Photophilous or light-resistant?

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In today's physiology the dominating principle of division is based on photophilous and shade-enduring plants.

Such divnision at first glance seems reasonable. It is known, that after fires and deforestation of large spaces, there is a consecutive change of species. At first the photophilous species appear and create a thick canopy. Light exposure under the canopy is considerably reduced, decreasing below a point at which the photophilous plants can grow. But plant species, classified as"shade-enduring plants", thrive in these conditions.

The "shade-enduring" plant canopy creates even thicker shade in which only shade-enduring plants alone can grow. Then photophilous plants which have appeared right in the beginning, gradually age and die off, without producing a new generation of photophilous plants. Therefore, only shade-enduring species stay in the forest.

This process is called natural succession.

The upper part of the canopy of these shade-enduring plants has a strong exposure to sunlight where the rate of photosynthesis is reduced. These plants survive only due to the photosynthesis in the lower part of the canopy.

This theory forces the scientists to search for the plants' mechanisms of adaptation to lower amounts of light.

At first, scientists were looking for the cause of evolution of a shade-enduring plants at a morphological level, then on a cellular level, and finally - on molecular level. However, none of these searches have lead to the root of the problem.

Strong variability of Curves of Photosynthesis (LCP - Dependence of Iintensity of Photosynthesis on Light exposure) not considered a sufficient factor in defining of "photophilousing" or "shade-enduring" anymore. It is necessary to take into account a resulting effect of low light exposure on the growth of a plant. This requirement strongly reduces the value of such classification?

In [1] author writes: " … Considering the importance of changes in the gain of organic matter, it is possible to tell that the increase in the leaves' surface area and decrease of relative weight? of non-assimilating organs contributes to increase of quantity of assimilating matter and reduction of it's expenditures on respiration. Hence, these changes are adaptive [1]"

Obviously, this is a teleologic approach. We used to interpreter the natural changes of plants in the low light exposure conditions as useful for their survival. This way the matter is presented as if the shade enduring plants adapt to the lack of light by developing some signaling systems, that react on the lack of light or the changes of it's spectrum by launching some mechanisms to compensate those adverse conditions. But these mechanisms were never found.

The reason of this failure is probably because, researchers did not consider changes in climate during all the history of flora's phylognesis.

However it is known, that Earth climat at early stages of the plant phylogenesis was very different. As Tahtadjan [2, the page 86] correctly emphasizes " … a climate and forms of a life during the most part of Jurassic period were the most uniformed in the Earth history. In the end of the Jurassic period the development of mountains took place and the areas of arid climate appeared. Conditions of environment gradually became more diverse, and eventually changed the organic world. It is not clear why, but the prevailing plants of Jurassic period-gymnosperms, were succeed by angiosperms.

They either have completely died out, or have faded into the background. The angiosperms started to dominate first in highlands (!), and then in the plains. "

And further: "The water-supply system of mesozoic gymnosperms was ineffective. It provided water only for rather small leaves .The total area of a photosynthesizing surface of gymnosperms has been limited by the level of development of their water supply system, that dramatically decreased their survival ability. The ability to substantial growth of organic synthesis directly depend on the perfection a water-supply systems". [2, page 88-89]

In work [1] and in those quotes as well in the implicit form it is affirmed, that the crucial factor for survival is the efficiency of photosynthesis and the maximum productivity. If it was so the high-efficiency man cultivated agricultural plants should replace wild-growing species very quickly. However, we see quite opposite in practice. So, the high efficiency is not a major survival factor.

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Why these geographical changes promoted fast spreading of angiosperms, and not some other groups of plants?

It is well known fact that, that on early stages the earth's atmosphere contained higher level of CO_2, than now. As a result of accompanying "hotbed effect" the cloudy cover was much more dense, and the climate was much warmer and damp. Therefore the level of light exposure was almost in 10 times less, than now.The light spectrum was "redder" for the same reason.

In these conditions multicellular plants could have the big sizes even without the specialized systems of water supply. Some of them survived till now. They are the most moistureloving and "shade-requiring" plants of a wood - mosses, horsetails, ferns.

These plants did not have good water-supply system as there was no need in it: plants were not over heated by the Sun.

As time went by atmospheric conditions were changing slowly concentration of oxygen increased, concentration of CO_2 decreased. The density of clouds therefore decreased, radiation from a surface of Earth to space increased, the average temperature of air at a surface went down, average and maximal light exposure (insulation) increased. The big dry territories have appeared.

In these conditions ferns were unable to survive on open spaces and in the upper story of vegetation. But not because of low photosynthesis , but because the leaves of ferns were overheated in direct sun. Therefore ecological niches for those who could not function in changed conditions, decreased. These changes have begun first of all in highlands areas. In valleys the density of clouds was reduced more slowly.

The plants that could provide sufficient cooling of leaves for maintenance of their temperature within the limits of effective photosynthesis, were resistant to insulation.

The increase of insulation in the valleys, the light resistant plants were moving down from mountains to valleys. Their place on mountains was taken by even more light tolerant species. These plants had means for effective cooling of their leaves. The temperature of leaves of these plants could be supported in limits necessary for photosynthesis for a long time.

So extensive high-mountainous territories were cleared from a powerful cover of Gymnosperms, and angiosperms (resistant to radiation) began to concur their place.

From this moment on the further evolution of flora in the great deal is defined by the factor of increase of insulation. This adaptation could go in several ways.

Thickness of a leaves could change; photosynthesis in the top layers of multilayered tissue of a leave have stopped at overheat, but upper layers protected under layers from superfluous light.

The shape of a canopy could also change; the top or lateral branches stopped photosynthesis at overheat, but created a shadow for bottom and internal layers which would continue photosynthesis.

Plants used also other ways of protection of leaves from a direct sunlight. But development water-supply systems was the most reliable, effective and thus the most widespread way of protection of leaves from overheating.

At the further increase of insulation, grasses appear - plants with even more powerful capillary water supply system. It helps them to survive in especially hard climatic conditions and the short period of vegetation. This is not the only way for grasses to protect themselves from overheating, but we shall not discuss it in this study.

If we were to take into consideration all the ways of evolution of plants described above, their division on shade-enduring (SE) and photophilous (PP) looks incorrect. For example, the "shade-loving" fur-tree perfectly grows in southern breadths in high mountains where it there is lots of light but low temperatures and high wind chill. This fact alone is enough to suggest the concept of light-resistance.

Another examples of this are pine trees and birches. Both plants are considered to be photophilous, but the birch tree cannot grow in the southern states and poor, dry soil while the pine tree thrives in these environments. Why? Because although the photosynthesis in the pine is less productive than birch's, the overheating of needles during hot hours of the day are not as deadly for a pine. For a birch leaf with advanced water-supply system but a lack of water in soil, the overheating can be fatal.

Therefore, the modern category of "light-loving" plants cannot be considered to be a proper way of distinguishing between plan groups.

The modern classification would be acceptable if the change of a level of solar radiation in phylogenesis the exact opposite of what it is. In other words, if in the beginning of evolution first appeared the "photophilous plants " with physiological processes possible only in harsh sunlight, and "shade-tolerant" species would have evolved under the protection of their canopy.

Then the theory of plant adaptation to reduced solar radiation could be considered. But the data of an evolutionary science does not confirm this theory.

On the contrary, the concept offered in this article allows to connect photosynthetic properties of plants the structure to their transpiration systems and the food supply systems. These issues are usually ignored in the attempts to explain "shade-tolerance" at a physiological level.

Therefore we suggest to abandon the classification of plants on "shade-tolerant" and «light-loving» (photophylous), and to use concept of the «light-resistance». This term was offered by Prof. O.A.Semihatova to the author of this article. Light resistance is the ratio of the level of endurance of the given plant specie to a level of insulation.
Certainly, (as marked J.L.Tselniker) it cannot be a universal parameter as long as the light endurance of a plant depends on a degree of available moisture in the soil, available nutrients in the soil and on cooling factors such as the temperature of air, wind chill etc. However, with all other factors being equal, the endurance of plants to an increase in solar radiation will vary for different species of plants.

All the conclusions above concur with the hypothesis of light-resisting plants that evolved with the change of climate on Earth.This theory arises many new questions that need proper experimental proof . Some of them are mentioned below.

Photosynthesis

The relation of photosynthesis to the solar radiation is expressed in the characteristic curve (fig. 1) which is usually called " the light curve of photosynthesis" (LCP - dependence of intensity of photosynthesis on the stream of light)

In darkness, the plants use CO_2 for their metabolism, which they obtain from the air. This process is referred to as"plant breathing". As the light intensity increases, so does the amount of available energy for photosynthesis, i.e. for CO_2 transformation into substances which are necessary for a plant life. This implicates that a part of the energy of the nutrients necessary for the basic survival of the plant is now supplied by the light energy and not by the plant. At one particular stream of light, all its energy is exerted on consuming CO_2 to provide the minimal necessities for the survival of the plant. This point on a curve of photosynthesis (LCP) is referred to as the "Compensation Intensity Point" (CIP).

The growth of a plant can occur only if the intensity of light is above Compensation Intensity Point. The lower the rate of respiration, the lower is CIP. In other words, the lower the cost of production the more profit is gained. This particular quality allows shade-enduring plants to grow at lower levels of light.

The characteristics of the light curves of photosynthesis (LCP) is one of first questions that should be addressed. The basic results of the researches are listed bellow.

1. It is found out, that LCP of the shade-enduring plants has a noticable plateau. LCP of the photophilous plants do not reach such a plateau.

2. It is considered, that at high illumination levels photophilous plants have a higher intensity of photosynthesis (IPS) per area unit and a higher efficiency. Photophilous plants rely more on the carbon-fixing reaction and have higher levels of respiration that does not require light.

Nevertheless, the research done by Nichiporovich, as quoted by J. L. Tselniker, shows that the levels of photosynthesis of all plants are practically identical, and photosynthesis efficiency at a given light intensity depends only on the area surface of the leaves.

Note: At times conclusions based on the results of many previously made experiments can prove to be incorrect. So, for example, the absence of a plateau for photophilous plants can be a result of their effective transpiration system.

Therefore, the decline in photosynthesis, with all other variables being equal, can start at much higher levels of light intensity. It is clear that LCP of photophilous plants cannot increase indefinitely and, eventually, at higher heat and at light levels photosynthesis should end. This is a hypothesis and requires the confirmation of further experiments.

3. It is known for fact that Compensation Point on the LCP of photophilous plants (fig. 4) is always located further to the right of the graph, than that of shade-enduring plants, because of the greater intensity of their carbon-fixing reactions.

4. With photophilous plants, the higher levels of light energy consumption appear to take place at the upper part of the canopy; shade-enduring plants have higher levels of photosynthesis activity in the bottom part of their canopy.

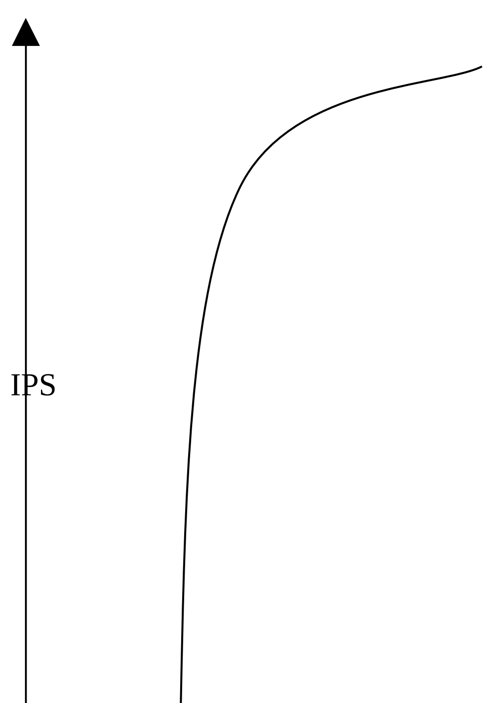
Note: Considering all the above conclusion #4 needs additional research.

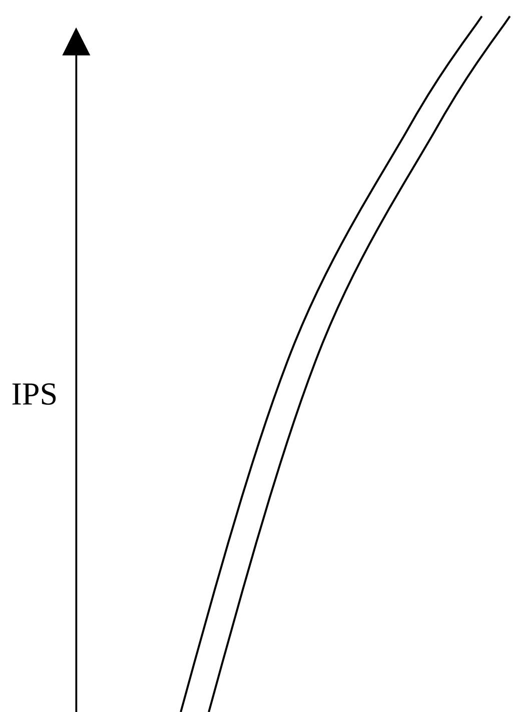
5. If a shade-enduring species were planted in conditions with varying light intensity, then the light intensity at which the plateau occurs will correspond to average amount of light exposure. A similar phenomenon takes place with the light and shade leaves of shade-enduring plants.

Note: It is not accurate to say that photophilous plants have no plateau at all. Most likely decline in photosynthesis still occurs, but at higher levels of light intensity.

6. The shaded leaves of a shade-enduring plants which have a lower level of the plateau also have a lower rate of respiration.

7. Therefore, the rate of exchange in the gas-cycle will increase at a lower levels of light.





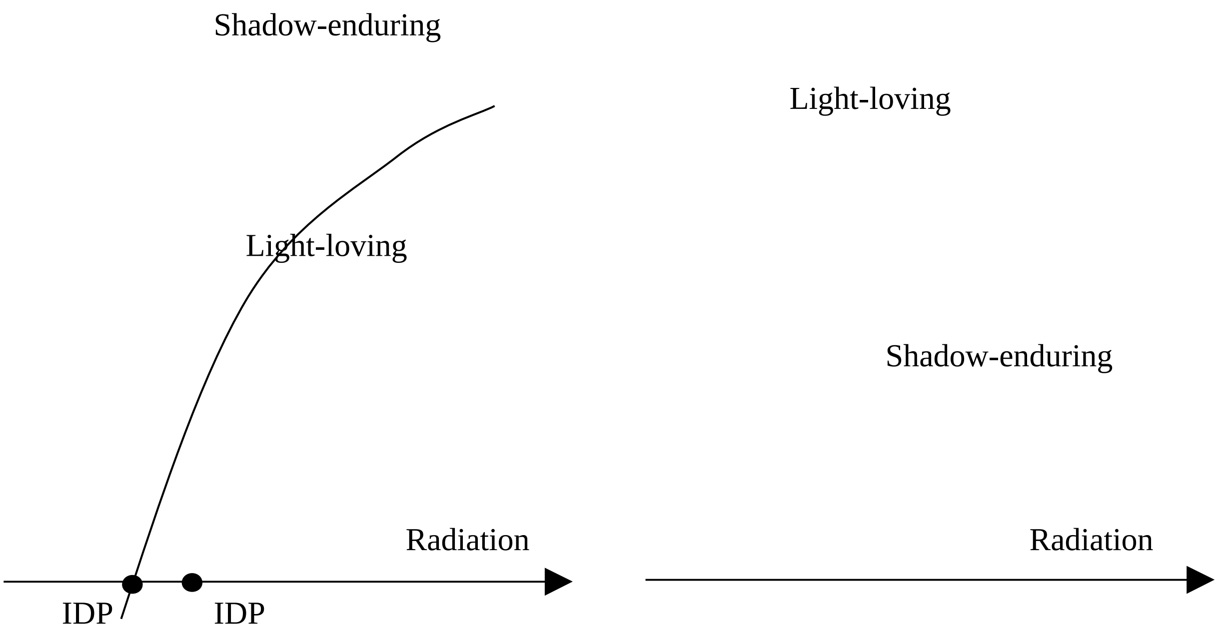


Fig.1

The increase in light-resistance thoughout plant evolution.

The data collected by J.L. Tselniker shows that plants in that are in the process of phylogenies had at least three ways to resist the decline in photosynthesis due to an increase of radiation, namely:

- change of the shape of a canopy
- change of leaf structure and its shape.
- improvement of the ways of cooling of the leaves by increase of water or volatile oils evaporation.

These ways could have been used in any combination.

Change of canopy shape.

The reliance of leaf and needle growth on the quantity of the previous year's stored nutrients can explain why the development of various kinds of canopies, even in gymnosperm plants may be beneficial to a plant.

In the beginning of a plant's development, the growth of the upper branches does not shade the lower branches, and they grow approximately at the same pace. Eventually, the growth in quantity and area surface of leaves in the upper part of a tree reduces the light exposure of the leaves in the lower levels. They accumulate less and less nutrition during the vegetation period and gradually die off. Branches in the middle story gradually grow out to the limit of their durability and until the water-supply system is unable to transport water to the tips of the branches and retrieve the products of photosynthesis

In open spaces, the majority of northern species basically grow horizontal, and not vertical canopies. Vertical growth occurs only in the forest where a lateral shading of canopies takes place. Photosynthesis is carried out mainly by the upper leaves of the canopy that's where its products are stored. This results in the primary growth of the upper part of a trunk. In open spaces, the trunk growth is more uniform and occurs with the same rate along the whole length of the trunk.

The more dense the forest (up to some extent), the higher are the trees, as long as all other variables are equal. This phenomenon is easier to observe in the northern regions because the more prominent lateral shading .

This helps explain the canopy shape of a chestnut and a linden tree. The lower branches of these "shade-enduring" trees are well developed, as there is enough light for them even in the second story of the forest. Therefore, linden trees can grow very tall in the forest. But in the open spaces the vertical growth of a tree is slowed down due to more radiation in the upper part of a canopy- midday decline in photosynthesis starts earlier in the upper canopy than at the lower levels, which are closer to optimal conditions.

Considering the above, species like pine, which did not evolve an effective enough water-supply system, develop a canopy which depends not just on genetic traits, but also on the surrounding environment. For example, the pines in Baltic Sea area experience overheating and photosynthesis decline almost simultaneously in all parts of a canopy. It happens not just because of high radiation but also because of a simultaneous increase in sea air humidity which prevents the cooling of the pine needles. Therefore, the screening of the lower parts of the canopy has very little importance and these pines have an identifiable, flat canopy.

As the cooling factors improve and the radiation increases, the pine needles will get wider and longer. P.A.Hurshudjan bred pines with extremely long and thick needles on the shores of Lake Sevan. In contrast, in wetlands, pines cannot grow long and wide needles due to overheating and few cooling factors.

Change in leaf structure and shape.

It can be assumed that the leaf grows in length and width up to the point when certain limiting factors stunt its growth.

The bottom layer of a leaf eventually reaches the Compensation Intensity Point (CIP) and, as a result, the bottom layer of a leaf cannot produce the next layer because of a shortage in the nutrients needed for an effective cell reproduction.

During the growth of a leaf in width, there can be limitations due to the leaf's inability to cool intself; the long and thin capillaries cannot transport a sufficient amount of water to the cells in the outer areas of the leaf so photosynthesis slows down. This leads to a lower rate of cell reproduction in the outermost edges of the leaf.

At the same level of light intensity, photophilous plants expose more cells to unbeneficial conditions than shade-enduring plants. Theoretically, the ratio of the rate of respiration to the surface area of a leaf (and not the volume) should be greater in photophilous plants, than in shade-enduring plants. *This hypothesis is confirmed by field observations.*

Experiment. From these conclusions, follows the need in carrying out a comparative experiment. The leaves that are found in conditions with similar light exposure but with varying cooling factors should differ greatly in leaf area. Leaves found in areas that vary in light exposure but have similar cooling factors should differ mainly in thickness.

Problem. Consequently, it is important to answer the question: " How do the nutrient producing cells work for the whole plant? Do they always give to the plant the same percentage of synthesized nutrients, or does this percentage depend on the intensity of photosynthesis? "

Experiment. The overheating of a leaf can be decreased by evaporation or by a cool air breeze. It is quite possible that for a wide leaf of a "shade-enduring" plant, the overheating factor causes a decrease in water supply of the marginal areas of the leaf. The can be tested by the means of infrared photography of the leaf at different light intensities. The maximum level of light exposure should exceed the level at which the decline in photosynthesis begins.

If a leaf is small but relatively thick (multi-layered), its water supply is relatively well adjusted. Optimal temperature can be maintained in the lower layers of a leaf because they are insulated by the upper tissues from strong sunlight. In any case, can have only as many layers as allow for proper light exposure in the lower layers for the maintenance of photosynthesis slightly above the CIP.

The water-supply system development.

Development of a water-transport system is very well tracked in evolutionary morphology. It is proven that the is a direct correlation in the improvement of water transport in the trunk and the improvement of water transport in the leaves. However it is strange, that Тахтаджян [2] relates the evolution of the "waterpipe" with an appearance of arid climates, but, for some reason, holds back relating this phenomenon to the increase of solar radiation rates which began at the end of Jurassic Period. From all the above it follows that this was the cause for the development of a waterpiping system. During the entire Jurassic Period, the isolation rates were low and the humidity levels were high so the water supply systems improved very little. Even the early angiosperm species did not have good water-supply system.

An aether-contained plants can better survive in conditions where water is difficult to obtain and where plants with water cooling system survive can barely survive. In Israel, for example, эфироносы with a good water transport system (Eucalyptus) and with enough soil moisture available can reach very large heights just like it appears in its wetland habitat. On the other hand, the Eucalyptus is also able to survive in the arid zones of Israel due to its ability to cool its leaves with the evaporation of oils.

Experiment. Consequently, it would be interesting to compare the amount transpiration in the overall area to the surface area and volume of leaves of coniferous and deciduous trees and grasses. Almost for certain they will correlate with the degree plant resistance to solar radiation.

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