

**PLASTICITY NOISE AND THE ELECTION OF BIOMASS RATIOS,
BIOMASS FRACTIONS OR ALLOMETRIC ANALYSIS FOR TEST
OPTIMAL PARTITIONING PREDICTION**

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**UNIVERSIDAD INDUSTRIAL DE SANTANDER
FACULTAD DE CIENCIAS
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BUCARAMANGA
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Trabajo de grado presentado para optar al título de Biólogo

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RESUMEN

TÍTULO: ASIGNACIÓN DE BIOMASA EN *Lippia alba* (VERBENACEAE): ONTOGENIA, “EQUILIBRIO FUNCIONAL O ALOMETRÍA”^{*}

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PALABRAS CLAVES: *Lippia alba*, patrones de asignación de biomasa, deriva ontogénica, análisis del crecimiento.

DESCRIPCIÓN:

Nosotros probamos si plantas de *Lippia alba* reducen la razón raíz:tallo, raíz:hoja, raíz:vástago, para compensar las limitaciones de los recursos arriba del suelo en una manera consistente con las teorías de partición óptima o si estas razones de biomasa reflejan “ruido plástico” debido a trayectorias ontogénicas plásticas de tan solo uno de sus componentes. Para esto, plantas clonales crecieron en condiciones de campo bajo alta media y baja disponibilidad de luz. Los análisis de las fracciones de biomasa en función del tamaño de la planta mostraron que la raíz es el único carácter que alteró los patrones de asignación de biomasa en respuesta a la variación en la disponibilidad de luz. La plasticidad acorde con las teorías de partición óptima observada en las razones raíz:tallo, raíz:hoja, raíz:vástago fue una consecuencia de asignación plástica de biomasa a la raíz (“ruido plástico”) in respuesta a la variación en la disponibilidad de luz, y no necesariamente fue debida a asignación plástica de biomasa en hojas y vástago. Una única trayectoria alométrica entre los componentes de biomasa de las razones podría explicar el crecimiento de la raíz vs hoja, raíz vs vástago y hoja vs vástago en respuesta a la variación en la disponibilidad de la luz. Estos resultados no soportan la predicción para diferentes disponibilidades del factor luz de las teorías de partición óptima. Mantener funcionalmente activas las plantas en diferentes disponibilidades de luz podría explicar la plasticidad en la asignación de biomasa de las raíces y sus mayores valores en alta disponibilidad de luz. Alcanzar la misma biomasa total al final del periodo de crecimiento vegetativo puede explicarla aparición de plasticidad en las tasas de crecimiento del área foliar, la razón de área foliar y el área foliar específica y sus mayores valores en bajas disponibilidades de luz.

^{*} Trabajo de Grado

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ABSTRACT

TITLE: PLASTICITY NOISE AND THE ELECTION OF BIOMASS RATIOS, BIOMASS FRACTIONS OR ALLOMETRIC ANALYSIS FOR TEST OPTIMAL PARTITIONING PREDICTION *

AUTHOR: IVÁN DARÍO CAMARGO RODRÍGUEZ **

KEY WORDS: *Lippia alba*, biomass allocation patterns, ontogenetic drift, growth analysis

DESCRIPTION

We tested whether plants of *Lippia alba* decrease root:shoot, root:leaf, root:stem to compensate for limitations of above-ground resources in a manner consistent with optimal partitioning theories or whether these biomass ratios reflect “plasticity noise” due to plastic ontogenetic trajectories of some of its components. Clonal plants were grown in field conditions under high-, medium- or low-light availability. Analyses of biomass fractions as a function of plant size showed that root is the unique character that altered allocation patterns in response to light availability. Plasticity agree with prediction of optimal partitioning theories observed in biomass root:shoot, root:leaf, root:stem ratios was a consequence of plastic biomass allocation in root (i.e. plasticity noise) in response to variation in light availability and not necessarily was due a plastic biomass allocation in leaves and stem. A single allometric trajectory between the biomass components involve can explain root vs leaf, root vs stem and leaf vs stem growth in response to variation in light availability. These results do not support prediction of optimal partitioning theories to light availability. Keep functionally active plants in different light environments could explain biomass allocation plasticity in roots and its mayor values in high-light. Reach the same total biomass at final of vegetative growth period can explain the apparition of plasticity in leaf-area growth-rates, leaf-area ratio and specific leaf-area and its mayor values in low-light environments.

* Work of Degree

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INTRODUCTION

Light availability is fundamental in regulating plant life cycles (Cosgrove 1986). The responses of plants to variation in light availability are a central question in physiological plant ecology. Optimal partitioning models and theories have been pointed out (Brouwer 1962a, b, 1983; Bloom, Chapin & Mooney 1985; Wilson 1988; Thornley 1972, 1998) that exist preferential partitioning to the part of the plant which acquires the currently most limiting resource. The general prediction of these theories is that plants shift their allocation toward shoots if the carbon gain of the shoot is impaired by a low level of above-ground resources, such as light and CO₂. Thus, plants shift allocation towards roots at a low level of below-ground resources, such as nutrients and water. These shifts could be seen as adaptative, as they enable the plant to capture more of those resources that most strongly limit plant growth (Poorter, Remkes & Lambers 1990; Poorter & Nagel 2000). Moreover, allocation patterns largely determine the ability of plants to compete with neighbors (Grime 1979; Tilman 1988) and to produce vegetative offspring and seeds (Abrahamson & Gadgil 1973; Bazzaz & Reekie 1985; Schmid & Weiner 1993). However, resource capture may or may not be dependent on the biomass allocated to different organs (Coleman & McConnaughay 1995).

Changes in allocation may result as a normal consequence of plant growth and development (i.e. ontogenetic drift) and “true” adjustments in biomass allocation, that is, those that require an adjustment in biomass allocation beyond that due to ontogenetic drift (McConnaughay & Coleman 1999). To date, some studies have reported “true”

adjustments in biomass allocation in response to light availability agree with predictions of optimal partitioning theories using root vs shoot allometry (Pearsall 1927; Troughton 1956), biomass fractions at a common age, that is, biomass allocation of plants of widely different size (see Coleman, MacConnaughay & Ackerly 1994) were examined (Givnish 1988; Olf, Van Andel & Bakker 1990; Callaway 1992; Latham 1992; Lei & Lechowicz 1998; Poorter & Nagel 2000). This evidence of plants that grew under different light conditions led to the common paradigm that plants shift allocation toward leaves or shoot when grown at a low-light (Reich 2002). However, other studies that account for ontogenetic drift, that is, plants were examined at a common size, and use biomass fractions, biomass ratios or allometric analyses have not found increasing allocation to leaf or shoot mass in low-light (e.g. Evans & Hughes 1961; Hughes & Evans 1962; Steinbrenner & Rediske 1964; Ledig *et al.* 1970; Rice & Bazzaz 1989, Gonzalez & Gianoli 2004).

In this study, we examine biomass allocation patterns throughout vegetative growth phase of *Lippia alba* (Mill) N.E.Br., family Verbenaceae, along three levels of light availability. A comparative approach was chosen to test if the use of different characters (i.e. biomass fractions, biomass ratios or the allometry of characters) could affect biological interpretations of biomass allocation patterns. A decrease in root/shoot at low-light accounted for ontogenetic drift may be interpreted like supportive evidence of optimal partitioning prediction (MacConnaughay & Coleman 1999) in part because of apparent increase in shoot production at a faster rate. What would happen if a decrease in root/shoot ratio is a consequence of plants following different developmental trajectories for root mass fraction (plastic biomass allocation patterns) but the same for shoot or its organs involve

(i.e. stem, leaves)? We hypothesized those same size comparisons of biomass ratios could contain “plastic noise” of some of its components and could affect biological interpretations. We asked the following questions: (1) Is the predicted decreased in root:shoot, root:leaf, root:stem ratios corroborate by examine biomass fractions of organs involucrate? (2) A single allometric trajectory between the biomass components involve can explain root vs leaf, root vs stem and leaf vs stem growth in response to variation in light availability?

1. MATERIALS AND METHODS

We use growth analysis and allometric regression techniques for compare biomass ratios, biomass fractions (Poorter & Nagel 2000) as a function of plant age and plant size (Coleman, McConnaughay & Ackerly 1994) in *L. alba* . Examining plasticity of biomass partitioning in three light levels allowed us to ascertain the source of morphological and physiological plasticity for this specie.

We grew clonal plants of *L. alba* (Herbario Nacional Colombiano COL, N° 480749, J.L. Fenrnández-Alonso) from a population of disturbed area of Bucaramanga city, we chose clonal plants for reduce genetic variability (Gianioli 2004a), the first experimental population of clonal plants grew at plenty solar exposition during 4 months in Granja Experimental Guatiguara seat of Universidad Industrial de Santander. Then, we grew vegetative offspring of this population. Once the first true leaves appeared (1-2 wek of age), individual seedlings were transplanted to 0.05 m³ plastic bags (one seedling per bag) containing 1:2:1 mixture of forest topsoil, river sand and organic mater, the mixture was

standardized (whit nutrient analysis) for assure nutrients during seedlings growth and for that its texture were consistent within that specie experience in the field. Plants were maintained under natural air temperature and relative humidity, and were watered two times daily at 600 and 1600 to field capacity with tap water. Day/night temperatures were $33^{\circ}\text{C}/18^{\circ}\text{C} \pm 1^{\circ}\text{C}$. Seven harvest (seven seedlings per light level per harvest) were performer beginning 1 wek (20 days of age), and were subsequently performed every third day to six harvest and every 5 day to seven harvest (40 days of plant age and before of flower). The plants were partitioning into roots, leaves, stems. All plant fractions were dried to a constant mass at 70°C , before leaf-area was determined. Stems and leaves were combined and are referred to as “shoot”.

The experimental setup included a random distribution of clones of *L. alba* into three treatments: (1) open field (100% sunlight); (2) medium-light (53% light); and (3) low-light (37% light). The second and third treatments were produced using shade cloth over a wooden structure. They were brought into the experimental setup on 27 April.

1.1 Growth Analysis and Statistical Methods

Developmental trajectories of whole-plant growth and biomass allocation were analyzed using the functional approach outlined by Causton and Venus (1981) and Hunt (1982). A “triming” method for minimizes the outliers was used (Barnett & Lewiss 1978), therefore five plants per harvest per light level were plotted. Sequential polynomial regression determined in most cases curvilinear trajectories even when biomass variables were transformed to their natural logarithms. The curvilinearity of the allometric precludes the

use of more appropriate model 2 linear regression (Jolicoeur 1989). Therefore, second-order polynomial regression equations were used for comparisons of biomass ratios (i.e. root:shoot, R/S; root:stem, R/ST; root:leaf, R/L; leaf:stem, L/ST), biomass fractions (i.e. root mass fraction, RMF; stem mass fraction, SMF and leaf mass fraction, LMF) as a function of time and of plant size, the allometric relationships of ratios and fractions were used too. Whole plant leaf-area, leaf-area ratio (LAR), and specific leaf-area (SLA) were examined as functions of time and plant size, third order polynomial regressions were used. Biomass variables and whole plant leaf-area parameters were transformed to their natural logarithms before analysis to meet the assumptions of normality and homoscedasticity associated with model 1 regression techniques. Log transformed variates and their residuals were judged to be normally distributed and homoscedastic by a combination of histograms, normality statistics, and normal probability plots. These fitted curves were statistically compared using methods described by Mead and Curnow (1983) and Potvin, Lechowicz & Tardif (1990).

Derived growth functions (i.e. relative growth rate, RGR; relative leaf-area growth-rate, RGR_L and unit leaf rate, ULR) were obtained and statistically compared using methods of Hunt & Parsons (1974).

2. RESULTS

2.1 Biomass Ratios

Comparisons of biomass ratios (i.e. R/S, R/ST, R/L, L/ST) at the same age showed that plants, whether or not were grown in shade, had similar ratios (Fig. 1a, d, g, j). Biomass

R/S, R/ST, R/L ratios declined (Fig. 1a, d, g) and L/ST increased (Fig. 1 g) throughout 40 days period.

Comparisons of R/S, R/ST and R/L as a function of plant size displayed significant plasticity across three light levels, plants in high-light had higher R/S, R/ST and R/L ratios than those grown in low-light environments throughout all growing period but these ratios declined across three light treatments (Fig 1b, e, h). Increased allocation to leaf observed in L/ST was not apparent when plants were compared as a function of plant size (Fig. 1k).

Allometric plots of root vs shoot mass (Fig. 1c) revealed that *L. alba* altered allocation patterns in response to light availability, and that shifts in the partitioning programs observed were dramatic early in development but decreased throughout growth. Other allometric analyses (i.e. stem vs root, leaf vs root and stem vs leaf) were insensitive to light availability (Fig 1f, i, l).

2.2 Biomass Fractions

Comparisons of biomass fractions (i.e. LMF, RMF and SMF) at the same age revealed that plants had similar biomass fractions across three light environments (Fig. 2a, d, g), that is, increased allocation to leaf (Fig 2a) and decreased allocation to stem and root (Fig. 2d, g) were not apparent throughout 40 days period.

Analyses of biomass fractions as a function of plant size showed that root is the unique character that altered allocation patterns in response to light availability (Fig. 2h); plants in

high-light had higher RMF than those grown in low-light environments but RMF decline across three light treatments. Allometric plots of root vs total mass were sensitive to light availability (Fig. 2i).

2.3 Growth Functions

L. alba plants displayed significant plasticity in total biomass, in high-light had higher total biomass throughout the growth period than those grown in low-light (Fig. 3a).

Comparisons of the derived growth-functions showed that ULR and RGR not differed significantly throughout the period of the observations (Fig. 3b, c). There were some exceptions, for 40 day plants in high-light magnified ULR but in low- light decreased.

L. alba plants displayed significant plasticity for RGR_L throughout the mayor period of the observations except for 26 to 32 day (Fig. 3d).

2.4 Leaf-Area Parameters

Comparisons of leaf-area, LAR and SLA as a function of plant age and size displayed significant plasticity across three light levels; plants in high-light had low leaf-area, LAR and SLA than those grown in low-light environments throughout all growing period (Fig. 4).

3. DISCUSSION

Same size comparisons of biomass ratios were false-supportive evidence of optimal partitioning theories. Biomass R/S, R/ST and R/L ratios were higher in high-light-grown plants than those grown in low-light environments; this was apparent supportive evidence of optimal partitioning due to shoot production increased at a faster rate in low-light environments. However, analyses of RMF suggested that plasticity observed in biomass R/S, R/ST and R/L ratios was a consequence of plastic biomass allocation in root in response to variation in light availability and not necessarily was due a plastic biomass allocation in leaves and stem (as was corroborate by same size LMF and SMF comparisons). Here, it is important said that when root was remove of biomass ratios (i.e. same size comparisons of L/ST ratio) plasticity in biomass allocation was not the answer, therefore, the former is a supportive evidence of root plasticity noise in testing plastic allocation of biomass ratios in response to light availability at same size in *L. alba*.

A closer analysis of ontogenetic drift throughout biomass fractions suggested that the changes in allocation were due solely to a shift in investment from roots (Fig. 2h) to leaf (Fig. 2b) and that the change in R/S with size (Fig. 1b) is not caused by a shift in the biomass allocation to stems due to that allocation remained remarkably constant (Fig. 2e) throughout almost all growing period.

Optimal partitioning models predict that adjustment in partitioning might lead to the optimization of growth rate by making all resources equally limiting. Nonetheless, contrasting interpretations of experimental results of LMF and SMF supported a single

allometric trajectory of leaf vs stem growth in response to variation in light availability in *L. alba*. Therefore, while acknowledging that stems may have their own specific role in increased the plant's rate of photosynthesis (Poorter & Nagel 2000), these observations nevertheless do not comply with the predictions of optimal partitioning theories. That is, the plant does not invest more in the leaves, the organ that will cause the strongest growth limitation at low-light availability. Observation of not plasticity in LMF at varying light intensities has been reported more often (Corré 1983; Lehto & Grace 1994; Van der Werf *et al.* 1996).

In the literature is often neglected that plasticity is not a property of a entire genotype it needs to be studied to a specific environments and traits: a given genotype can be plastic for one trait in response to one set of environmental conditions but not to another set, or it can be plastic for some traits but not others in response to the same set of conditions (Bradshaw 1965). The evidence of this experiment plea in line with former concept for an analysis of allocation using at least three compartments: leaves, stems and roots that not join stem and leaves into one compartment (i.e. shoot) does not acknowledge the very different functions these organs have (Poorter & Nagel 2000, see Körner 1994). Moreover, biomass ratios are compound characters that could reflect plasticity noise when one of its character is not plastic (e.g. leaf and stem in this experiment) and make obscure functional interpretations for self changes throughout growth and development.

In a physiological context a higher irradiance implies a higher rate of photosynthesis per unit leaf mass, but also a higher rate of water uptake due of an increased transpiration and

higher need for nutrient uptake because growth is stimulated (Poorter & Nagel 2000). Following optimal partitioning prediction it is expected that not only allocation to leaves decreases but to roots increases too in high-light. Now, if the prediction for optimal partitioning theories only be fulfilled for root, that is, root showed more biomass allocation in high-light than in low-light environments, then more explicit interpretations imply said that at least in *L. alba* this happen in order to lead to the optimization of growth rate in low-light availability. But these is not the case, differences in growth rate and plasticity in allocation for leaves throughout tree light environments was not apparent.

Now, how reached *L. alba* to decrease grade plasticity in total biomass throughout growing period? Plasticity in RGR_L may be the answer. The grade of plasticity in total biomass of *L. alba* decrease over time and plants of low-light environments reached very close total biomass of high-light environments. This can be traced to a much higher initial relative leaf-area growth-rate of low-light-grown plants than that observed in high-light-grown plants. However, the slight differences in total biomass for high-light-grown plants are due, not to superiority in the efficiency of its leaf-area as a producer of dry material for all experiment but remarkably turn to significant to final of experiment. Thus, increase in ULR to the final of experiment was compensated for dramatic increase in low-light RGR_L . Increase in leaf-area raised photon capture due to maximization of photosynthetic-active surface (see Crawley 1997). Total vegetative biomass has been strongly correlated with fitness (e.g. Farris & Lechowicz, 1990), the mechanism underlying to maximize total vegetative biomass in *L. alba* not involve plasticity in biomass allocation to leaves but to reach throughout plasticity in leaf-area. Here, is relevant said that high-light habitats

(thick-grain) were *L. alba* grow, conduct to strong developmental constraints in above ground biomass and that the adaptation to new environments imply plasticity in other character that not necessarily use differential allocation. It has been pointed out, amongst others, Ackerly *et al.* (1999, and references there in) that thick-grain species show reduction in phenotypic plasticity when suffer exposition to habitats different to species habitat affinity (see Gianoli 2004b, cf. González & Gianoli 2004), this is a possible explanation for find not plasticity in biomass allocation to leaves in this experiment.

In the literature the mayor leaf-area ratio compared among same-sized low-light-grown plants has been interpret as a result of optimal partitioning (e.g. Coleman *et al.* 1994), in particular for interpret that increases in the relative production of leaf-area in low-light represents functional adjustments in allocation as optimal partitioning models predict but at least for this experiment high LAR in low-light-grown plants is a consequence of the expression of mayor area in this environments that was not accompanied with a mayor allocation to leaves. The increases in SLA in low-light-grown plants implies that leaves invest less biomass per unit leaf-area and this counterbalance the decreased carbon fixation per unit leaf-area at final of experiment by increasing the total leaf-area at a given size and therefore conserve to some extent the rate of carbon dioxide fixation per unit plant biomass (see Poorter 2002).

The idea that phenotypic plasticity could be an evolutionary pathway in certain circumstances (Bradshaw & Hardwick 1989, Schlichting 1986, Sultan 1987, Gianoli 2004a) may explain plasticity in root biomass allocation of this study. *L. alba* is a shrub common

in disturbed areas (Stevens Montiel *et al.* 2001) where high-light is the norm, the adaptation to this environment imply develop response mechanism to water, a resource very fluctuant in time and space and very necessary for high demand of transpiration in high-light environments. Although we did not measure physiological water and parameters in this study, perhaps the not plastic biomass allocation response of above ground organs to light availability in *L.alba* should be compensated with increase biomass allocation to roots system for respond to hight demand in transpiration. Thus, water could be a limiting resource in time, that is, tap water in this experiment was added to field capacity at 600 and after at 1600 daily leaving a reasonable time where demands for transpiration raise up water like a more limiting time resource that light.

Former explication appears to be reasonable as it is unlikely that plants growing in nature are ever truly at a dynamic equilibrium whit respect to biomass allocation, as supply rates of light and soil resources fluctuate continuously in time and space. Thus, plasticity in biomass allocation better comes out in responses to reduce any imbalance between carbon fixation by leaves and soil resource acquisition by roots (Shipley & Meziane 2002). Then, if above ground biomass of *L. alba* present strong constraint in developmental patterns in response to light availability, the cost for keep functional plant may comes out plasticity in biomass allocation of bellow ground organ and should be related to temporal variability in water supply rates.

Differences in biomass ratios and leaf-area ratios at a given plant age may determine the outcome of competitive interactions among plants (Coleman, McConnaughay & Ackerly

1994) at least in this experiment not differences in biomass ratios and biomass fractions at same age can explain with the fact that plants throughout period of experiment never had attained sizes and therefore do not go through consequences of neighbouring shoots, that is, disturbed biomass allocation patterns (McConnaughay & Bazzaz 1992).

All these results are not in agreement with predictions based in optimal partitioning theories and are consistent with other studies that have accounted for ontogenetic drift and have found a lack of plasticity in allocation in response to variable light availability in conifers (Ledig *et al.* 1970, Steinbrenner & Rediske 1964), another woody plant seedlings (Walters, Kruger & Reich 1993; Stoneman & Bell 1993; Reich, *et al.* 1998), weedy annuals (Evans and Hughes 1961, Hughes and Evans 1962, Rice & Bazzaz 1989), other herbs (Philippot *et al.* 1991; Casper, Chaill & Hyatt 1998), *Chenopodium album* (McConnaughay & Coleman 1999), crop plants (Terry 1968; Corré 1983). However, other studies accounted for ontogenetic drift are inconsistent with this results in pea (Pearsall 1927) and forage grasses (Troughton 1956), it is relevant said that these studies use R/S and would faced plasticity noise if one of its character was not plastic.

Other studies that not accounted for ontogenetic drift (i.e. compared at a common time) support optimal partitioning theories (Olf *et al.* 1990; Callaway 1992; Latham 1992; Lei & Lechowicz 1998; Poorter & Nagel 2000) and led to the common paradigm that plants shift allocation toward leaves when are growing at low-light (Reich 2002). But, environmentally-induced changes in traits representing any aspect of plant biomass partitioning need to be examined as a function of plant size in order to draw any

conclusions as to the functional significance of the phenotypic variation (Evans 1972; Coleman, McConnaughay & Ackerly 1994) because plants growing in different environments will be of different sizes and stages of development at a particular age (Coleman, McConnaughay & Ackerly 1994)

The results of this study support a more general explanation of same allometric trajectory for components of plant biomass different to root vs. shoot in 27 herbs (Müller, Schmid & Weiner 2000; Weiner 2004) and are in disagree with Meziane & Shipley (2002) that support optimal partitioning models in 22 herbs. However, recent controversy between Müller, Schmid & Weiner (2000) and Meziane & Shipley (2002) using herbs could have basis in the comparisons of the values of the parameters of regressions were highly depend upon the model chosen and could easily lead to biologically different interpretations (Potvin, Lechowicz & Tardif 1990). Comparing overall curves (on the basis of residual ss, like this study) incline balance to Müller, Schmid & Weiner (2000) interpretation. In general, if the fit is good “without regard to whether it is the best possible fit” (Mosteller & Tukey 1977), then comparing the curves should be consistent regardless of the model used (Potvin, Lechowicz & Tardif 1990).

Finally, there are few caveats that should be considered when interpreting the results of this field study. Reach the same total biomass in a gradient of light at final of vegetative-growth period in this plant might be argued as a result of bag binding. However it is highly unlikely that this was the case for at least two reasons. First the plants in high-light continued add root mass to levels above those low-light environments (as evidenced by

allometric plot of root *vs* total mass), suggesting that there was plenty of bag space available. Second the grade of plasticity in root allocation suggested that plants added root mass constantly throughout all growth. Plasticity in allocation to roots may be argued by nutrient limitations (nutrients in this study was secured for all growing season calculating your availability from correct mixture of soil); water is delivered to roots via mass flow, while nutrients are delivered via bulk flow in soil water or via slower diffusion along soil particles, depending of the mobility of the ion (Nye & Tinker 1977). Increased biomass allocation to root systems may be a responses to increased rooting densities required to maintain nutrient uptake rates of less mobile nutrients become limiting (Nye & Tinker 1977).

We grew plants in a field under natural light, air temperature and relative humidity and varied as they would in nature. Thus, water levels were controlled to field capacity two times daily and nutrients were insured for growing period. We can not rule out that possible fluctuations in water and nutrients might have been so extreme that they preclude plants from being able to partitioning biomass of root and therefore this response was not consequence of keep functional plant in high-light environments. Nevertheless, the unrealistic nature of total constant water and nutrient levels could lead to artificial results as well. It is likely that confront a variety of different experimental designs, using both field and greenhouse conditions will be the only way to satisfy all possible criticism of experimental designs in one experiment (Gedroc, McConnaughay & Coleman 1996). Empiric comparisons be of great utility because stimulate scientific progress (Grant 2002:105) and will be needed to come to a final conclusion regarding to if plant behaviour

is define actually for predictions of optimal partitioning theories (Gedroc, McConnaughay & Coleman 1996). However, this study show that for test optimal partitioning theories is required a standard methodology that combine the comparisons of biomass fractions (Poorter & Nagel 2000) throughout the potential for contrasting interpretations at same age and same size (Coleman, McConnaughay & Ackerly 1994) and that the comparisons throughout different environments could be beneficiary for more powerful biological outcomes with the comparisons of fitted equations on the basis of the residual ss in the cases on the allocational trajectories are curvilinear (i.e. test always for non-linear components).

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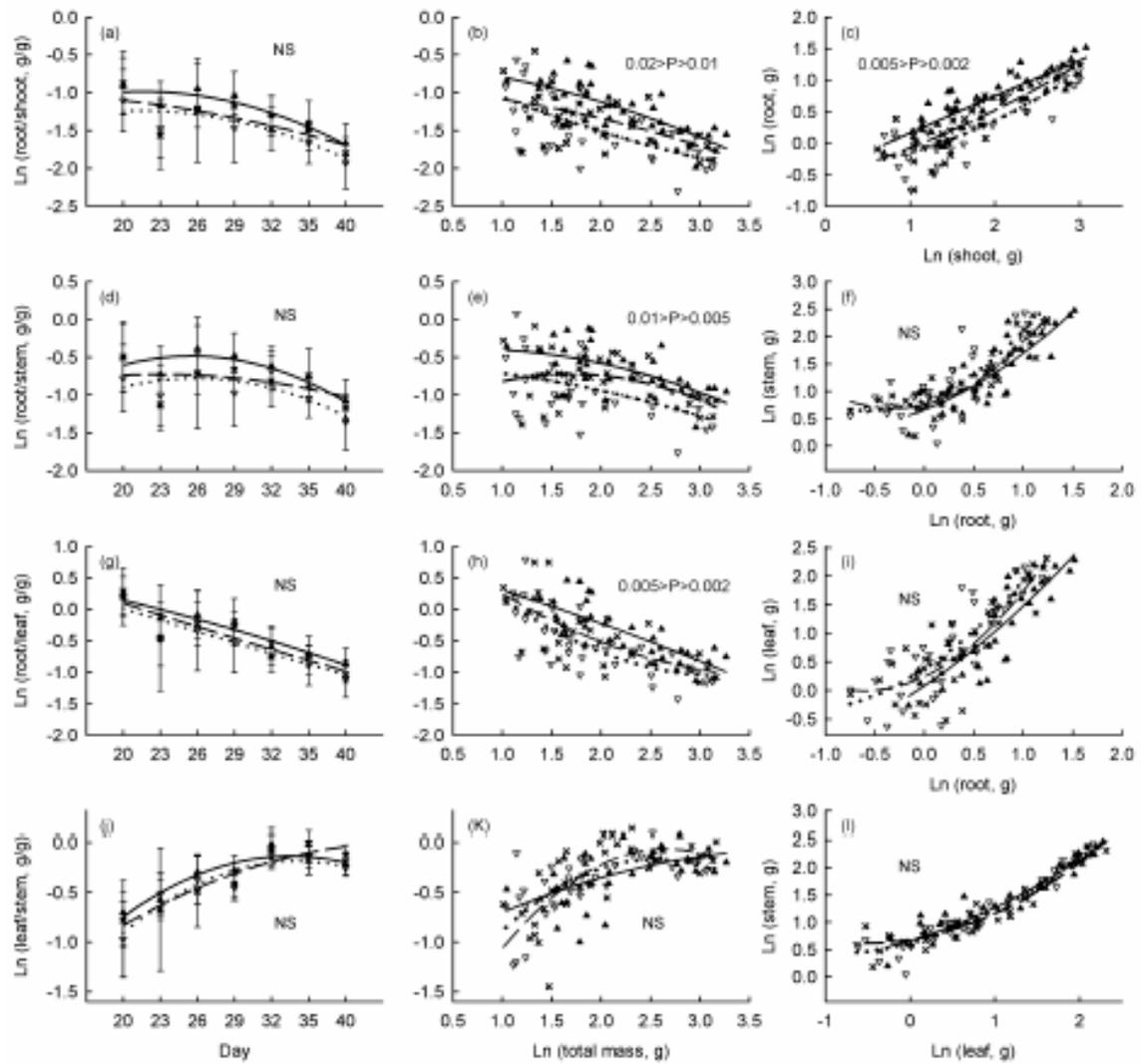


Figure 1.

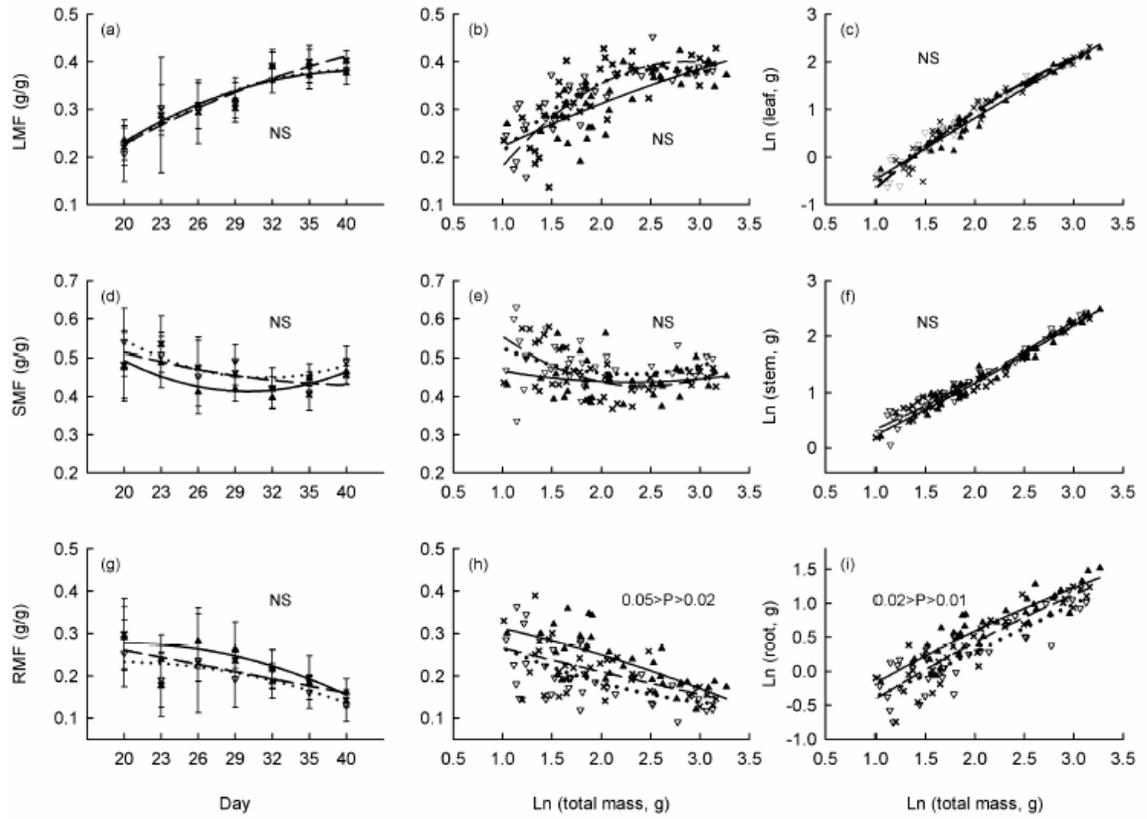


Figure 2.

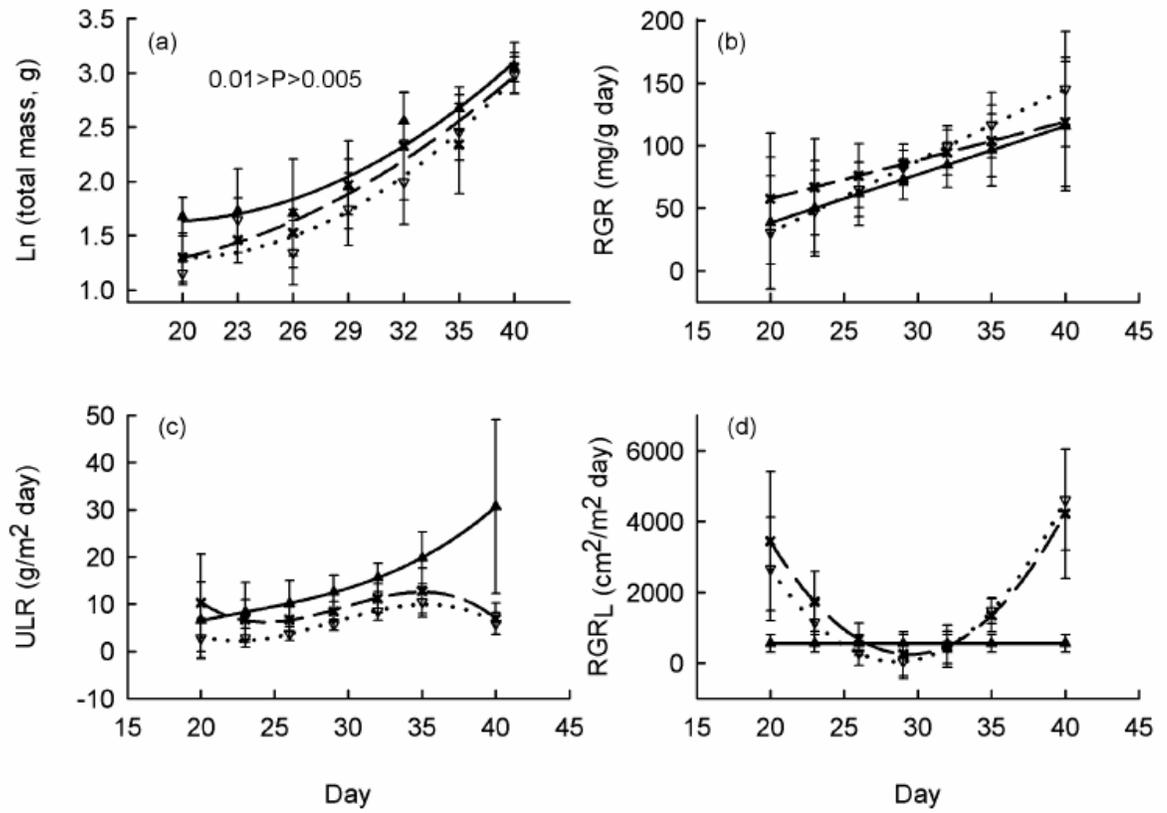


Figure 3.

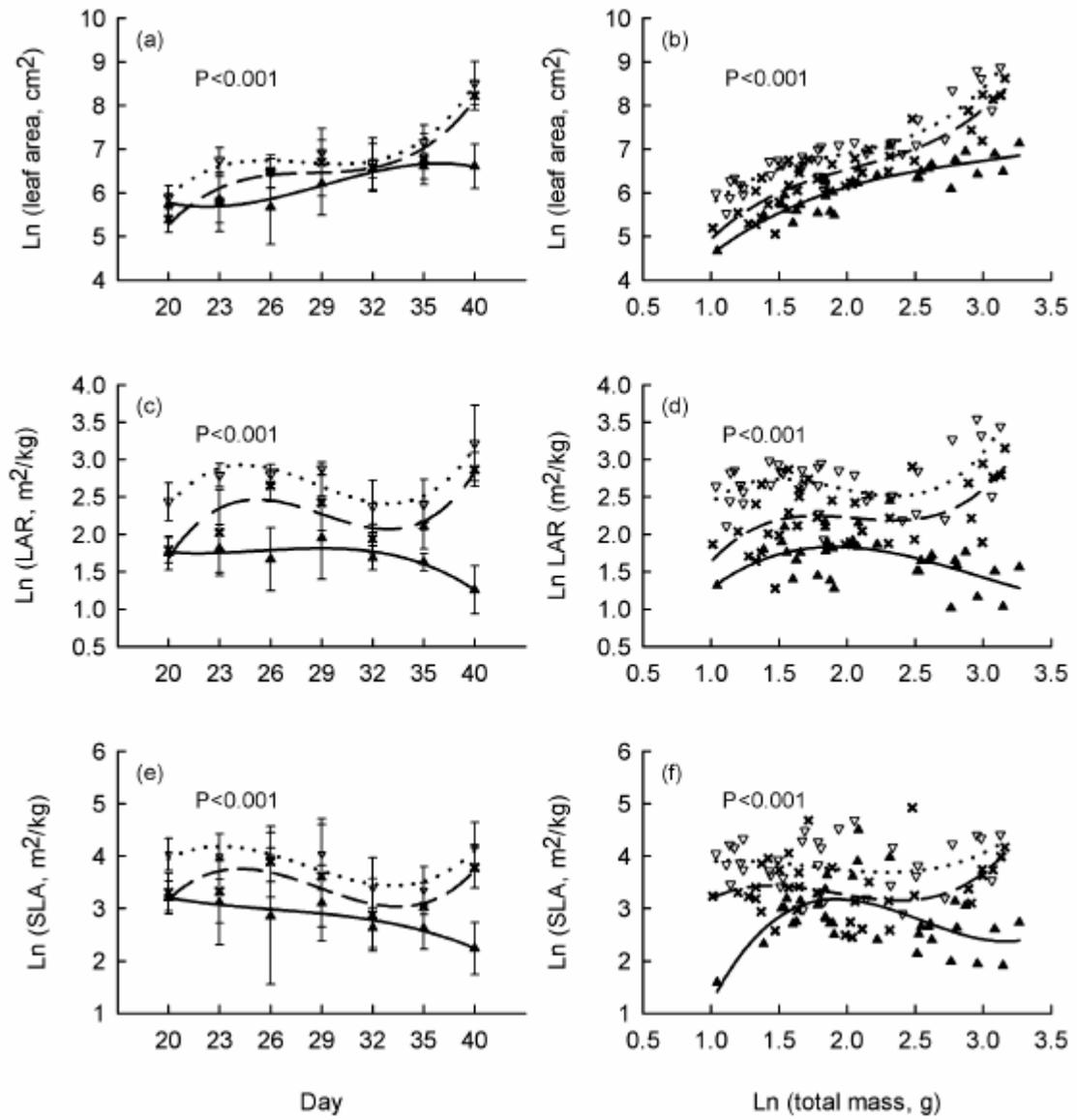


Figure 4.