

Communication

# Soybean Seed Growth in Response to Long-Term Exposures to Differing Oxygen Partial Pressures

Received for publication November 6, 1986

THOMAS R. SINCLAIR\*, JUDITH P. WARD, AND CAROLYN A. RANDALL  
*Environmental Physiology Project, United States Department of Agriculture, Agricultural Research Service, Bldg. 164, Agronomy Department, University of Florida, Gainesville, Florida 32611*

## ABSTRACT

Short-term studies have indicated that alterations in the oxygen partial pressure ( $pO_2$ ) around developing soybean (*Glycine max* [L.] Merr.) seeds may alter seed growth characteristics. A 2-year field study was undertaken to determine the effects on seed development of long-term exposures of individual pods to either sub-ambient or supra-ambient  $pO_2$ . Pod chambers were used through which fixed  $pO_2$  were continuously flowed throughout seed development. No effects on maturity date were observed from exposures to either sub-ambient or supra-ambient  $pO_2$ . On the other hand, seed weight was reduced by 0.10  $pO_2$  in both years of the study implicating an  $O_2$  limitation on seed growth rate at this fairly high  $pO_2$ . In 1 of the 2 years, supra-ambient  $pO_2$  resulted in increased seed weight.

## MATERIALS AND METHODS

A 2-year study was conducted on the University of Florida Agronomy Farm where the soil type was Arredondo fine sand (loamy, siliceous, hyperthermic Grossarenic Palendalf). Before sowing, the field was broadcast with 56 g  $m^{-2}$  of 0-10-20 (N-P<sub>2</sub>O<sub>5</sub>-K<sub>2</sub>O) fertilizer. In each year the soybean cultivar Williams was sown in rows spaced 0.76 m apart with a spacing of 26 to 33 plants per m within the row. The sowing date in 1983 was 8 April and in 1984 it was 2 April. The crop was irrigated to avoid any drought stress.

Young pods 10 to 30 mm long on primary racemes between the 5th and 8th nodes were enclosed in chambers on 31 May in 1983 and on 29 May in 1984. These chambers, similar to those used by Spaeth and Sinclair (8) in the measurements of pod respiration rates, were 10 cm<sup>3</sup> plastic syringe bodies from which the plungers had been removed. Only one pod per plant was placed in a syringe and the syringe was attached to the plant with rubber bands around the plant stem. Air was flowed continuously at 1.7 cm<sup>3</sup> s<sup>-1</sup> into the chamber from an air line attached to the needle end of the syringe at the distal end of the pod. The gas in the chamber was allowed to escape freely from the chamber around the plant stem at the proximal end of the pod.

In 1983 pods were exposed to one of four  $pO_2$ : 0.10, 0.21 (ambient), 0.42, and 0.62. The three  $pO_2$  differing from atmospheric partial pressure were obtained by adding either N<sub>2</sub> or O<sub>2</sub> gas to ambient air. No attempt was made to reestablish ambient CO<sub>2</sub> levels in the treatments derived by dilution with either N<sub>2</sub> or O<sub>2</sub>. Ambient CO<sub>2</sub> dilution (50%) was equal in the 0.10 and 0.62  $pO_2$  treatments and it was less in the 0.42  $pO_2$  treatment. The  $pO_2$  was confirmed daily at the pod chambers with a paramagnetic O<sub>2</sub> analyzer (model 570A, Sybron Instruments<sup>2</sup>) and the  $pO_2$  was confirmed to be within 0.02 atm of the prescribed treatment. Forty chambers received each gas mixture, for a total of 160 chambers used in this experiment. Pods were harvested at physiological maturity, the date noted and the dry weight of individual seeds obtained. Physiological maturity was judged to have occurred when pod walls changed to a yellowish color (1, 9, 11).

In 1984, the 0.62  $pO_2$  treatment was eliminated but a set of control pods was included on which no chambers were used. Eighty pods were identified for each treatment. Two intermediate harvests of 20 pods each were made on 12 and 26 June. Forty pods were harvested from each treatment on the final date, which was 6 July when most pods were yellow or brown. Pod color and individual seed dry weights were recorded.

---

Several studies have demonstrated that soybean (*Glycine max* [L.] Merr.) seed growth traits are affected by short-term exposures of developing seeds to atmospheres differing in  $pO_2$ <sup>1</sup> from ambient. Decreases in  $pO_2$  have been found to decrease seed respiration rates (3) and sucrose uptake rates (12). Conversely, increases in  $pO_2$  above ambient were found to increase seed respiration rates (4) and sucrose uptake rates (12). These results from short-term studies implicate O<sub>2</sub> as an important factor regulating seed growth.

Only one set of long-term experiments of altered  $pO_2$  has been reported from which effects on soybean seed growth can be inferred. Quebedeaux and Hardy (5, 6) sealed the entire shoots of soybean into chambers in which  $pO_2$  was maintained at 0.05, 0.21, or 0.40 for extended periods. Plants exposed to 0.05  $pO_2$  during the period of seed development produced little or no seed. Plants exposed to 0.40  $pO_2$  during seed development produced less seed mass than those in 0.21  $pO_2$ . However, exposure of the entire shoot to 0.40  $pO_2$  confounded the influence of O<sub>2</sub> on seed growth because photorespiration in the leaves was probably stimulated at this high  $pO_2$ , resulting in less net carbon fixation by the plant.

This study was undertaken to examine the effects of altering  $pO_2$  in the atmosphere around individual pods during seed growth. Small chambers were placed around developing pods to allow them to be exposed to  $pO_2$  below, at, or above ambient levels. The results from this 2-year field study demonstrated that altered  $pO_2$  had no effect on pod maturity date, but significantly influenced final seed weight.

<sup>2</sup> Mention of company names or commercial products does not imply recommendation or endorsement by the United States Department of Agriculture over others not mentioned.

<sup>1</sup> Abbreviation:  $pO_2$ , oxygen partial pressure.

## RESULTS AND DISCUSSION

Pod development in the chambers was visually observed to be no different than those pods outside of chambers. Similar to the natural situation some of the pods in the chambers were aborted and abscised. No differences in pod abortion rate among the pO<sub>2</sub> treatments was observed with all treatments having about 5% pod abscision.

No significant difference was found in maturity date among the four pO<sub>2</sub> treatments in the 1983 experiment (Table I). On the other hand, significant differences were found in mean seed dry weight. When compared to the seed weights produced by pods exposed to ambient pO<sub>2</sub>, the 0.10 pO<sub>2</sub> produced significantly lower seed weights and the 0.42 and 0.62 pO<sub>2</sub> produced significantly greater seed weights. The derived seed growth rate at 0.21 pO<sub>2</sub> was approaching 90% of the maximum achieved at 0.42 pO<sub>2</sub>.

The results from 1984 essentially confirmed those from the previous year. The distribution in pod color at the final harvest was similar among the four treatments with over 95% of the pods in each treatment having attained a yellow or brown color. These results indicated no difference in maturity among the treatments. However, significantly lower seed dry weights were obtained from the pods subjected to 0.10 pO<sub>2</sub> as compared to those treatments receiving greater pO<sub>2</sub> (Table II). The data from this second year confirmed that the main effect of altered pO<sub>2</sub> was to alter seed growth rate rather than maturity date.

These results, then, indicate that seed growth rate is regulated at the individual pod level. Alteration of pO<sub>2</sub> around an individual pod resulted directly in a change of the seed growth rates in that pod. Yet, changes in individual seed growth rate did not

result in a change in the date of physiological maturity for the pod. Consequently, it is inferred that pod maturity is regulated at the whole-plant level rather than at the individual pod. Spaeth and Sinclair (9) similarly concluded in studies of seed maturation of an indeterminate soybean cultivar that maturation occurred uniformly on plants regardless of individual seed growth rate or seed weight. The failure of individual seed growth rate and mass to correlate well with yield (2, 7, 10) further confirms the importance of the regulation of the overall seed development and maturation at the whole-plant level.

Nevertheless, the more than 20% decrease in seed dry weight in each of the 2 years for the 0.10 pO<sub>2</sub> treatment as compared to the other treatments is somewhat surprising. The *K<sub>m</sub>* of mitochondria for dissolved O<sub>2</sub> is approximately 100 nM, or about 1 × 10<sup>-4</sup> atm gaseous O<sub>2</sub>. Respiration should have been easily O<sub>2</sub> saturated in the 0.10 pO<sub>2</sub> treatment unless a substantial drop in pO<sub>2</sub> occurred somewhere in the seeds. Since the seed growth rate was in fact decreased at 0.10 pO<sub>2</sub>, it can be inferred that a physical barrier to O<sub>2</sub> diffusion exists in soybean seeds that results in major decreases in pO<sub>2</sub> at the respiratory sites of the rate-limiting steps for seed growth rate. The magnitude of the barrier is apparently such that under ambient pO<sub>2</sub> the decrease in O<sub>2</sub> within the seed results in very little respiratory inhibition, but at lowered pO<sub>2</sub> the restriction becomes important. Interestingly, Thorne (12) found sucrose uptake rates by isolated soybean embryos subjected to anaerobic conditions were still 68 to 77% of those under ambient pO<sub>2</sub>. Consequently, it is suggested that the diffusion barrier and much of the sensitivity to pO<sub>2</sub> resides in the seed coat rather than the embryo. However, additional work is required to verify the existence of a diffusion barrier and to identify the specific site of the O<sub>2</sub> sensitivity in growing soybean seeds.

Table I. Mean Harvest Dates and Seed Weights of 1983 Experiment

Treatment	Mean Harvest Date	Mean Seed Dry Weight
pO <sub>2</sub>		mg
0.10	15 July (a) <sup>a</sup>	129 (a)
0.21	15 July (a)	167 (b)
0.42	14 July (a)	199 (c)
0.62	13 July (a)	194 (c)

<sup>a</sup> Means followed with the same letter are not significantly different at the 5% level according to Duncan's multiple range test.

Table II. Seed Weights at Three Harvest Dates in 1984 Experiment

Treatment	Seed Weight		
	12 June	26 June	6 July
pO <sub>2</sub>			mg
0.10	46 (a) <sup>a</sup>	142 (a)	167 (a)
0.21 (chamber)	65 (bc)	174 (b)	213 (b)
0.21 (natural)	60 (b)	187 (c)	224 (c)
0.42	67 (c)	191 (c)	214 (b)

<sup>a</sup> Means followed with the same letter are not significantly different at the 5% level according to Duncan's multiple range test within each harvest date.

## LITERATURE CITED

- CROOKSTON RK, DS HILL 1978 A visual indicator of the physiological maturity of soybean seed. *Crop Sci* 18: 867-870
- EGLI DB, JE LEGGETT, JM WOOD 1978 Influence of soybean seed size and position on the rate and duration of filling. *Agron J* 70: 127-130
- GALE J 1974 Oxygen control of reproductive growth: possible mediation via dark respiration. *J Expt Bot* 25: 987-989
- OHMURA T, RW HOWELL 1962 Respiration of developing and germinating soybean seeds. *Physiol Plant* 15: 341-350
- QUEBEDEAUX B, RWF HARDY 1973 Oxygen as a new factor controlling reproductive growth. *Nature* 243: 477-479
- QUEBEDEAUX B, RWF HARDY 1975 Reproductive growth and dry matter production of *Glycine max* (L.) Merr. in response to oxygen concentration. *Plant Physiol* 55: 102-107
- SALADO-NAVARRO LR, TR SINCLAIR, K HINSON 1986 Yield and reproductive growth of simulated and field grown soybeans. II. Dry matter allocation and seed growth rates. *Crop Sci* 26: 971-975
- SPAETH SC, TR SINCLAIR 1983 Carbon exchange rate of intact individual soybean pods. I. Response to step changes in light and temperature. *Ann Bot* 51: 331-338
- SPAETH SC, TR SINCLAIR 1984 Soybean seed growth. I. Timing of growth of individual seeds. *Agron J* 76: 123-127
- SPAETH SC, TR SINCLAIR 1984 Soybean seed growth. II. Individual seed mass and component compensation. *Agron J* 76: 128-133
- TEKRONY DM, DB EGLI, J BALLE, T PFEIFFER, RJ FELLOWS 1979 Physiological maturity in soybean. *Agron J* 71: 771-775
- THORNE JH 1982 Temperature and oxygen effects on <sup>14</sup>C-photosynthate unloading and accumulation in developing soybean seeds. *Plant Physiol* 69: 48-53