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Leaf area development strategies of cover plants used in banana plantations identified from a set of plant traits

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ABSTRACT

Cover crops introduced into cropping systems can lead to chemical input reductions and pollution mitigation because they enhance ecological functions. The choice of the best cover crops for a specific cropping system is, however, difficult because of the large range of potential cover species. A promising method involves functional traits as simplified indicators of plant functions. In banana cropping systems, cover crops are used especially to control weeds by development of their leaf area to boost competition for light. The aim of this study was to seek trait-based leaf area development strategies among tropical cover species, based on four plant traits chosen because of their mathematical link with leaf area development: specific leaf area (SLA), aboveground leaf mass fraction (LMF_a), seed mass (SM) and aboveground relative growth rate (RGR_a). We measured trait values and leaf areas of 17 tropical cover species grown for 1 month in a growth chamber. Strong positive and negative covariations were observed between SM, LMF_a and RGR_a, revealing a "syndrome" of traits and suggesting trade-offs between traits. Four groups of species were identified based on PCA and cluster analyses and were characterized by significantly different sets of trait values. They showed four leaf area development strategies: species that allocate a large part of biomass to leaf area (G1), species that develop large biomass and leaf area at emergence (G2), species with rapid biomass growth and low biomass investment in leaves (G3) and species with a non-specialized strategy (G4). After 1 month, species of groups G1 and G2 had higher leaf area, although not significantly, than species of groups G3 and G4. Comparisons between this functional classification and the taxonomic monocot/dicot classification showed that the functional classification captured a larger part of the variability in traits involved in leaf area development than the taxonomic monocot/dicot classification. This encourages the use of such a classification to describe plant functioning, to understand plant roles in plant–plant interactions and guide the choice of the best cover species to introduce into cropping systems.

1. Introduction

The reintroduction of biodiversity in agrosystems has been encouraged for more than a decade to enhance ecological functions and reduce chemical inputs recognized for their negative impacts on the environment (Altieri, 1999; Malézieux et al., 2009; Koohafkan et al., 2012). Growing cover species is one way to increase the biodiversity of agrosystems. There has been recent renewed interest in these plants, which have long been used by farmers as green manure or fodder, because of their roles in erosion control, weed and pest control, N input by atmospheric fixation, improvement of nutrient cycling, and limitation of water and nutrient losses (Lu et al., 2000). Cover species have different abilities to deliver these services and the choice of the best one for a specific cropping system depends on the services expected and constraints imposed on the plants. This choice is crucial because it determines the system performances in terms of services delivered and thus the reduction of chemical inputs allowed.

Banana plantations of the French West Indies (FWI 14°39′48.07″ N, 60°59′57.54″ W) are characterized by a high level of weed pressure due to favorable growth conditions all year round under wet tropical climate. Weeds strongly compete with the banana for soil resources and impair banana growth and production. To maintain yields, large quantities of herbicides are used in export banana plantations (5.8 kg ha^{-1} $year^{-1}$ of herbicide active product in Guadeloupe, IT2, 2013). These chemical input applications represent a particular threat for the fragile insular tropical areas of FWI, because of the proximity of agrosystems to forest, freshwater and

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coastal resources (Bonan and Prime, 2001; Bocquene and Franco, 2005). Cover species have been proposed for less than a decade as a way to reduce chemical inputs in banana plantations, to alleviate environmental threats. Banana cropping systems are composed of two phases: a one year sanitation fallow driven to sanitize the soil and maintain productivity, followed by five or six cycles of production lasting from 9 to 11 months in wet tropical conditions (Gowen, 1995). Cover species can be grown during both phases, to control weeds and deliver different sets of other services (Damour et al., 2015).

Cover species are expected to control weeds with one of three main processes: competition for resources, development of a physical barrier to germination and emergence, and allelopathy (Teasdale et al., 2007; Mediene et al., 2011). We focused on competition for resources and competition for light in particular, as it is considered as the main source of weed control in early stage of plant development, the critical stage for weed control in banana cropping systems (Minotti, 1991; Damour et al., 2015). Competition for light between weeds and cover species depends on the way species shade each other by their leaves (called thereafter "leaf development strategy"). The ability of a plant to shade another one and so to compete with it for light was related to its size—evaluated through its aboveground biomass or height (Gaudet and Keddy, 1988; Westoby, 1998; Reynolds and Rajaniemi, 2007)—and to its leaf area (e.g. crop-weed competition models) (Spitters and Van den Bergh, 1982; Kropff and Spitters, 1991). Because we wanted to embrace a large range of growth forms (from erected to twining plants, which are able to climb onto other plants), we choose to focus on leaf area, which is a better descriptor of the shading potential of species of different growth forms. We believe that there could be different ways species develop their total leaf area (called thereafter "leaf area development strategy") and shade each other within tropical cover species. We assume that better knowledge of these strategies could help understand how cover species interact with weeds.

Plant functional traits may be used to describe these strategies. Functional traits are morphological, physiological and phenological features of an individual organism that determines its effect on or response to the environment (Violle et al., 2007; Wood et al., 2015) and are then considered as simplified indicators of plant functions. Trait syndromes (i.e. a set of linked traits, Reich et al., 1999) may reveal trade-offs between traits and enable to identify functional groups, groups of species sharing a similar functioning at an organism level, having different strategies (Cornelissen et al., 2003; Wright et al., 2004; Reich, 2014). Functional groups can provide more mechanistic classifications than taxonomic groups, basically constructed on reproductive organs descriptors (Wood et al., 2015).

Table 1
Abbreviation list.

Traits	
$BM_{a,0}$	Aboveground dry biomass at first leaf emergence
$BM_{a,1}$	Aboveground dry biomass 1 month after first leaf emergence
$BM_{a,t}$	Aboveground dry biomass at time t
LA_0	Leaf area at first leaf emergence
LA_1	Total leaf area 1 month after first leaf emergence
LA_t	Total leaf area 1 month at time t
LAR_a	Aboveground leaf area ratio
LMF_a	Aboveground leaf mass fraction
RGR_a	Aboveground relative growth rate
SLA	Specific leaf area
SLA_{ps}	Plant-scale specific leaf area
SM	Seed mass
t	Time t

While extensively used for decades in comparative ecology studies to describe relationships between plant diversity, community structure, and ecosystem properties (e.g. Grime, 1979; Reich et al., 1992; Lavorel and Garnier, 2002; McGill et al., 2006; Diaz et al., 2007b; Suding et al., 2008), their interest to deal with agronomic issues has arisen and strongly increased over the last decade (Wilke and Snapp, 2008; Duru et al., 2009, 2014; Gunton et al., 2011; Fried et al., 2012; Garnier and Navas, 2012; Damour et al., 2014, 2015; Gaba et al., 2014; Gagliardi et al., 2015; Martin and Isaac, 2015; Tardy et al., 2015; Tribouillois et al., 2015a,b; Wood et al., 2015). In previous studies on cover species used in banana cropping systems of the French West Indies, we discussed how a trait-based approach can be used to assess the ecosystem services delivered (Damour et al., 2015), we presented trait-based characterizations of cover species' potential to deliver ecosystem services (Damour et al., 2014; Tardy et al., 2015) and trade-offs between traits associated to different services were explored (Tixier et al., 2011). In the present paper, we defend the idea that understanding syndromes of traits related to leaf area development enables to better understand species leaf area development strategies and that grouping species according to their strategies would facilitate the choice of the better species to control weeds.

The aim of this study was thus to seek trait-based leaf area development strategies among tropical cover species. We sought responses to four questions: (1) Do covariations exist between traits related to the leaf area development, enable the identification of "syndromes" of traits (sensu Reich et al., 1999) and of physiological trade-offs? (2) Can we identify groups of cover species with close trait values reflecting the same leaf area development strategy? If so, (3) do these trait-based groups perform differently in terms of the leaf area actually developed? and (4) How does this functional

Table 2
The 17 cover plants studied, code used throughout the text and figures, taxonomical groups and trait-based groups constructed according to the cluster analysis (see Fig. 2).

Code	Full names	Family	Taxonomic classification	Trait-based group
BD	*Bracharia decumbens*	Poaceae	Monocot	G1
BR	*Bracharia ruzziziensis*	Poaceae	Monocot	G1
CC	*Cajanus cajun*	Fabaceae	Dicot	G2
CD	*Cynodon dactylon*	Poaceae	Monocot	G3
CP	*Centrosema pascorum*	Fabaceae	Dicot	G4
CPal	*Crotalaria palida*	Fabaceae	Dicot	G1
CS	*Crotalaria spectabilis*	Fabaceae	Dicot	G4
CZ	*Crotalaria zanzibarica*	Fabaceae	Dicot	G1
EC	*Eleusine coracana*	Poaceae	Monocot	G4
PN	*Paspalum notatum*	Poaceae	Monocot	G3
PP	*Pueraria phaseolides*	Fabaceae	Dicot	G1
NCNC	*Vigna unguiculata* var. CNC	Fabaceae	Dicot	G2
NSPLM	*Vigna unguiculata* var. splm1	Fabaceae	Dicot	G2
NW	*Neonotonia wightii*	Fabaceae	Dicot	G1
RC	*Ricinus communis*	Euphorbiaceae	Dicot	G2
SG	*Stylosanthes guanensis*	Fabaceae	Dicot	G4
TP	*Tagetes patula*	Asteracea	Dicot	G1