

Parameterization of a leaf gas-exchange model for *Fagus sylvatica* L. using microcosms grown under ambient and elevated CO₂

Jörn Strassemeier & Manfred Forstreuter

Synopsis

One year old beech stands (*Fagus sylvatica* L., provenance Niederdeutsches Tiefland) were exposed to ambient ($370 \pm 40 \mu\text{mol mol}^{-1}$) and elevated CO₂ ($700 \pm 10 \mu\text{mol mol}^{-1}$) for three vegetation periods. These microcosms - consisting of 49 (first year), 36 (second year) and 25 (third year) saplings - were grown in closed cubical mini-glasshouses with unlimited nutrient supply. Single leaf gas exchange measurements (CO₂ and H₂O) and leaf nitrogen analyses were performed every year at various canopy depths (LAI 4 to 6). In order to parameterize a leaf gas-exchange model, a series of A_n/C_i curves were measured with a mini-cuvette system (CMS 400, Walz) under constant environmental conditions (PPFD > $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, $T_{\text{leaf}} = 25^\circ\text{C}$, VPD=1.4 kPa). In the second year A_n/C_i curves was also measured at four additional temperatures (17°, 21°, 29°, 35 °C).

A widely used photosynthesis model integrating photosynthesis and stomatal conductance was employed to interpret the gas-exchange data. The key parameters of this model, V_{cmax} and J_{max} , were derived for each leaf. The temperature dependency of these parameters was derived using a modified Arrhenius function.

Adjustments of the photosynthesis apparatus to elevated CO₂ were not detected in any of the three years. V_{cmax} and J_{max} , showed no significant change as a result of the increase in the growth CO₂ concentration.

The derived model parameters showed a wide variability. We propose that this variability in physiological properties can be explained with the varying light climate in the canopy. In former studies a relationship of SLA to canopy depth and of SLA to leaf nitrogen could be demonstrated. We therefore proposed that SLA or leaf nitrogen would correlate with the estimated model parameters. Confirming our assumptions we found a linear relationship of V_{cmax} and J_{max} to leaf nitrogen and a exponential relationship to SLA. This indicates the need to incorporate such relationships into leaf- and canopy-scale models.

Keywords

Fagus sylvatica, elevated CO₂ concentration, net photosynthesis, acclimation, stomatal conductance, transpiration, intercellular CO₂ concentration, temperature dependence, leaf nitrogen

Introduction

In the context of global change plant communities will be subject to changing environmental conditions i.e. temperature and CO₂ concentration (NEFTEL & al. 1985, SARIMENTO & BENDER 1994, KEELING & WHORF 1994, FORSTREUTER & al. 1994, HOUGHTON & al. 1990). These changes will have great impact on physiological reactions such as photosynthesis (GODELEWSKY 1873, FARQUHAR & al. 1980, CURE & ACOCK 1986, EAMUS & JARVIS 1989, OVERDIECK 1993, SAGE 1994) and respiration (CEULEMANS & MOUSSEAU 1994). A considerable amount of research on these processes has been performed at leaf level whereas measurements at the canopy level of woody plants are difficult to accomplish due to financial and technical restrictions. Simulation models are therefore important tools for integrating physiological information across scales of organisation. To achieve realistic predictions with the help of such models it is essential to establish a well founded parameterization.

Another elegant way of predicting the reaction of ecosystem responses to a changing environment is the microcosm technique (FORSTREUTER 1995, 1996). This technique enables the investigation of the behaviour of canopies and ecosystems under field-like conditions and the verification of models which have been parameterized on the same ecosystem. We therefore conducted a long-term research (1994 - 1996) of the carbon and water vapour exchange of beech microcosms growing under ambient and elevated CO₂ concentrations (FORSTREUTER 1996).

In this study a photosynthesis model first proposed by FARQUHAR & al. (1980) and a version of a model for stomatal conductance proposed by BALL & al. (1987) and subsequently modified by LEUNING (1995) were combined to describe the gas exchange at leaf scale. Similar model set-ups have been applied successfully in scaling up gas exchange from leaf to canopy (HARLEY & al. 1992, HARLEY & BALDOCCHI 1995, WANG & al. 1996). Although there has been considerable research on gas exchange of beech, we found no information which was sufficiently detailed to allow rigorous parameterization of these models. Therefore, we focused in this study on the gas exchange of beech at leaf level. Of particular interest were the effects which CO₂ elevation had on the physiological properties of the photosynthesis apparatus and the effects of varying leaf nitrogen and temperature on the photosynthesis parameters.

Method

Microcosms of one year old beech stands (*Fagus sylvatica* L., provenance Niederdeutsches Tiefland) were exposed to ambient ($370 \pm 40 \mu\text{mol mol}^{-1}$) and elevated ($700 \pm 10 \mu\text{mol mol}^{-1}$) CO₂ for three vegetation periods. These microcosms - consisting of 49 (first year), 36 (second year) and 25 (third year) saplings - were grown in closed cubical mini-greenhouses under unlimited nutrient supply. Single leaf gas exchange measurements (CO₂ and H₂O) and leaf nitrogen analysis were performed every year in various canopy depths (LAI 4 to 6). In order to parameterize a leaf gas-exchange model, a series of A_n/C_i curves were measured with a mini-cuvette system (Fig. 1; CMS400, Walz) at constant environmental conditions (PPFD > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $T_{\text{leaf}} = 25^\circ\text{C}$, VPD = 1.4 kPa). In the second year A_n/C_i curves were also measured at four additional temperatures (17°, 21°, 29° and 35° C).

In this study, the model described by FARQUHAR et al. (1980) and modified by von CAEMMERER & FARQUHAR (1981) was used to estimate the net photosynthesis of beech leaves.

As one molecule of CO₂ is released in photorespiration for every two oxygenations of RuBP, net CO₂ assimilation A_n may be expressed as

$$A_n = V_c - 0.5 \cdot V_o - R_d = V_c \left| 1 - 0.5 \frac{V_o}{V_c} \right| - R_d \quad (1)$$

where the V_c and V_o are the rates of carboxylation and oxygenation, respectively, and R_d is the rate of CO₂ evolution in the light resulting from processes other than photorespiration.

The underlying assumption of the model is, that the rate of carboxylation is either being limited by the amount, the activation state and the kinetics of RuBisCO or by the rate of RuBP regeneration. The RuBP saturated rate of net CO₂ assimilation (A_c) is formulated by eqn. 2.

$$A_c = V_{c \max} \frac{C_i + \Gamma^*}{C_i + K_c \left| 1 + \frac{O_i}{K_o} \right|} - R_d \quad (2)$$

where Γ^* is the CO₂ compensation point in the absence of day respiration (R_d). At Γ^* eqn. 1 gives the ratio $V_o/V_c=2$ if $R_d=0$ and $A_n=0$. Γ^* can be expressed as:

$$\Gamma^* = \frac{V_{c \max} 0.5 K_c O_i}{V_{o \max} K_o} = \frac{O_i}{2\tau} \quad (3)$$

The formulation of the RuBP regeneration limited net CO₂ assimilation is

$$A_j = J \frac{C_i - \Gamma^*}{4(C_i + 2\Gamma^*)} - R_d \quad (4)$$

and the estimated rate of net photosynthesis, under a given set of environmental conditions, is then given by the minimum of the predicted RuBisCo limited and RuBP regeneration limited rates

$$A_n = \min\{A_j, A_c\} \quad (5)$$

In the model described above six parameters are dependent on temperature. For the temperature dependencies of $V_{c \max}$, K_c , K_o , τ and R_d exponential functions are used as described by HARLEY & BALDOCCHI (1995).

$$f(T_k) = f^* e^{\frac{H_a(T_k - T^*)}{RT_k T^*}} \quad (6)$$

where $f(T_k)$ is the value of one of the above parameters at leaf temperature T_k [K], f^* is the value of that parameter at the temperature T^* [K], R is the gas constant ($8.31 \text{ J mol}^{-1} \text{ K}^{-1}$) and H_a is the activation energy for that parameter.

The temperature dependence of J_{max} is described by a humped temperature function:

$$f(T_k) = f(T^*) \cdot e^{\frac{H_a(T_k - T^*)}{RT_k T^*}} \cdot \frac{1 + e^{\frac{\Delta ST^* - H_d}{RT^*}}}{1 + e^{\frac{\Delta ST - H_d}{RT}}} \quad (7)$$

where $f(T_k)$ is the value of J_{max} at leaf temperature T_k [K], f^* is the value of J_{max} at T^* [K], R is the gas constant, H_a is the activation energy, H_d is the energy of deactivation and S is an entropy term.

Regressions to gas-exchange data were made according to the Secant-Method (SAS Institute 1988), deriving V_{cmax} , J_{max} and R_d simultaneously. The values used for the kinetic properties of RuBisCO are shown in Tab. 1.

Tab. 1: Values for parameters describing the kinetic properties of RuBisCO

| | | |
|-------------|---------------------|--------------------------|
| $K_c(298)$ | 404* | $\mu\text{mol mol}^{-1}$ |
| $H_a(K_c)$ | 59500 ^x | J mol^{-1} |
| $K_o(298)$ | 248* | mmol mol^{-1} |
| $H_a(K_o)$ | 35900 ^x | J mol^{-1} |
| $\tau(298)$ | 2710* | - |
| $H_a(\tau)$ | -29000 ⁺ | J mol^{-1} |

* von CAEMMERER & al. 1994

x BADGER & COLLATZ 1977

+ JORDAN & OGREN 1984

The intercellular CO_2 concentration C_i , which is the driving variable of the model is not only determined by photosynthesis. External CO_2 concentration and stomatal conductance are further factors which influence C_i . Therefore, in order to predict net photosynthesis at varying environmental conditions a model for stomatal conductance must be integrated. Stomatal conductance (g_s) is modelled with a version of the model proposed by BALL & al. (1987) modified by LEUNING & al. (1995):

$$g_s = g_0 + \frac{a_1 \cdot A}{(C_a - \Gamma) \cdot (1 + D_s / D_0)} \quad (8)$$

where g_0 is the conductance as $A_n \rightarrow 0$ when leaf irradiance $\rightarrow 0$, a_1 and D_0 are empirical parameters and D_s and c_s are the humidity deficit and the CO_2 concentration at leaf surface.

Results

Adjustments of the photosynthesis apparatus to CO_2 elevation were not detected after three years of measurement (Fig. 1). The key parameters for photosynthesis, V_{cmax} and J_{max} , showed no significant change as a result of CO_2 elevation (Tab. 2).

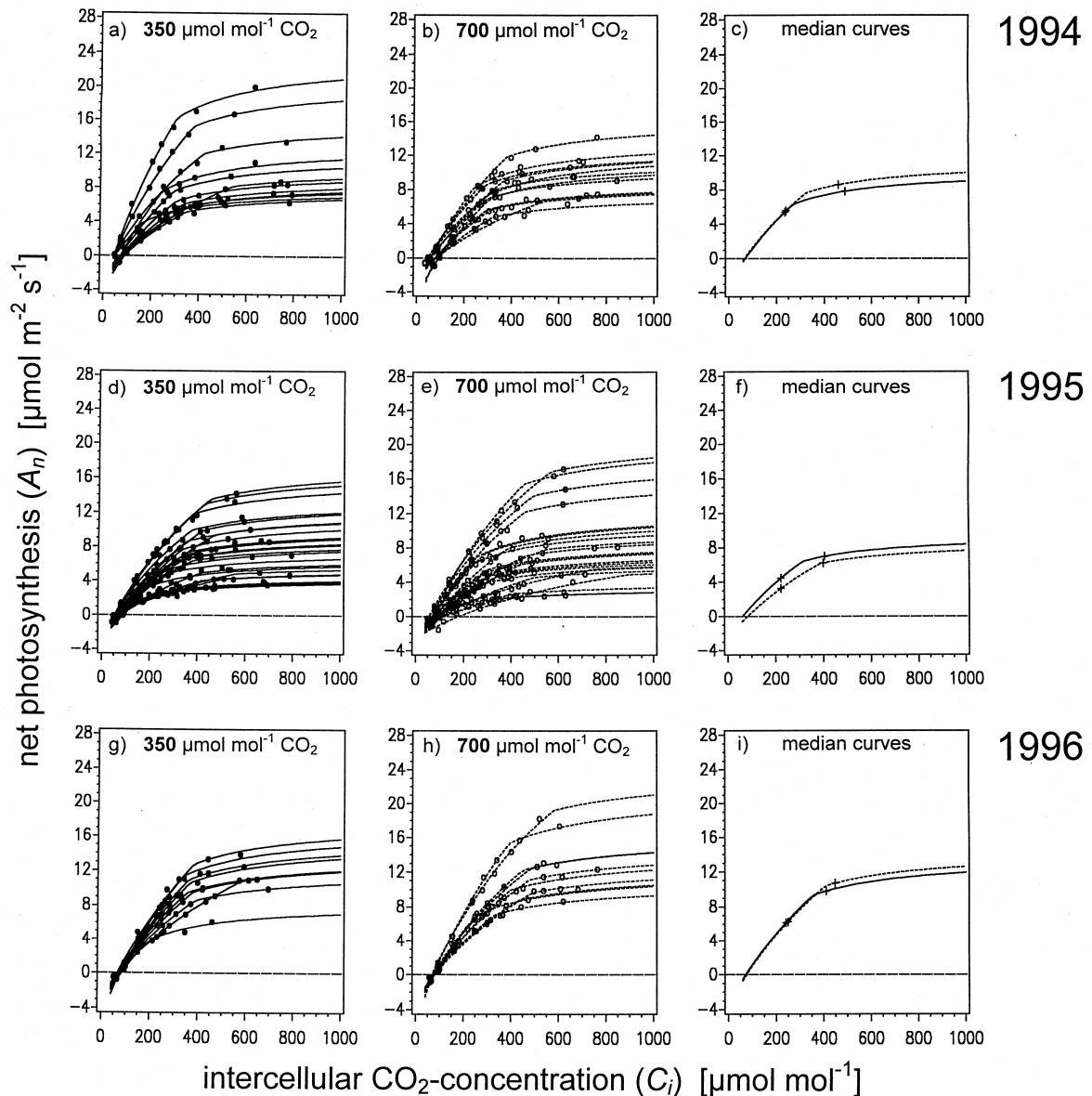
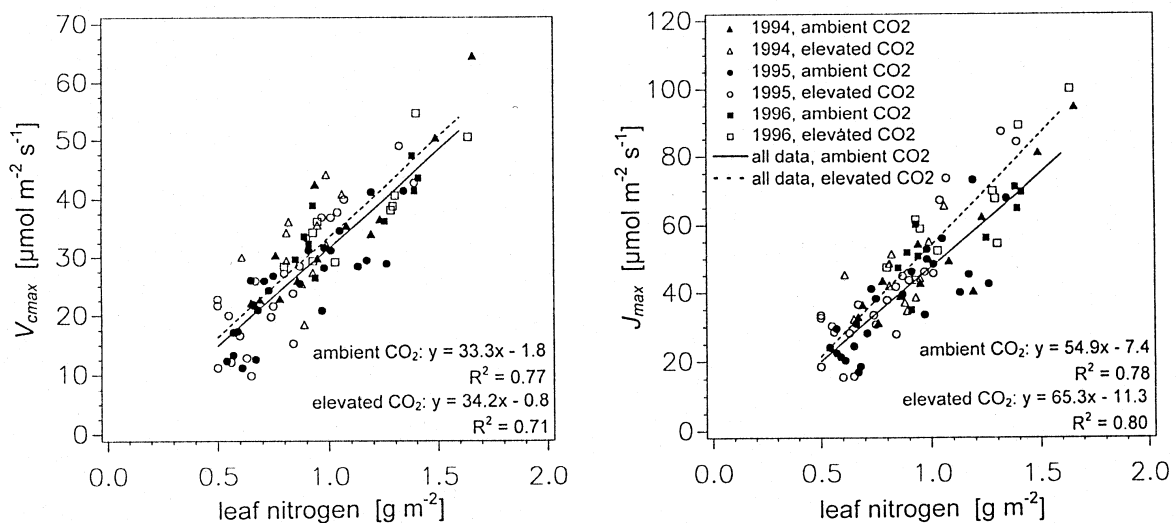


Fig. 1: A_n/C_i curves measured in 1994 (a-c), 1995 (d-e) and 1996 (g-i). Single leaf measurements and regression models at 350 $\mu\text{mol mol}^{-1}$ (a, d, g, — ●) and 700 $\mu\text{mol mol}^{-1}$ CO_2 growth concentration (b, e, h, --- ○). Median of the regression models (c, f, i), +: marks the C_i concentration corresponding to the CO_2 growth concentrations (350 and 700 $\mu\text{mol mol}^{-1}$).

Tab. 2: Photosynthesis and conductance parameters at 25°C of *Fagus sylvatica*

| | | 1994 | | 1995 | | 1996 | |
|---|----------|------------------------------------|-------------------------------------|------------------------------------|-------------------------------------|-----------------------------------|-------------------------------------|
| | | ambient CO ₂ n=13 | elevated CO ₂ n=12 | ambient CO ₂ n=24 | elevated CO ₂ n=24 | ambient CO ₂ n=9 | elevated CO ₂ n=10 |
| $V_{cmax}(298)$ [$\mu\text{mol m}^{-2} \text{s}^{-1}$] | M | 34.8 | 34.3 | 28.2 | 25.0 | 41.1 | 39.6 |
| | I_{50} | 16.8 | 13.8 | 11.5 | 20.4 | 7.4 | 8.4 |
| | p | 0.99 | | 0.68 | | 0.96 | |
| $J_{max}(298)$ [$\mu\text{mol m}^{-2} \text{s}^{-1}$] | M | 45.6 | 49.3 | 40.9 | 39.7 | 60.2 | 64.1 |
| | I_{50} | 22.1 | 16.8 | 26.6 | 20.6 | 11.2 | 15.8 |
| | p | 0.99 | | 0.94 | | 0.73 | |
| $R_d(298)$ [$\mu\text{mol m}^{-2} \text{s}^{-1}$] | M | 1.1 | 0.9 | 0.7 | 1.2 | 1.4 | 1.6 |
| | I_{50} | 1.0 | 0.5 | 0.6 | 0.7 | 0.4 | 0.4 |
| | p | 0.72 | | 0.01 | | 0.11 | |
| g_0 [$\text{mmol m}^{-2} \text{s}^{-1}$] | M | 5.0 | 5.0 | 1.0 | 1.0 | 1.0 | 1.0 |
| | I_{50} | 1.0 | 1.0 | 0 | 0 | 0 | 0 |
| | p | 1 | | 1 | | 1 | |
| a_1 [mol mol^{-1}] | M | 5.06 | 4.97 | 4.96 | 4.94 | 5.17 | 5.05 |
| | I_{50} | 2.43 | 2.03 | 1.81 | 1.33 | 0.46 | 1.03 |
| | p | 0.98 | | 0.99 | | 0.95 | |
| D_0 [kPa] | M | 1.2 | 1.2 | 1.2 | 1.2 | 1.2 | 1.2 |

M : median of single leaf measurements, I_{50} : interquartile range, p : significance level for the U-Test. All measurements were carried out with: PPFD > 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $T_{\text{leaf}}=25^\circ\text{C}$, VPD=1.4 kPa. Variation in A_n and g_s was due to a change in C_a .


Fig. 2: Nitrogen dependence of V_{cmax} and J_{max} .

The measured leaves indicate a high variability within the canopy, which explains the large values of the interquartile range in Tab. 1. This variability could be resolved by setting the derived parameters in relation to the total leaf nitrogen. The derived parameters V_{cmax} and J_{max} show a strong linear correlation with the leaf nitrogen level (Fig. 2). The slopes and the y-intercepts of these of these relationships are given in Tab. 2

V_{cmax} and J_{max} change with leaf temperature according to eqn. 6 and eqn. 7 (Fig. 3). The parameter values of the temperature dependencies are summarised in Tab. 3. There was no significant difference between the parameter values of the two CO₂ growth concentrations. Increasing the CO₂ growth concentration had therefore no significant effect on the temperature response.

The semi-empirical model of stomatal conductance used in this study successfully describes the response of stomata of beech saplings to variations in the assimilation rate and external CO₂ concentration with high probability ($R^2 > 0.7$, Fig. 4) The parameters of the conductance model show no significant difference between the two CO₂ growth concentrations (Tab. 2).

Tab. 3: Parameters derived from measurements

| | ambient CO ₂ | elevated CO ₂ | regression to both data sets | units |
|-----------------|----------------------------|-----------------------------|---------------------------------|--------------------------------------|
| $R_d(298)$ | 0.88 | 1.17 | 0.99 | $\mu\text{mol m}^{-2} \text{s}^{-1}$ |
| $H_a(R_d)$ | 27000 | 27800 | 26500 | J mol^{-1} |
| $V_{cmax}(298)$ | 27.2 | 25.1 | 26.3 | $\mu\text{mol m}^{-2} \text{s}^{-1}$ |
| $H_a(V_{cmax})$ | 33038 | 33087 | 31584 | J mol^{-1} |
| $J_{max}(298)$ | 41.1 | 39.18 | 40.2 | $\mu\text{mol m}^{-2} \text{s}^{-1}$ |
| $H_a(J_{max})$ | 28300 | 44100 | 33700 | J mol^{-1} |
| $H_d(J_{max})$ | 573000 | 594000 | 654000 | J mol^{-1} |
| $dS(J_{max})$ | 1851 | 1923 | 2113 | J mol^{-1} |
| $V_{cmax}a$ | -1.8 | -1.8 | - | $\text{mmol m}^{-2} \text{s}^{-1}$ |
| $V_{cmax}b$ | 33.3 | 34.2 | - | $\text{mmol g}^{-1} \text{s}^{-1}$ |
| $J_{max}a$ | -7.4 | -11.3 | - | $\text{mmol m}^{-2} \text{s}^{-1}$ |
| $J_{max}b$ | 54.9 | 65.3 | - | $\text{mmol g}^{-1} \text{s}^{-1}$ |

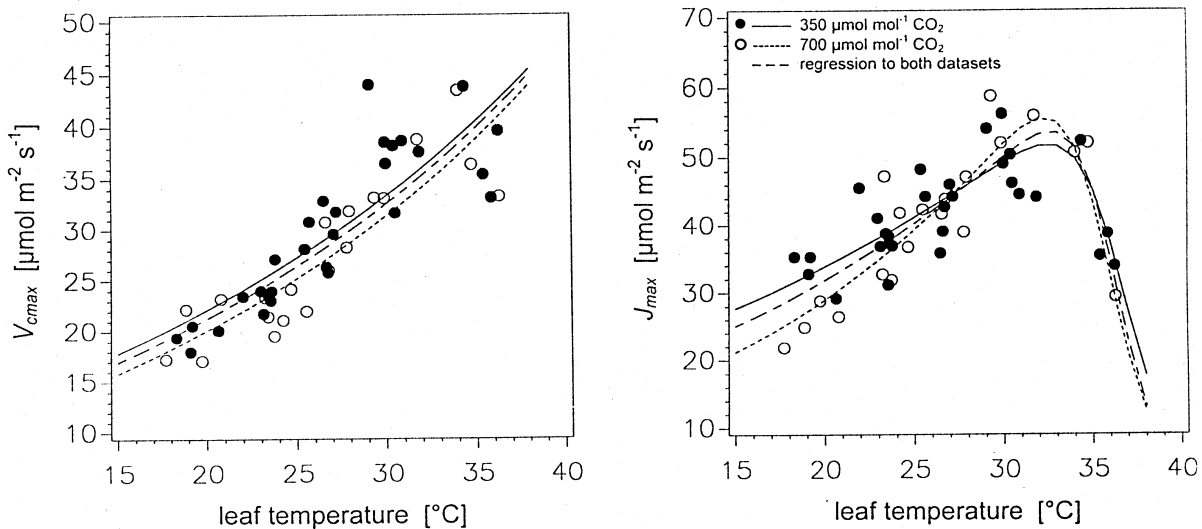


Fig. 3: Temperature dependence of V_{cmax} and J_{max} .

Discussion

We found no adjustment of the photosynthesis apparatus to the elevated CO_2 concentration. Neither V_{cmax} nor J_{max} showed a significant difference between the two CO_2 treatments in any year or at any temperature level. No acclimation of the photosynthesis apparatus to high CO_2 concentrations could be found in other long term CO_2 experiments on woody plants. (GUNDERSON & al. 1993, HARLEY & al. 1992). On the other hand the derived model parameters exhibit a wide variability which characterises the photosynthetic capacity of the foliage area (FORSTREUTER 1996, STRASSEMAYER & al. 1997). We propose that this variability in physiological properties can be explained with the varying light climate in the canopy. In former studies a relationship of SLA to canopy depth (FORSTREUTER 1995, GUTSCHICK & WIEGEL 1988) and of SLA to leaf nitrogen could be demonstrated (FORSTREUTER, personal communication). These results indicate that both SLA and leaf nitrogen are determined by the position of the leaf in the canopy and therefore by the light climate, which the leaf had been exposed to in the canopy. A decrease of leaf nitrogen content with the canopy depth was also found in studies of LEUNING & al. (1991) and CHEN & al. (1992). Considering these relationships SLA or leaf nitrogen should correlate with the estimated model parameters. In confirmation of our assumptions we found a linear relationship of V_{cmax} and J_{max} to leaf nitrogen and an exponential relationship to SLA. These results are in accordance with the studies of HARLEY & al. (1992) and HARLEY & BALDOCCHI (1995) who also expressed V_{cmax} and J_{max} as a function of leaf nitrogen content.

Canopy photosynthesis models need to incorporate such relationships characterising the partitioning factors (e.g. nitrogen allocation). The recognition that adjustments of the canopy structure to elevated CO_2 rather than adjustments of leaf photosynthesis, indicates the importance of ecophysiological studies in canopies at changing environmental conditions.

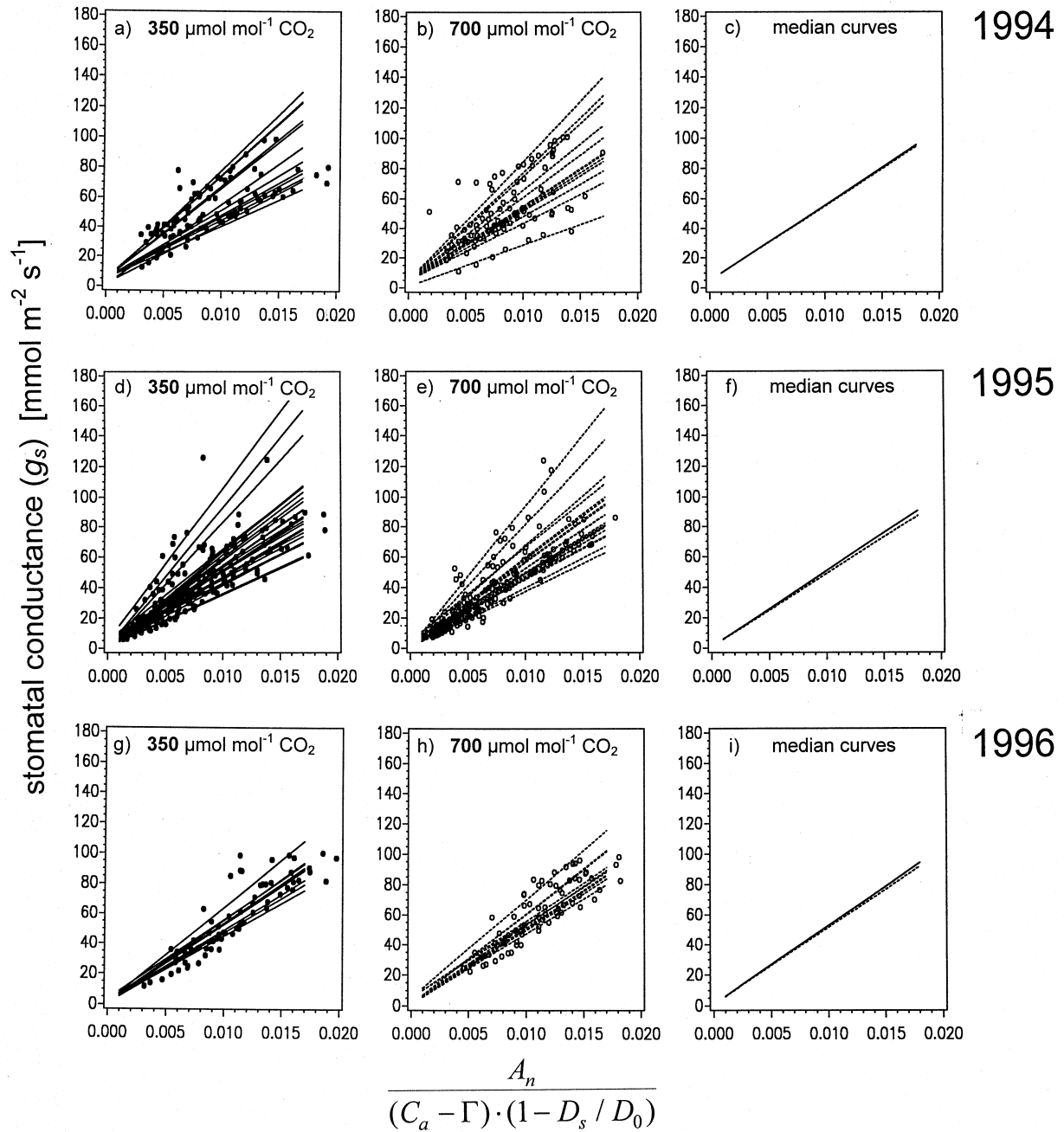


Fig. 4: Test of the conductance model (BALL et al.1987, LEUNING 1995) in 1994 (a-c), 1995 (d-e) and 1996 (g-i). Single leaf measurements and regression models at $350 \mu\text{mol mol}^{-1}$ (a, d, g, — ●) and $700 \mu\text{mol mol}^{-1}$ CO_2 growth concentration (b, e, h, ---- ○). Median of the regression models (c, f, i).

Acknowledgement

This work was supported by the EU Project ECOCRAFT (EV 50 CT92-0127) and the Deutsche Forschungsgemeinschaft.

Literature

- BADGER, M.R. & COLLATZ, 1977: Studies on the kinetic mechanism of ribulose-1,5-bisphosphate carboxylase and oxygenase reactions, with particular reference to the effect of temperature on kinetic parameters. - Carnegie Inst. Washington Yearb. 76, 355-361.
- BALL, J.T., WOODROW, I.E. & BERRY, J.A., 1987: A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: BIGGINS, I. (ed.), Progress in photosynthesis research, Vol. IV. Proceedings of the VII International Congress on Photosynthesis. - Martinus Nijhoff, Dordrecht, pp 221-224.
- CEULEMANS, R. & MOUSSEAU, M., 1994: Tansley review No. 71. Effects of elevated atmospheric CO₂ on woody plants. - New Phytol. 127: 425-446.
- CHEN J.L., REYNOLDS J.F., HARLEY P.C. & TENHUNEN J.D., 1993: Coordination theory of leaf nitrogen distribution in a canopy. - Oecologia: 93, 63-69.
- CURE, J.D. & ACOCK, B., 1986: Crop responses to carbon dioxide doubling: A literature survey. - Agricultural Forest Meteorology 38: 127-145.
- EAMUS, D. & JARVIS, P.G., 1989: The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. - Adv. Ecol. Res. 19: 1-15.
- FARQUHAR G.D. & VON CAEMMERER S., 1982: Modelling of photosynthetic response to environmental conditions. In: LANGE O.L, NOBEL P.S., OSMOND C.B., ZIEGLER H. (eds.): Encyclopedia of Plant Physiology, N.S. 12A. - Springer-Verlag, Berlin, pp. 550-587.
- FARQUHAR, G.D., VON CEAMMERER, S. & BERRY, J.A., 1980: A biochemical model of photosynthetic CO₂ fixation in C₃ species. - Planta 149: 178-190.
- FORSTREUTER, M., 1995: Bestandesstruktur und Netto-Photosynthese von jungen Buchen (*Fagus sylvatica* L.) unter erhöhter CO₂-Konzentration. - Verh. Ges. Ökol. 24: 283-292.
- FORSTREUTER, M., 1996: CO₂-Abhängigkeit (CO₂/H₂O) von jungen Buchenbeständen (*Fagus sylvatica* L.) nach Langzeitbegasung bei 350 und 700 µmol mol⁻¹. Verh. Ges. Ökol. - 26: 629-636.
- FORSTREUTER, M., TSCHUSCHKE, A. & OVERDIECK, D., 1994: Atmospheric CO₂ record from Osnabrück. In: BODEN, T.A, KAISER, D.P., STEPANSKI, R.J & STOSS, F.W (eds.), Trends' 93: A compendium of data on global change. ORNL/CDIAC-65. - Carbon Dioxide Information Analysis Center, Oak Ridge, U.S.A.: 157-160.
- GODELEWSKI, E., 1873: Abhängigkeit der Sauerstoffausscheidung der Blätter von dem Kohlensäuregehalt der Luft. - Arbeiten des Botanischen Instituts in Würzburg, Leipzig, Bd. I Heft 3: 343-370.

- GUNDERSON, C.A., NORBY, R.J. & WULLSCHLEGER, S.D., 1993: Foliar gas exchange responses of two deciduous hardwoods during 3 years of growth in elevated CO₂: No loss of photosynthetic enhancement. - *Plant Cell Environ.* 16(7): 797-807.
- GUTSCHICK, V.P. & WIEGEL, T.J., 1988: Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. - *American Naturalist*: 132, 67-86.
- HARLEY, P.C. & BALDOCCHI, D.D., 1995: Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. I. Leaf model parameterization. - *Plant Cell Environ.* 18: 1146-1156.
- HARLEY, P.C., THOMAS, R.B., REYNOLDS, J.F. & STRAIN, B.R., 1992: Modelling photosynthesis of cotton grown in elevated CO₂. - *Plant Cell Environ.* 15: 271-282.
- HOUGHTON, J.T., JENKINS, G.J. & EPHRAUNS, J.J., (eds.), 1990: *Climate Change. The IPCC scientific assesment.* - Cambridge University Press, Cambridge 7(3): 611-617.
- JORDAN, D.B. & OGREN, W.L., 1984: The CO₂/O₂ specificity of ribulose-1,5-bisphosphate concentration, pH and temperature. - *Planta* 161: 308-313.
- KEELING, C.D. & WHORF, T.P., 1994: Atmospheric CO₂ records from sites in the SIO air sampling network. In: BODEN, T.A., KAISER, D.P., STEPANSKI, R.J. & STOSS, F.W. (eds.), *Trends' 93: A compendium of data on global change.* ORNL/CDIAC-65. - Carbon Dioxide Information Analysis Center, Oak Ridge, U.S.A.: 16-26.
- LEUNING, R., CROMER, R.N. & RANCE, S., 1991: Spatial foilar nitrogen and phosphorous in crowns of *Eucalyptus grandis*. - *Oecologia*: 88, 504-510.
- LEUNING, R., 1995: A critical appraisal of a combined stomatal-photosynthesis model for C₃ plants. - *Plant Cell Environ.* 18: 339-335, 1995.
- NEFTEL, A., MOORE, E., OESCHGER, H. & STAUFFER, B., 1985: Evidence from polar ice cores for the increase in atmospheric CO₂ in the past two centuries. - *Nature* 315: 45-47.
- OVERDIECK, D., 1993: Effects of atmospheric CO₂ enrichment on CO₂ exchange rates of beech stands in small model ecosystems. - *Water Air and Soil Pollution* 70(1-4): 259-277.
- SAGE, R.F., 1994: Acclimation of photosynthesis to increasing atmospheric CO₂: The gas exchange perspective. - *Photosyn. Res.* 39: 351-368.
- SARIMENTO, J.L. & BENDER, M., 1994: Carbon biogeochemistry and climate change. - *Photosyn. Res.* 39: 209-234.
- SAS INSTITUTE, 1988: *SAS/STAT User's Guide, Release 6.03 Edition.* - Cray NC: 675-712.
- STRASSEMAYER, J., FORSTREUTER, M. & OVERDIECK, D., 1997: Temperatur und CO₂-Abhängigkeit von *Fagus sylvatica* L. nach Wachstum unter erhöhter atmosphärischer CO₂-Konzentration. - *Verh. Ges. Ökol.* 27: 303-309.
- VON CAEMMERER, S. & FARQUHAR, G.D., 1981: Some relationships between the biochemistry of photosynthesis and gas exchange in leaves. - *Planta* 153: 376-387.
- VON CAEMMERER, S., EVANS, J.R., HUDSON, G.S. & ANDREWS, T.J., 1994: The kinetic of ribulose-1,5-bisphosphate carboxylase/oxygenase in vivo inferred from

measurements of photosynthesis in leaves of transgenic tobacco. - *Planta* 195: 88-97.

WANG, Y.P. & 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, 1995.

Adresse der Autoren:

Dipl.-Biol. Jörn Strassemeier
Dr. Manfred Forstreuter
Technische Universität Berlin
Institut für Ökologie
Fachgebiet: Ökologie der Gehölze
Königin-Luise-Str. 22
D-14195 Berlin