Chapter 2
Response of Trees to CO_2 Increase

Among the principal abiotic requirements for plant growth, namely, light, water, nutrients and carbon dioxide, CO_2 is an anthropogenic gas associated with potential global warming. Any change in the availability of the above abiotic elements will impact not only plants, but the entire living systems. The current annual rate of increase in CO_2 ($\sim$0.5 %) is expected to continue with concentrations exceeding 600 ppm by the end of this century from the current 380 ppm (Houghton et al. 2001). Such an increase in the CO_2 levels will certainly affect the globally important process of photosynthesis, which sustains the life on this planet. Hence this has been the subject of intensive research during the past half a century. Since this book is going to deal with only the impact of climate change on fruit trees, the reader is referred to a number of general publications on this subject (e.g. Koch and Mooney 1996; Murray 1997; Luo and Mooney 1999; Reddy and Hodges 2000; Karnosky et al. 2001; Ziska and Bunce 2006; Kallarackal and Roby 2012). It is important to remember that as the methodology for artificial CO_2 enrichment experiments is improving around the groups concentrating on this research, our understanding of the response of plants to elevated CO_2 has been changing. All methods used during the past, namely, chamber methods and Free-Air-Carbon dioxide-Enrichment (FACE) have both positive and negative attributes and hence data obtained through any method should be treated with caution. Moreover, there is much interaction of CO_2 with other biotic and abiotic factors, which is usually ignored in many studies.

The primary effects of rising CO_2 on plants have been well documented and include reduction in stomatal conductance and transpiration, improved water-use efficiency, higher rates of photosynthesis, and increased light-use efficiency (Fig. 2.1) (Drake and González-Meler 1997). As may be noticed in the review on FACE facilities around the world, hardly any of them concentrate on horticultural tree crops (Ainsworth and Long 2005). Very few studies are available for fruit trees in open or closed chambers too.

F. Ramírez and J. Kallarackal, *Responses of Fruit Trees to Global Climate Change*,
SpringerBriefs in Plant Science, DOI 10.1007/978-3-319-14200-5_2

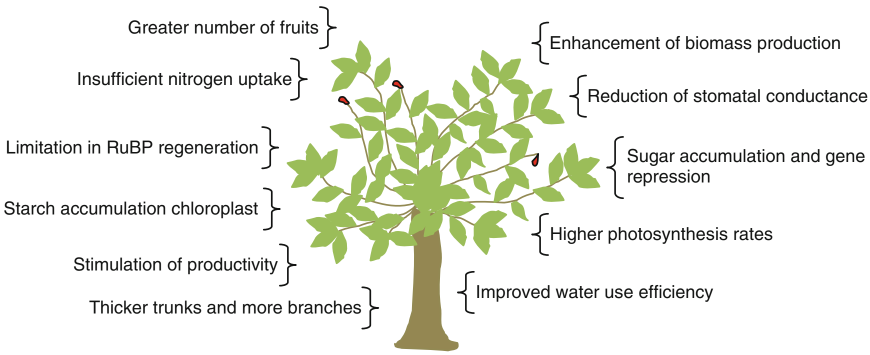

Fig. 2.1 Effects of elevated CO_2 on trees

Although photosynthesis is stimulated to approximately 37 % in the short-term elevated CO_2 experiments (Farquhar et al. 1980), when the CO_2 is raised from an ambient level of 350–550 ppm at 25 °C, over time the photosynthetic rates decline in some species relative to plants grown at ambient levels of CO_2. This phenomenon termed photosynthetic acclimation, although not very common, is reported in several species (Thomas and Strain 1991; Hogan et al. 1996). This acclimation at elevated CO_2 has been ascribed to at least five potential mechanisms at the cellular level: (a) sugar accumulation and gene repression (Krapp et al. 1993), (b) insufficient nitrogen uptake by the plant (Stitt and Krapp 1999), (c) a tie-up of inorganic phosphate with carbohydrate accumulation and a subsequent limitation in RuBP regeneration capacity (Sharkey 1985), (d) starch accumulation in the chloroplast (Lewis et al. 2002), and (e) triose phosphate utilization capability (Hogan et al. 1996).

An important point to be discussed with regard to the impact of elevated carbon dioxide (eCO_2) on fruit trees is the stimulation of productivity as noticed in certain other crops. In general, the FACE studies have reported 47 % stimulation in photosynthesis in trees compared to 7–8 % stimulation in yield in crops such as wheat or rice (Kim et al. 2003; Kimball et al. 1995; Ainsworth and Long 2005). However, in chamber studies the reports have been just the opposite, where the trees have not responded as in FACE experiments and the annual crops have responded much better. Many projections on the future food productivity have been made based on chamber studies, which would prove wrong if FACE studies are taken into account. Most of the increase in productivity reported for trees in FACE studies shows an increase in vegetative biomass including leaf area. Does it mean that only vegetative productivity is increased due to an elevation in CO_2 in the atmosphere? If productivity cannot be translated to reproductive parts, then we cannot expect the horticultural fruit crops to yield more.

When compared to the natural vegetation, studies on eCO_2 impacts on fruit trees are very limited. Sour orange trees grown for 17 years in open-top chambers reported by Kimball et al. (2007) in eCO_2 atmosphere is probably the longest experiment available for any fruit tree. Two to four years into the experiment, there was a productivity plateau, and at about a 70 % enhancement of annual fruit and incremental wood production over the last several years of the experiment. When summed over the duration of the experiment, there was an overall enhancement of 70 % of total biomass production. Much of the enhancement came from greater numbers of fruits produced, with no change in fruit size. Thicker trunks and branches and more branches and roots were produced, but the root/shoot ratio was unaffected. Also, there was almost no change in the elemental composition of the biomass produced, perhaps in part due to the minimal responsiveness of root-symbiotic arbuscular mycorrhizal fungi to the treatment.

In *Citrus aurantium*, Idso et al. (2002) observed a long-term 80 % increase in trunk, branch and fruit biomass in response to a 75 % increase in atmospheric CO_2 concentration. They were able to recover from the soluble fraction three CO_2-sensitive proteins with apparent molecular masses of 33-, 31-, and 21-kDa, which they concluded as vegetative storage proteins (VSPs). According to them these storage proteins possibly enhance the growth due to eCO_2. The existence of these proteins may be the key that allows the CO_2-enriched trees to temporarily stockpile the unusually large pool of nitrogen that is needed to support the large CO_2-induced increase in new branch growth that is observed in the spring, which ultimately sustains the large increase in wood and fruit biomass production throughout the rest of the year. Penuelas et al. (1997) have reported that the nitrogen concentrations of leaves of sour orange (*Citrus aurantium* L.) trees growing in the field with 700 ppm CO_2 were considerably less than those of leaves on trees growing in ambient air of 400 ppm CO_2 after three years of a long-term experiment (Idso and Kimball 1997). However, by the time 8 years had elapsed the nitrogen concentrations of the CO_2-enriched leaves had gradually risen to become identical to those of the ambient-treatment leaves. This suggests that given enough time or a slow enough change in atmospheric CO_2 concentration, plants may be able to adjust their rates of nitrogen acquisition to maintain foliage nutritive characteristics similar to those of the recent past, that is, when CO_2 concentrations were somewhat lower than they are today (Newbery et al. 1995). Expressed on a per-unit-leaf-area basis, leaves from the CO_2-enriched trees contained 4.8 % less chlorophyll and nitrogen than leaves from the trees exposed to ambient air. Because of their greater leaf numbers, however, the CO_2-enriched trees contained 75 % more total chlorophyll and nitrogen than the ambient-treatment trees; the total productivity of the CO_2-enriched trees was 175 % greater. Consequently, although per-unit-leaf-area chlorophyll and nitrogen contents were slightly lowered by atmospheric CO_2 enrichment in their experiment, their use efficiencies were greatly enhanced (Idso et al. 1996).

It has been demonstrated by Rogers et al. (1996) and Kimball et al. (2001) that the provision of high levels of nitrogen fertilizer to the soil has the capacity to totally offset the reduced foliage nitrogen concentrations caused by higher levels of atmospheric CO_2. As Rogers et al. (1996) have described it, "the widely reported reduction in leaf or shoot nitrogen concentration in response to elevated CO_2 is highly dependent on nitrogen supply and virtually disappears when nitrogen is freely available to the roots." This probably means that we have to supplement the soil with more nitrogen in a climate change situation to maintain the productivity.

Vu et al. (2002) found that in Ambersweet orange (*Citrus reticulata*) grown for 29 months under eCO_2 in temperature gradient greenhouses, in the absence of other environmental stresses, photosynthesis would perform well under rising atmospheric CO_2. Their results show a photosynthetic acclimation for both new and old leaves of Ambersweet orange to eCO_2. This photosynthetic acclimation was accompanied by down-regulation of rubisco protein concentration and activity, and was correlated with high accumulation of starch and sucrose. The new leaves acclimated very well to eCO_2, compared to old leaves, in terms of gas exchange parameters, photosynthetic capacity and sucrose synthesis. In addition, starch accumulation in new leaves during the day was much higher than in old leaves under eCO_2. According to them photosynthetic acclimation of both young and mature leaves of Ambersweet orange to a future rise in atmospheric CO_2 would allow an optimization of plant nitrogen use, either by reallocating the nitrogen resources away from rubisco to other catalytic or structural proteins within the leaves, or redistributing nitrogen from the photosynthetic proteins of source leaves to sink tissues (Stitt 1991; Bowes 1993). Also, the optimization of inorganic carbon acquisition and greater accumulation of the primary photosynthetic products would be beneficial for citrus vegetative growth. In the above study, the productivity aspects of this crop have not been considered.

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http://www.springer.com/978-3-319-14199-2

Responses of Fruit Trees to Global Climate Change
Ramírez, F.; Kallarackal, J.
2015, XI, 42 p. 3 illus., Softcover
ISBN: 978-3-319-14199-2