



Review

Response and potential of agroforestry crops under global change

C. Calfapietra^{a,*}, B. Gielen^b, D. Karnosky^c, R. Ceulemans^b, G. Scarascia Mugnozza^d^a Institute of Agro-Environmental & Forest Biology (IBAF), National Research Council (CNR), Via Salaria km 29,300, 00015 Monterotondo Scalo (Roma), Italy^b University of Antwerpen, Campus Drie Eiken, Department of Biology, Research Group of Plant and Vegetation Ecology, Universiteitsplein 1, B-2610 Wilrijk, Belgium^c Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931, USA^d Department of Agronomy, Forestry and Land Use (DAF), Agricultural Research Council of Italy (CRA), Via del Caravita 7/a 00186 Roma, Italy

Growth and management of agroforestry plantations will be influenced by climate change.

ARTICLE INFO

Article history:

Received 24 August 2009

Received in revised form

29 August 2009

Accepted 3 September 2009

Keywords:

SRF

Elevated CO₂

Climate change

Ozone

Poplar

ABSTRACT

The use of agroforestry crops is a promising tool for reducing atmospheric carbon dioxide concentration through fossil fuel substitution. In particular, plantations characterised by high yields such as short rotation forestry (SRF) are becoming popular worldwide for biomass production and their role acknowledged in the Kyoto Protocol. While their contribution to climate change mitigation is being investigated, the impact of climate change itself on growth and productivity of these plantations needs particular attention, since their management might need to be modified accordingly. Besides the benefits deriving from the establishment of millions of hectares of these plantations, there is a risk of increased release into the atmosphere of volatile organic compounds (VOC) emitted in large amounts by most of the species commonly used. These hydrocarbons are known to play a crucial role in tropospheric ozone formation. This might represent a negative feedback, especially in regions already characterized by elevated ozone level.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

1.1. Agroforestry crops: agricultural approach applied to forest plantations

Over the last thirty years, trees have been utilized in agroforestry plantations involving agriculturally productive landscapes and management techniques. Often, their yield and management are more similar to agricultural crops than to forest plantations (Weih, 2004). Short rotation forestry (SRF) plantations, also called short rotation cultures (SRC), have been introduced with the aim of producing biomass for energy and industry both in the USA (Hohenstein and Wright, 1994) and in Europe (Grassi et al., 1990) over the past two decades. These SRF plantations are now justifiably defined as bioenergy tree crops in addition to the more traditional use of their biomass for pulp, paper, construction wood or fodder (Weih, 2004).

SRF plantations usually have a rotation cycle less than 10 years, usually ranging from 3 to 6 years, in some cases even 1–2 years. They involve fast growing tree species planted at very high density with up to 10,000 trees per hectare. Typically, the higher the density, the

shorter the length of the rotation cycle. Short rotation periods are advantageous because they reduce the risk of growth reduction or mortality due to disease or wind-throw and allow for the use of more convenient agricultural techniques to harvest the crop.

Furthermore, the fact that no resource is allocated to sexual reproduction for several years after coppicing is beneficial to vegetative yield (Pontauiller et al., 1999). The most common species utilized for such plantations in temperate climates belong to the genera *Populus* and *Salix*; *Eucalyptus* is utilized in mild climates. In a few cases, species of the genera *Betula*, *Alnus*, *Robinia* and *Nothofagus* are also utilized. For several species and hybrids of *Populus* and *Salix* a large number of genotypes have been selected to allow the distribution of these plantations at very different latitudes and climatic conditions (Heilman et al., 1994; Ceulemans and Deraedt, 1999; Mitchell et al., 1999; Karacic et al., 2003). Biomass production rates are variable according to the clone, climate and limiting factors but are often in the range of 8–12 Mg of dry matter ha⁻¹ year⁻¹ as woody aboveground biomass (Mitchell et al., 1999) although it is also possible to achieve productivities above 20 Mg of dry matter ha⁻¹ year⁻¹.

Short rotation forestry crops are currently assuming growing importance in many countries where surplus agricultural land is becoming available. In addition to an increasing interest in renewable energy sources, Article 3.3 of the Kyoto Protocol attributes a crucial role to forest plantations in sequestering the

* Corresponding author. Tel.: +39 06 90672530; fax: +39 06 9064492.

E-mail address: carlo.calfapietra@ibaf.cnr.it (C. Calfapietra).

atmospheric CO₂ to meet commitments towards a reduction of CO₂ emissions. Thus, SRF plantations represent an ideal tool to maximize yields and sequester CO₂.

The perennial character of the tree crops usually allows a reduction in herbicide application compared to traditional agricultural crops. In addition to this environmentally advantageous attribute, SRF crops can also offer a buffering effect on nitrogen leaching thanks to the dense rooting systems which allow better nutrient utilization and consequently a greater yield compared to agricultural crops (Goor et al., 2000). Finally, SRF plantations are gaining interest given their potential for phytoremediation through the uptake of large quantities of nutrients from municipal and industrial wastewater (Aronsson and Perttu, 2001) and of heavy metals (Laureysens et al., 2004, 2005).

1.2. Manipulative experiments to simulate climate change on SRF species

Among the characteristics which distinguish tree from agricultural crops, size is probably the most important. This, of course, increases the difficulty when manipulative experiments to simulate climate change are established, and is the primary reason why most of the studies available in literature are carried out in laboratories with seedlings that often show different responses from those of mature trees. Another limitation to the responses observed in the literature is the length of many experiments which last for just few days or for one growing season. It is clear that some responses are affected by seasonality or changing growth patterns over many years. Furthermore, experiments that use small enclosures to grow trees alter the microclimatic conditions, constraints at the root system (typical in trees grown in pots) or limitations in light, water or nutrients availability.

In this review we will focus on three aspects of climate change: increase of atmospheric CO₂ concentration, increase of

tropospheric O₃ concentration and increase in air temperature (Table 1). When the SRF species are native it is possible to use regional or altitudinal gradients of O₃ or temperature on natural populations to simulate the climate change (Winner et al., 1989; Karnosky et al., 1999; Rood et al., 2007). But often genetic changes influence the response more than the experimental factor itself. In the case of elevated CO₂ simulations, natural springs are being used for studies on trees, although the lack of an experimental control is a major deficiency.

The exposure systems to study the impacts of climatic changes on forest trees have evolved drastically over the last decades (Ceulemans and Mousseau, 1994; Karnosky et al., 2007). Free Air CO₂ Enrichment (FACE) technology was developed during the 1990s to overcome the limitations of chamber studies. This technique allowed for the direct fumigation of trees growing in the ground without any alteration of the microclimatic and soil conditions (McLeod et al., 1985; Hendrey et al., 1999). This technique has also been applied to CO₂ and O₃ fumigation in FACE systems (Hendrey et al., 1999). Two FACE facilities examining agroforestry tree crops are AspenFACE experiment in Rhinelander, Wisconsin, USA where a high-density *Populus tremuloides* stand is fumigated alone and in combination with elevated CO₂ and elevated O₃ (Karnosky and Pregitzer, 2006) and the POP-EUROFACE experiment in Italy where elevated CO₂ and N fertilization are tested alone or in combination on a multispecies SRF poplar plantation (Scarascia-Mugnozza et al., 2006) (Fig. 1). A modification of the FACE approach with a technique called web-FACE based on a fine web of tubes woven into tree canopies with the help of a construction crane has also been applied both for CO₂ and O₃ fumigation (Körner et al., 2005; Matyssek et al., 2007) although not on SRF tree species.

Air temperature is more difficult to manipulate than CO₂ or O₃ in experiments outside of growth cabinets, and there have, therefore, been far fewer ecosystem-scale warming experiments (Rustad

Table 1

List of the studies including global change manipulations on SRF species. The review includes field studies except few cases of laboratory or pot experiments.

Location (experiment name)	Facility	Factors examined	Species	Main references
Viterbo, Italy (POP-EUROFACE)	FACE	CO ₂ N	<i>Populus alba</i> , <i>Populus nigra</i> , <i>Populus deltoides</i> × <i>Populus nigra</i>	Miglietta et al. (2001), Calfapietra et al. (2001), Scarascia-Mugnozza et al. (2006)
Rhineland, WI, USA (AspenFACE)	FACE	CO ₂ O ₃	<i>Populus tremuloides</i> (different clones)	Karnosky et al. (2003, 2007)
Oracle, AZ, USA (Biosphere 2)	Mesocosms	CO ₂ Temperature	<i>Populus deltoides</i>	Zabel et al. (1999), Barron-Gafford et al. (2005)
Rapolano, Italy	mini-FACE	CO ₂	<i>Populus deltoides</i> × <i>Populus nigra</i> , <i>Populus deltoides</i>	Miglietta et al. (1997), Tognetti et al. (1999)
Antwerp, Belgium	Open-top chambers	CO ₂	<i>Populus deltoides</i> × <i>Populus nigra</i> <i>Populus trichocarpa</i> × <i>Populus deltoides</i> <i>Populus tremuloides</i> (different clones)	Ceulemans et al. (1995, 1996), Kalina and Ceulemans (1997)
Alberta, MI, USA	Open-top chambers	CO ₂ O ₃	<i>Populus trichocarpa</i>	Kull et al. (1996), Karnosky et al. (1998)
Gunnarsholt, Iceland	Closed-top chambers	CO ₂ N	<i>Populus trichocarpa</i>	Sigurdsson et al. (1998), Sigurdsson et al. (2001)
Headley, UK	Open-top chambers	CO ₂ O ₃	<i>Populus trichocarpa</i> × <i>Populus deltoides</i>	Taylor et al. (1995), Gardner et al. (2005)
Pellston, MI, USA	Cooling boxes	Temperature N	<i>Populus tremuloides</i>	King et al. (1999)
Gainesville, FL, USA	Tunnels	CO ₂ Water stress	<i>Populus trichocarpa</i> × <i>Populus deltoides</i> , <i>Salix sagitta</i>	Johnson et al. (2002)
Mekrijärvi, Finland	Closed-top chambers	CO ₂ Temperature	<i>Salix myrsinifolia</i>	Kellomäki and Wang (1998), Veteli et al. (2002)
Melbourne, Australia	Glasshouse	CO ₂ Water stress	<i>Eucalyptus cladocalix</i>	Palanisamy (1999)
Darwin, Australia	Chambers	CO ₂	<i>Eucalyptus tetrodonta</i>	Berryman et al. (1993), Eamus et al. (1995)
Edinburgh, UK	Open-top chambers	O ₃	<i>Eucalyptus grandis</i> , <i>E. urophylla</i> , <i>E. camaldulensis</i> , <i>E. torelliana</i> , <i>E. phaeotrica</i>	Lima et al. (2003)
Canberra, Australia	Growth chambers	CO ₂ Temperature Water stress	<i>Eucalyptus macrorhyncha</i> , <i>Eucalyptus rossii</i>	Roden and Ball (1996)



Fig. 1. The two Free Air CO₂ Enrichment (FACE) experiments on agroforestry tree crops: a) The AspenFACE experiment in Rhinelander, Wisconsin (USA) where elevated CO₂ and elevated O₃ treatments are tested alone or in combination (field station with 12 experimental plots, photo by Dave Karnosky) and b) the POP-EUROFACE experiment in Tuscania, Viterbo (Italy) where elevated CO₂ treatment and N fertilization treatments are tested alone or in combination (particular of one experimental plot, photo by Steve Bunn).

et al., 2001). Many warming experiments elevate soil temperatures (using buried heating cables) or canopy temperatures (using infrared heaters), making the interpretation of results difficult (Rustad et al., 2001). The largest facility utilized so far for warming experiments on SRF tree species is the Biosphere 2 Research Center in USA where elevated CO₂ levels in combination with night time warming are tested on a *Populus deltoides* mesocosm encased in a glass and metal shell (Walter and Lambrecht, 2004).

1.3. Single vs. combination of factors and the importance of the ecosystem approach

Climate change is a phenomenon involving numerous processes such as increase of elevated CO₂ concentration, air temperature and tropospheric O₃ levels, variation in the UV-B radiation and in the atmospheric events, depositions of pollutants, etc. Simulating all these processes together to study the response of plants especially in field experiments is not feasible also because some processes vary their extent in the different parts of the planet or during the

day. Usually the simulation of one factor at a time or two–three factors combined is done. An exception is the Jasper Ridge Experiment where four factors (CO₂, temperature, water, nutrients) were varied in a full factorial design (Shaw et al., 2002) on a grassland community.

Single-factor responses can be misleading because of interactions between these factors, and indirect effects such as increased nutrient availability from temperature-induced decomposition. In the long-term the strength of feedbacks, for example the increasing demand for nutrients from increased growth, will dominate over short-term responses to single factors (Hyvönen et al., 2007). This is particularly important for SRF crops. For example, nutrient availability can compromise the resprouting capacity over multiple rotation cycles as well as the potential yield. Thus, it is crucial to conduct long-term ecosystem-scale multifactor experiments testing the same protocol on different ecosystems and climatic zones. Also, a multidisciplinary approach involving researchers covering multiple ecosystem scales is necessary for understanding the processes and interactions of factors at the different levels (Beier, 2004). For instance elevated CO₂ is supposed to stimulate growth of crops but when experiments are moved at ecosystem scale it is observed that elevated CO₂ might exacerbate pests and insect attacks. In SRF plantations this might be of particular importance as spray treatments are sometimes difficult and economically disadvantageous. Although single-factor experiments cannot directly inform us on ecosystem response to simultaneous changes in multiple factors, these are important to provide critical information on the response to single vectors of change (Rustad, 2006) and to focus on specific mechanisms which are directly or indirectly driven by a change in one factor.

Indirect effects will likely be even more important than the direct effects in the longer-term but are more complex and require an ecosystem-scale approach. It is however, difficult to predict the indirect effects of multiple, interacting factors (Shaver et al., 2000). Thus, models are essential tools for conceptually and empirically integrating existing knowledge to make longer-term projections of ecosystem-scale responses of multiple interacting vectors of global change (Deckmyn et al., 2004; Classen and Langley, 2005).

Another potential complication arising from experimental studies is the application of the treatment. In nature, environmental changes are often gradual and plants, especially trees are able to adapt and acclimate. The sudden manipulation of several environmental factors may therefore elicit an un-natural response to the treatment. Even if the treatment starts at the establishment of an SRF plantation for example, thus exposing the plant under treated conditions throughout its life cycle, the impact on the long-term carbon pools in the soil could be sudden and dramatic. In an SRF, for instance, it has been found that step changes may induce a sudden, significant increase of labile C in the soil, stimulating rhizosphere activity with consequent priming of the decomposition of old stable organic matter (Hoosbeek et al., 2004).

2. Effects of global change on growth and productivity

2.1. Short rotation forestry productivity

As in agricultural crops, the maximization of yields represents the main objective in SRF plantations. Thus, the role of climate change on their productivity is a primary concern to assess whether these tree crops will be economically competitive in the future. Although in SRF plantations only aboveground woody biomass is economically relevant, the accumulation of carbon in the below-ground compartment and in the soil is also of interest for the CO₂ mitigation strategies and might acquire economic value in the future. Moreover the below-ground carbon is sequestered during

the entire life of the plantation whereas carbon in the aboveground compartment is usually re-emitted at the end of each rotation cycle when the biomass is burned for energy.

An overall positive response to CO₂ enrichment was reported for poplars with a stimulation of total biomass or stem biomass ranging from 22 to 90% (Gielen and Ceulemans, 2001). In OTC experiments, two different clones of *P. trichocarpa* × *P. deltoides* exhibited an increase in stem biomass by 38 and 39% (Ceulemans et al., 1995; Gardner et al., 2005). In another OTC experiment *P. trichocarpa* exhibited increased above- and below-ground biomass production under elevated CO₂ by 45% and 58%, respectively, but only when nitrogen availability was high whereas no effect or slightly negative effect was observed when nitrogen availability was low (Sigurdsson et al., 2001). If the effect of elevated CO₂ is higher on the below-ground biomass than on the aboveground biomass then the root/shoot ratio is modified as reported in some experiments with trees (Janssens et al., 2000). This might be of primary importance for SRF plantations because the increased accumulation on the below-ground compartments could favour sprouting in the year following the harvest.

Over the 4-year Biosphere 2 experiment, cumulative below-ground and total aboveground biomass of *P. deltoides* increased in both elevated CO₂ treatments (Barron-Gafford et al., 2005). In particular, the 800 and 1200 ppm CO₂ treatments produced 27% and 28% more total aboveground biomass, respectively, than the 400 ppm. Also, trees in the 800 and 1200 ppm CO₂ treatments produced an average of 27% and 37% more cumulative root biomass, respectively, per tree than the 400 ppm control treatment after 3 years of growth.

In both FACE experiments involving *Populus* species, a significant stimulation for both above- and below-ground biomass was observed which was maintained even after canopy closure (Norby et al., 2005). Aboveground stimulations ranged between 15 and 29% according to the different species and the rotation cycle at the POP-EUROFACE site and were similar to the stimulation on the below-ground biomass (Calfapietra et al., 2003a; Liberloo et al., 2006). However, when fine roots were considered the stimulation by elevated CO₂ increased drastically being 113% at the AspenFACE and 64% at the POP-EUROFACE as average of the aspen clones in the first case and poplar species in the second (King et al., 2001; Lukac et al., 2003).

Such investment in fine roots under elevated CO₂ has also been described in other tree species (Norby et al., 1999) and is of particular value for short rotation cultures because it would theoretically guarantee good yields over several growing seasons. This type of mechanism could however imply a shift in the tree's functional balance between carbon acquisition vs. water and nutrient acquisition (Norby et al., 1999) possibly compromising productivity especially when SRF plantations are not fertilised and/or irrigated.

In an experiment with *Salix myrsinifolia*, elevated CO₂ increased stem dry weight by 28% (Veteli et al., 2002) whereas in an experiment with *Eucalyptus pauciflora*, it has been shown how elevated CO₂ might delay cold acclimation inducing frost damages and reducing biomass production (Barker et al., 2005).

Observations on natural vegetation and experiments in OTC confirm that *Populus* spp. and *Salix* spp. are among the most sensitive genera to ozone pollution (Novak et al., 2003; Bussotti et al., 2007). *Populus tremuloides* clones planted along a natural O₃ gradient showed increased damage at higher O₃ concentrations (Karnosky et al., 1999). In a recent review it is reported that ozone causes adverse effects on most components of growth of aspen, but root growth appears to be most severely impacted (Karnosky et al., 2007). In OTC experiments, stem biomass production of *P. tremuloides* was decreased under ozone exposure by 11–40% according

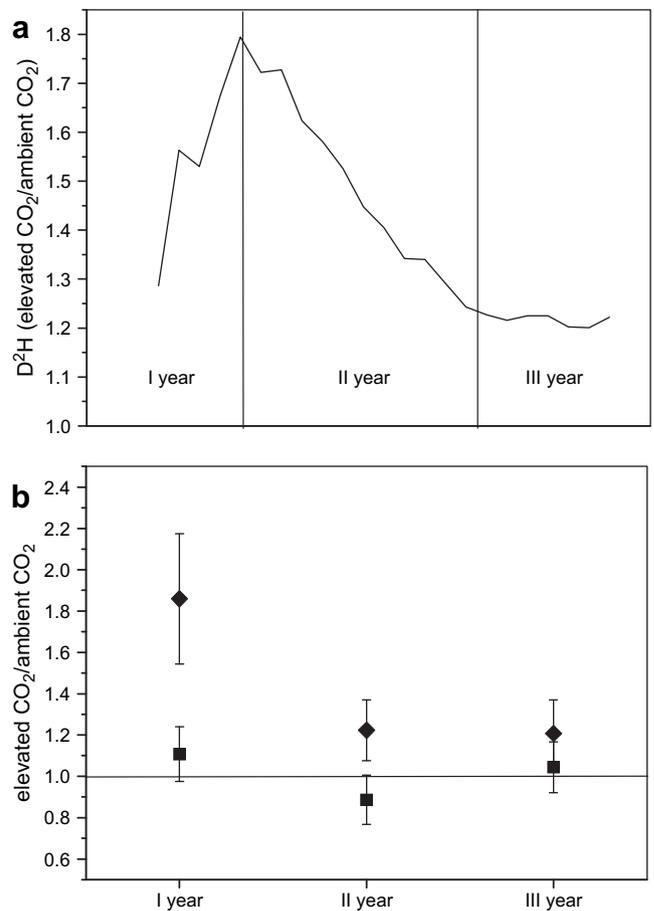


Fig. 2. E/A (elevated over ambient CO₂) for a) the volume index D²H over the first rotation cycle at the POP-EUROFACE site; b) the relative growth increment (RGI, black squares) and the absolute growth increment (AGI, black rumbles) of D²H for each of the three years.

to the clone in ambient ozone compared to filtered air and by 30–46% in the O₃-enriched treatment (Dickson et al., 2001).

At AspenFACE, *P. tremuloides* growth was strongly inhibited for most of the clones although not for the ozone tolerant one (Karnosky et al., 2005). Although shifts in carbon allocation were found previously for this species (Karnosky et al., 1996) and for other species exposed to ozone (Andersen, 2003), no changes in root/shoot ratios emerged at the AspenFACE (Karnosky et al., 2005). Interestingly, the O₃ treatment caused more rapid root turnover and a smaller crop of standing fine-root biomass (Karnosky et al., 2005). Some species of *Eucalyptus* also appeared sensitive to ozone: *E. microcorys* and *E. gomphocephala* exhibited a reduction in biomass production by 30% under ozone exposure while *E. globulus* did not in OTC experiments (Monk and Murray, 1995). Experiments with warming showed an increased whole-plant growth for *P. tremuloides* by 37% when soil was warmed by 2–7 °C (King et al., 1999) whereas in *Salix myrsinifolia* higher temperature had a positive effect on stem biomass production although not on the total aerial biomass (Veteli et al., 2002).

In a meta-analysis of warming experiments, the response of aboveground productivity varied inversely with the mean annual temperature of the experimental site (Rustad et al., 2001). However a great difference exists among species: Tjoelker (1997) found that conifers had the highest mean relative growth rate (RGR) and mass at intermediate temperatures, while broadleaved species such as *Populus tremuloides*, exhibited the highest mean RGR and mass at the highest temperatures. It is not clear what might be the role of

warming on the below-ground biomass accumulation in SRF plantations: it is likely that this might differ among the latitude and the species considered. Usually higher temperatures are associated with increased fine-root production and mortality, and therefore turnover rates (Pendall et al., 2004). This, as suggested due to elevated CO₂ might have positive repercussions on the sustainability of enhanced productivities over multiple rotation cycles in SRF plantations.

2.2. Growth analysis in tree crops under global change

Agroforestry tree crops differ from most of the agricultural crops because they occupy the land for many years. Thus the study of the effects of climate change on this particular kind of crop requires an approach at an ecosystem level that takes into account interactions and feedbacks between plant and soil over the entire period. Given the complexity of interactions the response might change among the different years or even within a single growing season. In manipulative experiments over multiple years these transient effects, which are driven by particular often unknown mechanisms, might be masked because we only observe the cumulative effects when we measure or sample at the end of a predicted period. Growth analysis in SRF crops might be a typical example. At the POP-EUROFACE experiment, we showed how growth patterns manifested in different ways may lead to contrasting interpretations of the effect of elevated CO₂ on growth. At the end of the first rotation cycle differences in volume index between elevated and ambient CO₂ was slightly higher than 20%, however, this ratio changed over the three years (Fig. 2a). This is a result of changes in growth rates as evidenced by Fig. 2b. Focussing on the relative growth increment, it is evident that the stimulation by CO₂ occurred only in the first and in the third year. Conversely, trees grew less under elevated CO₂ in the second year. However, when focussing on absolute growth increment, it is evident that the stimulation by elevated CO₂ was present even in the second year which means trees accumulated more biomass and carbon than under ambient CO₂.

From this example, it is evident that growth can provide contrasting indications whether it is presented as relative growth or absolute growth. Moreover, when we compare different years in multiannual experiments, we should consider tree condition at the onset of each year, as it often happens that trees start from different sizes in the treatments.

Relative growth increment (RGI) offers a good tool to normalize growth for initial size, but unfortunately RGI is affected by size and tends to decrease with increasing size (Evans, 1972). Accordingly, the higher values of second-year RGI in the ambient CO₂ treatment

can be simply explained by the larger size of the trees under elevated CO₂.

An alternative to RGI is evaluating growth of trees in the different treatments at the same size rather than at the same time. This is done by plotting the absolute growth increment of trees (AGI) in short periods against their size, and analysing the curves of the different treatments using analysis of covariance. This can yield useful information provided that growth in the different treatments is evaluated at the same phase in the growing season (Calfapietra et al., 2003b). In the case of SRF plantations where the primary objective is to maximize yield and carbon sequestration, AGI should be primarily considered as it gives a direct measure of the sequestration potential in the different treatments.

If multiple years and heterogeneity in size between treatments is a trait common to other tree crop experiments, growth estimates on SRF plantations are complicated by the fact that aboveground biomass is removed at the end of each rotation cycle (as short as one year), whereas below-ground biomass and soil carbon continue to accumulate over the entire life of the plantation.

For instance, it is difficult to ascribe to SRF plantations any of the four models of growth that have been proposed by Körner (2006) to compare growth of plants under elevated CO₂ vs. ambient CO₂ over the duration of the experiment. In particular, he presented four possible situations: i) No CO₂ effect; ii) continuous CO₂ effect combined with compound interest effects (expanding system), leading to exponential growth; iii) initial effects as in (ii) but no further stimulation after completion of canopy and root volume expansion; and iv) initial effect as in (ii) but return to control biomass after completion of the expansive phase.

In Fig. 3 we adapt these models to SRF plantations over multiple rotation cycles. In Fig. 3a the growth is largely stimulated by elevated CO₂ during the first rotation cycle especially after the establishment of a conspicuous below-ground apparatus. Differences between treatments become evident both in the above- and below-ground biomass although the stimulation decreases when competition starts to be limiting. In the second rotation cycle (Fig. 3b) the below-ground biomass only slightly increases in both treatments as most of the volume is already occupied by roots at the end of the first cycle. Aboveground biomass production is higher than in the first cycle because resources in stump and roots allow a vigorous resprouting at the onset of the second cycle but CO₂ stimulation tends to decrease as the length of the cycle gets longer. In Fig. 3c we hypothesize what would be the CO₂ effect and the biomass production once nutrients are becoming limiting. In very poor sites this might be even typical of the third cycle but it is more likely such a pattern for a following cycle. Of course, there is no additional accumulation in below-ground biomass as soil has been already fully occupied by roots in the previous cycle. However,

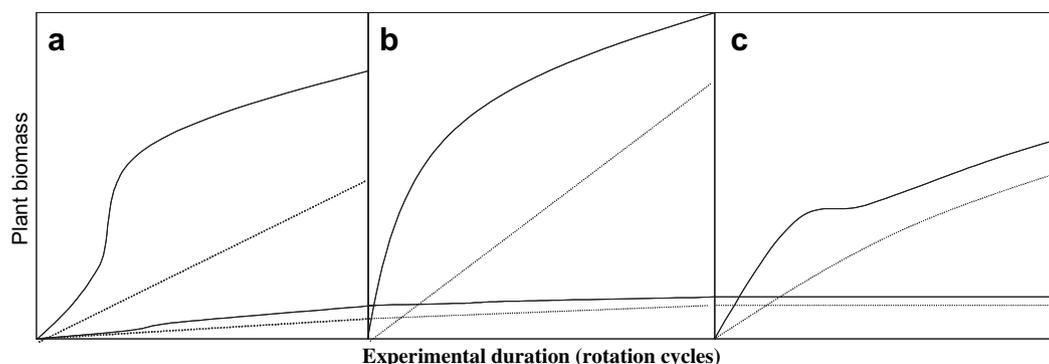


Fig. 3. Growth pattern for SRF plantations under elevated CO₂. a) first rotation cycle; b) second rotation cycle; c) rotation cycle when strong nutrient limitation occurs. Upper lines represent above-ground biomass, while lower lines represent below-ground biomass; full line: elevated CO₂ and dashed line: ambient CO₂.

differences between treatments might persist because under elevated CO₂ roots are usually able to colonize deeper layers of soil (Lukac et al., 2003). Aboveground production might be even lower than the first cycle and the CO₂ stimulation is restricted to a very short period in the first part of the rotation cycle. This should be the sign for a replacement of the plantation or for a fertilization treatment once it is verified that this behaviour is determined by scarcity of nutrients. Obviously, it is desirable not to reach these conditions in productive plantations as the yields might be heavily compromised.

2.3. Effects on soil C

The role of soil in the carbon mitigation strategies is being investigated with growing interest because it is still uncertain what the potential of carbon accumulation might be, especially under future atmospheric levels of CO₂. In a recent review, van Groenigen et al. (2006) found that total soil C increased significantly by 4.1% at elevated CO₂ but the effect was relevant depending on N fertilization. Unfortunately, only one study included in the review was on woody plants whereas greatest interest is on natural forests and tree crops. Deckmyn et al. (2004) compared the benefits for carbon sequestration of afforestation with a multifunctional oak–beech forest vs. a poplar SRF through model simulations. SRF resulted more sensitive to global change with a yield increase of 65%, compared to 25% in an established forest (Table 2).

At the POP-EUROFACE experiment, total soil C increased with time under ambient and elevated CO₂ by 12 and 3%, respectively, suggesting that the establishment of the plantation itself induces a considerable input of carbon into the soil (Hoosbeek et al., 2004). Despite the fact that total soil carbon increased more under ambient CO₂ than under elevated CO₂, the new carbon deriving from litter incorporation was sequestered considerably more under elevated CO₂ rather than under ambient CO₂. Hoosbeek et al. (2004) hypothesized that these opposite effects may be caused by a priming effect of the newly incorporated litter, where priming effect is defined as the stimulation of soil organic matter (SOM) decomposition caused by the addition of labile substrates.

At the Biosphere 2 experiment, tree growth at elevated CO₂ increased inputs to SOM by increasing the production of fine roots and accelerating the rate of root C turnover. However, soil carbon content decreased as CO₂ in the atmosphere increased and inputs of new C were not found in SOM. The huge increase in soil respiration under elevated CO₂ led to net loss of soil C at a rate that was between 10 and 20 times faster at elevated CO₂ than at ambient conditions (Trueman and Gonzalez-Meler, 2005).

At the AspenFACE experiment, the elevated ozone treatment heavily affected the soil carbon sequestration in the aspen plantation. In particular, the less depleted δ¹³C signature of total soil carbon from the elevated O₃ + CO₂ treatment compared to the elevated CO₂ treatment indicates that less carbon entered the soil

when aspen was exposed to both elevated O₃ and CO₂. Elevated O₃ reduced total soil carbon formation by approximately 300 g cm⁻² compared to the amount formed under elevated CO₂ alone (Loya et al., 2003).

Some experiments show a loss of soil C under elevated temperature (Melillo et al., 2002); however, it seems possible that global soils will lose less carbon in response to warming than currently anticipated, because the decomposition of old organic matter is not greatly accelerated by increasing temperatures, may be because microbes lack substrates, old organic matter is recalcitrant or increasing temperature increases physico-chemical protection (Saxe et al., 2000).

2.4. Interactions with abiotic factors: resource use efficiency

The variations induced by global change on SRF ecosystems and in particular on plant growth induce a series of feedback on resource use especially because typically fast growing species consume resources at high rates.

Water and nitrogen are usually the resources which might become limiting and compromise the yields in SRF plantations, although in some cases irrigation and fertilization might be provided regularly like agricultural crops. When tree species have been tested in open fields under elevated CO₂ they usually exhibited decreased stomatal conductance (Medlyn et al., 2001), whereas Norby et al. (1999) provided evidence that the effect is in many cases negligible. Most of the studies on *Populus* showed a decrease of stomatal conductance although not in all studies (Gielen and Ceulemans, 2001). Although this effect might result in an increased WUEi (Intrinsic Water Use Efficiency), it should be taken into account that at the ecosystem level LAI of the plantation is usually stimulated by elevated CO₂ and, thus, the transpiration rate at the ecosystem level might be heavily increased.

At the POP-EUROFACE experiment, stomatal conductance has been always inhibited by elevated CO₂ throughout the different years of the experiment (Bernacchi et al., 2003; Calfapietra et al., 2005) and this resulted in a significant increase in WUEi (Tricker et al., 2004). On the other hand, LAI was stimulated by elevated CO₂ at the onset of each rotation cycle (Gielen et al., 2001; Liberloo et al., 2006) but not when canopy closure occurred (Gielen et al., 2003; Liberloo et al., 2006) suggesting a different repercussion on total water consumption by the plantation.

At the Biosphere 2 experiment, leaf-level transpiration rates in *P. deltoides* were approximately equivalent across CO₂ treatments when soil water was not limiting. In contrast, during drought stress, canopy-level transpiration rates were approximately equivalent across CO₂ treatments, indicating that leaf-level fluxes during drought stress were reduced in elevated CO₂ by a factor equal to the leaf area ratio of the two canopies (Engel et al., 2004).

Water use efficiency was increased in *P. tremuloides* at AspenFACE under elevated CO₂ both under ambient ozone and in combination with high ozone. However, ozone itself induced a significant decrease of water use efficiency (Sober et al., 2000).

Elevated temperature leads to increased evapotranspiration; without commensurate increases in precipitation, water stress can affect both plant and soil processes (Norby and Luo, 2004) which are particularly relevant for agroforestry plantations, usually requiring high water availability. However, increasing temperature at the Biosphere 2 did not result in any significant change in WUE (Water Use Efficiency) on *P. deltoides* both calculated at leaf level and at ecosystem level (Barron-Gafford et al., 2007).

Furthermore, while water can be limiting depending on the weather conditions, nitrogen limitation is exacerbated throughout the lifetime of the plantation as SRF crops uptake large amounts of nitrogen each year.

Table 2
Comparison of C pools modelled from different ecosystem compartments in short rotation forestry (SRF) and mixed forests under actual and global change conditions (adapted from Deckmyn et al., 2004).

	C wood (t ha ⁻¹)	C root (t ha ⁻¹)	C soil (t ha ⁻¹)	Total (t ha ⁻¹)	Yield (t ha ⁻¹ yr ⁻¹)
ACTUAL					
SRF	14.2	5.2	143.0	162.4	6.2
Mixed forest	61.5	210	170.5	264.6	2.2
GLOBAL CHANGE					
SRF	22.3	8.3	154.2	184.8	10.3
Mixed forest	123.7	41.7	160.3	337.4	3.1

When plants are exposed to elevated atmospheric CO₂ concentrations, they often exhibit enhanced growth with increased biomass accumulation, which in the long-term can lead to an increased nitrogen uptake from the soil. Increased N uptake was observed under elevated CO₂ in three of the forest FACE experiments: AspenFACE, DukeFACE, and OakRidgeFACE (Finzi et al., 2007). By contrast, at the POP-EUROFACE experiment none of the three *Populus* species exhibited increased N uptake even if the biomass increased considerably under elevated CO₂ (Calfapietra et al., 2007). This resulted in increased nitrogen use efficiency (NUE) under elevated CO₂ although the depletion of total N in the soil suggested a potential limitation under elevated CO₂ for the following rotation cycles of the poplar plantation. Also, at Biosphere 2 elevated CO₂ accelerated depletion of soil nutrients, phosphorus, calcium and potassium, after 3 years of growth, although total N showed no change (Barron-Gafford et al., 2005). An increase in ozone concentration could exacerbate the negative feedbacks of elevated CO₂ on soil N availability through a decrease on gross N mineralization as found by Holmes et al. (2006) at AspenFACE.

Nitrogen mineralization may be stimulated by warming and act as a positive feedback to plant productivity (Stromgren and Linder, 2002). However, over a longer-term period this might result in an accelerated depletion of available soil N with negative feedbacks on plant productivity itself. This is particularly relevant in SRF plantations because at the end of each rotation cycle the soil remains uncovered and therefore favours soil warming, especially in southern climates. In general, warming tends to have a negative effect on plant NUE (Fuhrer, 2003).

2.5. Interactions with biotic factors

Both damaging and beneficial insects, as well as disease susceptibility, can be affected by changing environmental conditions, either directly or indirectly via changes in host physiology and chemical composition, or via effects on predators, competitors, and insect pathogens (Patterson, 1995). In perennial tree crops, these effects can even be exacerbated because they accumulate year after year. Moreover, in SRF plantations farmers often avoid any insecticide treatments because extremely expensive but on the other hand damages by insects can dramatically compromise the yields.

In the *Populus* plantation at POP-EUROFACE, elevated CO₂ did not have a clear effect on the defoliator *Melasoma populi* attacks but increased the percentage of trees attacked by the stem borer *Cryptorhynchus lapathi* on *P. × euramericana* (Speranza and Calfapietra, unpublished results).

At the same site the results concerning both *Marssonina* spp. and *Melampsora* spp. attacks on three different poplar species did not show any significant variation between CO₂ treatments, whereas the only clear and direct effect of elevated CO₂ was an increase in the intensity of attacks of sooty moulds (Scarascia-Mugnozza et al., 2006).

At AspenFACE, elevated CO₂ did not have any significant effect on aspen aphids (Percy et al., 2002) but it decreased Aspen Blotch Leafminer (Kopper and Lindroth, 2003) and increased attacks by *Oberea* woodborer (Karnosky et al., 2003). Food consumption by herbivores and population development should be lower in O₃-exposed plants, contrary to the situation with CO₂, but as seen above experimental evidence often suggests otherwise (Fuhrer, 2003). As for diseases, elevated O₃ considerably enhanced susceptibility of aspen trees to *Melampsora medusae* (Karnosky et al., 2002).

Increase in temperature might lead to a possible exacerbation of insect attacks in SRF plantations especially in case of warmer winters which might result in reduced mortality of the over-

wintering insects. Moreover, the extension of the growing season might lead to the onset of an additive generation of *Melasoma populi* in poplar plantations (Speranza and Calfapietra, unpublished results). Increase in temperature is expected also to increase leaf rust and decrease leaf blotch diseases, especially when combined with less precipitation levels (Jahn et al., 1996).

3. Implications for management

The role that SRF plantations and more generally tree crops can have in the future depends on the understanding of their role in relation to climate change both in terms of response and of mitigation potential. So far forest plantations cover 190 Mha worldwide, with planting rates of 8.5–10.5 Mha year⁻¹ resulting in an annual net gain of 1.96 Mha year⁻¹ between 1965 and 1990 (FAO, 2005). In particular, SRF plantations are gaining importance for biomass production substituting for fossil fuel and therefore reducing GHG emissions. The management of this particular kind of crop has to take into account the change in climatic conditions and in the atmospheric composition. On one hand the warming will allow northern expansion of the forest plantations, on the other hand it will exacerbate the dry conditions in the south requiring the use of irrigation practices in most cases. The possibility to expand SRF plantations in the boreal regions has potential value represented by the increase in the abundance and diversity of many organisms in boreal landscapes dominated by either agricultural fields or managed coniferous forests (Weih, 2004). Ozone pollution together with the increase in ultraviolet-B (UV-B) radiation will certainly reduce yields both in the boreal and in the southern regions where it could even compromise the use of some sensitive species. A combination of climatic and environmental stresses might exacerbate the extent of pest and insects attacks with possible dramatic repercussions on the productivity. However, the negative factors mentioned above might easily be counterbalanced by some other processes included in global change such as increase in CO₂ concentration and warming and by the activities of breeding and selection. While warming could sometimes be self-defeating in southern climates, the fertilization effect by the increase in CO₂ concentration is usually recognized worldwide (Norby et al., 2005). Moreover, modern biotechnology offers exciting possibilities for plant breeding towards increased yields, improved stress resistance, and pest tolerance (Wullschleger et al., 2002).

The increase in productivity due to global change opens new perspectives in the management strategies of SRF plantations because it might exacerbate nutrient deficiencies over multiple rotation cycles. From this point of view, it appears crucial that nutrient cycling in an SRF system is managed to provide sustainable biomass production and land use. In the meantime, estimating the right amount of fertilizer to apply is important in order to minimize production costs and to limit off-site effects of fertilization (Heilman and Norby, 1998). The variations in growth patterns originated by global change as suggested in the previous paragraphs for the increase in CO₂ levels might lead to change the number and length of the rotation cycles. If stimulating effect of CO₂, warming and selection will prevail over the negative factors as suggested by Deckmyn et al. (2004), the length of the rotation cycles will need to be reduced in order to avoid the collapse in growth rate observed when competition becomes a limiting factor. On the other hand, the number of cycles will be determined by the analysis of the costs for increasing nutrient demand and the income derived from decreased yields over time.

According to FAO (2005), SRF plantations of just poplars and willows account for 2 million hectares worldwide but areas of poplars in SRF plantations are increasing in several countries such as Bulgaria, Canada, China, Germany, Serbia & Montenegro, Spain,

and the United States of America. Considering that substitution for fossil fuels for SRF plantations accounts for a yearly reduction in C emissions of 7–8.5 Mg ha⁻¹ yr⁻¹ which can increase under global change up to 14 Mg ha⁻¹ yr⁻¹ (Deckmyn et al., 2004) it is easy to believe that these plantations will gain importance in the next decades.

A negative feedback might derive from the emission of volatile organic compounds (VOC) which have a crucial role in the oxidizing potential of the atmosphere. In particular, isoprenoid oxidation leads to the formation of tropospheric ozone and other secondary pollutants. VOC emission is particularly relevant for poplar and eucalyptus species which are most commonly used in SRF plantations, therefore, a massive diffusion of VOC might have serious repercussions on the atmospheric composition. In this regard, willow species might be more suitable because they are known to emit considerably less isoprenoids compared with poplar species. Engineering non-emitting poplars through the suppression of the isoprene synthase gene could overcome this limitation (Miller et al., 2001). Moreover, there is some evidence that both elevated CO₂ and increases in ozone levels might lead to decreased isoprene emission in *Populus* species with a possible positive feedback on the air quality (Rosenstiel et al., 2003; Calafapietra et al., 2008). On the other hand, it is also expected that VOC emission will increase considerably under a warmer climate. Despite the added value and the potentiality, increasing the range of SRF plantations appears to be mainly regulated by sociopolitical issues such as investment in agroforestry products for energy purposes and market developments.

4. Conclusions

Short rotation forestry plantations are becoming increasingly important in many parts of the world. Like agricultural crops, the objective of agroforestry tree crops production is maximizing yields. Consequently, research is often focussed on the most productive genotypes to use in different climates. It is, however, also important to consider that tree crops occupy soil for multiple years and therefore the same cultural practices used for annual crops cannot be directly applied.

Agroforestry tree crops also have the potential to be an important tool for fossil fuel substitution aimed at drawing down atmospheric CO₂ to mitigate global warming. It is expected that in the near future millions of hectares of land will be occupied by these plantations. It is, therefore, critical to assess the likely impact of global change on the growth and productivity on the candidate species to maximize yields and carbon sequestration potential. It is economically and logistically difficult to design experiments that investigate the effects of multiple, interacting global changes. As a result, many of the observed experimental responses are from experiments examining one main global change factor. The main findings from large-scale experiments where elevated CO₂, ozone pollution and warming have been simulated in open environments are reported here. While elevated CO₂ will guarantee higher yields, ozone pollution may offset or negate the stimulation. Warming will probably produce contrasting effects according to the climate and the interaction with drought. Furthermore, it is also important to consider other factors such as soil fertility and pest attacks.

Acknowledgement

The authors wish to thank the POP-EUROFACE and the AspenFACE communities for the helpful suggestions on the contents of this review, as well as Paolo de Angelis for productive discussions over the last few years and Victoria Wittig for language revision.

References

- Andersen, C.P., 2003. Source-sink balance and carbon allocation below ground in plants exposed to ozone. *New Phytologist* 157, 213–228.
- Aronsson, P., Perittu, K., 2001. Willow vegetation filters for wastewater treatment and soil remediation combined with biomass production. *Forestry Chronicle* 77, 293–299.
- Barker, D.H., Loveys, B.R., Egerton, J.J., Gorton, H., Williams, W.E., Ball, M.C., 2005. CO₂ enrichment predisposes foliage of a eucalypt to freezing injury and reduces spring growth. *Plant Cell and Environment* 28, 1506–1515.
- Barron-Gafford, G.A., Martens, D., Grieve, K., McLain, J.E.T., Lipson, D., Murthy, R., 2005. Growth of eastern cottonwoods (*Populus deltoides*) in elevated [CO₂] stimulates stand-level respiration and rhizodeposition of carbohydrates, accelerates soil nutrient depletion, yet stimulates above and belowground biomass production. *Global Change Biology* 11, 1220–1233.
- Barron-Gafford, G.A., Grieve, K., Murthy, R., 2007. Leaf- and stand-level responses of a forested mesocosm to independent manipulations of temperature and vapor pressure deficit. *New Phytologist* 174, 614–625.
- Beier, C., 2004. Climate change and ecosystem function – full-scale manipulations of CO₂ and temperature. *New Phytologist* 162, 243–245.
- Bernacchi, C.J., Calafapietra, C., Davey, P.A., Wittig, V.E., Scarascia-Mugnozza, G.E., Raines, C.A., Long, S.P., 2003. Photosynthesis and stomatal conductance responses of poplars to free-air CO₂ enrichment (PopFACE) during the first growth cycle and immediately following coppice. *New Phytologist* 159, 609–621.
- Berryman, C.A., Eamus, D., Duff, G.A., 1993. The influence of elevated atmospheric CO₂ on growth, nutrient content and biomass allocation of *Maranthus corymbosa*. A closed forest species of the wet-dry tropics of Australia. *Australian Journal of Botany* 41, 195–209.
- Bussotti, F., Desotgiu, R., Cascio, C., Strasser, R.J., Gerosa, G., Marzuoli, R., 2007. Photosynthesis responses to ozone in young trees of three species with different sensitivities, in a 2-year open-top chamber experiment (Curno, Italy). *Physiologia Plantarum* 130, 122–135.
- Calafapietra, C., Gielen, B., Sabatti, M., De Angelis, P., Scarascia Mugnozza, G., Ceulemans, R., 2001. Growth performance of *Populus* exposed to "Free Air Carbon dioxide Enrichment" during the first growing season in the POPFACE experiment. *Annals of Forest Science* 58, 819–828.
- Calafapietra, C., Gielen, B., Galema, A.N.J., Lukac, M., De Angelis, P., Moscatelli, M.C., Ceulemans, R., Scarascia-Mugnozza, G., 2003a. Free-air CO₂ enrichment (FACE) enhances biomass production in a short-rotation poplar plantation (POPFACE). *Tree Physiology* 23, 805–814.
- Calafapietra, C., Gielen, B., Sabatti, M., De Angelis, P., Miglietta, F., Scarascia-Mugnozza, G., Ceulemans, R., 2003b. Do above-ground growth dynamics of poplar change with time under CO₂ enrichment? *New Phytologist* 160, 305–318.
- Calafapietra, C., Tulva, I., Eensalu, E., Perez, M., De Angelis, P., Scarascia-Mugnozza, G., Kull, O., 2005. Canopy profiles of photosynthetic parameters under elevated CO₂ and N fertilization in a poplar plantation. *Environmental Pollution* 137, 525–535.
- Calafapietra, C., De Angelis, P., Gielen, B., Lukac, M., Moscatelli, M.C., Avino, G., Lagomarsino, A., Polle, A., Ceulemans, R., Scarascia Mugnozza, G., Hoosbeek, M., Cotrufo, M.F., 2007. Nitrogen use efficiency of a short-rotation poplar plantation is increased under elevated CO₂. *Tree Physiology* 27, 1153–1163.
- Calafapietra, C., Scarascia Mugnozza, G., Karnosky, D.F., Loreto, F., Sharkey, T.D., 2008. Isoprene emission rates under elevated CO₂ and O₃ in two field-grown aspen clones differing for their sensitivity to O₃. *New Phytologist* 179, 55–61.
- Ceulemans, R., Deraedt, W., 1999. Production physiology and growth potential of poplar under short-rotation forestry culture. *Forest Ecology and Management* 121, 9–24.
- Ceulemans, R., Jiang, X.N., Shao, B.Y., 1995. Effects of elevated atmospheric CO₂ on growth, biomass production and nitrogen allocation of two *Populus* clones. *Journal of Biogeography* 22, 261–268.
- Ceulemans, R., Shao, B.Y., Jiang, X.N., Kalina, J., 1996. First- and second-year aboveground growth and productivity of two *Populus* hybrids grown at ambient and elevated CO₂. *Tree Physiology* 16, 61–68.
- Ceulemans, R., Mousseau, M., 1994. Tansley review No. 17. Effects of elevated atmospheric CO₂ on woody plants. *New Phytologist* 127, 425–446.
- Classen, A.T., Langley, J.A., 2005. Data-model integration is not magic: modeling ecosystem responses to global change: techniques and recent advances. *New Phytologist* 166, 367–370.
- Deckmyn, G., Muys, B., Garcia Quijano, J., Ceulemans, R., 2004. Carbon sequestration following afforestation of agricultural soils: comparing oak/beech forest to short-rotation poplar coppice combining a process and a carbon accounting model. *Global Change Biology* 10, 1482–1491.
- Dickson, R.E., Coleman, M.D., Pechter, P., Karnosky, D.F., 2001. Growth and crown architecture of two aspen genotypes exposed to interacting ozone and carbon dioxide. *Environmental Pollution* 115, 319–334.
- Eamus, D., Duff, G.A., Berryman, C.A., 1995. Photosynthetic responses to temperature, light flux-density, CO₂ concentration. Pressure deficit in *Eucalyptus tetrodonta* grown under CO₂ enrichment and vapour. *Environmental Pollution* 90, 41–49.
- Engel, V.C., Griffin, K.L., Murthy, R., Patterson, L., Klimas, K., Potosnak, M.J., 2004. Growth CO₂ concentration modifies the transpiration response of *Populus deltoides* to drought and vapor pressure deficit. *Tree Physiology* 24, 1137–1145.

- Evans, G.C., 1972. Relative growth rate. In: Anderson, D.J., Greigh-Smith, P., Pitelka, F.A. (Eds.), *The Quantitative Analysis of Plant Growth*. Blackwell Scientific Publications, Oxford, pp. 246–254.
- FAO, 2005. Report of the 22nd Session of the International Poplar Commission and 42nd Session of its Executive Committee, Santiago, Chile, 28 November–2 December 2004.
- Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., Ceulemans, R., 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *Proceedings of the National Academy of Sciences of the United States of America* 104, 14014–14019.
- Fuhrer, J., 2003. Agroecosystem responses to combinations of elevated CO₂, ozone, and global climate change. *Agriculture, Ecosystems and Environment* 97, 1–20.
- Gardner, S.D.L., Freer-Smith, P.H., Tucker, J., Taylor, G., 2005. Elevated CO₂ protects poplar (*Populus trichocarpa* × *P. deltoides*) from damage induced by O₃: identification of mechanisms. *Functional Plant Biology* 32, 221–235.
- Gielen, B., Ceulemans, R., 2001. The likely impact of rising atmospheric CO₂ on natural and managed *Populus*: a literature review. *Environmental Pollution* 115, 335–358.
- Gielen, B., Calfapietra, C., Sabatti, M., Ceulemans, R., 2001. Leaf area dynamics in a closed poplar plantation under free-air carbon dioxide enrichment. *Tree Physiology* 21, 1245–1255.
- Gielen, B., Liberloo, M., Bogaert, J., Calfapietra, C., De Angelis, P., Miglietta, F., Scarascia-Mugnozza, G., Ceulemans, R., 2003. Three years of free-air CO₂ enrichment (POPFACE) only slightly affect profiles of light and leaf characteristics in closed canopies of *Populus*. *Global Change Biology* 9, 1022–1037.
- Goor, F., Jossart, J.-M., Ledent, J.F., 2000. ECOP: an economic model to assess the willow short rotation coppice global profitability in a case of small scale gasification pathway in Belgium. *Environmental Modelling & Software* 15, 279–292.
- Grassi, G., Gosse, G., Dos Santos, G., 1990. Biomass for Energy and Industry. In: *Policy, Environment, Production and Harvesting*, vol. I. Elsevier Applied Science, UK.
- van Groenigen, K.J., de Graaff, M.A., Six, J., Harris, D., Kuikman, P., van Kessel, C., 2006. The impact of elevated atmospheric [CO₂] on soil C and N dynamics: a meta-analysis. In: *Nosberger, J., Long, S.P., Norby, R.J., Stitt, M., Hendrey, G.R., Blum, H. (Eds.), Managed Ecosystems and Elevated CO₂: Case Studies, Processes and Perspectives*. Springer Verlag, Berlin Heidelberg, pp. 373–391.
- Heilman, P.E., Ekuon, G., Fogle, D., 1994. Above- and below-ground biomass and fine roots of 4-year-old hybrids of *Populus trichocarpa* × *Populus deltoides* and parental species in short rotation culture. *Canadian Journal of Forest Research* 24, 1186–1192.
- Heilman, P.E., Norby, R.J., 1998. Nutrient cycling and fertility management in temperate short rotation forest. *Biomass & Bioenergy* 14, 361–370.
- Hendrey, G.R., Ellsworth, D.S., Lewin, K.F., Nagy, J., 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO₂. *Global Change Biology* 5, 293–309.
- Hohenstein, W.G., Wright, L.L., 1994. Biomass energy production in the United States – an overview. *Biomass & Bioenergy* 6, 161–173.
- Holmes, W.E., Zak, D.R., Pregitzer, K.S., King, J.S., 2006. Elevated CO₂ and O₃ alter soil nitrogen transformations beneath trembling aspen, paper birch, and sugar maple. *Ecosystems* 9, 1354–1363.
- Hoosbeek, M.R., Lukac, M., van Dam, D., Godbold, D., Velthorst, E., Biondi, F., Peressotti, A., Cotrufo, M.F., De Angelis, P., Scarascia-Mugnozza, G., 2004. More new carbon in the mineral soil of a poplar plantation under free air carbon enrichment (POPFACE): cause of increased priming effect? *Global Biogeochemical Cycles* 18, GB1040.
- Hyvönen, R., Agren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A., Jarvis, P.G., Kellomäki, S., Lindroth, A., Loustau, D., Lundmark, T., Norby, R.J., Oren, R., Pilegaard, M., Ryan, M.G., Sigurdsson, B.D., Strömgren, M., van Oijen, M., Wallin, G., 2007. The likely impact of elevated [CO₂], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist* 173, 463–480.
- Jahn, M., Kluge, E., Enzian, S., 1996. Influence of climate diversity on fungal diseases of field crops – evaluation of long-term monitoring data. *Annals of Applied Biology* 45, 247–252.
- Janssens, I.A., Mousseau, M., Ceulemans, R., 2000. Crop ecosystem responses to global climate change: tree crops. In: *Reddy, K.R., Hodges, H.F. (Eds.), Climate Change and Global Crop Productivity*. CAB International, Wallingford, pp. 245–270.
- Johnson, J.D., Tognetti, R., Paris, P., 2002. Water relations and gas exchange in poplar and willow under water stress and elevated atmospheric CO₂. *Physiologia Plantarum* 115, 93–100.
- Kalina, J., Ceulemans, R., 1997. Clonal differences in the response of dark and light reactions of photosynthesis to elevated atmospheric CO₂ in poplar. *Photosynthetica* 33, 51–61.
- Karacic, A., Verwijst, T., Weih, M., 2003. Above-ground woody biomass production of short-rotation *Populus* plantations on agricultural land in Sweden. *Scandinavian Journal of Forest Research* 18, 427–437.
- Karnosky, D.F., Gagnon, Z.E., Dickson, R.E., Coleman, M.D., Lee, E.H., Isebrands, J.G., 1996. Changes in growth, leaf abscission, and biomass associated with seasonal tropospheric ozone exposures of *Populus tremuloides* clones and seedlings. *Canadian Journal of Forest Research* 16, 23–27.
- Karnosky, D.F., Podila, G.K., Gagnon, Z., Pechter, P., Akkapeddi, A., Coleman, M., Dickson, R.E., Isebrands, J.G., 1998. Genetic control of responses to interacting O₃ and CO₂ in *Populus tremuloides*. *Chemosphere* 36, 807–812.
- Karnosky, D.F., Mankovska, B., Percy, K., Dickson, R.E., Podila, G.K., Sober, J., Noormets, A., Hendrey, G., Coleman, M.D., Kubiske, M., Pregitzer, K.S., Isebrands, J.G., 1999. Effects of tropospheric O₃ on trembling aspen and interaction with CO₂: results from an O₃-gradient and a FACE experiment. *Water Air and Soil Pollution* 116, 311–322.
- Karnosky, D.F., Percy, K.E., Xiang, B., Callan, B., Noormets, A., Mankovska, B., Hopkin, A., Sober, J., Jones, W., Dickson, R.E., Isebrands, J.G., 2002. Interacting elevated CO₂ and tropospheric O₃ predisposes aspen (*Populus tremuloides* Michx.) to infection by rust (*Melampsora medusae* f.sp. *tremuloidae*). *Global Change Biology* 8, 329–338.
- Karnosky, D.F., Zak, D.R., Pregitzer, K.S., Awmack, C.S., Bockheim, J.G., Dickson, R.E., Hendrey, G.R., Host, G.E., King, J.S., Kopper, B.J., Kruger, E.L., Kubiske, M.E., Lindroth, R.L., Mattson, W.J., McDonald, E.P., Noormets, A., Oksanen, E., Parsons, W.F.J., Percy, K.E., Podila, G.K., Riemenschneider, D.E., Sharma, P., Thakur, R.C., Sober, A., Sober, J., Jones, W.S., Anttonen, S., Vapaavuori, E., Mankovska, B., Heilman, W.E., Isebrands, J.G., 2003. Tropospheric O₃ moderates responses of temperate hardwood forests to elevated CO₂: a synthesis of molecular to ecosystem results from the Aspen FACE project. *Functional Ecology* 17, 289–304.
- Karnosky, D.F., Pregitzer, K.S., Zak, D.R., Kubiske, M.E., Hendrey, G.R., Weinstein, D., Nosal, M., Percy, K.E., 2005. Scaling ozone responses of forest trees to the ecosystem level in a changing climate. *Plant Cell and Environment* 28, 965–981.
- Karnosky, D.F., Skelly, J.M., Percy, K.E., Chappelka, A.H., 2007. Perspectives regarding 50 years of research on effects of tropospheric ozone air pollution on US forests. *Environmental Pollution* 147, 489–506.
- Karnosky, D.F., Pregitzer, K.S., 2006. Impacts of elevated atmospheric [CO₂] and [O₃] on northern temperate forest ecosystems: results from the AspenFACE experiment. In: *Nosberger, J., Long, S.P., Norby, R.J., Stitt, M., Hendrey, G.R., Blum, H. (Eds.), Managed Ecosystems and Elevated CO₂: Case Studies, Processes and Perspectives*. Springer Verlag, Germany, pp. 213–229.
- Kellomäki, S., Wang, K.Y., 1998. Sap flow in Scots pines growing under conditions of year-round carbon dioxide enrichment and temperature elevation. *Plant, Cell and Environment* 2, 969–981.
- King, J.S., Pregitzer, K.S., Zak, D.R., 1999. Clonal variation in above- and belowground growth responses of *Populus tremuloides* Michaux: influence of soil warming and nutrient availability. *Plant and Soil* 217, 119–130.
- King, J.S., Pregitzer, K.S., Zak, D.R., Sober, J., Isebrands, J.G., Dickson, R.E., Hendrey, G.R., Karnosky, D.F., 2001. Fine root biomass and fluxes of soil carbon in young stands of paper birch and trembling aspen as affected by elevated atmospheric CO₂ and tropospheric O₃. *Oecologia* 128, 237–250.
- Kopper, B.J., Lindroth, R.L., 2003. Responses of trembling aspen (*Populus tremuloides*) phytochemistry and aspen blotch leafminer (*Phyllonorycter tremuloidiella*) performance to elevated levels of atmospheric CO₂ and O₃. *Agricultural and Forest Entomology* 5, 17–26.
- Körner, C., 2006. Plant CO₂ responses: an issue of definition, time and resource supply. *New Phytologist* 172, 393–411.
- Körner, C., Ashhoff, R., Gibnuolo, O., Hättenschwiler, S., Keel, S.G., Pelàez-Riedl, S., Pepin, S., Siegwold, R.T.W., Zotz, G., 2005. Carbon flux and growth in mature deciduous forest trees exposed to elevated CO₂. *Science* 309, 1360–1362.
- Kull, O., Sober, A., Coleman, M.D., Dickson, R.E., Isebrands, J.G., Gagnon, Z., Karnosky, D.F., 1996. Photosynthetic responses of aspen clones to simultaneous exposures of ozone and CO₂. *Canadian Journal of Forest Research* 26, 639–648.
- Laureysens, I., Bogaert, J., Blust, R., Ceulemans, R., 2004. Biomass production of 17 poplar clones in a short-rotation coppice culture on a waste disposal site and its relation to soil characteristics. *Forest Ecology and Management* 187, 295–309.
- Laureysens, I., De Temmerman, L., Hastir, T., Van Gysel, M., Ceulemans, R., 2005. Clonal variation in heavy metal accumulation and biomass production in a poplar coppice culture. II. Vertical distribution and phytoextraction potential. *Environmental Pollution* 133, 541–551.
- Liberloo, M., Calfapietra, C., Lukac, M., Godbold, D., Luo, Z.-B., Polle, A., Hoosbeek, M.R., Kull, O., Marek, M., Raines, C., Rubino, M., Taylor, G., Scarascia-Mugnozza, G., Ceulemans, R., 2006. Woody biomass production during the second rotation of a bio-energy *Populus* plantation increases in a future high CO₂ world. *Global Change Biology* 12, 1094–1106.
- Lima, W.P., Jarvis, P., Rhizopoulou, S., 2003. Stomatal responses of Eucalyptus species to elevated CO₂ concentration and drought stress. *Scientia Agricola* 60, 231–238.
- Loya, W.M., Pregitzer, K.S., Karberg, N.J., King, J.S., Giardina, C.P., 2003. Reduction of soil carbon formation by tropospheric ozone under elevated carbon dioxide. *Nature* 425, 705–707.
- Lukac, M., Calfapietra, C., Godbold, D.L., 2003. Production, turnover and mycorrhizal colonisation of root systems of three *Populus* species grown under elevated CO₂ (POPFACE). *Global Change Biology* 9, 838–848.
- Matyssek, R., Bahnweg, G., Ceulemans, R., Fabian, P., Grill, D., Hanke, D.E., Kraigher, H., Oßwald, W., Rennenberg, H., Sandermann, H., Tausz, M., Wieser, G., 2007. Synopsis of the CASIROZ case study: carbon sink strength of *Fagus sylvatica* L. in a changing environment – experimental risk assessment of mitigation by chronic ozone impact. *Plant Biology* 9, 163–180.
- McLeod, A.R., Fackrell, J.E., Alexander, K., 1985. Open-air fumigation of field crops: criteria and design for a new experimental system. *Atmospheric Environment* 19, 1639–1649.

- Medlyn, B.E., Barton, C.V.M., Broadmeadow, M.S.J., Ceulemans, R., De Angelis, P., Forstreuter, M., Freeman, M., Jackson, S.B., Kellomäki, S., Laitat, E., Rey, A., Roberntz, P., Sigurdsson, B.D., Strassemeier, J., Wang, K., Curtis, P.S., Jarvis, P.G., 2001. Stomatal conductance of forest species after long-term exposure to elevated CO₂ concentration: a synthesis. *New Phytologist* 149, 247–264.
- Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298, 2173–2176.
- Miglietta, F., Lanini, M., Bindi, M., Magliulo, V., 1997. Free air CO₂ enrichment of potato (*Solanum tuberosum*, L.): design and performance of the CO₂-fumigation system. *Global Change Biology* 3, 417–427.
- Miglietta, F., Peressotti, A., Vaccari, F.P., Zaldei, A., De Angelis, P., Scarascia-Mugnozza, G., 2001. Free-air CO₂ enrichment (FACE) of a poplar plantation: the POPFACE fumigation system. *New Phytologist* 150, 465–476.
- Miller, B., Oschinsky, C., Zimmer, W., 2001. First isolation of an isoprene synthase gene from poplar and successful expression of the gene in *Escherichia coli*. *Planta* 213, 483–487.
- Mitchell, C.P., Stevens, E.A., Watters, M.P., 1999. Short rotation forestry – operations, productivity and costs based on experience gained in the UK. *Forest Ecology and Management* 121, 123–136.
- Monk, R.J., Murray, F., 1995. The relative tolerances of some *Eucalyptus* species to ozone exposure. *Water Air and Soil Pollution* 85, 1405–1411.
- Norby, R.J., Wullschlegel, S.D., Gunderson, C.A., Johnson, D.W., Ceulemans, R., 1999. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant Cell and Environment* 22, 683–714.
- Norby, R.J., Delucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Oren, R.E., Schlesinger, W.H., 2005. Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America* 102, 18052–18056.
- Norby, J., Luo, Y., 2004. Evaluating ecosystem responses to rising atmospheric CO₂ and global warming in a multi-factor world. *New Phytologist* 162, 281–289.
- Novak, K., Skelly, J.M., Schaub, M., Krauchi, N., Hug, C., Landolt, W., Bleuler, P., 2003. Ozone air pollution and foliar injury development. *Environmental Pollution* 125, 41–52.
- Palanisamy, K., 1999. Interactions of elevated CO₂ concentration and drought stress on photosynthesis on *Eucalyptus clacocalix* F. Muell. *Photosynthetica* 36, 635–638.
- Patterson, D.T., 1995. Weeds in a changing climate. *Weed Science* 43, 685–701.
- Pendall, E., Bridgham, S., Hanson, P.J., Hungate, B., Kicklighter, D.W., Johnson, D.W., Law, B.E., Luo, Y., Mezonigal, J.P., Olsrud, M., Ryan, M.G., Wan, S., 2004. Belowground process response to elevated CO₂ and temperature: a discussion of observations, methods, and models. *New Phytologist* 162, 311–322.
- Percy, K.E., Awmack, C.S., Lindroth, R.L., Kubiske, M.E., Kopper, B.J., Isebrands, J.G., Pregitzer, K.S., Hendrey, G.R., Dickson, R.E., Zak, D.R., Oksanen, E., Sober, J., Harrington, R., Karnosky, D.F., 2002. Altered performance of forest pests under CO₂- and O₃-enriched atmospheres. *Nature* 420, 403–407.
- Pontaiiller, J.Y., Ceulemans, R., Guittet, J., 1999. Biomass yield of poplar after five 2-year coppice rotations. *Forestry* 72, 157–163.
- Roden, J.S., Ball, M.C., 1996. The effect of elevated [CO₂] on growth and photosynthesis of two *Eucalyptus* species exposed to high temperatures and water deficits. *Plant Physiology* 11, 909–919.
- Rood, S.B., Berg, K.J., Pearce, D.W., 2007. Localized temperature adaptation of cottonwoods from elevational ecoregions in the Rocky Mountains. *Trees* 21, 171–180.
- Rosenstiel, T.N., Potosnak, M.J., Griffin, K.L., Fall, R., Monson, R.K., 2003. Increased CO₂ uncouples growth from isoprene emission in an agriforest ecosystem. *Nature* 421, 256–259.
- Rustad, L.E., 2006. From transient to steady-state response of ecosystems to atmospheric CO₂-enrichment and global climate change: conceptual challenges and need for an integrated approach. *Plant Ecology* 182, 43–62.
- Rustad, L.E., Campbell, J., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., Gcte-News, 2001. A meta-analysis of the response of soil respiration, net N mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543–562.
- Saxe, H., Cannell, M.G.R., Johnsen, Ø., Ryan, M.G., Vourlitis, G., 2000. Tree and forest functioning in response to global warming. *New Phytologist* 149, 369–399.
- Scarascia-Mugnozza, G., Calfapietra, C., Ceulemans, R., Gielen, B., Cotrufo, F., DeAngelis, P., Godbold, D., Hoosbeek, M.R., Kull, O., Lukac, M., Marek, M., Miglietta, F., Polle, A., Raines, C., Sabatti, M., Taylor, G., 2006. Responses to elevated CO₂ of a short rotation, multispecies poplar plantation: the POPFACE/EUROFACE experiment. In: Nosberger, J., Long, S.P., Norby, R.J., Stitt, M., Hendrey, G.R., Blum, H. (Eds.), *Managed Ecosystems and Elevated CO₂: Case Studies, Processes and Perspectives*. Springer Verlag, Berlin Heidelberg, pp. 173–195.
- Shaver, G.R., Canadell, J., Chapin III, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L., Rustad, L., 2000. Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience* 50, 871–882.
- Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A., Field, C.B., 2002. Grassland responses to global environmental changes suppressed by elevated CO₂. *Science* 298, 1987–1990.
- Sigurdsson, B.D., Aradóttir, Á.L., Strachan, I.B., 1998. Cover and canopy development of a newly established poplar plantation in south Iceland. *Icelandic Agricultural Sciences* 12, 15–26.
- Sigurdsson, B.D., Thorgerisson, H., Linder, S., 2001. Growth and dry matter partitioning of young *Populus trichocarpa* in response to carbon dioxide concentration and mineral nutrient availability. *Tree Physiology* 21, 941–950.
- Sober, A., Noormets, A., Isebrands, J.G., Sober, J., Karnosky, D.F., 2000. Hydraulic properties of aspen leaves as affected by leaf age and elevated concentrations of carbon dioxide and (or) ozone. *Proc. Annual Meeting of the American Society of Plant Physiologists*. *Plant Biology* 2000, 97.
- Stromgren, M., Linder, S., 2002. Effects of nutrition and soil warming on stemwood production in a boreal Norway spruce stand. *Global Change Biology* 8, 1195–1204.
- Taylor, G., Gardner, S.D.L., Bosac, C., Flowers, T.J., Crookshanks, M., Dolan, L., 1995. Effects of elevated CO₂ on cellular mechanisms, growth and development of trees with particular reference to hybrid poplar. *Forestry* 68, 379–390.
- Tjoelker, M.G., 1997. Acclimation in Plant Growth and its Determinants to Elevated Carbon Dioxide and Temperature: Interspecific Variation among Five Boreal Tree Species. PhD thesis, University of Minnesota, USA.
- Tognetti, R., Longobucco, A., Raschi, A., Miglietta, F., Fumagalli, I., 1999. Responses of two *Populus* clones to elevated atmospheric CO₂ concentration in the field. *Annals of Forest Science* 56, 493–500.
- Tricker, P.J., Calfapietra, C., Kuzminsky, E., Puleggi, R., Ferris, R., Nathoo, M., Pleasant, L.J., Alston, V., De Angelis, P., Taylor, G., 2004. Long-term acclimation of leaf production, development, longevity and quality following three years exposure to free-air carbon dioxide enrichment during canopy closure in *Populus*. *New Phytologist* 162, 413–426.
- Trueman, R.J., Gonzalez-Meler, M.A., 2005. Accelerated belowground C cycling in a managed agriforest ecosystem exposed to elevated carbon dioxide concentrations. *Global Change Biology* 11, 1258–1271.
- Veteli, T.O., Kuokkanen, K., Julkunen-Tiitto, R., Roininen, H., Tahvanainen, J., 2002. Effects of elevated CO₂ and temperature on plant growth and herbivore defensive chemistry. *Global Change Biology* 8, 1240–1252.
- Walter, A., Lambrecht, S.C., 2004. Biosphere 2 Center as a unique tool for environmental studies. *Journal of Environmental Monitoring* 6, 267–277.
- Weih, M., 2004. Intensive short rotation forestry in boreal climates: present and future perspectives. *Canadian Journal of Forest Research* 34, 1369–1378.
- Winner, W.E., Lefohn, A.S., Cotter, I.S., Greitner, C.S., Nellessen, J., McEvoy Jr., L.R., Olson, R.L., Atkinson, C.J., Moore, L.D., 1989. Plant responses to elevational gradients of O₃ exposures in Virginia. *Proceedings of the National Academy of Sciences of the United States of America* 86, 8828–8832.
- Wullschlegel, S.D., Gunderson, C.A., Hanson, P.J., Wilson, K.B., Norby, R.J., 2002. Sensitivity of stomatal and canopy conductance to elevated CO₂ concentration – interacting variables and perspectives of scale. *New Phytologist* 153, 485–496.
- Zabel, B., Hawes, P., Hewitt, S., Marino, B.D.V., 1999. Construction and engineering of a created environment: overview of the Biosphere 2 closed system. *Ecological Engineering* 13, 43–63.