FLOATING CAPITAL PATTERN AND BIOMASS SLOPE ALLOCATION METHOD IN THE LIFE HISTORY OF *CALOTROPIS PROCERA* (AIT.) AIT. F.

By

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نمــط رأس المـــال العــائم في توزيع المادة الجافـة في
دورة حيـــاة نبـــات العُشـــار (العشــــر)
باستخــــدام طريقـــة الانحــــدار

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أجري هذا البحث على نبات العشار الخشبي المعمر ، حيث تمت زراعته بالبذور في
حقل مفتوح واستمر في النمو إلى مرحلة النضج والتكاثر بإنتاج بذور جديدة . وقد تم
دراسة توزيع المادة الجافة في النبات باستخدام طريقة انحدار سميث وطريقة النسبة
المئوية المستخدمة من قبل . وجد أن هناك تبايناً في كلتا الطريقتين بالنسبة لتوزيع المادة
الجافة لأعضاء النبات المختلفة ، حيث وجد أن هناك تغير في نسبة المادة الجافة بالجذر
إلى المجموع الخضري سواء بالزيادة والنقصان ، ثم الثبات . وكان متوسط نسبة
الجذر/المجموع الخضري تعادل ٠,١٢ / ١,٠ خلال المرحلة اليافعة ، ٠,٦٨ / ١,٠ قبل
الازدهار ، بينما وصلت ٠,٥٠ / ١,٠ قبل مرحلة التكاثر . ووصلت نسبة المادة الجافة
الموزعة إلى أعضاء التكاثر ٢٠٪ ، وكان معامل الحصاد ٩٪ . ويرجع نقص نسبة المادة
الجافة الموزعة إلى أعضاء التكاثر إلى النمو الخضري الغزير لكل من المجموع الخضري
والجذري بعد مرحلة إنتاج البذور . وتميل دورة حياة نبات العشار إلى استراتيجية مثلث
جـرايم C - S - R عنها في K - r لماك أرثـر .

Key Words: Biomass allocation, *Calotropis*, Fractional allocation, Life-history, Perennial, Ruderal, Slope allocation.

ABSTRACT

Plants of the woody perennial *Calotropis procera* (Asclepediaceae) were grown from seed to seed-set in an open field. Smith's slope allocation and fractional allocation or percentage methods were used to study dry matter partitioning in the species. The two methods differed in thier predictions of the biomass allocated to the various organs. There were differences in the direction of change in the root/shoot ratio: increase, decrease and no change. The mean root/shoot ratio was 0.21:1 during the juvenile phase, rising to 0.68:1 and stabilized at 0.5:1 prior to and following the reproductive phase. Reproductive effort was 20% of biomass and harvest index was 9%. The relatively small biomass allocated to reproduction was caused by vigorous vegetative growth and root growth following seed shed. The set type of life-history strategy to which *Calotropis* can be assigned is in accordance with the C-S-R triangle for ordination rather than the r-K selection theory.

INTRODUCTION

Current concept of life-history strategies which are often used to describe a particular species include annual, biennial, pauciennial, perennial, r- and K- strategists. fugitive, colonist, ruderal, weed and Grime's C-S-R model (Baker 1965; MacArthur and Wilson, 1967; Harper, 1977; Grime. 1977; Reinartz, 1984a and b; Matlack, 1987; Shipley, Keddy, Moore and Lemky, 1989).

Some life history strategies are described in the literature. For example, an annual is a plant that completes its life-cycle and dies within 12 months and it only reproduces by seed. A monocarpic pauciennial (a biennial or a triennial) is a species who lives for 2-3 years but will die after flowering once. The perennial (a polycarpic pauciennial) is a species able to flower for several years and it may reproduce either vegetatively or by seed or by both.

Grime's (1979) triangle of ordination accounted for what he called the intensity of 'stress' which plants may experience in different habitats; Grime (1979) classified habitats in terms of the levels of disturbance, competition and stress and thereafter suggested three primary strategies for plants' life-cycles: competitors, stress-tolerators and ruderals (hence Grime's C-S-R-model).

MacArthur (1972) proposed two life history strategies: the r and K- selection. The r-selected species should possess superior fitness at low population density, i.e. poor competitive abilities. In K- selected plants are found: small number of large seeds, large adult size and strong competitive abilities.

Numerous studies have examined life-history strategies for annual species, e.g. *Senecio vulgaris.* (Harper and Ogden, 1970) and for perennial species, e.g. *Ranunculus repens* (Smith, 1986) and *Mikania micrantha* (Swamy and Ramkrishnan. 1988).

From these studies a consensus has emerged that the proportion of biomass allocated to reproduction in annuals is greater than that allocated in perennials. These studies also give a correspondence between patterns of allocation and the different groups of plants in several different communities.

The allocation pattern of a plant defines its ecological role and is an important factor in understanding plant distribution and adaptation to different niches Bazzaz, Chiariello and Coley, (1987). Smith (1986) argued that the traditional method of calculating allocation by relative dry weights of plant components (fractional allocation) must also be accompanied by plotting the actual organs' weights against total plant weight. For example, the straight line relationship of a plant organ (stem) dry weight with total dry weight can be expressed as:

$$y = a + b x \qquad (1)$$

where y = stem dry weight
        x = total plant dry weight
        b = gradient of line
        a = y-axis intercept.

Smith (1986) pointed out that 'b' can be constant which implies a constancy of dry weight allocation to any plant organ independent of total dry weight, and it follows that 'slope allocation' or 'b' can be expressed as:

$$\text{Slope allocation} = b = (y-a)/x \qquad (2)$$

and therefore the traditional fractional allocation

$$= y/x \qquad (3)$$

which implies that (Equation 3) is equivalent to (Equation 2) when 'a' = 0 (i.e. this is only true when y and x have large values) and consequently "the value of 'a' in the term 'y-a' becomes insignificant towards y". Smith (1986) concluded that in biomass allocation studies both methods, the 'allocation slope' and the 'fractional allocation', must be attempted.

This study was carried out to (a) compare biomass allocation in terms of 'slope allocation' and 'fractional allocation' (b) investigate whether the allocation of resources to roots, vegetative and reproductive organs (flowers) has achieved a compromise between plant size and reproductive effort and (c) examine the relationship between life-history and pattern of biomass allocation in *C. procera.*

MATERIALS AND METHODS

Description of study species: *C. procera* was chosen as especially suitable for this study because of its exceptional presentation and its wide distribution in a variety of ecologically distant habitats.

Calotropis procera (Ait.) (Asclepediaceae) is a soft-wooded shrub or small tree up to 2.5 m. high, with milky juice, the leaves are fleshy, sessile or shortly petiolate (Andrews, 1952). *C. procera* is a cosmopolitan species and is common through tropical Africa, extending through Egypt into Arabia, India, and also found in Brazil (Chadwick and Obeid, 1963). In the Sudan *C. procera* is ubiquitous in areas of human disturbance such as fields, abandoned fields, pastures, roadsides, riverine banks, conservation areas, domestic lawns, vacant urban and utility areas and timber plantations. The invasion of these areas has resulted in an increased fire hazard, degradation of aesthetically valuable regions including arable areas, and the likelihood of decreased livestock carrying capacity as the species is unpalatable. The occurrence of *C. procera* in the vicinity of villages is an indicator of heavy grazing pressure (Obeid, Wickens, Bari and Williams, 1982). *C. procera*, if not eradicated as a weed, quickly produces dense forests. *Calotropis* does not reproduce vegetatively, but by producing wind-dispersed propagules. A remarkable phenological feature of *Calotropis* is that it is an opportunist in its germination and seedling emergence, responding to soil moisture or rain in all seasons.

EXPERIMENTS

Seeds used in this study were collected in June 1987 from *C. procera* plants growing in the Sudan Gezira. The plants were grown from seed (weight 3.0 ± 0.17 mg.) within experimental plots (University of Qatar) established in September 1987. Plot soil textures vary from loamy sand to sandy loam with electric conductivity 0.8 - 0.1 mmho cm^{-1}, field capacity of 11%, maximum water holding capacity of 28%, pH 8.2. The monthly average temperature ranges between 18°C in January and 35°C in July. Average annual precipitation on the study site is scanty, erratic and does not exceed 55-76 mm over the period December-March. Four plots (0.65 x 0.70 m) were arranged in a completely randomized design. The seeds were sown by hand on 1 October 1987 at 0.13 m (8 plants row^{-1}) spacing within four rows 0.13 m apart and ran north-south to give 70 plants m^{-2}. Before sowing, the plots were irrigated to field capacity, thereafter they were irrigated twice a week.

One plant was selected at random from each plot at monthly intervals starting 1 November and ending by the end of May 1989. The sampled plants were separated into leaves, roots, stem (caudex + twigs) and reproductive parts only during April-May 1989. Once this was done each component from each plant was bagged and dried at 80°C for six days, and weighed to obtain their dry weights. Monthly net production and its allocation to each part was estimated from these data. Firstly, the 'slope allocation' method was used (see Introduction) by carrying out regressions between (i) leaf dry weight (ii) stem dry weight (iii) root dry weight and total plant dry weight and then testing for significance using the correlation coefficient (r). Secondly, the 'fractional allocation' method was used. Thirdly, an attempt was made to quantify biomass partition of below ground (roots) and above ground components (shoot = stem + caudex + twigs + leaves +reproductive parts), i.e. root/shoot ratio; and, lastly, reproductive effort (RE) was calculated using the formula

RE = (S + E) / B

where

S = weight of seeds plant^{-1}
E = total weight of empty inflorescence or fruits plant^{-1}
B = above ground biomass = weight of vegetative components + S+ E plant^{-1}

90

To determine if there were any shifts in the amount of biomass allocated to each plant component analyses of variance were performed.

RESULTS

The average dry mass of the plant's organs increased steadily with increasing level of the total plant weight (Fig. 1, a, b, c). When data from the treatment were pooled there was a highly significant relationship between stem dry weight (r = 0.999), root weight (r = 0.999), leaves' weight (r = 0.997) and plant dry weight. Rank of order of increasing biomass based on the regression lines was stem > root > leaves.

The general forms of the fractional allocation curves show that recovery of the allocated biomass did not differ significantly (P > 0.5) beyond the intitial instability period (referred to as 'floating capital period' henceforth) during November 1987 - July 1988 for leaves, stem and root (Fig. 2). The mean leaf fraction changed gradually (negative slope) from > 60% to level off at a minimum biomass threshold of 31% (Fig. 2a). This change corresponded in time with a similar increase in the percentage (positive slopes) of biomass recovered from the stem (Fig. 2b) and root (Fig. 2c);
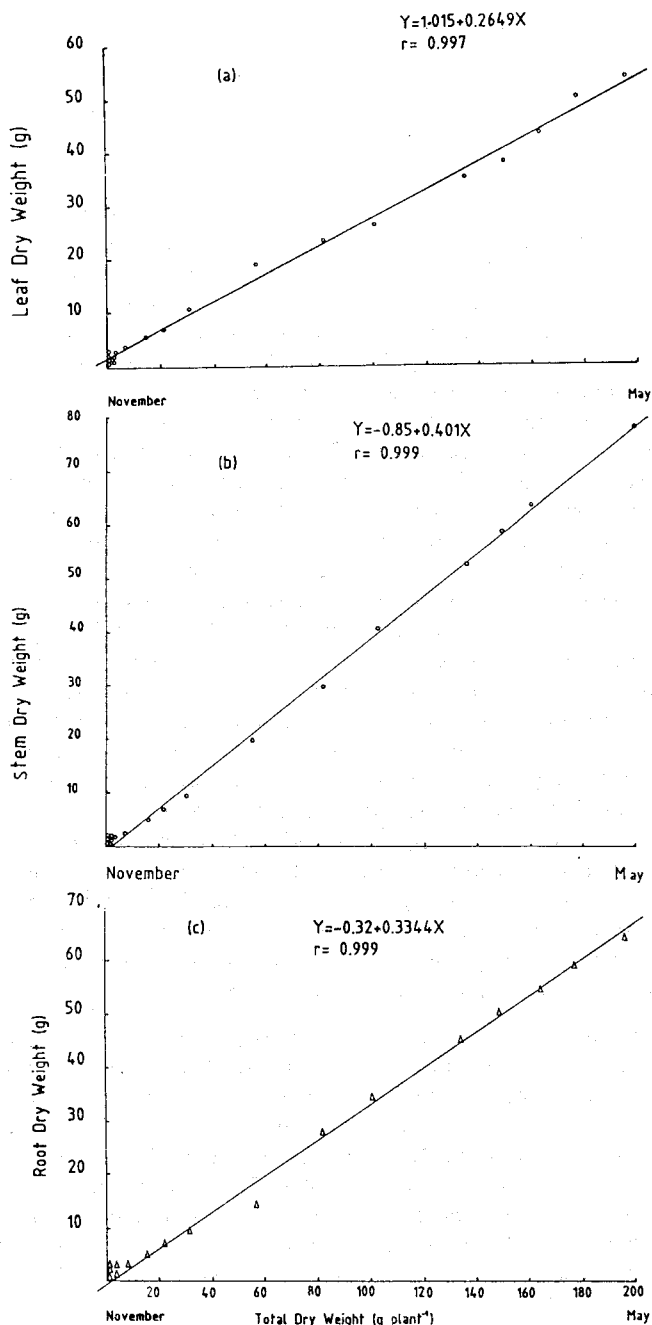
$$Y = 1.015 + 0.2649X$$
$$r = 0.997$$

$$Y = -0.85 + 0.401X$$
$$r = 0.999$$

$$Y = -0.32 + 0.3344X$$
$$r = 0.999$$

Fig. 1a, b, c: The relationship between organ weight and total plant weight during November (1987) - May (1989.
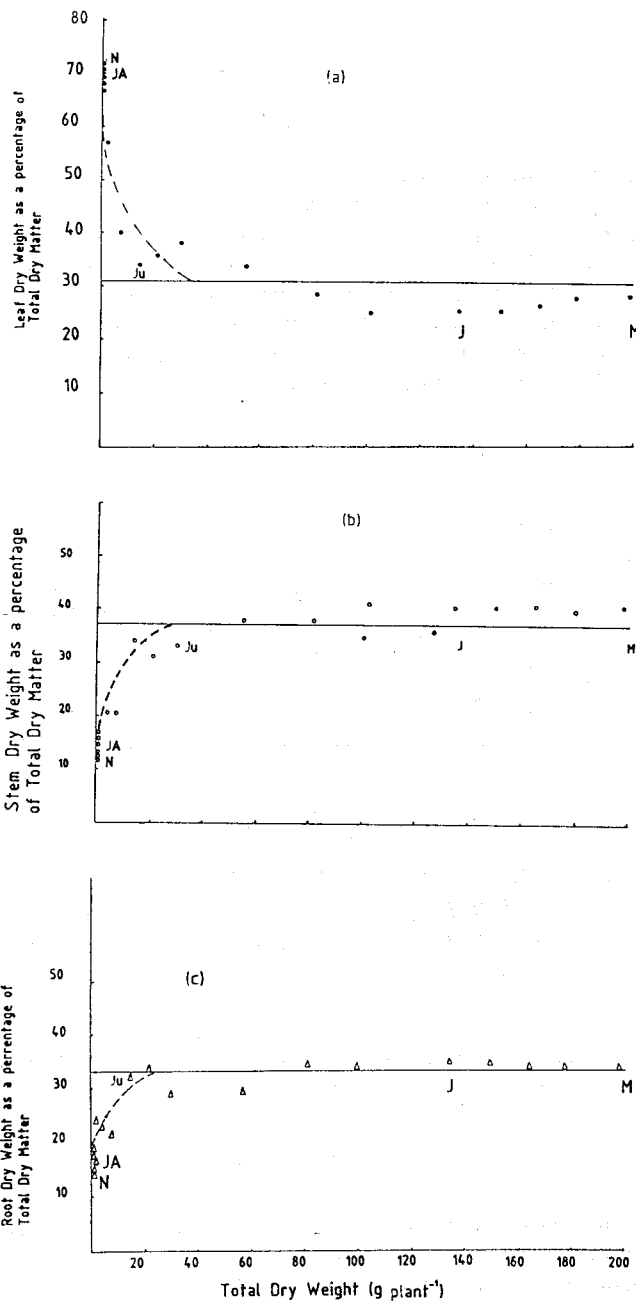
Fig. 2a, b, c: Plant components dry weight (............) Leaf (○○○) stem (△△△) root as a percentage of total plant dry weight. (———) calculated minimum or maximum biomass threshold (see text for explanation). N = November 1987, JA = January 1988, Ju = July 1988, J = January 1989, M = May 1989.

stem and root weight increased substantially (P < 0.05) from 11-13% over the floating capital period to a maximum biomass threshold of 36% and 33% respectively. The values 31%, 36% and 33% for the leaves, stem and root respectively were maintained thereafter.

The results show that the root/shoot ratio was 0.21:1 during the juvenile phase (November 1987 - March 1988) but this value rose sharply with time and the highest ratio (0.68:1) occurred by June 1988. Thereafter the root/shoot quotient declined to a value 0.41 over the period July-November 1988, but later the situation stabilized (November 1988-May 1989) when similar proportions of the biomass allocated were equally shared between the root and the shoot, and this ratio of 0.5:1 was maintained till the end of the experiment. The root/shoot ratio curve (Fig. 3) can be divided into three phases according to the life-history strategy of *C. procera*. Firstly, biomass allocated to roots increased exponentially at the expense of that allocated to shoot (environmental). Secondly, some biomass is allocated to canopy formation with no further addition to root (physiological). Thirdly, a parity in the biomass allocated between shoot and root is reached until the appearance of flowers and formation of follicles (reproductive and innate).
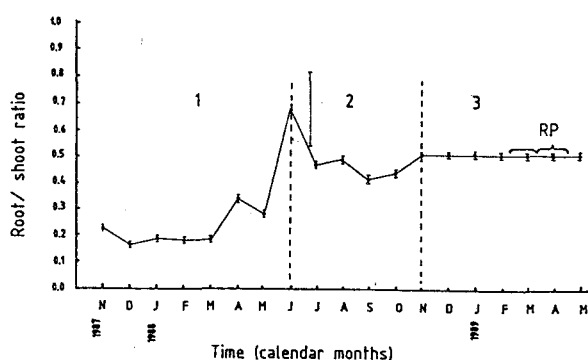

Fig. 3: The root/shoot dry weight ratios over time in *Calotropis procera* (RP = Reproductive Period). 1, 2, and 3 plant-life phases. Vertical bars indicate ± ISE.

The reproductive effort of *C. procera* was 20% of biomass and the harvest index was about 8-9%.

DISSCUSSION

In almost all previous published literature on dry matter allocation it has been the relative dry weights of plant components, rather than actual weights, which have received thorough study. In the present study dry weight allocations expressed as percentages were variable compared to organs' weights when plotted against total plant dry weight, for example, with leaves. The data show a decrease in percentage of leaf dry weight with increase in total dry weight of *C. procera* (Fig. 2a). Conversely, the data show an increase in percentage shoot and root dry weights with increased total *Calotropis* dry weight (Fig. 2 b, c). However, when the actual separate dry weights of leaves, shoot (caudex + stem + flowers) and root are plotted separately against total dry weight of *Calotropis* there was a highly

significant relationship (correlation) between the three plant components' dry weights and *Calotropis* total dry weight (Fig. 1a, b, c). The present results support (Smith's 1986) argument that the traditional method of calculating biomass allocation has a built-in assumption (an Achille's heel) that the y-axis intercept 'a' = 0. This is not the case for the results obtained with *Calotropis* (Fig. 1, 2) as in none of the relationships between any plant component dry weight and total plant dry weight was 'a' = 0. This explains the decrease (leaves) and the increase (shoot and root), and subsequent levelling off, of percentage allocation with increasing total dry weight (see Smith, 1986). Evidence of the applicability of the above findings to other plants has been found in data by (Smith 1986) working with *Ranunculus repens*, and by (Reinartz 1984b) working with *Verbascum thapsus* L. Whether the slope allocation model is common to many plant species awaits further study. Also, it would be of interest to investigate the consequences of the model on the interpretation of competition effects at the individual species level.

Life-histories and population dynamics are related to biomass partitioning and plant size (Sarukhan and Harper, 1973). The biomass allocation pattern in *C. procera* consists of several phases that blend subtlely into one another. *Calotropis* typically has an extended juvenile period following seedling emergence-all available resources are allocated to vegetative growth-during which vegetative growth is supposed to be optimal, maximizing fitness of the seedling (Kachi and Rorison, 1989). The lesser amounts of root to shoot ratio during this vegetative growth stage is indicative of survival potential under competition (Chadwick and Obeid, 1963; Grime, 1977; Swamy and Ramakrishnan, 1988). This prediction is also supported by the general trend that the root/shoot ratio of a plant decreases in response to increasing nutrient and moisture availability. By the end of the season (June 1988) excess biomass was stored in the root for use in the next year (Fig. 3). In turn, the resources were allocated to the caudex, stem and leaves (June-November 1988). Perennials have a much more complex growth due to several complicating factors, i.e. unlike annuals perennials need to store energy for perennation. Additional complications arise from the fact that in *Calotropis* vegetative growth continued during the short (2-3 months) reproductive episode. The preferential allocation of resources to caudices, vegetative organs, and root rather than to reproductive organs may be strategic in that individual *Calotropis* plants are likely and destined to survive until a subsequent year. Over the last phase of the life-history (November 1988-May 1989) *Calotropis* accumulated resources and became large in size to produce seeds. Plants at this phase allocated resources equally to both shoot and root.

Plants are reported to possess root/shoot ratios as 10:1 in cold deserts and close to unity in warm deserts (Sisson, 1989). This is not the case for the results obtained with *C. procera* shown here. The mean root/shoot ratio of *Calotropis* at the different life phases were in turn 0.21:1, 0.41:1, 0.68:1 and 0.50:1 respectively, with a composite range of 0.45-0.55. These results suggest that the root/shoot ratio in *C. procera* is of a satisfactory balance between the above-ground biomass (caudex + stem + leaves) and below-ground biomass (root) for successful growth (Kramer, 1983; Robinson, 1986).

Reproductive effort is the proportion of a plants' total resources allocated to reproduction. However, measurement of the currency used in reproductive effort is a controversial topic (Bazzaz and Reekie, 1985; Ohlson, 1988). In this study the

harvest index was 9% and reproductive allocation was 20%; these values are similar to those of other perennials (Reinartz, 1984b). A plant-controlled restriction of resources which limited the fecundity was most probably responsible for the low reproductive effort encountered with *Calotropis*. Harper and Ogden (1970) stated that the life history of a plant species is to some extent predetermined. The success of an individual plant in a given environment is often determined by the allocation of limited available resources between competing ends: maintenance, growth and reproduction (Abrahamson and Gadgil, 1973). Thus an organism which colonizes disturbed but stable habitats, e.g. *C. procera*, optimizes the partitioning of biomass allocation in a way that maximizes fitness by *vigorous vegetative growth* (Harper, 1977). The reproductive strategy of *C. procera* can be described as iteroparous (Sterns, 1976) or polycarpic (Harper, 1977; Brock, 1983) as it produces a huge number of seeds over several years of its life span.

Calotropis has (a) a large number of small seeds capable of wind-dispersal and speedy germination-juvenile traits (b) a strong competitive ability (*sensu* Chadwick and Obeid) and (c) a large size (see results) - adult traits. Shipley, Keddy, Moore and Lemky (1989) argued that the concept of r-K strategists predisposes an association between juvenile and adult traits. In Grime's C-S-R ordination triangle of plant strategies (1974, 1977, 1979) this association between juvenile and adult traits is not found. Rather than conforming to a set type of life-history strategy, the results in the present investigation may describe *Calotropis* as (a) a perennial (b) a stress-tolerant ruderal (Grime, 1977) and (c) a weed.

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