

**Plant responses to elevated CO₂ levels in soils: distinct CO₂ and O₂-
depletion effects.**

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Running Title

16 **extreme CO₂ in soils**

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Key Words: extreme CO₂, soils, gas exchange, O₂ depletion, hypoxia, crops, carbon
20 capture and storage, CCS, roots

22

Abstract

24 To investigate potential environmental effects in the context of carbon dioxide (CO₂)
leakage from Carbon Capture and Storage (CCS) schemes, the University of
26 Nottingham ASGARD (Artificial Soil Gassing And Response Detection) facility,
was used to inject CO₂ into the soil in replicated open-air field plots over several
28 seasons to measure the effects on UK crop species. However, this system lacked a
way of distinguishing the concomitant effects of oxygen (O₂)-depletion (occurring as
30 a consequence of high CO₂ levels in the soil). As plants are aerobic, they require O₂
for functional integrity of root processes. Here a complementary laboratory system
32 was used to specifically identify distinct CO₂ and O₂-depletion effects on two crop
species, beetroot and wheat. Parameters measured (photosynthetic rate, transpiration
34 rate, stomatal conductance and biomass) between CO₂-gassed, nitrogen (N₂)-gassed
(O₂-depletion control) and non-gassed control plants showed distinct differences in
36 response to CO₂ gassing and O₂-depletion. Differences between field and laboratory
studies illustrate effects of variable meteorological conditions in the field, whilst
38 more stable laboratory conditions show differences between crop species. Results
show that the interactions of these two stresses (very high soil CO₂ and O₂ depletion
40 on crop physiology are discrete and complex.



The Don Valley Power Project is co-financed by the European Union's European Energy Programme for Recovery
The sole responsibility of this publication lies with the author.
The European Union is not responsible for any use that may be made of the information contained therein.

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48 **Introduction**

49 Rising atmospheric carbon dioxide (CO₂) levels and links with climate change have
50 led to the development of innovative technologies to facilitate Carbon Capture and
51 Storage (CCS). CCS is currently regarded as a critical mitigation strategy for the
52 global reduction of the atmospheric CO₂ accumulation (IPCC 2007) with the UK
53 Government committed to reducing emissions by 80% of 1990s levels by 2050
54 under the Climate Change Act of 2008. CCS is reported as being capable of
55 providing 19% of the global CO₂ emission reductions required by 2050 to facilitate a
56 smooth transition to sustainable energy production and use (L'Orange Segio *et al.*
57 2014). Many high CO₂ emitting industries (e.g. power stations) in the UK are distant
58 from potential carbon storage sites (offshore geological reservoirs) and therefore an
59 infra-structure of CO₂ transportation must be initiated to carry the CO₂ to safe
60 storage. As such there is a need to understand the risks involved and mitigation of
61 potential leaks associated with CCS and dense-phase CO₂ transportation networks
62 into the environment. As most transportation pipelines are likely to be routed
63 through agricultural land, assessment of the impacts in the unlikely event of a leak
64 on the environment and in particular on economically grown vegetation (crops) is
65 required from the outset to inform stakeholders, industry and policy makers with the
66 aim of providing industry best practice.

67
68 Although other studies have been carried out with regard to potential CCS leakage
of CO₂ (Zhou *et al.* 2013, Sharma *et al.* 2014), these studies utilised a non-replicated

70 CO₂-gradient experiment with soil CO₂ levels of between 1 and 16%. Previous
replicated field studies, the first of their kind, specifically designed to assess impacts
72 of a hypothetical CO₂ pipeline leak were carried out at the ASGARD (Artificial Soil
Gassing And Recovery Detection) facility (details in Smith *et al.* 2016 - this issue)
74 over several crop seasons. Various crops and species assemblages were investigated
including winter bean (*Vicia faba* cv. Clipper) (Patil *et al.* 2010), field bean (*Vicia*
76 *faba*), maize (*Zea mays*) (Al-Traboulsi *et al.* 2012a,b, 2013), commercial turf (Pierce
and Sjörgesten 2009) and a cover of grass/clover mix (Smith *et al.* 2013). These
78 studies investigated germination, biomass and root production and reported varied
responses to the effects of high CO₂ within the rooting zone from no change,
80 through to moderate and severe. These studies, however, could not differentiate
between effects directly caused by CO₂ or by hypoxia (a lack of oxygen (O₂)). As
82 gases compete on a volume basis, increases in CO₂ result in substantial decreases in
O₂ (Gal *et al.* 2012) (Zhou *et al.* 2013); severe O₂-depletion in the root zone is a
84 consequence of the experimental design at ASGARD and therefore, two stresses are
imposed simultaneously. As plants are aerobic organisms there is a requirement for
86 O₂ to be present in the root zone for functional integrity. Hypoxia responses in
plants have been widely reported as a consequence of waterlogging; with a recent
88 notable review specifically on wheat varieties (Herzog *et al.* 2016). Here we report
the results of a comparative study of the impacts on two crop species grown both in
90 the field and in the laboratory to isolate responses to both high soil CO₂ and low soil
O₂.

92

Materials and methods

94 *Field studies*

ASGARD is a purpose-built facility located at the University of Nottingham's
96 Sutton Bonington campus in the UK (location, N52°, 49'60; W01°, 14'60) for the
study of agro-ecosystem responses to elevated soil CO₂ concentrations. This was
98 the same facility as used and described previously (Al-Traboulsi *et al.* 2012a, b
2013) but with newly prepared test sites for the current investigation. Briefly, CO₂
100 gas is delivered to up to 16 field plots via 20 mm (Inside Diameter (ID)) medium
density polyethylene (MDPE) gas pipes. The pipes are sealed at the end, perforated
102 over the final 210 mm and inserted into the ground at an angle of 45° to the vertical
so that the CO₂ is delivered into the soil 0.5-0.6 m below the centre of each gassed
104 plot. Food-grade, CO₂ is delivered by 16 individual mass flow controllers (Alicat,
Tucson, USA) to individual experimental plots. The mass flow controllers are
106 operated, and the system data logged, by a PC-based control system (TVC, Great
Yarmouth, UK).

108

The experimental area was divided by crop type into three blocks of eight replicated
110 2.5 m × 2.5 m plots. In each block, four randomly selected plots were treated with
injected CO₂ and four were left as untreated controls for each crop species. CO₂ was
112 supplied to each plot at a constant rate of 1 L min⁻¹. The single point injection
scheme generates a distribution of CO₂ in the soil ranging from high concentrations,

114 sometimes above 50%, in the plot centre down to values approaching control levels
at the plot edges.

116

Gas measurement

118 Soil CO₂ and O₂ concentrations were measured using a GA5000 landfill gas analyser
(Geotech, Warwickshire, UK) on a weekly basis via permanently installed tubes
120 located at 0.15 and 0.70 m from the centre of the plot. Sampling areas within the
plots were zoned into low, medium and high CO₂, corresponding to soil
122 concentrations of approximately 0-4%, 4-10% and >10% respectively.

Crop species

Studies were carried out on spring wheat (*Triticum aestivum* v Tybault - a
126 monocotyledon, grass) and beetroot (*Beta vulgaris* v Pablo F1 - a dicotyledon,
vegetable). These crops were chosen to examine any differential effect on
128 monocotyledonous and dicotyledonous plant forms as well as differences in root
structure; grasses have fibrous roots, whilst beetroots form storage roots (the beet).
130 Following establishment of the crop, CO₂ gas was delivered continuously to the
gassed plots until harvest.

Plant gas exchange

134 Plant gas exchange (photosynthetic rate, stomatal conductance and transpiration
rate) was measured using an infra-red gas analyser (Licor 6400x, Licor Inc., Utah,

136 USA). A minimum of 3 replicate plants in each plot in areas of high CO₂ (>10%)
were measured respectively.

138

Laboratory studies

140 *Plant material and methods*

The same crop species (and varieties) grown in field trials were used in laboratory
142 studies to examine potential differences between field and laboratory plant responses
measured under both varied and standardised conditions respectively. Crops were
144 sown and grown in Levington's no. 3 multipurpose compost within the growth room
for 1 to 2 weeks before being transplanted into the soil chambers. They were then
146 left to allow sufficient root growth before gassing commenced (approximately 2
weeks). The gassing period lasted for up to 7 days. After that time, plants become
148 pot-bound which affects physiology and plant responses no longer reflect those
under field conditions.

150

Soil chambers were constructed of acrylic plastic with pipe inlets to allow CO₂ or N₂
152 gassing of the soil environment exclusively, which was isolated from the above
ground environment to reduce the effects of physiologically relevant atmospheric
154 CO₂ (Fig. 1A & B). The experimental system was housed in a controlled
environment growth facility (UNIGRO, UK) to standardise all other environmental
156 variables: irradiance was 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (at plant height), day/night as 12/12
hours; temperature 21/18°C; relative humidity 60%. Gas was supplied from either an

158 integral supply (pure CO₂) or a gas cylinder (nitrogen - N₂) and separated prior to
entering each individual soil chamber by 2 flow rate step-down manifolds. Gas was
160 delivered to each individual chamber at a rate of 30 (±15) mL min⁻¹ to maintain CO₂
and N₂ levels at steady state. Gases were exhausted to atmosphere via a separate
162 manifold to prevent build up within the growth room. Gas concentrations (CO₂ and
O₂) were measured daily using the GEOTECH GA5000 gas analyser (Geotech,
164 Warwickshire, UK). Each experiment consisted of 3 levels of control: CO₂-gassed
soil (experiment), N₂-gassed soil (O₂-depleted control), air-gassed soil and non-
166 gassed soil. Replication for each species was 24, 24, 16 and 16 respectively.

Plant gas exchange

168 Gas exchange was measured on each replicate plant prior to and then daily during
gassing until harvest using a Licor 6400x IRGA (Licor Inc, Utah, USA).

170 *Biomass (shoot and root)*

Plants were harvested between days 5 and 7. Shoots were taken from each plant,
172 washed and dried at 80° C for 2 days. Biomass was measured as fresh and dry
weight.

174 Roots were carefully removed from the chambers, washed, patted dry, weighed and
dried for 4 days at 50°C. They were then re-weighed. The beet (storage root) was
176 separated from the lateral roots from beetroot plants and analysed independently.
Beets were dried until the constant dry weight was measured. Wheat roots were
178 measured as dry weight only.

Statistical analyses were all carried out using Minitab v 12 (USA). One-way
180 ANOVA and Student's t tests of each treatment from each other (comparison of
means).

182

Results

184 *Gas concentrations*

In the field study, CO₂ injection caused elevated concentrations of soil CO₂ which
186 were highest above the delivery point and rapidly decreased radially towards the
edge of the gassed plots. Concentration varied in each plot due to the variability of
188 the soil conditions. Table 1 shows the mean soil CO₂ and O₂ concentration achieved
in the plots measured from the permanently installed gas measurement tubes.

190

There was a strong negative correlation ($R^2=0.95$ $P<0.001$) between the CO₂ and
192 O₂ concentration measured at 150 mm from the centre of the plot as O₂ was
displaced by CO₂.

194

In the laboratory studies, mean gas concentrations in both CO₂-gassed and N₂-gassed
196 chambers, also in Table 1, showed a reduction in O₂ levels comparable to the field
conditions, with the N₂-gassed chambers being generally slightly lower in O₂
198 concentration than the CO₂ chambers. Air-gassed plants were not statistically

different to the non-gassed controls (Table S1 – Supplementary Information) and so
200 data is shown for non-gassed controls only (as comparable to the field study).

202 *Gas exchange*

Fig 2A-L shows the mean gas exchange parameters in both the field and laboratory
204 for both species over time. Both were measured from the onset of gassing, however
measurements continued in the field for 15 days (weather permitting) whilst the
206 laboratory studies were terminated after 6/7 days. Photosynthetic rate (*A*) (Fig. 2A-
D) for both species differed in magnitude between the field and laboratory;
208 measurements were normally higher in the field due to higher light levels, but
measurements varied according to the prevailing weather conditions on the day.
210 Both experimental sets show an initial effect of CO₂ gassing on *A*, however this
difference diminishes in field grown crops. By day 15, wheat showed a reduction in
212 *A* compared to non-gassed controls, but beetroot remained the same as control
plants.

214

Stomatal conductance (*g_s*) levels were comparable for both species in the laboratory
216 and the field (Fig. 2E-H). Again an immediate and sustained reduction in *g_s* is
recorded under both CO₂-gassing and O₂-depletion. Transpiration rate (*E*) (Fig. 2I-
218 L) was also lower in the laboratory than the field for beetroot, but comparable in
wheat. Both species showed an immediate and sustained effect of CO₂ gassing on *E*
220 compared to non-gassed controls. N₂-gassed (O₂-depletion) showed an intermediate

effect in beetroot for A, g, and E (Fig 2A, E & I), but in wheat there is no statistical
222 difference for A (Fig 2C). E is recorded as higher in N₂-gassed plants compared to
controls from days 1 to 3 (Fig 2K).

224 Laboratory studies show greater differences between crop species than field
measurements. This is a consequence of both larger error rates under field conditions
226 and greater stability in laboratory conditions. Percentage (%) change from non-
gassed controls at the end of experimental gas exchange measurements is shown to
228 allow comparison between the field and laboratory results (Table 2). Fig 3A-C
graphically shows the relative effect of O₂-depletion. CO₂-gassing has a separate
230 and greater effect on reducing all three gas exchange parameters in the laboratory,
with only A remaining higher (lower % reduction) in the field in beetroot over the
232 measured time course (Fig 3A). Wheat is more sensitive to CO₂-gassing under field
compared to lab conditions (Fig 3A, B & C).

234

Whilst a one-way ANOVA for each gas exchange parameter between all treatments
236 reports highly significant differences ($p < 0.000$), Table 3 is more useful in
demonstrating the differences between CO₂-gassed and N₂-gassed plants via
238 individual Student's t-test results for individual treatments (comparison of means).
CO₂ versus N₂-gassed plants all show highly significant differences.

240 *Shoot biomass*

Table 4 gives the dry weight (g) for the total shoot and total root. Beetroot has a
242 greater shoot biomass (after drying) under CO₂-gassing than non-gassed controls,
while wheat has the smallest shoot biomass when CO₂-gassed.

244 *Root biomass*

Root biomass is severely affected by both CO₂ and N₂-gassed O₂-depletion, with
246 wheat roots affected more by O₂-depletion than CO₂ gas.

248 *Root to shoot ratio*

Table 4 also gives the root to shoot ratio (R/S). Non-gassed control plants show
250 healthy root to shoot ratios of 0.96 (beetroot) and 0.51 (wheat). Wheat has more
shoot to root biomass, whereas beetroot at this developmental stage has an equal
252 amount of both. CO₂-gassing has an effect on roots only in beetroot, while in wheat
both leaves and roots are affected. Wheat R/S is most severely affected under O₂-
254 depletion.

256 **Discussion**

There are differences in time series responses of gas exchange measurements
258 between the field and laboratory studies for both species. Field conditions varied due
to the dynamic weather conditions and therefore changes in air temperature, vapour
260 pressure deficit and water availability would all impact on measurements of A, E and
g_s on daily basis. In the laboratory, CO₂ is delivered directly and efficiently to the
262 roots, whereas in the open field system lateral diffusion may take the CO₂ away

from any individual plant, so that responses in the laboratory may be expected to be
264 more severe. Nevertheless, the impacts of CO₂ gassing were immediate (within 1
day) in both species for all parameters in both field and laboratory settings. Both g_s
266 and E exhibit similar responses in the laboratory as the field, with significant
reductions under elevated CO₂ soil levels. This is in contrast to g_s measured for both
268 dandelion and orchid grass leaves in a study carried out at the ZERT site (Montana,
USA) where stomatal conductance was recorded as higher under the highest CO₂
270 level (16%) (Sharma *et al.* 2014) with near-normal O₂ levels (recorded separately) of
~19% (Zhou *et al.* 2013), despite localised death of vegetation over time. It may be
272 that higher CO₂/lower O₂ levels recorded in the field at ASGARD here (Table 1)
produce a more severe stomatal response.

274 N₂-gassed O₂-depletion responses are more complex. Although each species
responded differently to all gassing scenarios the % reduction (Fig. 3) shows that O₂-
276 depletion effects are always less severe than CO₂ effects, illustrating that O₂
depletion and CO₂ responses are clearly separate and distinct. Whilst not exactly the
278 same growth conditions and developmental stage to the present study, several wheat
varieties were found to show similar decreases in A and g_s after 1 to 3 days of
280 waterlogging imposed O₂-depletion. Other varieties showed no response to this
treatment (Herzog *et al.* 2016), suggesting that both variety and age of the plant can
282 have differential effects on root responses to O₂-depletion.

284 Shoot biomass as dry weight is not affected in beetroot and only slightly affected in
wheat with either CO₂ or N₂-gassing (Table 4). Examination of dry root biomass

286 shows that the effect of both CO₂ gassing and O₂-depletion is severe. Comparison of
% change in dry weight against non-gassed control plants in the laboratory,
288 reductions for wheat are 71% and 75% for CO₂-gassed and N₂-gassed, respectively.
The same measurements for beetroot record a reduction of 71% and 65%
290 respectively.

292 The root to shoot ratio (Table 4) is considered a measure of plant health, with a
balanced amount of both roots and shoots contributing to below ground resources
294 (nutrients, water) and carbon acquisition respectively. A change in this ratio suggest
that an unfavourable environment (stress) has had an effect on either or both the root
296 or shoot. The ratio is different for different plant forms and for different age classes
of the same plant (Werger 1998, Kozłowski *et al.* 2012). Here, only comparisons
298 between treatments are taken into account; previous studies on wheat show R/S for
non-experimental control plants of between 1.32 and 0.33 comparable to a control
300 for wheta here of 0.51. Changes in R/S under O₂-depleted waterlogging experiments
decreased from 0.4 to 0.2 (Herzog *et al.* 2016) which also is comparable to a
302 reduction reported here to 0.22 under N₂-gassing. This suggests that O₂-depletion is
having a greater effect than CO₂-gassing and that it is largely an effect on root
304 biomass; wheat is known to be sensitive to low O₂ in the root zone (Herzog *et al.*
2016). Little information is available about beetroot in terms of O₂-depletion
306 sensitivity, but two values for R/S have been previously reported; the first in non-
stressed hydroponic systems of between 0.41 and 0.57 (Egilla 2012), which
308 suggests that beetroot in the present study is healthy at 0.96 under non-gassed

conditions. The second gives an R/S for non-treated beetroot as 2.57, but the plants
310 were 75 days old, so it is expected that the storage organ would have been much
bigger at that stage and contributed to a larger root biomass.

312 A more detailed analysis of root fresh weight versus dry weight for beetroot (Fig. 4)
shows that most losses occur in the form of true roots; the beet (storage root)
314 showing a greater loss under CO₂-gassing than O₂ depletion. Furthermore, the
difference between control plants (fresh weight to dry weight) shows that CO₂-
316 gassed plants are severely short of water at the end of the experiment. This is in
agreement with the time course measurements of *E* and *g_s*, which show greater
318 reductions under CO₂ gassing than either control or N₂-gassed plants in this crop.
This suggests that stomatal function and normal hydraulic mechanisms of water
320 transport are disrupted under CO₂-gassing for both species, and constitutes a specific
CO₂ response. As the aerial organs are isolated from treatment in the laboratory
322 studies, the effects can only be due to changes imposed on the root zone i.e.
increases in CO₂ and decreases in O₂; all other variables in the root zone are the
324 same and therefore standardised for each treatment (sufficient water availability,
temperature and growth medium) which allows for our interpretation of results. It is
326 noted that each species responds in a specific and different way. This may reflect the
differences in root architecture, however, as both crops are severely affected in the
328 root zone, such differences are subtle and don't impact hugely on the end result of
CO₂-gassing.

330

The aim of this study was to determine the differential effects of high CO₂ and low
332 O₂ levels in the soil. Data presented clearly demonstrate a separate and distinct effect
of elevated levels of CO₂ in the root zone. However, aspects of CO₂-gassed and
334 concomitant O₂-depletion effects show that both environmental stresses interact in a
complex manner. Gas exchange characteristics for beetroot show an intermediate
336 effect of O₂-depletion between non-gassed and CO₂-gassed plants, suggesting that
CO₂ and O₂-depletion effects may potentially be additive. Wheat was more sensitive
338 to CO₂-gassing under field conditions than in the lab, suggesting that field
conditions may contribute to the degree of sensitivity in the species. Roots were
340 affected differentially with beetroot more sensitive to CO₂-gassing (or an additive
effect of both CO₂ and O₂-depletion) whereas wheat was more severely affected by
342 O₂-depletion. Further investigations are required to elucidate the specific
mechanisms of each species to each stress.

344

346 **Acknowledgements**

JAL was funded by National Grid, UK and the European Union Energy Programme
348 for recovery (EEPR) under the COOLTRANS research programme. Research
carried out at the ASGARD site was part of a collaboration with the RISCs project
350 (Research into Impacts and Safety in CO₂ Storage, 2010-2013), funded by the EC 7th
Framework Programme and industrial partners ENEL I&I, Statoil, Vattenfall AB,
352 E.ON and RWE. The sole responsibility of this publication lies with the authors. The

European Union is not responsible for any use that may be made of the information
354 contained herein.

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Figure legends:

446 **Figure 1.** Schematic diagram of the soil chamber showing CO₂ diffusion in the root
zone and isolation from the aerial environment and graphic *in situ* of beetroot (A)
448 and wheat (B).

Figure 2. Gas exchange parameters for laboratory (left hand panels) and field (right
450 hand panels) experiments: photosynthetic rate (A) beetroot A, B; wheat C, D:
stomatal conductance (g_s) beetroot E, F; wheat G, H: transpiration rate (E) beetroot
452 I, J; wheat K, L. (n = 24, 24 and 16 for CO₂-gassed, N₂-gassed and non-gassed
control laboratory experiments respectively , n = 12 for CO₂-gassed and non-gassed
454 control in field experiments. Error bar = SE_{mean}).

456 **Figure 3.** Comparison of % change from non-gassed controls in photosynthetic rate
(A), stomatal conductance (B) and transpiration rate (C) showing relative effects and
458 clear differences of CO₂-gassing and O₂-depletion (as N₂-gassing) in both field and
laboratory experiments.

460

Figure 4. Effects of CO₂-gassing and N₂-gassing root biomass for beetroot
462 comparing fresh and dry weight of separated lateral and storage (beet) roots.

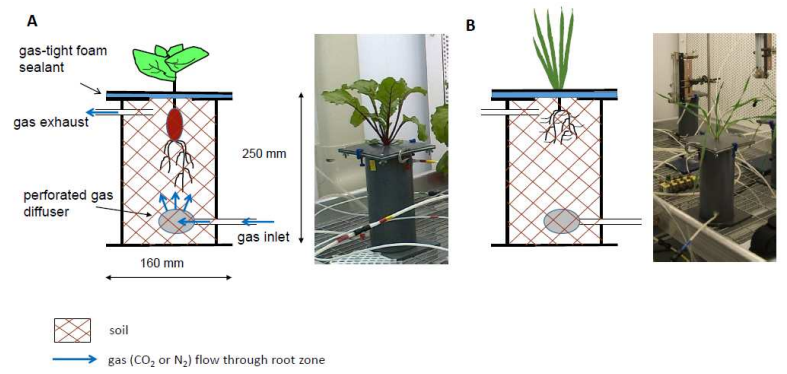
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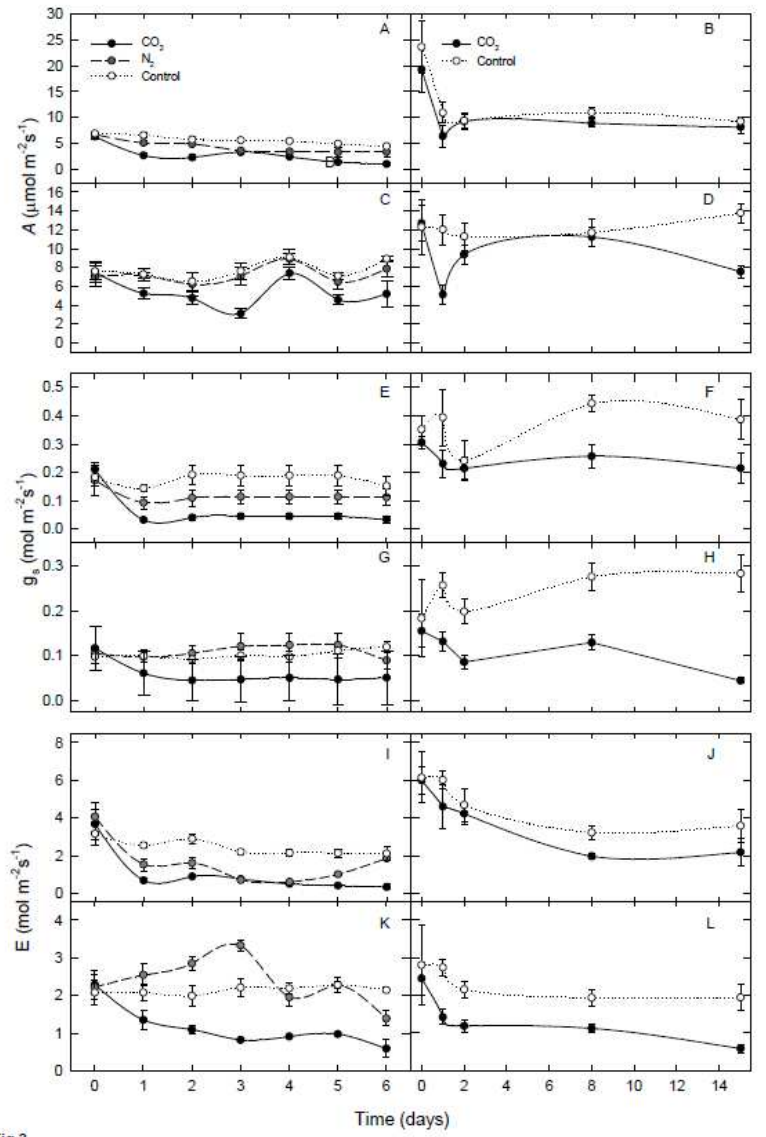
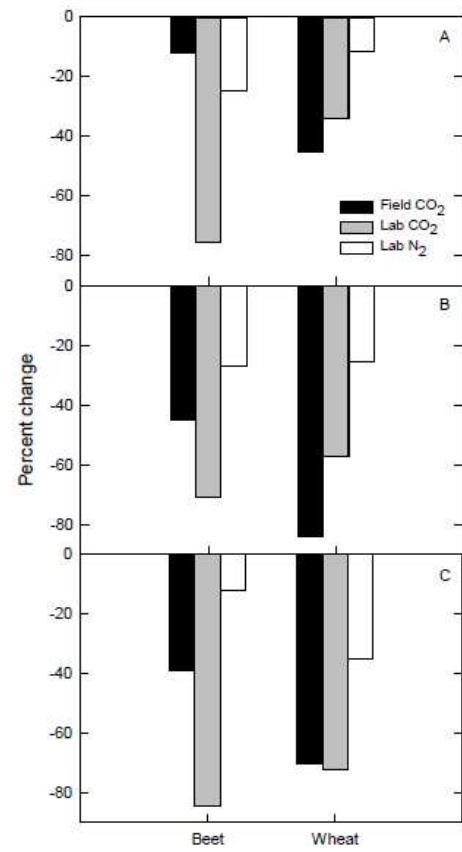


Fig.2. Lake et al. (2015).



486 Fig. 3.
Lake et al. (2015).

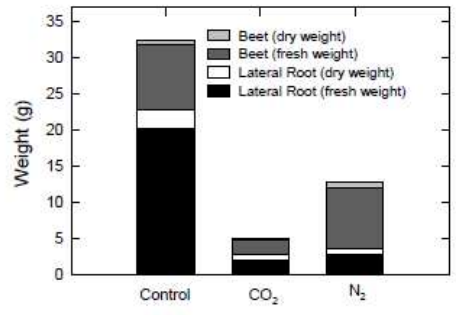


Fig. 4.
Lake et al. 2016

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498 **Table 1.** Mean CO₂ and O₂ concentrations measured in both field and laboratory
500 experiments. Laboratory experiments replicate the highest mean values measured in
the field.

Mean gas level	CO ₂ concentration (%)		O ₂ concentration (%)	
	CO ₂ -gassed	control	CO ₂ - gassed	control
field	42.2	0.7	12.7	19.6
laboratory	42.3	0.4	11.1	9.4 (N ₂ - gassed)

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516 **Table 2.** Mean % changes in gas exchange parameters from non-gassed control plants

Crop species	beet									wheat								
	A (photosynthetic rate)			E (transpiration rate)			g _s (stomatal conductance)			A (photosynthetic rate)			E (transpiration rate)			g _s (stomatal conductance)		
Day	field CO ₂	lab CO ₂	lab N ₂	field CO ₂	lab CO ₂	lab N ₂	field CO ₂	lab CO ₂	lab N ₂	field CO ₂	lab CO ₂	lab N ₂	field CO ₂	lab CO ₂	lab N ₂	field CO ₂	lab CO ₂	lab N ₂
0	-18.3	-8.5	-2.3	-2.4	+16.4	+28.9	-13.1	+22.7	-5.9	+3.3	+6.9	-7.5	-12.7	+10.2	+6.9	-15.3	+19.4	+6.9
1	-40.7	-58.7	-22.2	-23.4	-73.3	-39.9	-41.7	-66.5	-35.7	-57.4	-26.6	-1.7	-48.3	-34.9	+22.6	-48.6	-38.5	-2.4
2	-1.4	-59.1	-15.1	-9.8	-69.4	-44.4	-11.4	-63.8	-42.8	-17.0	-23.7	-4.4	-45.2	-45.1	+43.1	-56.6	-50.7	+14.4
3		-40.4	-35.4		-66.1	-67.9		-61.5	-40.2		-56.0	-7.1		-62.9	+50.7		-52.9	+20.2
4		-54.5	-36.4		-76.7	-72.1		-61.5	-40.2		-17.0	-2.2		-58.4	-10.8		-48.2	+20.2
5		-70.0	-32.0		-81.2	-53.1		-61.5	-40.2		-29.5	-8.7		-57.1	0		-57.5	+11.3
6		-75.6	-24.6		-84.4	-12.2		-71.0	-26.8		-34.0	-11.7		-72.5	-35.2		-57.1	-25.3
8	-19.0			-39.2			-42.1			-4.0			-42.1			-53.0		
15	-12.0			-39.4			-44.7			-45.2			-70.2			-84.2		

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522 **Table 3.** Student's t-test *p* values between gassing treatment and controls and
 524 between CO₂-gassing and N₂-gassing. (>0.05 is significantly different; * = test
 variables). Non-significant results are highlighted.

species	beet			wheat			beet			w
	lab			lab			field			
study	A	g _s	E	A	g _s	E	A	g _s	E	A
parameter										
treatment										
CO ₂ *control	<0.000	<0.000	<0.000	<0.000	<0.000	<0.000	0.21	0.02	0.04	<0.000
N ₂ * control	0.095	0.049	<0.000	0.028	0.86	0.53				
CO ₂ * N ₂	<0.000	<.0000	<0.000	<0.000	<0.000	<0.000				

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528 **Table 4.** Dry weight (g), total shoot and total root and root to shoot ratio (R/S) of
 beet and wheat (n = 6 per treatment, SE_{mean} in parentheses).

crop	beetroot			wheat		
	shoot biomass	root biomass (total)	root to shoot ratio	shoot biomass	root biomass	root to shoot ratio
non-gassed control	3.34 (0.35)	3.22 (0.75)	0.96	1.68 (0.8)	0.87 (0.32)	0.51
CO₂-gassed	4.47 (1.0)	0.88 (0.21)	0.19	1.33 (0.24)	0.34 (0.12)	0.26
N₂-gassed	3.42 (0.6)	1.44 (0.22)	0.42	1.62 (0.1)	0.22 (0.1)	0.14

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