A Study of Photosynthetic Activities of Eight Asparagus Genotypes under Field Conditions

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ADDITIONAL INDEX WORDS. *Asparagus officinalis*, photosynthesis, genetic variability, specific leaf weight, yield, stomatal conductance

ABSTRACT. Net photosynthesis from whole plants of eight asparagus (*Asparagus officinalis* L.) genotypes was measured at two locations in an open infrared gas analysis system. Measurements started at about the completion of full fern growth, which occurred at the end of July and lasted through the season until fern senescence in late September. Net photosynthesis of the eight genotypes ranged from 15.67 to 27.79 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Significant differences ($P < 0.1$) in net photosynthesis were found among the eight genotypes. Both yield and specific leaf mass (SLM) were correlated significantly with net photosynthesis. We suggest that specific leaf mass can be used as a criterion for selecting genotype of high photosynthetic ability. Daily photosynthetic rate patterns were studied and appear to be related to daily changes of stomatal conductance. Seasonal changes of asparagus' photosynthetic activity were studied. High photosynthetic activity was observed from July through August. Photosynthetic activity decreased greatly in September along with the fern maturation and unfavorable changes in environmental conditions.

Asparagus (*Asparagus officinalis*) is an important perennial vegetable crop in Michigan. Yield trials of asparagus genotypes have been conducted in southwestern and west central Michigan since 1988. A wide variation of yield performance was observed, and genotypic variation in photosynthetic ability was suggested as a major factor. Genotypic variability in photosynthetic rate has been reported in a number of crops, i.e., tomato (*Lycopersicon esculentum* L.) (Augustine and Stevens, 1976), soybean (*Glycine max* L.) (Dornhoff and Shibles, 1970), tobacco (*Nicotiana tabacum* L.) (Zelitch and Day, 1968), peanut (*Arachis hypogaea* L.) (Pallas and Samish, 1974), and oats (*Avena sativa* L.) (Criswell and Shibles, 1971). This study was established to characterize the photosynthetic variability of asparagus genotypes and to test the hypothesis that the yield variability observed among genotypes is correlated with differences in net photosynthesis.

Asparagus is a C_3 plant, and the architecture of the shoot canopy is thought to be conducive to high photosynthetic capacity (Downton and Torokfalvy, 1975). The cladophylls are shaped like needles, and thus the shading effect of leaves is minimal. Light can penetrate into the lower levels of the asparagus canopy, so that the whole canopy should be able to photosynthesize effectively.

The earliest work on asparagus photosynthesis was the report from Sawada et al. (1962), who reported that the carbon assimilate content of ferns increased steadily with an increasing number of hours of daylight, until $\approx 3:30$ PM. Assimilation rates were estimated by taking the difference between assimilate content, measured in the lab, from samples collected in the field at different times in the day. Assimilation rates as glucose varied from 18 to 33 $\text{mg}\cdot\text{g}^{-1}$ of fresh cladophylls. They also determined that assimilation was affected directly by weather conditions, hours of sunshine and light intensity and that assimilation of staminate and pistillate plants did not differ. They reported that stomata are scattered over the entire surface of the cladophyll.

In another study (Lin and Hung, 1978), using an assimilation chamber with individual branches, photosynthetic activity of developing asparagus at various growth stages was studied. When young cladophylls are developed, about one month after the emergence of a spear, the net photosynthetic rate (CO_2 fresh mass basis) can be as high as 48.9 $\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$. The photosynthetic rate reached a maximum when the plant reached the vigorous cladophyll stage, about two months after spear emergence; the net assimilation rate can be as high as 65.3 $\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$. The photosynthetic rate dropped to 8.6 $\text{mg}\cdot\text{g}^{-1}\cdot\text{h}^{-1}$ when cladophylls were senescing. They also found no statistical differences in the photosynthetic rates of male and female plants, confirming the conclusion reached by Sawada et al. (1962).

Downton and Torokfalvy (1975), using an assimilation chamber, showed that net photosynthesis occurred once the spears began to assume a fern-like form, when CO_2 exchange rate was measured in detached shoots of greenhouse-grown plants. The photosynthetic rate (CO_2 fixed per unit of chlorophyll) at this prefern stage, was about 17 $\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{mg}^{-1}$ chlorophyll, but the dark respiration rate was higher (26.3 $\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{mg}^{-1}$ chlorophyll), whereas net photosynthetic rate in a fully differentiated fern exceeded dark respiration (20.9 $\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{mg}^{-1}$ chlorophyll versus 11.7 $\mu\text{mol}\cdot\text{h}^{-1}\cdot\text{mg}^{-1}$ chlorophyll).

Zelitch (1982) concluded that measuring photosynthetic rates of individual leaves or detached plants in either indoor or outdoor conditions gives a less reliable estimate of net canopy photosynthesis than measuring photosynthetic rates of whole plants under field conditions. The above studies on asparagus photosynthetic activity were performed with a small portion of the whole plant, and measurements were carried out under indoor conditions for a short period of time. No research has been conducted under field conditions measuring whole asparagus canopy gas exchange at various developmental stages or over sequential daylight periods. For this reason, and because it allows for daily integration of the canopy under field environmental conditions, we adopted the method of measuring whole-canopy gas exchange in our study.

Eight asparagus genotypes exhibiting large differences in yield from two preexisting yield trial experiments were selected for study of their photosynthetic efficiency, to test the hypothesis that net daily photosynthesis per plant is correlated positively with yield performance.

Received for publication 7 Nov. 1997. Accepted for publication 1 July. 1998. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

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Table 1. Source and characteristics of asparagus cultivars and lines sampled at Southwest Michigan Research and Extension Center and Michigan Asparagus Research Farm.

Genotype	Source	Cultivar type	Mean yield 1990–95 (lb/acre)	Mean ht $\pm$ sd of 10 plants (cm $\pm$ cm)
Hart-3	Michigan Agr. Expt. Sta.	All-male clone	4934	198 $\pm$ 5.5
Franklin	Netherlands	All-male hybrid	3870	165 $\pm$ 7.6
44Px22-8	N.J. Agr. Expt. Sta.	All-male clone	3724	196 $\pm$ 2.3
Jersey Giant	N.J. Agr. Expt. Sta.	All-male hybrid	3767	192 $\pm$ 5.1
86Ram3	Michigan Agr. Expt. Sta.	All-male clone	2914	171 $\pm$ 3.7
UC86-11	California Agr. Expt. Sta.	Open-pollinated	2819	188 $\pm$ 2.0
Tainan No.3	Taiwan	Open-pollinated	1464	176 $\pm$ 3.8
86Sam3	Michigan Agr. Expt. Sta.	All-male clone	1220	192 $\pm$ 3.3

Materials and Methods

The experiment was conducted on two preexisting cultivar trials established at the Southwest Michigan Research and Extension Center (SWMREC), Benton Harbor and the Michigan Asparagus Research Farm (MARF), Hart by planting 1-year-old crowns in April 1988. All the cultivars were grown in the same blocks on Spinks sandy loam type of soil at SWMREC and Montcalm sandy loam at MARF and were managed the same way over the years (Zandstra et al., 1992). Table 1 summarizes the sources and characteristics of these eight genotypes.

Photosynthetic rates were estimated on canopies of the eight genotypes. All the shoots that emerged from a crown were measured in an open system using a portable infrared gas analyzer (IRGA), (model LCA2; Analytical Development Co., Hoddesdon, Herts, U.K.) throughout the season (Corelli-Grappadele and Magnanini, 1993). A clear polyester material (Mylar; Du Pont, Wilmington, Del.), which has good light transmission properties, was used to make two similar transparent chambers; the second chamber was used after the first one began to show signs of wear. These totally enclosed the asparagus plants and functioned as an assimilation chamber. Foam rubber was wrapped around the bases of stalks to form a mat structure. The bottom part of the chamber was collected and tied tightly around the mat structure to seal the chamber and isolate the plant gas exchange system from the soil respiration.

For each of the eight genotypes, two individual plants were selected at each location for measurements. Every time a genotype was measured at each location, throughout the season, the same two plants were used. A fan was used to blow air into the chamber through a pipe connected at the bottom of the chamber. A hole in the middle of the pipe permitted insertion of a tube of a flow meter (Tri-Sense Air Velocity/Humidity/Temperature Meter, Cole-Parmer Instrument Company, Vernon Hills, Ill.) for the measurement of flow velocity. Flow rate was determined by multiplying flow velocity by the cross-sectional area of the pipe through which the air was blown into the tent. Flow rates ranged from 4100 to 5900 L·min⁻¹. The outlet air was directed to the IRGA by inserting a sampling tube connected to the IRGA into the outlet opening at the top of the chamber. No increase in temperature compared to ambient was observed inside the chamber. It took about half an hour to complete the measurement of one plant, from setting up the chamber to taking down everything. The actual time used to make measurements was about ten minutes for each plant.

Measurements of photosynthetic rates were made from the end of July to the end of September, after which each plant was cut at the ground level to obtain its dry mass. Each plant was separated into stem and fern. The dry mass of the fern portion was used in the

calculation of total leaf area of each plant by multiplying total dry mass of each plant times the leaf area per unit dry mass of the sample measured. Total leaf area of each plant was used in the calculation of photosynthetic rate.

Leaf area was measured with an electronic area meter (LI-3000; LI-COR). The fresh cladophylls were spread out to minimize overlap before they were fed into the leaf area meter. Three subsamples were used for the measurement of leaf area of each genotype. The same method was used to estimate leaf area as that employed by Benson (1982) in his study of asparagus plant morphology.

Daily trends in photosynthesis were evaluated on sunny days during the active growing season. Stomatal conductance, vapor pressure deficit and intercellular CO₂ concentration were calculated. The formulas used for the calculation of these parameters were developed by Moon and Flore (1986). Seasonal changes in asparagus photosynthetic activity were evaluated by multiple measurements on the same pair of plants throughout the season. Because it was not always possible to measure all eight genotypes in a single day, the genotypes were divided into two groups based on their proximity to one another in the field (to minimize time lost in relocating the chamber). Generally four cultivars were measured on 1 day and the other four on the next day. Group A included '86Ram-3', 'Hart-3', '86Sam-3', and 'Franklin'. These were measured on 25 and 31 July; 8 and 15 Aug.; 1, 10, and 23 Sept. Group B included 'Tainan No. 3', 'Jersey Giant', 'UC86-11', and '44Px22-8'. These were measured on 26 July; 12 and 27 Aug.; and 1, 2, 11, and 23 Sept.

A significant confounding factor in assessing genotypic differences in photosynthetic rates was the time of day of photosynthetic rate measurement. Thus, the experiment was designed to measure genotypes in a rotating sequence over the whole season to reduce such an effect. A split-plot experimental design of two blocks was used in this study; the main plot was the eight genotypes at each location; the subplot was the seven measurements throughout the season. Analyses of variance (ANOVA) were conducted on the photosynthetic rate data. The total variation was composed of the variation caused by 1) the genotypic differences on photosynthetic rate, 2) the measurement date effect, which reflected the seasonal change of photosynthetic rate, and 3) the interaction between main plots and subplots. Photosynthetic rates were calculated by using a BASIC computer program developed by Moon and Flore (1986) for open gas exchange systems. To evaluate the effect of time-of-day measurements, on 13 Aug. 1995, the photosynthetic rates of one plant of 'Franklin' and one plant of 'Jersey Giant' were measured ten times each from 0900 to 1800 HR, once every hour at SWMREC. At MARF, rates were measured on one plant of 'Franklin' on 22 Aug. 1995, nine times from 1000 to 1800 HR, once every hour.

Table 2. Whole-plant photosynthetic rates of eight asparagus genotypes, expressed as an average 14 measurements ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and specific leaf weight (SLW) ($\text{mg}\cdot\text{cm}^{-2}$).

Ranking	Genotype	Mean Pn rate ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	SLW ($\text{mg}\cdot\text{cm}^{-2}$)
1	Franklin	27.8 A ^z	13.55 A
2	Hart-3	24.1 B	11.55 B
3	Jersey Giant	22.5 B	12.44 B
4	44Px22-8	21.6 B	12.44 B
5	UC86-11	21.3 B	12.32 B
6	Tainan No.3	17.1 C	11.59 B
7	86Ram3	17.0 C	12.23 B
8	86Sam3	15.7 C	10.43 C
	Mean	20.9	12.1
	LSD 5%	3.5	1.1

^zGenotypes sharing the same letter are not significantly different in their photosynthetic rates.

Results and Discussion

VARIABILITY OF PHOTOSYNTHETIC RATE IN ASPARAGUS GENOTYPES (GROUP A). Analysis of variance indicated that there is significant genotypic variation in asparagus photosynthetic rate ($P < 0.1$). Average asparagus photosynthetic rates ranged from $15.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for '86Sam-3' to $27.8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 'Franklin' in this study. Other genotypes with relatively high photosynthetic rates were 'Hart-3' and 'Jersey Giant' (Table 2). 'Franklin', 'Hart-3', and 'Jersey Giant' all exhibited good performance in yield trial experiments (Table 1).

Prior studies have not indicated a consistent relationship between photosynthetic rate and yield. Elmore (1980) concluded that there is no direct relationship between photosynthetic rate and yield; but Zelitch (1982) reported that they were positively correlated. The no-correlation conclusions generally are derived from single-leaf or small-plant-portion measurements or are not integrated over a season. The positive-correlation conclusions were results of whole-canopy measurements of photosynthetic rate (Biscoe et al., 1975; Christy and Porter, 1982; Peterson and Zelitch, 1982). In this study, a positive correlation ($r = 0.8$) was observed between our measurements of seasonal photosynthesis rate and the yield of these cultivars (Fig. 1).

These results suggest that average seasonal photosynthetic rate (rate/leaf area) would be a good predictor of yield and might be used as a selection criterion in breeding programs. There is evidence that CO_2 exchange rate is a trait of high heritability (Crosbie et al., 1978; Vietor and Musgrave, 1979), which suggests that progress could be made in a breeding program in which canopy photosynthesis is selected. Improvements in crop yield generally have been realized largely by increasing harvest index (Frey, 1981), which is the ratio of the economic yield to total plant mass. Our observations of foliar size relative to long-term yields of 36 cultivars indicate that there is no relationship between size of plants and economic yield. Improvement in a plant's photosynthetic rate may become an important factor in yield enhancement.

Specific leaf mass (SLM = leaf dry mass

per unit leaf area), often is found to correlate with photosynthetic rate per unit leaf area (Augustine et al., 1979; Barnes et al., 1969; Dornhoff and Shibles, 1970; Pearce et al., 1969). The highest photosynthetic rate genotype, 'Franklin', had the highest specific leaf mass ($13.55 \text{ mg}\cdot\text{cm}^{-2}$) and the lowest photosynthetic rate genotype, '86Sam-3', had the lowest specific leaf mass ($10.43 \text{ mg}\cdot\text{cm}^{-2}$) (Table 2). However, the others showed no correlation. Least significant difference (LSD) test indicates that SLM of 'Franklin' was significantly higher than SLWs of the other seven cultivars.

A significant positive correlation, 0.74, was found ($P < 0.05$) between specific leaf mass and photosynthetic rate (Fig. 2). This is in agreement with a similar finding with other species that high photosynthetic rate often is correlated with high specific leaf mass (Augustine et al., 1979; Barnes et al., 1969; Dornhoff and Shibles, 1970). SLW is easier to measure than photosynthetic rate. When interests arise to select genotypes with high photosynthetic rate from a large pool of materials, it could be worthwhile to select high SLM genotypes in preliminary studies to reduce the amount of work involved.

DAILY PHOTOSYNTHETIC ACTIVITIES OF ASPARAGUS PLANT (GROUP B). Photosynthetic rates of one plant of 'Franklin' measured throughout the day of 13 Aug. indicated that photosynthetic rate increased between the first measurement at 0900 HR, 2.5 h after sunrise, and 1000 HR (Fig. 3). Photosynthetic rates then remained relatively constant until 1400 to 1500 HR, after which photosynthetic rates dropped sharply from 33.7 to $22.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Photosynthesis was maintained at this lower level until the last measurement at 1800 HR, which was ≈ 2.5 h before sunset. Similar trends in daily photosynthetic activity were observed with two other measurements using 'Franklin' and 'Jersey Giant'. The daily fluctuations in ambient CO_2 , photosynthetically active radiation (PAR) and temperature (data not shown) showed similar patterns of fluctuation.

Table 3 shows the daily changes of vapor pressure deficit (VPD), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of the cultivar Franklin. Closely related to the drop of

Fig. 1. Correlation between average photosynthetic rate of multiple measurements of a season and 6 years' average yield of eight asparagus genotypes.

Fig. 2. Correlation between average photosynthetic rate of multiple measurements of a season and specific leaf weight of eight asparagus genotypes.

photosynthetic rate between 1300 and 1400 HR (Fig. 2), was a sharp decrease of g_s (from $515.7 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 1300 HR to $196.9 \text{ μmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 1400 HR). During this time, intercellular CO_2 concentration dropped from 244.9 to $190.2 \text{ μmol}\cdot\text{mol}^{-1}$. VPD increased after 1300 HR, which correlated negatively with the change in stomatal conductance ($r = -0.87$). The decrease in photosynthetic rate after 1300 HR was correlated negatively with the changes in VPD ($r = -0.79$), versus positive correlations with the changes in g_s ($r = 0.72$), and C_i ($r = 0.69$). These correlations support the speculation that the higher photosynthetic rates may be a result of the lower stomatal conductance.

SEASONAL VARIATION OF ASPARAGUS PHOTOSYNTHETIC RATE (GROUP C). Field measurements of asparagus photosynthetic rates made it possible to study the seasonal photosynthetic activities of asparagus plants. However, because many measurements were made at different dates through the season, the environmental parameters could not be held constant and are a source of variation. For example, photosynthetic rates measured on a cloudy day in July might be lower than what it could be if the day were sunny; this may lead to an incorrect interpretation of seasonal trends. To minimize light effects, measurements were conducted under full sunlight or as near to full sunlight as daily weather changes permitted.

Since no individual cultivar was measured at the same time of day for each of its measurements through the season, the average assimilation rate of all the cultivars measured at each date was used to represent the assimilation rate of asparagus plants on that date.

Both groups A and B (Fig. 4) show a similar pattern of seasonal photosynthetic rate change. The highest rate was the first measurement in both groups in late July. Depletion of underground carbohydrate storage at the end of the harvest in the middle of June (Shelton and Lacy, 1980; Taga et al., 1980), termination of vigorous fern growth by the end of July and a response to a high demand for carbohydrates by depleted sinks may have contributed to the high photosynthetic demands of the fern during that period. Photosynthetic rates were also relatively high during August. Upon entering September, there was a trend toward decreasing photosynthetic rates.

The ferns were growing vigorously from July to the middle of

Fig. 3. Diurnal changes of photosynthetic rates of three asparagus plants measured at 2 sunny days in August 1995.

Table 3. Daily changes of temperature, photosynthetically active radiation (PAR), vapor pressure deficit (VPD), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of the cultivar Franklim on 13 Aug. 1995 at SWMREC.

Time (HR)	Temp (°C)	PAR ($mmol \cdot m^{-2} \cdot s^{-1}$)	VPD (kPa)	g_s ($mmol \cdot m^{-2} \cdot s^{-1}$)	C_i^2 ($\mu mol \cdot mol^{-1}$)
0900	30	1170	0.94	1050.1	365.1
1000	31	1545	0.22	1100.5	374.2
1100	33	1515	0.26	2137.0	311.0
1200	34	1635	0.81	911.4	283.2
1300	36	1650	1.44	515.7	244.9
1400	38	1635	2.34	196.9	190.2
1500	37	1695	2.22	398.5	246.3
1600	36	1575	2.40	185.7	194.0
1700	35	1335	2.13	75.1	68.5
1800	34	1290	1.78	206.1	203.7

²During the day, the ambient CO_2 concentration decreased from 348 ppm at 0900 HR to 306 ppm at 1800 HR.

Fig. 4. Seasonal changes of asparagus photosynthetic rate at SWMREC. Assimilation rate for each date of Group A was the average of '86Ram-3', '86Sam-3', 'Hart-3', and 'Franklim'. Assimilation rate for each date of group B was the average of 'Jersey Giant', 'UC86-11', '44Px22-8', and 'Tainan No.3'. The seven measurements in group A were conducted on 07/25, 07/31, 08/08, 08/15, 09/01, 09/23. The seven measurements in group B were conducted on 26 July, 12 and 27 Aug., and 1, 2, 11, and 23 Sept.

September. Foliage color of some genotypes began to turn yellow, indicating senescence after the middle of September, and others began to turn yellow near the end of September. The change of fern color was accompanied by the dropping of cladophylls to the ground at the end of the growing season. Unfavorable environmental conditions and the maturity and senescence of the cladophylls largely explain the decrease of photosynthetic rate in September.

Conclusion

Genetic variability in photosynthetic rates was found among eight different asparagus genotypes grown at two sites. This variability in photosynthetic capacity was correlated positively with the long-term economic yields of these asparagus genotypes.

Genotypes having high photosynthetic rates were found to have high specific leaf mass. Selecting for high specific leaf mass could be adopted as a method for preliminary selection of genotypes with high photosynthetic rates. The method of whole-canopy measurement was shown to be a valid method for determining asparagus photosynthetic rates, but the diurnal and seasonal variation must be factored into photosynthetic rate studies using whole-canopy measurements.

Literature Cited

Augustine, J.J. and M.A. Stevens. 1976. Genotypic variation in carboxylation of tomatoes. *Plant Physiol.* 57:325–333.
Augustine, J.J., M.A. Stevens, and R.W. Breidenbach. 1979. Physiological, morphological, and anatomical studies of tomato genotypes varying

- in carboxylation efficiency. *J. Amer. Soc. Hort. Sci.* 104: 338–341.
- Barnes, D.K., R.B. Pearce, and G.E. Carlson. 1969. Specific leaf weight differences in alfalfa associated with variety and plant age. *Crop Sci.* 9:421–423.
- Benson, B. 1982. Sex influence on foliar trait morphology in asparagus. *HortScience* 17:625–627.
- Biscoe, P.V., R.K. Scott, and J.L. Monteith. 1975. Barley and its environment. III. Carbon budget of the stand. *J. Appl. Ecol.* 12:269–293.
- Christy, A.L. and C.A. Porter. 1982. Canopy photosynthesis and yield in soybean. In: Govindjee (ed.). *Photosynthesis—Applications to food and agriculture*. Academic Press, New York.
- Corelli-Grappadeli, L. and E. Magnanini. 1993. A whole-tree system for gas-exchange studies. *HortScience* 28:41–45.
- Criswell, J.G. and R.M. Shibles. 1971. Physiological basis for genotypic variation in net photosynthesis of oat leaves. *Crop Sci.* 11:550–553.
- Crosbie, T.M., J.J. Rock, and R.B. Pearce. 1978. Inheritance of photosynthesis in a diallel among eight maize inbred lines from Iowa stiff stalk synthetic. *Euphytica* 27:657–664.
- Dornhoff, G.M. and R.M. Shibles. 1970. Varietal differences in net photosynthesis of soybean leaves. *Crop Sci.* 10:42–45.
- Downton, W.J.S. and E. Torokfalvy. 1975. Photosynthesis in developing asparagus plants. *Austral. J. Plant. Physiol.* 2:367–375.
- Elmore, C.D. 1980. The paradox of no correlation between leaf photosynthetic rates and crop yields, p. 155–167. In: J.D. Hesketh and J.W. Jones (eds.). *Predicting photosynthesis for ecosystem models*. vol. 2. CRC Press, Boca Raton, Fla.
- Frey, K.J. 1981. Capabilities and limitations of conventional plant breeding, p. 15–62. In: K.O. Rachie and J.M. Lyman (eds.). *Genetic engineering for crop improvement*. The Rockefeller Foundation, New York.
- Lin, A.C. and L. Hung. 1978. The photosynthesis of asparagus plant. *Mem. College Agr., Natl. Taiwan Univ.* 18(1):88–95.
- Moon, J.W. and J.A. Flore. 1986. A BASIC computer program for calculation of photosynthesis, stomatal conductance, and related parameters in an open gas exchange system. *Photosynthesis Res.* 7:269–279.
- Pallas, Jr., J.E. and Y.B. Samish. 1974. Photosynthetic response of a peanut. *Crop Sci.* 14:478–482.
- Pearce, R.B., G.E. Carlson, D.K. Barnes, R.H. Hart, and C.H. Hanson. 1969. Specific leaf weight and photosynthesis in alfalfa. *Crop Sci.* 9:423–426.
- Peterson, R.B. and I. Zelitch. 1982. The relationship between net CO₂ assimilation and dry weight accumulation in field-grown tobacco. *Plant Physiol.* 70(3):677–685.
- Sawada, E., T. Yakuwa, and S. Imakawa. 1962. On the assimilation of asparagus ferns, p. 479. In: A. Lecrenier and I.P. Goeseels (eds.). *Proc. XVIth Intl. Hort. Congr.* vol. 2.
- Shelton, D.R. and M.L. Lacy. 1980. Effect of harvest duration on yield and on depletion of storage carbohydrates in asparagus roots. *J. Amer. Soc. Hort. Sci.* 105(3):332–335.
- Taga, T., H. Iwabuchi, K. Yamabuki, and S. Sato. 1980. Analysis of cultivation environments on the growth of asparagus in Hokkaido. I. Effect of harvesting term on the yields and the carbohydrate in the stock root. *Shuho Bul. Hokkaido Prefect. Agr. Expt. Sta. Hokkaido Chuo Nogyo Shikenjo Naganuma* 43:63–71.
- Vietor, D.M. and R.B. Musgrave. 1979. Photosynthetic selection of *Zea mays* L. II. The relationship between CO₂ exchange and dry matter accumulation of two hybrids. *Crop Sci.* 19:70–75.
- Zandstra, B.H., J.F. Kelly, M. Hausbeck, E.J. Grafius, and H. Price. 1992. Commercial vegetable recommendations: Asparagus. *Mich. Ext. Bul.* E-1304.
- Zelitch, I. 1982. The close relationship between net photosynthesis and crop yield. *BioScience* 32:796–802.
- Zelitch, I. and P.R. Day. 1968. Variation in photorespiration. The effect of genetic differences in photorespiration on net photosynthesis in