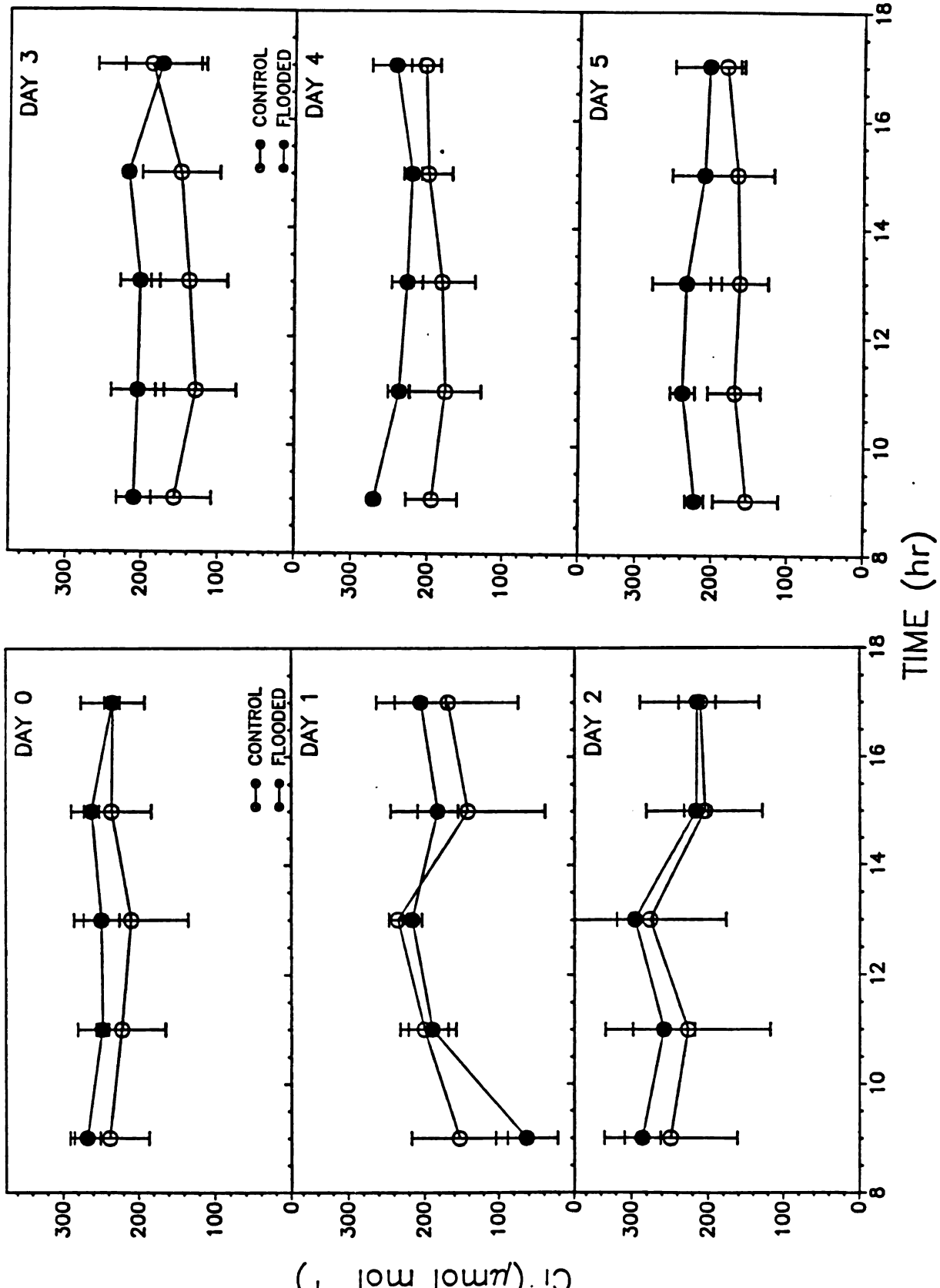

DAY 0
DAY 1
DAY 2
DAY 3
DAY 4
DAY 5
FLOODED
CONTROL
TIME (hr)
g_f(mmol m^{-2} s^{-1})

Figure 5. Effects of 1-5 days of flooding on intercellular CO_2 (Ci) of sour cherry trees (Montmorency/Mahaleb). Data points are means of 2 plants/time ± sd. Significance of difference between 2 treatments at each time indicated at the 10% (+) or 5% (*) level, otherwise ns, t test.

FIGURE 5


DAY 0
DAY 1
DAY 2
DAY 3
DAY 4
DAY 5
CONTROL
FLOODED
Ci (μmol mol⁻¹)
TIME (hr)
0
100
200
300
8
10
12
14
16
18

Davies and Flore (1986a and 1986c) observed that initial decline of A in flooded blueberries appeared to be primarily caused by stomatal closure since Ci declined also. However, as flooding continued, reduction in A appeared to be due to decreases in both stomatal aperature and residual conductance. In contrast, Smith and Ager (1988) concluded that in pecan seedlings subjected to soil flooding, reduction in A was primarily due to loss of CO_2 assimilation capacity since Ci did not decline in flooded plants throughout the treatment period. Guy and Wample (1984) also observed a decline in A of flooded sunflowers independent of changes in stomatal conductance suggesting a loss of carbon assimilation capacity.

Flooded trees displayed a reduced A at all light levels from day 1 (Figure 6). Both treatments light saturated at ca. 600-800 micromols m^{-2} s^{-1} PPF initially. Saturation light level is lower than that reported previously for sour cherries (Sams and Flore, 1982). This is possibly the result of the trees having been grown in a partially shaded environment. From day 2 on, the light saturation point of flooded trees gradually dropped to ca. 400 micromols m^{-2} s^{-1} PPF. This could be due to chlorophyll loss during flooding. However, this seems unlikely since we have previously observed no change in chlorophyll content in leaves of sour cherry trees during short term flooding (Beckman et al., in preparation). Alternatively, this might be the result of some limitation in the capacity of the light harvesting components to transfer captured light energy to the chemical reactions of photosynthesis.

Apparent quantum yield, as estimated from light response curves decreased for flooded plants compared to controls after 1 day and

Figure 6. Net CO_2 assimilation as a function of incident PPF in sour cherry trees (Montmorency/Mahaleb) before and after 1-5 days of flooding.

Fitted curves:

Day 0, Control: $A = 7.14 - 7.72 \times e^{(-.00459 \times PPF)}$, $r^2 = 0.98$
Flooded: $A = 7.01 - 7.54 \times e^{(-.00339 \times PPF)}$, $r^2 = 0.99$

Day 1, Control: $A = 9.47 - 10.0 \times e^{(-.00379 \times PPF)}$, $r^2 = 0.99$
Flooded: $A = 6.27 - 7.06 \times e^{(-.00394 \times PPF)}$, $r^2 = 0.92$

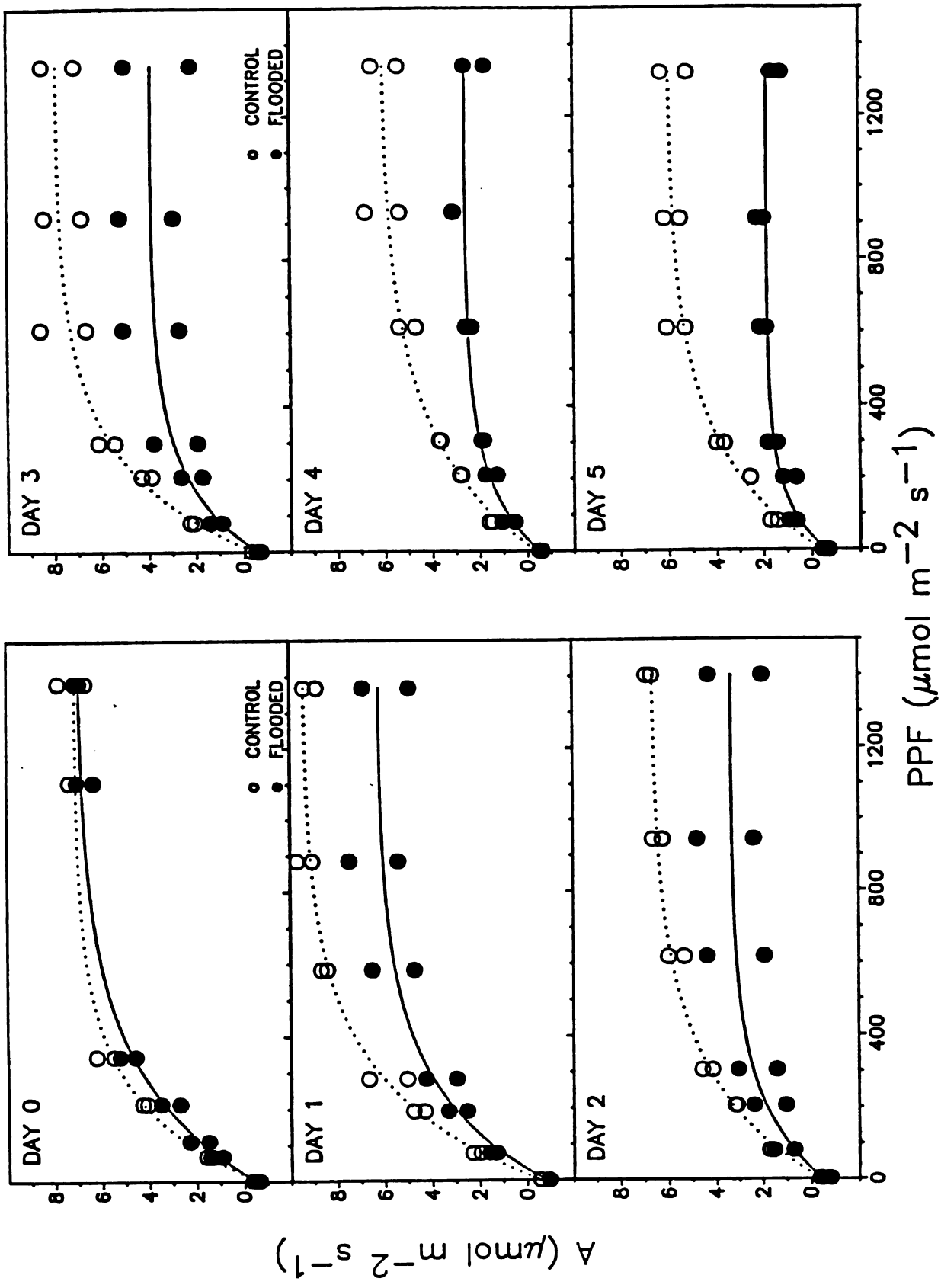
Day 2, Control: $A = 6.69 - 7.05 \times e^{(-.00354 \times PPF)}$, $r^2 = 0.99$
Flooded: $A = 3.34 - 3.79 \times e^{(-.00458 \times PPF)}$, $r^2 = 0.67$

Day 3, Control: $A = 7.94 - 8.34 \times e^{(-.00428 \times PPF)}$, $r^2 = 0.96$
Flooded: $A = 3.89 - 4.46 \times e^{(-.00517 \times PPF)}$, $r^2 = 0.74$

Day 4, Control: $A = 6.14 - 6.47 \times e^{(-.00326 \times PPF)}$, $r^2 = 0.97$
Flooded: $A = 2.61 - 3.08 \times e^{(-.00539 \times PPF)}$, $r^2 = 0.91$

Day 5, Control: $A = 6.01 - 6.40 \times e^{(-.00370 \times PPF)}$, $r^2 = 0.97$
Flooded: $A = 1.82 - 2.39 \times e^{(-.00739 \times PPF)}$, $r^2 = 0.88$

FIGURE 6


DAY 0
DAY 1
DAY 2
DAY 3
DAY 4
DAY 5
CONTROL
FLOODED
A (μmol m⁻² s⁻¹)
PPF (μmol m⁻² s⁻¹)
0
2
4
6
8
400
800
1200

generally continued to decline through end of experiment (Table 1). At the conclusion of the experiment the quantum yield of flooded plants was only 36% that of controls. Quantum yield is comparable to that reported for blueberries (Davies and Flore, 1986a), but lower than that previously reported for sour cherries (Sams and Flore, 1982). Davies and Flore (1986a) observed a similar decrease in quantum efficiency during soil flooding of blueberries. In contrast, Bradford (1983a) found no change in quantum efficiency of tomato plants subjected to 1 day of flooding.

Dark respiration of flooded trees was significantly greater than that of controls after 1 day of flooding and remained higher throughout the treatment period (Table 1), although differences from day 2 through 5 were not significant. Estimated light compensation point of flooded trees also increased after 1 day of flooding and remained higher throughout experiment (Table 1), probably as a reflection of increased dark respiration in flooded trees.

Response of g_l to varying ambient CO_2 concentrations after 2 and 5 days of flooding in Experiment 2 is shown in Figure 7. On both occasions flooded and control trees show a negative linear response to increasing ambient CO_2 in the range tested. Differences in g_l of flooded and control plants increased with flooding duration. Relatively flatter slope of regression line for flooded trees after 5 days indicates a decrease in stomatal responsiveness to ambient CO_2. Davies and Flore (1986b) observed a similar pattern in blueberries subjected to short term flooding.

Response of A to varying ambient CO_2 concentrations after 2 and 5 days of flooding is shown in Figure 8. On day 2, net CO_2 assimilation

Table 1. Effects of 1-5 days flooding on estimated apparent quantum efficiency, dark respiration (R_d) and estimated light compensation points of sour cherry trees (Montmorency/Mahaleb).

Day	Hours After Flood	Treatment	Apparent Quantum Efficiency (mol CO_2 mol^{-1} PPF)	R_d (micromol CO_2 m^{-2} s^{-1})	Light Compensation Point (micromol m^{-2} s^{-1} PPF)
0	-7	Control	0.0224	0.44 ± 0.07 ns[z]	17
		Flooded	0.0182	0.50 ± 0.21	21
1	13	Control	0.0260	0.58 ± 0.04 **	15
		Flooded	0.0187	0.95 ± 0.02	30
2	43	Control	0.0175	0.49 ± 0.06 ns	15
		Flooded	0.0110	0.59 ± 0.31	27
3	67	Control	0.0233	0.42 ± 0.13 ns	12
		Flooded	0.0138	0.65 ± 0.07	27
4	91	Control	0.0152	0.53 ± 0.10 ns	16
		Flooded	0.0097	0.56 ± 0.06	31
5	115	Control	0.0163	0.46 ± 0.07 ns	17
		Flooded	0.0085	0.65 ± 0.06	37

[z] Mean of 2 trees per treatment ±sd. Significance of difference between control and flooded treatments indicated at the 1% level (**) or ns, t test.

Figure 7. Stomatal conductance to CO_2 (g_l) as a function of ambient CO_2 (Ca) in sour cherry trees (Montmorency/Mahaleb) after 2 and 5 days of flooding.

Fitted Lines:

Day 2, Control: $g_l = 104.9 - (0.0565 \times Ca)$, $r^2 = 0.52$
Flooded: $g_l = 99.4 - (0.0852 \times Ca)$, $r^2 = 0.45$

Day 5, Control: $g_l = 100.5 - (0.0832 \times Ca)$, $r^2 = 0.54$
Flooded: $g_l = 57.3 - (0.0490 \times Ca)$, $r^2 = 0.83$

FIGURE 7

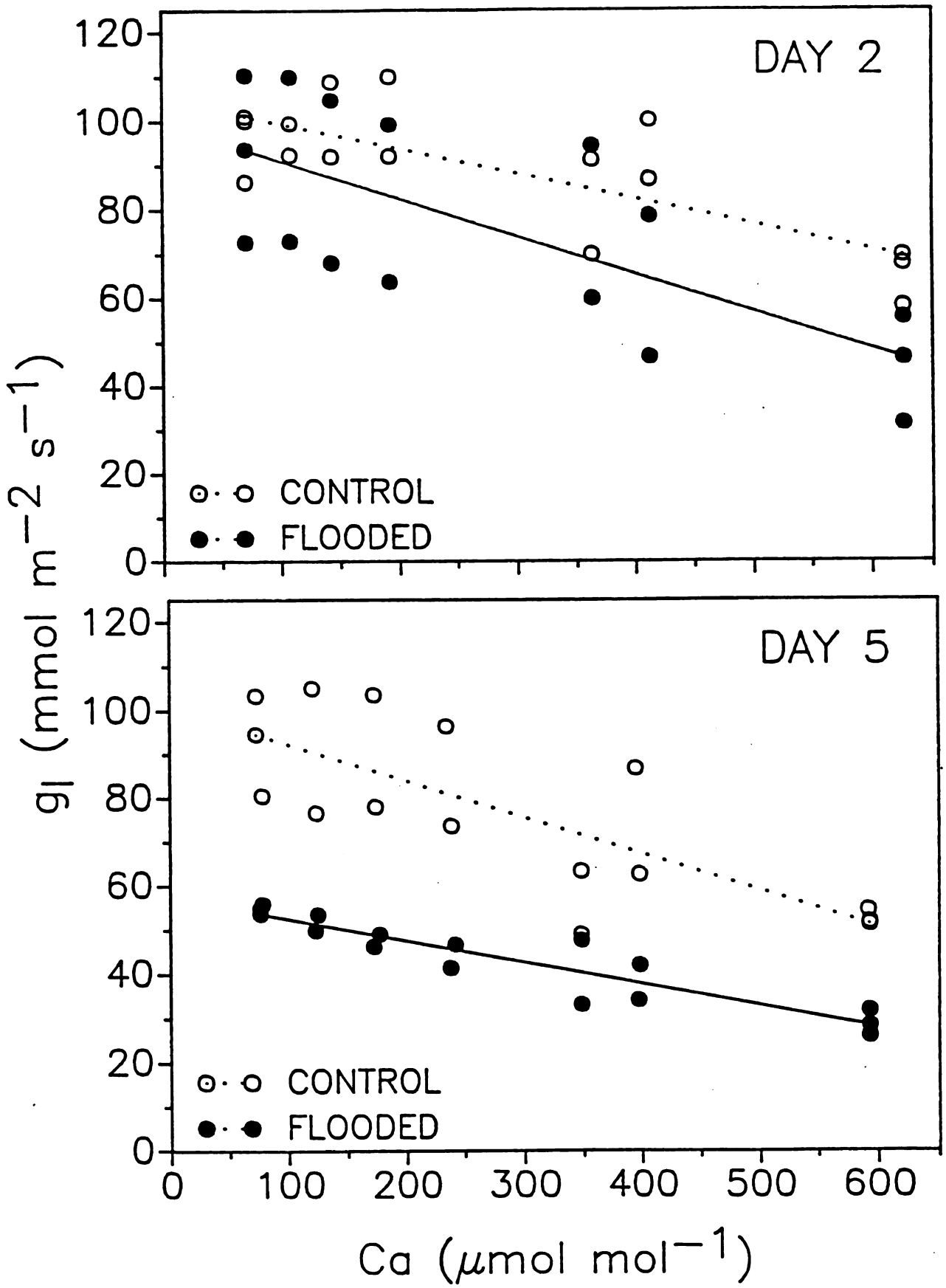

DAY 2
DAY 5
CONTROL
FLOODED
CONTROL
FLOODED
120
100
80
60
40
20
0
0
100
200
300
400
500
600
gl (mmol m−2 s−1)
Ca (μmol mol−1)

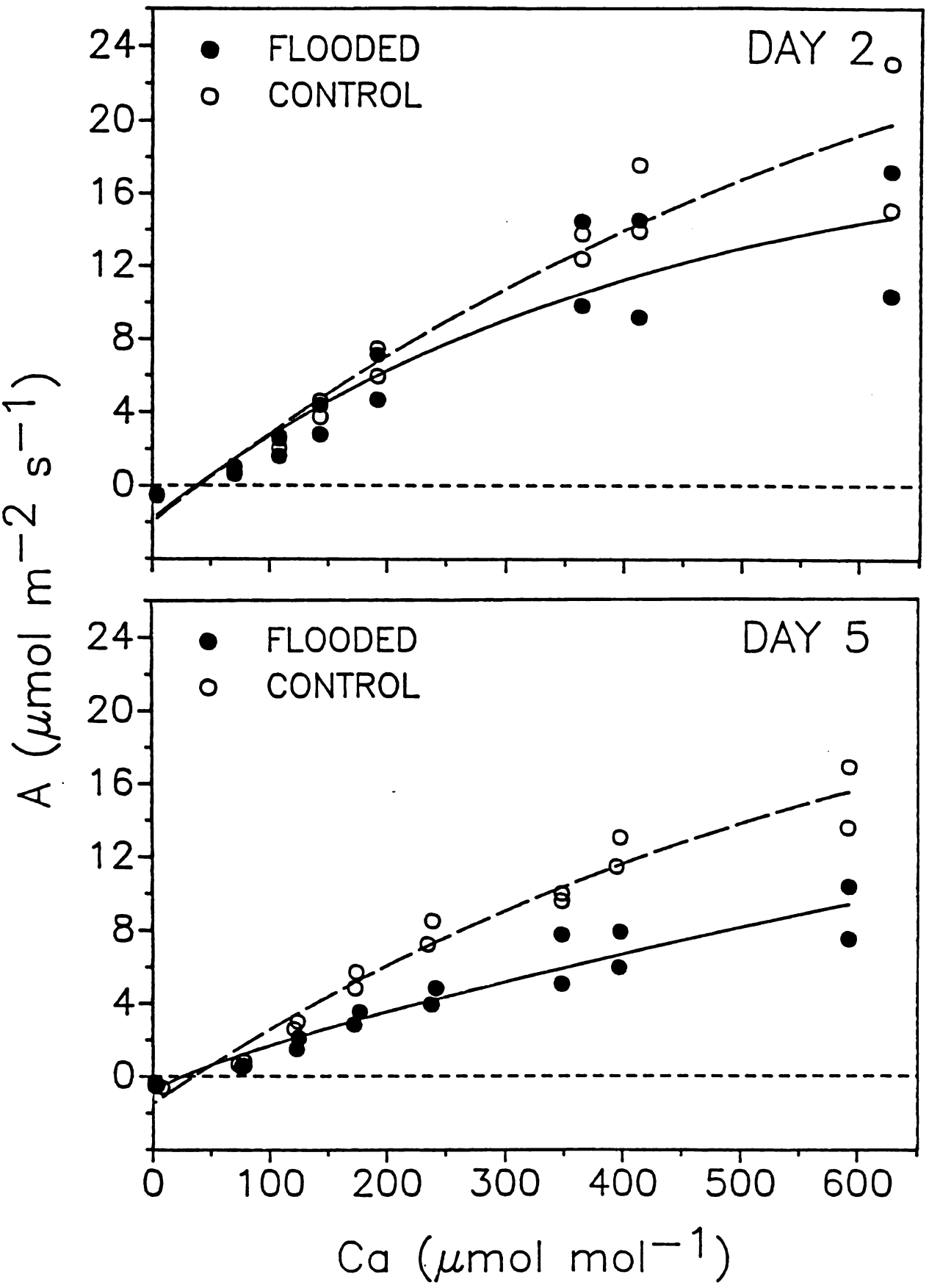
Figure 8. Net CO_2 assimilation (A) as a function of ambient CO_2 (Ca) in sour cherry trees (Montmorency/Mahaleb) after 2 and 5 days of flooding. Dashed and solid curves, control and flooded treatments, respectively.

Fitted curves:

Day 2, Control: $A = 35.9 - 38.0 \times e^{(-0.0014 \times Ca)}$, $r^2 = 0.93$
Flooded: $A = 19.3 - 21.2 \times e^{(-0.0024 \times Ca)}$, $r^2 = 0.87$

Day 5, Control: $A = 26.6 - 28.1 \times e^{(-0.0016 \times Ca)}$, $r^2 = 0.97$
Flooded: $A = 0.0728 \times Ca^{(0.07746)} - 0.9164$, $r^2 = 0.92$

FIGURE 8


FLOODED
CONTROL
DAY 2
FLOODED
CONTROL
DAY 5
A (μmol m⁻² s⁻¹)
Ca (μmol mol⁻¹)
0
4
8
12
16
20
24
0
100
200
300
400
500
600

of control plants was roughly linear throughout the range tested, while A of flooded plants was linear only up to ca. 250 micromol CO_2 mol^{-1}. On day 5 the situation was reversed, with control plants responding in a linear fashion only up to ca. 300 micromol CO_2 mol^{-1} and flooded plants responding in a roughly linear fashion throughout the range tested. Sams and Flore (1982) observed a linear response of A in sour cherry trees to increasing ambient CO_2 up to ca. 300 micromol CO_2 mol^{-1}. After 2 days, carbon assimilation of flooded plants was lower than controls at all ambient CO_2 concentrations greater than ca. 300 micromol mol^{-1}. After 5 days, carbon assimilation of flooded plants was lower than controls at all CO_2 concentrations greater than ca. 100 micromol mol^{-1}. Additionally, differences between controls and flooded trees were larger after 5 days compared to differences observed between the two treatments after 2 days of flooding. Estimated CO_2 compensation points (calculated from A/Ca regression curves) were lower for flooded plants on both dates (40.5 and 38.1 micromol mol^{-1} CO_2 for control and flooded trees, respectively, on day 2 and 35.4 and 26.3 micromol mol $^{-1}$ CO_2 for controls and flooded trees, respectively, on day 5), probably as a reflection of increased dark respiration in flooded plants.

Figure 9 shows the relationship between A and intercellular CO_2 concentration (Ci) for flooded and control trees after 2 and 5 days flooding. Pattern is similar to that of A vs ambient CO_2 concentration. Carbon assimilation of flooded plants was lower than controls at virtually all Ci on both days. However, differences were very small at low Ci on day 2. Differences between control and flooded trees were larger after 5 days of flooding than they were after only 2 days of flooding.

Figure 9. Net CO_2 assimilation rate (A) as a function of intercellular CO_2 (Ci) in sour cherry trees (Montmorency/Mahaleb) after 2 and 5 days of flooding. Dashed and solid curves, control and flooded treatments, respectively. Dotted vertical lines represent supply curves for infinite g_l.

Demand Curves:

Day 2, Control: $A = 19.8 - 34.4 \times e^{(-0.0088 \times Ci)}$, $r^2 = 0.84$
Flooded: $A = 20.1 - 27.8 \times e^{(-0.0057 \times Ci)}$, $r^2 = 0.87$

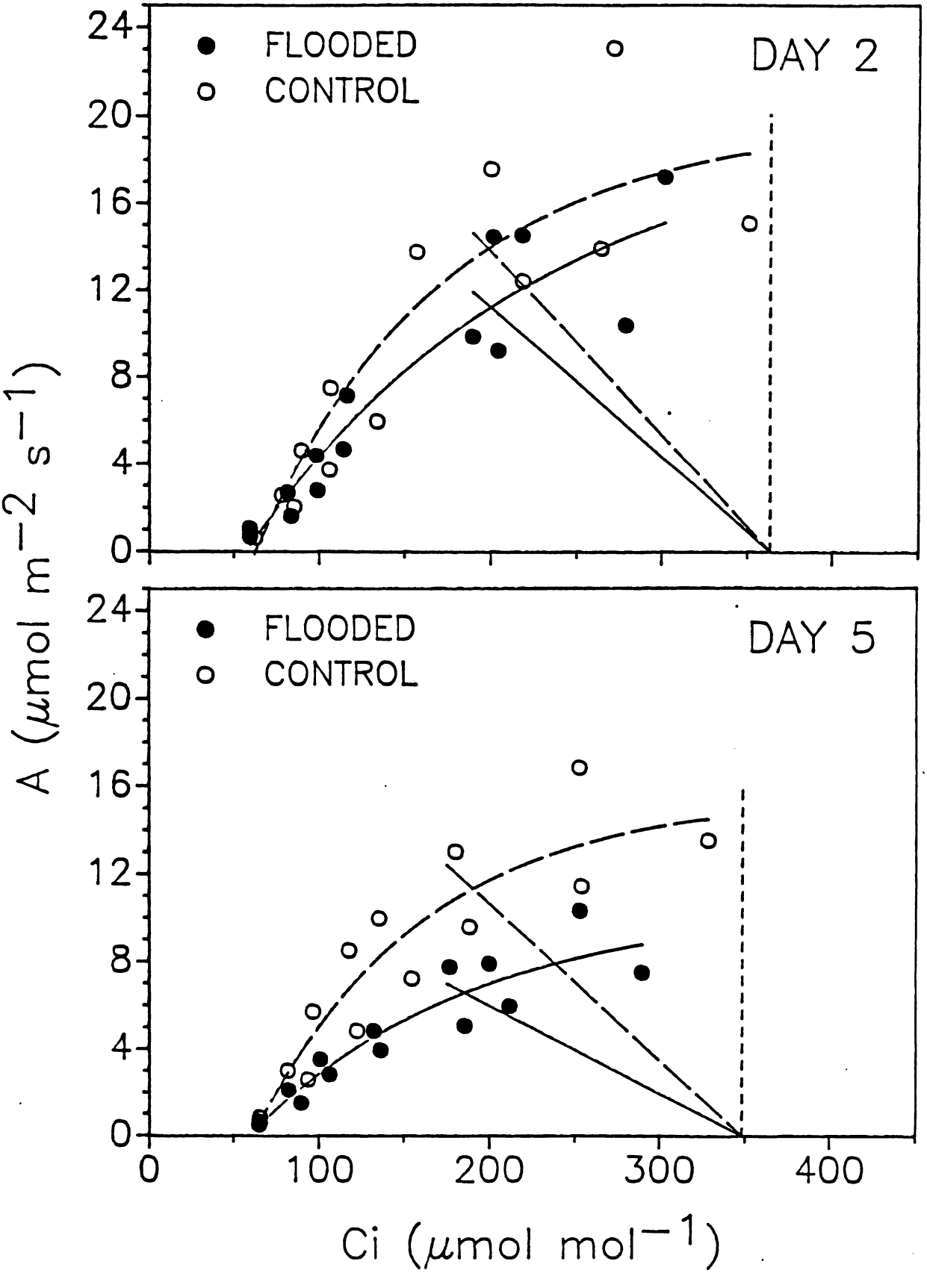
Day 5, Control: $A = 15.5 - 28.7 \times e^{(-0.0101 \times Ci)}$, $r^2 = 0.86$
Flooded: $A = 10.5 - 16.5 \times e^{(-0.0077 \times Ci)}$, $r^2 = 0.87$

Supply Curves:

Day 2, Control: $A = 0.084 \times (363 - Ci)$
Flooded: $A = 0.069 \times (363 - Ci)$

Day 5, Control: $A = 0.072 \times (348 - Ci)$
Flooded: $A = 0.040 \times (348 - Ci)$

FIGURE 9


FLOODED
CONTROL
DAY 2
FLOODED
CONTROL
DAY 5
A (μmol m⁻² s⁻¹)
Ci (μmol mol⁻¹)
0
4
8
12
16
20
24
0
100
200
300
400

Estimates of stomatal limitations to A on day 2 were 24.8% and 32.5% for control and flooded trees, respectively, and on day 5 were 22.8% and 29.9%, respectively. The relative importance of stomatal limitations to A in flooded plants can be estimated by assuming that the flooded plants had stomatal limitations similar to controls and recalculating net assimilation rates at ambient CO_2 concentrations from the equations in Figure 9. Such an analysis shows that increased stomatal limitations in flooded plants account for 48% and 14% of the observed reductions in A at ambient CO_2 concentrations on days 2 and 5, respectively. Clearly increased stomatal limitations are a significant factor initially in reducing net CO_2 assimilation rates in flooded plants but their importance declines as flooding continues.

Recent contributions to models of leaf gas exchange (Farquhar and von Caemmerer, 1982; Farquhar et al., 1980; von Caemmerer and Farquhar, 1981) have identified the low Ci portion of the A vs Ci curve (i.e. initial slope) as reflecting the relative activity/amount of ribulose bisphosphate carboxylase/oxygenase (Rubisco) in the leaf, and the high Ci region reflecting the relative ribulose bisphosphate (RuBP) regeneration capacity. Based on this model, it appears that flooding initially impairs the RuBP regeneration capacity of sour cherries and not its activity or amount. However, as flooding continues both the activity of Rubisco and the RuBP regeneration capacity are diminished. Initial response in flooded trees is similar to that observed by Bradford (1983a) in tomato plants flooded for 1 day.

According to the model (Farquhar and von Caemmerer, 1982; von Caemmerer and Farquhar, 1981) reductions in RuBP regeneration capacity may be due to limitations in photosynthetic electron transport, NADPH

and ATP synthesis and the reductive pentose phosphate cycle. The decline in quantum efficiency of flooded cherry trees, observed in Experiment 1, indicates some limitation in the light harvesting component of the leaf. This is probably not due to loss of chlorophyll, however, since we have previously observed no change in chlorophyll content of cherry trees during short term flooding under greenhouse conditions (Beckman et al., in preparation). Bradford (1983a) suggested that reduced RuBP regeneration in flooded tomato plants might be due to depletion of Pi needed for RuBP regeneration, possibly because of a buildup in sucrose and/or starch due to reduced sink activity.

Reduced activity of Rubisco after prolonged flooding might be related to alterations of plant growth regulators normally supplied by the root system. Burrows and Carr (1969) demonstrated that flooding reduced cytokinin export from the roots of flooded sunflowers. Cytokinins have been shown to retard leaf senescence and loss of protein, and maintain photosynthetic capacity (Adedipe et al., 1971; Richmond and Lang, 1957). This suggests that reduced cytokinin export from the root system of sour cherry during soil flooding could be the cause of a number of the symptoms typically observed in the canopy of sour cherries during soil flooding. Bradford (1983b) demonstrated that cytokinin applications not only prevented stomatal closure in flooded tomato plants, but it also prevented much of the decline in photosynthetic capacity normally observed after imposition of flooding.

ABA and ethylene (or its precursor ACC) have often been shown to increase in plants subjected to soil flooding and in some experiments they appear to be directly related to the symptoms observed (Bradford and Yang, 1980 and 1981; Hiron and Wright, 1973; Wadman-van Schravendijk

and van Andel, 1985 and 1986). Applications of ABA to unstressed plants can depress A, although effects are generally exercised through reductions in stomatal conductance (Bradford, 1983b; Dubbe et al., 1978; Hiron and Wright, 1973). In contrast, Raschke (1982) reported non-stomatal limitation of A by ABA in a number of species. Ethylene, once thought to have no effect on either g_s or A, has recently been shown to have both stomatal and non-stomatal effects on A (Govindarajan and Poovaiah, 1982; Pallas and Kays, 1982). Nevertheless, ability of ABA and ethylene to cause non-stomatal reductions in A appears to be species-specific (Pallas and Kays, 1982; Raschke, 1982). Therefore, further research will be necessary to determine the role, if any, of these plant growth regulators in flooding stress of sour cherries.

Response of A and g_l to varying VPD's in Experiment 3 is similar for both control and flooded plants after 2 days, except at VPD's less than 1 kPa, where A of flooded plants was higher than that of controls (Figures 10 and 11, respectively) . After 5 days of flooding, both A and g_l were lower in flooded trees than in controls at all VPD's tested. Davies and Flore (1986c) observed a similar drop in stomatal responsiveness to VPD in blueberries subjected to flooding.

In summary, data indicates that flooding affects carbon assimilation of sour cherries in a number of ways, whose relative importance change as flooding persists. Loss of assimilative capacity and increased stomatal limitations seem to be of primary importance; initially the effect on assimilative capacity appears to be confined to RuBP regeneration capacity. As flooding continues, reductions in A due to stomatal limitations decline while reductions in A due to reduced Rubisco activity/amount appear.

Figure 10. Effect of vapor pressure deficit (VPD) on net CO_2 assimilation (A) of sour cherry trees (Montmorency/Mahaleb) after 2 and 5 days of soil flooding.

FIGURE 10

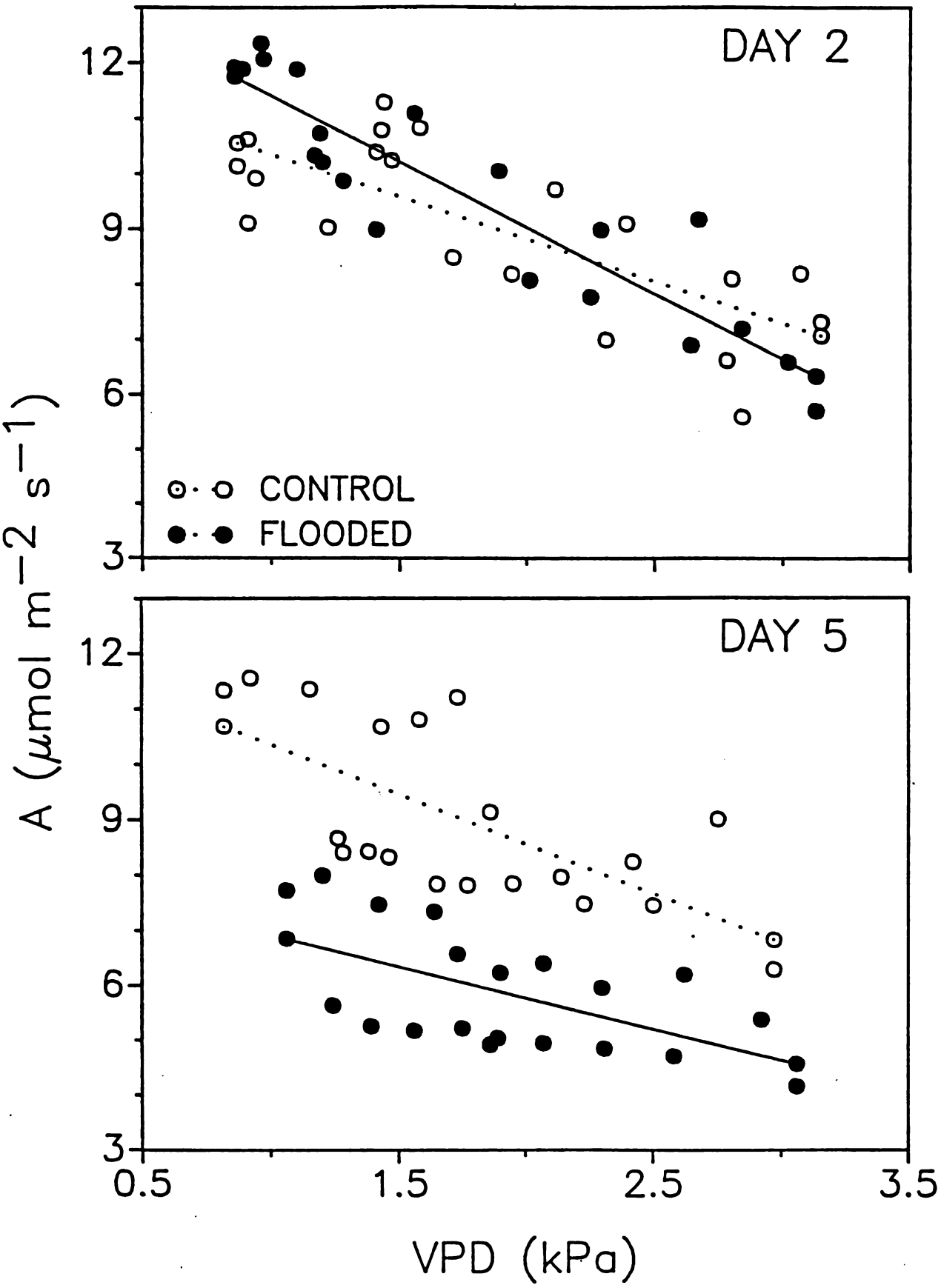
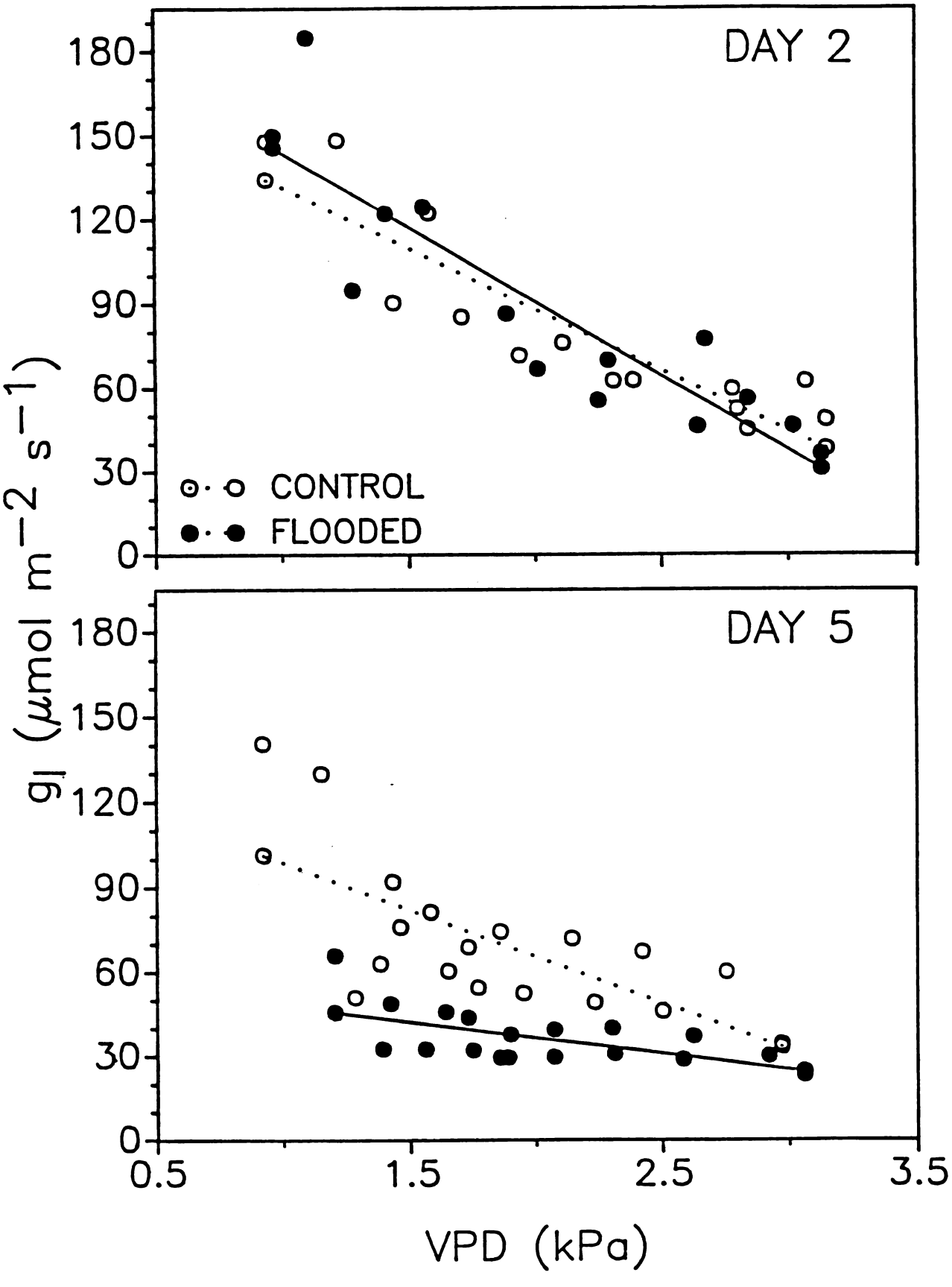

DAY 2
DAY 5
CONTROL
FLOODED
A (μmol m⁻² s⁻¹)
VPD (kPa)
12
9
6
3
0.5
1.5
2.5
3.5

Figure 11. Effect of vapor pressure deficit (VPD) on stomatal conductance to CO_2 (g_l) of sour cherry trees (Montmorency/Mahaleb) after 2 and 5 days of soil flooding.

FIGURE 11


DAY 2
DAY 5
CONTROL
FLOODED
180
150
120
90
60
30
0
0.5
1.5
2.5
3.5
VPD (kPa)
g_l (μmol m^{-2} s^{-1})

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SUMMARY AND CONCLUSIONS

Although cherry trees are rarely planted on uniformly poorly drained sites, significant numbers of trees within an orchard block may be subjected to the effects of soil flooding due to the presence of locally restrictive soils commonly found in midwestern glacial soils. Researchers at MSU have observed that prematurely declining cherry trees in Michigan are typically situated in such soils. Research with a number of temperate fruit species has invariably found even short term flooding to have significant deleterious effects on both long and short term productivity of an orchard. Moreover, both of the commonly utilized cherry rootstocks, Mahaleb and Mazzard seedlings, have been consistently found to be extremely sensitive to soil flooding in controlled tests; conclusions which are supported by many years of field observations.

This study was undertaken to determine the effects of short and long term effects of soil flooding on cherry trees, which, if any, of the available cherry rootstocks differed in their sensitivity to flooding and what were the physiological causes of plant injury during flooding.

Our observations on symptom dvelopment of Montmorency/Mahaleb during soil flooding were similar to those made by other researchers working with various flooding intolerant plant species. All gas exchange characteristics and growth parameters dropped rapidly following imposition of flooding. Wilting was observed during flooding only when environmental conditions were conducive, i.e. high temperature and low relative humidity. Stem water potential was observed to drop transiently in flooded plants during one experiment. Significant leaf chlorosis developed only during prolonged flooding, i.e. longer than 8

days, and then was slow to develop. However, significant leaf abscission was subsequently observed if trees were flooded for more than 2 days.

Recovery of gas exchange rates was possible only if flooding stress was brief, i.e. 2-4 days, but required a recovery period 7-8 times the length of the flooding stress. Gas exchange rates appeared normal during a subsequent growth cycle following dormancy. However, flooding stress as brief as 2 days brought shoot extension and leaf expansion to a permanent halt for that growth cycle and tended to reduce shoot growth during the subsequent growth cycle following dormancy. It was estimated that fifty percent of trees subjected to flooding for 6 days during active growth would subsequently die, as would all trees subjected to flooding for 16 or more days.

Our results indicate that short term flooding stress, i.e. 2-4 days, was survivable, albeit with profound reductions in current season's growth. On the other hand, long term flooding stress, i.e. 8 or more days, was usually fatal. These observations have profound implications for cherry growers since their profitability is a function of both consistent annual productivity and longevity of their orchard blocks.

In a survey of both standard and experimental rootstocks we found remarkably little variability in sensitivity to flooding. We were able to statistically separate very few rootstocks on the basis of parameters measured in the survey study. Nevertheless, MxM 2 appeared to be the most tolerant stock tested, while GC 196/4 and MxM 39 were the most sensitive. Clearly there is much work to be done by breeders and horticulturists in the production and identification of more flooding

tolerant materials for use as cherry rootstocks.

During some preliminary experiments with Montmorency/Mahaleb, we occasionally observed trees survive and recover from 10-14 days of flooding. Following dormancy fulfillment, several of these individuals produced suckers from the Mahaleb rootstock and, thus, could be clonally propagated and retested against an unselected population of Mahaleb seedlings. If these selections proved to be more flooding tolerant than the unselected population then this method would lend itself to the selection of superior individuals in seedling lines which could in turn be utilized as superior clonal rootstocks or as parents in breeding programs.

The major limitation of these studies was that they were performed exclusively on containerized plants and involved flooding of the entire root system. In field plots and containerized systems where the entire root system was not flooded we have observed that plant injury was somewhat ameliorated and presumably more survivable. Therefore, one research area deserving of attention is to determine the importance of root system architecture, i.e. horizontal vs. vertical rooting patterns, as a flooding avoidance strategy. Should this prove to be a viable strategy then presumably this trait could be a selection criteria in a breeding program.

A related area also deserving attention is the role of compensatory root growth in reducing plant injury and mortality during soil flooding. This might come into play either in those parts of the root system situated in a portion of the soil profile not subjected to flooding or in roots damaged by flooding. In the first case, elaboration of those portions of the root system not subjected to flooding might allow the

plant to compensate for the loss of function in other roots damaged or lost during flooding. In the latter case rapid replacement of damaged roots might allow the plant to continue to grow and function optimally following flooding. In either case maintenance of photosynthetic rates during flooding or rapid recovery of photosynthetic capacity following flooding would play a major role in providing the necessary photosynthates to support root growth.

Many questions remain as to how flooding causes plant injury. While we were able to demonstrate that a translocatable factor from the roots may reduce photosynthetic rates in the canopy during flooding, its identity remains unknown. A number of possibilities exist: a toxin produced by the roots or imported into them during flooding, a reduced quantity of some essential metabolite or hormone from the rootsystem, or perhaps a CO_2 source which releases CO_2 in the leaves thus appearing to reduce net photosynthesis. The use of fluorescence to measure gas exchange would allow one to determine whether the electron transport pathway is inhibited during soil flooding. Determinations of leaf hormone and starch levels during flooding or exogenous applications of hormones may also help elucidate the mechanism of apparent photosynthetic inhibition. Indeed, such experiments may point the way to treatments that would reduce the negative effects of flooding in trees grafted onto flooding sensitive rootstocks.

APPENDIX A

APPENDIX A

EFFECT OF XYLEM SAP FROM FLOODED AND CHECK TREES ON GAS EXCHANGE CHARACTERISTICS OF SOUR CHERRY LEAF EXPLANTS.

The purpose of this experiment was to determine if the xylem sap from flooded plants had an effect on photosynthesis of sour cherry leaf explants.

Exudate was collected from flooded and check trees (2 of 4 reps) at conclusion of Experiment 1 described in Section I. Trees were gently removed from pots and roots washed clean in tap water (ca. 22 °C). Trunks were severed ca. 25 cm above the graft union. A neoprene stopper with an appropriate diameter hole was slipped down the trunk to within a few cm of the graft union. Assembly was then sealed into a large custom made pressure bomb filled with enough tap water to completely cover root system. System was pressurized to ca. 8 bars and ca. 1 ml of expressed sap collected in a short length of plastic tubing attached to the cut end of the tree stem protruding from the top of the pressure bomb. Sap was transferred with a pipette to a small vial (ca. 20 ml). Vial was immediately sealed, placed on ice and stored at 2 °C until commencement of experiment the next day.

Explant system consisted of a single fully expanded sour cherry leaf (Montmorency) with ca. 4 cm of attached stem. Well exposed shoots (ca. 20 cm long) were collected from field grown trees the morning of the experiment and cut ends immediately recut while submerged in tap water. Explants were prepared by cutting stem ca. 0.5 cm above and ca. 3.5 cm below point of petiole attachment, taking care that all cuts were performed under water to maintain continuity of water column to leaf.

Stems were placed in 5 ml vials filled with deionized water and held in place with a small lump of modeling clay. Leaves were then sealed in environmentally controlled plexiglass chambers (Sams and Flore, 1982) with petioles, stems and vials protruding.

Gas exchange measurements were made every 15 minutes (900 hr -1700 hr), using an open gas-exchange system described previously (Sams and Flore, 1982). Gas exchange measurements were made within optimum environmental conditions for sour cherries (Sams and Flore, 1982), photosynthetic photon flux (PPF) of 1000 micromols m^{-2} s^{-1}, leaf temperature of 25 ^{o}C, ambient carbon dioxide concentration of 350 micromol mol^{-1} and leaf to air vapor pressure deficit (VPD) of 0.5-1.0 KPa. Flow rate through individual chambers was ca. 1.65 l min^{-1}. Carbon assimilation and conductance values were calculated as described previously (Moon and Flore, 1986).

Leaves were allowed to equilibrate ca. 3 hr at which time deionized water was suctioned from explant vials and immediately replaced with a 50% solution (v/v) of deionized water and sap collected from eith control or flooded trees (sap from 2 reps of each treatment combined before dilution). Vials were replenished periodically during experiment with deionized water to maintain ca. 2 ml of fluid in each vial.

At conclusion of experiment leaves were released from chambers, petioles severed at point of attachment to stem and leaf water potential measured with a portable pressure bomb (PMS Instrument Co., Corvallis, OR). Measurements were made in the manner of Boyer (1967). Hydraulic conductivity of explant stem was measured by first trimming ca. 1 mm of tissue from the apical portion of stem. A short piece of water filled tubing was attached to the basal portion and the stem inserted tightly

into the collar of the portable pressure bomb. The free end of the water filled tubing was placed in a small water filled beaker in the bottom of the chamber to maintain continuity of water column and the system sealed. A pressure of ca. 3.5 bar was applied and flow through stem section collected in a short length of tubing attached to the protruding stem end. Hydraulic conductivity was estimated as:

$$K = \frac{QL}{PA} \text{ where,}$$

K equals hydraulic conductivity (cm s^{-1}), Q equals flow (mg s^{-1}), L equals length of stem (cm), P equals pressure (mg cm^{-2}) and A equals mean cross sectional area of stem (cm^2).

Net carbon assimilation of explants receiving exudate from flooded plants dropped more rapidly than explants receiving exudate from check plants, differences becoming significant 2 hours after introduction of exudate as shown in Table 1. Residual mesophyll conductance to CO_2 of explants receiving exudate from flooded plants also dropped significantly below that of explants receiving exudate from control plants, differences becoming significant 2.75 hours after introduction of exudate. No significant differences in transpiration or stomatal conductance to CO_2 was observed between the 2 treatments. No significant differences were detected in LWP or hydraulic conductivity of stem sections of the two treatments at conclusion of the experiment as shown in Table 2.

Results indicate that some factor contained (or missing) in exudate from flooded plants causes net carbon assimilation to fall in explant leaves. Effect is probably not via plugging of the xylem since no differences in hydraulic conductivity of stems or in LWP of the two treatments was detected at conclusion of experiment.

Table 1. Effects of xylem exudate from flooded[z] and check sour cherry trees (Montmorency/Mahaleb) on net CO_2 assimilation (A), residual mesophyll conductance to CO_2 (g_r'), and stomatal conductance to CO_2 (g_l) of Montmorency leaf explants.

Parameter	Trt	Hours after introduction of exudate																
		0.00	0.25	0.50	0.75	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00	3.25	3.50	3.75	4.00
A	C	11.6	11.0	10.7	10.4	10.6	9.9	9.9	8.9	9.0a[y]	8.4a	7.9a	7.6A	7.3A	6.7A	6.8A	5.9A	5.5A
(umol m^{-2} s^{-1})	F	12.7	12.3	11.6	11.4	10.9	9.4	8.2	6.7	5.5b	4.9b	4.2b	3.7B	3.1B	2.8B	2.7B	2.2B	1.9B
g_r'	C	50.8	72.8	46.4	52.4	68.4	44.8	38.6	61.2	38.9	48.0	42.4	34.9a	29.0A	27.6A	32.4	23.3A	24.1
(mmol m^{-2} s^{-1})	F	55.6	80.8	50.0	56.0	51.2	44.4	32.0	44.8	21.0	30.8	15.6	13.7b	10.5B	9.2B	8.7	7.2B	6.1
g_l	C	164	96	164	79	105	97	189	108	135	79	116	99	136	81	102	53	102
(mmol m^{-2} s^{-1})	F	180	103	195	134	187	119	175	98	140	55	104	109	119	60	127	116	103

[z] Plants flooded 4 days.
[y] For each parameter, values in same column followed by different lower or upper case letter significantly different at the 5% or 1% level respectively, F test.

Table 2. Leaf water potential (LWP) and stem hydraulic conductivity (K) of leaf explants (Mont) receiving xylem exudate from either flooded[z] or check sour cherry trees (Mont/Mahaleb).

Exudate	LWP (MPa)	K ($cm\ s^{-1}$)
Check	-0.58	0.000377
Flood	-0.43	0.000247

[z] Trees flooded 4 days.

APPENDIX B

APPENDIX B

ETHANOL AND ACETALDEHYDE CONCENTRATION IN ROOT EXUDATE FROM FLOODED AND CONTROL SOUR CHERRY TREES (MONTMORENCY/MAHALEB).

The purpose of this experiment was to determine the concentration of ethanol and acetaldehyde in root exudate from flooded and control sour cherry trees.

Containerized two year old sour cherry trees (Montmorency/Mahaleb) were flooded for 12 days in manner described in Section 1, Experiment 1. Exudate was collected from 6 flooded and 8 check trees at conclusion of flooding treatments in manner described in Appendix A. First ml of exudate was drawn off with a pipette and placed in 20 ml vial. Vials were immediately sealed, placed on ice and stored overnight at 2 °C before analysis. Ethanol and acetaldehyde standards (1000 ppm) were prepared with deionized water. One ml of each sample and standard was transferred with a pipette to a 25 ml flask which was then sealed with a rubber septum. Flasks were placed in a stirred water bath at 32 °C and allowed to equilibrate for ca. 1 hour. Gas samples (1 ml) were then drawn from the headspace above each sample. Analyses were performed using a Varian 1200 gas chromatograph (Varian Associates Inc., Sunnyvale, CA) with a H flame detector on a Porapak Q 80/100 mesh column at 120 °C and N_2 carrier. Concentrations were estimated from peak heights. Each exudate sample was analyzed twice and the results averaged.

Results are reported in Table 1. Within the limits of detection (ca. 160 and 50 ppm for ethanol and acetaldehyde, respectively) no ethanol or acetaldehyde was found in any exudate samples from control

Table 1. Concentration of ethanol and acetaldehyde in xylem exudate from flooded[z] and control sour cherry trees (Montmorency/Mahaleb).

Treatment	Ethanol (ppm)	Acetaldehyde (ppm)
Flooded	789 ±436	699 ±617
Control	<160[y]	<50[y]

[z] Trees flooded 14 days.
[y] Limits of detection.

trees. However, exudate samples from flooded trees contained a mean concentration of 789 and 617 ppm of ethanol and acetaldehyde, respectively. Ethanol concentration ranged from 191 to 1413 ppm, while acetaldehyde concentration ranged from 47 to 1670 ppm.

APPENDIX C

APPENDIX C

EFFECTS OF ETHANOL, ACETALDEHYDE AND SODIUM BICARBONATE ON GAS EXCHANGE CHARACTERISTICS OF SOUR CHERRY LEAF EXPLANTS MONTMORENCY.

The purpose of these experiments was to determine if ethanol, acetaldehyde or sodium bicarbonate reduced photosynthesis of leaf explants and, if so, whether or not this reduction occurred in a manner similar to that produced by xylem exudate from flooded sour cherry trees.

Sour cherry leaf explants (Montmorency) were prepared from containerized trees (Montmorency/Mahaleb) in manner described in Appendix A. Explants were placed in the walk-in growth chamber described in Section III. Chamber was operated at 25 °C and ca. 50% relative humidity. Light levels at leaf surfaces were maintained between 1000 and 1400 micromols m^{-2} s^{-1} PPf. Ambient CO_2 concentrations were not controlled but typically ranged between 400 and 450 micromol mol^{-1} CO_2. Plants were allowed to equilibrate for ca. 2 hours prior to start of experiments. Treatments were imposed by replacing the deionized water in each vial with a solution of ethanol, acetaldehyde or sodium bicarbonate (and deionized water) ranging in concentration from 1 to 1000 ppm (10 to 1000 ppm in ethanol study). Five replications of each treatment were used (4 in ethanol study). Gas exchange characteristics were measured with the portable system described in Section I, Experiment 1. Cuvette temperature typically ranged from 25 to 30 °C and vapor pressure deficit from 2.5 to 3.5 KPa. CO_2 concentration of air stream entering cuvette was maintained at ca. 400 micromol mol^{-1} CO_2. Light levels during measurements typically ranged

between 1100 and 1400 micromol m^{-2} s^{-1} PPF. A single measurement was made every hour on each explant until end of experiment.

Effects of ethanol, acetaldehyde and sodium bicarbonate on gas exchange characteristics are summarized in Tables 1, 2 and 3, respectively. No treatment produced a significant reduction in any of the characteristics measured indicating that none of these materials is by itself capable of reproducing the effects of xylem exudate from flooded trees observed in experiments described in Appendix A.

Table 1. Effects of various concentrations of ethanol on net CO_2 assimilation (A), residual mesophyll conductance to CO_2 (g_r'), and stomatal conductance to CO_2 (g_l) of Montmorency leaf explants.

Parameter	Treatment (ppm EtOH)	Hours after introduction of treatment				
		0	1	2	3	4
A ($\mu mol\ m^{-2}\ s^{-1}$)	0	9.2	10.4	8.7	8.6	10.3
	10	6.9	9.6	8.5	8.6	9.7
	100	9.8	9.1	8.5	8.4	9.4
	1000	10.2	9.3	8.5	8.5	9.3
g_r' ($mmol\ m^{-2}\ s^{-1}$)	0	26.8	27.3	27.1	26.5	26.6
	10	18.2	25.4	26.8	26.2	25.9
	100	27.4	22.8	24.9	23.7	23.6
	1000	29.7	23.7	25.4	25.1	23.3
g_l ($mmol\ m^{-2}\ s^{-1}$)	0	92	88	81	81	84
	10	95	79	75	79	74
	100	97	87	86	87	82
	1000	103	86	86	84	82

Table 2. Effects of various concentrations of acetaldehyde on net CO_2 assimilation (A), residual mesophyll conductance to CO_2 (g_r'), and stomatal conductance to CO_2 (g_l) of Montmorency leaf explants.

Parameter	Treatment (ppm Acet)	Hours after introduction of treatment				
		0	1	2	3	4
A (μmol m^{-2} s^{-1})	0	11.5	11.4	10.5	9.7	9.1
	1	10.6	10.3	9.7	10.8	8.6
	10	9.9	9.8	10.4	9.8	9.1
	100	10.1	10.1	10.0	8.8	8.7
	1000	12.2	11.0	12.2	11.6	9.2
g_r' (mmol m^{-2} s^{-1})	0	29.2	31.6	31.9	30.7	27.4
	1	26.1	28.2	28.3	33.9	24.7
	10	25.1	25.4	29.5	30.6	25.3
	100	26.3	28.8	30.6	28.3	26.8
	1000	31.2	30.3	36.7	35.7	27.5
g_l (mmol m^{-2} s^{-1})	0	112	112	97	86	88
	1	107	105	93	91	86
	10	93	104	96	84	94
	100	93	94	90	81	83
	1000	110	116	106	103	98

Table 3. Effects of various concentrations of sodium bicarbonate on net CO_2 assimilation (A), residual mesophyll conductance to CO_2 (g_r'), and stomatal conductance to CO_2 (g_l) of Montmorency leaf explants.

Parameter	Treatment (ppm $NaHCO_3$)	Hours after introduction of treatment				
		0	1	2	3	4
A ($\mu mol\ m^{-2}\ s^{-1}$)	0	10.3	8.4	9.7	8.8	8.9
	1	9.6	10.1	9.5	9.2	9.2
	10	8.4	8.0	9.1	8.3	8.0
	100	9.0	8.5	8.9	7.8	8.0
	1000	9.6	9.9	9.3	9.1	9.0
g_r' ($mmol\ m^{-2}\ s^{-1}$)	0	29.0	26.3	30.3	28.4	26.6
	1	26.1	30.1	29.8	30.0	27.6
	10	21.9	22.7	27.5	26.4	23.0
	100	24.7	23.8	27.3	24.3	22.8
	1000	25.6	28.8	28.3	29.4	26.1
g_l ($mmol\ m^{-2}\ s^{-1}$)	0	107	91	106	107	105
	1	96	101	96	97	92
	10	92	93	102	94	88
	100	110	119	103	101	100
	1000	104	115	106	107	104

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