
The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric CO₂ concentration and climate

Bart Kruijt, Craig Barton, Ana Rey and Paul G. Jarvis

Institute of Ecology and Resource Management, Darwin Building, Mayfield Road, Edinburgh EH9 3JU, UK
Tel. +44 131 650 5427, Fax. +44 131 662 0478, Email: b.kruijt@ed.ac.uk

Abstract

The 3-dimensional forest model MAESTRO was used to simulate daily and annual photosynthesis and transpiration fluxes of forest stands and the sensitivity of these fluxes to potential changes in atmospheric CO₂ concentration ([CO₂]), temperature, water stress and phenology. The effects of possible feed-backs from increased leaf area and limitations to leaf nutrition were simulated by imposing changes in leaf area and nitrogen content. Two different tree species were considered: *Picea sitchensis* (Bong.) Carr., a conifer with long needle longevity and large leaf area, and *Betula pendula* Roth., a broad-leaved deciduous species with an open canopy and small leaf area.

Canopy photosynthetic production in trees was predicted to increase with atmospheric [CO₂] and length of the growing season and to decrease with increased water stress. Associated increases in leaf area increased production further only in the *B. pendula* canopy, where the original leaf area was relatively small. Assumed limitations in N uptake affected *B. pendula* more than *P. sitchensis*. The effect of increased temperature was shown to depend on leaf area and nitrogen content. The different sensitivities of the two species were related to their very different canopy structure. Increased [CO₂] reduced transpiration, but larger leaf area, early leaf growth, and higher temperature all led to increased water use. These effects were limited by feedbacks from soil water stress. The simulations suggest that, with the projected climate change, there is some increase in stand annual 'water use efficiency', but that actual water losses to the atmosphere may not always decrease.

Introduction

As a result of the current imbalance in the global carbon cycle, atmospheric CO₂ concentrations [CO₂] are increasing and climates are likely to change (Carter *et al.*, 1994). General Circulation Models (GCMs) predict increases in temperature of the order of 3 °C in the next 50 years and changes in rainfall patterns, but at regional scales uncertainties are still large. One of the key areas in GCM development is to predict the response of vegetation to climate change as well as to subsequent feedbacks to the atmosphere resulting from changed carbon uptake rates or water use.

Climate change is likely to be gradual, and consequent vegetation changes should be predicted as a function of such gradual change. But, to understand the *sensitivity* of vegetation to different aspects of climate change, it is useful to study step changes, both in experiments and modelling studies. This separates the short (seasonal) time scale responses of photosynthesis and water relations from longer time scale responses of growth, carbon and nutrient

cycling, that feed back to the short time scale (Comins and McMurtrie, 1993; Wang and Polglase, 1995). Photosynthesis and water relations depend mainly on the existing biomass in foliage and roots, and current soil N availability. Long-term changes in cycles and stocks of carbon and nutrients are determined largely by soil processes but plant physiology also plays a significant role. McMurtrie and Comins (1996), using a steady-state model, show that the equilibrium productivity of vegetation after a step change in atmospheric CO₂ depends critically on the ability of the ecosystem to sustain diminished nitrogen concentrations per unit biomass or dead organic matter (N:C ratios) in plants and soil. Short time-scale models can shed some light on this by analysing the sensitivity of primary productivity to nutrition and foliage density with changed [CO₂] and climate, whilst taking into account the full diurnal, daily and seasonal variability in the weather, as well as spatial variation in vegetation structure and nutrient concentrations. This is the approach followed in the present study.

Several modelling studies have in the past addressed the direct sensitivity of photosynthesis to atmospheric CO₂ and temperature (e.g. Kirschbaum, 1994). Lloyd and Farquhar (1996) also modelled long-term ecosystem-scale CO₂ exchange and the relative sensitivity of photosynthesis and growth to [CO₂], and they demonstrated the important role of the respiratory costs of investment in nutrient acquisition. Many experimental studies have been made on trees in environments with artificially increased and 'current' atmospheric [CO₂], comparing both immediate and medium-term effects on photosynthesis and growth (e.g. Poorter, 1993; Ceulemans and Mousseau, 1994). Doubling of [CO₂] usually results in a 40–50% increase in net photosynthetic rates and this increase is positively correlated with temperature and water stress (see Luxmoore *et al.*, 1993).

An important effect, often observed but still poorly understood, is the apparent acclimation of photosynthesis when (young) trees are exposed to elevated [CO₂] over long periods. The leaf nitrogen content, and with it photosynthetic capacity, often decreases, diminishing the effects of higher availability of CO₂. Productivity, however, is still higher in elevated [CO₂], resulting in higher leaf areas and total tree photosynthetic rates. Acclimation to elevated [CO₂] has been hypothesised to be the result of limitations to growth set by factors other than [CO₂], most notably nitrogen availability. When the plants grow bigger, N is more likely to become limiting, and leaf N content becomes 'diluted'. This in itself reduces leaf photosynthetic capacity but, especially if there is a tendency to conserve N:C ratios, reduced growth results in an accumulation of assimilation products, which have been shown to inhibit photosynthesis (Van Oosten *et al.*, 1995).

Temperature also affects growth in other ways. For example, the timing of leaf emergence and the length of the growing season in temperate climates depends on the temperatures in winter and early spring. In warm years, bud burst occurs earlier in the season (Hänninen, 1990; Murray *et al.*, 1994; Kramer, 1995a). Such changes increase potential annual productivity at the risk of spring frost damage but earlier leaf emergence also implies higher whole-plant respiratory costs (Kramer, 1995b). Using satellite information, Myneni *et al.* (1997) claimed that, on average, over the past 20 years, the length of the growing season in the northern hemisphere has increased by about seven days and that net ecosystem CO₂ exchange rates have probably increased by about 20%.

There are also likely to be effects of [CO₂] increase and climate change on transpiration of vegetation on both short and long time scales. Empirical evidence suggests a decrease of stomatal conductance if [CO₂] increases; this may not be universal, particularly in trees, and there is little evidence of any 'acclimation' analogous to that with photosynthesis (Sellers *et al.*, 1996; Jarvis, 1998).

In this study, the sensitivity to several factors associated with climate change of leaf annual net photosynthesis and

transpiration, integrated over the foliage of forest stands of two species, has been investigated. Photosynthesis as presented here, includes losses from leaf respiration during day-time and night-time. Focus is on time scales of a year and less, assuming a prescribed canopy structure, phenology and tree N content. Thus, the short-term behaviour of tree stands in a changed climate has been investigated, and the consequences of hypothetical changes in leaf area. Leaf C:N ratios, which were shown to be both critical and little understood by McMurtrie and Comins (1996), have also been varied.

The model MAESTRO was used, parameterised for stands of two species, *Picea sitchensis* (Bong.) Carr. (Sitka spruce) and *Betula pendula* Roth. (silver birch), both of which have been studied intensively in experiments in relation to the impact of elevated ($\times 2$) atmospheric [CO₂]. The effects have been investigated of increases in 1) [CO₂], 2) air temperature, 3) water stress, 4) leaf area and 5) the length of the growing season as well as of changes in 6) leaf nitrogen content per unit leaf area (from now on: N_L). The working hypotheses were as follows: i) that elevated ($\times 2$) [CO₂] has an effect of about 40% on net photosynthesis; ii) that increased water stress and temperature (through enhanced respiration) will decrease the CO₂ effect on net primary productivity; and iii) that increased leaf area will lead to lower N_L , depending on soil nutrition. The approach is to compare annually integrated values of net canopy photosynthesis and transpiration for well-watered baseline conditions in the current climate with conditions in which combinations of the above factors (1–6) were altered, for stands of both species. The extent to which sensitivities to the variables differ between the two species is also considered.

Methods

THE MODEL: MAESTRO

MAESTRO allows a three-dimensional representation of a forest stand (Fig. 1; Wang and Jarvis, 1990a). The location, shape, height, crown diameter and total leaf area of each tree can be specified separately. Within one tree, the leaf area distribution with height and radial distance from the stem for up to three foliage age classes can be specified, as well as the degree of randomness of the leaf area distribution and the leaf angle distribution. If there are more than three age classes, such as in *Picea sitchensis*, all older foliage is lumped into the third class. Although the stand structure and leaf area are prescribed, it is also possible to prescribe variation of these over time and, for example, to simulate phenological changes and growth responses.

In this 'target' tree, the absorbed radiation is calculated in each of up to 120 'sub-volumes' arranged in up to 10 layers, at three radial distances and with four azimuthal directions, for near infrared radiation and PPFD in diffuse

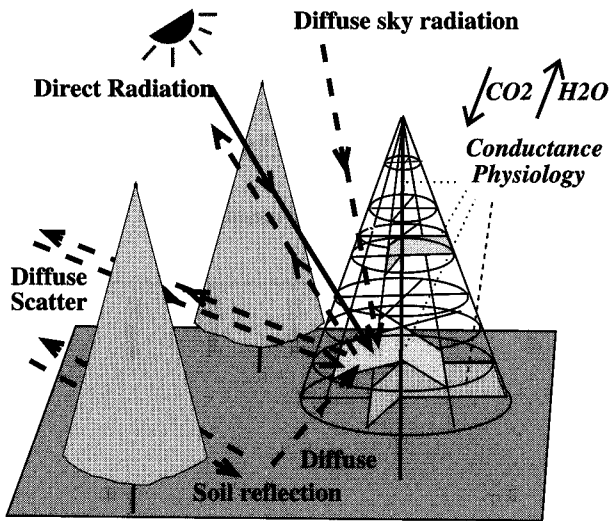


Fig. 1. Schematic representation of the MAESTRO model. The diagram shows the free arrangement of trees in a plot and the arrangement of sub-volumes within the 'target' tree. Note that tree shape can be conical, as shown, but also ellipsoidal, and that in reality the number of sub-volumes at each level is larger. The diagram also shows the various radiation components that are taken into account for three wavebands, and the localisation of CO₂ and water vapour flux calculations.

and beam radiation, over hourly intervals for any day of the year. Transmission of diffuse radiation to each sub-volume is calculated initially as a Lambert-Beer extinction along straight lines from up to 55 hemisphere points. For direct radiation, only the path of the beam from the sun to the sub-volume is considered. Extinction of radiation takes into account the total leaf area along the path, including neighbouring sub-volumes and trees, and also accounts for the average leaf angle distribution and clumping (Wang and Jarvis, 1990a). First-order scattering is calculated according to Norman and Welles (1983). Subsequent absorption of radiation by leaves can be specified independently for each of the three foliage age classes and is integrated over all the sub-volumes.

Because of the strong coupling between tree canopies and the atmosphere, temperature, humidity and CO₂ concentration are held constant with height, and leaf temperatures are assumed equal to the air temperature, but wind speed decreases exponentially with depth, according to Landsberg and Jarvis (1973). The leaf boundary layer resistance in each sub-volume is calculated from local windspeed and leaf dimensions.

Based on the microclimatic information, stomatal conductance, net photosynthesis and transpiration are calculated for each model sub-volume. The sub-models used to represent these processes can be interchanged fairly easily, but the present model calculates stomatal conductance, g_s , following Jarvis (1976), transpiration using the Penman-Monteith approach (Jarvis and McNaughton, 1986), and

photosynthesis by the Farquhar and Von Caemmerer (1982) approach. Stomatal conductance increases hyperbolically with photosynthetic photon flux density (PPFD), is inversely related to the vapour pressure deficit (VPD), decreases in proportion to the inverse of atmospheric [CO₂] and predawn water potential, and has a symmetrical, bell-shaped optimum dependence on temperature (Jarvis, 1976; *cf.* Table 1).

In the photosynthesis model, the CO₂ compensation concentration in the absence of mitochondrial respiration, Γ^* , and the Michaelis-Menten constants of Rubisco are calculated according to Harley *et al.* (1992). Electron transport depends on absorbed PPFD according to a non-rectangular hyperbola with initial slope (α) and convexity (θ) obtained from experimental data. The maximum carboxylation rate, V_{cmax} , and maximum photosynthetic electron transport rate, J_{max} , depend linearly on N_L (g N m⁻²), and these relationships are calibrated against experimental data. N_L varies spatially, in the canopy, and temporally, over the season. The temperature dependencies of V_{cmax} and J_{max} follow Lloyd *et al.* (1995), where V_{cmax} has no optimum but J_{max} has an optimum, in this case at 23 °C. This choice of an optimum temperature is fairly arbitrary because of lack of experimental data, but the underlying assumption is that the optimum should be near the average growing season maximum temperature (*cf.* Fig. 3). Mitochondrial respiration of leaves is modelled as an exponential function of temperature, and is scaled with N_L , as in Field (1983). Daytime respiration is assumed to be reduced to 60% of what it would have been at night at the same temperature, as a result of switching to chloroplastic ATP supply (Brooks and Farquhar, 1985). Daily integrals of hourly canopy net photosynthesis (A_c) were obtained by integrating over all crown sub-volumes, over 24 hour-periods, and thus include the night-time CO₂ losses from the leaves. The model was run for a full year, and the daily integrals of A_c were further integrated to yield annual net photosynthesis, here denoted P_n .

The model includes a simple routine to simulate soil water status. Canopy interception loss is estimated following Rutter *et al.* (1971). The remaining fraction of precipitation enters the soil sub-model, which consists of a 'bucket' model of three layers that fill up, starting with the topmost one, from which excess water drains to the layer below as well as being lost by transpiration of the trees. A simple linear relationship between soil water content of the top two layers and predawn water potential of the trees sets a limit to stomatal conductances for each day. Evaporation from the soil was ignored.

The model was run on an hourly time scale, with measured climatic data, that included global radiation input, windspeed, air temperature, humidity and precipitation. Other variables, such as incoming PPFD, near-infrared radiation and the fraction of beam solar radiation were calculated from the global radiation input following Weiss and Norman (1985). MAESTRO has been tested against

extensive canopy transmitted radiation data (Wang and Jarvis 1990b), and recent simulations of photosynthesis have been successfully tested against several canopy CO₂ flux data sets measured with eddy covariance, for Scottish spruce forest, Amazon rain forest and Sahel shrubland/savanna (Kruijt *et al.*, 1994), and for Boreal spruce forest (Rayment *et al.*, 1995). These tests have shown that the model reproduces the diurnal course of the fluxes with acceptable accuracy. The accuracy in predicting the magnitude of the fluxes depends on the quality of the input parameters. This makes MAESTRO especially suited for sensitivity analysis.

EXPERIMENTAL DATA AND PARAMETERISATION

For a sensitivity analysis, it is not strictly necessary to parameterise a model for a real canopy, since the parameters are going to be varied. But, because the number of possible combinations of parameters is very large, it is useful to ensure that the part of the parameter set that is not subject to sensitivity analysis is as realistic as possible and actually refers to an existing situation. An overview of the most important fitted and assumed parameters for the two species is given in Table 1. The sources of the experimental data are summarised below. Details are given in Jarvis (1998) and in the references cited here.

The experiments on *P. sitchensis* consisted of a set of branch bags mounted initially on whorl three of six, 12-year-old trees in 1991, in a dense stand, planted at standard 2.5 m spacing. Average tree height was 6 m in 1991 and 10 m in 1994. Yield class (average annual stem volume increment over one rotation) was estimated to be *ca* 16 m³ ha⁻¹. At the same whorl on each tree, there were treatments with air containing ambient and elevated (ambient + 350 μmol mol⁻¹) [CO₂] (Barton *et al.*, 1993). The branches had been growing in these bags for three years before extensive gas-exchange measurements were made on them, and by this time the whorls were in mid-canopy. The measurements determined the dependence of photosynthesis and stomatal conductance on CO₂ and PPFd, for needles of current and one-year-old age classes. Parameter values of *V*_{cmax}, *J*_{max} and stomatal functions were fitted to these data using a non-linear least squares procedure. One of the main results from the branch bag work was that the photosynthesis and stomatal conductance of needles on these branches showed no acclimation to elevated [CO₂] in the first two year classes, but that needles of three years and older did acclimate, resulting in reduced photosynthetic capacities (Barton, 1997). In the present simulations, the photosynthetic parameters and *N*_L were not varied with needle age directly, but they did generally decrease with needle age because of acclimation to the more heavy shade deeper in the canopy (Field, 1983), where the older needles are located. To model the leaf area and its variation over the year, a visual estimate of the peak leaf area index was used (estimated as 7 m² m⁻²,

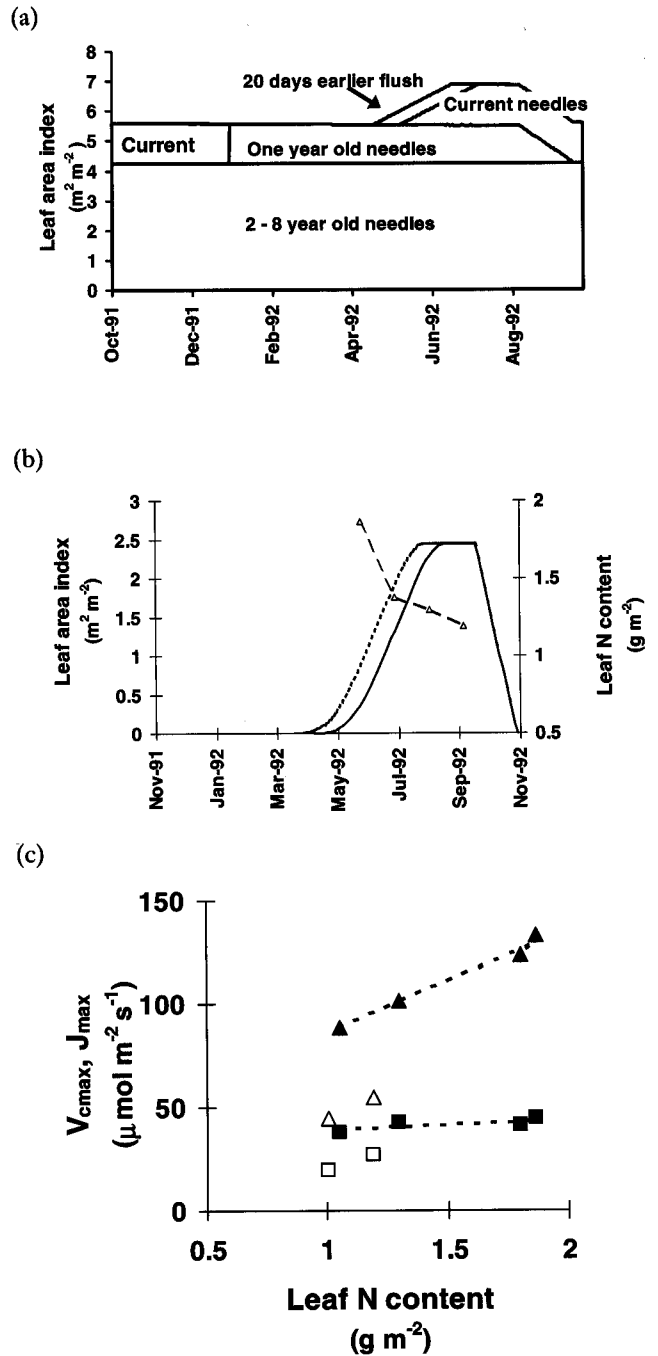


Fig. 2. Seasonal variation of leaf area index (LAI) as used in the model, for the baseline conditions. In the sensitivity analysis, area was sometimes increased by 40% uniformly over the year and over all needle ages. a) The variation in *P. sitchensis*, showing the proportions of the needle age classes and the contribution of early flush of needles. Note that the simulated 'season' starts in October of the previous year. b) The variation of leaf area in the *B. pendula* simulations (—), and the effect of early leaf flush (.....), as well as the measured variation of *N*_L over the year (—▷—▷—▷). c) the measured relationship with *N*_L of *V*_{cmax} (squares) and *J*_{max} (triangles) and the fitted linear relationships used in the model. Open symbols represent the lower values in September, when a reduction was imposed on the model parameters.

in agreement with earlier work) combined with data on stand and needle age structure. The model assumed the amount of two to eight-year-old needles to be constant over time, as a result of a balance between senescence and recruitment of younger needles. Dates of bud burst, elongation of current needles as well as senescence of one-year-old needles were prescribed, and the transition from current to one-year-old was arbitrarily set at the start of the calendar year (see also Fig. 2a, Jarvis *et al.*, 1990). The exact timing of this transition does not influence the calculated results since N_L was assumed to decrease with increasing shading only. Vertical and radial leaf area distributions in the tree crowns were assumed to be similar to those used by Wang and Jarvis (1990b).

The *B. pendula* trees were grown from seed in 1991 in elevated or ambient $[\text{CO}_2]$, first in polythene tunnels and then in open-top chambers for two years, before 12 trees were transferred to individual open-top chambers, where they were rooted in the ground. They continued to receive air with ambient and elevated $[\text{CO}_2]$ (ambient + 350 $\mu\text{mol mol}^{-1}$), as in the *P. sitchensis* stand (Rey and Jarvis, 1997). Measurements were made in 1995 during the fourth growing season to describe variation in photosynthetic parameters and in N_L over the season. By then, the average height of the trees was 3.7 m at the beginning of the growing season and had reached 4.3 m at the end, when the trees were harvested. The experiment showed that photosynthetic capacity was lower in elevated than in ambient $[\text{CO}_2]$, and this was associated with a decrease in N_L . The relationship of V_{cmax} , and J_{max} with N_L had been chosen such that the measured variation in N_L predicts the measured temporal variation in photosynthesis as closely as possible but, late in the season, a correction accounting for a disproportional decrease in V_{cmax} , and J_{max} (Fig. 2c) had to be introduced.

The data on stomatal conductance for *B. pendula*, however, were not very detailed and we have therefore assumed similar functions as in *P. sitchensis*, but with a higher maximum conductance. Data of leaf area phenology were used directly in the model (Fig. 2b; Wang, Rey and Jarvis, 1998). The open top chambers stood in relatively open space, so that the amount and distribution of foliage on the experimental *B. pendula* trees were not likely to be representative of a closed stand. In the model, a young stand with trees of similar dimensions as in the chambers, was assumed but with less leaf area and taller stems (Table 1).

Both leaf-scale photosynthesis data sets were collected in the lower half of the respective crowns. In the model it was assumed that N_L , photosynthetic capacity and maximum stomatal conductance acclimate partly to the local light environment, such that the change in these variables with canopy depth is 30% of the calculated spatial variation in PFD (Wang and Jarvis, 1990b; Kruijt, *et al.*, 1997). Using this assumption, the measured variables were extrapolated upwards as well as downwards in the canopy.

THE SENSITIVITY ANALYSIS

Hourly time scale. Although the emphasis here is to study annually integrated photosynthesis and transpiration, it is useful to consider the sensitivity of canopy photosynthesis, A_c , to elevated atmospheric $[\text{CO}_2]$ at the scale of the basic model time step (one hour) and to explore how this sensitivity varies with other key environmental variables. The model for *P. sitchensis* was run over a whole season, in both ambient and elevated $[\text{CO}_2]$, recording predicted canopy net photosynthesis every third hour. The relative effect of doubling CO_2 was then expressed as:

$$\mathfrak{R}_h = \frac{A_c(700) - A_c(350)}{A_c(350)} \quad (1)$$

Where $A_c(\text{CO}_2)$ is the hourly average rate of net canopy photosynthesis ($\mu\text{mol m}^{-2}_{\text{ground}} \text{s}^{-1}$) in a given $[\text{CO}_2]$ growth treatment ($\mu\text{mol mol}^{-1}$).

Annual time scale. The analysis compared annual integrals of net daily photosynthesis (P_n , $\text{mol m}^{-2}_{\text{ground}} \text{y}^{-1}$) and transpiration fluxes (mm y^{-1}) in a range of conditions. To this end, MAESTRO was run for every third day in the foliated season for *B. pendula*, and between 1 October and 30 September for *P. sitchensis*, using weather data for 1991 and 1992 (Fig. 3). Actual measurements of $[\text{CO}_2]$ were not used; instead in the baseline conditions the concentration was assumed to vary diurnally between 350 $\mu\text{mol mol}^{-1}$ in the afternoon and 390 $\mu\text{mol mol}^{-1}$ at night. Sensitivity of fluxes to changes in model input variables and parameters has been expressed for each species as relative differences between a baseline run, for which variables and parameters reflect the real, present situation as closely as possible, and a run for which various combinations of variables and parameters have been changed. These combinations were made up of one or several of the changes given below. In Table 2, where the results are listed for each combination, these changes are identified with the short phrases given in bold below:

- 1 Elevated atmospheric $[\text{CO}_2]$, applied uniformly over the year as an increase of 350 $\mu\text{mol mol}^{-1}$ over the baseline, still allowing for diurnal fluctuations in $[\text{CO}_2]$. This condition is called ' $2 \times \text{CO}_2$ ', as opposed to ' $1 \times \text{CO}_2$ ' in tables and graphs.
- 2 A 40% increase in leaf area, similar to that measured in the elevated $[\text{CO}_2]$ treatment of the *B. pendula* experiment. In the *B. pendula* simulations, there was an increase in initial canopy height of 10% associated with the leaf area increase. This increase was imposed, rather than being the consequence of any modelled growth response. Referred to as '**Increased leaf**' or '**Incr. leaf**'.
- 3 Variation in the total nitrogen content of the trees, reflecting three degrees of N uptake capacity from the soil. Firstly, total canopy N was assumed invariant with leaf area, and this leads to a 'dilution' of N_L by 100% ($1 - 100/140$) = 30%. Secondly, a slightly increased N uptake was assumed, not fully tracking the increase in

Table 1. Overview of the most important input parameters and their values for MAESTRO in the present study. The values are given for the standard, baseline conditions. Variation of leaf area and N_L over the year are shown in Fig. 2. Temperature dependences of V_{cmax} and J_{max} are given in the text. Note that several relationships derived from experimental data are not generally applicable, since they were chiefly meant to reproduce the observed variation. Parameters for the soil and canopy water balance submodel are not shown, since they do not relate to the data and were chosen only to ensure high soil water deficits.

Parameter	Sitka spruce (<i>Picea sitchensis</i>)		Silver Birch (<i>Betula pendula</i>)	
	Value or function	Source	Value or function	Source
Stand structure				
Spacing	2.5 m	Barton (1997)	1.2 m	Estimate
Height-crown depth	10 m	Barton (1997)	5 m-3 m	Estimate
Crown radius	2.5 m	Barton (1997)	0.7 m	As in chambers
Leaf area index	7, varies over season (Fig 2)	Barton (1997)	2.4, varies over season (Fig 2)	Adapted from Rey (1997)
Leaf area distribution	Beta-function along height and radius	Wang and Jarvis (1990a)	Uniform	Rey (1997)
Stomatal conductance model				
	Jarvis (1976)		Jarvis (1976)	
Maximum conductance	0.2 mol m ⁻² s ⁻¹	Barton (1997)	0.3 mol m ⁻² s ⁻¹	Data from Rey (1997)
Initial slope of light response	0.01 mol/μmol	Wang and Jarvis (1990a)	0.01 mol/μmol	Wang and Jarvis (1990)
Relative VPD (kPa) dependence	1/(1+1.5×VPD)	Jarvis and Sandford (1986)	1/(1+0.5×(VPD-0.5))	Jarvis and Sandford (1986)
Rel. Predawn water potential (Ψ_{p} , Mpa) dependence	0< (1-0.5×(Ψ_{p} -0.4)) <0.25	Jarvis <i>et al.</i> (1990)	0< (1-0.5×(Ψ_{p} -0.4)) <0.25	Jarvis <i>et al.</i> (1990)
Temperature dependence	Min. -5; opt. 15; Max. 40°C	Wang and Jarvis (1990)	Min. -5; opt. 15; Max. 40°C	Wang and Jarvis (1990a)
Rel. CO ₂ (C_a , ppm) dependence	0< (1-4×10 ⁻⁴ C_a) <1	Barton (1997)	0< (1-4×10 ⁻⁴ C_a) <1	Barton (1997)
Photosynthesis model				
	Farquhar and Von Caemmerer (1982)		Farquhar and Von Caemmerer (1982)	
V_{cmax} at 25°C	-4+25× N_L (μmol m ⁻² s ⁻¹)	Data from Barton (1997)	34+5× N_L (μmol m ⁻² s ⁻¹)	Data from Rey (1997)
J_{max} at 25°C	-3 + 66× N_L (μmol m ⁻² s ⁻¹)	Data from Barton (1997)	35 + 50× N_L (μmol m ⁻² s ⁻¹)	Data from Rey (1997)
Quantum efficiency	0.2 (μmol el. / μmol quanta abs.)	Data from Barton (1997)	0.2 (μmol el. / μmol quanta ab.)	Data from Rey (1997)
Leaf PPFD absorptance	0.15	Wang and Jarvis (1990a)	0.15	Wang and Jarvis (1990a)
Convexity of J vs. PPFD response	0.7	Data from Barton (1997a)	0.9	Data from Rey (1997)
Leaf N content (N_L)	1 g m ⁻² (no seasonal variation)	No data. Only used as scaling parameter.	1.3 g m ⁻² , varies over season (Fig 2)	Data from Rey (1997)

Table 2. Annually integrated values and relative (δ) effects of A) net canopy photosynthesis (P_n , mol m⁻² year⁻¹ (ground area)) and B) transpiration (E mm year⁻¹), as well as C) water use efficiency, the ratio of those two values (mol CO₂ (mol H₂O)⁻¹ ×1000), for *P. sitchensis*. Relative effects are increases relative to the '1×CO₂, low temperature' baseline.

A: <i>P. SITCHENSIS</i> net photosynthesis	Low temperature		High temperature		Hi T+ early flush		Hi T+ water stress		Hi T+ water stress+ early flush	
	P_n	δ	P_n	δ	P_n	δ	P_n	δ	P_n	δ
1 × CO ₂	112	0.00	108	-0.03	110	-0.02	102	-0.09	103	-0.08
2 × CO ₂ no acclimation	125	0.19	125	0.20	128	0.22	122	0.17	124	0.19
2 × CO ₂ Increased leaf area, <i>N</i> limiting	133	0.09	133	0.11	136	0.13	130	0.08	132	0.10
2 × CO ₂ Increased leaf area, intermediate <i>N</i>	121	0.12	123	0.12	126	0.15	120	0.09	123	0.11
2 × CO ₂ Increased leaf area no <i>N</i> limit	131	0.17	126	0.13	129	0.16	122	0.10	125	0.12
B: <i>P. SITCHENSIS</i> transpiration	Low temperature		High temperature		Hi T+ early flush		Hi T+ water stress		Hi T+ water stress + early flush	
	E	δ	E	δ	E	δ	E	δ	E	δ
1 × CO ₂	394	0.00	454	0.15	463	0.18	339	-0.14	341	-0.14
2 × CO ₂ no acclimation	430	-0.13	496	0.01	506	0.03	348	-0.22	349	-0.21
2 × CO ₂ Increased leaf area <i>N</i> limiting	344	0.09	396	0.26	404	0.28	308	-0.12	310	-0.11
2 × CO ₂ Increased leaf area intermediate <i>N</i>	430	0.09	496	0.26	506	0.28	348	-0.12	349	-0.11
2 × CO ₂ Increased leaf area no <i>N</i> limit	430	0.09	496	0.26	506	0.28	348	-0.12	349	-0.11
C: <i>P. SITCHENSIS</i> water use efficiency	Low temperature		High temperature		Hi T+ early flush		Hi T+ water stress		Hi T+ water stress + early flush	
	WUE	δ	WUE	δ	WUE	δ	WUE	δ	WUE	δ
1 × CO ₂	5.09	0.00	4.28	-0.16	4.27	-0.16	5.39	0.06	5.43	0.07
2 × CO ₂ no acclimation	5.23	0.37	4.53	0.19	4.54	0.19	6.30	0.49	6.39	0.51
2 × CO ₂ Increased leaf area <i>N</i> limiting	6.95	-0.01	6.05	-0.12	6.04	-0.12	7.61	0.22	7.68	0.24
2 × CO ₂ Increased leaf area intermediate <i>N</i>	5.06	0.03	4.47	-0.11	4.48	-0.11	6.23	0.24	6.33	0.26
2 × CO ₂ Increased leaf area no <i>N</i> limit	5.46	0.07	4.58	-0.10	4.60	-0.10	6.33	0.24	6.43	0.26

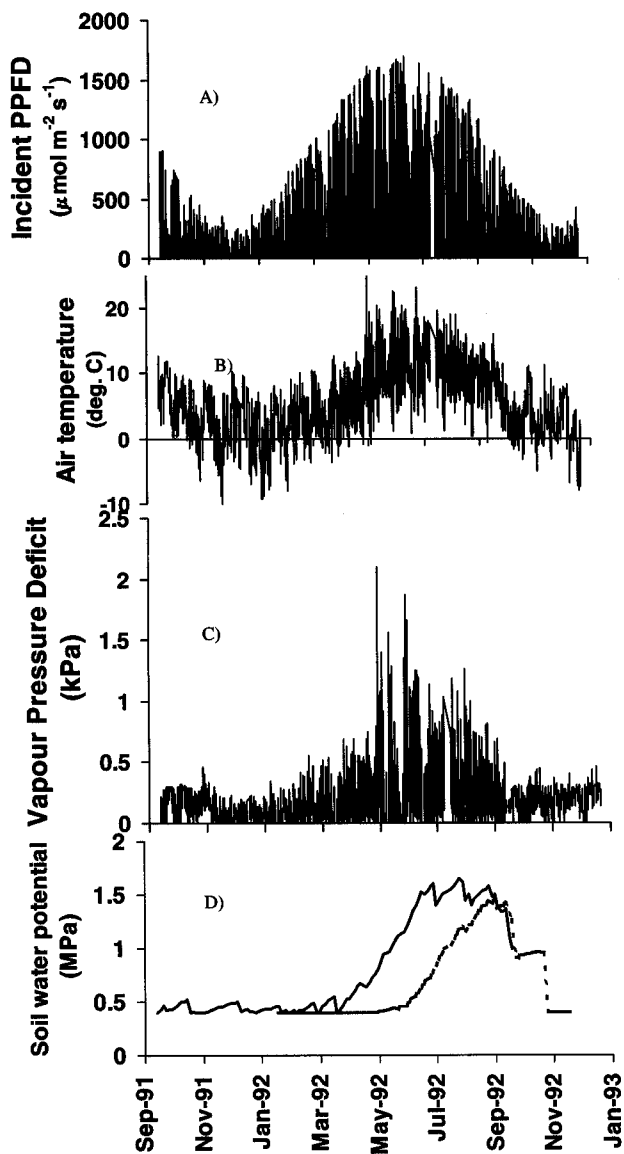


Fig. 3. The hourly meteorological (and derived) baseline conditions for 1992 at Glencorse used as inputs to the simulations: a) Incoming Photosynthetic Photon Flux Density (PPFD); b) Air temperature; c) Vapour Pressure Deficit (VPD); d) Daily soil water potential as simulated under the *P. sitchensis* (—) and *B. pendula* (----) stands, in elevated temperature (+3°C) conditions. The data were measured at the Glencorse experimental site, south of Edinburgh, by Alan Crossley, ITE-Bush.

leaf area, as was measured in the *B. pendula* experiment. This leads to a 20% reduction in N_L . Thirdly, a total absence of N limitation was assumed, allowing N_L to be the same in both ambient and elevated $[CO_2]$ treatments. These different conditions are referred to as 'N limiting' (or 'N limit'), 'Intermediate N', and 'No N limit', respectively, and were applied together only with an increase in leaf area.

- 4 Temperature increase by 3 °C, applied uniformly over the year. Together with this increase, the *wet bulb temperature depression* was assumed constant, with the consequent effect of a slight (0.2–0.3 kPa) increase in the associated VPD. This is referred to as 'High temperature' or 'Hi T'.
- 5 Variation in soil water stress, achieved by either switching off the sensitivity of stomata to pre-dawn water potentials (no water stress) or by allowing water stress to affect the stomata. A low soil water holding capacity was assumed to ensure that substantial stress develops in response to the water use in each model plot. This condition is referred to as 'Water stress' or 'w.stress'.
- 6 A change in start of the growing season, by bringing the date of leaf emergence forward by 20 days whilst keeping the dates for leaf senescence and fall the same (Fig. 2), referred to as 'Early flush'.

The effects of these conditions were considered not only independently but in combinations likely to occur, such as increased leaf area together with elevated CO_2 and changes in N supply, or an early start of the growing season in a warmer climate only.

Results

Figs 4a and 4b show the sensitivity of A_c to $[CO_2]$ in *P. sitchensis* (Eqn. 1) for a range of temperatures or absorbed PPFD. This is not the same as the combined effects of rises in $[CO_2]$ and temperature. The scatter in these plots is the result of the natural variation in the other environmental variables and is especially large when absolute rates of photosynthesis are low. Clearly, the dependence of photosynthesis on air temperature is stronger than the dependence on PPFD: the relative effect increases dramatically with temperature, especially above 15 °C. There is a much less clear dependence of the $[CO_2]$ effect on absorbed PPFD, and much of the increase with PPFD may be caused by correlation of PPFD with temperature.

DAILY INTEGRALS OVER THE YEAR

Fig. 3 shows the variation over the year of *measured* climate data and *modelled* soil water potentials. Soil water potentials peak at similar values, but the soil under the *B. pendula* canopy dries out later, as a result of the different leaf area dynamics. Fig. 5 shows examples of the simulated annual course of daily net photosynthesis (daily integrals of A_c in $mol\ m^{-2}\ day^{-1}$) and daily transpiration ($mm\ day^{-1}$). The fluxes under baseline conditions were compared with those in which $[CO_2]$, temperature and leaf area are elevated, bud burst is early, water stress is allowed to occur, but N_L is unchanged (no N limitation). Variability is strong, associated with variations in incoming PPFD. The figure shows that the combined conditions affect photosynthesis only slightly in *P. sitchensis*, where

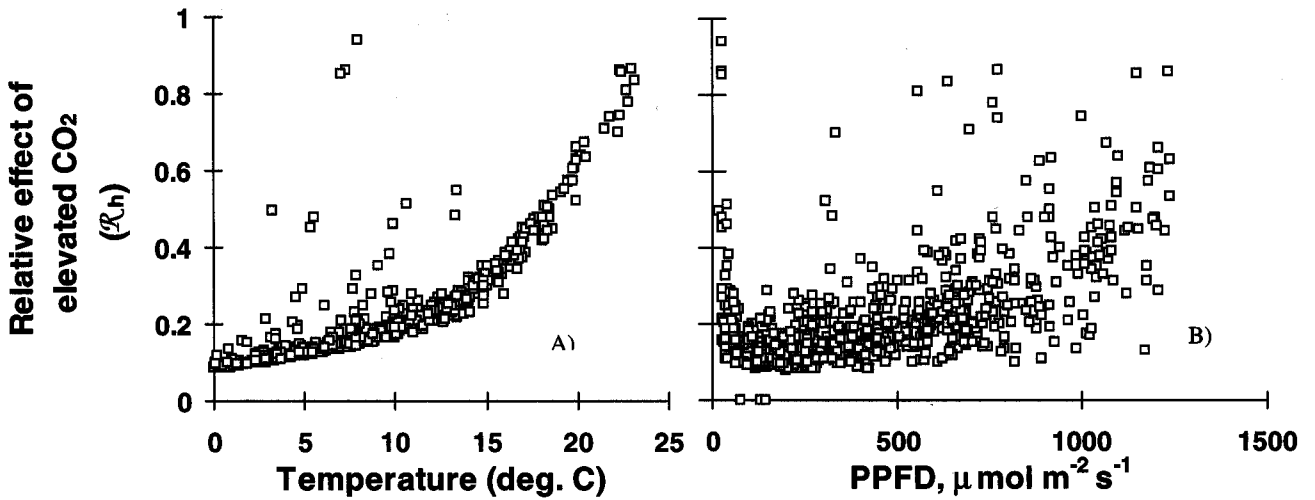


Fig. 4. Simulated relative effect of doubling CO₂ on hourly canopy net photosynthesis of *P. sitchensis* throughout the 'season' of 1991–1992, as it varies with temperature and absorbed PPFD. The scatter in these relationships is the result of other variables changing at the same time, since these measurements were forced by real meteorological data.

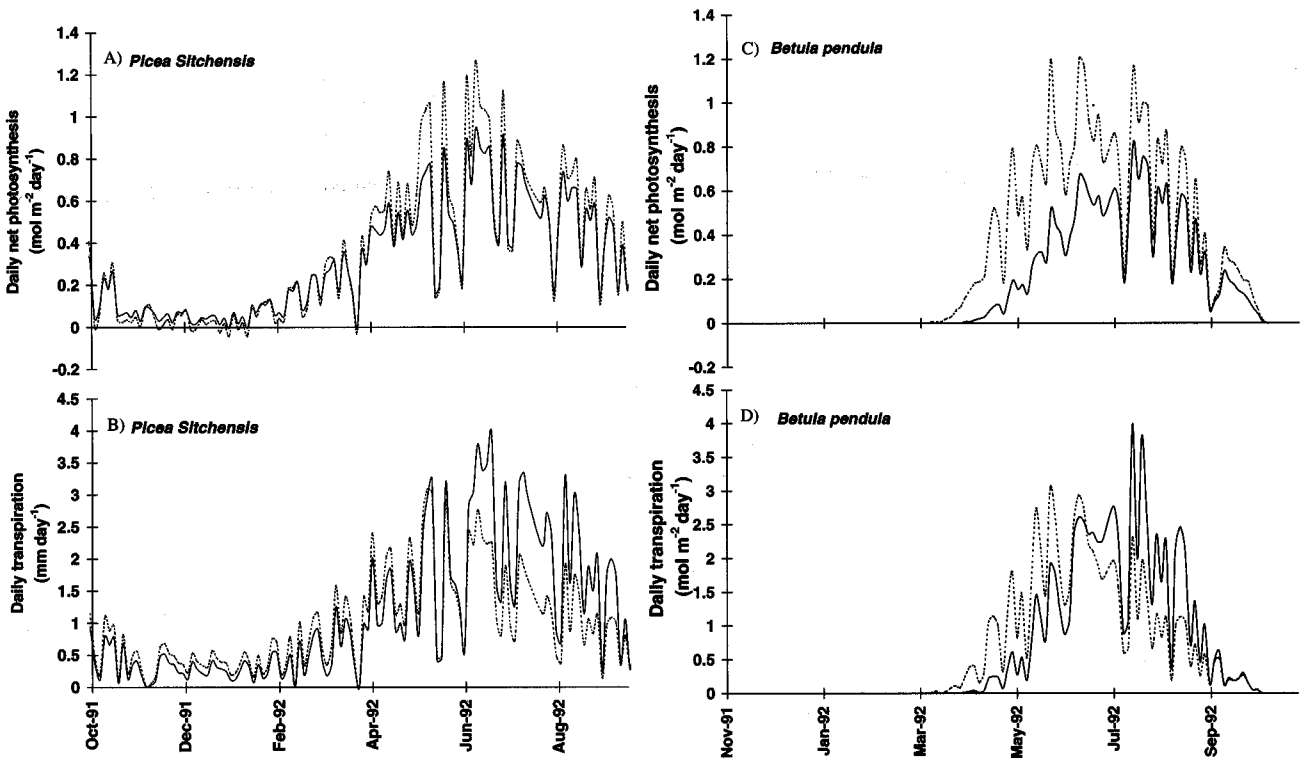


Fig. 5. The modelled annual course of net photosynthesis a) and c) and transpiration b) and d) for *P. sitchensis* a) and b) and for *B. pendula* c) and d). Solid lines represent the current baseline conditions in current climate, and dotted lines represent conditions in which [CO₂], temperature and leaf area are elevated, bud burst is early, water stress is allowed to occur, but N_L is unchanged (no N limitation). Note the different offsets in the horizontal axes.

phenology hardly changes in total spring leaf area and water stress feeds back relatively strongly on fluxes. Only in the early summer are the fluxes clearly enhanced. In *B. pendula*, the combined effects on photosynthesis are strong. In the spring, higher leaf areas have a strong influence. Water stress reduces fluxes later in the season.

Water use in *P. sitchensis* is not much increased by early bud burst in spring, but water stress has a strong effect later. In *B. pendula*, enhanced transpiration in spring compensates for reductions in late summer.

SENSITIVITY OF ANNUAL CANOPY PHOTOSYNTHESIS AND TRANSPIRATION TO CLIMATE CHANGE

Tables 2 and 3 present the results of the sensitivity analysis in terms of relative differences in P_n and transpiration in altered conditions, compared with the baseline CO_2 and

temperature conditions. Fig. 6 summarises those results for the two extremes in terms of temperature, water stress and phenology.

In summary, the responses are as follows. A percentage indicates a difference relative to the baseline value:

- An increase of $[CO_2]$ by $350 \mu mol mol^{-1}$ led to an increase in P_n of up to 20% and a decrease in transpiration of up to 16% of the baseline simulation. The effect on photosynthesis was stronger in *P. sitchensis* than in *B. pendula* and the effect on transpiration was stronger in *B. pendula*.
- An increase of canopy leaf area by 40% (keeping N_L the same) led to an increase in P_n of 26 to 27% in *B. pendula*. In *P. sitchensis*, this increase in leaf area was predicted to lead to a decrease in P_n of 2% at reference temperature, but of 7% at elevated temperatures. Transpiration increased strongly with leaf area, especially in *B. pendula* when bud burst was early.

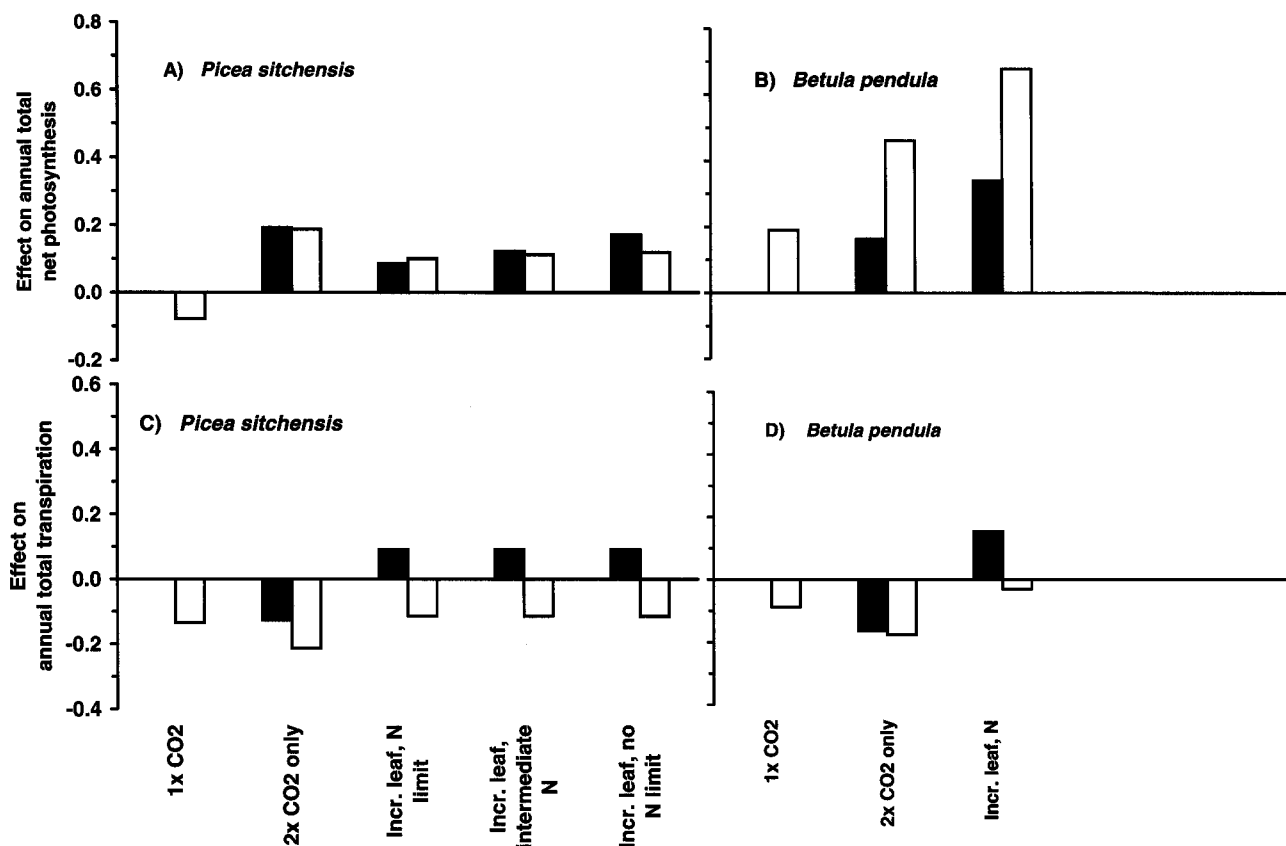


Fig. 6. The relative effect on annually integrated net canopy photosynthesis (P_n) of a) *P. sitchensis*, and b) *B. pendula*, of increasing CO_2 by $350 \mu mol mol^{-1}$, increasing leaf area by 40% and varying N_L between -30% of the baseline in the case of full N limitation, via intermediate limitation as observed by Rey and Jarvis (1997), of -20%, to no limitation, with leaf N the same as in the baseline conditions (black bars). These effects are compared with the situation of increased temperature (+3°C), soil water stress and early leaf emergence occurring simultaneously (white bars). All effects are expressed as the difference normalised with the standard, $1 \times CO_2$ condition. In the lower histograms the same relative effects are shown for canopy transpiration c), d).

Table 3. As Table 2, but for the *B. pendula* simulations.

A: <i>B. PENDULA</i> net photosynthesis	Low temperature		High temperature		Hi T+ early flush		Hi T + water stress		Hi T + water stress + early flush	
	P_n	δ	P_n	δ	P_n	δ	P_n	δ	P_n	δ
1 × CO ₂	59	0.00	59	0.01	73	0.24	58	-0.02	70	0.19
2 × CO ₂ no acclimation	68	0.16	71	0.20	87	0.48	80	0.19	86	0.46
2 × CO ₂ Increased leaf area N limiting	79	0.34	82	0.40	100	0.70	81	0.38	98	0.68
2 × CO ₂ Increased leaf area intermediate N	80	0.37	83	0.42	101	0.73	82	0.40	100	0.70
2 × CO ₂ Increased leaf area no N limit	84	0.43	86	0.46	104	0.78	85	0.45	103	0.75
B: <i>B. PENDULA</i> transpiration	Low temperature		High temperature		Hi T+ early flush		Hi T + water stress		Hi T + water stress + early flush	
	E	δ	E	δ	E	δ	E	δ	E	δ
1 × CO ₂	212	0.00	244	0.15	307	0.45	171	-0.19	194	-0.09
2 × CO ₂ no acclimation	178	-0.16	204	-0.04	257	0.21	153	-0.28	175	-0.18
2 × CO ₂ Increased leaf area N limiting	245	0.15	281	0.33	254	0.67	183	-0.14	206	-0.03
2 × CO ₂ Increased leaf area intermediate N	245	0.15	281	0.33	354	0.67	183	-0.14	206	-0.03
2 × CO ₂ Increased leaf area no N limit	245	0.15	281	0.33	354	0.67	183	-0.14	206	-0.03
C: <i>B. PENDULA</i> water use efficiency	Low temperature		High temperature		Hi T+ early flush		Hi T + water stress		Hi T + water stress + early flush	
	WUE	δ	WUE	δ	WUE	δ	WUE	δ	WUE	δ
1 × CO ₂	4.97	0.00	4.37	-0.12	4.25	-0.14	6.06	0.22	6.48	0.30
2 × CO ₂ no acclimation	6.91	0.39	6.22	0.25	6.05	0.22	8.25	0.66	8.82	0.77
2 × CO ₂ Increased leaf area N limiting	5.77	0.16	5.23	0.05	5.07	0.02	7.95	0.60	8.59	0.73
2 × CO ₂ Increased leaf area intermediate N	5.91	0.19	5.30	0.07	5.15	0.04	8.07	0.62	8.72	0.75
2 × CO ₂ Increased leaf area no N limit	6.15	0.24	5.47	0.10	5.30	0.04	8.32	0.68	8.97	0.81

- Increases in N_L led to moderately strong increases in P_n of *B. pendula* (a 6 to 9% increase in P_n for a 30% increase in N_L), and less in *P. sitchensis* (2 to 8%). Transpiration did not depend on N_L in this study, because there was no implied dependence of stomatal conductance on photosynthesis.
- There were only moderate effects of temperature and VPD on P_n (3 to 6% increases) for rises of 3°C and 0.3 kPa in *B. pendula*. In *P. sitchensis*, the effect was very slightly positive (1 to 2%) in high $[CO_2]$ with low N_L and leaf area, but negative in either low $[CO_2]$ or high N_L . Strong (12 to 17%) effects of increased temperature and VPD on transpiration were predicted in both species.
- Water stress had a small negative effect (-3 to -6%) on P_n in *P. sitchensis*, and a still smaller effect on *B. pendula* (-1 to -3%). In the case of early phenology the effect in *B. pendula* was similar to that in *P. sitchensis*. The effects of water stress on transpiration were large: -22 to -38% in *P. sitchensis* and -32 to -40% in *B. pendula*, increased to -70% in *B. pendula* if bud burst was early.
- Early leaf emergence on its own showed the sensitivity to increased leaf area. The effect was small in *P. sitchensis* (1 to 3% increase in P_n and transpiration), but substantial in *B. pendula* (21-32% increase in P_n and transpiration), but with water stress transpiration was less sensitive to phenology.

These sensitivities are not independent. At the high temperatures, the sensitivities to CO_2 of both P_n and transpiration were higher, but sensitivity of P_n to N_L was lower. Also, high leaf area and high N_L increased the effects of early leaf emergence and water stress.

An annual 'water use efficiency' (WUE) was computed as the total of net photosynthetic production over the year per unit of total transpiration over the year. Tables 2c and 3c give the values and relative differences. For both species WUE decreased with increasing leaf area in well-watered conditions, but WUE increased with leaf area under water stress. WUE increased with increasing N_L . The most efficient canopy in terms of water use was the drought-stressed, well-fertilised, *B. pendula* stand with early bud burst.

The main difference between the results of the simulations for the two species was the smaller responsiveness of P_n in *P. sitchensis* to increased leaf area, temperature and N_L , and the stronger response to water stress, in comparison with *B. pendula*. The two species behave fairly similarly with respect to transpiration, except that early leaf emergence greatly increased both transpiration itself and its sensitivity to water stress in *B. pendula*, whilst there was only a small effect on transpiration in *P. sitchensis*.

Discussion

RESPIRATION AND FLUXES FROM THE SOIL

The sensitivity of net carbon sequestration to $[CO_2]$ presented by Wang and Polglase (1995) and by Lloyd and Farquhar (1996), as well as the observation of increased CO_2 exchange in the northern Hemisphere (Myneni *et al.*, 1997), all relate to *Net Ecosystem Productivity* (NEP), i.e. the time integral of the net ecosystem flux as measured by eddy covariance methods. NEP includes large respiration effluxes from the woody biomass, roots and heterotrophic soil organisms, which often almost cancel the net photosynthetic influx. Modelling these fluxes is beyond the scope of this study, and *relative* effects of climate change at this scale are highly sensitive to the very small baseline NEP, which may even be zero or negative (e.g. Goulden *et al.*, 1996). If, for example, the very substantial annual soil respiration term had been subtracted from our calculated annual fluxes, the *relative* effects presented here would have been substantially larger. Thus, the results of this study represent minimum sensitivities with respect to ecosystem carbon exchange.

Evaporation of surface water from the leaves (interception loss) and from any understorey and soil surface would, if included, have responded slightly to increases in canopy leaf area. But since these fluxes are small and of the same sign as the transpiration fluxes, effects of including surface water evaporation were neglected.

DEPENDENCE ON BACKGROUND CONDITIONS

This sensitivity analysis was made in the context of a set of background conditions and parameters that were the same in all simulations. These background conditions are important, because many of the processes involved are non-linear with respect to the variables. For example, the sensitivity of P_n to temperature may well have been different if different temperature functions had been chosen for the photosynthetic parameters, or if the baseline climate had been at higher temperatures.

INFLUENCE OF THE STOMATAL MODEL

The model for stomatal conductance is empirical and does not specify direct dependence of stomatal conductance on N_L or photosynthesis. Alternative models, such as the Ball-Woodrow-Berry-Leuning approach (Ball *et al.*, 1987; Leuning, 1995), do specify such dependence, and would have predicted rather different results, especially for the sensitivity of transpiration and water use efficiency to $[CO_2]$ and N_L . There is, however, little experimental justification for using such an approach with these species, particularly when elevated $[CO_2]$ is the variable of interest (Rey, 1997; Barton, 1997).

SENSITIVITY OF P_n AND TRANSPIRATION TO $[CO_2]$, NITROGEN AND WATER STRESS

Elevated $[CO_2]$ on its own resulted in similar increases in P_n , of about 20%, in both species. The slightly stronger response of *P. sitchensis* to $[CO_2]$ is explained below. In comparing this with as much as 40–50% from a number of other studies (Luxmoore *et al.*, 1993) it should be realised that average temperatures in Scotland are low (Fig. 3c), even during the growing season. The marked effect of temperature on the sensitivity of photosynthesis to CO_2 is evident from the analysis of hourly simulations, but it is also clear from the annual integrals. The decreases in transpiration with increasing $[CO_2]$ are the result of the dependence of stomatal conductance on $[CO_2]$. The slightly higher sensitivity of transpiration of *B. pendula* to this variation in stomatal conductance is because the *B. pendula* leaves are more closely coupled to the atmosphere, as a result of lower LAI and, therefore, higher windspeeds inside the canopy. The resulting sensitivity of WUE to $[CO_2]$, however, is similar in both species.

The two species differ with respect to the dependence of P_n and transpiration on leaf area, N_L and water stress, but the role of leaf area is overriding in this case. The already dense *P. sitchensis* canopy does not, with the assumed parameter set, benefit from substantial increases in leaf area. The question arises whether even a small increase in leaf area has a negative effect on P_n in *P. sitchensis* in elevated $[CO_2]$. This was investigated by running the model also for *P. sitchensis* for leaf area increases of 5%, 10%, 20% and 30% relative to the baseline leaf area, at current and elevated temperatures, elevated CO_2 and without nutrient limitations (Fig. 7). This

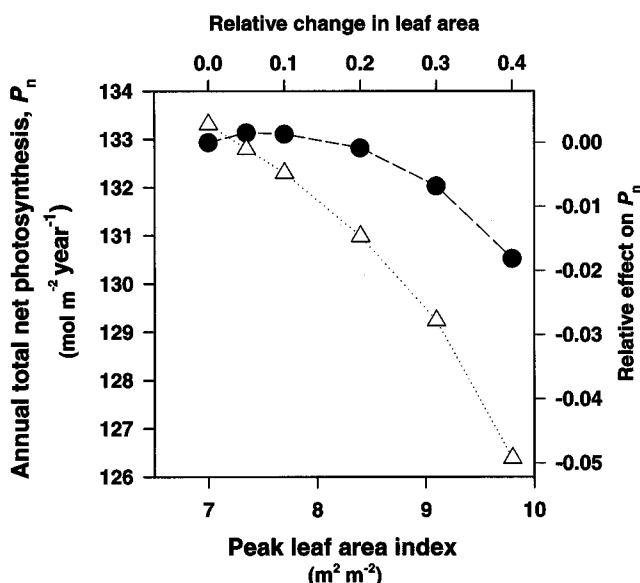


Fig. 7. The simulated dependence of the peak leaf area index (LAI, in summer) on P_n , for current temperatures (circles) and elevated (+3 °C) temperatures (triangles), for *P. sitchensis*.

shows that the effect of increased leaf area is not linear and that increases of up to about 20% (LAI = 8.5) have a neutral effect on P_n in current temperatures, but that in elevated temperatures P_n declines with any increase in leaf area, as a result of increased leaf respiration. Of course, where there is a simulated negative effect of increased leaf area, this increase in leaf area would never occur in reality. In contrast, the relatively open *B. pendula* canopy shows a substantial increase in P_n when leaf area is increased.

Theory predicts that N_L and water stress are more important variables for light-saturated photosynthesis than for light-limited photosynthesis (Farquhar and Von Caemmerer, 1982). Indeed, increasing N_L does not increase P_n in *P. sitchensis* very much, as a result of intense shading within the canopy. In elevated temperature, the effect of increasing N_L almost becomes negative as a result of respiratory costs of N maintenance. The effect of N_L on P_n in *B. pendula* is only moderately larger, since in these trees V_{cmax} , and J_{max} are already large and light saturation occurs only at high PPFD.

Sensitivity to the initial quantum efficiency of electron transport, α , was also tested in *P. sitchensis*, with its dense canopy, by doubling its value. In the case of high α , the effects of increasing N_L and leaf area were enhanced, because in this case photosynthesis was light-saturated in a larger proportion of the foliage.

Transpiration in these simulations did not depend on N_L , whereas photosynthesis did, leading to increased WUE with increasing N_L . There was also a clear dependence of WUE on water stress and leaf area, through the canopy-integrated stomatal conductance. The dependence on leaf area was stronger in *B. pendula*, as a result of lower initial leaf area, as discussed above, and because of the dominant difference in response of P_n .

SENSITIVITY OF P_n AND TRANSPIRATION TO PHENOLOGY

The potential impact of phenological change on primary productivity is sometimes overestimated. Conifers with long-lived needles (such as *P. sitchensis*) replace only a part of their foliage in spring, so that the relative gain in leaf area by early leaf emergence is small (Fig. 2a). If, in addition, there is low sensitivity of P_n to increased leaf area because the canopy is very dense already, then the effect of early leaf emergence is further reduced. By contrast, in the deciduous *B. pendula* canopy, advanced leaf emergence made a very big difference to P_n because the canopy photosynthesis was responsive to increases in leaf area. Similar arguments hold for canopy transpiration, and as a result the annual WUE was not affected by early leaf emergence in the *P. sitchensis* simulations, but was reduced slightly in the *B. pendula* simulations. However, at present, the model does not account for any risk of damage to the leaf area by spring frost, and this is very likely to be an important

factor on longer time scales, limiting the benefits of early leaf emergence (Murray *et al.*, 1994).

CONCLUSIONS AND IMPLICATIONS FOR LONG-TERM DEVELOPMENT OF FORESTS

The results in this study demonstrate that the key factors that determine the responses of P_n are the distribution of PPFD through the canopy, as a function of leaf area, and the value of PPFD at which photosynthesis starts to saturate.

The conditions considered in this sensitivity analysis represent several potential stages of development of *P. sitchensis* and *B. pendula* forests under a changed climate. These were imposed, static conditions and the model results enable us to assess whether they may occur in reality. Clearly, a substantial increase in leaf area is not likely to occur in closed *P. sitchensis* forests, since this leads to a decrease in productivity, even if nutrition is not limiting. In *B. pendula* woodlands, on the other hand there definitely is scope for leaf area increases in relatively young stands, but higher LAI will inevitably lead to saturating responses similar to those in *P. sitchensis*.

Higher [CO₂] leads to less transpiration on a unit leaf area basis, but higher temperature and VPD counteract this, and larger leaf areas may well increase water use beyond that in the present-day climate. In most cases, it will be the strength of the feed-backs, such as between soil water, nutrient supply and the climate itself, that will determine whether in a future climate CO₂ uptake and/or WUE will be increased. The simulations suggest that, on the whole, there will be some increase in annual 'water use efficiency', but that the absolute amounts of water transpired into the atmosphere will not always decrease, even if leaf areas remain the same.

Acknowledgements

The authors are grateful to Alan Crossley, Institute for Terrestrial Ecology, Edinburgh, for the hourly climate data set from Glencorse, Penicuik, Midlothian, Scotland, and to the anonymous referees who made several helpful comments. The experimental work was done as part of the EC-ECOCRAFT project (EC CT95-0077) and a Leverhulme Trust Grant (F/158/A). B. Kruijt was supported by the NERC-TIGER thematic programme grant GST/02/597.

References

Ball, J.T., Woodrow, I.E. and Berry, J.A., 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: *Progress in Photosynthesis Research*, Vol. VI (Biggens, S., Hrg.), Dordrecht: 221–224.

Barton, C.V.M., 1997. Effects of elevated atmospheric carbon dioxide concentrations on growth and physiology of Sitka spruce (*Picea sitchensis* (Bong.) Carr.), PhD Thesis, University of Edinburgh.

Barton, C.V.M., Lee, H.S.J. and Jarvis, P.G., 1993. A branch bag and CO₂ control system for long-term CO₂ enrichment of mature Sitka spruce (*Picea sitchensis* (Bong.) Carr.): technical report. *Plant, Cell Environ.* 16, 1139–114.

Brooks, A. and Farquhar, G.D., 1985. Effect of temperature on the CO₂/O₂ specificity of ribulose-1,5-bisphosphate carboxylase oxygenase and the rate of respiration in the light—estimates from gas-exchange measurements on spinach. *Planta*, 165, 397–406.

Carter, T.R., Parry, M.L., Harasawa, H. and Nishioka, S., 1994. *IPCC Technical Guidelines for Assessing Climate Change Impacts and Adaptations*. IPCC Special Report, UCL, London.

Ceulemans, R. and Mousseau, M., 1994. Effect of elevated atmospheric CO₂ on woody plants – Tansley review No. 71. *New Phytologist*, 127, 425–446.

Comins, H.N. and McMurtrie, R.E., 1993. Long-term biotic response of nutrient limited forest ecosystems to CO₂-enrichment: equilibrium behaviour of integrated plant-soil models. *Ecol. Applic.*, 3, 661–681.

Evans, J.R. and Farquhar, G.D., 1991. Modelling canopy photosynthesis from the biochemistry at the chloroplast level. In: Boote, K.J. and Loomis, R.S. (eds.): *Modelling Crop Photosynthesis – From Biochemistry to Canopy*. CSSA Special publication no., 19, Crop Science Society of America, Madison, 1–16.

Farquhar, G.D. and von Caemmerer, S., 1982. 'Modelling of photosynthetic response to environmental conditions.' In: Lange, O.L., Nobel, P.S., Osmond, C.B. and Ziegler, H. (eds.): *Water Relations and Carbon Assimilation. Encyclopaedia of Plant Physiology*, 12-B, 550–587.

Field, C., 1983. Allocating leaf nitrogen for the maximisation of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56, 341–347.

Goulden, M.L., Munger, J.W., Fan, S.M., Daube, B.C. and Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance—methods and a critical-evaluation of accuracy. *Global Change Biology*, 2, 169–182.

Hänninen, H., 1990. Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica*, 47 pp.

Harley, P.C., Thomas, R.B., Reynolds, J.F. and Strain, B.R., 1992. Modelling photosynthesis of cotton grown in elevated CO₂. *Plant, Cell Environ.* 15, 271–282.

Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. Roy. Soc. Lond. Series B-273*, 593–610.

Jarvis, P.G. (Ed.), 1998. *The Likely Impact of Rising CO₂ and Temperature on European Forests*. Cambridge University Press, Cambridge. In press

Jarvis, P.G. and McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. *Adv. Ecol. Res.* 15, 1–49.

Jarvis, P.G. and Sandford, A.P., 1986. Temperate forests. In: (eds. N.R. Baker and S.P. Long) *Topics in Photosynthesis, vol. 7. Photosynthesis in Contrasting Environments*, Elsevier: Amsterdam. pp., 199–236.

Jarvis, P.G., Barton, C.V.M., Dougherty, P.M., Teskey, R.O. and Massheder, J.M., 1990. MAESTRO. In *Development and Use of Tree and Forest Response Models. Acidic Deposition: State of Science and Technology*, Report 17. Ed. Kiester, A.R., NAPAP, Government Printing Office, Washington, DC 20402–9325. 167–178.

- Kirschbaum, M.U.F., 1994. The sensitivity of C₃ photosynthesis to increasing CO₂ concentration: a theoretical analysis of its dependence on temperature and background CO₂ concentration. *Plant, Cell Environ.*, **17**, 747–754.
- Kramer, K., 1995a. Phenotypic plasticity of the phenology of seven European tree species, in relation to climatic warming. *Plant, Cell Environ.*, **17**, 367–377.
- Kramer, K., 1995b. Modelling comparison to evaluate the importance of phenology for the effects of climate change in growth of temperate-zone deciduous trees. *Climate Res.*, **5**, 119–130.
- Kruijt, B., Levy, P., Massheder, J., McIntyre, J., Grace, J., Moncrieff, J.B. and Jarvis, P.G., 1994. Modelling forest CO₂ and water fluxes for a range of biomes—retaining the critical sensitivities *Annales Geophysicae*, **12**, C457.
- Kruijt, B., Onger, S. and Jarvis, P.G., 1997. Scaling PAR absorption, photosynthesis and transpiration from leaves to canopy. In: P. van Gardingen, G. Foody and P. Curran (eds.) 'Scaling-up from Cell to Landscape', Cambridge University Press.
- Landsberg, J.J. and Jarvis, P.G., 1973. A numerical investigation of the momentum balance of a spruce forest. *J. Appl. Ecol.*, **10**, 645–655.
- Leuning, R., 1995. A critical appraisal of a combined stomatal-photosynthesis model for C-3 plants. *Plant Cell Environ.*, **18**: 339–355
- Lloyd, J. and Farquhar, G.D., 1996. The CO₂ dependence of photosynthesis, plant growth responses to elevated atmospheric CO₂ concentration and their interaction with soil nutrient status. I. General principles and forest ecosystems. *Functional Ecology*, **10**, 4–32.
- Lloyd, J., Grace, J., Miranda, A.C., Miranda, H.S., Meir, P., Wong, S.C., Gash, J.H.C. and Wright, I.R., 1995. A simple calibrated model of Amazonian rainforest productivity based on leaf biochemical properties. *Plant, Cell Environ.*, **18**, 1129–1145.
- Luxmoore, R.J., Wullschlegel, S. and Hanson, P.J., 1993. Forest responses to CO₂ enrichment and climate warming. *Water, Air Soil Pollut.*, **70**, 309–323.
- McMurtrie, R.E. and Comins, H., 1996. The temporal response of forest ecosystems to doubled atmospheric CO₂ concentration. *Global Change Biol.*, **2**, 49–57.
- Murray, M.B., Smith, R.I., Leith, I.D., Fowler, D., Lee, H.S.J., Friend, A.D. and Jarvis, P.G., 1994. Effects of elevated CO₂, nutrition and climatic warming on bud phenology in Sitka spruce (*Picea sitchensis*) and their impact on the risk of frost damage. *Tree Physiol.*, **14**, 691–706.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. and Neman, R.R., 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature, Lond.*, **386**, 698–702.
- Norman, J.M. and Welles, J.M., 1983. Radiative transfer in an array of canopies. *Agron. J.* **75**, 481–488.
- Poorter, H., 1993. Interspecific variation in the growth response of plants to an elevated CO₂ concentration. *Vegetatio*, **104/105**, 77–97.
- Rayment, M.B., Kruijt, B. and Jarvis, P.G., 1995. Sub-canopy scale carbon fluxes in BOREAS, *Annales Geophysicae*, **13**, C 523
- Rey, A., 1997. Response of young birch trees (*Betula pendula* Roth.) to increased atmospheric carbon dioxide concentration. PhD Thesis, University of Edinburgh.
- Rey, A. and Jarvis, P.G., 1997. Growth response of young birch trees (*Betula pendula* Roth.) after four and a half years of CO₂ exposure. *Ann. Bot.* **80**, 809–816.
- Rutter, A.J., Kershaw, K.A., Robins, P.C. and Morton, A.J., 1971. A predictive model of rainfall interception in forests, 1. derivation of the model from observations in a plantation of Corsican pine. *Agric. Met.* **9**, 367–384.
- Sellers, P.J., Bounoua, L., Collatz, G.J., Randall, D.A., Dazlich, D.A., Los, S.O., Berry, J.A., Fung, I., Tucker, C.J., Field, C.B. and Jensen, T.G., 1996. Comparison of radiative and physiological effects of doubled atmospheric CO₂ on climate. *Science*, **271**, 1402–1406
- Van Oosten, J.J., Wilkins, D. and Besford, R.T., 1995. Acclimation of tomato to different carbon dioxide concentrations. Relationships between biochemistry and gas exchange during leaf development. *New Phytologist*, **130**, 357–367
- Wang Y.P. and Jarvis, P. G., 1990a. Description and validation of an array model—MAESTRO. *Agric. For. Meteorol.*, **51**, 257–280
- Wang, Y-P. and Jarvis, P.G., 1990b. Effect of incident beam and diffuse radiation on PAR absorption, photosynthesis and transpiration of Sitka spruce—A simulation study. *Silva Carelica* **15**, 167–180.
- Wang, Y.P. and Polglase, P.J., 1995. Carbon balance in the tundra, boreal forest and humid tropical forest during climate change: scaling up from leaf physiology and soil carbon dynamics. *Plant, Cell Environ.*, **18**, 1226–1244.
- Wang, Y.P., Rey, A. and Jarvis, P.G., 1998. Carbon balance of young birch trees grown in ambient and elevated CO₂ concentrations. *Global Change Biology*, in press.
- Weiss A. and Norman, J.M., 1985. partitioning solar radiation into direct and diffuse, visible and near infra-red components. *Agric. For. Meteorol.*, **34**, 205–214.