

THE RESPONSE OF WILD OATS TO CLIMATE CHANGE

Chris C. O'Donnell and Steve W. Adkins

Department of Agriculture and The Co-operative Research Centre for Tropical Pest Management,
The University of Queensland, Brisbane, Queensland, Australia

Summary Six lines of wild oat (*Avena fatua* L.) were grown in controlled environment growth chambers under either ambient (357 ppmv) CO₂ or elevated (480 ppmv) CO₂. Three soil-moisture regimes (-0.01 MPa – field capacity, -0.1 MPa or -1.0 MPa) were also imposed. In the first experiment, using a day/night temperature of 20/16°C, the elevated CO₂ plants produced an average of 27% more seed, plant dry-weights were 45% higher, physiological maturity was attained seven days earlier and the plants grew 7% taller. In the second experiment using a day/night temperature of 23/19°C, seed production for elevated CO₂ plants was 14% higher, plant dry-weights were 50% higher and plants were 34% taller. In an addition series experiment between *A. fatua* and wheat (*Triticum aestivum* cv. Hartog) a reciprocal yield model indicated that under elevated CO₂, the competitive ability of *T. aestivum* was reduced.

INTRODUCTION

Human activities are changing the composition of the Earth's atmosphere. Climate modelling studies indicate that an equilibrium doubling of CO₂ is likely to cause global mean surface temperatures to increase by 1.5 to 4.5°C and these increases will be accompanied by changes in precipitation patterns (Houghton *et al.* 1990).

As well as affecting the Earth's radiative flux, increases in atmospheric CO₂ concentrations directly enhance plant growth – a phenomenon commonly referred to as the 'CO₂ fertilization effect'. This has been reported to enhance plant growth by as much as 30 to 40% for C₃ species at doubled current CO₂ concentrations (Kimball 1983, Cure and Acock 1986, Gifford 1988). Increasing the atmospheric CO₂ concentration does not confer as large an advantage on C₄ species because the internal leaf CO₂ concentration is already near saturation. Studies between C₃ crops and C₄ weeds and between C₄ crops and C₃ weeds usually show an improved fitness for the C₃ species (Patterson and Flint 1980).

There are however situations where interacting crops and weeds share the same photosynthetic pathway. *A. fatua* is a persistent annual weed of the world's temperate cereal growing regions. It's persistence is caused by an ability to produce large numbers of viable seeds that shatter before the crop is harvested thereby ensuring continual recruitment into the seed bank, coupled with a dormancy mechanism that ensures discontinuous

germination over long periods of time (Naylor 1983). *A. fatua* uses the C₃ photosynthetic pathway as does *T. aestivum*, the main crop plant with which *A. fatua* competes. Any shift in competitive interactions between *A. fatua* and *T. aestivum* are therefore likely to be less prominent than those between C₃ crops and C₄ weeds or between C₄ crops and C₃ weed species.

The objectives of this study were to examine the response of six lines of *A. fatua* to the interactive effects of temperature, CO₂ fertilization and soil-moisture deficit and also to examine how competitive interactions between one line of *A. fatua* and one cultivar of *T. aestivum* might alter in response to CO₂ fertilization.

MATERIALS AND METHODS

Experiments 1 and 2 The wild oat seed used in these studies (Table 1) were developed on Australian isogenic lines in a previous study (Armstrong 1994). Caryopses were pre-germinated then transplanted, 3 per pot, into 25 cm diameter plastic pots containing 7.8 kg of a University of California potting mix (UC Mix B; 1:1 by volume, river sand and peat with 4 kg stock fertilizer per 0.5 m³ of mix). The pots were then placed in two identical controlled environment growth chambers (Conviron model PGW36). Each chamber held 36 pots. Light intensity was adjusted to 500 μmol m⁻² s⁻¹ at mean canopy height and temperature was set at 20.0 ± 0.5°C day/16.0 ± 0.5°C night (experiment 1) or 23.0 ± 0.5°C day/19.0 ± 0.5°C night (experiment 2) with a 12 hour square-wave photoperiod and relative humidity of 70–90%. One cabinet was enriched with food grade CO₂ (Air Liquide Australia Ltd) to 480 ppmv, a concentration that could realistically be expected to occur by the middle of the 21st Century. Supply of CO₂ was monitored and controlled using an ADC 2000 CO₂ monitor (ANRI Instruments and Controls Pty. Ltd., Victoria). Using de-ionised water the potting mix in each pot was watered daily, by weight, to either -0.01 MPa (field capacity), -0.1 MPa, or -1.0 MPa. Every 10 days Aquasol, (Hortico Industries Australia Pty. Ltd.) soluble liquid fertilizer, at the rate of 0.8 g L⁻¹ was applied as part of the normal watering regime.

Times to anthesis and maturity were recorded. Heights were measured from soil level to the top of the tallest panicle. Root, shoot and leaf fractions were placed in a drying oven at 80°C for 72 hours to obtain dry weights. The number of glume-pairs on each panicle

Table 1. Australian isogenic lines of wild oat used in experiments 1 and 2 showing the abbreviations used in accompanying figures and the latitude of original isolation of each line.

Line name	Abbreviation	Latitude
Springsure	Sp	24° 08'S
Toowoomba	Tb	27° 32'S
Narrabri	Nb	30° 19'S
Wellington	Wt	32° 35'S
Wickepin	Wn	32° 47'S
Rutherglen	Rg	36° 05'S

were counted and multiplied by the number florets that were observed present therein during maturation, to give total seed production per plant. In experiment 1, water-use was determined gravimetrically as each pot was weighed daily. Stomatal conductance and transpiration rates were measured with a Li-Cor 1800 steady-state porometer (Li-Cor Industries, Lincoln, Nebraska).

Statistical analysis These experiments were a $6 \times 3 \times 2$ (line:water:CO₂) factorial completely randomized design with two replications. Data were evaluated with an ANOVA model generated within the General Linear Models procedure of SAS. Where a significant F-value was obtained, pairwise multiple comparisons of means were conducted with an LSD test ($P < 0.05$).

Experiment 3 An addition series experiment examined the effects of CO₂ fertilization on competition between *A. fatua* (Toowoomba line) and *T. aestivum* (cv. Hartog). Three total plant densities of 3, 6 or 12 plants per pot of both *A. fatua* and *T. aestivum* were planted at ratios of; 1:0, 2:1, 1:1, 1:2, 0:1 (1:1 was not used at a density of three plants per pot). Each density by planting ratio was replicated three times. Plants were grown in 25 cm diameter pots at a day/night temperature of $20 \pm 0.5/16 \pm 0.5^\circ\text{C}$. Soil type, photoperiod, light intensity and growth chambers were as previously described for experiments 1 and 2. Soil moisture was maintained at field capacity.

Plants were harvested at 43 days after planting by cutting shoots level with the soil surface and then dried at 70°C for 72 hours. Results were analysed using the reciprocal yield model of Spitters (1983). This model assumes that biomass response can be fitted with a rectangular hyperbola

$$y = N / (b_0 + b_1 N) \quad \text{Eqn 1}$$

where y is biomass and N is plant density.

Average per plant weight (w) is then calculated as

$$w = y/N = 1/(b_0 + b_1 N) \quad \text{Eqn 2}$$

The constant b_0 and coefficient b_1 are estimated by rearranging the equation in linear regression form

$$1/w = b_0 + b_1 N \quad \text{Eqn 3}$$

The intercept b_0 is the reciprocal of the theoretical biomass of an isolated plant in the absence of competition and b_1 , the slope, indicates intraspecific competition or 'crowding effect'. Spitters (1983) argued that if adding a plant of the same species affected $1/w$ additively then adding a plant of another species should also affect this value in the same manner and by expanding the linear regression equation for a second species to

$$1/w_1 = b_{1,0} + b_{1,1}N_1 + b_{1,2}N_2 \quad \text{Eqn 4}$$

inter- and intra-specific competitive effects could be studied and separated mathematically. In equation 4 the coefficient $b_{1,1}$ quantifies intraspecific competition whilst the coefficient $b_{1,2}$ quantifies interspecific competition. N_1 and N_2 are the densities of species 1 and 2 respectively.

RESULTS AND DISCUSSION

Experiments 1 and 2: Plant growth and development

When averaged across lines and water treatments elevated CO₂ plants responded with increases in dry weight of 45% at 20/16°C and 50% at 23/19°C. All lines responded with significant increases at -0.01 MPa (Figures 1a,b). Soil-moisture stress decreased assimilation processes in both experiments and although greater absolute dry weight reductions occurred at 23/19°C, the elevated CO₂ plants at this temperature suffered relatively smaller reductions, relative to the -0.01 MPa soil moisture level, than the ambient CO₂ controls. At 20/16°C soil-moisture stress caused smaller absolute reductions in dry weights in both CO₂ treatments and both CO₂ treatments also had similar reductions at -0.10 and -1.0 MPa when compared to their respective -0.01 MPa level treatments (Figures 1a,b).

At 20/16°C the average time to maturity was 109 days for elevated CO₂ plants and 116 days for the ambient controls whilst at 23/19°C these times were reduced by 26 days. Earlier work has shown that when temperature was increased by 5°C from 20 to 25°C maturation times for Canadian *A. fatua* lines were reduced by about 24 days (Adkins *et al.* 1987) which is consistent with what was found in these experiments. If CO₂ fertilization causes a differential maturation response between *A. fatua* and the competing crop then, depending on the direction of the response, *A. fatua* populations could either increase or decrease. If the relative maturation rates were shortened then an increase in *A. fatua* populations could be expected as more seed will be deposited to the soil-seed bank, whereas if rates are slower more seed would

Table 2. Percentage yield loss of *T. aestivum* when *A. fatua* plants were added to a constant density of 100 *T. aestivum* plants m⁻².

<i>A. fatua</i> m ⁻²	Percentage yield loss	
	357 ppmv CO ₂	480 ppmv CO ₂
10	2.9	4.0
20	5.6	7.6
30	8.2	11.0
40	10.7	14.2

be removed with the harvested crop with a consequent decline in *A. fatua* populations.

Seed characters At 20/16°C elevated CO₂ plants generally produced more seed per plant. As the seed is the basic unit of the *A. fatua* population, CO₂ fertilization at this temperature indicates a potential for populations to increase. At 23/19°C only two elevated CO₂ treatments

produced significantly more seed (Sp -0.01 MPa and Wt -0.01 MPa) than the ambient CO₂ controls (Figure 2b). The CO₂ fertilization benefit observed at 20/16°C was not realised at 23/19°C. Soil-moisture stress at 23/19°C also reduced seed production by a larger factor than at 20/16°C. These findings imply that under climate change, if the expected warming is of a sufficient rate and magnitude then the interactive effects of warmer temperatures and soil-moisture stress could serve to reduce the fitness of *A. fatua*.

Water use Elevated elevated CO₂ plants had a reduced stomatal conductance and lower transpiration rates per unit leaf area but total plant water usage was 21% higher as a consequence of the 39% increase in leaf area.

Height At 20/16°C elevated CO₂ plants were, on average, 7% taller than ambient CO₂ plants whilst at 23/19°C elevated CO₂ plants were 45% taller. An ability to grow

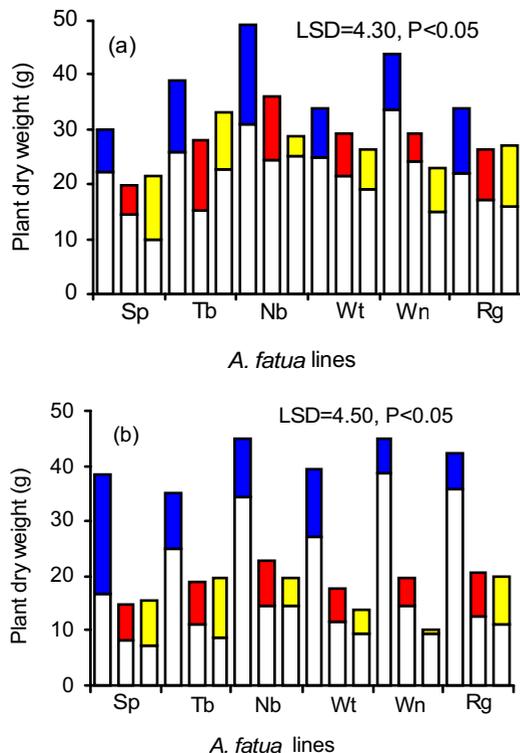


Figure 1. Plant dry weights at (a) 20/16°C and (b) 23/19°C for six lines of *A. fatua* grown at ambient CO₂ (no colour) or elevated CO₂ (coloured bar at rear). The soil-moisture levels have been indicated with colours on the elevated CO₂ bars: -0.01 MPa (blue), -0.10 MPa (red), -1.00 MPa (yellow).

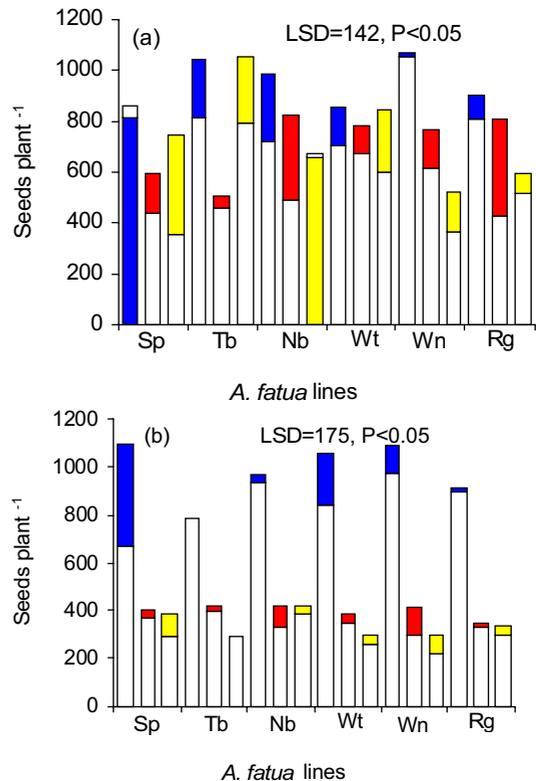


Figure 2. Seed production at (a) 20/16°C and (b) 23/19°C for six lines of *A. fatua* grown at ambient CO₂ (no colour) or elevated CO₂ (coloured bar). Refer to Figure 1 for full legend.

taller with a consequent ability to intercept more radiation could increase the competitive ability of *A. fatua*, however the response will be relative to that of competing crops.

Competitive interactions Using the equations described above the following models for *A. fatua* in monoculture at 357 ppmv CO₂ (Eqn 5) and at 480 ppmv CO₂ (Eqn 6) were derived:

$$1/w = 0.151 + (0.00148 \times N) \quad r^2 = 0.82 \text{ Eqn 5}$$

$$1/w = 0.0925 + (0.00142 \times N) \quad r^2 = 0.97 \text{ Eqn 6}$$

where w is dry shoot biomass per plant (g), and N is plant density per square metre.

For *T. aestivum* in mixture with *A. fatua* the following models at 357 ppmv CO₂ (Eqn 7) and at 480 ppmv CO₂ (Eqn 8) were derived:

$$1/w_{\text{wheat}} = 0.0695 + (0.00147 \times N_{\text{wheat}}) + (0.000646 \times N_{\text{w/oat}}) \quad r^2 = 0.86 \text{ Eqn 7}$$

$$1/w_{\text{wheat}} = 0.0461 + (0.00130 \times N_{\text{wheat}}) + (0.000727 \times N_{\text{w/oat}}) \quad r^2 = 0.81 \text{ Eqn 8}$$

From equations 5 and 6 it can be seen from the constant b_0 , that *A. fatua* plants in the absence of competition, are expected to produce approximately 54% more biomass. Although this constant estimates biomass for isolated plants, it is in quite a good agreement with values for plants grown at the same soil moisture level (-0.01 MPa) and temperature from experiment 1 above – these plants produced 45% more biomass than the ambient CO₂ controls and were grown in monoculture at a density of three plants per pot (60 plants m⁻²). The coefficient b_1 shows that the reciprocal slope for elevated CO₂ plants is steeper, and therefore, that the per-plant weight will decline faster with each plant added to the population. Intraspecific competitive stress, as measured by the ratio b_1/b_0 , is greater for elevated CO₂ plants (0.017) than the ambient CO₂ controls (0.012).

From the models describing mixture effects (Eqn's 7 and 8), the coefficients b_0 have estimated that elevated CO₂ *T. aestivum* plants will produce 51% more biomass. Relative competitive ability of *T. aestivum*, as measured by the ratio $b_{1,1}/b_{1,2}$, was reduced from 2.28 under ambient CO₂ to 1.80 under elevated CO₂. The formula:

$$[1 - (b_{1,0} + b_{1,1}N_1) / (b_{1,0} + b_{1,1}N_1 + b_{1,2}N_2)] \times 100 \text{ Eqn 9}$$

was used to examine the percentage yield loss of *T. aestivum*, under both elevated and ambient CO₂ when *A. fatua* plants were added to a constant *T. aestivum* density (Table 2). In Eqn 9, *T. aestivum* is represented as species 1.

From these experiments it is concluded that the main climate change variables will have an impact on the growth

and life-cycle processes of *A. fatua*. Reduced stomatal conductance with associated lower transpiration rates per unit leaf area and reduction in transpiration stream activity could adversely affect the efficacy of both foliar and systemic herbicides, a problem that could be amplified by the additive effects of physically larger, more robust plants. A reduced competitive ability for *T. aestivum* relative to *A. fatua* under elevated CO₂ would also indicate potential for increase in *A. fatua* populations.

ACKNOWLEDGMENTS

The authors acknowledge the support and financial assistance of the National Greenhouse Advisory Committee, Department of Environment Sport and Territories, Commonwealth of Australia. Advice given by Dr. Bob Sutherst and Dr. Joel Brown is gratefully acknowledged. We also thank Jan Priest for advice on statistical analyses and Winston Bean for service with glasshouse and associated facilities.

REFERENCES

- Adkins, S.W., Loewen, M. and Symons, S.J. (1987). Variation within pure lines of wild oats (*Avena fatua*) in relation to temperature of development. *Weed Science* 35, 169-72.
- Armstrong, L.J. (1994). Studies on the biology of wild oats (*Avena fatua* L.): The effect of selected environmental factors on growth and reproduction. Ph.D. thesis, The University of Queensland, 241 pp.
- Cure, J.D. and Acock, B. (1986). Crop responses to carbon dioxide doubling: A literature survey. *Agricultural and Forest Meteorology* 38, 127-45.
- Gifford, R. (1988). Direct effects of higher carbon dioxide concentrations on vegetation. In 'Green-house: Planning for climate change', ed. G.I. Pearman, pp. 506-19. (CSIRO, Melbourne).
- Houghton, J.T., Jenkins G.J. and Ephraums, J.J. (eds.) (1990). 'Climate change – The IPCC scientific assessment', 365 pp. (Cambridge University Press, UK).
- Kimball B.A. (1983). Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agronomy Journal* 75, 779-88
- Naylor, J.M. (1983). Studies on the genetic control of some physiological processes in seeds. *Canadian Journal of Botany* 61, 3561-67.
- Patterson D.T. and Flint, E.P. (1980). Potential effects of global atmospheric CO₂ enrichment on the growth and competitiveness of C₃ and C₄ weed and crop plants. *Weed Science* 28, 71-5.
- Spitters, C.J.T. (1983). An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. *Netherlands Journal of Agricultural Science* 31, 1-11.