IMPROVING CROP PRODUCTIVITY IN AGROFORESTRY SYSTEMS: LOW LEAF RESPIRATION IS A KEY TRAIT

Rosati A[1]*, Pang K[2], Van Sambeek J[3], Gold M[2], Jose S[2]

(1) Consiglio per la ricerca in agricoltura e l'analisi dell'economia agraria, centro di ricerca Olivicoltura, Frutticoltura, Agrumicoltura (CREA – OFA), Spoleto (PG), Italy (2) School of Natural Resources, The Center for Agroforestry, University of Missouri, Columbia, MO, USA (3) USDA Forest Service Northern Research Station, Columbia, MO, USA

*Corresponding author: adolfo.rosati@crea.gov.it

Abstract

We studied the mechanisms of shade adaptation in gamagrass (*Tripsacum dactyloides*). We compared the photosynthetic response curves to light in leaves of plants grown in either full sun or shade, in a shade-tolerant and a control cultivar (total of 4 treatments). Plants grown in the shade had lower dark respiration rates and the shade-tolerant cultivar grown in the shade, had the lowest dark respiration rate. We also measured the actual light under the tree canopy in a variety of agroforestry situations. We then modeled the daily photosynthesis for each treatment in each agroforestry situation, using the measured light and the specific photosynthetic response curves to light. Lower leaf respiration rate in the shade-tolerant cultivar grown in the shade allowed maintaining a positive net photosynthesis at lower light conditions, than in the other cases. Low leaf respiration rate appears to be an important trait when breeding genotypes suitable for agroforestry conditions.

Keywords: shade-adaptation, photosynthesis, modeling, respiration, gamagrass

Introduction

The cultivation of crops and forages under tree plantations in agroforestry systems has been shown to be advantageous from both a productive and an environmental perspective (Jose et al. 2004). While the overall productivity of the land (trees + crop/forage) may be increased, tree shade generally decreases the crop/forage productivity. However, in most instances the crop/forage cultivars employed in agroforestry systems are the same as for open field situations, which have been selected to perform best in full sun. It has long been suggested that selecting shade-adapted genotypes could greatly improve the productivity of crops in agroforestry

considered this aspect, and no shade-adapted cultivars are available for most forages and crops. Even for those genotypes/species that have been shown to be more suitable for cultivation under tree shade, there is little if any information on the mechanisms that make such adaptation possible. Understanding these mechanisms is key to select and breed genotypes specifically adapted to grow under the shade of trees, and thus to increase the productivity of agroforestry systems.

Eastern gamagrass (*Tripsacum dactyloides*) is a native grass that can be found in North America, as well as in Central America, and Brazil. A selection if this grass, named "Bumpers" has been released (USDA, NRCS, 2006). Bumpers' appears to be more suitable than other cultivars to grow in shade, but no mechanisms for this adaptation have been investigated.

The aim of this study was to investigate the mechanisms of shade adaptation in Bumpers, compared to a control cultivar (Verl) that is not shade-tolerant. To do this we measured the photosynthetic response curves to the photosynthetically active radiation (PAR) of these genotypes, both when grown under tree shade and in full sun. We then used the measured curves to model photosynthesis under the actual PAR available below trees in different scenarios.

Materials and methods

Bumpers plants, together with plants of a common (i.e. non-shade-tolerant) cultivar of the same species (i.e. Verl) used as a control, were established in the Alley-Cropping Shade Laboratory (ACSL) at the Horticulture and Agroforestry Research Center during the 2010 and 2011 growing seasons. Plants were established in a 6 m-wide alley under oak trees, as well as in an adjacent open field.

During summer 2017, net photosynthetic response curves to light (i.e. PAR) were measured (between 9.00 and 12.00 h) on representative top-canopy leaves, both in the full sun and in the alleys. Curves were measured using a portable gas exchange system (LI-6400; LI-COR Inc., Lincoln, NE, USA), equipped with a cool light source (6400±02 LED) mounted on the leaf chamber. Leaves were exposed to high PAR (2000 μmol m±2 s±1) until photosynthesis was constant: this was defined as photosynthesis at saturating PAR (Amax). Then, PAR was decreased in steps down to zero (2000, 1500, 1000, 750, 500, 250, 100, 50, 20, 0 μmol m^{-2} s^{-1}). The rate of CO_2 emission at zero PAR was assumed to be the dark respiration rate (Rd) of the leaf. From the data, the curvature factor and the apparent quantum yield were calculated for each treatment combination (i.e. each cultivar in each light treatment) using the best fit to a non-rectangular hyperbola (Thornley 1976).

Curve parameters were then used to estimate net photosynthesis of top canopy leaves, when exposed to the actual incident light as measured in different alley cropping systems. To do this, the PAR transmitted under the trees (thus available for the understory crop) was measured (using 24 GaAsP photosensors, Hamamatsu, Japan) at different positions in a grid under the trees, in different adjacent chestnut orchards of different ages and with different tree spacing. In each position, PAR was measured every minute, from dawn to dusk, during different days (i.e. cloudy or sunny) in the summer of 2016. This provided a large and widely variable sample of daily light patterns, actually occurring under the trees.

The minute-by-minute PAR data for each position, day and orchard, was then coupled with the photosynthetic response curve of each treatment combination (i.e. each cultivar grown in shade or in full sun), to model the respective minute by minute photosynthetic performance in that position, day and orchard, of each treatment combination. The minute by minute photosynthesis was then summed up for all minutes in the day (from dawn to dusk), to obtain the daily net photosynthesis of each treatment combination, for each position, day and orchard. Further details on this approach are provided in Rosati et al. (2003, 2004).

Results

The photosynthetic response curves to light differed between cultivars and growing conditions (i.e. full light vs. shade) (Figure 1). Within cultivars, plants grown in full sunlight had both greater light saturated net photosynthesis (Amax) (Figure 1 Top) and greater (i.e. more negative values) dark respiration rate (Rd) (Figure 1 Bottom) than the respective plants grown in the tree shade.

'Bumpers', the shade-adapted cultivar, had both lower Amax and lower Rd than the control cultivar, both when grown in the sun or in the shade.

The respective photosynthetic response curves to light were then used to model daily photosynthesis (Figure 2 Top). Daily net photosynthesis (Daily An) increased less than proportionally, with increasing daily PAR, as expected. At any value of daily incident PAR, the possible value of the daily An was very variable, even within each treatment. This was due to the fact that the same daily PAR value can be obtained with brighter/longer days in more shaded positions (i.e. more variable light), or with more overcast/short days in less shaded positions (i.e. more uniform light), and this changes the radiation use efficiency (RUE), as longer times at average PAR values results in higher RUE than alternating high and low incident PAR values (Hirose and Bazzaz 1998; Rosati et al. 2003, 2004). This broad range of response makes it difficult to appreciate differences across treatments. To better visualize the data, therefore, the difference in daily An between the control cultivar grown in the sun (i.e. the treatment with the highest Amax) and all the other treatments was plotted against the daily incident PAR (Figure 2 bottom). This figure clearly shows that the control cultivar grown in the sun had the highest daily photosynthesis at high irradiance, reflecting its highest Amax (Figure 1 Top). However, below about 17 mol m^{-2} d^{-1} of PAR, the control cultivar grown in the shade surpassed the same CV grown in the sun, thanks to its lower (i.e. less negative) leaf respiration (Rd) (Figure 1 Bottom). Similarly, the shade-tolerant cv, both grown in the shade and in the sun, also became more efficient than the control cv in the sun at daily PAR lower than, respectively, 10 and 5 mol m^{-2} d^{-1} of PAR. More interestingly, at daily PAR lower than 6 mol m^{-2} d^{-1} of PAR, the shade tolerant cv (i.e. Bumpers) grown in the shade had the highest photosynthesis, and this was again related to its lowest Rd (Figure 1 Bottom).

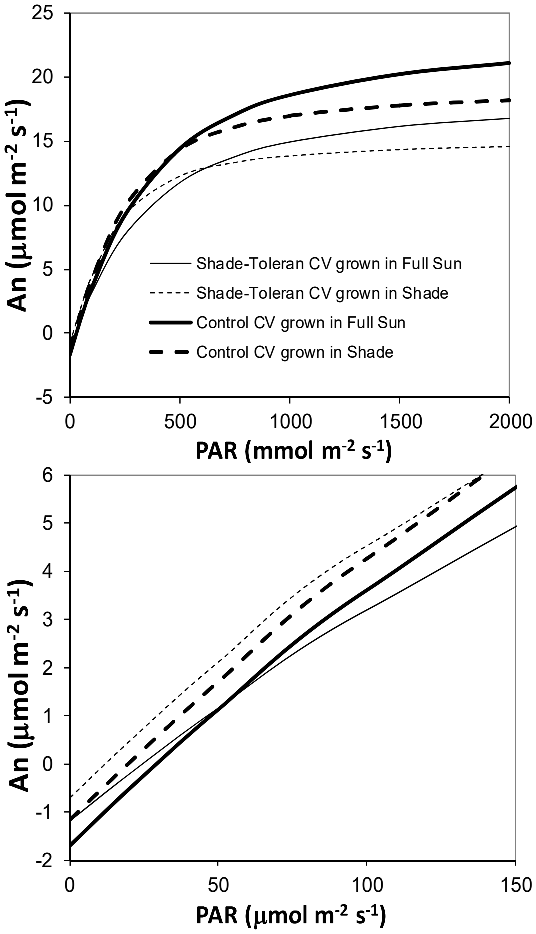

Figure 1: Photosynthetic response to light (i.e. photosynthetically active radiation: PAR) of a shade-tolerant cv (Bumpers) and a control cv (Verl) when grown in either full sun or in tree shade. Top panel: whole curves; bottom panel: details of the initial part of the curves.

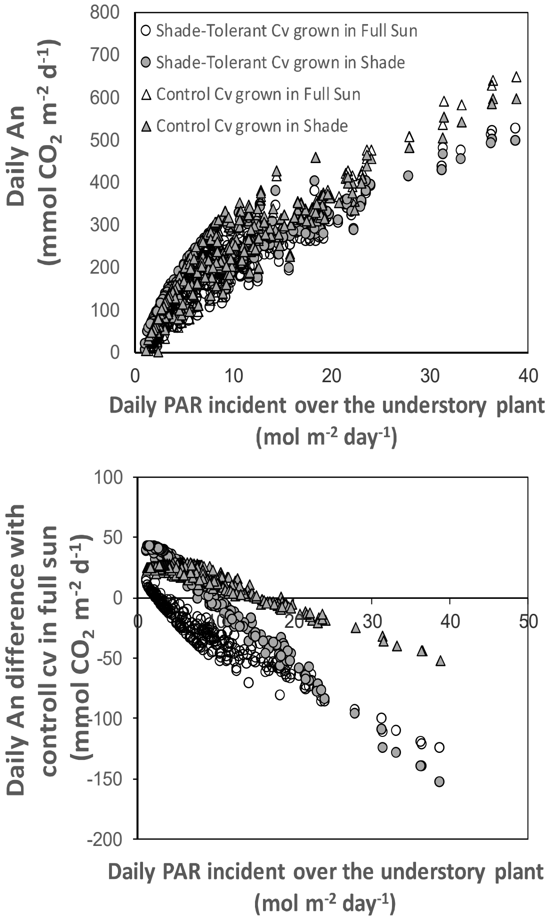

Figure 2: Daily photosynthetic response to daily incident light (i.e. photosynthetically active radiation: PAR) of a shade-tolerant cv (Bumpers) and a control cv (Verl) when grown in either full sun or in tree shade. Top panel: actual values; bottom panel: difference in daily net photosynthesis between each treatment and the control cultivar (Verl) grown in full sun.

Discussion

The different treatment combinations had different photosynthetic response curves to light (Figure 1). Plants grown in full sunlight had greater light saturated photosynthesis (Amax) than plants grown in the tree shade, as well as greater (i.e. more negative values) dark respiration rate (Rd). This shows that also in gamagrass, as in many species, leaf metabolisms tend to be adjusted to the illumination conditions under which the leaf develops (Rosati at al. 1999). For the same growing light conditions (i.e. full light or shade), however, the shade-tolerant cultivar (Bumpers) appeared to have an intrinsically lower leaf respiration rate.

The different Rd rates proved to be the key physiological feature to improve photosynthesis at low incident light. In fact, the radiation use efficiency is typically highest at intermediate PAR values, and decreases both at increasing PAR, due to saturation, and at decreasing PAR, due to respiration (Hirose and Bazzaz 1998; Rosati et al. 2003, 2004). At low PAR, therefore, a condition which is typical in agroforestry crops, it is the Rd that determines the RUE, and thus the level of net photosynthesis that can be obtained at low incident radiation. The higher (i.e. more negative) the Rd, the faster the RUE and the net photosynthesis decline at decreasing incident PAR.

Conclusion

The present data suggests that differences in metabolic activity (i.e. in leaf respiration), across different genotypes exist, and can be exploited to increase crop performance in agroforestry systems. Breeding for lower leaf respiration rates might prove a viable tool to increase crop performance in agroforestry systems, particularly in those systems with greater shade levels.

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