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The Shade Avoidance Syndrome Under the Sugarcane Crop

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1. Introduction

Sugarcane is grown mainly for sugar and ethanol production, belongs to the Poaceae family, genus *Saccharum* native to Southeast Asia and India and cultivated intensively in tropical and subtropical areas throughout the world, and it plays a significant role in the world economy and the area cultivated yields observed to have progressively increased to remarkable levels in the last 10 years (Azevedo et al., 2011). Commercial sugarcane, mainly the interspecific hybrids of *S. officinarum* and *S. spontaneum* would greatly benefit from biotechnological improvements due to the long duration (10-15 years) required to breed elite cultivars, more importantly there is an ongoing need to provide durable and disease and pest resistance in combination with superior agronomic performance (Lakshman et al., 2005).

There is an increasing pressure worldwide to enhance the productivity of sugarcane cultivation in order to sustain profitable sugar industries (Hanlon et al., 2000), for example, improvement of industrial processes along with strong sugarcane breeding programs in Brazil, brought technologies that currently support a cropland of 7 million hectares of sugarcane with an average yield of 75 tons/ha (Matsuoka et al., 2009). Besides, biomass has gained prominence in the last years as new technologies for energy production from crushed sugarcane stalks developed a sugarcane industry that currently is one of the most efficient systems for the conversion of photosynthate into different forms of energy, for example, the production of ethanol as a liquid fuel.

The crop is vegetatively propagated by stalk cuttings, having one to three buds, known as seed pieces or setts, is a perennial crop regrowing from these vegetative buds after the crop has been harvested giving subsequent regrowth or crop cycles known as ratoonings. The germinating bud develops its own root system, and several shoots arise by heavy tillering which produces a canopy of leaves during closing-in stages of crop growth; the term "closed crop" defines a community of plants, of uniform height, which extends indefinitely in the horizontal plane. Within a "closed crop" canopy, we might expect the leaves in any particular horizon to experience a uniform environment, and we might further expect the only significant source of environmental variation to be found in the vertical plane (Charles-Edwards, 1981), thus for the sugarcane crop the production of stalks, to quickly achieving a closed canopy, is important as a means of increasing competition with the weeds growing underneath and for crop protection against adverse conditions.

Sugarcane uses the C₄ pathway of photosynthesis where CO₂ is efficiently captured, in the mesophyll cells giving a four-carbon organic acid, oxaloacetate which is the first product of CO₂ fixation, and recycled inside the leaves because of the compartmentalized arrangement of leaf tissues into bundle sheath and mesophyll cells (Hatch & Slack, 1966). This photosynthetic specialization of cell types allows leaves to fix CO₂ at higher rates and at lower stomatal conductance; however other C₄ species dominate the list of the world's worst weeds which in many cases, like for the sugarcane crop, are among the most noxious plants to the crop. Failure to control weeds during early stages of crop growth can reduce yields appreciably. As a C₄ plant sugarcane grows better at high irradiances and temperatures and is also resistant to some environmental conditions very common in the field, especially in the tropics, such as water deficits. Because of these attributes improved cultivars with increased resistance to stressful conditions, adequate management of water and other resources have been developed.

Light interception is an important component of the environment within a crop canopy; in sugarcane solar radiation is intercepted by the extended leaves but canopy architecture can modify photosynthetic performance. Thus commercial sugarcane varieties may have erect or planophile leaves but in a closed canopy most of the light is intercepted by the top fully expanded leaves. Erect leaved varieties, appear to be more efficient capturing light than those with more planophile or droopy leaves, specially at high plant densities. In this context strategy for weed control in order to improve farm management must include the knowledge of the dynamic and biology of plants growing underneath the canopy.

Canopy shade is an important part of weed-crop interference, thus the effect of radiation quality (wavelength) and quantity (irradiance, photon flux) on the diversity of plant species is a serious constraint to production and crop management. The sugarcane crop canopy closes at about three months after planting/sprouting, and the population of plants under the canopy changes in number and diversity depending on the ability of some species to escape or avoid shade by a series of developmental changes at the individual and population levels. Under field conditions, for each sugarcane ratoon cycle (regrowth), recognition of the species diversity as well as their strategies for shade avoidance, before and after canopy closure, is relevant to agricultural applications and plant biology and as research on the shade avoidance syndrome has been mostly restricted to individual plants and under controlled conditions, the objective of the present study is to provide information about what happens under a sugarcane canopy under field conditions, as related to spectral shifts within the canopy and the changes in species diversity.

The shade avoidance syndrome (SAS) in plant neighborhoods such as those underneath a crop canopy, is associated with both the quality (wavelength) and quantity (energy) of light and the decrease in the red/far red ratio (R/FR), as the light environment becomes enriched in far red radiation that is reflected by the leaves of all plants, including the crop itself. A reduced R/FR is the proximity signal that is perceived by the plants alerting that they are being shaded, and in fact it is perceived in early developmental stages, as shown by Ballare & Casal, 2000; Ballare et al., 1991; Smith et al., 1990. Small changes in amounts of red relative to far red light have been shown to alter the equilibrium of different phytochrome forms appreciably, which plays a major role in plant development. Perception of light quality and quantity at the stem level may elicit morphological adaptations in the plants growing beneath the canopy, that may result in shade tolerance or avoidance, and under field

conditions, slight differences in height, degree of tillering, earlier flowering and increase in the shoot/root ratio among different species, might imply a greater potential to survive escaping shade; thus recognition of plant species before and after canopy closure as well as the changes in the light profiles under the canopy, are important for weed detection in cultivated crops as a means to ascertain which species avoid shade.

Shade avoidance responses are mediated by multiple forms of phytochromes; despite of initial attempts to ascribe the SAS to the action of a single member of the phytochrome family (Franklin & Whitelam, 2005). In this context and according to Schmitt (1997), the shade avoidance response has undergone adaptive evolution as quantitative genetic variation in R:FR ratio sensitivity has been detected in wild populations. The "Shade Avoidance Syndrome" has been described by Morgan et al (2002); Smith (1982); Smith & Whitelam (1997) as an accelerated extension growth (as seen by an increase in shoot and petiole elongation), reduced branching (increase in apical dominance), earlier flowering (i.e., rate of flowering markedly accelerated) and increase in the shoot to root ratios, changes in plant architecture and leaf shape, among other responses not easily seen under field conditions, however, we have used the term "Agronomic Shade Avoidance Syndrome" to include species that persist and compete successfully with the crop after canopy closure, but not by means of growth responses normally associated to the SAS under field conditions, such as morphological changes in leaf shape, stem elongation or plant architecture. The persistence of such species after canopy closure, may be associated to the seed bank, sunflecks in gaps within the canopy and the production of underground organs (that become well established and almost impossible to control by shade) as well as climbing strategies such as in tie-vines.

From another point of view, the shade avoidance syndrome is not restricted to terrestrial ecosystems but has also been studied in connection to other stress responses, such as submergence (Pierik et al., 2005). In complete submergence, well-adapted plants may overcome the effects by adopting an avoidance strategy to induce growth responses, phenotypically similar to those described when plants are shaded by proximate neighbors.

In this chapter, we will analyze light profiles within sugarcane canopies and how changing light conditions in a closed-in canopy, may affect the development and diversity of plant species, as seen in the field at the individual level. Then, based on the results of experimental trials and under controlled conditions, some of the strategies to escape or avoid shade and to capture light more efficiently, will be discussed for different species known to be noxious to the sugarcane crop.

2. Research methods

2.1 Field experiments

Field experiments were conducted in two different sites where sugarcane is a mayor crop in Venezuela. The first experiment was established with sugarcane plants (*Saccharum* spp hybrid var. PR-692176 (first ratoon crop) in a 625 m² plot inside a commercial regrowth of a sugarcane field in Chivacoa, Yaracuy State and the second experiment, in 2500 m² experimental area in the Agricultural Experimental Station at the College of Agriculture in the Central University of Venezuela in Maracay, Aragua State, using droopy and erect leaf commercial varieties planted from cane (initial or plant cane crop).

2.1.1 First field experiment

The objectives of the first trial were: 1) to acknowledge the species that were present before and after the sugarcane canopy closure; 2) to determine the effect of canopy shade on the developmental responses that could be associated to the SAS under field conditions and 3) to measure the amount of light in terms of photon flux density of photosynthetically active radiation (PAR), at different points within the crop and weed canopies.

Standard management practices included hand planting of 50 cm long stalks or seed pieces placed at rates of 24000 stalks/ha in the bottom of furrows spaced 1,5 m and covering the sugarcane seed pieces with soil. Soil was regularly irrigated every two weeks, or as needed, and fertilized before planting with ammonium phosphate and with a second application of Urea+KCl at 45 days after planting. Chemical weed control in the drive areas of the experimental plot was not performed for the experiments discussed in this chapter. For species recognition, ten 0,5 m² fixed wooden squares were randomly distributed in the field and all plant species (except for those of the crop) inside the squares were collected at 60 and 90 days after germination (sprouting of the buds from the seed pieces or stalks), to acknowledge for the presence and number of different species, and for plant height and leaf size determinations. Flowering and any other visual symptoms associated to the shade avoidance response were as well registered.

In order to compare the plants growing under a "canopy in a non-shaded condition", in some previously selected rows in the same plot the leaf arrangement of sugarcane plants, was artificially changed by loosely bounding the leaves in an upright position along the stem, simulating an plant biotype with erect leaves.

Light quantity was measured as Photosynthetically Active Radiation (PAR as $\mu\text{mol m}^{-2} \text{s}^{-1}$) using a quantum-radiometer-photometer LiCor 185B by positioning the quantum sensor at different heights above and below the sugarcane canopy and above the population of weeds growing in shaded and non-shaded sites beneath the crop, as shown in Fig. 1. Instant measurements, at five different points in each position (sites) within the canopy, were performed between 12M and 1PM at 60 days after germination of buds from the seed pieces or sugarcane stalks, for the two leaf arrangements described in the preceding paragraph.

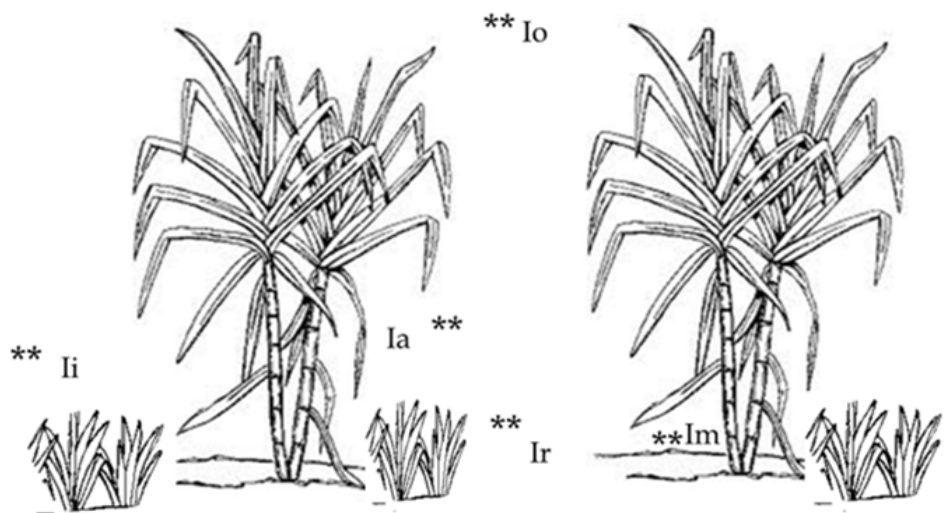


Fig. 1. Sugarcane plants and weed underneath the canopy showing quantum sensor positions (Io, Ii, Ia, Im) to register PAR values shown in Table 1.

2.1.2 Second field experiment

For the second field experiment, with the objective of recognizing weed species before and after canopy closure for two commercial sugarcane varieties with contrasting growth habits, and to register radiation profiles within the canopy, a plant crop (first cycle) was established in 2500 m² experimental area in the Agricultural Experimental Station at the College of Agriculture in the Central University of Venezuela in Maracay, Aragua State. The experimental area was divided into four 625 m² plots where droopy and erect leaf commercial varieties, C 266-70, which is a fairly typical variety, with planophile or droopy leaves and RB 85-5035 with more erect leaves, were planted from initial plant canes. Crop management practices were as described for the first experiment except for the fact that 10 randomly located fixed wooden 1m² squares, were used to collect the plants growing under the crop canopy and that weed control, in some previously selected drive areas between rows, was manually performed.

Spectral profiles within sugarcane canopy: energy distribution of visible and near infrared radiation above, within, and on the soil below a canopy a sugarcane plants with droopy or erect leaf commercial varieties were registered and light spectra (Spectral Irradiance, W m⁻² nm⁻¹ and Quantum Intensity, $\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1}$) were measured in the field plot during the growing season, at the beginning of canopy closure (three months from planting date), with a spectroradiometer ASD FieldSpecpro VNIR 350-1050 nm, using hyperspectral analysis, approximately at 20 cm above the crop, at 30 cm above and below the weed canopy and at 30 cm above the soil, in shaded and non shaded sites.

2.2 Greenhouse experiments

Three of the most abundant species known to be noxious weeds to the sugarcane crop and present in the experimental fields (*Rottboellia cochinchinensis*, *Leptochloa filiformis* and *Cyperus rotundus*), were selected for the study of growth responses associated to shade quality (wavelength) and quantity (Photon flux density, PFD 400 - 700 nm). Seeds of *Rottboellia* and *Leptochloa* and corms from *Cyperus* were sowed in pots, containing soil, shaded by cabinets covered with red, blue and green cellophane paper and under low PFD neutral shade while another group was left uncovered. Cabinets were directly exposed to daylight. Effects were compared separately for each species when plants in any of the groups showed visual symptoms of deterioration.

3. Research results

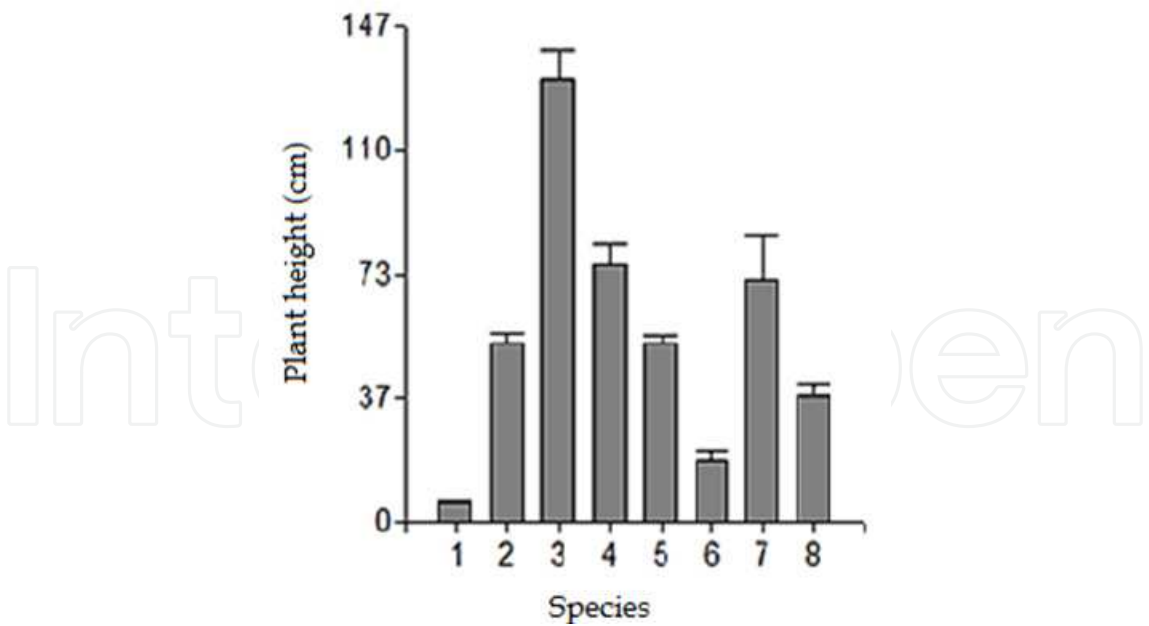
3.1 First field experiment

Under the sugarcane canopy in the **first field trial**, at 60 days after sprouting when canopy closure was not complete, a stratified pattern in plant height for the different species was observed. Plants species identified under the sugarcane canopy before canopy closure were (Lara & Ascencio, unpublished): *Ruellia tuberosa* L., *Trianthema portulacastrum* L., *Amaranthus dubius* Mart, *Eclipta alba* (L.) Hassk, *Tridax procumbens* L., *Lagascea mollis* Cav., *Heliotropium ternatum* Valhl and *H. indicum* L., *Cyperus rotundus* L., *Commelina diffusa* Burm, *Ipomoea indica* (Burm.) Merr and *I. batatas* (L.) Lam, *Momordica charantia* L., *Cucumis dipsaceus* Ehreimb. ex Spash, *Ceratosanthes palmata* (L.) Urb, *Euphorbia hirta* L. and *E. hypericifolia* L., *Croton lobatus* L. *Phylathus niruri* L., *Desmanthus virgatus* (L.) Willd, *Spigelia anthelmia* L., *Leptochloa filiformis*

(Lam.) Beauv, *Rottboellia cochinchinensis* (Lour) W. Clayton, *Panicum fasciculatum* Sw., *Echinochloa colona* (L.) Link, *Eleusine indica* (L.) Gaerth, *Cynodon dactylon* (L.) Pers, *Dactyloctenium aegyptium* (L.) Wild, *Portulaca oleracea* L., *Capraria biflora* L., *Physalis angulata* L., *Corchorus orinocensis* Kunth, *Priva lappulaceae* (L.) Pers, *Kallstroemia maxima* (L.) Hook & Arn.

It is important to note that 23% of the species listed above belong to the Poaceae (as sugarcane) and that the rest are distributed in 18 families, thus 8 species known to be noxious for the sugarcane crop were selected for this study, where, except for *Trianthema portulacastrum*, *Heliotropium ternatum* and *Cyperus rotundus* the other five (*Leptochloa filiformis*, *Rottboellia cochinchinensis*, *Panicum fasciculatum*, *Panicum maximum* and *Cynodon dactylon*) belong to the Poaceae.

When the first evaluation was made in the field 30 days after sprouting a reduction in the number of plants for the species *Cyperus rotundus* and *Leptochloa filiformis* was observed at first sight under the shade of other plants (either the crop or other plants in the neighbourhood), but not for other species in the site, a first indication that shade was affecting plant performance, plant loss or even causing plant death. Differences in plant height (stem or internode elongation) for the species growing below the sugarcane canopy were observed after 60 days in the following order: *Rottboellia cochinchinensis* > *Panicum maximum* > *Panicum fasciculatum* > *Heliotropium ternatum* > *Trianthema portulacastrum* > *Cyperus rotundus*. Thus, these species except for *Cyperus rotundus*, *Trianthema portulacastrum* and *Heliotropium ternatum*, escaped canopy shade by an increase in plant height. Maximal plant height approaching that of the crop after full canopy closure (90 days) was observed for *Rottboellia exaltata* and *Panicum maximum*, which effectively escaped shade, competing successfully with the crop for light (Fig 2).

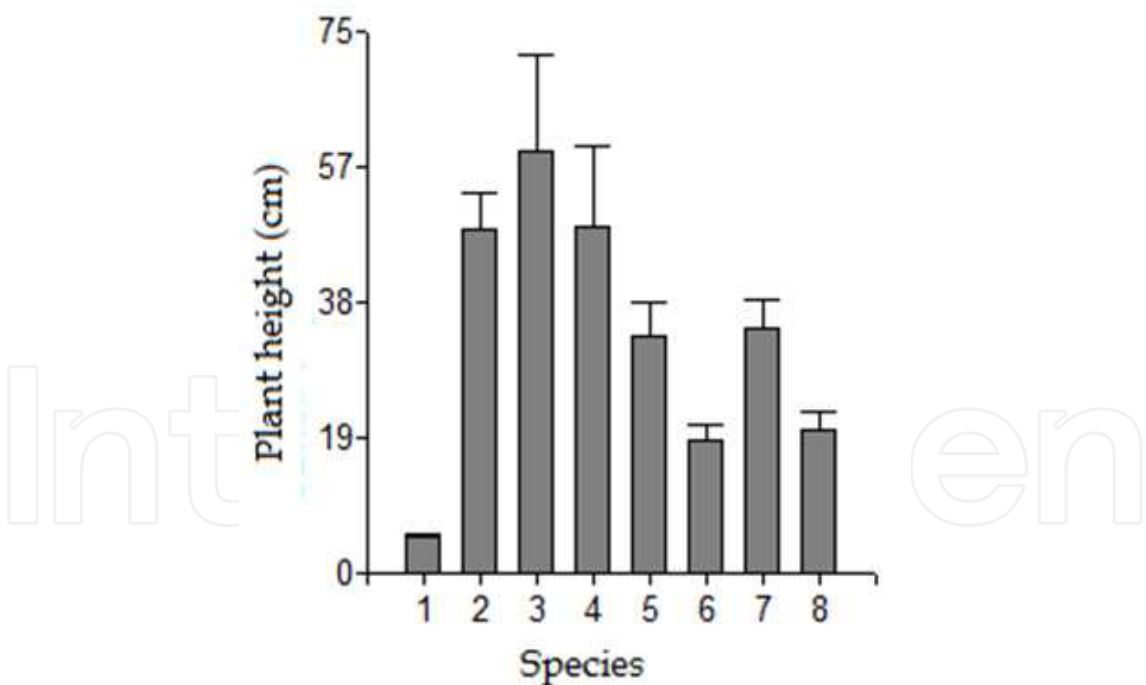


Species: 1. *Cyperus rotundus* L., 2. *Leptochloa filiformis* (Lam.) Beauv., 3. *Rottboellia cochinchinensis* (Lour.) W. Clayton, 4. *Panicum fasciculatum* Sw., 5. *Heliotropium ternatum* Vahl., 6. *Trianthema portulacastrum* L., 7. *Panicum maximum* Jacq., 8. *Cynodon dactylon* (L.) Pers. (Lara & Ascencio, unpublished).

Fig. 2. Plant height for species growing under a sugarcane (*Saccharum spp* hybrid) canopy with droopy leaves (*Saccharum spp* hybrid var PR692176) after 90 days of crope emergence.

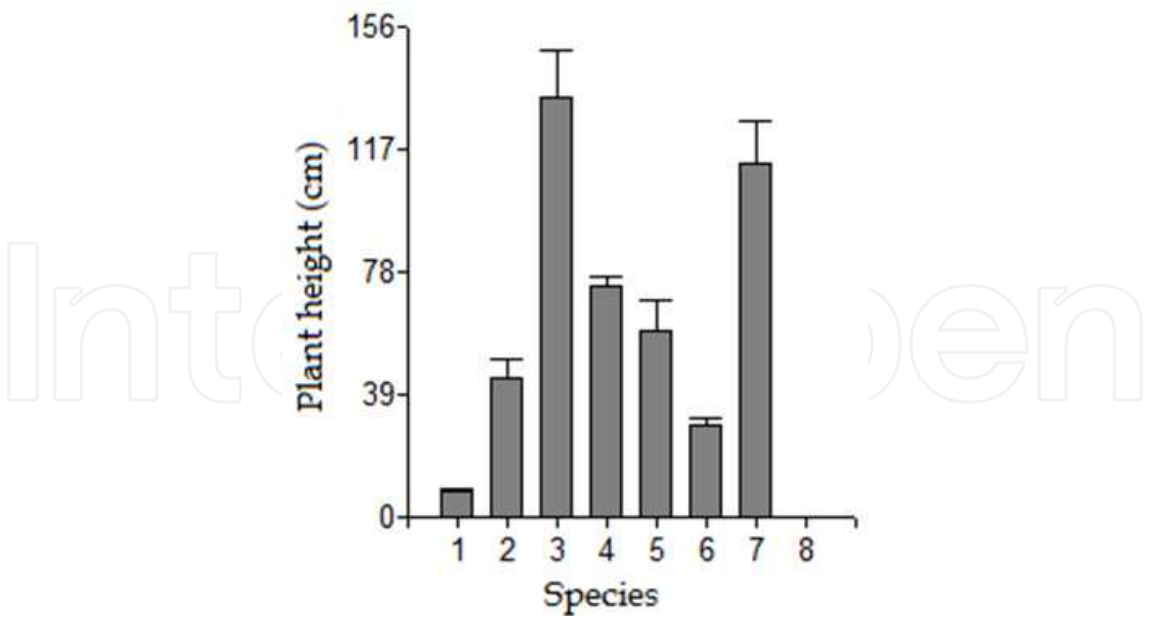
Two growth strategies associated to the SAS as seen in the field were observed: increased internodes length and decreased leaf size. The species that showed higher sensitivity towards canopy shade were *Cyperus rotundus* and *Trianthema portulacastrum*, as plants eventually died in this condition apart from *Leptochloa filiformis* in which changes in leaf morphology, such as broader but shorter leaves were observed, as well as an early flowering of the individuals in order to produce seeds, which is also a means of escaping shade for population survival; however, the plants eventually died under the shade. Changes in leaf shape were also observed for plants escaping canopy shade through stem elongation, as in the case of *Rottboellia cochinchinensis* and *Panicum fasciculatum* were shorter leaves were observed as compared to those growing before canopy closure.

The effect of weed canopy shade on the development of plants in the neighborhood was observed when sugarcane leaves, in some selected rows, where loosely bound around the stem simulating an extreme erect biotype. As seen from Figure 3, at beginning of the crop cycle (60 days after sprouting) plant height for the different species were: *Rottboellia cochinchinensis* > *Leptochloa filiformis* > *Panicum fasciculatum* > *Heliotropium ternatum* > *Panicum maximum* > *Trianthema portulacastrum* > *Cynodon dactylon* > *Cyperus rotundus*, and after 90 days at full canopy closure (Fig.4), a steeper gradient for plant heights was observed as follows: *Rottboellia cochinchinensis* > *Panicum maximum* > *Panicum fasciculatum* > *Heliotropium ternatum* > *Leptochloa filiformis* > *Trianthema portulacastrum* > *Cyperus rotundus*. Plants from *Cynodon dactylon* were absent from the stand, unable to tolerate shade.



Species: 1. *Cyperus rotundus* L., 2. *Leptochloa filiformis* (Lam.) Beauv., 3. *Rottboellia cochinchinensis* (Lour.) W. Clayton, 4. *Panicum fasciculatum* Sw., 5. *Heliotropium ternatum* Vahl., 6. *Trianthema portulacastrum* L., 7. *Panicum maximum* Jacq. y, 8. *Cynodon dactylon* (L.) Pers. (Lara & Ascencio, unpublished)

Fig. 3. Plant height for species growing under a sugarcane (*Saccharum* spp hybrid var PR692176) canopy for 60 days after emergence with their leaves loosely bound to the stem simulating and erect leaf arrangement.



Species: 1. *Cyperus rotundus* L., 2. *Leptochloa filiformis* (Lam.) Beauv., 3. *Rottboellia cochinchinensis* (Lour.) W. Clayton, 4. *Panicum fasciatum* Sw., 5. *Heliotropium ternatum* Vahl., 6. *Trianthema portulacastrum* L., 7. *Panicum maximum* Jacq. y 8. *Cynodon dactylon* (L.) Pers. (Lara & Ascencio, unpublished)

Fig. 4. Plant height for species growing under sugarcane (*Saccharum* spp hybrid var PR692176) canopy for 90 days after emergence with their leaves loosely bound to the stem simulating and erect leaf arrangement.

Light quantity, an important component of shade, was measured in shaded and non-shaded positions within the sugarcane canopy (see Fig. 1), and for two leaf arrangements along the stem: droopy (planophile leaves) and erect (leaves bound to the stem to an erect position). PAR was measured in full sunlight above the crop at different crop heights (I_o), above the canopy of weeds at 30 cm above soil level (which is in average the height of the population of weeds underneath the crop), under shaded (I_a) and non shaded (I_i) positions, at soil level at sites not shaded by plants (I_r) and also under the canopy of weeds growing beneath the canopy of sugarcane leaves (I_m). Values for (I_i) are more likely to be sunflecks reaching gaps inside the canopy, while I_a are PAR values above the canopy of weeds but underneath the sugarcane leaves.

As seen from the results shown in Table 1, maximum PAR values were observed above the crop ($I_o = 1310$) and above the canopy of weeds exposed to light in the erect leaf arrangement (1150) growing below the crop canopy at 30 cm above soil level (I_i) . PAR was 50% higher for (I_i) than under the shade of leaves (I_a), with low extinction values from I_o for droopy and erect leaf arrangement, equal to -9.3 and -12.2% respectively. Another characteristic of the light environment underneath a canopy of leaves, is that direct sunlight may arrive as high intensity light beams known as sunflecks. In Table 1, values for (I_i) are more likely to be sunflecks in drive areas between rows. For droopy leaf arrangement and underneath the crop canopy (I_a), extinction values from I_o were -38.3% above the weed canopy, and -70% at soil level, while for the erect leaf arrangement, higher values equal to -65.0 and -82.0% were observed for the extinction from I_o . There is no clear explanation for this difference except for the fact that for the erect or vertically inclined leaf arrangement,

sugarcane leaves were bound to the stalk allowing more light for the weeds to grow, so attenuation of radiation might have occurred by the scattering of radiation by the leaves. PAR values at soil level were dramatically lower under canopy shade (Im) as compared to that in between rows (Ir) with extinction values of -70 and -23% respectively; however it is worth noting that when these measurements were taken, crop canopy closure was about 20% of the maximum at full closure when values between rows may be much lower.

Leaf arrangement	Crop canopy		Weeds Underneath Crop Canopy*		Soil Level	
	PAR	Height	PAR		PAR	
	Above Crop (Io)	(cm)	Exposed to Light (Ii)	Shaded (Ia)	Exposed (Ir)	Shaded (Im)
Droopy	642**	66.4	582 (-9.3%)	396 (-38.3%)	494 (-23.1%)	194 (-70%)
Erect	1310	60.2	1150 (-12.2%)	460 (-65%)	1032 (-21.2%)	236 (-82%)

* Weed canopy average height, 30 cm above soil

** Heavy cloud

Table 1. Incident photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) within a sugarcane canopy (see Figure 1, for Io, Ii, Ia, Ir, and Im, quantum sensor positions). Values in parenthesis are expressed as percentages of Io.

Incident radiation transmitted by the leaves is a function of the extinction coefficient, which quantifies the influence of the arrangement of the leaves in the canopy. According to Tolenaar & Dwyer 1999, in the three-dimensional space above the soil, the leaf area arrangement is determined by (1) plant height, (2) plant spacing (i.e., row width vs. distance between plants in the row), (3) leaf length and width, (4) leaf angle with respect to the horizontal plane, and (5) leaf orientation with respect to north and south (i.e., azimuth angle). The extinction coefficient is relatively constant during the middle of the daytime when close to 90% of the total daily incident photosynthetic photon flux density is received.

Population dynamics (amount and diversity of species) below the canopy is highly influenced by the light environment (shade) and also by sunflecks which play an important role in the germination of new species not seen at the beginning of the crop cycle, as a great number of weed species have small, photoblastic seeds. This is discussed in the second field experiment as part of an strategy of escaping shade at a population level, as new species grown under shade conditions, are more likely to tolerate shade competing successfully with the crop for light. The importance of measurements of light (quantity and quality) in canopies is highlighted by Holt (1995) as a means to improve weed management as many plants possess the ability to adapt quickly to changes in light during the life cycle, species such as *Amaranthus palmeri*, *Crotalaria spectabilis*, *Cyperus rotundus*, *Cyperus esculentus*, *Imperata cylindrica* and *Abutilon theophrasti*, are mentioned as examples of weeds that respond to shade, thus, by understanding physiological and morphological mechanisms of

competition for light between weeds and crops will it be possible to manipulate crop canopies to suppress weeds.

3.2 Second field experiment

According to the results of the second field trial, a higher number of species survived after the closure of the canopy of sugarcane plants with erect leaves, as compared to those for droopy leaves, and new species appeared: *Amaranthus* sp, *Bidens pilosa*, *Cyperus rotundus*, *Euphorbia heterophylla*, *Sida* sp, *Aldana dentata*, *Desmodium* sp, *Phyllanthus niruri* and *Eclipta alba*; and the new species (*Aldana* sp., *Phyllanthus* sp. and *Eclipta* sp) appeared. Under the canopy of sugarcane plants with droopy leaves, *Amaranthus* sp, *Commelina diffusa* (new), *Bidens pilosa*, *Mimosa* sp, *Euphorbia heterophylla* and *Desmodium* sp, were observed. In the experimental field of the second experiment, *Rottboellia exaltata* (which is capable of avoiding shade) was not found, and plants of *Leptochloa filiformis*, *Cynodon dactylon*, *Echinochloa colona*, *Ipomoea* sp, *Cucumis melo*, *Ruellia tuberosa* and *Cyperus rotundus*, progressively died under the shade of the canopy with droopy leaves.

It is important to note that some of the species that persisted after canopy closure were located at points within the canopy where light penetration was higher, while others were part of the seed bank (new species that appeared after canopy closure) which, in our opinion, may be an strategy for "agronomic shade avoidance" at a population level. Plants are actually seen growing under the canopy, thus escaping or avoiding shade in some way. In this category, the morning glory group of species (*Ipomoea spp*) referred to as tie-vines, may also be included as they are capable of climbing and forming a dense mat that grows over the crop canopy, escaping shade. Perennial grasses, found under the sugarcane canopy are another example of "agronomic shade avoidance", as sugarcane itself is a grass and conditions able to its development are also conducive to grass weed growth. As seen from the results of this study, perennial grasses such as *Cynodon sp* and *Panicum spp*, persist after canopy closure. In short, during each crop cycle different species are found as part of the biodiversity of the seed bank and the changing environment associated to the quantity (PAR) and quality (wavelength) of light in a closed-in canopy.

Radiation measurements: Energy distribution of visible and near infrared radiation (irradiance and quantum intensity) was measured underneath the sugarcane canopy; as leaf angle with respect to the horizontal plane and leaf length and width, influence the extinction of light within the canopy, and that these variables are associated to variety types, in this second field trial radiation profiles were compared within sugarcane canopies with either planophile (droopy or horizontal leaf arrangement) or erect (vertically inclined) leaves and in selected rows with high and low weed populations.

The energy distribution of radiation above the sugarcane canopy (light profile), is shown in Fig. 5 in terms of Quantum Intensity (QI, in $\mu\text{mol m}^{-2}\text{s}^{-1}\text{nm}^{-1}$) of full sunlight on a clear day in Maracay, Aragua ($10^{\circ} 11'\text{N}$, 440 msl). Figures 6 and 7, show energy distribution of visible and near infrared radiation within a canopy of sugarcane leaves with planophile leaves and with low and high populations of weeds growing underneath and Fig. 8 and 9 for a canopy with erect leaves with low or a high populations of weeds respectively.

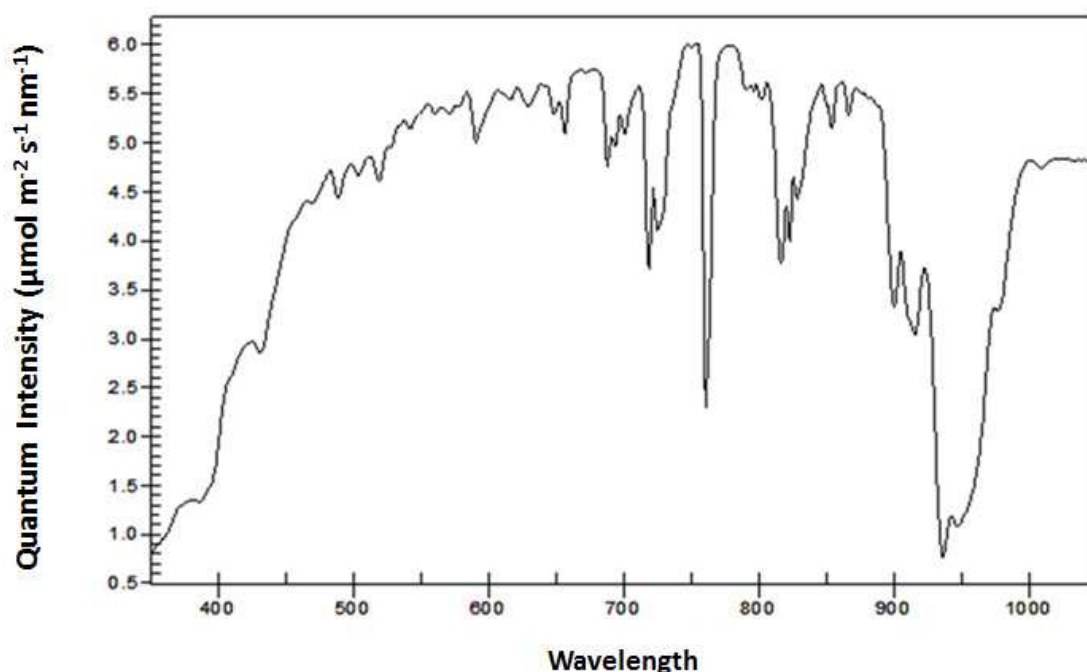


Fig. 5. Quantum energy distribution of full sunlight above a sugarcane canopy in Maracay ($10^{\circ}11' \text{ N}$, 440 msl). Values are given as Quantum Intensity (QI $\mu\text{mol m}^{-2} \text{ s}^{-1} \text{ nm}^{-1}$)

The spectroradiometric measurements clearly show that the decreased QI of radiant energy within a sugarcane canopy is not uniform at all wavelengths and that spectral composition of shade light differs from that above the canopy (Fig. 1), because of the selective absorption of PAR (400-700 nm) by the leaves. Therefore, plant responses that may be attributed only to a reduced number of photons, or light intensity of radiant energy, could be confused with responses to a shift in the spectral composition of light received by the shaded leaves. In fact, a decreased R/FR is the most important radiation component within canopies as transmittance of far red radiation (730 nm) is substantial. This is shown in Figs 6 to 11 for the sugarcane canopies of this study. The population of weeds below the crop canopy and also crop architecture, influences the QI distribution of wavelengths reaching the soil at 30 cm from the ground, i.e. above the canopy of weeds. As compared to spectral distribution of sunlight (Fig 1), QI increases at wavelengths in the far red (radiation mostly reflected and transmitted by the leaves of the whole plant population crop+weeds) but differences are also found for QI values in canopies with planophile (Fig. 6 and 7) or erect leaves (Figs. 8 and 9) with low or high weed populations growing underneath. In deep shade QI values are lower.

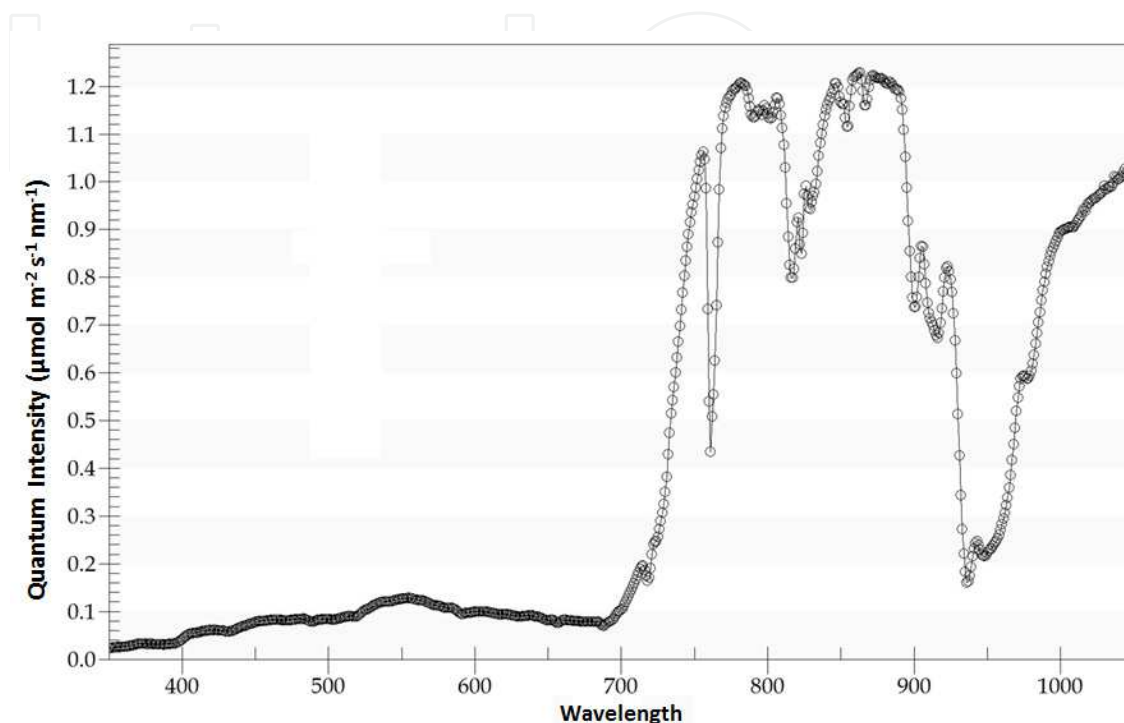


Fig. 6. Quantum energy distribution within and below a closed canopy of field grown sugarcane with planophile (droopy) leaves and a low population of weed growing underneath the canopy. Measurements were taken between adjacent rows at 30 cm from the ground. Values are given as Quantum Intensity (QI $\mu\text{mol m}^{-2} \text{s}^{-1} \text{nm}^{-1}$)

Shifts in the amount of radiation beneath the canopy with planophile leaves and a low population of weeds, indicates that QI in the visible (400-700 nm) was lower than for a high population of weeds and, as could be expected, a higher QI was observed for wavelengths in the far red when the population of weeds was high (Fig.7). When comparing these results with the radiation profiles, as QI and irradiance, within a canopy of sugarcane leaves with erect leaves (Fig. 8 and 9), radiation reaching the soil in the visible was higher than for a canopy with planophile leaves, but still a higher QI for wavelengths in the near infrared was observed when the population of weeds was high. Except for the near infrared water sensitive portion (940-1040 nm), this is the shade that plants actually "see" and it is perceived at very early stages of development, alters phytochrome photoequilibrium and initiates growth responses to avoid the shade (shade avoidance syndrome).

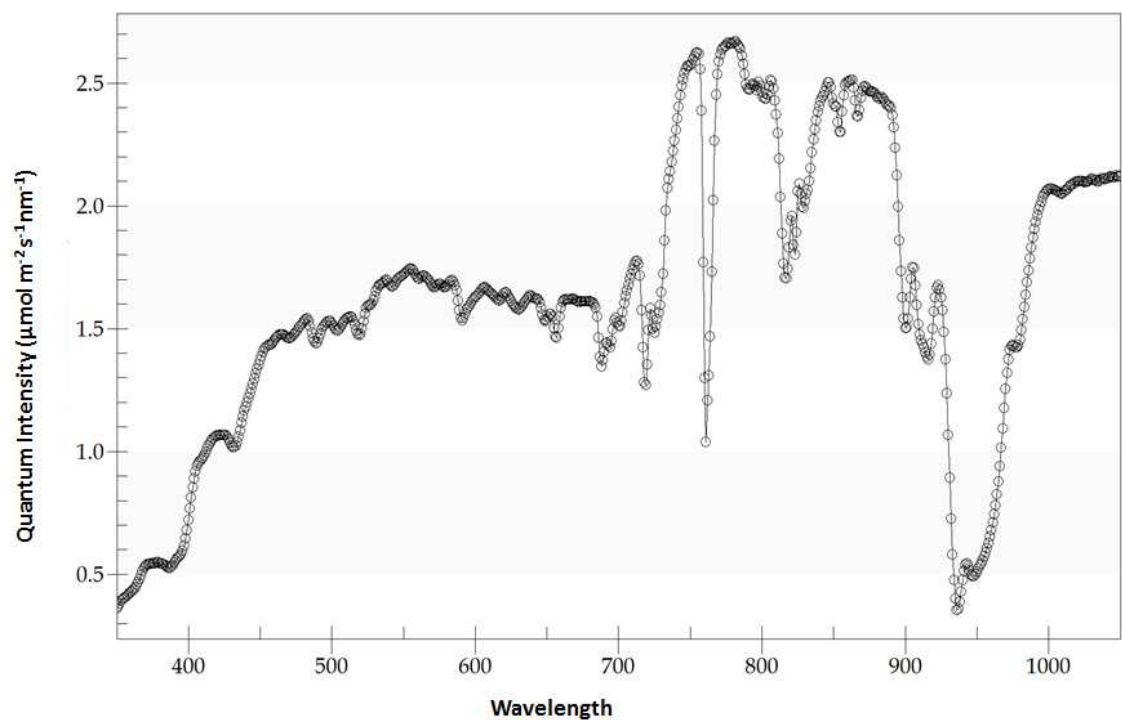


Fig. 7. Quantum energy distribution within and below a closed canopy of field grown sugarcane with planophile leaves and a high population of weeds growing underneath the canopy. Measurements were taken between adjacent rows at 30 cm from the ground. Values are given as Quantum Intensity (QI micromol m⁻² s⁻¹ nm⁻¹)

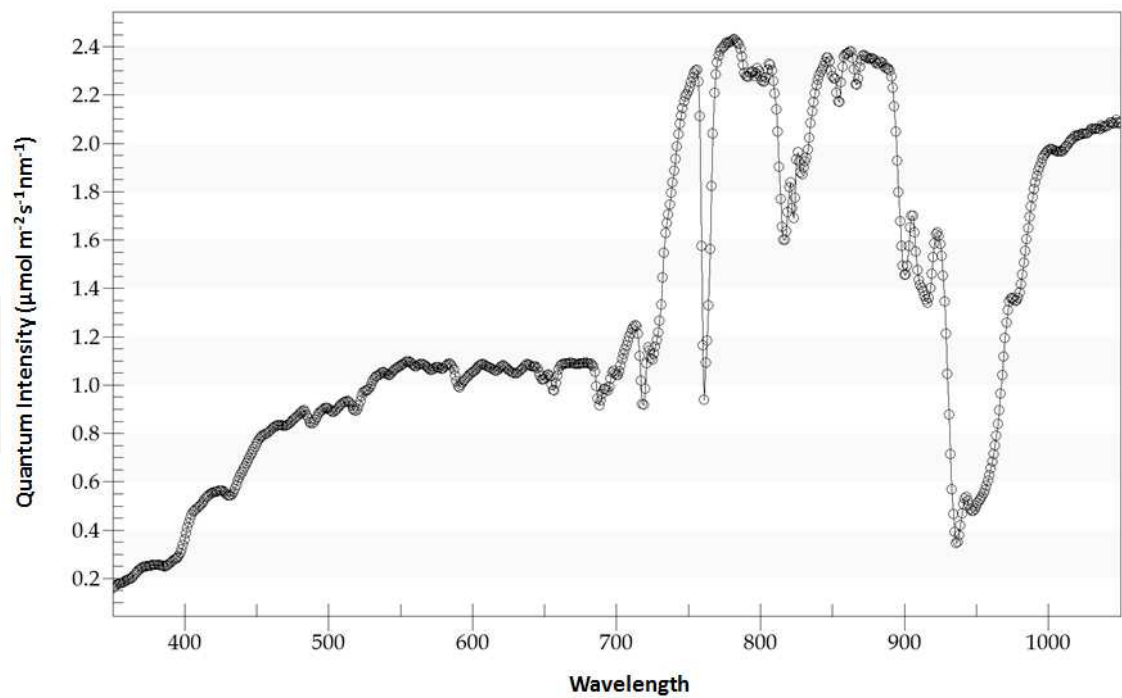


Fig. 8. Quantum energy distribution within and below a closed canopy of field grown sugarcane with erect leaves and a low population of weeds growing underneath the canopy. Measurements were taken between adjacent rows at 30 cm from the ground. Values are given as Quantum Intensity (QI micromol m⁻² s⁻¹ nm⁻¹)

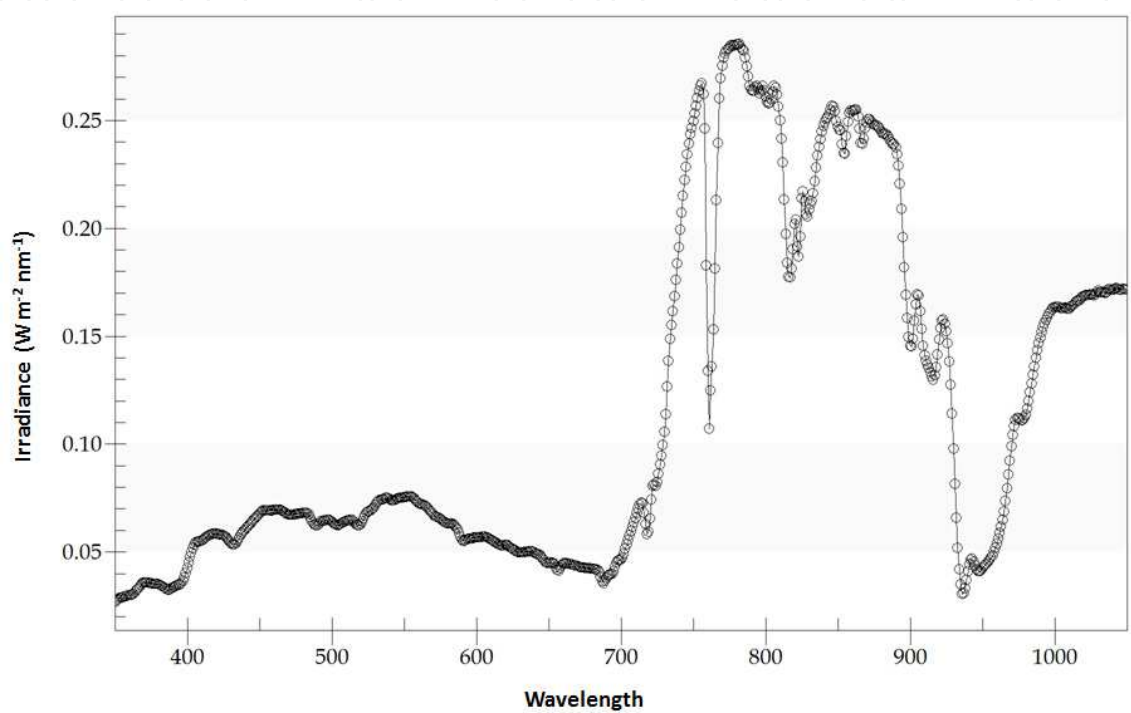


Fig. 9. Spectral irradiance within and below a close canopy of field grown sugarcane with erect leaves and a high population of weeds growing underneath the canopy. Measurements were taken between adjacent rows at 30 cm from the ground. Values are given as irradiance ($\text{W m}^{-2} \text{nm}^{-1}$)

In Fig 10 an 11 radiation profiles, are shown as spectral irradiance (energy units in Watt $\text{m}^{-2}\text{nm}^{-1}$), below and above the **canopy of the weeds** growing underneath the sugarcane canopy with planophile leaves. Under this circumstances, shade conditions are more accentuated and the amount of energy in the visible is almost at limits to sustain growth; in these figures extreme shade conditions are observed within a canopy architecture that favors shade conditions (as for planophile or more horizontal leaf arrangement).

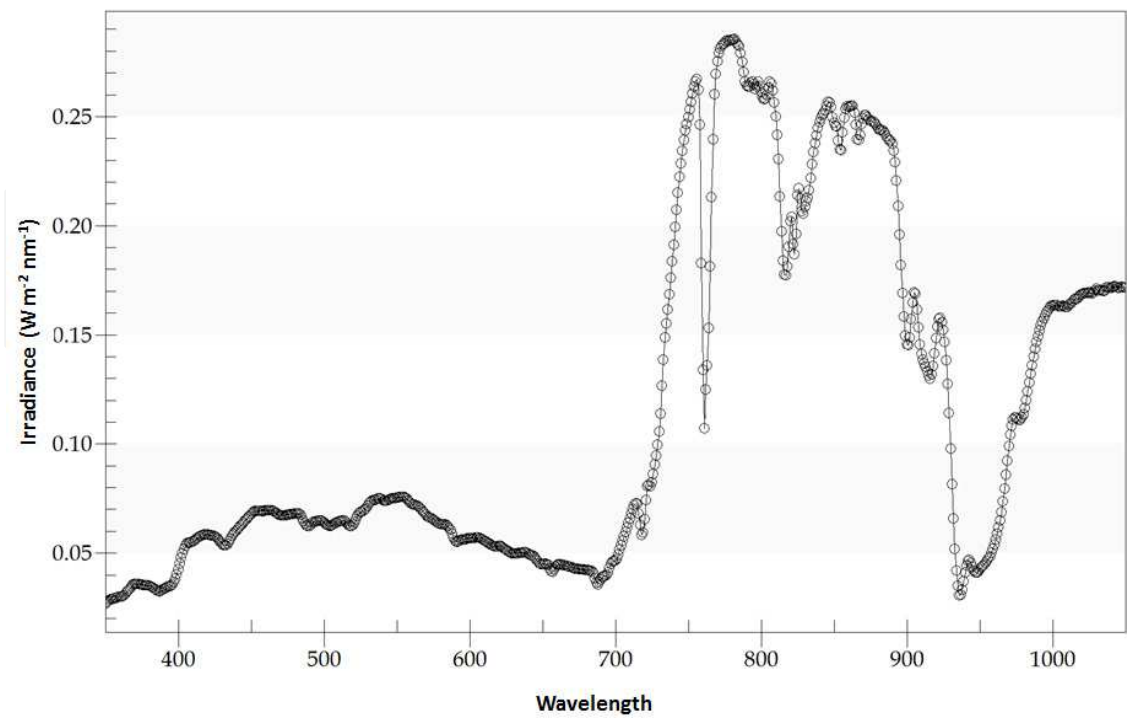


Fig. 10. Spectral irradiance beneath the canopy of the populations of weeds growing under a sugarcane canopy with planophile leaves. (Values are given in W m⁻² nm⁻¹)

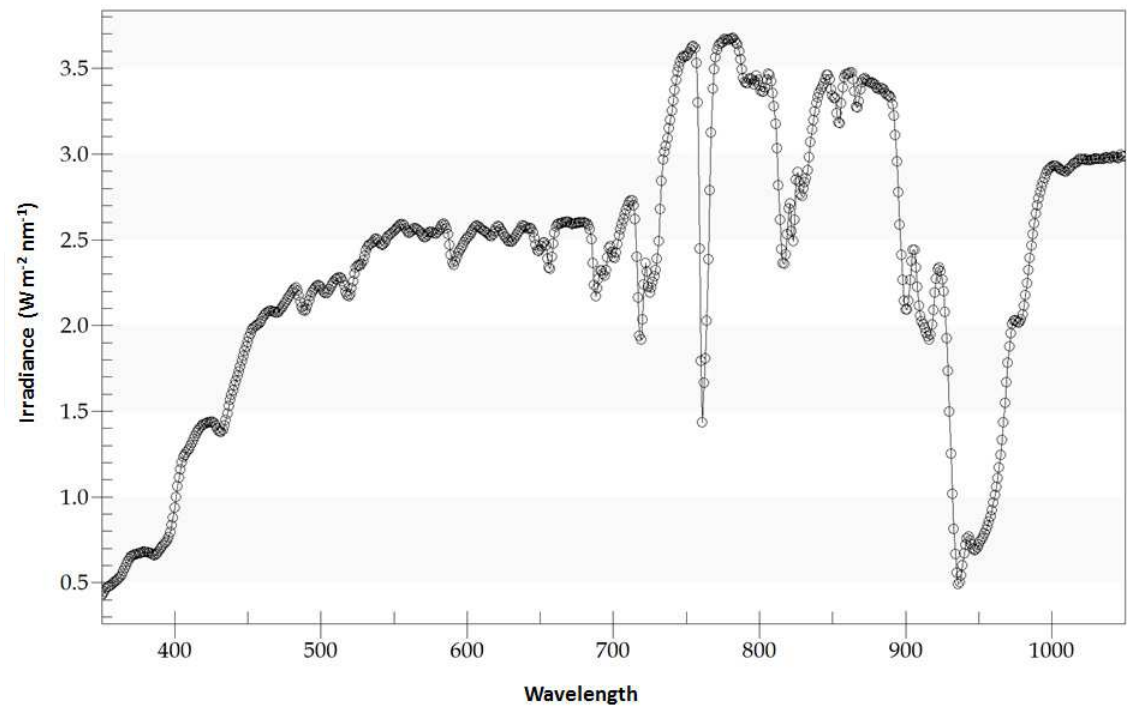


Fig. 11. Spectral irradiance above the canopy of the weed population growing under the sugarcane crop canopy with planophile leaves. (Values are given in W m⁻² nm⁻¹)

From the perspectives of this chapter, what is more important is to ascertain which species that were present before crop canopy closure persist. From the establishment of the crop to full canopy closure, different shade intensities are found, and also different species and plant types, then the question arises as to which are capable of developing a syndrome for shade avoidance? the first answer to this question is: those species capable of perceiving, early in their development, that they are being shaded and start building mechanisms or strategies to defend themselves from dying from the shade and to escape the shade; first thing, as seen under field conditions: acceleration of extension growth of stem and petioles. Adaptation takes a little longer.

In the next part of this chapter, experiments under controlled conditions are shown in order to investigate some of the growth strategies most commonly found for three important sugarcane weeds, under an artificial shade.

3.3 Greenhouse experiments

Experiments under controlled conditions are used to simulate and find the causes of plant behavior as seen in the field. The Shade Avoidance Syndrome has been mostly investigated in connection with the ratio of red to far red wavelengths as an indication of neighbor proximity and adaptive plasticity. According to the results obtained by Weing (2000), elongation responses to R:FR are more variable than previously realized and that the observed variability suggests competitive interactions in the natural environment. Other researchers have also stressed on the importance of plant development as influenced by light spectral quality and quantity (Rajcan et al. 2002; Wherley, Gardner & Metzger 2005); tillering dynamics in grasses in relation to R/FR (Evers et al. 2006; Monaco & Briske 2000) and also on the effects of canopy shade on morphological and phenological traits (Brainard, Bellinder & DiTommaso 2005). The effects of reduced irradiance and R/FR on the leaf development of papaya (*Carica papaya*) leaves to simulate canopy shade were studied by Buisson & Lee (1993) using experimental shadehouses; results indicate that although many morphological and anatomical characteristics were affected by reduction in irradiance, some were affected primarily by low R/FR. It is important to note that when vegetation shade is simulated by means of artificial filters in growth cabinets in which R/FR is low but PAR is sufficient to allow for sustained growth, phenological changes are exaggerated (Smith & Whiteham 1997).

In connection with these ideas, the results presented in this chapter were performed with simulated shades of different colors using cellophane paper to grow three of the more severe weeds for the sugarcane crop: *Cyperus rotundus* (purple nutsedge), *Rottboellia cochinchinensis* (ichgrass) and *Leptochloa filiformis*, in order to characterize their growth responses to different light qualities as an expression of the shade avoidance syndrome in these species.

The first species (*Cyperus rotundus*) have been studied mostly due to its susceptibility to canopy and artificial shading, which have been a basis, according to Neeser, Aguero & Swanton (1997) for integrated management under crop cultivation. For the experiment, the plants were grown for 48 days inside plant cabinets with red, blue and green artificial shade, low PFD neutral shade and full exposure to daylight. Results showed that *Cyperus rotundus* plants under low PFD neutral shade had lower values for the number of tillers and corms,

dry root and stolon and leaf biomass, which resulted in a lower total dry biomass and leaf area (Lazo & Ascencio 2010). Differences in growth were found between this environment and full exposure to daylight and under the red and blue filters. It is important to emphasize the larger leaf area ratio found under low PFD neutral shade, as resulted from a lower number and corm dry biomass as compared to the aerial part. This species, a C4 plant, is thus highly sensitive to shade as shown by its lower total dry biomass and leaf area under low PFD; this could possibly explain the wide distribution of *Cyperus rotundus* in high light intensity environments, which generally occurs in tropical areas (Bielinski, Morales-paya & Shilling, 1997). However, it is also seen under canopy shade, due to the corms germinating potential and that plants under the canopy flower ("emergency flowering"), to produce seeds that are promptly shed, thus enriching the seed bank. These features may explain its persistence from planting to canopy closure, where sunflecks may play an important role in the maintenance of the plant population seen under cultivation.

Different shade avoidance strategies in biomass production, tillering, leaf area, plant height and flowering, revealing different capacity of acclimation to shade are shown when comparing *Rottboellia exaltata* and *Leptochloa filiformis* (both of the Poaceae family as well as sugarcane). The effect on leaf dry biomass density in *Rottboellia* was similar to full exposure to daylight, under a shade with low PAR and artificial color filters, but a red stimulator effect was observed. In *Leptochloa*, on the other hand, it was observed under blue and red filters, but the differences were not significant when comparing groups among them. The effects on the accumulation of dry biomass of roots, showed higher values for *Rottboellia* in full exposure to daylight and red; in contrast, a remarkable increase in root biomass was observed in *Leptochloa* in full exposure to daylight, which was significantly higher than under low photon flux density shade and blue, red and green filters (Ascencio & Lazo 2009). These results show a higher sensitivity of *Leptochloa* to shade, as a consequence of a lower development of the root system, which did not permit a sustained growth of the plants. This hypothesis is supported by the fact that this species showed "emergency flowering" under conditions of low PAR neutral shade and blue filter, but not total solar exposition and red filters, which are non shade conditions (high R/FR). In contrast, *Rottboellia exaltata* showed shade avoidance responses such as increased petiole length and stem, rendering it capable of competing for a longer time with the sugarcane crop under cultivation. Early flowering was not observed. The effects of shading on *Rottboellia exaltata* were determined under controlled environment conditions by Patterson (1979) under 100, 60, 25 and 2% sunlight; according to the results, this species maintains the capacity for high photosynthetic rates and high growth rates when subsequently exposed to high irradiance, after being shaded, which may explain its competitiveness with crop species.

Besides accelerated shoot growth, decreased tillering and early flowering, and increase in the shoot to root ratio have been part of the responses that have been associated to the SAS; however, this is not always the case as increases or decreases in S/R have been observed. The apparent contradiction is probably due to the complex nature of plant weight as a character. The ability of *Rottboellia* to reduce the effects of shade appears related to increased dry matter partitioning to the shoots. In Table 2, shoot to root ratios on a dry basis are shown for the three species grown exposed to full sunlight, neutral shed of low photon flux density (PAR) and shed plant cabinets in open space under full sunlight and covered with

artificial filters made of red, blue and green cellophane paper. The values for S/R or dry matter partitioning are mainly related to biomass allocation to shoots in species capable of escaping shade as *Rottboellia*, however the highest value was found in full sunlight (2.27) but no significant differences were found for S/R with the rest of the light environments. In contrast, a remarkable increase in root biomass as compared to shoots, lowered the S/R in *Leptochloa* in full sunlight, while an increase was observed under shade conditions. The increase in S/A observed for this species and for *Cyperus* are more likely to be related to a lower root biomass allocation under shade conditions.

	<i>Rottboellia exaltata</i>	<i>Leptochloa filiformis</i>	<i>Cyperus rotundus</i>
	SA/SR	SA/SR	SA/SR
Exposed to Full Sunlight	2.27a	0.15b	0.74c
Neutral Shade (low PAR)	0.93a	0.54b	2.63a
Red cover	0.83a	0.83a,b	1.03c
Blue cover	1.01a	0.48b	0.98c
Green cover	1.58a	1.46a	1.82b

Values with the same letter, within the same column, do not differ according to Tukey HSD test; Homogenous Groups, alpha = .05000

Table 2. Shoot to root ratio (S/R) for *Rotboellia exaltata*, *Leptochloa filiformis* and *Cyperus rotundus* plants, grown: (1) exposed to full sunlight, (2) neutral shed of low PFD, and (3) shed, plant cabinets in open space under full sunlight and covered with red, blue and green cellophane paper.

The partitioning dry biomass to the roots and shoots for *Leptochloa* reflects a higher sensibility of this species to shade impairing the aerial parts to develop strategies to escape or avoid shade. This is shown in lower S/R for *Leptochloa* as compared to the other two species. The sensibility of *Cyperus rotundus* to shade is shown in the lower values of dry biomass for the subterranean parts (roots, corms and stolons) which produces higher values for S/R under low intensity neutral shade (2.63). This plant is totally intolerant to shade and under low intensity light, lower values for the number of tillers and corms, dry root, stolon and leaf biomass were observed (Lazo & Ascencio 2010). Because of the high plasticity of the S/R to environmental conditions, values are not easy to interpret and show less predictable responses to environmental variables such as light.

4. Conclusion

Sugarcane is an important crop in many tropical countries. Under these conditions, the major biotic limiting factor to productivity is the direct interference caused by weeds, especially during sprouting and the first three months of growth (initial stand establishment), when canopy closure has not been completed because crop growth is slow and foliage do not completely cover the area under cultivation. Weeds also serve as host plants of pests and diseases and interfere with crop management practices such as side dressing, sanitary inspection, sampling, maturation, etc., as well as with mechanical harvesting. Weed control is usually performed either by mechanical or the application of chemical herbicides, but the emergence and rapid evolution of weed species resistant to many herbicides, has prompted the search for new alternatives to control, and to consider

management strategies based on the knowledge of the dynamics and biology of plants that grow under the canopy of the crop.

When sucrose is the desired sugarcane product, sucrose yield is the ultimate concern, but when the production of ethanol is the main purpose, the accumulation of biomass is the goal to achieve. However, in both cases, the output is determined by the number of stalks, which in turn depends on adequate and timely management of weeds and the good use of agronomic practices. It is important to emphasize that one of the ways to control weeds in this perennial crop, is precisely to take advantage of the intense shading under the sugarcane canopy, which limits the density and biodiversity of plant population grown underneath the crop. At canopy closure, the light environment underneath can exclude a considerable number of plant species, since not all species can tolerate shade, without ruling out the possibility that there are some species that are able to tolerate the shade, and others remain in the seed bank, and become a delayed problem when it is activated by some environmental factor, such as sunflecks. In this connection, it is important to recognize which of the species can tolerate shade and which cannot; therefore, research and studies of the dynamics of weed populations in the sugar cane crop, are required from planting to canopy closure. Light profiles are rarely recorded in field conditions and may be the key to understanding some of the growth responses of different plant species under a crop canopy.

Light quality (wavelength) and quantity (number of photons, irradiance) interact to control growth responses under vegetation canopies and some species underneath sugarcane canopies under field conditions can escape shade competing successfully with the crop for light. Two strategies associated to the Shade Avoidance Syndrome, as seen in the field, were observed: increased internodes length and decreased leaf size, while others species showed a higher sensitivity towards canopy shade and eventually died in this condition. Energy distributions of visible and near infrared radiation above, within, near the soil and above a canopy of weeds underneath a sugarcane canopy, showed that the decreased intensity of radiant energy was not uniform at all wavelengths. Some species are also seen under canopy shade, due to the corms or other subterranean organs and the germinating potential of the seed bank. These features may explain their persistence from time of planting to canopy closure, where sunflecks may play an important role in the maintenance of the plant population seen under crop cultivation. Different shade avoidance strategies in biomass production, tillering, leaf area, plant height and flowering, revealing different capacity of acclimation to shade were shown using experimental shadehouses; experiments under controlled conditions were useful to simulate and find the causes of plant behavior as seen in the field. Even though sugarcane is a crop economically important, research is limited in this area and in our opinion more has to be done on the biology and performance of the population of plants growing underneath the canopy from the beginning of the crop cycle, to improve weed control practices under cultivation.

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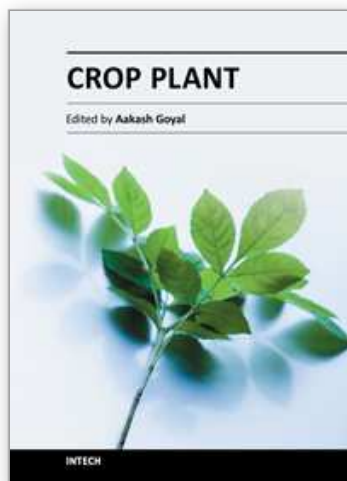
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