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Trait-based characterisation of cover plants' light competition strategies for weed control in banana cropping systems in the French West Indies

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ABSTRACT

Cover plants can be used as an ecological tool to manage weeds through competition for shared resources. Assessing the abilities of a large number of different plant species to compete for light remains difficult. Our aim was to characterise the light competition strategies of a range of species on the basis of a small number of traits related to both acquisition of light and interference abilities, to help farmers choose the most suitable cover plant species for banana cropping systems. Using a trait-based approach, we identified and measured the most representative plant morphological and functional traits to characterize the light acquisition strategies of 21 plant species including banana, cover plants, and weed species. We identified trade-offs between plant traits and light acquisition strategies. We identified light competition strategies by taking into account the aboveground interference abilities of plants as defined by their growth habit. There was a wide range of variations between species for all the traits. Two main trade-offs were identified: resource acquisition vs. conservation and carbohydrates investment in height vs. leaf area. Five traits selected in a multivariate analysis explained 80% of the variability of light acquisition strategies in our panel of species. These were related to plant morphology (height and plant crown width), light conversion efficiency (specific leaf area), carbohydrate allocation (aboveground leaf area ratio), and carbohydrates demand (aboveground biomass). The growth habit and the light acquisition strategies were related. The characterisation of plant species using functional traits enabled us to hypothesise three light acquisition strategies shaped by interference abilities in four light competing strategies. We propose a new method to characterise and distinguish species through their ability to acquire light and to interfere aboveground with their neighbours.

1. Introduction

Given the need to reduce chemical inputs, cover plants are being increasingly used in innovative cropping systems to favour biological regulation and to deliver agro-ecosystem services, including pest, weed, and erosion control (Altieri, 1999; Lu et al., 2000; Koohafkan et al., 2012). The choice of the best cover plant species to deliver these services and of the best spatial and temporal combinations of plants with the main crop determine the performances of the system (Vandermeer, 1989; Lu et al., 2000; Malezieux et al., 2009). For farmers, this choice is often complicated because no criteria and no formalised framework are available to help them choose among many species of cover plants based on their abilities.

In the French West Indies, banana is still mostly cultivated as intensive monoculture, using large amounts of chemical inputs, among which herbicides represent the largest proportion of the active ingredients (Bourgouin, 2013). In these systems, the use of cover plants to control weeds could help reduce herbicide inputs during two stages of the sequence of banana cropping systems: fallow and the following banana cycles (Damour et al., submitted). We assume that in these systems and in both stages, the biological regulation of weeds by cover plants mostly relies on competition, especially for light, as the other resources are seldom limiting for

Abbreviations: BMa, aboveground dry biomass; CW, crown width; FDR, false discovery rate; H, height; LARa, aboveground leaf area ratio; LDMC, leaf dry matter content; LMFa, aboveground leaf mass fraction; LSA, leaf soil area ratio; PCA, principal component analysis; SLA, specific leaf area.

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Table 1
Species studied (authorities according to *The Plant List* (2013). Version 1.1. Published on the Internet; http://www.theplantlist.org/) and its qualitative growth habit (according to expert knowledge).

Species	Abbreviation	Family	Growth habit
Arachis pintoi Krapov. & W.C.Greg.	AP	Fabaceae	Creeping
Musa spp., AAA group, 'Cirad925'	B925	Musaceae	Erect
Musa spp., AAA group, Cavendish subgroup, '902'	Bcav	Musaceae	Erect
Brachiaria decumbens Stapf	BD	Poaceae	Semi-Erect-Creeping
Bidens pilosa L.	BP	Asteraceae	Semi-Erect-Creeping
Brachiaria ruziziensis Germ. & C.M.Evrard	BR	Poaceae	Semi-Erect-Creeping
Cajanus cajan 'Guadeloupe' (L.) Millsp	CCG	Fabaceae	Erect
Centrosema pascuorum Benth.	CP	Fabaceae	Twining
Crotalaria spectabilis Roth	CS	Fabaceae	Erect
Crotalaria zanzibarica Benth.	CZ	Fabaceae	Erect
Dolichos lablab L.	DL	Fabaceae	Twining
Gliricidia sepium (Jacq.) Walp.	GS	Fabaceae	Erect
Mucuna deeringiana (Bort) Merr.	MD	Fabaceae	Erect
Vigna unguiculata 'David' (L.) Walp.	N	Fabaceae	Creeping
Neonotonia wightii (Wight & Arn.) J.A.Lackey	NW	Fabaceae	Twining
Momordica charantia L.	P	Cucurbitaceae	Twining
Paspalum notatum Flüggé	PN	Poaceae	Creeping
Pueraria phaseoloides (Roxb.) Benth.	PP	Fabaceae	Twining
Ricinus communis L.	RC	Euphorbiaceae	Erect
Stylosanthes guianensis (Aubl.) Sw.	SG	Fabaceae	Erect
Tagetes patula L.	TP	Asteraceae	Erect

plant growth (high fertilisation rates, high rainfall). Competition for light can be defined as the acquisition of a shared resource (see Zimdahl (2004) for a review of plant competition). The ability of a plant species to compete for light can be assessed by its light acquisition strategy, which may be affected by special abilities of aboveground interference (e.g. overgrowth ability, shading), by enhancing access to light for the plant itself and/or by reducing access to light by its neighbours. The interference abilities may be related to the growth habit of plants (e.g. twining plants).

Light is an essential resource for plant growth, as it is the driving force of photosynthesis, which produces the carbohydrates necessary for growth, development, and maintenance. Light acquisition relies on four processes: (i) interception of light by the plant leaf surface, (ii) conversion of light into energy which is used to synthesise carbohydrates, (iii) carbohydrates demand, and (iv), allocation of carbohydrates to the different plant organs for their growth, maintenance, and activity. Neighbouring plants can affect the quantity and quality of light received by a given plant (Taiz and Zeiger, 2006), and directly or indirectly affect the four processes described above. Each species may have different abilities with respect to each of those four processes.

Assessing the efficiency of the processes of light interception, light conversion, and carbohydrate demand and use may require extensive physiological studies. Studies to identify the most suitable plants to control weeds by light competition cannot be undertaken easily for a large range of cover plants. In this context, new tools and methods are needed to characterise the light competition abilities of a range of potential cover plant species in a tractable way.

Trait-based approaches, which originated in the field of comparative functional ecology, have a high potential. They are based on the use of functional traits, i.e. morpho-physio-phenological features, which are measurable at the plant level, and which have an impact on plant performances (Violle et al., 2007). Traits can be considered as indicators of plant-driven processes (e.g. aboveground biomass for carbohydrates demand) and make it possible to compare wide ranges of species based on their potential ability to participate in these processes.

In ecology, a combination of traits defines a strategy, and strategies confer different relative advantages (Fortunel et al., 2009). Wright et al. (2004) developed the "leaf economic spectrum" which is associated with combinations of traits related to leaf functions (e.g. photosynthesis efficiency, carbohydrate production, nitrogen consumption) allowing plant species to be ranked based on their strategies for the acquisition and conservation of resources. They proposed to use specific leaf area (SLA) and leaf dry matter content (LDMC) traits which, when they have high values, are representative of acquisition and conservation strategies (Garnier et al., 2004). LDMC provides information on leaf tissue density, which is related to nutrient conservation in the plant, and SLA is positively correlated with the net photosynthetic rate and relative growth rate (Violle et al., 2007). Combinations of traits defined to characterise these strategies and their correlations are reviewed in Garnier and Navas (2013). Knowing where species are placed on this continuum of resource use can provide information on the strategies of the plant species concerned. To go further in the characterisation of competitive processes, one can also describe plant species with traits related to each of the light acquisition processes. The light acquisition strategies of species can then be characterised by identifying the combination of traits reflecting the abilities of plant species to compete for light.

Although trait-based approaches have been extensively used in natural ecosystems for decades, applications of these approaches to systems such as managed grasslands (Ansquer et al., 2004; Maire et al., 2009; Duru et al., 2014) and agrosystems (Wilke and Snapp, 2008; Fried et al., 2012; Garnier and Navas, 2012; Damour et al., 2014; Gaba et al., 2014), are still rare, although currently increasing (Garnier and Navas, 2012). In banana cropping systems, a few recent studies have been conducted to enable farmers to choose cover plant species based on their traits (Tixier et al., 2011; Damour et al., 2014; Damour et al., submitted).

Following these works, we undertook deeper investigations into the trait-based characterisation of the abilities cover plant species to compete for light with the goal of introducing them in innovative banana cropping systems. Our aim was to characterise the light competition strategies of a range of species on the basis of a small number of traits related to both acquisition of light and their aboveground interference abilities. To do so, we asked the following questions: (i) What are the light acquisition strategies of our panel of plant species? (ii) What are their aboveground interference abilities and are they related to light acquisition strategies? (iii) What are the light competition strategies of our plant species? (iv) How could they be used to facilitate the choice of the best cover plant species? To answer these questions, we conducted a