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Stomatal conductance of forest species after long-term exposure to elevated CO_2 concentration: a synthesis

B. E. Medlyn[1,*], C. V. M. Barton[1], M. S. J. Broadmeadow[2], R. Ceulemans[3], P. De Angelis[4], M. Forstreuter[5], M. Freeman[6], S. B. Jackson[2], S. Kellomäki[7], E. Laitat[8], A. Rey[1], P. Roberntz[9], B. D. Sigurdsson[9,10], J. Strassemeyer[5], K. Wang[7], P. S. Curtis[11] and P. G. Jarvis[1]

[1]IERM, University of Edinburgh, King's Buildings, Edinburgh, UK; [2]Forestry Commission, Alice Holt Lodge, Farnham, Surrey, UK; [3]Department of Biology, University of Antwerpen, Wilrijk, Belgium; [4]DISAFRI, University of Tuscia, Viterbo, Italy; [5]Institut für Ökologie, Technische Universität Berlin, Germany; [6]Department of Economics and Natural Resources, Royal Veterinary and Agricultural University, Denmark; [7]Faculty of Forestry, University of Joensuu, Finland; [8]Department de Biologie Vegétalé, Faculte des Sciences Agronomiques de Gembloux, Belgium; [9]Department for Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden; [10]Agricultural Research Institute, Keldnaholt, Reykjavik, Iceland; [11]Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, OH, USA; *present address: School of Biological Science, University of New South Wales, UNSW Sydney 2052, Australia

Author for correspondence:
Belinda Medlyn
Tel: +61 29385 2213
Fax: +61 29385 1558
Email: B.Medlyn@unsw.edu.au

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Summary

• Data from 13 long-term (> 1 yr), field-based studies of the effects of elevated CO_2 concentration ([CO_2]) on European forest tree species were analysed using meta-analysis and modelling. Meta-analysis was used to determine mean responses across the data sets, and data were fitted to two commonly used models of stomatal conductance in order to explore response to environmental conditions and the relationship with assimilation.

• Meta-analysis indicated a significant decrease (21%) in stomatal conductance in response to growth in elevated [CO_2] across all studies. The response to [CO_2] was significantly stronger in young trees than old trees, in deciduous compared to coniferous trees, and in water stressed compared to nutrient stressed trees. No evidence of acclimation of stomatal conductance to elevated [CO_2] was found.

• Fits of data to the first model showed that growth in elevated [CO_2] did not alter the response of stomatal conductance to vapour pressure deficit, soil water content or atmospheric [CO_2]. Fits of data to the second model indicated that conductance and assimilation responded in parallel to elevated [CO_2] except when water was limiting.

• Data were compared to a previous meta-analysis and it was found that the response of g_s to elevated [CO_2] was much more consistent in long-term (> 1 yr) studies, emphasising the need for long-term elevated [CO_2] studies. By interpreting data in terms of models, the synthesis will aid future modelling studies of responses of forest trees to elevated [CO_2].

Key words: stomatal conductance, elevated [CO_2], meta-analysis, model parameters, forests, acclimation.

Introduction

It is well documented that stomatal conductance (g_s) declines when exposed to a transient increase in atmospheric CO_2 concentration; a doubling of [CO_2] from the present ambient concentration generally results in a reduction in g_s of the order of 40% (Morison, 1987). If this reduction in g_s should also occur in response to the current gradual increase in atmospheric [CO_2], there could be important implications for forest carbon and water balance (Field *et al.*, 1995). Using models based on the transient response of g_s to increasing [CO_2], it is generally predicted that forest canopy evapotranspiration is likely to be reduced, with a resulting increase in soil moisture, and possible consequences for a wide range of ecological processes

including run-off, production, soil mineralization, and regional climate change (Field *et al.*, 1995, Sellers *et al.*, 1996, Thornley & Cannell, 1996, Kellomäki & Vaisanen, 1997).

However, recent results have called into question whether longer-term exposure to elevated [CO_2] results in a similar reduction in stomatal conductance, particularly in woody species (Saxe *et al.*, 1998, Mooney *et al.*, 1999). For example, in a meta-analysis of 48 studies with woody plants, Curtis and Wang (1998) report a modest and nonsignificant reduction of just 11% in response to growth in elevated [CO_2]. Many of the studies incorporated in Curtis and Wang's review were, however, relatively short-term (< 1 yr), pot-based studies. Mature, field-grown trees are subject to extremely different environmental conditions and constraints, and therefore may not respond in the same way as pot-grown seedlings (Norby *et al.*, 1999). Thus, the first aim of this paper is to apply the meta-analysis approach of Curtis & Wang (1998) to examine how stomatal conductance changes in field-grown trees after several years' exposure to elevated [CO_2].

The second aim is to interpret the stomatal conductance data in terms of the models commonly used to extrapolate from leaf g_s responses to stand scale. To predict effects of elevated [CO_2] on stand carbon and water balance it is not enough to know the average effect of elevated [CO_2] on stomatal conductance; we also need to know how to incorporate that effect in models. Currently, there are two main models used to describe stomatal conductance. The first, proposed by Jarvis (1976), is based on empirical stomatal responses to environmental conditions including incident radiation, vapour pressure deficit (VPD), temperature, soil water potential, and atmospheric [CO_2]. These empirical responses may be altered in plants grown in elevated [CO_2]. For example, growth in elevated [CO_2] has been observed to cause reduced sensitivity of g_s to VPD (Heath, 1998), reduced sensitivity to drought (Heath & Kerstiens, 1997), and reduced sensitivity to atmospheric [CO_2] (Santrucek & Sage, 1996). Here, we investigate how the sensitivity of g_s to environmental conditions changed under elevated [CO_2] by fitting the Jarvis (1976) model to a range of data sets.

The second commonly used model of stomatal conductance (Ball *et al.*, 1987) is based on the observed correlation between stomatal conductance and assimilation (Wong *et al.*, 1978). Assimilation rates are often observed to acclimate to growth in high [CO_2] (Medlyn *et al.*, 1999) and many models assume implicitly that stomatal conductance acclimates in parallel, based on the Ball *et al.* (1987) function (Sellers *et al.*, 1996). The question of whether assimilation and g_s acclimate to elevated [CO_2] in parallel or independently is only just beginning to be tackled (Morison, 1998). In order to address this question, Drake *et al.* (1997) examined the Ci : Ca ratio (intercellular : atmospheric [CO_2]) and reported that there was no change in this ratio overall, suggesting that g_s and assimilation do acclimate in tandem. However, as noted by Santrucek & Sage (1996), this ratio is not a very sensitive indicator. In this paper, we address this problem by fitting the Ball *et al.* (1987) model to a range of experimental data sets, and observing whether the parameters of this model change in response to elevated [CO_2].

Materials and Methods

Measurements

The experimental data were obtained from experiments carried out under the auspices of two major European collaborative programmes: ECOCRAFT (Jarvis, 1998) and the Nordic Research Project 'The Likely Impact of Rising CO_2 and Temperature on Nordic Forests at Limiting and Optimal Nutrient Supply' (Roberntz *et al.*, Sigurdsson *et al.*, unpublished). Brief details of the experiments involved are given in Table 1. More information on the design of each experiment may be found in Pontailler *et al.* (1998) or in the individual references given in Table 2. The experiments differed in a number of ways. They used 15 different European forest tree species, including the most important commercial forestry species. Four main types of CO_2 exposure facilities were employed: branch bags (BB), open-top chambers (OTC), whole-tree chambers (WTC) and mini-ecosystems (ME). Some experiments also included nutrient, drought, temperature, or ozone factorial treatments. However, there were two factors common to all experiments: they were all done on freely rooted plants, and all continued for at least two growing seasons. In what follows, individual experiments will be referred to by the experiment names given in Table 1.

Brief details of the measurements of stomatal conductance are given in Table 2. Most measurements were made using gas exchange equipment, although porometers were also used in the English Mixed OTC experiment. Only data where stomata were given enough time to equilibrate with measurement conditions were included. Data from high-ozone treatments were also excluded from the analysis.

Statistical analysis

Meta-analysis was used to estimate the mean ratio of stomatal conductance of plants grown in elevated (700 μmol mol^{-1}) to that of plants grown in ambient (350 μmol mol^{-1}) [CO_2] (the E/A ratio). The meta-analysis techniques used are those described by Curtis & Wang (1998) and implemented in the statistical software MetaWin (Rosenberg *et al.*, 1997). The mean, standard deviation, and number of observations for each parameter value were required. The standard deviation was taken to be the between-chamber standard deviation, and the number of observations was taken as the number of chamber replicates. The standard deviation is used in the meta-analysis to weight each observation. Some observations in the dataset had no corresponding standard deviation because there was only one chamber replicate. These observations were included conservatively, by assigning to them the smallest of the weights of the other experiments. In order to satisfy the requirement

Table 1 Details of experiments from which stomatal conductance data were obtained

Experiment Name	Site Name, Institution[1]	Lat.	Long.	Species	Stress	Additional factors	Initial age (yr)	Length of exposure[2] (yr)	Stocking[3]	No. of Replicates
Branch bags										
Denmark *Fagus* BB	Grib Skov, RVAU	55°59′N	12°16′E	*Fagus sylvatica*	None		36	2	800	8
Scotland *Picea* BB	Glencorse, UE	55°31′N	3°12′W	*Picea sitchensis*	Nutrient		16	4	1600	6
Sweden *Picea* BB	Flakaliden, SLU	64°07′N	19°27′E	*Picea abies*	Nutrient, None	Nutrition	29	3.5	2400	6
Open-top chambers										
Belgium *Picea* OTC	Vielsalm, FUSAG	50°17′N	5°55′E	*Picea abies*	Nutrient, None	Nutrition	11	9	14	2
Belgium *Populus* OTC	UIA Campus, UIA	51°10′N	4°24′E	*Populus* cv. Robusta, *Populus* cv. Beaupre	None		0	3	15	2
England Mixed OTC	Headley, FC	52°08′N	00°50′W	*Quercus petraea, Fraxinus excelsior*	Water, None	Water, Ozone[4]	2	3	16	2
England *Quercus* OTC	Headley, FC	52°08′N	00°50′W	*Quercus petraea, Quercus robur* *Quercus rubra*	None	Ozone[4]	1	2	36	4
Finland *Pinus* OTC	Mekrijärvi, JOY	62°41′N	30°57′E	*Pinus sylvestris*	Nutrient	Temperature	20	4	1	4
Italy *Macchia* OTC	Montalto di Castro, UVT	42°22′N	11°32′E	*Quercus ilex, Pistacia lentiscus,* *Phillyrea angustifolia*	Water		30	6	13	3
Scotland *Betula* OTC	Glencorse, UE	55°31′N	3°12′W	*Betula pendula*	Nutrient		0	4	1	6
Mini-ecosystems										
Germany *Fagus* ME	TUB Campus, TUB	52°28′N	13°18′E	*Fagus sylvatica*	None		1	4	25	1
Germany *Quercus* ME	TUB Campus , TUB	52°28′N	13°18′E	*Quercus robur*	None		1	3	16	1
Whole-tree chambers										
Iceland *Populus* WTC	Gunnarsholt, ARI	63°51′N	20°13′W	*Populus trichocarpa*	Nutrient, None	Nutrition	4	3	1	4

Notes: (1) Institution Codes: ARI, Icelandic Agricultural Research Institute; FC, U.K. Forestry Commission Research Agency; FUSAG, Faculté Universitaire des Sciences Agronomiques de Gembloux; JOY, University of Joensuu; RVAU, Royal Veterinary and Agricultural University; SLU, Swedish University of Agricultural Sciences; TUB, Technical University of Berlin; UE, University of Edinburgh; UIA, Universitaire Instelling Antwerpen; UPS, Universite de Paris-Sud; UVT, University of Viterbo. (2) Length of exposure in growing seasons. (3) Stocking is in stems ha^{-1} for branch bag experiments, otherwise in plants per chamber. (4) Values from plants exposed to elevated ozone were omitted from this review.

Table 2 Details of stomatal conductance measurements from which data were obtained

Experiment Name	Equipment	Field/Lab	Climatic Conditions	Sampling	References
Branch bags					
Denmark *Fagus* BB	Ciras-1 (PP Systems)	Field	Light saturation. ambient T (23–30°C). Ambient VPD (1.7–3.2 kPa). Growth [CO_2]	Three leaves from each branch. (Branches in mid-canopy)	Freeman (1998)
Scotland *Picea* BB	ADC LCA3 + light source	Field	Light saturation. Ambient T (18–35°C). Ambient VPD (0.7–3.1 kPa). Growth [CO_2]	One shoot of each age class. (Branches of 3rd whorl)	Barton & Jarvis (1999)
Sweden *Picea* BB	Li-Cor 6200	Field	Light saturation. Ambient T (5–24°C). Ambient VPD (0–1.1 kPa). Growth [CO_2]	Current shoots. (Branches in mid-canopy)	Roberntz & Stockfors (1998)
Open-top chambers					
Belgium *Picea* OTC	Binos 100 IRGA	Field	Light saturation (> 800 μmol m^{-2} s^{-1}). T (15–20°C). VPD: < 1.0 kPa. Growth [CO_2].	Randomly sampled.	Laitat *et al.* (2000)
Belgium *Populus* OTC	ADC-LCA3	Field	Light saturation. T: 25–30°C. rh: 30–50%. Growth and reciprocal [CO_2].	2 or 3 ramets per clone.	Will & Ceulemans (1997)
England Mixed OTC	Delta-T AP4 porometer	Field	Ambient PAR (25–1100 μmol m^{-2} s^{-1}). Ambient T (20–35°C). Ambient VPD (0–4 kPa). Growth [CO_2]	Youngest fully expanded mature leaves sampled from top of canopy growing in full sun.	Broadmeadow & Jackson (2000)
England *Quercus* OTC	ADC-LCA3	Field	Ambient PAR (25–1200 μmol m^{-2} s^{-1}). Ambient T (10–34°C). Ambient VPD (0–4 kPa). Growth [CO_2]	Youngest fully expanded mature leaves sampled from top of canopy growing in full sun.	unpublished
Finland *Pinus* OTC	ADC-LCA4	Lab	T: 7.0–33.0°C. PAR: 50–1400 μmol m^{-2} s^{-1} [CO2]: 20–1400 μmol mol^{-1}. VPD: 0.3–2.0 kPa.	Current shoot from second whorl.	Kellomäki & Wang (1996)
Italy *Macchia* OTC	ADC-LCA4	Field	Ambient PAR. Ambient T (25–38°C). Ambient VPD (0–6 kPa). Growth [CO_2].	Five to 10 sun leaves for each species.	Scarascia-Mugnozza *et al.* (1996)
Scotland *Betula* OTC	Li-Cor 6200 + home-made light source	Field	Light saturation. Ambient T (20–30°C). Ambient VPD (0.8–3.0 kPa). Growth [CO_2]	Three leaves per tree from the middle-bottom crown.	Rey & Jarvis (1998)
Mini-ecosystems					
Germany *Fagus* ME	Walz CMS-400	Field	Light saturation. T (25°C). VPD (1.3 kPa). Eight [CO_2].	Range of canopy depths.	Strassemeyer & Forstreuter (1998)
Germany *Quercus* ME	Walz CMS-400	Field	Light saturation. T (25°C). VPD (1.3 kPa). Eight [CO_2].	Range of canopy depths.	unpublished
Whole-tree chambers					
Iceland *Populus* WTC	Li-Cor 6200 + QB6200 light source	Field	Light saturation. Ambient T (2–20°C). Ambient VPD (0.1–0.9 kPa). Growth and reciprocal [CO_2]	Youngest fully expanded sun leaves.	Sigurdsson *et al.* (2001)

VPD, Vapour pressure deficit; T, temperature.

Table 3 Mean values of stomatal conductance to water vapour at ambient and elevated [CO_2] taken from experiments listed in Table 1

Species	Date	Treatment	Treatment	Ambient SD	*n*	Mean	Elevated SD	*n*	E : A
CONIFERS									
Sweden *Picea* BB									
Picea abies	1994	Unfert.	107	20.1	5	91	29.8	5	0.85
Picea abies	1994	Fert.	103	8.6	4	107	38.9	4	1.04
*Picea abies**	1995	Unfert.	134	22.6	6	126	24.4	6	0.94
*Picea abies**	1995	Fert.	157	20.9	6	149	45.1	6	0.95
Belgium *Picea* OTC									
Picea abies	Jul 96	Fert.	47		1	48		1	1.01
Picea abies	Jul 96	Unfert.	75		1	53		1	0.70
*Picea abies**	Aug 97	Fert.	101		1	104		1	1.03
*Picea abies**	Aug 97	Unfert.	126		1	82		1	0.66
Scotland *Picea* BB		Needle age[1]							
Picea sitchensis	13/7/93	C + 1	75	28.1	6	30	3.4	3	0.40
Picea sitchensis	22/7/93	C + 1	77	52.1	4	74	57.1	4	0.96
Picea sitchensis	10/8/93	C + 1	89	56.3	5	56	28.7	5	0.64
Picea sitchensis	24/8/93	C + 1	79	34.6	6	56	35.7	6	0.71
Picea sitchensis	28/9/93	C + 1	93	38.8	6	47	25.5	6	0.50
Picea sitchensis	12/7/93	C	143	40.4	6	108	42.3	6	0.76
Picea sitchensis	22/7/93	C	117	51.8	4	124	35.5	3	1.05
Picea sitchensis	10/8/93	C	112	32.8	5	120	74.1	5	1.07
*Picea sitchensis**	24/8/93	C	98	30.9	6	94	39.6	6	0.96
Picea sitchensis	28/9/93	C	67	26.2	6	73	45.6	6	1.10
Finland *Pinus* OTC									
*Pinus sylvestris**	1994	Amb. T	145	10.6	4	121	10.4	4	0.84
*Pinus sylvestris**	1994	Elev. T	152	8.7	4	142	9.3	4	0.94
BROADLEAF EVERGREEN									
Italy *Macchia* OTC									
Measurements at low VPD (1 kPa)									
*Quercus ilex**	Jun 94		153	53.0	2	135	0.0	2	0.89
*Pistacia lentiscus**	Jun 94		305	14.1	2	183	102.5	2	0.60
*Phillyrea angustifolia**	Jun 94		234	1.8	2	188		1	0.80
Measurements at normal VPD (2–4 kPa)									
Quercus ilex	Jun 94		47	3.8	3	44	7.1	3	0.93
Pistacia lentiscus	Jun 94		105	28.5	3	59	5.0	3	0.56
Phillyrea angustifolia	Jun 94		103	10.3	3	88	34.9	3	0.85
DECIDUOUS									
England Mixed OTC									
*Quercus petraea**	Jun 96	$+H_2O$	213	47.5	2	156	37.5	2	0.73
*Quercus petraea**	Jun 96	$-H_2O$	152	19.6	2	99	23.7	2	0.65
*Fraxinus excelsior**	Jun 96	$+H_2O$	185	59.4	2	99	11.3	2	0.54
*Fraxinus excelsior**	Jun 96	$-H_2O$	68	4.9	2	44	6.3	2	0.65
England *Quercus* OTC									
*Quercus petraea**	Aug 98		175	4.6	4	122	27.0	4	0.70
*Quercus robur**	Aug 98		180	49.3	4	99	17.9	4	0.55
*Quercus rubra**	Aug 98		108	1.8	4	67	15.6	4	0.62
Germany *Quercus* ME									
Quercus robur	Aug 96		131		1	96		1	0.73
Quercus robur	Aug 97		116		1	102		1	0.87
Quercus robur*	Aug 98		80		1	51		1	0.63
Scotland *Betula* OTC									
Betula pendula	Jun 94		289	202.6	5	193	155.6	5	0.67
Betula pendula	Jul 94		279	102.4	6	235	136.0	5	0.84
*Betula pendula**	Aug 94		220	65.9	6	167	78.9	6	0.76
Betula pendula	Sept 94		177	39.3	6	103	24.3	6	0.58
Belgium *Populus* OTC									
Populus cv. Beaupré	May 95		214	18.4	2	200	2.3	2	0.94
Populus cv. Beaupré*	Aug 95		244	10.0	2	222	24.9	2	0.91
Populus cv. Robusta	May 95		231	3.3	2	203	7.9	2	0.88
Populus cv. Robusta*	Aug 95		243	9.0	2	217	41.5	2	0.89

Table 3 *continued*

Species	Date	Treatment	Treatment	Ambient SD	*n*	Mean	Elevated SD	*n*	E : A
Iceland *Populus* WTC									
Populus trichocarpa	15/6/96	Unfert.	143	43.2	4	153	9.6	4	1.07
Populus trichocarpa	15/7/96	Unfert.	239	89.0	4	260	21.6	4	1.09
*Populus trichocarpa**	30/7/96	Unfert.	352	80.1	3	400	114.0	4	1.14
Populus trichocarpa	15/8/96	Unfert.	344	76.3	4	448	109.0	4	1.30
Populus trichocarpa	11/9/96	Unfert.	346	62.6	4	400	263.4	4	1.16
Populus trichocarpa	15/6/96	Fert.	239	105.9	4	150	48.5	4	0.63
Populus trichocarpa	15/7/96	Fert.	377	33.8	4	375	53.8	4	1.00
*Populus trichocarpa**	30/7/96	Fert.	555	145.4	4	493	106.1	4	0.89
Populus trichocarpa	15/8/96	Fert.	507	76.7	4	437	71.1	4	0.86
Populus trichocarpa	11/9/96	Fert.	589	77.0	4	512	116.3	4	0.87
Germany *Fagus* ME									
Fagus sylvatica	1994		88		1	67		1	0.76
Fagus sylvatica	1995		74		1	42		1	0.57
Fagus sylvatica	1996		91		1	78		1	0.86
*Fagus sylvatica**	1997		74		1	62		1	0.85
Denmark *Fagus* BB									
*Fagus sylvatica**	Jul 96		179	72.1	8	171	61.6	8	0.96

Values are given in mmol m^{-2} s^{-1}. For conifers, values are expressed on a projected leaf area basis. Values indicated with * were included in the meta-analysis. SD, standard deviation of replicates; n, number of replicate chambers in which g_s was measured; E : A, ratio of mean value at elevated [CO_2] to that at ambient [CO_2]. Note: (1) C, current-year needles.

that observations be independent, the observation made in mid-growing season in the final year of the experiment was used if more than one observation was available (Table 3). The meta-analysis was done on the natural logarithm of the response ratios, as described by Hedges *et al.* (1999). A mixed-model analysis was assumed (Gurevitch & Hedges, 1993). Further details of the meta-analysis procedure are given by Medlyn *et al.* (1999).

Meta-analysis was first used to compare the results from the data set compiled here with that compiled by Curtis & Wang (1998), by combining the two data sets. We then performed a meta-analysis of long-term, field-based studies only; four of the studies considered by Curtis & Wang (1998) fitted these criteria and hence were retained in the data set for this meta-analysis. These four studies were on *Liriodendron tulipifera* and *Quercus alba* (Gunderson *et al.*, 1993), *Maranthes corymbosa* (Eamus *et al.* 1995) and *Pinus taeda* (Liu & Teskey, 1995).

In addition to the statistical meta-analysis, data were fitted where possible to one or both stomatal conductance models (Jarvis, 1976, Ball *et al.*, 1987). The Jarvis (1976) model expresses stomatal conductance as a multiplicative combination of responses to several environmental factors, for example:

$$g_s = g_{smax}\, f_1\,(C_a)\, f_2\,(D)\, f_3\,(T)\, f_4\,(I)\, f_5\,(\psi) \qquad \text{Eqn 1}$$

(g_{smax}, the maximum value of stomatal conductance under optimal environmental conditions; $f_1 \ldots f_5$, functions ranging from 0 to 1; C_a, atmospheric [CO_2] (μmol mol^{-1}); D, leaf to air vapour pressure deficit (kPa); T, leaf temperature (°C); I, incident PAR (μmol m^{-2} s^{-1}); ψ, soil water potential (MPa).)

The derivation of all parameters of this model requires measurements of g_s under varying conditions of all variables, and the variables should not be correlated (Jarvis, 1976). Such datasets are difficult to obtain in practice; in most cases the datasets we had available included responses to only one or two of these variables. Thus, in place of the full model, we individually fitted as many of the functions $f_1 \ldots f_5$ as possible to each dataset.

We also fitted the Ball *et al.* (1987) model, which relates stomatal conductance to assimilation as follows:

$$g_s = g_0 + g_1\, A_n\, h_s/C_a \qquad \text{Eqn 2}$$

(A_n, the net assimilation rate (μmol m^{-2} s^{-1}); h_s, the relative humidity at the leaf surface; g_0 and g_1, the parameters to be fitted.) All model fits were performed using SigmaPlot for Windows Version 5.0 (SPSS Inc.). Stomatal conductance parameters obtained were stored for future reference in the ECOCRAFT parameter database (Medlyn & Jarvis, 1999).

Results

Meta-analysis

Response of stomatal conductance to growth in elevated [CO_2] The mean values of stomatal conductance under ambient and elevated [CO_2] from each experiment in the Ecocraft/Nordic data set are given in Table 3. Meta-analysis was used to calculate the mean effect of [CO_2] on stomatal conductance from these values (Table 4). A significant reduction

Table 4 Output from the meta-analysis of the effect of growth in elevated [CO_2] on mean stomatal conductance, measured at the growth [CO_2] concentration. For each category, the estimate of the mean E : A ratio (value in elevated [CO_2] : value in ambient [CO_2]) and the 95% confidence interval on this ratio is given. *n*, number of observations in each category, and *P*, probability that response was different among the categories. *indicates probability significant at the 5% level.

	Mean Response	95% CI	*n*	*P*
All experiments	0.86	0.78–0.96	74	
Comparison with Curtis & Wang (1998)				
ECOCRAFT/Nordic experiments	0.79	0.67–0.95	25	
Curtis & Wang (1998)	0.90	0.79–1.03	49	0.24
Pot vs field based				
Pot-grown	0.84	0.74–0.97	40	
Freely rooted	0.89	0.75–1.04	34	0.63
Length of experiment				
< 1 yr	0.95	0.83–1.09	42	
> 1 yr	0.77	0.66–0.90	32	0.05*
Long-term, field-based experiments only				
Tree age				
Mature (> 10 yr)	0.91	0.82–1.02	10	
Young (< 10 yr)	0.75	0.69–0.82	19	0.01*
Functional group				
Coniferous	0.92	0.81–1.03	8	
Broadleaf evergreen	0.79	0.55–1.14	3	
Broadleaf deciduous	0.76	0.69–0.83	18	0.04*
Exposure facility				
Open-top chamber	0.76	0.69–0.83	20	
Branch bag	0.96	0.80–1.14	5	
Mini-ecosystem	0.76	0.56–1.04	2	
Whole-tree chamber	0.99	0.73–1.36	2	0.07
Stress				
Nutrient stress	0.90	0.79–1.03	7	
Water stress	0.69	0.56–0.86	5	
Unstressed	0.79	0.72–0.87	17	0.11

in g_s of 21% was found. By contrast, in the dataset compiled by Curtis & Wang (1998), there was a nonsignificant reduction in stomatal conductance of 10% in elevated [CO_2]. However, the probability that the mean responses in the two data setswere different was not significant ($P = 0.245$). To examine further the differences between the two datasets, we combined them and then tested for differences between pot-grown and freely rooted plants, and between short-term (< 1 yr) and long-term (> 1 yr) studies. As shown in Table 4, there was no significant difference in the [CO_2] effect on stomatal conductance between pot-grown and freely rooted plants. However, there was a difference between short-term and long-term studies. In studies of < 1 yr, there was no significant effect of [CO_2] on stomatal conductance, while in longer studies, there was a significant reduction of 23%.

Meta-analysis was also used to test for differences in stomatal response within the set of long-term, field-based experiments. There was a difference in response between functional groups of tree species, with the reduction in g_s being less for conifers than for deciduous species (Table 4). Responses were also found to differ between mature (> 10-yr-old) and young trees, with older trees showing a smaller response. However, there was a confounding effect with functional group, as most of the experiments with older plants were carried out on conifers. The test for differences in response between different types of exposure facility was not powerful because the majority of observations came from open-top chamber studies. There did appear to be a small difference between open-top chamber and branch-bag studies, with branch-bag studies showing a smaller reduction in g_s. This result is also confounded with other factors, however, since all the branch-bag studies were performed on mature trees. Finally, plants were also categorised according to stress level. Although the differences were not significant, there was a clear trend for the reduction in stomatal conductance in elevated [CO_2] to be greater when plants were water stressed, and less when plants were nutrient stressed.

Acclimation of stomatal conductance to growth in elevated [CO_2] Acclimation of photosynthesis to growth in elevated [CO_2] is commonly tested for by measuring photosynthesis of ambient- and elevated-[CO_2] grown plants at the same [CO_2] (e.g. Drake *et al.*, 1997, Curtis & Wang, 1998). However, a similar test for acclimation of stomatal conductance to growth in elevated [CO_2] is rarely performed. Here, we tested for acclimation by using meta-analysis to test whether stomatal conductance measured at 700 μmol mol^{-1} [CO_2] differed between treatments. Across the dataset compiled here, no significant effect of elevated [CO_2] on g_s at 700 μmol mol^{-1} [CO_2] was found (Table 5). This conclusion was unchanged when the database was expanded by including the data compiled by Curtis & Wang (1998). This result suggests that there was no acclimation of stomatal conductance to elevated [CO_2].

	Mean Response	95% CI	*n*	*P*
All experiments	0.94	0.84–1.05	21	
Comparison with Curtis & Wang (1998)				
ECOCRAFT/Nordic experiments	1.02	0.85–1.23	9	
Curtis & Wang, 1998	0.89	0.77–1.03	12	0.25

Table 5 Meta-analysis of the effect of growth in elevated [CO_2] on mean stomatal conductance, measured at a constant [CO_2] concentration (700 μmol mol^{-1}).

Experiment	Species/Treatment	Ambient [CO_2]	Elevated [CO_2]
Denmark *Fagus* BB		3.42 (0.60)	3.62 (0.34)
England Mixed OTC	Watered (*Q. robur*)	6.66 (0.99)	4.43 (0.41)
England Mixed OTC	Droughted (*Q. robur*)	5.75 (1.00)	5.95 (1.38)
Finland *Pinus* OTC	Ambient temperature	4.72 (0.38)	3.85 (0.26)
Finland *Pinus* OTC	Elevated temperature	7.30 (0.79)	6.29 (0.56)
Italy *Macchia* OTC	*Q. ilex*	8.56 (1.26)	7.92 (1.06)
Italy *Macchia* OTC	*P. angustifolia*	9.71 (5.61)	14.4 (5.34)
Scotland *Picea* BB	C + 1 needles[1]	4.00 (0.90)	3.64 (0.76)

Table 6 Values of D_0 (kPa), the Jarvis model parameter describing the response to VPD (eqn 5). The standard error is given in parentheses. [1]Needles from previous year.

The Jarvis (1976) model: Environmental effects on stomatal conductance

Response to vapour pressure deficit (VPD) For several of the datasets, the only independent variable to which stomatal conductance could be related was VPD. Light levels varied but did not appear to affect stomatal conductance, and temperature was highly correlated with VPD. The Finland *Pinus* OTC dataset, by contrast, included response curves of stomatal conductance to VPD with all other variables held constant. We chose to fit a simple linear response to VPD to ensure that the same model could be fitted to all data sets. The equation fitted (cf. eqn 1) was:

$$g_s = g_{smax}\,(1 - D/D_0) \qquad \text{Eqn 3}$$

(D_0, the value of VPD at which stomatal conductance becomes zero.)

We tested whether the response of g_s to VPD is affected by growth in elevated [CO_2], examining whether the parameter D_0 was altered between treatments. As a note of clarification: we chose to test for changes in D_0 rather than changes in the slope of the g_s-VPD response because it is well known that the slope is highly correlated with the magnitude of g_s at low VPD (e.g. Oren *et al.*, 1999), which is often reduced by growth in elevated [CO_2].

The values of D_0 found for each experiment are shown in Table 6, and the responses of g_s to VPD are illustrated in Fig. 1. The experiments included studies on mature conifers, mature beech, oak saplings, and water-stressed macchia species. In none of these experiments did the value of D_0 change significantly, indicating that the response of g_s to VPD is unaffected by growth in elevated [CO_2] for a wide range of environmental conditions and species.

Response to soil water content The response to soil water content was examined by comparing the watered and droughted low-ozone treatments in the England Mixed OTC experiment. A set of data with VPD < 1.0 kPa was used. Values from both irrigation treatments were combined to obtain a response of stomatal conductance to soil water content, shown in Fig. 2. To these responses the following simple model was fitted (cf. eqn 1):

$$g_s = g_{smax}\,(1 - \psi/\psi_0) \qquad \text{Eqn 4}$$

(ψ_0, the value of soil water potential (MPa) at which stomatal conductance becomes zero.) The parameter ψ_0 was examined to test whether sensitivity to soil water content changed in elevated [CO_2]. The values of this parameter are given in Table 7 and illustrate that, while sensitivity of g_s to soil water potential was much higher in *F. excelsior* than in *Q. robur*, there was no effect of growth [CO_2] on this sensitivity for either species.

Sensitivity to atmospheric [CO_2] The effect of long-term growth in elevated [CO_2] on stomatal conductance is indicated by the results of the meta-analysis (Table 4). However, one can also ask whether the sensitivity of stomata to transient changes in [CO_2] is affected by growth at elevated [CO_2]. To investigate this possibility, we utilised measurements of g_s made at ambient and doubled [CO_2] in both ambient and elevated [CO_2] treatments. To these data we fitted the linear model:

$$g_s = g_{smax}\,(1 - (1 - a)(C_a/350 - 1)) \qquad \text{Eqn 5}$$

(the parameter a, the fractional response in g_s to a doubling in [CO_2] from 350 to 700 μmol mol^{-1}, and is comparable to the E : A ratio obtained in the meta-analysis.) Values of this parameter are shown in Table 8. The sensitivity to [CO_2]

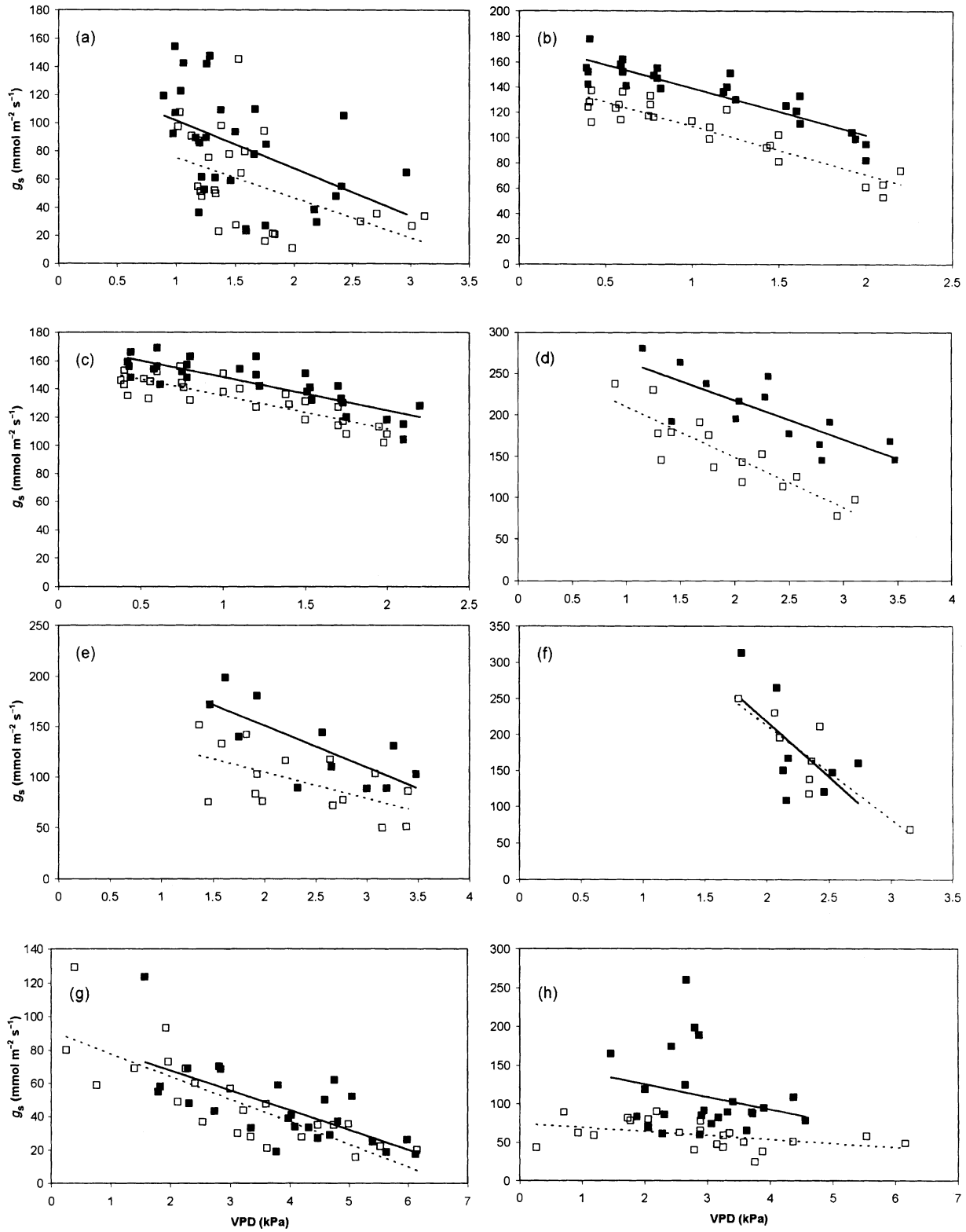

Fig. 1 Response of stomatal conductance to vapour pressure deficit (VPD). Closed squares, ambient [CO_2]; open squares, elevated [CO_2]. Solid and dotted lines show regressions fitted to ambient and elevated [CO_2] treatments, respectively. (a) Scotland *Picea* BB, C + 1 needles. (b) Finland *Pinus* OTC, ambient temperature treatment. (c) Finland *Pinus* OTC, elevated temperature treatment. (d) England Mixed OTC, *Quercus robur*, watered treatment. (e) England Mixed OTC, *Quercus robur*, droughted treatment. (f) Denmark *Fagus* BB. (g) Italy *Macchia* OTC, *Quercus ilex*. (h) Italy *Macchia* OTC, *Phillyrea angustifolia*.

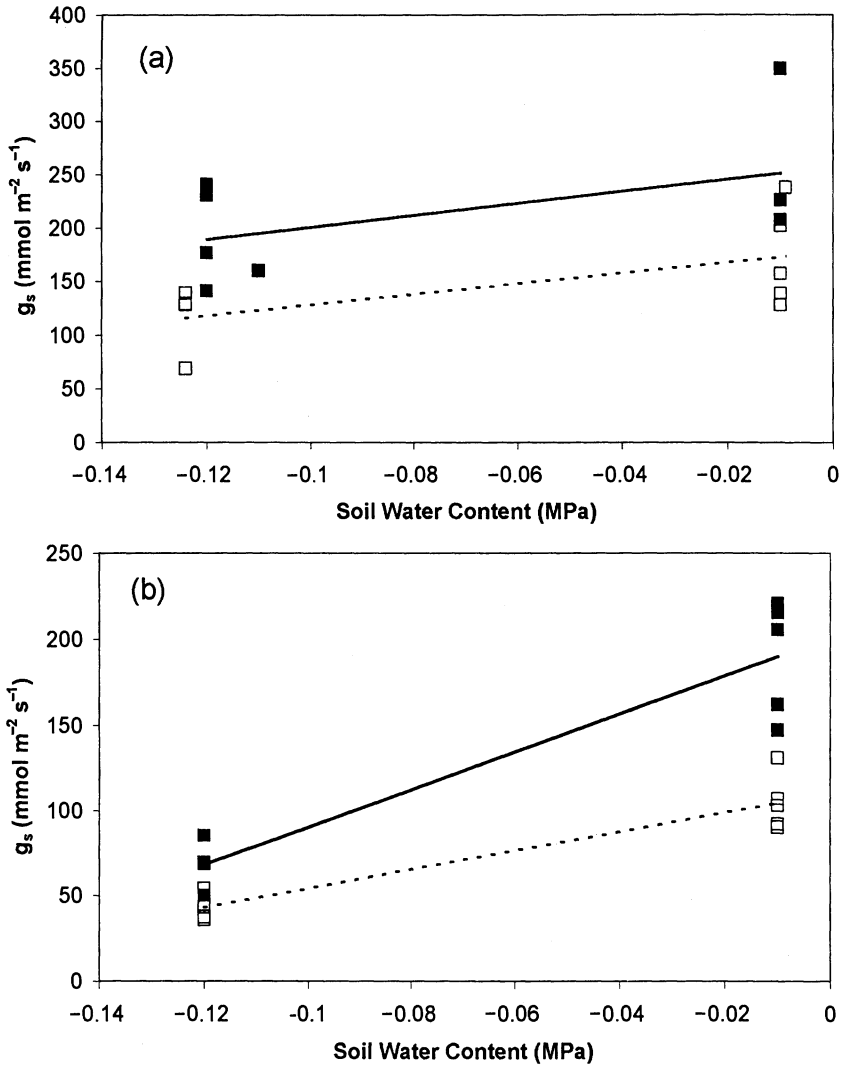

Fig. 2 Response of stomatal conductance to soil water potential. Closed squares: ambient [CO_2]; open squares: elevated [CO_2]. Solid and dotted lines show regressions fitted to ambient and elevated [CO_2] treatments, respectively. (a) England Mixed OTC, *Quercus robur*. (b) England Mixed OTC, *Fraxinus excelsior*.

over the range 350–700 μmol mol^{-1} in ambient conditions varied considerably between experiments. In the two conifer experiments, stomatal conductance showed a relatively small sensitivity to [CO_2] (a approx. 0.8–1.0), and this sensitivity was unchanged by growth in elevated [CO_2]. A similar pattern was seen for the two poplar cultivars in the Belgium Populus OTC experiment. By contrast, for the other broad-leaf species, the sensitivity of g_s to [CO_2] was strong in the ambient [CO_2] treatments (a approx. 0.6) but tended to be reduced slightly by growth in elevated [CO_2].

The Ball *et al.* (1987) model: relationship between stomatal conductance and assimilation

The meta-analysis of stomatal conductance measured at 700 μmol mol^{-1} [CO_2] indicated that there was no acclimation of stomatal conductance to elevated [CO_2] (Table 5). By contrast, a similar meta-analysis of photosynthesis data from the same experiments indicated that photosynthetic rates measured at 700 μmol mol^{-1} [CO_2] were significantly reduced by 9% in elevated [CO_2] (Medlyn *et al.*, 1999). Thus, a preliminary conclusion might be that stomatal conductance and photosynthesis do not respond to long-term growth in elevated [CO_2] in the same way. This question was investigated in more detail using the Ball *et al.* (1987) model (eqn 2), which is based on the relationship between photosynthesis and stomatal conductance. If photosynthesis and stomatal conductance acclimate to long-term growth in elevated [CO_2] in

Table 7 Values of ψ_0 (MPa), the Jarvis model parameter describing response to soil water potential (eqn 6). The standard error is given in parentheses

Experiment	Species	Ambient [CO_2] (MPa)	Elevated [CO_2] (MPa)
England Mixed OTC	*Q. robur*	−0.45 (0.23)	−0.36 (0.14)
England Mixed OTC	*F. excelsior*	−0.18 (0.02)	−0.20 (0.02)

Table 8 Values of *a*, the Jarvis model parameter describing the short-term response to atmospheric [CO_2] (eqn 7). The standard error is given in parentheses

Experiment	Species/Treatment	Ambient [CO_2]	Elevated [CO_2]
Belgium *Populus* OTC	*Populus* cv. Beaupré	1.02 (0.04)	0.94 (0.02)
Belgium *Populus* OTC	*Populus* cv. Robusta	0.93 (0.04)	0.91 (0.03)
Finland *Pinus* OTC	Ambient temperature	1.07 (0.06)	1.03 (0.07)
Finland *Pinus* OTC	Elevated temperature	1.04 (0.04)	1.00 (0.04)
Germany *Fagus* ME		0.61 (0.03)	0.76 (0.03)
Germany *Quercus* ME		0.60 (0.12)	0.67 (0.05)
Italy *Macchia* OTC	*Q. ilex*	0.60 (0.04)	0.71 (0.04)
Italy *Macchia* OTC	*P. lentiscus*	0.65 (0.04)	0.80 (0.09)
Scotland *Picea* BB	C needles	0.79 (0.02)	0.83 (0.02)

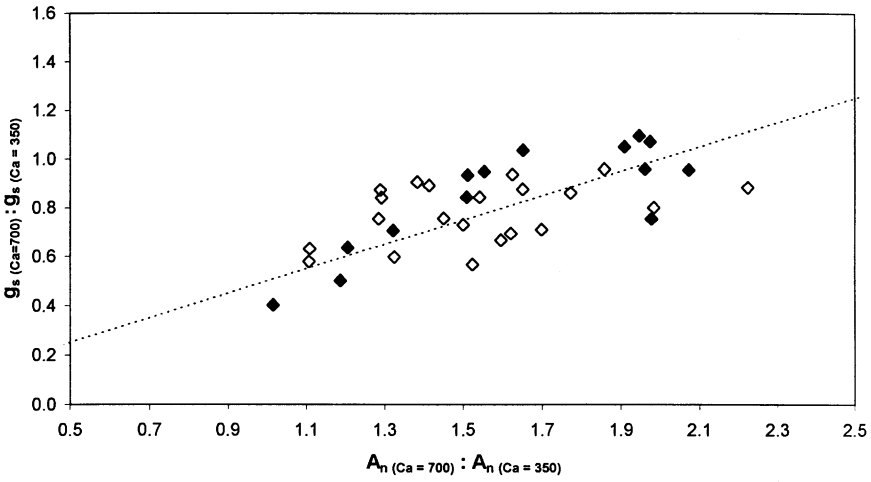

Fig. 3 Effect of elevated [CO_2] on stomatal conductance, expressed as a ratio of the elevated [CO_2] value to the ambient [CO_2] value, versus the effect on assimilation. Closed symbols, conifers; open symbols, broadleaved species. The dashed line indicates the 1:2 line.

Table 9 Parameters of the Ball *et al.* (1987) model (eqn 2). *P*, probability that fitted lines for ambient and elevated [CO_2] treatments are coincident

	Ambient equation	r^2	*n*	Elevated equation	r^2	*n*	Combined equation	r^2	*n*	*P*	CO_2 effect on slope
Denmark *Fagus* BB Italy *Macchia* OTC	$y = -0.02 + 12.7x$	0.95	8	$y = -0.003 + 12.1x$	0.91	8	$y = -0.008 + 12.3x$	0.93	16	0.26	0.95
Phillyrea angustifolia	$y = 0.033 + 10.09x$	0.66	24	$y = 0.048 + 1.85x$	0.22	23	$y = 0.039 + 6.47x$	0.36	47	< 0.001	0.18
Pistacia lentiscus	$y = 0.042 + 8.16x$	0.73	23	$y = 0.028 + 13.41x$	0.50	20	$y = 0.042 + 8.62x$	0.63	43	0.18	1.64
Quercus ilex	$y = 0.024 + 6.23x$	0.52	25	$y = 0.029 + 3.28x$	0.35	23	$y = 0.030 + 3.68x$	0.37	46	0.15	0.53
Scotland *Betula* OTC	$y = 0.084 + 9.37x$	0.15	69	$y = -0.018 + 18.62x$	0.42	66	$y = 0.043 + 12.1x$	0.30	135	0.06	1.99
Scotland *Picea* BB (C needles)	$y = 0.043 + 6.44x$	0.20	29	$y = 0.023 + 7.62x$	0.74	27	$y = 0.031 + 7.29x$	0.73	56	0.54	1.18
Scotland *Picea* BB (C + 1 needles)	$y = 0.027 + 5.19x$	0.71	29	$y = 0.009 + 7.05x$	0.83	28	$y = 0.018 + 5.88x$	0.88	57	0.15	1.36
Sweden *Picea* BB	$y = 0.054 + 2.93x$	0.67	21	$y = 0.032 + 4.56x$	0.53	21	$y = 0.052 + 3.21x$	0.59	42	0.07	1.56

parallel, then the parameters of the model should not change. Applying the model at ambient and elevated [CO_2] concentration, we have

$$g_{s(Ca=350)} = g_0 + g_1 A_{n(Ca=350)} h^s/350 \quad \text{Eqn 6}$$

and

$$g_{s(C_a=700)} = g_0 + g_1 A_{n(C_a=700)} h_s/700. \quad \text{Eqn 7}$$

Dividing eqn 7 by eqn 6, and assuming the parameter g_0 to be negligible, if the parameter g_1 is unchanged between ambient and elevated [CO_2] then the E/A ratio of photosynthesis ($A_{n(C_a=700)}/A_{n(C_a=350)}$) should be approximately twice the E/A ratio of stomatal conductance ($g_{s(C_a=700)}/g_{s(C_a=350)}$), whether or not acclimation has occurred. Thus, as a first test of whether stomatal conductance and assimilation acclimate (or do not acclimate) in parallel to growth in elevated [CO_2], we plotted the E/A ratio of g_s against the E/A ratio of A_n and

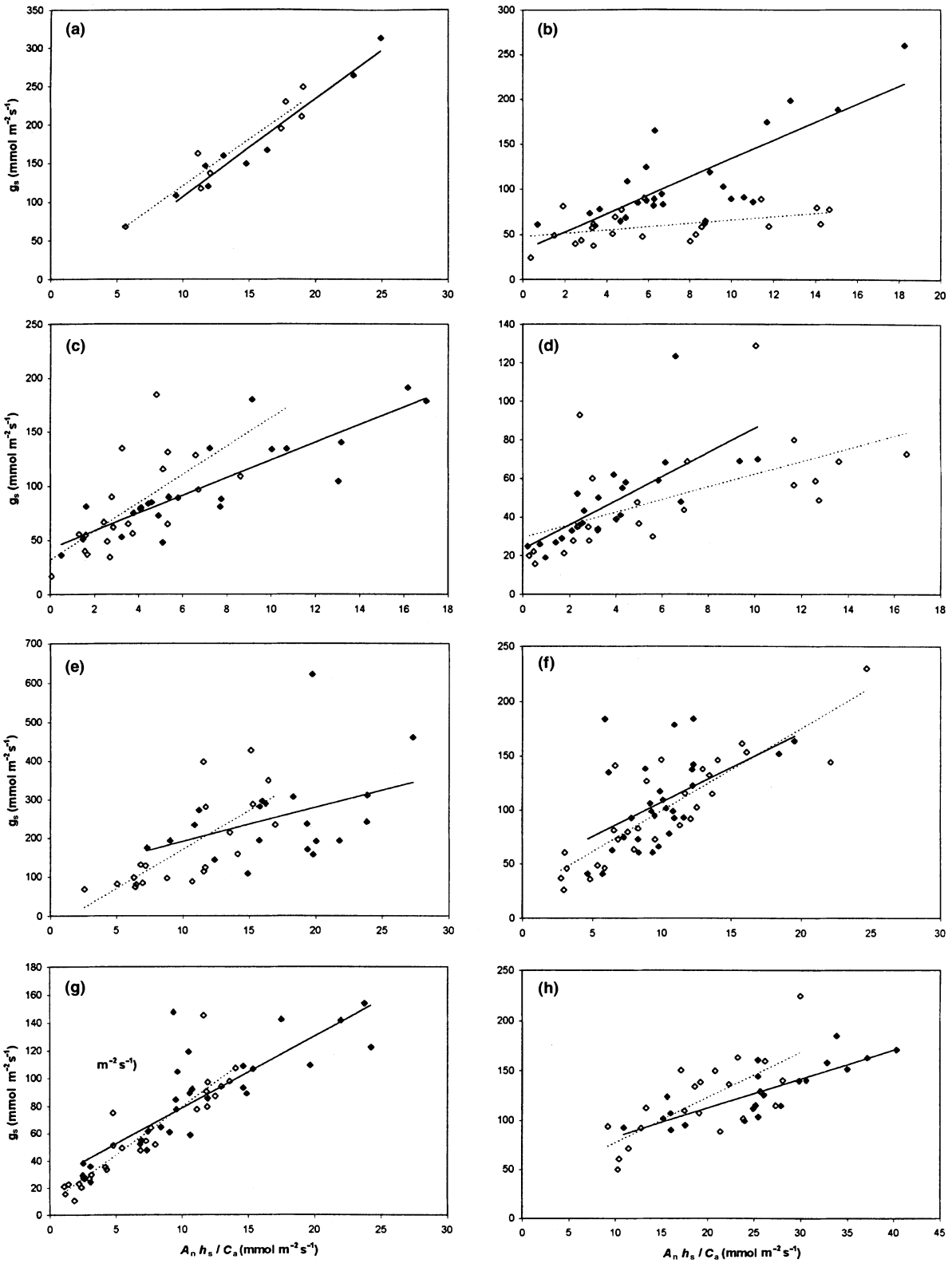

Fig. 4 Fits of the Ball *et al.* (1987) stomatal conductance model (eqn 2). Closed squares, ambient [CO_2]; open squares, elevated [CO_2]. Solid and dotted lines show regressions fitted to ambient and elevated [CO_2] treatments, respectively. (a) Denmark *Fagus* BB. (b) Italy *Macchia* OTC, *Phillyrea angustifolia*. (c) Italy *Macchia* OTC, *Pistacia lentiscus*. (d) Italy *Macchia* OTC, *Quercus ilex*. (e) Scotland *Betula* OTC. (f) Scotland *Picea* BB, C needles. (g) Scotland *Picea* BB, C + 1 needles. (h) Sweden *Picea* BB.

compared the plot to the 1 : 2 line (Fig. 3). Some scatter is to be expected, since g_s and A_n were not always measured under the same conditions. However, the plot appears to follow the 1 : 2 line, suggesting that the linkage between stomatal conductance and assimilation is unchanged by growth in elevated [CO_2].

A better test of this conclusion was made by fitting the Ball *et al.* (1987) model to a series of data sets to test how the relationship changed between ambient and elevated [CO_2] grown plants. Parameters from the model fits are given in Table 9, and the data are illustrated in Fig. 4. In the nonwater-stressed experiments (Sweden, Denmark, Scotland) the slope of the relationship tended to increase slightly but this shift was not significant. In the water-stressed Italian experiment, different species responded in strikingly different ways. For one shrub, *Phillyrea angustifolia*, there was a small increase in the slope of the relationship, as for the nonwater-stressed experiments, whereas for a different shrub, *Pistacia lentiscus*, there was a highly significant reduction in the slope of the relationship. These species clearly have different strategies to cope with water limitation (Scarascia-Mugnozza *et al.*, 1996). In summary, it seems fair to conclude that, in general, the slope of the Ball *et al.* (1987) relationship is unlikely to be changed significantly by growth in elevated [CO_2], indicating that stomata and photosynthesis do respond in parallel. However, the divergent results obtained in the Italian Macchia OTC experiment suggest that this conclusion should be further tested under water-stressed conditions.

Discussion

Effect of elevated [CO_2] on mean stomatal conductance

The meta-analysis of stomatal conductance values (Table 4) indicates that there was a significant 21% decrease of stomatal conductance in response to growth in elevated [CO_2] across this set of 13 long-term studies with woody species. This result contrasts with the study by Curtis & Wang (1998) who performed a similar meta-analysis on stomatal conductance in 48 studies with woody plants and found a modest and nonsignificant reduction of 11% in response to elevated [CO_2]. An analysis of our database combined with that of Curtis & Wang (1998) indicated that the chief difference between the two databases was the length of the studies included. Experiments of less than 1 year showed no reduction in g_s in elevated [CO_2], while experiments of > 1 yr showed a significant reduction in g_s of 23%. This result appears to run counter to the idea recently put forward that the transient reduction in g_s in response to elevated [CO_2] will be attenuated by long-term growth in elevated [CO_2] (Saxe *et al.*, 1998, Mooney *et al.*, 1999, Norby *et al.*, 1999). However, a plot of the response of g_s to elevated [CO_2] versus length of exposure (Fig. 5) illustrates that the key difference between 'short-term' (< 1 yr) and longer-term experiments is variability.

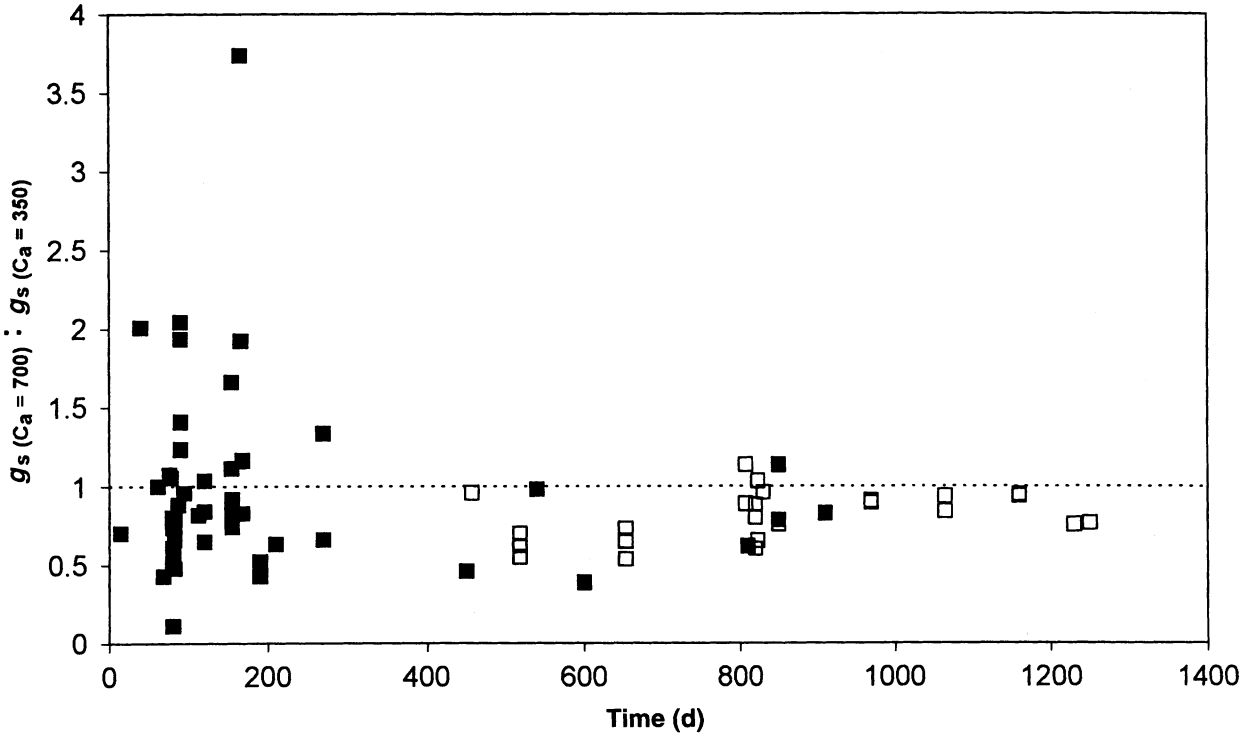

Fig. 5 Effect of elevated [CO_2] on stomatal conductance, expressed as a ratio of the elevated [CO_2] value to the ambient [CO_2] value, as a function of length of exposure to elevated [CO_2]. Filled symbols, data from Curtis & Wang (1998); open symbols, data from the current set of experiments. The dashed line indicates a ratio of 1.

Reported responses of g_s in short-term experiments are highly variable, whereas the responses in long-term experiments are much more consistent. The reason for the high variability in short-term experiments is not immediately evident. There is no similar distinction between pot-grown and freely rooted plants, thus ruling out any artefact related to restricted root volume, such as that proposed by Saxe *et al.* (1998). However, one conclusion that may be drawn from Fig. 5 is that long-term experiments are essential in studies of elevated [CO_2] effects on stomatal conductance.

The meta-analysis (Table 4) indicated a significant effect of functional type on the response of stomata to [CO_2], with conifers responding less strongly to elevated [CO_2] than deciduous and evergreen broadleaf species. Saxe *et al.* (1998) also reported a similar difference between functional groups. However, the meta-analysis also showed a significant effect of tree age on stomatal response. The two factors were confounded, with most experiments on older trees (> 10 yr) being on conifers, and most experiments on saplings being with deciduous species. Hence, from the meta-analysis, it was not possible to determine which was the principal cause of the difference between categories. Examination of nonconfounded cases tends to suggest that the difference may lie in tree age rather than functional type. In a branch bag study on mature beech there was no reduction in stomatal conductance or transpiration in elevated [CO_2] (Dufrêne *et al.*, 1993, Pontailler *et al.*, 1994). In a second study on mature beech, the [CO_2] effect on stomatal conductance varied through the season, with decreases in June and September but no effect in July and an increase in August (Freeman, 1998). On the other hand, literature reports from long-term field-based experiments with young conifers tend to show a strong reduction in g_s (−17% in *Pinus ponderosa*, Surano *et al.*, 1986, −38% in *P. taeda*, Fetcher *et al.*, 1988, up to −40% in *P. taeda*, Tissue *et al.*, 1997, −35% in current needles of *P. sitchensis*, C. Barton, unpublished). Differences in the stomatal response related to age or to functional type both appear plausible. The observation that stomata of conifers are generally unresponsive to C_a has been invoked to explain the difference in response of g_s to elevated [CO_2] between conifers and broadleaf species (Saxe *et al.*, 1998), while many studies have shown a reduction in stomatal conductance with increasing tree age (Kolb *et al.*, 1997). New FACE (free-air CO_2 enrichment) studies on mature trees may shed some light on this question (e.g. Ellsworth, 2000).

Effect of elevated [CO_2] on responses of g_s to environmental factors

Curtis (1996) found that the response of g_s to elevated [CO_2] was strongest in unstressed plants, and noted that this appeared to conflict with the observation by Sage (1994) that environmental stress accentuates the effect of elevated [CO_2] on g_s. Meta-analysis of our data suggests that this conflict may be resolved by observing that different kinds of stress affect the response of g_s to elevated [CO_2] in different ways. Nutrient stress (the most common type of stress in the dataset of Curtis (1996)) appeared to reduce the response of g_s to elevated [CO_2], whereas water stress increased the response, as noted by Sage (1994).

The response of g_s to elevated [CO_2] under water stress is of particular interest, since the higher temperatures predicted to follow increases in atmospheric [CO_2] are likely to increase potential evapotranspiration and thus the frequency of drought stress. The enhanced water-use efficiency almost universally observed under elevated [CO_2] seems to offer the potential for protection from this stress. For this reason we examined the effect of elevated [CO_2] on responses of stomatal conductance to two important factors influencing plant water relations, leaf to air vapour pressure deficit and soil water potential.

We found that stomatal sensitivity to VPD was unchanged by growth in elevated [CO_2] in any of the experiments (Fig. 1), in that the value of VPD at which stomatal conductance became zero (D_0) was unchanged. A number of studies have found similar results. Will & Teskey (1997) reported no change in VPD sensitivity in three species (*Quercus rubra*, *Populus deltoides* × *nigra*, *Pinus sylvestris*) with a small increase in sensitivity in a fourth species (*Cercis canadensis*). Goodfellow *et al.* (1997) and Tognetti *et al.* (1998) present data showing that D_0 is unchanged by growth in elevated [CO_2] in *Mangifera indica* and *Quercus ilex*, respectively. Morison & Gifford (1983) also noted that the most common pattern was for stomatal responses to humidity to remain unchanged by growth in elevated [CO_2]. However, there are exceptions to this pattern, such as the study by Heath (1998), where strongly decreased stomatal sensitivity to VPD was found in seedlings of *F. sylvatica*, *Castanea sativa* and *Q. robur*. Hollinger (1987) also reported reduced sensitivity to VPD in two young conifers. These two studies were, however, carried out on pot-grown seedlings exposed to elevated [CO_2] for less than 1 year and hence may be less likely to reflect responses of field-grown trees than the experiments considered here.

With regard to soil water potential, we present data indicating that stomatal sensitivity to soil water potential was unchanged by growth in elevated [CO_2] for young saplings of oak and ash (Fig. 2). Similar results have been demonstrated by Morison & Gifford (1984) and Centritto *et al.* (1999) for wheat and potted cherry (*Prunus avium*) seedlings, respectively. However, a convincing counter-example to this pattern was presented by Heath & Kerstiens (1997), who show a much-reduced response of stomatal conductance to soil water content in potted beech seedlings exposed to elevated [CO_2] for two growing seasons.

In summary, therefore, we found that mean stomatal conductance tended to be reduced strongly by growth in elevated [CO_2] when plants were water-stressed, but that the sensitivity of stomatal conductance to VPD and soil water potential was unchanged. Other literature studies are generally in

agreement with these observations, except for those presented by Heath & Kerstiens (1997) and Heath (1998), in which stomatal conductance was found to be less sensitive to VPD and soil water content when grown in elevated [CO_2]. We do not currently have a framework that would allow us to interpret these results. Optimality arguments, for example, would suggest that stomata should be more sensitive to soil water content at elevated [CO_2], since under elevated [CO_2] water availability is relatively more limiting to growth. The behaviour observed by Heath and Kerstiens (1997) would, as they note, lead to increased risk of drought damage.

Acclimation of stomatal conductance and relationship with assimilation

Although the acclimation of photosynthesis to elevated [CO_2] has been much studied (Gunderson & Wullschleger, 1994, Sage, 1994, Besford *et al.*, 1998, Medlyn *et al.*, 1999), less attention has been paid to the acclimation of stomatal conductance. A particularly important question, highlighted by Morison (1998), is whether stomata acclimate in parallel to photosynthesis, maintaining the tight linkage between the two processes observed at ambient [CO_2] (Wong *et al.*, 1978), or whether they can acclimate independently.

We examined whether stomatal conductance acclimated to growth in elevated [CO_2] by performing a meta-analysis of g_s data measured at a constant [CO_2] (700 μmol mol^{-1}) (Table 5). This analysis indicated that, overall, there was no acclimation of g_s to elevated [CO_2]. Pursuing this further, we also examined the sensitivity of stomata to [CO_2] under ambient and elevated [CO_2] growth conditions (Table 8). In ambient conditions, stomatal sensitivity to [CO_2] differed greatly between species, with responses ranging from zero to a 40% decrease in stomatal conductance in response to a doubling of [CO_2] from 350 to 700 μmol mol^{-1}. Growth in elevated [CO_2] appeared to slightly attenuate [CO_2] sensitivity in those species that were [CO_2] sensitive, but not to affect the species that were not. Other studies generally show no change in [CO_2] sensitivity of g_s (Radoglou *et al.*, 1992, Johnsen, 1993, Berryman *et al.*, 1994, Tuba *et al.*, 1994), although one study reports a greatly reduced sensitivity to [CO_2] (Santrucek & Sage, 1996).

While this analysis indicates little or no acclimation of stomatal conductance to elevated [CO_2], a similar meta-analysis of photosynthesis data from the same set of experiments suggested that photosynthesis did acclimate (Medlyn *et al.*, 1999). Hence, we examined whether the relationship between stomatal conductance and photosynthesis was changed under elevated [CO_2]. First, we compared the effect of elevated [CO_2] on stomatal conductance with the effect on photosynthesis (Fig. 3) and found a close coupling between the two processes, suggesting that they do acclimate in parallel. Taking this further, we applied a model of stomatal conductance that is based on the relationship with assimilation (Ball *et al.*, 1987) to eight separate datasets. We found that the model parameters did not change after growth in elevated [CO_2], except under conditions of water stress (Table 9).

Other studies using the Ball *et al.* (1987) model have generally also found no change in model parameters between ambient and elevated [CO_2] treatments (Kellomäki & Wang, 1997, Strassemeyer & Forstreuter, 1997; Liozon *et al.*, 2000). Other authors have examined the linkage between assimilation and stomatal conductance by examining the ratio of intercellular to atmospheric [CO_2] (C_i : C_a ratio) and have generally observed no effect of elevated [CO_2] on this ratio (Sage, 1994, Drake *et al.*, 1997). The exceptions noted by Sage (1994) were under conditions of water stress. Hence, we conclude that the relationship between assimilation and stomatal conductance is generally unchanged by growth under elevated [CO_2], but may change under conditions of water stress.

This conclusion appears difficult to reconcile with the observation that stomatal conductance does not acclimate to elevated [CO_2], while photosynthesis does. One problem is that stomata respond much more slowly to changes in environmental conditions (scale of hours) than does photosynthesis (scale of minutes). Although we attempted to exclude data where stomata would not have had time to respond fully to imposed measurement conditions, it is possible that stomata had not reached equilibrium conditions in some of the measurements, which would affect the observed relationship between g_s and assimilation. However, the more likely reason for the apparent contradiction is that significantly fewer datasets were available to assess the acclimation of stomatal conductance (9, Table 5) than acclimation of photosynthesis (17, Medlyn *et al.*, 1999). This limited number of data sets may not have been sufficient to detect a small acclimation in stomatal conductance.

Implications for modelling

To assess the implications of changes in stomatal conductance in elevated [CO_2] on future forest stand growth and water use, it is important to be able to predict stomatal conductance (Morison, 1998). Hence, in this paper, we have focused, not merely on the absolute size of the response of g_s to [CO_2], but also on how to model g_s under elevated [CO_2].

There are drawbacks to the way that the models were fitted. The meta-analysis was performed on mid-season values, omitting values from early and late-season, which could cause problems when scaling up to a whole year. However, there does not appear to be a strong seasonality in the response of g_s to elevated [CO_2] (Table 3), so this omission may not be grave. The parameterisation of the model of Jarvis (1976) requires an extensive dataset including measurements of g_s under varying conditions of all variables, and the variables should not be correlated. In the absence of such comprehensive data sets, we could only fit individual response curves (equations 3–5). Furthermore, we chose to use simple linear response

curves, instead of the nonlinear functions commonly used (Jarvis, 1976). This choice was made to minimise the number of parameters fitted and enhance comparability of parameters between datasets. For the second model, we chose to use the form presented by Ball *et al.* (1987) rather than the alternative formulation suggested by Leuning (1995) that is currently gaining ground amongst modellers (Van Wijk *et al.*, 2000). The Ball *et al.* (1987) form is easier to fit and more readily compared across experiments because it has fewer parameters and is linear.

Despite these drawbacks to the way the models were fitted, this study has enabled some general conclusions about modelling of stomatal conductance in elevated [CO_2] conditions – and highlighted several areas in which more data are required before we can have confidence in modelling.

To reflect the reduction in g_s indicated by the meta-analysis (Table 4), the maximum stomatal conductance (g_{smax}) in the Jarvis (1976) model (eqn 1) could be reduced by 21%. However, the meta-analysis indicated that either different functional groups, or different ages of trees, respond differently to elevated [CO_2]. This issue must be resolved before we can confidently model the response of g_{smax} to elevated [CO_2]. Also in the Jarvis (1976) model, our review has shown that the functions relating stomatal conductance to VPD ($f(D_0)$), soil water potential ($f(\psi_0)$) and atmospheric [CO_2] ($f(C_a)$) were generally unchanged in elevated [CO_2] and hence do not need to be modified. However, these functions have been shown to be altered in some studies: in particular, Heath & Kerstiens (1997) and Heath (1998) found reduced sensitivity to VPD and soil water potential in young deciduous trees. More careful, quantitative studies of the interactive effects of VPD, water stress and elevated [CO_2] on stomatal conductance in freely rooted plants are required to clarify whether, and how, the functions $f(D_0)$ and $f(\psi_0)$ are altered by growth in elevated [CO_2].

For the Ball *et al.* (1987) model it appears that parameters are unchanged under elevated [CO_2] and hence the model may be applied unmodified in most circumstances. However, the model may need to be modified for plants growing in water-limited environments, as suggested by the strongly significant shift in the relationship observed for the macchia shrub species *Phillyrea angustifolia*. Further work needs to be undertaken to investigate how this relationship is be affected by water stress and its interaction with [CO_2].

After many years of research, we thus now have a consistent body of data on which to base models of stomatal conductance under elevated [CO_2]. We note in conclusion, however, that the models of stomatal conductance used in this paper are entirely empirical, and our description of stomatal responses to elevated [CO_2] is essentially phenomenological. A major challenge that remains is to develop mechanistic models of stomatal conductance that will allow us to explain, rather than to merely describe, the response of stomatal conductance to elevated [CO_2] (e.g. Assmann, 1999).

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