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Comparison of the Carbon Partitioning and Photosynthetic Efficiency of Lettuce (*Lactuca sativa* L.) under Hydroponics and Soil Cultivation

M.A.M.S. Anver, D.C. Bandara[1] and K.R.E Padmathilake[1]

Postgraduate Institute of Agriculture
University of Peradeniya, Peradeniya
Sri Lanka

ABSTRACT. *It is claimed that hydroponically grown plants are superior in yield and resistance to pests and diseases. Although these attributes are explained on the basis of the principles of plant physiology, no specific research has been done to understand the physiological basis of such statements. Moreover, result of many molecular biology related experiments conducted using hydroponics to reveal basic processes in plants have been generalized to soil grown plants assuming that plants behave in the same manner in both soil and hydroponic culture. Thus, it is necessary to investigate this issue for evidence to pursue further research. In this study, lettuce (Lactuca sativa L.) was grown in hydroponics and soil and a number of basic physiological parameters were measured for comparison. Hydroponically grown lettuce plants showed high shoot: root ratio, photosynthetic rates per unit leaf area and stomatal conductance compared to soil grown lettuce. Transpiration rates were higher in hydroponically grown plants due to higher stomatal conductance. Number of leaves was also 53% higher in hydroponically grown plants. Chlorophyll concentration data were not statistically significant. Mean harvest index of plants grown under hydroponics was also significantly higher than that of soil grown plants.*

INTRODUCTION

Hydroponics is used extensively in crop production especially in vegetables such as lettuce and tomato. It is becoming more and more popular due to limitation of cultivatable lands and soil-related problems (Muckle, 1995). It is generally believed that the plants grown hydroponically are superior in growth quantitatively and qualitatively than soil grown plants. In reality carbon partitioning to leaves, flowers and fruits is comparatively higher in hydroponically cultivated crops than that of conventionally soil cultured plants (Gent, 1998).

Resh (2001) reported that many crops including rice, wheat, soybean, tomato and lettuce showed at least more than two times higher yields under hydroponics than under soil culture. However, specific studies have not been conducted to understand the underlying physiological basis of the above arguments. Thus, in this study a comparison of the carbon partitioning, photosynthetic efficiency and growth and development of crops grown under hydroponics and soil cultivation was done using lettuce (*Lactuca sativa*, L.) as a reference plant to generate some clues for further studies at molecular level.

[1] Department of Agricultural Biology, Faculty of Agriculture, University of Peradeniya, Peradeniya, Sri Lanka.

MATERIALS AND METHODS

Experimental crop and site

Lettuce (*Lactuca sativa*, L.) cv. Grand Rapids (TBR, USA) was used as the experimental crop and the experiment was conducted at the Department of Agricultural Biology of the Faculty of Agriculture, University of Peradeniya in a planthouse with a transparent roof, allowing more than 1000 $\mu molm^{-2}s^{-1}$ light intensity.

Soil culture

Soil used was prepared to a fine texture and mixed with 10 kg (approximately 250 g per plant) of (dried) cattle manure. Before adding inorganic fertilizers, soil was tested for the initial nitrogen; phosphorus and potassium contents which were 9.2, 8.5 and 42.1 mg/100 g soil, respectively. EC and pH values of the soil were 43.8 mS/min and 6.79, respectively. Black polythene bags (gauge 500) of 25 × 25 cm^2 size were used for soil cultivation. Bags were filled with equal compaction leaving 1.5" from the top. Plants established in seedling trays of 45 × 30 × 5 cm^3 (wells: 3.5cm diameter, 4cm height) in coir dust medium were transplanted one plant per bag, two weeks after germination. Each plant was applied with 1.075 g N, 1.175 g P and 0.375 g K according to the recommendations of the Department of Agriculture, Sri Lanka.

Hydroponic culture

Hoagland and Arnon (1950) hydroponic culture media was used. The solution comprised of 6.0mM KNO_3, 4.0mM $Ca(NO_3)_2.4H_2O$, 1.0mM $NH_4H_2PO_4$, 2.0mM $MgSO_4.7H_2O$, 0.009mM $MnCl_2.4H_2O$, 0.046mM H_3BO_3, 0.0008mM $ZnSO_4.7H_2O$, 0.0003mM $CuSO_4.5H_2O$ and 0.0001mM $H_2MoO_4.H_2O$. Fe-EDTA was prepared as a stock solution of 5g/l final concentration and 2ml was added to each liter of nutrient solution twice weekly as recommended by the protocol. 50 × 33 × 9 cm^3 size polystyrene boxes were used for the hydroponic culture with four plants per box (with 20 × 30 cm^2 spacing), anchored using net cups (6 cm diameter, 7 cm height) filled with coir dust.

Experimental design and sampling

Plants were arranged in completely randomized design and were sampled randomly. All the parameters were measured when the plants were 30, 37 and 45 days old. Four plants were taken each from hydroponic cultured and soil grown plants for destructive sampling. Number of leaves was counted from each plant.

Parameters measured by destructive sampling

Root lengths were measured from the bottom of the shoot to the tip of the longest root in centimeters to one decimal precision using a meter ruler. Root and shoot dry weights were measured by oven drying the samples in a dry oven at 105° C for 72 hours. Using the dry weights, shoot: root ratio was calculated. Leaf area of the fifth leaf from the bottom (the largest leaf) was measured using a leaf area meter (LI-3050A, LI-COR, USA) in square centimeters. Chlorophyll quantification was done in four weeks old plants using the method suggested by Witham *et al.* (1971). Four plants were selected randomly each from soil and hydroponic cultured plants and 0.5g of leaf was taken from each sample particularly from the fifth leaf. Optical density (absorbance) readings were measured using a UV spectrophotometer (UV-1201, Shimadzu, Japan). Using the chlorophyll a and b concentration data, chlorophyll a: b ratio was calculated.

Net photosynthetic rate, stomatal conductance and transpiration rate

Net photosynthetic rates, stomatal conductance and transpiration rates were measured with a portable infrared gas analyser (Model LI 6400, LI-COR Co. Ltd., Lincoln, Nebraska, USA). The leaf chamber was open type and the readings were taken around 10.00 a.m. each Monday particularly from the fifth leaf. The measurements were taken when the photosynthetically active radiation (PAR) was around 1000 $\mu molm^{-2}s^{-1}$ whenever possible and observations were recorded after the plant reached a steady photosynthesis state. All measurements were recorded three times and differences between the observations were negligible. Photosynthetically Active Radiation (PAR) was measured in the chamber near the leaf plane using a miniature GaAsP sensor and the external ambient PAR was measured with the optional LI-COR quantum sensor located outside the chamber to correct the readings for the comparison.

Harvest index

Since harvest index is one of the important parameters in agriculture, this was measured in 45 days-old plants. Generally harvest index is obtained by dividing weight of the marketable yield (g) by weight of the biological yield (g). In lettuce, the marketable yield is the leaves and the shoot whereas the biological yield is the total weight of the plant.

Statistical Analysis

The "t" test was performed for each parameter to check whether the data obtained for the two systems were statistically significant or not, using SAS System for Windows V8 (SAS Institute Inc. Cary, NC 27513, USA).

RESULTS AND DISCUSSION

Net photosynthetic rate, stomatal conductance and transpiration rate

Net photosynthetic rates in hydroponically grown plants (HGPs) were significantly higher (p-value=0.0021) than that of soil grown plants (SGPs) according to the results (Figure 1). Net photosynthetic rate is affected by many factors including solar energy use efficiency, stomatal conductance for CO_2, efficiency of ribulose diphosphate (RuBP) carboxylase enzyme, temperature etc. There was no difference between atmospheric temperatures in both types of plants. However, stomatal conductance of HGPs was shown to be significantly higher (p-value =0.0002) than that of SGPs (Figure 2). Thus, it is obvious that the photosynthetic rate will increase with increasing CO_2 supply. Being a C_3 plant, high stomatal conductance is highly advantageous for lettuce because an increase in leaf intercellular CO_2 concentration increases the efficiency of the CO_2 fixing enzyme RuBp carboxylase (Salisbury and Ross, 1992).

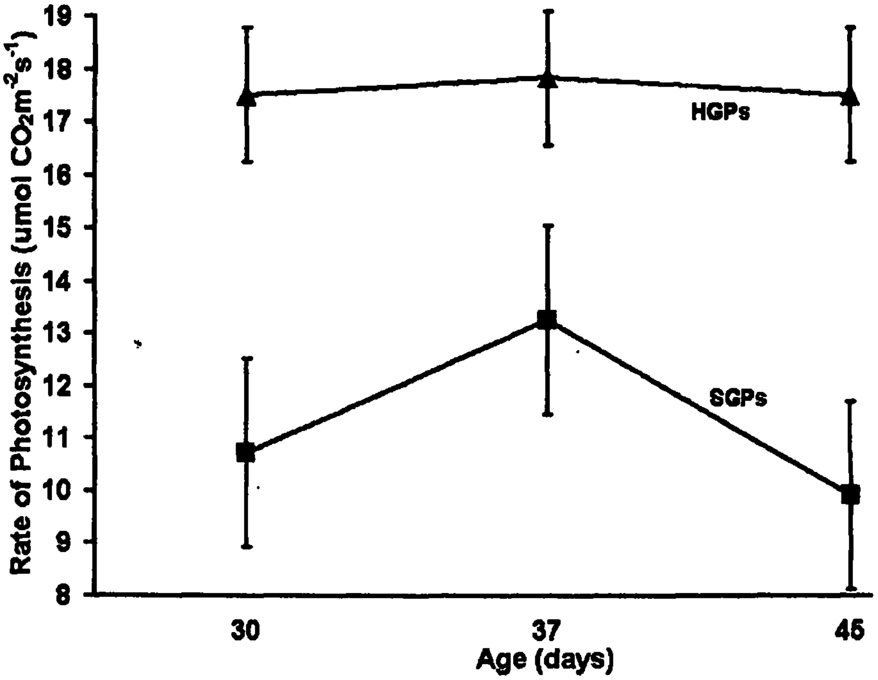

Fig. 1. Changes in photosynthetic rates with age in HGPs and SGPs

Transpiration rates were also significantly higher (p-value=0.002) in HGPs than that of SGPs (Figure 3). As the stomatal conductance was higher in HGPs, either the stomatal pore size should be larger or the number of stomates per unit leaf area should be higher (these parameters were not measured) leading to increased transpiration rates. Water supply is always satisfactory in hydroponic systems whereas short term or localized water stresses are always possible in soil grown plants although watered sufficiently. Wilkinson and Davies (1997) have shown that the flux of ABA to the leaves of even well watered plants may be enough to close the stomata if the hormone is able to reach the sites of action on the guard cells. They have also shown that a small alkalinization of the xylem sap (less than a pH unit) can be enough to close stomata significantly, without extra ABA. pH changes of this magnitude are routinely observed in soil grown plants in response to quite small reductions in soil water content (Wilkinson *et al.*, 1998). This may be one of the reasons for comparatively lower stomatal conductance in SGPs.

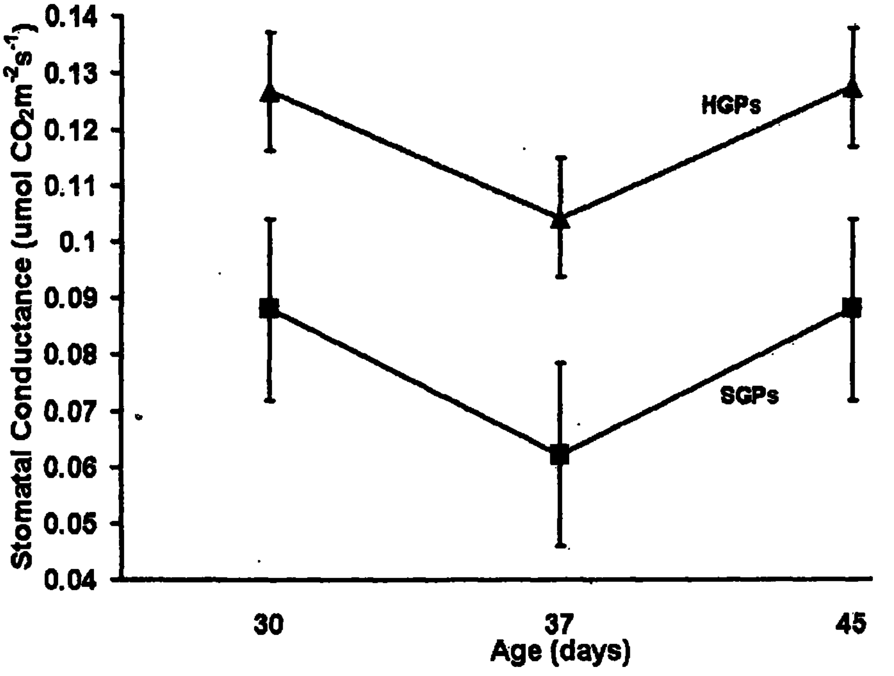

Fig. 2. Changes in stomatal conductance with age in HGPs and SGPs

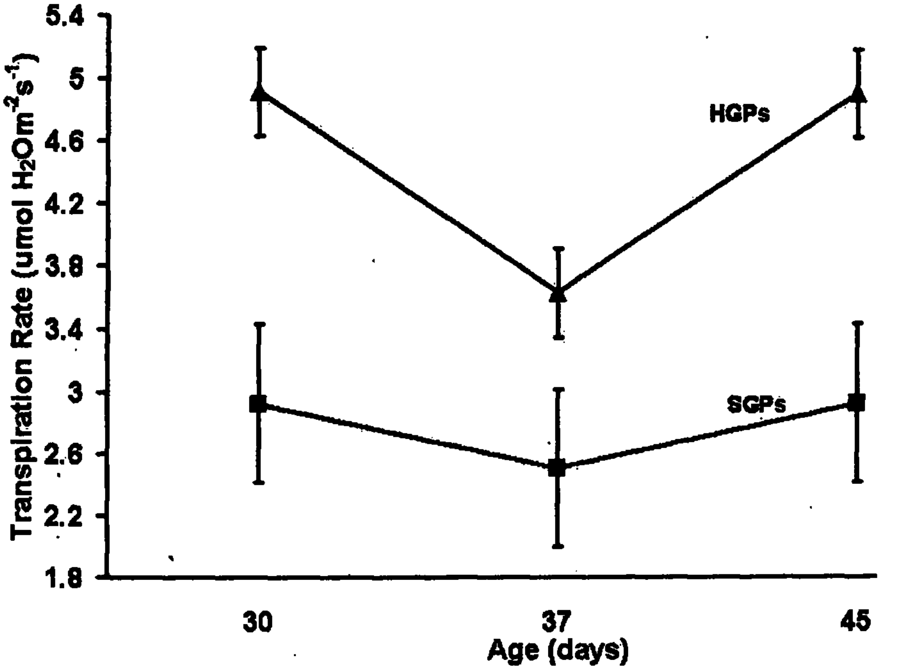

Fig. 3. Changes in transpiration rate with age in HGPs and SGPs
Chlorophyll Concentrations

There were no significant differences in chlorophyll a, b, total chlorophyll concentrations per unit leaf area and a: b ratio between SGPs and HGPs.

Root lengths, shoot and root dry weights and shoot: root ratio

Root lengths though higher in HGPs (Table 1) were not significantly different from SGPs. As the resistance to root growth was lesser under hydroponics than in soil, initial root lengths may be significantly higher in HGPs. Root dry weights were significantly higher in SGPs as expected whereas shoot dry weights were significantly higher in HGPs (Table 1). In soil, anchorage should be provided by the roots themselves whereas it is more or less artificial in hydroponics where nutrients are provided in solution. Thus, profuse growth of roots is not necessary or not encouraged under hydroponics. As a result it could be expected that carbon partitioning to roots would be lower in hydroponics.

Table 1. Mean root lengths, root dry weights, shoot dry weights and shoot:root ratios of HGPs and SGPs with age

Age (days)	R L		RDW		SDW		S:R Ratio	
	H	S	H	S	H	S	H	S
30	39.5^a	27.9^b	0.502^a	1.378^b	1.322^a	1.084^a	2.632^a	0.786^b
37	36.8^a	33.5^a	1.041^a	2.653^b	6.665^a	3.12^b	6.404^a	1.176^b
45	45.7^a	43.3^a	1.69^a	2.792^b	12.56^a	5.501^b	6.644^a	2.122^b

RL – Mean root length; RDW – Mean root dry weight; SDW – Mean Shoot dry weight; S:R Ratio – Mean Shoot:Root ratio; H – Hydroponically grown plants; S – Soil grown plants; Values with the same letter (a or b) within the same parameter and same age are not significantly different ($P > 0.05$)

For most ions, the rate limiting step in uptake is transport through soil and not across the root (Nye and Tinker, 1977). It is always possible to have localized deficiencies of soil nutrients under soil conditions although the plants are provided with sufficient amount of nutrients as recommended. Root growth is favoured when there is a short supply of nutrients (Ericsson *et al.*, 1997; Fitter and Hay, 1987). It was shown in lettuce itself that localized N deficiencies can favour root growth and reduces shoot growth (Broadely *et al.*, 2000). Moreover root exudation in the soil can account up to 20% of the total photosynthesis (Whips, 1990). Thus it was obvious that root dry weights were higher in SGPs whereas shoot dry weights were lower. As a result, shoot: root ratio was also significantly lower in SGPs (Table 1).

Furthermore, the same authors in two different studies (Broadely *et al.*, 2000; Broadely *et al.*, 2001) have shown that short supply of N is associated with a lower stomatal conductance, which resulted from adjustments to stomatal frequency or distribution. It could also be due to increased CO_2 partial pressure at the sites of carboxylation due to nitrogen deficiencies. This has been very obvious in our results (Figure 2). Thus there could be possibilities of localized nutrient deficiencies in SGPs although the soil that was selected for the experiment was ideal considering pH and EC values.

Leaf area and number of leaves per plant

Leaf area (Figure 4) and number of leaves per plant (Figure 5) were significantly higher in HGPs. Carbon partitioning depends on the strength of both source and sink. Number of leaves and leaf area indicates the strength of the source of a crop.

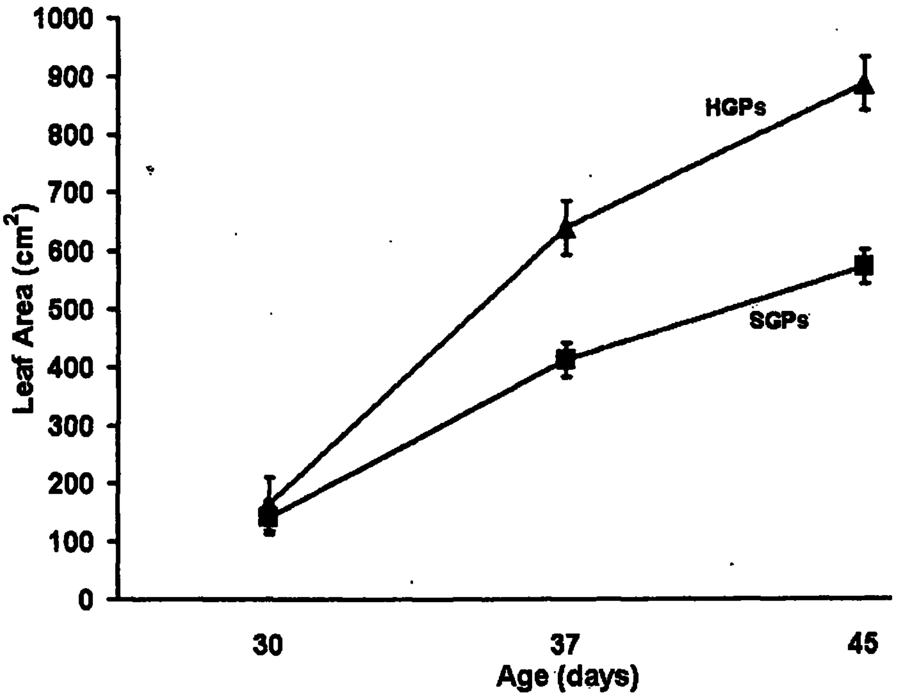

Fig. 4. Changes in leaf area with age in HGPs and SGPs

If the number of leaves or the leaf area is higher, the amount of light trapped and the rate of photosynthesis are also higher. However with increasing leaf numbers some of the leaves could function as parasitic leaves due to mutual shading, which is very prominent in lettuce as it has a short stem. Nevertheless the final harvest to be produced or highest carbon partitioning expected to, are also leaves in lettuce, as it is a leafy vegetable. Thus increasing the number of leaves is advantageous (whether parasitic or productive) since they can function either as a sink or a source.

As a result of all the above reasons mean harvest index of HGPs was significantly higher (p-value =0.0044) than that of SGPs. Mean harvest index values for HGPs and SGPs were 0.85 and 0.68 respectively.

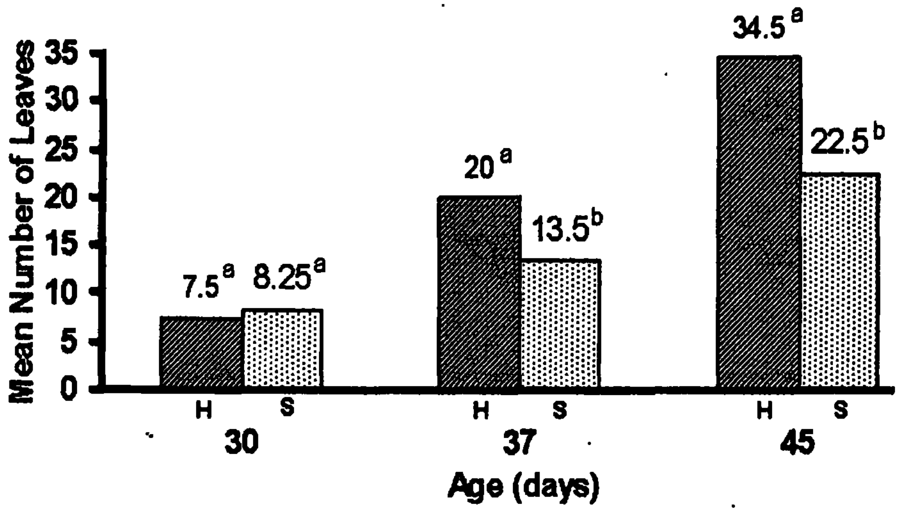

Fig. 5. **Changes in number of leaves/plant with age in HGPs and SGPs**

H – Hydroponically grown plants; S – Soil grown plants; Values with the same letter (a or b) within the same age are not significantly different ($P > 0.05$)

CONCLUSION

Shoot: root ratio, number of leaves, leaf area and stomatal conductance are significantly higher in hydroponically grown lettuce than that of soil grown lettuce whereas dry matter partitioning of roots is higher in soil grown lettuce. As a result photosynthetic rates and partitioning of photosynthates to above ground parts (leaves) are higher in hydroponically grown lettuce. Further investigations on stomatal number and distribution, chloroplast proteins and photosynthetic pigments are needed for better understanding of the physiological basis of the performance of HGPs. This understanding in turn might help in the future to exploit the plants to their maximum genetic potential towards much better yields.

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