A. TRANSLOCATION

Translocation is the movement of dissolved materials throughout the plant. The rate at which photosynthetic (Ps) products such as sucrose move from the leaves to the sink organs controls the rate of photosynthesis.

Plant species that have high Ps rates also have relatively high translocation rates. This is consistent with the idea that effective removal of Ps products maintains rapid CO_2 fixation. Severe infection of leaves by pathogens often so severely inhibits Ps rates that these leaves become sugar importers instead of sugar exporters. The adjacent healthy leaves then gradually attain marked increases in Ps rates, suggesting that enhanced translocation has reduced CO_2 fixation.

There are four principal pathways for translocation of materials after uptake by the roots of leaves of a plant.

a.   Movement in the xylem along the transpiration stream. It allows the upward movement of organic materials in the xylem from the soil solution into foliage.

b.   Through the phloem or other cells such as ray parenchyma. This is the major pathway of movement of materials applied to the leaves. Subsequently, phloem flow may take solutes up to the stem apex as easily as down to the lower parts of the plant.

c.   Through the cell walls. Aqueous network through the cell walls is described as apoplast (outside protoplast). It is the principal region of the apparent free space.

d.   Through the intercellular spaces. The rapid systemic permeation of gases and volatiles through the plants indicates a ready movement through the intercellular spaces.

Most of the metabolic sinks in plants are connected with the source by phloem elements in vascular strands. Sugars move from source to sink down the concentration gradients. Translocation occurs in the sieve tubes of the phloem and although other sugars and derivatives and also nitrogenous compounds

may be found in the phloem exudates, the most important and general constituent is the disaccharide sucrose.

The movement of photosynthate or metabolites from the surrounding mesophyll cells of the leaf into the conducting tissues of the phloem is known as "***phloem lading***". The process of loading is selective, as shown by the failure of certain sugars and organic acids to be transferred while others moved in readily. Entrance into the sieve tubes is apparently independent of concentration differences between the mesophyll and sieve tubes in the case of sucrose, amino acids and organic acids. Both the process of transport to the sieve tubes and the terminal step of passage into the sieve tubes may require ATP. The concentration of sugars in leaves where they are produced is usually higher than that in the sinks. Only a fraction of the products of photosynthesis remain at the site of production in fully expanded leaves, most of them are translocated to other organs where they are either used as building blocks for various cell-constituents or deposited as storage products. A certain part is always lost through respiration during transport and at the final storage site. Photosynthathes (PS) are distributed within the plant at a definite distribution pattern. The pattern of movement changes continuously during the growth of the plant and exerts a profound effect on both the morphological form and the yielding properties of the plant.

During the development of a single young leaf, it imports PS from other parts of the plant to build up its own structure; but very soon it becomes self-supporting and in a short time starts to export PS. As long as the plant is young, this export is mainly directed towards centres of active growth, such as developing leaves, root tips, or shoot apices; but later on much of the assimilate transport is diverted to storage organ such as fruits, grains, or tubers. Another expression of the distribution pattern is the fact that leaves in different positions on the plant may preferentially supply different growing organs with assimilates. The PS for the roots are thus mainly produced in the lower leaves and those for the apical parts in the upper leaves, whereas leaves in an intermediate position deliver assimilates in both

directions. This general pattern is only relative, however, and may be modified both by differences in the internal organizations of the vascular system. Different centres of active growth may exhibit various strengths of "demand" for assimilates and therefore, reproductive organs often (but not always) dominate vegetative organs; shoot apices dominate root tips.

The continues growth of higher green plants well supplied with water and inorganic nutrients depends primarily on

i.   the accomplishment of photosynthesis in the leaves of the plants

ii.   the transport of organic compounds from the leaves to heterotrophic cells which constitute metabolic sinks

Underground parts – roots and a variety of storage organs are obvious examples of plant parts leading a heterotrophic existence and developing tubers are regarded as the classical sink for products of photosynthesis. Non-green aerial plant paerts – bilbs, flowers and fruits and most of the cells in stems and petioles also constitute a drain on photosynthetic products. Even within leaves there are many cells without chloroplasts and the autotrophic cells themselves consume PS in their own growth and respiration..

In a germinating seedling, the sink is the rapidly growing embryo and this is supplied by mobile organic materials produced during hydrolytic activity in the source storage organs – cotyledon or endosperm.

In a vegetative plant, the developing green leaves are a sink not only for their own PS but also for that produced in older leaves with appropriate vascular connections, which also support apical growth. The oldest leaves near the base of the plant, provided they receive adequate illumination export sugars to the roots. Developing buds and meristematic regions in the roots place demands on the available assimilates and compete successfully as sinks with developing leaves. The onset of flowering and

subsequent fruit development have a marked effect on the redistribution of assimiliates. Fruits develop at then expense of vegetative growth and at this time the growth of roots may be restricted.

The principal carbohydrate translocated in the sieve tubes appears to be sucrose, but in trees and some other plants this molecule may have condensed with it one or more molecules of galactose, to give rafinose, starchyose or verbascose in order of decreasing concentrations. Sucrose is also the principal carbohydrate translocated in herbaceous plants. Amino and organic acids, minerals, viruses, hormones and steroids are also known to be translocated. As sucrose moves through the sieve tubes it may be withdrawn into surrounding cells and hydrolyzed there so that whole-phloem analysis may give misleading results.

B. PARTITIONING OF ASSIMILATES

Partitioning describes the distribution of new assimilates to growth of various plant parts and to respiration. Partitioning is subject to a control system whose flexibility is indicated by its capacity to respond appropriately to different environmental stimuli. Thus shading is likely to increase partition (relative to the total dry weight) to the laminae whereas water or nutrient stress improves partition to the roots. Removal of plant parts results in temporarily increased partition to other similar parts until partition relationship of intact control plants is re-established. All the vegetative sinks are potentially in competition during the vegetative phase, the dominant sink being sheath and stem. Yield depends on the translocation of assimilates in most species largely sucrose from the leaves or other photosynthetic tissues to the parts of economic importance – tubers, seeds, etc. Other parts – roots, stems, young leaves and fruits also rely on the assimilates produced by the mature leaves. The source and sinks are linked by a transport pathway of phloem sieve elements. Mature leaves are the primary sources of assimilates, from the current photosynthesis, but this can be supplemented by the mobilization of stored reserves/organs such as the stems, which may be described as secondary sources.

In most dicots, cotyledons initially serve as source of reserves, but are subsequently raised above ground, when they assume a photosynthetic function which supports further growth until the first true leaves are photosynthetically competent. Storage function is taken over by endosperm from which mobilized reserves are absorbed by the cotyledons and then translocated to the embryonic axis. Sucrose from the endosperm is accumulated in the phloem cells of the cotyledons largely sustain growth of the hypocotyls and roots. Elongation of the hypocotyls raises the cotyledon.

Dry matter partitioning between roots, above ground vegetative growth, and reproductive growth are usually modified by water deficits. The response depends upon the species, when the stress occurs, its duration, and its severity. The increase in root-shoot ratio of crops under water deficits may reflect an increase in the proportion of assimilates allocated to the roots, or a change in the rate of death or turn over of roots relative to the shoot. An increase in root growth may indicate a greater density or a greater depth of roots. Soil and root resistances to water uptake are reduced when root length density increases, thereby permitting higher water flow rates through the plant and delaying the onset of severe plant water deficits. Whilst partitioning of dry matter to roots may enhance water uptake, it represents a loss to above ground dry matter production. An exception is root crops, such as cassava, where water deficit could be beneficial to economic yield, provided that the increased proportion of dry matter partitioned to the roots goes mainly to the tubers. Since photosynthesis is inhibited more than translocation during stress, dry matter produced before flowering may be transferred from the stem and roots to the grain during grain filling – " **Compensatory translocation**" The amount of pre-anthesis assimilate partitioned to the grain is dependent on the timing and severity of water deficits as it affects the source-sink balance.

C. PHOTOSYNTHETIC POTENTIAL OF PLANTS

There are basically two types of plants C-3 and C-4.

In **C-3 plants,** the earliest labeled compound i**s 3-phosphoglycerate (PGA).** The 5-Carbon substance, ribulose diphosphate (RuDP) combines with one molecule of CO_2, presumably forming an unstable 6-carbon substance which immediately splits into two molecules of PGA, the 3-carbon substance which gives the C-3 cycle its name.

Ribulose diphosphate + CO_2 2 X PGA

   5C atoms   1 C atom   2 X 3C atoms

The reaction is catalyzed by RuDP carboxylase

C-4 plants, (most tropical grasses and cereals, except rice and a few dicots) have 4-carbon organic acid, malate or aspartate) as the immediately labeled product which is formed by the combination of 3-carbon phosphoenol pyruvate (PEP) with CO_2

PEP + CO_2 PEP carboxylase   malate or aspartate

3 C + 1 C   4C

A feature of the C-3 is photorespiration which reduces net CO_2 assimilation rates in all C-3 species especially at high leaf temperatures. C-4 plants actually contain the enzymes for C-3 photosynthesis including RuDP carboxylase but they are confined to certain cells in the leaf surrounding the smaller veins and called the bundle sheath cells. In the mesophyll cells, CO_2 is fixed to form the C-4 acid which are translocated to the bundle sheath cells where they dissociate to release CO_2 which is re-fixed by RuDP carboxylase. The other dissociated product, probably pyruvate, is translocated back to the mesophyll.

The net Ps rates of C-4 plants are higher than in C-3 plants, whereas the rate of water use is not greatly different from C-3 species, the WUE of C-4 plants may be 50-100% better than C-3 species.

SOME PHOTOSYNTHETIC CHARACTERISTICS OF C-3 AND C-4 PLANTS

Sn	CHARACTERISTIC	C-3	C-4
1	Leaf anatomy	No distinct bundle sheath of photosynthetic cells	Well organized bundle sheath , rich in organelles (starch storing chloroplasts)
2	Carboxylating enzyme	Ribulose diphosphate (RuDP) carboxylase	Phosphoenol pyruvate (PEP) carboxylase + RuDP carboxylase
3	Theoretical energy requirement (CO_2:ATP:NADPH)	1:3:2	1:5:2
4	Transpiration ratio g/H_2O/g dry wt increase	450-950	250-350
5	Leaf chlorophyll a to b ratio	2.8 ± 0.4	3.9 ± 0.6
6.	Requirement for Na^+ as a micronutrient	No	Yes
7.	CO_2 compensation point (ppm CO_2) i.e CO_2 conc. at which net Photosynthesis ceases	30-37	0-10
8.	Photosynthesis inhibited by 21% O_2	Yes	No. <3% largely independent of O_2 concentration

9.	Photorespiration detectable?.	Yes	Only in the bundle sheath
10.	Optimum temperature for photosynthesis	15-25°C	30-40°C
11.	Dry matter production tons/ha/year	22$\pm$0.3	39$\pm$17

D. TRANSPIRATION

Transpiration is the evaporation of water from the plant through the openings between the guard cells. The opening and the guard cells are collectively called **'stomatal apparatus'**. Adjacent to each guard cell are usually one or two other modified epidermal cells called **accessory or subsidiary cells**. Water evaporates inside the leaf from the palisade parenchyma and spongy parenchyma cell walls into the intercellular spaces, which are continuous with the outside air when the stomates are open. Many of the cell walls of palisade and spongy parenchyma cells are collectively called mesophyll cells and are exposed to the internal leaf atmosphere. Stomates often as the guard cells take up water and swell. The guard cell then curves during opening, partially because it is attached to each end of its partner.

Environmental Effects on Stomates

- Stomates of most plants open at sunrise and close in darkness, allowing entry of CO_2 needed for photosynthesis during the day time. Light intensity influences the rate of opening and the final aperture size, bright light causing a wider aperture.

- Low conc. of CO_2 cause stomates to open and removal of CO_2 during photosynthesis by parenchyma and mosophyll cells results in opening of stomates of most species in the day. High CO_2 conc causes the stomates to close in the light and dark.

- As water potential decreases (water stress increases), the stomates close.

- High temperatures (30-35°C) cause the stomates to close due to water stress or increase in CO_2 conc within the leaf.

- Exposure to gentle breeze can lead to partial closure of stomates because additional CO_2 is brought close to stomates where it can diffuse in faster.

Guard Cell Uptake of K+

When the stomates open, relatively large quantities of K+ move from the surrounding cells into the guard cells. Light causes a building of K+ in guard cells, as does CO_2-free air. When leaves are transferred to the dark, K+ moves out of guard cells into the surrounding cells and stomates close.

Stomates also close in response to the application of abscisic acid whose application causes loss of K+ from the guard cells.

Blue light under low light intensity can cause stomatal opening when red light has no effect by acting directly on guard cells that receive K+ and thereby open up.

Ecologists classify plants according to their response to water as follows:

a.   Hydrophytes – plants that grow where water is super abundant.

b.   Mesophytes – plants that grow where water availability is intermediate

c.   Xerophytes – Plants that grow where water is scarce

Solutes strongly influence water potential, so ecologists further classify plants that are sensitive to relatively high salt concentrations as GLYCOPHYTES and those that are able to grow in the presence of high salts as HALOPHYTES

Xerophytes are plants that escape, resist or endure drought. They can be described as being hardy. Annual plants in the desert escape the drought by existing as dormant seeds during the dry season. Succulent species resist drought by storing water in their succulent tissues (cactus). Enough water is stored and its rate of loss is so extremely low (due to an exceptionally thick cuticle and stomatal closure during the day time.

Non-succulent perennial perennials avoid drought by having extensive shallow root system capable of absorbing surface moisture after rain storm, reduction in size of leaf blades (which increases heat transfer by convection, lowers leaf temperature and thus reduces transpiration, sunken tomates, shedding of leaves during dry periods and such other factors as heavy pubescence on leaf surfaces.

Transpiration may also refer to sweating and hyperhydrosis.
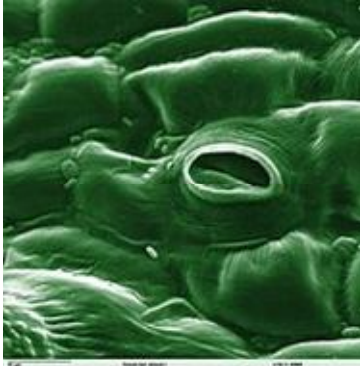
Stoma in a tomato leaf shown via colorized scanning electron microscope.

The clouds in this image of the Amazon Rainforest are a result of **transpiration**.

Transpiration is a process similar to evaporation. It is the loss of water from the aerial parts of plants, especially leaves but also stems, flowers and roots. Leaf surfaces are dotted with openings called stoma, and in most plants they are more numerous on the undersides of the foliage. The stoma are bordered by guard cells that open and close the pore. Collectively the structures are called stomata.[1] Leaf **transpiration** occurs through stomata, and can be thought of as a necessary "cost" associated with the opening of the stomata to allow the diffusion of carbon dioxide gas from the air for photosynthesis. **Transpiration** also cools plants and enables mass flow of mineral nutrients and water from roots to shoots.

Mass flow of liquid water from the roots to the leaves is caused by the decrease in hydrostatic (water) pressure in the upper parts of the plants due to the diffusion of water out of stomata into the atmosphere. Water is absorbed at the roots by osmosis, and any dissolved mineral nutrients travel with it through the xylem.

The rate of **transpiration** is directly related to the degree of stomatal opening, and to the evaporative demand of the atmosphere surrounding the leaf. The amount of water lost by a plant depends on its size, along with the surrounding light intensity, temperature, humidity, and wind speed (all of which influence evaporative demand). Soil water supply and soil temperature can influence stomatal opening, and thus **transpiration** rate.

A fully grown tree may lose several hundred gallons (a few cubic meters) of water through its leaves on a hot, dry day. About 90% of the water that enters a plant's roots is used for this process. The **transpiration** ratio is the ratio of the mass of water transpired to the mass of dry matter produced; the **transpiration** ratio of crops tends to fall between 200 and 1000 (*i.e.*, crop plants transpire 200 to 1000 kg of water for every kg of dry matter produced).[2]

Transpiration rate of plants can be measured by a number of techniques, including <u>potometers</u>, <u>lysimeters</u>, porometers, and heat balance sap flow gauges.

<u>Desert</u> plants and <u>conifers</u> have specially adapted structures, such as thick cuticles, reduced leaf areas, sunken stomata and hairs to reduce **transpiration** and conserve water. Many <u>cacti</u> conduct photosynthesis in <u>succulent</u> stems, rather than leaves, so the surface area of the shoot is very low. Many desert plants have a special type of <u>photosynthesis</u>, termed <u>crassulacean acid metabolism</u> or CAM photosynthesis in which the stomata are closed during the day and open at night when **transpiration** will be lower.

E. PLANT RESPONSES TO WATER STRESS

a.   Cellular growth appears to be the most sensitive to water stress. Decreasing the external water potential by only a bar or less results in a perceptible decrease in cellular growth. This sensitivity is responsible the common observation that many plants grow only at night when water stress is lowest.

b.   The response of cellular growth to water stress is manifested as a reduction in cell wall synthesis.

c.   Protein synthesis in the cell may be almost equally sensitive to water stress. These responses are observed only in tissues that are normally growing rapidly (synthesizing cell wall polysaccharides and proteins). The effects on protein synthesis are apparently controlled at the translational level, the level of ribosome activity.

d.   At slightly more negative water potentials, protochlorophyll formation is inhibited.

e.   Activities of certain enzymes e.g NO_3 – reductase decrease quite sharply as water stress increases. Whereas, a few enzymes, such as alpha amylase and ribonulease, show increased activities. It

was thought that such hydrolytic enzymes might break down starches and other materials to make the osmotic potential more –ve, thereby resisting the drought.

f.   Nitrogen fixation and reduction also drop with water stress. At levels of stress that cause observable changes in enzyme activities, cell division is also inhibited.

g.   The stomates begin to close leading to a reduction in transpiration and photosynthesis.

h.   At about this level of stress, Abscisic acid (ABA) begins to increase markedly in leaf tissues. This could be responsible for stomatal closure, since applied ABA causes stomates to close rapidly. At slightly higher stress levels, the amino acids praline begins to increase sharply, sometime building up to levels of 1% of the tissue dry weight. At higher level of stress (Water potential = 10 – 20 bars,) , respiration, translocation of assimilates and CO_2 assimilation drop to levels near zero. Hydrolytic enzyme activity increases considerably and ion transport can be slowed down.

i.   Parts of the transpiration stream in the xylem eventually cavitate so the xylem becomes blocked by vapour space.

j.   Since growth is especially sensitive to water stress, yields may be noticeably decreased even with moderate drought.

k.   Cells are smaller and leaves develop less during water stress, resulting in reduced area for photosynthesis. Furthermore, plants may be especially sesnsitive to drought during certain stages , such as tassel formation in maize.

Mechanism of plant response to water stress

1.   Water activity (its ability to enter into chemical reactions) is a function of water potential and is thus lowered by water stress.

2.   Solutes increase in concentration as water is lost.

3.   Water stress might result in special changes in membranes

4.   Water stress might upset the hydration of macro-molecules e.g. dehydration of key enzymes could cause disulfide within proteins to break and reform leading to enzyme denaturation when molecules are re-hydrated.

5.   Water stress can change the turgor pressure within the plant cells.

F. LIGHT UTILIZATION

Crops grow and use water because they intercept radiation from the sun, sky and atmosphere. Diurnal changes of solar radiation dictate the diurnal course of photosynthesis and transpiration and the vertical gradient of radiation flux in a canopy is a measure of the absorption of energy by foliage at different heights. The distribution of radiation within a plant community is the most important single element of microclimate.

Radiation: Features of solar radiation relevant to Crop Ecology.

1.   The angle of incidence of the sun's rays usually specified by the solar elevation ß.

2.   The spectral composition of the radiation. The wave band in which radiant energy is available for PS is usually defined by the limits 0.4 – 0.7 µm corresponding to the blue and red ends of visible spectrum PAR (**Photosynthetically Active Radiation).**

3.   The relative intensity of diffuse radiations from the blue sky, haze and clouds, and of direct radiation from the solar beam.

The ratio of PAR to total radiation changes slightly with the amount of water vapor and dust in the atmosphere but seems to be relatively insensitive to the presence of clouds.

Leaves

Most of the radiation intercepted by a field crop is absorbed by leaves, more specifically, by leaf laminae. Leaf sheaths, stems and inflorescences also absorb radiation and are capable of PS in some species.

The area of leaf laminae within any horizontal layer of a canopy is specified by a leaf area index, LAI, the area of leaves per unit area of ground beneath them. The transmission of radiation by leaves depends strongly on wavelength. In the region of 0.4 to 0.7µm where pigment absorbs most strongly, the leaves of many crop plants absorb 80-90% of incident radiation. Absorption is much smaller in the infra-red (0.7-3µm) often falling to 10-20% between 0.7-0.8 µm. The proportions of radiation transmitted and reflected by crop leaves are usually similar at about 5 – 10% in the visible spectrum and 30 – 40% in the infrared. It will be assumed here that leaves transmit 7% of PAR and 25% of total solar radiation because leaves absorb visible radiation preferentially, marked differences of spectral composition are observed in plant communities.

Light quantity is defined as the wavelength available and active in a particular biological phenomenon. The quality of light that arrives at the top surface of the canopy may be changed as it moves through a leaf or is reflected from a leaf.

Light intensity (quantity) – a product of irradiance and duration. The quantity of radiation increase sharply as day length increases. Species differ in their response to light intensity. With increasing light, a unit area of corn leaf shows increasing PH capacity when compared to the same area of soybean leaf. A soybean leaf is only 2/3 as efficient as a corn leaf in fixing carbon at full sunlight. It is common to observe that species botanically referred to as shade species (e.g. tobacco) are saturated (i.e. cease to respond to increased light intensity) more rapidly than do sun species. Tobacco is saturated near ¼ full sunlight. Sunflower and corn continue to respond to light intensity changes in the range near full sunlight.

One flat layer of leaves over a unit area would reflect 10% of the incoming radiation, absorb 80% and transmit only 10% to the next leaf area. The optimum leaf area index range for most crops is between **2.5 to 5.0** based on these facts.

1.   the LAI during growth should be sufficient to intercept as much of the incoming radiation as possible

2.   the LAI should be of a magnitude which prevents parasitism: i.e. a condition of lower leaves using carbohydrates at a greater rate than they photosynthesize.

3.   the LAI must suit the condition and purposes of which the crop is grown.

Max LAI does not always equal max grain yield, nor does it always yield maximum dry matter production.

Leaf Area Duration (LAD) is used to describe the length of time the leaf area is functional e.g. a field corn might have LAI of 4.5 at the time of pollination, but it could be useful also to know how long this LAI is maintained. It has been established that the grain yield of cereals is related to LAI after the ears emerge but not before.

Optimum vs Critical Leaf Area

Optimum Leaf Area is the leaf area at which the rate of dry matter production is max at a particular LAI and less at LAI below or above.

Critical Leaf Area is when the rate of dry matter production is constant after the maximum rate was reached. It is the LAI required to give 95% interception at noon.

Low Light Intensity

When light intensity limits full expression of a plant's photosynthetic potential, morphological adaptation can maximize interception of incident radiation. Leaves and leaflets of Leguminosae show coordinated movements which place leaflets perpendicular to incident light at low insolation. Such a 'day-sleep' phenomenon improves light utilization within a legume canopy by modifying community structure according to available light. The great majority of plants show some leaf movement in response to solar direction and intensity. Final position depends upon prevailing light and plant response.

In shade plants, leaves are generally in one layer and at right angles to incident light. In deep shade, leaf mosaics develop which maximize light interception but minimize mutual shading. Formation of larger thinner leaves confers additional ecological advantage in deep shade.

Plant morphology and community architecture govern the interception of solar radiation, and physiological processes in the leaf govern its utilization. Leaves on shade plants, have an impressive array of adaptive responses at low light intensity. Mesophyll cell size is reduced and laminar surface enlarges. Chloroplasts become rearranged in photosynthetic tissues, and they line upper

surfaces of cells under low light but align along vertical walls when sunlight is strong.

Most cultivated annuals and biennials bear typical sun leaves. Their photosynthetic apparatus is light saturated at ¼ to 1/5 of full sunlight, with an absolute capacity well in excess of that for shade leaves. Shade leaves are much thinner and have lower rates of dark respiration and a lower value for light compensation. Respiratory losses in particular can be a primary factor in shade adaptation. Shade tolerant plants show only moderate response to high temperature even at 35^0C.

High Light Intensity

Under high light intensity, leaves on a plant adopt a vertical orientation in a north south plane so that noon-time exposure is at an absolute minimum, maximum exposure occurring in early morning and late afternoon. Vertical orientation of foliage is thus a means of minimizing head load under strong irradiance but at the same time providing sufficient illumination to saturate the leafs photosynthetic apparatus for much of the day. Flat leaves, on the other hand, can reduce their energy absorption with epidermal hairs or other surface coverings (waxes) which increase reflectivity especially at high angles of incidence.

Under high light intensity, chloroplasts of most plants are saturated at intensities around 1/20 of full sun, because their light-harvesting capacity is well in excess of their ability to convert this absorbed energy into a chemically useable form.

Sustained bright light inhibits photosynthesis in shade-adapted plants whereas fluctuations in light intensity provide some opportunity for repair as well as favouring higher photosynthetic yield (CO_2 fixed per quantum of absorbed energy). Short intervals of light and darks of one second or less, can enhance energy conversions because dark reactions concerned with CO_2 assimilation can run to completion and thereby restore the photosynthetic apparatus to its full efficiency at the start of each new light phase.

Photosynthetically active radiation

Photosynthetically active radiation, often abbreviated **PAR**, designates the spectral range (wave band) of solar radiation from 400 to 700 nanometers that photosynthetic organisms are able to use in the process of photosynthesis. This spectral region corresponds more or less with the range of light visible to the human eye. Photons at shorter wavelengths tend to be so energetic that they can be damaging to cells and tissues, but are mostly filtered out by the ozone layer in the stratosphere. Photons at longer wavelengths do not carry enough energy to allow photosynthesis to take place.

Other living organisms, such as green bacteria, purple bacteria and Heliobacteria, can exploit solar light in slightly extended spectral regions, such as the near-infrared. These bacteria live in environments such as the bottom of stagnant ponds, sediment and ocean depths. Because of their pigments, they form colorful mats of green, red and purple. These organisms must make use of the leftovers discarded by the plant kingdom.
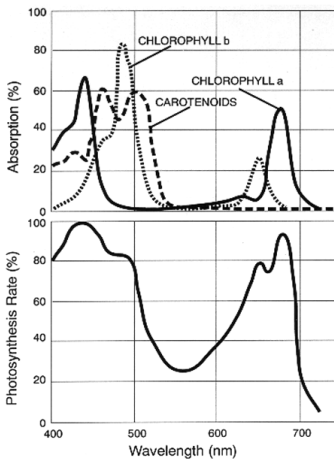
Typical PAR action spectrum, shown beside absorption spectra for chlorophyll-A, chlorophyll-B, and carotenoids

Chlorophyll, the most abundant plant pigment, is most efficient in capturing red and blue light. Horticulturists[who?] say that blue light is the most important for leaf growth and that red light encourages flowering. Accessory pigments such as carotenes and xanthophylls harvest some green light and pass it on to the photosynthetic process, but enough of the green wavelengths are reflected to give leaves their characteristic color. An exception to the predominance of chlorophyll is autumn, when chlorophyll is degraded (because it contains N and Mg) but the

accessory pigments are not (because they only contain $\underline{C}$, $\underline{H}$ and $\underline{O}$) and remain in the leaf producing red, yellow and orange leaves.

PAR measurement is used in agriculture, forestry and oceanography. One of the requirements for productive farmland is adequate PAR, so PAR is used to evaluate agricultural investment potential. PAR sensors stationed at various levels of the forest canopy measure the pattern of PAR availability and utilization. PAR measurements are also used to calculate the <u>euphotic</u> depth in the ocean. PAR is normally quantified as <u>μmol</u> <u>photons</u>/$\underline{m^2}$/<u>second</u>, which is a measure of the photosynthetic photon flux (area) density, or PPFD. PAR can also be expressed in W/m^2. Because photosynthesis is a quantum process PPFD is generally used by plant biologists, but W/m^2 measurements are important in energy balance considerations for photosynthetic <u>organisms</u>.