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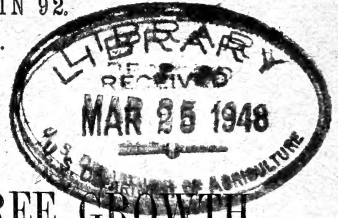
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Issued June 30, 1911.

U. S. DEPARTMENT OF AGRICULTURE,
FOREST SERVICE—BULLETIN 92.

HENRY S. GRAVES, Forester.



LIGHT IN RELATION TO TREE GROWTH.

BY

RAPHAEL ZON,
CHIEF OF SILVICS,

AND

HENRY S. GRAVES,
FORESTER.



WASHINGTON:
GOVERNMENT PRINTING OFFICE
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LETTER OF TRANSMITTAL.

U. S. DEPARTMENT OF AGRICULTURE,
FOREST SERVICE,
March 13, 1911.

SIR: I have the honor to transmit herewith a manuscript entitled "Light in Relation to Tree Growth," the major portion of which is the work of Mr. Raphael Zon, Chief of Silvics, and to recommend its publication as Bulletin 92 of the Forest Service.

Respectfully,

HENRY S. GRAVES, *Forester.*

HON. JAMES WILSON,
Secretary of Agriculture.

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LIGHT IN RELATION TO TREE GROWTH.

INTRODUCTION.

Light is indispensable for the life and growth of trees. In common with other green plants a tree, in order to live, must produce organic substance for the building of new tissues. Certain low forms of vegetable life, such as bacteria and fungi, do not require light. They exist by absorbing organic substance from other living bodies; but the higher forms of plants manufacture their own organic material by extracting carbon from the air. The leaves, through the agency of their chlorophyll, or green coloring matter, absorb from the air carbon dioxide, and give off a nearly equal volume of oxygen. The carbon dioxide is then broken up into its elements and converted into organic substances which are used in building up new tissues.

Light is not only indispensable for photosynthesis, but it is essential for the formation of chlorophyll itself. Only in exceptional cases, as in the embryo of fir, pine, and cedar seeds, does chlorophyll form in the dark, and, with the exception of some microbes, the green cell is the only place where organic material is built up from inorganic substances.

Light also influences transpiration, and consequently the metabolism of green plants. It influences largely the structure, the form, and the color of the leaf, and the form of the stem and the crown of the tree. In the forest it largely determines the height growth of trees, the rate at which stands thin out with age, the progress of natural pruning, the character of the living ground cover, the vigor of young tree growth, the existence of several-storied forests, and many other phenomena upon which the management of forests depends. A thorough understanding, therefore, of the effect of light upon the life of individual trees, and especially on trees in the forest, and a knowledge of the methods by which the extent of this effect can be determined are essential for successful cultural operations in the forest.

The aim of this bulletin is to bring together the principal facts with regard to the part which light plays in the life of the forest, and the different methods of measuring it. It should prove of ma-

terial assistance to students of the subject, and it is hoped that it may also stimulate an interest to further research in determining more accurately the light requirements of our forest trees, especially by actual measurements of light in the forest.

KINDS OF LIGHT.

DIRECT AND DIFFUSED LIGHT.

In discussing light with reference to tree growth a distinction must be made between direct sunlight and diffused light. If the earth were not enveloped by an atmosphere, all light would be direct sunlight, and its intensity at every point on the earth could be calculated mathematically from the position of the sun. The presence of the atmosphere, however, modifies essentially the distribution of light and heat on the earth's surface. Only a part of the light which emanates from the sun reaches the earth as direct sunlight. Another part is reflected from the small particles contained in the air, such as dust and minute drops of water, and forms diffused light. Still another part is absorbed and entirely disappears. The diffused light illumines the atmosphere and forms the skylight. When the sky is cloudless the total daylight consists of both direct and diffused light. On cloudy days all the light is diffused light.

Trees in the forest make use chiefly of the diffused skylight, and for this reason it plays the most important part in their life. Indeed, many plants have developed special contrivances for protecting themselves from the direct rays of the sun. There are, however, trees and other plants which, in addition to diffused light, need direct light either during their entire life or during a definite period of their life, as, for instance, during the period of flowering and leafing. Thus, the opening of the buds in many trees proceeds much faster when the tree is exposed not only to diffused light, but also to the direct rays of the sun. Therefore, in determining the effect of light on vegetative processes it may be essential to know what portion of the entire light affecting the tree is diffused and what is direct.

Both direct sunlight and diffused light decrease with increase in latitude, but not in the same proportion. The intensity of direct sunlight decreases much more rapidly with increase in latitude than does the intensity of diffused or sky light. This is well brought out in Table 1, computed on the basis of measurements taken by Bunsen and Roscoe, which gives the relative chemical intensities of the radiation received directly from the sun and from the sky upon a horizontal surface during a whole day at the spring equinox. It is of considerable interest as showing what kind of light is mostly available for tree growth at various latitudes.

TABLE 1.—*Light intensity of direct sunlight and of diffused light at various latitudes.*¹

Places.	Latitude.	Chemical intensity—		Total.
		Of sun- light.	Of sky- light.	
Pole.....	90	0	20	20
Melville Island.....	75	12	106	118
Reykjavik, Iceland.....	64	60	150	210
St. Petersburg, Russia.....	60	89	164	253
Manchester, England.....	53	145	182	327
Heidelberg, Germany.....	49	182	191	373
Naples, Italy.....	41	266	206	472
Cairo, Egypt.....	30	364	217	581
Bombay, India.....	19	438	223	661
San Jose, Costa Rica.....	10	475	226	701
Quito, Ecuador.....	0	489	227	716

¹ From Handbook of Climatology, by Dr. Julius Hann, p. 116.

Diffused light decreases with increase in altitude; direct sunlight, on the contrary, increases.

OVERHEAD, SIDE, AND REFLECTED LIGHT.

Besides direct and diffused light, light may be distinguished in accordance with the direction from which it comes and the effect it has upon the different parts of the crown. The light which reaches the crowns of trees from above is called overhead light. (Fig. 1, *a*.) This determines the arrangement of leaves on the shoots, their position in relation to the sun, and the arrangement of the branches. It is the strongest light, whether it consists of either direct or diffused light alone or both together. In the case of dominant trees it equals the total daylight.

The light which reaches the crowns of trees from the side is called side light. (Fig. 1, *b*.) It stimulates the development of buds on the lateral branches and is responsible for the development of the branches facing an opening in the forest.

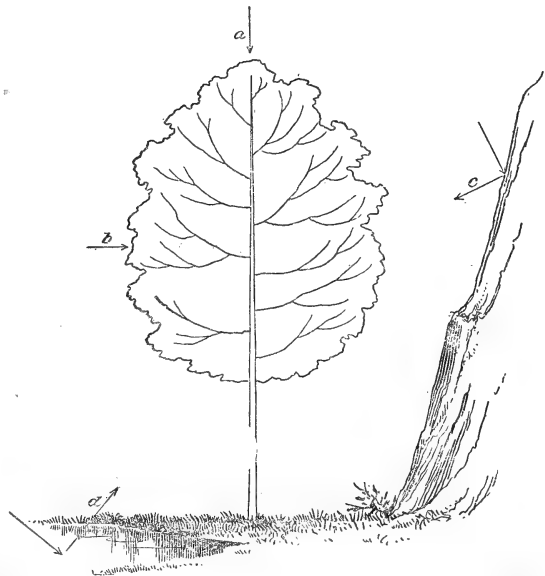


FIG. 1.—Overhead light (*a*); side light (*b*); reflected side light (*c*); reflected ground light, from a water surface (*d*).

In the case of trees growing near a wall or steep slope the tree may receive light which is reflected back upon the tree and is called reflected side light. (Fig. 1, *c*.)

In some cases, especially where trees are growing near bodies of water, their crowns are illumined by light which is reflected from the ground or from the water's surface. (Fig. 1, *d*.) This is called reflected ground light, and is not so insignificant as it may appear at first thought. Thus, actual measurements have shown that, at a height of 1 meter ($3\frac{1}{4}$ feet) the intensity of light reflected from a road illumined by the sun may be $1/12$ of the overhead light intensity; the intensity of light reflected from the water's surface may amount to $1/6$ of the overhead light intensity, measured at a height of about 5 feet from the surface.

The intensity of light varies with the direction from which it comes. Thus, the following results were obtained from measurements made at the end of April, at noon, in Vienna. If the light intensity coming from the north is taken as 1, then the intensity of light from the west is 1.19; from the east, 1.25; from the south, 3.12; while the intensity of the overhead light is 4.50.

LIGHT INTENSITIES AND TREE GROWTH.

Only in exceptional cases do forest trees make use of the total daylight. Isolated individual trees may do so, but, as a rule, the total daylight is considerably weakened by the configuration of the land and by the shade cast by the foliage of the individual tree itself or of neighboring trees. The bulk of forest trees and the interior parts or crowns of even isolated trees depend, therefore, only on a part of the total daylight. Actual measurements of light intensity have shown that on a clear, sunny day the light intensity on the edge of a forest is only about half that of the total daylight, while in the shade of the trees, even when they were still without any foliage, the light intensity was one-fourth that of the total daylight.

MINIMUM INTENSITIES.

The minimum intensity of light in which photosynthesis can take place is not sufficiently determined for all species; it differs in different species with the sensitiveness of the chloroplasts. Trees not only accumulate energy by building up new organic substance, but they also expend energy from the organic substance which they produce. This expenditure of energy is accompanied by oxidation of carbon and exhaling carbon dioxide, or respiration. As long as the light intensity is above the necessary minimum for the given species, the process of assimilating carbon from the air, and thus building up new organic substance, goes on with greater energy than the opposite

process of breaking up organic substance and giving off carbon into the air in the form of carbon dioxide. As the light intensity decreases the assimilation decreases correspondingly, and the amount of carbon assimilated from the air approaches the amount given off by respiration. As soon as the energy of assimilation falls so low that the amount of carbon assimilated is less than that needed for the maintenance of respiration, the leaf dies.

It is possible to gain an idea of the relation between light intensity and the activity of the green cell from the experiments made by Kreusler. He found that a square centimeter of a leaf of European hornbeam (*Carpinus betulus*) on a cloudy day decomposed in one hour 13.7 cubic millimeters of carbon dioxide,¹ or seven times as much as was given off by the leaf in breathing; with a 1,000-candlepower electric light (which has an effect upon assimilation similar to that of sunlight), at a distance of 31 centimeters (12.2 inches), a square centimeter of leaf surface decomposed 28.5 cubic millimeters of carbon dioxide,² an amount 15 times greater (by weight) than that which was given off; by removing the source of light to a distance of from 1 to 1.5 meters (39 to 59 inches), thus making it from one-ninth to one twenty-fifth as intense as before, the amount of carbon dioxide which was absorbed was barely enough to cover the amount given off by respiration.

According to Wiesner (1907), for Norway maple (*Acer platanoides*) the minimum light intensity under which photosynthesis can still take place is $1/55$ of the total daylight, for birch $1/50$, and for beech somewhat less than for birch. The fact that in light intensity of $1/70$ of the total daylight, such as prevails in dense spruce forests, no green vegetation occurs under the shade of the trees indicates that the minimum light intensity at which a green leaf can still function must lie between $1/60$ and $1/70$ of the total daylight intensity.

As far as woody species are concerned, Wiesner (1907) found in the shade of European hornbeam (*Carpinus betulus*), with a light intensity of $1/58$, an undergrowth of the following species still in a fairly good condition: Beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*), field maple (*Acer campestre*), common elm (*Ulmus campestris*), and dogwood (*Cornus sanguinea*). In the same light intensity, however, the undergrowth of elder (*Sambucus nigra*), *Euonymus europæus*, and *E. verrucosus*, was dying.

The minimum light intensity at which green vegetation disappears from under the shade of trees in the forest varies considerably with the climate. Thus, in the Temperate Zone no green vegetation occurs

¹ Equivalent to 1 square inch of leaf surface decomposing 0.0054 cubic inch of carbon dioxide.

² Equivalent to 1 square inch of leaf surface decomposing 0.0112 cubic inch of carbon dioxide.

in the shade where the light is only $1/70$ of the total daylight. In the Tropics the last vestige of green vegetation disappears from under the tree cover when the minimum light intensity falls to $1/120$ of the total daylight.

The minimum intensity of light which is needed for the formation of chlorophyll is much smaller than the minimum required for photosynthesis. Thus, while the green leaves of *Acer platanoides* cease to break up the carbon dioxide of the air and form organic substance in a light whose intensity is $1/55$ of the total daylight, the formation of chlorophyll still takes place in a light which is $1/400$ of the total daylight; in some herbaceous plants, such as peppergrass (*Lepidium sativum*), the formation of chlorophyll still goes on at a light intensity of $1/2,000$, while in light whose intensity is $1/50$ of the total daylight the leaves are just as green as in higher light intensities.

The decomposition of carbon dioxide is produced chiefly by the rays of the red portion of the spectrum, and the leaves in the interior of the crown are able to assimilate, because the largest part of the light which they receive penetrates not through the green leaves, which absorb the red rays, but through the places between the foliage. Chlorophyll may form in light which lacks the rays of the red portion of the spectrum. For this reason light which goes through the green foliage may still be effective in producing the green color of the leaves inside the crown, but is no longer effective in bringing about the process of assimilation of carbon.

MAXIMUM INTENSITIES.

In general the intensity of light varies directly with the height of the sun. The maximum light intensity, however, does not coincide with the intensity at noon, which is always less than the maximum. Thus, from measurements made at Vienna, the ratio of the average noon light intensity to the average maximum light intensity for the year was found to be as 1 : 1.08. This is analogous to the well-known fact that the highest temperature during the day occurs not at noon, but later, and is probably due to the same causes.

The maximum light available for tree growth is, of course, the total daylight. This varies, as has already been pointed out, with latitude, altitude, and the configuration of the earth.

The highest light intensities found by Wiesner (1905) in the United States were in Yellowstone Park. Thus, at Norris, on September 1, 1904, at 1 p. m., with the sun at an altitude of $52^{\circ} 56'$, the chemical intensity of the light was found to be 1.7 in Bunsen-Roscoe units.¹ At Old Faithful, on September 4, 1904, at noon, angle of sun

¹ Bunsen-Roscoe unit of chemical light intensity is the amount of light required to produce a standard color in one second on standardized sensitive paper.

52° 22', the light intensity was 1.9, and an hour later, with the sun forming an angle of 51° 47', 2.083. These measurements were taken on cloudless days. In Europe the highest light intensities measured were 1.5 near Vienna, at an elevation of 550 feet above sea level (Wiesner, 1896), between 1.5 and 1.6 at Kremsmunster at an elevation of 1,268 feet (F. Schwab, 1904), and 1.8 in Steiermark, at an elevation of 4,550 feet (Thomas V. Weinzierl, 1902).

OPTIMUM INTENSITIES.

The optimum light intensity at which different species thrive best has not been fully determined, especially since this optimum varies during the life of the tree, and is subject to variations even in different parts of the same vegetative season. In a general way it may be stated that with the majority of forest trees the optimum light intensity at which the leaves function best and at which the production of flowers and fruits is most abundant lies nearer to the maximum amount of light available for the use of the tree than to the minimum light under which it can still exist. In some species this optimum coincides with the total daylight or with conditions that surround a tree grown in the open; in other species both the vegetative and reproductive functions of the tree are most vigorous when the amount of light is less than the total daylight; that is, when the trees are grown in a stand.

TOLERANCE AND INTOLERANCE OF TREES.

The ability of trees to endure shade is called tolerance of shade, or often merely tolerance. Trees that are capable of enduring shade are tolerant; those requiring full light intolerant. Some species are able to absorb enough light for assimilation even in the shade of a forest canopy. Thus, hemlock and spruce spring up and live for many years under other trees. Other species, such as tamarack, aspen, gray birch, and most of the yellow pines, require full light and can not endure shade from above. All trees, however, thrive in full light, especially if they have it from the very start, and none requires shade except as a protection from drying or from frost. This does not mean, however, that all trees grown in the open absorb equally all the available light. Even in full light they need and use differing amounts of light for their best growth. This is accomplished by a definite orientation of the foliage in relation to the source of light, by the development of denser crowns which lessen the amount of light that can penetrate into the interior, or by a change in the structure of the leaves so as to decrease the assimilative energy. In the open they are able to make these modifications for their best growth to better advantage than in the shade of a dense forest, and

adapt themselves to their needs; therefore, open-grown trees usually appear the more thrifty.

The primary cause of this difference in tolerance must be sought in the anatomical structure and inherent qualities of the leaves and chlorophyll. Since, however, the anatomical structure of the leaves and even the character of the chlorophyll may be influenced by environment, the tolerance of trees is not a fixed quality, but is subject to variation. Each species, however, inherently requires a certain amount of light, which can not be changed by any environment.

LUBIMENKO'S EXPERIMENTS.

The latest experiments by Prof. Lubimenko¹ established with sufficient accuracy the difference in the sensitiveness of the chloroplasts of different tree species. The species with which he experimented were Scotch pine (*Pinus sylvestris*), noble fir (*Abies nobilis*), white birch (*Betula alba*), and linden (*Tilia cordata*). Of these, pine and birch are light-needing species and stand close to each other in this respect. The fir and basswood are classed as tolerant, and are also fairly similar in their demands upon light. Moreover, the anatomical structures of the leaves of pine and fir are very similar, and of birch and basswood practically identical.

These experiments brought out clearly the following points:

(1) The initial light intensity at which assimilation begins varies with the species, since the fir and basswood began assimilation at 1/5 of the light intensity at which pine and birch began to assimilate.

(2) If it be accepted that the light intensity at which assimilation equals respiration is the minimum for the existence of the leaf, then birch appears to be the most light-demanding species, followed by pine, basswood, and finally fir.

(3) With increase in light, the assimilation at first increases in all four species, but in direct sunlight, when the rays strike the surface of the leaves perpendicularly, the pine and birch still continue to show an increase in assimilation, while the fir and basswood show a decrease. This may be seen in Table 2.

TABLE 2.—Relative amounts of carbon dioxide absorbed by 1 gram of leaf during one hour of work.

	Pine.	Fir.	Birch.	Basswood.
Direct rays of the sun striking the surface of the leaf at an acute angle.....	49.74	53.10	68.08	68.71
Direct rays of the sun striking the surface of the leaf perpendicularly.....	56.83	38.50	75.69	43.21

Since the anatomical structures of the leaves of pine and fir are very similar, and of birch and basswood almost identical, this difference in assimilation must be explained exclusively by the difference

¹ Carried on in 1904 at the Laboratoire de Biologie Vegetale, in Fontainebleau, France.

in the sensitiveness of their chloroplasts. These figures show also, in a general way, that a unit (by weight) of leaf substance of broadleaf species assimilates considerably more than the same unit of leaf substance of coniferous species. This is probably due to the difference in the anatomical structure of the leaves of the broadleaf and coniferous species. The extremely small size of the cells of the leaf parenchyma in broadleaf species means the presence of a large amount of living protoplasm and chloroplasts, and consequently a larger amount of living, acting substance within the same space.

On the basis of these experiments, Lubimenko claims to have established the following facts in regard to the photochemical work of different forest trees:

(1) The photochemical work of the green leaf is determined by its anatomical structure and the inherent qualities of its chloroplasts.

(2) The influence of the anatomical structure of the leaf is felt mainly in light of medium intensity; the influence of the inherent qualities of the chloroplasts, on the other hand, is strongly apparent in light of low and high intensities.

(3) Chloroplasts of different species are sensitive to light in different degrees; chloroplasts of shade-enduring species are more sensitive than chloroplasts of light-needing species.

(4) Species with more sensitive chloroplasts begin to decompose carbon dioxide and reach a maximum of assimilative photochemical energy in light of a much lower intensity than species with less sensitive chloroplasts.

(5) The curve of the photochemical work of a green leaf has a distinct optimum, which is reached in different species under different intensities of light and is determined by the inherent qualities of the chloroplasts.

(6) It is very probable that the difference in sensitiveness of chloroplasts of different species is due to a difference in the absorptive capacity of the chlorophyll.

(7) The conception of "light-loving" and "shade-enduring" trees has a real foundation as far as the process of assimilation of carbon is concerned. Leaves of shade-enduring species are able to replace the carbon dioxide expended in the mere process of respiration in much weaker light than are leaves of light-loving species. The optimum of assimilation in tolerant species lies within the limits of normal sunlight, while the optimum of assimilation in light-needing species lies beyond those limits.

GRAFE'S EXPERIMENTS.

These conclusions are also corroborated by Grafe's experiments carried on at the Institute of Plant Physiology, at Vienna (Wiesner, 1907: 266-267), though for another purpose. Green leaves of birch (a light-demanding species) and of beech (shade enduring) were

exposed to light of various intensities and tested for the presence of starch. At a light intensity of $1/6$ of total daylight the leaves of beech showed distinctly the presence of starch, while birch gave a less distinct reaction. At a light intensity of $1/10$ beech still gave a pronounced reaction for starch, while in birch only traces of starch could be detected. At a light intensity of $1/50$ birch leaves showed no presence of starch, while the leaves of beech still continued vigorously to form it. These facts tend to show the same point brought out by Lubimenko, that there is a distinct difference in the sensitiveness of the chloroplasts of beech and birch.

FACTORS INFLUENCING TOLERANCE.

Tolerance varies not only with species, but even within the same species, according to conditions under which the tree is growing. These variations are due largely to changes in the structure of the leaves brought about by changes in transpiration. Among the important factors influencing transpiration, and therefore tolerance, are climate, altitude, moisture and nourishment in the soil, age of tree, and vigor and origin of the individual.

CLIMATE.

Plants need less light the higher the temperature and more light the lower the temperature. Consequently the higher the temperature of a given locality, the more shade a tree can stand. This explains, in part, the frequent differences of opinion regarding the tolerance of the same species when the observations are taken in different regions. For example, white pine in Maine is less tolerant than in the Southern Appalachians. In Vienna the minimum light intensity in which the leaves of Norway maple (*Acer platanoides*) can exist is $1/55$ of the total daylight. In Hamar, Norway, it is $1/37$; in Drottningholm, $1/28$; and in Tromsö, $1/5$.

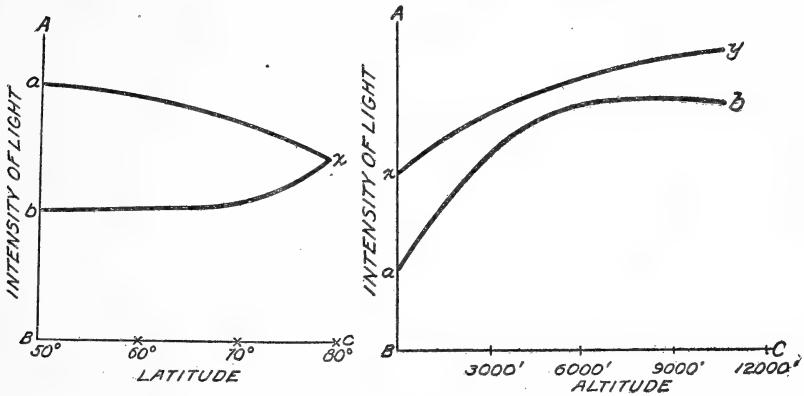
This substitution of light for heat in plant growth, and vice versa, was well demonstrated by Wiesner (1907) with regard to annual meadow grass (*Poa annua*). The minimum light necessary for annual meadow grass at the beginning of March, at Cairo, is equivalent to about 53 calories, while at Vienna it is equivalent to 109. The mean temperatures are 59.9° and 35.6° F., respectively.

ALTITUDE.

The light requirement of a species increases also with increase in altitude, but only to a certain limit, beyond which it remains constant or even decreases. For example, observations by Wiesner showed that lodgepole pine, at an elevation of 6,400 feet, required a

minimum light intensity of $1/6$ of the total daylight; at an elevation of 8,500 feet it sinks to $1/6.4$ and even to $1/6.9^\circ$.

Thus the behavior of trees in their extension toward higher latitudes and higher altitudes is not the same. This is due to the fact that the intensity of both direct and diffused light decreases with the increase in latitude, and the light limit of a species is reached when the intensity of the total daylight becomes equal to the tree's minimum light requirement. With increase in altitude, however, diffused light decreases, but direct sunlight increases. With an increase in the intensity of direct sunlight, even though there be a decrease in the diffused light and a lower temperature, the light requirements of a species remain constant or even become less at higher altitudes.



AB, total light intensity; *BC*, latitude; *ax*, total light intensity; *bx*, minimum light requirement of a species; *x*, point at which total light intensity equals minimum light needed by the species, also limit of latitudinal distribution of the species. (After Wiesner.)

AB, light intensity; *BC*, altitude; *xy*, curve of the total light intensity; *yz*, curve of the light requirements of trees. (After Wiesner.)

FIG. 2.—Variation of light requirements with increase in latitude and altitude.

This difference in the light requirements of trees in the horizontal and vertical distribution is well illustrated by the two diagrams shown in figure 2.

SOIL MOISTURE.

Tolerance of trees is emphatically influenced by moisture conditions in the soil, as well as by its quality. Fricke (1904: 315-325) clearly demonstrated by a series of convincing experiments that deficient moisture in the soil, brought about by competition of the roots of older trees, may cause the death of young growth under the shelter of mother trees. His experiments were made in a Scotch pine stand on poor, dry, sandy soil, on which, according to all authorities, the light requirements are greatest. In a stand from 70 to 100 years old,

with a crown density of 0.7, there were isolated groups of suppressed young pines, among which were no old trees. The young pines were 10 years old and but little over a foot and a half in height. Ditches 10 inches deep were cut around these groups, and in this way all the roots extending from neighboring old trees were cut through to the depth of the ditches. The relative amount of light received by these groups of undergrowth was not affected by the experiment, since not a single tree was cut down or trimmed.

The ditches were made in the spring. In the first summer the needles that appeared on the little pines within the isolated groups had doubled the length of the preceding summer, the terminal shoots became longer, and this thrifty growth continued up to the time the results of the experiments were described (1904), while the same undergrowth outside the areas surrounded by the ditches preserved the same suppressed character. The old trees, whose superficial roots were cut through, apparently did not suffer, and none of them were uprooted by the wind. On the areas inside the ditches a rich flora sprung up during the first summer. Entirely unexpected, there appeared bellflower (*Campanula*), wild strawberry (*Fragaria*), hawkweed (*Hieracium*), sorrel (*Rumex*), ironweed (*Veronica*), willow herb (*Epilobium*), star thistle (*Centaurea*), geranium (*Geranium*), violet (*Viola*), five finger (*Potentilla*), and other herbaceous plants, and in addition there sprung up a number of seedlings of birch and mountain ash. Most interesting and significant of all, however, is the fact that none of these species appeared in the neighboring stand. The herbaceous vegetation which was present on the ground before the experiment, such as sweet vernal grass (*Anthoxanthum*), hair grass (*Aira*), bentgrass (*Agrostis*), and woodrush (*Luzula*), and which had led a very precarious existence, developed luxuriantly, so that the areas surrounded by the ditches bore green, succulent vegetation, in striking contrast to the grayish-brown ground cover of the rest of the stand.

In another pine stand, 100 years old, growing on poor soil, several natural openings on which there were no old trees or young growth of any kind were surrounded by ditches and sown with seeds of Scotch pine, spruce, beech, and red oak without any preparation of the ground. Similar sowings were made on similar natural openings not surrounded by ditches. On the area inside the ditches there are now remarkably well-developed seedlings of pine and oak, although with characteristics peculiar to shaded plants, and also seedlings of beech and spruce. At a distance of some 7 or 10 feet outside of the ditches, although a part of the seeds did come up, the seedlings of pine, beech, and spruce were poorly developed from the start and soon died; the seedlings of oak which still persist have scarcely reached $1/5$ the height attained by those inside the ditches

and will hardly live very long. In this stand also there appeared in the openings surrounded by the ditches a luxuriant herbaceous vegetation strikingly different from that in the surrounding forest.

In order to prove also that deficient soil moisture brought about by the competition of the roots was the sole cause of the death of pine reproduction under the shelter of mother trees, Fricke determined the soil moisture in sample plots of which some were penetrated by living roots, while in others the competition of the living roots was eliminated. In all these experiments the proportion of moisture in the soil was invariably greater in the plats free from living roots—usually two or three times greater, and occasionally four and even six times.

The results of these experiments clearly show that the unsatisfactory condition of an undergrowth shaded laterally or from above is not due altogether to insufficient light, but to competition of the roots of the neighboring old trees; likewise that the presence and condition of shrubs, grasses, and mosses in the forest depends very little upon the amount of light, but are chiefly influenced by the degree of desiccation of the soil caused by the roots of the old trees. Thus the poor development of young growth directly under or near seed trees may be explained, not by shading alone, nor by the mechanical action of water dripping from the leaves and branches of the old trees, nor by excessive light reflected from the trunks, but by the moisture-sapping competition of the roots of the older trees.

In these experiments, however, Fricke, by eliminating competition of the neighboring roots, created artificial conditions which do not exist in nature. Moreover, no photometric measurements of any kind were made during these experiments, and without such measurements the question of light requirements of species can not be settled. While the experiments bring out the importance of considering other factors besides light in the life of the forest, they do not prove that the light requirements of all species is the same.

On fresh soils, with an abundant supply of moisture, root competition affects the growth of the seedlings only a little or not at all, and for this reason it is assumed that trees are more tolerant on fresh or moist soils than on dry soils. But even on the same kind of soil the effect of trees of different species upon the growth of seedlings is not the same. Trees with a strongly developed superficial-root system naturally desiccate the upper layers of the soil much more than trees with a compact, deep-root system.

In filling fail places in plantations, the competition of the roots determines the success or failure of the operation. It happens only too often that the planting of fail places on dry or only moderately fresh soils meets with entire failure, because growth of the new

seedlings is impossible in the dry soil produced by the roots of the older seedlings, which in the porous soils of the planting holes attain extra good development. In dry situations, therefore, fall places must be filled not later than three years after the first planting; otherwise it will be necessary to give up entirely the filling of the blank places, or the older competitors must be removed from small areas and these then replanted.

These facts show that the so-called "light increment," or increase of growth after logging or thinning, is not due alone to the greater access of light to the remaining trees. By thinning a stand not only are the light conditions changed, but the competition of the roots is diminished, which leads to an increase of moisture in the soil. The leaf litter is also more readily decomposed and the soil in this way becomes enriched with nutritive substances, all of which results, of course, in an acceleration of growth after thinning.

SOIL FERTILITY.

Plenty of chemical nourishment in and favorable physical conditions of the soil increases tolerance. At the same light intensity the assimilative energy of the green leaf increases with increase of nourishment in the soil. Thus, the assimilative energy of trees grown in a deficient light but on good soil may be the same as that of trees grown in full light but on poor soil; or, in short, trees on good soils can stand more shade than trees on poor soils. This has been clearly demonstrated by Hartig (1897:142-143), who thought that the weight of the young leaf-bearing shoots may, to some degree, serve as an indication of the amount of foliage in a tree. At the same time, the amount of wood produced in a tree for each pound of small leaf-bearing twigs serves as a criterion of the work of the leaves. Thus, measurements made by him on oaks in the Bavarian Spessart gave the average results shown in Table 3.

TABLE 3.—*Amount of wood produced annually for each pound of small twigs.*

Age (years).	Cubic inches of wood.
33	45.9
90	16.8
246	16.0
400	14.0

These figures show that the leaves of young trees function with greater energy than the leaves of older trees. The same method may be applied to determine the effect of nourishment upon the work of the leaves. It was found that on different soils the annual production of wood in trees of the five different classes (dominant, codomi-

nant, intermediate, oppressed, and suppressed) for each pound of small twigs was as given in Table 4.

TABLE 4.—Amount of wood produced annually by different classes of trees for each pound of small twigs.

Classes.	Good soils.	Poor soils.
	<i>Cu. in.</i>	<i>Cu. in.</i>
Dominant.....	85.7	15.8
Codominant.....	73.2	20.4
Intermediate.....	49.6	16.5
Oppressed.....	32.8	17.3
Suppressed.....	18.5

These figures clearly show the influence of soil conditions upon the assimilative activity of the leaves, and consequently upon the variation in tolerance of trees according to soil fertility.

AGE, VIGOR, AND ORIGIN OF TREE.

Trees are more tolerant in early youth than later in life. In fact, it may be said that during the first year or two all trees are tolerant. As they grow their demands for light increase and the distinctive light requirements of different species become more and more emphasized. This increase in light requirements becomes especially apparent at the time of the most rapid height growth, after which the light requirement remains stationary for a long time and increases again only late in life. White pine is a very good example of a tree which in early youth is tolerant, but in later life is distinctly intolerant. White pine seedlings will start in dense shade; but can not often live under such conditions for more than 10 to 15 years; and may perish from lack of light in the first 2 to 5 years, even if abundant moisture and nourishment are present.

The amount of light needed for flowering and fruiting is greater than for mere growth, so that demands for light vary not only with age, but with season. Thus, early in spring at the time of bursting of buds, the minimum light intensity for larch is $1/2$ of the total daylight, later it falls to $1/5$; for beech the minimum light intensity at the time of unfolding of buds is $1/4$; and later it sinks to $1/60$ of the total daylight. These differences in light demands are well known from common experience. Thus, in a coppice forest it is often necessary, in order to awaken the dormant buds of the stumps, to clear away the brush around them and expose them to higher light intensities. It is a well-known fact that trees in the open begin to bear seed earlier than trees in a close stand. Foresters estimate the average retardation due to close stand at 20 years. The preparatory cuttings for natural reproduction under the shelter-wood

system are based on this principle of allowing more light to the remaining trees in order to stimulate seed production.

In general, the more vigorous the individual, the greater is its tolerance. Any factor which reduces its vitality reduces its tolerance. trees from seed, all other conditions being equal, stand shade much better than sprouts, and in artificial plantations nursery stock is more tolerant than trees which have been started by direct seeding.

MEASURE OF TOLERANCE.

Since tolerance is affected by so many different factors, it is evident that the tolerance of any particular species is necessarily variable and exceedingly difficult to measure. Until recently, therefore, it has been customary not to attempt to measure tolerance of shade in positive, but only in relative terms.

SCALES OF TOLERANCE.

The tolerance of different species is usually compared in lists or scales, the most tolerant being usually placed first and the least tolerant last. The position which a species occupies in relation to these extremes is the expression of its tolerance. Broad and rather indefinite terms have been used, such as "very tolerant," "tolerant," "intermediate," "intolerant," "very intolerant." The following are examples of scales of tolerance prepared by European authorities, beginning with the most tolerant:

GAYER (1898).

Taxus baccata (English yew).
Abies pectinata (silver fir).
Fagus (beech).
Picea (Norway spruce).
Carpinus betulus (European horn-beam).
Pinus strobus (white pine).
Tilia parvifolia=*T. cordata* (small-leaf linden).
Alnus incana (hoary alder).
Acer (maple).
Ulmus montana (wych elm).
Fraxinus excelsior (European ash).
Quercus pedunculata (oak).
Populus tremuloides (aspen).
Pinus sylvestris (Scotch pine).
Betula verrucosa (birch).
Betula pubescens (birch).
Larix europæa (European larch).

BÜHLER (Morozov, vol. 2:1286-1295).

Taxus baccata (English yew).
Abies pectinata (silver fir).
Fagus (beech).
Picea (Norway spruce).
Pinus strobus (white pine).
Ulmus montana (wych elm).
Tilia (linden).
Alnus incana (hoary alder).
Quercus (oak).
Acer platanoides (Norway maple).
Pinus montana (Swiss pine).
Pinus sylvestris (Scotch pine).
Populus (poplar).
Betula (birch).
Larix europæa (larch).

TURSKY (1904:32).

Abies pectinata (silver fir).
Fagus (beech).
Picea (Norway spruce).
Carpinus betulus (European horn-beam).
Ulmus montana (wych elm).
Pinus laricio, var. *austriaca* (Austrian pine).
Alnus glutinosa (black alder).
Fraxinus excelsior (European ash).
Quercus (oak).
Populus (poplar).
Pinus sylvestris (Scotch pine).
Betula (birch).
Larix europæa (larch).

WARMING (1909:18).

Abies pectinata (silver fir).
Fagus (beech).
Carpinus betulus (European horn-beam).
Tilia (basswood).
Picea (Norway spruce).
Pinus montana (Swiss pine).
Acer pseudoplatanus (sycamore maple).
Ulmus effusa (spreading elm).
Quercus (oak).
Fraxinus excelsior (European ash).
Pinus strobus (white pine).
Pinus sylvestris (Scotch pine).
Alnus incana (hoary alder).
Populus tremula (aspens-poplar).
Betula (birch).
Larix europæa (European larch).

The following are scales of tolerance prepared for some of our American trees:

WESTERN SPECIES.

VERY TOLERANT.

Taxus brevifolia (western yew).
Picea engelmanni (Engelmann spruce).
Abies lasiocarpa (alpine fir).
Abies concolor (white fir).
Thuja plicata (western red cedar).
Tsuga heterophylla (western hemlock).
Tsuga mertensiana (mountain hemlock).
Picea sitchensis (Sitka spruce).

INTOLERANT.

Abies magnifica (red fir).
Pinus ponderosa (western yellow pine).
Pinus jeffreyi (Jeffrey pine).
Pinus lambertiana (sugar pine).
Pinus aristata (bristle-cone pine).

TOLERANT.

Chamæcyparis lawsoniana (Port Orford cedar).
Libocedrus decurrens (incense cedar).
Picea parryana (blue spruce).
Sequoia sempervirens (redwood).

VERY INTOLERANT.

Larix tyallii (alpine larch).
Larix occidentalis (western larch).
Pinus albicaulis (white-bark pine).
Pinus attenuata (knobcone pine).
Pinus balfouriana (foxtail pine).
Pinus coulteri (Coulter pine).
Pinus flexilis (limber pine).
Pinus monophylla (single-leaf pine).
Pinus edulis (piñon).
Pinus sabiniana (digger pine).
Pinus contorta (lodgepole pine).

INTERMEDIATE.

- Pseudotsuga taxifolia* (Douglas fir).
Pseudotsuga macrocarpa (bigcone spruce).
Abies amabilis (amabilis fir).
Abies grandis (grand fir).
Abies nobilis (noble fir).
Chamæcyparis nootkatensis (yellow cypress).
Sequoia washingtoniana (bigtree).
Pinus monticola (western white pine).

EASTERN SPECIES.

VERY TOLERANT.

INTOLERANT.

- | | |
|--|--|
| <i>Chamæcyparis thyoides</i> (southern white cedar). | <i>Pinus divaricata</i> (jack pine). |
| <i>Abies balsamea</i> (balsam fir). | <i>Pinus resinosa</i> (red pine). |
| <i>Abies fraseri</i> (Fraser fir). | <i>Oxydendrum arboreum</i> (sourwood). |
| <i>Tsuga canadensis</i> (hemlock). | <i>Liriodendron tulipifera</i> (tulip poplar). |
| | <i>Q. rubra</i> (red oak). |
| | <i>Q. velutina</i> (yellow oak and others). |
| | <i>Betula papyrifera</i> (paper birch). |
| | <i>Liquidambar styraciflua</i> (red gum). |
| | <i>Hicoria alba</i> (mockernut). |
| | <i>Hicoria ovata</i> (shagbark hickory). |
| | <i>Hicoria pecan</i> (pecan). |

TOLERANT.

VERY INTOLERANT.

- | | |
|---|--|
| <i>Picea canadensis</i> (white spruce). | <i>Pinus palustris</i> (longleaf pine). |
| <i>Picea rubens</i> (red spruce). | <i>Pinus echinata</i> (shortleaf pine). |
| <i>Thuja occidentalis</i> (northern white cedar). | <i>Taxodium distichum</i> (bald cypress). |
| <i>Fagus atropunicea</i> (beech). | <i>Larix laricina</i> (tamarack). |
| <i>Acer saccharum</i> (sugar maple). | <i>Robinia pseudacacia</i> (black locust). |
| <i>Acer saccharinum</i> (silver maple). | <i>Salix</i> (willows). |
| <i>Acer rubrum</i> (red maple). | <i>Populus deltoides</i> (cottonwood). |
| <i>Nyssa sylvatica</i> (black gum). | <i>Populus grandidentata</i> (largetooth aspen). |
| <i>Ulmus americana</i> (white elm). | |
| <i>Ulmus racemosa</i> (cork elm). | |
| <i>Tilia americana</i> (basswood). | |
| <i>Platanus occidentalis</i> (sycamore). | |

INTERMEDIATE.

- Pinus taeda* (loblolly pine).
Pinus virginiana (scrub pine).
Pinus rigida (pitch pine).
Pinus strobus (white pine).
Castanea dentata (chestnut).
Quercus alba (white oak).
Betula lenta (river birch).
Betula lutea (yellow birch).
Juglans nigra (black walnut).
Magnolia tripetala (umbrella-tree).
Magnolia acuminata (cucumber-tree).

MOST IMPORTANT SPECIES IN CENTRAL NEW YORK.

[Beginning with the most tolerant.]

<i>Ulmus americana</i> (white elm).	<i>Quercus coccinea</i> (scarlet oak).
<i>Acer rubrum</i> (red maple).	<i>Quercus velutina</i> (yellow oak).
<i>Pinus strobus</i> (white pine).	<i>Castanea dentata</i> (chestnut).
<i>Quercus alba</i> (white oak).	<i>Hicoria</i> (hickories).
<i>Quercus platanoides</i> (swamp white oak).	<i>Quercus prinus</i> (chestnut oak).
<i>Quercus rubra</i> (red oak).	<i>Fraxinus americana</i> (white ash).
	<i>Juniperus virginiana</i> (red cedar).

In actual practice there is seldom any doubt as to the light requirements of the extreme members of the tolerance scale. The doubt comes with species which, under certain conditions of climate and soil, may be classed either as tolerant or intolerant. Instead of dividing species into "very tolerant," "tolerant," "intermediate," "intolerant," and "very intolerant," it would therefore be more simple and practical to divide them into only three groups—"tolerant," "partially tolerant," and "intolerant." This classification does not, however, preclude the possibility of species with extreme requirements becoming, under certain conditions of climate and soil, partially tolerant. Thus, beech and fir, which are ordinarily very tolerant, on very poor soil and in a very cold climate may become only partially tolerant; and, on the other hand, pine and larch, which are ordinarily very intolerant, in most favorable soil and climate may become partially tolerant.

To the group of tolerant trees belong the following genera: *Taxus*, *Fagus*, *Abies*, *Picea*, *Tsuga*, *Pseudotsuga*, *Thuja*, *Æsculus*, evergreen oaks and other evergreen broadleaf trees, and others.

To the group of partially tolerant trees belong *Carpinus*, *Tilia*, *Acer*, *Fraxinus*, *Ulmus*, *Alnus*, the five-needled pines, *Chamæcyparis*, *Libocedrus*, *Sequoia*, white oaks, and others.

To the group of intolerant trees belong the black oaks; the two and three needled pines, such as *Pinus contorta*, *P. jeffreyi*, and others; *Larix*, *Salix*, *Populus*, *Betula*, *Taxodium*, *Magnolia*, *Robinia*, *Liriodendron*, and others.

Of the secondary trees and arborescent shrubs, the evergreen broadleaf shrubs, such as *Buxus*, are classed as tolerant; *Corylus*, *Cornus*, *Ligustrum*, *Euonymus*, *Lonicera*, and others are classed as partially tolerant; *Prunus*, *Spartium*, *Calluna*, *Cratægus*, *Viburnum*, and others as intolerant.

Of forest weeds, *Polytrichum*, *Hypnum*, *Aspidium*, *Vaccinium*, *Hedera*, and others are tolerant; *Anemone* and *Pteris*, partially tolerant; *Circium*, *Silene*, *Fragaria*, and most of the grass and clover species, intolerant.

PRACTICAL VALUE OF THE SCALES.

These scales have their practical use in silviculture, particularly in giving a broad comparison of the different species. If one is seeking a species for underplanting, he naturally concerns himself with the most tolerant. If he is developing a plan for reproduction cuttings, he knows that the least tolerant will require a clear cutting method, and that he can not reestablish new growth under the old cover. Thus, empirical knowledge of light requirements establishes the fact that young growth of a tolerant species under the shade of a fully stocked stand of a tolerant species begins to die off, as a rule, after from 10 to 20 years of suppression; intolerant trees under a tolerant species perish after about 5 years; a tolerant species under an intolerant species may continue to live indefinitely, because the amount of light that penetrates through the thin crowns of the light-demanding species is sufficient for the growth and development of the tolerant species. Reproduction of an intolerant species under the shade of an intolerant species is capable of enduring for from 10 to 20 years, or almost as long as reproduction of tolerant trees under the shade of tolerant species. Since the least amount of light is admitted to the ground in a fully stocked stand in its pole stage, only a tolerant species under the shade of an intolerant species can live through this period without injury.

Tolerance scales based on experience are of distinct value to the practitioner and to the student of forestry first learning the characteristics of the different species. For accurate and scientific investigation, however, they are defective, for they show only that one species is more or less tolerant than another. They do not show how much. What is needed is a mathematical expression for each species based on some definite scale. Thus, for example, that the tolerance of hemlock is 89, of yellow birch 61, of white oak 32, or whatever the actual values might be proved to be.

METHODS OF DETERMINING TOLERANCE.

The tolerance of trees may be determined by observation of their behavior in the forest in light of different intensities; by studying the anatomical structure and the functions of the different organs, especially the assimilative organs of trees grown in light and shade; and finally by measuring instrumentally the light intensities themselves. These methods may be classed respectively as empirical, anatomical or physiological, and physical.

EMPIRICAL METHODS.

The density of crowns of individual trees; the rate of natural pruning of different species in stands of the same density, or the same species in stands of different densities; the number of successive branch orders found on trees of different species; the rate of

natural thinning of stands; the rapidity of growth; the ability of young seedlings to come up under the shade of older trees; and the ratio between the diameter and height of a tree, may all be used as a basis for determining the relative tolerance of different species.

DENSITY OF CROWN.

Density of crown is, without doubt, a fairly good criterion for determining the tolerance of a tree. The denser the crown the less light is received by the leaves hidden within the crown, and consequently the more tolerant is the species, and vice versa, the more open the crown the more intolerant the species. The degree of density or looseness of the crown can not, however, be accurately measured and must always be ocularly estimated. This introduces a subjective element into the observation, and while it is possible to determine with a fair degree of accuracy the extreme members in the scale of tolerance, the intermediate species must always be arranged more or less arbitrarily.

SELF-PRUNING.

The rapidity with which the trunk clears itself of lower branches is a splendid indication of the degree of tolerance. The dying of live branches on the lower portion of the trunk and crown in dense stands is, without any question, due to lack of light, which is not sufficient for the assimilative processes of the leaves. The more intolerant the species and the denser the stand, the more rapid is the pruning. Light-needing species clear themselves of branches even in isolated positions, although of course in a less perfect way than in dense stands. Shade-enduring species, however, lose the lower branches only in dense stands, and in the open the crowns reach almost to the base of the trunk. This criterion of tolerance, however, has the same objection as the previous one; it leaves too much to the subjective impression of the observer. Furthermore, this process of self-pruning is often confused with the mere falling off of the dead branches, which is due not to light, but to mechanical causes.

NUMBER OF BRANCH ORDERS.

Mathematically, a tree or branch should contain as many successive orders of branches as there are years in the life of the tree or branch, minus one. Thus, a 100-year-old oak should have 99 successive orders of branches; as a matter of fact, there are found, as a rule, not more than five or six different orders of branches. In a 50-year-old sycamore there should be 49 branch orders; in reality there are found usually not more than 7. If a branch of a birch formed every year two lateral buds and each bud developed every year into a shoot, a 10-year-old branch would have 19,683 twigs, representing 9 yearly ramifications or orders of branches. As a mat-

ter of fact, on a 10-year branch of birch grown in the open Wiesner (1907) found only 238, and on a branch grown in the shade only 182 lateral branches; and instead of 9 successive orders of branches there were only 5. The reason for many of the buds failing to develop into shoots and the gradual dying of existing shoots must be sought chiefly in the minimum light intensities under which buds and foliage of a given species can develop and exist. This is especially true of the buds, since, as has already been pointed out, the unfolding of buds requires higher light intensities than the mere process of growth. It stands to reason that species capable of withstanding low light intensities will succeed in unfolding a proportionately larger number of buds every year and will preserve during their mature life a larger number of original ramifications than will light-needing species.

Wiesner (1907) prepared the following lists of trees and shrubs, arranged according to the number of branch orders found in them:

COMMON FOREST TREES.

Species.	Maximum number of branch orders.	Species.	Maximum number of branch orders.
Larix (larch).....	3-4	Quercus (oak).....	6
Gingko (gingko).....	4	Robinia (locust).....	7
Gleditsia (honey locust).....	5	Ulmus (elm).....	7
Populus (poplar).....	5	Fraxinus (ash).....	7
Picea (spruce).....	5	Carpinus (hornbeam).....	8
Pinus laricio (Austrian pine).....	5	Fagus (beech).....	8
Betula (birch).....	5	Taxus (yew).....	8

SHRUBS.

Cornus (dogwood).....	4	Philadelphus (mock orange).....	6
Sambucus (elder).....	6	Ligustrum (——).....	7
Viburnum (viburnum).....	6	Syringa (lilac).....	7

In these lists the species having the smallest number of branch orders must be classed as light-needing, and those with the largest number of branch orders as distinctly shade-enduring. The only apparent exception is spruce, which, by this method, would be grouped with the light-needing species. The small number of branch orders found in spruce may not, however, be due entirely to light, since many of the smaller branches of old spruce trees are bitten off by animals, especially squirrels. The interference by animals, insects, and other agencies with the successive branch formations in a tree constitutes a weak point in this method of determining light requirements of species; moreover, the method is, of course, altogether too complicated for practical use.

NATURAL THINNING OF STAND.

The rapidity with which stands thin themselves affords another indication of the light requirements of trees. As soon as the crowns

in a young stand touch each other there begins a struggle for existence among the individual trees, which finally results in the differentiation of the stand into dominant and suppressed trees with all the intermediate stages. The trees which lag behind their neighbors receive less light, their growth is retarded, and they become more and more suppressed, until finally they die and thus gradually reduce the number of individuals in the stand. The rate at which this process takes place depends largely upon the degree of tolerance of the species composing the stand. Natural thinning, however, is a very complex phenomenon which is conditioned by a number of factors. Although light plays an essential part in the process, it has thus far proved impossible to separate fully its influence from that of the other factors concerned.

CONDITION OF REPRODUCTION.

The condition of the young growth under an older stand as an indication of tolerance has the same objections, since the extent to which a species can stand suppression is far from being determined exclusively by its tolerance. This method, however, although entirely empirical in character, has accomplished a great deal of good, and is one of the most prevalent ways of determining the tolerance of trees in this country.

RELATIVE HEIGHT.

The relation between the height and the diameter of a tree varies with the amount of light which it receives. Thus a tree in the open grows more in thickness, while a tree in a dense stand grows more in height. The ratio between the height of a tree and its diameter, obtained by dividing the total height by the diameter at breastheight (expressed in the same unit of length), has been called its relative height, and it has been clearly demonstrated by actual measurements that it depends upon the amount of light received.

On the basis of such measurements, Medevév (1884), a Russian forester, obtained the following maximum and minimum figures of relative heights for isolated and suppressed trees:

	Isolated trees.	Suppressed trees.
Pine.....	24.9	126.0
Spruce.....	39.8	130.0
Beech.....	38.4	157.5

Between these extreme figures are included the relative heights of trees in all the intermediate degrees of illumination. The more shade-enduring a species the lower is the light intensity at which it can grow, and consequently the greater the relative height at which it becomes completely suppressed and dies. It is possible, therefore, by determining the relative height of a given species to determine

also its ability to endure low light intensities; that is, its tolerance. The best way to obtain such figures would be to determine the relative heights of trees which have grown without any influence upon one another, but under a uniform shading of some other stand. Since, however, such conditions were hard to find, Medevév, who was the author of this method, made use of the numerous results of his forest measurement work and of the data obtained in measuring sample areas, especially in the forests of Transcaucasus, where an unusual number of observations were made on spruce (*Picea orientalis*) and on Scotch pine.

He found, on the basis of such measurements, that the relative height of spruce is from 1.762 to 1.338, or on the average 1.500 times greater than that of pine; in other words, that the tolerance of spruce is one and a half times greater than that of pine. In the same way the following figures were obtained for the light relations of other species:

Spruce (<i>Picea</i>) to pine (<i>Pinus</i>)-----	1.500
Pine (<i>Pinus</i>) to birch (<i>Betula</i>)-----	1.333
Beech (<i>Fagus</i>) to spruce (<i>Picea</i>)-----	1.029
Hornbeam (<i>Carpinus</i>) to beech (<i>Fagus</i>)-----	.918
Yew (<i>Taxus</i>) to beech (<i>Fagus</i>)-----	2.816
Fir (<i>Abies</i>) to spruce (<i>Picea</i>)-----	1.125
Basswood (<i>Tilia</i>) to beech (<i>Fagus</i>)-----	.849
Oak (<i>Quercus</i>) to hornbeam (<i>Carpinus</i>)-----	.855
Aspen (<i>Populus</i>) to pine (<i>Pinus</i>)-----	1.199
Ash (<i>Fraxinus</i>) to birch (<i>Betula</i>)-----	1.400

If birch, as the most light-needing species, be taken as a unit, the relative tolerance of the other species would be expressed as follows:

Birch (<i>Betula</i>)-----	1.000	Hornbeam (<i>Carpinus</i>)-----	1.889
Pine (<i>Pinus</i>)-----	1.333	Spruce (<i>Picea</i>)-----	2.000
Ash (<i>Fraxinus</i>)-----	1.400	Beech (<i>Fagus</i>)-----	2.058
Aspen (<i>Populus</i>)-----	1.598	Fir (<i>Abies nordmanniana</i>)-----	2.450
Oak (<i>Quercus</i>)-----	1.645	Yew (<i>Taxus</i>)-----	5.795
Basswood (<i>Tilia</i>)-----	1.747		

Medevév's method, although less subjective than some of the others suggested, is nevertheless not entirely reliable, since it is still an open question whether or not the distribution of growth in a tree depends exclusively, or even chiefly, upon light. Investigations have shown that while the growth in diameter of suppressed trees is from one-third to two-fifths as much as that of dominant trees, their height growth is from two-thirds to three-fourths as much.

According to Hartig (1891: 271-274), the distribution of the increment of a tree is influenced by the density of the stand and whether the tree is dominant, intermediate, or suppressed. In dominant trees the increment is chiefly in the lower part of the trunk; in suppressed trees, in the upper part. Suppressed trees sometimes show

even an entire lack of annual rings at breastheight, and in such cases the relative height of the tree can not be a true indication of its tolerance.

ARTIFICIAL SHADING.

With empirical methods must also be classed the experiments in artificial shading, to determine the relative tolerance of forest trees. The first experiment of this kind was made in 1866 by Kraft (1878, v. 54: 164-167), who planted under the cover of a 50-year-old oak forest (of artificial origin) seedlings of other forest trees, and eight years later, in 1874, measured the heights and diameters of the planted seedlings. On the basis of the results of these experiments and observations on the forest in general, Kraft arranged the species, beginning with the most tolerant, in the following order:

<i>Fagus</i> and <i>Abies</i> (beech and fir).	<i>Betula</i> (birch).
<i>Carpinus</i> (hornbeam).	<i>Pinus strobus</i> (white pine).
<i>Acer</i> (maple).	<i>Larix</i> (larch).
<i>Picea</i> (spruce).	<i>Pinus austriaca</i> (Austrian pine).
<i>Fraxinus</i> (ash).	<i>Pinus sylvestris</i> (Scotch pine).

Another experiment of this kind was made in Russia by Nikolsky (1881) on three rows of pine (intolerant) and spruce (tolerant) for

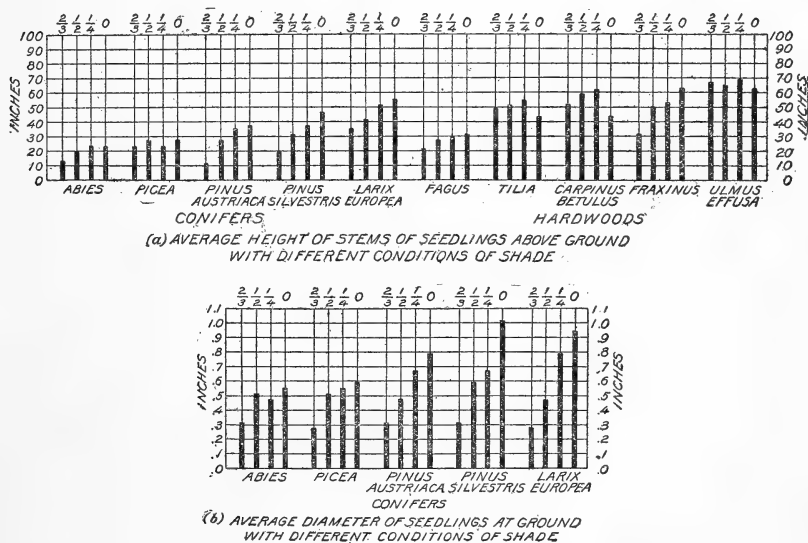


FIG. 3.—Results of experiments with shading seedlings.

the purpose of determining the influence which shade has upon the growth of 1-year-old spruce and pine. In this experiment the greatest length of stem (from the cotyledons to the terminal buds) was found in trees which grew in the shaded row; the length of the entire plant above ground increased with increase in shade; the length of the main root, as well as the number and the total length of the lateral roots, however, diminished with increase in shade, while the

total length of all roots in rows with great light intensity was greater than the total length of all the roots in the shaded rows; in pine seven and a half times and in spruce two times; at the same time the weight of the dry substance of seedlings which grew in full light was greater (in pine five times, in spruce three times) than that of seedlings which grew in heavy shade.

The Swiss experiment station¹ made, in 1893 and 1897 (Badoux, 1898, v. 6: 29-36), experiments on 11 tree species (5 rows of each) with different degrees of shading; rows entirely unshaded, one-fourth, one-half, and two-thirds shaded. In these experiments the least sensitive to shading proved to be spruce and fir, which had almost the same average height growth at different degrees of shading. With pines, larch, beech, and ash the growth in height, on the contrary, decreased in proportion to shading. Finally, with basswood, blue beech, and elm, the growth in diameter decreased in proportion to shading, while the growth in height was but little affected. The results of these experiments are presented in fig. 3, where for each species is given

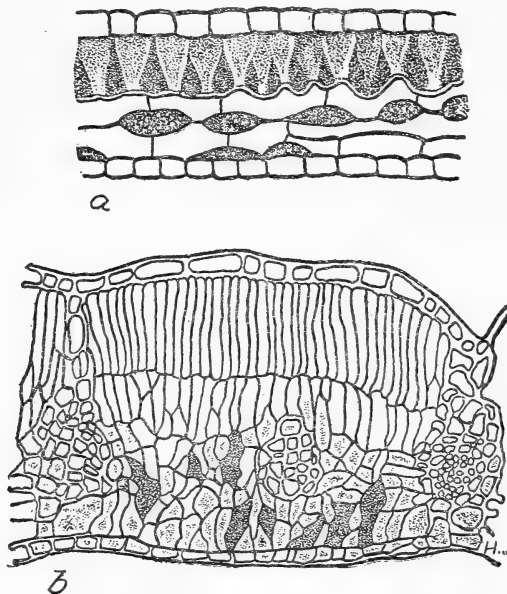


FIG. 4.—Cross section of a beech leaf. *a*, Grown in the shade; *b*, grown in full light.

the average height of the stem above the ground in inches, and for fir, spruce, Austrian pine, Scotch pine, and larch also the average diameter of the stem above ground.

ANATOMICAL AND PHYSIOLOGICAL METHODS.

The cause of the difference in the ability of plants to endure shade must, as already stated, be sought in the leaves, chiefly in their anatomical structure and in the character of the chlorophyll.

STRUCTURE OF LEAVES.

Stahl's (1880 and 1883) experiments have conclusively shown that light exerts a very powerful influence upon the external and internal structure of the leaves. Shade-enduring plants (for instance, *Oxalis*

¹ These experiments seem to show that the development of seedlings of an intolerant species is affected more by variation in light intensity than is that of a tolerant species, and therefore that their behavior in different light intensities may serve as a criterion to determine their tolerance.

acetosella) have their leaves made up almost exclusively of cells of the spongy parenchyma, while the leaves of extremely light-needing plants have hardly any cells of the spongy parenchyma, but are made up also exclusively of palisade parenchyma. Stahl's experiments have also demonstrated that the structure of leaves of the same species varies with different light intensities; in the shade the leaves are made up chiefly of spongy parenchyma; in full light, of palisade tissue. The spongy parenchyma is adapted to weak and the palisade tissue to strong light. The leaves of beech, for instance, in light are characterized by a dark-green color on their upper surface and

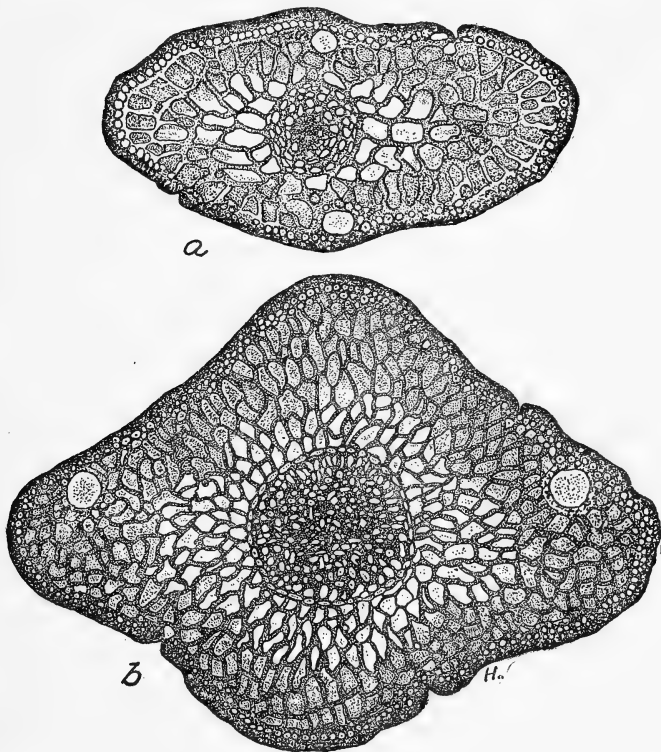


FIG. 5.—Cross section of a spruce needle. *a*, Grown in the shade; *b*, grown in full light.

strongly developed palisade tissue; in the shade they have a light-green surface, and are made up almost exclusively of spongy parenchyma. Leaves in light often have a crumpled surface and are frequently more densely covered with hair than leaves in the shade; the veins of leaves in light are also developed more strongly; and, finally, the thickness of the leaf is closely connected with the structure, a shaded leaf being so thin and limp that it readily rolls itself into a small tube, while the leaf in light has a dense structure. (See figs. 4 and 5.) In Table 5 is given a comparative thickness of leaf tissues.

TABLE 5.—Comparative thickness of leaf tissues in micromillimeters.

Species.	Thickness.					
	Epidermis.		Palisade parenchyma.		Spongy parenchyma.	
	Shaded leaves.	Illumined leaves.	Shaded leaves.	Illumined leaves.	Shaded leaves.	Illumined leaves.
<i>Sambucus racemosa</i> (elder).....	10	20	0	75	39	60
<i>Tilia europæa</i> ¹ (linden).....	10	20	0	38	24	44
<i>Sorbus aucuparia</i> (mountain ash).....	18	23	15	62	40	44
<i>Populus tremula</i> (aspen).....	20	24	50	96	44	58
<i>Betula verrucosa</i> (birch).....	17	22	45	80	45	52

¹ Refers to one of the following European lindens: *T. platyphyllos*, *T. vulgaris*, *T. cordata*.

Some shade-enduring plants, as *Oxalis*, for instance, when exposed to strong light become sickly, since they are unable to modify the mesophyllum of the leaves. The other extreme is shown by light-loving species, such as *Peucedanum*, which are unable to endure shade.

Trees occupy an intermediate position between these two extremes. They are capable of adapting themselves more or less, especially those species whose life tissues may be either chiefly in the form of a spongy parenchyma or chiefly in the form of a palisade parenchyma, in accordance with the light intensity. The stronger the parenchyma tissues developed, the more intolerant is the species, and vice versa. Therefore, by the thickness of the parenchyma of shaded leaves, especially of the palisade parenchyma, it is possible to determine the comparative adaptability of species to shading. Suroj (1891), on the basis of his experiments along this line, has arranged the different tree species in order of their tolerance (beginning with the most tolerant) as follows:

<i>Taxus baccata</i> (European yew).	<i>Alnus incana</i> (hoary alder).
<i>Abies pectinata</i> (silver fir).	<i>Quercus robur pedunculata</i> (pedunculate oak).
<i>Tilia</i> (linden).	<i>Fraxinus excelsior</i> (European ash).
<i>Picea</i> (spruce).	<i>Pinus strobus</i> (white pine).
<i>Sorbus aucuparia</i> (mountain ash).	<i>Betula verrucosa</i> (birch).
<i>Acer</i> (maple).	<i>Populus tremula</i> (aspen-poplar).
<i>Alnus glutinosa</i> (black alder).	<i>Pinus silvestris</i> (Scotch pine).
<i>Ulmus effusa</i> (spreading elm).	<i>Larix europæa</i> (European larch).

ASSIMILATIVE CAPACITY OF LEAF.

The assimilative capacity of the leaves furnishes another good basis for determining the comparative tolerance of different trees. It has already been brought out that there is a difference in the assimilative energy of light-needing and shade-enduring species as influenced by light, which is due to the inherent difference in the sensitiveness of the chloroplasts of the two groups of trees. The leaves of some species (shade enduring) apparently do not possess a great assimilative activity only in intense light. Assimilation means, in every species (light needing) are capable of developing the greatest assimi-

lative activity only in intense light. Assimilation means, in every case, growth, and therefore it is natural to expect a similar difference in the capacity of growth of shade-enduring and light-needing species. It is known experimentally that if light-needing and shade-enduring species are raised in full light, the most rapid growth of the young seedlings will be found among the light-needing species, but if the two kinds of seedlings are raised under shade, the result will be the reverse. It is known further that in older trees also there is a direct relationship between the capacity for height growth and the tolerance of the species; the more light needing the species the more rapid is its growth. Otherwise a slow-growing but light-needing species would not be able to compete with other more tolerant species. Comparison between species, arranged in order of their tolerance and rapidity of growth, brings out clearly this relationship:

Tolerance and rate of growth.

ACCORDING TO GAYER (1898).

Tolerance. (Most intolerant first.)	Rapidity of growth. (Most rapid growing first.)
<i>Larix europæa</i> (European larch).	<i>Larix europæa</i> (European larch).
<i>Pinus sylvestris</i> (Scotch pine).	<i>Pinus sylvestris</i> (Scotch pine).
<i>Picea</i> (spruce).	<i>Picea</i> (spruce).
<i>Abies pectinata</i> (silver fir).	<i>Abies pectinata</i> (silver fir).
<i>Betula</i> (birch).	<i>Betula</i> (birch).
<i>Populus tremula</i> (aspen-poplar).	<i>Populus tremula</i> (aspen-poplar).
<i>Fraxinus excelsior</i> (European ash).	<i>Alnus incana</i> (hoary alder).
<i>Quercus</i> (oak).	<i>Acer</i> (maple).
<i>Alnus incana</i> (hoary alder).	<i>Fraxinus excelsior</i> (European ash).
<i>Ulmus effusa</i> (elm).	<i>Tilia</i> (linden).
<i>Tilia</i> (linden).	<i>Ulmus effusa</i> (spreading elm).
<i>Acer</i> (maple).	<i>Quercus</i> (oak).
<i>Carpinus betulus</i> (European horn-beam).	<i>Carpinus betulus</i> (European horn-beam).
<i>Fagus</i> (beech).	<i>Fagus</i> (beech).

ACCORDING TO HEYER (1893).

Tolerance. (Most tolerant first.)	Rapidity of growth. (Most rapid growing first.)
<i>Larix europæa</i> (European larch).	<i>Larix europæa</i> (European larch).
<i>Pinus sylvestris</i> (Scotch pine).	<i>Pinus sylvestris</i> (Scotch pine).
<i>Picea</i> (spruce).	<i>Picea</i> (spruce).
<i>Abies</i> (fir).	<i>Abies</i> (fir).
<i>Populus tremula</i> (aspen-poplar).	<i>Populus tremula</i> (aspen-poplar).
<i>Betula</i> (birch).	<i>Betula</i> (birch).
<i>Alnus incana</i> (hoary alder).	<i>Alnus incana</i> (hoary alder).
<i>Acer</i> (maple).	<i>Acer</i> (maple).
<i>Ulmus effusa</i> (spreading elm).	<i>Ulmus effusa</i> (spreading elm).
<i>Acer pseudoplatanus</i> (sycamore maple).	<i>Acer pseudoplatanus</i> (sycamore maple).
<i>Quercus</i> (oak).	<i>Tilia</i> (linden).
<i>Carpinus betulus</i> (European horn-beam).	<i>Quercus</i> (oak).
<i>Tilia</i> (linden).	<i>Carpinus betulus</i> (European horn-beam).
<i>Fagus</i> (beech).	<i>Fagus</i> (beech).

Müller (1877) attempted to determine the comparative light requirements of different species by arranging leaves of the same species in layers, one above the other, until no light could penetrate through them. This he accomplished by placing the leaves over a small aperture in a perfectly dark room and by causing the sun rays to penetrate into this dark room through the aperture perpendicularly to the surface of the leaves. Light was entirely prevented from entering the dark room by a thickness of 10 leaves of ash, 11 of elm and basswood, 13 of alder and oak, 15 of aspen and maple, 17 of blue beech, and 20 of beech. These figures are indicative of the shade which each species can endure, and may therefore serve as a criterion of their tolerance.

PHYSICAL METHODS.¹

A more direct way of determining the light requirements of forest trees is to measure with instruments the light itself, just as weight is measured by means of scales, temperature by means of thermometers, air pressure by means of barometers, and air humidity by means of psychrometers.

Sunlight is not homogenous, but is composed of rays of many different wave lengths. The white sun ray in passing through a prism reveals seven different colors, known as the solar spectrum, and these in turn are made up of an infinite number of color gradations. The different rays composing the solar spectrum produce different effects upon matter. Thus, the rays which produce by their action upon the retina the sensation of vision are luminous rays and are found chiefly in the yellow portion of the spectrum, decreasing toward the red and the violet. The rays producing the heating effect are calorific rays and are centered in the red portion. They are very low in the ultraviolet and high in the infra-red. The rays which affect photographic paper or other light-sensitive substances are actinic or chemical rays. They are usually greatest in the violet or ultraviolet portion of the spectrum. In measuring light, therefore, it is possible to measure either the luminous effect or the heating effect or the chemical effect.

Plant life is differently affected by different rays of the solar spectrum. In order to determine accurately, therefore, the effect of light upon tree life, not merely the luminous effect or the chemical effect, but the effect of each separate ray of the spectrum should be measured. Unfortunately, up to the present time no accurate and practical instrument has been invented by which the effect of the different rays of the spectrum can be measured. The methods of

¹ This discussion is based largely on a detailed description of the physical methods prepared by G. A. Pearson, in charge of the Coconino Forest Experiment Station, Forest Service.

measuring light in the forest so far have been based to some extent on the measurement of its luminous intensity, but principally on the measurement of its chemical intensity.

MEASUREMENT OF LUMINOUS LIGHT INTENSITY.

In physics the usual method of determining the intensity of a luminous source is to compare it with a light of known intensity. For this purpose there have been adopted a number of lights which are used as the standard of comparison; among these may be mentioned the "standard candle," the Hefner-Alteneck lamp, and the Vernon Harcourt lamp. The use of such standards in field work, however, has been found very inconvenient and impracticable, and a number of attempts have been made to devise an instrument by which the luminous intensity of light could be measured without the use of the standard light. None of these attempts has, however, resulted in a generally adopted instrument. The best-known instruments for this purpose are the smoked-glass photometer and the polarization photometer, for which the inventor Wagner (1907), claims great simplicity and accuracy. Nobody, however, except the inventor himself has used these instruments for field work, and no definite results of any permanent value have been obtained with them.

The principle upon which these two instruments are based is that of measuring the amount of light which is intercepted, in one case by a graduated, sliding, smoked glass of uneven thickness (wedge shaped), and in the other case by two Nichol's prisms whose planes of vibration form various angles with each other. If the amount of light intercepted by the thinner and thicker portions of the wedge-shaped smoked glass, or by the two prisms at various angles of their planes of vibration, is known, then the intensity of light in the open and in the forest may be determined. Thus, if the observer looks through the tube of the smoked glass photometer in the open and obtains complete absorption of light by the smoked glass at a point at which its light absorption is equal to 25 units, while in the forest complete darkness is obtained at a point at which its absorption of light is equal to 20 units, then the light intensity in the forest is to that in the open as 20 is to 25, or, expressed in per cent, the light in the forest is 80 per cent of that in the open.

In the case of the polarization photometer, the amount of light absorption in the open and in the forest is measured not by a smoked glass of uneven thickness but by the angle between the planes of vibration of the two Nichol's prisms.

These two photometers are very simple, but they are not free from error, since with both the accuracy of the measurements depends

chiefly on the ability of the observer to determine the point at which total darkness begins. The chance for subjective error, owing to the variability of the human eye, is therefore very great.

MEASUREMENT OF CHEMICAL LIGHT INTENSITY.

Of all the physical methods of measuring light, the measurements of its chemical intensity have proved most satisfactory, and have contributed in a large measure to a better understanding of climate (Bunsen and Roscoe, 1862) and of the effect of light upon plant life.

USE OF PHOTOGRAPHIC PAPER.

The Austrian botanist, Prof. Julius Wiesner, was really the first who employed in a practical and thoroughly scientific manner the action of light upon silver chloride paper (photographic paper) for determining the light requirements of plants. Before Wiesner, Theodore Hartig attempted to determine quantitatively the light requirements of forest trees by means of photographic paper, but he did not succeed in developing a thoroughly satisfactory instrument. Use of photographic paper for measuring light intensities was first made by Bunsen and Roscoe for climatological investigations, but Wiesner was the first to adapt this method to studies of plant life.

The measurement of the chemical intensity of light is based on the well-known law formulated by Bunsen and Roscoe that products of light intensity and time of exposure correspond to darkenings of silver chloride paper of like sensitiveness. In other words, if two exposures produce the same tints on the same kind of paper in different lengths of time, the light intensities are inversely proportional to the corresponding periods of exposure. Thus, if a certain shade is reached in light I by an exposure of t seconds, and the same shade is reached in light I_1 by an exposure of t_1 seconds, then $I:I_1=t_1:t$, or $It=It_1$. By varying, therefore, the time of exposure, it is possible to obtain identical shades at very different light intensities.

"NORMAL SHADE" AND "NORMAL PAPER."

In order to have a uniform and constant unit of measure of the light intensity a standard or "normal shade" and a standard or "normal paper" has been adopted. The "normal shade" adopted by Bunsen and Roscoe is prepared as follows: One thousand parts of chemically pure white zinc oxide are mixed with one part pure lampblack heated to incandescence in the absence of air. The mixture is pulverized to a fine grayish powder. This powder is then spread, with the aid of a gelatinous solution, in an even coat on a piece of white paper or pasteboard, and produces a constant, uniform, and somewhat grayish color. This color is the "normal shade" to which all other shades are compared.

The "normal paper" is prepared in a very simple way. Ordinary paper used for photographic purposes is soaked in a 3 per cent solution of common salt, and then hung up to dry. After the paper has become thoroughly dry it is immersed for two minutes, in the absence of chemically active rays, in a 12 per cent solution of silver nitrate. After this the paper is dried in a dark place.

The light intensity which produces in one second on such "normal paper" a shade equal to the "normal shade" is the Bunsen-Roscoe unit of measure of the chemical light intensity. Thus, if the color of the "normal shade" is reached in 1, 2, 3, 4 n seconds, the corresponding light intensities are $1/1$, $1/2$, $1/3$, $1/4$ $1/n$.

WIESNER'S INSOLATOR.

The measurement of the chemical light intensity is carried on by means of a very simple device called an insulator (see fig. 6) and a stop watch. The insulator devised by Wiesner consists of a piece of soft wood 3 to 4 inches long, $2\frac{1}{2}$ to 3 inches wide, and about one-fourth of an inch thick, covered, with the exception of a narrow slit at one end (S), with black opaque paper. The strip of "normal paper" (N. P.) is pushed in beneath the black paper, and the standard ("normal shade") is placed in the slit beside the "normal paper." When a reading is to be made the insulator is held in a horizontal position. The photographic "normal paper" is drawn out until a section of it is brought into the open slit, thus exposing it to light. At the same moment that the "normal paper" is exposed to the light the time is taken. As soon as the "normal paper" assumes a shade identical with the "normal shade" the watch is stopped and the time of exposure is recorded. The light intensity is determined by dividing the light value of the standard by the time which has elapsed from the beginning to the end of the exposure. Thus, if at a given light intensity eight seconds are required to produce the "normal shade" on the "normal paper," then the intensity $I=1:8=0.125$, Bunsen-Roscoe units.

As long as low light intensities are measured, the "normal shade" is sufficient; as soon, however, as high light intensities are to be measured, in which the "normal shade" is assumed in fractions of a second, and therefore the time of exposure can not be accurately recorded, standards of different light values greater than that of the "normal shade" become necessary. Such standards are readily obtained simply by a comparison with the "normal shade." Thus, if it is desired to obtain a standard 10 times greater than the "normal shade," a strip of "normal paper" is exposed in the insulator 10 times the number of seconds required to reach the tint of the "normal shade." Since such standards to be of any value must remain un-

changed when exposed to the light, the shades obtained by different exposures of the "normal paper" are reproduced in permanent water colors. The different standards are then placed in the insulator beside the "normal paper" for facilitating comparison. (See fig. 6, *N. S.* 10.)

In field work, instead of the "normal paper," ordinary photographic paper, especially Rodamin-B paper, invented by A. Andersen, of Berlin, may be used. The chief drawback to the use of the "normal paper" is its poor keeping quality. It can be kept at most only 24 hours, and therefore a fresh supply must be made every day. Any commercial silver chloride or silver bromide photographic papers may be used, provided they are of a uniform known sensitiveness with reference to the "normal paper."

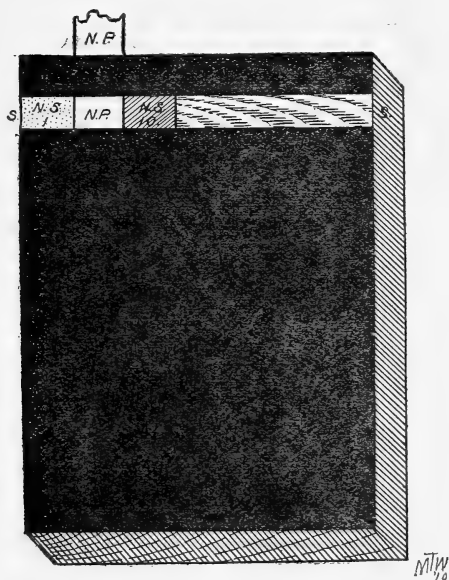


FIG. 6.—Wiesner's insulator. *S*, Slit in the black paper; *N. P.*, "normal paper"; *N. S.* 1, "normal shade" (1 unit); *N. S.* 10, a shade equal to 10 units of "normal shade."

CLEMENTS' PHOTOMETER.

Prof. F. E. Clements (1905: 38-63), in his studies of the influence of light upon vegetation, has used a photometer of his own invention which in many ways is simpler than Wiesner's insulator. Like Wiesner's photometer, it is also based on the blackening of silver salts in the light. The construction of the instrument is shown in fig. 7. It is made in two cases, outer *A* and inner *B*, which fit closely together, forming a tight metal case. A strip of sensitive paper is fastened upon the shoulder of *B*, which fits into the outer case *A*.

The two parts are held together by means of a central screw *C*. In the outer case is a hole one-fourth of an inch square, which is opened and closed by means of a slide *S* working between two flanges (*f*). By turning the inner case *B* the strip of paper is made to revolve past the opening. The outer face of *B* is graduated into 25 equal parts, which are numbered consecutively in such a manner that the number opposite the opening will always indicate the number of the exposure. On the edge of the shoulder bearing the strip of paper are 25 holes, which are engaged by a spring catch as the case *B* is turned, thus allowing only one twenty-fifth of a revolution to be

made at a time. The photometer is made of aluminum; it weighs but a few ounces and may be conveniently carried in the pocket.

The sensitive paper is a commercial printing paper sold on the market as "solio." The photographic paper, the most convenient size of which to use in the photometer is the 8 by 10 inch sheet, is cut into strips one-quarter of an inch wide. The strip is placed in position on the shoulder of the photometer so that the two ends meet

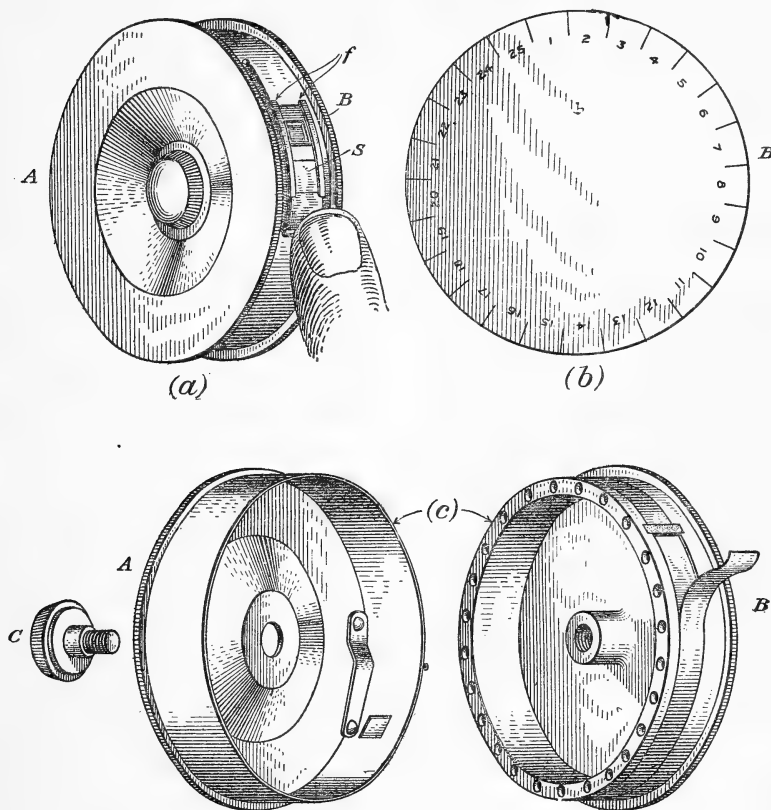


FIG. 7.—Clements' photometer. *a*, Perspective view of the photometer in use; *b*, rear view of the inner case; *c*, perspective view, showing the inside construction.

at *E*, care being exercised that the strip fits into the groove all around. The strip is then drawn tight and the ends are wedged into the slit with a piece of cork.

In this way Clements dispensed with the "normal paper" of Wiesner. He has also done away with the "normal shade," substituting for it what he calls a "multiple standard." This "multiple standard" consists of a strip of paper exposed for 1, 2, 3, 4, and 5 seconds successively, thus producing a series of shades. For the unit

of measure is taken the shade made by an exposure of one second at meridian at a given day and place when the sun is not obscured by clouds.

Since the standard is not "fixed," it should therefore always be kept in a dark, cool place. The exposures are made by quickly drawing back the slide, thus exposing a section of the sensitive paper. The paper is usually exposed until a medium shade is obtained, because very light or very dark shades are difficult to match with the standard. After each exposure the disk *B* is turned to the next number. When the entire strip has been exposed, it is removed, labeled, and placed in an envelope or light-proof box, where it is kept until it is compared with the standard.

At the end of the day's field work the exposed strips are compared with the standards, in the absence of chemically active rays. The standard is laid upon the table and fastened at each end with pins to prevent curling. The exposure to be compared is passed along the standard until the shade is found with which it matches. The relative light intensity is then found from the time ratio between the particular shade in the standard and the exposure with which it matches. Thus, if the tint has been obtained by an exposure of 60 seconds in the forest, while the shade of the standard which it matches has been obtained by an exposure of only 3 seconds in the open, then the light intensity in the forest is $3/60$, or $1/20$, or 0.05 of that of meridional sunlight in the open. The difficulty with Clements' method, even more than Wiesner's, lies in matching the tints obtained in the forest with those of the standard; yet with some practice fairly accurate results are obtained by means of Clements' photometer.

ABSOLUTE AND RELATIVE LIGHT INTENSITY.

Since plants seldom make use of the total daylight but only of a portion of it, it is of greater practical value to know how much of the total daylight a given species actually requires for its growth than simply to know the light intensity in the crown expressed in absolute figures without relation to the light intensity in the open. The ratio between the light intensity which a given plant actually enjoys and the light intensity in the open is the "relative" light intensity. The light intensity in the open, expressed in Bunsen-Roscoe units, is the "absolute" light intensity. Thus, if the light in the open has a chemical intensity equal to 0.80, Bunsen-Roscoe units, while at the same time the light intensity in a tree crown is only 0.20, then the relative light intensity, or the amount of light the tree actually receives, is $20/80$, or one-fourth of the total daylight.

METHOD OF MAKING MEASUREMENTS.

Measurements of light should be made on perfectly clear days, since cloudy, smoky, and hazy skies reduce the light intensity and are apt to lead to errors. For the same reason no measurements should be made when the sun is at the horizon or low altitude, for the composition of the solar spectrum at that time differs considerably from that when the sun is at a high altitude. Absolute light intensity is also influenced by the altitude above sea level. Its influence, however, is noticeably felt only when the difference in elevation is 3,000 feet or more.

The measurement of the relative light intensity enjoyed by forest trees presents considerable difficulties because the different parts of the crown are differently illumined. It is not enough, therefore, in measuring the relative light intensity to measure only the light on the periphery of the crown, but rather the minimum light intensity at which green leaves still continue to live or assimilate carbon from the air. This minimum light intensity is of the greatest importance in forestry, since it indicates the limit of light beyond which a given species can not exist, and consequently serves as a basis for classifying species as tolerant and intolerant. The maximum light intensity under which forest trees grow best does not differ as much with different species as does the minimum light intensity which is characteristic of each species and which must be taken into account in carrying on cultural operations in the forest.

It is evident that in attempting to measure the maximum and minimum light intensities which are enjoyed by different species we are necessarily dealing with a variable quantity. Not only does the light vary with the altitude of the sun, but the light intensity within the crown varies with the density of the crown and the arrangement of the foliage.

There are two possible ways of measuring the amount of light which is received by a given tree. One way is to obtain a summation of the light intensities for the vegetative period. Another way, much simpler and yet probably as serviceable for the comparison of different species, is to make a series of measurements during the day at points within the crown where the foliage just continues to exist. An average of these measurements gives the average minimum light intensity for that species. The measurements should be taken every hour, so as to include the periods of greatest and least illumination of the interior of the crown.

These periods vary considerably with different species. Thus, thinly foliaged trees have a light intensity in the interior of the crown in direct proportion to the intensity of the daylight, and the relative minimum light intensity remains about constant through-

out the day. In densely foliated trees in which the foliage has a more or less horizontal position, as a rule the light intensity in the interior of the crown at noon, or when the sun is at its highest altitude, is greatly reduced, since the position of the leaves prevents to a large extent the entrance of the vertical rays. In such trees the greatest light intensity within the interior of the crown occurs in the forenoon and in the afternoon when the sun is in the east and west—that is, when the light penetrates into the interior of the crown, not from above, but from the side. The light intensity at noon, therefore, lies between two maxima, which occur in the forenoon and the afternoon. In thinly foliated trees of species, such as locust, whose

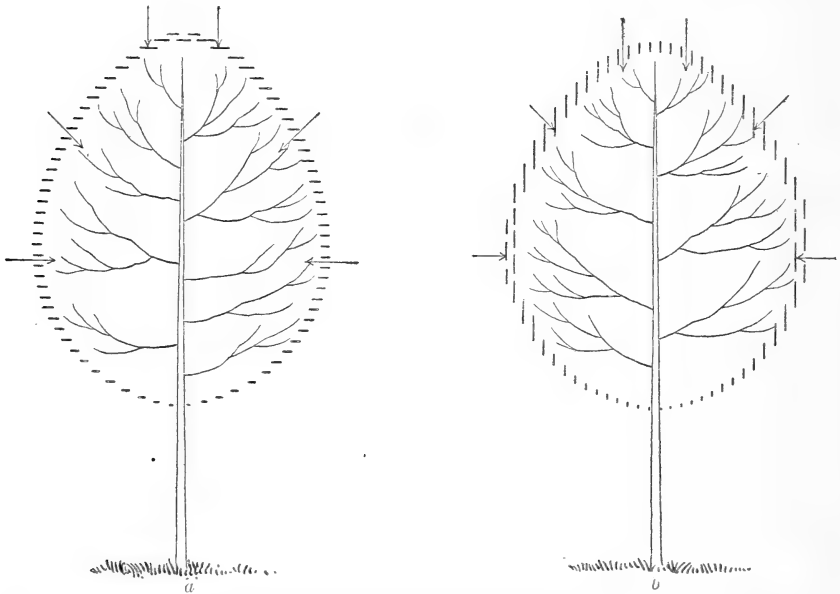


FIG. 8.—Maximum and minimum light intensities within crowns of trees with different arrangement of foliage. *a*, Tree with horizontal arrangement of foliage, in which noon light intensity lies between two maxima; *b*, tree with vertical foliage in which the maximum illumination of the crown occurs at noon.

leaves avoid the midday light by assuming a profile position, a maximum intensity may be attained at noon. In trees of the same species which have a dense foliage, however, only the uppermost leaves assume a profile position at noon, and the relative light intensity within the interior of the crown, therefore, remains more or less constant during the day. (See fig. 8.) This difference in the occurrence of maximum and minimum light intensities within the tree crowns during the day is clearly brought out in the diagrams (figs. 9 and 10), which represent actual hourly measurements of light intensities in the interior of the crown of ailanthus (*Ailanthus glandulosa*) and black locust (*Robinia pseudacacia*).

MEASUREMENTS OF DIRECT AND DIFFUSED LIGHT.

Plants depend chiefly for their growth and development on diffused light; yet for certain functions, such as leafing, flowering, and fruiting, direct sunlight is essential, and it is therefore desirable to determine the requirements of trees for direct and diffused light. By means of Wiesner's insulator the intensity of direct and diffused light may be measured separately in the manner suggested by Roscoe. The observer faces the sun, holding the insulator in a horizontal position before him.

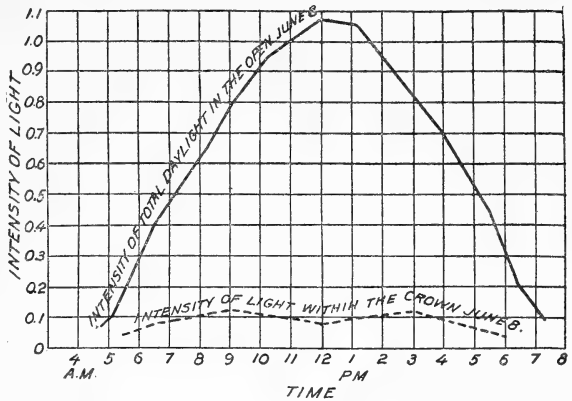


FIG. 9.—Hourly light intensities within the crown of ailanthus (*Ailanthus glandulosa*). Horizontal arrangement of leaves.

The time required to obtain the shade of a given standard is recorded. He then turns 180° so that his back is toward the sun, and holding the insulator in the shadow of his body again observes the time

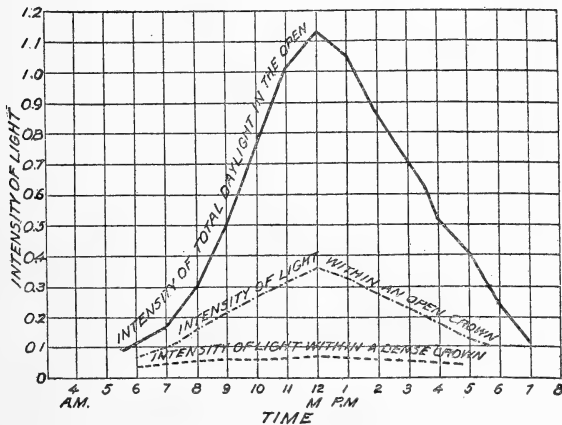


FIG. 10.—Hourly light intensities within the crown of black locust (*Robinia pseudacacia*). Vertical arrangement of leaves.

required for the "normal paper" to reach the tint of the same standard. The reading taken facing the sun gives the intensity of the total light—that is, the sum of the direct and diffused light. The one facing away from the sun gives only the diffused light, since here the direct light is cut off by the body of

the observer. The intensity of the direct light alone is then found by subtracting the value of the diffused light from that of the total light.

If, for instance, 8 seconds are required to obtain the "normal shade" in full sunlight and 27 seconds are required when the insulator is held in the shadow of the body, then the intensity of the total light (direct plus diffused light) $It = \frac{1}{8} = 0.125$; the intensity of the diffused light $Id = \frac{1}{27} = 0.037$, and the intensity of the direct light $ID = It - Id = 0.125 - 0.037 = 0.088$. Since the body of the observer absorbs a portion of the diffused light, this method gives correct values for the total light, but does not give correct values for the diffused light. In order to minimize the error for diffused light it is suggested that the insulator be held as far from the body as possible and in such a position as to receive only the shadow cast by the head.

WIESNER'S INVESTIGATIONS.

By means of the chemical method Wiesner (1907) determined the average minimum light intensities of a comparatively large number of forest trees of the temperate and tropical climates, as follows:

Species.	Average minimum light intensities.	Species.	Average minimum light intensities.
<i>Boxus sempervirens</i> (box).....	1 1/108	<i>Populus alba</i> (white poplar).....	1/15
<i>Fagus silvatica</i> (beech).....	1/60	<i>Populus nigra</i> (black poplar).....	1/11
<i>Æsculus hippocastanum</i> (horse chestnut).....	1/37	<i>Pinus laricio</i> (Austrian pine).....	1/11
<i>Carpinus betulus</i> (hornbeam).....	1/56	<i>Betula verrucosa</i> (birch).....	1/9
<i>Acer platanoides</i> (Norway maple).....	1/55	<i>Liriodendron tulipifera</i> (tulip tree).....	1 7/5
<i>Acer campestre</i> (field maple).....	1/43	<i>Populus deltoides</i> (cottonwood).....	1/6
<i>Acer negundo</i> (box elder).....	1/28	<i>Fraxinus excelsior</i> (ash).....	1/5.8
<i>Quercus pedunculata</i> (oak).....	1/26	<i>Larix decidua</i> (larch).....	1/5
<i>Allanthus glandulosa</i> (tree of heaven).....	1/22	<i>Corylus avellana</i> (hazel).....	1/3
<i>Thuja occidentalis</i> (arborvitæ).....	1/20	<i>Prunus spinosa</i> (cherry).....	1/3

¹ Measurements of light intensities below 1/80 are unsafe.

This scale of tolerance corresponds very closely to the empirical scales that have been worked out by foresters, with the exception perhaps of ash, whose minimum light requirement is given as greater than that of birch, which is scarcely correct.

Of special interest are the minimum light requirements found by Wiesner (1905: 77-150) for some of our native trees and shrubs and European species commonly grown here:

Species.	Region.	Elevation.	Minimum light intensity.
<i>Pinus contorta</i> (incl. <i>P. murr</i>).....	Yellowstone Park, Wyo.....	6,400	1/6
Do.....	do.....	8,500	1/6.4-1/6.9
<i>Pinus flexilis</i>	do.....	6,000	1/8-1/9
<i>Picea parryana</i>	do.....	8,000	1/60-1/62
Do.....	Salt Lake City, Ogden, Utah.....	4,000	1/64-1/70
<i>Pseudotsuga taxifolia</i>	Yellowstone Park, Wyo.....	5,500-6,000	1/20
<i>Juniperus virginiana</i>	do.....	6,000	1/5-1/7
<i>Juniperus communis nana</i>	do.....	6,000-8,000	1/9-1/9.6
<i>Acer glabrum</i>	do.....	6,000	1/30
<i>Acer saccharinum</i> L.....	Niagara Falls (600 ft.) and Pocatello, Idaho.....	4,000	1/25-1/40

Species.	Region.	Elevation.	Minimum light intensity.
Populus alba.....	Utah and Idaho.....	3,000-4,000	1/8 -1/10
P. tremuloides.....	Yellowstone Park, Wyo.....	6,000	1/4.2-1/6
P. acuminata.....	Livingston, Mont.....	4,500	1/8 -1/9.1
P. deltoides.....	Colorado Springs, Colo.....	6,000	1/4
Do.....	Billings, Mont.....	3,100	1/9
P. balsamifera.....	Colorado Springs, Colo.....	6,000	1/16
P. nigra italica.....	Salt Lake City, Utah.....	4,250	1/21
Betula fontinalis.....	Mammoth Hot Springs, Wyo.....	6,000	1/14
Symphoricarpos oreophilus.....	do.....	6,000	1/20
Shepherdia argentea.....	Yellowstone region near Livingston.....	4,500	1/14
Vaccinium myrtillus.....	Yellowstone region.....		1/16.6

CLEMENTS' INVESTIGATIONS.

Clements determined, by the aid of his photometer, the light requirements of a number of forest trees in Colorado in the lodgepole pine zone of the Rocky Mountains. He found that the light values in mature lodgepole pine forests range from 0.12 to 0.05 (1/8.3 to 1/20). The values most frequently found were 0.08 (1/12.5) and 0.07 (1/14.3), which he accepts as the normal. At intensities of 0.20 to 0.14 (1/5 to 1/7.1), germination and growth of lodgepole pine were found to be fairly good, though much below that in sunshine. No vigorous seedlings were found in forests with light values from 0.08 to 0.05 (1/12.5 to 1/20). These light values tend to show that the minimum light intensity for lodgepole pine is very low, much lower than the values obtained by Wiesner. Wiesner determined the minimum light intensity for lodgepole pine as 1/6 of full daylight, while the light intensities under which lodgepole pine seedlings still persist, according to Clements, may be even as low as 1/20. This difference is due partly to the difference in the methods of measuring light, partly to the difference in the accuracy of the two instruments, but probably chiefly to the difference in the standard with which the light intensities were compared. Clements' measurements of the light requirements of limber pine (*Pinus flexilis*) gave him values approximately the same as those for lodgepole pine (*Pinus contorta*). This again does not agree with the results obtained in Yellowstone Park by Wiesner, who found the minimum light intensity for limber pine to be from 1/8 to 1/9. For Douglas fir the minimum light intensity, according to Clements, apparently lies below 0.05 (1/20). In Estes Park he found that Douglas fir very rarely thrives in light intensities below 0.05 (1/20), though it grows fairly well in light of 0.02 (1/50) at Pikes Peak. Wiesner determined the minimum light intensity for Douglas fir in the Rocky Mountains also as 1/20. Engelmann spruce (*Picea engelmanni*) and alpine fir (*Abies lasiocarpa*) were found by Clements to be almost identical in their tolerance, and no forest light measured was too weak for fair reproduction of both species.

FOREST SERVICE INVESTIGATIONS.

G. A. Pearson took a number of light readings, by means of Clements' photometer, on several species of forest trees at the Coconino Forest Experiment Station near Flagstaff, Ariz., in 1909, and on the Willowa National Forest in northeastern Oregon in 1907.

At the Coconino Forest Experiment Station, at an elevation of 7,200 feet, on a limestone formation, he found the following light values for western yellow-pine seedlings at five different places:

Condition of seedlings.	Average light intensity.	Condition of seedlings.	Average light intensity.
Fair.....	0.385	Good.....	0.570
Do.....	.309	Do.....	.630
Good.....	.414		

In a sapling stand of western yellow pine 24 years old, on rocky, volcanic soil, elevation 7,300 feet, readings around an old, full-crowned tree at the inner limit of thrifty sapling growth gave the following light values: 0.579, 0.547, 0.379, 0.328. Readings in a group of suppressed saplings in a near-by stand gave values of 0.088 and 0.026.

From these observations it appears that the seedlings of western yellow pine grow fairly well in a light intensity of from 0.309 to 0.414, while the older saplings evidently require a light intensity of 0.328.

In a thick stand of white fir (*Abies concolor*) saplings from 4 to 12 feet high under Douglas fir, white fir, and western yellow pine, on a steep, very rocky south slope, he obtained the following light values:

Condition.	Light intensity.	Condition.	Light intensity.
Suppressed.....	0.020	Good.....	0.068
Good.....	.048	Do.....	.027
Do.....	.028		

In a stand of Douglas fir (*Pseudotsuga taxifolia*) saplings from 4 to 6 feet high under western yellow pine, aspen, and Douglas fir, on a gentle, northwesterly slope, at the edge of draw, with rocky but fresh soil, he obtained the following values:

Condition.	Light intensity.	Condition.	Light intensity.
Poor.....	0.049	Good.....	0.192
Fair.....	.097	Do.....	.133
Poor.....	.016		

In a stand of very healthy and fast-growing saplings of Engelmann spruce (*Picea engelmanni*), in small groups on the top of a ridge, under Engelmann spruce, he obtained the following values: 0.050, 0.062, and 0.033.

Arranging the species in the order of their light requirements, as determined by these observations, with the most intolerant first, gives the following scale:

Western yellow pine.

Douglas fir.

White fir and Engelmann spruce.

On the Wallowa National Forest, in northeastern Oregon, the light readings were not taken in so systematic a manner as at the Coconino Experiment Station, but in most cases three or more light readings were taken in each situation. The values given for each species are the average of all the readings taken at a number of situations:

TABLE 6.—*Light intensities, Wallowa National Forest.*

Species.	Elevation.	Number of readings.	Light intensity—condition of saplings—	
			Good.	Poor.
	<i>Feet.</i>			
<i>Abies lasiocarpa</i>	7,000–7,500	12	0.029	0.006
<i>Picea engelmanni</i>	7,000–7,500	24	.021	.004
<i>Tsuga heterophylla</i>	6,000	3	.027
<i>Abies grandis</i>	5,000–6,000	12	.025	.011
<i>Pseudotsuga taxifolia</i>	6,000–7,000	17	.052	.025
<i>Pinus contorta</i>	6,000–7,000	31	.086	.019
<i>Larix occidentalis</i>	6,500	7353

The species are arranged according to their tolerance as determined by experience, with the most tolerant first. It will be seen that the recorded light values roughly bear out this arrangement.

DEFECTS OF THE METHOD.

The inaccuracies of the photochemical method of measuring light intensity are not great. Ordinarily the error does not amount to more than 10 per cent, and by repeated measurements it can be reduced to 5, and even to 2.5 per cent.

A more serious objection to the method is that it measures only the chemical rays of the solar spectrum—that is, the rays of high refrangibility in the blue and violet end of the spectrum. It is assumed, however, that the intensity of the red and yellow rays is proportional to the intensity of the chemical rays, and that measurement of the chemical rays therefore gives at the same time an approximate measure of all other rays of the solar spectrum which affect plant growth.

This would be true if the clearness of the atmosphere remained always the same. As a matter of fact, when the atmosphere is not clear the different rays are not equally absorbed by it, and the result is that the measurement of the chemical rays alone does not give a correct value for the intensity of all other rays.

Furthermore, the light which is measured in the forest under the shade of the crowns is a "mixed" light, which consists of diffused and direct light passing unchanged through the openings between the crowns; of light which is reflected from the leaves, branches, and trunks; and, finally, of light which has passed through the foliage. By the photochemical method it is possible to measure accurately only light which penetrates into the forest through the openings between the crowns and foliage, and which is of the same composition as the sunlight in the open, except that all the rays composing it are equally weakened. If the light in the forest consisted only of this kind of light, then it would be possible to compare its intensity with that in the open. Since, however, the light in the forest is a "mixed" light, which partly consists also of reflected light and light transmitted through the green foliage, such comparison is apt to lead to errors.

Helmholtz has pointed out that landscapes rich in green vegetation appear as a rule too dark in photographs. He ascribes this to the fact that the rays which act upon the photographic paper are not reflected by the green leaves of living vegetation. Roscoe has expressed the same idea, and has demonstrated further that "chemical" rays do not pass through green leaves. It is easy to become convinced of the truth of this statement by a very simple experiment. If fresh green leaves are placed on sensitive photographic paper and exposed for several minutes to light, the parts covered by the green leaves, even very thin leaves, such as those of basswood, remain entirely or nearly white, while the paper all around them assumes a dark color.

These facts prove that green leaves not only do not reflect the chemical rays, but do not even transmit them. Investigations of Krause, Engelmann, Reincke, and Timiriazev have shown that fresh green leaves, as well as the alcoholic solution of such leaves, absorb the rays of different wave lengths unequally. Sachs demonstrated by direct experiments that rays of different wave lengths penetrate plant tissues differently. He found that the ultraviolet rays of the solar spectrum were absorbed more fully than other rays, and were retained by the most superficial layers of the tissues. The violet, blue, and yellow penetrated somewhat deeper into the tissues, while the red and partly the green rays penetrated most. In other words, the rays which are most active in producing the blackening of the

photographic paper—that is, the ultraviolet, violet, and blue rays—are absorbed by the leaves first of all.

It is evident, therefore, that the light intensities in the forest measured by the photochemical method are necessarily too low. Furthermore, the composition and intensity of light in the forest are influenced by the character of the bark of the tree and of the under surfaces of the leaves.

SPECTROSCOPIC MEASUREMENT OF LIGHT INTENSITY.

All these facts tend to show that the photochemical method of measuring light in the forest determines only that the denser the forest canopy and the fewer the openings in it, the less will be the chemical intensity of light in the forest. The more light demanding is the species, the more open is its crown, the more will be the chemical intensity of light under its shade. The photochemical method, however, apparently can not establish the absolute amount of light which the green leaf utilizes. There were, therefore, many criticisms of measuring light in the forest merely by this method. It was suggested that light measurement in the forest should be qualitative as well as quantitative; in other words, that it is necessary to know not only how much light in general, but how much of each kind of light a plant receives.

ZEDERBAUER'S INVESTIGATIONS.

The most recent attempt in measuring separately the intensity of the different rays of the solar spectrum was made by Dr. Zederbauer (1907; 325-330) of the Austrian forest experiment station at Maria-brunn. Since individual green leaves, as is now well established, exercise a selective power of absorption, he concludes that the tree crown, merely an aggregation of leaves, should show a similar if not identical absorption. It would seem, therefore, that the light in the forest must be of a different composition from that in the open.

This conclusion is apparently verified by his observations with the spectroscope. He finds that the leaf canopy exerts a selective power of absorption similar to that of individual leaves, and that the degree and kind of absorption varies with the species. Thus the absorption in a beech stand is found to be different from that in an oak or a pine stand. Common to all species is the absorption between the Fraunhofer lines B and C in the red portion of the spectrum, also in the blue portion approximately at the line F, and in the violet beyond H. Some species absorb practically all of the rays between F and H (blue-violet), while others allow most of the indigo rays to pass through unabsorbed. He finds that the species generally

recognized as most light-demanding, namely, the pine and larch, absorb, in addition to the deep band in the red, only small portions of the blue and violet, while the shade-enduring spruce and beech absorb, besides the red, some orange and a large amount of blue, indigo, and violet.

For measuring light intensities of the different rays of the solar spectrum he used a modified form of the Winger "light measurer," manufactured by A. Krüss, Hamburg. The principle of the instrument is to measure the monochromatic light transmitted through a colored glass by comparing it with the standard light of a benzine lamp passed through a glass of the same color. Two defects in the apparatus are pointed out. First, its capacity is not sufficient for all measurements; second, the glasses of the slide, with the exception of the red, are not of perfectly homogeneous color, with the result that the light which is transmitted through them is not absolutely monochromatic. The first of these difficulties is easily overcome by increasing the capacity of the instrument; the second, however, presents a more serious obstacle, since perfectly monochromatic glasses, with the exception of red, are at present unobtainable. He presents the results of a number of measurements taken in stands of different composition. These results, with the exception of those for red light, are admitted to be inaccurate because of the defects in the apparatus; however, they are regarded by Zederbauer as sufficiently conclusive to demonstrate the correctness of the method. Measurements for the red rays only made by him at Purkersdorf, near Vienna, July 21, 1906, 9 a. m., sky clear, gave the following results:

	Amount of red light transmitted.
	<i>Units.</i>
<i>Picea excelsa</i> (young) (Norway spruce).....	10
<i>Fagus sylvatica</i> (young) (beech).....	10
<i>Larix europæa</i> (young) (larch).....	125

Experiments at Mariabrunn, near Vienna, August 8, 1906, 6 p. m., sky rather cloudy, gave the following:

	Amount of red light transmitted.
<i>Picea excelsa</i> (young) (Norway spruce).....	About 2 units.
<i>Pinus sylvestris</i> (young) (Scotch pine).....	About 12 units.
<i>Larix europæa</i> (young) (larch).....	About 11 units.
<i>Quercus robur pedunculata</i> (young) (pedunculate oak).....	About 10 units.
In the open.....	220 units.

The results show a different absorption for each species, it being almost 10 times as great for the tolerant as for the intolerant species.

Measurements for all the colors of the spectrum at Krems, April 22, 1907, 10 a. m., sky partly cloudy, gave the following results:

	Units of transmitted light.						
	Red.	Orange.	Yellow.	Green.	Blue.	Indigo.	Violet.
<i>Picea canadensis</i> (white spruce).....	75	100	200	250	300	500+	100
<i>Pinus sylvestris</i> (Scotch pine).....	225	320	500	500+	450	500+	300

Measurements at Mariabrunn, June 14, 1907, 3-4 p. m., sky cloudy, gave the following results:

	Units of transmitted light.						
	Red.	Orange.	Yellow.	Green.	Blue.	Indigo.	Violet.
<i>Picea excelsa</i> (Norway spruce).....	2	7	12	100	40	200	100
<i>Pinus sylvestris</i> (Scotch pine).....	150	200	470	500+	500+	500+	200
<i>Larix europæa</i> (European larch).....	50	80	90	250	200	500+	100
<i>Quercus robur pedunculata</i> (pedunculate oak)	24	50	100	100	150	250	50

These measurements show a different absorption for each species, not only in the red but also in the other colors of the spectrum.

According to Zederbauer, the results of his investigations, including measurements not given here, show that the intolerant species, pine, larch, and birch, absorb very little in the indigo, and less than the tolerant species in the red, blue, and violet. It will thus be seen that a tolerant species such as spruce growing beneath an intolerant species such as pine is capable of utilizing a great deal of the light which is let through by the latter. The light beneath the overshadowed spruce will be found to have undergone a second sifting, as it were, thus producing a spectrum deficient in red, blue, and violet.

WIESNER'S INVESTIGATIONS.

Zederbauer's criticism of the photochemical method of measuring light in the forest probably holds good for dense forests, such as those of spruce or hemlock in this country, in which the light is mostly transmitted or reflected light and therefore of a different composition from light in the open. In open forests, such as the longleaf pine and western yellow pine forests of the South and Southwest, in which most of the light is of the same composition as that in the open except that it is of lower intensity, the photochemical method undoubtedly gives correct values. Wiesner, while not denying the possible change in the composition of the light after it passes through the crowns of the trees, maintains that the light even in dense forests is practically of the same composition as that in the

open, and therefore the measurement of light by means of photographic paper gives the measure of the entire spectrum as well as of the chemical rays. The reason for this he finds in the fact that under ordinary conditions the light in the forest instead of being transmitted directly through the leaves enters almost wholly by reflection through openings in the crowns. Thus, according to his calculations, the open, illumined space within the crown of a Norway maple (*Acer platanoides*) is 670 times and that of cottonwood (*Populus deltoides*) 1,000 times larger than the space occupied by the solid substances of the two respective crowns. Hence the amount of light which is transmitted through the green leaves is comparatively small as compared with the amount of unchanged light which passes through the openings in the crowns. Spectroscopic observations by Wiesner showed no difference in the composition of the light inside and outside the forest, even at light intensities in the forest as low as one-eightieth of that in the open, where the absolute light intensity ranged from 0.5 to 1.0.

Zederbauer's experiments in themselves are not sufficiently accurate to be entirely conclusive. They were apparently made at different times and therefore probably at various conditions of the atmosphere, and, with one exception, on cloudy or partly cloudy days. Furthermore, only the visible rays of the solar spectrum are measured by means of Zederbauer's instrument. Consequently his method fails to measure all the rays of the solar spectrum which affect plant life, since this is influenced by the invisible as well as the visible rays. As a matter of fact, by the photochemical method a much larger portion of the solar spectrum is measured than by Zederbauer's method.

RELATIVE VALUE OF DIFFERENT METHODS.

Since no practical instrument has so far been devised by which the intensity of the different rays of the solar spectrum can be measured, the measurement of the chemical light intensity remains for the present the nearest approach to the ideal. The photochemical method doubtless can be used to great advantage in open forests and forests of moderate density. To what extent the light in dense forests may be different in composition from that in the open is still debatable. If its composition differs as the critics of the photochemical method claim, then the measurement of chemical intensity alone gives too low values for the forest. If it does not, as Wiesner's investigations apparently show, then the measurement of the chemical light intensity is correct, even in forests of great density. While the physical methods of measuring light in the forest are more direct and express the light requirements of forest trees in a mathematical

form, yet they are not the absolute quantities of light used by different species.

An apparent drawback to all the instruments used for measuring light directly is that they record only the light intensity at the given moment. The effect of light upon plants depends not only on its intensity but also on its duration during the day and during the entire vegetative period. The ideal method, therefore, of measuring light directly would be by a self-registering photometer, which would record the light intensities in the forest during the entire day and for the entire vegetative period. Such self-recording photometers, which would give the minima and maxima as well as the sum of the light enjoyed by trees, would make it possible to determine accurately the light requirements of our forest trees. They are, however, not yet in existence, and the best that can be done at present is to select typical clear days, determine the time of occurrence of the minimum and maximum illumination of the interior of the crown, and in this way obtain the relative minima and maxima of light endured by different species. In interpreting the results of the light readings, account must be taken also of other factors of tree growth, such as moisture content of the soil, age and vigor of the specimen, quality of the soil, and relative humidity.

With these precautions and some experience, it is possible by means of the photochemical method to obtain results of great practical value, and to determine, if not the absolute quantities of light required by different species, at least their relative light demands. The method still seems to be the one quick and practical method for measuring the light requirements of forest trees and expressing them in an accurate and mathematical form, and it has been already effectively used in a number of studies here and abroad. Though it is not free from drawbacks, these are bound to be eliminated more and more as the method itself receives greater recognition on the part of foresters and is tested by repeated observations.

The relative importance of light in the life of the tree has long been recognized, but too little understood. Only recently have methods been devised for measuring light intensities, and all are admittedly imperfect. It is not the aim of this bulletin to recommend any particular method or instrument for measuring light, but to stimulate interest in this important problem and to indicate the different lines along which future practice may be developed.

BIBLIOGRAPHY.

- ANDRESEN, M. Zur Aktinometrie der Sonne. (In Photographische Korrespondenz, Wien, 1898.)
- BADOUX, H. Lichtversuche mit Deckgittern. (In Mitteilungen der Schweizerischen Centralanstalt für das forstliche Versuchswesen, 1898, vol. 6: 29-36.)
- BARANETZKI, J. Die tägliche Periodicität im Längenwachstum. (In Mémoires de l'Académie de science de St. Pétersbourg, 1879.)
- BATALIN, A. Ueber die Wirkung des Lichtes auf die Entwicklung der Blätter. (In Botanische Zeitung, 1871, Spalte 675.)
- BATES, CARLOS G. Windbreaks; their influence and value. Washington, D. C., 1911. (U. S. Forest service. Bulletin 86.)
- BERGEN, J. Y. Relative transpiration of old and new leaves of the Myrtus type. (In Botanical gazette, 1904, vol. 38.)
- Transpiration of sun leaves and shade leaves of *Olea europea* and other broad-leaved evergreens. (In Botanical gazette, 1904, vol. 38.)
- BONNIER, G. and FLAHAULT, C. Observations sur les modifications des végétaux suivant les conditions physiques du milieu. (In Annales des sciences naturelles, Paris, 1879, ser. 6, vol. 7.)
- Influence des hautes altitudes sur les fonctions. (In Comptes rendus des séances de l'Académie des sciences, Paris, 1890, vol. 111.)
- Recherches expérimentales sur l'adaptation des plantes au climat alpin. (In Annales des sciences naturelles, Paris, 1894, ser. 7, vol. 20.)
- Influence de la lumière électrique continue sur la forme et la structure des plantes. (In Revue générale de botanique, 1895, vol. 7.)
- BORGGREVE, BERNARD R. Die Holzzucht. Berlin, 1891.
- BROWN, HORACE T., and MORRIS, G. HARRIS. A contribution to the chemistry and physiology of foliage leaves. (In Journal of the Chemical society of London, 1893, vol. 63: 604-677.)
- BUNSEN, R., and ROSCOE, H. Meteorologische Lichtmessungen. (In Poggen-dorff's Annalen, 1862, vol. 117.)
- BURGERSTEIN, A. Die Transpiration der Pflanzen. Jena, 1904.
- BÜSGEN, MORITZ. Bau und Leben unserer Waldbäume. Jena, 1897.
- CANDOLLE, C. DE. Étude de l'action des rayons ultraviolets sur la formation des fleurs. (In Annales des sciences physiques et naturelles, Genève, 1897.)
- CIESLAR, ADOLPH. Einiges über die Rolle des Lichtes in Walde. Wien, 1904.
- Licht- und Schattholzarten. Lichtgenuss und Bodenfeuchtigkeit. Wien, 1909.
- CLEMENTS, E. S. The relation of leaf structure to physical factors. (In Transactions American microscopical society, 1905, vol. 25.)
- CLEMENTS, FREDERIC E. Research methods in ecology. Lincoln, Nebr., 1905.
- Plant physiology and ecology. New York, 1907.
- The life history of lodgepole burn forests. Washington, 1910. (U. S. Forest service. Bulletin 79.)

- DANCKELMANN, BERNHARD. Lichtmessung und Lichtverhältnisse im Walde. (In Zeitschrift für Forst- und Jagdwesen, 1899, vol. 31: 321-345.)
- DUFOUR, L. Note sur les relations qui existent entre l'orientation des feuilles et leur structure anatomique. (In Bulletin de la Société botanique de France, 1886, vol. 33.)
- Influence de la lumière sur la forme et la structure des feuilles. (In Annales des sciences naturelles, Paris, 1887, ser. 7, vol. 5.)
- FAMINTZIN, A. Die Wirkung der Intensität des Lichtes auf die Kohlensäurezersetzung durch Pflanzen. (In Bulletin de l'Académie impériale des sciences, St. Petersburg, 1880.)
- FISCHBACH, CARL VON. Lehrbuch der Forstwissenschaft. Berlin, 1886.
- FISCHER, A. Beiträge zur Physiologie der Holzgewächse. (In Pringsheim's Jahrbücher für wissenschaftliche Botanik, 1891, vol. 22.)
- FLAHAULT, CH. Nouvelles observations sur les modifications des végétaux suivant les conditions physiques du milieu. (In Annales des sciences naturelles, Paris, 1881, ser. 6, vol. 9.)
- FRICKE, KARL. "Licht- und Schattenholzarten," ein wissenschaftlich nicht begründetes Dogma. (In Centralblatt für das gesamte Forstwesen, 1904, vol. 30: 315-325.)
- GAYER, KARL. Der Waldbau. Berlin, 1898.
- GÉNEAU DE LAMARLIÈRE, L. Recherches physiologiques sur les feuilles développées à l'ombre et au soleil. (In Revue générale de botanique, 1892, vol. 4: 481.)
- Sur la respiration, la transpiration et le poids sec des feuilles développées au soleil et à l'ombre. (In Comptes rendus des séances de l'Académie des sciences, Paris, 1892, v. 115: 521-523.)
- GILTAY, E. Ueber die vegetabilische Stoffbildung in den Tropen und in Mitteleuropa. (In Annales Jardin botanique, Buitenzorg, 1898, vol. 15.)
- Die Transpiration in den Tropen und in Mittel-Europa. (In Pringsheim's Jahrbücher für wissenschaftliche Botanik, 1898, 1900, vols. 32, 34.)
- Vergleichende Studien über die Stärke der Transpiration in den Tropen und im mitteleuropäischen Klima. (In Pringsheim's Jahrbücher für wissenschaftliche Botanik, 1897, vol. 30.)
- GÖBEL, K. Organography of plants. Oxford, 1900-1905.
- Einleitung in die experimentelle Morphologie der Pflanzen. Leipzig and Berlin, 1908.
- GROOM, PERCY. The influence of external conditions on the form of leaves. (In Annals of botany, 1893, vol. 7.)
- HABERLANDT, GOTTLIEB. Vergleichende Anatomie des assimilatorischen Gewebesystems der Pflanzen. (In Pringsheim's Jahrbücher für wissenschaftliche Botanik, 1881, vol. 13.)
- Physiologische Pflanzenanatomie. Leipzig, 1904.
- HANN, JULIUS. Handbook of climatology. N. Y., 1903.
- HARTIG, ROBERT. Lehrbuch der Anatomie und Physiologie der Pflanzen. Berlin, 1891.
- HARTIG, THEODOR. Photometrisches. (In Allgemeine Forst- und Jagdzeitung, 1877, vol. 53: 35-36.)
- HEMPEL, GUSTAV, and WILHELM, KARL. Die Bäume und Sträucher des Waldes. Wien, 1889.
- HESS, RICHARD A. Die Eigenschaften und das forstliche Verhalten der Holzarten. Berlin, 1895.
- HEYER, CARL J. Der Waldbau. Leipzig, 1893.

- HEYER, GUSTAV. Das Verhalten der Waldbäume gegen Licht und Schatten. Erlangen, 1852.
- Lehrbuch der forstlichen Bodenkunde und Klimatologie. Erlangen, 1856.
- HÖHNEL, FRANZ R. VON. Ueber den Ablösungsvorgang der Zweige einiger Holzgewächse und seine anatomischen Ursachen. (In Mittheilungen aus dem forstlichen Versuchswesen Oesterreichs, 1878, vol. 1: 255–268.)
- Weitere Untersuchungen über den Ablösungsvorgang von verholzten Zweigen. (In Mittheilungen aus dem forstlichen Versuchswesen Oesterreichs, 1881, vol. 2: 247–256.)
- HUNDESHAGEN, JOHANN C. Encyclopädie der Forstwissenschaft, Bd. I. Tübingen, 1828.
- JOST, LUDWIG. Ueber Beziehungen zwischen der Blattentwicklung und der Gefäßbildung in der Pflanze. (In Botanische Zeitung, 1893, vol. 51.)
- Ueber den Einfluss des Lichtes auf das Knospentreiben der Rothbuche. (In Berichte der Deutschen botanischen Gesellschaft, 1894, vol. 12: 188.)
- Ueber die Abhängigkeit des Laubblattes von seiner Assimilationsfähigkeit. (In Pringsheim's Jahrbücher für wissenschaftliche Botanik, 1895, vol. 27: 403–480.)
- KIENITZ, MAX. Ueber den Einfluss der Freistellung bisher beschatteter Blätter auf die Entwicklung des Baumes, als Beitrag zur Durchforstungslehre. (In Bericht über die 16. Versammlung deutscher Forstmänner, 1887: 128–135.)
- KISSLING, P. B. Beiträge zur Kenntnis des Einflusses der chemischen Lichtintensität auf die Vegetation. Halle, 1895.
- KOHL, FRIEDERIK GEORG. Die Transpiration der Pflanzen und ihre Einwirkung auf die Ausbildung pflanzlicher Gewebe. Braunschweig, 1886.
- KRAFT, GUSTAV. Ueber das Beschattungserträgniss der Waldbäume. (In Allgemeine Forst- und Jagd-Zeitung, 1878, vol. 54: 164–167.)
- Beiträge zur Lehre von den Durchforstungen, Schlagstellungen und Lichtungshieben. Hanover, 1884.
- Beiträge zur Durchforstungs- und Lichtungsfrage. Hanover, 1889.
- KRAVCHINSKIĪ, D. Lyesovozraschenie. Osnovaniya lyesokhozyaistvennagho rastenievodstva. (Silviculture. Principles of forest production.) St. Petersburg, 1903.
- KREUSLER, W. Eine Methode für fortlaufende Messungen des Tageslichtes und über deren Anwendbarkeit für pflanzenphysiologische Untersuchungen. (In Landwirtschaftliche Jahrbücher, 1878, vol. 2.)
- Ueber eine Methode zur Beobachtung der Assimilation und Athmung der Pflanzen und über einige dieser Vorgänge beeinflussende Momente. (In Landwirthschaftliche Jahrbücher, 1885, vol. 14: 913–965.)
- LAZNIENSKI, W. VON. Beiträge zur Biologie der Alpenpflanzen. (In Flora, 1896, vol. 82.)
- LEIST, K. Einfluss des alpinen Standortes auf die Ausbildung der Laubblätter. Bern, 1889.
- LESAGE, PIERRE. Recherches expérimentales sur les modifications des feuilles chez les plantes maritimes. (In Revue générale de botanique, 1890, vol. 2: 55–65; 106–121; 163–175.)
- Sur les rapports des palissades dans les feuilles avec la transpiration. (In Comptes rendus des séances de l'Académie des sciences, Paris, 1894, vol. 118.)

- LÜBIMENKO, V. N. O chuvstvitelnosti khlorofillonosnagho apparata svyeto-lübivuiikh i tyenevuiinoslivuiikh rastenii. (Sensitiveness of the chlorophyll apparatus of light-loving and shade-enduring plants.) (In *Lyesnoi zhurnal*, 1905, vol. 35: 1269-1281, 1435-1449).
- Novi data o chuvstvitelnosti khlorofillonosnagho apparata svyeto-lübivuiikh i tyenevuiinoslivuiikh rastenii. (New data on the sensitiveness of the chlorophyll apparatus of light-loving and shade-enduring plants.) (In *Lyesnoi zhurnal*, 1906, vol. 36: 17-34.)
- MAYR, HEINRICH. *Waldbau auf naturgesetzlicher Grundlage*. Berlin, 1909.
- MEDEVEV. (In *Lyesnoi zhurnal*, 1884, vol. 14.)
- METZGER, DR. Studien über den Aufbau der Waldbäume und Bestände nach statischen Gesetzen. (In *Mündener forstliche Hefte*, 1895, vol. 7: 45-97.)
- MIYAKE, K. On the starch of evergreen leaves and its relation to photosynthesis during the winter. (In *Botanical gazette*, 1902, vol. 33.)
- MONTEMARTINI, LUIGI. Intorno alla anatomia e fisiologia del tessuto assimilatore della piante. (In *Atti dell' Istituto botanico della R. Università di Pavia*, 1897, vol. 4: 89-128.)
- MOROZOV, G. Tienevuiinoslivost drevisnikh porod. (Tolerance of trees.) (In *Enciklopedia russkago lesnogo choziastvo*, 1908, vol. 2: 1286-1295.)
- MULLER, N. J. CARL. *Botanische Untersuchungen*. Heidelberg, 1877.
- NIKOLSKY. (In *Transactions of Petrovsky Academy*, 1881.)
- PEARSON, GUSTAF A. Reproduction of western yellow pine in the Southwest. Washington, 1910. (U. S. Forest service. Circular 174.)
- PFEL, FRIEDRICH W. L. Pflanzenphysiologischen Aphorismen. (In *Kritische Blätter für Forst- und Jagdwissenschaft*, 1840(?)—1859, vol. 20-42, regular contributions.)
- PRINGSHEIM, N. Ueber Lichtwirkung und Chlorophyllfunction in der Pflanze. (In *Pringsheim's Jahrbücher für wissenschaftliche Botanik*, 1881, vol. 12.)
- RAMANN, EMIL. *Forstliche Bodenkunde und Standortslehre*. Berlin, 1893.
- *Bodenkunde*. Berlin, 1905.
- ROSCOE, H. E., and BEXENDELL. Ueber die relativen chemischen Intensitäten des direkten und zerstreuten Sonnenlichtes. (In *Poggendorff's Annalen*, 1866, vol. 204.)
- and THORPE. On the relation between the sun's altitude and the chemical intensity of total daylight in a cloudless sky. (In *Philosophical transactions of the Royal society of London*, 1870, vol. 160.)
- SACHS, FERDINAND GUSTAV JULIUS VON. Ueber die Durchleuchtung der Pflanzentheile. (In *Sitzungsberichte der K. Akademie der Wissenschaften*, Wien, 1860, vol. 43, pt. 1.)
- Ueber den Einfluss des Tagelichtes auf Neubildung und Entfaltung verschiedener Pflanzenorgane. (In *Botanische Zeitung*, 1863, vol. 21.)
- Wirkung des Lichtes auf die Blütenbildung der Laubblätter. (In *Botanische Zeitung*, 1864, vol. 22.)
- *Handbuch der Experimental-Physiologie der Pflanzen*. Leipzig, 1865.
- Ein Beitrag zur Kenntniss der Ernährungsthätigkeit der Blätter. (Arbeiten aus dem botanischen Institut zu Würzburg, 1884, vol. 3.)
- *Lectures on the physiology of plants*. Oxford, 1887.
- SCHIMPER, ANDREAS F. W. *Pflanzen-Geographie auf physiologischer Grundlage*. Jena, 1898.
- SCHRAMM, W. Ueber die Verteilung des Lichtes in der Atmosphäre. Kiel, 1901.

- SCHWAB, F. Ueber das photochemische Klima von Kremsmünster. (In Denkschriften der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1904, vol. 74.)
- STAHL, E. Ueber den Einfluss der Lichtintensität auf Struktur und Anordnung des Assimilationsparenchyms. (In Botanische Zeitung, 1880, vol. 38.)
- Ueber den Einfluss des sonnigen oder schattigen Standortes auf die Ausbildung der Laubblätter. (In Jenaische Zeitschrift für Naturwissenschaften, 1883, vol. 16.)
- Einige Versuche über Transpiration und Assimilation. (In Botanische Zeitung, 1894, vol. 52.)
- STÖHR, A. Ueber das Vorkommen von Chlorophyll in der Epidermis der Phanerogamen-Laubblätter. (In Sitzungsberichte der K. Akademie der Wissenschaften, Wien, 1879, vol. 79.)
- SUROJ. (In Lyesnoi zhurnal, 1891, vol. 21.)
- TURSKIĀ, M. K. Lyesovodstvo. (Silviculture.) Moscow, 1904.
- TIMIRIAZEFF, C. État actuel de nos connaissances sur la fonction chlorophyllienne. (In Annales des sciences naturelles, Paris, 1885, ser. 7, vol. 2, no. 2.)
- Enregistrement photographique de la fonction chlorophyllienne par la plante vivante. (In comptes rendus des séances de l'Académie des sciences, Paris, 1890, vol. 110.)
- The cosmical function of the green plant. (In Proceedings of the Royal society of London, 1903, vol. 72.)
- VESQUE, J., and VIET, C. De l'influence du milieu sur la structure anatomique des végétaux. (In Annales des sciences naturelles, Paris, 1881, ser. 6, vol. 12.)
- VÖCHTING, H. Ueber die Abhängigkeit des Laubblattes von seiner Assimilationsthätigkeit. (In Botanische Zeitung, 1891, vol. 49.)
- Ueber den Einfluss des Lichtes auf die Gestaltung und Anlage der Blüten. (In Pringsheim's Jahrbücher für wissenschaftliche Botanik, 1893, vol. 25.)
- WAGENER, GUSTAV. Der Waldbau und seine Fortbildung. Stuttgart, 1884.
- WAGNER, A. Zur Kenntnis des Blattbaues der Alpenpflanzen und dessen biologischer Bedeutung. (In Sitzungsberichte der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1892, vol. 101, pt. 1.)
- WAGNER, MAX. Pflanzenphysiologische Studien im Walde. Berlin, 1907.
- WARMING, EUGENIUS. Oecology of plants; an introduction to the study of plant communities. Oxford, 1909.
- WEBER, LEONARD. Resultate der Taglichtmessungen in Kiel, 1890-1892. (In Schriften des naturwissenschaftlichen Vereins für Schleswig-Holstein, 1893, vol. 10.)
- WEBER, RUDOLPH. Lehrbuch der Forsteinrichtung. Berlin, 1891.
- WEINZIERL, TH. VON. Alpine Futterbauversuche. Bericht über die im alpinen Versuchsgarten auf der Sandlingalpe durchgeführten wissenschaftlich-praktischen Untersuchungen in den Jahren 1890-1900. Wien, 1902.
- WESNER, JULIUS. Orientirende Versuche über den Einfluss der sogenannten chemischen Lichtintensität auf den Gestaltungsprocess der Pflanzenorgane. (In Sitzungsberichte der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1893, vol. 102, pt. 1: 291-350.)
- Bemerkungen über den factischen Lichtgenuss der Pflanzen. (In Berichte der Deutschen botanischen Gesellschaft, 1894, vol. 12: (78)-(98).)

- WIESNER, JULIUS. Untersuchungen über den Lichtgenuss der Pflanzen mit Rücksicht auf die Vegetation von Wien, Cairo und Buitenzorg, Java. (In Sitzungsberichte der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1895, vol. 104, pt. 1: 605-711.)
- Beiträge zur Kenntniss des photochemischen Klimas im arktischen Gebiete. (In Denkschriften der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1898, vol. 67.)
- Untersuchungen über den Lichtgenuss der Pflanzen im arktischen Gebiete. (In Sitzungsberichte der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1900, vol. 109, pt. 1.)
- Ueber den Einfluss des Sonnen- und des diffusen Tageslichtes auf die Laubentwicklung sommergrüner Holzgewächse. (In Sitzungsberichte der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1904, vol. 113, pt. 1.)
- Untersuchungen über den Lichtgenuss der Pflanzen im Yellowstone-Gebiete und in anderen Gegenden Nordamerikas. (In Sitzungsberichte der K. Akademie der Wissenschaften, Wien, Mathematische-naturwissenschaftliche Klasse, 1905, vol. 114, pt. 1: 77-150.)
- Der Lichtgenuss der Pflanzen. Leipzig, 1907.
- ZEDERBAUER, EMERICH. Das Lichtbedürfniss der Waldbäume und die Lichtmess Methoden. (In Centralblatt für das gesamte Forstwesen, 1907, vol. 33: 325-330. Translation in Forestry quarterly, 1908, vol. 6: 255-262.)
- ZON, RAPHAEL. A new explanation of the tolerance and intolerance of trees. (In Proceedings of Society of American foresters, 1907, vol. 2: 79-94.)



