

Growth Performance of *Cephalosphaera usambarensis* Seedlings: Effect of Canopy Cover, Other Tree Species and Herbaceous Plants

**Stephen Maina Kiama, Kenya Forests Working Group, Kenya.
Munezero H. Kanyangemu, Sokoine University of Agriculture,
Tanzania.**

INTRODUCTION

Ecologists have studied the dynamics of forests, and have realised that plants have evolved and responded to the vagaries of nature, by developing coping mechanisms. According to Pickett & White (1985), tropical forests are dynamic systems which, to a large extent, are regulated by disturbance, (adapted from Hamilton & Bensted-Smith, 1989). Gap formation, forest regeneration and forest maturation are nowadays believed to be essential processes in tropical forest dynamics, (Binggeli in Hamilton & Bensted-Smith 1989).

Tropical forests undergo a dynamic process of rejuvenation following a disturbance, which creates a gap in the forest canopy. The effect of the disturbance is often to knock the community back to an earlier stage of succession. Re-growth occurs from three sources: seeds, plants established prior to gap formation, and lateral growth of branches from trees on the gap periphery, (Begon, Harper & Townsend, 1990). According to them, more rapid growth of surrounding trees as they extend their branches into the sunlit place that has been created is usually the first response. Near ground level, colonisation often takes place by the fast growth of saplings that were already present but suppressed. These are released and grow up rapidly into the gap.

The establishment and growth of saplings will depend on numerous factors (e.g. seed production, dispersal and viability, light, humidity, soil substrate, herbaceous competition among others).

In trees, mortality is high in the early stages of life, so that the selection of survivors, and thus the determination of species composition in forest, operates most strongly in young plants, hence the importance of the “regeneration niche”, (Swane & Hall, 1994). Under closed canopy forest, seedlings are probably the most important regeneration pool of the so-called “shade-tolerant”, “non-pioneer”, “mature-phase”, “climax” or “persistent” long-lived tree species (Benitez-Malvido, 1998, adapted from Denslow 1987; Whitemore 1989; Martinez-Ramos & Suto-Castro 1993).

Swane & Hall, (1994) note that canopy openings may stimulate faster growth in groups of juveniles capable of responding, or may allow the establishment of pioneer species previously absent. Conversely, continued overshadowing may cause differential mortality and growth amongst shade-tolerant species, which differ in their requirement for light. Brown & Jennings (undated) makes a similar suggestion, by pointing that seedling growth is stimulated by release from shade suppression and perhaps by locally diminished root competition.

There has been, however, over generalisation to some extent. There is indeed an observed difference in germination requirements (Kennedy & Swaine, 1992, adapted from Brown & Jennings (date?)); growth response to light (Thompson et al, 1992 a and b, Zipperlen & Press, submitted, adapted from Brown & Jennings); and light energy dissipation (Scholes et al, submitted, adapted from Brown & Jennings).

Whereas plants can generally be classified as either pioneer-species or climax-species as they undergo succession processes following disturbance, it is not always true that all climax species respond equally during the process, nor do pioneer species. Brown and Jennings, for instance, mention those differences between climax species in seedling growth responses and physiological traits have been demonstrated experimentally on numerous occasions.

Native tree species, even those that are shade tolerant, have high divergence in terms of their growth rate under different environmental conditions, especially light level. In some tree species seedlings/saplings show a positive response when exposed to light while others have their growth retarded.

Hamilton & Benstead-Smith (1989), in their analysis of the priorities for research in the East Usambara Forest, point out that each of the over 200 species of tree in the forests must be ecologically unique and that caution is necessary in classifying them into few, especially just two, ecological categories. What needs to be known is how these plants flower, produce and distribute their seeds, under what conditions the seeds germinate, the factors influencing seedling survival, how the species grow thereafter, the effects of pathogens and the ways in which they interact with soil, with animals and with other plants.

In Amani Nature Reserve, East Usambara, United Republic of Tanzania, preliminary observations have shown that *Cephalosphaera usambarensis* a shade-tolerant species, especially in the juvenile stage, respond differently to different light regimes penetrating the canopy. Where the light level penetrating the canopy is high following disturbance, the seedlings and saplings show a poor growth pattern. On the other hand, where the light level is low, for example in intact forest that has undergone minimal disturbance, the seedlings and saplings show higher growth rates.

These observations seem to suggest that the growth of seedlings /saplings of *C. usambarensis* is very specific to light regime and that growth is optimal in conditions where light level is minimal.

It was against this background that the research project was undertaken. Essentially, the study sought to prove or disprove the following hypotheses:

1. *C. usambarensis* seedlings display high growth vigour and abundance in high canopy cover than in low canopy cover,
2. The abundance and growth vigour of *C. usambarensis* decreases with increase of other trees and herbaceous plants,
3. There is a marked difference in growth performance of *C. usambarensis* seedlings between disturbed and undisturbed habitat.

Study objectives were to test the following null hypotheses vis-a-vis the alternate hypothesis:

◆ Hypothesis 1

Ho: The abundance of *C.usambarensis* does not show a corresponding increase with the increase of canopy cover,

Hi: The abundance of *C.usambarensis* shows a corresponding increase with the increase of canopy cover

Ho: The growth vigour of *C. usambarensis* does not show a corresponding increase with increase of canopy cover

Hi: The growth vigour of *C. usambarensis* shows a corresponding increase with increase of canopy cover

◆ Hypothesis 2

Ho: The abundance of *C.usambarensis* does not show a corresponding increase with increasing abundance of other trees and herbaceous plants,

Hi: The abundance of *C.usambarensis* shows a corresponding increase with increasing abundance of other trees and herbaceous plants

Ho: The growth vigour of *C. usambarensis* does not show a corresponding increase with increasing abundance of other trees and herbaceous plants

Hi: The growth vigour of *C. usambarensis* shows a corresponding increase with increasing abundance of other trees and herbaceous plants

◆ Hypothesis 3

Ho: The abundance of *C.usambarensis* seedlings is not markedly higher in undisturbed habitats than it is in disturbed habitats

Hi: The abundance of *C. usambarensis* seedlings is markedly higher in undisturbed habitats than it is in disturbed habitats

Ho: The growth vigour of *C.usambarensis* seedlings is not markedly better in undisturbed habitat than it is in disturbed habitat

Hi: The growth vigour of *C.usambarensis* seedlings is markedly better in undisturbed habitat than it is in disturbed habitat.

METHODS

Study Species

Cephalosphaera usambarensis (Warb.) Warb (Myristicaceae) is a tall rain forest tree with a straight, cylindrical and tall bole, brown to grey often ring-grooved bark. In East Usambaras, *C. usambarensis* occur between 900m and 1400m a.s.l., with mean annual rainfall of 1919mm. According to Holmes (1995), it occurs in free drainage valleys, rarely on slopes or ridges. Its regeneration survival rate is better in intermediate light, though light requirement change with age. Distribution is strongly related to the number of mother trees.

Study site

This study was carried out in Amani Nature Reserve (ANR), East Usambara Mountains, Tanzania from 16th –21st September 2005. The forest type of ANR is evergreen sub-montane forest (Hamilton, 1989). Mean rainfall for the area is 1918mm and the mean temperature ranges from 20.6°C to 24.6°C with high humidity (Hamilton, 1989b).

Three different forest sites were chosen, given that they had different disturbance histories and to avoid the influence of the surrounding matrix (Milne & Formen, 1986; Stongfer & Bierregaard, 1995 adapted from Benitez-Malvido, 1995). These were Monga forest which represented a natural undisturbed forest. Within this site two strata were considered; the intact forest and natural gaps here referred to as Undisturbed Habitat Increasing Canopy Cover (UHIC) and Undisturbed Habitat Decreasing Canopy Cover (UHDC) respectively. The second site was Kwamkoro forest which is referred to as Disturbed Habitat Decreasing Canopy Cover (DHDC) and lastly the Amani west forest referred to as Disturbed Habitat Increasing Canopy Cover (DHIC).

Experimental design

In each forest type a total of ten sample plots measuring $5\text{ m} \times 5\text{ m}$ were obtained by first choosing randomly the starting point and then the direction to be followed. The direction was taken such that transect passed almost the diagonal line of the forest. The rest of the sample plots were laid down 30m apart in the direction chosen. Plots representing natural gaps, however, were selected without necessarily following a specific direction. The sample plots were divided into four subplots of equal size measuring $2.5\text{ m} \times 2.5\text{ m}$.

Data Collection

Canopy cover

Four densiometer readings were taken from the four corners of the $5\text{ m} \times 5\text{ m}$ plot facing the centre and their mean was taken to be the percentage shade cover of that particular plot.

Counts

Counts for *C. usambarensis* and other trees were taken in each plot to determine the abundance. The herbaceous plants were determined by counting all plants that were within a 1 m^2 quadrat set at the middle of each subplot, and the sum taken to represent the sample plot.

Plant measurements

Within each subplot three *C. usambarensis* seedlings less than two years old (having no more than one branching level), were randomly selected. The stem diameter, stem height, leaf length and leaf breadth measurements were then taken. For stem diameter, measurements were taken just below the branching level using a pair of vernier callipers and the stem height was taken from the ground to the branching level. A pair of youngest leaves was used to determine leaf breadth and leaf length measurements, and the specific average taken to represent the seedling.

Data Analysis

Spearman rank correlation, simple linear regression and Mann-Whitney were used to estimate and test the significant effect of canopy cover, other trees and herbaceous plants, and the difference between the selected habitat.

RESULTS

Abundance of *C. usambarensis* seedlings in relation to canopy cover

The figure below illustrates the mean values of % canopy cover and *C. usambarensis* counts in each stratified block

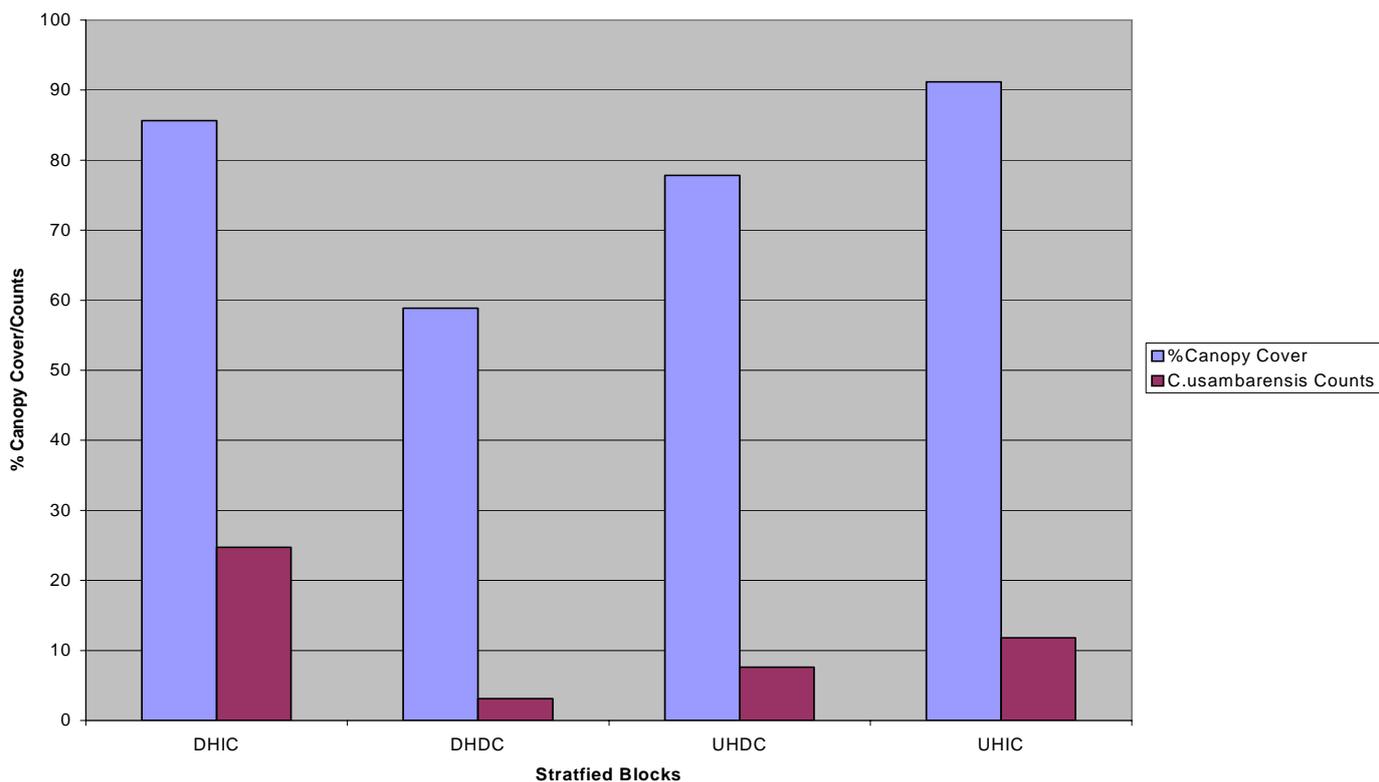


Fig. 1: % Canopy cover and *C. usambarensis* in different stratified blocks

Fig. 2 illustrates the relation between % canopy cover and the corresponding counts of *C. usambarensis*. As shown, there were no *C. usambarensis* seedlings recorded below 60% canopy cover in any of the stratified blocks.

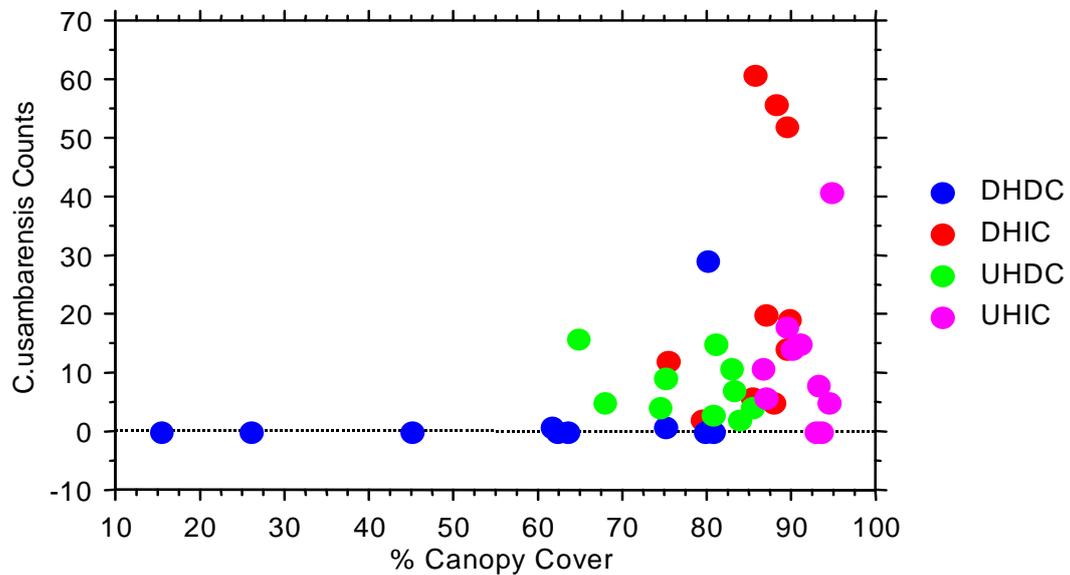


Fig. 2: The Scattergram showing the relationship between *C. usambarensis* counts and % canopy cover

Spearman rank correlation test on the data shown on Fig. 2 indicates that the counts of *C.usambarensis* increasing with increasing % canopy cover, ($z = 2.922$, $p=0.0035$).

Growth performance of *C. usambarensis* seedlings in relation to Canopy Cover

Figure 3 illustrates the relation between canopy cover and stem diameter .

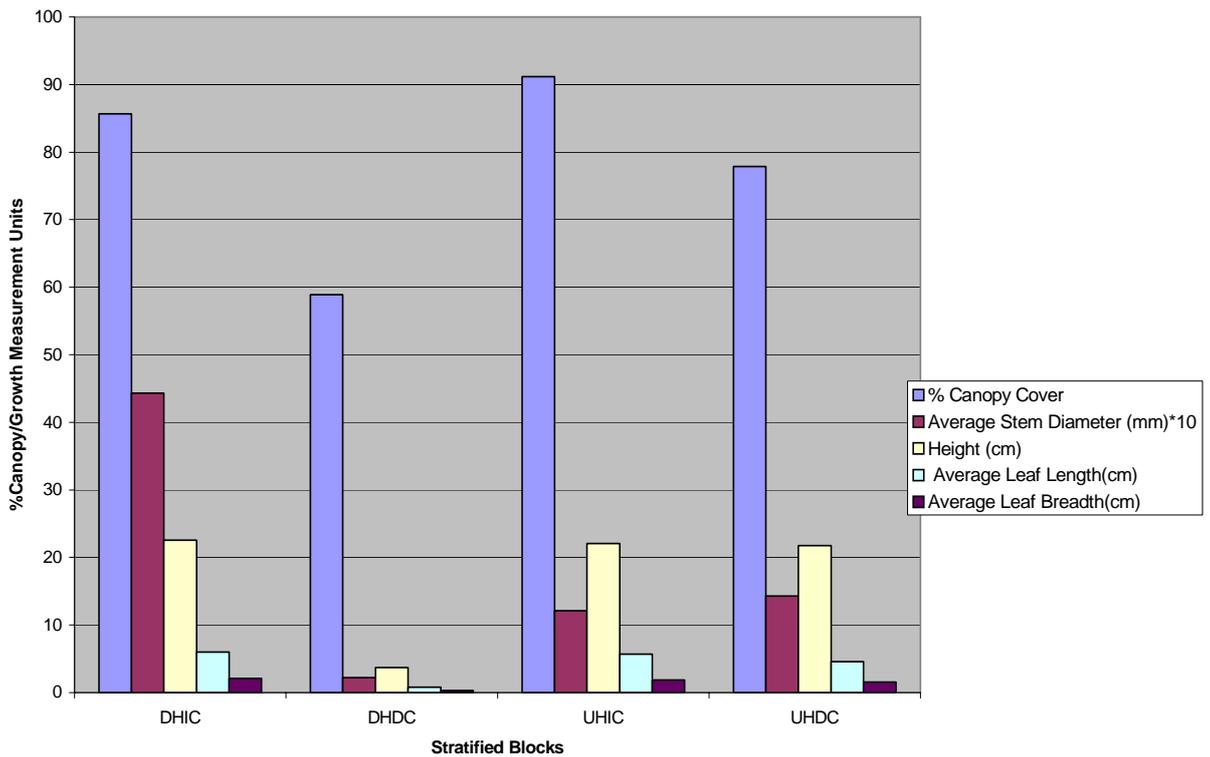


Fig. 3: % Canopy Cover & Seedlings Growth Parameters

Figure 4 (a) and (b) represents mean values of canopy cover, growth vigour/performance of *C. usambarensis* seedlings in terms of stem diameter, height, leaf length and leaf breadth in each of the stratified blocks.

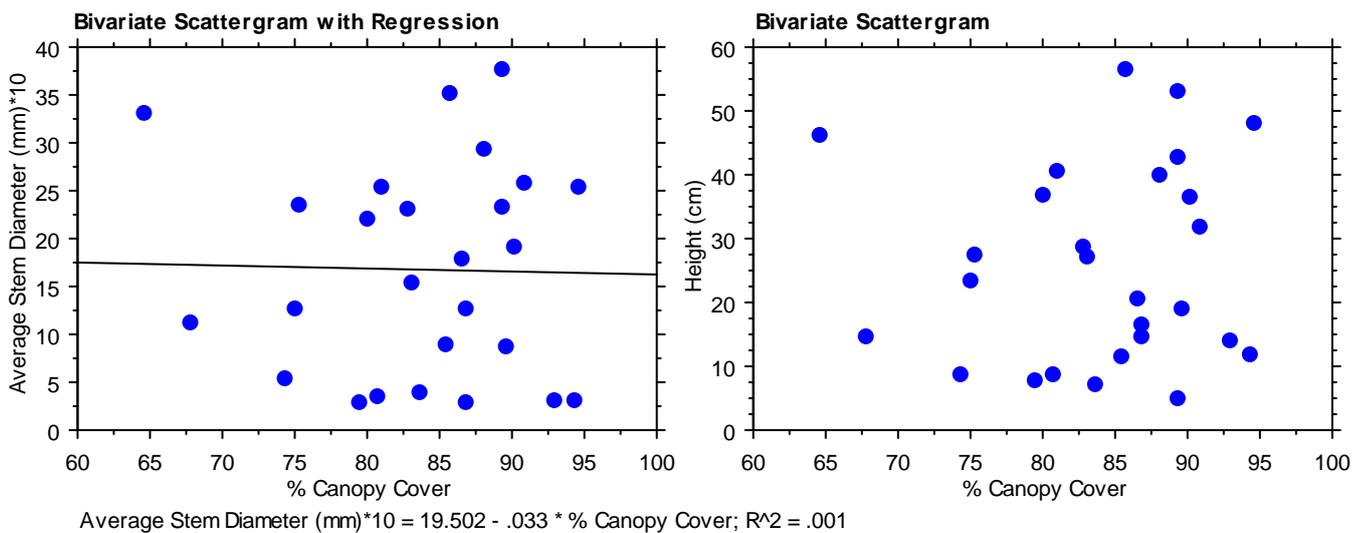


Fig. 4 (a) & (b): Relationship between stem diameter /height and % canopy cover

A linear regression analysis on the data shown in Fig. 4, indicates that change in % canopy cover cause significant change in some growth vigour measurement parameters of *C.usambarensis* seedlings, including height ($r_2=0.121$, $p=0.0277$); average leaf length ($r_2=0.104$, $p=0.0421$); and average leaf breadth ($r_2=0.113$, $p=0.0338$). However, change in %canopy cover does not significantly change the average stem diameter of *C. usambarensis* seedlings, ($p=0.0721$).

Abundance of *C. usambarensis* seedlings in relation to abundance of other trees and herbaceous plants

Fig.5 illustrates the counts of *C.usambarensis* seedlings and the counts of other trees and herbaceous plants, for each of the four stratified blocks.

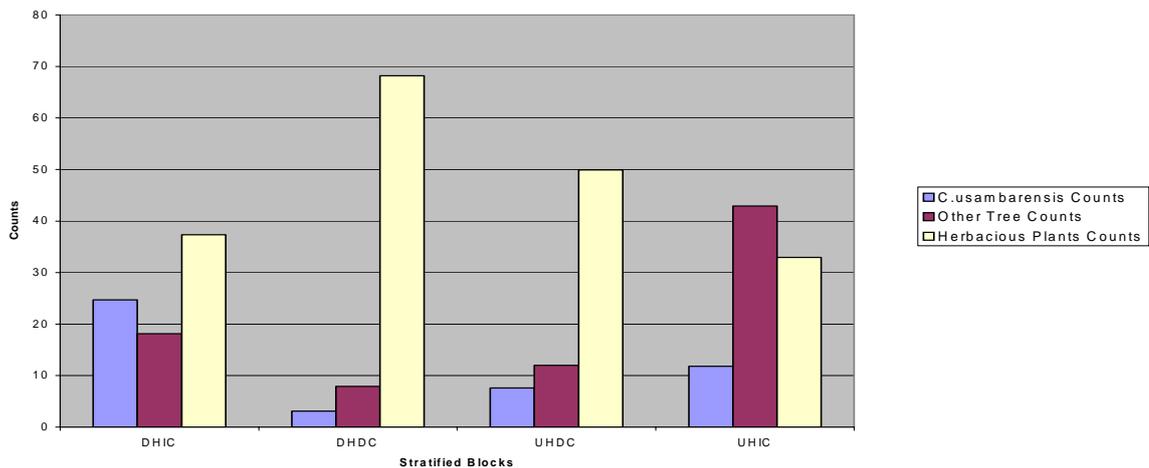


Fig. 5: *C. usambarensis* seedlings counts and Other Trees and Herbacious Plants in all stratified blocks

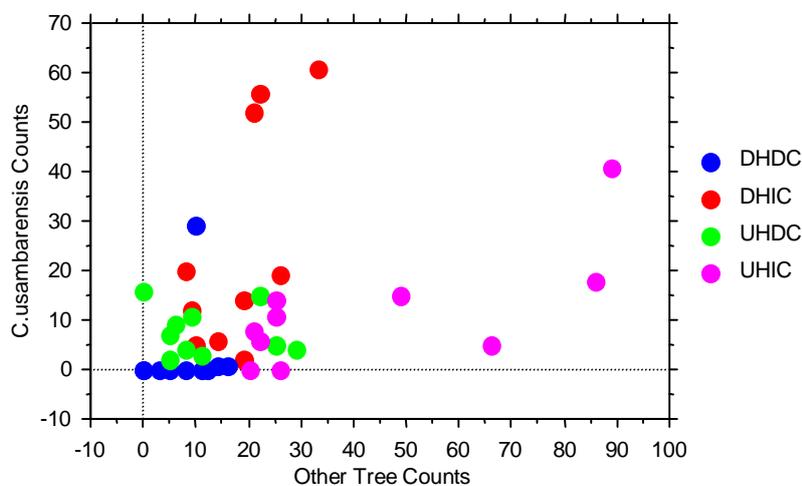


Fig. 6: Abundance of *C. usambarensis* in relation to abundance of other trees

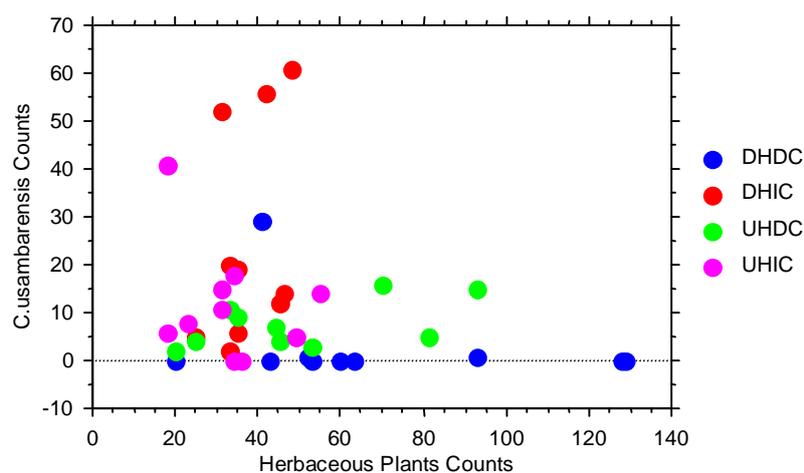


Fig. 7: Illustration of Abundance of *C.usambarensis* in Relation to Herbaceous Plants

Spearman Rank Correlation for the data on Fig.6 & 7 indicates that the abundance of *C. usambarensis* shows a strong relationship with the abundance of other trees, ($z_{40}=2.555$, $p=0.0106$). On the other hand, abundance of *C.usambarensis* has no significant relationship with the abundance of herbaceous plants ($z_{40} = -1.449$, $p=0.1472$).

Growth performance of *C. usambarensis* in relation to abundance of other tree and herbaceous plants

Figures 8 represent mean values of other tree counts, measurements of the growth parameters of seedlings, including the stem diameter, height, leaf length and leaf breadth for each of the four stratified blocks

Linear regression analysis for the data on Fig.9 indicates that change in abundance of tree counts is significantly related to change in seedlings' height ($r^2=0.173$, $F_{1, 40} = 7.960$, $t=2.821$, $p=0.0076$), leaf length ($r^2=0.182$, $F_{1,40}=8.442$, $t=2.832$, $p=0.0061$), leaf breadth ($r^2=0.174$, $F_{1,40}=8.019$, $t=2.832$, $p=0.0074$). Change in abundance of tree counts does not contribute to a significant change in seedling stem diameter, ($r^2, =0.093$, $F_{1,40}=3.912$, $p=0.0552$)

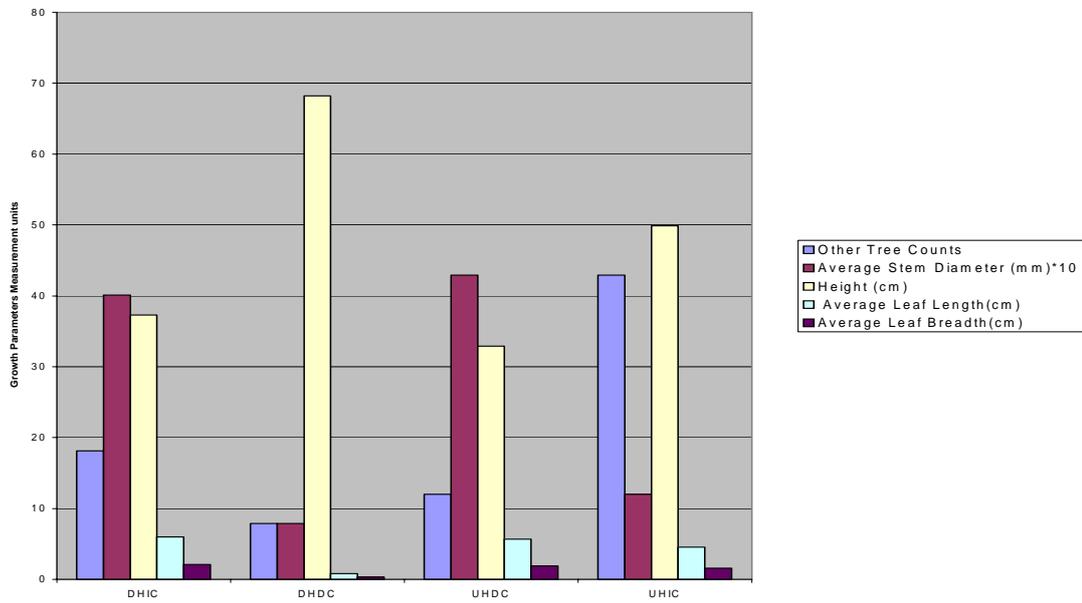


Fig. 8: Plant growth performance of *C.usambarensis* seedlings in relation to abundance of other Trees

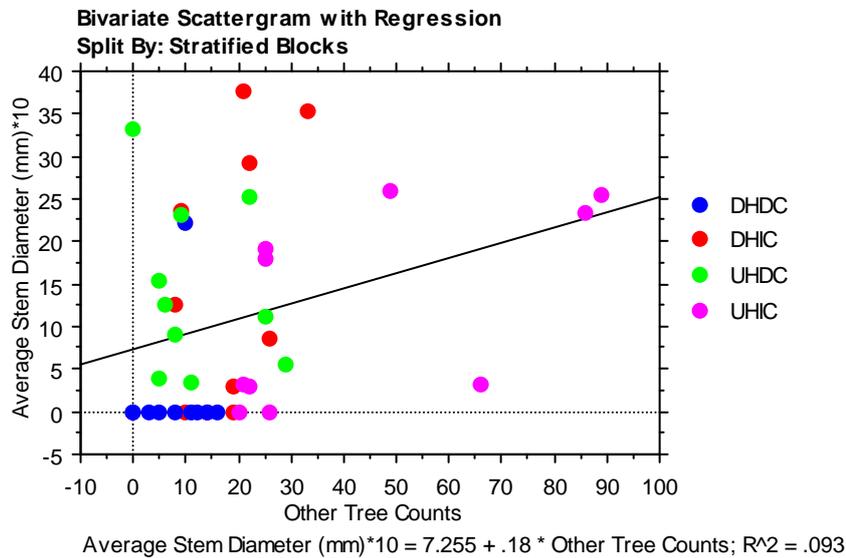


Fig. 9: Bivariate Scattergram illustrating the plant growth performance of *C.usambarensis* seedlings in relation to abundance of other trees

Fig.10 represent the mean values of herbaceous plant count, stem diameter, height, and leaf length and leaf breadth.

Spearman Rank Correlation analysis for the data shown on Fig.11, indicates that the abundance of herbaceous plants had no significant relationship with stem diameter ($z=-1.67$, $p=0.2858$), nor with the height ($z=-1.069$, $p=0.2850$), nor with leaf length ($z=-1.308$, $p=0.1909$), nor with leaf breadth ($z=-1.395$, $p=0.1630$).

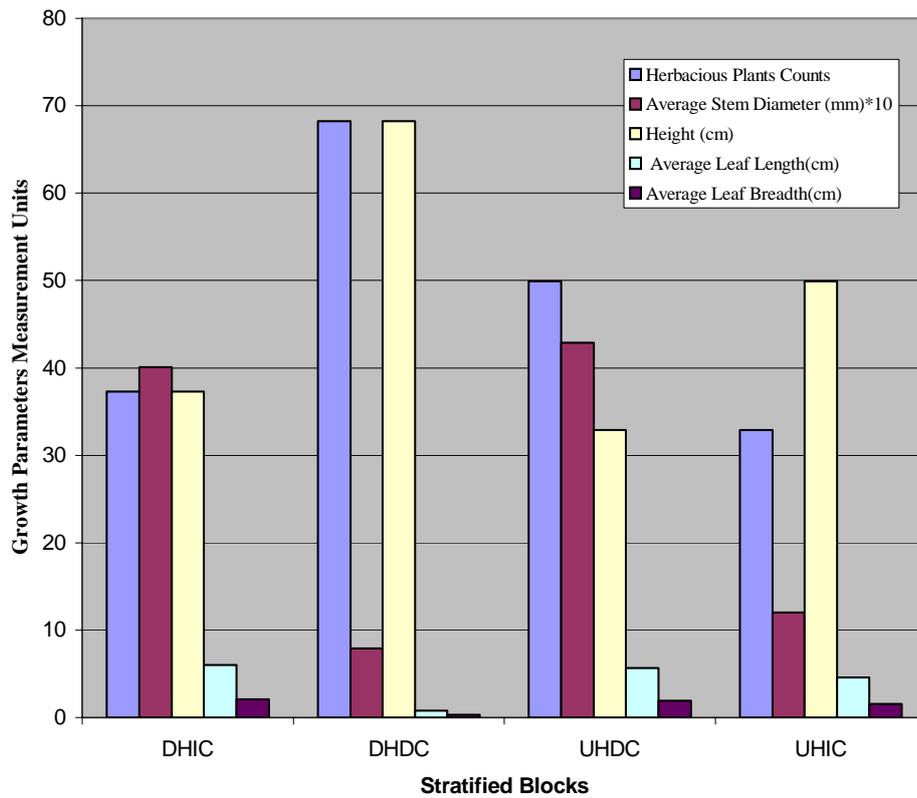


Fig.10:Herbaceous plant counts, stem diameter diameter,height,leaf length and leaf breadth in all stratified blocks

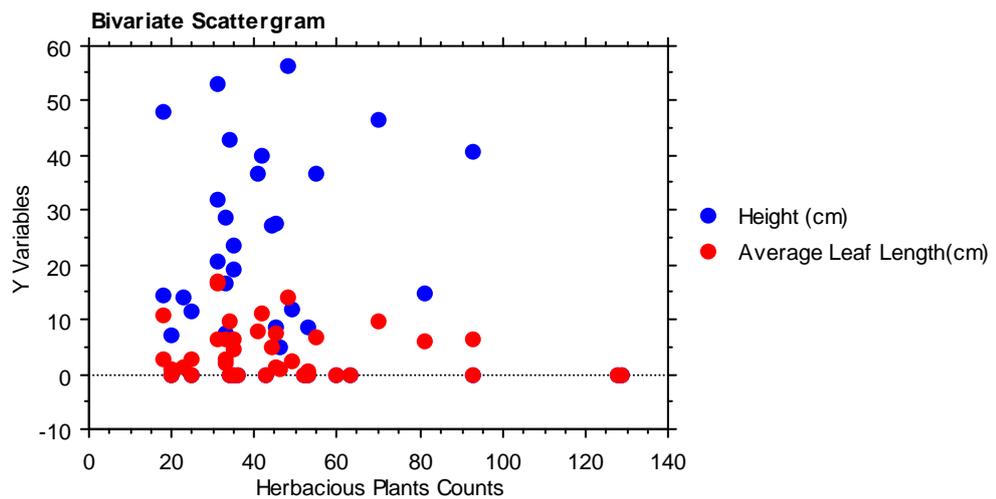


Fig.11: Bivariate Scattergram illustrating the growth performance of *C.usambarensis* seedlings in relation to abundance of herbaceous plants

Growth performance of *C. usambarensis* seedlings in relation to habitat difference

Figs.12 and 13 illustrates the mean growth vigour /performance of *C.usambarensis* seedlings in relation to habitat difference.

The height measurement was higher in the DH habitat than in the UH habitat. However, stem diameter, leaf length and leaf breadth were relatively higher in the UH habitat than in the DH habitat.

Mann-Whitney showed that there was no significant difference in seedlings performance between the two habitats, for instance, leaf length ($U=64.000$, $z= -0.874$, $p=0.0.3819$).

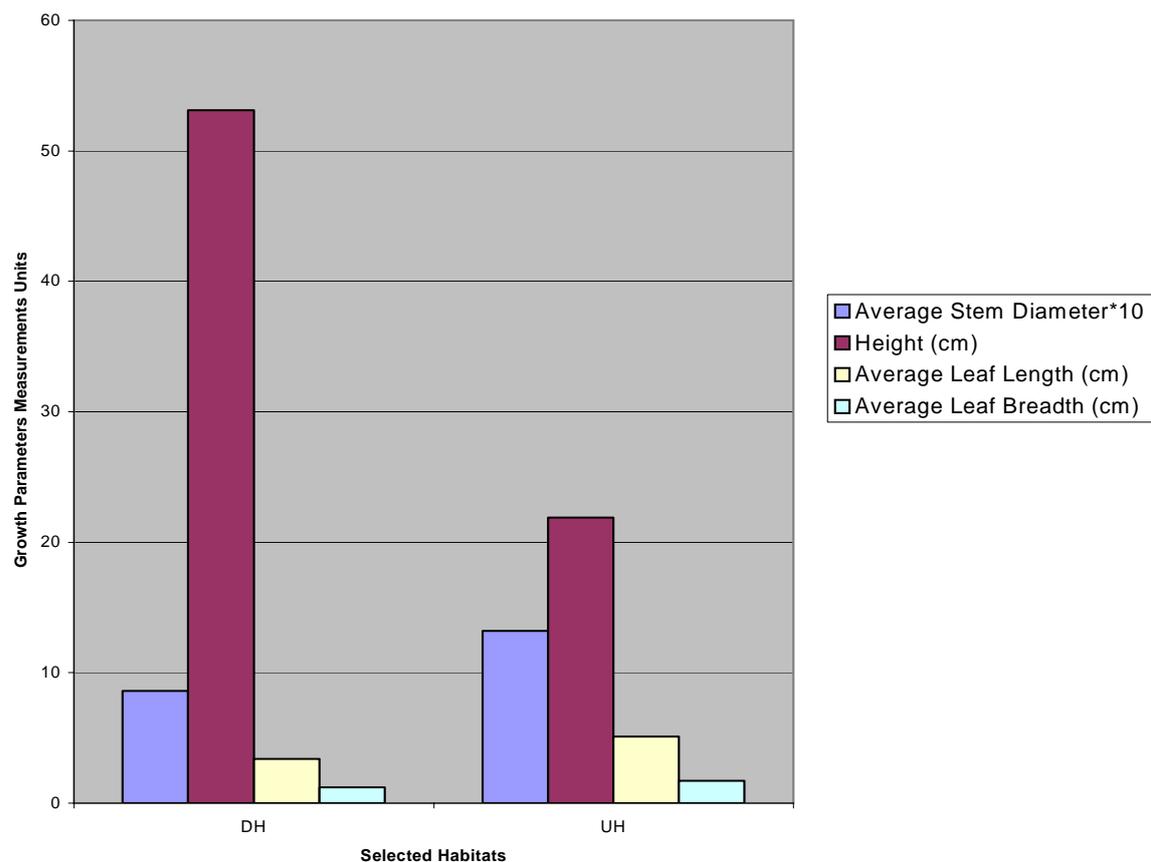


Fig. 12: Growth performance in disturbed and undisturbed habitats

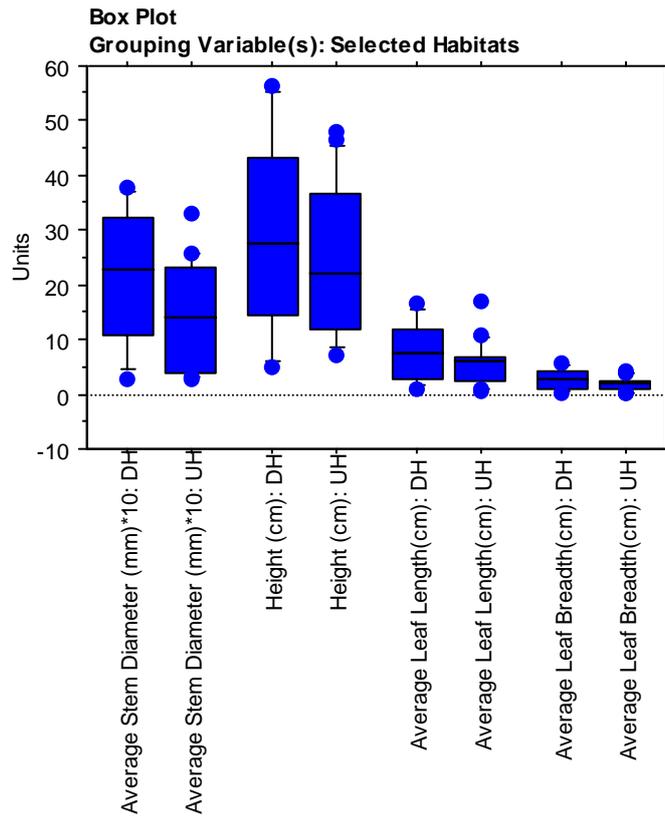


Fig. 13: Box plot illustrating growth performance of *C.usambarensis* seedlings in different habitats

Abundance of *C. usambarensis* seedlings in Relation to Habitat difference

Fig. 14 illustrates the mean counts of *C. usambarensis* seedlings in the two different selected habitats.

Using the Mann-Whitney analysis to test the null hypothesis, it was found that there was no significant relationship between the choice of habitat and the abundance of *C. usambarensis* seedlings, ($U=174.500$, $Z=-0.694$, $p=0.4876$).

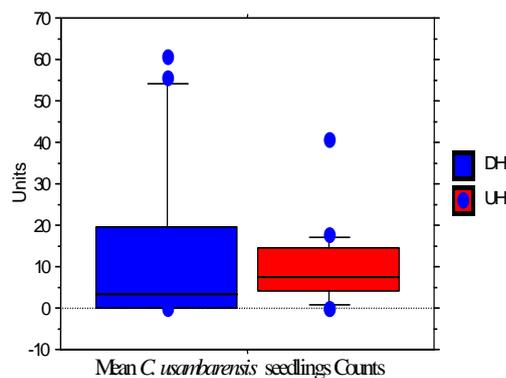


Fig. 14: Abundance of *C.usambarensis* seedlings in different habitats

DISCUSSION

Abundance of *C.usambarensis* seedlings in relation to canopy cover

The study revealed that there exists a strong correlation between % canopy cover and the abundance of *C. usambarensis* seedlings, and that the relative increase/decrease of the latter can be predicted for any increase/decrease of canopy cover. In trees, as in almost all organisms, mortality is high in the early stages of life, so that the selection of survivors operates most in young plants, (Grubb, 1977 in Swane & Hall, 1984). According to Swane and Hall (1984), canopy openings may stimulate faster growth in groups of juveniles capable of responding. Indeed, different species differ in their light requirements. The fact that the seedlings of *C. usambarensis* were found to be abundant under high canopy cover and vice versa, suggests that they have low response mechanism to take advantage of increase in light. For *C. usambarensis*, light requirement change with age (Holmes, 1995). This infers that the juveniles are shade demanders and may not survive when exposed to light.

Growth performance of *C.usambarensis* seedlings in relation to Canopy Cover

The study found that increase in canopy cover enhances the performance of *C. usambarensis* seedlings, especially with regard to height, leaf length and leaf breadth. Canopy cover does not contribute to increase in stem diameter. This scenario suggests that seedling recruitment for shade tolerant species like *C. usambarensis* is affected by a trade off mechanism in their growth in shade against their survival. They concentrate their dry mass in shoots and leaves.

According to Bjorkman (1981), decreasing irradiance tends to cause an increase in the relative proportion of plants dry mass as shoots and leaves. This differentiation may support the hypothesis that there is a spectrum of architectural types for shade-tolerant saplings of lowland tropical forest in Sumatra, as pointed by Kohyama and Hotta (1990). They labelled representatives of the end-points of this spectrum as “optimists” and “pessimists” with respect to the length of time between establishment and gap creation. When present, “optimists” are favoured because tall seedlings are most likely to become established in the gap (Brown and Whitmore, 1992) while “pessimists” are favoured at a site if the time between germination and gap creation is long relative to the survivorship of the “optimists” seedlings in the shade, (Kohyama, 1987).

Further studies could assess the extent to which the life history strategies of *C. usambarensis* correlate with the above hypothesis.

Abundance of *C. usambarensis* seedlings in relation to abundance of other trees and herbaceous plants

Our study showed that the abundance of *C. usambarensis* seedlings decreases with increasing abundance of other trees. Resource competition, especially for water and nutrients, may increase whenever fast growing early (pioneering) species are present. This explanation concurs with Burslem, Grubb and Turner, (1996)'s view, that availability of water and nutrients are significant factors potentially limiting the growth of tropical rain forest tree seedlings. This is because the rate of photosynthesis per unit area of leaf is generally higher in early species (Begon *et al*, undated), and thus their requirement for resources is high.

Growth performance of *C. usambarensis* in relation to abundance of other tree species and herbaceous plants

As described in the above section, resource competition may be a key factor limiting the growth performance of *C. usambarensis* seedlings growing side by side with other trees. Our study shows that the growth performance of *C. usambarensis* seedlings, especially height, leaf length and leaf breadth, decreases with increasing abundance of other trees. Stem diameter, however, was found to be independent of abundance of other trees.

It was found that seedlings of *C. usambarensis* concentrate most of their energies into the development of the height, leaf length and breadth, more than stem diameter, as an in-built mechanism. Competition from other trees, therefore, impedes the steady accumulation of biomass that was directed to height and leaf development. The outcome is a significant reduction in increase of height, leaf length and breadth of the seedlings, relative to reduction in stem diameter. Further study to establish the proportional ratio of reduction in growth due to competition from other trees between height, leaf length and breadth on one hand and stem diameter on the other is essential.

Herbaceous plants were found to have little effect on the abundance of *C. usambarensis* seedlings, possibly due to the earlier explanation that most of them are annuals and have low nutrient demand. Therefore their competition edge is not significant to affect the growth performance of *C. usambarensis* seedlings.

Abundance of *C.usambarensis* seedlings in Relation to Habitat difference

Holmes (1995) points out that in unexploited forest, few saplings of *C. usambarensis* are found, and little regeneration grows above 1m in height, despite abundant seed fall and initial germination. However, as pointed by Benitez-Malvido, forest destruction increases the vulnerability of the advance regeneration (seedlings and saplings in the shade understorey of the tree community). Our study found out that there is no significant difference in abundance of *C. usambarensis* seedlings between the two habitat types- contrary to our earlier expectation that there would be a difference given the differing histories of disturbance between the two habitats. A possible explanation of this deviation may be accounted for by other factors apart from canopy cover and competition from other tree species and herbaceous plants.

Growth performance of *C. usambarensis* seedlings in relation to habitat difference

Growth performance seedlings in terms of stem diameter leaf length and height did not show a significant difference between the habitats, contrary to our prediction. A possible explanation of this deviation may be accounted for by other factors apart from canopy cover and competition from other tree species and herbaceous plants.

CONCLUSION

The establishment and growth of saplings will depend on numerous factors (e.g. seed production, dispersal and viability, light, humidity, soil substrate, herbaceous competition among others).

The study revealed that canopy cover and other trees had significant effect on the abundance and performance of *C. usambarensis* seedlings. The study also indicated that comparing the two habitats, abundance of *C. usambarensis* seedlings did not differ significantly, though their stem diameter, height and leaf length did.

Under closed canopy forest, seedlings are probably the most important regeneration pool of the so-called “shade-tolerant”, “non-pioneer”, “mature-phase”, “climax” or “persistent” long-lived tree species.

C. usambarensis being one of the endemic species within Amani Nature Reserve needs to be highly considered for conservation. Given that in trees, mortality is high in the early stages of life, effort should be put to protect the destruction of habitat, since this will increase the vulnerability of advance regeneration to disturbance.

It is recommended that studies be carried out to establish the proportional ratio of reduction in growth due to competition from other trees between height, leaf length and breadth on one hand and stem diameter on the other is essential. Also, further studies could assess the extent to which the life history strategies of *C. usambarensis* correlate with the above hypothesis.

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