Host Suitability of *Phaseolus lunata* for *Trichoplusia ni* (Lepidoptera: Noctuidae) in Controlled Carbon Dioxide Atmospheres

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ABSTRACT Elevated atmospheric carbon dioxide (CO_2) levels of 1,000 parts per million (ppm) significantly increased consumption of foliage by *Trichoplusia ni* (Hübner) and significantly enhanced growth of *Phaseolus lunata* L. when compared with ambient levels of 340 ppm. Mean pupal weight was less under treatments with elevated atmospheric CO_2 under a high fertilization regime, but larval survival and percent nitrogen content of pupae were not affected by level of CO_2 treatments at high, medium, or low fertilizer rates. Regardless of CO_2 concentration, larval survival and pupal weight were reduced in absence of fertilizer. Nitrogen and protein consumption increased with fertilization rate. Because percent leaf area of plants consumed by *T. ni* larvae was not affected by CO_2 concentration, this study suggests that increased plant growth resulting from elevated atmospheric CO_2 may benefit the plant proportionately more than the insect.

KEY WORDS *Trichoplusia ni*, *Phaseolus lunata*, atmospheric CO_2

CONCENTRATION OF global atmospheric carbon dioxide (CO_2) is increasing at a rate of ca. 4% a year, which, if this rate continues, will result in a doubling of CO_2 levels in the atmosphere in the next 60 yr (Baes et al. 1977). Such changes can be expected to affect world agriculture, because elevated atmospheric CO_2 levels have been demonstrated to enhance the productivity of plants utilizing the Calvin (C3) cycle (Lemon 1983, LaMarche et al. 1984, von Caemmerer & Farquhar 1984). In addition, nitrogen levels and the nitrogen/carbon ratio of plants grown in elevated CO_2 may be decreased (Wong 1979, Sionit 1983). This decrease in available nitrogen has caused accelerated feeding rates of some herbivorous insects, thereby suggesting that increased levels of gross plant productivity at higher CO_2 concentrations could be offset or even reduced below the current levels (Lincoln et al. 1984). Thus, the increase in atmospheric CO_2 could have a profound effect on insect/plant interactions in both natural and agricultural communities.

We report here how increased atmospheric carbon dioxide, combined with three fertilization regimes, changes various growth and nutritional parameters of lima beans, *Phaseolus lunata* L., and how this affects host plant suitability for the cabbage looper, *Trichoplusia ni* (Hübner).

Materials and Methods

Chamber. All tests were conducted in two identical greenhouse-type chambers. The frames of the chambers (137 by 99 by 92 cm) were assembled from wood waterproofed with white marine paint (Fig. 1). Acetate plastic was used to construct the lower transparent wall panels and transparent teflon film was used for the remainder of the walls and ceiling. Teflon film was used because of its durability, lack of static charge, and permeability to long-wave radiation. All joints were sealed with silicone caulking to prevent air leaks. A dynamic, flow-through, air exchange system was constructed from flexible vinyl ducting (10 cm diameter), and 115-V shade pole blowers provided an air flow rate of 2.5 complete air exchanges per minute (3.13 m^3/min) as determined with a jeweled anemometer (Taylor Biram's). This rate of air exchange was designed to prevent CO_2, O_2, and excessively high temperatures from accumulating in the chambers. Exhaust ports were ducted outside the greenhouse in which the chambers were located, and a slight negative pressure maintained within the chambers prevented contamination of intake air of the control chamber (Heck et al. 1978).

One chamber was equipped with a CO_2 regulating system, which consisted of an air pump (common aquarium type) that drew an atmospheric sample from the intake port of the chamber and forced it through a sample line (polypropylene tubing, 3 mm i.d.) into an infrared gas analyzer (IRGA) (Beckman model 15A) and returned the sample to the chamber (Fig.1). The standard panel meter of the IRGA amplifier was replaced with a solid-state double-setpoint meter relay (Simpson, model 3324AIXA) to provide switching for control of CO_2 concentration. A general-purpose, solid-state switch was constructed to control power to a solenoid valve

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Table 1. Effect of atmospheric CO_2 and fertilization regimes on consumption of *P. lunata* by *T. ni*

Fertilizer regime	CO_2[a]	Consumption per larva ($\bar{x}$ ± SEM)					
		Dry matter (mg) (*n*)	Wet matter (g) (*n*)	Leaf area (cm^2) (*n*)	% leaf area (*n*)	Nitrogen (mg) (*n*)	Protein (mg) (*n*)
LFR	0	271.03 ± 48.66 (15)c	1.18 ± 0.21 (15)b	87.43 ± 15.70 (15)c	35.73 ± 6.25 (15)bc	4.92 ± 0.88 (15)d	5.95 ± 1.07 (15)d
LFR	+	311.98 ± 73.71 (21)b	1.26 ± 0.30 (21)b	94.54 ± 22.34 (21)bc	41.05 ± 11.56 (21)ab	4.90 ± 1.16 (21)d	9.04 ± 2.13 (21)c
MFR	0	177.09 ± 37.28 (30)d	1.14 ± 0.24 (30)b	84.33 ± 17.75 (30)c	29.38 ± 7.32 (21)c	6.15 ± 1.29 (30)c	10.36 ± 2.18 (30)c
MFR	+	257.33 ± 40.75 (22)c	1.12 ± 0.18 (22)b	102.93 ± 16.30 (22)ab	27.45 ± 5.09 (19)c	6.34 ± 1.00 (22)c	10.39 ± 1.64 (22)c
HFR	0	237.61 ± 62.75 (33)c	1.14 ± 0.30 (33)b	99.01 ± 26.15 (33)b	46.90 ± 16.17 (33)a	11.43 ± 3.02 (33)b	14.96 ± 3.95 (33)a
HFR	+	464.54 ± 76.65 (32)a	1.47 ± 0.24 (32)b	110.61 ± 18.25 (32)a	49.29 ± 16.17 (32)a	13.72 ± 2.26 (32)a	12.94 ± 2.14 (32)b

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] 0, ambient (340 ± 20 ppm) atmospheric CO_2 levels; +, increased (1,000 ± 15 ppm) atmospheric CO_2 levels.

in the CO_2 line (schematic available upon request from the authors). The chamber with elevated CO_2 concentration was operated slightly below the opening point of the meter relay, causing shutdown of CO_2 flow only when desired concentrations were exceeded.

A cylinder of compressed CO_2 with a two-step gas regulator, needle valve, and flow meter was connected with polypropylene tubing through the solenoid valve to the intake ducting of the chamber. With the appropriate flow setting, CO_2 passed into the intake port uninterrupted, and maintained a constant concentration of atmospheric CO_2 flow into the chamber. CO_2 concentrations were recorded constantly with a strip chart recorder attached to the IRGA amplifier. The IRGA was calibrated with standardized gasses (Liquid Carbonic, Los Angeles, Calif.) to function in the range of 300–1,100 ppm. Measurements of CO_2 concentrations at various locations in the chamber, both with and without plants, were taken with the CO_2 IRGA sensor of a LiCor 6000 photosynthesis system to determine if intrachamber heterogeneity of gas concentrations existed.

Insect/Plant Interactions. Effects of CO_2 and fertilizer regimes on plant and insect development were tested using a factorial blocked design with two levels of atmospheric CO_2 (ambient, 340 ± 20 ppm; elevated, 1,000 ± 15 ppm) and three levels of fertilization as the factors. Fertilization regimes were as follows: no fertilizer (LFR), 100 ml of Hoagland's nutrient solution (Downs & Hellmers 1975) the day after unfolding of the primary leaves (MFR), and 100 ml of Hoagland's nutrient solution applied every 48 h beginning the day after unfolding of the primary leaves until termination of the experiment (HFR). Two chambers were used, one maintained at elevated CO_2 levels and the other at ambient CO_2 levels. The three fertilization regimes were randomly sequenced in time. Each fertilization treatment was replicated three times at each of the CO_2 levels. Data were analyzed with analysis of variance (ANOVA) and Duncan's (1955) multiple range test using the general linear models (GLM) procedure of SAS (SAS Institute 1985). Pearson's product moment correlations (r) were determined using the Proc Corr procedure of SAS (SAS Institute 1985).

Lima beans were grown from seeds in plastic pots (10 by 10 cm, 0.4 liter) containing soil mix (Matkin & Chandler 1957). Twenty-four plants were germinated and grown in each of the chambers for each replicate maintaining approximate CO_2 regimes and located in an air-conditioned greenhouse under full sunlight. Midday irradiance (400–700 nm) averaged 1,500 $\mu mol \cdot s^{-1} \cdot m^{-2}$ (quanta) measured with a quantum sensor (LiCor, Lincoln, Nebr.). Only primary and first trifoliate leaves were allowed to develop; all other foliage was pruned. *T. ni* were obtained from a laboratory colony at University of California, Riverside. Neonate larvae were placed individually on each of

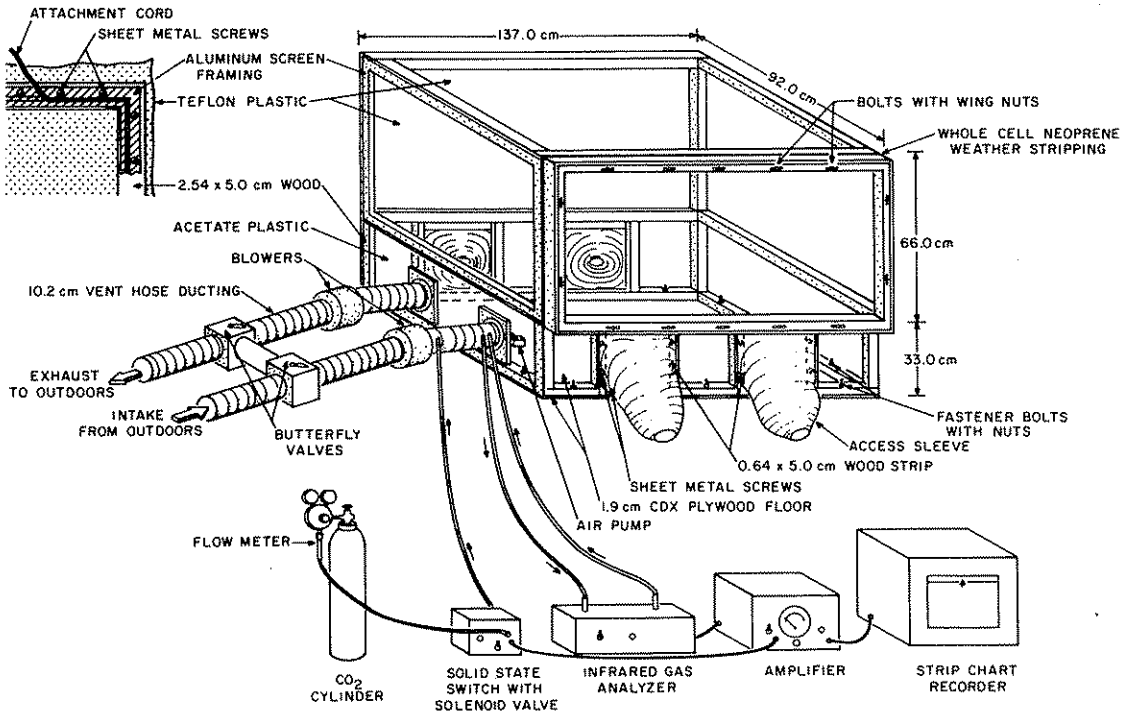

Fig. 1. Chamber with CO_2 gas regulation system.

the bean plants when they had only their primary leaves unfolded (ca. 7 days after planting). Interplant movement of larvae was prevented by a suitable spacing of plants. Larvae were allowed to develop to pupation, at which time the plants were harvested. Number of larvae surviving to pupation and pupal weights were recorded. Insects not found were considered dead. Leaves were photocopied and frozen. Photocopies were utilized for leaf area and feeding area determination using a leaf area meter (LiCor). Ten leaf disks (3.80 cm^2) were cut from primary leaves selected randomly from each treatment to determine wet and dry leaf weight and fresh weight/dry weight ratio. Leaf protein was determined from frozen leaf samples (0.50 g) using the Bio-Rad Protein Assay (Bio-Rad Chemical Division, Richmond, Calif.) (see tables for sample sizes). Percent nitrogen content of leaves and pupae was determined with oven-dried (70°C) leaf samples (50.00 mg [dry weight]) and whole dried (70°C) pupae by the microkjeldahl procedure (McKenzie & Wallace 1954) in which copper sulfate was substituted for the catalyst mercuric oxide red. *T. ni* consumption of wet weight, dry weight, nitrogen, and protein was calculated from leaf disk data and feeding area determinations.

To evaluate further the effects of increased atmospheric CO_2 on the host, 40 lima beans were grown in each of the two chambers at high and ambient CO_2 levels. Half of the plants in each chamber were fertilized once with Hoagland's nutrient solution (100 ml) the day after unfolding of the primary leaves (MFR) and the other half of the plants remained unfertilized (LFR). The plants were allowed to grow ad libitum (no pruning). At 17 d after planting, photosynthetic rate and stomatal resistance were determined using the LiCor photosynthetic system. At 21 d after planting, all

Table 2. Interactions of atmospheric CO_2 and fertilization rate on *T. ni* development ($\bar{x}$ ± SEM)

Fertilizer regime	CO_2[a]	Larval survival (%) (*n*)	Pupal wt (mg) (*n*)	Pupal nitrogen content (%) (*n*)
LFR	0	25.94 ± 4.76 (72)c	118.77 ± 19.91 (13)c	10.27 ± 0.02 (4)a
LFR	+	32.71 ± 0.00 (72)bc	123.76 ± 19.22 (20)c	9.53 ± 1.30 (4)a
MFR	0	42.59 ± 6.35 (72)a	173.04 ± 26.55 (30)a	9.86 ± 1.30 (5)a
MFR	+	36.90 ± 2.87 (72)ab	178.53 ± 22.17 (24)a	10.30 ± 0.53 (5)a
HFR	0	42.60 ± 2.39 (72)a	170.34 ± 18.57 (32)a	9.93 ± 0.10 (4)a
HFR	+	41.75 ± 5.63 (72)a	158.59 ± 13.15 (32)b	10.05 ± 0.67 (4)a

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] 0, ambient (340 ± 20 ppm) atmospheric CO_2 levels; +, increased (1,000 ± 15 ppm) atmospheric CO_2 levels.

Table 3. Effect of atmospheric CO_2 and fertilizer regime on selected growth and nutritional parameters of *P. lunata* ($\bar{x} \pm$ SEM)

Fertilizer regime	CO_2[a]	Leaf area (cm^2) (*n*)	Dry density (mg/cm^2) (*n*)	Nitrogen (% dry wt) (*n*)	Protein (mg/g wet wt) (*n*)	Wet wt (g) (*n*)	Dry wt (mg) (*n*)	Wet wt/dry wt ratio (*n*)
LFR	0	247.86 ± 39.68 (15)c	3.05 ± 0.39 (10)bc	1.82 ± 0.14 (10)e	5.04 ± 1.04 (8)c	3.35 ± 0.54 (15)b	755.74 ± 120.98 (15)b	4.51 ± 0.76 (10)b
LFR	+	235.28 ± 38.07 (21)c	3.34 ± 0.28 (10)b	1.57 ± 0.18 (13)e	7.19 ± 1.24 (7)b	3.12 ± 0.50 (21)bc	786.08 ± 127.19 (21)b	3.99 ± 0.31 (10)b
MFR	0	293.70 ± 66.41 (30)b	2.10 ± 0.26 (10)d	3.47 ± 0.60 (9)e	9.10 ± 2.62 (6)b	3.98 ± 0.90 (30)a	615.90 ± 139.42 (30)c	6.25 ± 1.19 (10)a
MFR	+	386.63 ± 59.80 (22)a	2.51 ± 0.14 (10)cd	2.47 ± 0.66 (14)d	9.26 ± 2.62 (6)b	4.22 ± 0.65 (22)a	970.38 ± 150.10 (22)a	4.35 ± 0.66 (10)b
HFR	0	236.70 ± 67.09 (33)c	2.36 ± 0.25 (10)d	4.81 ± 0.58 (10)a	13.14 ± 2.68 (10)a	2.71 ± 0.80 (33)c	558.57 ± 158.33 (33)c	4.82 ± 1.53 (10)b
HFR	+	256.13 ± 110.09 (32)bc	4.27 ± 1.39 (10)a	2.95 ± 0.64 (14)c	8.80 ± 1.82 (12)b	3.41 ± 1.47 (32)b	1,092.93 ± 469.75 (32)a	3.05 ± 0.69 (10)c

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] 0, ambient (340 ± 20 ppm) atmospheric CO_2 levels; +, increased (1,000 ± 15 ppm) atmospheric CO_2 levels.

plants were harvested and leaf area was determined using a leaf area meter. Dry weight of leaves, stems, and roots; length of stems and roots; number of nodes; and number of trifoliate leaves (>0.5 cm long) were determined. This test was replicated twice. ANOVA and Duncan's (1955) multiple range tests were computed using the GLM procedure of SAS (SAS Institute 1985).

Results and Discussion

Maximum and minimum air temperatures reached in each chamber were 35°C during the day and 25°C at night, respectively. CO_2 levels were homogenous and stable throughout the chambers either with or without plants, indicating that problems associated with inadequate mixing or slow flow rates causing photosynthetic depletion of CO_2 did not occur (Patterson & Hite 1975, Pallus 1979).

Elevated atmospheric CO_2 significantly increased dry matter consumption under all fertilization regimes and leaf area consumption at MFR and HFR compared with ambient CO_2 concentrations ($P < 0.05$) (Table 1). Nitrogen consumption increased significantly with fertilization rates ($P = 0.001$; ANOVA). These results are consistent with previous research (Lincoln et al. 1984), but in our study the percent leaf area consumed as well as wet weight consumption were not significantly different between CO_2 treatments within any fertilization regime; thus, the impact of increased dry matter consumption was nullified by increased gross productivity of the plants.

Pupal weight was significantly lower in elevated CO_2 at HFR as compared with ambient CO_2, although larval survival was not affected ($P < 0.05$) (Table 2). At MFR, larval survival rates and pupal weights were equivalent regardless of CO_2 concentration. Pupal weights and larval survival were lowest in the LFR treatments and were not affected by CO_2 levels. There were no differences in nitrogen content of pupae between any fertilizer or CO_2 treatment.

In the fertilized treatments, elevated CO_2 decreased nitrogen content in the leaf material at MFR and HFR and reduced protein content in HFR (Table 3). In addition, we found a significant correlation between protein consumption and insect survival ($r = 0.68$; $P = 0.0001$; $n = 155$), and nitrogen consumption and survival ($r = 0.76$; $P = 0.0001$; $n = 155$). Lighter pupae and increased leaf consumption were apparently an adjustment by the insect to a lack of available or assimilable nitrogen (Mattson 1980, Scriber & Slansky 1981). Similar results were reported by Lincoln et al. (1984) for the soybean looper, *Pseudoplusia includens* (Walker), feeding on soybean plants. Because weight is related directly to fecundity in *T. ni* (Shorey 1963), elevated CO_2 levels resulting in the occurrence of lighter pupae under conditions of HFR, which is typical of commercial agricultural

Table 4. Growth of *P. lunata* in ambient and elevated atmospheric CO_2 and interactions of elevated CO_2 and fertilizer regimes in test chambers

Growth parameter	No. plants tested	Treatment ($\bar{x} \pm$ SD)			
		LFR		MFR	
		Ambient CO_2[a]	High CO_2	Ambient CO_2	High CO_2
Leaf area (cm^2)	80	162.25 ± 7.12d	208.50 ± 12.68c	268.19 ± 9.38b	360.56 ± 21.61a
Photosynthesis[b]	20	0.486 ± 0.078c	0.540 ± 0.039c	0.960 ± 0.053b	1.232 ± 0.041a
Stomatal resistance[c]	20	1.056 ± 0.312a	1.410 ± 0.253a	0.670 ± 0.050a	0.884 ± 0.066a
Dry leaf wt (g)	80	0.289 ± 0.028b	0.319 ± 0.046b	0.459 ± 0.035a	0.465 ± 0.075a
Dry stem wt (g)	80	0.084 ± 0.018c	0.206 ± 0.032b	0.224 ± 0.022b	0.328 ± 0.043a
Stem length (cm)	80	34.28 ± 2.26c	81.56 ± 3.56b	74.13 ± 4.85b	102.12 ± 2.84a
Root length (cm)	80	23.59 ± 0.84a	24.26 ± 1.12a	21.15 ± 1.01a	23.83 ± 0.96a
Dry root wt (g)	80	0.308 ± 0.048ab	0.197 ± 0.035b	0.206 ± 0.026b	0.403 ± 0.073a
Total dry wt (g)	80	0.677 ± 0.062b	0.763 ± 0.095b	0.888 ± 0.068b	1.190 ± 0.148a
No. of trifoliates	80	1.4 ± 0.5b	2.0 ± 0b	2.8 ± 0.4a	2.9 ± 2.4a
No. of nodes	80	3.8 ± 0.6d	5.2 ± 0.6c	6.0 ± 0.6b	7.0 ± 0a

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Duncan's [1955] multiple range test).
[a] Ambient CO_2 = 340 ± 20 ppm; elevated atmospheric CO_2 = 1,000 ± 15 ppm.
[b] $mg \cdot s^{-1} \cdot m^{-2}$.
[c] $cm \cdot s^{-1}$.

practices, could profoundly affect the population dynamics of this pest.

The fertilization effect demonstrated for other plant species (Lemon 1983, LaMarche et al. 1984, von Caemmerer & Farquhar 1984) was also evident in our study for *P. lunata*. Significant increases in the number of plant nodes, leaf areas, photosynthetic rates, dry stem weights, stem lengths, dry root weights, and total dry weights were found for the MFR-high CO_2 treatment when compared with plants grown under ambient CO_2 concentrations ($P \leq 0.05$) (Table 4). Similar trends were evident for the LFR treatment, but the differences were not as great. These results are in agreement with results of nitrogen/CO_2 enrichment studies by Wong (1979) on cotton and are indicative of the increased gross productivity caused in many plants using the basic C3 photosynthetic cycle under conditions of elevated atmospheric CO_2. Stomatal resistance was consistently but not significantly higher for *P. lunata* under conditions of increased atmospheric CO_2, which demonstrated a trend consistent with significant increases reported by Sionit et al. (1984). Such effects of CO_2 on stomatal resistance are of considerable interest, because changes in both water use efficiency and leaf microclimate may in turn affect host-plant survival and suitability for arthropods (Perring et al. 1986).

Increased photosynthetic rate induced by elevated atmospheric CO_2 apparently competes with plant nitrogen metabolism for energy and reducing capacity from electron transport system (Lemon 1983). This may shift the carbon nitrogen balance in favor of the carbon, decreasing the nutritional value of the leaf material, thereby increasing consumption by herbivores. In study, increased leaf consumption was offset, however, by the increased amount of leaf material produced in the elevated CO_2 environment. Thus, because the percent leaf area of the plant consumed by *T. ni* larvae was not affected by CO_2 concentration (Table 1), and elevated CO_2 reduced pupal weight under the high fertilization regime typical of modern agriculture, increased plant growth resulting from elevated atmospheric CO_2 may benefit the plant proportionally more than the insect.

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