PHYSIOLOGICAL GROWTH ANALYSIS OF THE LIFE-HISTORY OF *CALOTROPIS PROCERA* (AIT.) AIT. F.

By

A. M. A. ISMAIL

Department of Botany, Faculty of Science, University of Qatar, Doha, Qatar

تحليل النمو الفسيولوجي في دورة حياة نبات العُشـــار

أحمـد محمـد علي إسماعيل

تناول هذا البحث دراسة تحليلية للنمو في نبات العشار من خلال توزيع المادة الجافة لأعضاء النبات في مراحل نموه المختلفة . وقد تم قياس تراكم المادة الجافة ، مساحة الأوراق وكتلتها ، ومعدل النمو شهريا خلال ١٩٨٧ إلى ١٩٨٩م . بينت الدراسة ان تخزين نواتج التمثيل الغذائي يستمر خلال مرحلة النمو الخضري ومرحلة التكاثر ، مما يوضح ان نبات العشائر لا يمر بالمرحلة الانمائية المعروفة بالقطع (cut - out) . وجد ان المادة الجافة الكلية تزداد تدريجيا مع التقدم في العمر لكل من الورقة والسـاق والجذر . وكانت الزيادة في معامل مساحة الورقة (L A I) حادة بعد مرحلة البادرة والتي وصلت ٩ في مرحلة النضـج والتكاثر . ويرجـع سبب زيادة كمية المادة الجافة في حجم معين من المجموع الخضري لنبات العشار إلى أوراقه التي تتميز بقلة مساحة الورقة بالنسبة لوزنها (S L A) ومن جهة أخرى وجد أن نسبة مساحة الورقة (L A R) ونسبة وزن الورقة (L W R) قد وصلت أعلى معدلاتها خلال مرحلة البادرة ثم قلت تدريجيا مع التقدم في العمر ، وقد ينسب ذلك إلى زيادة تراكم المادة الجافة في الجذر والساق على حساب باقي أعضاء النبات . وقد تبادلت قيمة معدل التمثيل الصـافي (N A R) بين الصعود والهبوط مع التقدم في العمر حتى بداية مرحلة النضـج والتكاثر . وبالنسبة لمعدل النمو النسبي (R G R) فقد وصل أعلى معدلاته خلال مرحلة البادرة وأقلها في مرحلة النضـج والتكاثر ، بينما استمر معدل نمو المحصول (C G R) ووصل أعلى معدلاته خلال مرحلة النمو الخضري وبداية مرحلة التكاثر . أوضـحت الدراسة ان التكيف البيئي ـ فسيولوجي في دورة حياة نبات العشار تمكنه من تحاشي الظروف غير المناسبة التي قد يتعرض لها خلال مراحل نموه المختلفة . وقد نوقشت النتائج بالنسبة للادارة والتحكم في انتشار نبات العشار .

Key Words: Pest management, Growth analysis, Perennial, Weedy ruderal.

ABSTRACT

Growth of *Calotropis procera* was analysed by distribution of dry weight throughout the plant at various stages in growth. Dry biomass, leaf area index, specific leaf area, leaf weight ratio, leaf area ratio, net assimilation rate, relative growth rate and crop growth rate were monitored monthly during 1987-1989. In *Calotropis* storage of assimilates seems to dominate both vegetative and reproductive phases, thus *Calotropis* does not undergo the developmental phenomenon known as "cutout". Total biomass increased steadily for all three major organs. i.e. leaves, stem and root. LAI increased sharply following the seedling stage and reached 9.0 during the reproductive phase. The amount of biomass packed into a given volume of canopy space was high in *Calotropis procera* achieved by having leaves with low SLA. LAR and LWR reached a maximum during the seedling phase and thereafter consistently declined. The decreasing value of LAR was due to greater contribution to stem and root dry matter to the total dry matter. *Calotropis* has alternating peaks of rise and fall in NAR with time until the beginning of the reproductive phase. RGR was highest during the seedling phase and the least during the reproductive phase. CGR continued at a higher level during late vegetative and early reproductive stages. *Calotropis* has ecophysiological adaptations in its life-cycle which enable it to avoid the consequences of a season unfavourable to active growth. These findings are discussed in relation to the management and control of *C. procera.*

INTRODUCTION

A fundamental purpose of growth analysis and yield component analysis is to increase quantitative understanding of the growth of plants or vegetation (Warren Wilson, Hunt and Hand, 1986).

Leaf area index (LAI) is frequently used as an indicator of plant growth for measuring assimilation, transpiration and biomass production. Leaf area ratio (LAR) expresses the amount of leaf area developed per unit plant weight and is a component of relative growth rate. Specific leaf area (SLA) is used to estimate total leaf area at various stages of plant growth and to predict leaf area from leaf dry weight. In general, SLA is sensitive to environmental change and more prone to ontogenetic drift (Hunt, 1982). Reddy, Acock, Baker and Acock (1989) pointed out that the most variable component of leaf dry weight was starch content and that SLA will vary inversely with leaf starch content. Leaf weight ratio (LWR) or leaf fraction is the proportion of plant weight devoted to leaf material. Net assimilation rate (NAR) is the net growth rate (of dry matter) expressed per leaf area. Relative growth rate (RGR) is defined as the rate of dry matter accummulation per unit of existing dry matter (Warren Wilson, 1981) or is defined as the rate of growth divided by size. Shipley and Keddy (1988) pointed out that RGR was an important variable because it measured the rate of return of new tissue for a given investment in existing tissue. Relative growth rate is dependent on the area of leaf displayed by unit plant weight (LAR) and on the assimilatory efficiency of this leaf area, i.e. NAR (Warren Wilson, Hunt and Hand, 1986). However, RGR decreases with increasing plant size. Crop Growth Rate (CGR) is defined as the rate of dry matter production per unit area (Warren Wilson, 1982).

In the companion paper (Ismail, 1992, this volume) it was reported that Calotropis procera is (a) certainly ruderal in the sense that it colonizes abandoned lands that are too exhausted for growing crops (b) stress tolerant in its ability to thrive on such lands as well as over-grazed grasslands (c) weed in the sense that it grows in areas touched by man and his stock (d) iteroparous in the sense that it reproduces more than once a year, and (e) consistent with the findings of (Crick and Grime, 1987) in Scirpus sylvaticus, Calotropis procera (as a plant characteristic of exhausted soils) developed a large root/shoot ratio and also showed a constancy in final root biomass.

Whilst an extensive literature on growth analyses performed on annuals, especially crops, exists (Cotton: Ibrahim and Buxton, 1981; Soybean: Harris, Smith and Mackender, 1986; Sugar cane: Singh and Gururaja Rao, 1987; Tomatoes: Heuvelink, 1989) there is relatively little information available for well adapted perennials in semi-arid and tropical environments. Lack of knowledge of these responses hinders management options of weedy ruderals like Calotropis procera growing on thousands of hectares of range and arable lands. This paper describes the development trends in most of the growth parameters in C. procera and tries to understand the physiological qualities behind its success as a versatile weed.

MATERIALS AND METHODS

Description of study species

Calotropis procera (Ait) (Asclepediaceae) is a soft-wooded shrub or small tree up to 2.5 m. high, much branched from the base, with milky juice, the leaves are fleshy, sessile or shortly petiolate (Andrews, 1952). C. procera is a cosmopolitan species and is common through out tropical Africa, extending through Egypt into Arabia, India, and also found in Brazil (Chadwick and Obeid, 1963). C. procera occurs widely in the Sudan Gezira, occupying a diversity of habitats including arable and pastoral farm land, river banks, waste places bulldozed or scraped conservation areas and road sides. The species reproduces by small parachute-bearing propagules which are wind-borne. In the Sudan Gezira germination takes place largely during July-August in response to rains but seedlings may also arise any time of the year near irrigated sown crops (plot walkways or alleys) but were never observed to grow successfully as a week amongst crops. Calotropis plants flower all the year round.

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 0.8-1.0 dSm^{-1}. The mean soil physical characteristic (0-60cm) were: soil water at -0.03 MPa 11.0%, at -1.5 MPa 7.0%, bulk density 1.30g/^{3}c. The soil was calcareous and very low in nitrogen (0.01%), medium in phosphorus and potassium (4-5%) and slightly alkaline in reaction.

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 55.0-76.0 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} by the beginning of the experiment and 20 plants m^{-1} by the end of the experiment (due to self-thinning and sequential harvesting). Before sowing, the plots were irrigated to field capacity, thereafter they were irrigated twice a week.

Growth analysis

One plant was selected at random from each plot at monthly intervals starting 1 November 1987 and ending by the end of May 1989. They were separated into leaves, roots, stem (caudex + twigs) and reproductive parts (at appropriate time). The leaves prior to being subjected to the oven, had their areas determined by graph-paper tracing. Leaf area index (LAI) was determined:

LAI = Leaf area plant^{-1} (mean leaf area plant^{-1} in m^2) x density (the number of plants m^{-2})   (1)

Once this was done, each component from each plant was bagged and dried at 80°C for six days to obtain their dry weights. If A = total plant leaf area (cm^2); DW = total dry weight of the plant (g); DW$_L$ = total dry weight of the leaves, then the following growth functions were calculated:

Specific leaf area (SLA) = A/DW$_L$ (2)
Leaf area ratio (LAR) = A/DW   (3)
Leaf weight ratio (LWR) = DW$_L$/DW   (4)

Therefore LAR = LWR x SLA   (5)
Mean Net Assimilation Rate (NAR) =

$$NAR = \frac{DW_2 - DW_1}{t_2 - t_1} \times \frac{\ln A_2 - \ln A_1}{A_2 - A_1} \qquad (6)$$

Mean relative growth rate (RGR) = $\ln DW_2 - \ln DW_1 / t_2 - t_1$ (7)

Therefore RGR = LAR x NAR   (8)

Cropt growth rate (CGR) = LAI x NAR   (9)

Also

CGR = Biomass x RGR   (10)

Where: Biomass = n x W = Total above ground plant dry weight per unit area of ground

n = number of plants^{-2}

W = total dry weight plant^{-1}.

The relationship between LAI, SLA, LAR, LWR and RGR respectively and time (19 months) were determined by curves fitted by least-squares linear regression.

RESTULTS

LAI

The patterns of LAI overtime in response to increasing age and the total LAI the plant reached are shown in (Fig. 1) LAI of *C. procera* increased linearly following the initial instability period (= floating capital period) and reached a maximum of about 9 just before flowering began. There was a highly significant relationship (r = 0.997, P < 0.001) between LAI increase as the plant aged. Following reproductive phase middle and lower leaves senesced and had fallen (results not shown).
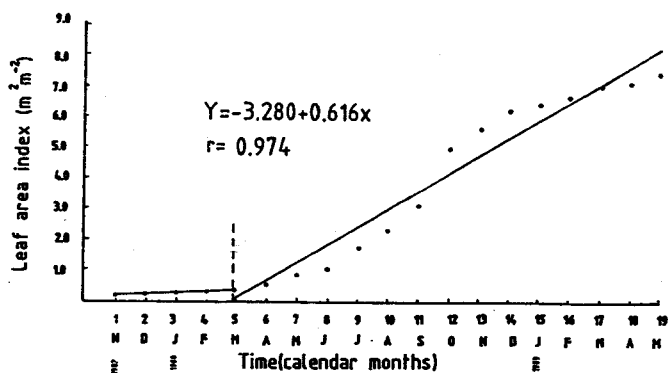

Fig. 1: Seasonal progress in leaf area index of *Calotropis procera* from seedling emergence to seed-set. (----------) End of floating capital phase (1-19 duration of experiment in months).

SLA

SLA peaked two months after emergence (MAE) to reach a value of 225 cm^{2}g^{-1}. During seedling stage the value was maintained between 180-190 cm^{2}g^{-1} and thereafter it showed a continuous decline (r = −0.86, P < 0.001). From January 1989 (15 MAE) flowering began and 18 MAE most of the follicles (fruits) had matured. As the follicles opened to shed seeds, their demands for assimilates might have decreased resulting in surplus of photosynthate availability and thus decreased SLA to 100.0 cm^{-1}g (Fig. 2).
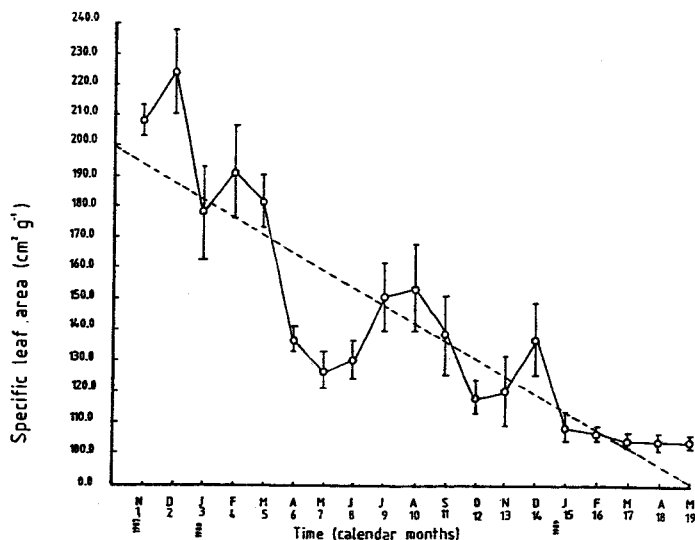

Fig. 2: Seasonal changes in specific leaf area of *C. procera*. Bars represent ±1SE. ---------Line fitted by least -squares linear regression Y= 199.68 − 5.65 x r = −0.86, P < 0.001 (1-19 duration of experiment in months).

LAR

There was a greater proportion of shoot weight e.g. more leaf area per total shoot weight (120-150 cm^{2}g^{-1}) that was lamina during the seedling stage. During subsequent growth stages LAR showed a stark decline (r = −0.91, P < 0.001) to maintain a value of 25 cm^{2}g^{-1} till the end of the experiment (Fig. 3).
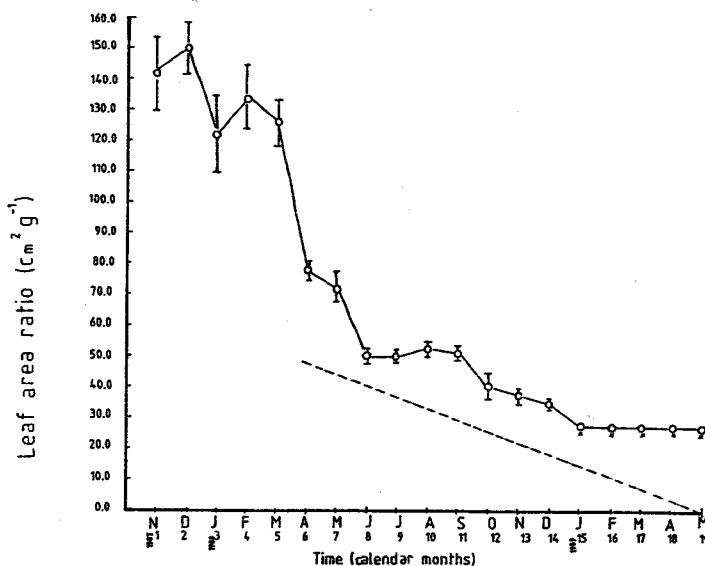

Fig. 3: Seasonal change in leaf area ratio of *Calotropis procera*. Bars represent ±1SE. The magnitudes of SE of measurements (x) were smaller than the symbols. ------- Line fitted by least -squares linear regression Y = 70.86 − 3.62 x, r = −0.92, P < 0.001. (1-19 duration of experiment in months).

LWR

The form of the curve shows a stepwise decrease (Fig. 4) in the amount of biomass devoted to leaf material as the plant aged. For example, 71% of the plants biomass was in leaf fraction during the seedling stage. This value dropped to 55% by the beginning of the vegetative stage and this value decreased to 40% and 30% during the vigorous vegetative and reproductive stages respectively (r = −0.94, P < 0.001).
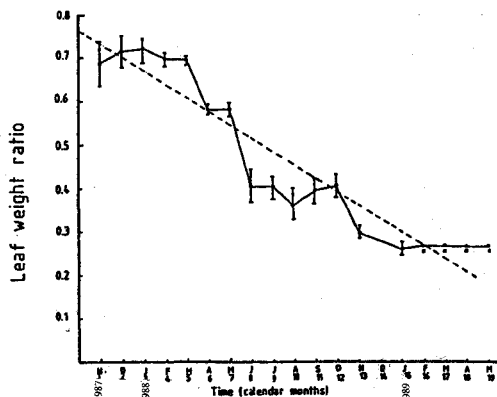

Fig. 4: Seasonal changes in leaf weight ratio of *Calotropis procera*. Bars represent ±ISE. The magnitudes of measurements (x) were smaller than the symbols. --------Line fitted by least -squares linear regression, Y= 0.755 − 0.31 x, r = −0.94, P < 0.001 (1-19 duration of experiment in months).

RGR

Generally RGR declined with time (Fig. 5). The relative growth rate (RGR) peaked (0.63 month⁻¹) during the seedling phase (two cotyledonary leaves + first pair of decussate foliage leaves). This value was maintained following unfolding and expansion of the second to the seventh pairs of leaves (5 MAE). RGR dropped to 0.48 month⁻¹ by the beginning and during the vigorous vegetative stage. RGR was 0.25 by the beginning of the reproductive phase. Thereafter, it continued to decrease at a lower rate till it reached 0.19 month⁻¹ by the end of the experiment (r = −0.69, P < 0.01).
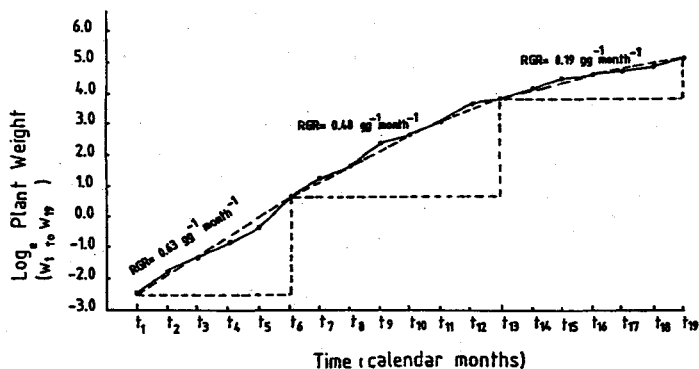

Fig. 5: RGR of *Calotropis procera* during 19 months period. Note that RGR_{max} = 0.63 gg⁻¹ month⁻¹ occurred during the first month of the life -span (the seedling stage) t_1 = November 1987, t_3 = January 1988 and t_{15} = January 1989.

NAR

NAR peaked five times during the present investigation. The first peak (19 mg cm⁻² month⁻¹) was associated with the seedling stage. The second, third and fourth peaks occurred over the period May-October 1988, during which vigorous vegetative growth was taking place. The fifth peak occurred just before flowering and thereafter the NAR value gradually declined to 2.0 mg cm⁻² month⁻¹ (Fig. 6).
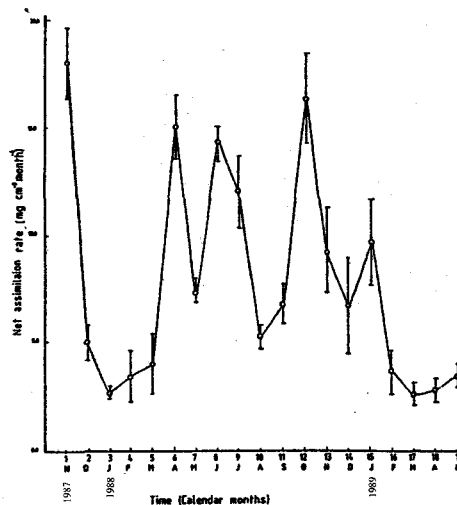

Fig. 6: Net assimilation rate of *C. procera* from seedling emergence to seed-set. Bars represent ± ISE. (1-19 duration of experiment in months).

CGR

Crop growth rate was minimal during the seedling stage, then it began to rise slowly over the period April 1988-January 1989 to reach a value between 110-140 mg cm⁻² month⁻¹ (during the vigorous vegetative growth). Thereafter, CGR declined to a value of 45 mg cm⁻² month⁻¹ and this value was maintained till the end of the experiment (Fig. 7).
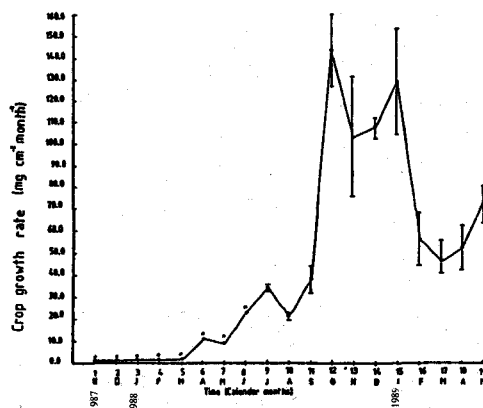

Fig. 7: Crop growth rate of *C. procera* from seedling emergence to seed-set. Bars represent ± ISE. The magnitudes of SE of measurements (x) were smaller than the symbols. (1-19 duration of experiment in months).

DISSCUSSION

Growth of plants can be divided into accumulation of photosynthate and subsequent partitioning of photosynthate into various plant organs (Ismail and Sagar, 1981; Ismail, 1984). Seasonal changes in plant growth and form (plant phenomorphology) are decisive in determining the plants adaptation to a seasonally changing environment (Diaz Barradas and Garcia Novo, 1990). Vegetative phase is primarily concerned with structural development of the plant necessary to provide an adequate framework with sufficient leaf area and fruiting points to ensure sexual reproduction. Ismail (this volume) showed that in *Calotropis* the main stem and the taproot are very efficient sinks that compete successfully for assimilates with the fruits. Annuals undergo a developmental phenomenon known as "cutout", i.e. when fruiting begins vegetative growth slows and may finally cease (Radin, Mauney and Kerridge, 1990). This phenomenon is not found in perennials such as *Calotropis*.

Leaf area was measured in terms of leaf area index. Although the maximum LAI values attained in the present study were somewhat larger than any other reported species (Bannister, 1979; Fitter and Hay, 1987) yet a LAI value of nine was reported for maize (Manrique and Hodges, 1991). In the event the increase in LAI suggested that more light might be intercepted by *Calotropis* canopy. Fitter and Hay (1987) attributed the increased plant growth to a better interception of photosynthetically active radiation (PAR) and to a higher conversion efficiency of the radiation. However, leaf area is probably most critical during the seedling stage when in *Calotropis procera* LAI was slow and moisture was available. Slayter (1970) reported that the presence of a relatively large leaf area early in the growing season (seedling phase) may be an extremely important mechanism allowing the plant to capitalize on soil moisture when soil water content is near field capacity and other conditions are favourable.

The results show that LAI increased slowly until the beginning of the main stem elongation and thereafter increased rapidly and that *Calotropis* has rather a long vegetative phase (15 months). Such an increased vegetative duration phase which is associated with a steady increasse in LAI value could be of an adaptive significance to allow both an increased accumulation of assimilates (source) and an increase in the size of the sink (stem + root). This combination of attributes is conducive to meet two basic requirements (a) to maximize fitness by optimizing partitioning of biomass allocated to different organs (Harper, 1977; Ismail, 1992) and (b) to reach and surpass a minimum plant size below which no seeds can be produced.

The results show that subsequent to seedling emergence there was a marked rise in SLA caused by expansion of the first pair of leaves whose dry weight changes slowly and slightly during expansion, but this value declined rapidly thereafter. Presumably during the seedling phase starch content was low as demand for photosynthate from growing parts is high. Later in the life of *Calotropis* starch content substantially increased thereby decreasing SLA (Reddy, Acock, Baker and Acock, 1989). The maximum SLA attained by *Calotropis* is well within the range of other species. For example, in mesomorphic species SLA ranges upwards from 200 cm^2 g^{-1} (Hiroi and Mohsi, 1966); the SLA of *Pinus sylvestris* is 84 cm^{-3} g^{-1} (Hunt, 1982); in sclerophyllous species, e.g. *Banksia ericifolia* the SLA is about 50 cm^2 g^{-1} (Morris and Myerscough, 1988). Morris and Myerscough (1988)

indicated that possession of low SLA (as is the case with *C. procera* over the reproductive phase period) will increase plant weight several times relative to plants with a high SLA. Watson (1937) argued a priori that SLA must decrease with increasing leaf weight, because as the leaf grows in area, it also increases in thickness. Bruggink and Heuvelink (1987) indicated that leaf thickness equals the reciprocal of SLA provided that the density of plant material is close to I. However, in the present investigation leaf thickness was only considered in the last harvest and density of the plant material was well below 0.8 g cm^{-3}, and therefore no comparisons can be made for *Calotropis* leaf thickness due to lack of data from the previous 18 harvests.

LAR can be considered as the result of SLA times LWR; generally LAR represents the ratio of photosynthesizing to respiring material within the plant (Hunt, 1981). Both SLA and LAR are a ratio of leaf area to mass and both decrease in values as leaves become thicker. The results show that the fall in LAR occurred despite continuing and steady increments in LAI. This decline in LAR is probaby ascribable to the increasing amount of secondary growth occurring in *Calotropis* plant as it matured. The decline in LAR during the life-cycle of *Calotropis* is caused mainly by decline in SLA (Hunt, 1982; Bruggink and Neuvelink, 1987).

Important as SLA is, LWR is even more so and might be by far the dominant factor in *Calotropis* whole plant physiology. In the present investigation LWR was significantly reduced during the period May 1988-February 1989 (see Evans, 1982, p. 307). This time period corresponds to vegetative and early reproductive stages. The reduced LWR value illustrates that *Calotropis* partitioned more dry matter into storage organs i.e. caudex, stalks and root. An increased LAI and NAR were also maintained during this period so that *Calotropis* was able to continue producing dry matter and to partition it into other organs.

NAR was significantly greater for *Calotropis* at four or five points during the experimental period. The NAR fluctuated with an increase in LAI following seedling establishment; before flowering NAR decreased with increase in LAI possibly due to mutual shading between plants and self-shading between leaves resulting in attenuation of the intensity of light reaching the leaves and thus reducing photosynthesis. The decrease in SLA was associated with an increase in NAR, as was expected (Bunce, 1986).

Crop growth rate continued at a higher level during late vegetative and early reproductive stages. The maximum CGR during the period 13-16 MAE when LAI was between 10-15 which coincided with an increase in NAR (as CGR is a product of both LAI and NAR). The noted decrease in NAR and CGR during the reproductive stage was due partially to the unusually larger LAI which attained its maximum value at 19 months and partially due to yellowing and drying of a large number of lowermost leaves (Singh and Gururaja Rao, 1987).

Grime and Hunt (1975); Burdon and Harper, (1980) emphasized the importance of RGR in the adaptation of the plant to its environment and that different plant species have different potential growth rates. Dijkstra and Lambers (1989) reported that within *Plantago major* L., inbred lines of subspecies *major* had 14% lower RGR than ssp. *pleiosperma*. The RGR of *Calotropis* was significantly greater at only one month during the sampling period and thereafter it smoothly declined. A lower

SLA, coupled with a lower LWR, explained the steady decrease in RGR. The decline in RGR with time in higher plants is well documented the world over. However, the reason for the decline is not fully understood (Wareing and Phillips, 1980). It has been suggested that in a growing plant, that plant material formed during peak vegetative growth is permanently incorported into structural tissues (mechanical, vascular and secondary) therewith contributing to no further synthesis of new plant material. Woledge (1988) argued that the NAR of leaf surface coupled with the assimilates allocated and thereof invested in expansion of new leaf area are from the factors determining a plant's RGR. Grime and Hunt (1975) reported that seedlings of woody species yielded consistently low values of R_{max} (= RGR_{max}). Maximum RGR recorded in the present investigation (0.63 g g week) was well within the range of other species with low R_{max} (Grime and Hunt, see their Table 5). Grime and Hunt (1975) stated that there were at least three ways in which low growth could be adaptive to plants like *Calotropis* in order to confer resistance to environmental stresses (a) low demands upon limited resources (b) lower rates of incorporation of assimilates and mineral nutrients, and (c) survival of seasons in which little or no growth is possible (see Crick and Grime, 1987). The extremely low RGR shown by *Calotropis procera* is consistent with responses to resource limitation pointed out by Grime (1977); it is pertinent to conclude that such a low RGR during the reproductive phase coincides with the diversion of photosynthates into the flowers and fruits thereby safeguarding the survival of *Calotropis* which depends on its re-establishment from seed (Boot, Raynal and Grime, 1986).

There are ecological factors which may confer selective advantage to *Calotropis procera* after attaining a large stature before reproducing (Jong and Klinkhamer, 1987) as it may receive more visits form pollinators and because of possessing larger flowering stalks it may disperse its seeds more efficiently. Similar to *Scirpus sylvaticus* (Crick and Grime, 1987) *Calotropis* takes a stable situation with resources to spare to be able to adapt to new infertile and exhausted environments in a rational planned way. Crick and Grime (1987) attributed the success of *Scirpus sylvaticus* on infertile soils (see their Fig. 3) to the large root: shoot ratio (0.48-0.72) i.e. extensive roots, that "provided a large absorption system which remains functional throughout the year, allowing capture of mineral nutrients released unpredictably".

The growth analysis of the life-cycle of *Calotropis* as now exposed would seem to possess no Achilles heel; it would therefore appear from this that it is necessary to prevent the seedlings from entering the vegetative phase and if a herbicide application could be accurately timed to coincide with the seedlings' emergence *Calotropis procera* will disappear at least from arable lands. More work is needed to determine if the relationships established here are general in other weedy ruderals and to discover where the weaknesses of species like *Calotropis* lie, thus enabling the formulations of sound management practices and guidelines for effective control.

ACKNOWLEDGEMENT

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