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UNDERSTORY LIGHT AND HERBACEOUS PLANT PHOTOSYNTHESIS IN OKLAHOMA FORESTS

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CHAPTER I

INTRODUCTION

The growth of herbaceous species in diverse natural light regimes suggested to early workers that a distinction could be made between sun and shade plants on the basis of assimilation rates. Sparling (1967) reporting on earlier work of Lundegardh (1921, 1924) states that the sssimilation curves of sun and shade plants could be distinguished and that the leaf morphology differs according to the level of light exposure during differentiation. Daxter (1934) concluded that light intensity is a controlling factor of dry weight of herbaceous florá even at the high light intensities of the edges of woodlands.

Blackman and Rutter (1946, 1948) reported that light, among other factors, controlled the distribution and net assimilation rate of bluebell, _Scilla_ _non-scripta_, with bluebell occurring in decreasing light regimes down to a mean value of 0.089 daylight. Light levels illuminating leaves during initial growth were observed to control leaf area and possibly the leaf photosynthetic mechanism. Pretreatment in reduced light favored subsequent growth in shade.

Bohning and Burnside (1956) using single leaves of greenhouse cultivated plants reported light saturation curves for apparent photosynthesis of 8 sun and 5 shade species. Their data indicated that the maximum apparent photosynthesis of shade species to be about 1/6 that of sun species and the maximum rate of shade species was reached at about ½ the light intensity required of sun species to attain the maximum rate.

Wolf (1969) studied several species growing them at 2 light intensities and 3 temperatures. He concluded that the "light intolerant" group had a peak photosynthetic rate at about 5000fc, whereas the tolerant group peaked at higher light intensities.

Went (1957) in a review of plant growth suggested that the "woodland adaptation" to low light intensity was low metabolism. This concept received indirect support from Grime and Jeffrey (1965) who conclude that plants which are slow growing and endure long periods of shade replace other types.

Bjorkman and Holmgren (1963, 1966) used single leaves from contrasting sun and shade ecotypes of each of various species grown from propagules under controlled light regimes. He concluded that the shade ecotypes had higher photosynthetic rates at low, light limiting, intensities. Sun ecotypes although not as efficient at low light intensities had higher photosynthetic rates at higher, enzyme limiting, light intensities.

Sparling (1967) using single leaves grouped several understory woodland species according to their growth period in relation to tree canopy expansion: (1) those plants which complete active growth prior to canopy expansion were considered shade intolerant, (2) those which grow during canopy expansion were considered semi-shade tolerant, while (3) those which grow after canopy expansion were considered shade tolerant. His data although variable indicate that tolerance to shade is correlated to reaching maximum photosynthetic rates at lower light intensities. He further indicates that shade tolerant species are injured by high light intensities and should thus be considered shade obligate.

In summary, the present understanding of the photosynthetic capacity of various herbaceous species based on their distribution in various light regimes suggests a division into two groups. The first group is the sun type which is characterised by high respiration, high rates of CO_2 fixation per unit of plant (either area or weight) in strong light, low fixation rates in weak light, and a wider range of tolerance to increasing light without injury. The second group is the shade type characterised by a lower respiration, lower rate of CO_2 fixation per unit of plant in strong light, higher fixation rates in weak light, and limited tolerance to strong light without injury.

Therefore it seemed likely that typical prairie species would exhibit sun type characteristics and that herbaceous understory plants occurring in forests would exhibit shade type characteristics. The open prairie and forests in Oklahoma provide contrasting open and shaded habitats from which herbaceous species could be selected. The objective of this study is to determine examples of contrasting expression of sun type and shade type characteristics between species occurring in these habitats.

CHAPTER II

METHODS AND MATERIALS

Herbaceous species[1] were selected from those occurring in 3 forest stands and from adjacent open prairie. One bottom land stand (Oliver) and adjacent open area are located in Cleveland county, R3W T8N sec. 1. One upland stand (Thunderbird) and adjacent open area are located in Cleveland county, R1E T9N sec. 32. The third stand located in Southeast Oklahoma is found in McCurtain county, R25E T5S sec. 19. The open area in McCurtain county was in the same range and township, but in section 13. Eight 1m^2 quadrats were sampled for herbaceous species in the wooded and open areas. Four 1/10 acre quadrats in each slope of the 4 cardinal directions in Lookout stand and four 1/10 acre quadrats in the other stands were sampled for woody species. The Lookout exposures sloped from 10-15° from horizontal toward each direction. Thunderbird stand sloped gently to the northeast while Oliver stand was almost level representing the uppermost floodplain of the South Canadian River.

From the sampling data herbaceous species were selected for analysis. Further criteria for selection were that propagules for obtaining replicate individuals

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[1] Voucher specimens of study species deposited in The Bebb Herbarium, University of Oklahoma, Norman, OK., USA

of the same age could be obtained and that the leaf structure was suitable for leaf area determinations. Replicate individuals were necessary in order to obtain an estimate of variance of the characteristics measured and leaf structure was critical because leaf area was used in CO_2 exchange rates.

Several aspects of the natural light regime were measured during portions of the spring and summer of 1969 and 1970. Both instantaneous illumination values and light energy values were measured. Illumination measurements were made by a Weston Illumination meter while energy values were obtained by a recording Belfort Pyroheliometer or by an anthracene technique (Marquis 1962) calibrated by the pyroheliometer. The change in light energy penetration as the forest canopy becomes more dense was monitored in Oliver and Thunderbird stands. The variability of the illumination reaching the understory plants was measured in all stands by multiple illumination readings after the canopy had fully developed. The relation of the understory light energy availability to the distance and to the basal area of nearly trees was measured for Thunderbird stand.

Plants were grown in sand culture from propagules in 3 light regimes. A Percival growth chamber provided light intensities of 200 and 2000fc. The chamber was adjusted to provide a 16 hr day (75^{o}F) and an 8 hr night (65^{o}F). The third light regime was obtained by placing the plants outdoors. Temperatures and light varied with the weather but were restricted to spring and summer months. All plants received regular amounts of mineral solution, FeEDTA modified from Hoagland and Arnon (1950).

The photosynthetic rate responces of plants selected for study were measured by monitoring the CO_2 gas exchange of whole plants within a known volume of air enclosed in a Plexiglass chamber. The leaf area of the individual plant was measured at the time of each separate analysis and was used for calculation of the CO_2 exchange rates. Temperatures were maintained at 70^{o}F by refrigeration of the chamber. Exact CO_2 concentration changes were measured by a calibrated recording Beckman 215A infra-red analyzer. Light of different intensities was provided by tungsten filament bulbs of various wattage combinations filtered by 2 cm running water.

CHAPTER III

RESULTS AND DISCUSSION

Vegetation of the forest stands.

The importance values of major woody species in the three stands is given in Table 1. Between exposures in Lookout stand most species are similar with the highest number in the north and the least in the west exposure. The most striking differences are the absence of *Pinus echinata*[2] in the east exposure, *Quercus velutina* in the east exposure, and *Carya tomentosa* in the north exposure. Single individuals of *Juniperus virginiana* and *Ulmus alata* account for their appearance on the north exposure. *Pinus echinata* shows the highest importance value within the north and west exposures while *Quercus marilandica* shows the highest importance value within the east and south exposures.

The Thunderbird stand included only 3 tree species whereas Lookout stand contained 7. The relation between the importance values of *Quercus marilandica* and *Q. stellata* reverses, *Q. marilandica* showing the higher value in Lookout stand but the lower value in Thunderbird stand.

The species composition of Oliver stand is totally

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[2]Nomenclature follows Waterfall (1966) unless suthority is given.

Table 1. Importance values of major woody species in Lookout north exposure (L-O N), Lookout east exposure (L-O E), Lookout south exposure (L-O S), Lookout west exposure (L-O W), Thunderbird stand (Thbrd) and Oliver stand (Oliv).

Species	Importance values of woody species					
	L-O N	L-O E	L-O S	L-O W	Thbrd	Oliv
Quercus marilandica	45	179	103	71	89	-
Quercus stellata	31	53	33	36	114	-
Pinus echinata	113	-	77	99	-	-
Quercus alba	43	20	45	55	-	-
Carya tomentosa	-	30	34	39	-	-
Carya texana	-	-	-	-	97	-
Fraxinus pennsylvanica	-	-	-	-	-	209
Quercus velutina	11	18	9	-	-	-
Populus deltoides	-	-	-	-	-	34
Juniperus virginiana	7	-	-	-	-	-
Ulmus alata	7	-	-	-	-	-
Diospyrus virginiana	-	-	-	-	-	30
Ulmus americana	-	-	-	-	-	27

different from the other stands. Fraxinus pennsylvanica makes up a larger portion of the importance value within the stand than any one species in the other 2 stands.

The importance values of herbaceous species in the 3 stands is given in Table 2. The most obvious distinction between the 4 exposures of Lookout stand is the reduction in number of species in the east exposure where there are about ½ as many species as in the other exposures. About the same number of species occur in and several are common to the north, south, and west exposures of Lookout stands.

The most unexpected species in the three stands were Andropogon gerardii and Schizachrium scoparium (Mich.) Nash in Lookout and Thunderbird stands respectively. A possible explanation will be considered from the light data presented later. During the period of observation only vegetative growth of these 2 species was observed in the forest stands and they tended to occur in more open sites.

Rhus radicans and Parthenocissus quinquefolia were most common, occurring in all three stands. Clitoria mariana was common to Lookout and Thunderbird stands. Although the sampling procedure did not include Antennaria plantaginifolia in Thunderbird stand, nor did Parthenocissus quinquefolia appear in the Lookout stand data, both species were observed outside the quadrats which were recorded in the data but are common species to Lookout and Thunderbird stands.

Table 2. Importance values of herbaceous species in Lookout north exposure (L-O N), Lookout east exposure (L-O E), Lookout south exposure (L-O S), Lookout west exposure (L-O W), Thunderbird stand (Thbrd) and Oliver stand (Oliv).

Species	Importance values of herbaceous species					
	L-O N	L-O E	L-O S	L-O W	Thbrd	Oliv
Antennaria plantaginifolia	82	-	106	89	-	-
Andropogon gerardii	47	-	48	20	-	-
Galactia volubilis	37	40	-	33	-	-
miscellaneus	27	69	-	24	14	21
Rhynchosia latifolia	25	-	33	-	-	-
Rhus radicans	22	82	-	15	26	58
Tephrosia virginiana	18	-	-	27	-	-
Panicum linearifolium	13	-	-	-	-	-
Erigeron strigosis	11	-	-	-	-	-
Rudbeckia hirta	10	-	-	-	-	-
Callicarpa americana	10	-	-	24	-	-
Clitoria mariana	-	77	-	40	31	-
Brachchyelytrum erectum	-	32	-	-	-	-
Panicum malacophyllum	-	-	24	-	-	-

Table 2. continued

Species	Importance values of herbaceous species					
	L-O N	L-O E	L-O S	L-O W	Thbrd	Oliv
Scutellaria ovata	-	-	13	-	-	-
Galium pilosum	-	-	12	-	-	-
Veronia baldwinii	-	-	11	-	-	-
Panicum dichotomum	-	-	10	-	-	-
Panicum microcarpon	-	-	-	15	-	-
Chasmanthium sessiliflorum (Poir.) Yates	-	-	-	15	-	-
Viola pedata	-	-	-	-	51	-
Schizachrium scoparium	-	-	-	-	38	-
Panicum lanuginosum	-	-	-	-	25	-
Parthenocissus quinquefolia	-	-	-	-	21	80
Aster sp.	-	-	-	-	15	-
Galium pilosum	-	-	-	-	10	-
Eleocharis sp.	-	-	-	-	7	-
Carex sp.	-	-	-	-	7	-
Cirsium undulatum	-	-	-	-	7	-

Table 2. continued

Species	Importance values of herbaceous species					
	L-O N	L-O E	L-O S	L-O W	Thbrd	Oliv
Panicum virgatum	-	-	-	-	7	-
Sphenopholis obtusata	-	-	-	-	7	-
Viola missouriensis	-	-	-	-	-	61
Phryma leptostachya	-	-	-	-	-	34
Senicula canadensis	-	-	-	-	-	18
Commelina communis	-	-	-	-	-	15
Galium circaezans	-	-	-	-	-	13

The species composition of Thunderbird and Oliver stands differs except for poison ivy and virginia creeper which are common species. Thunderbird stand has the greatest number of species of the stands. A relationship between the number of species and the light values measured in the stand will be suggested later in the discussion.

Vegetation of the open areas.

The importance values of herbaceous species in open areas adjacent to Lookout stand, Thunderbird stand and Oliver stand are given in Table 3. The open areas have a wide variation of species composition with *Erigeron strigosus* and *Andropogon virginicus* common to the areas.

Lookout open area was recently cleared of tree species. The occurrence of *Parthenocissus quinquefolia* which also occurs in the forested area appears to be an indicator of the prior vegetation. In the season following the one in which the area was sampled it appeared that the bluestem grasses had increased in number and size much more than any other species of herbaceous plants in the open area. It seems therefore likely that the species composition was shifting toward the other areas sampled.

Thunderbird and Oliver open areas appeared to have been free of woody species for some time. The high importance value for *Schizachrium scoparium* is as expected. The importance value given *Bromus tectorum* in Oliver open area is the result of density and frequency. During this

Table 3. Importance values for herbaceous species in open areas adjacent to Lookout stand, Thunderbird stand, and Oliver stand.

Species	Importance value		
	Lookout	Thunderbird	Oliver
Lespedeza striata	144	-	-
Erigeron strigosus	40	12	59
Aira elegans	20	-	-
Festuca octoflora	16	-	-
Cynoglossum amabile	12	-	-
Andropogon virginicus	12	17	7
Hedeoma pulegioides	10	-	-
Plantago aristata	9	-	-
Andropogon gerardii	7	-	-
Bromus tectorum	7	-	-
Stipa leucotricha	7	-	-
Panicum linearifolium	6	-	-
Parthenocissus quinquefolia	5	-	-
Panicum ravenelii	5	-	-

Table 3. continued

Species	Importance value		
	Lookout	Thunderbird	Oliver
Schizachrium scoparium	-	110	51
Echinacea angustifolia	-	32	-
Sisyrinchium angustifolium	-	27	-
Bouteloua hirsuta	-	20	-
Thelosperma ambiguum	-	17	-
Cirsium undulatum	-	14	-
Ruellia sp.	-	12	-
Hedyotis nigricans	-	9	-
Hymenopappus tenuifolius	-	9	-
Psoralea linearifolia	-	9	-
Eleocharis sp.	-	9	-
Bromus tectorum	-	-	98
Ambrosia psilostachya	-	-	39
Panicum virgatum	-	-	16
Solanum torreyi	-	-	9
Helianthus annuus	-	-	7
Budbeckia hirta	-	-	7

study this species demonstrated heavy late winter growth, flowering and setting fruit before other species present in the area became active. Although the plants were past their active growth at the time of sampling the species was identifiable and was included in the data.

Light measurements in the forest stands.

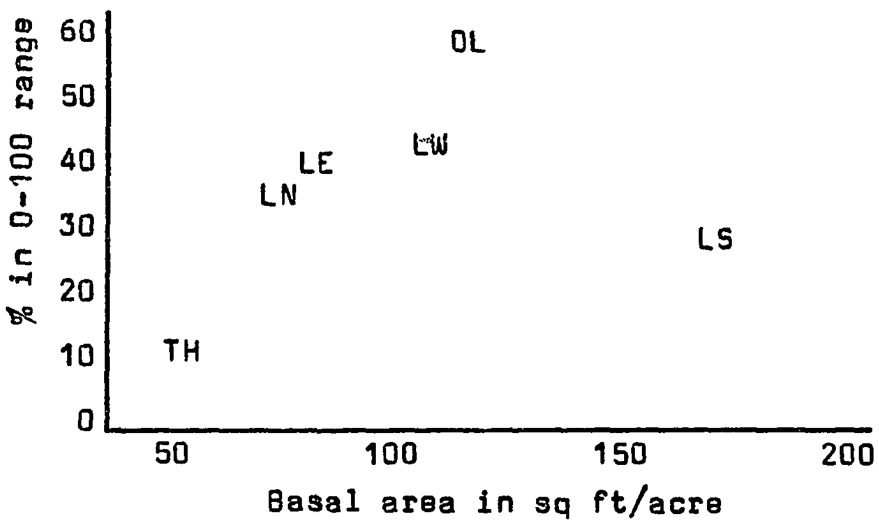
The frequency distribution of different light intensity ranges and total basal area per acre of woody species are given in Table 4. In Lookout stand the most frequent occurrence of the light intensity range above 700 fc occurs in the south exposure. The high light intensity would occur in those areas where the canopy failed to intercept the light. In the southern exposure where the light source is most nearly vertical, more frequent high illumination values would be expected. In the same fashion more light would be available in this exposure and, provided moisture were adequate, more plant growth would be expected. The data show such an agreement because the total basal area is greatest in the south exposure of Lookout stand.

With an increasing frequency of readings in the lowest intensity range in Lookout stand, except for the south exposure, basal area increases (Table 4). This appears to show a relationship between light interception and basal area (Fig. 1). In general, as basal area increases the percent of illumination values falling in the lowest range increases. As the trees become larger they become

Table 4. Comparative distribution of light readings in foot candles as percent of measurements within each stand after tree leaf expansion near noon on clear days. Total basal area per acre is given for Lookout north exposure (L-O N), Lookout east exposure (L-O E), Lookout south exposure (L-O S), Lookout west exposure (L-O W), Thunderbird stand (Thbrd), and Oliver stand (Oliv).

	Percent of readings in each range					
	L-O N	L-O E	L-O S	L-O W	Thbrd	Oliv
above 700 fc	0	0	3	0	16	7
401 - 700 fc	3	8	7	6	13	0
301 - 400 fc	2	5	3	6	6	1
201 - 300 fc	9	13	13	12	6	2
101 - 200 fc	45	27	44	32	46	27
0 - 100 fc	41	47	30	44	13	63
ft^2/acre	79	84	181	112	48	123

Figure 1. Relation between the percent of illumination values falling in the 0-100 fc range and the basal area of woody species in Lookout north exposure (LN), Lookout east exposure (LE), Lookout south exposure (LS), Lookout west exposrre (LW), Thunderbird stand (TH), and Oliver stand (OL).



more efficient in intercepting light which is indicated by the increased frequency of low light intensity readings.

Light readings in Thunderbird and Oliver stands show the same relationship between basal area and light intensity. Light measurements in Thunderbird, with a lower basal area, tended more to fall in higher light intensity ranges whereas light measurements in Oliver stand, with a higher basal area, tended more to fall in low light intensity ranges. Although the lowest light intensity range occurs most frequently in Oliver stand the highest basal area was measured in the southern exposure of Lookout stand. The factor which may explain this exception is slope, since Oliver stand is about level. The relationship cannot be compared as neither a southern exposure of Oliver nor a level portion of Lookout was studied. However as the light reaching the canopies was assumed equal, Oliver stand intercepts more sunlight as indicated by the higher frequency of the lowest light intensity range.

A higher than expected frequency of light intensity readings above 701 fc was measured in Oliver and Thunderbird stands. A possible explanation could be that canopy openings are the result of the death of very large individuals either from the present or a preceeding successional stage. If large individuals were to die, replacement lag would permit canopy openings indicated by the high light intensity readings. The occurrence of large, isolated individuals of cottonwood suggest a transition from the termination of a cottonwood-willow stage to the present stage. By comparison at Thunderbird the openings seem to result from the loss of dominant species as dead blackjack oak can be seen on the forest floor. The canopy openings resulting from the death of very large cottonwood individuals in Oliver stand appear less frequent, although the openings are larger than the openings resulting from the death of blackjack oak individuals in Thunderbird stand.

The light data appear to show an agreement to the herbaceous plant sampling data. A greater range of plants might be expected to occur where a greater range of light was available. There appears to be an agreement between the more evenly distributed light ranges measured in Thunderbird stand and the larger number of species occurring there. The prairie species Andropogon gerardii occurs only in the Lookout exposure with the most frequent light readings above 400 fc. Likewise, another prairie species, Schizachrium scoparium occurs in Thunderbird stand. In this stand, the highest occurrence of the highest light intensity range was measured. These two prairie species would be expected to occur where light of a higher intensity is available.

The effect of tree leaf expansion on the energy reaching the understory plants is given in Figure 2 for Oliver stand in two spring seasons and Thunderbird stand

Figure 2. Light energy penetration as percent of unshaded open area values in two forest stands during three spring months measured at one site in each stand.

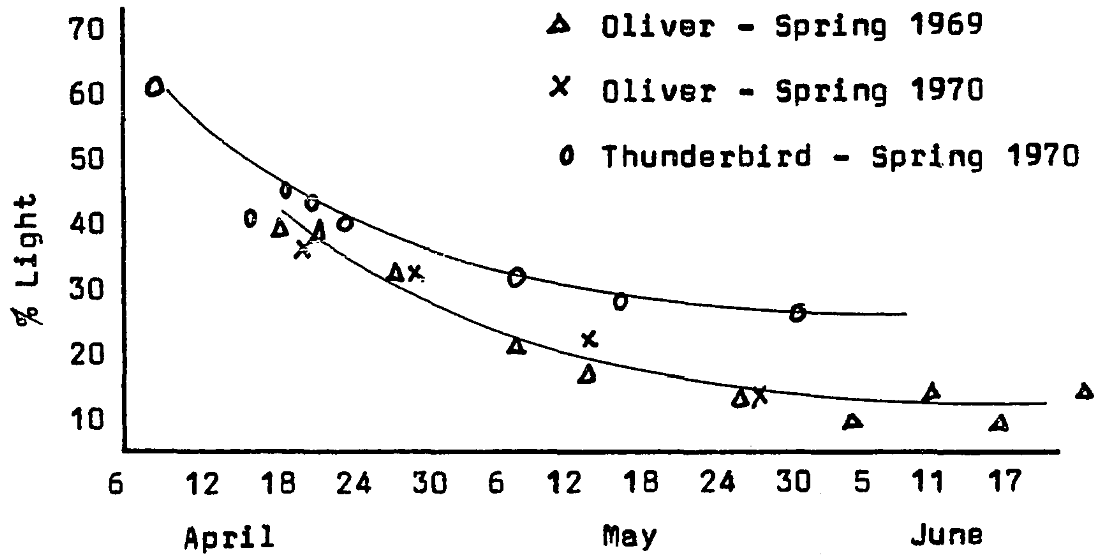
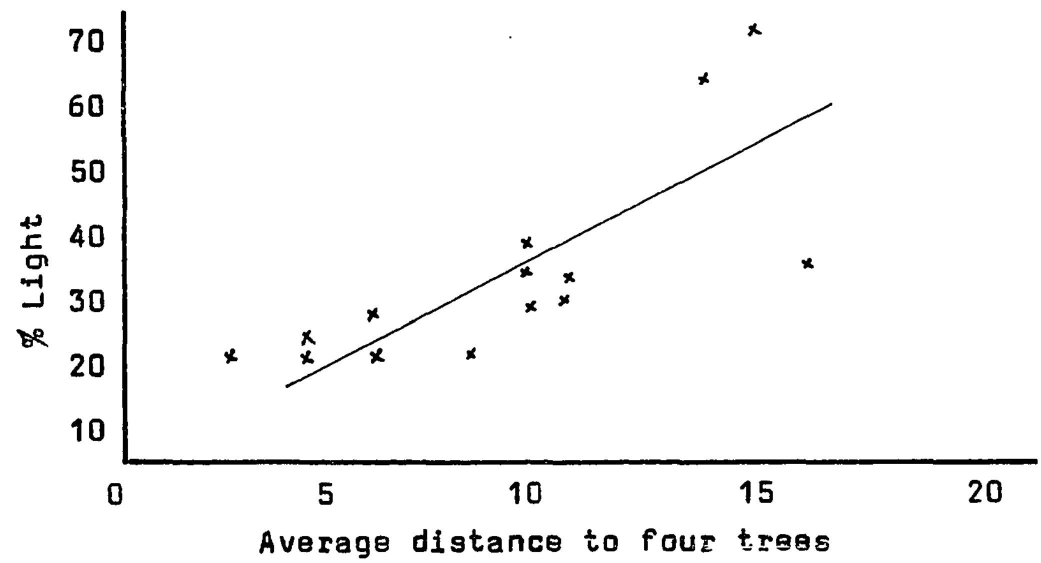


Figure 3. Relation between the average of four distances from a point to the nearest tree in four directional quarters and light energy penetration as percent of unshaded open area in Thunderbird stand after canopy closure.



for one spring. The percent of light interception in the middle of April is about equal for both stands but the canopy in Oliver stand intercepts more light in the following periods. This appears to agree with the values which would be predicted from the illumination data.

The relation of light energy interception by the canopy to the average of four distances from a point to the nearest tree in four directional quarters in Thunderbird stand is given in Figure 3. In general, light energy increases as the distance from the nearest trees increases. By comparison no relation can be seen between light energy interception by the canopy and the average basal area of four trees nearest a point in each of four directional quarters in Thunderbird stand. These data suggest a relation between density, since density can be measured by the distance to nearest trees, and light energy interception by the forest canopy. A greater light interception would be found to follow a greater density. The relation between the percent of illumination values measured in the three stands falling in the lowest illumination value range and density in the same stands, however, does not show a pattern. This lack of correlation would in part be expected since density does not include other factors regulating light in forest stands. According to Marquis (1965), the determinants regulating the pattern of sunlight and shade within forests include the sun's angle of elevation, the shadow length of the trees, and the horizontal angle between the sun and due south. The differences in exposure and angle of slope between stands in this study would change both the sun's elevation, and consequently also the shadow length of the trees. The lack of correlation therefore in this case appears to indicate that these differences are responsible for the differences in light measurements.

Gas exchange measurements of selected plant species.

The mean gross photosynthetic rates of individual species selected for gas analysis measured at 500 fc and the maximum mean gross photosynthetic rate measured at any light intensity with the variance of the replicate measurements are given in Table 5. The measurements represent the mean of the measured values of from 2 - 6 individuals. In the case of Helianthus annuus grown at 200 fc light intensity the values reported for the growth period under 3 weeks are means of 6 individuals measured whereas the values reported for growth over 3 wks are means of the 2 individuals which survived. The values in the growth period over 3 wks therefore represent those remaining in the light regime for this species. A drop in the variance value occurs between these two growth periods which may demonstrate selection for one type gas exchange rate response.

In general, fixation rates tend to increase with increased light intensity of the growth treatment. This appears to indicate that the plants become photosynthe-

Table 5. Mean gross photosynthetic rates measured at 500 fc and the maximum photosynthetic rate measured at any light intensity for various species grown in 3 light regimes for less than and more than 3 wks. Growth light intensities were 200 fc, 2000 fc, and direct sunlight (sun). Photosynthetic rates reported in mg $CO_2/dm^2/hr$. Variance (s^2) reported with each rate.

Species	Growth	Under three weeks		Over three weeks	
		500fc	max.	500fc	max.
Shade habitat species.					
Aster	200fc	2.61	2.61	2.64	2.64
sp.	s^2	0.34	0.34	0.13	0.13
	2000fc	4.51	7.03	7.88	10.25
	s^2	0.05	0.04	0.02	0.15
	sun	6.42	11.49	5.92	12.1
	s^2	4.29	0.91	2.33	5.81
Clitoria	200fc	9.81	12.75	3.11	8.91
mariana	s^2	2.42	22.45	8.82	1.84
	2000fc	7.69	24.2	1.8	5.79
	s^2	1.28	14.58	2.38	3.92
	sun	6.55	13.28	8.14	25.35
	s^2	0.41	35.28	17.41	7.61
Commelina	200fc	4.06	5.45	2.75	4.01
communis	s^2	4.56	0.02	0.25	0.03
	2000fc	7.51	14.77	3.66	4.11
	s^2	2.46	12.05	0.61	1.28
	sun	3.47	5.39	3.01	4.10
	s^2	1.50	3.56	0.98	0.42
Galactia	200fc	4.34	5.50	6.47	11.88
volubilis	s^2	1.13	0.88	1.13	2.99
	2000fc	4.44	7.59	5.01	7.65
	s^2	3.65	0.99	0.08	18.64
	sun	5.10	9.59	5.48	13.33
	s^2	0.04	4.51	4.92	12.03
Chasmanthum	200fc	2.84	7.56	6.41	11.85
sessiliflorum	s^2	0.13	0.85	0.50	10.13
	2000fc	2.35	8.51	4.23	7.64
	s^2	0.02	0.03	0.66	0.08
	sun	3.6	8.05	10.84	12.79
	s^2	0.88	0.13	2.22	2.88

Table 5. continued

Species	Growth	Under three weeks		Over three weeks	
		500 fc	max.	500 fc	max.
Shade habitat species continued.					
Viola	200fc	5.55	5.89	5.20	5.90
missouriensis	s^2	15.79	2.33	0.02	0.18
	2000fc	11.89	12.69	3.64	4.06
	s^2	2.14	0.01	0.61	1.35
	sun	6.01	7.28	4.10	6.45
	s^2	1.23	0.32	0.33	2.64
Sun habitat species.					
Andropogon	200fc	5.21	7.95	5.70	6.51
virginicus	s^2	3.92	1.44	2.78	11.55
	2000fc	4.36	16.90	4.85	16.5
	s^2	1.12	8.00	2.21	58.32
	sun	3.81	12.96	3.44	18.15
	s^2	3.38	9.24	12.51	37.84
Cynoglossum	200fc	7.73	9.52	7.55	7.55
amabile	s^2	17.66	14.30	0.99	0.12
	2000fc	3.41	20.45	8.01	8.64
	s^2	0.39	3.65	1.28	0.12
	sun	7.91	27.83	8.16	24.20
	s^2	4.02	3.11	0.25	38.72
Helianthus	200fc	10.20	15.49	4.01	7.36
annuus	s^2	8.06	38.01	0.05	0.04
	2000fc	15.10	17.75	4.00	4.63
	s^2	9.42	79.44	0.26	0.09
	sun	12.65	12.85	5.75	10.06
	s^2	33.33	14.87	0.55	10.8

tically more efficient as the light intensity in which they are grown increases. One exception was Commelina communis in which after 3 wks pretreatment the maximum photosynthetic rate is the same at each pretreatment. That is, reducing the pretreatment light level does not reduce the photosynthetic efficiency. A similar pattern can be seen with Clitoria mariana, Galactia volubilis, and Chasmanthium sessiliflorum for 2 of the 3 light pretreatments. This pattern does not appear in the sun types.

The greatest rates measured for plants grown in sunlight occur in sun types Cynoglossum amabile and Helianthus annuus. Most photosynthetic rates measured at 500 fc are higher for sun than for shade habitat types. This finding seems to disagree with the data reported by Bjorkman and Holmgren (1963, 1966) concerning the higher efficiency of shade types in weak light. It is important, however, to consider that whole plants were used in this study whereas single leaves were used by Bjorkman and Holmgren. This difference, among others, could account for the differences in data. Because all plant leaves of the measured individual participated in the photosynthetic rate measurement, a leaf age factor may possibly account for differences in data. Of the sun habitat forbs used in this study, it was observed that the oldest leaves tended to dry and drop whereas all the leaves of shade habitat types tended to remain green and attached to the plant. It has been reported that the photosynthetic capacity of a leaf peaks during developement and that it declines in some cases even before full leaf expansion (Smillie 1962). Sun habitat plants therefore appear to expose on the average younger and thus more efficient leaves to the sun's light than shade habitat plants. Support for this difference in growth habit is suggested by the data in Table 6 where in 5 of 6 comparisons, the sun types have higher dark respiration rates. An additional interpretation could possibly explain the high photosynthetic rates in reduced light by the sun habitat types. Grime and Jeffrey (1965) suggest that dense grasslands produce shade conditions in the area between the soil surface and the upper level of the herbaceous foliage. It therefore seems that prairie species could demonstrate microhabitat light regime adaptations to low light intensity. Light interception by herbaceous prairie foliage was not measured in this study. The measuring device was positioned about 6 in. above the soil surface and was not effected by herbaceous growth.

Of the highest photosynthetic rates measured for plants grown in sunlight and measured at their maximum photosynthetic rates, the species include the sun types and possibly also the shade types _Clitoria mariana_ and _Chasmanthium sessiliflorum_ (Table 7). Most values for sun plants show higher rates than for shade plants. In 4 of 6 comparisons the shade plants reach a higher percentage of their maximum photosynthetic rates at 500 fc measurement

Table 6. Mean dark respiration rates of sun and shade habitat plants measured after growth periods of less than and more than 3 wks. Pretreatment light regimes were 200 fc, 2000 fc, and direct sunlight (sun). Respiration rates in mg $CO_2/dm^2/hr$.

Mean Values - Under Three Weeks

Shade Plants

	200 fc	2000 fc	sun
$\bar{X}$ =	0.75	3.24	2.10
s^2 =	19.49	3.24	104.06

Sun Plants

	200 fc	2000 fc	sun
$\bar{X}$ =	4.32	3.20	11.4
s^2 =	441.28	248.19	124.24

Mean Values - Over Three Weeks

Shade Plants

	200 fc	2000 fc	sun
$\bar{X}$ =	0.64	2.10	1.51
s^2 =	14.47	3.10	107.91

Sun Plants

	200 fc	2000 fc	sun
$\bar{X}$ =	0.80	2.98	3.91
s^2 =	9.34	131.49	121.06

light intensity than sun plants (Table 7). It would therefore appear that the shade habitat types demonstrate adaptations to lower light. These data, although some species do not completely agree, tend to support the distinctions between sun and shade types reported by Bohning and Burnside (1956) and Bjorkman and Holmgren (1963, 1966).

In general, from the data in Table 7, the percent of the maximum photosynthetic rate increases with an increase in the light intensity at which the habitat types are grown. One exception is the shade habitat types under 3 wks growth in which case those grown under 2000 fc demonstrate the maximum photosynthetic rates, and not those grown under sunlight. It appears that this is an adaptation to the lower light levels in which they occur.

Differences in growth not shown by the gas exchange data concern the success of plants grown in the three light regimes. Most growth for all species was demonstrated in the 2000 fc light regime. The reduction in growth of all species between this light treatment and sunlight was considered due to temperature and transpirational stress. Shade types however did not appear injured by the sunlight regime as suggested by Sparling (1967). This difference could not be explored further without a better understanding of the light regime used by Sparling (1967).

The most dramatic distinction between species grown in the 200 fc pretreatment was shown by a very much

Table 7. Mean gross photosynthetic rates measured at 500 fc and the maximum photosynthetic rate measured at any light intensity after growth periods of less than and more than 3 wks. Growth light intensities were 200 fc, 2000 fc, and direct sunlight (sun). Photosynthetic rates of various species summarized and given in mg $CO_2/dm^2/hr.$, with variance (s^2), and percent of the maximum rate (%) for each type and growth period.

Mean Values - Under Three Weeks

	500			max.		
Shade Plants						
	200fc	2000fc	sun	200fc	2000fc	sun
$\overline{X}$ =	4.86	6.4	5.19	6.62	12.46	9.17
s^2=	95	122	26	142	451	73
% =	39	51	42	53	100	74
Sun Plants						
$\overline{X}$ =	8.39	9.44	9.66	12.17	18.16	19.91
s^2=	109	351	258	267	102	183
% =	42	47	49	61	91	100

Mean Values - Over Three Weeks

	500			max.		
Shade Plants						
$\overline{X}$ =	4.43	4.38	6.37	6.79	6.58	12.34
s^2=	43	46	106	170	68	581
% =	35	35	52	55	53	100
Sun Plants						
$\overline{X}$ =	5.77	5.62	6.05	6.57	9.92	17.47
s^2=	17	22	46	15	205	288
% =	33	32	35	38	57	100

reduced growth of one shade type _Aster sp._ and one sun type _Helianthus annuus_. Of 10 individuals started in each light regime for these 2 species only 2 of each kind survived the 200 fc regime. The surviving individuals were small, fragile, and seemed unlikely to be able to complete their life cycle as the other species seemed able to do. This would be expected of the sun type _Helianthus annuus_. Of the shade types, the poor growth of _Aster sp._ would seem most likely since the light level where it occurs in Thunderbird stand is higher than in the other stands.

Most vigorous growth in the 200 fc light regime was demonstrated by _Commelina communis_. This would be expected considering the light data because Oliver stand where it occurs has the lowest light level of the stands.

Most vigorous growth in the sunlight light regime was shown by _Helianthus annuus_ and also by _Commelina communis_. The response of the former would be expected, but the implications of the success of _C. communis_ are not clear.

In summary, shade species tend to reach the same photosynthetic rates at lower light intensities as at higher light intensity pretreatments. This appears to demonstrate an adaptation to the reduced light in which they occur. Unexpectedly the average photosynthetic rates of sun species is higher when measured at 500 fc than shade types. This appears contrary to what would be expected of shade species, since the reduced light of the shaded habitat would be expected to select for higher photosynthetic rates in reduced light.

CHAPTER IV

CONCLUSIONS

Plant species in Oklahoma forests vary with differences in exposure and location. Exposure within the southeast area accounted for differences in woody and herbaceous species. Greater differences, however, occurred between the Lookout stand and the others, and between the upland and bottomland locations.

The light regime within the stands shows strong correlation to various characteristics of the woody species. Among these factors are the expansion of tree leaves in the forest canopy, basal area of the woody species, and the distance from a point to the nearest woody plant.

Gas exchange characteristics of plants occurring in the stands show characteristics which appear to be adaptations to the regime within the stands. The species occurring in the shade attain the maximum rate of photosynthesis at light intensities below those required for species of open habitats to reach the maximum rate. However, the actual rate of photosynthesis in the species of open habitats was as high or higher in low light intensities as that of shade species.

Growth characteristics generally demonstrated what appeared to be adaptations to the light in which they occur. Most successful were shade types grown in reduced light and sun types grown in higher light. Shade types, however, were more successful when grown in high light than sun types when grown in low light. It appears therefore that shade types are more tolerant to wider ranges of light regimes than sun types.

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