Plant Physiol. (1986) 80, 59–62
0032-0889/86/80/0059/04/$01.00/0

Acclimation to High CO_2 in Monoecious Cucumbers[1]

I. VEGETATIVE AND REPRODUCTIVE GROWTH

Received for publication June 17, 1985 and in revised form July 30, 1985

MARY M. PEET
Department of Horticultural Science, Box 7609, North Carolina State University,
Raleigh, North Carolina 27695-7609

ABSTRACT

CO_2 concentrations of 1000 compared to 350 microliters per liter in controlled environment chambers did not increase total fruit weight or number in a monoecious cucumber (*Cucumis sativus* L. cv Chipper) nor did it increase biomass, leaf area, or relative growth rates beyond the first 16 days after seeding. Average fruit weight was slightly, but not significantly greater in the 1000 microliters per liter CO_2 treatment because fruit numbers were changed more than total weight. Plants grown at 1000 and 350 microliters per liter CO_2 were similar in distribution of dry matter and leaf area between mainstem, axillary, and subaxillary branches. Early flower production was greater in 1000 microliters per liter plants. Subsequent flower numbers were either lower in enriched plants or similar in the two treatments, except for the harvest at fruiting when enriched plants produced many more male flowers than the 350 microliters per liter treatments.

CO_2 enrichment increases growth and yield in many species. Compared to nonenriched cotton, high CO_2-grown plants had twice the dry weight at 40 d (18). Enrichment to 700 compared to 350 $\mu l\ L^{-1}$ CO_2 raised dry matter production from 14 to 73% in six agronomic species (7). Seed yield increased 56 to 81% in soybean cultivars (8) and 17% in wheat (9) with enrichment.

There are numerous reports also of cucumber yields responding to CO_2 enrichment in greenhouses. In the Netherlands, enrichment of gynoecious cucumber plants to 790 $\mu l\ L^{-1}$ CO_2 increased fruit weight 41% and fruit number 36% compared to plants grown at 245 $\mu l\ L^{-1}$ (10). In Japan (11) fruit weight of gynoecious cucumbers increased 31 to 40% with enrichment to 1130 $\mu l\ L^{-1}$ CO_2.

In a preliminary study, we compared growth at 350 and 675 $\mu l\ L^{-1}$ CO_2 of a field-type monoecious cucumber. We noted considerable necrosis of lower leaves and fruit fresh weight did not increase with enrichment (1.01 ± 0.13 *versus* 1.07 ± 0.11 kg). Fruit number (4.00 ± 0.99 *versus* 2.75 ± 0.50) and total dry weights (4.62 ± 0.46 *versus* 2.34 ± 0.11 g) did increase with enrichment. To our knowledge there are no previous reports of enrichment effects on cultivars developed for outdoor production.

In this experiment we determine the effect of a CO_2 concentration of 1000 $\mu l\ L^{-1}$ imposed at seeding on morphology, growth, and yield of a monoecious cucumber cultivar. Nutrient and starch concentrations and the activities of a number of enzymes in these plants are reported elsewhere (15).

MATERIALS AND METHODS

Cucumis sativus cv Chipper seeds were planted November 10, 1980 in controlled environment facilities in the Southeastern Plant Environmental Laboratory unit at Duke University in 0.24 L styrofoam cups at an initial spacing of 97 cups m^{-2} with two seeds per cup. Seedlings were thinned at emergence to one per cup and transplanted 15 d later (first true leaf stage) to 24.5 cm diameter plastic pots at a spacing of 10.8 plants m^{-2}. The potting medium was a 1:1:1 mixture of gravel, vermiculite, and calcined clay.

From the time of planting, growth chambers were maintained on a 12 h, 25/20°C thermoperiod, 70% RH, and 500 $\mu E\ m^{-2}\ s^{-1}$ irradiance at pot level. CO_2 concentrations were maintained at either 350 or 1000 $\mu l\ L^{-1}$ CO_2. Nighttime CO_2 levels were not controlled and ranged from 400 to 600 $\mu l\ L^{-1}$ in the 350 treatment but remained at approximately 1000 $\mu l\ L^{-1}$ in the 1000 treatment. Pots were watered to the drip point automatically once daily until d 33 when watering was increased to 3 times daily. At that time plants were sprayed with iron chelate.

Flowers and all axillary shoots but one were removed up to d 36. Flowers were left on the plant after d 36 and pollinated daily starting on d 44. This corresponded roughly to the vegetative, flowering, and fruiting period lengths observed in the field for monoecious cucumbers. Dry weights of mainstem, axillary, and subaxillary leaves, roots, stems, and fruit were recorded at the time of transplanting (16 d), end of vegetative growth (36 d), flowering (43 d), and during fruiting (60 d). Numbers, sex, and location of flowers were also recorded on those dates. Dry or missing fruit (resulting from unsuccessful pollination) and undeveloped fruit (resulting from successful pollination but restricted growth) were also recorded. Mainstem, axillary, and subaxillary leaf areas were measured on a LI-COR LI-3100 wide belt leaf area meter.

Relative growth rates on an area and dry weight basis and net assimilation rates (13) were calculated based on 8 plants per sampling period except for a final harvest of 12 plants.

RESULTS

Total Weights. CO_2 enriched plants were 83% heavier than control plants at d 16, but only 11% heavier by d 36. For the next two harvests total weights were virtually identical in the enriched and nonenriched treatments (Table I).

Root Weights. CO_2 enrichment increased root weights 69% and 58% for the first two harvests, respectively, but root weights did not differ significantly in the last two harvests (Table I). Root/shoot ratios which are generally reported to be higher in

---

[1] Paper No. 9929 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, NC 27695-7601. Supported in part by grant DEB 77-156845 to the Duke University Phytotron, DEB 78-23640 to B. Strain, and PCM 76-20595 to P. J. Kramer and M. M. Peet and PCM 77-11142 to P. J. Kramer.

Table I. *Growth of CO_2 Enriched and Nonenriched Cucumbers Harvested at d 16, 36, 43, and 60 After Seeding*

	Growth CO_2 level	Days after Seeding							
		16		36		43		60	
	$\mu l\ L^{-1}$	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Root dry wt (g)	350	0.072	0.0048	1.34	0.11	3.46	0.24	5.19	0.48
	1000	0.122	0.007	2.12	0.17	3.49	0.46	5.40	0.42
Stem wt (g)	350	0.039	0.0018	5.86	0.43	16.11	1.27	32.97	1.78
	1000	0.051	0.006	6.00	0.26	16.92	1.54	36.91	2.45
Leaf wt (g)	350	0.157	0.012	11.55	0.70	21.56	1.60	32.87	2.55
	1000	0.322	0.039	12.79	0.44	21.50	2.62	29.40	1.46
Total wt (g)	350	0.347	0.017	18.76	1.20	41.13	2.92	71.0	6.20
	1000	0.636	0.06	20.92	0.73	41.92	4.52	71.71	4.18
Total leaf area (dm^2)	350	0.652	0.041	32.93	1.79	64.79	3.80	98.05	6.63
	1000	0.918	0.07	31.12	1.06	52.25	4.72	93.28	4.15
Leaf number	350	2.3	0.145	24.1		50.47		106.67	
	1000	2.5	0.158	22.5		43.49		107.41	

CO_2 enriched plants (2), were only increased by enrichment at the second harvest (Table II).

Stem Weights. Mainstem, axillary, and subaxillary stem weights were recorded separately, but only total weight is shown (Table I) as responses to enrichment were similar. Stem weights were increased significantly by enrichment in the first (seedling—d 16) and last (fruiting—d 60) harvests only.

Leaf Growth. Leaf numbers in the two CO_2 treatments were similar except for the flowering harvest (d 43) at which time enriched plants had 14% fewer leaves (Table I). Leaf areas were 41% higher in enriched plants during seedling growth but subsequently, leaf areas were similar in both treatments (Table I). Leaf weights were much higher in enriched plants during seedling growth (105%) but were only 11% higher by the second harvest and did not differ significantly during the flowering or fruiting periods.

Plant Development. Morphologically, there were few differences between enriched and nonenriched plants. Plants in both treatments produced 7 axillaries at the time of the first pruning which was 26 d after initial exposure to high CO_2. Enriched plants still had an advantage in numbers of mainstem and axillary nodes at this time, indicating a slightly more rapid growth (7.06 ± 0.14 mainstem nodes and 1.89 ± 0.14 axillaries in enriched plants *versus* 6.21 ± 0.13 axillaries and 1.29 ± 0.1 nodes in nonenriched plants).

After 33 d (second pruning) the enriched treatments were actually growing at a reduced rate compared to the nonenriched treatments. Nonenriched plants produced 4.29 ± 0.11 mainstem and 2.58 ± 0.12 axillary nodes in the week since the previous trimming while enriched plants produced only 3.69 ± 0.09 mainstem and 2.15 ± 0.136 axillary nodes in the same time period.

Growth Analysis. The more rapid early growth of CO_2 enriched plants followed by equal or faster growth in nonenriched plants can also be seen in the growth analysis data (Table II). Relative growth rates based on dry weight were much higher in CO_2-enriched plants during seedling growth (0–16 d), but subsequently they were higher in the nonenriched plants. Relative leaf area expansion rates and net assimilation rates cannot be calculated for the seedling growth period since there was no initial leaf area. Relative leaf area expansion rates were higher, however, in nonenriched plants during vegetative growth and flowering. This

Table II. *Growth Rates and Root/Shoot Ratios ± SEM for Cucumbers Grown at 350 or 1000 $\mu l\ L^{-1}$ CO_2 for the Periods 0 to 16 d, 16 to 36 d, 36 to 43 d, and 43 to 60 d*

These represent periods of seedling growth up to 1st true leaf stage, vegetative growth, flowering and fruiting, respectively.

Growth Period	Relative Growth Rate				Net Assimilation Rate		Root/Shoot	
	Weight basis		Area basis					
	350	1000	350	1000	350	1000	350	1000
d	$g \cdot g^{-1} \cdot d^{-1}$		$dm^2 \cdot dm^{-2} \cdot d^{-1}$		$g \cdot dm^{-2} \cdot d^{-1}$		*ratio*	
0–16 $\bar{X}$	0.1518	0.2151					0.3670	0.3270
16–36 $\bar{X}$	0.1896	0.1681	0.1869	0.1690	0.1064	0.1136	0.0770	0.1128
SE	± 0.0030	0.0095	0.0060	0.0080	0.0070	0.0074		
36–43 $\bar{X}$	0.0988	0.0827	0.0852	0.0617	0.0594	0.0615	0.0919	0.0907
SE	± 0.0075	0.0257	0.0128	0.0210	0.0044	0.0250		
43–60 $\bar{X}$	0.0946	0.0907	0.0253	0.0445	0.1039	0.1036	0.0789	0.0813
SE	± 0.0069	0.0136	0.0142	0.0163	0.0041	0.0126		

trend reversed at fruiting, with relative expansion higher in the CO_2 enriched plants. Net assimilation rates, which are calculated as the dry weight increases per unit of leaf were similar in both treatments.

Flowering. To have flowering and fruit set correspond approximately to field developmental patterns, flowers were removed up to d 36. On d 26, enriched treatments produced 28.58 ± 1.11 flowers compared to 22.48 ± 1.35 flowers in the nonenriched treatment. By d 33, nonenriched plants produced 21.31 ± 1.05 mainstem and 10.23 ± 0.61 axillary flowers compared to only 16.62 ± 0.63 mainstem and 9.47 ± 1.37 axillary flowers in enriched plants. On d 42 mainstem and axillary flowering were unaffected but subaxillary flowering was increased by enrichment (Table III). The number of pollinated flowers which subsequently developed into fruit peaked on d 48 to 49 (3–4 d after the start of pollination). No fruit developed on flowers pollinated after d 51. Staminate flowers continued to be produced through fruiting, especially in the 1000 $\mu l\ L^{-1}$ CO_2 grown plants. No pistillate flowers were present at the final harvest.

Fruit Weight. Fruit weights and numbers on mainstem and subaxillary nodes were similar in the two treatments (Table IV) but axillary nodes of 1000 $\mu l\ L^{-1}$ grown plants produced significantly more than nodes of 350 $\mu l\ L^{-1}$ plants. Since most of the fruits were produced at the subaxillary nodes, total weights were similar in the two treatments.

There was an average of 3.25 (significant at $p = 0.05$) more undeveloped fruit per plant at the subaxillary nodes of enriched plants than nonenriched, but the number of undeveloped fruits at mainstem and axillary nodes did not differ significantly. The number of dry or missing fruit was, however, significantly greater in nonenriched plants at the axillary nodes by an average of 0.75 fruit per plant. At other nodes the differences were not significant.

DISCUSSION

Our data show that monoecious cucumbers do not fit the model (12) of the high-CO_2 crop, which, with a doubling of atmospheric CO_2 will be 40% heavier and have a larger leaf area and a much larger root system. The CO_2 used to enrich the chambers was checked for ethylene contamination as was the phytotron itself so ethylene pollution does not account for the reduced growth.

There are a few other reports of lack of long-term response to CO_2 enrichment. Dry weight of potato was lower than nonenriched controls (7) and growth of tobacco was not promoted beyond the seedling stage (16). Seed production in *Datura stramonium* and *Abutilon theophrasti* did not increase at 600 or 900 compared to 300 $\mu l\ L^{-1}$ CO_2, and seed number in fact, declined in *A. theophrasti* (6) as did biomass. Lack of effect of CO_2 enrichment on soybean leaf area has been reported by Acock *et al.* (1), but Mauney *et al.* (14) and Ford and Thorne (5) both report more and larger leaves in enriched plants of several species.

Cucumbers are particularly variable in their response to CO_2 enrichment. In the eight reports on greenhouse cucumbers listed by Kimball (12) increases of from 14 to 61% in fruit fresh weight

Table III. *Flower Production and Distribution of Cucumber Plants Grown at 350 or 1000 $\mu l\ L^{-1}$ CO_2 on d 43 and 58*

Time After Seeding	Growth CO_2 Level	Flower Production: Mainstem Male	Mainstem Female	Axillary Male	Axillary Female	Subaxillary Male	Subaxillary Female
d	*$\mu l\ L^{-1}$*			*number*			
43	350 $\bar{X}$	4.00	1.12	3.00	1.0	1.00	1.12
	SE	0.35	0.28	0.31	0.0	0.35	0.33
	1000 $\bar{X}$	3.87	0.87	3.25	1.0	0.75	2.25
	SE	0.33	0.28	0.49	0.31	0.38	0.63
58	350 $\bar{X}$	2.00	0	1.92	0	13.42	0
	SE	0.49	0	0.49	0	2.48	0
	1000 $\bar{X}$	5.75	0	5.92	0	19.17	0
	SE	1.18	0	0.70	0	2.8	

Table IV. *Fruit Production and Distribution on Cucumbers Grown at 350 or 1000 $\mu l\ L^{-1}$ CO_2*

Growth CO_2 Concn.	Mainstem 350	Mainstem 1000	Axillary 350	Axillary 1000	Subaxillary 350	Subaxillary 1000	Total 350	Total 1000	Avg Wt 350	Avg Wt 1000
					Fruit Fresh Wt					
					g/plant					
$\bar{X}$	74.58	76.98	7.35	65.97	1542.1	1472.03	1624.03	1614.98		
SE	22.49	23.21	2.22	19.87	465	443.83	489.66	489.93		
					Fruit Production					
					no./plant				*g/f*	
$\bar{X}$	0.25	0.25	0.08	0.50	8.67	7.33	9.00	8.08	187.13	203.76
SE	0.08	0.08	0.03	0.15	2.61	2.21	2.71	2.44	56.42	61.44

were reported. In Japan the yield advantage of CO_2 enrichment persisted for only the first 45 d of the harvest period. Subsequently, yields were 30% lower than in controls (11). Daunicht (4) reported that CO_2 enrichment of cucumbers was most effective early in plant development and that the final vegetative mass on continually enriched plants may not be different. He reported that the main advantage of enrichment was earliness, but that this could be rapidly overcome by control plants. Daunicht also found that for the greater part of the vegetative period the distribution of dry matter was essentially unchanged in cucumbers.

Cultivars used in the above cucumber studies set fruit parthenocarpically, and normally develop many large fruit simultaneously. The cultivar used in this study required pollination to set fruit and normally only 1 or 2 fruits develop at a time. When the first pollinated 1 to 2 fruits are removed by picking or by completion of seed development, subsequently pollinated fruits develop. The mechanism of this first fruit inhibition is not understood (see citations in Uzcategui and Baker [17]). Whatever the mechanism, however, this cultivar would have a more restricted sink than cucumber cultivars in the other studies. This study also provided a longer daily period of enrichment on the average than was possible in the other studies which were conducted in greenhouses. In greenhouses, high temperatures can cause venting for long periods each d with the consequence that CO_2 cannot be maintained above atmospheric levels. Thus, if a high source/sink ratio reduced photosynthetic response to enrichment, as was suggested by studies with soybeans (3), less response to enrichment would be expected in this study than in the other cucumber studies. In a related study, we reported on carbon exchange rates, nutrient concentration, enzyme activities, and starch concentrations in the leaves of these plants (15).

Acknowledgments—For seed, the original suggestion to conduct the experiment and subsequent comments, I am indebted to Dr. D. Mason Pharr, Department of Horticultural Science, N.C.S.U. Excellent assistance in all phases of the research was provided by Dr. Elizabeth Flint and members of the Duke University Phytotron staff.

LITERATURE CITED

1. Acock B, DN Baker, VR Reddy, JM McKinion, FD Whisler, D del Castillo, HF Hodges 1982 Soybean responses to CO_2: Measurement and simulation. *In* series 'Response of Vegetation to Carbon Dioxide. Dept of Energy and Dept of Agriculture
2. Baker DN, HZ Enoch 1983 Plant growth and development *In* ER Lemon, ed, CO_2 and Plants. Westview Press, Boulder, CO, pp 107–130
3. Clough JM, MM Peet, PJ Kramer 1981 Effects of high atmospheric CO_2 and sink size on rates of photosynthesis of a soybean cultivar. Plant Physiol 67: 1007–1010
4. Daunicht HJ 1974 Control of plant growth and development by carbon dioxide concentration. Acta Hortic 39: 167–174
5. Ford MA, GN Thorne 1967 Response of CO_2 concentration on growth of sugar-beet, barley, kale, and maize. Ann Bot 31: 629–644
6. Garbutt K, FA Buzzaz 1984 The effects of elevated CO_2 on plants. III. Flower, fruit and seed production and abortion. New Phytol 98: 433–446
7. Goudriaan J, HE de Ruiter 1983 Plant growth in response to CO_2 enrichment, at two levels of nitrogen and phosphorus supply. 1. Dry matter, leaf area and development. Neth J Agric Sci 31: 157–169
8. Havelka UD, RC Ackerson, MG Boyle, VA Wittenbach 1984 CO_2-enrichment effects on soybean physiology. I. Effects of long-term CO_2 exposure. Crop Sci 24: 1146–1150
9. Havelka UD, WA Wittenbach, MG Boyle 1984 CO_2 enrichment effects on wheat yield and physiology. Crop Sci 24: 1163–1168
10. Heij G, JAM van Uffelen 1984 Effects of CO_2 concentration on growth of glasshouse cucumber. Acta Hortic 162: 29–36
11. Ito T 1978 Physiological aspects of carbon dioxide enrichment to cucumber plants grown in greenhouses. Acta Hortic 87: 139–146
12. Kimball BA 1983 Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. Agron J 75: 779–788
13. Kvet J, JP Ondok, J Necas, PG Jarvis 1971 Methods of growth analysis. *In* Z Sestak, J Catsky, PG Jarvis, eds, Plant Photosynthetic Production: Manual of Methods. Dr W Junk, NV, The Hague, pp 343–391
14. Mauney JR, KE Fry, G Guinn 1978 Relationship of photosynthetic rate to growth and fruiting of cotton, soybean, sorghum and sunflower. Crop Sci 18: 259–263
15. Peet MM, SC Huber, DT Patterson 1986 Acclimation to high CO_2 in monoecious cucumbers. II. Carbon exchange rates, enzyme activities, and starch and nutrient concentrations. Plant Physiol 80: 63–67
16. Thomas JF, CD Raper Jr, CE Anderson, RJ Downs 1975 Growth of young tobacco plants as affected by carbon dioxide and nutrient variables. Agron J 67: 685–689
17. Uzcategui NA, LR Baker 1979 Effects of multiple-pistillate flowering on yields of gynoecious pickling cucumbers. J Am Soc Hortic Sci 104: 148–151
18. Wong SC 1979 Elevated atmospheric partial pressure of CO_2 and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C_3 and C_4 plants. Oecologia 44: 68–74