Growth Responses of Sun and Shade Plants in Simulated Vegetation Shade and Neutral Shade*

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Light environment in natural vegetation shade can be characterized by reduced light intensity and modified spectral quality due to selected attenuation of radiation by the canopy. Spectral property of diffused light under canopies has been summarized such that the photon fluence rates in the blue and red wavebands are very low, with a small peak (usually) in the green and a large peak in the far-red¹⁷⁾. This results in a decrease in the red : far-red ratio from that observed in natural daylight⁸⁾.

Established plants have been known to exhibit basically two types of response to vegetation shade; one is "shade avoidance" and another "shade tolerance"¹⁵⁾. A number of herbaceous seedlings have been reported to show marked morphogenic responses to simulated shade-light at the equal photosynthetically active photon fluence rate. These responses are similar to those of the shade avoiders¹⁷⁾, such as the increase in stem elongation^{9,14)}, increase in petiole length¹³⁾, decrease in leaf area development^{7,13)}, decrease in branching²⁰⁾, and change in chlorophyll content^{4,13)}.

However, these responses are much different between species of open habitats and woodland shade habitats¹⁵⁾, and between shade-tolerant and shade-intolerant species⁴⁾. Moreover, Some arboreous species did not show a large response to a simulated shade-light¹⁶⁾. Thus, the present study was carried out to investigate the growth responses of seedlings in sun and shade plant species to

simulated vegetation shade and neutral shade. In this study we used the following two shade plant species, cacao and *Sagittaria pygmaea*. Cacao, an important economic tree in tropics, needs shading for raising the seedlings in the nursery. It has been considered that the aim of shading rate would be about 50 percent for a great part of the nursery time¹⁹⁾. We found that the most favorable growth of the seedlings could be obtained at a photon fluence rate about $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ (400—700nm) with an artificial source¹¹⁾. *S. pygmaea*, a perennial paddy weed, is widely distributed throughout Japan and much troublesome in rice culture. It has been described that the growth is better in 25 percent shade than in full sunlight¹²⁾, and the shoot growth is greatly accelerated under filtered sunlight through either green or blue PVC film compared with under clear one⁶⁾.

Materials and Methods

Plant materials

Rice (*Oryza sativa* L. cv. Nipponbare) and soybean (*Glycine max* Merr. cv. Norin No.2) were used as sun plants, and cacao (*Theobroma cacao* L.) and *Sagittaria pygmaea* Miquel. as shade plants. These plants were grown with vermiculite and Hyponex solution, except *S. pygmaea* which were grown on submerged paddy soil. For rice plants, pH of medium was adjusted to about 5. These plants were precultivated in a natural-light growth chamber at day/night temperatures 25/20°C and relative humidity about 70% for certain days after seeding or planting (*S. pygmaea*), then exposed to different light environments. The periods of the precultivation and light treatment were 4 and 21 day for rice, 6 and 14 days for soybean, 26 and 35 days for cacao, and 26 and 21 days for *S. pygmaea*. The average sizes of seedlings at the start of treatment were as

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follows : rice, 0.8 cm in shoot length ; soybean, 4.2 cm in stem length ; cacao, 5.4 cm in stem length ; and *S. pygmaea*, 2.8 in normal leaf number. During the treatment, these seedlings except cacao were grown 14-h day and 10-h night cycles, day/night temperatures 25/20°C and relative humidity about 70%, while cacao seedlings were under 13-h day and 11-h night cycles and the temperatures 28/23°C. Number of seedlings per treatment was 30 for rice, 8 for soybean, 6 for cacao and 12 for *S. pygmaea* at the end of treatment.

Preparation of leaf-simulated filters

A leaf-simulated filter, which gives a spectral transmission curve similar to that of "mean leaf", was prepared to simulate a natural vegetation shade. The transmission curve of the mean leaf was provided from the data of 33 plant species including 7 arboreal species described in the previous paper¹⁰⁾. A polyacrylate sheet (2-mm thickness) was formed in Kyowa Gas Chemical Ind. Co. Tokyo, according to our prescription that the following dyes should be dissolved in the monomer at the final concentration ; 0.01% Diaresin H3G, 0.06% Diaresin Brown A, 0.015% Macrolex Yellow 3G and a fixed concentration of ultraviolet adsorber. The transmission curve of the sheet was partly corrected by a yellow PVC film. Transmission spectra of the mean leaf and the simulated filter are shown in Fig. 1.

Another filter, bored leaf-simulated filter, was prepared to simulate a bright vegetation shade with sunflexs, by boring holes in the leaf

-simulated filter with 2.1-cm diameter and 10-cm interval. Rate of total area of the holes per unit area of the filter was 13.3%, which can be comparable to that of sunflexs per unit land area under a relatively bright canopy of trellised grapevine orchard.

Light sources

Sixteen, 400W "BOC lamps" (Mitsubishi MLBOC 400F-U, reflected type) mixed with 6 halogen quartz lamps (Mitsubishi J210 V500W) installed in the ceiling of a growth chamber (Koito KG-206, special type) were used as the primary source. Characterized lights for treatments were isolated from the source with respective filter frames [60×45×60 (H) cm] having ventilating slits.

Names of the treatments and the filter systems are as follows : A, control, without filter frame ; B, simulated bright shade, hole-bored simulated filter ; C, neutral bright shade, a combination of each one layer of cheese cloths (Kuraray Co. Ltd.), #100, #200 and #610 ; D, simulated dark shade, the leaf-simulated filter ; and E, neutral dark shade, a combination of cheese cloths (ditto), #300, #610 and #600×2. Average photosynthetically active photon fluence rate at the upper level of plants was measured with Quantum Sensor, LI-190S and Integrating Light Meter, LI-188 (Lambda Instruments Corp.), and those expressed in $\mu\text{mol m}^{-2} \text{s}^{-1}$ (400–700 nm) were : A, 708 ; B and C, 157 ; and D and E, 73. The three levels of fluence rate can be comparable to about 1/2, 1/10 and 1/20 of daylight under a clear summer sky, respectively. Spec-

Fig. 1. Comparison of transmission spectra between mean leaf and leaf-simulated filter. Actual values of transmittance at 800 nm were 38% for mean leaf and 83% for leaf-simulated filter.

Fig. 2. Spectral photon distribution curves of incident lights under the experimental conditions. A, unshaded control, indicated by about 1/2 scale in the ordinate; B, simulated bright vegetation shade; C, neutral bright shade; D, simulated dark vegetation shade; and E, neutral dark shade.

tral photon distributions of the lights under the experimental conditions were obtained by conversion from the data of energy unit measured with a spectroradiometer (Iio SRP-1465, revised model).

The ratio of photon fluence rates in 10 nm wide wavelengths at 660 nm and to those at 730 nm, which is known to have a close correlation with phytochrome photoequilibrium¹⁸⁾, was calculated by the each spectral photon distribution curve and expressed as R/FR ratio or ξ value, according to SMITH and HOLMES¹⁸⁾. The spectral photon distribution curves, R/FR ratio and photon fluence rate (400–700 nm) of radiation under the experimental conditions are given in Fig. 2. The R/FR ratios 1.31–1.52 for the control and neutral shade lights are somewhat higher than the mean ratio 1.16 for natural daylight described by HOLMES and SMITH¹⁸⁾. The values 0.51 for the simulated bright shade and 0.26 for the simulated dark shade correspond well with those observed by the same authors at ground level under a wheat canopy with leaf area indices about 2 and 3, respectively. The low R/FR values like these could be found also

under various natural vegetations including crop fields, woodlands and tropical rain forests¹⁷⁾.

Chlorophyll assay

Chlorophyll was extracted from full-grown leaf blades with 80% acetone solution. Chlorophyll a and b contents in the extract were analyzed with a spectrophotometer (Hitachi, Model 100-60) and calculated according to MACKINNEY-ARNON equation¹¹⁾.

Results

Elongation growth

Elongation growth, expressed in terms of plant height increase for rice, stem length extension for soybean and cacao, and maximal leaf length for *S. pygmaea*, was generally promoted by the shade treatments, especially in soybean and cacao. The promotion was more or less greater in the simulated shades than in the neutral shades at the equal photon fluence rate (Fig. 3). To distinguish between the effect of neutral shade and that of simulated shade, the ratio of neutral shade/control at the equal R/FR ratio, and that of simulated shade/neutral shade at the equal fluence rate

were calculated for each growth parameter (Fig. 1). In the former case, growth responses in the neutral shades at R/FR ratio of 1.31 equal to that in the control were interpolated on the assumption that each response has a

linear relation with R/FR ratio. The neutral shade caused a remarkable promotion in elongation for dicotyledonous soybean and cacao, but none or little for monocotyledonous rice and *S. pygmaea*. In the dicots the response was

Fig. 3. Growth responses of seedlings grown under simulated vegetation shade and neutral shade. See Fig. 2 for the symbols of treatments. Δ PH, plant height increase; Δ SL, stem length increase; LL, maximum leaf length; Δ LN, leaf number increase; Δ LA, leaf area increase; LA, leaf area; Chl, chlorophyll content; and Δ DW, dry weight increase.

generally greater at the lower fluence rate and in the early stage of the treatment.

On the other hand, the ratios of simulated shade/neutral shade for the sun plants, rice and soybean, were high (123–157%) in the early stage of treatment but decreased at the final determination, in either level of fluence rate. However, the ratios for the shade plants, cacao and *S. pygmaea*, were low (98–113%) in the early stage but increased in most cases

at the end of treatment.

Leaf development

Leaf growth, expressed in terms of leaf number per plant for rice and leaf area per plant for the other species, was strongly affected by the shade treatments in different ways among the species (Fig. 3, Table 1). In rice and soybean, leaf growth was evidently inhibited with the lowering of fluence rate particularly in soybean. In either level of

Table 1. Discrimination of the effects between the neutral shade and simulated shade on the growth responses of seedlings.

		Effect of light intensity ^{b)} (neutral/control, %)				Effect of light quality (simulated/neutral, %)			
		Bright shade		Dark shade		Bright shade		Dark shade	
		Early ^{c)}	Final ^{d)}	Early	Final	Early	Final	Early	Final
Rice	$\Delta PH^a)$	88	106	96	106	140	119	157	116
	ΔLN		71		59		109		106
	ΔDW		17		4		129		124
	Chl		136		117		88		75
Soybean	ΔSL	247	268	344	314	131	111	123	114
	ΔLA		58		30		98		90
	ΔDW		23		4		85		83
	Chl		98		90		107		82
Cacao	ΔSL	194	159	233	173	98	115	113	118
	ΔLA		261		237		128		112
	ΔDW		307		161		122		90
	Chl		101		95		80		80
<i>S. pygmaea</i>	LL	96	103	101	113	100	100	111	117
	LA		79		73		100		146
	ΔDW		53		82		133		80
	Chl		218		191		76		75

^{a)} See Fig. 3 for the abbreviations. ^{b)} Calculated from interpolated values at R/FR ratio 1.31 equal to that of the control. ^{c)} Early stage indicates for 6 (rice), 7 (soybean) or 8 days (cacao and *S. pygmaea*) from the start of treatment.

^{d)} Final value was obtained at the end of treatment.

Table 2. Leaf and stem dry weights per plant, leaf/stem ratio and areal weight of leaf of the seedlings grown in the simulated shade and neutral shade.

	Soybean				Cacao				<i>S. pygmaea</i>
	Leaf (mg)	Stem (mg)	L/S ratio	AW (mg cm ⁻²)	Leaf (mg)	Stem (mg)	L/S ratio	AW (mg cm ⁻²)	AW (mg cm ⁻²)
Control	957 ^a	607 ^a	1.58 ^a	3.31 ^a	468 ^b	408 ^a	1.14 ^b	4.45 ^a	1.32 ^{ab}
Simulated bright shade	257 ^b	273 ^b	0.96 ^{bc}	1.53 ^{bc}	1035 ^a	521 ^a	2.05 ^a	3.13 ^b	1.02 ^c
Neutral bright shade	311 ^b	271 ^b	1.14 ^b	1.81 ^b	910 ^a	436 ^a	2.10 ^a	3.16 ^b	1.06 ^{bc}
Simulated dark shade	93 ^c	153 ^c	0.61 ^d	1.22 ^d	674 ^b	538 ^a	1.88 ^a	2.26 ^c	1.00 ^c
Neutral dark shade	118 ^c	138 ^c	0.87 ^c	1.36 ^c	683 ^b	356 ^a	1.93 ^a	2.57 ^c	1.42 ^a

Petioles were included in stem. L/S and AW indicate leaf/stem ratio in dry weight and areal weight, respectively. Figures followed by a different letter are significantly different at the 5% level.

fluence rate, the inhibitory effect in the neutral shade was somewhat larger for rice, but rather smaller for soybean compared with that in the simulated shade. Leaf area development in *S. pygmaea* was considerably inhibited by the shade treatments, excepting the simulated dark shade.

Contrary to these, leaf area development in cacao greatly promoted in all the shade treatments. The promotion was more in the higher fluence rate than in the lower one in either light quality, and more in the simulated shade than in the neutral shade in either light intensity.

Areal weight of leaf, which was expressed in terms of leaf dry weight/leaf area for estimating leaf thickness, decreased with lowering of the fluence rate, particularly in the simulated shade in all of the species. This response was much greater in soybean than in cacao and *S. pygmaea* (Table 2).

Effects of shade treatments on dry weights of leaf blades (leaf) and stem plus petioles

(stem) per plant and their ratio were compared between soybean and cacao (Table 2). In soybean, leaf and stem weights and leaf/stem ratio were remarkably reduced with the decrease of fluence rate. The decrease of leaf/stem ratio was greater in the simulated shade than in the neutral shade at either fluence rate level. However, in cacao leaf weight was increased by shading especially in the bright shades. Stem weight was not significantly affected by shading, but showed a tendency to increase in the simulated shades. As the results leaf/stem ratio was greatly increased in all the shade treatments.

Dry matter production

In rice and soybean, dry matter production was strongly inhibited by the shade treatments (Fig. 3, Table 1). Dry weight increment in both species was reduced to approximately 20% in the bright shade and 4% in the dark shade. In *S. pygmaea*, however, the inhibition by shading was much less than that in the above two species, showing the relative dry

Fig. 4. Effects of photon fluence rate on the ratio of dry matter production to leaf area development of seedlings grown under simulated vegetation shade and neutral shade. Closed circle, simulated shade; open circle, neutral shade. Vertical lines show the standard deviations. Data of *S. pygmaea* are expressed as DW/LA ratio at the end of treatment.

weight increment much more than 50% of the control. It should be noted that in the neutral shades dry matter production was rather more in the dark shade than in the bright shade.

On the contrary, dry matter production in cacao was greatly promoted by the shade treatments, especially in the bright shade with values more than 3 times of the control. The promotion in the simulated shade was greater than that in the neutral shade at the higher fluence rate level, whereas it was reversed in the lower level. It was also noticed that the simulated shade/neutral shade ratios in rice and soybean are not much different between the two fluence rates, but those in cacao and *S. pygmaea* are evidently greater in the bright shade than in the dark shade.

To estimate the photosynthetic response to fluence rate, the ratio of dry weight increment/leaf area development ($\Delta DW/\Delta LA$) for soybean and cacao, and dry weight/leaf area (DW/LA) at the end of treatment for *S. pygmaea* were calculated and shown in Fig. 4. In soybean the ratio was sharply decreased with lowering the fluence rate. However, in cacao and *S. pygmaea* the ratios at the low fluence rates were evidently higher than those in soybean. The maximum ratio was found in the bright shades for cacao and in the neutral dark shade for *S. pygmaea*.

Chlorophyll content and chlorophyll a/b ratio

Chlorophyll (a+b) content of leaf blades was greatly increased by the shade treatments in *S. pygmaea*, while generally less increased in rice. However, the contents in soybean and cacao tended to decrease in the simulated

shades (Fig. 3, Tables 1 and 3). The content in the simulated shade was mostly lower than that in the neutral shade at the equal fluence rate regardless of the species. Chlorophyll a/b ratio was found to be somewhat decreased by shading in the sun plants, rice and soybean, but rather increased in the shade plants, cacao and *S. pygmaea*. Effect of the spectral quality of shade-lights was similar to that in the chlorophyll content (Table 3).

Discussion

The present study clearly indicated that most of the growth responses are much more affected by the reduced fluence rates than by the lowered R/FR ratios. The responses of the seedlings to the shade-lights were different between the sun and the shade species, and specific effects of the simulated shade could be found in some growth parameters. These facts are in good agreement with the result of MORGAN et al.¹⁵⁾ who observed for kiwifruit and grapevine trees.

In the sun plants, rice and soybean, the shade treatments caused an increase in elongation, a decrease in leaf development and a great decrease in dry matter production. Although the elongation promotion was much greater in soybean than in rice, an additional elongation effect in the simulated shade was observed for both species, particularly in the early stage (within about 1 week) of treatment. This rapid response indicates the characteristics of shade avoiders categorized by SMITH¹⁷⁾. However, effects of the simulated shade on leaf development and dry matter

Table 3. Chlorophyll content and chlorophyll a/b ratio of leaf blades of the seedlings grown in the simulated shade and neutral shade.

	Rice		Soybean		Cacao		<i>S. pygmaea</i>	
	a+b(mg gFW ⁻¹)	a/b	a+b(mg dm ⁻²)	a/b	a+b(mg dm ⁻²)	a/b	a+b(mg dm ⁻²)	a/b
Control	2.57 ^c	3.44 ^a	1.77 ^a	2.86 ^a	2.72 ^{ab}	2.48 ^{ab}	1.16 ^c	2.29 ^a
Simulated bright shade	3.16 ^b	3.09 ^b	1.84 ^a	2.33 ^b	2.18 ^b	2.53 ^{ab}	2.04 ^b	2.36 ^a
Neutral bright shade	3.60 ^a	3.28 ^a	1.72 ^a	2.43 ^b	2.72 ^{ab}	2.71 ^a	2.67 ^a	2.39 ^a
Simulated dark shade	2.31 ^c	2.90 ^c	1.34 ^b	1.94 ^d	2.26 ^{ab}	2.33 ^b	1.69 ^{bc}	2.26 ^a
Neutral dark shade	3.07 ^b	3.21 ^{ab}	1.63 ^a	2.13 ^c	2.82 ^a	2.52 ^{ab}	2.26 ^{ab}	2.41 ^a

The values indicate averages of 5 (rice) or 4 (the others) separate determinations. Figures followed by a different letter are significantly different at the 5% level.

production were different between both species; the simulated shade caused a promotion for rice but an inhibition for soybean, in the same fluence rate levels.

On the other hand, the shade plants, cacao and *S. pygmaea*, responded to the shade-lights mostly in the same way, but partly in different way each other. The shade-lights caused marked increases in stem elongation, leaf area development and dry matter production for cacao, whereas an increase in leaf length, and decreases both in leaf area and dry matter production for *S. pygmaea*. The decrease in dry matter production in *S. pygmaea* was, however, much less than those seen in rice and soybean.

Both of the shade plants exhibited the following characteristics: a) promotive effect of the simulated shade on the elongation growth was smaller in the early stage of treatment, unlike that found in the sun plants; b) The simulated shade caused greater leaf area and smaller leaf thickness compared with the neutral shade at the equal fluence rate; and c) dry matter production and $\Delta DW/\Delta LA$ or DW/LA ratio in the shade-lights were remarkably higher than those observed in the sun plants, while the effect of simulated shade to these parameters were promotive in the bright shade but inhibitive in the dark shade.

The slow response of elongation to the simulated shade-light found in the shade plants seems to be characteristic of a shade tolerance reaction¹⁷⁾. However, the wider and thinner leaves developed in the simulated shade clearly indicate that both species have an adaptability to utilize the insufficient light intensity more effectively for photosynthesis in natural vegetation shades. Relationship between the $\Delta DW/\Delta LA$ or DW/LA ratio and the fluence rate shown in Fig. 5 coincides well with the result of BJÖRKMAN and HOLMGREN³⁾ who investigated photosynthetic rates of the sun- and shade-habitat species at a high and a low light intensities.

BJÖRKMAN and HOLMGREN²⁾ described that the chlorophyll content in the shade habitat species is often lower in the plants grown in strong light, whereas that in the exposed habitat species is mostly higher in the leaves grown in strong light. In the present study, however, the changes in chlorophyll content with the fluence rate was not clearly distinguished between the sun and the shade

species, though the content in *S. pygmaea* was much higher in the shades than in the unshaded control. It was revealed that both chlorophyll content and chlorophyll a/b ratio were lower in the simulated shade with a low R/FR ratio than in the neutral shade with a high R/FR ratio at the equal fluence rate, for all the species used. Similar result has been reported by MORGAN and SMITH¹⁴⁾ on the chlorophyll content in leaf and stem of *Chenopodium album*.

From these results, it can be concluded that the sun plants, particularly for soybean, exhibit the responses to shade-lights similar to those in shade-avoiding species¹⁷⁾, whereas the shade plants partly respond like to those seen in shade-tolerating species¹⁷⁾. A high adaptability of the shade plants to reduced light quantity may mostly be due to a remarkable increase in leaf area for cacao, while an extremely high level in chlorophyll content for *S. pygmaea*. A favorable growth of cacao seedlings can be expected in natural bright vegetation shades with a certain amount of sunflecks.

Summary

Seedlings of sun plants, rice (*Oryza sativa* L.) and soybean (*Glycine max* Merr.) and shade plants, cacao (*Theobroma cacao* L.) and *Sagittaria pygmaea* Miquel. were grown in a strong light and at two photon fluence rate levels of simulated vegetation shade and neutral shade-lights, under suitable daylengths for 2–5 weeks, to investigate the responses of these seedlings to the intensity and quality of the shade-light.

In the sun plants, the shade-light caused an increase in elongation, a decrease in leaf development and a great decrease in dry matter production. The elongation growth in the early stage of treatment was much greater in the simulated shade than in the neutral shade. In the shade-lights, cacao seedlings exhibited marked increases in stem elongation, leaf area and dry matter production, whereas *S. pygmaea* showed a decrease in leaf area and dry matter production. The shade plants showed the following common responses to the shade-lights: a) the elongation growth in the later stage of treatment was greater in the simulated shade than in the neutral shade; b) the simulated shade induced wider and thinner leaves compared with the neutral shade at the equal levels of fluence rate; and c) dry

matter production and dry weight per leaf area in the shade-lights were remarkably higher than those in the sun plants.

Chlorophyll content of leaves in the neutral shades was greatly increased in *S. pygmaea* but not much changed in the other species compared with that in the control. Chlorophyll content and chlorophyll a/b ratio were mostly lower in the simulated shade than in the neutral shade at the each light level, for all the species used.

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〔和 文 摘 要〕

人工緑陰および中性遮光下における
陽地および陰地植物の生育反応

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植物群落内の光環境に対する植物の生育反応を明らかにするため、植物葉類似の分光透性を示す試作フィルター透過光（人工緑陰）と寒冷紗透過光（中性遮光）下で、陽地植物としてイネ（日本晴）とダイズ（農林2号）、陰地植物としてカカオとウリカワを用いて2-5週間における幼植物の生育反応を調べた。光強度は、対照の白色強光区（BOC ランプ+ハロゲンランプ、W 比 6.4:3.0）では $708 \mu\text{mol m}^{-2} \text{s}^{-1}$ (400-700 nm)、人工緑陰区および中性遮光区ではともに同 157 および 73 の明・暗2段階とした。赤色光 ($660 \pm 5 \text{ nm}$) と遠赤色光 ($730 \pm 5 \text{ nm}$) の光量子比 (R/FR) で表わした光質は、対照区および中性遮光区では 1.31-1.52、人工緑陰区では 0.26-0.51 であった。

イネとダイズでは、遮光下で伸長促進、葉の発達抑制および乾物生産の著しい低下がみられた。伸長促進程度は、ダイズで大きくイネでは小さかったが、両種とも人工緑陰下の方が同じ光強度の中性遮光下よりも明らかに大で、とくに処理初期（約1週間以内）に著しかった。一方、カカオでは、遮光によって茎の伸長、葉の発達および乾物生産が著しく増大した。ウリカワでは、葉の伸長促進、葉面積の抑制および乾物生産の低下が起るが、その変化の程度は上記陽地植物よりも小さかった。

カカオとウリカワに共通した反応は次のとおりである：a) 人工緑陰下の光質によって引き起される伸長促進反応は、陽地植物と異なり、処理初期に小さくその後増大する：b) 葉の発達は、同一光強度レベルでは、人工緑陰下でより強く促進される：c) 遮光下における乾物生産および葉面積当たり乾物重の相対値は、陽地植物よりも明らかに高く、人工緑陰の光質の効果は光強度および R/FR 比が高い場合に促進的に、低い場合には抑制的に作用する。

葉緑素含量は、ウリカワでは遮光下で著しく増大し、イネでもやや大となったが、他は大差がなかった。葉緑素 a/b 比は、遮光によってイネとダイズではやや低下したが、カカオとウリカワでは増大する傾向を示した。人工緑陰下の光質は葉緑素含量および同 a/b 比の両方を低下させることが、供試4種に共通して認められた。

以上から、遮光下では、陽地植物とくにダイズは弱光回避種と類似の反応をし、供試した陰地植物は部分的に弱光耐性種に似た反応を示すことが判明した。後者の高い弱光適応性は、カカオでは主に葉面積の発達により、ウリカワでは葉緑素含量の増加によると考えられた。