Growth and photosynthetic responses of dwarf apple saplings (Malus domestica Borkh. cv. Fuji) acclimated to 3 years of exposure to contrasting atmospheric CO2 concentrations (360 and 650 µmol mol–1) in combination with current ambient or elevated (ambient +5°C) temperature patterns were determined. Four 1-year-old apple saplings grafted onto M.9 rootstocks were each enclosed in late fall 1997 in a controlled environment unit in nutrient-optimal soil. Soil moisture regimes were automatically controlled by drip irrigation scheduled at 50 kPa of soil moisture tension. For the elevated CO2 concentration alone, overall tree growth was suppressed. However, tree growth was slightly enhanced when warmer temperatures were combined with the elevated CO2 concentration. Neither temperature nor CO2 concentration affected leaf chlorophyll content and stomatal density. The elevated CO2 concentration decreased mean leaf area, but increased starch accumulation, thus resulting in a higher specific dry mass of leaves. An elevated temperature reduced starch accumulation. Light-saturated rates of leaf photosynthesis were suppressed due to the elevated CO2 concentration, but this effect was removed or enhanced with warmer temperatures. The elevated CO2 concentration increased the optimum temperature for photosynthesis by ca. 4°C, while the warmer temperature did not. The results of this study suggested that the long-term adaptation of apple saplings to growth at an elevated CO2 concentration may be associated with a potential for increased growth and productivity, if a doubling of the CO2 concentration also leads to elevated temperatures.

Keywords Apple · Elevated carbon dioxide concentration · Temperature · Photosynthesis · Growth

Introduction

Evidence suggests that higher plants respond to a rising ambient atmospheric CO2 concentration by increasing their CO2 uptake (Ciais et al. 1995). According to global climate change scenarios, atmospheric CO2 concentrations are predicted almost double within the twenty-first century if current emissions are not reduced, and this doubling of the CO2 concentration will increase the mean surface temperature of the earth by about 2–6°C (Burroughs 2001). The atmospheric CO2 concentration and temperature are concomitant factors influencing the global environment (Morison and Lawlor 1999), so the response of higher plants to rising CO2 concentration, temperature, and their possible interactions is of significant interest for future agricultural and natural productivity (Fritschi et al. 1999). Recent studies confirm that the impact of global warming beyond a certain limit may have serious consequences for agricultural productivity (Lal et al. 1998).

One of the more sensitive and intriguing responses of plants to elevated CO2 and temperature is the acclimation of photosynthesis (Stitt 1991). There is abundant evidence that photosynthesis acclimates to elevated CO2 (Curtis 1996; Weber et al. 1994). Short-term exposure of plants to elevated CO2 stimulates the rate of photosynthesis and biomass production (DeLucia et al. 1999). However, the effects of long-term exposure among dif-
different plant species are conflicting. In general, prolonged exposure to elevated CO$_2$ reduces the initial stimulation of photosynthesis in many species, and frequently suppresses photosynthesis, due in part to excess accumulation of starch in leaves, which probably hinders CO$_2$ diffusion within the chloroplast (Makino 1994; Nafziger and Koller 1976). However, such photosynthetic suppression cannot be so great for species which have strong sink organs for carbohydrate accumulation (Makino and Mae 1999).

In general, an increase in temperature counters the suppression of photosynthesis due to an elevated CO$_2$ concentration (Drake et al. 1997), but the effects on plant growth are either positive or negative depending on the species (Reddy et al. 1998). From this interaction, it is deduced that the optimum temperature for the maximal rate of CO$_2$ assimilation must increase by about 6°C with an increase in the CO$_2$ concentration to 670 µmol mol$^{-1}$ (Long 1991). This interaction between CO$_2$ and temperature could, therefore, be of profound importance for future agricultural productivity, but there is little information regarding the nature of this interaction (Morison and Lawlor 1999).

The effect of an increased CO$_2$ concentration on plant growth is primarily due to changes in the composition and dry mass per unit area of leaves (Roderick et al. 1999), and the factors influencing these changes are primarily temperature dependent. Stomatal density is indicative of the extent of the acclimation of photosynthesis to a changing CO$_2$ concentration (Sage 1994), and generally decreases with an increase in CO$_2$. However, this decrease is not universally observed, and varies among species (Estiarte et al. 1994; Woodward et al. 1991). In contrast to the general response to an elevated CO$_2$ concentration, Maherali and DeLucia (2000) observed an increased leaf-specific hydraulic conductivity of Ponderosa pine exposed to elevated temperature. They hypothesized that this response should increase stomatal conductance and, therefore, transpirational cooling.

Apple, one of the commercially important temperate fruits, has been widely cultivated from prehistoric times. The global demand for apples and their products has not slowed down, and thus apple producers face the challenge of producing more apples from less area in an energy-efficient way (Ro and Park 2000). However, it is not clear whether such an increase in productivity can be sustained or achieved if global warming occurs. As elevated atmospheric temperature and CO$_2$ concentration are expected to be part of our future climate, it is important to understand and quantify the responses of apple trees to these two interactive environmental factors.

We measured the growth responses of dwarf apple (Malus domestica Borkh. cv. Fuji) saplings after 3 years of exposure to elevated CO$_2$, to elevated temperature, and to these factors in combination. To understand the mechanisms of the responses, leaf photosynthesis was measured. We hypothesized that: (1) high temperatures would ameliorate the effects of elevated atmospheric CO$_2$; (2) fruit yield would interact with the effects of atmospheric CO$_2$, temperature, and their interactions; and (3) long-term exposure to elevated CO$_2$ would shift the optimum temperature for photosynthesis to a higher temperature.

**Materials and methods**

CO$_2$- and temperature-controlled closed environment facility for plant growth

The closed-environment plant-growth facility, sunk into the soil, consists of two rows of four experimental units each. Each unit comprises a soil compartment (3×3×3 m), a transparent canopy enclosure (4×3×6 m), and a utility space for the temperature-control unit located on the north side. A weather station measures air temperature and relative humidity, wind speed and direction, solar radiation, and rainfall using a datalogger (21X, Campbell Scientific, USA). An open-architecture, distributed control system (DCS), POREX 6800 (POSCON Institute 1996), developed by POSCON of POHANG Steel, Korea, was used to control the facility and the automated collection of the sensors’ data. POREX 6800 DCS consists of two UNIX-based workstations (SPARCrstation 20, Sun Microsystems, USA) providing user-friendly man-machine interfaces for process operation and engineering works, and a process control station performing various real-time processing for field input/output points, and scheduled transfer of real-time data to a central database.

Each unit individually controls atmospheric CO$_2$ and air temperature. Compressed CO$_2$ gas is mixed with the flow of fresh air depending on the preset CO$_2$ concentration of the bulk air in the enclosure, and the mixture is brought into the enclosure by the air blower. The purity of the CO$_2$ gas was regularly inspected. Chilled or heated water is supplied to the fan coil unit depending on whether cooling or heating is required. Conditioned air passes through the plant canopy with sufficient flux to cause slight leaf flutter, and returns to the outlet duct just above the soil level.

An atmospheric CO$_2$ concentration at ±1 Pa of a predetermined set value and temperature at ±0.5°C of an ambient regime were individually controlled in each unit. Reference values for the ambient regime were taken real-time from a weather station. The solar radiation, air temperatures and relative humidity inside the enclosure were measured and multiplexed to a 21X datalogger. Atmospheric CO$_2$ concentrations in the enclosure are measured using infrared CO$_2$ analysers (ZH, Fuji Electric, Japan), and the addition of CO$_2$ prior to inlet points is thus controlled. Elevated temperatures included a 5°C step above the ambient regime. Four profiles of time-domain reflectometry probes were installed horizontally with respect to roots at 0.15-m intervals, 0.15–1.20 m below the soil surface, and three tensiometers at depths of 0.15, 0.45, and 0.75 m were also installed. Soil temperatures were measured from calibrated RTD temperature sensors.

Tree culture under controlled climate conditions

Apple (Malus domestica) cv. Fuji was selected because it represents a large portion of commercial apple production in Korea. Each soil compartment was back-filled with a sandy loam soil (Ro and Park 2000) in 1996, and was stabilized for 2 years. Four nursery apple trees each grafted onto a M.9 rootstock were transplanted in each compartment during late fall in 1997. Four units were maintained at 360 µmol CO$_2$ mol$^{-1}$, while the other four were maintained at 630 µmol CO$_2$ mol$^{-1}$. The air temperature inside two of the units maintained at 360 µmol CO$_2$ mol$^{-1}$ mimicked the ambient temperature pattern, while that of the remaining two was kept at an elevated temperature of +5°C. The same temperature treatments were used for the four elevated-CO$_2$ units. Both CO$_2$ and temperature treatments were initiated after transplanting and lasted three con-