ORNL/CDIAC-124
NDP-073

A Database of Herbaceous Vegetation Responses to Elevated Atmospheric CO2

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ORNL/CDIAC-124
NDP-073

A DATABASE OF HERBACEOUS VEGETATION RESPONSES TO ELEVATED ATMOSPHERIC CO_2

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Environmental Sciences Division
Publication No. 4909
Date Published: November 1999

Prepared for the
Environmental Sciences Division
Office of Biological and Environmental Research
U.S. Department of Energy
Budget Activity Number KP 12 04 01 0

Prepared by the
Carbon Dioxide Information Analysis Center
Environmental Sciences Division
OAK RIDGE NATIONAL LABORATORY
Oak Ridge, Tennessee 37831-6335
managed by
LOCKHEED MARTIN ENERGY RESEARCH CORP.
for the
U.S. DEPARTMENT OF ENERGY
under contract DE-AC05-96OR22464

CONTENTS

ABSTRACT

Jones, M. H., P. S. Curtis, R. M. Cushman, and A. L. Brenkert. 1999. *A Database of Herbaceous Vegetation Responses to Elevated Atmospheric CO_2*. ORNL/CDIAC-124, NDP-073. Carbon Dioxide Information Analysis Center, U.S. Department of Energy, Oak Ridge National Laboratory, Oak Ridge, Tennessee, U.S.A. 84 pp.

To perform a statistically rigorous meta-analysis of research results on the response by herbaceous vegetation to increased atmospheric CO_2 levels, a multiparameter database of responses was compiled from the published literature. Seventy-eight independent CO_2-enrichment studies, covering 53 species and 26 response parameters, reported mean response, sample size, and variance of the response (either as standard deviation or standard error). An additional 43 studies, covering 25 species and 6 response parameters, did not report variances. This numeric data package accompanies the Carbon Dioxide Information Analysis Center's (CDIAC's) NDP-072, which provides similar information for woody vegetation.

This numeric data package contains a 30-field data set of CO_2-exposure experiment responses by herbaceous plants (as both a flat ASCII file and a spreadsheet file), files listing the references to the CO_2-exposure experiments and specific comments relevant to the data in the data sets, and this documentation file (which includes SAS®[1] and Fortran codes to read the ASCII data file).

The data files and this documentation are available without charge on a variety of media and via the Internet from CDIAC.

Keywords: carbon dioxide, meta-analysis, vegetation

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[1] SAS® is a registered trademark of the SAS Institute, Inc., Cary, North Carolina 27511.

1. BACKGROUND INFORMATION

To perform a statistically rigorous synthesis of research results on the response by vegetation to increased atmospheric CO_2 levels, a multiparameter database of herbaceous-plant responses was compiled from the published literature (Wand et al. 1999, included in this report as Appendix D; Jones et al. submitted). Seventy-eight independent CO_2-enrichment studies, covering 53 species 1and 26 response parameters, reported mean response, sample size, and variance of the response. An additional 43 studies, covering 25 species and six response parameters, did not report variances. The plant species included in the database are listed in Appendix A. Meta-analytical methods (Cooper and Hedges 1994; Gurevitch and Hedges 1993; Gurevitch et al. 1992) have been applied to part of this database (Wand et al. 1999). This numeric data package accompanies the Carbon Dioxide Information Analysis Center's (CDIAC's) NDP-072 (Curtis et al. 1999), which provides similar information for woody vegetation.

Physiological "acclimation" or "downward regulation" of photosynthetic rates, stomatal conductance, dark respiration, and water-use efficiency of plants exposed to elevated CO_2 levels can be analyzed according to the following definitions. "Acclimation" is in general defined as "diminishing enhancement of photosynthesis by elevated CO_2 with time" (Mousseau and Saugier 1992). "Downward regulation" can be defined as "the initial stimulation of enhanced photosynthesis and growth by atmospheric enrichment eroding with time" (Idso and Kimball 1992). The phenomenon is also called "downward acclimation": "following prolonged exposure to high CO_2, photosynthetic capacity measured at either elevated or ambient CO_2 partial pressure falls to below that of plants exposed only to ambient CO_2" (Curtis and Teeri 1992).

Data were compiled for the database according to the following guidelines. The durations of experimental exposures are always reported. When more than one elevated-CO_2 treatment level is reported, only the level that is approximately twice the ambient level is included. For photosynthetic rates, stomatal conductance, dark respiration, and water use efficiency, only final-exposure experiment results are included; multiple measurements over time for the same plant are not. For acclimatory responses, only data for (1) plants grown at ambient CO_2 levels and measured at elevated CO_2 levels and (2) plants grown at elevated CO_2 levels and measured at elevated CO_2 levels are included.

2. APPLICATIONS OF THE DATA

This database was produced to support a meta-analysis of the effects of elevated CO_2 on herbaceous vegetation (Wand et al. 1999), and it was formatted accordingly. For other applications, the user should be aware that the data may be reported in more than one unit for a given variable (e.g., aboveground weight is reported in units of grams, grams per square meter, grams per plant, grams per pot, kilograms per hectare, kilograms per square meter, milligrams, milligrams per plant, and tons per hectare); this is not a problem for meta-analysis, but for other applications the user may need to convert the data to consistent units.

The effects of environmental factors (e.g., nutrient levels, light intensity, temperature), stress treatments (e.g., drought, heat, ozone), and the effects of experimental conditions (e.g., duration of CO_2 exposure, pot size, type of CO_2 exposure facility) on plant responses to elevated CO_2 levels can be explored with this database.

3. DATA LIMITATIONS AND RESTRICTIONS

In many papers, the data were reported graphically rather than numerically. In such cases, values reported in the database were digitized from the printed figures and may therefore be less accurate.

Some of the standard deviations (and derived standard errors and coefficients of variation) in this database may be incorrect. When a "standard deviation" was reported in a published paper, it was not generally possible to verify whether this value was a *sample* standard deviation or the standard deviation *of the mean*, which is sometimes used synonymously with standard error (i.e., standard error of the mean). Unfortunately, it was not possible to settle this issue definitively without personally contacting the authors of the published papers. In all cases, where not specified or known to be otherwise, a reported standard deviation was taken to be the sample standard deviation. If this assumption was in error, then the standard deviation, standard error, and coefficient of variation reported in this database would be incorrect.

In some cases an error bar in a figure or confidence interval in a table was not specified as standard deviation or standard error. If it was not possible to determine whether the reported variability was standard deviation or standard error, a missing-value indicator (-9.99) is entered under standard deviation and standard error for that observation.

In some cases (e.g., in long-term exposures), the duration of CO_2 exposure was approximated.

As noted in Sect. 2, various units may be used for the same parameter, so the user should apply caution in integrating observations from more than one paper. Units are reported in the database.

4. DATA CHECKS AND PROCESSING PERFORMED BY CDIAC

An important part of the data-packaging process at CDIAC involves the quality assurance (QA) of data before distribution. To guarantee data of the highest possible quality, CDIAC performs extensive QA checks, examining the data for completeness, reasonableness, and accuracy, through close cooperation with the data contributor.

All entries in the data file were visually inspected for reasonableness, and selected entries were spot-checked against the original publications.

The following paragraphs describe the additional data checks that were performed in the preparation of this numeric data package and the resulting revisions to the database.

Excel®[2] was used to convert the spreadsheets provided by the principal investigators to Lotus 1-2-3®[3] format. Two separate databases, one including observations for which standard deviation or standard error was reported ("weighted") and the other consisting of observations without reported standard deviation or standard error ("unweighted"), were merged into one.

Lists of entries for each field were generated to identify possible spelling variants, typographical errors, or order-of-magnitude errors in the original literature or in the compilation and data entry of the database.

Where a cited paper reported standard error, standard deviation was calculated and tabulated (such occurrences are indicated in the database with a **SDC** flag-code).

The ratio of elevated/ambient for X, SE, SD, and N was calculated for all parameters and all observations; then all observations were ranked on the basis of each ratio, whenever possible (all these variables were not present for all observations), to identify suspect values (defined as jumps of greater than twofold between adjacent observations). The ranked ratios of **X_ELEV/X_AMB** ranged without abrupt jumps from 0.19 to 3.5, except for the ratio for variable AGWT reported from **PAP_NO** 2440 (**X_ELEV/X_AMB** = 9.2); the individual values for **X_ELEV** and **X_AMB** were verified in that publication (they were digitized from Fig. 5). The ranked ratios of **SE_ELEV/SE_AMB** and **SD_ELEV/SD_AMB** ranged without abrupt jumps from 0.05 to 18, except for the ratios of 0 for variables TOTWT, RGR, PN, and GS reported from **PAP_NO** 2363; the individual values for which standard error was reported as 0 were verified in that publication. The ranked ratios of **CV*_ELEV/CV*_AMB** ranged without abrupt jumps from 0.07 to 29.25, except for the same observations for **PAP_NO** 2363, for which the reported standard error of 0 was verified. The ranked ratios of **N_ELEV/N_AMB** ranged without abrupt jumps from 0.4 to 1.43. Thus, this analysis did not reveal any aberrant and unverifiable observations in the databases.

To search for possible confusion between standard error and standard deviation (see Sect. 3), coefficients of variation **CV*** (after Sokal & Rohlf 1981) were calculated, whenever possible, for each **PARAM** from each mean, standard deviation, and sample size. It was expected that, for any **PARAM**, an anomalously low coefficient of variation for a given observation might signal that a standard error was mis-labeled as a standard deviation. The database was sorted by **PARAM**, then by **CV*_AMB** and **CV*_ELEV**, and was inspected for jumps of greater than fourfold

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[2] Excel® is a registered trademark of the Microsoft Corporation, Redmond, Washington 98052.

[3] Lotus 1-2-3® is a registered trademark of the Lotus Development Corporation, Cambridge, Massachusetts 02142.

between adjacent observations. Where the standard error, rather than standard deviation, was reported in the cited publication, no mislabeling should have been possible. This analysis identified two pairs of adjacent observations that warranted further scrutiny. The following list contains those pairs of adjacent observations, along with the results of the checks.

PAP_NO = 3034
PARAM = PN
SPECIES = *Echinochloa crusgalli*
SOURCE = F1
X_ELEV = 44.400
SE_ELEV = 0.100
CV*_ELEV = 0.694

and

PAP_NO = 2723
PARAM = PN
SPECIES = *Poa alpina*
SOURCE = F4
X_ELEV = 40.120
SE_ELEV = 0.505
CV*_ELEV = 2.955

Data for both of the above observations were verified in the original publications.

PAP_NO = 2184
PARAM = TILLERS
SPECIES = *Phleum pratense*
SOURCE = T2
X_ELEV = 726.000
SE_ELEV = 52.000
CV*_ELEV = 28.203

and

PAP_NO = 2717
PARAM = TILLERS
SPECIES = *Bromus erectus*
SOURCE = F1
X_ELEV = 4.590
SE_ELEV = 0.400
CV*_ELEV = 129.991

Data for both of the above observations were verified in the original publications. However, the error bars in Fig. 1 of **PAP_NO** 2717 were not labeled as to their meaning; they were assumed to represent standard error (see Sect. 3).

5. INSTRUCTIONS FOR OBTAINING THE DATA AND DOCUMENTATION

This database (NDP-073) is available free of charge from CDIAC. The files are available via the Internet, from CDIAC's World-Wide-Web site (**http://cdiac.esd.ornl.gov**), or from CDIAC's anonymous file transfer protocol (FTP) area (**cdiac.esd.ornl.gov**) as follows:

1. FTP to cdiac.esd.ornl.gov (128.219.24.36).
2. Enter "ftp" as the user id.
3. Enter your electronic mail address as the password (e.g., fred@zulu.org).
4. Change to the directory "pub/ndp073" (i.e., use the command "cd pub/ndp073").
5. Set ftp to get ASCII files by using the ftp "ascii" command.
6. Retrieve the ASCII database documentation file by using the ftp "get ndp073.txt" command.
7. Retrieve the ASCII data files by using the ftp "mget *.dat" command.
8. Set ftp to get binary files by using the ftp "binary" command.
9. Retrieve the binary spreadsheet files by using the ftp "mget *.wk1" command.
10. Exit the system by using the ftp "quit" command.
11. Uncompress the files on your computer if they are obtained in compressed format.

For non-Internet data acquisitions (e.g., diskette or 8-mm tape) or for additional information, contact:

User Services
Carbon Dioxide Information Analysis Center
Oak Ridge National Laboratory
P.O. Box 2008
Oak Ridge, Tennessee 37831-6335, U.S.A.

Telephone: 1-865-574-3645
Telefax: 1-865-574-2232
Email: cdiac@ornl.gov

6. REFERENCES

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7. LISTING OF FILES PROVIDED

The database consists of seven files (see Table 1), including this documentation file. The data files (**ndp073.dat** and **ndp073.wk1**), reference files (**refs.dat** and **refs.wk1**), and comment files (**comments.dat** and **comments.wk1**) are available in two formats: as flat ASCII files and as binary spreadsheet files (in Lotus 1-2-3® format, but readable by other spreadsheet programs).

The 30-field **ndp073.dat** and **ndp073.wk1** files contain data (954 observations in all) relevant for CO_2-exposure meta-analysis for herbaceous plants. The **ndp073.dat** file can be read into SAS® or Fortran programs, using the access codes provided in Sect. 11 of this numeric data package. The

ndp073.dat file can also be converted into a spreadsheet file for processing, although it is simpler to use the corresponding **ndp073.wk1** spreadsheet file provided.

The **refs.dat** file (included in this report as Appendix B) and **refs.wk1** file list the selected literature represented in the data file (119 references), and the **comments.dat** file (included in this report as Appendix C) and **comments.wk1** file provide additional information about the studies, beyond what appears in the **ndp073.dat** and **ndp073.wk1** data files. The reference numbers in the **refs.dat, refs.wk1, comments.dat**, and **comments.wk1** files correspond to the paper numbers in the **ndp073.dat** and **ndp073.wk1** data files.

Table 1. Data files in the database

File number	File name	File size (kB)	File type	File description
1	**ndp073.txt**	85	ASCII text	Documentation file
2	**ndp073.dat**	223	ASCII text	Data file
3	**ndp073.wk1**	507	Binary spreadsheet	Data file
4	**refs.dat**	24	ASCII text	Reference file
5	**refs.wk1**	30	Binary spreadsheet	Reference file
6	**comments.dat**	21	ASCII text	Comment file
7	**comments.wk1**	29	Binary spreadsheet	Comment file

8. DESCRIPTION OF THE DOCUMENTATION FILE

The **ndp073.txt (File 1)** file is an ASCII text equivalent of this document.

9. DESCRIPTION, FORMAT, AND PARTIAL LISTINGS OF THE ASCII DATA FILES

Table 2 describes the format and contents of the ASCII data file **ndp073.dat (File 2)** distributed with this numeric data package. Table 2 also indicates the column in the corresponding spreadsheet file **ndp073.wk1** in which each variable is found. The missing-value indicator in this database is the period (.), except for the real numeric fields **SE_AMB, SD_AMB, CV*_AMB, SE_ELEV, SD_ELEV**, and **CV*_ELEV**, in which the missing-value indicator is -9.99, and the integer numeric fields **N_AMB** and **N_ELEV**, in which the missing-value indicator is -9.

Table 2. Contents and format of ndp073.dat (File 2)

Variable	Variable type	Variable width	Starting column	Ending column	Units	Spreadsheet column	Definition and comments
PAP_NO	Numeric	6	1	6		A	Cited paper number
PARAM	Character	7	7	13		B	Measured parameter
P_UNIT	Character	14	14	27		C	Unit for PARAM
GENUS	Character	13	28	40		D	Plant genus name
SPECIES	Character	13	41	53		E	Plant species name
DIV1	Character	6	54	59		F	Functional division #1
DIV2	Character	7	60	66		G	Functional division #2
DIV3	Character	5	67	71		H	Functional division #3
DIV4	Character	6	72	77		I	Functional division #4
AMB	Character	3	78	80	See CO2_UNIT	J	Ambient CO_2 treatment level
ELEV	Character	4	81	84	See CO2_UNIT	K	Elevated CO_2 treatment level
CO2_UNIT	Character	10	85	94	See text following table	L	Units for CO_2 exposure concentration
TIME	Character	5	95	99	Days	M	Maximum duration of CO_2 exposure
POT	Character	13	100	112		N	Growing method
MTHD	Character	4	113	116		O	CO_2-exposure facility
STOCK	Character	9	117	125		P	Planting stock

Table 2 (continued)

Variable	Variable type	Variable width	Starting column	Ending column	Units	Spreadsheet column	Definition and comments
XTRT	Character	6	126	131		Q	Interacting treatment
LEVEL	Character	7	132	138		R	Interacting treatment level
QUANT	Character	17	139	155		S	Quantity and unit associated with LEVEL
SOURCE	Character	6	156	161		T	Figure, table, or page from which data taken
X_AMB	Numeric	8	162	169	See P_UNIT	U	Mean response of plants grown in ambient CO_2
SE_AMB	Numeric	8	170	177	See P_UNIT	V	Standard error of X_AMB
SD_AMB	Numeric	8	178	185	See P_UNIT	W	Standard deviation of responses of plants grown in ambient CO_2
CV*_AMB	Numeric	7	186	192	%	X	Coefficient of variation of responses of plants grown in ambient CO_2
N_AMB	Numeric	5	193	197		Y	Sample size of responses of plants grown in ambient CO_2
X_ELEV	Numeric	9	198	206	See P_UNIT	Z	Mean response of plants grown in elevated CO_2
SE_ELEV	Numeric	7	207	213	See P_UNIT	AA	Standard error of X_ELEV

Table 2 (continued)

Variable	Variable type	Variable width	Starting column	Ending column	Units	Spreadsheet column	Definition and comments
SD_ELEV	Numeric	8	214	221	See P_UNIT	AB	Standard deviation of responses of plants grown in elevated CO_2
CV*_ELEV	Numeric	8	222	229	%	AC	Coefficient of variation of responses of plants grown in elevated CO_2
N_ELEV	Numeric	6	230	235		AD	Sample size of responses of plants grown in elevated CO_2
SDC	Character	3	236	238		AE	Calculated versus reported standard deviation

Where:

For **PARAM**, the following list defines the possible measured parameters:

plant parts

AGPROD: aboveground productivity (= AGWT + clippings)
AGWT: total aboveground weight
BGWT: total belowground weight
LFWT: total leaf weight
RGR: relative growth rate
ROOTWT: root weight
SHTWT: shoot weight
STWT: stem weight
TILLERS: number of tillers
TOTWT: whole plant weight

leaf area components

INDLA: maximum individual leaf area
MAXLA: maximum canopy leaf area
SLA: specific leaf area (leaf area/unit mass of leaf)
SLW: specific leaf weight (leaf mass/unit area of leaf)

gas-exchange parameters

GR: stomatal resistance of ambient-grown plants measured at ambient CO_2 levels (**X_AMB**) and of elevated-grown plants measured at elevated CO_2 levels (**X_ELEV**)

GR_AC: stomatal resistance of ambient-grown plants measured at elevated CO_2 levels (**X_AMB**) and of elevated-grown plants measured at elevated CO_2 levels (**X_ELEV**)

GS: stomatal conductance of ambient-grown plants measured under ambient CO_2 (**X_AMB**) and elevated-grown plants measured under elevated CO_2 levels (**X_ELEV**)

PN: net CO_2 assimilation of ambient-grown plants measured under ambient CO_2 (**X_AMB**) and elevated-grown plants measured under elevated CO_2 levels (**X_ELEV**)

PN_AC: net CO_2 assimilation of ambient-grown plants measured at elevated CO_2 (**X_AMB**) and elevated-grown plants measured at elevated CO_2 levels (**X_ELEV**)

RD: dark respiration of ambient-grown plants measured under ambient CO_2 (**X_AMB**) and elevated-grown plants measured under elevated CO_2 levels (**X_ELEV**)

WUE: water use efficiency of ambient-grown plants measured under ambient CO_2 (**X_AMB**) and elevated-grown plants measured under elevated CO_2 levels (**X_ELEV**)

WUE_AC: water use efficiency of ambient-grown plants measured at elevated CO_2 (**X_AMB**) and elevated-grown plants measured at elevated CO_2 levels (**X_ELEV**)

biochemical constituents

AGN: aboveground N
BGN: belowground N
LFN: leaf N
STEMN: stem total N
TOTN: total N

The value of **PARAM** is linked to that shown for **P_UNIT** (parameter units), **X_AMB** (parameter value for plants grown under ambient CO_2 exposure conditions), and **X_ELEV** (parameter value for plants grown under elevated CO_2 exposure conditions).

The only entry for **DIV1** (functional division #1) is ANGIO (angiosperms)

Entries for **DIV2** (functional division #2) are

GRASS
GRASS_C: typically monotypic crop; generally does not include pasture species
SEDGE

Entries for **DIV3** (functional division #3), if known, are

C3

C4
C3/C4: C3/C4 intermediate, as reported by the authors of the cited paper

Entries for **DIV4** (functional division #4) are general habitat or location:
ALPINE
BOREAL
GRASS (grassland)
MEAD (meadow)
WETL (wetland)

The values of **AMB** and **ELEV** are linked to those shown for **CO2_UNIT**.

Entries for **CO2_UNIT** are
Pa (Pascals)
μbar (1 μbar = 0.1 Pa)
ppm
μl/l
cm^3/m^3
μmol/mol
μmol/l
ml/l

TIME represents the maximum duration (days) of the CO_2 exposure.

For **POT** (growing method), a numeric entry signifies pot size (in liters) used during the major part of the experiment; the other entries are
GRND: plants rooted in the ground
HYDRO: solution or aeroponic culture

Entries for **MTHD** (CO_2-exposure facility) are
FACE: Free-Air CO_2 Enrichment
GC: indoor, controlled environment: growth chambers
GH: sunlit greenhouses and chambers within greenhouses; also includes closed-top chambers in the field, covering ecosystems
OTC: field-based open-top chambers
SACC: screen-aided CO_2 control

Entries for **STOCK** (planting stock codes) are
CLONE: experimental plants started from cuttings (graminoids); published paper refers to specific genotype
ECOSYS: entire ecosystem exposed
MATURE: mature plants exposed
MIXED: typically ecosystems where species are propagated from multiple sources

RAMETS: small plants (with 2 to 3 tillers) propagated from cuttings, rather than grown from seed
SEED: plants started from seeds
SEEDLINGS: young plants grown from seed
TILLERS: equivalent to rhizomes or stolons, depending upon species; that is, more-or-less horizontal stems or culms

Entries for **XTRT** (codes for interacting treatment, used together with CO_2) are
COMP: plant competition
DEFOL: defoliation (clipping by any means)
FERT: soil fertility
FLD: flooding treatment
F+O3: fertility plus ozone
H2O: well-watered versus drought
LIGHT: light treatment
NONE: no additional treatment beyond CO_2 enrichment; usually optimal growth conditions
O3: ozone exposure
SALT:
TEMP: temperature treatment

The entries for **LEVEL** (which qualitatively describes the treatment level) are treatment-dependent; this field is linked with **XTRT** (which characterizes the treatment type) and **QUANT** (which quantifies the treatment level).

For **XTRT** = COMP, FERT+L, NATIVE, NONE, or SALT, **LEVEL** = . (missing value) (see entry for corresponding paper in **comments.dat** and **comments.wk1** files)

For soil fertility treatment:
CONTROL
HI
LOW
MED
TRT-1
TRT-2
TRT-3
missing (.) when treatment cannot be clearly described (see entry for corresponding paper in **comments.dat** and **comments.wk1** files).

For H2O treatment:
DRT: drought
FLD: flooding
PRECIP: natural levels of precipitation

WW: well-watered

For LIGHT, TEMP, OZONE, and UVB treatments:
CONTROL
HI
LOW

Entries for **QUANT**, which quantify the interacting treatment level, are treatment-dependent. The combination of quantity and unit is reported in this one field (see also the corresponding entry in **comments.dat** and **comments.wk1** file). If **QUANT** data are not available or inappropriate, a missing value (.) is present.

Possible entry formats for **SOURCE** (figure, table, or page from which data were extracted) are:
F1a (Fig. 1a)
T1 (Table 1)

Entries for **X_AMB**, **SE_AMB**, **SD_AMB**, **X_ELEV**, **SE_ELEV**, and **SD_ELEV** are linked to the units given for **P_UNIT**. The suffix "**AMB**" refers to measurements of plants grown under ambient CO_2 exposure conditions, and the suffix "**ELEV**" refers to measurements of plants grown under elevated CO_2 exposure conditions.

For **CV*_AMB** and **CV*_ELEV**, corrected (for small sample size) coefficient of variation was calculated according to Sokal and Rohlf (1981) as follows:

$$CV^* = (1 + 1/4N)(SD \times 100)/X$$

where SD = standard deviation, X = mean, and N = sample size.

SDC indicates whether the tabulated values for standard deviation (used to calculate coefficient of variation) were extracted directly from the cited publications or calculated from reported values for standard error. The tabulated values of **SDC** are either Y (yes) or N (no).

First two data records:

```
    38AGWT   G PLANT-1     TRITICUM      AESTIVUM     ANGIO GRASS_CC3   GRASS 330
660UL L-1       461.45         GC  SEED      H2O   LO     10 ML PL-1 D-1   F4
3.61   -9.99   -9.99  -9.99   10      5.13  -9.99   -9.99   -9.99    10  .
    38AGWT   G PLANT-1     TRITICUM      AESTIVUM     ANGIO GRASS_CC3   GRASS 330
660UL L-1       371.45         GC  SEED      H2O   CTL    40 ML PL-1 D-1   F4
2.98   -9.99   -9.99  -9.99   10      3.97  -9.99   -9.99   -9.99    10  .
```

Last two data records:

```
  3042PN     UMOL M-2 S-1  ZEA          MAYS         ANGIO GRASS_CC4   GRASS 330
640UBAR         305            GH  SEED     FERT  HI     .                F2
64.80    2.10    5.94   9.45    8    52.40   0.90    2.55    5.01     8  Y
  3042PN     UMOL M-2 S-1  ZEA          MAYS         ANGIO GRASS_CC4   GRASS 330
640UBAR         305            GH  SEED     FERT  LO     .                F2
27.90    1.84    5.20  19.24    8    21.90   2.10    5.94   27.97     8  Y
```

The **refs.dat (File 4)** ASCII file provides citations of papers included in the database. A full listing of the file is included as Appendix B.

The **comments.dat (File 6)** ASCII file provides experimental details from papers included in the database. A full listing of the file is included as Appendix C.

10. DESCRIPTION AND FORMAT OF THE LOTUS 1-2-3® BINARY SPREADSHEET FILES

Three Lotus 1-2-3® binary spreadsheet files (files 3, 5, and 7) contain the same information as the corresponding ASCII files (files 2, 4, and 6).

File **ndp073.wk1 (File 3)** corresponds to ASCII file **ndp073.dat (File 2)**.

Table 2, which describes the contents and format of **ndp073.dat**, also indicates the column of **ndp073.wk1** in which each variable is found.

File **refs.wk1 (File 5)** corresponds to ASCII file **refs.dat (File 4)**.

File **comments.wk1 (File 7)** corresponds to ASCII file **comments.dat (File 6)**.

11. SAS® AND FORTRAN CODES TO ACCESS THE DATA

The following is SAS® code to read file **ndp073.dat**.

```
*SAS data retrieval routine to read ndp073.dat;

data ndp073;
infile 'ndp073.dat';
input PAP_NO 6. @7 PARAM $char7. P_UNIT $ 14-27 GENUS $ 28-40
      SPECIES $ 41-53 DIV1 $ 54-59 DIV2 $ 60-66 DIV3 $ 67-71
      DIV4 $ 72-77 AMB $ 78-80 ELEV $ 81-84
      CO2_UNIT $ 85-94 TIME $ 95-99 POT $ 100-112 MTHD $ 113-116
      STOCK $ 117-125 XTRT $ 126-131 LEVEL $ 132-138 QUANT $ 139-155
      SOURCE $ 156-161 X_AMB 162-169 SE_AMB 170-177 SD_AMB 178-185
      CV_AMB 186-192 N_AMB 193-197 X_ELEV 198-206 SE_ELEV 207-213
      SD_ELEV 214-221 CV_ELEV 222-229 N_ELEV 230-235 SDC $ 236-238 ;

* In the above INPUT statement, the variables CV*_AMB and CV*_ELEV have
  been renamed CV_AMB and CV_ELEV, respectively.;
```

```
proc print;
run;
```

The following is Fortran code to read file **ndp073.dat**.

```
C *** Fortran program to read the file "ndp073.dat"
C
      INTEGER PAP_NO, N_AMB, N_ELEV
C
      REAL X_AMB, SE_AMB, SD_AMB, CV_AMB, X_ELEV, SE_ELEV,
     +     SD_ELEV, CV_ELEV
C
      CHARACTER PARAM*7, P_UNIT*14, GENUS*13, SPECIES*13, DIV1*6,
     + DIV2*7, DIV3*5, DIV4*6, AMB*3, ELEV*4, CO2_UNIT*10,
     + TIME*5,  POT*13, MTHD*4, STOCK*9, XTRT*6, LEVEL*7,
     + QUANT*17, SOURCE*6, SDC*3
C
      OPEN (UNIT=1, FILE='ndp073.dat')
C
C     Note that the variables CV*_AMB and CV*_ELEV have
C     been renamed CV_AMB and CV_ELEV, respectively
C
   10 READ (1,100,END=99) PAP_NO, PARAM, P_UNIT, GENUS, SPECIES,
     + DIV1, DIV2, DIV3, DIV4, AMB, ELEV, CO2_UNIT, TIME, POT,
     + MTHD, STOCK, XTRT, LEVEL, QUANT, SOURCE, X_AMB, SE_AMB,
     + SD_AMB, CV_AMB, N_AMB, X_ELEV, SE_ELEV, SD_ELEV, CV_ELEV,
     + N_ELEV, SDC
C
  100 FORMAT (I6,A7,A14,2A13,A6,A7,A5,A6,A3,A4,A10,A5,A13,A4,A9,
     + A6,A7,A17,A6,3F8.2,F7.2,I5,F9.2,F7.2,2F8.2,I6,A3)
C
      GO TO 10
   99 CLOSE (UNIT=1)
      STOP
      END
```

APPENDIX A. SPECIES INCLUDED IN THE DATABASE

Agropyron caninum
Agropyron smithii
Agrostis capillaris
Andropogon gerardii
Avena barbata
Avena fatua
Avena sativa
Bouteloua curtipendula
Bouteloua eriopoda
Bouteloua gracilis
Briza subaristata
Bromus erectus
Bromus hordaeceus
Bromus willdenowii
Calamagrostis epigejos
Carex curvula
Dactylis glomerata
Digitaria macroblephara
Digitaria sanguinalis
Echinochloa crusgalli
Eleusine indica
Eriophorum vaginatum
Festuca arundinacea
Festuca durviscula
Festuca elatior
Festuca idahoensis
Festuca ovina
Festuca pratense
Festuca rupicola
Festuca vivipara
Hordeum vulgare
Lolium boucheanum
Lolium multiflorum
Lolium perenne
Nardus stricta
Oryza sativa
Panicum antidotale
Panicum laxum
Panicum millioides
Pascopyrum smithii
Paspalum dilatatum
Pennisetum clandestinum
Phalaris aquatica
Phleum pratense
Poa alpina
Poa annua
Poa pratensis
Puccinellia maritima
Rottboellia exaltata
Schizachyrium scoparium
Scirpus olneyi
Setaria faberi
Sorghum bicolor
Sorghum helpense
Spartina patens
Sporobolus kentrophyllus
Stipa occidentalis
Themeda triandra
Triticum aestivum
Vulpia microstachys
Zea mays

APPENDIX B. FULL LISTING OF REFS.DAT (FILE 4)

The number at the beginning of each entry corresponds to **PAP_NO**, the cited paper number, as defined in Sect. 9.

38. Andre, M., and H. Du Cloux. 1993. Interaction of CO2 Enrichment and Water Limitations on Photosynthesis and Water-Use Efficiency in Wheat. Plant Physiology and Biochemistry 31:103-112.

186. Drake, B. G. 1992. A Field Study of the Effects of Elevated CO2 on Ecosystem Processes in a Chesapeake Bay Wetland. Australian Journal of Botany 40:579-595.

488. Nie, D., H. He, M. B. Kirkham, and E. T. Kanemasu. 1992. Photosynthesis of a C3 Grass and a C4 Grass under Elevated CO2. Photosynthetica 26:189-198.

618. Ryle, G. J. A., C. E. Powell, and V. Tewson. 1992. Effect of elevated co2 on photosynthesis, respiration and growth of perennial ryegrass. Journal of Experimental Botany 43:811-818.

754. Ziska, L. H., and J. A. Bunce. 1993. Inhibition of Whole Plant Respiration by Elevated CO2 as Modified by Growth Temperature. Physiologia Plantarum 87:459-466.

765. Baker, J. T., L. H. Allen Jr., and K. J. Boote. 1992. Response of Rice to Carbon Dioxide and Temperature. Agricultural and Forest Meteorology 60:153-166.

2066. Samarakoon, A. B., W. J. Muller, and R. M. Gifford. 1995. Transpiration and leaf area under elevated CO2: Effects of soil water status and genotype in wheat. Australian Journal of Plant Physiology 22:33-44.

2119. Greer, D. H., W. A. Laing, and B. D. Campbell. 1995. Photosynthetic responses of thirteen pasture species to elevated CO2 and temperature. Australian Journal of Plant Physiology 22:713-722.

2125. Baxter, R., M. Gantley, T. W. Ashenden, and J. F. Farrar. 1994. Effects of elevated carbon dioxide on three grass species from montane pasture. Journal of Experimental Botany 45:1267-1287.

2132. Rao, M. V., B. A. Hale, and D. P. Ormrod. 1995. Amelioration of ozone-induced oxidative damage in wheat plants grown under high carbon dioxide. Plant Physiology 109:421-432.

2133. Tuba, Z., K. Szente, and J. Koch. 1994. Response of photosynthesis, stomatal conductance, water use efficiency and production to long-term elevated CO2 in winter wheat. Journal of Plant Physiology 144:661-668.

2158. Gloser, J., and M. Bartak. 1994. Net photosynthesis, growth rate and biomass allocation in a rhizomatous grass Icalamagrostis epigejos grown at elevated CO2 concentration. Photosynthetica 30(1):143-150.

2159. Ziska, L. H., and J. A. Bunce. 1994. Increasing growth temperature reduces the stimulatory effect of elevated CO2 on photosynthesis or biomass in two perennial species. Physiologia Plantarum 91:183-190.

2168. Knapp, A. K., E. P. Hamerlynck, and C. E. Owensby. 1993. Photosynthetic and water relations responses to elevated CO2 in the C4 grass Andropogon geradii. International Journal of Plant Science 154(4):459-466.

2184. Saebo, A., and L. M. Mortensen. 1995. Growth and regrowth of Phleum pratense, Lolium perenne, Trifolium repens and Trifolium pratense at normal and elevated O2 concentration. Agriculture, Ecosystems and Environment 55:29-35.

2192. Knapp, A. K., J. T. Fahnestock, and C. E. Owensby. 1994. Elevated atmospheric O2 alters stomatal responses to variable sunlight in a C4 grass. Plant, Cell and Environment 17:189-195.

2202. Wilsey, B. J., S. J. McNaughton, and J. S. Coleman. 1994. Will increases in atmospheric O2 affect regrowth following grazing in C4 grasses from tropical grasslands? Oecologia 99:141-144.

2208. Crush, J. R. 1994. Elevated atmospheric O2 concentration and rhizosphere nitrogen fixation in four forage plants. New Zealand Journal of Agricultural Research 37:455-463.

2211. Morgan, J. A., W. G. Knight, L. M. Dudley, and H. W. Hunt. 1994. Enhanced root system C-sink activity, water relations and aspects fo nutrient acquisistion in mycotrophic Bouteloua gracilis subjected to CO2 enrichment. Plant and Soil 165:139-146.

2227. Bowler, J. M., and M. C. Press. 1993. Growth responses of two contrasting upland grass species to elevated CO2 and nitrogen concentration. New Phytologist 124:515-522.

2229. Mitchell, R. A. C., V. J. Mitchell, S. P. Driscoll, J. Franklin, and D. W. Lawlor. 1993. Effects of increased CO2 concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. Plant, Cell and Environment 16:521-529.

2246. Baxter, R., T. W. Ashenden, T. H. Sparks, and J. F. Farrar. 1994. Effects of elevated carbon dioxide on three montane grass species. Journal of Experimental Botany 45 (272):305-315.

2300. Bassirirad, H., D. T. Tissue, J. F. Reynolds, and F. S. Chapin. 1996. Response of Eriophorum vaginatum to CO2 enrichment at different soil temperature: effects on growth, root respiration and PO-4 uptake kinetics. New Phytologist 133:423-430.

2312. Wilsey, B. J. 1996. Urea additions and defoliation affect plant responses to elevated CO2 in a C3 grassland from Yellowstone National Park. Oecologia 108:321-327.

2315. Casella, E., J. F. Soussana, and P. Loiseau. 1996. Long-term effects of CO2 enrichment and temperature increase on a temperate grass sward. 1. Productivity and water use. Plant and Soil 182:83-99.

2316. Soussana, J. F., E. Casella, and P. Loiseau. 1996. Long-term effects of CO2 enrichment and temperature increase on a temperate grass sward. 2. Plant nitrogen budgets and root fraction. Plant and Soil 182:101-114.

2329. Jones, M. B., M. Jongen, and T. Doyle. 1996. Effects of elevated carbon dioxide concentrations on agricultural grassland production. Agricultural and Forest Meteorology 79:243-252.

2330. Stewart, J., and C. Potvin. 1996. Effects of elevated CO2 on an artificial grassland community: competition, invasion and neighbourhood area. Functional Ecology 10:157-166.

2337. Saebo, A., and L. M. Mortensen. 1996. The influence of elevated CO2 concentration on growth of seven grasses and one clover species in a cool maritime climate. Acta Agriculturae Scandinavia Section B-Sorland Plant Science 46:49-54.

2341. Schappi, B., and C. Korner. 1996. Growth responses of an alpine grassland to elevated CO2. Oecologia 105:43-52.

2342. Jackson, R. B., and H. L. Reynolds. 1996. Nitrate and ammonium uptake for single and mixed species communities grown at elevated CO2. Oecologia 105:74-80.

2345. Hakala, K., and T. Mela. 1996. The effects of prolonged exposure to elevated temperatures and elevated CO2 leveles on the growth, yield and dry matter partitioning of filed-sown meadow fescue. Agricultural and Food Science in Finland 5(3):285-298.

2347. Jackson, R. B., Y. Luo, Z. G. Cardon, O. E. Sala, C. B. Field, and H. A. Mooney. 1995. Photosynthesis, growth and density for the dominant species in a CO2 enriched grassland. Journal of Biogeography 22:221-225.

2350. Teughels, H., I. Nijs, P. Van Hecke, and I. Impens. 1995. Competition in a global change environment: The importance of different plant traits for competitive success. Journal of Biogeography 22:297-305.

2351. Campbell, B. D., W. A. Laing, D. H. Gree, J. R. Crush, H. Clark, D. Y. WIlliamson, and M. D. J. Given. 1995. Variation in grassland populations and species and the implications for community responses to elevated CO2. Journal of Biogeography 22:315-322.

2357. Chu, C. C., C. B. Field, and H. A. Mooney. 1996. Effects of CO2 and nutrient enrichment on tissue quality of two California annuals. Oecologia 107:433-440.

2358. Ferris, R., I. Niy, T. Bejaeghe, and I. Impens. 1996. Contrasting CO2 and temperature effects on leaf growth of perennial rye grass in spring and summer. Journal of Experimental Botany 47:1033-1043.

2362. Wheeler, T. R., G. R. Batts, R. H. Ellis, P. Hadley, and J. J. L. Morison. 1996. Growth and yield of winter wheat (Triticum aestium) crops in response to CO2 and temperature. Journal of Agricultural Science 127:37-48.

2363. Volin, J. C., and P. B. Reich. 1996. Interaction of elevated CO2 and O3 on growth, photosynthesis and respiration of three perennial species grown in low and high nitrogen. Physiologia Plantarum 97:674-684.

2364. Miglietta, F., A. Giuntoli, and M. Bindi. 1996. The effect of free air carbon dioxide enrichment (FACE) and soil nitrogen availability on the photosynthetic capacity of wheat. Photosynthesis Research 47:281-290.

2366. Ziska, L. H., W. Weerakoon, O. S. Namuco, and R. Pamplona. 1996. Influence of nitrogen on the elevated CO2 response in field-grown rice. Australian Journal of Plant Physiology 23:45-52.

2367. Saebo, A., and L. M. Mortensen. 1996. Growth, morphology and yield of wheat, barley and oats grown at elevated atmospheric CO2 concentration in a cool maritime climate. Agriculture, Ecosystems and Environment 57:9-15.

2369. Ziska, L. H., P. A. Manalo, and R. A. Ordonez. 1996. Intraspecific variaiton in the response of rice (Oryza sativa L) to increased CO2 and temeprature: growth and yield response of seventeen cultivars. Journal of Experimental Botany 47:1353-1359.

2372. Nijs, I., H. Teughels, H. Blum, G. Hendrey, and I. Impens. 1996. Simulation of climate change with infrared heaters reduces the productivity of Lolium perenne L in summer. Environmental and Experimental Botany 36:271-280.

2379. Veisz, O., N. Harnos, L. Szunies, and T. Tischner. 1996. Overwintering of winter cereals in Hungary in the case of global warming. Euphytica 92:249-253.

2383. Nijs, I., and I. Impens. 1996. Effects of elevated CO2 concentration and climate-warming on photosynthesis during winter in Lolium perenne. Journal of Experimental Botany 47:915-924.

2387. Leadley, P. W., and J. Stocklin. 1996. Effects of elevated CO2 on model calcareous grasslands: Community, species, and genotype responses. Global Change Biology 2:389-397.

2395. Tuba, Z., K. Szente, Z. Nagy, Z. Csintalan, and J. Koch. 1996. Responses of CO2 assimilation, transpiration and water use efficiency to long-term elevated CO2 in perennial C3 xeric loess steppe species. Journal of Plant Physiology 148:356-361.

2398. Mortensen, L. M., and A. Saebo. 1996. The effects of elevated CO2 concentration on growth of Phleum pratense L. in different parts of the growth season. Acta Agriculturaie Scandinavia Section B-Soil and Plant Science 46:128-134.

2401. Jackson, R. B., and A. L. Reynolds. 1996. Nitrate and annomium uptake for single- and mixed species communities grown at elevated CO2. Oecologia 105:74-80.

2403. Fanymeier, A., U. Geuters, U. Hesstein, H. Sandhagel, A. Hoffmann, B. Vermebren, and A. J. Jager. 1996. Effects of elevated CO2, nitrogen supply and tropospheric ozone on spring wheat. 1. Growth and Yields. Environmental Pollution 91:381-390.

2407. Kinball, B. A., P. J. Pinter, R. L. Garcia, R. L. La Mort, G. W. Wall, D. J. Hunsaker, G. WEchsung, F. Wechsung, and T. Kartschall. 1995. Productivity and water use of wheat under free-air CO2 enrichment. Global Change Biology 1:429-442.

2420. Hunt, H. W., E. T. Elliot, J. K. Detling, J. A. Morgan, and D. X. Chen. 1996. Responses of a C3 and a C4 perennial grass to elevated CO2 and temperature under different water regimes. Global Change Biology 2:35-47.

2427. Samarakoon, A. B., and R. M. Gifford. 1996. Elevated CO2 effects on water use and growth of maize in wet and drying soils. Australian Journal of Plant Physiology 23:53-62.

2430. Ruget, F., O. Bethenod, and L. Combe. 1996. Repercussions of increased atmospheric CO2 on maize morphogenesis and growth for various temperature and radiation levels. Maydica 41:181-191.

2440. Frank, A. B., and A. Bauer. 1996. Temperature, nitrogen and carbon dioxide effects on spring wheat development and spikelet numbers. Crop Science 36:659-665.

2441. Read, J. J., and J. A. Morgan. 1996. Growth and partitioning in Pascopyrum smithii (C3) and Bouteloua graciles (C4) as influenced by carbon dioxide and temperature. Annals of Botany 77:487-496.

2443. Polley, H. W., H. B. Johnson, H. S. Mayeux, D. A. Brown, and J. W. C. White. 1996. Leaf and plant water use efficiency of C4 species grown at glacial to elevated CO2 concentrations. International Journal of Plant Sciences 157:164-170.

2444. Bowler, J. M., and M. C. Press. 1996. Effects of elevated CO2 nitrogen form and concentration on growth and photosynthesis of a fast- adn slow-growing grass. New Phytologist 132:391-401.

2448. RowlandBamford, A. J., J. T. Baker, H. L. Allen, and G. Bowes. 1996. Interactions of CO2 enrichment and temperature on carbohydrate accumulation and partitioning in rice. Environmental and Experimental Botany 36:111-124.

2454. Bagash, D. Z., M. J. Paul, M. A. J. Parry, A. J. Keys, and D. W. Lawlor. 1995. Increased capacity for photosynthesis in wheat grown at elevated CO2. The relationship between electron-transport and carbon metabolism. Planta 197:482-489.

2468. Rao, M. V., and L. J. Dekok. 1994. Interactive effects of high CO2 and SO2 on growth and antioxidant levels in wheat. Phyton-Annales Rei Botanicae 34:279-290.

2474. Newbery, R. M., J. Wolfenden, T. A. Mansfield, and A. F. Harrison. 1995. Nitrogen, phosphorus and potassium uptake and demand Agrostis capillaria. The influence of elevated CO2 and nutrient supply. New Phytologist 130:565-574.

2480. Lenssen, G. M., W. E. Vandium, P. Jak, and J. Roxema. 1995. The response of Aster tripolium and Puccinellia maritima to atmospheric carbon dioxide enrichment and their interaction with flooding and salinity. Aquatic Botany 50:181-192.

2492. Schenk, U., R. Manderscheid, J. Hugen, and H. J. Weigel. 1995. Effects of CO2 enrichment and intraspecific competition on biomass partitioning, nitrogen content, and microbial biomass carbon in soil of perennial rye grass and white clover. Journal of Experimental Botany 46:987-993.

2502. Jacob, J., C. Greitner, and B. G. Drake. 1995. Acclimation of photosynthesis in relation to Rubisco and non-structural carbohydrate contents and in-situ carboxylase activity in Scirpus olnei grown at elevated CO2 in the field. Plant, Cell and Environment 18:875-884.

2503. Jongen, M., M. B. Jones, T. Hebeisen, H. Blum, and G. Hendrey. 1995. The effects of elevated CO2 concentrations on the root growth of Lolium perenne and Trifolium repens grown in a FACE system. Global Change Biology 1:361-371.

2504. Kleemola, J., J. Peltonen, and P. Peltonen-Sainio. 1994. Apical development and growth of Barley under different CO2 and nitrogen regimes. Journal of Agronomy and Crop Science 173:79-92.

2510. Demothes, M. A. G., and D. Knoppik. 1994. Effects of long term enhanced CO2 partial pressure on gas exchange parameters and saccharide pools of wheat leaves. Photosynthetica 30:435-445.

2521. Balaguer, L., J. D. Barnes, A. Panicucci, and A. M. Borland. 1995. Production and utilization of assimilates in wheat leaves exposed to elevated O3 and/or CO2. New Phytologist 129:557-568.

2522. Barnes, J. D., J. H. Ollerenshaw, and C. P. Whitfield. 1995. Effects of elevated CO2 and/or O3 on growth, development and physiology of wheat. Global Change Biology 1:129-142.

2525. Hattenschwiler, S., and C. Korner. 1996. System-level adjustments to elevated CO2 in model spruce ecosystems. Global Change Biology 2:377-387.

2531. Owensby, C. E., P. I. Coyne, J. M. Ham, L. M. Avea, and A. K. Knapp. 1993. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO2. Ecological Applications 3:644-653.

2541. Jackson, R. B., O. E. Sala, C. B. Field, and H. A. Mooney. 1994. CO2 alters water use, carbon gain, and yield for the dominant species in a natural grassland. Oecologia 98:257-262.

2547. Baker, J. T., L. H. Allen, and K. J. Boote 1992. Temperature effects on rice at elevated CO2 concentration. Journal of Experimental Botany 43:959-964.

2579. Billes, G., H. Rouhier, and P. Bottner. 1993. Modifications of the carbon and nitrogen allocations in the plant Triticum aestivum L. soil system in response to increased atmospheric CO2 concentration. Plant and Soil 157:215-225.

2580. Baker, J. T., S. L. Albrecht, D. Pan, L. H. Allen, N. B. Pickering, and K. J. Boote. 1994. Carbon dioxide and temperature effects on rice (Oryza sativa L., CV 1R-72). Soil and Crop Science Society of Florida, Proceedings 53:90-97.

2595. Santruce, J., H. Santurckova, J. Kueton, M. Simkoua, and K. Rohacek. 1994. The effect of elevated CO2 concentration on photosynthetic CO2 fixation, respiration and carbon economy of wheat plants. Rostlinna Vyroba 40:689-696.

2597. Ingaurdsen, C., and B. Veierskov. 1994. Response of young barley plants to CO2 enrichment. Journal of Experimental Botany 45:1373-1378.

2644. Reeves, D. W., H. H. Royers, S. A. Prior, C. W. Wood, and G. B. Runion. 1994. Elevated atmospheric carbon dioxide effects on sorghum and soybean nutrient status. Journal of Plant Nutrition 17:1939-1954.

2654. Jackson, R. B., Y. Lou, Z. G. Cardon, O. E. Sala, C. B. Field, and H. A. Mooney. 1995. Photosynthesis, growth and density for the dominant species in a CO2 enriched grassland. Journal of Biogeography 22:221-225.

2666. Samarakoon, A. B., and R. M. Gifford. 1995. Soil water content under plants at high CO2 concentrations and interaction with the direct CO2 effects: A species comparison. Journal of Biogeography 22:193-202.

2669. Schenk, U., A. J. Jager, and H. J. Weigel. 1996. Nitrogen supply determine responses of yeild and biomass partitioning of perennial rye grass to elevated atmospheric carbon dioxide concentrations. Journal of Plant Nurtition 19:1423-1440.

2692. Kimball, B. A., P. J. P. Pinter, R. L. Garcia, R. L. LaMorte, G. W. Wall, D. J. Hunsaker, G. Wechsung, F. Wechsong, and T. Kartschall. 1995. Productivity and water use of wheat under free-air CO2. Global Change Biology 1:429-442.

2698. Potvin, C., and L. Vasseur. 1997. Long-term CO2 enrichment of a pasture community: species richness, dominance, and succession. Ecology 78:666-677.

2709. Hebeisen, T., A. Luscher, and J. Nosberger. 1997. Effects of elevated atmospheric CO2 and nitrogen fertilisation on yield of Trifolium repens and Lolium perenne. Acta Oecologica/Oecologia Plantarum 18:277-284.

2710. Hebeisen, T., A. Luscher, S. Zanetti, B. U. Fischer, U. A. Hartwig, M. Frehner, G. R. Hendrey, H. Blum, and J. Nosberger. 1997. Growth response of Trifolium repens L and Lolium perenne L as monocultures and bi-species mixture to free air CO2 enrichment and management. Global Change Biology 3:149-160.

2711. Ghannoum, O., S. vonCaemmerer, E. W. R. Barlow, and J. P. Conroy. 1997. The effect of CO2 enrichment and irradiance on the growth, morphology and gas exchange of a C3 (Panicum laxum) and a C4 (Panicum antidotale) grass. Australian Journal of Plant Physiology 24:227-237.

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APPENDIX C. FULL LISTING OF COMMENTS.DAT (FILE 6)

Listed are

paper number (**PAP_NO**, as defined in Sect. 9.)
    CO_2 exposure facility
    light
    temperature
    watering
    humidity
    nutrient
    interacting treatment
    biome
    location, and
    comments.

Abbreviations are as described in the body of this report for data files **ndp073.dat** and **ndp073.wk1**.

```
38
     GC
     600+/-90 UE M-2 S-1
     14/10
     24/18
     40 OR 10 ML PL-1 D-1
     0.588235294
     HOAGLAND'S
     H2O
     GRASS
     EU

186

     OTC
     AMB
     AMB
     AMB
     AMB
     AMB
     NONE
     CO2 ONLY
     WETL
     NA

488
     GH
     AMBIENT
     AMBIENT

     FIELD CAPACITY OR NONE
```

```
     NONE
     CO2 AND WATER
     GRASS
     NA
     2ND YEAR; NO TEMP DATA; FIELD PLANTS.

618
     GC
     AMB
     12H
     20/15 C  (DAY/NIGHT)
     WW
     AMB
     NITRATE' SOLUTION
     NONE
     GRASS
     EU
     .

754
     GC
     0.6 MMOL M-2 S-1
     14 H
     "15, 20, 25, 30 DEG C CONSTANT DAY/NIGHT"
     WW
     >50 %
     COMPLETE NUTRIENT SOLUTION ADDED DAILY
     TEMP
     MEAD
     NA
     MAINTENANCE RESPIRATION RECORDED HERE. GROWTH RESPIRATION
      ALSO REPORTED ONE GC PER CO2 TREATMENT

765
     GC
     AMB
     AMB
     .
     WW
     .
     .
     TEMP
     GRASS_C
     NA
     CONTROL: 28/21/25 C;  HI: 40/33/37 C

2066
     GH
     24.8 MOL M-2 D-1
     16 H
     20/14
     .
     .
     COMPLETE FERTILIZER ADDED
     H2O
     GRASS_C
```

AU
TWO VARIETIES USED

2119
GC
700 UMOL M-2 S-1
1/12/00
12/7; 18/13; 28/23
WW
0.4/0.3 +- 0.05 KPA VPD
HALF-STRENGTH HOAGLAND'S
TEMP
GRASS
AU
"USABLE DATA ON 4 SPP ONLY, FOR PN"

2125
OTC
AMB
AMB
AMB
WW DAILY FC
AMB
0.2 MOL M-3 N AND 0.05 MOL M-3 P
CO2 ONLY
GRASS
EU
"OTHER NUTRIENT DATA, EFFICIENCIES - P,"

2132
GC
500 UMOL M-2 S-1
14/10
25/18
WW
50-70
HOAGLAND'S ALTERNATE DAYS
O3
GRASS
NA

2133
OTC
AMB
AMB
AMB
.
.
NPK APPLIED
.
GRASS_C
EU

2158
GC
200 UMOL M-2 S-1
16 H

```
     220
     WW
     0.8
     SURPLUS NUTRIENTS
     NONE
     BOREAL
     EU
     "1 GC AT EACH CO2 LEVEL. QY, RHZWT, LWR, LAR"

2159
     GC
     .6 MMOL M-25-1
     14H
     "15,20,25,30"
     WW
     >50%
     """COMPLETE"" IN DAILY WATER"
     TEMP
     GRASS
     NA

2168
     OTC
     AMBIENT
     AMBIENT
     AMBIENT
     AMBIENT
     AMBIENT
     AMBIENT
     NONE
     GRASS
     NA
     1991 PRECIPITATION: 17.1 CM; 1992 PRECIPITATION: 26.8 CM; SAMPLE
      SIZE INFERRED FROM DESIGN. LFY.MD

2184
     OTC
     AMBIENT
     15-18
     12-Nov
     AMB AND DRIP
     .
     ADDED WITH DRIP WATER; AMT NOT STATED
     HARVEST
     GRASS
     EU
     CLIPPED TO 5CM AT EACH HARVEST

2192
     OTC
     AMB
     AMB
     AMB
     AMB
     AMB
     .
     CO2
```

```
     GRASS
     NA
     "DATA USED FROM LAST MEASUREMENT PRIOR TO SHADING, F2."

2202
     GC
     725-890 UE
     .
     .
     WW
     .
     HOAGLAND'S; 2 G/M2 N WEEKLY
     CLIPPING TO 5 CM
     GRASS
     AF
     C4; SPOROBOLUS KENTROPHYLLUS;  ADDT'L LF NUTRIENTS AVAILABLE IN T1

2208
     GC
     700 UMOL M-2
     12 H
     .
     WW
     AMB
     FERT
     TEMP
     GRASS_C
     NA
     THERE ARE TWO LOLIUM HYBRIDS (2N AND 4N).  EACH ONE WAS TREATED AS A
      SPECIES.

2211
     GH
     ~900 UMOL M-2 S-1
     14/10
     25/16
     WW
     35/90
     NONE
     NONE
     GRASS
     NA

2227
     GC
     600 UMOL M-2 S-1 AT SEEDLING HT
     15/9
     20/15
     WW
     65/70
     0.8 NM NH4NO3 + 50% LONG ASHTON SOLUTION
     "HI N, LOW N"
     GRASS
     EU

2229
     GC
```

```
     AMB
     .
     +4C
     .
     .
     HI/LOW
     TEMP/FERT
     GRASS_C
     EU

2246
     OTC
     AMBIENT
     AMBIENT
     AMBIENT
     WW
     AMBIENT
     "WEEKLY 1/5 MODIFIED LONG ASHTON- 0.2 MOL M-3 N, 0.05 MOL M-3 P"
     NONE
     GRASS
     EU
     "NAR, LAR, LWR"

2300
     GC
     800 UMOL/M2S ACTIVE RADIATION
     18 H
     15 C
     WATERED DAILY TO SATURATION
     .
     HALF-STRENGTH MODIFIED HOAGLAND SOLUTION WITH AMMONIUM NITRATE AND P
      CONCENTRATION OF 32 PPM
     "SOIL TEMPERATURE (5,15, AND 25 C)"
     TUNDRA
     NA
     THIS STUDY FOCUSES ON THE EFFECTS OF SOIL TEMPERATURE. RATE OF PO4
      ABSORPTION WAS LEFT OUT.

2312
     GC
     615 UE (603-621)

     23/11
     100 ML EACH 3 D
     NOT CONTROLLED
     C= HOAGLAND'S  T=HOAGLAND'S + UREA (40 G/M2)
     "UREA, CLIPPING"
     GRASS
     NA
     RINSED SAND;  CONTROLS HAD HOAGLAND'S

2315
     GH
     AMB/SEASONAL
     AMB/SEASONAL
     AMB/SEASONAL
     SEASONAL; SUMMER WW/DEFICIT
```

.
N-= 160 KG/HA YR; N+=530 KG/HA YR
"N HI, LO"
GRASS
EU
2 YR STUDY; MICROCLIMATE DETAILS AVAIL. PKS ALSO APPLIED. DATA USED FROM SUMMER DROUGHT ONLY.

2316
GH
AMB
AMB
AMB
IRRIGATION AT AMB LEVELS
AMB
160 OR 530 KG N HA-1 YR-1
FERT
GRASS
EU
"PLASTIC TUNNELS. SWARDS, SOWN. PERIODIC CLIPPING OF ALL PLOTS."

2329
OTC
REDUCED ~20%
AMB
"AMB + 1-2 DAY, 0-1 NIGHT"
WW
.
NPK; 600 KG N/HA FOR SEASON
CLIPPING
GRASS
EU
SOWN IN GROUND. DATA FROM 2 GROWING SEASONS. CO2 TMNT YR-ROUND

2330
OTC and GC
"OTC= AMBIENT, GC NOT AVAILABLE"
"OTC=AMBIENT, GC=NOT AVAILABLE"
"OTC= AMBIENT, GC= FOLLOWED AMBIENT"
"OTC= AMBIENT, GC= EVERY 1-3 DAYS"
"OTC= AMBIENT, GC= NOT AVAILABLE"
GROWTH CHAMBERS; 5-10-15 NPK PLUS MICRONUTRIENTS. 2 ML/H EVERY TWO WEEKS
COMPETITION AND METHOD (OTC AND GC)
GRASS
NA
"GC (PH = 6.5) PHOTOPERIOD, LIGHT AND HUMIDITY ARE REPORTED IN WANT, LECHOWICZ AND POTWIN (1994). COMPETING SPECIES (TRIFOLIUM REPENS, POA PRATENSIS, PHLEUM PRATENSE, AGROSTIS STOLONIFERA) NO INDIVIDUAL POTS."

2337
OTC
AMB
AMB
AMB; X=11.3
DRIP
AMB
"YES, UNKNOWN"

NONE
MEAD
EU
COMMON SPP + CULTIVARS; NORWAY; MARITIME

2341
OTC
AMB
AMB
AMB
AMB/WW
AMB
NPK 1.5:1:1.5; =40 KG N HA-1 Y-1
"CO2, NUTRIENTS"

EU
3 YR EXP. OTCS UP 98-108 D Y-1. SOME DATA ALSO FROM YEARS 1 & 2

2342
OTC
AMBIENT
AMBIENT
AMBIENT
AMBIENT
AMBIENT
"N, P, K 20 G M-2, 120 DAY TIME-RELEASE OSMOCOTE"
"ADDITIONAL NUTRIENTS N, P, K"
GRASS
NA
MONOCULTURES OF SIX SPECIES AND ONE MIXED COMMUNITY. SERPENTIME SOIL

2345
otc
amb
AMR
AMB; AMB +3
WW
.
NPK + NUTRIENTS
TEMP
GRASS
EU
OTCS PLACED IN GH FOR WARMING

2347
OTC
AMB
AMB
AMB
AMB
AMB
NONE
CO2 ONLY
GRASS
NA
JASPER RIDGE

2350
GH
AMB
AMB
17
WW
.
7 G M-2 N; 5 G M-2 P; 7 G M-2 K
CLIPPING EVERY 4 WK
GRASS
EU
"ALSO INCLUDED TEMP, CO2 X TEMP, MIXTURES OF SPP"

2351
GC
700 UMOL M-2 S-1
12
12/7; 18/13; 28/23
WW
.
HALF-STRENGTH HOAGLAND'S GX D-1
TEMP
GRASS
AU
GROWN IN STERILE SAND

2357
OTC
AMB
AMB
AMB
AMB
AMB
OSMOCOTE: 20 G M
NUTRIENTS
GRASS
NA
JASPER RIDGE

2358
GH
AMB; 640 UMOL M-2 S-1
AMB; 640 UMOL M-2 S-1
13-26
WW
0.08
13 G N M-2; 3.18 G P M-2; 10.61 G K M-2
TEMP (+4)
GRASS
EU
GERMINATION IN POTS IN FIELD; CO2 BEGAN AFTER ~6.5 MONTHS

2362
GH
AMB
AMB
13;10

WW
.
NOT LIMITING
NONE
GRASS
EU
TUNNELS = GH

2363
GC
552 UMOL M-2 S-1
14 H
26/21
WW
60-70%
HALF STRENGTH HOAGLAND'S; N=6 OR .5 mM
O3 + FERT
GRASS
NA
"OZONE = 3 +/- .3, 92 +/- .4 nMOL MOL-1; FERT = 6 OR .5 nM N. MACRONUTRIENTS SAME FOR HI/LO FERT TMNT."

2364
FACE
AMB
.
.
.
.
.
.
GRASS_C
EU
MINIFACE

2366
OTC
89% OF AMB
AMB
32 / 24.9
WW
.
.
FERT
GRASS_C
AS
NO SUPPLEMENTAL N

2367
OTC
AMB
AMB
AMB
WW
.
IRRIGATED WITH NUTRIENT ENRICHED WATER
NONE

```
     GRASS_C
     EU
     .

2369
     GH
     AMB
     AMB
     29/21 OR 37/29
     WW
     70 +/- 5
     PROVIDED
     WETL
     WETL
     AS
     29/21= CTL;  37/29 = HI TEMP (PC.1354).  17 CULTIVARS TREATED AS REPS

2372
     FACE
     AMB
     AMB
     "AMB/AMB+2.5, 18-30"
     WW
     AMB
     7 G N M-2
     TEMP
     GRASS
     EU
     "TEMP INCREASE USING INFRA-RED LAMPS ALL MATERIAL CLIPPED PRIOR
      TO START OF TEMP TMT.  EFFECTIVE CO2 DURATION USED.  12- AGWT, LFN, PN"

2379
     GC
     AMB
     AMB
     AMB
     .
     .
     .
     NONE
     GRASS_C
     EU
     10 CULTIVARS TREATED AS REPS.

2383
     GH
     .
     AMB
     AMB AND AMB+4
     WW
     .
     FERTILIZED
     TEMP
     GRASS_C
     EU

2387
```

```
     GH
     AMB- ~MAX=800 UMOL M-2 S-1
     "16, W LIGHTS"
     18/10-24/18
     WW 1X WK-1
     .
     NO ADDITIONAL
     "330, 500, 660  UL L-1 CO2"
     GRASS
     EU
     "CALCEROUS GRASSLAND. SPP AND ECOSYS 76 PLANTS/ CONTAINER
      REPRESENTING FIELD %, PESTICIDES USED."

2395
     OTC
     AMB
     AMB
     AMB
     WATERED OCCASIONALLY
     AMB
     .
     .
     GRASS
     EU
     THE SPECIES GROW IN A XERIC TEMPERATE LOESS STEPPE.

2398
     OTC
     AMB
     AMB
     AMB (~11)
     WW
     . .
     "ADDED, BUT NOT SPECIFIC; SEE TEXT."
     SEASONALITY
     GRASS
     EU
     USING GRAND MEANS AND SE ONLY; NOT USING SEASONAL DATA.

2401
     OTC
     AMB
     AMB
     AMB
     WW
     AMB
     LOW/HI NPK
     FERT
     GRASS
     NA

2403
     OTC
     AMB
     AMB
     AMB
     WW
```

```
     .
     150 KG N HA-1 AND 270 KG N HA-1
     FERT/OZONE
     GRASS_C
     EU

2407
     FACE
     AMB
     AMB
     3 C LESS THAN AMB
     WW + DROUGHT
     .
     .
     H2O
     GRASS_C
     NA
     .

2420
     GC
     550 UMOL M-2 S-1
     SEASONAL
     SEASONAL
     WW
     .
     NONE
     TEMP
     GRASS
     NA
     "WATER TMT ALSO, BUT NOT USED IN DATASET. ""WINTER"" TEMP = 3"

2427
     GH
     AMB + SUPPL (28.4 MOL M-2 S-1)
     16
     28/22
     WW/DRY
     .
     5KG M-3 15:10:10:2 NPK MG 3 MO RELEASE
     H2O
     GRASS
     AU

2430
     GH
     AMB 2-3.9 MJ M-2 D-1
     AMB
     19 - 22.5
     WW
     .
     SUPPLEMENTED
     NONE
     GRASS
     EU
     NOT USING 1992 DATA
```

```
2440
     GC
     1115 UMOL M-2 S-1
     16/8
     25/15
     WW
     .
     N= 0 OR 300 KG HA-1;  P= 56 KG HA-1; K= 46 KG HA-1
     "FERT, TEMP"
     GRASS
     NA

2441
     GC
     1000 UMOL M-2 S-1
     12/12/98
     "DAY 20, 35; NIGHT 15"
     WW
     60/~100
     HALF STRENGTH HOAGLAND'S; =400 UL L-1 N
     TEMP 20 = CTL
     GRASS
     NA

2443
     GH
     SEASONAL
     SEASONAL
     SEASONAL
     WW
     .
     HOAGLAND'S + - N;  SEE METHODS AND RESULTS
     NONE.  SEE RESULTS
     GRASS
     NA
     "N HAD NO EFFECT ON PN, OR APPARENTLY ON TOTWT"

2444
     GC
     600 UMOL/M2S PFD
     15 H
     20/15 DEGREES C
     WW
     "65/70 % (DAY,NIGHT)"
     "NITROGEN CONCENTRATIONS (.01, .1, 1.0, AND 5.0 MG N/L)"
     NITROGEN CONCENTRATIONS BY N SUPPLY (AMMONIUM OR NITRATE)
     GRASS
     EU
     SAMPLE SIZE OF GAS EXCHANGE MEASUREMENTS WAS USED FOR ALL MEASUREMENTS
      BECAUSE IT WAS THE ONLY ONE AVAILABLE. AGROSTIS CAPILLARIS IS A FAST
      GROWING GRASS.  NARDUS ESTRICTA IS A SLOW GROWING GRASS.

2448
     GC
     AMB
     AMB
     AMB
```

WW
.
.
TEMP
GRASS_C
NA
.

2454
GC
AMB
14 HR
AMB
WW
60-70%RH
NUTRIENTS SUPPLEMENTED TWICE A WEEK
NONE
GRASS
EU
.

2468
GC
200 UMOL M-2 S-1
14H
19/15 C
.
.
.
.
GRASS_C
EU
ANOTHER SET OF DATA (CO2 * SO2) CAN BE EXTRACTED

2474
GH
AMBIENT
AMBIENT
.
WW
.
MODIFIED HOAGLANDS
"N= 5, 20, OR 50 MG L-1; P= 2, 11, OR 30 MG L-1; K=5, 20, 50 MG L-1"
GRASS
EU
"CO2= AMB, AMB+250...1:1 SAND:PEAT;   DATA TAKEN FROM P=3 + K=3 ONLY. AGN, AGC, AGK, AGP"

2480
GH
200 UMOL M-2 S-1
14 H
25/18
"WW, FLD"
.
NATIVE SOIL
"FLD, SALT"

WETL
EU
PLANTS ROTATED BETWEEN 2 GHS

2492
GC
220-250 UMOL M-2 S-1
14/10
23.5/19
80% OF FIELD CAPACITY
30/55
"194 MG N, 13 MG P, 24 MG K, 39 MG MG POT-1"
DENSITY
GRASS
EU
"USING LOWEST AND HIGHEST DENSITIES ONLY, AS REPS"

2502
OTC
AMB
AMB
AMB
PRECIP
AMB
NONE
NONE
WETL
NA
"SAME PARAMETERS WERE MEASURED AT DIFFERENT YEARS AND/OR THE SAME YEAR, BUT DIFFERENT MONTHS. EACH MONTH AND/OR YEAR WAS CONSIDERED A SEPARATE DATA POINT BECAUSE TIME OF EXPOSITION CHANGED. THE PAPER INCLUDES DATA ON LEAF RUBISCO AND LEAF SOLUBLE PROTEIN."

2503
FACE
AMB
AMB
SEASONAL; -5-25
AMB
SEASONAL
N (100 OR 420 KG HA-1 Y-1); 120 KG HA-1 P205; 240 KG HA-1 K2O; 16 KG HA-1 MGO
FERT: 100 OR 420 KG N HA-1 Y-1
GRASS
EU
OOT IN GROWTH BAGS. ETHANOL SOLUBLE TNC USED IN DATABASE. WATER-SOLUBLE TNC ALSO AVAILABLE.

2504
GH
AMB; 180 UMOL M-2 S-1 + 100 UMOL M-2 S-1
16/8
20
WW
.
HI N=54 G M-2; LO N=9.5 G M-2; + OTHER NUTRIENTS
FERT

```
     GRASS
     EU
     .

2510
     GC
     AMB
     .
     AMB
     WW
     AMB
     FERTILIZED WEEKLY
     .
     .
     EU

2521
     GC
     500 UMOL M-2 S-1
     13.5 H
     23/17
     WW
     60-70
     .
     OZONE
     GRASS_C
     EU
     .

2522
     GC
     500 UMOL M-2 S-1
     14/10
     24/14
     WW
     65+/-5
     INITIAL AND EVERY 21 DAYS
     O3
     GRASS
     EU

2525
     OTC
     AMB
     AMB
     AMB
     WW
     AMB
     .
     .
     WETL
     NA
     CARBON CONTENT WITH SE/SD & N; ADDT'L VAR

2531
     OTC
     AMB - 11%
```

AMB
AMB
AMB
AMB
NONE
NONE
GRASS
NA
CO2 FROM APRIL/ MAY THRU OCT EACH OF 3 YRS

2541
OTC
AMB
AMB
AMB+
AMB
AMB
NO ADDITIONAL
CO2
GRASS
NA
"JASPER RIDGE. GS, E, LFY, PN, SEEDS, HT, AGWT, WVE, DNSITY, ISOTOPE, SEED WT, FRUITWT, SEED C, SEED N."

2547
GH
AMB
AMB
28/21/25(H20)
WW
.
NPK INITIAL; VARIABLE N ADDED DURING SEASON
CO2 ONLY APPROPRIATE
WETL
NA

2579
GC
1000 UMOL M-2 S-1
16/8
23/16
WW
70-80
ALL: 4.6 MG P; 5.8 MG K; N= 0 OR 32 MG POT-1
FERT
.

.

2580
GH
amb
amb
32/23; 35/26; 38/29
ww
.
"12.6, 6.3, 6.3, G N M-2 AT 7, 31 + 63 D"

```
     NONE
     WETL
     NA
     .

2595
     GC
     350 UMOL M-2 S-1
     15/9
     20/17
     WW
     .
     .
     .
     .

     .

2597
     GH
     AMB
     AMB
     AMB
     WW
     .
     .
     NONE
     GRASS_C
     EU
     .

2644
     OTC
     AMB
     AMB
     AMB
     WW
     .
     101 KG N HA-1; SEE ALSO T1
     NONE
     GRASS
     NA

2654
     OTC
     AMB
     AMB
     AMB
     AMB
     AMB
     AMB
     NONE
     GRASS
     NA
     JASPER RIDGE

2666
```

GH
AMB 25-29 MOL M-2 D-1
16 H
20/14
WW / DRY
.
SOLUBLE OR SLOW RELEASE ADDED
H2O
GRASS_C
AU

2669
GC
220-250 UMOL M-2 S-1
14/10
17-Dec
WW
0.571428571
N: 0 OR 765 MG POT-1; 114 MG P; 193 MG K; 26 MG MG
FERT
GRASS
EU
USING ONLY CTL; HIGHEST FERT LEVELS

2692
FACE
AMB
AMB
32/23; 35/26; 38/29
WET/DRY
AMB
NON-LIMITING; REPEATED APPLICATIONS
H2O
GRASS
NA
DRY = HALF OF WET (WW). USE WET AS CTL

2698
OTC
AMB
AMB
AMB
AMB
AMB
NONE
NONE
GRASS
NA
"SUM Y EXPERIMENT. 2 OTC'S W/ CO2, OTC'S - CO2"

2709
FACE
AMB
AMB
AMB
.
.

.
FERT/COMP
GRASS
EU
TIME ASSUMED TO BE 730 BECAUSE AGWT WAS SUM OF TWO SEASONS

2710
FACE
AMB
AMB
AMB
AMB
AMB
LO: 10-14 G N M-2 Y-1; HI: 42-56 G N M-2 Y-1
DEFOL: 4 OR 7-8 Y-1; FERT
GRASS
EU
MET IN TABLE 1

2711
GH
9.2 + 24.9 MOL M-2 S-1
AMB
30/25
WW
>90
"30 MG N POT-1 + 60 G N POT-1, SEASONALLY"
LIGHT
GRASS
AU

2715
GC
300 UMOL M-2 S-1
16/8
18/4
WW; 14% H20
0.928571429
28 MG P + 50 MG K KG-1 + N TREATMENTS
N 8KG N HA-1 OR 278 KG N HA-1
GRASS
EU

2718
GC
794
AMB
25/13 (DAY/NIGHT)
WW
AMB
HOAGLAND'S SOLUTION EVERY 3 D
DEFOL
GRASS
NA
.

2723

```
     GH
     85-90% AMB
     14-H
     AMB/AMB + 3 C
     WW
     AMB
     .
     TEMP
     .
     EU
     GS WITH NO SE/SD.  Vc MAX WITH SE/SD AND N IN FIG. 4

2735
     GH
     AMB
     AMB
     "AMB, AMB+4"
     WW
     AMB
     10 G M-2 N; 15 G M-2 P; 15 G M-2 K
     TEMP
     GRASS
     EU
     80% OF UVB

2737
     GH
     25 MOL M-2 DAY-1
     16/8
     17
     WW
     65
     "COMPLETE, INCLUDE 188 MG L-1 N"
     "O3, SOIL"
     GRASS
     EU
     O3 NOT USED FOR PHYL DATASET

2756
     OTC
     AMB
     AMB
     AMB
     AMB + DROUGHT
     AMB
     NONE
     H2O
     GRASS
     NA
     "UNDISTURBED TALL GRASS PRAIRIE; EARLY, MID + LATE SEASON DATA; EXP. RAN
      4Y PRIOR TO THIS STUDY"

2758
     OTC
     AMB
     AMB
     AMB
```

```
     .
     .
     .
     NONE
     GRASS
     EU
     .

2785
     OTC
     AMBIENT
     AMBIENT
     AMBIENT
     AMBIENT
     AMBIENT
     HI FERT TRT ONLY
     FERT. 20 G M-2 NPK OSMOCOTE
     GRASS
     NA
     JASPER RIDGE. SERPENTINE SOIL

2793
     OTC
     AMB
     AMB
     AMB
     AMB
     AMB
     .
     .
     GRASS
     EU
     MINI-RHIZOTRONE. DATA USED FROM 10 CM

2802
     GH (TUNNEL)
     AMB
     AMB
     0.3 C HIGHER DURING DAY;  0.2 C LOWER AT NIGHT
     .

     .
     FERT
     GRASS
     EU
     .

2821
     GH
     79% OF AMB
     AMB
     AMB
     WW
     .
     8 G N M-2 PER 24 DAYS
     CO2
     GRASS
```

EU

2834
GC
750 UMOL M-2 S-1
16/8
16
WW
0.54 KPA
0.2 OR 2.5 MOL M-3 N; 0.04 OR 0.5 MOL M-3 P
LOW N+LOW P OR HI N + HI P
GRASS
EU
"P, OTHER MINERALS"

2835
GC
1000 UMOL M-2 S-1
16
30/20
WW
0.0025
"HOAGLAND'S, ALTERNATE WATERING"
.
GRASS
NA

2839
OTC
85% OF AMB
AMB
"25/29 (AMB, AMB+4)"
WW
.
220 KG N HA-1
TEMP
WETL
AS

2855
GH
AMB+
16/8
20/15
WW
70
NPK (HOAGLAND'S) OR 0.1 N (MODIFIED HOAGLAND'S)
FERT
GRASS
EU

2856
GH
AMB
AMB
26/16 C DAY/NIGHT
WW

```
     .
     .
     FERT
     GRASS_C
     AS
     .

2892
     GC
     645 UMOL M-2 S-1
     16/8
     24/18
     WW
     .
     MODIFIED SHIVE'S SOLUTION
     O3
     GRASS
     EU
     TIME FOR BIOMASS ASSUMED > 42 D; SEE FIG 6

2893
     OTC
     AMB
     AMB
     19
     WW
     67-71%
     0.4 G L-1 N; 0.3 G L-1 P205; 0.4 G L-1 K20
     NONE
     GRASS_C
     EU
     INTRODUCED IN 1890

2895
     OTC
     AMB
     AMB
     AMB
     AMB
     .
     .
     NONE
     GRASS
     NA

2911
     OTC
     AMB
     AMB
     AMB
     AMB
     AMB
     AMB
     O3
     GRASS
     EU
     CTL O3 = 26-29  NMOL MOL-1; HI O3= 84 NMOL MOL-1 AVE FOR ALL DAYS
```

```
2919
     GC
     AMB
     AMB
     15 C MEAN
     .
     .
     "150 MG N, 18.1 MG P AND 34 MG K"
     H20
     GRASS_C
     EU

2924
     GH
     AMB; PN >1200 UMOL M-2 S-1
     AMB
     32/23; 35/26; 38/29
     WW
     .
     "P, K= 9 G M-2; N (UREA) 12.6-6.3 G M-2 X3 DATES"
     TEMP
     WETL
     NA

2928
     OTC
     85% OF AMB
     AMB
     X= 25; AMB+4
     WW
     .
     N: 110 KG HA-1 WET SEASON;  220 KG HA-1 DRY
     TEMP
     WETL
     AS
     DATA ON DEVELOPMENT STAGES

2935
     OTC
     AMB
     .
     28/21 (DAY / NIGHT)
     .
     .
     .
     H2O
     GRASS_C
     NA
     SPAR:  SOIL-PLANT-ATMOSPHERE-RESEARCH CHAMBER

3034
     GC
     1000 UMOL M-2 S-1
     14/10
     28/22; 24/18; 21/25
     WW
     70
```

```
     .
     TEMP. NOTE ECOTYPES
     GRASS
     NA
     "TEMPS: MISS:  CTL=28, L0=2, . ;  N.C: CTL=24, LO=21, HI=28;  QUEBEC:
      CTL=21, . , HI =28"

3033
     GC
     65 UE M-2 S-1
     14/10
     28/22
     WW
     0.7
     HALF STRENGTH HOAGLANDS
     NONE
     MIXED
     NA

3035
     GC
     1000 UMOL M-2 S-1
     14/10
     28/22; 24/18; 21/15
     WW
     70
     .
     TEMP NOTE ECOTYPES
     GRASS
     NA
     "TEMPS:  MISS: CTL=28, LO=21, . ;  N.C: CTL=24, LO-21, HI=28;  QUEBEC:
      CTL=21, . ,       HI=28"

3036
     GC
     150 OR 1000 UMOL M-2 S-1
     14/10
     29/23
     WW
     70
     HALF STRENGTH HOAGLANDS
     LIGHT
     GRASS
     NA

3038
     GH
     AMB
     AMB
     34
     WW
     .
     .
     NONE
     GRASS
     NA
     MIXED AND UNMIXED CULTURES
```

```
3042
     GH
     AMB; 2ME M-2 S-1
     AMB
     32/20
     WW
     50-70
     "4 LEVELS OF HENITTS:  24,12, 4, OR MM NITRATE"
     FERT
     GRASS_C
     NA
     ONLY MAIZE DATA WERE TAKEN

3401
     GH
     AMB + LOW INTENSITY INCANDESCENT
     1/16/00
     28/23
     "AT PLANTING ONLY, DRYING THEREAFTER"
     60-70
     ..
     H20
     GRASS
     AU
     ASSUMING THAT TIME COURSE FOR WATER LOSS IS SIMILAR FOR ALL GRASS SPECIES
      (USING WHEAT (COMPANION PAPER)); WE USE TIME CLASSES FOR ANALYSES.
```

APPENDIX D: REPRINT OF PERTINENT LITERATURE

Wand, S. J. E., G. F. Midgley, M. H. Jones, and P. S. Curtis. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a test of current theories and perceptions. *Global Change Biology* 5:723-741.

Global Change Biology (1999) 5, 723–741

Review Article

Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: a meta-analytic test of current theories and perceptions

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Abstract

C4 plants contribute ≈20% of global gross primary productivity, and uncertainties regarding their responses to rising atmospheric CO_2 concentrations may limit predictions of future global change impacts on C4-dominated ecosystems. These uncertainties have not yet been considered rigorously due to expectations of C4 low responsiveness based on photosynthetic theory and early experiments. We carried out a literature review (1980–97) and meta-analysis in order to identify emerging patterns of C4 grass responses to elevated CO_2, as compared with those of C3 grasses. The focus was on nondomesticated Poaceae alone, to the exclusion of C4 dicotyledonous and C4 crop species. This provides a clear test, controlled for genotypic variability at family level, of differences between the CO_2-responsiveness of these functional types. Eleven responses were considered, ranging from physiological behaviour at the leaf level to carbon allocation patterns at the whole plant level. Results were also assessed in the context of environmental stress conditions (light, temperature, water and nutrient stress), and experimental growing conditions (pot size, experimental duration and fumigation method).

Both C4 and C3 species increased total biomass significantly in elevated CO_2, by 33% and 44%, respectively. Differing tendencies between types in shoot structural response were revealed: C3 species showed a greater increase in tillering, whereas C4 species showed a greater increase in leaf area in elevated CO_2. At the leaf level, significant stomatal closure and increased leaf water use efficiency were confirmed in both types, and higher carbon assimilation rates were found in both C3 and C4 species (33% and 25%, respectively). Environmental stress did not alter the C4 CO_2-response, except for the loss of a significant positive CO_2-response for above-ground biomass and leaf area under water stress. In C3 species, stimulation of carbon assimilation rate was reduced by stress (overall), and nutrient stress tended to reduce the mean biomass response to elevated CO_2. Leaf carbohydrate status increased and leaf nitrogen concentration decreased significantly in elevated CO_2 only in C3 species.

We conclude that the relative responses of the C4 and C3 photosynthetic types to elevated CO_2 concur only to some extent with expectations based on photosynthetic theory. The significant positive responses of C4 grass species at both the leaf and the whole plant level demand a re-evaluation of the assumption of low responsiveness in C4 plants at both levels, and not only with regard to water relations. The combined shoot structural and water use efficiency responses of these functional types will have consequential implications for the water balance of important catchments and range-

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lands throughout the world, especially in semiarid subtropical and temperate regions. It may be premature to predict that C4 grass species will lose their competitive advantage over C3 grass species in elevated CO_2.

Keywords: C4 grasses, C3 grasses, climate change, elevated CO_2, gas exchange and growth responses, meta-analysis

Received 2 October 1998; resubmitted and accepted 5 January 1999

Introduction

The effects of atmospheric CO_2 enrichment have been studied in great detail for agricultural crops (Cure & Acock 1986), trees (Ceulemans & Mousseau 1994), and other plant types (Bazzaz 1990; Poorter 1993; Idso & Idso 1994). The great majority of these studies have been carried out on C3 species. Much of the early research into CO_2-responses of C4 species focused on weedy and old-field dicotyledonous (dicot) species (e.g. *Amaranthus* sp., Bazzaz & Carlson 1984), or important planted C4 crop species (e.g. *Zea mays* and *Sorghum* sp., Morison & Gifford 1984). Despite the fact that about half of the world's grass species possess the C4 photosynthetic pathway, fewer studies have tested the responses of wild temperate C4 grasses to elevated CO_2, and only a handful have used tropical C4 grasses. These plants account for ≈ 18% of the total global productivity, mainly due to the extensive grasslands and savannas of the tropics (Ehleringer *et al.* 1997), but they also play an important role in mixed temperate grasslands such as the North American prairies. Lloyd & Farquhar (1994), using a modelling approach based on ^{13}C discrimination, estimated a contribution of 21% by C4 plants to global gross primary productivity (GPP) under current atmospheric conditions. Any changes in C4 productivity driven by CO_2 and other climatic perturbations will, consequently, have a substantial impact on global GPP.

By far the greatest proportion of C4 species are monocotyledonous (monocot), whereas C4 dicots are relatively uncommon, both in terms of species representation and abundance (Ehleringer *et al.* 1997). Many C4 dicots are noxious weeds and old-field invaders, and gain importance only in disturbed sites. Thus, studies using C4 dicots and bred crops may not represent the potential CO_2-responsiveness of natural, relatively undisturbed ecosystems with a significant C4 monocot component, such as prairies, tropical grasslands, and savannas. Nevertheless, results obtained from many of these studies, and from the first field-based study of a C4-containing ecosystem, a salt marsh on Chesapeake Bay (Curtis *et al.* 1989), appeared to confirm the theory that C4 plants should not show significant growth responses to elevated CO_2, due to their CO_2-concentrating mechanism in the bundle sheath cells (Osmond *et al.* 1982; Pearcy & Ehleringer 1984; Bowes 1993). This mechanism increases the effective concentration of CO_2 at the site of carboxylation, thereby masking photorespiration and apparently ensuring saturation of photosynthesis at current atmospheric CO_2 concentrations. It follows, in theory, that C4 plants should not benefit from increased atmospheric CO_2 availability, and may suffer reduced competitive advantage over C3 species (Bazzaz 1990; Bowes 1993; Ehleringer & Monson 1993). As a result of this common perception, the potential contribution of C4-dominated ecosystems to the global carbon budget in a future high-CO_2 environment, especially in the highly productive tropics, has been largely discounted or ignored.

It is now becoming increasingly clear that the response of C4 species to elevated CO_2 is not as clearcut as previously thought (Henderson *et al.* 1994), and that many C4 plants show significant photosynthetic and growth responses to CO_2. In a recent review, Poorter (1993) found an average growth enhancement of 22% for C4 species. Owensby *et al.* (1993) have also reported significant above-ground biomass increases in the C4 component of a tall-grass prairie site exposed to elevated CO_2. This was explained by the reduced water loss under high CO_2 of C4 species relative to competing C3 species, especially during a dry year. However, there also appears to be a primary direct enhancement of photosynthetic activity in elevated CO_2 in a number of C4 species (Sionit & Patterson 1984; Knapp *et al.* 1993), suggesting that the assumption of photosynthesis saturation at current CO_2 concentration may need to be re-evaluated.

Interacting environmental stresses can influence the response to elevated CO_2 in plants (Idso & Idso 1994; Curtis 1996; Lloyd & Farquhar 1996; Curtis & Wang 1998), and may do so differentially for different functional types. The literature of C4 responses to elevated CO_2 shows that environmental factors, especially those known to be of importance to C4 productivity and biogeographic distributions (high minimum temperatures and high light levels), may influence the relative CO_2-response. Responses of C4 species under stressful conditions may not emerge clearly from experiments employing growth conditions optimal for C3 plants. These factors could account for some of the poor responses to high CO_2 previously reported for environmentally controlled experiments, as opposed to significant responses measured more recently under natural field conditions (Owensby *et al.* 1993).

The purpose of this review is to assess critically from the literature, using meta-analytic methods (e.g. Curtis 1996; Curtis & Wang 1998), the physiological and growth responses of wild C4 grass species (family: Poaceae) to elevated atmospheric CO_2. To enable a critical test of current theories and perceptions, a similar literature review was carried out for the CO_2-responses of wild C3 grass species (Poaceae). This provides a clear comparison, controlled for genotypic and morphological variability. The influences of exposure and growth conditions were also analysed, in order to determine whether current understanding of the relative responses of C3 and C4 species, and resulting uncritical extrapolation to natural environments, may be biased by experimental conditions very different from natural conditions.

Materials and methods

Database compilation

The data analysed in this study were taken from published sources by investigators at the National Botanical Institute, South Africa, and the CO_2 Meta-Analysis Project, Ohio State University, USA. In cases where the two individual databases overlapped, data were used from the CO_2 Meta-Analysis Project only. Non-overlapping data were checked for consistency. The studies addressing C4 pathway grass species that were included in our analyses were as comprehensive as possible for all years (1980–97), while the studies addressing C3 pathway grass species were as comprehensive as possible for 1991–97, with most studies from 1980 to 1990 also included. The following criteria were used for incorporation of studies in the database:

(a) The species was wild or semiwild, a member of the family Poaceae, and the photosynthetic pathway (C3 or C4) was either clearly stated or otherwise unambiguous.

(b) Only data which included response means, sample sizes (N), and either standard deviation (SD) or standard error (SE) were used, since a weighted meta-analysis gives a more robust analysis than if resampling tests must be used to estimate variances or if an unweighted analysis is used (Rosenberg *et al.* 1997).

(c) The paper was published between 1980 and 1997.

(d) The ambient CO_2 treatment concentration was between 300 and 400 $\mu mol\ mol^{-1}$, and the elevated CO_2 treatment was between 550 and 750 $\mu mol\ mol^{-1}$.

(e) Data were presented for individual plants, or for individual species where plants were grown in stands or in mixture with other species.

(f) Only absolute data were used, not relative data such as relative growth rates.

(g) At least one of the following parameters was measured:

- *A*: Leaf-based light-saturated net CO_2 assimilation rates measured at the growth CO_2 concentration
- G_S: Leaf-based stomatal conductance measured at the growth CO_2 concentration
- WUE: Instantaneous leaf water use efficiency at the growth CO_2 concentration, either published as such or calculated from net CO_2 assimilation rates and transpiration rates
- TOTWT: Total plant biomass, either presented as such or calculated as the sum of above-and below-ground biomass.
- AGWT: Above-ground biomass
- BGWT: Below-ground biomass
- INDLA: Individual leaf area
- TILLERS: Number of tillers
- SLA: Specific leaf area either presented as SLA, or calculated as the inverse of specific leaf mass
- TNC: Concentration of total nonstructural carbohydrates in leaves, either presented as such or calculated as the sum of total sugar and starch concentrations, and expressed on a dry mass basis
- N: Leaf total nitrogen concentration expressed on a dry mass basis

The responses at elevated and ambient CO_2 were extracted either from tables, or manually digitized from figures. Where the interaction between CO_2 treatments and deliberately imposed light, temperature, water, or nutrient stress treatments was reported, the CO_2-response was entered separately under both levels of the stressful environmental factor. For those analyses testing a response to stress, all possible data in which plants were not stressed were included as controls for the meta-analysis ('no stress'), rather than only the data for nonstressed plants in studies reporting the response under intentional factorial stress treatments (controls within those studies). This necessitated careful decisions about how to code some treatment responses. For example, we determined that 'high nutrient levels' or normal nutrient levels (comparable to the field situation) were equivalent to 'no nutrient stress', and that 'high light levels' or light levels which were deemed normal or sufficiently high, were similarly equivalent to 'no light stress'. In these instances, we recorded 'none' for the level of stress. Furthermore, we utilized only the extreme levels of any given stress. That is, we included only 'low nutrients' (nutrient stress) and 'high nutrients' (no nutrient stress, or normal) in our analyses, and did not include intermediate levels (e.g. 'medium nutrient levels'). Studies which provided data on interactions with environmental stresses are identified in Appendix 3 (C3) and Appendix 4 (C4).

Where additional environmental stresses (such as salinity or ozone treatments) were imposed factorially, only the CO_2-response at the ambient, nonstressful level of this other factor was used. Unintentional stresses were not taken into account, except in the case of separately reported data for wet and dry years in some prairie studies. Where competition treatments were intentionally and differentially imposed, only the CO_2 response at the lowest level of competition was used.

Response parameters were combined whenever appropriate in order to overcome the problem of low sample sizes. For example, rather than differentiate between what some authors termed root biomass and others termed below-ground biomass, we pooled these data and report them as below-ground biomass. Thus, while we lost some potential detail in the analysis, we improved our ability to generalize and distinguish among effects (Gurevitch & Hedges 1993).

In order to test for potential influences of exposure methodology on the responses to elevated CO_2, the following categorical variables were assigned to each data entry:

(i) Pot size: ≤ 10 L, > 10 L, or in-ground. These size classes have been previously used in a similar meta-analytic review (e.g. Curtis 1996).

(ii) Duration of exposure (from treatment initiation until measurement): ≤ 60 days, 61–120 days, > 120 days. Where repeated measurements were taken, only the last measurement was used (usually at harvest). However, in some field studies showing marked seasonal responses, declining towards the end of the growth season, a single date at or just after the mid-season peak was chosen.

(iii) Exposure method: GC=indoor controlled-environment growth chamber, GH=outdoor enclosed mini-greenhouse or enclosed portion of greenhouse, OTC=open-top chamber in the field or greenhouse, FACE=free-air CO_2 enrichment.

The database used for the meta-analysis comprised 62 papers (Appendix 1). Other papers on C4 grass responses to elevated CO_2 which did not meet the criteria for meta-analysis are given in Appendix 2 to provide a complete reference list.

Meta-analyses

Meta-analyses were conducted with MetaWin (Rosenberg *et al.* 1997), using the natural log of the response ratio (response in elevated CO_2/response in ambient CO_2) as our metric (Hedges *et al.* 1999). We used the mixed-effects model in our analyses, because of the large number of diverse studies examined and the assumption that there is random variation among studies in the effects in which we are interested. Consequently, the confidence intervals generated are larger than those of a fixed-effects model, and as such represent potentially more conservative interpretation. In general, means of single response variables were considered significantly different from zero (significant response to elevated CO_2) if their 95% confidence intervals did not overlap zero. Similarly, means of two different response variables (e.g. stress treatment classes) were considered significantly different from each other if their 95% confidence intervals did not overlap. Some results are also discussed in terms of trends and tendencies in order to highlight interesting comparisons, even if they did not satisfy this statistical guideline. For a more detailed description of the statistical approach see Curtis & Wang (1998) and Hedges *et al.* (1999).

Results

Sample sizes for all variables presented in the Figures are given in Table 1.

Relative CO_2-responses of C3 and C4 species

CO_2 responses of the full data set, including responses under interacting stress variables, are presented as the mean percentage change in elevated CO_2 (Fig. 1a). Net CO_2 assimilation rates (*A*) increased significantly in both C3 and C4 species, by 33% and 25%, respectively. Stomatal conductances (G_S) decreased significantly by 24% and 29% for C3 and C4, respectively. Increases in instantaneous leaf water use efficiency (WUE) were significant only in C4 species (72%); the sample size for C3 was small and variability high. Total plant biomass (TOTWT) was enhanced in both C3 (44%) and C4 species (33%). C3 species showed greater CO_2-induced increases in above-ground biomass (AGWT, 38%) and below-ground biomass (BGWT, 44%), where these were reported individually, than C4 species. This suggests a deficiency in data for C4 biomass partitioning into above- and below-ground components, as the smaller effect here does not concur with the larger positive result for TOTWT. Due to reporting shortcomings, the data set for above- and below-ground biomass was often drawn from a different set of publications than that for total plant biomass, likely contributing to the lack of correspondence between the results for the three variables. Individual leaf area (INDLA) increased by 15% and 25% and tiller numbers increased by 27% and 14% in C3 and C4 species, respectively. C3 species showed greater decreases in specific leaf area (SLA, 19%) and foliar total nitrogen (N) concentrations (21%) than C4 species. Only C3 species showed significantly increased foliar total nonstructural carbohydrate (TNC) concentrations (37%) in elevated CO_2.

Table 1 Number of data entries (N) used for analyses of the CO_2-responses of C_3 and C_4 grasses. Abbreviations of variables as for Fig. 1. 'None' refers to no stress; 'low' or 'high' refers to stress. For pot size, category numbers represent (1) <10 L (2) >10 L (3) in-ground. For duration, category numbers represent (1) <60 days (2) 61-120 days (3) >120 days. For method, category numbers represent (1) GC (2) GH (3) OTC (4) FACE.

		CO_2-responses (Fig. 1)		Environmental stress (Fig. 2)			Exposure methods/Growth conditions(Figs 3-5)			
Variable	Photo pathway	All stresses	No stress	Light none;low	Temp. none; low/high	Water none;low	Nutrients none;low	Pot size cat.1;2;3	Duration cat. 1;2;3	Method cat. 1;2;3;4
A	C_4	48	15		38 ; 8	42 ; 6		34 ; - ; 12	29 ; 7 ; 12	29 ; 6 ; 13 ; -
	C_3	68	8				41 ; 19	27 ; 32 ; 9	55 ; 8 ; 5	50 ; 11 ; 3 ; 4
Gs	C_4	47	16		40 ; 5	41 ; 6	44 ; 3	35 ; - ; 10	28 ; 7 ; 12	27 ; 7 ; 13 ; -
	C_3	7	3					4 ; - ; -	4 ; - ; 3	4 ; - ; 3 ; -
WUE	C_4	13	7							
	C_3	2	2							
TOTWT	C_4	25	6	22 ; 3				20 ; - ; 2	18 ; 2 ; 5	
	C_3	71	9				54 ; 13	49 ; 17 ; 5	49 ; 13 ; 9	
AGWT	C_4	19	10			16 ; 3		19 ; - ; -	19 ; - ; -	18 ; - ; - ; -
	C_3	40	23		36 ; 3		37 ; 3	18 ; 13 ; 9	7 ; 15 ; 18	11 ; 10 ; 17 ; 2
BGWT	C_4	9	4					9 ; - ; -		
	C_3	30	8				21 ; 9	19 ; 10 ; -		
INDLA	C_4	14	5			10 ; 4		9 ; - ; 2	9 ; - ; 5	10 ; 2 ; 2 ; -
	C_3	8	0					6 ; - ; -	2 ; 2 ; 4	7 ; - ; - ; -
TILLERS	C_4	9	5						4 ; - ; 5	5 ; 2 ; 2 ; -
	C_3	12	6						2 ; 7 ; 3	8 ; - ; 4 ; -
SLA	C_4	19	6							
	C_3	21	5							
TNC	C_4	4	0							
	C_3	12	11							
N	C_4	15	5							
	C_3	37	10				22 ; 11			

Influence of environmental stress

Under nonstressful growth conditions (Fig. 1b), the relative mean stimulation of photosynthetic rate in C3 species increased from 33% to 53%, and below-ground biomass enhancement rose from 44% to 57%. However, both changes were not significant according to the 95% confidence interval (CI) overlap test. The CO_2-responses of all other variables remained similar compared to the 'all stresses' analysis (Fig. 1a). By contrast, when interacting stresses were removed from the database for C4 species, the response of total biomass to elevated CO_2 decreased from 33% to 26%, the tillering response was reduced (from a 14% increase to a 10% increase), but stimulation of individual leaf area rose from 25% to 30%. Again, these responses were not significant according to the CI overlap test.

The influence of environmental stresses was further explored by comparing the CO_2-responses of deliberately stressed plants with the responses of all other plants (not deliberately stressed) for each stress variable individually (Fig. 2). Only results which can be interpreted with reasonable confidence, taking into account the sample size (>2), the confidence interval, and the power to draw robust statistical conclusions, are presented. For example, no studies addressing the interactions between elevated CO_2 and light or water stress in C3 grass species existed or were suitable for use in the meta-analysis, and in many other cases the number of studies for a particular measurement category and stress factor were too small, or did not exist.

In C4 species (Fig. 2a), low light, low temperature, or low nutrient supply levels did not alter the mean responses to elevated CO_2. Droughting treatments (low water supply) similarly did not alter the CO_2-responses of gas exchange in C4 species, but resulted in the loss of a significant CO_2-response for above-ground biomass and individual leaf area (95% confidence intervals overlap zero), compared to plants that were not water stressed. There were no data for C4 plants under high temperature stress, probably because high temperatures are not regarded as being potentially harmful to C4 plants as they are for C3 plants. In C3 species (Fig. 2b), on the other hand, abnormally high temperatures increased the mean

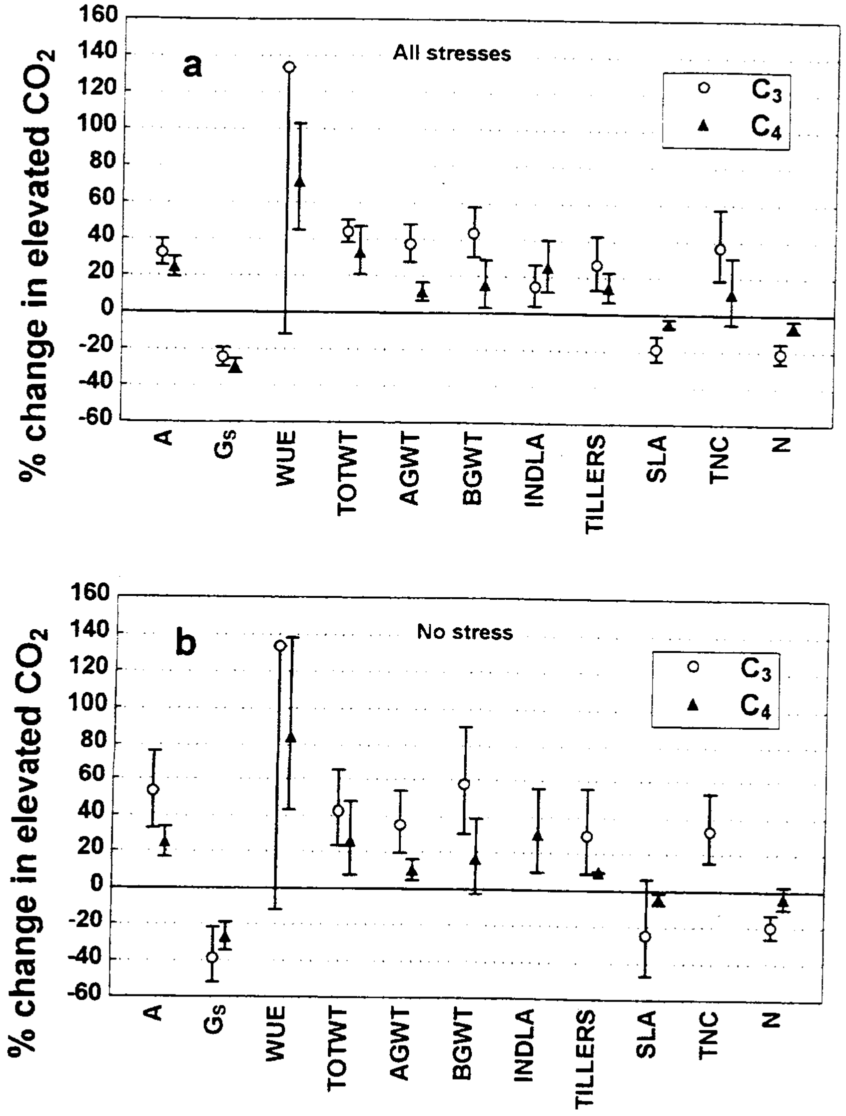

Fig. 1 Comparative photosynthetic, growth, morphological, and chemical responses of wild C3 and C4 grass species to elevated atmospheric CO_2 concentrations. (a) full data set including responses under all levels of environmental interactions other than CO_2. (b) selected data set of CO_2-responses under nonstressful environmental conditions. Abbreviations: A, net CO_2 assimilation rate; G_S, stomatal conductance; WUE, instantaneous leaf water use efficiency; TOTWT, total plant dry weight; AGWT, above-ground dry weight; BGWT, below-ground dry weight; INDLA, individual leaf area; TILLERS, tiller number; SLA, specific leaf area; TNC, leaf total nonstructural carbohydrate concentration; N, leaf total nitrogen concentration. No data were available for INDLA (C3 species) and TNC (C4 species) for nonstressful environmental conditions. Data represent percentage change in elevated CO_2 with 95% confidence intervals.

above-ground biomass response to elevated CO_2, but this tendency was not significant. Low nutrient stress did not alter the mean CO_2-response of photosynthesis and leaf nitrogen concentration in C3 species. By contrast, mean CO_2-induced increases in total plant, above- and below-ground biomass tended to diminish under low nutrient supply levels, although these changes were not significant.

Exposure methods and growth conditions

The effects of exposure methods and growth conditions on the relative responses to elevated CO_2 are presented in Figs 3,4,5. Those variables for which data for at least two categories were available for either the C3 or C4 data set, and which had reasonable sample sizes and the potential for meaningful statistical inferences, are presented. These are matched with the results for the corresponding variable in the other (C3 or C4) data set, even if the sample sizes are small and categories missing. This was done in order to allow at least a rudimentary comparison between C3 and C4 species. Even though this comparison is largely fragmentary, it exposes gaps in the knowledge base, particularly with regard to the lack of information from long-term studies in the field, and could provide a guideline for future studies (and publication of existing data).

An increasing volume of available rooting space ('pot size', Fig. 3) allowed for slightly greater CO_2-induced increases in photosynthetic rate in C3 species, although not significantly according to the CI overlap test. The mean photosynthetic CO_2-response in C4 species was not altered. Stomatal conductances were reduced more strongly in C4 species growing in open ground than in small pots. Large positive responses in

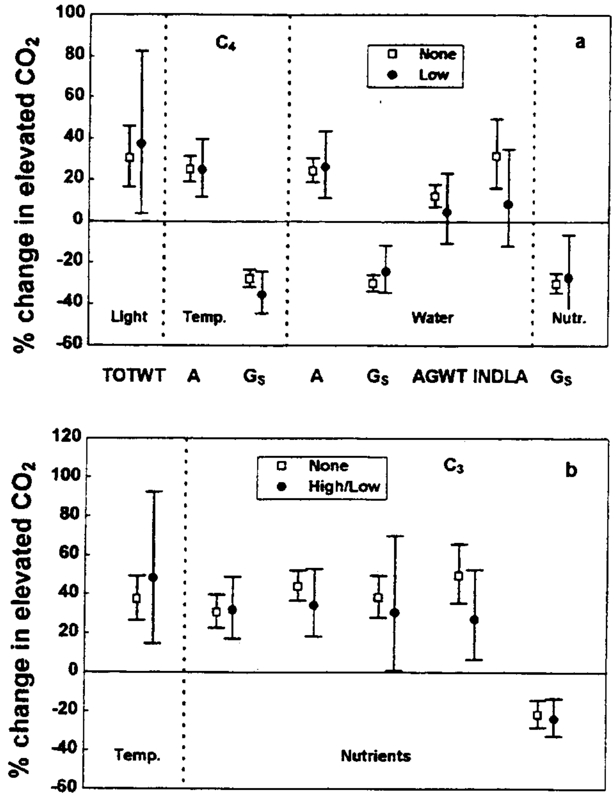

Fig. 2 CO_2-responses of wild C4 (a) and C3 (b) grass species as influenced by interaction with low light, low or high temperature, low water, or low nutrient stress. Abbreviations as for Fig. 1. Data represent percentage change in elevated CO_2 with 95% confidence intervals.

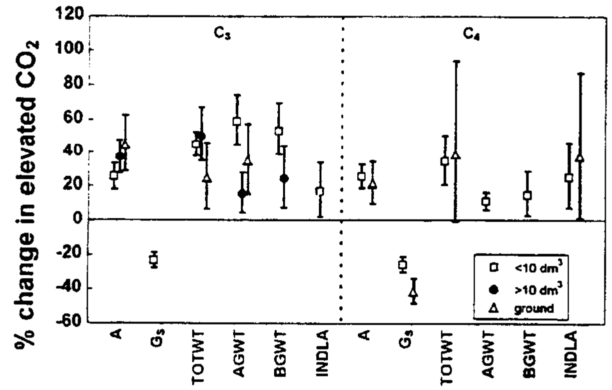

Fig. 3 Effect of pot size on CO_2-response of C3 and C4 grass species. Legend refers to pot size in dm^3, or plants grown in-ground. Abbreviations as for Fig. 1. Data represent percentage change in elevated CO_2 with 95% confidence intervals.

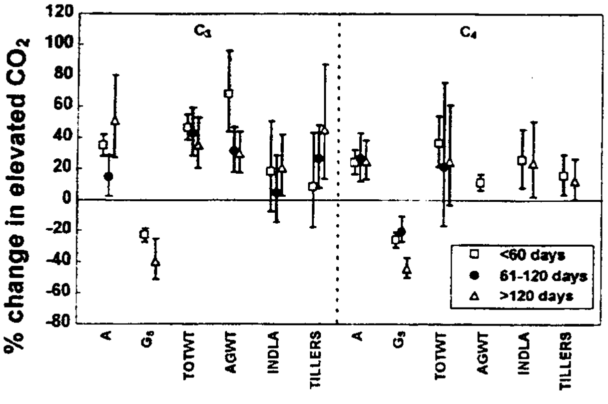

Fig. 4 Effect of duration of exposure on the CO_2-response of C3 and C4 grass species. Abbreviations as for Fig. 1. Data represent percentage change in elevated CO_2 with 95% confidence intervals.

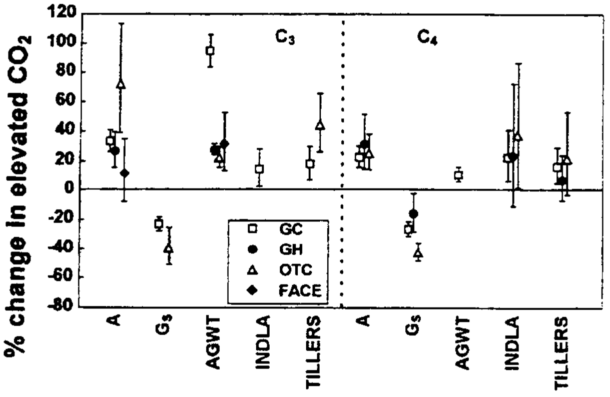

Fig. 5 Effect of exposure method on the CO_2-response of C3 and C4 grass species. Abbreviations as for Fig. 1. In the legend, GC, growth chamber; GH, greenhouse; OTC, open-top chamber; FACE, free-air CO_2 enrichment. Data represent percentage change in elevated CO_2 with 95% confidence intervals. Note that GC, GH and OTC treatments typically have 2× ambient $[CO_2]$ (650–700 $\mu mol\,mol^{-1}$), and that FACE is typically about 550 $\mu mol\,mol^{-1}$ $[CO_2]$.

biomass in C3 species were favoured by growth in smaller rooting volumes, as supported by no or only minimal overlap in the confidence intervals between pot size classes. This effect on biomass was not discernible in C4 species, although interpretation here is strongly limited by insufficient sample sizes. Significant increases in individual leaf area in C4 species in high CO_2 were measured in plants growing both in small pots and in the ground.

The mean CO_2-responses for photosynthetic rate and conductance in C3 species were greater in the longer term (> 120 days, Fig. 4) than in the medium term (61–120 days). The mean above-ground biomass response, by contrast, was greatest in the short term (< 60 days). The positive tillering response to elevated CO_2 achieved significance (95% confidence interval not overlapping zero) only after 60 days of exposure to high CO_2, and continued to increase with experimental duration, although not significantly. In C4 species, relative decreases in conductance were significantly greater in the longer term (> 120 days). The biomass response to elevated CO_2 appeared to decrease somewhat after 60 days (although small sample sizes and large confidence limits preclude a clear interpretation), so that mean biomass increases were no longer significant after 60 days (confidence intervals overlap zero). Similar increases in leaf area in elevated CO_2 were found both in the short and longer term.

Increases in photosynthetic rates in elevated CO_2 appeared to be greatest when C3 species were grown in open-top chambers (73%), and smallest in FACE systems (12%, Fig. 5), although the latter is probably attributable to the generally lower CO_2 concentrations used in these systems than in the other types of growth facilities. In both C3 and C4 species, mean decreases in conductances were greatest in OTCs. Above-ground biomass increases were found for all exposure methods in C3 species, but responses were particularly high in growth chambers (95% increase in GC compared to 23–32% increases in other facilities). The mean tillering response was greater in OTCs (45% increase) than in growth chambers (18%). In C4 species, CO_2-induced increases in photosynthetic rates were similar in all exposure facilities. Leaf area increases were found for most exposure methods (with the possible exception of greenhouses, where confidence intervals overlapped zero), and the tillering response to elevated CO_2 was small for all methods and not significant in GHs and OTCs (CI overlapped zero), but in both cases interpretation was hampered by insufficient sample sizes.

Discussion

Relative CO_2-responses of C3 and C4 species

The results of this meta-analysis confirm the widely held view that the relative responses of C4 species to elevated CO_2 are usually smaller than those for C3 species, especially for growth under nonstressful environmental conditions. Nevertheless, differences in CO_2 response between C3 and C4 grass species are not as large as current perceptions have it. A similar conclusion was drawn from a previous semiquantitative minireview of C3 vs. C4 responses (Poorter 1993). The present analysis shows that C4 grasses are certainly responsive to elevated CO_2 particularly with regard to gas exchange and leaf area development.

Photosynthetic stimulation of C4 species is, surprisingly, comparable to that of C3 species. This contradicts the general view that C4 photosynthesis does not increase in elevated CO_2, due to the specialized CO_2 concentrating mechanism in C4 leaves (Bowes 1993). Many of the definitive early studies of C4 photosynthesis were performed on crop species, such as maize, which appears to be CO_2-saturated at ambient CO_2 levels and shows very low responsiveness to higher CO_2 concentrations, compared to wild C4 species (Ziska & Bunce 1997). A closer examination of gas exchange in other C4 grasses reveals that photosynthesis is not necessarily saturated at current CO_2 levels and can increase at higher c_i (Sionit & Patterson 1984; Imai & Okamoto-Sato 1991). This simple explanation may account for the majority of cases of photosynthetic stimulation in C4 species. For example, LeCain & Morgan (1998) showed that photosynthesis was not saturated at ambient CO_2 concentration in any of the six wild C4 grass species studied. Ziska & Bunce (1997) similarly measured higher photosynthetic rates at elevated CO_2 in 8 out of 10 C4 species studied, due to the effect of increased c_i. Another study has shown that under favourable growth conditions (high light), the operational c_i of a tropical C4 grass was close to the inflection point of the A/c_i response, so that increasing CO_2 supply caused slight enhancements in the CO_2 assimilation rates, and improved growth (Ghannoum *et al.* 1997). On the other hand, under growth-limiting conditions (low light), the operational c_i was well above the CO_2 saturation level for photosynthesis, and no photosynthetic or growth response to elevated CO_2 was measured. The relative 'saturation level' may therefore change with changing conditions, and this may play a role in photosynthetic responses to elevated CO_2 in wild C4 grasses.

Stimulation of photosynthetic rates due to increases in c_i represents a simple short-term effect. In addition, longer term biochemical changes, such as altered enzyme efficiencies, or altered regeneration rates of phosphoenolpyruvate (PEP) or ribulose-1,5-bisphosphate (RuBP), may develop in elevated CO_2. These are termed 'regulatory' or 'acclimatory' responses and change the shape of the A/c_i response. Unlike for many C3 species (Wullschleger 1993), instances of up- or downregulation of photosynthetic capacity in C4 species have not been given much attention in the literature as they have appeared to be rare. Sage (1994) concluded that little adjustment is found in the A/c_i response in C4 species under elevated CO_2 (see also Ziska & Bunce 1997), except possibly downregulation under conditions of nutrient deficiency (Wong 1979; Morgan *et al.* 1994; Ghannoum & Conroy 1998). Nevertheless, photosynthetic downregulation has also been measured under conditions not apparently stressful (Read *et al.* 1997; LeCain & Morgan 1998). Many earlier reports of unchanged or reduced photosynthetic rates in C4 species in elevated CO_2 may have been due to the acclimation phenomenon, but are not identifiable without full A/c_i measurements (e.g. Wray & Strain 1986). The mechanisms of photosynthetic acclimation in C4 species are apparently not related to feedback inhibition resulting from carbohydrate (TNC) accumulation, or to reductions in leaf nitrogen (N) concentrations (Read *et al.* 1997; LeCain & Morgan 1998), as they are in C3 species (Stitt 1991; Sage 1994; Cotrufo *et al.* 1998). The meta-analysis confirmed that accumulation of TNC and reductions in leaf N in elevated CO_2 are insignificantly low in C4 species. There is currently no available information on the possible mechanisms of photosynthetic acclimation in C4 species, and this warrants further attention.

Natural seasonal dynamics of photosynthetic capacity in C4 species may also influence the response to elevated CO_2. In young *Themeda triandra* (red grass) plants with high assimilation rates, photosynthetic upregulation resulted in increased photosynthetic rates in high CO_2 (Ludwig 1996), but downregulation was measured in the same set of plants later in the season (when absolute rates were reduced), which led to similar or reduced photosynthetic rates at high compared to ambient CO_2 (Wand, unpublished data). Growth enhancement, particularly of leaf area, was linked to this early response. Detailed measurements of A/c_i responses in C4 and C3 grass species growing in elevated CO_2 in a field experiment in South Africa (utilization of a natural CO_2 spring) have also shown photosynthetic upregulation in *Themeda triandra* during the active growth season (Wand, unpublished data). Similarly, significant increases in CO_2 assimilation rates in the salt marsh C4 species *Spartina patens* in high CO_2 were confined to the early season, when absolute rates of assimilation were highest (Ziska *et al.* 1990). Knapp *et al.* (1993) have also reported upregulation in *Andropogon gerardii* (big bluestem), and Chen *et al.* (1994) modelled this response. Recent reports indicate that C4 photosynthetic physiology may change with progressive developmental stages, showing more similarities with C3 physiology (lower CO_2-concentrating ability) when leaves are young or senescent, compared to mature leaves (Dai *et al.* 1995; He & Edwards 1996). This was tentatively proposed as an explanation for ontogenetic shifts in CO_2-responsiveness (Ghannoum *et al.* 1997), but subsequent work on C4 grass species does not support this explanation, as C4 photosynthetic characteristics were already fully developed in young leaves (Ghannoum *et al.*, 1998). In conclusion, this aspect of C4 response to elevated CO_2 requires more attention, as conflicting evidence also exists. For example, photosynthetic downregulation was found in both young and older *Bouteloua gracilis* (blue grama) plants (Read *et al.* 1997). Furthermore, seasonal dependencies of C4 growth responses, in contrast with responses of carbon assimilation, are not evident in many field-based elevated CO_2 experiments (Curtis *et al.* 1989; Kirkham *et al.* 1991; Hamerlynck *et al.* 1997).

The issue of whether biochemical differences between C4 photosynthetic subtypes may shed light on the reasons for interspecific differences in CO_2 responsiveness (Henderson *et al.* 1994) is beyond the scope of the present review, but we make some brief comments. The three C4 subtypes (NADP-ME (NADP-malic enzyme), PCK (phosphoenolpyruvate carboxykinase), and NAD-ME (NAD-malic enzyme)) exhibit increasing levels of 'leakiness' to CO_2 from the bundle sheath to the mesophyll, in the above order (Hattersley 1982; Furbank & Hatch 1987; Jenkins *et al.* 1989; Brown & Byrd 1993; but see Hatch *et al.* 1995). This amounts to a loss of between 10 and 40% of carbon fixed by PEP carboxylase, which could, conceivably, be counteracted by increased CO_2 supply from the atmosphere. Recent studies investigating the relative responsiveness of the subtypes to elevated CO_2 yielded counter-intuitive results, with the least 'leaky' NADP-ME showing the largest responses (LeCain & Morgan 1998; Wand, unpublished data). Nevertheless, this line of investigation may well contribute to an improved understanding of photosynthetic responses of C4 plants to elevated CO_2.

Elevated CO_2 has significant positive effects on plant water relations in both C3 and C4 grass species, via reductions in stomatal conductance (G_S). In fact, this response, coupled with reduced transpirational water loss and the corresponding increases in WUE, are probably the most ubiquitous responses to elevated CO_2 for almost all plant functional types (Gifford & Morison 1985; Chaves & Pereira 1992; Tyree & Alexander 1993). C4 and C3 responses in G_S to elevated CO_2 were similar (Fig. 1a), but clear interpretation is hampered by the fact that fewer data are available for C3 Poaceae. The decrease in G_S in C4 species is consistent across a range of environmental stresses, but greatest in plants grown in the ground and exposed to elevated CO_2 for more than 120 days. This suggests that developmental changes in G_S, possibly related to altered stomatal sizes or densities, may occur as leaves mature in high CO_2. Information on long-term changes in G_S (e.g. changing stomatal densities) is limited (Ghannoum *et al.* 1997). It is generally thought that CO_2-induced reductions in G_S are primarily short-term effects, but some researchers have measured acclimatory responses in stomatal physiology in C4 species, as shown by the responses of conductance to increasing CO_2 (G_S/c_i curves) (Morgan *et al.* 1994; Read *et al.* 1997; LeCain & Morgan 1998). This can take the form of either upregulation (higher G_S at equivalent c_i for leaves grown in elevated CO_2), or downregulation (reduced G_S at low c_i in elevated CO_2). Studies in the greenhouse and field (Wand, unpubl. data) showed that G_S was significantly reduced under increasing CO_2 levels in the short term (changes in the cuvette CO_2 concentration) in all seven C4 grass species studied. In addition, either upregulation or downregulation of G_S was also found in the longer term (a treatment effect) in some species, and this developmental response appeared to depend on season or environmental conditions (e.g. water stress). Reduced transpirational water loss in elevated CO_2 and the resulting improvement in soil water content over the course of the growing season, as reported for the tall-grass prairie (Kirkham et al. 1993), are likely to be reflected in longer term changes in stomatal conductances.

The stimulation of C4 whole plant growth under elevated CO_2 (mean of 33%, 95% confidence interval 21%–47%) is slightly higher than the 22% reported by Poorter (1993). Growth stimulation could be either a direct effect of greater carbon assimilation rates (discussed above), or an indirect effect of improved soil and leaf water relations resulting from reduced stomatal conductances and transpirational water loss (Knapp et al. 1993; Owensby et al. 1993). Cell elongation and blade extension rates in developing grass leaves are positively correlated with leaf water potentials (Boyer 1970; Toft et al. 1987). Although not included in the meta-analysis, the C4 literature database clearly showed a consistent and significant positive increase in shoot water potentials in grasses exposed to elevated CO_2 (e.g. Kirkham et al. 1993; Hamerlynck et al. 1997).

The growth response of C3 species in this review is a little larger than that for C4 species (44%) and comparable to the C3 herbaceous monocot component of Poorter's database (42%). We tentatively support Poorter's conclusion that differences in growth stimulation between C3 and C4 plants are probably not as large as suggested by current perceptions. Unfortunately, the responses for above- and below-ground biomass in C4 species in this meta-analysis do not match those for whole-plant biomass, and care must be taken in interpretation. Also, many field studies using C4 species have not reported biomass responses adequately, probably due to logistical difficulties and an unwillingness to disturb the ecosystem in longer term experiments. We need more information on whether increased carbon assimilation rates will lead to sustained enhanced biomass production in C4-grass-dominated ecosystems such as prairies and savannas, which comprise a large percentage of productive land surface (Hall et al. 1995). This would help to improve our models of global carbon dynamics. Currently, the potential of C4-grass-dominated ecosystems as significant carbon sinks is considered small, but this may need to be re-assessed.

An interesting contrast emerged regarding the morphological development of C3 and C4 species under elevated CO_2. C3 species generally develop more tillers, with only small increases in leaf area, but decreased specific leaf areas (increased leaf density or thickness). C4 species, on the other hand, appeared to respond mainly with increased leaf areas, and smaller increases in tiller numbers. This contrast may indicate a greater sensitivity in C4 species to self-shading of the basal nodes from which tillers are initiated (Deregibus et al. 1985; Everson et al. 1988), and may provide the mechanism for growth stimulation even under moderate photosynthetic enhancement. Gradually increasing canopy leaf areas, leading to a progressive increase in whole-canopy carbon assimilation rates, would result in a continuously greater supply of carbon products to support enhanced growth. Early increases in leaf area, leaf area duration (the cumulative leaf area over the growth period), leaf area ratio (the proportion of leaf area to plant biomass), plant height and total plant biomass of C4 species in elevated CO_2 have been reported by Patterson & Flint (1980), Riechers & Strain (1988) and Ackerly et al. (1992). Early responses in biomass and leaf area, which persist for the whole growth period, have also been found for some C3 species (Bowler & Press 1993), but the stimulation of leaf area, in particular, appears to be characteristic of the CO_2-response of C4 species. Coleman & Bazzaz (1992) and Ackerly et al. (1992) came to the conclusion that standing photosynthetically active leaf area (net leaf area production and loss) in a C4 species was the primary influence on growth responses in elevated CO_2.

Influence of environmental stress and growth methodology

Environmental stresses tend to reduce (although not significantly) the potential CO_2-response in C3 species, as evidenced by the suppression of mean photosynthetic and below-ground biomass responses when all stresses are included in the analysis (Fig. 1a,b), as well as the reductions in mean growth responses when nutrients are limiting (Fig. 2b). By contrast, C4 species were generally not negatively impacted by environmental stresses, although leaf area stimulation was sensitive to water stress (Fig. 2a). The current view that CO_2-responses in C4 graminoids are particularly marked under conditions of water stress (Nie et al. 1992; Knapp et al. 1993; Owensby et al. 1993; Ham et al. 1995) was not borne out by the meta-analysis, possibly due to the lack of data suitable for inclusion in the database. Many of these studies do not present plant- and leaf-level responses, concentrating on canopy-level gas fluxes instead.

C4 graminoids may well benefit from increased CO_2 supply under some stressful environmental conditions, such as low soil fertility. However, there is a lack of information about the changes in plant nitrogen use efficiency in C3 and C4 graminoids in elevated CO_2. This understanding may be critical in predicting changes in their relative competitive abilities, as it has been suggested that competitive advantage,

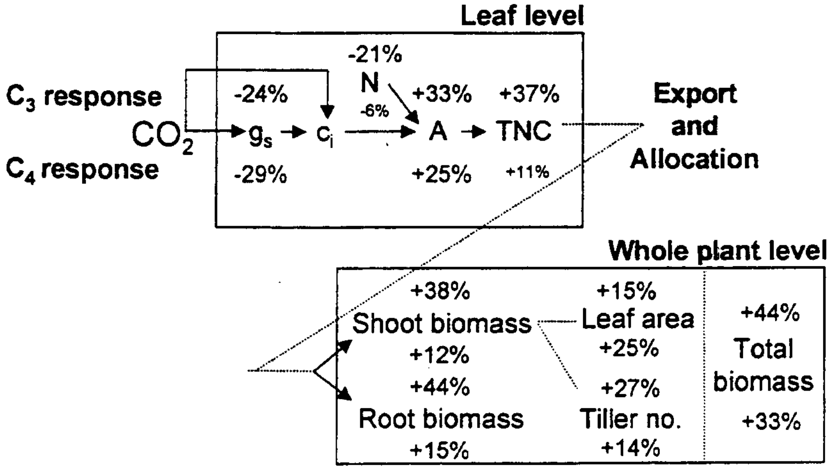

Fig. 6 Summary scheme of the CO_2-response levels (% change) and their relationships under all conditions (full data set). C3 responses are given above and C4 responses given below the stated parameter. Response levels printed in small font are not significantly different from zero. Abbreviations as for Fig. 1, and c_i=intercellular CO_2 concentration.

especially in grasslands, may be due to a greater ability to extract nitrogen from the soil (Tilman 1990). This in turn may be associated with greater plant and photosynthetic nitrogen use efficiency (Richardson *et al.* in press).

Contrary to strong evidence for nongraminoid C3 species showing reduced CO_2-responsiveness in small rooting volumes (Arp 1991; McConnaughay *et al.* 1993, 1996), C3 grass species were more responsive in small pots, with respect to above- and below-ground growth. In C4 species, rooting volume did not appear to play a role in the biomass response to CO_2, but more data are needed to confirm this as the sample size was too small for a confident interpretation. Nevertheless, field studies with C3 species have not supported the expected significant productivity increases based on earlier pot studies, and predictions of competitive advantages over C4 species should be cautiously reviewed. In addition, aboveground biomass enhancement of C3 species diminished with increasing duration of exposure to elevated CO_2, even though tiller number appeared to be stimulated, which suggests that individual tiller size is progressively reduced in this group.

In conclusion, responses to elevated CO_2 in wild C4 and C3 Poaceae at the leaf and whole plant levels are summarised in Fig. 6, and demonstrate many trends common to both photosynthetic types. At the leaf level, the greater carbohydrate accumulation and greater reductions in leaf nitrogen concentration in the C3 type alone differentiated the types, and constituted the only evidence for so-called 'sink limitation' which is often invoked in elevated CO_2 studies on C3 dicots. Average photosynthetic responsiveness did not concur with predictions based solely on photosynthetic theory. However, at the shoot level, there were clearcut differences between types resulting from disparate effects on aboveground morphologies. These, rather than photosynthetic differences between the types, might be of greater importance when evaluating responses to elevated CO_2.

The combined shoot structural and water use efficiency responses of these functional types are likely to have consequential implications for the water balance of important catchments and rangelands throughout the world, especially in semiarid subtropical and temperate regions. Improved water relations would be highly beneficial to C4 grasses growing in marginal semiarid sites where growing season may be limited by soil water availability, such as over much of southern Africa and parts of North America. The results of this meta-analysis suggest that it may be premature to predict that the C4 type will lose its competitive advantage in certain regions as CO_2 levels rise, based solely only on differential photosynthetic mechanisms (Collatz *et al.* 1998).

Acknowledgements

We thank B.G. Drake of the Smithsonian Environmental Research Centre, Edgewater, USA, for stimulating our interest in C4 plant responses to elevated CO_2. We are also grateful to W.D. Stock, O. Ghannoum and J.A. Morgan for suggestions and valuable discussion. P. Moran-Palma, X. Wang, N. Ceja, E. Lai, T. Goodwin and M. Rheinhardt are thanked for their assistance. M.B. Kirkham and two anonymous referees made valuable comments that helped improve the manuscript.

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Appendix 3

References, C3 species, exposure and growth conditions, and interaction with other environmental stresses, for studies used in the analysis. GC, growth chamber; GH, greenhouse; OTC, open-top chamber; FACE, free-air CO_2 enrichment

					Interacting stresses		
Reference	C3 species	Exposure facility	Pot size (L)	Duration (days)	Nutr.	Temp.	Water
Baxter *et al.* (1994a)	*Agrostis capillaris*	OTC	0.7	79			
	Festuca vivipara	OTC	0.7	189			
	Poa alpina	OTC	0.7	105			
Baxter *et al.* (1994b)	*Agrostis capillaris*	OTC	0.4	43			
	Festuca vivipara	OTC	0.4	189			
	Poa alpina	OTC	0.4	105			
Baxter *et al.* (1995)	*Agrostis capillaris*	OTC	0.7	79			
	Festuca vivipara	OTC	0.7	189			
	Poa alpina	OTC	0.7	105			
Baxter *et al.* (1997)	*Poa alpina*	GC	2.5	50			
Bowler & Press (1993)	*Agrostis capillaris*	GC	3.8	58	*		
	Nardus stricta	GC	3.8	63	*		
Bowler & Press (1996)	*Agrostis capillaris*	GC	25	42	*		
	Nardus stricta	GC	25	49	*		
Campbell *et al.* (1995)	*Agrostis capillaris*	GC	0.8	28		*	
	Bromus willdenowii	GC	0.8	42		*	
	Dactylis glomerata	GC	0.8	28		*	
	Festuca arundinacea	GC	0.8	42		*	
	Lolium multiflorum	GC	0.8	28		*	
	Lolium perenne	GC	0.8	42		*	
	Phalaris aquatica	GC	0.8	28		*	
Casella *et al.* (1996)	*Lolium perenne*	GH	220	720	*		
Ferris *et al.* (1996)	*Lolium perenne*	GH	3.7	133		*	
Fischer *et al.* (1997)	*Lolium perenne*	FACE	G	426	*		
Fitter *et al.* (1996)	*Festuca ovina*	OTC	G	730			
Ghannoum *et al.* (1997)	*Panicum laxum*	GH	7.0	49			
Gloser & Bartak (1994)	*Calamagrostis epigejos*	GC	0.5	21			
Greer *et al.* (1995)	*Lolium perenne*	GC	1.2	28/56		*	
	Agrostis capillaris	GC	1.2	28/56		*	
Hakala & Mela (1996)	*Festuca pratensis*	OTC	G	510		*	
Jackson & Reynolds (1996)	*Avena fatua*	OTC	30	135	*		
	Bromus hordeaceus	OTC	30	135	*		
	Lolium multiflorum	OTC	30	135	*		
	Vulpia microstachys	OTC	30	135	*		
Jackson *et al.* (1994)	*Avena barbata*	OTC	G	430			
Jackson *et al.* (1995)	*Avena barbata*	OTC	G	790			
	Avena sativa	GH	3.1	30			
Jones *et al.* (1996)	*Lolium perenne*	OTC	G	735			
Larigauderie *et al.* (1988)	*Bromus mollis*	GC	3	129	*		
Leadley & Stöcklin (1996)	*Bromus erectus*	GC	24.3	126			
	Festuca ovina	GC	24.3	126			
Lenssen *et al.* (1995)	*Puccinellia maritima*	GH	1.8	28			
Marks & Clay (1990)	*Lolium perenne*	GC	0.5	70	*		
Morgan *et al.* (1994a)	*Pascopyrum smithii*	GC	20.4	460		*	
Newton *et al.* (1995)	*Lolium perenne*	GC	150	340			
Nie *et al.* (1992)	*Poa pratensis*	GH	G	61			*
Nijs *et al.* (1996)	*Lolium perenne*	FACE	G	23		*	
Nijs *et al.* (1997)	*Lolium perenne*	FACE	G	143		*	
Read *et al.* (1997)	*Pascopyrum smithii*	GC	6	49		*	
Ryle *et al.* (1992)	*Lolium perenne*	GC	2	49			
Saebo & Mortensen (1995)	*Lolium perenne*	OTC	48	147			
	Phleum pratense	OTC	48	147			
Saebo & Mortensen (1996)	*Agrostis capillaris*	OTC	48	60			
	Dactylis glomerata	OTC	48	64			

Reference	C3 species	Exposure facility	Pot size (L)	Duration (days)	Interacting stresses Nutr.	Temp.	Water
	Festuca arundinaceae	OTC	48	64			
	Festuca duriuscula	OTC	48	72			
	Festuca pratensis	OTC	48	72			
	Festuca rubra	OTC	48	71			
	Poa pratensis	OTC	48	72			
Schäppi & Körner (1996)	*Poa alpina*	OTC	G	310	*		
Stewart & Potvin (1996)	*Poa pratensis*	GC	27.4	61			
	Poa pratensis	OTC	G	61			
	Elymus athericus	GH	1.8	65			
Stirling *et al.* (1997)	*Poa alpina*	GH	4.7	75		*	
	Poa annua	GH	4.7	75		*	
Teughels *et al.* (1995)	*Lolium perenne*	GH	6.2	60			
	Festuca arundinaceae	GH	6.2	30			
van de Staaij *et al.* (1993)	*Elymus athericus*	GH	1.8	65			
Volin & Reich (1996)	*Agropyron smithii*	GC	2.5	58	*		
Wilsey (1996)	*Stipa occidentalis*	GC	2	86	*		
Wilsey *et al.* (1997)	*Agropyron caninum*	GC	2.0	75			
	Festuca idahoensis	GC	2.0	75			
	Briza subaristata	GC	2.0	75			
	Stipa occidentalis	GC	2.0	75			
Zanetti *et al.* (1997)	*Lolium perenne*	FACE	G	913			
Ziska *et al.* (1991)	*Pharus latifolius*	OTC	12.5	100			

Appendix 4

References, C$_4$ species, exposure and growth conditions, and interaction with other environmental stresses, for studies used in the analysis. GC, growth chamber; GH, greenhouse; OTC, open-top chamber

Reference	C4 species	Exposure facility	Pot size (L)	Duration (days)	Interacting stresses Temp.	Water	Light
Bowman & Strain (1987)	*Andropogon glomeratus*	GC	1	56			
Campbell *et al.* (1995)	*Digitaria sanguinalis*	GC	0.8	42	*		
	Paspalum dilatatum	GC	0.8	42	*		
Carlson & Bazzaz (1982)	*Setaria faberii*	GH	1	32			
	Setaria lutescens	GH	1	32			
Curtis *et al.* (1989)	*Spartina patens*	OTC	G	124			
Curtis *et al.* (1990)	*Spartina patens*	OTC	G	580			
Garbutt *et al.* (1990)	*Setaria faberii*	GH	1	78			
Ghannoum *et al.* (1997)	*Panicum antidotale*	GH	7	49			*
Gifford & Morison (1985)	*Paspalum plicatulum*	GC	3.2	131		*	
Hamerlynck *et al.* (1997)	*Andropogon gerardii*	OTC	G	1255		*	
Kirkham *et al.* (1991)	*Andropogon gerardii*	OTC	G	214		*	
Knapp *et al.* (1993)	*Andropogon gerardii*	OTC	G	480		*	
Marks & Clay (1990)	*Tridens flavus*	GC	0.5	70			
Marks & Strain (1989)	*Andropogon virginicus*	GC	0.5	16		*	
Morgan *et al.* (1994a)	*Bouteloua gracilis*	GC	8	76		*	
Morgan *et al.* (1994b)	*Bouteloua gracilis*	GC	20	190			
Newton *et al.* (1995)	*Paspalum dilatatum*	GC	150	340			
Nie *et al.* (1992)	*Andropogon gerardii*	GH	G	61		*	
Polley *et al.* (1996)	*Schizachyrium scoparium*	GH	30	480			
Potvin & Strain (1985a)	*Echinochloa crus-galli*	GC	1	48	*		
	Eleusine indica	GC	1	48	*		
Read *et al.* (1997)	*Bouteloua gracilis*	GC	6	49	*		
Sionit & Patterson (1984)	*Digitaria sanguinalis*	GC	1	22			*
	Echinochloa crus-galli	GC	1	22			*
	Eleusine indica	GC	1	22			*
	Setaria faberii	GC	1	22			*
Sionit & Patterson (1985)	*Digitaria sanguinalis*	GC	2	43		*	
	Echinochloa crus-galli	GC	2	43		*	
	Eleusine indica	GC	2	43		*	
	Setaria faberii	GC	2	43		*	
Thompson & Drake (1994)	*Spartina patens*	OTC	G	1600			
Volin & Reich (1996)	*Bouteloua curtipendula*	GC	2.5	58			
Wand *et al.* (1996)	*Themeda triandra*	OTC	3.9	210			
Wilsey *et al.* (1994)	*Sporobolus kentrophyllus*	GC	4.2	42			
Wilsey *et al.* (1997)	*Sporobolus kentrophyllus*	GC	2	75			
	Paspalum dilatum	GC	2	75			
	Digitaria macroblephara	GC	2	75			
	Themeda triandra	GC	2	75			
Wray & Strain (1986)	*Andropogon virginicus*	GC	0.5	56		*	
Wray & Strain (1987)	*Andropogon virginicus*	GC	0.5	63			
Ziska *et al.* (1990)	*Spartina patens*	OTC	G	500			