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MELiSSA

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Yield Responses of MELiSSA Candidate Crops to Environment Conditions

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Yield Responses of MELiSSA Candidate Crops to Environment Conditions

1.0 - Introduction

Earlier higher-plant studies in the MELiSSA program have involved stead-state mass transfer simulations between higher plant chambers and the four MELiSSA micro-biological compartments (Poughon, 1997). These simulations incorporated wheat, soybean, potato, lettuce, rice, onion, spinach and tomato as candidate crops. Edible and inedible biomass production values used in these simulations were largely derived from field cultivation trials. Closed environment crop production, however, eliminates many of the stresses of field cultivation (water deficits, nutrient deficiency) and offers the opportunity to enhance crop productivity in other ways, such as through unique lighting configurations and CO_2 enrichment (Dixon et al., 1997). Earlier technical notes outlined the physiological basis of closed environment culture and recommended a set of cultural management strategies for each candidate crop (TN 40.1). They also have also provided estimates of the mineral and proximate composition of crops grown in controlled environments (TN 40.2). The purpose of this technical note is to summarize observed relationships between crop yield and various controllable environment conditions and to improve edible and inedible biomass estimates for candidate crops produced in these controlled conditions. These improved estimates may then serve as input parameters for future MELiSSA-HPS steady-state simulations.

A review of literature in the area of controlled environment cultivation (both greenhouse and growth chamber studies) was conducted. As explained in earlier technical notes, little information could be obtained for onion cultivation in closed systems and so, for the purposes of this technical note, has been excluded from future consideration. For each of the remaining seven candidate crops (lettuce, potato, tomato, rice, soybean, spinach, wheat) a summary of crop yield response to CO_2 enrichment, light intensity (Photosynthetic Photon Flux, PPF), photoperiod, temperature and nutrient supply (if present in the literature) is presented. The role of each of these key environment variables in crop production has been described earlier and the reader is therefore referred to TN 40.1 (Cloutier and Dixon, 1997). Water supply (root zone and atmospheric) is not discussed as an environment factor since it is assumed that all crops are produced using a hydroponics system which confers an unlimited water supply to the crop. Simple models relating crop photosynthesis (yield) to PPF and CO_2 are also presented. These models serve to identify how further enhancements in the crop yields presented in Section 3.0 can be made.

2.0 - Yield Responses of Crops to Environment Conditions

2.1 - Lettuce

Crop: **Lettuce (Lactuca sativa L.)**			
Variable	Variable Range	Yield Response	Reference
CO_2	350-3200 (ppm)	- An increase in leaf dry weight on the order of 40 - 75% has been observed when CO_2 was enriched to 1000 ppm at moderate (450 $\mu molm^{-2}s^{-1}$ PAR) light intensities, relative to 350 ppm, This gain was observed only during the first 15 days of growth. - At CO_2 concentrations greater than 1000 ppm, lettuce leaf growth was most responsive to a combination of high PPF (850 $\mu molm^{-2}s^{-1}$ PAR) and CO_2 enrichment. No increase in growth was observed when CO_2 concentrations were at 2000 ppm.	Knight and Mitchell (1988); Knecht and O'Leary; (1983); Ikeda et al (1988)
Light Intensity (PPF)	50 - 950 ($\mu molm^{-2}s^{-1}$ PAR)	- An increase in light intensity confers an increase in lettuce leaf yield but at the expense of greater incidences of tip burn. - Tip burn is a result of low calcium levels and is associated with environmental conditions conducive to rapid dry matter accumulation	Gaudreau et al, (1994); Tibbitts and Rao (1968); Cox et al, (1976); Knight and Mitchell (1983); Ikeda et al, (1988);
Photoperiod	16, 20 and 24 (hrs)	- Significant increases on the order of 100 - 135% were observed at photoperiods of 24 hrs relative to 16 hr photoperiods. The incidence of tip burn increases with increasing daily integrated PPF, thus longer photoperiods warrant a reduced instantaneous PPF. - A doubling of the photoperiod at ½ the PPF confers a greater yield	Gaudreau et al, (1994); Koontz and Prince (1986); Craker and Seibert (1983);

Temperature		- The relationship between lettuce growth and temperature is not simple and is dependent upon light intensity. A positive relationship was established between temperature and lettuce yield but only at high PPFs -Temperatures above 21-22 °C promote seed-stalk elongation (bolting), puffy heads and bitterness	Kanaan and Economakis (1992); Whitaker et al, (1974)
Nutrient Supply	30 mM NO_3^- ; 5 mM NH_4^+ + 25 mM NO_3^- ; 1 mM NO_3^-	- Application of N as 25 mM NO_3^- and 5 mM NH_4^+ resulted in a 31% percent increase in leaf dry weight relative to application rates as 30 mM NO_3^- ; the degree of chlorosis decreased with increasing nitrogen nutrition and with application of NH_4^+ as an N source; - A leaf dry weight increase on the order of 16% was observed when the N concentration was doubled from 15 mM NO_3^- to 30 mM NO_3^-	Knight and Mitchell (1983)
Water Supply (Atmospheric and Root zone)	50 - 85% R.H.	- Significantly higher growth rates and leaf dry weights (increases of about 62%) were observed in plants grown under 85% R.H. compared to 50% R.H. - This increase was greatest for soil grown plants - Water supply to the root zone through hydroponics reduces the degree of water stress and enhances yield	Tibbitts and Bottenberg (1976)

2.2 - Potato

Crop: **Potato (Solanum tuberosum L.)**			
Variable	Variable Range	Yield Response	Reference
CO_2	300 - 1000 ppm	- CO_2 enrichment to 1000 ppm increased total plant dry weight and tuber yield by 39 and 34% respectively - These increases were greater under lower PPF and shorter photoperiods	Wheeler et al, (1991); Wheeler et al, (1994b);
Light Intensity (PPF)	400 - 800 $\mu molm^{-2}s^{-1}$ PAR	- Increasing PPF from resulted in a 24% increase in tuber yield at 350 ppm CO_2 and a 12 hr photoperiod. - The magnitude of increased yield resulting from a PPF increase was greatest under shorter photoperiods and lower CO_2 concentrations. At CO_2 concentrations of 1000 ppm, and a 24 hr photoperiod tuber dry weight decreases were observed on the order of 10 %	Wheeler et al, (1991)
Photoperiod	12 and 24 hrs	- Tuber yields increased with long days (by about 10%). Short days followed by longer days had an enhancing effect as well - Early reports indicate that short days are required for tuber growth but some cultivars are not obligate in the photoperiod requirement and benefit from longer days if temperature is lower	Wheeler and Tibbitts (1997); Cary (1986);

Temperature	33/25 °C; 20/10 °C	- Tuber growth rates and yields were greatest under lower temperatures and decreased with increasing temperature and higher daily integrated PPF. This is consistent with the idea that increased photoperiods warrant cooler temperatures in order for tuber formation to occur	Midmore and Prange (1992)

2.3 - Rice

Crop: **Rice (Oryza sativa L.)**			
Variable	Variable Range	Yield Response	Reference
CO_2	350 - 900 (ppm)	- Rice photosynthetic and growth rate and yield increased for CO_2 concentrations up to 500-600 ppm but saturated at higher values	Rowland et al (1991); Rowland et al (1990); Baker et al (1990);
Light Intensity (PPF)	350 -1000 $\mu molm^{-2}s^{-1}$ PAR	- high PPF values increased grain yield by as much as 2-3 times the yields obtained under greenhouse cultivation	Kozai et al (1995);
Photoperiod	8 - 24 hrs	- grain yield was not shown to increase under continuous lighting, harvest index decreased - a switch to continuous lighting did not promote or delay the time to harvest	Volk and Mitchell (1995); Azmi and Ormrod (1971)
Temperature	35/18 °C; 35/27 °C; 35/35 °C; 41/18 °C	- highest photosynthetic rates were observed at temperatures of 41/18 or 35/35 °C	Azmi and Ormrod (1971)

2.4 - Tomato

Crop: **Tomato (Lycopersicon esculentum L.)**			
Variable	Variable Range	Yield Response	Reference
CO_2	300 - 1500 ppm	- CO_2 enrichment at 1500 ppm increased the fruit yield by as much as 80% of early and 22% of total yields. This effect was growth stage dependent with the greatest effects occurring during the first few weeks of treatment - the effects of CO_2 enrichment were greatest at a day/night temperature difference of 9 °C, as compared to 3 °C. - enhanced yield due to CO_2 enrichment has been attributed to a re-allocation of assimilates from roots to fruits	Yelle et al, (1990); Tripp et al, (1991); Willits et al, (1989);
Light Intensity (PPF)	400 - 2000 $\mu molm^{-2}s^{-1}$ PAR	- a positive relationship existed between PPF and tomato yields, with absolute yields dependent upon ambient PPF in the greenhouse - supplementary lighting increased yields by 100% as compared to tomatoes grown in ambient conditions - a light curve for tomato production in closed chambers could not be located in the literature	McAvoy et al, (1989); Boivin et al, (1987); Vezina et al, (1991); Tremblay et al, (1984)
Temperature	Day Temperature: 13 - 22 °C Night Temperature: 12 - 21 °C	- day night temperatures of 9 °C accelerated fruit growth ripening - low greenhouse air temperatures did not have a significant impact on fruit yield providing deviations from the optimal day/night temperatures of 22/17 °C did not exceed 3 °C - cooler night temperatures than 14 °C are reported to have resulted in increased root dry mass and reductions in the rate of fruit development - day/night temperature differences increased the effect of CO_2 enrichment on yield	Gent (1988); Papadopoulos and Tiessen (1983); Gosselin et al, (1983);

Nutrient Supply	5-20 meq L^{-1}	- increasing nitrate concentrations increased yields if sulphate was less than 25 meq L^{-1} - fruit yield was higher at higher nutrient solution concentrations	Martinez et al, (1984); Pardossi et al, (1987);

2.5 - Soybean

Crop: **Soybean (Glycine max L.)**			
Variable	Variable Range	Yield Response	Reference
CO_2	160 - 5000 ppm	- A positive yield response is observed with increasing CO_2 concentration. Seed yields increased from between 20% and 57% relative to ambient CO_2 concentrations - Increases in photosynthetic rates and the number of pods per plant were observed but highest yields were observed at 1000 ppm, with higher concentrations being supra-optimal at study PPF levels	Cooper and Brun (1967); Campbell et al, (1990); Egli et al, (1970); Acock et al, (1985); Wheeler et al, (1994b); Sionit et al., (1987); Wheeler et al., (1993);
Light Intensity (PPF)	250 - 1500 $\mu molm^{-2}s^{-1}$ PAR	- Increased photosynthetic and growth rates were observed with increasing PPF - the degree of increase was found to be dependent upon CO_2 concentration, with the greatest responses occurring at concentrations near 1000 ppm	Campbell et al, (1990); Acock et al, (1985); Egli et al, (1970);
Photoperiod	12 - 22 hrs	- Soybean is a photoperiod sensitive crop. Photoperiods less than 12 hours were found to be flower-inducive while longer (22 hrs) photoperiods were found to low or non-inducive	Wilkerson et al, (1989); Acock and Acock (1995)
Temperature	18/12 °C; 22/16 °C; 26/20 °C;	- Number of pods and seeds and seed yields increased with greater day and night temperatures. This increases were on the order of 50% at 1000 ppm CO_2 relative to the lowest temperature treatment	Sionit et al, (1987)

2.6 - Spinach

Crop: **Spinach (Spinacea oleracea L.)**			
Variable	Variable Range	Yield Response	Reference
CO_2	350 - 1500 ppm	- spinach showed a positive response to CO_2 enrichment up to 1% No increase in leaf dry weight was observed at higher concentrations - fresh weight harvest increased 1.5-2.0 over 350 ppm CO_2 controls when grown at 750 ppm CO_2. This conferred a 7-10 day earlier harvest. - CO_2 enrichment is reported to affect fresh weight and leaf length rather than leaf number - the effect of increasing CO_2 concentrations was greatest at cooler temperatures (20 °C) rather than at warmer temperatures (30 °C)	Pfeufer and Krug (1984); Kawashima and Kurozumi (1990)
Light Intensity (PPF)	10 - 22 $molm^{-2}day^{-1}$ PAR	- Spinach yield was found to be highly correlated with daily integrated PPF. Yield was found to increase by 0.89% for every 1% increase in integrated daily PPF. - Individual spinach plant PPF saturation occurred at 25$molm^{-2}day^{-1}$ PAR	Both et al, (1997); Glenn et al, (1984)
Photoperiod	13 - 16 hrs	- a day length of 16 hrs increased leaf number from an average of 8.9 to 16.9 per plant - dry weight under 16 hr photoperiods increased plant weight by 160% of masses obtained under 13 hrs. Relative growth rate and leaf area were also observed to increase - longer photoperiods stimulated bolting	Sugiyama (1990); Both et al, (1997);

Temperature	5 - 25 °C	- Spinach is reported to have developed normally at air temperatures near 5 °C. Higher temperatures resulted in greater yields though no atmospheric temperature optimum could be located in the literature - an inverse relationship between hydroponics solution temperature and spinach yield was observed during summer cultivation in the greenhouse. The converse was observed in the winter months	Both et al, (1997); Boese and Huner (1990); Ikeda et al, (1995)
Nutrient Supply	0.5 - 12 mM	- A positive relationship was found between N application and spinach yield and photosynthesis	Biemond et al, (1996); Evans and Terashima (1988)

2.7 - Wheat

Crop: **Wheat (Triticum aestivum L.)**			
Variable	Variable Range	Yield Response	Reference
CO_2	350 - 1000 ppm	- A positive relationship exists between atmospheric CO_2 concentrations and grain yield. An increase in wheat relative growth rate on the order of between 20% and 50% has been observed when atmospheric CO_2 concentrations approached 1000 ppm . - Studies have also shown a saturation of wheat photosynthetic capacity near 1000 ppm - Intraspecific competition has also been noted, suggesting that planting density may be a factor in the efficacy of CO_2 enrichment through the effects of light attenuation - Some reports indicate that there is no response (tiller numbers or plant development) to CO_2 enrichment	Du Cloux et al (1987); Wheeler et al, (1993); Moot et al, (1996); Gifford (1977)

Light Intensity (PPF)	400 - 2000 $\mu molm^{-2}s^{-1}$ PAR	- Grain yield approached 60g $m^{-2}day^{1}$(total yield aprx: 4.5 Kg m^{-2}) as PPF increased to 2000 $\mu molm^{-2}s^{-1}$ PAR. This corresponds to an 200% increase relative to 500 $\mu molm^{-2}s^{-1}$ PAR. - The number of heads, seed per head and mass per seed increased as PPF approached 2000 $\mu molm^{-2}s^{-1}$ PAR. - Harvest index increased from 41 to 44% as PPF increased	Bugbee and Salisbury (1988)
Photoperiod	8, 12 and 16 hrs	- Days to anthesis decreased with increasing photoperiod - As total daily integrated PPF increased, so did the average crop growth rate, seed yield, head yield and mass per seed	Ortiz-Ferrara et al, (1995); Bugbee and Salisbury (1988)
Temperature	13/10 °C and 23/18 °C	- Rate of growth was less at cooler temperatures but total growth over the same period of development was greater in cooler grown crops - Main shoot and tiller leaves were shorter in cooler grown plants - Temperature increases conferred advances in anthesis and grain filling	Lawlor et al, (1988); Moot et al, (1996)
Nutrient Supply	0.45 mM NO_3^- twice weekly and 2.0 mM NO_3^- twice weekly	- Increased nitrate significantly increased tiller and grain mass	Lawlor et al, (1988)
Water Supply (Atmospheric and Root zone)	No specific information on the influences of R.H. or water supply sould be found for wheat in closed systems		

3.0 - Yield Estimates of MELiSSA Candidate Crops Grown Under Specific Environment Conditions

Crop	*Environment Conditions*				Edible Biomass[1]	Non-Edible Biomass	Harvest Index[2] (%)	Days to Harvest	Source
	CO_2 Conc. (ppm)	PPF ($\mu molm^{-2}s^{-1}$ PAR)	Photoperiod (Length of Day)	Temperature (Day/Night, °C)					
Wheat cv. Yecora Rojo Edible: grain[1]	1200	2000 (HPS & Metal Halide)[3]	20 hr	20/15	2.3 g plant^{-1}	2.9 g plant^{-1}	44	79	Bugbee and Salisbury (1988)
Soybean cv. McCall Edible: seed	1000	300 (HPS)	12 hr	26/20	33.3 g plant^{-1}	40.7 g plant^{-1}	45	90	Wheeler *et al* (1993)
Potato cv. Norland Edible: tuber	1000	400 (HPS)	12 hr followed by 24 hr	19/16	1100 g plant^{-1}	1100 g plant^{-1}	50	112	Wheeler and Tibbitts (1997)
Tomato cv. Calypso Edible: Fruit	350	ambient (400 - 2000) (sun; glasshouse)	ambient (Jan-Nov)	22/17	20.6 Kg plant^{-1}	3.9 Kg plant^{-1}	84	-----	de Koning and de Koning (1989)
Lettuce cv. Waldmann's Green Edible: Leaf	1000	290 (HPS)	16 hr	22/22	8.8 g plant^{-1}	0.61 g plant^{-1}	94	28	Wheeler *et al* (1994a)
Spinach cv. Nordic Edible: Leaf	350	190-380 (Greenhouse with HPS as a supplement)	16 hr	24/18	6.8 g plant^{-1}	2.3 g plant^{-1}	74	33	Both *et al* (1996)
Rice cv. Ai-Nan-Tsao Edible: Grain	350	350 (HPS)	8 hr	37/25	1.6 g plant^{-1}	1.5 g plant^{-1}	52	83	Volk and Mitchell (1995)

[1] Edible fraction refers to that presented for each crop type; [2] Harvest Index = Edible Biomass/Total Plant Biomass; [3] Lamp type used is given in brackets.
Abbreviations: cv. = cultivar; PPF = Photosynthetic Photon Flux;

4.0 - Simple Models of Crop Response to Light and Carbon Dioxide

4.1 - Light

Figure 1 presents a typical relationship between light intensity (PPF) and net photosynthesis (growth), expressed as net carbon exchange rate (NCER) for a single plant or leaf. This same profile was presented in TN 40.1 but it is used here to model the relationship between crop growth, yield and light intensity.

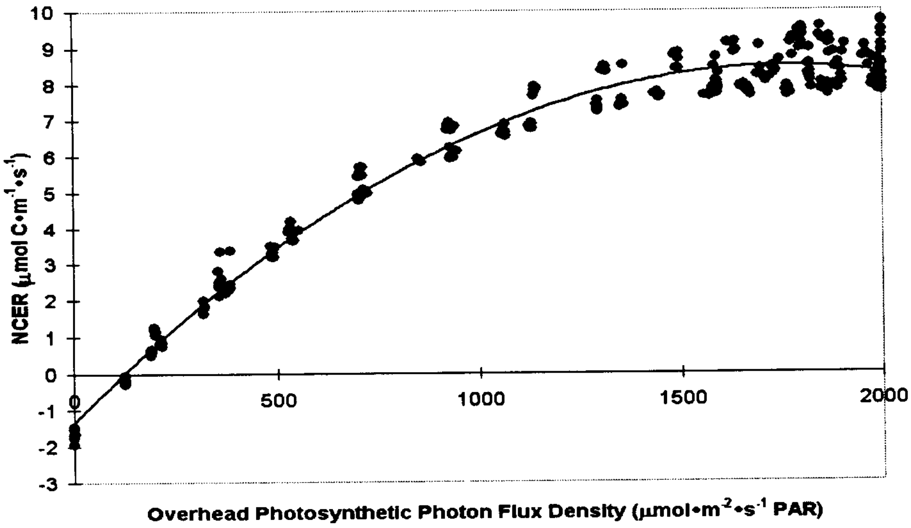

Figure 1. Net carbon exchange rate (NCER) for 40 day old whole soybean plants in small plant growth chambers containing four plants measured over a range of photosynthetic photon fluxes. Carbon dioxide concentration was maintained at 375 µmol/mol (adapted from Stasiak et. al., 1998).

The x-intercept of this curve is known as the light compensation point. At PPF levels lower than the compensation point, respiratory losses of CO_2 are greater than photosynthetic fixation and no net biomass accumulation (yield) is possible. At PPF levels greater than the compensation point, photosynthetic rates are greater than respiration rates and there is a net accumulation of biomass. At high PPF levels there is a saturation of the photosynthetic complexes. Above the point of saturation there is no net return on increased radiation supply.

The curve in Figure 1 shows how photosynthesis in single leaves or plants changes with irradiance level. This curve is not typical of the response of full canopy systems. Light attenuation in full canopies results in a situation where leaves of the upper canopy are light saturated while those of the lower canopy are not. Because of this attenuation, full canopy systems are saturated at irradiance levels much greater than those of single plants. Further, some C_4 plants show even less tendency to saturation (Baker and Musgrave, 1964). Despite the fact that full canopies systems exhibit a higher point of saturation, crop yield response to PPF is given by the profile presented above, but shifted to the right. It is important to note that full canopy saturation has is difficult to demonstrate at moderate to high canopy leaf area indexes. As a result, many of the yields presented in Section 3.0 can be further augmented by changing the geometry of radiation supply and by using very high powered lighting systems. This is the rationale behind the inclusion of an micro-wave based inner-canopy lighting system in one of the University of Guelph chambers (Dixon *et al*, 1997).

4.2 - Carbon Dioxide

The net photosynthetic response model for CO_2 is very similar to the light curve presented in Figure 1. At high CO_2 levels, depending on the crop, there is a saturation of RuBP and hence the net photosynthetic rate plateaus. These points of saturation have been identified in Section 2.0 for each crop, where possible. It is important to note that there is an interaction between CO_2 supply and PPF. At higher PPF, there is a tendency for the CO_2 saturation point to shift to the right since crop photosynthesis is not limited by products of the light reactions.

4.3 - Simple Models of Plant Photosynthetic response to CO_2 and PPF

Numerous models have been fitted to net photosynthesis data, but the two most frequently used are the rectangular hyperbola and the exponential model. A general form of the rectangular hyperbola equation as suggested in Iqbal et al (1996) is:

$$P_n = \frac{aIP_{g_{max}}}{aI + P_{g_{max}}} + R_d \qquad [1]$$

Where P_n = net photosynthetic rate, I = photon flux density, a = the initial slope of the Pn-I curve, P_{gmax} = the maximum gross photosynthesis as $I \rightarrow \infty$, and Rd = the dark respiration rate which is negative.

The form of the exponential model proposed by a number of authors and reviewed in Iqbal et al (1996) is:

$$P = P_{n_{max}}[1 - e^{-(\frac{aI}{P_{max}})}] \qquad [2]$$

Where P is gross photosynthesis, P_{nmax} is maximum net photosynthesis, P_{max} is maximum photosynthesis, I is photon flux density and a is the initial slope of the Pn-I curve or photosynthetic efficiency. This model passes through the origin and hence P = Pg. Modified versions of the model have accounted for dark respiration and do not pass through the origin. Both model forms can apply to the Pn-I response curve and re-parameterization will also allow for their application to modelling Pn-CO_2 responses. A knowledge of crop specific PPF and CO_2 compensation and saturation points (i.e. P_{nmax}) will do much to improve the predictability of yield response.

5.0 - References

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