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How does elevated atmospheric CO_2 concentration affect vegetation productivity?

A study based on Free Air CO_2 enrichment (FACE) experiments and two generalised vegetation models

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1. Introduction

Human activities, particularly burning fossil fuel, have increased the atmospheric CO_2 concentration (Hungate et al., 2003). This has led to the major changes that are occurring in the chemical composition of our atmosphere. (Baldocchi et al., 1996). The atmospheric CO_2 concentration has risen from 280 ppm at the beginning of the industrial revolution to ca 370 ppm today, and is projected to exceed 600 ppm by the end of the present century. Never in history have the earth experienced so large increase during a so short period. (IPCC, 2001)

The increase in atmospheric CO_2 concentration is not as large as expected and this imbalance has been called the "missing sink". It has been showed that the terrestrial ecosystem have a higher ability to assimilate CO_2 than what have been measured before. (Schlesinger, 1997) CO_2 and water vapour play an important role in the functioning of your earth's climate and biology. Regarding climate, CO_2 and water vapour are strong absorbers of infrared energy. Their presence in the atmosphere causes the mean surface temperature of the earth to be warmer than the radiating temperature that would otherwise occur due to the balance between absorbed solar and outgoing terrestrial radiation (Baldocchi et al., 1996). Forests account for more than 75% of the carbon stored in terrestrial ecosystems and the current atmospheric CO_2 concentration acts like a fertilizer since the vegetation is limited by CO_2 (Hamilton et al., 2002). Elevated CO_2 stimulates tree growth and forest net primary production (NPP). NPP represents the amount of carbon incorporated into biomass and is the difference between total carbon assimilated by photosynthesis and that lost by autotrophic respiration. (Hamilton et al., 2002)

Direct measurements of canopy CO_2 exchange under elevated CO_2 on daily and annual scales are useful for improving our understanding of the carbon dioxide budget of ecosystems and for providing data sets for testing and parameterization of carbon balance models (Baldocchi et al., 1996). Previous studies conducted in growth chambers and open-top chambers showed that the size and the scale of the chamber caused a significant chamber effect that often confounded the results. Therefore a new more realistic technology where invented, called the Free Air Carbon Enrichment (FACE) (Nowak et al., 2004). The FACE experience has the advantage of a size large enough to encompass the small-scale spatial structure of the ecosystem (Nowak et al., 2004).

Cramer et al., (2001) made a study of how ecosystems will change with the increased CO_2 concentration, using six dynamic vegetation models, one of them the LPJ-DGVM. The six models carried out three different simulations, increased CO_2 only, climate only and CO_2 and climate together (see figure 1). All the models showed the same results, only increasing CO_2 concentrations would have high impact on the plant productivity. Climate only on the other hand shows a slight decrease in productivity. Cramer et al., (2001) study shows that understanding the processes behind plant productivity are of great importance to predict the future climatic changes. To understand the essential matter around these processes it's of great importance to comprehend the structure of photosynthesis.

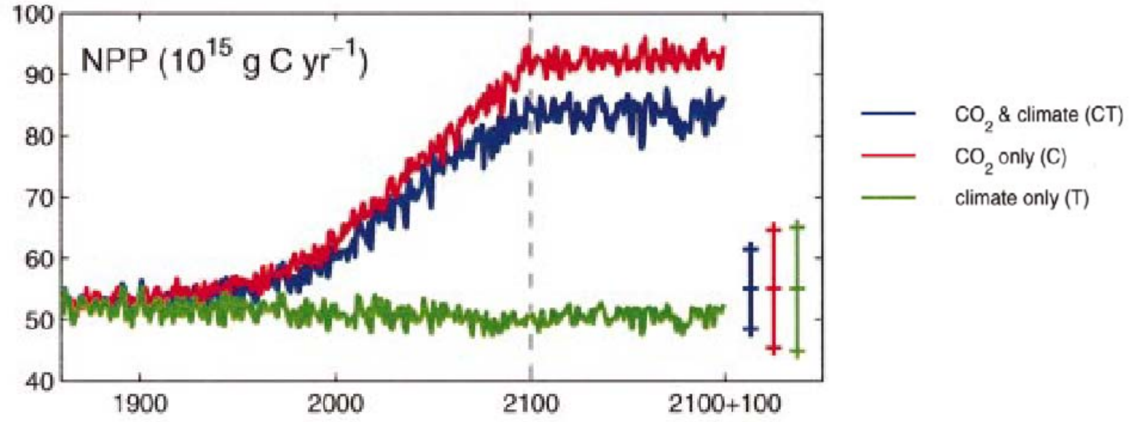


Figure 1. Time series of simulated global net primary production (NPP) from six dynamic vegetation models, showing the average across models between the three different simulations. The error bars show the variation among models. Cramer et al. (2001) fig. 4

In this study, two generalized vegetation models LPJ-DGVM and GUESS were used on FACE, experiment sites to see how well the models simulated results agrees with the observed results from the FACE sites.

2. Background

2.1 Plant physiology

Photosynthesis

The assimilation of carbon by the plants leaves follows the general reaction;

$$CO_2 + H_2O + \text{light} \rightarrow CH_4O + O_2$$

where CH_4O represents Carbohydrates such as starch or sucrose. Assimilation involves many chemical reactions which occurs inside the chloroplasts in leaf mesofyll cells and are catalyzed by enzymes. The substrates for assimilation consist of CO_2, water and light. The carbon dioxide comes from the atmosphere and diffuses into the leaf through the stomata. The water is available in excess within the leaf, the biochemical reactions occurs within a highly hydrated cell. Light is from solar radiation in the range between 400 to 700 nm, called the photosynthetic active radiation (PAR). (Campbell, 1998)

The photosynthesis begins with absorption of photons from sunlight by pigments. Some of the chlorophyll molecules are oxidized, passing an electron to a sequence of electron transfer proteins that ultimately leads to a reduction of a high-energy molecule, known as nicotinamide adenine dinucleotide phosphate (NADP), to NADPH. The energy from the photons is used to split water with the simultaneous production of oxygen. The photosynthetic pigments and proteins are embedded in a cell membrane, allowing protons to build up high concentrations on one side of the membrane and for this potential energy to be used to synthesize another high-energy compound, adenosine triphosphate, ATP. The reactions are dependent of light energy and are there for called the light reactions of the photosynthetic.

The high energy compounds NADPH and ATP are then used with enzymes to reduce CO_2 and build carbohydrate molecules, the Calvin cycle. The reaction begins with the enzyme ribulose biphosphate carboxylase, known as Rubisco, which assimilates CO_2 and leads to the synthesis compounds. This process does not require light and are referred to as the dark reaction. (Schlesinger, 1997)

Respiration

Respiration is the plant metabolism and is a result of mitochondrial activity in plant cells. The equation for respiration is the opposite of photosynthesis;

$$CH_4O + O_2 \rightarrow CO_2 + H_2O + \text{energy}$$

Measurements of respiration show that one-half of the gross carbon fixations by photosynthesis are respired by the plants. A large fraction of the respiration is contributed by stems and root owing to their large contribution to total plant biomass in woody plants. For long-lived woody plants, respiration increases with stand age. (Schlesinger, 1997)

2.2 Net primary Production

Net primary production (NPP) is the net biomass gain by vegetation per unit time (Lambers, 1998). For plants in nature, the expression is (Schlesinger, 1997)

$$\begin{array}{ccccc} \multicolumn{5}{c}{\text{Gross primary production – plant respiration = net primary production}} \\ (\text{GPP}) & - & (R_p) & = & (\text{NPP}) \end{array}$$

Net primary production is not directly equal to plant growth because some fraction of the NPP is in dead and lost tissues. NPP is generally expressed in units of g m^{-2} yr^{-1}. About 45 to 50% of the plant tissue contains carbon, by dividing by two is a simple way to convert units of organic matter to carbon fixation (Schlesinger, 1997). Below are factors that affect the NPP descried shortly.

2.3 Environmental effects on photosynthesis and NPP

Water

The stomatal conductance is one factor that determines the rate of the photosynthesis. Stomatal conductance is primary controlled by the availability of water from the roots up to the leaf, the CO_2 concentration inside the leaf and the relative humidity in the air surrounding the leaf. When plant stomatas are open it allows CO_2 to diffuse inward and O_2 together with H_2O to diffuse outward to the atmosphere. The loss of water relative to photosynthesis is referred to as water-use efficiency, (WUE). When the CO_2 concentration in the atmosphere increases it allows the same rate of photosynthesis to occur at lower stomatal conductance, thus increasing WUE. When well watered plants are actively photosynthesizing, internal CO_2 is relatively low and stomatas show maximum conductance. Under such conditions the amount and activity of Rubisco may determine the rate of the photosynthesis. (Schlesinger, 1997)

Much of the interest in the response of stomatal conductance to atmospheric CO_2 enrichment relates to a need for quantitative estimates of leaf transpiration (Norby et al., 1999b). Of great interest are ecosystems with low precipitation where it has been suggested that these will show the strongest response to rising atmospheric CO_2 due to strong water limitations in these systems (Nowak et al.(2), 2004). An increased CO_2 concentration may stimulate plant growth by reducing plant water consumption and hence slower soil moisture depletion (Morgan et al., 2004). Naumburg et al. (2003) on the other hand predicts that the response to elevated CO_2 for vegetation in dry climate will depend on precipitation patterns and only have a small CO_2 effect during dry years due to the lack of water.

Nutrients

The rate of photosynthesis is directly correlated to leaf nitrogen content, expressed on mass basis. This gives a good index of the metabolic activity in most plants since it's correlated with respiration. Most of the leaf nitrogen is in enzymes. The photosynthetic potential is directly related to the content of Rubisco and leaf nitrogen in many species. When leaf nutrient content increases, nutrient-use efficiency declines. Nutrient-use efficiency is also inversely correlated to WUE among many species. (Schlesinger, 1997)

Nowak et al.,2004, are saying that the high increase in NPP due to CO_2 fertilization seen now are transient because ecosystem quickly developed nitrogen limitations and this will in turn decrease the enhancement, called a downregulation. Long et al., 2004, made a summary of the results from the FACE sites and provided results showing that the elevation of CO_2 concentration predicted for the mid-century will result in a substantial increase in vegetation and reproduction, decreased transpiration, and decreased tissue quality, with respect to protein and N content of leaves. Chamber studies have suggested that a decline in Rubisco reflects an overall decline in leaf nitrogen and protein content, implying that a downregulation is part of a general decrease in investment in proteins under elevated CO_2 concentration. In the summary from Long et al., 2004, the result shows a 20% decrease in Rubisco, but just 4% decrease in nitrogen per unit leaf area.

Temperature

A strong influence on the rate of all metabolic processes is temperature. The inside of the plant enzymes that catalyses the photosynthesis reactions are strongly temperature dependent (Campbell, 1998). The higher the temperature gets the oxygenating reaction of Rubisco increases more than the carboxylation, leading to more photorespiration. This explains the decline in net photosynthesis at high temperatures (Lambert, 1998).

Light

As soon as the plant gets light the photosynthesis starts. The more irradiance, the faster the assimilation gets. The light-compensation point is where assimilation compensates for the respiration. At low irradiance the assimilation is light limited and increases linearly with irradiance. At high irradiance the assimilation becomes limited by the carboxylation rate and the photosynthesis becomes light-saturated. (Lambert, 1998)

CO_2

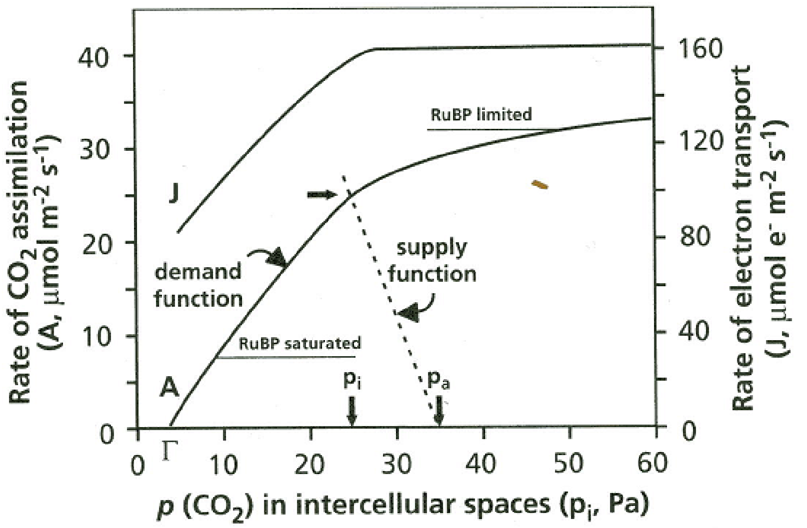


Figure 2. The relationship between the rate of assimilation, A, and the partial pressure of CO_2 in intercellular CO_2 partial pressure, p_i. (Lambert, 1998)

Plants need carbon to build up there tissue and supply carbon from carbon dioxide in the atmosphere. The demand for CO_2 is determined by the rates of the processes in the chloroplasts and environmental factors. The response of photosynthetic rate to CO_2 concentration shows the demand for CO_2. Figure 2 illustrates the CO_2 assimilation (A) as a function of intercellular CO_2 partial pressure (p_i). The CO_2 concentration is expressed as mole fraction in air. There is no net CO_2 assimilation until the production of CO_2 in respiration is compensated by the fixation of CO_2 in photosynthesis. This is showed in the CO_2 compensation point (Γ) and this point is determined by the kinetic properties of Rubisco. At the lower p_i the CO_2 concentration is limiting the rate of functioning Rubisko, while ribulose-1,5-bisphosphate (RuBP) is saturated. This linearly relationship is referred to as the carboxylation efficiency and it shows the carboxylation capacity, which depends on the amount of active Rubisco in the leaf. In the region at high p_i CO_2 no longer restricts the carbodylation reaction, but the rate where RuBP becomes available and the Rubisco activity is limited. This depends on the activity of the Calvin cycle and depends on the rate which ATP and NADPH are produced in the light reaction. The photosynthetic rate is here limited by the rate of electron transport, for example limitation of light. (Lambert, 1998)

To summarise (se figure 3) the plants appear to sense and respond directly to rising CO_2 concentration by direct effects of increased carboxylation by Rubisco and decreased stomatal opening. An increase in CO_2 concentration by increasing efficiency of light use in net CO_2 uptake, results in increased growth and therefore an increased rate of production of leaf area These changes, which both increase the efficiency of CO_2 uptake and water use, produce a wide range of secondary responses, most notably large increases in leaf nonstructural carbohydrates, improved plant water status including increased leaf water potential, and in many cases increases in plant carbon to nitrogen ratio (C:N), and decreases in leaf Rubisco activity, stomatal density, and root/shoot mass. (Long et al., 2004)

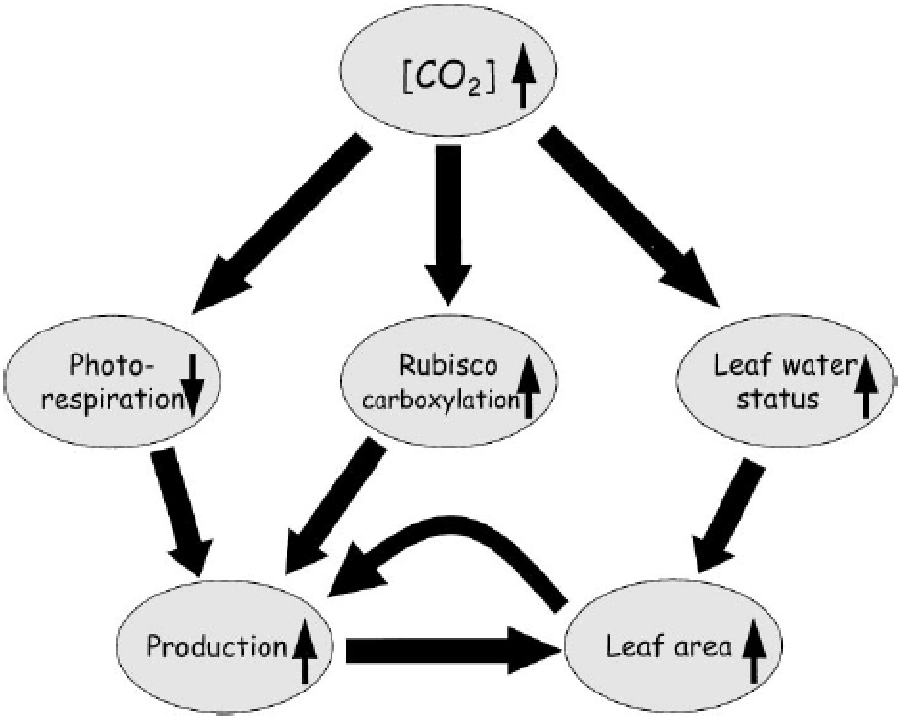


Figure 3. Increased CO2 concentration increases the rate of carboxylation at Rubisco while inhibiting the oxygenation reaction and thus decreasing photorespiratory loss of carbon. Increased production allows increased leaf area development, leading to a positive feedback on plant photosynthetic rate. This is further reinforced by decreased transpiration and improved leaf water status, which also favour increased leaf area growth. (Long et al., 2004)

2.4 Free Air CO_2 Enrichment (FACE)

Before the Free Air CO_2 Enrichment (FACE) experiments, studies were conducted in controlled environment, glasshouses with herbaceous plants and tree seedlings in pots or in the field with transparent enclosure or open-top chambers (Nowak et al., 2004). From here comes the most information about plant responses to elevated CO_2 concentration (Long et al., 2004). Because of the space limitation most of these studies are conducted at an early stage of the plant growth, this contributes to an inability to scale seedling responses to whole trees and forest stands (Nowak et al., 2004). A second limitation is that most studies, including field studies, use plants grown in a pot and the response under elevated CO_2 concentration is suppressed because of the limiting rooting volume (Long et al., 2004) It has been suggested that this suppression is due to nutrient exhaustion, but experiments have showed that independent of nutrients there is a strong feedback when roots encounter a barrier (Long et al., 2004). To bee able to study plant in there natural environment open-top chambers were used. Even though the top of the chamber are in contact with the atmosphere these experiments are constrained by the chamber effect, in which the camber itself alters a micro-climate around the plots being investigated. Still with the open chambers the problem to scale the results to whole trees or ecosystems remains. (Nowak et al., 2004)

This led to an extensive network of FACE, studies that have a size large enough to encompass the small-scale spatial structure of the ecosystem. (Nowak et al., 2004)

FACE experiments (see figure 4) commonly have plot diameters of 25-30m. Air enriched with CO_2 is blown into the rings from just above the surface to just above the top of the canopy. Wind direction, wind speed, and CO_2 concentration are measured at the centre of each ring. A computer-control system uses the wind speed and CO_2 concentration information to adjust the CO_2 flow rates to maintain the desired CO_2 concentration at the centre of the FACE ring. The system uses the wind direction information to turn on only those pipes upwind of the plots, so that CO_2-enriched air flows across the plots, no matter which way the wind blows. The CO_2 flow rate is updated every second, and the choice of which vertical pipes to release from is updated every 4 seconds (Long et al., 2004).

Figure 4. Example of how a FACE experiment looks like. These photos are taken at the Oak Ridge forest FACE site.

The FACE experiments are not without limitations. Long term records shows that one minute average is usually within ±10% of the target concentration, for about 90% of the time in low vegetation. For forest the one minute average lays within ±20% for 90% of the time. It's not yet clear if these fluctuations are sensed by the plants and if they affect the net CO_2 exchange. The photosynthesis response nonlinear to CO_2 concentration. If the concentration fluctuates assimilation will decrease as the amplitude of variations around the mean increases, providing that the chloroplasts are exposed to the fluctuation. Another disadvantage is that even though the centre is close to the CO_2 concentration target, it may differ ±100ppm depending if it is the side upwind or the side downwind. A third disadvantage is that the system depends on continuous air movements. During daytime still periods are rare due to the convective currents that the solar radiation provides, but during the dawn and at night still conditions are common. When the CO_2 enriched air is pumped into a still condition the cold air at the surface with warm air above is replaced by warm air at the surface and cold above. (Long et al., 2004)

A total of 24 noncrop FACE sites are situated around the world, with results from 16 sites. The majority of these sites are in Europe. Five different types of global ecosystems are represented in the network, where 75% of the current sites are either temperate forest or grassland vegetation (Nowak et al., 2004).

2.5 Model description

Models are used to upscale and/or predict the future. They can be in a small scale like the photosynthesis in a leaf up to global models. In this thesis two global dynamic vegetation models, the Lund-Postsdam-Jena dynamic generalized vegetation model (LPJ-DGVM), (Sitch et al., 2003), and the General Ecosystem Simulator (GUESS), (Smith et al., 2001), were used to simulate how elevated CO_2 affects plant production for five FACE sites.

The models use the same representations of ecophysiological processes. GUESS includes more-detailed representations of vegetation dynamics and canopy structure, while LPJ-DGVM has been optimized for applications on large scales, where computing power is still limiting. GUESS has been shown to give more accurate descriptions of vegetation at the stand scale (Smith et al. 2001), but it is not known if the two models simulate different responses to elevated CO_2. Below are first the ecophysiological core which both models have in common described and then the differences between them.

The models are constructed to be applied both on regional and global bases (Hickler et al., 2004). The models are driven by using daily values of temperature, precipitation, percentage sunshine hours (or solar radiation), latitude, soil texture and atmospheric CO_2 concentration (Hickler et al., 2004).

The vegetation is represented by Plant Functional Types (PFT). There are two general groups of PTFs the woody group and the herbaceous group, were the woody group consists of 8 subgroups (two tropical, tree temperate and tree boreal) and the herbaceous of two (C_3 and C_4 plants) (Sitch et al., 2003). The PFTs are central to the models because they are assigned different parameterizations with respect to physiological processes (e.g. phenology [evergreen or deciduous], leaf thickness, minimum stomatal conductance, photosynthetic pathway, allocation, rooting depth). The vegetation composition in terms of different PFTs defines the structural characteristics of vegetation (Cramer et al., 2001). The models also take in consideration the dynamics and competition between PFT population, and soil biogeochemistry (Sitch et al., 2003). For the woody PFTs the individuals are defined by its crown mass and the size of four tissue pools, leaf mass, sapwood mass, heartwood mass and fine root mass. The herbaceous PFTs are only defined as leaf mass and fine root mass (Sitch et al., 2003).

NPP for the different PTFs is derived from photosynthesis, respiration, canopy energy balance, the controls of stomatal conductance and canopy boundary-layer conductance, the allocation of carbon and nitrogen within the plant, tissue turnover and reproduction (Cramer et al., 2001).

Calculated every day are photosynthesis, canopy conductance, plant maintenance, respiration, plant transpiration, water percolation in the soil and plant root-weighted water uptake (Hickler et al., 2004). Vegetation dynamics (establishment, mortality and distribution) are based on annual net primary production and biomass growth, including competition among PFTs, probabilities of natural disturbance (fire, general mortality) and succession (Cramer et al., 2001). Soil hydrology depends on the soil texture and vegetation biophysical processes and influences both plant and soil behaviour (Cramer et al., 2001).

One major difference between the two models is that GUESS differentiates age- and size classes within a population of PFTs, while LPJ-DGVM only simulates one "average" individual for each PFT (Hickler et al. 2004). When simulating even-aged forest stands or non-woody vegetation, as done in this study (see section 3.2), this difference should not influence the results. However, simulating competition for light between different age-classes requires more-detailed parameterization of different PFTs and representations of light interception through the canopy, which are therefore included in GUESS but not in LPJ-

DGVM (Smith et al. 2001). These differences between the two models may influence the simulated response to elevated CO_2.

In GUESS the PFTs are divided further into shade tolerant and shade intolerant. The shade-tolerant uses a different life strategy than the intolerant. The shade intolerant needs more solar radiation so it allocates more carbon of sapwood into heartwood this makes it grow high faster and thereby reach the solar radiation. The shade intolerant species are the ones that first invade an open ground (e.g. clear cuts, after fires) growing fast and high. Below it the tolerant species grows slowly in the shade. When the intolerant species dies or cant grow any higher the tolerant species takes over and the intolerant species can't re-establish. (Smith et al., 2001)

3. Method

3.1 Site description

From all the FACE sites, five were chosen. The sites had to fulfil three demands. They must have presented results over a few years (more than tree), climate data for the site must be available and the sites should represent different vegetation sites. Below follows a detailed description of all the chosen sites. A shorter summarise of the most central facts are showed in table 1.

Oak Ridge
The research site is a planted sweetgum (*Liquidambar styraciflua*) monoculture located on the Oak Ridge National Environmental Research Park (35^o 54' N; 84^o 20' W) in south-eastern United States. Oak Ridge, eastern Tennessee in the Ridge and Valley province between the Cumberland and Blue Ridge Mountains. (Norby et al., 2003)

The plantation was established in fall, 1988, on an old terrace of the Clinch River (elevation 230 m). One-year-old, bare-rooted sweetgum seedlings were planted at a spacing of 2.3 m × 1.2 m. There is a total of 1.7 ha planted with sweetgum in two areas — a 185 × 70 m area and a smaller 85 × 50 area. No fertilizer has been added to the sweetgum; herbicide was used in 1989 and 1990 to control competition from weeds. (Gundeson et al., 2002)

When the experiment was initiated in 1997, stand basal area was 29 m^2 / ha with an average tree height of 12.4 m and stem diameter of 13 cm (Gundeson et al., 2002). The height and basal area are very uniform across both areas planted in sweetgum. The sweetgum stand has a closed canopy with a leaf area index (LAI) of 5 (Norby et al., 2003). The CO_2 fumigation began in April 1998, and has continued during the growing season, April – November, since then with a CO_2 concentration of 550 ppm. (Gundeson et al., 2002)

The soil at the site, which is classified as Wolftever, an Aquic Hapludult, developed in alluvium washed from upland soils derived from a variety of rocks including dolomite, sandstone, and shale. It has a silty clay loam texture and is moderately well drained. The soil is slightly acid (water pH approximately 5.5-6.0) with high base saturation largely dominated by exchangeable Ca. (Belote et al., 2003)

The climate is typical of the humid southern Appalachian region. Mean annual temperature is 13.9 °C and mean annual precipitation is 1322 mm. Precipitation is generally evenly distributed throughout the year. (Belote et al., 2003)

Daily temperature (^oC), precipitation (mm) and PAR ($mol/m^2/day$) where collected from the Oak Ridge FACE web site from 1999 to 2003. For missing values and gap filling see appendix.

Duke

The Duke Forest lies near the eastern edge of the North Carolina piedmont plateau and supports a cross section of the woodlands found in the upper coastal plain and lower piedmont of the Southeast. The FACE site is located in the Blackwood Division of Duke Forest in Orange County, N.C. (35^o 58' N, 79^o 5' W), near Durham, N.C., USA. Site elevation is 174 m. (Ellsworth, 1999)

This section of the Duke forest where farmed a century ago (Hamilton et al., 2002), and the current plantation was established in 1983 after a regenerating forest was clear-cut in 1979. The 90-ha block of the stand is even-aged, and was established from seedlings following clear-cutting and burning of the site. Loblolly pine trees from a Piedmont provenance were planted at 2m x 2.4m spacing. (Schäfer et al., 2002)

This site has six 30-m diameter experimental FACE plots. Tree treatment plots have been fumigated with elevated CO_2 beginning 27 august 1996. The elevated CO_2 plots have target concentrations of 200 ppm above ambient. CO_2 enrichment is provided 24 hours per day when air temperature is above 5° C and wind speed is below 5 m/s. (Schäfer et al., 2002)

The soil is a moderately well-drained low-fertility acidic Hapludalf of the Enon Series with a clayey loam in the upper 0.3 m, and clay below down to the bedrock. (Schäfer et al., 2002)

The first full year (1997) of FACE operation included a dry summer (Ellsworth et al., 1999). Total pine carbon was 5394g C /m in 1998 and peak growing-season LAI was 2,87 for the pine canopy. (Hickler et al., 2004)

Centrally located between the mountains to the west and the ocean to the south and east, the Forest has a moderate climate. The average annual temperature is 15,5 C. Precipitation averages about 1140 mm annually and is well distributed throughout the year. July and August are normally the wettest months with an average of 129.5 mm of rainfall; October and November are normally the driest with an average of 68.9 mm. (Schäfer et al., 2002)

Half hourly data for temperature (^oC), precipitation (mm) and solar radiation (W/m^2) were collected from the Duke forest FACE web site from 1998 to 2003. The half hourly data were after gap filling calculated into daily average values. For missing values and gap filling see appendix.

Aspen

The study site is in Oneida County, Wisconsin, USA (45^o 30' N. 89^o 30' W). (Noormets et al., 2001)

The vegetation consists of two trembling aspen (*P.tremuloides*) clones, differing in ozone sensitivity. The plant material was propagated from greenhouse-grown stock plants. The rooted cuttings were 6 months old by the time of planting in July 1997 and about 2,5 m tall in 1999. (Noormets et al., 2001)

CO_2 treatments began in 1998, with a CO_2 concentration of 200 ppm above ambient and where applied during daytime over the growing season from May to September. (Noormets et al., 2001)

The Soil is mixed, frigid, coarse, loamy Alfic Haplorthod topsoil. Clay lenses at 30 – 60 cm deep are found throughout the field. (King et al., 2001)

In the end of each growing season growing parameters where measured. From the diameter the basal area where calculated. The difference in growth between the years where calculated, the results where used instead of NPP.

In 1998 there was a high increase of dieback in the site. The dieback symptoms were dead buds and discoloured steams. The dieback appeared to be associated with the prolonged growing season that the region experienced in the autumn of 1999 (Iselbrands et al., 2001).

Half hourly data for temperature (^{o}C), precipitation (mm) and PAR (W/m^2) where collected from the Aspen FACE web site from 1999 to 2003. The half hourly data were after gap filling calculated into daily average values. For missing values and gap filling see appendix.

Nevada

This facility is located on the Nevada Test Site near the northern ecotone of the Mojave Desert (36^{o} 49' N, 115^{o} 55' W). This area is a fairly homogeneous area on a broad gently sloping bajada, elevation 960 m. (Naumburg, 2003)

The vegetation is characterized as a *Larrea tridentata*, *Lycium* spp., *Ambrosia dumosa* plant community. Unlike the grassland studies, there are no management practices, nor are the plants destructively sampled. (Morgan et al., 2004)

At the Nevada FACE site the concentration of CO_2 is elevated by 50% (550 ppm) above the present atmospheric levels in three plots. Six other plots remain at the current level. CO_2 exposure started April, 1997. The CO_2 fumigation is on during the entire year when the temperature is over 3^{o} C and wind is over 7 m/s. (Morgan et al., 2004)

The soil at the site is an Aridosol soils, sandy with rock fragments and has a well developed cryptogamic crust. (Morgan et al., 2004)

The Mojave Desert is the driest region in the United States. Long-term records average 74 mm of precipitation a year. Temperatures here range from 48^{o}C in summer to -19^{o}C in winter. Rainfall at the site is expressed as hydrologic years which have its beginning in October. In 1998 the precipitation was ~3.5x normal, with profuse winter annual germination and growth. In contrast, 1999 hydrologic year had half the normal rainfall, with little winter precipitation and no winter annuals. (Naumburg et al., 2003)

Hourly data for temperature (^{o}C), precipitation (mm) and solar radiation (W/m^2) where collected from the Nevada FACE web site from 1999 to 2003. The hourly data were after gap filling calculated into daily average values. For missing values and gap filling see appendix.

Swiss
The Swiss FACE site is located at Eschikon, 20 km north-east of Zurich, Switzerland (8^o 41' E. 47^o 27' N), 550 m above sea level. (Ainswoeth et al., 2003)

In one experiment Lolium perenne (ryegrass) was sown in monocultures (2.8 m x 1,9 m plots with 3.2 g seed m^{-2}) in mid-August 1992. There were two cutting frequencies and two N fertilization treatments. The swards were cut frequently from 1993 to 1995, six times in 1993 and eight times in 1994 followed by 1995 and infrequently four times. All the swards were cut five times per year from 1996 to 1998 at a height around 5 cm. The swards were exposed to two different N treatments, low nitrogen 14 $gm^{-2}y-^{1}$ and high nitrogen 56 $gm^{-2}y^{-1}$. (Deapp et al., 2000)

In another experiment 12 plant species Lolium perenne, L multiflorum, Arrhenathecult elatius, Dactylis glomernata, Festuca pratensis, Holcus lanatus, T. flavescens, Rumex obtusifolius, R. acetosa, Ranunculus friesianus, Trifolium repens, T.pratense. At the end of May 1993, the plants were transplanted into artificial gaps (initial diameter 8 cm) in established L. pernenne swards. L. perenne was chosen as a matrix for the species studied since it is the most important grass species for intensively managed temperate grassland. Since L perenne is relatively short it would not intensively shade the experimental plants. The plants were grown for three growing seasons (1993-1995) and were cut for three times per year. (Luscher et al., 1998)

The experiment is made up by three blocks; each consisting of two, 18m in diameter, circular rings, one fumigated 600 ppm CO_2 concentration and one control (ambient CO_2) were established in 1993. The CO_2 enrichment lasted for the entire growing period, from March to November. Fumigation began when mean air temperature reaches a threshold of 5 ^oC and ended when air temperature were below that threshold. (Deapp et al., 2000)

The soil is classified as a, fertile, eutric cambisol with sufficient phosphorus and potassium with pH values between 6.5 and 7.6. (Luscher et al., 1998)

The site has an average yearly temperature of 8 ^oC, and an average precipitation of 94 mm over the year. The precipitation is higher during the summer. (Luscher et al., 1998)

Daily temperature (^oC), precipitation (mm) and PAR ($mol/m^2/day$) where collected from the Swiss FACE web site from 1993 to 2003. There were no missing values for Swiss.

3.2 Modelling protocol

Two instruction files were made for each site, one for LPJ-DGVM and one for GUESS. The instruction file tells the model;

- which gridcell the site belongs to (defined by the nearest south-west corner)
- where to take input from
- where to put the output
- which site it should run for
- how long spinnup time
- if the site is under ambient or elevated CO_2
- how high the concentration for the elevated CO_2 are
- which year the forest were planted
- what plant functional type the vegetation belongs to

- parameters for each plant functional type

in the model where the following described;

- the soiltype for each site, using Sitch et al., 2003 classification.
- when the station climate starts,
- when the elevated CO_2 started
- when during the year the elevated CO_2 is on

From the Climate Research Unit (CRU), (New et al., 2000), mean temperature, precipitation and cloud cover (solar radiation) is used as input values for each gridcell (0.5° x 0.5°) from 1901 to1998. To get a more accurate climate, daily temperature, precipitation and PAR/solar radiation where collected from each site. Since there are no data from the sites before the FACE experiments the CRU climate where used until the FACE experiment started at each site. The atmospheric CO_2 concentration under ambient conditions from 1901 to 2000 was collected from the Carbon Cycle Model Linkage Project. This data derived from ice core measurements and atmospheric observations (Sitch et al., 2003). The CO_2 file ends at 2000 so an increscent of 2,725 ppm (difference between the two last years) was added to update the file until 2003.

The simulation starts from a bare ground (no plant biomass present) and spins up until equilibrium is reached with respect to carbon pools and vegetation cover. When the spinnup has established the vegetation, the forest where cut down one year before it was planted again. The new forest was planted with the same density (number of seedling per square meter) as in the FACE experiments. After the plant year the mortality where set to zero. All forest sites are young, managed forest plantations, where substantial tree mortality caused by competition for light and canopy closure has not yet occurred.

Fire disturbance was turned of during the whole simulation, since the ecosystems investigated are planted forest and no fires has been documented.

Plantyear were set so that the LAI and / or biomass correspond with the sites at the time the experiment started.

The species occurring at the FACE sites were parameterized as the corresponding PFT in the models. Where the simulated ratio of tree biomass to LAI deviated substantially from the site observations and the planted tree species has been reported to have a leaf-to-sapwood cross-sectional area ratio that differs from the one of the corresponding PFT, this parameter was adjusted to the observations. This adjustment had to be carried out for the Duke, Oak Ridge and Aspen site.

4. Results

4.1 NPP

The results from the simulations are shown as percentage enhancement, which is the quotient between annual NPP in elevated CO_2 concentration and annual NPP in ambient CO_2 concentration in.

Figure 5 shows the average quotient. The results span over different years and numbers of years. The Swiss site is not included in the histogram since the site was under fertilization.

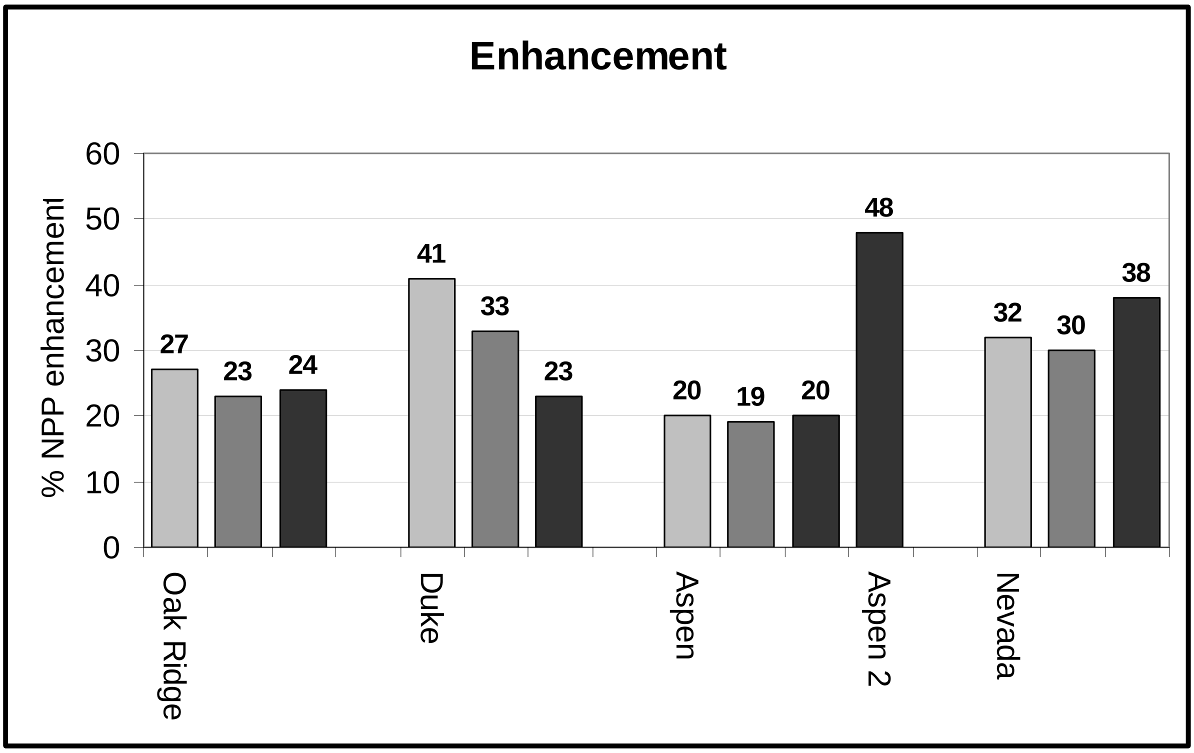


Figure 5. Results from the simulations are shown as the quotient between annual NPP in elevated CO_2 concentration and ambient CO_2 concentration in percentage enhancement. The results from LPJ-DGVM are represented in light grey, GUESS are represented in dark grey and the FACE sites are represented in black.

The average for all the sites is showed in the table 2 below.

Table 2. The averages NPP enhancement are calculated from the values in fig 5.

Averages NPP enhancement for all the sites (%)		
LPJ	GUESS	FACE
29,6	26,1	26,5

Figure 6 to figure 10 shows the interannual variation for all sites, and the table 3 to table 9 shows the unit values for the simulations and the observed results from the FACE sites. For all of the sites the LPJ-DGVM and GUESS simulated similar patterns of interannual variation and had NPP enhancement values that where more or less close to each other.

Oak Ridge

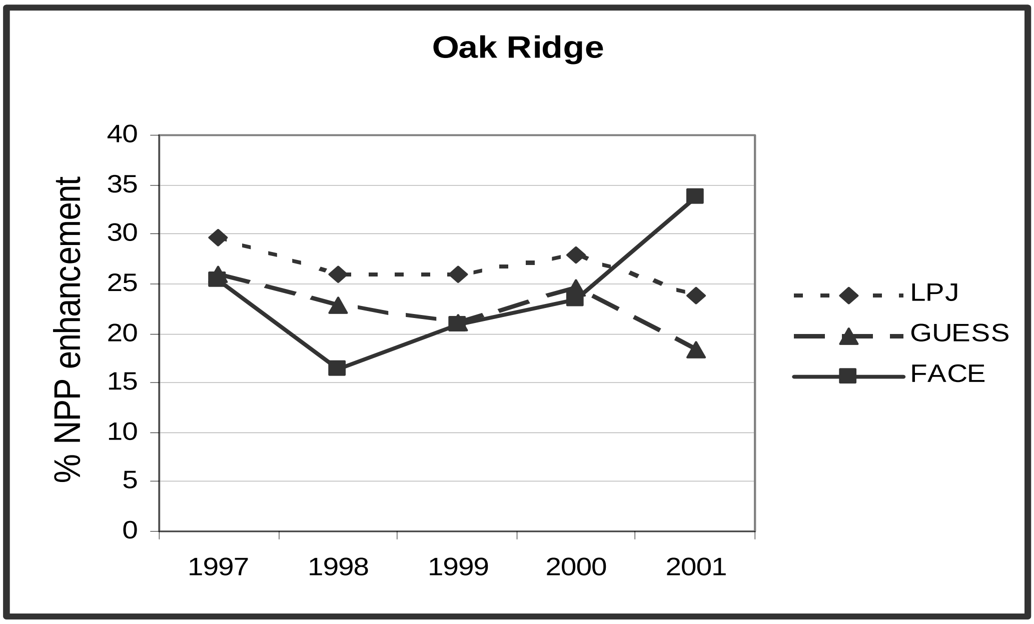


Figure 6. Year by year results from the Oak Ridge site, shown as the quotient between annual NPP in elevated CO$_2$ concentration and ambient CO$_2$ concentration in percentage enhancement.

Table 3. Year by year results from the Oak Ridge site. All values for NPP are shown. The values from the FACE site are from 1; Norby et al., 2002, table 1, and 2; Norby et al 2003, table 4.
*Dry Mass is 2 x carbon.

	LPJ kgC/m^2/yr			**GUESS** kgC/m^2/yr			**FACE** Dry Mass*/m^2/yr		
Year	**Ambient**	**Elevated**	**E/A**	**Ambient**	**Elevated**	**E/A**	**Ambiant**	**Elevated**	**E/A**
1998	0,439	0,569	1,296	0,587	0,739	1,259	1,815[1]	2,277[1]	1,255
1999	0,463	0,583	1,259	0,652	0,801	1,229	1,877[1]	2,184[1]	1,164
2000	0,470	0,592	1,260	0,629	0,762	1,211	2,120[1]	2,564[1]	1,209
2001	0,449	0,574	1,278	0,539	0,672	1,247	2,254[2]	2,781[2]	1,234
2002	0,521	0,645	1,238	0,687	0,813	1,183	2,030[2]	2,715[2]	1,337
Mean			**1,266**			**1,226**			**1,240**

The NPP for the sweetgum stand in the Oak Ridge FACE experiments was measured on annual bases through independent measurements of leaf, wood and fine-root production. Net annual production of leaves was determined by collection leaves as the abscise in baskets. Annual wood increase was determined by using an allometric equation that relates aboveground woody biomass increase to the change in basal area. Coarse root production was determined through an allometric equation relation root mass to tree basal area. Fine root production where determine every second week from observations of root length production. (Norby et al., 2002)

The LPJ-DGVM was around 5 % higher than GUESS. The observed data from the FACE site lie in the same range as GUESS for the years 1997, 1999 and 2000. In 1998, both models overestimated the NPP enhancement; and in 2001, both models underestimated the observed response.

Duke

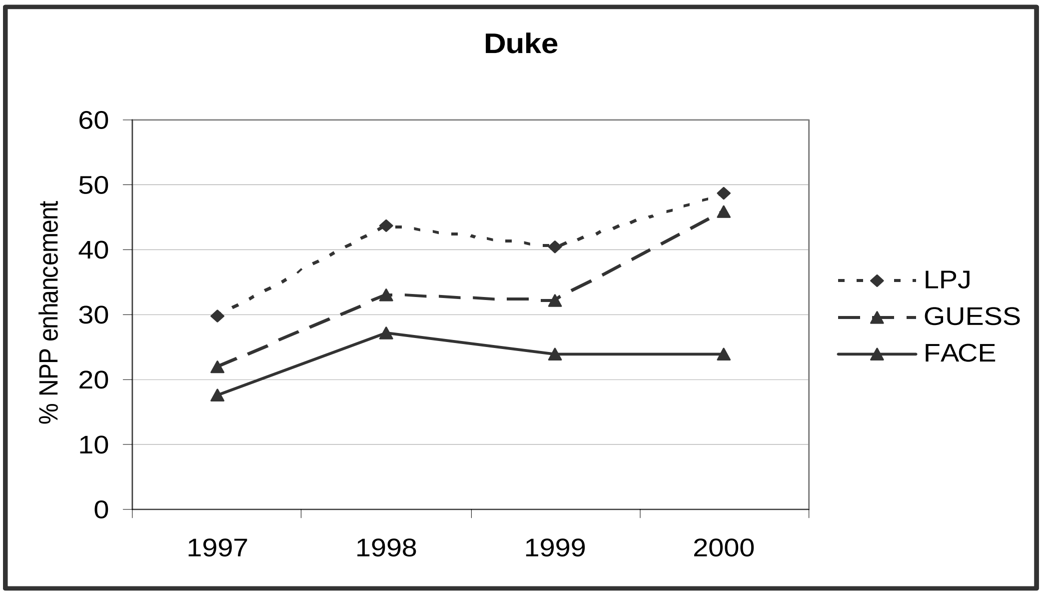


Figure 7. Year by year results from the Duke forest site, shown as the quotient between annual NPP in elevated CO_2 concentration and ambient CO_2 concentration in percentage enhancement.

Table 4. Year by year results from the Duke site. All values are for NPP are shown. The values from the FACE site are from 1; DeLucia et al 1999 2; Hamilton et al 2002 and 3; Schäfer et al 2003, table 4,

	LPJ	kgC/m^2/yr		**GUESS**	kgC/m^2/yr		**FACE**	kgC/m^2/yr	
Year	**Ambient**	**Elevated**	**E/A**	**Ambient**	**Elevated**	**E/A**	**Ambiant**	**Elevated**	**E/A**
1997	0,399	0,518	1,298	0,864	1,054	1,220	0,633 ^{1}	0,744 ^{1}	1,175
1998	0,332	0,477	1,437	0,676	0,900	1,331	0,705 ^{2}	0,897 ^{2}	1,272
1999	0,361	0,507	1,404	0,714	0,943	1,321	0,909 ^{3}	1,127 ^{3}	1,240
2000	0,289	0,430	1,488	0,394	0,575	1,459	1,060 ^{3}	1,313 ^{3}	1,239
Mean			**1,407**			**1,333**			**1,232**

NPP was calculated for the Duke FACE site as the difference of current- to previous-year standing biomass together with fine root turnover. To this litterfall was added, representing needle turnover. (Schäfer et al., 2003).

The first three years the modelled and the observed results had the same patterns of interannual variability. The LPJ-DGVM was on average around 10 % units higher than GUESS and the observed FACE results was on average around 6 % units below the GUESS over these three years. In the last year the LPJ-DGVM and GUESS showed an increase in NPP, GUESS more than the LPJ-DGVM, while the observed FACE results are similar to the previous year.

Aspen

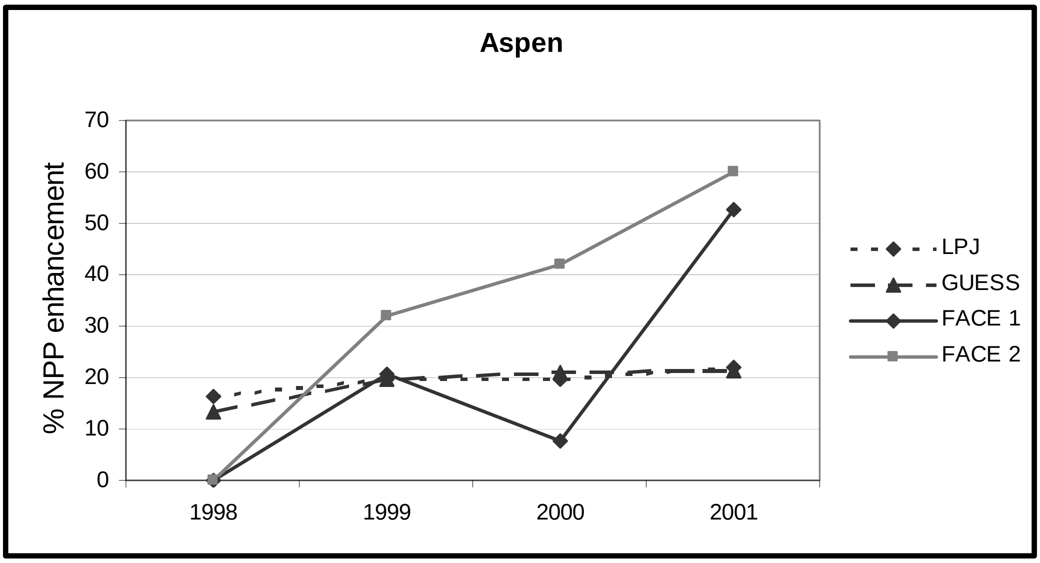


Figure 8. Year by year results from the Aspen site, shown as the quotient between annual NPP in elevated CO_2 concentration and ambient CO_2 concentration in percentage enhancement. FACE 1 results are from Percy et al., (2002) fig. 1 and are expressed as difference of current- to previous-year in basal area. FACE 2 results are from Nowak et al., (2004) fig. 10 and are above ground production

Table 5. Year by year results from the Aspen site. All values are for NPP are shown. The values from the FACE site are from 1; Percy et al., 2002, figure 1 and 2; Nowak et al., 2004, figure 10.

	LPJ	kgC/m^2/yr		**GUESS**	kgC/m^2/yr		**FACE**	**1**		**2**
Year	**Ambient**	**Elevated**	**E/A**	**Ambient**	**Elevated**	**E/A**	**Ambiant**	**Elevated**	**E/A**	**E/A**
1998	0,177	0,206	1,164	0,247	0,280	1,134			1,000^1	1,000^2
1999	0,152	0,182	1,197	0,353	0,423	1,198	1,563^1	1,888^1	1,208^1	1,320^2
2000	0,162	0,194	1,198	0,469	0,568	1,211	0,340^1	0,366^1	1,077^1	1,420^2
2001	0,159	0,194	1,220	0,548	0,664	1,212	0,213^1	0,325^1	1,526^1	1,600^2
Mean			**1,195**			**1,189**			**1,203**	**1,475**

In the end of each growing season growing parameters where measured. From the diameter the basal area where calculated. The difference in growth between the years where calculated, the results where used instead of NPP in FACE 1.

The GUESS results was on average less the 2 % units higher than the LPJ-DGVM except for the first year where the LPJ-DGVM was 3 % units higher. The observed FACE 1 results shift widely over the years, from zero increase the first year to an increase of around 50 % units between the last two years. The FACE 2 was more stable, increasing year by year but lays high above the modelled values except for the first year.

Nevada

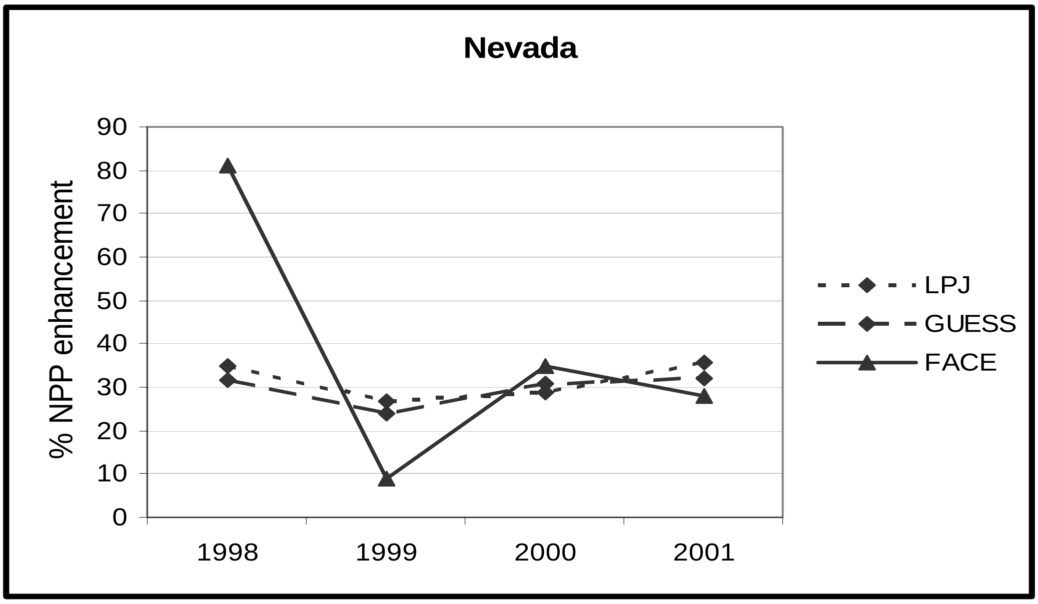


Figure 9. Year by year results from the Nevada site, shown as the quotient between annual NPP in elevated CO_2 concentration and ambient CO_2 concentration in percentage enhancement. The FACE results are estimated from Nowak et al., (2002) figure 10.

Table 6. Year by year results from the Nevada site. All values are for NPP are shown. The values from the FACE site are estimated from Nowak et al. (2002) and are above ground production.

	LPJ	kgC/m^2/yr		**GUESS**	kgC/m^2/yr		**FACE**		
Year	**Ambient**	**Elevated**	**E/A**	**Ambient**	**Elevated**	**E/A**	**Ambiant**	**Elevated**	**E/A**
1998	0,336	0,453	1,348	0,344	0,453	1,317	-	-	1,81
1999	0,16	0,203	1,269	0,162	0,201	1,241	-	-	1,09
2000	0,157	0,202	1,287	0,149	0,195	1,309	-	-	1,35
2001	0,132	0,179	1,356	0,134	0,177	1,321	-	-	1,28
Mean			**1,315**			**1,297**			**1,383**

As an index of NPP in a year, shoot production for three shrub and two perennial grass species was first weighted by plant cover, then perennial shoot production was averaged with the total production of four dominant annual species using a 2:1 weighting to estimate total above-ground production. Root length density where used to calculate below-ground production. (Nowak et al., 2004)

The GUESS result was on average 2 % units lower than LPJ-DGVM. The observed FACE results had a difference of 70 % units the first two years but then stabilised the last two years in the same range as the modelled results.

Swiss

The Swiss FACE site has been divided into three different groups depending on what nitrogen fertilization treatment the site where under and what vegetation that were included in the results.

In FACE and FACE 2 the vegetation was a monoculture consisting of ryegrass. The ambient and elevated CO_2 concentration were combined with nitrogen fertilization at 56 g N m^{-2} y^{-1} in FACE and 14 g N m^{-2} y^{-1} in FACE 2. FACE 3 consist of a polyculture of grasses and had the low nitrogen fertilization 14 g N m^{-2} y^{-1}.

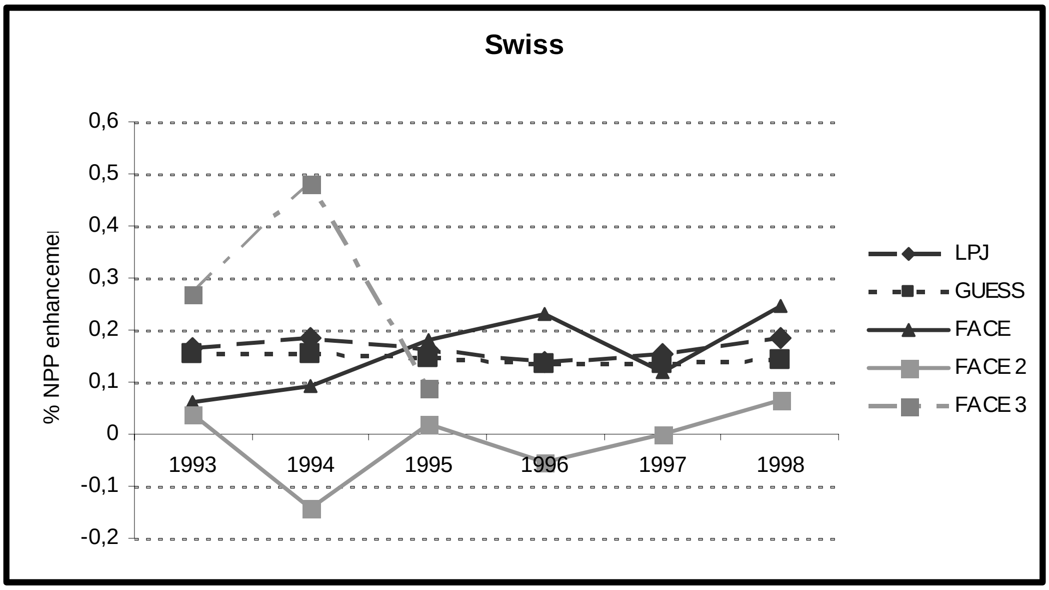


Figure 10. Year by year results from the Swiss site, shown as the quotient between annual NPP in elevated CO_2 concentration and ambient CO_2 concentration in percentage enhancement. The FACE and FACE 2 results are estimated from Deapp et al. (2000) figure 1 and FACE 3 results are from Lûscher et al., 1998 tabel 3.

GUESS was a little lower than LPJ-DGVM, around 2 % units, except in 1996 where LPJ-DGVM decreased to GUESS value. The high nitrogen fertilization, FACE, was on average around 20 % units higher than the low nitrogen fertilization, FACE 2. FACE 2 had negative values for 1994 and 1996 and it was only in the year 1998 that the results claimed over the zero line. Even though the FACE and FACE 2 only differed in the fertilization they did not follow each others fluctuations. From figure 10 the high fertilized results are in the same range as the models even though the models do not follow the fluctuations. The FACE and FACE 2 in this site only represent one of all the grass spices. Looking at the results of FACE 3 where all grasses are represented at low nitrogen fertilization these values are high above the rest of the values.

FACE

Table 7. Year by year results from the Swiss site. All values are for NPP are shown. The values from the FACE site are from Deapp et al., (2000).

	LPJ kgC/m^2/yr			**GUESS** kgC/m^2/yr			**FACE** DryMass/m^2/yr		
Year	**Ambient**	**Elevated**	**E/A**	**Ambient**	**Elevated**	**E/A**	**Ambiant**	**Elevated**	**E/A**
1993	0,864	1,008	1,167	0,49	0,565	1,153	1,150	1,220	1,061
1994	0,903	1,070	1,185	0,478	0,551	1,153	1,280	1,400	1,094
1995	0,841	0,978	1,163	0,482	0,553	1,147	1,500	1,770	1,180
1996	0,877	0,997	1,137	0,486	0,551	1,134	1,300	1,600	1,231
1997	0,884	1,019	1,153	0,502	0,569	1,133	1,790	2,000	1,117
1998	0,837	0,990	1,183	0,479	0,547	1,142	1,300	1,620	1,246
Mean			**1,164**			**1,144**			**1,155**

FACE 2

Table 8. Year by year results from the Swiss site. All values are for NPP are shown. The values from the FACE site are from Deapp et al., (2000).

	LPJ kgC/m^2/yr			**GUESS** kgC/m^2/yr			**FACE** DM/m^2/yr		
Year	**Ambient**	**Elevated**	**E/A**	**Ambient**	**Elevated**	**E/A**	**Ambiant**	**Elevated**	**E/A**
1993	0,864	1,008	1,167	0,49	0,565	1,153	0,410	0,425	1,037
1994	0,903	1,070	1,185	0,478	0,551	1,153	0,700	0,600	0,857
1995	0,841	0,978	1,163	0,482	0,553	1,147	0,800	0,815	1,019
1996	0,877	0,997	1,137	0,486	0,551	1,134	0,720	0,680	0,944
1997	0,884	1,019	1,153	0,502	0,569	1,133	1,980	1,980	1,000
1998	0,837	0,990	1,183	0,479	0,547	1,142	0,750	0,800	1,067
Mean			**1,164**			**1,144**			**0,987**

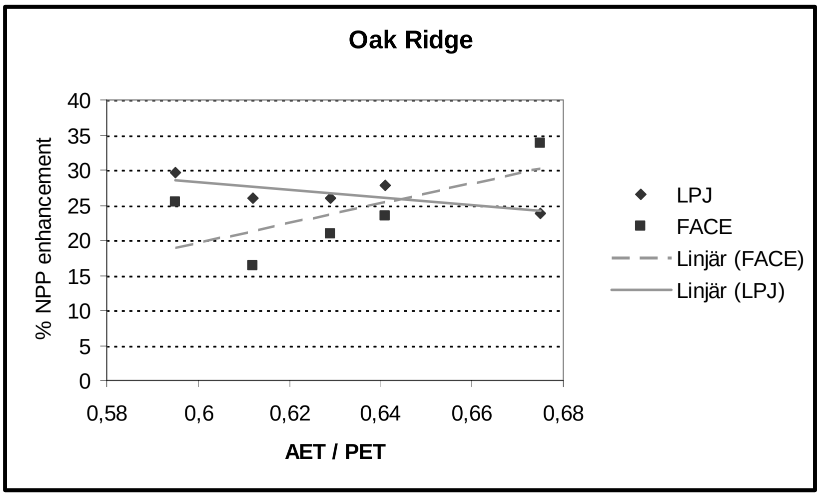
FACE 3

Table 9. Year by year results from the Swiss site. All values are for NPP are shown. The values from the FACE site are from from Lûscher et al., 1998.

	LPJ kgC/m^2/yr			**GUESS** kgC/m^2/yr			**FACE** DM/m^2/yr		
Year	**Ambient**	**Elevated**	**E/A**	**Ambient**	**Elevated**	**E/A**	**Ambiant**	**Elevated**	**E/A**
1993	0,864	1,008	1,167	0,49	0,565	1,153	-	-	1,27
1994	0,903	1,070	1,185	0,478	0,551	1,153	-	-	1,48
1995	0,841	0,978	1,163	0,482	0,553	1,147	-	-	1,09
Mean			**1,164**			**1,144**			**1,28**

4.2 Effects of water availability

The models were using the index actual evapotranspiration divided by potential evapotranspiration (AET / PET as a drought measurement. In figure 11 to figure 18 the percentage enhancement, for both FACE and LPJ-DGVM, are compared with the quotient between AET / PET followed by the relation between precipitation and percentage enhancement.



Values for AET / PET trendlines in the Oak Ridge site:

FACE
$y = 141x – 65$
were $R^2 = 0,45$
and $P = 0,218$

LPJ
$y = -55,5x + 62$
were $R^2 = 0,60$
and $P = 0,130$

Figure 11. The relationship between enhancement ratio (in percent) and AET / PET for the Oak Ridge site.

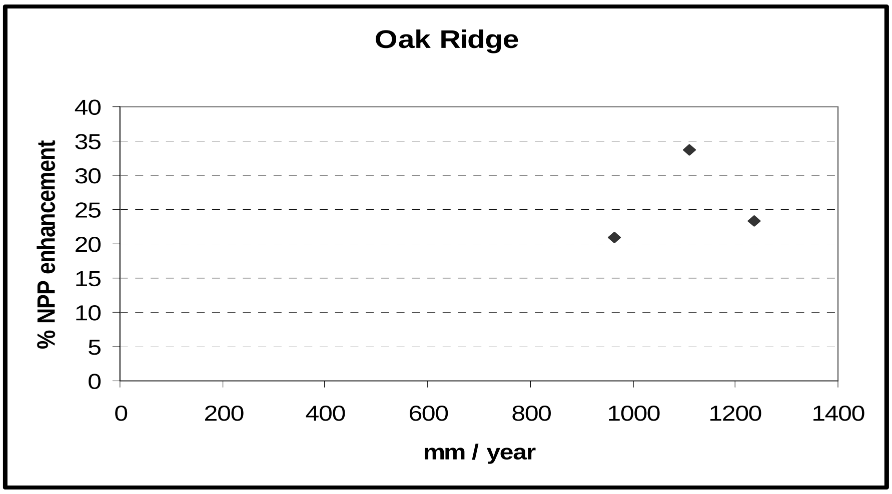
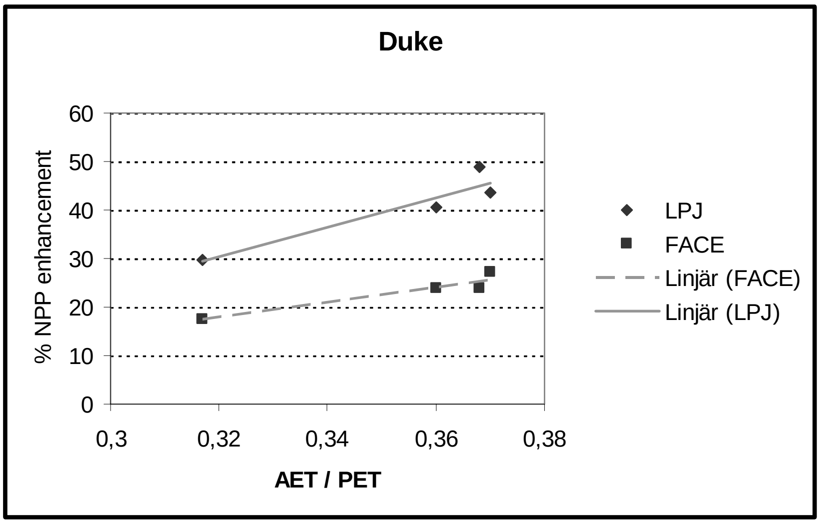


Figure 12. The relationship between enhancement ratio (in percent) and precipitation for the Oak Ridge site

The results from Oak Ridge, figure 11 and 12, showed that there were no significant relationships between the drought index, AET / PET, or between precipitation and NPP enhancement.



Values for AET / PET trendlines in the Duke site:

FACE
y = 155x – 32
were $R^2 = 0,9$
and P = 0,049

LPJ
y = 303x - 66
were $R^2 = 0,88$
and P = 0,060

Figure 13. The relationship between enhancement ratio (in percent) and AET / PET for the Oak Ridge site

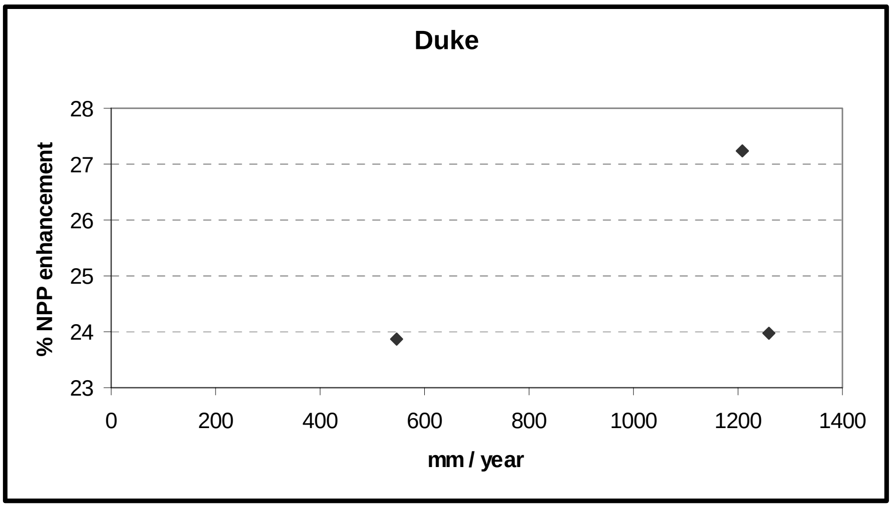
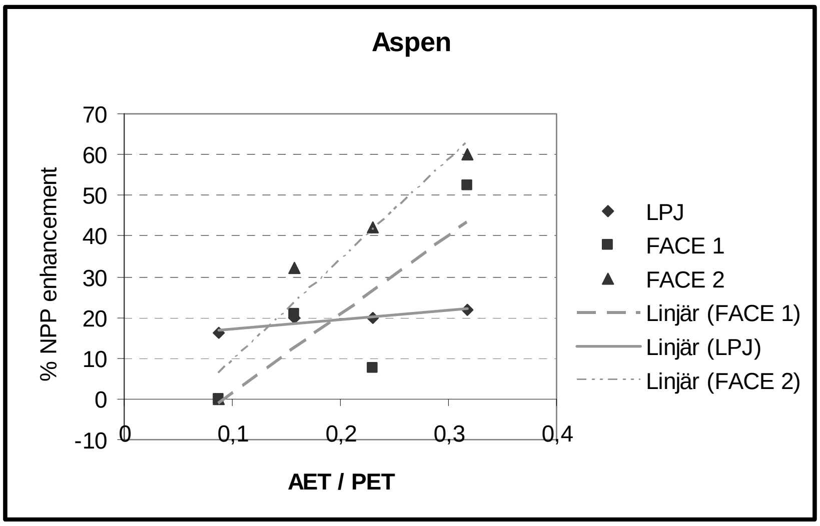


Figure 14. The relationship between enhancement ratio (in percent) and precipitation for the Duke site.

The results from Duke, figure 13, showed that there were significant relationships between the drought index, AET / PET and NPP enhancement for both the modelled and observed results. Figure 14 that describe the relation between precipitation and NPP enhancement did not show any relationship.



Values for AET / PET trendlines in the Aspen site:

FACE 1
y = 195x – 18
were R^2 = 0,68
and P = 0,822

FACE 2
y = 246,48x -15,365
were R2 = 0,9343
and P = 0,033

LPJ
y = 22x + 15
were R^2 = 0,88
and P = 0,739

Figure 15. The relationship between enhancement ratio (in percent) and AET / PET for the Aspen site.

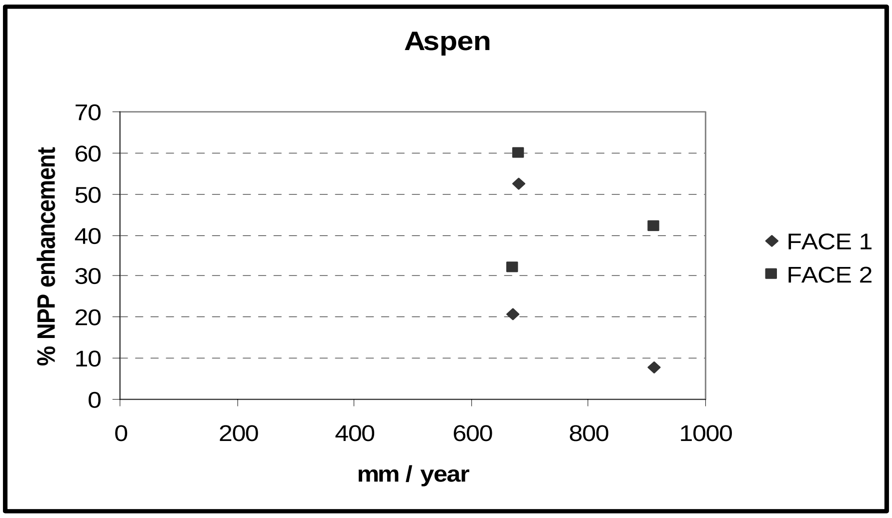
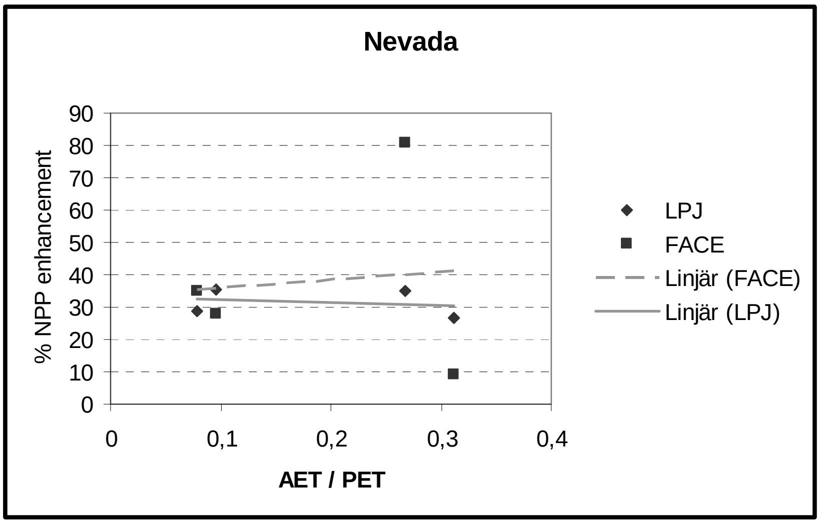


Figure 16. The relationship between enhancement ratio (in percent) and precipitation for the Aspen site

In figure 15 there are no significant relationship between AET / PET and NPP enhancement for LPJ-DGVM and FACE 1. The FACE 2 on the other hand showed significant relation between AET / PET and NPP enhancement in figure 15. There were no relationships between yearly precipitation and NPP enhancement.



Values for AET / PET trendlines in the Nevada site:

FACE
y = 26x – 33
were $R^2 = 0,01$
and P = 0,900

LPJ
y = -9x + 33
were $R^2 = 0,06$
and P = 0,739

Figure 17. The relationship between enhancement ratio (in percent) and AET / PET for the Nevada site

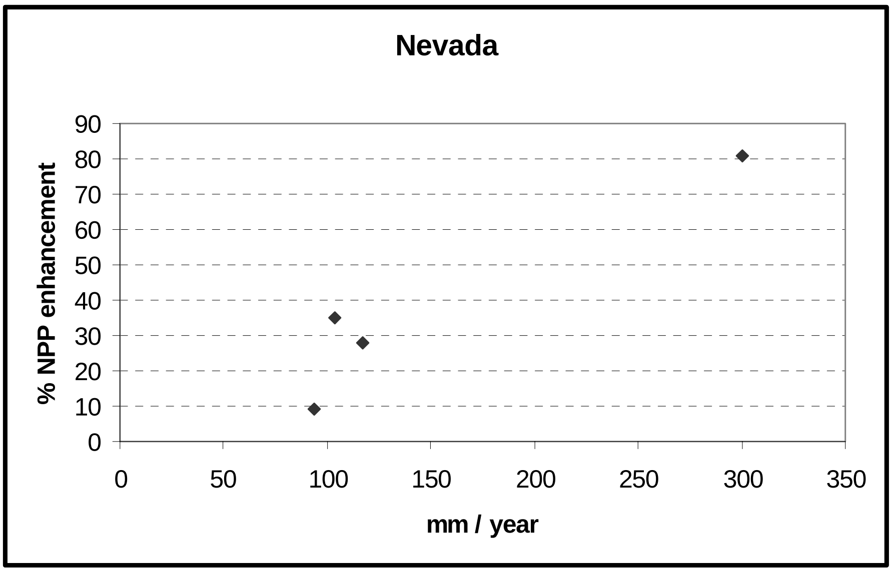


Figure 18. The relationship between enhancement ratio (in percent) and precipitation for the Nevada site.

In figure 17 there are no relation between AET / PET and NPP enhancement. However in figure 18 there are significant relationship between yearly precipitation and NPP enhancement.

5. Discussion

From the average enhancement from the sites (table 2) one can draw the conclusion that the vegetation responds positive to an elevated CO_2 concentration, around 25 %. Since the vegetation accounts for a large part of carbon uptake and carbon storage this leads to a big subject how well models can simulate this enhancement to make future predictions of the increasing atmospheric CO_2 concentration and its consequences. The models in this study simulate an increase in the same range as the FACE experiments, by only looking on the averages from all the sites in table 2. This is a crucial test for any ecosystem model to be applied for projections of future dynamics of vegetation productivity. These results indicate that a future CO_2 fertilisation effect as large as shown by Cramer et al. (2001) may be realistic.

5.1 Interannual variation

The models do generally fail to reproduce the observed interannual variations in the CO_2 response. One potential explanation for this is that the generalised representations of soil hydrology in the models do not adequately represent site-specific hydrological patterns and water-availability. To get a better understanding for the results its of great interest to look at the different sites year by year. Below follows a discussion for each site.

Oak ridge

By only looking at figure 5 the models showed a result in the same range as the observed. In figure 6 the results are explained by the fluctuation in the observed FACE result. Especially the last year that increases the overall average. The fluctuations at this site are hard to explain. One difference can be explained by Norby et al. (2002) that showed that the allocation of the carbon changes over the years. In the first year the elevated CO_2 resulted in increase in aboveground woody increment and where then declining the following years. This decline was matched by an increasing response of fine-root production. A possible explanation is that the increase in CO_2 and photosynthetic production as a delayed response of fine root production (Norby et al., 2002) and this is not included in the models.

Duke

Even though figure 5 indicates that the models strongly overestimate the CO_2 response, the interannual variation, table 4, indicates that the model and the observed values follow the same pattern. This shows that even if the models have results at higher values they have manage to simulate the same fluctuations as the observed FACE values. The low value in 1997 can be explained by exceptional low precipitation over the growing season (Ellsworth, 1999).

Duke FACE site when the results for AET / PET had a significant relationship for both the modelled and the observed values. This could be explaining why the Duke FACE site was the only site with similar pattern in the interannual variation (figure 7) between the observed and modelled results.

Aspen

Trembling Aspen has a rapid growth rate and a competitive growth strategy designed to take advantage of favourable environmental conditions. Because of these characteristics (high photosynthetic rates and stomatal conductance, rapid leaf growth and rapid height growth) the trembling aspen is quite sensitive to environmental stress (Dickson et al., 2001). This together with the fact that the FACE site is very young (the seedlings where only one year old when the experiment started) can explain the big fluctuation in the FACE 1 results, figure 8.

The results from the FACE 1 site are based on the change in annual basal area using the method DeLucia et al. (1999) used in their study over the Duke FACE site. The FACE 2 results come from Nowak et al. (2004) and he does not explain how the results were calculated therefore the difference between the two results can not be explained in this study.

The low values in FACE 1 year 2000, figure 8, can be explained by the dieback the site experienced (Iselbrands et al., 2001). This led to down cutting of trees, leading to a lower value of trees per square meter the following years and this is not implemented in the model. The FACE 2 instead continues increase this year.

Nevada

It has been suggested that desert vegetation will show the strongest response to elevated CO_2 concentration due to strong water limitation by both photosynthetic enhancement and reduction in stomatal conductance (Naumburg et al., 2003). The year 1998 was a year with a large amount of precipitation. This year is unfortunately not represented in the station climate but is instead represented by the CRU climate. This explains the high value in the observed FACE site and why the models do not show a higher value for this year. The year 1998 evidently shows that the vegetation under a reduced amount of waterstress leads to increase in the NPP due to a higher CO_2 concentration.

The vegetation in the site is not well represented in the models. They do not have a PFT for shrub so the vegetation is represented only by C_3 and C_4 grasses in the models while the observed values are calculated from both shrubs and grasses. Morgan et al., 2004 found that the biggest NPP enhancement was found in elevated CO_2 from new shoot biomass during wet years and in dry years, the CO_2-induced increase in shoot production typically was small. This could explain why the models did not manage to simulate the big fluctuations that the observed values showed.

Swiss

The Swiss site differs from the others since the use different nitrogen fertilizations. The models do not have a nitrogen limitation and it's therefore hard to make a comparison since the site does not have an experiment without fertilization. The nutrient issue is discussed in section 5.4.

5.2 Difference between the two models

LPJ-DGVM over simulates by 3 % units and the GUESS is almost the same as the observed results. Thus, simplified representations of vegetation dynamics, canopy light interception and PFT parameterizations, used LPJ-DGVM, seem to be sufficient for accurate projections of the effects of elevated CO_2 on NPP. The differences between GUESS and LPJ-DGVM do not influence the simulated CO_2 effect.

5.3 Effects of water availability

Many studies use a relationship between annual NPP and precipitation to show that the water stress is of great importance for the NPP. This can be discussed since the ability for water is controlled by more factors than precipitation. There are, for example, many places in the higher latitude that have a very low precipitation but still have an overflow of water. In this study the ratio between actual evapotranspiration and potential evapotranspiration were used as a value to indicate drought in the sites.

The short-term exposure of plants to elevated CO_2 has long been known to decrease stomatal conductance. Recent studies at the FACE sites, however, indicate little or no effect of atmospheric CO_2 on stomatal conductance (Norby et al., 1999).

The results in this study do not confirm the hypothesis that the NPP enhancement as a result of elevated CO_2 is larger under water limitation, showing no relation between enhancement ratio and the drought index AET / PET or precipitation.

For all the FACE sites except the Duke (figure 13) the drought index, the modelled and the observed enhancement ratio showed no similarity or relationship between each other. The differences between modelled and observed effects of water availability can explain discrepancies in the interannual variation. The drought index the model is using may be accurate applied on the Duke site.

In the Nevada FACE site there was a relationship between precipitation and enhancement ratio but no one for the drought index. Studies conducted at the site has showed that occasional increase in stomatal conductance as a result of water savings during preceding dry years under elevated CO_2 were observed in the Nevada FACE site (Pataki et el., 2000) but there are no indication that the soil water would be conserved (Nowak et al.,2004).

5.4 Are the results valid in the longer-term?

The forests are young plantations. To what extent mature forests behave similarly is very uncertain. A great issue here is how the vegetation will respond due to its demands for nutrients. Hungate et al., 2003 strongly criticise models that do not have nutrient limitations (there including the LPJ-DGVM), saying that these models highly overestimates the effects from elevated CO_2. The demand for nitrogen (N) set by rapid plant growth under elevated CO_2 could be met by increasing soil N availability or by greater efficiency of N uptake. Alternatively, plants could increase their nitrogen-use efficiency, thereby maintaining high rates of growth and NPP in the face of nutrient limitation (Finizi et al., 2002).

Nowak et al., 2004 tried to show how much nitrogen limits the NPP in a CO_2 enriched environment. His results are confusing when he calculates the difference between low nitrogen fertilization in ambient CO_2 concentration and high nitrogen fertilization in elevated CO_2 concentration (see figure 19). This leads to a result that includes both the nitrogen and the CO_2 fertilization. A more accurate result is shown in figure 20 showing the enhancement ratio between low and high nitrogen fertilization. As shown in figure 20 nitrogen may limiting the CO_2 response in some cases, but not as much as Nowak et al. (2004) are saying. In Nowaks et al. (2004) sites, figure 19, the estimated average differed around 3,45 units between low and high nitrogen fertilization, and the recalculated values had a difference of 0,49. This study shows that a model without nutrient limitation can reproduce the overall magnitude of the CO_2 effect on NPP observed at a number of experimental sites. This result indicates that nutrient availability does not crucially limit the CO_2 fertilization effect.

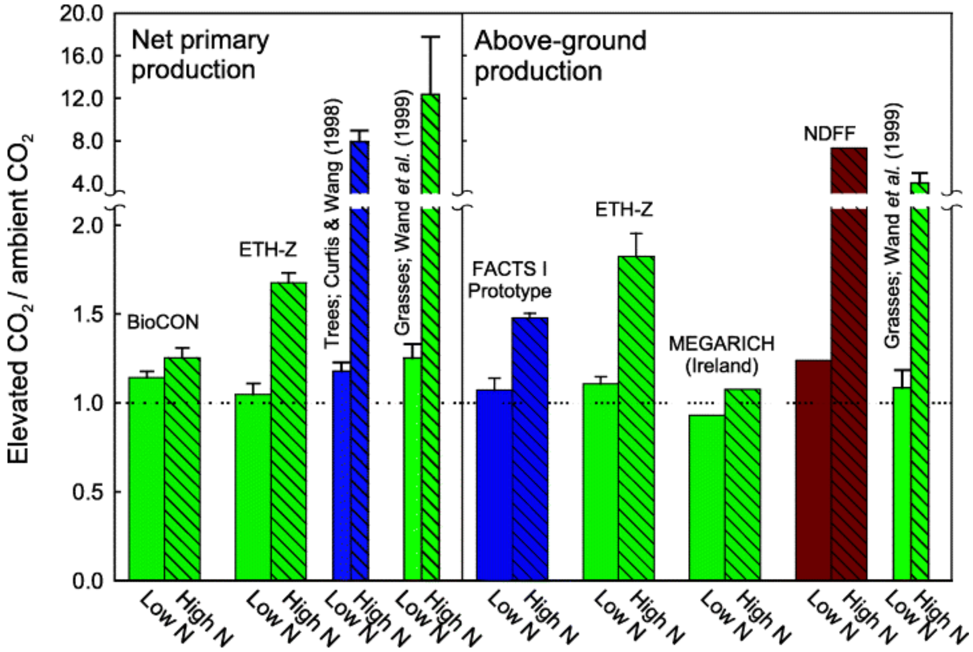


Figure 19. Nowak et al. (2004) figure on effects of increased nitrogen availability on the enhancement of primary production by elevated [CO2]. Wide, dark-colored bars are results from ecosystem free-air CO2 enrichment (FACE) experiments whereas narrow, light-colored bars are from meta-analysis of controlled environment and open-top chamber (OTC) experiments. The ratio of response under elevated [CO2] to that under ambient [CO2] (E/A) for low nitrogen (N) availability (closed bars) are production under elevated [CO2] and low N availability divided by production under ambient [CO2] and low N. The E/A ratio for high N availability (hatched bars) are production under elevated CO2 and high N availability divided by production under ambient [CO2] and low N.

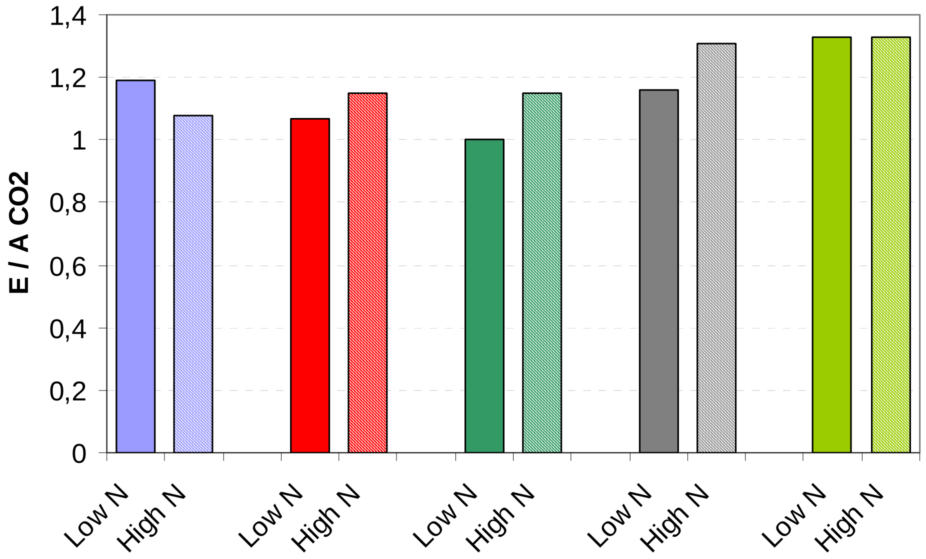


Figure 20. Recalculatation of Nowak's et al. (2004) figure 9. Showing the enhancement ratio between low and high nitrogen fertilization. Blue represents BioCON average of 4 month (june and august 1998 and1999) for 16 grassspecies (Reich et al., 2001), red represents Duke forest (Oren et al., 2001) in woody tissue (FACTS 1 in Nowak, et al., 2001 figure), dark green represents ETH-Z (Swiss), gray represents Curtis & Wang (1998) in woody plant biomass and light green represents Wand et al, (1999) in total biomass.

From the Swiss FACE experiment site there was little loss of Rubisco at elevated CO_2 concentration in ryegrass grown with a high nitrogen supply, but there was a significant loss at low nitrogen supply. However, the enhancement of assimilation by elevated CO_2

concentration was the same in both nitrogen treatments. The findings imply that nitrogen is not sequestered into Rubisco that would otherwise be in excess at elevated CO_2 concentration when grown in strongly nitrogen limited, but the increase in Rubisco is insufficient to remove any enhancement of assimilation by elevated CO_2 concentration (Long et al., 2004). The Swiss FACE experiment ran for 10 years and there is no evidence of a decline in the simulation of assimilation during the experiment, either in the high or low nutrient treatment (Long et al., 2004).

The fact that two models without nutrient limitation successfully simulates the observed magnitude of the CO_2 effect also indicates that nutrients availability does not strongly limit vegetation responses to elevated CO_2 productivity.

5.5 General conclusions

The models manage to provide results that were close the observed values in the FACE experiments when presenting the average NPP enhancement for all the sites over all the years. Thus strong CO_2 effects on NPP and carbon sequestration may occur in the future, but longer experimental time series are necessary to evaluate how the vegetation will respond. However the models fail to simulate the interannual variation in the CO_2 response. The explanation for this is probably the soil hydrology that the models do not adequately represent. The results do not confirm the hypothesis that the NPP enhancement as a result of elevated CO_2 is larger under water limitation. This study also manages to show that nutrient availability does not strongly limit vegetation response to elevated CO_2 productivity in the medium term.

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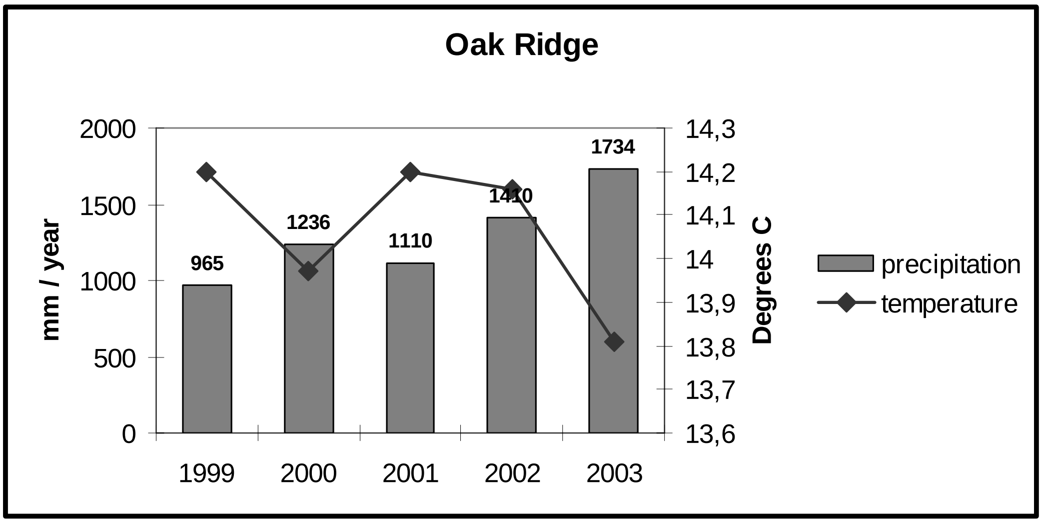
Appendix

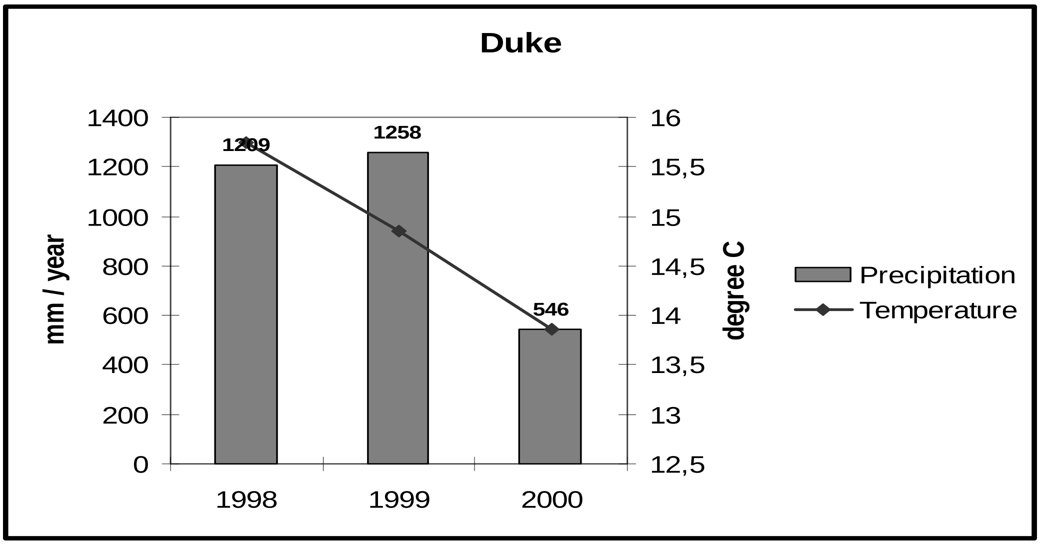


The Oak Ridge station climate was collected from the website:

www.esd.ornl.gov/facilities/ORNL-FACE/data.html

The data were in daily averages for temperature and PAR and precipitation were total over the day during the period 1999 – 2003.

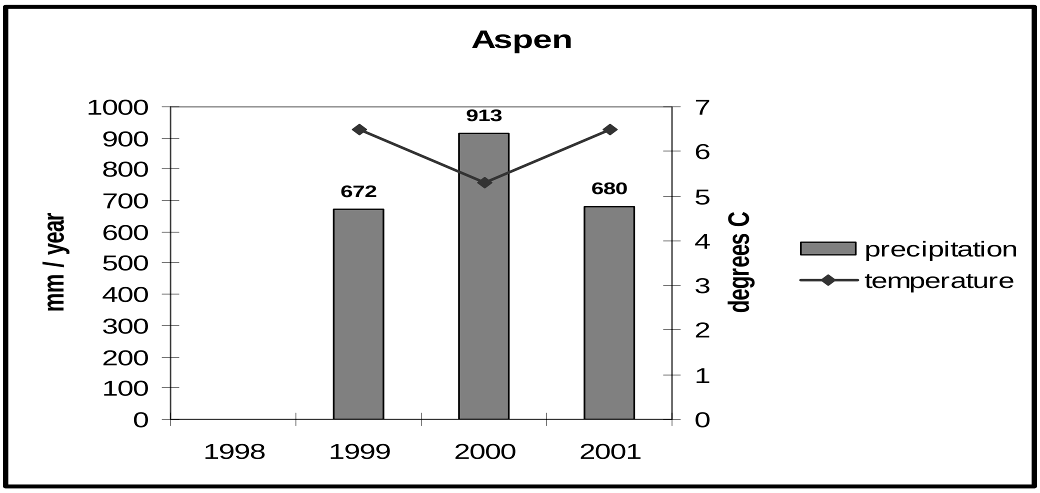
61 days were missing for precipitation and for the temperature 7 days were missing. For the PAR data 85 days were missing, to get the relationship between precipitation, temperature and solar radiation, temperature and precipitation were also changed for the days PAR was missing. Missing values were taken from the next year during the same days values were missing.



The Duke forest station climate was collected from the web site:

http://c-h2oecology.env.duke.edu/site/facedata.html

The data was presented as half hour data during 1998 – 2003. During this period 6290 (=131 days) half hours were missing for temperature and out of these 2560 (=53,3 days) could not be found in other rings at the same site. For PAR 9 089 (=228 days) half hours were missing and of these 4602 (= 95,8 days) could not be found in other rings at the same site. 9254 (=192,8 days) half hours were missing for precipitation.

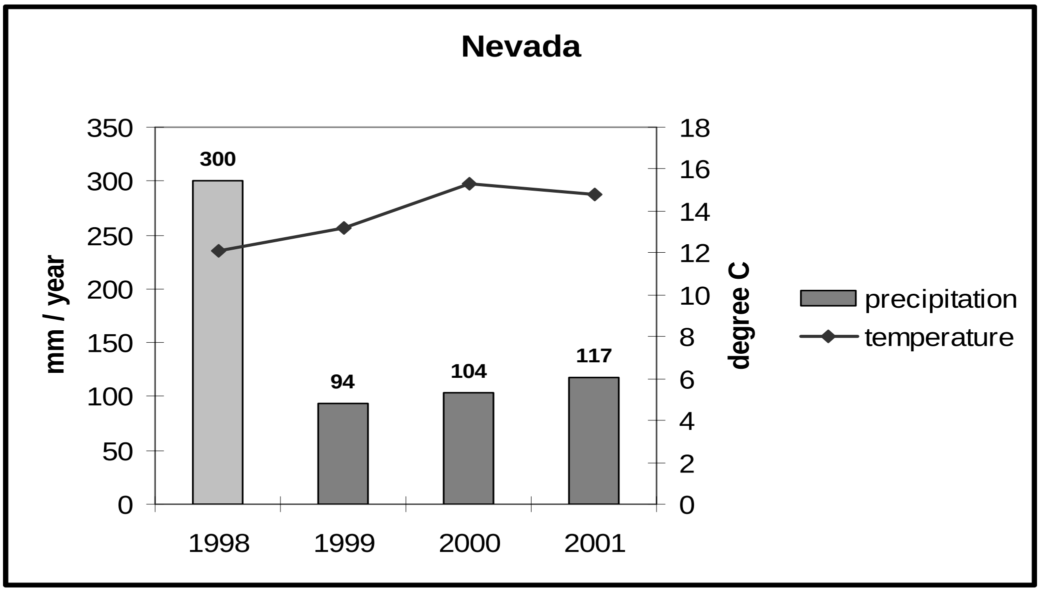


The Aspen station climate was collected from the website:

www.fs.fed.us/nc/face/

The data was presented as half hour data during 1999 – 2003. During this period 5455 (=113,6 days) half hours were missing for temperature and out of these 543 (=11,3 days)could not be found in other rings at the same site. For PAR 10 941 (=228 days) half hours were missing and of these were 5535 (=115,3) during dark hours of the day. 9750 (=203 days) half hours were missing for precipitation.

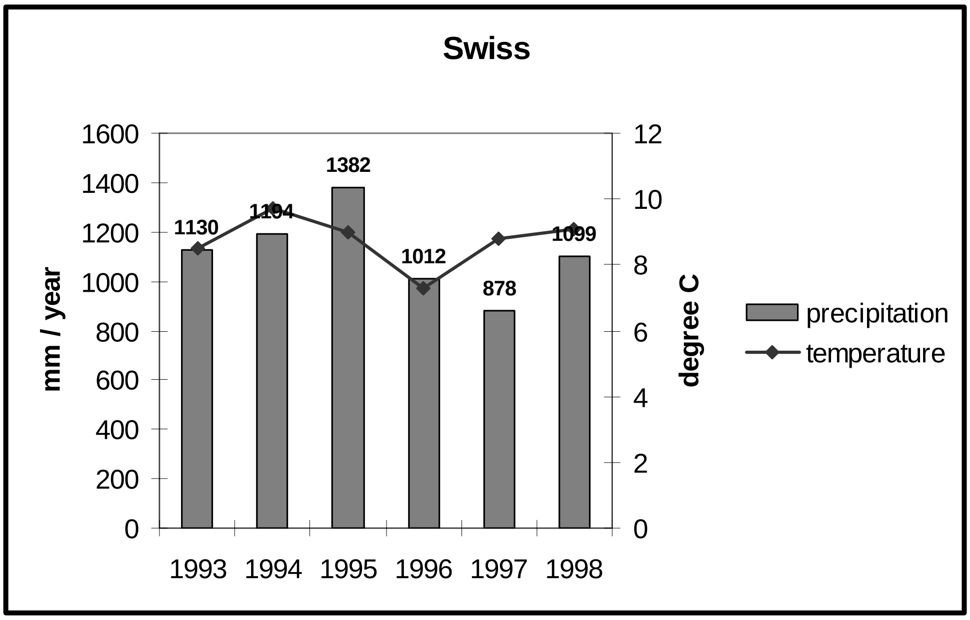
When a value was missing it depended on how long the sequences of missing values were. Separate missing half hours were collected from the half hour before. A few (up to tree days) hours missing were taken from the day before and long (over tree days) periods, missing days, were taken from the next year the same time period.



The Nevada station climate was collected from the website:

www.unlv.edu/Climate_Change_Research/Data_Bases/data_index.htm

Precipitation was presented as days it was raining and no values were missing. Station climate are 1999 – 2003. Temperature and PAR were hourly values. 117 (= 4,9 days) hours were missing for temperature and 169 (=7 days) hours for PAR. Missing data were taken from the day before at the same hours.



The Swiss station climate was collected from the website:
www.fb.ipw.agrl.ethz.ch/FACE.html
The data was presented as daily values data during 1993 – 2003. No values were missing at the Swiss site.

When a value was missing it depended on how long the sequences of missing values were. Separate missing half hours were collected from the half hour before. A few (up to tree days) hours missing were taken from the day before and long (over tree days) periods, missing days, were taken from the next year the same time period.

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