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Photosynthetic and respiratory characterization of field grown tomato

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Abstract

The photosynthetic responses of tomato (*Lycopersicum esculentum* Mill.) leaves to environmental and ontogenetic factors were determined on plants grown in the field under high radiation and high nitrogen fertilization. Response curves showed net photosynthesis to only approach light saturation at a photosynthetic photon flux density (PPFD) of 2200 μmol $m^{-2} s^{-1}$, with rates of approx. 40 μmol CO_2 $m^{-2} s^{-1}$. A broad temperature optimum was observed between 25° and 35°C, with 50% of the photosynthetic rates remaining even at 47°C. The high rate, the lack of saturation at the equivalent of full sunlight, and the tolerance to high temperature of tomato were unusual in light of the literature on this C_3 species. Apparently, acclimation to the field environment of high radiation and hot daytime temperature, coupled with the high nitrogen nutrition, made possible the high photosynthetic performance normally associated with C_4 species.

Photosynthetic ability of the leaf reached a maximum near the time of its full expansion and declined steadily thereafter, regardless of the time of leaf initiation. Leaf nitrogen content showed a similar decline with leaf ontogeny. Photosynthesis was linearly correlated with nitrogen content, whether the nitrogen variation was due to leaf age or rates of nitrogen fertilization. Internal CO_2 concentrations (C_i) of the leaf indicated that stomatal function was well coordinated with photosynthetic capacity as leaf age and fluence rate varied down to a PPFD of 500 μmol $m^{-2} s^{-1}$. As PPFD decreased further, there was less stomatal control and C_i increased to as high as 320 μbar bar^{-1}.

Dark respiration was highest for expanding leaves and increased nearly exponentially with temperature. Respiration was also highest for young and expanding fruits, and next highest for fruits just turning pink. Fruit respiration increased approximately linearly with temperature, and was estimated to be an important component of the CO_2 flux of the plant near maturity because of the heavy fruit load and low leaf photosynthesis at that time. The results are significant for model simulation of tomato productivity in the field.

Introduction

Plant growth and productivity rest ultimately on the photosynthetic acquisition of carbon dioxide from the atmosphere. Process-based plant growth models consider photosynthesis as the starting point for growth, resulting in biomass production when accumulated over time (Loomis et al. 1979, Penning de Vries 1983). Photosynthetic rates per unit leaf area, however, generally do not correlate with crop yields (Gifford and Evans 1981). This is particularly true when yield consists of only a part of the shoot biomass,

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as the partition of biomass into the harvested organ, reflected in the harvest index, can be very different among cultivars and species (Jordan 1983, Gifford et al. 1984). One major difficulty in relating yields to photosynthesis is that crop canopies are made up of leaves of different ages usually experiencing quite different, variable and non-optimal environments for CO_2 assimilation. The integration and extrapolation from photosynthetic response curves of single leaves to canopy assimilation still present major challenges (Penning de Vries 1983). Inevitably, computer simulation has been resorted to. Another difficulty is that photosynthesis is frequently studied on leaves grown in controlled environments but the results are extrapolated to field performance of the crop. It is well known that photosynthetic characteristics are altered by the environment in which the plant is grown (Berry and Downton 1982). Hence, analysis and simulation of performance in the field must be based on response curves obtained from field grown plants.

Processing tomato is an important crop in California and elsewhere and realistic photosynthetic data bases for evaluating its performance are lacking. This investigation characterized the photosynthetic and respiratory responses of leaves and fruits of field grown tomato to environmental and ontogenetic factors.

Materials and methods

A determinate processing cultivar (UC-82B) of tomato (*Lycopersicum esculentum* Mill.) was grown in an experimental field at the University of California at Davis in 1983, 1984 and 1985. In addition, plots at the West Side Field Station of the university at Five Points, California, were also used during 1982 and 1983. At both locations, the weather during the season was sunny (weekly mean solar radiation of 29 MJ m^{-2} day^{-1} in June, falling to 22 MJ m^{-2} day^{-1} in early September) with warm days and cool nights, and little or no rainfall. The soil at Davis was a deep Yolo silt loam, fertilized with 200 kg N ha^{-1} as NH_4NO_3. As in commercial practices, seeds were planted in double rows on wide beds spaced at 1.5 m, and thinned to 2 to 4 plants per meter (average density of 44 000 plants ha^{-1}). Irrigations were applied by sprinklers, first to establish the stand, then weekly to replenish the water evapotranspired (5–6 cm at full canopy) and maintain the soil at high water status. The plots at the West Side Field Station were cultivated similarly, except irrigation was weekly by furrow.

In Davis at planting, large plastic pots (8 and 12 l) with large drainage holes were filled with field soil, buried to the top rim within the plant rows, and also planted with seeds. In time, roots grew out through the holes into the soil outside and plants appeared very similar to the rest of the field. Some pots, with the drainage holes sealed to prevent root extrusion, were also planted and various amounts of nitrogen were applied to the pots. Due to high residual nitrogen in the soil, it was necessary to confine the roots to the pot to obtain plants of low nitrogen status. Since the sprinkler irrigation was controlled only to replenish the water evapotranspired, there was very little drainage and no problem of aeration was encountered with the sealed pots as judged by plant appearance and soil moisture.

To determine photosynthetic response, the pots were dug out, brought to the laboratory, and measured the same day in a gas exchange apparatus operating as an open system. Most of the branches of the plant, other than that selected for measurement, were covered with a plastic bag and aluminium foil to reduce transpiration and minimize water stress. This was necessary since the roots outside the pot were severed when dug up. Water potential measured with a pressure chamber at the end of gas exchange determination was nearly always above −0.4 MPa. Previous tests with other species indicated that the severance of some roots had no effect for many hours on photosynthesis and stomatal behavior other than that induced by water stress. In this study, there was no obvious difference in photosynthetic behavior of the plants with roots outside the pot severed and those grown in pots with drainage holes sealed and roots intact.

Air of ambient CO_2 and known water vapor pressure was passed over a leaf or leaflet enclosed in the chamber of the gas exchange apparatus. The chamber was made of nickel-plated aluminum, 20.8 × 11.3 cm, topped by glass and was vigorously stirred with two Micronel (Vista, California) fans. Boundary layer conductance was estimated to be 2 mol $m^{-2} s^{-1}$ using wet filter-paper leaf replicas. Vapor pressure was controlled by saturating the air over warm water and then condensing to the desired dew point (accuracy of 0.1°C) in a copper condenser, and measured by both a dew point hygrometer (EG&G model 880-C1, Waltham, Massachusetts) and a Vaisala (Helsinki, Finland) humidity capacitance sensor operating at 42°C to minimize hysteresis. Leaf temperature was controlled by Peltier blocks attached to the chamber and monitored with two 40 gauge (80 μm diameter) thermocouples pressed on the abaxial side. CO_2 concentration was controlled by mixing air of different concentrations with mass flow controllers (Tylan, Torrance, California) and monitored with a differential infrared gas analyzer (IRGA) (Horiba Model VIA 500, Kyoto, Japan) capable of resolving 0.05 μbar CO_2 bar^{-1} air. To reduce water vapor interference, the air was passed through an ice trap prior to entrance to the IRGA. Photosynthetic photon flux density (PPFD) of over 2500 μmol $m^{-2} s^{-1}$, supplied by a G.E. 1000-watt metal halide lamp, was modulated with screens and measured with a quantum sensor (Licor, Lincoln, Nebraska). The rate of CO_2 assimilation, epidermal (mostly stomatal) conductance for water vapor, CO_2 pressure of the intercellular air spaces (C_i), and related gas exchange parameters were calculated according to the methods of von Caemmerer and Farquhar (1981) and Cowan (1977).

Instantaneous rates of assimilation were also measured periodically in the field at Davis and West Side. Leaves were tagged shortly after appearance for age identification. Photosynthesis was measured at midday with the leaf held perpendicular to sunlight by a clamp-on photosynthetic cup (1.8 cm^2 in area) connnected to a Binos (Leybold-Heraeus, Hannau, West Germany) IRGA operating in the differential mode. Air from a tank of approx. 340 μbar CO_2 bar^{-1} was passed sequentially over the abaxial and adaxial sides of the leaf in the cup at approx. 375 μmol air s^{-1} (500 ml min^{-1}) until a steady photosynthetic rate was achieved. Depletion in CO_2 due to assimilation was usually less than 20 μbar bar^{-1}. Humidity and temperature were not controlled, but measurements generally took less than 30 s. The clamp-on cup was designed for high air velocity to maximize boundary layer conductance, estimated to be 1.0 to 1.3 mol $m^{-2} s^{-1}$ using wet filter-paper leaf replicas. The flow rate through the cup was monitored by pressure drop across viscous flow resistances using a pressure transducer and was calibrated with a bubble flow meter.

Dark respiration of leaves was determined in the gas exchange apparatus. Plants in pots were covered in the field with aluminum foil at dawn and brought to the laboratory. Leaves were kept in darkness for 6 to 9 h prior to measurement to ensure a steady-state rate of respiration.

Fruit of four developmental stages were picked and measured immediately for respiration in the field along two diurnal cycles to obtain the full range of temperatures experienced by them. Measurements were completed in less than 5 min after picking. Air of known CO_2 concentration (around 340 μbar bar^{-1}) from a tank was passed over the fruit in a stirred (Micronel fan) glass chamber wrapped in aluminum foil to maintain darkness. The difference in CO_2 concentration between the incoming and outgoing air streams was measured with the portable Binos IRGA, and the flow rate through the chamber, with floating ball rotometers. Temperature was monitored by inserting a thermocouple into the fruit.

For nitrogen content, leaves were harvested after measuring photosynthesis, oven-dried at 70°C and finely ground. A subsample of 250 mg or less was digested on a digestion block at 370°C for 2.5 h in 5 cm^3 H_2SO_4, 3.5 g K_2SO_4, and 3 cm^3 30% H_2O_2 in the presence of a selenized boiling chip. After cooling and dilution to volume, ammonium in the solution was passed selectively through a permeable microtubing and determined by conductivity, as described by Carlson (1978). The apparatus was calibrated with standard solutions of NH_4Cl.

Results and discussion

For all the response curves presented here, environmental and ontogenetic factors were kept near optimal except the one being varied. In general, youngest, uppermost, fully expanded and fully exposed leaves of high nitrogen content were used to determine the responses to environmental variables, in air of ambient CO_2 concentration (approx. 340 μbar bar^{-1}).

Light

Light response curves are shown in Fig. 1A. Light saturation, although approached, was not reached at 2000 μmol m^{-2} s^{-1} of PPFD, a level just below midday sunlight in Davis on clear summer days. This is in contrast to the prevailing impression that most C_3 species tend to saturate at levels substantially below full sunlight (Berry and Downton 1982). In addition, the rates of photosynthesis by these leaves were normally close to 40 μmol CO_2 m^{-2} s^{-1} under high irradiance, rates that also exceed common values in the literature using plants grown in greenhouses or growth chambers.

Leaves of many species have been shown to have photosynthetic responses to light intensity in accordance with their growth conditions, typical examples being 'sun' and 'shade' leaves of some plants (Berry and Downton 1982, Björkman 1981). For tomato grown under glass in England, one study (Peat 1970) showed photosynthesis to saturate nearly at an irradiance of 150 W m^{-2} (probably equivalent to considerably less than 300 μmol m^{-2} s^{-1} of PPFD) with rates in the range of 10 to 20 μmol m^{-2} s^{-1}, another (Acock et al. 1978) showed near saturation at 200 W m^{-2} of PPFD with rates near 23 μmol m^{-2} s^{-1}. Martin et al. (1981) found tomato photosynthesis in air of 1500 μbar CO_2 bar^{-1} to be nearly saturated at a PPFD of 1800 μmol m^{-2} s^{-1} when grown at a PPFD of 450 μmol m^{-2} s^{-1} in a growth chamber. Their maximal photosynthetic rate in air of 300 μbar CO_2 bar^{-1}, however, was only 21 μmol m^{-2} s^{-1}. The latter is in loose agreement with the near saturation rates of approx. 18 μmol m^{-2} s^{-1} at 1000 μmol m^{-2} s^{-1} of PPFD in air of 350 μbar CO_2 bar^{-1} reported (Jun et al. 1988) for three cultivars of marketing tomato grown under 400 μmol m^{-2} s^{-1} of PPFD at mid-plant height. We grew the same processing tomato cultivar (UC-82B) under 600 μmol m^{-2} s^{-1} in a growth chamber in Davis and found photosynthesis to saturate at 1200 μmol m^{-2} s^{-1} with rates around 25 μmol m^{-2} s^{-1} (unpubished). In contrast, our field grown plants only approached light saturation at a PPFD of 2000 μmol m^{-2} s^{-1} with rates close to 40 μmol m^{-2} s^{-1}. Other studies also reported high rates of leaf photosynthesis for field grown tomato: 30 μmol m^{-2} s^{-1} on sunny afternoons in the eastern United States for marketing tomato (Bunce 1988), and 40 μmol m^{-2} s^{-1} at light saturation in the desert of western United States (Sage and Sharkey 1987).

Conductance to water vapor also increased continuously with increasing PPFD, up to at least 2300 μmol m^{-2} s^{-1} (Fig. 1B). It thus appears that stomatal behavior is coordinated with photosynthetic capacity when PPFD is varied for tomato leaves. Similar results have been found with other species (Wong et al. 1979, Björkman 1981). This allowed the maintenance of nearly constant C_i for the range of irradiance down to 500 μmol m^{-2} s^{-1}, below which C_i increased (Fig. 1C). For the range where C_i stays nearly constant, it is not possible to resolve from these correlative phenomena whether stomatal opening is causing faster rates of photosynthesis, or whether higher rates of photosynthesis are responsible for the wider stomatal aperture. For the range where C_i increases with decreasing PPFD, stomata do not play a substantial role in controlling photosynthesis, but do appear to open in response to reductions in C_i.

Temperature

Curves of photosynthetic response to temperature are presented in Fig. 2. A broad maximum fell between 25 and 35°C. This range corresponds closely to the temperatures experienced by the crop for much of the daylight hours on most days during the season at Davis. Below 20°C and above 40°C, photosynthesis was substantially reduced. Considerable photosynthesis remained, however, even at 47°C! Many plants are known to acclimate to temperature (Berry and Downton 1982) with shifts in their temperature optima as growing conditions vary. Bar-Tsur et al. (1985) reported peaks of photosynthesis between 22 and 27°C for tomato grown at day/night cycles of 24°C/18°C. Jun et al. (1988)

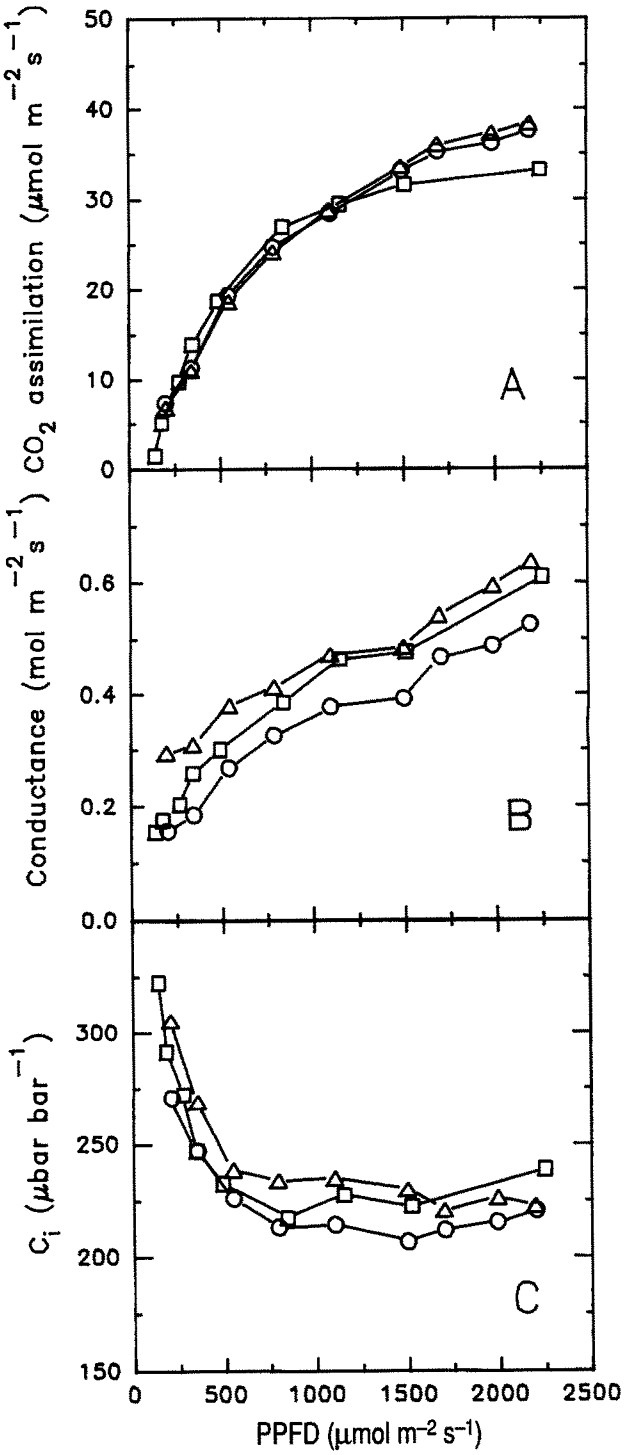

Fig. 1. Response of (A) net CO_2 assimilation; (B) leaf epidermal conductance for water vapor; and (C) calculated intercellular CO_2 concentration (C_i) of youngest, fully expanded and fully exposed field grown tomato leaves of high nitrogen status to photosynthetic photon flux density (PPFD). Air CO_2 partial pressure was ambient. Leaf temperature was 29°C and vapor pressure difference between leaf intercellular space and bulk air (VPD) was 12 to 14 mbar. Each line represents a leaf from a different plant. Data are from Davis in 1983 and 1984.

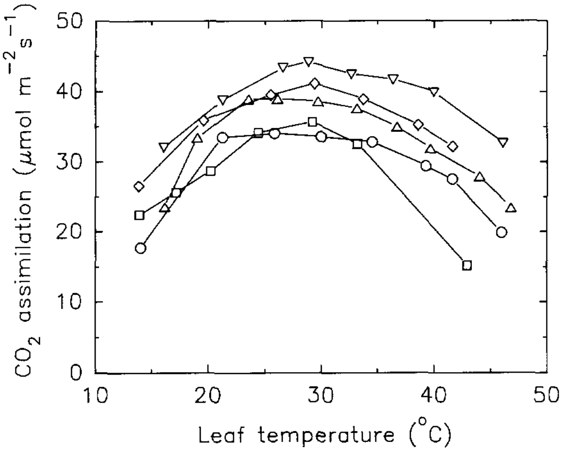

Fig. 2. Response of net CO$_2$ assimilation of youngest, fully expanded and exposed tomato leaves to leaf temperature. Air CO$_2$ was ambient and fluence rate was 2200 µm^{-2} s^{-1}. VPD was 12 to 14 mbar up to 25 to 30°C, then increased with further increases in temperature. Each line represents a leaf from a different plant. Data are from Davis in 1983.

found photosynthetic peaks at 30°C for their three cultivar of tomato grown at either 30°C/30°C or 30°C/15°C day/night cycles. For tomato grown outdoors in a desert environment at 1500 m in the western U.S., photosynthesis reached an apparent maximum at 28°C; but measurements were not carried out beyond 32°C (Sage and Sharkey 1987).

In the variable temperature experiment (Fig. 2), vapor pressure difference (VPD) between leaf and bulk air was maintained nearly constant (12–14 mbar) up to 25 to 30°C. Humidification of the air to dewpoints above those temperatures was not possible, however, because of water condensation in the air lines. Therefore in the data of Fig. 2, VPD increased with increases in temperature above approximately 30°C, to 50 mbar or higher at 45°C. We found stomata of tomato to be sensitive to VPD. At a constant leaf temperature, photosynthesis and C$_i$ decreased steadily as VPD was increased (Bolaños and Hsiao, in preparation), indicating stomatal closure was limiting supply of CO$_2$ to the mesophyll. It follows that some of the decline in assimilation rate at temperatures much higher than 30°C in Fig. 2 is attributable to partial stomatal closure and reduced C$_i$ in response to high VPD.

Leaf nitrogen content and age

The dependence of CO$_2$ assimilation of the most recently matured and fully exposed leaves on their nitrogen content is shown in Fig. 3 for two different years. The rate of maximum photosynthesis (i.e., at nearly saturating light, optimal temperature, and high water status and humidity) increased almost linearly with increases in nitrogen content although the data showed considerable scatter. The variation in leaf nitrogen was achieved by varying the levels of soil nitrogen. Maximum nitrogen levels for these leaves rarely exceeded 5% and it was difficult to obtain green leaves with less than 2% nitrogen. The dependence of leaf photosynthesis on nitrogen is expected (Field 1983, Hunt et al. 1985) and high nitrogen levels are associated with higher levels of enzymes and photosynthetic machinery (Thomas and Stoddart 1980, Seeman et al. 1987, Evans 1989).

The dependence of photosynthesis on age of tagged leaves of plants grown in the field is shown in Fig. 4A. Net photosynthesis, measured

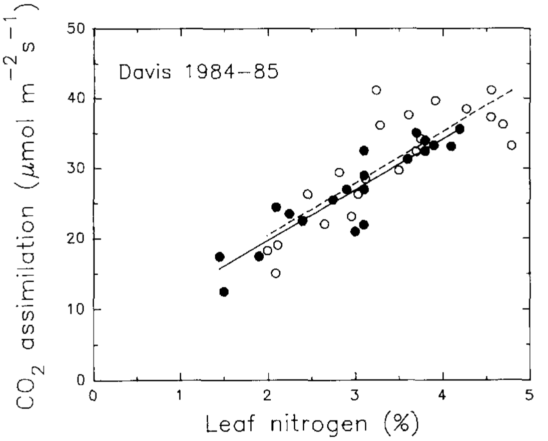

Fig. 3. Relationship between net CO$_2$ assimilation of youngest, fully expanded and exposed leaves and their nitrogen content as % of dry matter. The variation in leaf nitrogen content was achieved by varying levels of soil nitrogen. PPFD was 1700 µmol m^{-2} s^{-1} or higher. Open circles (○) represent data from plants grown in pots in the field in Davis in 1984 and brought to the laboratory for measurements in the steady state gas exchange apparatus. Regression equation for the line is $y = 5.70 + 7.34x$. Closed circles (●) represent data obtained in Davis in 1985 in the field using a newly available portable steady state gas exchange apparatus. Regression equation is $y = 5.28 + 7.22x$.

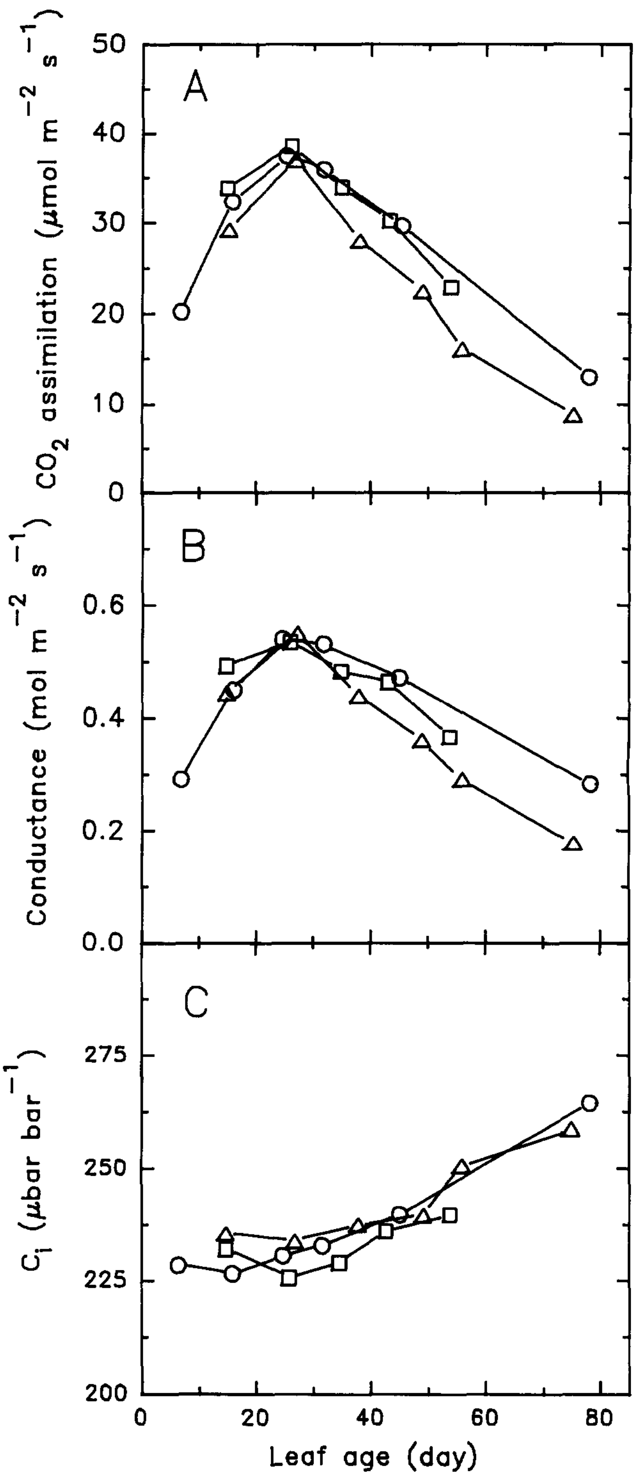

Fig. 4. Relationship between: (A) net CO_2 assimilation; (B) epidermal conductance; and (C) calculated internal CO_2 concentration of tomato leaves and their chronological age. Measurements were made on tagged leaves of different ages on plants grown in pots in the field and brought to the laboratory in 1983. PPFD was approx. 2200 $\mu mol^{-2} s^{-1}$; leaf temperature was 28 to 30°C; and VPD was 12 to 14 mbar. Each line represented leaves initiated on a different date.

in the laboratory gas exchange apparatus, reached a maximum almost coincidental with leaf full expansion (20–25 days old), and declined linearly with further aging. Similar results were obtained when instant rates of photosynthesis were measured at midday on age-tagged tomato leaves in the field with the portable photosynthetic cup (Fig. 5). The general pattern is similar to that reported by Peat (1970) for glasshouse grown tomato, except that his rates were much lower and leaf longevity shorter. In the present work, considerable photosynthesis was still evident (Fig. 5) in leaves at the beginning of visible senescence (about 80 day old). It should be noted that the decline in photosynthesis with leaf age was similar, regardless of the growth stage when the leaf first appeared (Fig. 5). Besford et al. (1985) correlated RuBP carboxylase activity to the changes in photosynthetic rates with tomato leaf age.

Diffusion conductance (Fig. 4B) paralleled the pattern of photosynthesis with leaf ontogeny, reaching a maximum also coincidental with full leaf expansion, and then declined steadily with further aging. The calculated C_i (Fig. 4C) showed a tendency to increase with leaf age, but only slightly. The near constancy of C_i is indicative of the close coordination between photosynthetic capacity and stomatal behavior manifested by tomato leaves. Results obtained with maize (Wong 1979) and other species (Woodward and Rawson 1976, Davis and McCree 1978) have suggested a near constant C_i with aging as well.

Tomato leaves lost nitrogen as they aged (Fig. 6), presumably the result of dilution by structural dry matter high in carbon at the early stage and the later export of nitrogen to other developing organs (Thomas and Stoddart 1980). The decline in nitrogen per unit of dry matter was not the result of an increase in specific leaf weight (dry weight per unit area) with age. Mean specific leaf weight (for all leaves of the canopy) was 9.0 mg cm^{-2} at 35 days after emergence, declining steadily to 6.0 mg cm^{-2} until day 49, then remained between 5.6–6.0 mg cm^{-2} thereafter. If the decline in leaf nitrogen was responsible for the decline in photosynthetic rate with leaf maturation, then photosynthesis should correlate with leaf nitrogen regardless of leaf age. In general, that was found to be the case for two different years in the field (Fig. 7A, B). Photosynthesis rates, measured at midday with the photosynthetic cup, were generally lower than those determined in a steady-state gas exchange apparatus (Fig. 3). Probably the rates did not reflect the maximum possible for these leaves, since at midday in the field water deficits, high temperatures, or low humidity may inhibit

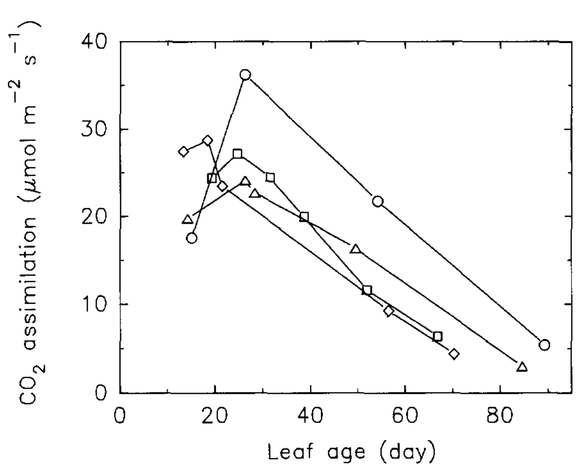

Fig. 5. Relationship between net CO_2 assimilation at midday and leaf age in the field in Davis. Assimilation was measured periodically with a portable photosynthetic cup on tagged leaves as they aged naturally in 1983. Data are means of six leaves, with each line representing leaves of the same appearance date, ranging from 25 to 55 days after emergence.

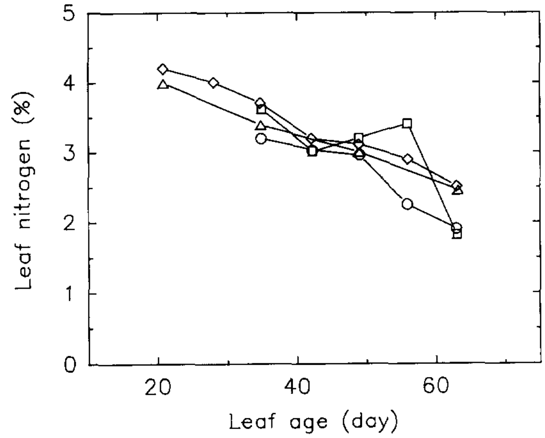

Fig. 6. Nitrogen content as % of dry matter of tomato leaves as a function of leaf age. Data are from plots fertilized with 200 kg nitrogen ha^{-1} at West Side Field Station in 1982 and 1983. Data are means of approximately six leaves, with each line representing leaves of the same appearance date.

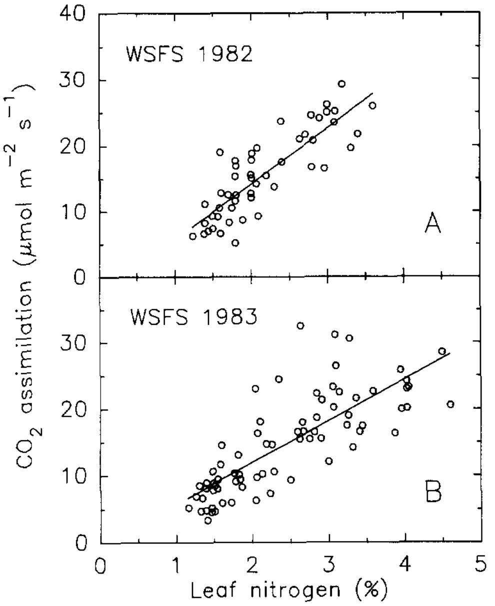

Fig. 7. Midday net CO_2 assimilation of tomato leaves of different ages in the field in relation to their nitrogen content as % of dry matter. Measurements were made with a photosynthetic cup at West Side Field Station (WSFS). The variation in nitrogen was the result of two rates of nitrogen fertilization and the natural decline in nitrogen content as the leaves aged over the season. Regression equation for the line is $y = -1.69 + 7.91x$ for 1982 and $y = -0.52 + 6.25x$ for 1983. Temperatures of the leaves during the measurements were generally in the range of 25 to 34°C.

photosynthesis. Nonetheless, the data still show a dependence of photosynthesis on nitrogen content for leaves of all ages. These findings suggest the possibility of reducing the two variables, age and nitrogen, to a single one, nitrogen content, on which tomato leaf photosynthesis partially depends. A similar suggestion based on data obtained from other species was made earlier by Field (1983).

Respiration

The carbon balance of a crop is also dependent on respiration rates. The temperature dependence of respiration by recently matured and fully exposed leaves was determined in the gas exchange apparatus (Fig. 8). As temperature increased, respiratory losses increased markedly, in nearly an exponential fashion. Nonetheless, the respiration rate at 30 to 35°C (2–3 μmol $m^{-2}\,s^{-1}$) was still only a small fraction of the net photosynthesis of these leaves (35–40 μmol $m^{-2}\,s^{-1}$). At 45° or higher, however, respiration approached 10 μmol $m^{-2}\,s^{-1}$ and apparently accounted for the major part of the drop in net CO_2 assimilation at this temperature (Fig. 2).

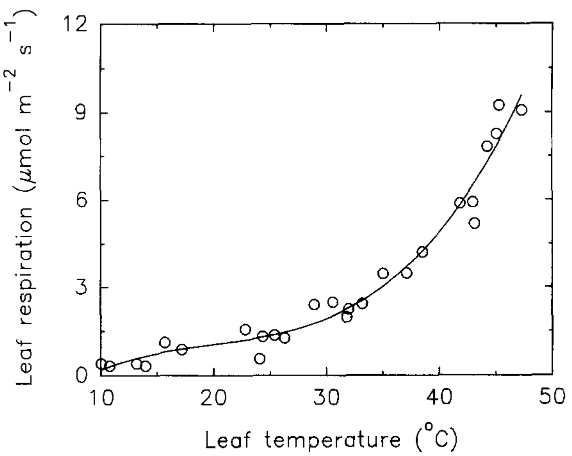

Fig. 8. Response of dark respiration of youngest, fully expanded and exposed leaves of field grown tomato to leaf temperature. Measurements were made in the gas exchange apparatus in the laboratory after the plants were kept for 6 to 9 h in darkness. Data are single measurements taken in Davis in 1984.

Respiration as a function of leaf age was also determined in the laboratory on age-tag leaves of field grown plants (Fig. 9). Very young leaves had relatively high rates of respiration (3.5 μmol $m^{-2}\,s^{-1}$ at 29°), probably reflecting the high costs of leaf construction and biosynthesis. With

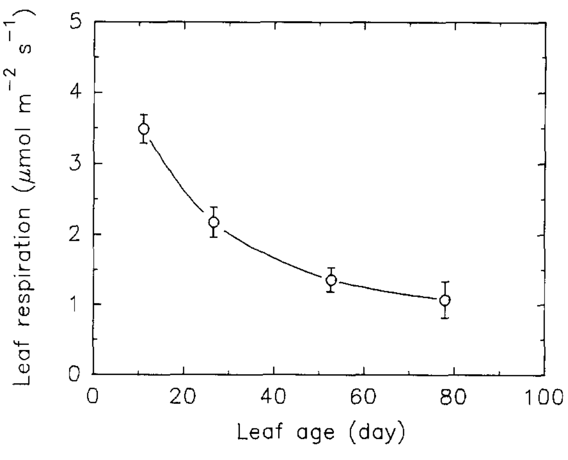

Fig. 9. Dark respiration of field grown tomato leaves as function of leaf age. Measurements were done at 29°C after 6 to 9 h of darkness. Data (±S.E.) are from Davis in 1984.

age, respiration gradually decreased, reaching a low level of 1 μmol m^{-2} s^{-1} as the leaves neared senescence.

Fruit respiration was estimated using a modified gas exchange system in the field. To evaluated respiration as a function of temperature, fruits at four developmental stages were harvested over two diurnal cycles, to obtain the full range of fruit temperatures in situ. For all the four developmental stages, respiration, expressed on a dry weight basis, increased with temperature (Fig. 10). Fruits in the 'B1' stage (green, and less than 25 mm in diameter) had relatively high rates of respiration, probably reflecting high biosynthetic activities. As the fruits grew but still remained green (B2 stage), the respiration rate at any given temperature declined. Respiration became high again when the fruits turned pink (B3 stage), probably reflecting the climacteric state. Respiration of red, fully mature fruits (B4 stage) was lower than at the B3 stage but higher than at the B2 stage. Fruit respiration increased only approximately linearly with temperature (Fig. 10), in contrast to the near exponential increase with temperature for leaves (Fig. 8).

The dry weight of the fruits at harvest from an adjacent area was nearly 700 g m^{-2} land area (Nyabundi 1985). Using the data of Fig. 10 for B4 fruits, fruit respiration rates of 8 to 10 μmol

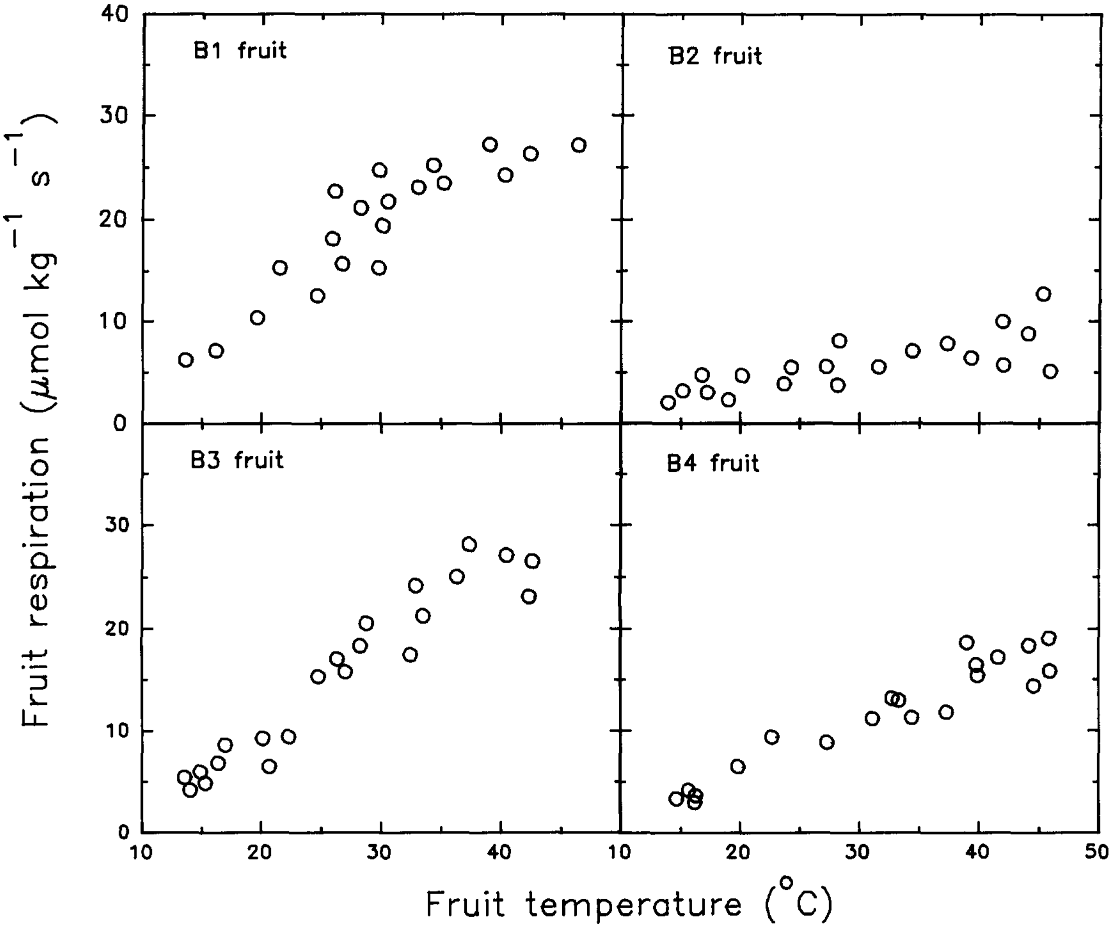

Fig. 10. Dark respiration per unit of dry matter of tomato fruits at four developmental stages in relation to fruit temperature. B1 fruits were green and smaller than 25 mm in diameter; B2 fruits were green and larger than 25 mm in diameter; B3 fruits were pink and maturing; and B4 fruits were fully mature and red. Each point represents a single measurement on a different fruit taken at Davis in 1984.

m^{-2} land s^{-1} may be estimated for much of daytime near harvest. This represents a substantial portion of the gross carbon assimilated at the late growth stages of tomato, when net canopy assimilation was in the range of 15 to 25 μmol m^{-2} land s^{-1} for the major part of the day (A.A. Held and T.C. Hsiao, unpublished).

Concluding discussion

The high rate of net photosynthesis, the lack of light saturation at PPFD levels equivalent to full sunlight (Fig. 1), and the retention of most of the CO_2 assimilation at a leaf temperature as high as 40°C (Fig. 2) reflected the adaptation of tomato leaves to the growth environment. These photosynthetic behaviors are in contrast with what may be inferred from the published photosynthetic literature on C_3 crops and on tomato. Most of the literature data on tomato were obtained from plants grown in controlled or protected environments of relatively low irradiance and mild temperature. In contrast, the plants studied here were grown in the field in a Mediterranean climate, a high radiation environment with high daytime temperature and cool nights. The high rate of nitrogen fertilization, in line with some of the local commercial practices for processing tomato, undoubtedly contributed significantly to the high photosynthetic rates and the high fluence rate required for light saturation. Cotton, another C_3 crop, was also observed to photosynthesize at high rates in the field at Davis, with net assimilations of as much as 50 μmol m^{-2} leaf s^{-1} or higher under full sunlight (Puech-Suanzes et al. 1989).

In spite of the high rates of nitrogen fertilization, the nitrogen content of the leaves began a continuous decline after full expansion of the leaves. That decline was associated with reductions in photosynthesis. The dependence of photosynthesis on nitrogen content and on leaf age could not be separated in the present study, suggesting the possible use of leaf nitrogen content as the overall factor in assessing photosynthetic capability of tomato leaves of diverse age.

Dark respiration of recently matured leaves (Fig. 8) was relatively insignificant at low temperatures when compared to their rates of photosynthesis, but became substantial at the upper end of the temperature range experienced by the crop. For example, at 40°C, a temperature occasionally encountered in the early afternoon on hot summer days in Davis, respiration was 5 μmol CO_2 m^{-2} s^{-1}. Cool nights prevail in Davis even in the summer, with temperatures ranging generally from 12 to 20°C. Using the data of Fig. 8, night respiration of recently matured leaves may be estimated to fall in the range of 20 to 30 mmol m^{-2} per night. That is not too significant when compared with the net assimilation of 80 to 120 mmol m^{-2} per hour at midday in the field (Fig. 5). Thus, leaves are highly efficient when it comes to its carbon gain vs. its carbon cost for maintenance. Because leaves constitute only a minor part of the total biomass, however, the dominant respiratory loss of carbon is by other plant parts, particularly fruits and stems.

The effect of leaf age on the ratio of rates of dark respiration to net CO_2 assimilation can be assessed from the data of Figs. 4 and 9. Before reaching maturity, respiration was relatively high, about 14% of the net assimilation rate, presumably the result of the cost of relatively high synthetic activities in the still growing leaf. Upon reaching maturity, the ratio dropped to 6 or 7%. As senescence was approached, the ratio rose again to 12%. For the crop as a whole, over its life cycle the fruit load increased as well as the structural biomass, with the corresponding increases in their respiratory loss of carbon. In terms of the leaf population, the ratio of respiration to photosynthesis probably declined initially. Later during the maturity and senescence stage, the ratio rose again. The net result for the crop in the later half of the season would be less and less net carbon gain during the day and greater and greater carbon loss at night. In fact, a reversal of the direction of net CO_2 flux, indicative of a switch from net assimilation to net carbon loss, was observed over a tomato canopy with a heavy fruit load near maturity about 1 h before sunset (A.A. Held and T.C. Hsiao, unpublished).

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