

Bibliographic review

Importance of light quality among weed-crop plants

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ABSTRACT

Plants have the ability to detect the presence of neighboring weeds through the R: RL ratio reflected on the surfaces of weed leaves. The role of the R: RL ratio as a weed management tool has not been sufficiently explored. It is believed that the competition of plants is due to the limitation of resources (water, light, space and nutrients). The competition of plants is initially triggered by the ratio of red to far-red (R: RL) that originates from neighboring plants, followed by a series of complex physiological processes, which exclude direct competition from resources. In this paper, the importance of the weed management system based on the quality of light is disclosed. In addition, mention is made of the crop - weed competition, as well as the perception of neighboring plants through the spectral composition of the light and how the shadow influences the management of weeds.

Key words: crop competition, management, physiological processes, plant growth

INTRODUCTION

Competition in plants is traditionally seen, as a process driven by limited resources. It is believed that weeds limit crop yield by direct competition from light, water and nutrients. These emerge with the crop or later; it has been shown to cause greater yield loss than weeds that emerge in more advanced stages of crop development ⁽¹⁻³⁾.

Most plant species respond differently to the quality of the radiation (color or wavelength) and the amount of it (density of photonic flux-DDF or irradiance), as well as the combinations of both, which represents a fundamental factor in interference between crops

and weeds. The effect of the quality and quantity of radiation is with the environmental shadow component combined that produces a characteristic radiation spectrum under the canopy of plants. The leaves absorb photons in the blue and red of the spectrum of photosynthetically active radiation (RFA), while absorption in the green and especially in the far-red region is weaker and much of these photons are as diffuse radiation (radiance) reflected ⁽⁴⁾.

Research carried out with respect to weeds in different crops demonstrated the importance of the ratio between red and far-red (R: RL), as a fundamental component of the shade between neighboring plants. The early uptake of this signal by internodes and its relationship with the density of foliage modulates the amount of radiation, which shows that plants can detect the presence of neighboring plants, long before they are shaded ⁽⁵⁾.

Resources are not limiting at the beginning of the crop growth stage. The competition at this time is mainly due to the time of appearance of the weed in relation to the crop and the yield losses cannot be compensated despite the elimination of the weeds, so some variable not accounted for should be the basis of weed competition. One of the variables to consider is the quality of light, that is, the relationship between red and far-red, R: RL. The ability of a plant to perceive and adjust to changes in the quality of light acts as an early warning signal of imminent competition, since a reduction in the R: RL signal reflected from the plants, precedes the shading ^(6,7).

Early detection of neighboring plants (plants that grow around others) can be an important mechanism that affects competition between plants ⁽⁸⁾. Although, the relation R: RL has manifested itself as a key factor that signals the start of competition between plants; As far as we know, R: RL has not been integrated into the general concept of competition. Plant responses to low R: RL signals include molecular, physiological and morphological changes ⁽⁷⁾.

Based on the above, it is the objective of the present work, to propose an alternative view of the competition between the plants, where the importance of the quality of the light is recognized, specifically R: RL and its role in the competition. Competition occurs to limit resources, but this is a series of complex physiological processes, initially activated by the R: RL signal, followed by the development of shadow avoidance characteristics (stem elongation, apical dominance and distribution changes of biomass).

Importance of light in plants

The perception of light allows living beings to adapt to changes in lighting, and greatly influences the control of morphogenesis, photosynthesis and the prevention of damage caused by harmful radiation. In the vast majority, plant species have the ability to respond in different ways to the quality of light, understood as color or wavelength, its intensity, that is, the density of photonic flux or irradiance and the combination of both ⁽⁹⁾.

This aspect is of great relevance in plant communities such as crops, plant ecosystems, because plants absorb certain ranges of incident radiation, and transmit non-absorbed radiation to neighboring plants. The effect of light quality and intensity is with the shadow component in the environmental offer combined and produces a unique radiation spectrum in the surroundings of the plants ⁽¹⁰⁾. Photosynthetic organs of plants (green leaves and stems) absorb photons in the blue and red stripes of the spectrum of visible radiation, while absorption in the green and infrared stripe is poor and most of these photons are they reflect as diffuse radiation ⁽¹¹⁾.

The efficiency of light, whose energy is stored in photosynthates after a complex process, is a very useful measure to determine the productivity of cultivated plants ⁽¹²⁾. However, the incorporation of the quality of light into measurements of its efficiency has shown that it improves the sharpness of the models with which it is intended to express or predict the productivity of ecosystems ⁽¹³⁾.

The plants have different types of photoreceptors that are useful for relating to the variables of the environmental offer and the capture of light facilitates the control of all the processes involved in the development and conservation of homeostasis. These photoreceptors are of various types and capture radiation in different ranges of the spectrum. Some of them capture light in the UV-B range, while cryptochromes and phototropins receive light in the UV-A stripes and blue ⁽¹⁴⁾. Chlorophylls, meanwhile, absorb the radiation in the blue and red stripes, the carotenes capture the green and yellow colors ^(15,16), and the phytochromes absorb in the red and infrared bands ⁽⁹⁾. The joint action of these pigments in terms of their absorption ranges induces photomorphogenic responses in plants; however, among these groups of photoreceptors, phytochromes and cryptochromes are in relation to photomorphogenesis in plants the most studied ⁽¹⁷⁻¹⁹⁾.

The quality of solar radiation, measured in terms of the color of the light captured by plants, could become a very useful tool in the management of cultivated plants to achieve an increase in the quantity or quality of the harvested product ⁽²⁰⁾.

The growth and development of a plant are influenced, among other factors, by the intensity and quality of the light captured by the organs that perform photosynthesis. When changes in the quality or intensity of the incident radiation are generated, changes occur in the plant that affect its anatomy and physiology, as well as its growth and development, strongly influenced by the quality of light in terms of color or wavelength that reaches the surface of the leaves ^(21,22). It has been found that the quality of light affects the photosynthetic rate, the quantum efficiency for CO₂ assimilation and the maximum activity of phosphoenolpyruvate carboxylase ⁽²³⁾. An example of these is that, these values were significantly lower in *Zea mays* L. (corn) and *Miscanthus giganteus* (eulalia) plants when exposed to blue light, compared to the values obtained when the plants were exposed to light white, red and green. For this reason, it was concluded that the quality of the light affected the rate of CO₂ assimilation in these plants, but not the efficiency of the mechanism of concentration of CO₂ ⁽²³⁾.

The use of coverage in the propagation and production of species of agricultural interest is a practice that arouses more and more the interest of many agricultural science researchers. The modifications of the light environment in which the plant carries out its growth and development, induce in the plant several morphogenetic responses that, on the one hand, counteract adverse conditions and, on the other, promote physiological responses that improve its functioning and increase the quantity and quality of harvested product ⁽²⁰⁻²⁴⁾.

Despite the many studies aimed at determining and clarifying the effects of light and its influence on the growth and development of plants, the results regarding the different responses of plants to stimuli mediated by changes in the light environment have been contradictory. Even sometimes, they are inconsistent, given that the variables that make up the environmental offer are numerous and in many cases, these responses depend on the ability of the plant itself to react to changes in its environment. Plants have different types of photoreceptors, each with a function defined by the wavelength that affects the leaf ⁽²⁵⁻²⁷⁾.

Similarly, the efficiency with which each photoreceptor is capable of capturing a certain color of light can be measured, indirectly, by various methodologies. Plant growth is one of these resources and to measure it there are variables such as dry weight, leaf area and growth rates ⁽²⁸⁾.

Light as a growth factor

The participation of light in plant growth is complex. The characteristics of the light change with the wavelength. There are harmful electromagnetic waves, such as cosmic rays and gamma rays that can injure living organisms. However, living beings can use most of the electromagnetic spectrum that affects the surface of the earth, in particular the visible part of this spectrum, which we call "light." In general, it is known that visible light has approximately the same wavelength as active photosynthetic radiation ⁽²⁹⁾.

Light has two important functions in plant growth: as a source of energy for photosynthesis, because without their participation the upper plants cannot grow and as a stimulus, for example, for the control of plant growth, or for regulate the moment of flowering or morphogenesis ^(30,31).

Therefore, the growth of plants and their development are sometimes in response to changes in the color of the irradiated light altered ⁽¹⁰⁾. On the other hand, due to the great variation of natural lighting conditions and their sessile nature, the plants are forced to acclimatize at the cellular and molecular level due to changes in the environmental offer. Changes in the intensity or quality of light induce alterations in the oxidation and reduction (redox) states of the electron transport chain for photosynthesis, which acts as the start of compensatory acclimatization responses, including functional adjustments and Structural photosynthesis and metabolism ^(32,33).

The quality of light and its influence on plant growth

Photo-selective filters guarantee the plant controlled environments with a certain percentage of opacity (decrease in direct radiation), which depends on the color and nature of the cover material and cause modifications with respect to photosynthetically active radiation (RFA) available for the plant ^(27,34).

Light also influences the total dry weight of the plant. Plants of various crops of agricultural interest have significant differences in biomass production when they are, by the quality of light, affected. The wavelengths between 400 and 550 nm, which correspond to the blue-green range, have induced a decrease in the total dry weight of the plant in some crops such as strawberry ⁽³⁵⁾, beet ⁽³⁶⁾ and broccoli ⁽³⁴⁾. However, they also found that in creek plants (*Anthurium nymphaefolium* C. Koch) ⁽³⁷⁾, the green color (500-550 nm) favored the accumulation of dry matter. It was found that the blue light emitting diode light increased the total dry weight of the plant in cherry tomatoes. The photosynthesis and growth of these tomato plants under the influence of blue light was superior compared to the control plants ⁽³⁸⁾.

According to the same authors, this result could be explained by the findings by some authors ⁽³⁹⁾, who state that blue light becomes a stimulus to induce acclimatization responses in plants, aimed at the distribution of energy in photo-system II (FSII) and in turn, it has to do with the assimilation of CO₂ under high irradiation conditions.

In studies carried out ⁽³⁵⁾, strawberry plants showed an increase in the total dry weight of the plant when they grew under a selective red photo filter, compared to blue, green and yellow color filters ⁽⁴⁰⁾. Some authors found that by exposing the *Chlorella vulgaris* (clorera) microalgae to yellow, red and white monochromatic lights, the total accumulated biomass was increased compared to the micro-algae exposed to blue, green and purple colored lights. Similarly, it was also found those 35 days after sowing, chive plants (*Cyperus rotundus* L.) showed an increase in total dry mass when growing exposed to a red cellophane paper filter compared to filters green and white colors ⁽⁴¹⁾.

The Fv/Fm ratio (ratio between variable and maximum fluorescence), or maximum quantum efficiency of the FSII, decreased significantly in the leaves of the plants that grew under photo-selective filters of yellow and transparent colors compared to the plants exposed to color coverages Blue, green and red. This result was due to the increase in the initial fluorescence (F₀) caused by a high reduction of the first electron receptor. The aforementioned mentioned directly influenced a variation in the electron transport rate that modified the photosynthetic yield of the plant, while the high values of this same variable in the blue, green and red color coverages were related to the efficiency of the mechanisms photo-protectors of the plant that are responsible for modulating the probability of light

damage ⁽³⁶⁾. On the other hand, they found that in *Brassic napus* L. a low value of the relationship between red and far-red reduced not only the value of the Fv/Fm coefficient, but also the contents of chlorophylls a, b, and carotenes ⁽⁴²⁾.

These findings demonstrate that the exposure of plants to different light environments either mediated by photo-selective filters or by additional light sources. It modifies the photochemical performance of the plants and their photosynthetic efficiency, which directly affects the synthesis of photoassimilates and in the total dry weight of the plant.

When the lighting environment undergoes modifications, the plants use various strategies to counteract some conditions that can be considered adverse depending on the physiological state of the plant. In the case of red, blue and green colors, the expansion of the leaf area could be related to the percentage of opacity in each of the filters. In studies conducted on strawberry cultivation, the largest foliar area was presented by plants that grew under red cover, with an opacity close to 71 %. However, in that same experiment, strawberry plants that grew under green cover, with a percentage of opacity of 73.7 %, showed lower leaf area values ⁽³⁵⁾. In the case of beet plants ⁽³⁶⁾ and broccoli ⁽³⁴⁾, the researchers found that the opacity percentages of the blue photoselective filters induced higher leaf area values compared to the red filters. However, the expansion of the leaf area of the plants that grew under the red cover was the highest compared to the other color covers and the control without coverage ^(34,36).

Cultive competition–arvenses

Weeds compete with crops for resources such as light, water, nutrients and space ⁽⁴³⁾. The magnitude of the crop yield loss depends on their emergence time in relation to the crop, density and species ^(2,3). Through the management of weeds in integral systems ⁽⁴⁴⁾, the biological basis of their competence is used to make decisions about their management. MIM systems include a multitude of weed control techniques that include mechanical, cultural and biological methods and incorporate fertilization, rotation, competition, and succession and soil management to reduce weed pressure and maintain crop yields ^(44,45). Specific Integrated Weed Management Systems (MIM) such as the critical period for weed control and weed threshold studies has emphasized the importance of their emergency time in relation to cultivation to understand their competitive interactions ⁽⁴⁶⁾.

The crop - weed competition can also occur under conditions that do not limit resources^(1,5,43). A series of interrelated events, involving so many processes dependent on or independent of the different resources (light and hormonal signals) can provide a sensible explanation for this rapid onset of loss of performance. The ability of crops to detect the presence of neighboring weeds by alterations in the light spectral composition (defined by the red/far-red ratio, that is, R: RL) and then respond through the avoidance response of the Shade mediated by phytochromes, can play an important role in determining the onset and outcome of resource-dependent competition. The role of light quality and the shadow avoidance response in weed competition and crop development are mentioned below in detail⁽¹⁾.

Light as information vehicle: detection of plants in the environment

Since plants are static and fixed organisms, unable to move, except during reproductive processes, they rely heavily on the perception of their environment to make decisions about how to grow and reproduce successfully. One of the variables that deliver essential environmental information to plants is light energy. As an environmental resource, light energy is not only crucial for the creation of biochemical energy through photosynthesis, but it is also vital for the initiation of physiological processes that can alter the morphology of plants. The competition of plants for light can, therefore, change the availability of resources or redirect plant growth so that the ability to obtain the necessary resources to support growth is modified⁽⁴⁷⁾.

Within the atmosphere, the energy of light consists of both direct radiation from the sun and diffuse radiation dispersed from the atmosphere⁽⁴⁸⁾. Regardless of these distinctions, the energy of light itself can be defined as quantity of light or quality of light. The amount of light refers to the amount of photons incident on a surface or the photosynthetic photonic flux density (DFFF) within the spectral range of 400 to 700 nm⁽⁴⁹⁾. The amount of light received by the plant depends on the solar elevation (time of day and year), latitude and cloudiness, as well as the density of the plant in the surrounding environment⁽⁶⁾.

Light quality refers to the spectral distribution of the incident light within the range of 400 to 700 nm. The ratio between red (600-700 nm) and far-red light (700-800 nm), R: RL⁽⁵⁰⁾ ratio is a stable indicator of the light quality environment compared to the incoming DFFF.

This is because the R: RL ratio is strongly influenced by the density of the surrounding canopy, but is less affected by solar elevation and cloud cover ⁽⁴⁹⁾. Solar elevation will influence the R: RL ratio under a canopy when the sun provides sufficient direct radiation in the far light to decrease the R: RL ratio to just 0.2 ⁽⁵⁰⁾. Otherwise, the R: RL ratio remains relatively high (between + 15° and 80° solar angles) and is approximately 1.15 ± 0.02 on clear and cloudy days ⁽⁴⁹⁾. Photosynthetically active radiation (RFA) (radiation required to boost photosynthesis) is available to plants between the spectral ranges of 400-700 nm. Therefore, the green leaves will absorb approximately 90 % of the violet and red light of the ARF and will reflect and transmit approximately 30 % of the green light and 90 % of the distant red light ⁽⁵¹⁾. Due to this selective absorption of violet and red light, plants will transmit and reflect light that has a greater proportion of distant red light ^(51,52).

The detection of the R: RL ratio by plants is perceived by the phytochrome, one of the four photoreceptors, cryptochromes, phototropins and the unidentified ultraviolet B photoreceptors (UVB) capable of controlling changes in the light spectrum within the environment ⁽⁵³⁾. Phytochromes are photochromic pigments that exist in two forms: P, (inactive form) that optimally absorbs around 665 nm and P_{rr} (active form) that absorbs at 730 nm ⁽⁵³⁻⁵⁵⁾. The phytochrome structure consists of a dimeric chromoprotein with two structural domains per dimer, an amino terminal and a carboxyl terminal ⁽⁵⁵⁾. Each dimer contains a light-sensitive chromophore linear tetrapyrrole phytychromobilin that covalently binds to the phytochrome apoprotein through a cysteine residue at the amino terminal ^(53,55). Since the absorption spectra overlap between 600 and 700 nm, P, and P_{rr} allow the four-ring chromophore to be conformationally modified, rearranging the structure of the apoprotein ^(54,55).

The phytochrome remains in the inactive P_r form until the red photons are absorbed, which allows a conformational change to the P_{rr} form, when the far-red photons are preferentially absorbed. When the P_{rr} form absorbs the distant red light, it is converted back to P_r. The relationship between the P_{rr} form and the total phytochrome (P_{total}) is known as the phytochrome equilibrium ⁽⁵⁶⁾. Under conditions of high red light, the phytochrome becomes mainly P_{rr} with the phytochrome balance around 0.54 ± 0.01 ⁽⁵⁷⁾. Phytochrome equilibrium is sensitive to small increases in the R: RL ratio. With an increasing R:RL ratio between

0.02 and 1.61, the phytochrome equilibrium can subsequently increase from 0.09 to 0.65⁽⁵⁷⁾.

Each organ of the plant will show different developmental responses to light, although they depend on the same photoreceptors. The phytochrome remains in the cytosol, regulating both cell and ionic equilibria within the cytoplasm that modulates the growth of the extent and the selected expression of target genes. Through the regulation of genetic expression, phytochromes have been considered to act as kinases that drive the cascade of several biochemical processes or through interactions mediated with transcription factors that direct signal transduction into gene expression⁽⁵⁵⁾.

Phytochromatic signaling can also be initiated by the hormones auxins, ethylene, gibberellic acid, the path of brassinosteroids and cytokinins. Phytochrome has been shown to mediate phosphorylation of auxin-regulated SY_2 genes, which encode AIA (indolic acid) and other related proteins⁽⁵⁸⁾. Auxin is necessary for many processes in plants, including elongation and root development, maintenance of meristems and senescence, as well as cell division and differentiation at the cellular level. The elongation response of Arabidopsis seedlings at a low R: RL ratio has been shown to be auxin dependent⁽⁵⁹⁾. It is argued that elongation depends on the location of auxin synthesis in bud and hypocotyl cells that is transported from the root in shady environments⁽⁵⁸⁾. On the other hand, the redistribution of auxin retards root development since an environment with a high R: RL ratio stimulates the location of auxin in the root, which has been correlated with increases in root length⁽⁵⁸⁾. The production of ethylene hormones will also increase during low light intensity and in an environment of low R: RL ratio. The transgenic lines insensitive to ethylene of tobacco have a reduced elongation response and fail to relocate the leaves in spaces with a lot of light in the canopy. Elongation responses induced by ethylene have been shown to be dependent on gibberellic acid⁽⁶⁰⁾.

The brassinosteroid pathway also activates stem elongation in plants and participates in the lateral distribution of auxin signaling in hypocotyls⁽⁶¹⁾. Other hormones, such as cytokinins, control the activation of cell division, inhibition of root growth, apical domain and senescence. Exogenous cytokinin applications have been shown to restore poor hypocotyl elongation in Arabidopsis, as well as photomorphogenic responses in *Pisum sativum* L. From these studies, several factors (light and hormonal signaling)

influence signal transduction and expression gene that regulate the morphogenic responses of plants; and it has been shown that signal transduction breaks down proteins targeting ubiquitination, which makes it difficult to distinguish between the two signaling processes ⁽⁵⁸⁾.

Shadow avoidance

Interactions between species as a struggle to limit light and nutrient water resources have often been the focus of competition studies ⁽⁴⁴⁾. However, it has been proposed that competition theory is composed of factors that limit resources (direct competition) and that do not restrict them (indirect competition) that is, the quality of light or condition factors that are not consumed ⁽⁴⁷⁾. Although the yield losses of weed competition may be due to limited resources, it has been suggested that non-limiting effects of resources, including hormonal changes and light signaling, may contribute to the onset and result of the limitation competition of resources ⁽⁶²⁻⁶⁴⁾.

Light signaling, specifically the R: RL ratio, has been considered as a preventive indicator of imminent competition for resources, specifically light ⁽⁵²⁾. This indicator results in shadow avoidance responses that include stem and petiole lengthening, branch suppression, accelerated flowering and changes in biomass distribution. While the term "shadow avoidance" clearly suggests that shade is avoided, it has been documented that these responses can also occur in full sun conditions ⁽⁵¹⁾.

The R: RL signal, we can see as an integral component of the competition rather than as a separate process, that drives both morphological and physiological changes. This vision would relocate competition that limits resources consequently rather than as the initial cause of competition ⁽⁴³⁾. Competition is considered as a series of complex physiological processes initiated by light signaling (the R:RL ratio) followed by the expression of shadow avoidance responses so that alterations in the morphology and phenology of the plant can be further aggravated lowering the limiting competition ^(1,65). The degree to which a plant can express these responses depends on its inherent ability to demonstrate phenotypic plasticity ⁽⁶⁶⁾.

Since plants are static organisms, it has been assumed that plasticity has an adaptive value in nature, allowing the development of phenotypes suitable for competitive situations,

particularly when light is limiting ^(4,6). In addition, these plastic responses are expected to convey substantial benefits to fitness ^(8,66).

In the agronomic environment, these shadow avoidance responses are also considered beneficial as they reduce size hierarchies within a crop canopy ⁽⁷⁾. As smaller individuals increase in height to match taller individuals in the canopy, a reduction in intraspecific competition should increase plant productivity ⁽⁴⁾, particularly in high-density environments ⁽⁸⁾.

The expression of shadow avoidance responses can also produce maladaptive phenotypes. If an individual fails to grow taller than his neighbors do, the resources spent on stem production are never recovered, since the interception of the light remains low ^(4,8).

Therefore, if the plastic responses are not balanced with the greatest capture of resources, reproductive costs can occur (defined as the number and weight of the offspring produced). Suggesting that reproductive costs may be the result of morphological and phenological costs (ie, reductions in biomass accumulation and plant development rate) ⁽⁸⁾.

For soy, it is considered to have both vegetative and reproductive plasticity ⁽⁶⁷⁾. The adaptive response of this phenotypic plasticity in soybeans has been reported in numerous studies that include planting density ^(68,69), seedling emergence ⁽⁷⁰⁾ planting density ⁽⁶⁷⁾ and row spacing ⁽⁶⁹⁾. Soy's ability to express phenotypic plasticity has been to its pattern of indeterminate growth attributed; variable branching and seed sink potential ⁽⁵¹⁾. As a result, soy is considered to be more plastic than other specific crop species, such as corn and sunflower ⁽⁶⁷⁾.

Agronomic practices of soy production are designed to optimize the uniformity of the plant (reduce plasticity) within the cultivation platform. The presence of weeds that emerge early and the subsequent light signaling between the weed and the crop can alter this uniformity by triggering the phenotypic responses that follow the avoidance of the shadow. However, when these same weeds are controlled with post-emergence herbicides, this phenotype can be maladaptive for the new environment. The impact of these maladaptive phenotypes on soybean yield is unknown. It is hypothesized that the low proportion of R: RL would trigger typical responses to the avoidance of shade in soybeans and that the subsequent phenotype would result in reproductive costs under conditions without limited resources ⁽⁶⁸⁾.

The combination of physiological and morphological alterations made by phytochrome photoconversion is considered a demonstration of phenotypic plasticity, which is the expression of various phenotypes that arise from a genotype in response to a changing environment ⁽⁸⁾. The shadow avoidance response is the best-known example of phenotypic plasticity and starts with both low reception (shadow) DFFF and low R: RL ⁽⁵²⁾ environments.

Studies conducted by ⁽⁴⁾ showed that the perception of R: RL by phytochrome allows the detection of neighboring plants before the actual shading begins. Plants respond to both reductions in the quantity and quality of light through the expression of shadow avoidance and a set of responses that allows the redistribution of those assimilated towards elongation of the stem ⁽⁵²⁾.

The elongation response is proposed to guarantee the competitive success of a plant when the availability of light decreases ⁽⁴⁾. Other responses to avoid shade include increased apical dominance, accelerated flowering and changes in the distribution of biomass and leaf area. It is proposed that the plants will start the elongation of the stem after detecting a change in the R: RL ratio of the light, which will allow the repositioning of the leaves in regions with a lot of canopy light. Plants probably cause apical dominance simultaneously, to avoid overlapping branches within the canopy ⁽⁵⁵⁾.

When elongation and deletion of the branch are unsuccessful, the other responses such as accelerated flowering and early seed production will begin to increase the probability of survival ⁽⁵⁵⁾. While the redistribution of dry matter to buds and petioles may be at the expense of the expansion of the area of roots and leaves, it has been suggested that these responses are evolutionarily adaptive and critical for plant survival, allowing plants to overcome to its competitors ⁽⁴⁾.

Several aspects of vegetative growth are by mediated responses, influenced for phytochrome. Increases in height and lengths are the most common shadow avoidance responses reported in all plant species and have been linked to a depression in the balance of Prr and Ptotal. An example of the aforementioned is the case of soybean seedlings having a greater length when grown on red and black soil surfaces that reflected a low R: RL ratio ⁽⁵¹⁾.

Similarly, with a reduction in the R: RL ratio by mirrors that simulated plant reflection and elongation increased inside *Sinapsis alba* L. (white mustard), *Datura ferox* L. (chamico) and *Chenopodium album* L. (White ash)⁽⁴⁾, these changes observed in plant height depend on the habitat of the species, as well as on the site of perception of the changing ratio R: RL has been shown. For example, species found in open and arable land, such as common lamb rooms, are more susceptible to changes in the R: RL ratio than species found in closed forest environments⁽⁵⁶⁾. In addition, genetic variation has been found in the phenotypic expression of shadow avoidance in natural populations of *Impatiens capensis* (madama) that evolve in sunny open sites versus closed forest sites⁽⁷¹⁾. The decrease in the response capacity of wood species to red light can prevent the useless allocation of resources since the overflow of neighboring species would never be achieved under these environmental conditions⁽⁵⁶⁾.

Where plants receive, their environmental signals they have an impact on the magnitude of morphological responses that accompany the avoidance of shade. It was shown that the primary leaves perceive changes in the R: RL ratio. In this study, white mustard seedlings that received a localized irradiation of distant red on the stem increased their stem extension rate after 10-15 minutes, while irradiation on the leaf, initiated the elongation of the stem after a 3-4 hours delay. In addition, when the red light was increased in any of these treatments, the stem elongation rate decreased⁽⁷²⁾.

After the onset of stem lengthening, the low R: RL ratio can alter the production of the leaf area of the plant and the rate of leaf appearance. In response to a decreasing R: RL ratio, *Trifolium repens* L. (white clover) increased the production of the leaf area⁽⁷³⁾. In contrast, the leaf area was reduced in soybeans grown in an environment of low R: RL ratio reflected from the adjacent row of soybeans⁽⁵¹⁾. The leaf area was also reduced in tobacco seedlings irradiated with far-red compared to seedlings irradiated with red light. The reduction in the rate of appearance of the leaves has been less documented in all species after the expression of shadow avoidance⁽⁷⁴⁾.

The distribution of plant biomass can also be altered in response to a low R: RL ratio. An increase in the bean sprout biomass was observed in relation to the root biomass (sprout/root ratio) after receiving a pulse of distant red light at the end of the day⁽⁵¹⁾. A low R: RL ratio of the reflected upward light reduced the weights of the stem and root and the

size of the lateral roots of soybeans grown on red and black soil panels ⁽⁷⁴⁾. The leaf: dry weight ratio of the white mustard seedling stem was reduced by 10 % when grown near a green grass fence against yellow grass ⁽⁴⁾. Contrary to these studies, other authors found that both stem weight and total plant biomass of tobacco seedlings increased when they were exposed to a distant red light signal at the end of the day ⁽⁷⁴⁾.

It has been shown that a low R: RL ratio affects chlorophyll content, photosynthesis and leaf structure in plants, depending on the level of incoming irradiation. Some author ⁽⁷³⁾ found that reducing the R: RL index was only sufficient to reduce the total chlorophyll content in white clover leaves while providing a low R: RL ratio (100 $\mu\text{mol m}^{-2} \text{sec.}$) of incoming irradiance, could reduce CO₂ assimilation rate, stomatal conductance, FS11 efficiency and RuBisCo activity as well as reductions in chlorophyll content. In the absence of shade, the effects of a low R: RL ratio of light reflected upward from painted surfaces were sufficient to increase the proportion of chlorophyll concentrations to: by LHC-11 in *Gossypium hirsutum* L. (cotton) cultivated in the field and indoor soybean plants ⁽⁴⁾. A similar effect was found when the tobacco seedlings received red light, which increased the proportion of chlorophyll a: b and total chlorophyll per gram of lamina leaf ⁽⁷⁴⁾.

Changes in the proportion of chlorophyll a: b can be expected in seedlings after irradiation with far-red light because chlorophyll b absorbs only violet and red light and not far-red light. Similarly, because the radiation reaching LHC-11 complexes reaches a maximum of approximately 700 nm, a change in the relative proportions of LHC-11 concentrations versus LHC-I in red light conditions could also be expected far away. The general change in chlorophyll content is not well understood and it is proposed to be positive ⁽⁴⁾ and negatively ⁽⁵⁶⁾ correlates with the avoidance of shade and, presumably, will vary between species and environments.

Phytochrome-mediated shadow avoidance responses are expressed in a wide range of crops and are more frequent when crops are grown at high densities ⁽⁵⁵⁾. Importantly, shading between seedlings can be rare in cultivated fields despite being at high densities planted ⁽⁶⁵⁾. Under non-limiting resource conditions (without shading), corn seedlings grown in the presence of weeds (reflects a low R: RL ratio) increased in height, leaf area and bud: root ratio ⁽⁶⁵⁾. In this study, it was also discovered that corn seedlings reorient their leaves away from weeds in anticipation of future light limitations. In a similar study, the reductions in

the R: RL ratio caused a shadow avoidance response (height increased and the bud: root ratio was reduced) in the growth stage of 4 to 8 leaves in corn ⁽¹⁾. When corn seedlings were exposed to a low R: RL ratio reflected by a substitute weed competitor, there was an increase in plant height and a reduction in the root ratio: emergence, followed by a reduction in the rate of appearance of the leaf and production of biomass and leaf area ⁽⁶³⁾.

It has been suggested that shadow avoidance responses convey substantial fitness benefits when anticipating future limiting resources in natural environments ⁽⁸⁾. Within an agronomic environment, it is proposed that the reproductive efforts of individual plants and canopy size dynamics, canopy growth rate and yield depend on the time and accuracy of shadow avoidance responses ⁽⁵⁵⁾. An example is that taller neighboring plants can quickly suppress individuals through asymmetric competition if retarded individuals are not able to demonstrate shade avoidance responses ⁽⁵⁵⁾. Therefore, within a monoculture, shadow avoidance responses have been a stabilizing force of benefits considered, where smaller individuals can increase their height to reduce the formation of size hierarchies ^(62,67). It is not well understood if the benefits of expressing shadow avoidance responses are altered in situations of interspecific competition of weeds. In addition, the expression of shadow avoidance in crops from agricultural environments can result in phenotypic costs (reductions in the growth of roots, leaves or fruits) if there are no net benefits for the energy expenditure used during the initial lengthening ⁽⁸⁾.

Several studies have discussed the costs associated with the expression of shadow avoidance ⁽⁷²⁾. Maladaptive phenotypes may be the result of an environmental signal that is unreliable or when environmental changes occur suddenly ⁽⁷⁵⁾. The elongation of *Ranunculus repens* L was discovered. In response to competition from plants, it was beneficial in open environments, but the plant presented difficulties when there were flood problems ⁽⁷⁶⁾. In these examples, a plant may be unable to assume an appropriate phenotype when the environment is changing rapidly so that it suffers damage before it fully adapts (stress situations). Plants that have expressed an early shadow avoidance response can also be phenotypically limited in later stages of growth ^(75,76).

Seedlings of *Abutilon theophrasti* Medic show shade invitation in response to a low R: RL ratio and were less receptive when they were exposed to a second low R: RL treatment compared to seedlings that had not experienced an initial shadow avoidance response.

These studies suggest that shadow avoidance responses expressed during the early stages of crop development can avoid phenotypic adjustments during subsequent abiotic stress and competition that limits resources ⁽⁷⁶⁾.

CONCLUSIONS

For all the above, it is necessary to continue providing research, which demonstrates the importance of the quality of light in crops specifically in the ratio between red and far-red (R: RL). It is a fundamental component that it influences the shade between neighboring plants and in most of the cultivated fields are weed plants that also interfere in economic crops by establishing a marked competition with them for light, water, nutrients, CO₂ and physical space, or for the production of substances harmful to the crop. Therefore, the early detection of neighboring plants can be an important mechanism for the management of weed plants to avoid competition between the light factor and arable plants.

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