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Ontogeny of Photosynthetic Performance in *Fragaria virginiana* under Changing Light Regimes[1]

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ABSTRACT

Apparent photosynthesis and dark respiration were followed during development in four light environments of leaves of *Fragaria virginiana* Duchesne. Leaf expansion was completed more rapidly the higher the growth photon flux density and leaves senesced more quickly in high light. Maximum photosynthetic capacity coincided with the completion of blade expansion and declined quickly thereafter. Leaves were transferred from high to low and low to high photon flux densities at several stages during expansion. Leaf photosynthetic performance and anatomy were subsequently analyzed. Leaf anatomy and apparent photosynthesis per unit dry weight can be modified during expansion to reflect the predominant light conditions. Adaptive potential is greatest early in blade expansion and decreases as expansion is completed.

The capacity of plants to adapt to differing light conditions has long been recognized and investigated in some detail. Under contrasting light regimes, leaves have different anatomical, morphological, and biochemical properties leading to differences in apparent photosynthetic rates (3). Most experimental studies of leaf adaptation have used static environmental conditions—irradiances were maintained at constant levels throughout the growth period. Because light, in nature, changes daily and seasonally throughout the course of leaf development, leaves initiated under one set of conditions often face quite different conditions during expansion and at maturity. The importance of changes in light levels during development on subsequent photosynthetic capacity has received little attention.

We were interested in determining whether the photosynthetic capacity of leaves is adaptable to changes in light at different stages of expansion. Is the photosynthetic capacity of the leaf equally responsive to the light environment at all ages or is it essentially determined at some early stage of development? Leaf anatomy was characterized and photosynthetic rates were measured following transfers of plants between contrasting light environments at different stages of leaf expansion. Inasmuch as photosynthetic capacity is also affected by leaf age, we studied the effect of light environment on the rate of attainment and decline of apparent photosynthesis.

MATERIALS AND METHODS

Plant Material and Growth Conditions. Vegetative material of *Fragaria virginiana* Duchesne, the common wild strawberry of the eastern United States, was collected near Ithaca, N.Y. in April and July, 1976. Runner plantlets derived from the original material, probably including several genotypes, were grown in 500-cm^3 plastic pots in peat-Vermiculite (Jiffy Mix) at a PPFD[2] of approximately 275 μE m^{-2} s^{-1} for 4 to 6 weeks. Plantlets which had produced two to three leaves since rooting were used in the experiments.

Four light levels were established in a single controlled environment chamber. A combination of sodium vapor, color-improved mercury vapor, and incandescent lamps was used to achieve a high PPFD of 678 ± 10 μE m^{-2} s^{-1} as measured at the top of the pots by a Lambda Instruments LI-190S Quantum Sensor. Nylon screen cloth and wire mesh screen were used to produce lower irradiances of 286 ± 3, 151 ± 6, and 64 ± 2 μE m^{-2} s^{-1}. Standard deviations indicate spatial variation within each treatment. Spectral distributions of the four light conditions as measured with a Gamma Scientific model 3000 scanning spectroradiometer were essentially the same. Photoperiod was 15-h centered on a 12-h thermoperiod with day/night temperatures of 25/18 C. Plants were watered daily with distilled H_2O and fertilized weekly (50 ml, Peters 20-20-20) throughout the experiments.

Experimental Treatments. Two sets of experiments were performed. In the first, the effects of irradiance and leaf age on photosynthetic performance were studied. Leaves were individually tagged as they appeared in each of the four light treatments. Length and width of leaflets were measured to the nearest 0.5 mm at 1- to 3-day intervals until expansion was essentially complete and at longer intervals thereafter. Longevity was estimated by allowing some leaves to die naturally. Apparent photosynthesis and dark respiration were measured on leaves of different ages.

A second experiment examined adaptive capacity as a function of leaf age at the highest and lowest growth chamber light levels. Leaves which appeared after the plants had been in the high or low light levels for at least 1 week were individually tagged. A plant was transferred to the contrasting light level when its tagged leaf was at one of three stages of development (Fig. 1): (*a*) "bud" stage, age 0 days—the leaf was first visible to the unaided eye; (*b*) "folded" stage, age 3 days—leaflets were still folded together; (*c*) "90% FA" stage, age 11 days for high-light leaves and 13 days for low-light leaves—the leaf had reached 90% of the full area it would have achieved had it remained in the same light condition. Predictions of final area were based on the pattern of leaf expansion determined from the first experiment as compared with daily measurements of leaf length and width in the second experiment. Gas exchange measurements and anatomical samples were taken when the leaves were either age 17 days (all controls, bud, and folded transfers), 18 days (high to low 90% FA transfers), or 20 days (low to high 90% FA transfers). All transfers were in the contrasting light condition for at least 7 days. This procedure insured that all leaves were measured at ages at which they

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[2] Abbreviations: PPFD: photosynthetic photon flux density (400–700 nm); FA: full area; GE: General Electric Company; SLW: specific leaf weight (weight/area); RuBPcase: ribulose-1,5-bisphosphate carboxylase-oxygenase.

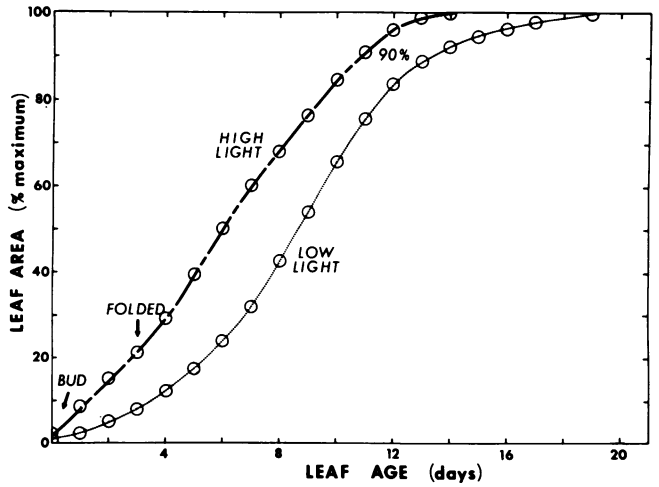

FIG. 1. Leaf blade expansion in two light regimes. Relative size as a per cent of maximum area is given as a function of age from first appearance of the bud. Maturity stages at which leaves were transferred between light treatments are indicated.

exhibited their maximum photosynthetic rates, as predicted from the results of the first experiment. This avoided introducing the confounding effects of differential rates of senescence between light treatments. CO_2 exchange measurements were made on four to seven single attached leaves per treatment.

Gas Exchange Measurements. Apparent photosynthesis and dark respiration of single attached leaves were measured using a Beckman 315 IR gas analyzer modified for differential analysis in an open system. Light was supplied by two to four GE Quartzline 500-w lamps filtered through 11 cm of water and variable amounts of wire screen and cotton cheesecloth. Air temperature, leaf temperature, air dew point, and wind speed were controlled and monitored. Air stream humidity was measured with matched narrow range LiCl sensors in a controlled temperature bath. Leaf temperatures were maintained to within one degree of the nominal 25 C measurement temperature. Leaf area was calculated by comparing total leaf weight to weight of discs of known area. Dry weight was determined after drying to constant weight in a forced-air oven at 70 C.

Anatomical Measurements. Samples for leaf anatomy analysis were taken from three leaves per treatment, often, but not always, from the leaves used for CO_2 exchange measurements. Tissue was fixed in 5% glutaraldehyde in 0.1 M phosphate or cacodylate buffer, postfixed in 1% OsO_4 in the same buffer, dehydrated, and embedded in Araldite. Uniform 0.2-μm-thick sections were stained with 0.05% toluidine blue. Mesophyll regions were photographed, then printed at 500× for quantitative measurements as described by Chabot and Chabot (5). Specific leaf weight was determined from four to seven leaves per treatment.

Statistics. Treatment means of the transfer experiments were compared using analysis of variance (20). If this test revealed differences, the means were then compared using the Student-Newman-Keuls procedure for multiple comparisons (21). Correlation tests were made using programs in the MINITAB package, Pennsylvania State University.

RESULTS

Effects of Irradiance and Leaf Age. Leaves from the high light treatment essentially completed their expansion by age 14 days. Cessation of expansion was abrupt, with no measurable increase in area after age 14 to 15 days (Fig. 1). Low-light leaves continued to expand until age 18 to 20 days, several days after the high-light leaves had stopped. The low-light leaves only gradually approached their maximum area; they increased in area for 6 to 8

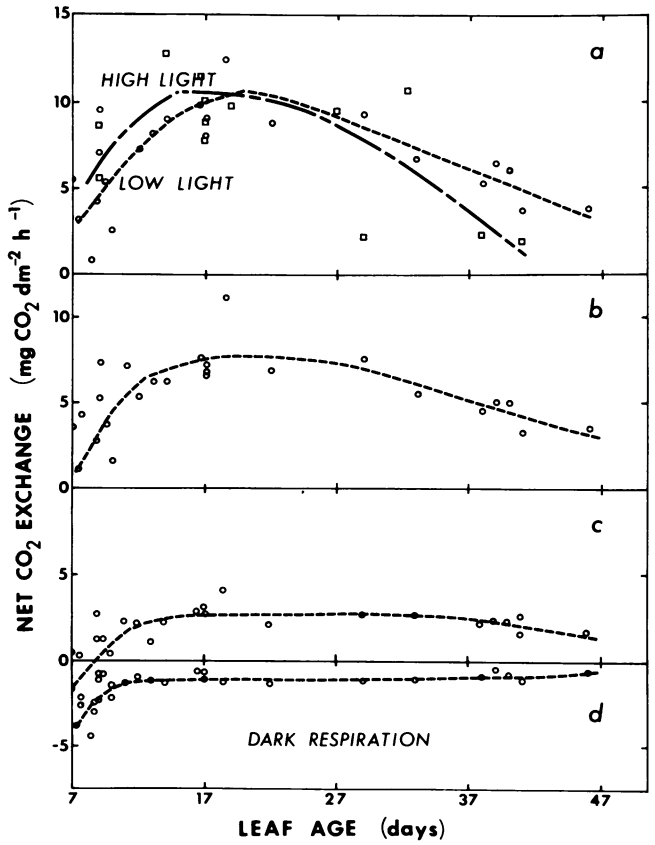

FIG. 2. Apparent photosynthesis and dark respiration as a function of leaf age. Earliest gas exchange measurements were taken just after the leaflets unfolded, approximate age of 7 days. a: Light-saturated rates at 1,490 μE m^{-2} s^{-1} for leaves in two light regimes; b: apparent photosynthesis at 245 μE m^{-2} s^{-1} for leaves grown under low light conditions; c: apparent photosynthesis at 68 μE m^{-2} s^{-1} for leaves grown under low light conditions; d: dark respiration for leaves grown under low light.

days after reaching 90% of their final size, while high-light leaves ceased expanding 3 to 4 days after that point. The low-medium and high-medium treatments produced results intermediate between those of the low and high treatments; only the low and high treatment results are presented here.

High-light leaves reached their maximum apparent photosynthesis rate slightly sooner than low-light leaves (Fig. 2a). In both cases, maximum rates were achieved 0 to 3 days after leaf expansion ceased. There was a progressive loss of photosynthetic capacity with age starting 4 to 7 days after the maximum was reached. Photosynthetic capacity at lower measurement PPFDs was lost progressively as age increased; leaves maintained their maximum rates at low measurement PPFDs longer than they maintained their maximum rates at high measurement PPFDs (Fig. 2, a, b, and c). Net photosynthesis declined more rapidly with increasing growth light level. For example, photosynthetic rate at high measurement PPFD declined faster in high-light leaves than in low-light leaves (Fig. 2a). The slope of decline was not significantly different between treatments; rather, high-light-grown leaves initiated the decline earlier and had a shorter lifespan than low-light leaves. Dark respiration rates in both treatments changed similarly with increasing age. The initially high rates decreased as the leaves expanded then stabilized near the completion of expansion (Fig. 2d). Fully expanded high-light leaves had rates about 50% higher than low-light leaves. Dark respiration rates were nearly constant for most of the leaves' lifetimes, with decline occurring late in life.

Median lifespan was 51 days ($N = 42$) for high-light leaves and 79 days ($N = 36$) for low-light leaves. Lifespan in the low-medium

environment was 74 days ($N = 21$) and was 62 days ($N = 28$) in the high-medium treatment. Apparent photosynthesis rates became more variable toward the end of leaf lifespan. This variability was due to variation in leaf longevity and to practical difficulties in determining the time of death. Physiological death appeared to be signaled by characteristic sequences of color change at each growth irradiance. Under high light, senescing leaves first turned yellowish green, then yellow, then bright red, finally becoming brown and dry. In low light, the green leaves faded into the final brown color with no distinct yellow or red stage. Frequently, parts of a leaf senesced at different rates as indicated by the pattern of color change. This suggests high within-leaf variation in metabolic rates.

Leaf Transfer Experiments. Maximum apparent photosynthesis rate expressed on a dry weight basis was higher in the low-light controls and significantly different ($P < 0.05$) from that of the high-light controls (Fig. 3). The low-light controls also had lower light compensation points than did the high-light controls.

Rates of net photosynthesis and dark respiration of the transferred leaves reflected the light regime prevailing during leaf age 3 to 12 days, the period of greatest blade expansion. Leaves transferred from high to low light at the bud and folded stages of development had maximum rates not significantly different from the low-light controls (Fig. 3). Leaves that were transferred to low light when they reached 90% FA had apparent photosynthetic rates that were intermediate between the low- and high-light controls and were significantly different from both.

The low to high light transfers had a somewhat different pattern of response (Fig. 4). The 90% FA transfers were not significantly different from the low-light controls. Leaves transferred at the bud and folded stages did not differ from each other, but were significantly different from the 90% FA transfers and the high-light controls. These two transfers did not achieve the same rate as the high-light controls, in contrast to the corresponding high to low light transfers, which had the same rate as the low-light controls.

Photosynthetic rates expressed on an area basis (Table I) did not differ significantly among the treatments. Table I also lists photosynthetic rates per area of mesophyll cell surface. These were obtained from average values of physiological and anatomical parameters in each treatment since different leaves were sampled in each case.

Leaf Anatomy. The low-light controls had lower specific leaf weights than did the high-light controls (Table II). The lower SLW of the low-light controls was a result of a thinner leaf coupled with a relatively poorly developed mesophyll. In contrast, the high-light controls had a well developed palisade region two to three cell layers thick and also had a denser spongy mesophyll region. Quantitative measures of leaf anatomy reflect this greater mesophyll development (Table II). Mesophyll cells comprised a high percentage of the total leaf volume of the high-light controls, while there was correspondingly little air space. This high percentage is also reflected in the high values for mesophyll volume/leaf surface area and mesophyll area/leaf surface area. The per cent volume devoted to epidermis was the same in the high- and low-light controls.

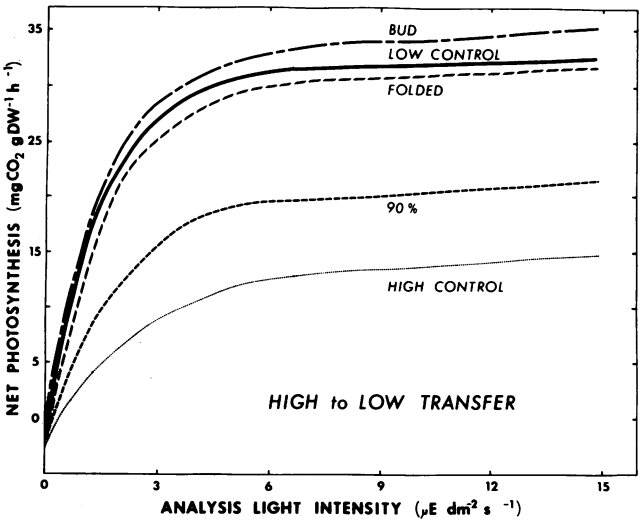

FIG. 3. Apparent photosynthesis as a function of irradiance for leaves transferred from high to low growth regimes. Maturity stages are indicated along with high and low light controls.

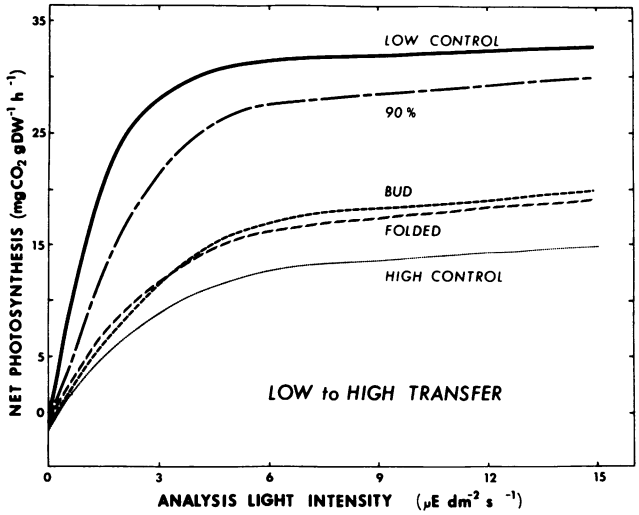

FIG. 4. Apparent photosynthesis as a function of irradiance for leaves transferred from low to high growth regimes. Maturity stages at which transfers were made are indicated along with high and low light controls.

The patterns of anatomical development of the transferred leaves closely resembled the photosynthetic response patterns of those leaves. As with photosynthesis, anatomical development reflected the light regime prevailing during the period of greatest leaf expansion. Anatomy of leaves transferred from high to low light at the bud and folded stages generally resembled the low-light controls (Table II). Most anatomical measures for the bud transfers were not significantly different from the low-light control values. The folded transfers tended to be intermediate between the low- and high-light controls, although the differences from the low-light controls were often not significant. The 90% FA transfers were intermediate, but closest to the high-light controls.

For the low to high light transfers (Table III), the 90% FA transfers were intermediate between leaves grown continuously in the two contrasting light regimes, but most like the low-light controls. The folded transfers were more like the high-light controls than were the bud transfers, however. This was consistent with the pattern of photosynthetic performance, although different from the high to low transfer pattern. The high standard deviations associated with the means for the folded transfers suggest that sample error was unusually large in this case.

Maximum apparent photosynthesis per unit dry weight was highly correlated ($P < 0.01$) with SLW ($r = -0.983$), leaf thickness ($r = -0.935$), per cent mesophyll ($r = -0.944$), mesophyll volume/leaf area ($r = -0.967$), and mesophyll area/leaf area ($r = -0.953$). Correlations of anatomical parameters with maximum apparent photosynthesis on a leaf area basis were insignificant.

DISCUSSION

It is clear from these results that the leaves of *F. virginiana* are capable of adaptation to altered light conditions experienced throughout the period of blade expansion. This means that leaves

Table I

Light Saturated Rates of Apparent Photosynthesis in Leaf Transfer Experiment

Data are given as mg CO_2 h^{-1} based upon external leaf surface area (dm^2) and mesophyll surface area (dm^2) with 1 standard deviation indicated. Measurements were taken at 1492 $\mu E\ m^{-2}\ s^{-1}$. Sample size is given in parentheses. Photosynthesis values for mesophyll area were determined from averages for the treatments.

TREATMENT	PHOTOSYNTHESIS LEAF AREA	MESOPHYLL AREA
LH* - BUD	11.42 ± 1.93 (5)	0.429
LH - FOLDED	11.17 ± 1.62 (4)	0.364
LH - 90% FA	12.90 ± 2.72 (4)	0.763
LOW CONTROLS	8.77 ± 0.95 (4)	0.559
HIGH CONTROLS	10.27 ± 1.83 (7)	0.355
HL - 90% FA	11.88 ± 1.31 (4)	0.440
HL - FOLDED	9.72 ± 0.46 (4)	0.509
HL - BUD	9.87 ± 0.95 (4)	0.609

*LH = Low to high light transfer; HL = High to low light transfer.

Table II

Anatomy of Leaves Transferred from High to Low Light Intensities

Leaves at different stages of expansion were transferred from a high light intensity (678 $\mu E\ m^{-2}\ s^{-1}$) to a low light intensity (64 $\mu E\ m^{-2}\ s^{-1}$) growth regime. One standard deviation is given where appropriate. Values in the same row followed by the same letter are not significantly different.

LEAF PARAMETER	LEAF TREATMENT BUD	FOLDED	90% FULL AREA	LOW CONTROL	HIGH CONTROL
Specific leaf weight ($mgDW/cm^2$)	2.85^a ± .24	3.22^a ± .51	5.62 ± 1.13	2.69^a ± .04	6.96 ± .59
Leaf thickness (μm)	108 ± 8^a	128 ± 22^b	140 ± 12^{bc}	121 ± 3.6^{ab}	153 ± 8.9^c
Cell volume/leaf volume (%)					
Epidermis	34.9	28.5	32.0	24.8^a	23.7^a
Mesophyll	34.5^a	40.3	48.3	32.7^a	55.6
Air	30.5^b	30.3^b	19.7^a	42.7	20.7^a
Mesophyll volume / leaf surface area ($\mu m^3/\mu m^2$)	36.8 ± 4.0^a	52.3 ± 15.7	68.8 ± 10.3	39.6 ± 4.8^a	83.8 ± 6.6
Mesophyll surface area / leaf surface area ($\mu m^2/\mu m^2$)	16.2 ± 1.6^a	19.1 ± 5.8^a	27.0 ± 4.0^b	15.7 ± 1.2^a	28.9 ± 2.9^b

are able to adjust to natural, changing PPFDs and, thus, more fully exploit altered light environments. In strawberry these adjustments occur in both anatomical and physiological characteristics. The potential for adaptation does change, decreasing as expansion nears completion. The physiological and anatomical character of the leaf was determined by the conditions to which it was exposed longest during development. Leaves that had reached approximately 90% of their final area under one light treatment retained anatomical and physiological traits typical of that light regime when transferred to a different PPFD. In addition to this evidence for the effects of previous light treatment on photosynthetic competence, a more subtle influence was observed. Leaves

Table III

Anatomy of Leaves Transferred from Low to High Light Intensities

Treatment conditions and forms of data are similar to Table II.

LEAF PARAMETER	LEAF TREATMENT				
	BUD	FOLDED	90% FULL AREA	LOW CONTROL	HIGH CONTROL
Specific leaf weight (mgDW/cm^2)	6.01[a] ± .61	6.16[a] ± .67	4.31 ± .69	2.69 ± .04	6.96 ± .59
Leaf thickness (μm)	139 ± 9	158 ± 22[b]	125 ± 12[a]	121 ± 3.6[a]	153 ± 8.9[b]
Cell volume/leaf volume (%)					
Epidermis	32.0	26.2[a]	26.5[a]	24.8[a]	23.7[a]
Mesophyll	45.0[a]	48.4[a]	39.7	32.7	55.6
Air	23.1[a]	25.2[a]	33.9	42.7	20.7[a]
Mesophyll volume / leaf surface area (μm^3/μm^2)	64.1 ± 6.1	77.3 ± 18.6[a]	49.9 ± 11.0	39.6 ± 4.8	83.8 ± 6.6[a]
Mesophyll surface area / leaf surface area (μm^2/μm^2)	26.6 ± 3.3[b]	30.7 ± 11.1[b]	16.9 ± 5.2[a]	15.7 ± 1.2[a]	28.9 ± 2.9[b]

transferred from high to low PPFD early in their development became substantially similar to low-light leaves while those leaves initiated in low light were not able to adapt fully to high light. Since adaptation to high light requires increased energy investment in cell structure and enzyme content (3, 5, 12, 13), it is possible that plants which have been grown for a period of time in low light simply do not have energy reserves sufficient to produce high-light leaves. Alternatively, since the major period of cell division occurs in the bud, perhaps this process is influenced by light environment and constrains later anatomical development.

Previous studies (4, 8, 16) have transferred leaves between light treatments only after full expansion. All of these studies have shown that fully expanded leaves retain some capacity to adapt to altered light environments, but that their adaptive response is determined by environmental history. Most of this adaptation probably occurs through biochemical reorganization. The report (4) that leaf anatomy can change subsequent to completion of expansion may simply indicate that morphological and anatomical development are not entirely coincident.

That maximum apparent photosynthesis per unit leaf area does not change significantly with light pretreatment may be a feature common to shade-adapted species. Similar findings have been reported for *Impatiens parviflora* (6), *Fragaria vesca* (5), and shade genotypes of *Solanum dulcamara* (8). Lugg (11) found that photosynthetic rates in soybean, a shade-adapted species, did not differ between leaves which expanded at different times in the growing season, in spite of significant differences in leaf thickness and specific leaf weight. The reason why leaf area-based photosynthetic rates do not change with light treatment is not clear. Leaf thickness does increase with growth PPFD along with mesophyll cell volume and surface area as reported by others (12, 13). Our data are consistent with the hypothesis that photosynthesis is depressed in high light by photodestruction of light-harvesting pigments (2, 8). This effect seems to increase with duration of exposure to high light, but interacts with anatomical changes which occur after leaves are transferred between contrasting PPFDs. Bunce *et al.* (4) found that high-light leaves transferred to low light conditions for several days yielded the highest photosynthetic rates in their series of treatments as a result of high internal mesophyll area produced under high light and brief protection from photodestruction. Low-light-grown leaves which were transferred to high light conditions had the lowest rates of apparent photosynthesis. Low light transfer leaves had low internal mesophyll development and suffered from high light photodestruction. A similar pattern occurs in our data.

Apparent photosynthesis per unit dry weight was negatively correlated with most anatomical parameters as was also found in *F. vesca* (5) and some other species (17). Possible explanations for this relationship were discussed by Chabot and Chabot (5). An additional factor may be the increase in SLW with increasing growth PPFD. A large fraction of SLW may consist of labile materials such as protein, carbohydrates, and minerals which may accumulate in the cell without necessarily affecting photosynthesis (11, 16). If, as growth PPFD increases, the greater accumulation of these materials is not matched by increases in the biochemical capacity for photosynthesis, then the apparent rate of photosynthesis per unit weight may decrease without any real decrease in the cellular capacity for photosynthesis. This phenomenon could be accentuated in those plants such as *F. virginiana* which appear to suffer high light inhibition.

The effects of age on light-saturated apparent photosynthesis in *F. virginiana* were similar to those observed in a variety of other species (1, 10, 14, 15, 19, 22). The early increase in rate generally paralleled leaf expansion, with maximum rates being attained at or very soon after full expansion was achieved. Maximum rates of photosynthesis were maintained for only 3 to 7 days in all four treatments. Smillie (19) found that peak rates were maintained for approximately 2 days in pea, although most other species observed to date seem to maintain maximum rates for longer periods, on the order of 1 to 3 weeks (10, 14, 22) up to years in some evergreen species (7, 18). A few studies have demonstrated that deterioration of photosynthetic capacity after the peak is related to a loss of nitrogen (11), RuBPcase activity (9), and Chl (18) with increasing leaf age.

Growth PPFD had a strong effect on the decline of maximum photosynthetic rates, with high-light leaves declining most quickly, while low-light leaves showed a more gradual decline. Osman and Milthorpe (14) found a similar pattern in wheat leaves grown at four irradiances. We also found that rates at low measurement PPFDs did not decline until near the end of leaf life, while rates at increasing measurement PPFDs exhibited intermediate patterns, with increasing rates of decline. The few previous studies of photosynthetic senescence have dealt largely with maximum rates,

although Aslam *et al.* (1) reported practically no change in low-light photosynthetic rate of cassava (*Manihot esculenta*) over a period of 6 weeks. Lugg (11) found that maximum photosynthetic rates declined rapidly in soybean leaves which were produced early, but were maintained for increasingly longer periods of time in leaves at successively higher nodes. This corresponds with a stabilizing of the light climate as plants reach maturity. In *F. virginiana,* photosynthetic rates at high light declined more rapidly in plants grown at high light than those grown at low light. Loss of high light capacity has little relevance to plants in low light conditions, except that in nature there will be a loss of ability to utilize high PPFD light flecks. Maximum response time for a step change in irradiance is about 80 s for *F. virginiana* so that light flecks probably are of major importance in leaf carbon balance. Under field conditions, strawberries begin growth in the early spring at a time when the competing herbaceous vegetation has been flattened by winter snow. Light conditions remain favorable for several months and strawberry is able to compete with surrounding vegetation by producing leaves with increasingly long petioles. Maximum petiole length is about 40 cm so that leaves become increasingly shaded in June. Leaf production also slows at this time. Our laboratory results seem to correspond to field conditions in that leaves produced under high light conditions are generally discarded when shaded and low-light leaves live longer and retain photosynthetic capacity for longer periods of time.

The effect on the photosynthesis-light-age response surface of changing the light regime, as distinguished from the different response surfaces for leaves in constant high or low light environments, remains unclear. For example, does a leaf transferred from high to low light continue to follow a high light senescence pattern, or react in some other way? Further study of such effects and their relationship to leaf anatomy is clearly needed for understanding the behavior of plants in natural environments.

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