# DEMOGRAPHIC STUDIES ON SELECTED SPECIES OF THE GENUS *CALAMUS* L. (ARECACEAE)

The thesis submitted to the University of Calicut in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

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## CERTIFICATE

This is to certify that the thesis entitled 'Demographic studies on selected species of the genus *Calamus* L. (Arecaceae)' submitted to the University of Calicut by Mr. Anto P. V. in partial fulfillment for the award of the degree of Doctor of Philosophy in Botany is a bonafide record of the research work carried out by him, under my guidance. No part of this work has formed the basis for the award of any degree or diploma previously.

15-10-2005

Dr. A. K. Pradeep
(Research Guide)

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**ANTO P.V.**

# DECLARATION

I hereby declare that the thesis entitled 'Demographic studies on selected species of the genus *Calamus* L. (Arecaceae)' submitted by me in partial fulfillment for the degree of Doctor of Philosophy in Botany of the University of Calicut incorporates the results of the work done by me. This thesis has not been submitted by me to any other University for the award of any other degree, diploma, or any other titles, and it represents the original research work done by me.

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# CONTENTS

MATERIALS AND METHODS

RESULTS

DISCUSSION

# INTRODUCTION

# INTRODUCTION

Demography is the study of the population changes and their causes throughout the life cycle. Demographic approach to the study of plant populations makes a valuable contribution to the conservation of wild populations whose numbers are in decline. Populations respond to both their outer environment and their own internal state. Their response is complex and multivariate, including changes in birth, death, immigration and emigration rates, growth rates at both the individual and the population level.

Demographic studies of rare species can provide a logical basis for the planning of conservation management, the design of monitoring programmes and the interpretation of fluctuations in population size. Recently there has been a great interest in basic population including estimates of growth rates, age specific mortality rates, birth rates and factors influencing these (Wilson, 1972; Harper and White, 1974).

The palm family, Arecaceae (Palmae) comprising about 200 genera and 2700 species is distributed throughout the tropics and subtropics (Uhl and Dransfield, 1987). Throughout the tropics, due to over exploitation and habitat destruction palm species are being destroyed at an alarming rate. Therefore, palm conservation has a very practical application, and conservation recommendations must have a balance between conservation and utilization.

Climbing palms or rattans are the conspicuous element in South East Asian forests. Most rattan species belong to the genus *Calamus* L. (Calamoideae). The genus has about 370 species and is the largest among the palm family (Uhl and Dransfield, 1987). The long flexible stem of these palms is an important natural resource, used primarily for furniture production. The global trade and subsistence value of rattan and its product is estimated to be over US $ 7 billion per annum (Manokaran, 1990; Sastry, 2000; Abdul Latif, 2000). Nearly all marketed cane is harvested from the wild *Calamus* populations. The most highly demanded species are severely threatened due to over-exploitation in many areas.

In India, rattans are represented by 60 species under four genera, *Calamus* L., *Daemonorops* Blume, *Korthalsia* Blume and *Plectocomia* Mart. Kerala has 15 species of rattans belonging to the genus *Calamus*, mostly found in the Western Ghats (Renuka, 2000). But all these species are not utilized in the furniture or handicraft industries, mainly due to their insufficient availability. In Kerala, nine species are used commonly in making furniture as well as handicraft items (Renuka and Bhat, 2002). Due to scarcity of the material in Kerala, a considerable quantity of the raw material is procured from the north-eastern states and from the Andaman Islands. Hence, resource enhancement is urgently needed. For effective resource management or conservation programmes to be developed, thorough knowledge of the performance of the existing population is essential. A demographic study of the population changes and their causes throughout the life cycle will helps us to understand exactly at what stage the population is affected adversely and the reason for the decreasing population size. Accordingly a management strategy can be developed for the conservation programme.

During the last 25 years, the exploitation of rattans from the Western Ghats was very extensive and this has led to the disappearance of rattans from all the accessible areas. Large scale destruction and fragmentation of forests have further aggravated the situation. The extraction of young plants, before they flower, affects the regeneration. At present rattans are restricted mostly to remote forest areas in Kerala. The alarming rate of forest destruction and the over exploitation of rattans are leading to the depletion of genetic resources of this group of plants in Kerala (Renuka, 2000).

Palms, in general, have a relatively fixed pattern of morphological development that provides convenient features for population analysis and are attractive subject for studies of demographic process (Bannister, 1972; Bullock, 1980; Piñero *et al.*, 1984; Oyama, 1984). Rattans also are being subjected to such studies recently (Bøgh, 1995).

Four species used commonly in the furniture and handicraft industries were selected for this study, *Calamus thwaitesii* Becc. & Hook.f., *C. hookerianus* Becc., *C. vattayila* Renuka and *C. delessertianus* Becc. with the following two major objectives.

1. To study the population structure and the changes taking place in it over a period of time.
2. To develop conservation strategies for the species selected.

# REVIEW OF LITERATURE

## REVIEW OF LITERATURE

A number of demographic studies on palm species have been published during the last three decades. Most of the studies have sought a general understanding of population and community dynamics (Piñero *et al.*, 1984; Olmsted and Alvarez-Buylla, 1995; Pena-Claros and Zuidema, 1999; Silva Matos *et al.*, 1999; Pinard, 1993; Svenning and Balslev, 1997; Bernal, 1998; Bullock, 1980; Enright and Watson, 1992; Padmakumar, 2003). However, there is only one demographic study in rattan species (Bøgh, 1995). Many of the demographic studies used transition matrix models (Caswell, 2001).

Tomlinson (1960) studied the pattern of emergence of leaves in seedlings of palms of different species and explained the morphological significance of these patterns in further growth and development of leaves. Tomlinson (1971) has also studied the details of shoot apex and its dichotomous branching in *Nypa fruticans* Wurmb. From those studies it was revealed that in palms a specific pattern of development and growth exists. Tomlinson (1979) has given a very detailed account on the systematics and ecology of the members of the family Palmae. Davis *et al.* (1975) studied the morphology and anatomy of juvenile *Elaeis guineensis* Jacq.

Waterhouse and Quinn (1978) studied the growth pattern in the stem of *Archontophoenix cunninghamiana* (H. Wendl.) H. Wendl. & Drude. Breure (1994) has studied the development of leaves in *Elaeis guineensis* and determined the leaf opening rate. The rachis length was determined on primordia dissected from palms planted in four densities. A sudden increment of light accelerated leaf production at both the rapid expansion stage and the preceding slow expansion stage. The greatest acceleration of leaf production began 24 months after thinning probably because of the effect of the extra light on the rate of leaf initiation.

Rich *et al.* (1995) studied the leaf development and crown geometry of two Iriarteoid plams. Changes in the morphology of pinnately compound leaves and crown geometry during height growth of *Socratea exorrhiza* (Mart.) H. Wendl. and *Iriartea deltoidea* Ruiz and Pavon of tropical wet forest of Costa Rica revealed that light availability increased with height. The number of leaves per plant was relatively constant. Total leaf area, however, was much larger in taller individuals. Increases in linear dimension of leaves were responsible for less than half of this greater surface area. More important was the transition from a basically dorsi-ventral display of leaflets in small individual to a more radial display in taller plants. Production of leaflets in more than one plane resulted leaves whose surface area was more than twice the horizontally projected area and whose lateral light interception was gradually enhanced.

Stages of leaf development especially growth was described by Carvalho *et al.* (1999) based on the studies in infant and juvenile stages of *Euterpe edulis* Mart. in a natural forest. The growth rhythm and longevity of leaves of palms were studied by Freiberg and Freiberg (2000) in the natural forests of Costa Rica. They noted the production of leaves in defined interval throughout the year, which showed a slower rate of leaf production in the dry season. The maximum leaf-age of the palm *Cryosophila warscewiczii* (H. Wendl.) Bartlett, *Iriartea deltoidea* Ruiz & Pavon and *Calyptrogyne trichostachys* Burret were estimated to be more than five years.

The reproductive behaviour and its individual variability study in a tropical palm showed that light gaps and seed predation were acting as selective pressures on *Astrocaryum mexicanum* Liebm. ex Mart. These findings were presented by Piñero and Sarukhan (1982). De Steven *et al.* (1987) studied the vegetative and reproductive phenologies of a palm assemblage in Panama and accordingly the palm species displayed substantial variation in reproductive phenology despite a shared uniform growth architecture. It might be seasonal, initiated by the commencement of rainy season and might have multiple flowering episodes, but all predictable. Fruiting again showed more synchronous nature. Palm vegetative phenology was also seasonal and appeared more responsive than the reproductive phenology to annual climatic variation. In many species rates of leaf expansion slowed during the dry season and in a species the total leaf production was relatively constant from year to year. Leaf production was correlated with individual height in certain species, but not generally related to the degree of canopy opening.

Voeks (1988) noted the changing sexual expression of a Brazilian rain forest palm, *Attalea funifera* Mart. which produced male and female inflorescences and rarely inflorescences with male and female flowers and suggested that there is a possibility that sexual expression related to size, competition, and the differential cost of male and female function. The field data suggested that *Attalea* changed sexual function during its life cycle, from male, under various conditions to increasingly female as it became taller and less crowded. The cost of reproducing through female as opposed to male function was found to be 13.2 to 1 and the allocation of resources of reproduction was shown to increase with size. It was found that varying accesses to sunlight in the rain forest environment set thresholds to gender expression. Mortality, number of leaves, stem height increment, number of inflorescences and probability of reproduction in *Chamaedorea tapejilote* Liebm. ex Mart. were studied by Oyama (1991). The study indicates the seedlings and non reproductive plants of both sex had high mortality rates. The mean stem height increment of mature male and female plants ranged from 6 - 12 cm per year. Male plants showed influence of spatial variation in growth rate but the females did not. Males produced significantly more leaves per year than females. Both sexes had different rates of production of leaves during each year. The number of inflorescences produced per plant was positively correlated with height in both male and female plants but males produced significantly more inflorescences than females. The expression of sexes did not have any correlation with spatial variation of individuals in a plot. The irregular reproductive behaviour due to various factors was more expressed in females than in males.

Basu and Basu (1993) noted the sex expression in some Caryotoid palms such as *Arenga pinnata* (Wurmb) Merr., *Arenga undulatifolia* Becc., *Caryota urens* L., *Caryota mitis* Lour. and *Wallichia densifolia* (Mart.) Mart. They have observed the basipetal emergence of inflorescence after a definite period of vegetative growth was very characteristic in Caryotoid palms. In all monocarpic (hapaxanthic) palms there is a distinctive vegetative phase followed by a reproductive phase that ends in the death of the palm. In pleonanthic palms the flowering shoot only wither. The effect of canopy shading on the growth of *Calamus manan* Miq. seedlings were studied by Sutiyono and Sukardi (1991), and concluded that seedling growth much faster as the shade condition decreases.

The abundance and site performance of *Calamus exilis* Griff. and *Calamus zollingeri* Becc. were noted in two Indonesian National Parks by Siebert (1993, 2004, 2005). Populations of *C. exilis* were negatively related to high light intensities, conversely, population of *C. zollingeri* were positively related to high light intensities. According to him the abundance of *C. exilis* and *C. zollingeri* were in conjunction with their clustering growth habits. Vegetative propagation capabilities and varied light performance provide opportunities to develop sustainable cane harvesting system in combination with a variety of land use practices. Jong *et al.* (1994) studied the effects of plant spacing on the growth and development of sago palm on undrained deep peat with a spacing of 4.5, 7.5, 10.5 and 13.5 meters apart. At 4.5 m spacing the palm had the lowest frond emergence rate, a small trunk circumference at the base and 1 m height, the longest fronds, thinnest rachis, the smallest crown size, and the shortest creeping trunk. The canopy closed over within 3 - 4 years. At 7.5 m and 10.5 m spacing the canopy closed over within 5 - 6 and 8 years respectively. With the increases in space, there was an increase in the prostrate stem length, trunk height of leader, and in number of suckers.

Troy (1995) studied the spatial distribution and abundance of *Desmoncus polyacanthos* Mart. to quantify the relationship between forest canopy characteristics and the abundance and distribution. Soemarna and Anwar (1994) have studied the distribution and ecology of rattans in the Pasir Tugu Natural forest which has potential for rattan production. The growth of 12 rattan species was measured using strap and line plot method. Phyto-sociological data were tabulated for all the rattan species and also for the 54 supporting tree species which had an average of 140 stems / ha and an average basal area of 12 $m^2$ / ha.

Setiadi and Harisetijono (1994) studied the growth of *Daemonorops pericanthus* Miq. seedlings cultivated under *Cassia* trees. The effects on soil cultivation on the survival, height, growth, and number of leaves per plant over 3 years were tested. The results showed that the survival and growth were best in the plots cultivated once a year and the poorest in those not cultivated at all, although difference between plots were not significant for survival. Germination and seedling growth of *Calamus tenuis* Roxb. were studied by Siddiqi *et al.* (1997). They recorded 70 percent germination for the whole fruit, 10 percent for seeds with pulp and 86.66 percent for cleared seeds. Survival of seedlings in the field was 96.6 percent, and with one and half years, the sustained seedlings showed an average height of 109.78 cm with an average of 3.34 culms per plant.

Chia (1995) in his studies on the stem characteristics and growth of planted and wild *Calamus subinermis* H. Wendl. ex Becc., tried to understand the growth rates at 2 sites in Sabah. Canes planted at Kolapis had a mean annual increment of about 2.4 m at the age of 12 years. The mean stem diameter and mean internode length were 29 mm and 26.3 cm respectively. Wild canes on Berhala island had a mean diameter of 22 mm and mean internodal length of 26.5 cm. Length of stem covered with dried leaf sheaths was positively related to total stem length.

Jose *et al.* (1995) studied the competition of *Areca catechu* L. in mixed cropping system. The inter and intra component competitions were studied and found that intracomponent competition with intercomponent competition became significant only during 11th to 14th year of planting and in other periods neither inter nor intra component competition were significant. The effect of forest disturbance and soil moisture levels on establishment of red alder (*Alnus rubra* Bong.) seedlings were studied by Haeussler *et al.* (1995) at four sites representing a climatic moisture gradient with in the Central Coast Range of Oregon. First year survival rates were correlated with minimum summer soil moisture levels ($R^2 = 0.71$). Best establishment occurred skid trials and landings, suggesting that young seedlings may suffer less from heat or moisture stress on these heavily disturbed micro environment. The spatial distribution of a mixed natural rattan population, environmental effect on rattan growth and shadow adjustments in Sabah, Malaysia were discussed by Rao (1998), and a model to estimate rattan growth from yield data was developed. Relationship between microhabitat variables like altitude, inclination, topographic position, drainage, canopy height, etc. and the distribution and abundance of palms at natural habitat of Amazonian Ecuador were examined and studied by Svenning (1999). Cluster analysis showed that palm species distribution was strongly structured by topography. The main difference in species composition was between plots in the bottom land and plots on the upper slopes and hilltops. Logistic and logic analysis showed that 20 of the 31 palms and palm-like taxa analyzed had distribution that were significantly related to the microhabitat variables measured mainly not to topography but also to drainage and canopy height. Spatial autocorrelation in the overall community structure was not explained by the microhabitat variables. Analysis of distributions or abundance of single species showed neighbourhood effects for seven taxa. Antagonistic pattern of microhabitat performance were recognizable among some species pairs of small palms, medium sized palm and palm-like plants, but not among canopy palms. The conclusion was that microhabitat specialization was an important factor in maintaining the diversity of these palm community while, mass effects might also be important. Correlations between geographical range-size, and plant structural and ecological characteristics of 45 palm taxa of natural forest of Peru were studied by Ruokolainen and Vormisto (2000). They observed that the most wide spread palms tended to be tall and had relatively wide tolerance to difference in soil fertility and habitat quality. Caespitose growth form and fruit size were not related to the variation in range size. Tallness may be associated with better seed dispersers which contributed to wider ranges. The positive link between range size and edaphic and habitat generality demonstrated the importance of relatively deterministic environmental factors in controlling the distributions of plants.

Naturally occurring variation in micro-site features to determine correlation of post-dispersal seed survival and the performance of established seedlings of Amazonian palm *Astrocaryum murumuru* Mart. was studied by Cintra and Terborgh (2000) in the natural habitat of Peru. According to them, at small spatial scales variation in leaf litter, under-storey vegetation and incident light had significant effect on the palms. Seedling growth and survival of the species were affected by variations in the biotic and abiotic component of microsites. Green and Ostling (2003) studied the quantitative models to isolate the effects of relative species abundance and conspecific spatial distribution on the endemics-area relationships. They also illustrated how species abundance distribution and species spatial distributions have a strikingly different influence on total and endemic species diversity patterns, respectively. Increased dominance and conspecific aggregation in a region will act to decrease the total species diversity of smaller sampled subregions, but to increase subregional endemic species diversity.

The effect of natural fruit size of *Euterpe edulis* Mart. on seedling germination vigour and seedling growth was evaluated by Fleig and Rigo (1998). Medium-sized fruits have higher germination percentage and speed followed by small and larger-sized fruits. Evaluation of total dry weight, shoot height, collar diameter, etc. of plants showed that significantly taller plants with a greater dry weight were obtained from larger fruits.

Basu and Mukherji (1972) studied the details of germination of seeds of certain palms. The studies brought to light the details of germination percentage, mode of germination, viability of seeds, barriers of seed germination, and special methods that can be adopted to increase the germination rate and mortality of seedlings.

The major causes of mortality associated with major functions served by seeds were discussed by Cavers (1983). He proved that seed mortality, somewhat paradoxically, had an integral role in its major functions. He suggested that the fate of a plant population may be decided by the pattern of mortality exhibited by its seeds. And the interaction between populations of different species may be decided by the relative mortality patterns of the seeds of those populations.

Demographic studies of *Astrocaryum sciophilum* (Miq.) Pulle an understorey palm of French Guiana was studied by Sist (1989), where the dynamics and seed dispersal of three populations of tropical forest were explained. Growth and survival of seedlings of *Welfia georgii* H. Wendl. ex Burret was noted by Vandermeer (1990). Majority of the populations showed a decrease in size over time due to their position in the understorey. Overall survival was 61 percent. The mean rate of growth of leaflet width was approximately 0.09 cm per year and was related to the size of the seedlings in a complicated non-linear manner, in which very small individuals and larger seedlings grew relatively rapidly and intermediate individuals degrew.

Vandermeer (1993) studied the successional pattern of understorey palm in an old Cacao plantation on the Caribbean coast of Costa Rica. The study determined the proximity of forest and the methods of seed dispersal to test the hypothesis that mammal-dispersed palm species are concentrated closer to the forest than the bird dispersed species and the observation supported the hypothesis. Other observations were that, bird dispersed species were distributed throughout the plantation and that mammal dispersed species showed clumped distribution close to the forest and along a path.

Kiew (1972) studied the natural history of a Malayan undergrowth palm

*Iguanura reonomaeformis* Mart. Hnatiuk (1977) studied the population structure of *Livistona eastonii* C. A. Gardner. Savage and Ashton (1983) studied the population structure of five endemic palms in the Vallee de Mai, on Praslin Island and recorded the reproductive activity. They concluded that the mortality in the populations of *Lodoicea* Comm. ex DC. and *Phoenicophorium* H. Wendl. occurred in two unrelated stages, that is juvenile and senile. De Steven and Putz (1985) studied the mortality rates of *Bactris barronis* L. H. Bailey, *B. coloniata* L. H. Bailey, *B. major* Jacq., *Chamaedorea wendlandiana* (Oerst.) Hemsl. , *Elaeis oleifera* (Kunth) Cortes, *Geonoma cuneata* H. Wendl. ex Spruce, G. *interrupta* (Ruiz & Pavon) Mart., *Synechanthus warscewiczianus* H. Wendl. (understory palms), *Astrocaryum standleyanum* L. H. Bailey, *Cryosophila warscewiczii* (H. Wendl.) Bartlett, *Oenocarpus mapora* H. Karst., *Scheelea zonensis* L. H. Bailey and *Socratea durissima* (Oerst.) H. Wendl. (canopy and sub-canopy palms). The mortality rate of palms, according to the authers was between 1 - 3 per cent which was similar to the mortality rate of dicot trees of that area. But some palms appeared to suffer much higher mortality rate which reflected the extreme susceptibility of palms to death as a result of their growth by single terminal meristem. Age calculation was done using leaf growth rates.

The effective population size was used for the estimation of relative importance of genetic drift in tropical palm *Astrocaryum mexicanum* Liebm. in the natural habitat in Mexico (Sarukhan and Piñero, 1993). The genetic neighbourhood area was fixed and effective population size and different overlapping generation method was used to estimate an effective density with demographic data. The effective density ranged from 0.040 to 0.351 individuals per $m^2$. The product of effective density and neighbourhood area yielded a direct estimate of the neighbourhood effective population size. Ataroff and Schwargkopf (1994) observed the vegetative growth in *Chamaedorea bartlingiana* H. Wendl., a dioecious, solitary, understorey palm of Andean cloud forest. The main changes in vegetative morphology from germination to adult stages were described by them. A demographic study of *Arenga westerhoutii* Griff. and *A. obtusifolia* Mart. was carried out for a total period of 17 months at Bakit Lagogng Forsest Reserve of Malaysia by Zakaria *et al.* (1999). Three life stages had been defined for both species: seedling, juveniles and adults. In every population observed *A. westerhoutii* had seedlings as the most abundant stage but, *A. obtusifolia* had seedlings and juveniles as the dominant stage. The rate of increment was higher in *A. westerhoutii.* For both species the highest mortality occurred during the seedling phase.

The demography of natural population of *Euterpe edulis* Mart. was analyzed by Reis *et al.* (2000). According to them, the natural populations showed a pyramid-shaped demographic structure with a large base of juvenile plants and a small number of reproductive individuals. These data suggested a strong dependence of a large population on a proportionally small number of genetically effective individuals. These individuals are responsible for the maintenance of genetic diversity, genetic structure and demographic structure for the entire population.

Bruna (2003) studied the effect of limited recruitment on plant population on fragmented habitat. This study reveals that the decreased recruitment to be a primary mechanism driving the local extinction of a plant species from fragmented landscapes. He suggested additional demographic studies of plant populations in fragmented areas are urgently needed to identify other potential mechanisms responsible for population declines.

Leslie (1945) used mathematical matrices for studying biological populations. Sarukhan and Gadgil (1974) conducted detailed studies on plant demography, in which a mathematical model incorporating multiple modes of reproduction was exemplified with three *Ranunculus* species. Mathematical models were developed to examine the population level response of a herbaceous plant species, *Dipsacus sylvestris* Huds. (Dipsacaceae) by Werner and Caswell (1977).

Sarukhan (1978) studied the demography of tropical trees and explained the tropical plant communities which showed conspicuous seasonal patterns in vegetative and reproductive phenologies at both community and species level, despite the apparent absence of very dramatic photoperiodic and climatic fluctuations that regulate temperate *zone* plant phenologies.

Bullock (1980) studied the demography of an undergrowth palm in littoral Cameroon. Piñero *et al.* (1984) studied the demography of *Astrocaryum mexicanum* Liebm. ex Mart. in six plots in a tropical rainforest in Mexico. According to them there were differences between the plots in transition probabilities, survival and fecundity estimates of different age classes. Yearly estimates of transition probabilities from one age to the next were very less. Mortality rate during the first stage of life cycles was high and there was no mortality after its first reproduction. Individual fecundity showed an initial increase followed by constant values after the palm became aged.

Genet and ramet demography of *Oenocarpus mapora* subsp. *mapora,* a palm of Barro Colorado Island, Panama tropical moist forest was studied by De Steven (1989). He proved that a static population structure in the 'mature forest' site was evident in its low genet population density, high dominance of large adult clones and poor seedling recruitment. Population dynamics, that is, survival, growth rate and fecundity of a population of Nikau palm *Rhopalostylis sapida* H. Wendl. *et* Drude was studied by Enright and Waston (1992) in the natural habitat of New Zealand. Transition matrix analysis was compared for groups with classified height and groups with classified frond-scars. Estimates of 1.004 (height) and 1.007 (scars) were obtained for the finite rate of increase, suggesting that the population was a numerically stable component of the temperate forest in which it was found. Difference between the initiated and stable stage distribution, especially for the height-classified analysis indicated that the present population size structure was not constant with the measured rates of growth and survival. Measures of sensitivity, elasticity and selective pressure revealed that the high survival rate of palms in the mature and immediately pre-reproductive stages had the strongest influence on population growth rate. Faster growth through the seedling and juvenile stage would also markedly increase population growth rate. Fecundity was relatively insensitive to changes in growth rate.

The impact of stem harvesting in the population of the Brazilian *Iriartea deltoidea* was explained by Pinard (1993) by using Population projection matrices. Projections were based on survival probability estimates derived from size class distributions, growth rates which is calculated from leaf production rates and leaf scar records and fecundity estimates obtained from seedling densities. Matrix analysis indicates all the five populations studied were stable. Elasticity analysis indicated that population stability was most sensitive to changes in survival probabilities in palms of 10 -15 m tall.

Setiyo (1994) has developed a model for the vegetative and total growth in oil palm. This dynamic model explains the relation between the growth and yield with climatic factors and plant characteristics. Olmsted and Alvarez-Buylla (1995) developed demography and matrix model of two palm species of Mexico *viz., Thrinax radiate* Lodd. ex J. A. & J. H. Schult. and *Coccothrinax readii* H. J. Quero. Patterns of survivorship, growth and reproduction were obtained from four populations. The abundance and population structure varied depending on habitat, flowering and fruiting. Leaf production varied in both the species, apparently as a function of rainfall and site. Seedling survival was high in comparison with other tree species. Growth rates of seedlings were directly related in the rate of adult survival and growth. From the data, a sustainable harvesting model was developed.

The dynamics of a remnant population of *Neodypsis decaryi* Jum. was characterized using a linear, stage structure demographic model by Ratsirarson *et al.*, (1996). This palm is a threatened key-stone species restricted to a narrow ecological zone in Madagascar. The population showed high mortality rate in early stage of life cycle followed by a period of lower adult mortality. Demographic results indicated that the population was either stable or increasing inside the reserve. Sensitivity and elasticity analysis indicated that adult state classes were the most sensitive to the changes in population growth rates. Restricted leaf collection and seed collection were recommended for conservation. An assessment of the impact of leaf harvesting of the Asian palm *Livistona rotundifolia* (Lam.) Mart. was done by OBrien and Kinnaird (1996). Harvest intensity on subsequent growth and ecological sustainability were studied and recommendations for sustainable harvesting were also formulated.

Demographic studies were used to unify the evolutionary theories of senescence and niche conservatism by Holt (1996). He argues that both phenomena, senescence and niche conservatism, arise from demographic asymmetries.

Bernal (1998) studied the demography of the vegetable ivory palm *Phytelephas seemannii* Cook on the Pacific coast of Colombia and a female-based matrix model was used to determine the proportion of seed that can be sustainably harvested from the population. The density of the adult palm stands ranged from 240 to 420 per hectare. The sex ratio was 1:1, and juveniles and adults of both sexes produced an average of 1.8 and l6.107, 4 leaves per year respectively. Adult females had fewer leaves than males. Leaves of females lasted for about 2.7 years in the crown, and those of males about 3.2 years. These figures reflected differences in growth habits. The population growth rate percent (1.059) was most sensitive to changes in survival of juveniles and adult, and relatively insensitive to changes in fecundity and growth. River channel migration was the most important cause of adult mortality. *Phytelephas seemannii* is apparently an efficient colonizer of the understorey in the late phase of riverine forest succession. Individuals of widespread *Serenoa repens* (Bartl.) H. Wendl. and endemic *Sabal etonia* swingle ex Nash were monitored for growth performance and reproduction in natural habitat. Logistic regression models were developed for each palm species to estimate the probability of flowering in each vegetative association. These models accurately predicted flowering and non-flowering individuals. However, probability of flowering model that were generalized across vegetative associations of each species were less accurate than the association-specific model, which indicated the specific nature of flowering responses.

A comprehensive analysis was conducted by Barot *et al.* (1999) on the spatial pattern of *Borassus aethiopum* Mart. population and its environment to interlink between demographic process, plant spatial patterns and environmental heterogeneity. Map data was analyzed for individual palms of all stages in the natural forest of West Africa. Juveniles and seedlings were aggregated, while adults had a random pattern or were more loosely aggregated. All stages except female adults were spatially associated with nutrient-rich patches but association distances increased with stage in the life cycle, and seedlings were associated with female adults; whereas the associations of juvenile at longer distances were not clear cut. The initial pattern of seedlings (close to maternal trees) resulted from low dispersal distance, while later stages (older seedling and juveniles) were mostly restricted to nutrient-rich patches while others occur away from these patches (environment induced mortality) and form dense clumps of immature palms. Competition on nutrient rich patches then favoured the few juveniles that managed to survive farther from these patches (density dependent mortality). The last surviving juvenile of a clump suddenly experienced almost no competition with conspecifics due to the long distance between clump of juveniles and root forming ability of the individuals of a clump.

Experimental demography of rhizome populations of establishing clones of *Solidago altissima* L. was studied by Meyer and Schmid (1999). They found that the removal of close neighbor plants led to increased rhizome densities and number of newly produced rhizomes per parent rhizome was positively correlated with mean rhizome length per genet.

Abrahamson (1999) came to the conclusion that the long-lived palms were highly vulnerable to anthropogenic disturbances because of their very limited ability to recolonize former habitats. Ludwig (1999) tried to calculate probability of quasi-extinction of natural populations from time series of census data or estimated abundance. In this study he suspected about the meaningful estimation of extinction due to errors in estimated abundance and natural catastrophes. The local-scale spatial distribution of an abundant arborient palm *Iriartea deltoides* in natural habitat in Amazonian Ecuador was studied by Svenning and Balslev (1999). The seedling recruitment rate of *Iriartea* as influenced by environmental heterogeneity at the scale of 10 x 10 m and the influence of microhabitat heterogeneity on the survival probability of immature individuals after the early seedling phase were assessed. The seedlings and small juveniles were correlated with the presence of streams and the presence of abundant number of adults was also seen correlated with the presence of stream. They concluded that microhabitat conditions act as a filter not only on germination and initial seedling establishment, but also in the survival of seedling and juvenile stages, and environmental heterogeneity strongly influenced local distribution and the effect is established both through differential germination or seedling establishment and differential mortality until the larger juvenile stage.

Data on growth, survival and reproduction were recorded by Mendoza *et al.* (1999) for *Astrocaryum mexicanum* Liebm. ex Mart., *Chamaedorea alternans* H. Wendl. and *Reinhardtia graciis* var. *gracilis* (H. Wendl) Drude ex Dammer of the Mexican tropical rain forest. Transition probability was estimated for each size class of each species. The demographic data were incorporated into Lefkovitch matrices to estimate population finite growth rates ($\lambda$) and results showed values of $\lambda$ as 1.0142 for *Astrocaryum,* 1.3623 for *Chamaedorea* and 1.0184 for *Reinhardtia.* Elasticity analysis showed that fecundity had a relatively low value and thus had a small contribution to the population growth rate. The extent to which demographic variables like relative growth, rate of leaf area and height together with mortality and recruitment were important determinant of the competitive ability of endemic palms *Phoenicophorium borsigianum* (K. Koch) Stuntz and aggressively invasive dicotyledonous alien *Cinnamomum verum* Presl. were studied by Maarel -E-van-der (1999).

The mortality and growth models prepared by Kobe (1999) revealed that differences in species performance would lead to light gradient partitioning. Light gradient partitioning provides an explanation for successional dynamics and suggests that tropical tree species coexistence and diversity is at least partly maintained through niche differentiation. An “integral projection model” introduced by Easterling *et al.*,(2000) eliminates the need for division into discrete classes, without requiring any additional biological assumptions .This model avoids stage class's sensitivity problem and yields size specific sensitivities that are not affected by stage duration.

Prospective and retrospective perturbation analysis and their roles in conservation biology were discussed by Caswell (2000). Perturbation analysis is a powerful tool with important implications for conservations. That helps managers to avoid misleading of conservation strategies. By this method he compare the contributions of past changes in vital rates, not the effects of future changes.

Life stage simulation analysis used in estimating vital-rate effects on population growth for conservation was studied by Wisdom *et al.* (2000). They developed life stage simulation analysis (LSA) for species conservation planning. Demography, dispersal and invasion speed were calculated for structural populations using calculations and sensitivity analysis by Neubert and Caswell (2000). They constructed a discrete time model for biological invasions that couples matrix population's models with integrodifference equations (for dispersal). They suggested that sensitivity and elasticity of invation speed is highly correlated with the sensitivity and elasticity of population growth rate.

A "Partial life cycle model" has been developed by Oli and Zinner (2001) on the basis of age-specific demographic data. The partial life cycle model helps to compare favourably with those obtained from the corresponding age-classified models.

van Tienderen (2000) suggested a hierarchial frame work for analysis, using elasticity path diagrams, "elastogram". In this framework he made link between phenotypic traits and fitness components of a population. Elasticity, the relative contribution of demographic parameters to the population growth rate was studied by de Kroon *et al.* (1986). In this work they developed a sensitivity index (elasticity), from Caswell's (1978) growth rate sensitivity measure. Elasticity analysis provides a tool for comparing potential shifts with realized life history patterns.

By using "Loop analysis" de Kroon *et al.*,(2000) revealed the underline pathway structure of the life cycle graph, which qualifies population growth rate changes in a demographic transition. In this paper they discussed the application of elasticity analysis and its extension, loop analysis, in the life history studies and conservation.

Selection pressures on vital rates in density dependent populations were drawn by Grant (1997). In this approach he proved that individual population growth rate changes indicate the strength of selection on different parts of the life history.

Grant and Benton (2000), discussed the extension of elasticity analysis to populations with density-dependent demographic parameters and examined the circumstances in which the standard density dependent analysis gave useful information for populations that are, in reality, density dependent.

Density dependant elasticity analysis was illustrated by Grant and Benton (2003) using LPA model in *Tribolium castaneum* (Herbst) Dennis *et al.* they concluded that a full density-dependent analysis was vital when concerned with effects on population numbers, as in population management, pest control and prediction of population effects of toxins.

Kaye and Pyke (2003) studied the effects of stochastic technique on estimates of population viability from transition matrix models. They estimated stochastic population growth rate using a matrix-selection method, in which whole observed matrices were selected at random at each time step of the model. They concluded that the absolute value of population viability estimates is sensitive to a model assumption, but the relative ranking of population is robust. Those results are applicable to a range of perennial plants and possibly other life histories.

# MATERIALS AND METHODS

# MATERIALS AND METHODS

## MATERIALS.

The species selected are *Calamus thawaitesii* Becc. & Hook.f., *C. hookerianus* Becc., *C. delessertianus* Becc., and *C. vattayila* Renuka. The first two species are generally seen in evergreen, semi evergreen and moist deciduous forests. Both the species are clump forming. *C. vattayila* and *C. delessertianus* are single stemmed and occur in the evergreen forests. Of the different species occurring in Kerala, *C. thwaitesii* and *C. hookerianus* have wider range of distribution and their population size also is comparatively larger. *C. vattayila* and *C. delessertianus*, though have an extended distribution along the Western Ghats of Kerala, their population size is very small and the plants are scattered (Renuka, 2001).

### Study area

The study plots were selected in the forests of the Western Ghats. Plots were taken at Athirapilly, under Vazhachal Forest Division in Central Circle (Thrissur district) and at Nelliyampathy under Nemmara Forest Division in Olavakkode Circle (Palakkad district). Athirapilly plot represents moist deciduous habitat with two dominant clustering *Calamus* species, *C. thwaitesii* and *C. hookerianus*. The plot was located at an altitude of 350 - 400 m, ($76^0$ 9'- $76^0$ 40' E; $10^o$ 7'- $10^0$ 18' N).

29A

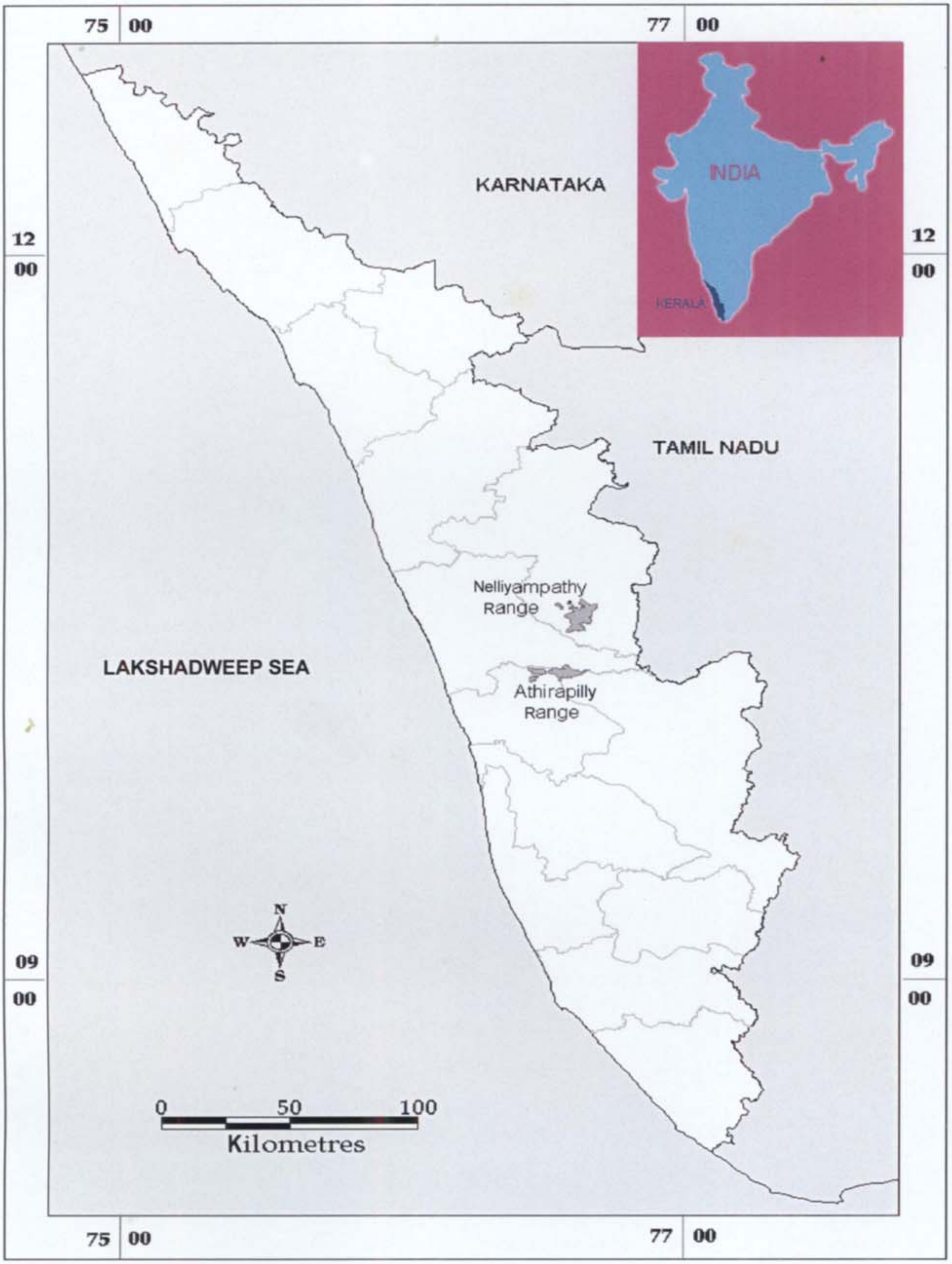

Figure 1. Map of Kerala showing study area

Nelliyampathy, having evergreen habitat has two single stemmed *Calamus* species, *C. delessertianus* and *C. vattayila*. The plot was located at an altitude of 950-1000 m, ($76^0$ 32'-$76^0$ 45' E; $10^0$ 26'-$10^0$ 36' N). The study area was selected based on the population size. In the area selected the population was scattered in an area of about one hectare. For effective study these main plots were divided into 10 x 10 m subplots.

**Habitat and vegetation**

Athirapilly forest area is represented by moist deciduous forest type with a few evergreen trees. In the study area the tree canopy is discontinuous with large interspaces and hence more light is available to the understorey plants. Total canopy coverage is contributed by 53 trees, above 15 cm of girth at breast height (gbh), belonging to 32 species coming under 15 families. The dominant trees were *Grewia tiliifolia* (Tiliaceae), *Xylia xylocarpa* (Mimosaceae), *Lagerstroemia microcarpa* (Lythraceae), *Olea dioica* (Oleaceae) and *Dalbergia* species (Fabaceae). The strong trees provide mechanical support to the selected two *Calamus* species. Both species studied in this area produce suckers as means for vegetative reproduction. Large numbers of suckers are produced by *C. hookerianus* and they are very closely packed. In the case of *C. thwaitesii*, the clump density is rather very low (Table 8).

Nelliyampathy forest areas are represented by evergreen forests. The tree canopy of the study area is continuous with little light penetration. 47 trees above 15 cm gbh representing 17 species coming under 13 families constituted the canopy. The dominant trees are *Palaquium ellipticum* (Sapotaceae), *Cullenia exarillata* (Bombacaceae), *Knema attenuate* (Myristicaceae), *Garcinia gummi-gutta* (Clusiaceae) and *Agrostistachys indica* (Euphorbiaceae). Storey stratification is very clear. The two selected species of *Calamus* is solitary in nature. But they show a specific nature of stem growth at early stages of stem formation. In the case of *C. delessertinus* basal part of the stem is as thicker as the other part of the stem whereas in the case of *C. vattayila* basal portion is very narrow. Both these species show very short internodal length at the basal region (Table 8).

## Morphology of *Calamus*

Most of the species of *Calamus* in Kerala are clump forming (clustering). Four species out of 15 are single stemmed (solitary).The unbranched stem (cane) is covered with spiny leaf sheath, which fall off when matures. The stem possesses well defined nodes. Diameter varies from 3 mm to 30 mm, depending on the species.

The leaves are large, pinnately compound and are spirally arranged on the stem showing 5/2 phyllotaxy. Leaves spirals on the stem is clockwise or anticlockwise. Spiny, whip like structure, which is the extended portion of rachis beyond the leaflets is called 'cirrus'. The whip like structure originating from the leaf sheath is called flagellum. Both flagellum and cirrus are climbing organs.

*Calamus* is dioecious, male and female plants are separate and the flowering is annual. The time of initiation of flowering varies with the species (Table.1). The inflorescence may branch into 2 or 3 orders. Rachillae are the ultimate branchlet which bears flowers. Fruits are usually produced in abundance. Each fruit is covered with vertical rows of reflexed overlapping scales. The scales are often hard and shiny. In general mature fruits are available from March to June. The germination period vary from 2 weeks to 1 year depending on the species.

Table 1. Flowering and fruiting periods of selected species of *Calamus*

| Name of the species | Flowering period | Fruiting period |
|---|---|---|
| *C. thwaitesii* | June-August | April-May |
| *C. hookerianus* | April-July | April-May |
| *C. vattayila* | September-October | May-June |
| *C. delessertianus* | August-September | May-June |

***Calamus thwaitesii* Becc. & Hook. f.**

This is the thickest cane available along the Western Ghats. This is a very robust, clump forming, large diameter rattan. Stem with sheaths measures to 6 cm in diameter and without sheaths to 3.5 cm. Leaves about 3m long; leaf sheath yellow, densely armed with black spines; spines arising from a raised rim-like surface, the largest 3 x 0.7 cm, flat, smaller spines scattered in between; knee absent; petiole and rachis yellowish, armed with black spines which are grouped and arranged into oblique whorls; leaflets usually grouped, sharply spinulose along the margins. Inflorescence about 6 m long, partial inflorescence about 70 cm long. Fruit about 2 x 1.3 cm, ovoid, scales arranged in 12 vertical rows with median grooves, yellow with deep brown margins.

Distribution: This cane grows in evergreen, semi evergreen and moist deciduous forests between 75 to 900 m throughout the Western Ghats. The distribution extends to Sri Lanka also.

***Calamus hookerianus*** **Becc.**

A clustering, moderate sized rattan. Stem with sheaths measures about 4 cm in diameter, without sheaths to 2.5 cm. Leaves to 2 m long; leaf sheath brownish green, densely armed with spines, spines triangular, the longest to 2.5 cm long, 0.5 cm wide at the base, interspersed with numerous smaller spines and abundant brown tomentum, mouth of the sheath, with long papery spines to 18 cm long; knee sometimes present, not conspicuous; leaflets regularly arranged. Inflorescence to 5 m long, partial inflorescence to 75 cm long. Fruits about 1 x 0.8 cm, subglobose, scales in 18 rows, yellowish brown with a dark brown border.

Distribution: This species is seen in the evergreen forests up to 1000 m throughout the Western Ghats in Kerala, Tamil Nadu and Karnataka.

***Calamus vattayila*** **Renuka**

A single stemmed moderate sized rattan. Stem with sheaths measures up to 5 cm in diameter at apex and 2.5 cm at base, without sheaths 1.8 cm. Leaf 1m long; leaf sheath dark green and sparingly spiny; spines generally point upwards; leaf- lets alternate, about 40 x 10 cm; inflorescence to 1m long; partial inflorescence to 40 cm long; getting shorter towards the tip of the inflorescence. Fruits in heavy bunch; a single fruit measures about 2.5 x 0.8 cm, oblong, scales in 27 rows, longer than broad, chestnut brown coloured. The shape of the leaflet is similar to that of a reed. The local name "vattayila" comes from the shape of the leaflet.

Distribution: Seen sporadically in evergreen forests between 200 to 950 m. This is reported from Thenmala, Ranni, Nilambur, Wayanad, Nemmara, Thekkady, Chalakkudy and Vazhachal Forest Divisions in Kerala. The distribution also extends to Tamil Nadu and Karnataka.

***Calamus delessertianus* Becc.**

Solitary, medium diameter rattan. Stem with sheaths 3 cm in diameter at base, 5-6 cm at the apex, without sheaths 2 -2.5 cm. Leaves about 1.5 to 2 m long; leaf sheath is green with bulbous based spines; leaflets regularly arranged along the rachis, about 55 x 2.5 cm, veins ciliated on the upper surface; cilia to 1.5 cm long, black tipped, leaf margin spinulose. Female inflorescence rather large, partial inflorescence to 30 cm long, arising erect at first and then spreading. Fruit globose, 1.5 cm in diameter, distinctly stalked, scales straw yellow, in 28 rows, spirally arranged, deeply channelled in the middle.

Distribution: Fairly common in the evergreen forests between 700-1200 m along the Western Ghats of Kerala, Tamil Nadu and Karnataka.

Figure 2. Habit and fruits of the *Calamus* species studied in Deciduous Forest

a. Habit of *Calamus thwaitesii* b. Fruits of *Calamus thwaitesii*

c. Habit of *Calamus hookerianus* d. Fruits of *Calamus hookerianus*

Figure 3. Habit and fruits of the *Calamus* species studied in Evergreen Forest
a. Habit of *Calamus vattayila* b.Fruits of *Calamus vattayila*
c. Habit of *Calamus delessertianus* d. Fruits of *Calamus delessertianus*

## METHODOLOGY

The four life stages such as seedling, juveniles, sub-adults and adults were defined on the basis of the changes in growth mode and reproductive status, which occur during the life of an individual (Table 2).

Table 2. Life stages and size of individuals recorded

| Life stages | Seedlings (acaulescent, < 4 leaves) | Juveniles (acaulescent, ≥ 4 leaves), Suckers | Sub-adults (well defined stems, non-flowering) | Adults (climbing stems with flowering) |
|---|---|---|---|---|
| Size units | Number of leaves | Length of longest leaf (m) | Length of stem (m) | Length of stem (m) |
| *C. thwaitesii* | 1 – 3 | 0.22 - 3.0 | 0 – 25 | 25 – 100 |
| *C. hookerianus* | 1 – 3 | 0.18 – 1.8 | 0 – 10 | 10 – 50 |
| *C. vattayila* | 1 – 3 | 0.10 – 1.2 | 0 – 26 | 26 – 75 |
| *C. delessertianus* | 1 – 3 | 0.23 – 2.1 | 0 - 22 | 22 – 75 |

The number of individuals coming under each class was observed periodically, at four months intervals for 3 years. The height and girth of each stem in a clump, and the number of individuals in each clump were noted.

Seedlings (S):- Seedlings are acaulescent (rosette) plants; it will remain in this stage till 1 to 3 leaves are produced.

Juveniles (J):- Juveniles are large acaulescent rosette plants bearing four or more leaves. The new shoot produced in the form of suckers, also are considered as juveniles regardless of number of leaves.

Sub-adult (SA):- Sub-adults are plants with elongated climbing stem. It will remain in this stage till on first flowering.

Adult (A):- Flowered plants are called adults.

**Data collection**

All rattans rooted in the plot were marked with numbered plastic tags. In clusters, each shoot was treated as a separate individual. For all individuals the following information was recorded: position (as coordinates), species, number of leaves (including spear leaves when they were at least as long as the petiole of fully expanded leaves), habit (clumped, solitary, acaulescent), and size. Size was measured as the number of leaves in the seedling stage, as the length of the longest leaf in juveniles, and as stem length in sub-adults and adults. The lengths of climbing stems were measured with a rod if they were accessible from the ground, from a ladder, or by climbing nearby trees. On each stem one leaf was marked, by removing a few pinnae near the leaf base. The position of the marked leaf relative to the apical leaf was carefully recorded. Production of new leaves was calculated from the position of the marked leaves in later surveys. Number of leaves and suckers were recorded. Average internode lengths of *C. thwaitesii and C. hookerianus* were determined by measuring all the internodes on ten stems that were chosen randomly among all stems longer than 4 m and 20 m, respectively. All internodes including basal part of stem of adult and sub-adult individuals of *C. delessertianus* and *C. vattayila* in the plot were measured (Table 8).

For reference the following voucher specimens are deposited at the Calicut University Herbarium(CALI) : *C. thwaitesii* (*Anto 3318*), *C. hookerianus* (*Anto 3325*), *C. vattayila* (*Anto 3331*), *C. delessertianus* (*Anto 3336*).

## Data analysis

### Population matrix

The data analysis was based on the method formulated by Bøgh (1995). For each of the four stages, defined in Table 2, yearly transition probabilities, $G_i$, and yearly probabilities of surviving and remaining in the same stage, $P_i$, were calculated. Average yearly fecundities, $F_{ij}$, were calculated for the reproductive stages. All estimates of growth and survival rates were calculated assuming that the rates were equal for all individuals in each stage.

$G_i$ was calculated as:

$G_i = \sigma_i / \bar{T}_i$; i= 1, 2, 3

where $\sigma_i$ is the survival probability and $\bar{T}_i$ is the average stage duration. For the seedling and juvenile stages $\bar{T}_i$ was calculated from the proportion of individuals that survived through the study period. Among sub-adults and adults deaths were rare. In these stages the defining size ranges (Table 2) were divided into halves. The survival probabilities were calculated from the decrease in number of individuals from the first half to the second half of the stage. The calculations of $\bar{T}_i$ and the survival probability, $\sigma_i$; of the sub-adult and adult stages were based on the assumption that the size distribution within the stages was stable. Stage durations, $\bar{T}_i$, were calculated as the average time required for surviving individuals to pass through a given stage at the observed growth rates. Seedling growth rates were calculated as the increase in number of leaves, and, for juveniles as the increase in the lengths of the longest leaves. The growth rates of sub-adults and adults were calculated by multiplying the number of new leaves produced by the average internodal lengths.

The number of months taken for the first four leaves is considered as seedling stage duration. It is converted to years. Juvenile stage duration was calculated by using the rate of growth in length of seedlings to the longest leaf length of juveniles. It is by using the formula

Stage Duration of Juveniles =

$$\left(\frac{\text{Length of largest juvenile - Average length of seedlings}}{\text{Average length of seedlings}}\right)\text{Seedling stage duration}$$

It gives the age of the juvenile directly in years. The sub-adult stage duration is calculated by using the formula

$$\text{SD OF SA} = \left\{\frac{\text{Length of largest SA plant}}{\text{Average inter nodal length of SA}}\right\}\text{Average new leaf per year in SA}$$

Where SD OF SA = Stage duration of sub adult.

In the case of *Calamus*, the sub adult and adult stage duration is very easy to calculate because of unbranched nature of stem with distinct nodal and inter nodal regions. Adult stage duration is calculated using the same formula, used for sub-adult stage duration. But the value got from that is the sum of adult and sub-adult stages. To get the adult stage duration in years, sub-adult stage duration is subtracted from the formula value. Here the arbitrary value for maximum height of the adult plant is taken which is comparable and reliable to the existing length of the adult plant in study plot or area other than the study plot.

$P_i$ was calculated as:

$P_i = \sigma_i - G_i;\quad i = 1, 2, 3, 4$

Estimates of sexual fecundities, $F_{14}$ were calculated as the ratio between the number of new seedlings and the total number of adults. This was done under the assumption that the import and export of seeds from the plot were equivalent. The calculation of the probability of growing into the next stage, $G_i$ and the survival rates of the sub-adult and adult stages were done under the assumption that the size distribution within the stages was stable. Since $P_i$ was calculated by subtracting $G_i$ from the survival rate the assumption also applies to $P_i$.

In clump forming species, the growth rates of suckers from clumps were significantly different from seedlings (Bøgh 1995). In case of *C.thwaitesii* and *C.hookerianus* the growth rates (leaf length increment) of suckers from clumps were significantly different from that of seedlings. Therefore new vegetative shoots were regarded as juveniles. The largest shoot in each clump was regarded as the parent of all new shoots. The vegetative fecundities of the sub-adult and adult stages, $F_{23}$ and $F_{24}$, were calculated as the average production of new shoots per individual in each stage. Occasionally acaulescent individuals produced new shoots. This vegetative fecundity, $F_{22}$ was added to $P_2$.

The above mentioned parameters were used to construct transition matrices as shown in Table 3. From these matrices the finite rates of population increase, $\lambda$, were calculated as the dominant eigenvalues, whereas the stable stage distributions, w, were given by the corresponding right eigenvectors. Finally, elasticity values for the matrix coefficients were calculated (Caswell, 1989).

Table 3. Matrix elements

| | Seedling | Juvenile | Sub-adult | Adult |
|---|---|---|---|---|
| Seedling | $P_1$ | R | 0 | $F_{14}$ |
| Juvenile | $G_1$ | $P_2$ | $F_{23}$ | $F_{24}$ |
| Sub-adult | 0 | $G_2$ | $P_3$ | 0 |
| Adult | 0 | 0 | $G_3$ | $P_4$ |

### Sensitivity and elasticity

Sensitivities are the sensitivity of $\lambda$, the asymptotic population growth rate, to an absolute change in each element in the projection matrix. The sensitivities allow one to see what would happen to the population growth rate if we could improve survival and fecundity values in the projection matrix one at a time of particular value.

Elasticity quantifies the proportional change in the population growth rate that will result from a proportion change in each matrix element. It indicates that to a given per cent change in life history transition will result in much percentage change in population growth rate.

The asymptotic rate of population growth is given by the dominant eigen value, $\lambda$, of the above projection matrix. The stable stage structure and reproductive values are given by the corresponding right and left eigen vectors W and V. The sensitivity, $S_{ij}$, of $\lambda$ to change in the matrix element $a_{ij}$, of projection matrix is given by the partial differential, $\partial$.

$$S_{ij} = (\partial\lambda / \partial a_{ij}) = (V_1 W_1) / <W,V>$$

where < > represents the scalar product of vectors. Sensitivity measures, how $\lambda$ changes with an absolute change in $a_{ij}$. The effect of proportional changes in $a_{ij}$ can be explained by scaling the sensitivities and calculating elasticities ($e_{ij}$) using formula,

$$e_{ij} = ( a_{ij}\, \partial\lambda ) / (\lambda \;\; \partial a_{ij} ) = ( \partial \log \lambda ) / (\partial \log a_{ij} )$$

Elasticity also has the useful properties that they sum to 1.0, and thus also represent the proportional contribution of each element to $\lambda$. Even though, both sensitivity and elasticity are used in management programmes, generally, elasticities are considered more useful for management consideration.

Sensitivity only gives a proportional clue to the change of $a_{ij}$ to $\lambda$. In this proportional changes, it does not give equal weightage to fecundity and survival. It gives more importance to sensitivity changes of fecundity than survival. Moreover, $s_{ij}$ is very large even though $a_{ij} = 0$. When we are comparing the plants which show similar life history parameters with growth rate differences in field condition, an analytical measure of proportional sensitivity i.e. elasticity is used. Here proportional change in $a_{ij}$ gives proportional change in $\lambda$ (de Kroon, *et al.* 1986).

**Population dynamics**

The data analysis was based on the method formulated by Zar (1974). For studying the varying pattern of each group of plants in the plots in the consecutive observations of the whole period, regression was formulated. The varying factors used for the regression studies were the numbers of plants at each observation and the corresponding months. In order to find out the trends in total number of seedlings from time to time equations were developed with total number of seedlings as dependent variable and months as independent variable. Different functional forms were tried and the best fitted functions were selected based on $R^2$ values.

### Seasonal variations in recruitment and death rates

The transition from one stage to another e.g., from seedling to juvenile and from juvenile to sub-adult and adult is called recruitment. Recruitment may occur from seeds or as is the case in many plants, by the production of vegetative suckers. These suckers were initially physically attached to the parent, each capable of an independent existence if they were detached.

Rate of new recruitment was found out as follows:

Rate of new recruitment = $(n/N)\ 100$,

where *'n'* is the number of new recruitment, *'N* is the total number of plants at the time of starting of the observation.

Rate of death could be calculated with the following formula

Rate of death = $(d/N)100$,

where *'d'* is the number of deaths noted for that particular period, *'N'* is the total number of plant observed in that particular plot at the time of starting of the measurement.

### Population flux

Summarization of the population dynamics for each species is the population flux. It was calculated for an annual basis for the whole period. From the Population flux the variations in the annual recruitment and death of the three year period were calculated. It gives the changing pattern of population in the consecutive years. The result would give information of change in population size, cumulative gains and cumulative losses yearly or for the total period and the different trends in the population yearly or for total period.

The rate of increase can be calculated by a / b,

where 'b' is the total number of plants in the final measurement and 'a' is the number of plants in the initial measurement. The total arrival and total mortality in the total period or year-wise also is included in the population flux. From the data, the total plants recorded during the period can be calculated by 'a + e' where 'a' is the initial number of plant and 'e' the number of new arrival during the period.

The percentage of death of the whole period or for one year is included in the population flux which can be calculated with the following formula.

Percentage of death = (f / g) 100

where 'f' is the total mortality of the period and 'g' is the number of total plants recorded.

The percentage of annual recruitment is also included in the population flux, which can be calculated with the following formula.

Percentage of recruitment = (e / g) 100

Here 'e' is the total arrival between the period and 'g', the number of total plants recorded. The values will give the changes in population by time with the net population size, the cumulative totals and the cumulative losses. The cumulative losses were tabulated below the original population size annually or total time, so that addition with the cumulative totals gives the next population size.

# RESULTS

# RESULTS

## Number of plants under each life stage

Number of seedlings ranged from 65 to 243 in case of *C. thwaitesii* and from 16 to 64 in *C. hookerianus*. Juveniles ranged from 137 to 222 in *C. thwaitesii* and from 66 to 159 in *C. hookerianus*. Number of sub-adults ranged from 60 to 81 in *C. thwaitesii* and 37 to 45 in *C. hookerianus*. Number of adults ranged from 41 to 47 in *C. thwaitesii* and 18 to 25 in *C. hookerianus*. Total number of individuals ranged from 346 to 582 in *C. thwaitesii*, and 171 to 251 in *C. hookerianus*.

Table 4. Number of individuals of *Calamus thwaitesii* in each stage at different time point

| Period | Seedlings | Juveniles | Sub-adult | Adult | Grand Total |
|---|---|---|---|---|---|
| January 2000 | 140 | 137 | 60 | 44 | 381 |
| May | 107 | 138 | 60 | 41 | 346 |
| September | 97 | 149 | 61 | 41 | 348 |
| January 2001 | 101 | 170 | 73 | 41 | 385 |
| May | 65 | 170 | 74 | 43 | 352 |
| September | 70 | 188 | 78 | 43 | 379 |
| January 2002 | 85 | 185 | 81 | 43 | 394 |
| May | 72 | 184 | 81 | 43 | 380 |
| September | 243 | 185 | 78 | 47 | 553 |
| January 2003 | 233 | 222 | 80 | 47 | 582 |

Table 5. Number of individuals of *Calamus hookerianus* in each stage at different time points

| Period | Seedlings | Juveniles | Sub-adult | Adult | Grand Total |
|---|---|---|---|---|---|
| January 2000 | 47 | 67 | 39 | 18 | 171 |
| May | 64 | 66 | 37 | 18 | 185 |
| September | 43 | 92 | 36 | 21 | 192 |
| January 2001 | 36 | 114 | 42 | 19 | 211 |
| May | 18 | 125 | 42 | 23 | 208 |
| September | 16 | 139 | 42 | 23 | 220 |
| January 2002 | 16 | 133 | 43 | 23 | 215 |
| May | 19 | 130 | 43 | 23 | 215 |
| September | 24 | 128 | 44 | 23 | 219 |
| January 2003 | 22 | 159 | 45 | 25 | 251 |

Table 6. Number of individuals of *Calamus vattayila* in each stage at different time points

| Period | Seedlings | Juveniles | Sub-adult | Adult | Grand Total |
|---|---|---|---|---|---|
| January 2000 | 6 | 2 | 5 | 1 | 14 |
| May | 7 | 4 | 6 | 1 | 18 |
| September | 5 | 6 | 6 | 1 | 18 |
| January 2001 | 12 | 6 | 4 | 2 | 24 |
| May | 10 | 8 | 4 | 2 | 24 |
| September | 9 | 8 | 4 | 2 | 23 |
| January 2002 | 16 | 8 | 4 | 2 | 30 |
| May | 13 | 9 | 4 | 2 | 28 |
| September | 5 | 12 | 5 | 2 | 24 |
| January 2003 | 2 | 12 | 5 | 1 | 20 |

Table 7. Number of individuals of *Calamus delessertianus* in each stage at different time points

| Period | Seedlings | Juveniles | Sub-adult | Adult | Grand Total |
|---|---|---|---|---|---|
| January 2000 | 134 | 38 | 13 | 2 | 187 |
| May | 152 | 51 | 11 | 3 | 217 |
| September | 196 | 76 | 14 | 4 | 290 |
| January 2001 | 282 | 104 | 13 | 5 | 404 |
| May | 280 | 106 | 13 | 5 | 404 |
| September | 229 | 122 | 12 | 5 | 368 |
| January 2002 | 198 | 152 | 14 | 5 | 369 |
| May | 131 | 188 | 14 | 5 | 338 |
| September | 82 | 217 | 14 | 5 | 318 |
| January 2003 | 73 | 243 | 14 | 5 | 335 |

In the case of *C. vattayila* number of seedlings ranged from 2 to 16, juveniles 2 to 12, sub-adult 4 to 6 and adult 1 to 2. Only the juvenile stage showed gradual increase in number of individuals from first to last observation. The total number of individuals of this species ranged from 14 to 30. The number of seedlings drastically reduced at the last observation. But there is no change in the number of adults in first and last observations.

In the case of *C. delessertianus* number of seedling ranged from 73 to 282, juveniles 38 to 243, sub-adult 11 to 14 and adult 2 to 5. The total number of individuals of this species ranged from 187 to 404. Only the juvenile stage showed gradual increase in number of individuals from first to last observation.

Number of seedlings decreased towards the last observation. Number of adults increased from first to last observation.

**Girth and internodal length**

*C. thwaitesii*, showed almost same internodal length (27.5 cm) and girth (8 cm) from base to tip of the stem. *C. hookerianus*, showed an average internodal length of 14.4 cm. *C. vattayila* showed short internodal length (2.5 cm) and smaller girth (1.5 cm) at the basal region when compared to upper part of the stem (internodal length-25 cm and girth-4 cm). In *C. delessertianus* the internodal length was shorter at the basal region (4.5 cm) than in the middle (27 cm). In case of girth there was a slight increase at the basal region.

Table 8. Comparison of growth characteristics of four species

| Species | Internodal length (cm.) | | | Girth in (cm.) | | | Average number of leaves | | Average number of suckers | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Base | Middle | Average | Base | Middle | Average | SA | A | J | SA | A |
| *C. thwaitesii* | 27.5 | 27.5 | 27.5 | 7 | 8 | 7.5 | 5 | 6 | 1 | 8 | 15 |
| *C. hookerianus* | 14.4 | 14.4 | 14.4 | 5 | 6 | 5.5 | 4 | 4.5 | 2 | 15 | 33 |
| *C. vattayila* | 2.5 | 25 | 16.1 | 1.5 | 4 | 3.5 | 4 | 5 | - | - | - |
| *C. delessertianus* | 4.5 | 27 | 19.2 | 9 | 8 | 8.5 | 4.5 | 5.5 | - | - | - |

**Production of leaves and suckers**

In *C. thwaitesii* average number of leaves produced per year in sub-adult and adult stage was 5 and 6 respectively. Average number of suckers produced in juvenile, sub-adult and adult stages was 1, 8 and 15 respectively.

In *C. hookerianus* average number of leaves was 4 and 4.5 per plant per year in sub-adult and adult stages respectively. Average number of suckers produced in juvenile, sub-adult and adult was 2, 15 and 33 respectively.

In *C. vattayila* average number of leaves was 4 and 5 per plant per year in sub-adult and adult stages respectively. Annual leaf production of *C. delessertianus* was 4.5 and 5.5 in sub-adult and adult stages respectively (Table 8). No suckers were produced in the case of *C. vattayila* and *C. delessertianus*.

### Yearly production of stem

Yearly production of stem is shown in Table 9. Maximum yield was given by *C. thwaitesii*, about 1.51 m per plant per year. Minimum yield was given by *C. hookerianus*, about 0.61 m per plant per year. Average stem production of *C. vattayila* and *C. delessertianus* was 0.72 m and 0.96 m respectively per plant per year

Table 9. Annual stem production in the plot

| Name | Annual stem production per plant per year | Total stem in the plot |
|---|---|---|
| *C. thwaitesii* | 1.51 m | 157.04 m |
| *C. hookerianus* | 0.61 m | 34.16 m |
| *C. vattayila* | 0.72 m | 4.32 m |
| *C. delessertianus* | 0.96 m | 14.4 m |

### Stage duration

The calculated stage durations for the four species are listed in Table 10. Generally, the seedling stage durations of 4 species ranged from 1.2 to 2 years. The duration was slightly greater in *C. hookerianus* (2 years), when compared to that of the co existing species *C. thwaitesii* (1.2 years).

Table 10. Stage duration in years

| Species | Seedling | Juvenile | Sub-adult | Adult | Age |
|---|---|---|---|---|---|
| *C. thwaitesii* | 1.2 | 15.16 | 16.9 | 39.5 | 72.76 |
| *C. hookerianus* | 2.0 | 18.0 | 17.4 | 59.8 | 97.2 |
| *C. vattayila* | 1.8 | 19.8 | 40.08 | 52.8 | 114.48 |
| *C. delessertianus* | 1.4 | 11.1 | 25.46 | 59.2 | 97.16 |

The duration of juvenile stage of 4 species ranged from 11.1 years to 19.8 years. There was a pronounced difference in juvenile stage duration between *C. vattayila* (19.8 years), and the co-existing species *C. delessertianus* (11.1 years), and between *C. thwaitesii* (15.6) and *C. hookerianus* (18).

The stage duration of sub-adult varied from 16.9 years to 40.08 years among the species. *C. thwaitesii* and *C. hookerianus* showed almost similar stage duration where as, there was a drastic difference between *C. vattayila* and *C. delessertianus*. Stage duration of sub-adults of *C. vattayila* and *C. delessertianus* is higher than that of *C. thwaitesii* and *C. hookerianus*.

The stage duration of adults varied from 39.5 years to 59.8 years among the four species. A pronounced difference was noticed in the case of *C. thwaitesii*, which showed 39.5 years duration and is smaller than that of all other three species studied. The other three species showed stage duration greater than 50 years (*C. hookerianus* 59.8, *C. vattayila* 52.8, *C. delessertianus* 59.2).

The sum of the stage durations are estimates of the longevities of the species. The values of these parameters were 72.76, 97.2, 114.48 and 97.16 years for *C. thwaitesii, C. hookerianus, C. vattayila and C. delessertianus* respectively (Table 10).

**Population matrix**

The transition matrices given in Tables 11 to 14 are the calculated demographic rates. A visual representation of the rates is given in Figures 4 to 5. The probabilities of surviving and remaining in the same stage $P_i$ values are listed on the matrix diagonals. Due to high seedling mortalities in all four species the $P_1$ values were relatively small especially in the case of *C. thwaitesii* and *C. delessertianus.* Both of them showed relatively higher birth and death rates when compared to other two species. $P_1$ values of *C .hookerianus* and *C. vattayila* were comparatively greater due to decreased birth and death rates. $P_3$ values were greater than 0.8 in three species except in *C. vattayila* where it was lower than $P_2$. In all four species $P_4$ values were greater than $P_3$ values. But it is less than $P_2$ value in the case of *C. vattayila*.

Yearly transition probabilities gradually decreased from $G_1$ to $G_3$ in *C. vattayila* and in *C. delessertianus*. In the case of *C. thwaitasii* and *C. hookerianus* $G_2$ was smaller than $G_3$. Sexual fecundities $F_{14}$ was about 4.333 and 53.3 in *C. vattayila* and *C. delessertianus* and 3.472 and 1.17 in *C. thwaitesii* and *C. hookerianus* respectively. Sexual fecundities in *C. delessertianus* are very high because the number of seedlings is very high compared to number of adults in that population. The vegetative fecundities ($F_{22}$, $F_{23}$, and $F_{24}$) of *C. thwaitesii* were 0.006, 0.157, and 0.469 for the juvenile, sub-adult and adult stages respectively. These values in the case of *C. hoookerianus* were 0.021, 0.364, and 1.668. The other two species are single stemmed and they do not produce suckers during their life period. Hence $F_{22}$, $F_{23}$ and $F_{24}$ are zeroes in these cases.

Table 11. Projection matrix for *Calamus thwaitesii*

**$\lambda = 1.01$**

| Stages | Seedling | Juvenile | Sub-adult | Adult | w |
|---|---|---|---|---|---|
| Seedling | 0.036 | 0 | 0 | 3.472 | 0.289 |
| Juvenile | 0.178 | 0.749 | 0.157 | 0.469 | 0.446 |
| Sub-adult | 0 | 0.052 | 0.882 | 0 | 0.184 |
| Adult | 0 | 0 | 0.055 | 0.883 | 0.081 |

Table 12. Projection matrix for *Calamus hookerianus*

**$\lambda = 1.05$**

| Stages | Seedling | Juvenile | Sub-adult | Adult | w |
|---|---|---|---|---|---|
| Seedling | 0.128 | 0 | 0 | 1.170 | 0.093 |
| Juvenile | 0.128 | 0.797 | 0.364 | 1.668 | 0.684 |
| Sub adult | 0 | 0.046 | 0.842 | 0 | 0.150 |
| Adult | 0 | 0 | 0.051 | 0.947 | 0.073 |

Table 13. Projection matrix for *Calamus vattayila*

**$\lambda = 0.94$**

| Stages | Seedling | Juvenile | Sub-adult | Adult | w |
|---|---|---|---|---|---|
| Seedling | 0.204 | 0 | 0 | 4.333 | 0.167 |
| Juvenile | 0.255 | 0.870 | 0.000 | 0.000 | 0.635 |
| Sub adult | 0 | 0.046 | 0.764 | 0 | 0.169 |
| Adult | 0 | 0 | 0.020 | 0.818 | 0.028 |

Table 14. Projection matrix for *Calamus delessertianus*

$\lambda = 1.21$

| Stages | Seedling | Juvenile | Sub-adult | Adult | w |
|---|---|---|---|---|---|
| Seedling | 0.095 | 0 | 0 | 53.300 | 0.573 |
| Juvenile | 0.238 | 0.806 | 0.000 | 0.000 | 0.338 |
| Sub adult | 0 | 0.080 | 0.862 | 0 | 0.078 |
| Adult | 0 | 0 | 0.035 | 0.983 | 0.012 |

In the calculation of the $P_1$ values $G_1$ values were subtracted from the survival rate, but the differences in growth probabilities are not sufficient to explain the low $P_3$ value of *C. vattayila*. Low $G_1$ and $P_1$ values of *C. thwaitesii* indicated the high seedling death rate. Low $P_1$ value and high $G_1$ value of *C. delessertianus* indicated the high rate of transition probabilities of seedling. Low $G_3$ value of *C. vattayila* showed the long stage duration of sub-adult stage. A non stable size distribution could explain the low sub-adult survival rates (eg. *C. vattayila* and *C. delessertianus*). *C. delessertianus* showed comparatively large $G_2$ value due to high rate of root establishment in large juvenile individuals.

The stable stage distributions (w) varied among the species (Tables 11 - 14). *C. thwaitesii* and *C. hookerianus* showed much greater stable stage distribution in the adult stage. The adult stages of *C. delessertianus* and *C. vattayila* was much less, than the other two clustering species. The observed stage distributions were significantly different from w in all four species (Tables 11 - 14).

The finite rate of population λ (Tables 11 - 14) was slightly greater than one for three species except for *C. vattayila*. It was 1.01 for *C. thwaitesii*, 1.05 for *C. hookerianus* and 1.21 for *C. delessertianus*. The λ value greater than one shows that the populations are stable if the demographic rate remains constant. The lower λ value of *C. vattayila* indicated that the population was decreasing. The values indicated a population increase of one per cent per year for *C. thwaitesii*, five per cent per year for *C. hookerianus* and 21 per cent per year for *C. delessertianus*. The λ value of *C. vattayila* was 0.94 which indicated a population decrease by six per cent per year. As the λ value of *C. delesertianus* was very high (21 per cent per year), the population increase was higher in this species than all other species studied.

Figures 4 and 5 indicate the stable stage duration and the transition rates of the four populations graphically. The areas of numbered circles show the relative proportions of the four stages at the stable stage distributions. Numbers 1 to 4 corresponds to the seedling, juvenile, sub-adult and adult stages, respectively. The value of $P_2$ for *C. thwaitesii* and *C. hookerianus* are lower than value given in table 11 and 12. In the figure the value of $F_{22}$ has been subtracted.

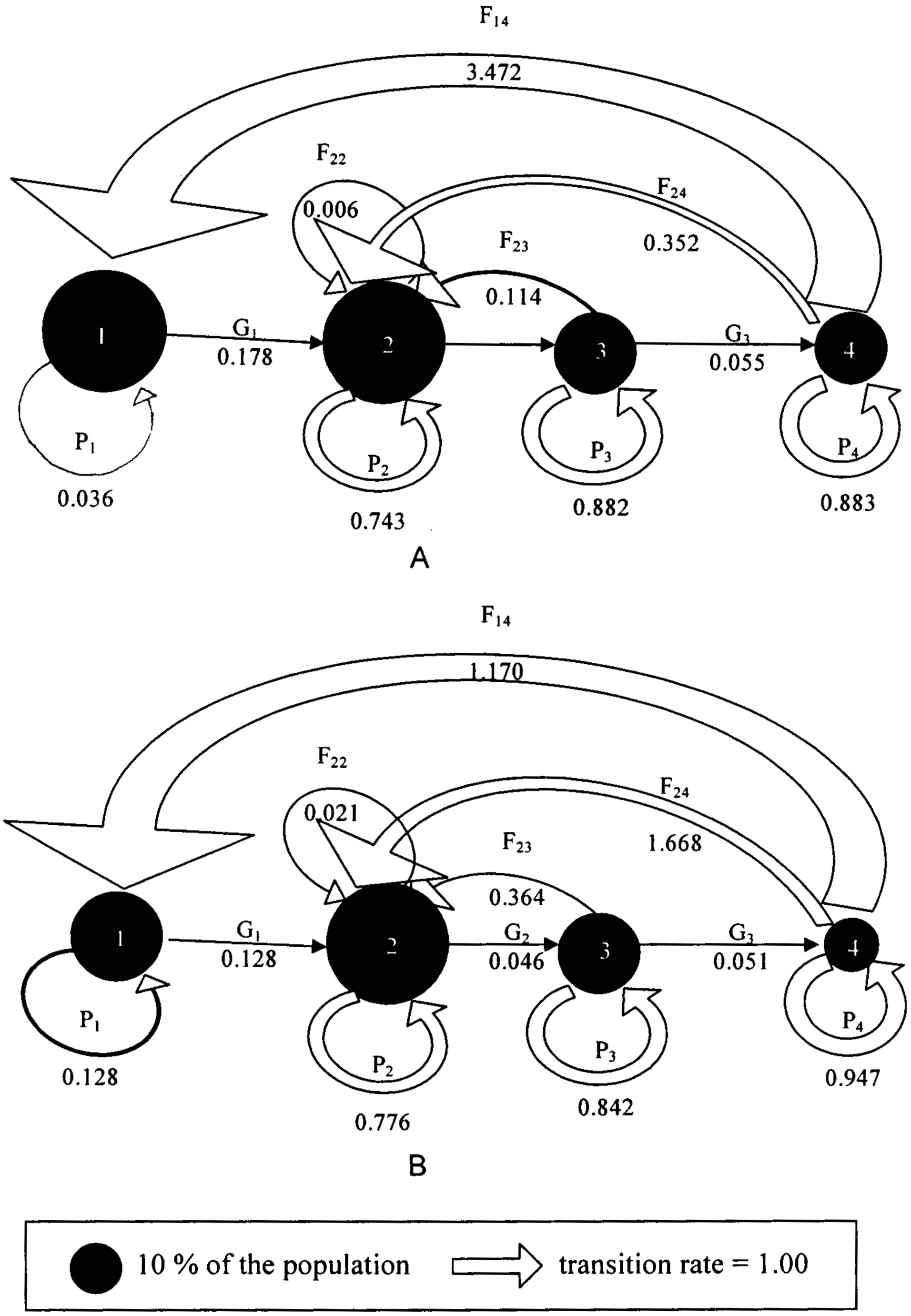

Figure 4. Graphical representation of the stable stage distribution and the transition rates with respect to population matrix of the two *Calamus* species studied in Deciduous Forest

A. *Calamus thwaitesii*
B. *Calamus hookerianus*

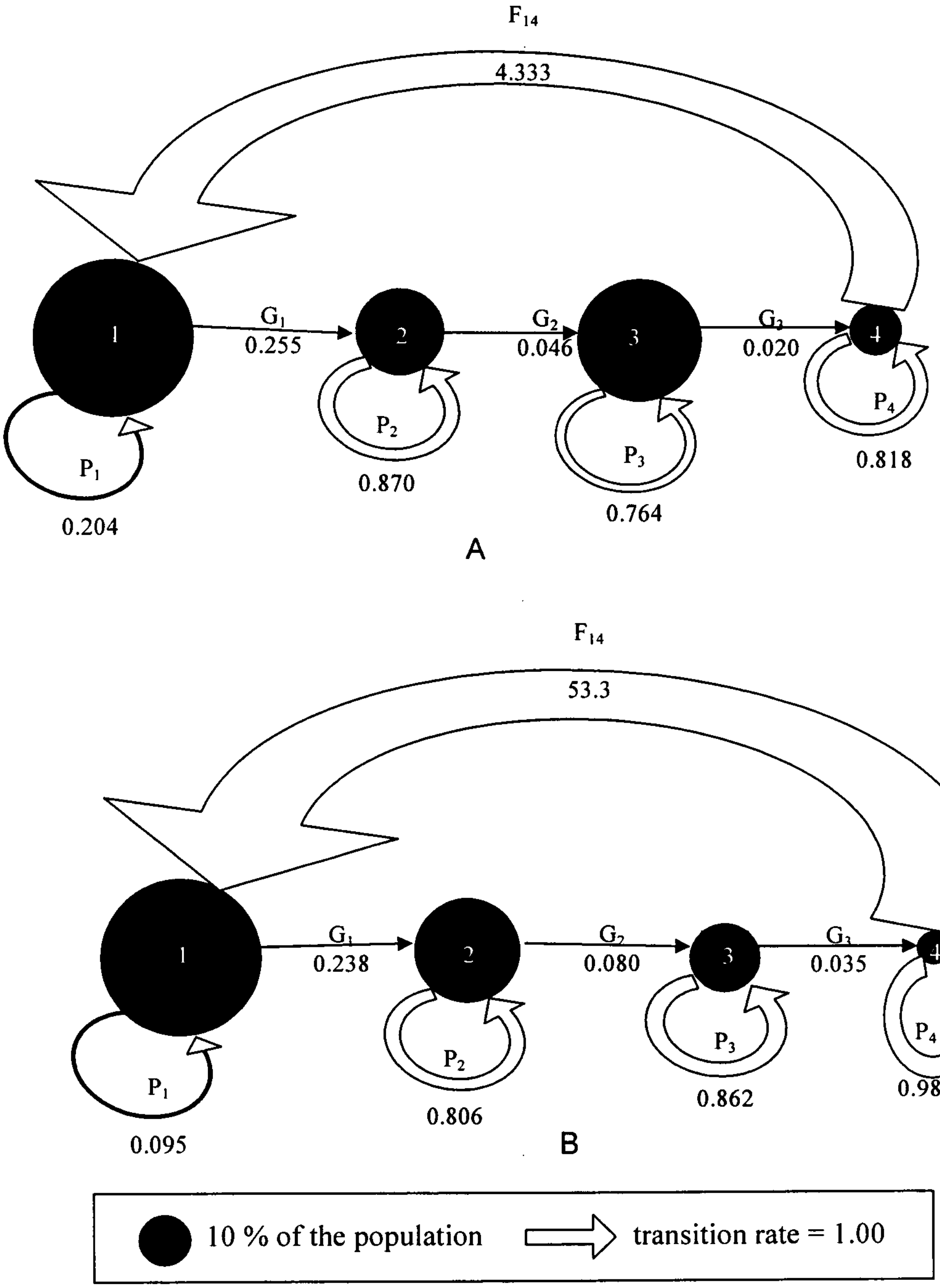

Figure 5. Graphical representation of the stable stage distribution and the transition rates with respect to population matrix of the two *Calamus* species studied in Evergreen Forest

A. *Calamus vattayila*
B. *Calamus delessertianus*

### Elasticity

The elasticity values given in Tables 15 - 18 express the relative contributions of the corresponding transitions to the population growth rates (Caswell, 1989). The highest elasticity values were those of sub-adult survival rates in *C. thwaitesii* (0.312) and adult survival rates in *C. hookerianus* (0.401) and *C. delessertianus* (0.336). In the case of *C. vattayila* the highest elasticity values was that of juvenile survival rate (0.453).

The adult survival elasticity ranked second in *C. thwaitesii* and *C. vattayila.* In both *C. hookerianus* and *C. delessertianus* sub-adult survival elasticity ranked second.

Adult and sub-adult stages were critical in changing the λ value in *C. thwaitesii* and *C. hookerianus.* But in the case of *C. vattayila*, adult and juvenile stages have the major role in changing the λ values where juveniles played a major role than adult stages. In the cases of *C. delessertianus*, only seedling stage has least importance in changing the λ values and adult stage is the most important one. In this case, juvenile and sub-adult play equal importance in changing λ values.

Table 15. Elasticity of *Calamus thwaitesii*

| Stages | Seedling | Juvenile | Sub adult | Adult |
|---|---|---|---|---|
| Seedling | 0.007 | 0.000 | 0.000 | 0.194 |
| Juvenile | 0.019 | 0.126 | 0.011 | 0.014 |
| Sub adult | 0.000 | 0.045 | 0.312 | 0.000 |
| Adult | 0.000 | 0.000 | 0.034 | 0.238 |

Table 16. Elasticity of *Calamus hookerianus*

| Stages | Seedling | Juvenile | Sub adult | Adult |
|---|---|---|---|---|
| Seedling | 0.001 | 0.000 | 0.000 | 0.004 |
| Juvenile | 0.004 | 0.181 | 0.018 | 0.040 |
| Sub adult | 0.000 | 0.062 | 0.251 | 0.000 |
| Adult | 0.000 | 0.000 | 0.045 | 0.401 |

Table 17. Elasticity of *Calamus vattayila*

| Stages | Seedling | Juvenile | Sub adult | Adult |
|---|---|---|---|---|
| Seedling | 0.010 | 0.000 | 0.000 | 0.035 |
| Juvenile | 0.035 | 0.453 | 0.000 | 0.000 |
| Sub adult | 0.000 | 0.035 | 0.154 | 0.000 |
| Adult | 0.000 | 0.000 | 0.034 | 0.240 |

Table18. Elasticity of *Calamus delessertianus*

| Stages | Seedling | Juvenile | Sub adult | Adult |
|---|---|---|---|---|
| Seedling | 0.007 | 0.000 | 0.000 | 0.077 |
| Juvenile | 0.078 | 0.155 | 0.000 | 0.000 |
| Sub adult | 0.000 | 0.077 | 0.192 | 0.000 |
| Adult | 0.000 | 0.000 | 0.078 | 0.336 |

The elasticities of transition from one stage to the next were small in all the species. There was little intraspecific variation between the stages. The highest transition values of stages were exhibited by *C. delessertianus.* In *C. hoookerianus* and *C. vattayila* sexual fecundities ($F_{14}$) contributed little to the population growth rates, while its contribution was considerable in case of *C. thwaitesii* and *C. delessertianus* where it was 0.194 and 0.077. *C. thwaitesii* showed the lowest elasticity values of vegetative fecundities than *C. hookerianus.*

In the case of *C. vattayila* $P_2$ value was greater than $P_1$, $P_3$ and $P_4$. $P_1$ value of *C. vattayila* was greater than all other three species. *C. delessertianus* showed a gradual increase from $P_1$ to $P_4$ values and $F_{14}$ value was also greater than *C. hookerianus* and *C. vattayila.* In the case of *C. hookerianus*, $P_4$ value is greater than $P_1$, $P_2$ and $P_3$. In the case of *C. thwaitesii*, $P_3$ value was greater than $P_1$, $P_2$ and $P_4$. $F_{14}$ value is highest in *C. thwaitesii* than all other species (Tables 15 -18).

Figures 6 and 7 indicate the elasticity corresponding to the transition shown in Figures 4 and 5. The areas of the circles show the relative proportions of the four stages at the stable stage distributions. The width of the arrows indicates the elasticities of the transitions. The values express the relative contribution of the corresponding transition to the $\lambda$ value. They also express the proportional change in $\lambda$ resulting from a proportional change in transition rates.

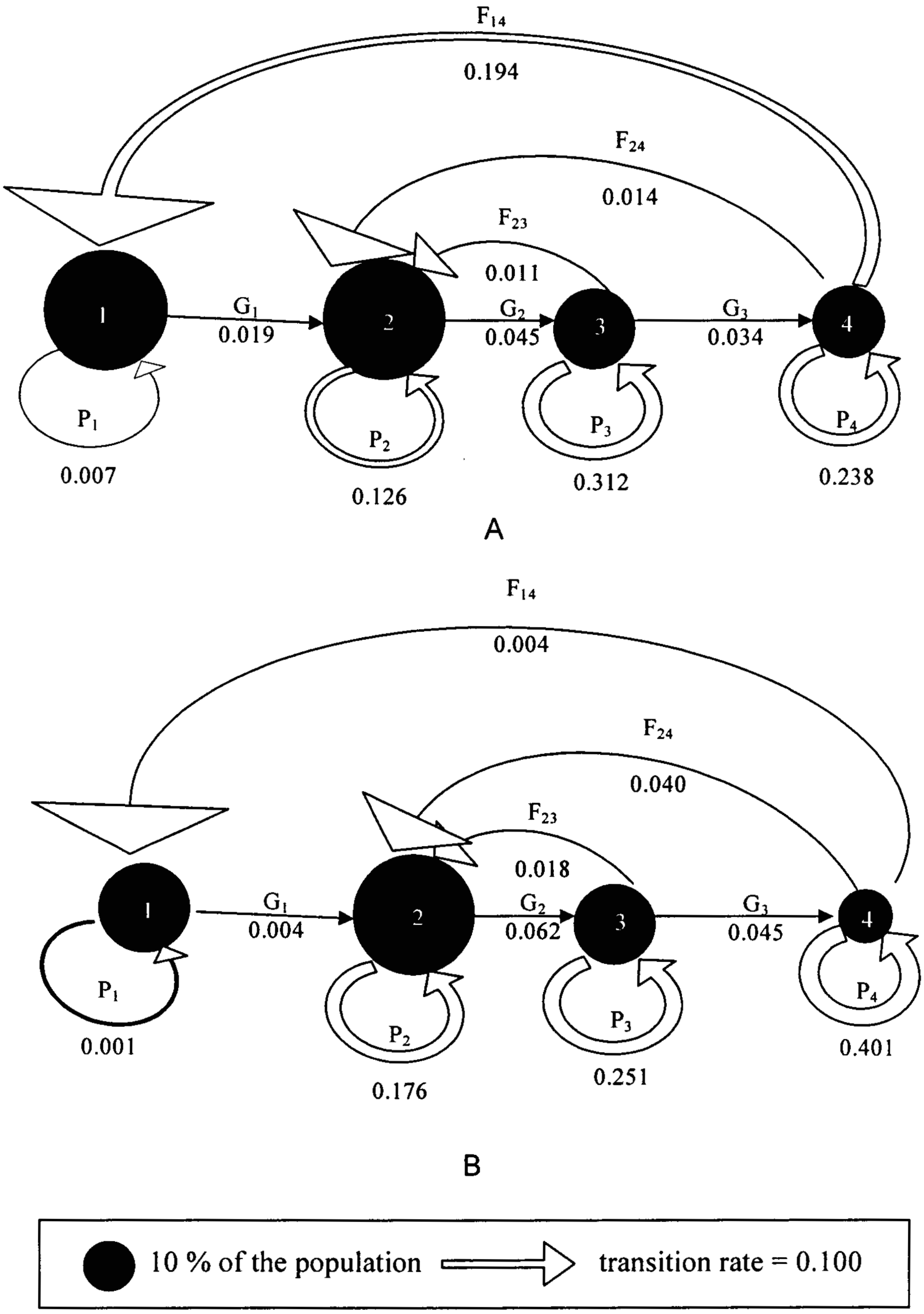

Figure 6. Graphical representation of elasticity with respect to transition of the two studied species of *Calamus* in Deciduous Forest.

A. *Calamus thwaitesii*
B. *Calamus hookerianus*

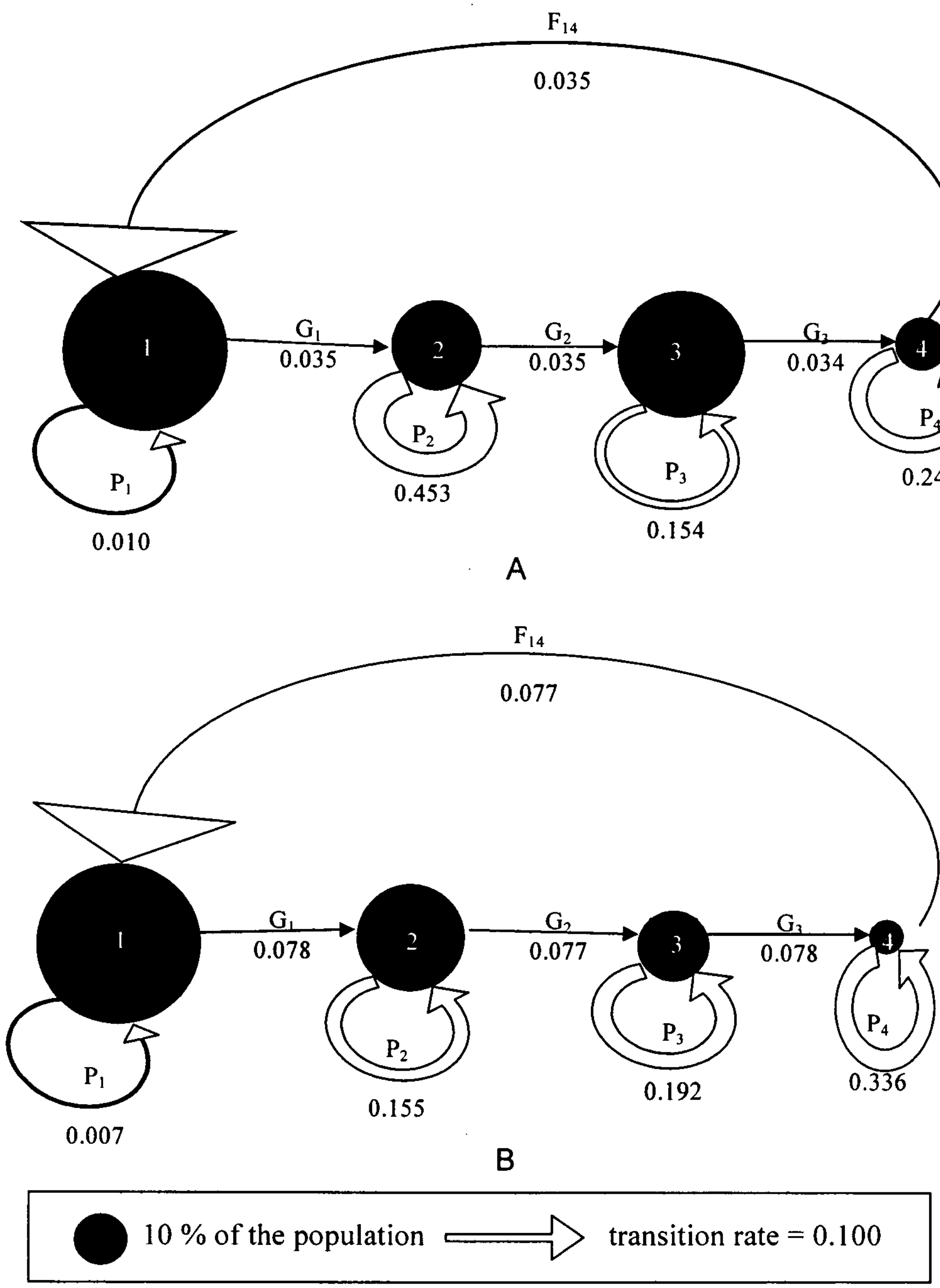

Figure 7. Graphical representation of elasticity with respect to transition of the two studied species of *Calamus* in Evergreen Forest.

A. *Calamus vattayila*
B. *Calamus delessertianus*

## $\chi^2$ Test

The fact that the observed stage distribution was significantly different from the stable distribution raises the question whether this assumption was justifiable. If the actual distribution (Table 19) is skewed towards smaller individuals the calculated $G_i$ estimates would overestimate the actual probabilities. Consequently $P_i$ would be an underestimate. A distribution skewed towards smaller individuals would cause the survival probability, $\sigma_i$, of the sub-adult and adult stages to be underestimated.

Table 19. The observed stage distribution of the four species studied (DF = 3)

| Species | Seedling | Juvenile | Sub-adult | Adult | $X^2$ value |
|---|---|---|---|---|---|
| *C. thwaitesii* | 36.75 | 35.96 | 15.75 | 11.55 | 79.94 ** |
| *C. hookerianus* | 27.49 | 39.18 | 22.81 | 10.53 | 28.84 ** |
| *C. vattayila* | 42.86 | 14.29 | 35.71 | 7.14 | 4.86 ns |
| *C. delessertianus* | 71.66 | 20.32 | 6.95 | 1.07 | 231.67 ** |

ns - Non significant(equal distribution)

** - Significant at one per cent level

## Population dynamics

The population dynamics of four species of *Calamus* is given in the Tables 4 - 7. Tables 4 and 5 represent clump forming species confined to moist deciduous habitat.

Seedling stage was predominant in the case of *C. thwaitesii* and individuals of juvenile stage were more in the case of *C. hookerianus*. In *C.*

*thwaitesii* number of seedlings and total individuals varied with each observation and there was no definite pattern for this change. In case of juvenile and sub-adult the number increased with periodic observations. No such trend was found in the case of *C. hookerianus*. The number of seedlings decreased very much during the last few observations.

Table 6 and 7 represent solitary species which are confined to the evergreen forests. In the case of *C. vattayila* grant total of individuals of the 4 stages were limited to a maximum of 30 individuals. The number of adult and sub-adult individuals showed no increment during the observed period. Only the juvenile stage showed gradual increase in number from first to last observations. There were only a very limited number of seedlings and this too decreased from first to last observation. A similar pattern was observed in *C. delessertianus* also.

**Birth and death rates**

The birth and death rates of four species are shown in Tables 20 to 23. *C. thwaitesii* and *C. delessertianus* showed very significant birth rates 52 per cent and 48 per cent respectively. This was followed by *C. vattayila* with 43 per cent. But in the case of *C. hookerianus* birth rate was comparatively poor only 15 per cent. *C. hookerianus* and *C. vattayila* showed reduced sexual fecundity. Birth rates of different species over the period of time are shown graphically in Figure 7.

Table20. Death and birth rate of *Calamus thwaitesii* over time

| Month | No. death | No. birth | Death rate | Birth rate |
|---|---|---|---|---|
| January 2000 | 0 | 0 | 0 | 0 |
| May | 39 | 4 | 10.24 | 1.05 |
| September | 21 | 23 | 6.07 | 6.65 |
| January 2001 | 54 | 91 | 15.52 | 26.15 |
| May | 42 | 9 | 10.91 | 2.34 |
| September | 16 | 43 | 4.55 | 12.22 |
| January 2002 | 26 | 41 | 6.86 | 10.82 |
| May | 14 | 0 | 3.55 | 0.00 |
| September | 27 | 200 | 7.11 | 52.63 |
| January 2003 | 6 | 35 | 1.08 | 6.33 |

There was no definite periodicity for maximum death rate. Maximum death rate of four species, *C. thwaitesii*, *C. hookerianus*, *C. vattayila*, *C. delessertianus* was 15.52, 7.21, 16.67 and 14.67 respectively. Among the four species, maximum death rate was exhibited by *C. vattayila* (Tables19 - 22). Figure 8 shows the graphical representation of death rate of different species over the period of time.

*C. hoookerianus* showed maximum death rate on 21st month, i.e., September 2001. *C. thwaitesii* showed maximum death rate on 13th month, ie, January 2001. The high death rate may be influenced by the high temperature during the month of May during that year. *C. delessertianus* showed maximum death rate during rainy season. This may be due to the washing away of seedlings or due to damage caused by heavy rain.

Table 21. Death and birth rate of *Calamus hookerianus* over time

| Month | No. of death | No. of birth | Death rate | Birth rate |
|---|---|---|---|---|
| January 2000 | 0 | 0 | 0 | 0 |
| May | 3 | 17 | 1.75 | 9.94 |
| September | 1 | 8 | 0.54 | 4.32 |
| January 2001 | 8 | 27 | 4.17 | 14.06 |
| May | 10 | 7 | 4.74 | 3.32 |
| September | 15 | 27 | 7.21 | 12.98 |
| January 2002 | 14 | 9 | 6.36 | 4.09 |
| May | 4 | 4 | 1.86 | 1.86 |
| September | 14 | 18 | 6.51 | 8.37 |
| January 2003 | 1 | 33 | 0.46 | 15.07 |

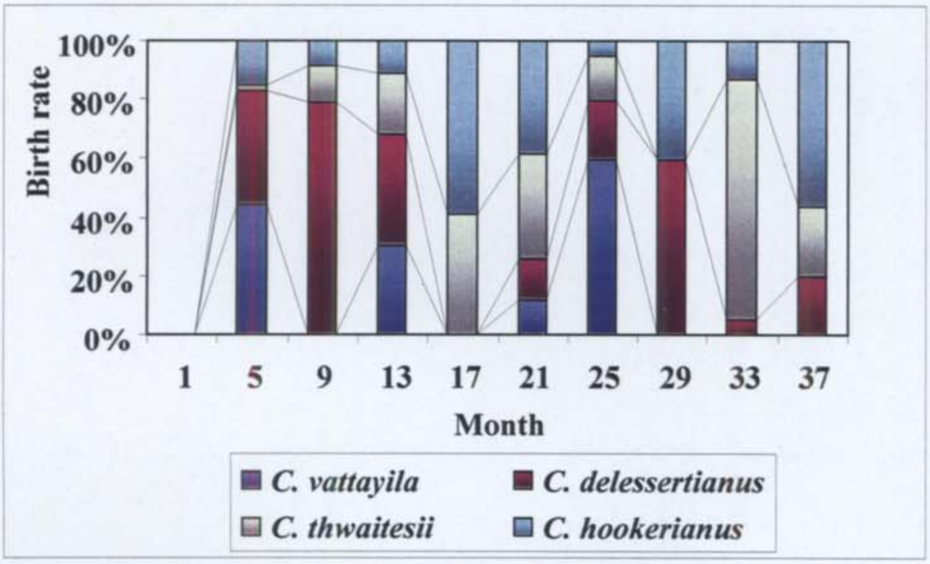

Figure 8. Birth rate of different species over the period of time

Table 22. Death and birth rate of *Calamus vattayila* over time

| Month | No. of death | No. of birth | Death rate | Birth rate |
|---|---|---|---|---|
| January 2000 | 0 | 0 | 0 | 0 |
| May | 0 | 4 | 0.00 | 28.57 |
| September | 0 | 0 | 0.00 | 0.00 |
| January 2001 | 1 | 7 | 5.56 | 38.89 |
| May | 0 | 0 | 0.00 | 0.00 |
| September | 2 | 1 | 8.33 | 4.17 |
| January 2002 | 3 | 10 | 13.04 | 43.48 |
| May | 2 | 0 | 6.67 | 0.00 |
| September | 4 | 0 | 14.29 | 0.00 |
| January 2003 | 4 | 0 | 16.67 | 0.00 |

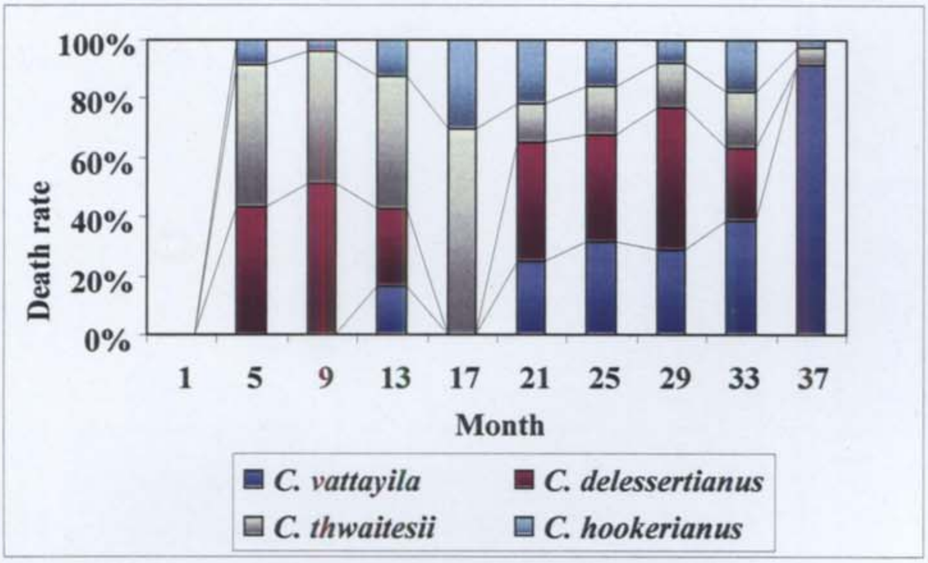

Figure 9. Death rate of different species over the period of time

Table 23. Death and birth rate of *Calamus delessertianus* over time

| Month | No. of death | No. of birth | Death rate | Birth rate |
|---|---|---|---|---|
| January 2000 | 0 | 0 | 0 | 0 |
| May | 17 | 47 | 9.09 | 25.13 |
| September | 15 | 88 | 6.91 | 40.55 |
| January 2001 | 26 | 140 | 8.97 | 48.28 |
| May | 0 | 0 | 0.00 | 0.00 |
| September | 55 | 19 | 13.61 | 4.70 |
| January 2002 | 54 | 55 | 14.67 | 14.95 |
| May | 41 | 10 | 11.11 | 2.71 |
| September | 31 | 11 | 9.17 | 3.25 |
| January 2003 | 0 | 17 | 0.00 | 5.35 |

**Seasonal variations in recruitment and death rates**

First observation was taken in January and further observations were taken at four months interval. In *C. vattayila* and *C. delessertianus* the maximum number of seedling appeared in January. In the case of *C. thwaitesii*, maximum number of seedling was observed in January for the first two years and in the September in the third year. In the case of *C. hookerianus*, the maximum number of seedling for the first year was observed in May, for the second year was January and for the third year it was observed in September (Tables 4 - 7).

In general, mortality rate also was higher during September and January for all the species. Deviations may occur due to summer rain in the habitat to an extent. But no seasonal mortality was observed in adult and sub-adult stages.

An analysis of the pattern of variations during the study period showed (Figure 10 - 14) that predominant variations were exhibited by *C. thwaitesii* and *C. delessertianus* in the seedling stage. Juvenile and sub-adult stage showed gradual increase during the study period. Adult stage also showed a slight increase in the number of individuals after an initial decrease. There was an increase in total number of individuals. All the stages of *C. thwaitesii* showed a positive trend towards growth (Figures 10 - 14).

*C. hookerianus* showed an initial decrease in the seedling stage but gradually it got stabilized. The increase in number in juvenile stage of *C.*

*hookerianus* is similar to *C. thwaitesii*. Adult and sub-adult stages showed a little increment with its small variations in the first year and second year. Total number showed slight increase in the second year onwards.

In *C. vattayila* there was no considerable increase in the number of seedlings, juveniles and sub-adults. Adults also show no increase in number after an initial increase. In *C. delessertianus* the number of seedlings increased in the initial stages but later decreased drastically. But in juveniles there was a steady increase. Sub-adults and adults became more or less steady over the entire period of observation. The adult stage showed a small increase in the beginning then became steady. Sub-adult stage showed uneven nature at the beginning but became steady at the third year. Total number of plants showed a prominent increase in the first year and then decreased slightly in the following years (Figure 10 - 14).

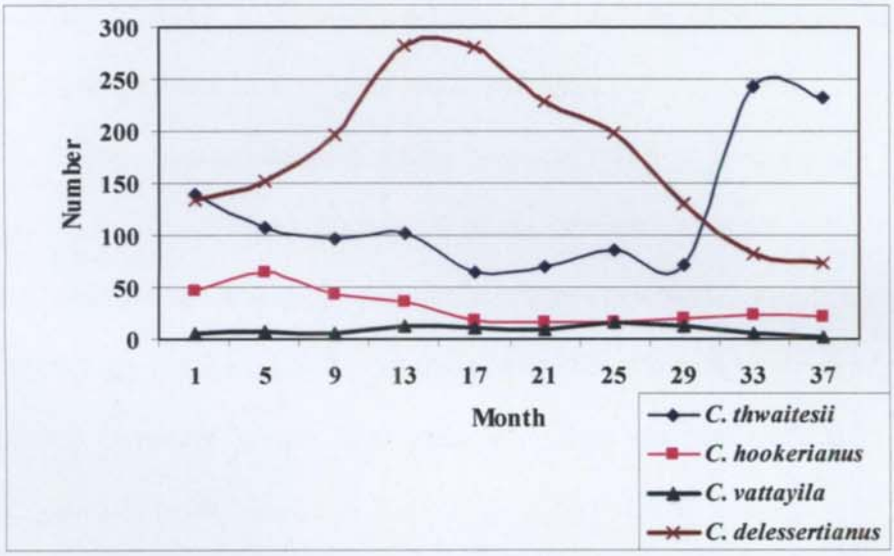

Figure 10. Seasonal variation in the seedlings of the four species

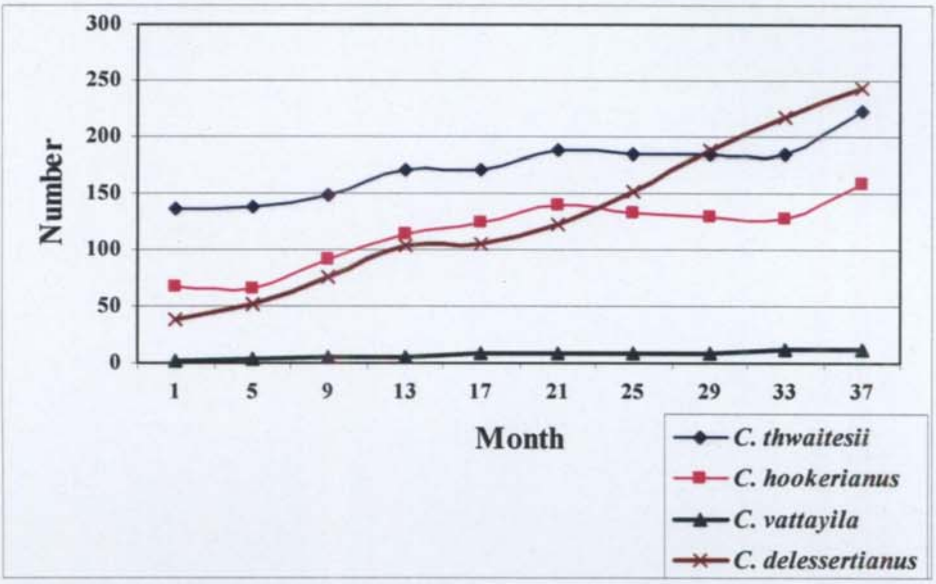

Figure 11. Seasonal variation in the Juveniles of the four species

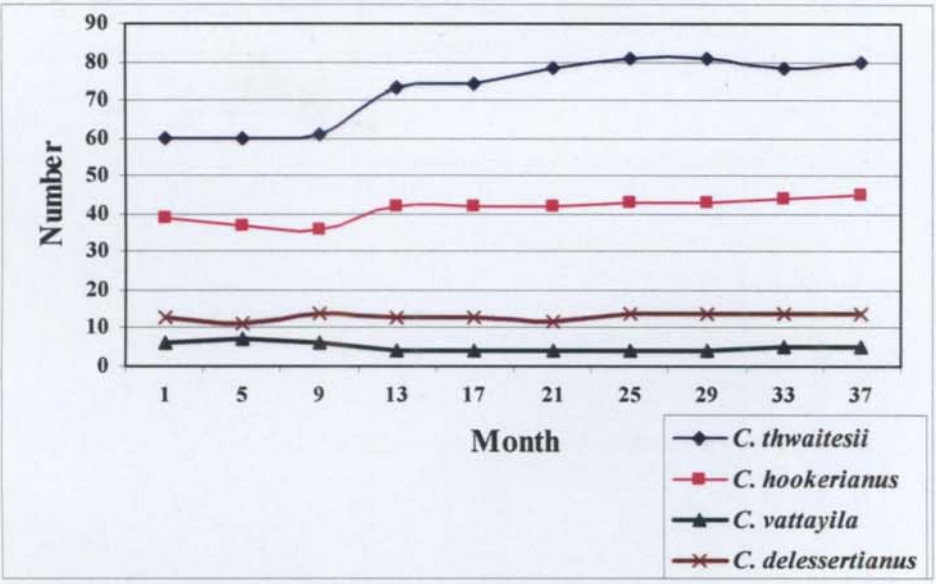

Figure 12. Seasonal variation in the sub-adults of the four species

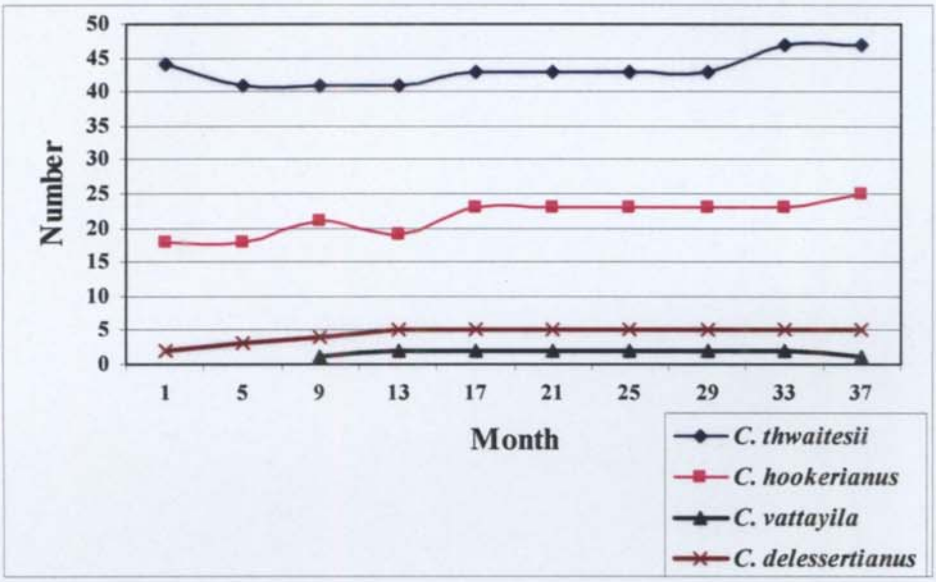

Figure13. Seasonal variation in the adults of the four species

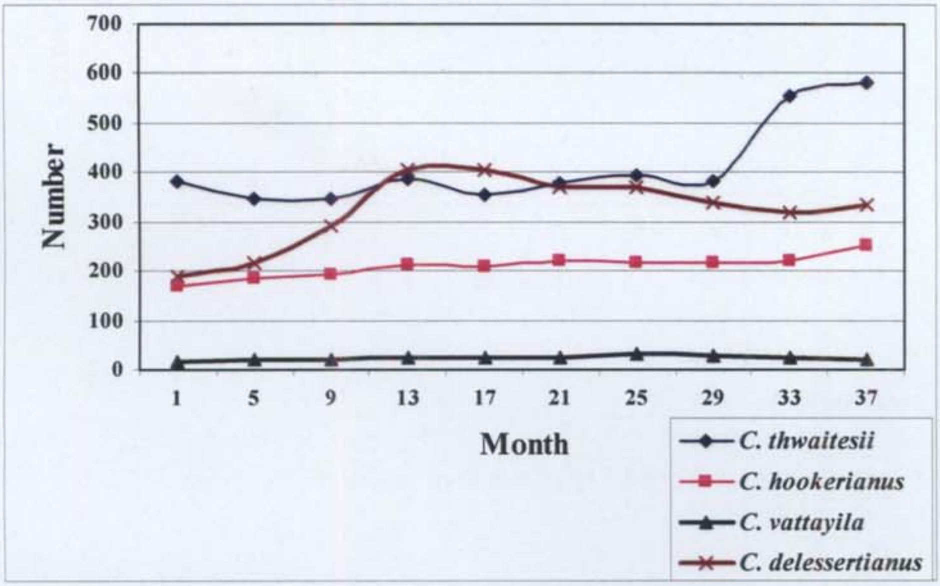

Figure 14. Seasonal variation in the total number of the four species

**Regression**

In order to find the trend in total number of seedling from time to time, equations were developed with total number of seedlings as dependent variable and month as independent variable. The results of analysis are showed in Tables 24 - 27, where 'Y' is the total number of plants and 'X' is the time (month) of observation.

The seedling pulse with its new recruitments which travels through seedling to adult in an observed period is indicated in regression. It shows a trend in the form of change in number of individuals, through their lifecycle, with respect to unchanged periodical duration.

*C. thwaitesii* showed no particular trend in seedling stage. The percentage of variations explained due to regression is 86.5, 81.4, and 48.6 in juvenile, sub-adult and adult number respectively. $R^2$ value for finding the trend in total number is 0.55. Slope coefficient of the fitted equations gives the change in depending variable due to unit change in time period. Here in the case of *C. thwaitesii*, the slope coefficient in all cases are positive indicating that there is an increasing trend from time to time in all stages like juvenile, sub-adult, adult and total number of individual. Among, adult, sub-adult and juvenile, slope coefficient was highest in juvenile stage which indicate that rate of increasing number of individuals was higher in juvenile stage.

Table 24. Regression functions fitted to number of plants in *Calamus thwaitesii*

| Status | Regression function | $R^2$ |
|---|---|---|
| Seedling | No trend | |
| Juvenile | Y = 134.338 + 2.035 X | 0.865 |
| Sub-adult | Y = 59.941 + 0.670 X | 0.814 |
| Adult | Y = 40.854 + 0.129 X | 0.486 |
| Total | Y = 310.389 + 5.270 X | 0.550 |

Table 25. Regression functions fitted to number of plants in *Calamus hookerianus*

| Status | Regression function | $R^2$ |
|---|---|---|
| Seedling | Y = 50.586 -1.063 X | 0.604 |
| Juvenile | Y = 71.138 - 2.337 X | 0.819 |
| Sub-adult | Y = 37.206 + 0.217 X | 0.753 |
| Adult | Y = 18.120 + 0.184 X | 0.801 |
| Total | Y = 177.050 + 1.675X | 0.825 |

In the case of *C. hookerianus*, a good fit of linear trend was observed in number of seedlings, sub-adult, adult and total number. Slope coefficient was negative in the case of seedling (-1.063) and juvenile (-2.337). this implies that the number of seedling and juveniles showed aa decreasing trend. Positive value of coefficients for sub-adult, adult and total number indicate that the number of sub-adult, adult and total number shows an increasng trend. Small values of slope coefficients indicate that the rate of increase is very small. $R^2$ for the fitted equations were 0.604, 0.819, 0.753, 0.801 and 0.825 for number of seedlings, juveniles, sub-adults, adults and total number of individuals respectively.

Table 26. Regression functions fitted to number of plants in *Calamus vattayila*

| Status | Regression function | $R^2$ |
|---|---|---|
| Seedling | No trend | |
| Juvenile | $Y = 2.653 + 0.256\ X$ | 0.934 |
| Sub-adult | No trend | |
| Adult | No trend | |
| Total | $Y = 17.284 + 0.260\ X$ | 0.415 |

In the case of *C. vattayila* no trend was observed for number of seedlings, sub-adult and adult. But number of juveniles and total number of individuals showed an increasing trend. $R^2$ prediction for fitted equation for juvenile number is 0.934. Which indicate that about 93% of variation in number of individual is explained by the change in period of time. $R^2$ for the fitted equation for total number is relatively low (0.415). Only 41.5% is explained by change in period of time. 58.5% of the variation is kept as unexplained.

In the case of *C. delessertianus*, no trend was observed in the number of seedling, sub-adult and total number of individual. Number of individuals in juvenile and adult shows a positive trend. Rate of increase is relatively very high in number of juveniles (5.713) than number of adult (0.0711). $R^2$ for number of juvenile is 0.973 and that for the number of adult is 0.625.

Table 27. Regression functions fitted to number of plants in *Calamus delessertianus*

| Status | Regression function | $R^2$ |
|---|---|---|
| Seedling | No trend | |
| Juvenile | Y = 21.723 + 5.713 X | 0.973 |
| Sub-adult | No trend | |
| Adult | Y = 3.056 + 0.0711 X | 0.625 |
| Total | No trend | |

## Population flux

### *Calamus thwaitesii*

Total number of plants in the initial observation on *C. thwaitesii* showed 381 plants which increased into 385 at the end of first year. In the second year this species showed 394 individuals and in the third year, 582. In the first year new arrival was 118 and its total mortality was 114. It almost balanced the population with the least rate of increase, 1.01. In the second year new arrival was 93 and the mortality was 84, so the rate of increase was1.02. In the third year rate of increase was 1.48. It shows a stable rate of population increase from year to year. Percentage of annual death decreased from first year to third year. Percentage of new recruitment decreased in second year and increased in third year (Table 28).

Table 28. Population flux of *Calamus thwaitesii.*

| | First year | Second year | Third year |
|---|---|---|---|
| No. of plants in the initial observation (a) | 381 | 385 | 394 |
| No. of plants in the final observation (b) | 385 | 394 | 582 |
| Net change (c=b-a) | 4 | 9 | 188 |
| Rae of increase (d) | 1.01 | 1.02 | 1.48 |
| Total new arrivals (e) | 118 | 93 | 235 |
| Total mortality (f) | 114 | 84 | 47 |
| Total plants recorded (g) | 499 | 478 | 629 |
| Percentage annual death ( $h = \frac{f}{g} \times 100$ ) | 22.85 | 17.57 | 7.47 |
| Percentage annual recruitment ( $(i = \frac{e}{g} \times 100)$ | 23.65 | 19.46 | 37.36 |

***Calamus hookerianus***

The total number in the initial observation of *C. hookerianus* showed 171 plants which increased to 211 at the end of the first year. In the second year, there were 215 individuals and in the third year it became 251. In the first year new arrivals were 52 and the total death was 12. Hence the rate of increase was 1.23. In the second year new arrivals were 43 and the mortality was 39, so the rate of increase was, 1.02. In the third year the rate of increase was 1.17. Hence there was a stable rate of population increase from year to year. The recruitment rate decreased in the second and third years when compared to the first year. But from second to third year the rate of recruitment increased slightely. The percentage of annual death was very high in the second year (15.35) when compared to first and third years (Table 29.)

Table 29. Population flux of *Calamus hookerianus*

| | First year | Second year | Third year |
|---|---|---|---|
| No. of plants in the initial observation (a) | 171 | 211 | 215 |
| No. of plants in the final observation (b) | 211 | 215 | 251 |
| Net change (c=b-a) | 40 | 4 | 36 |
| Rae of increase (d) | 1.23 | 1.02 | 1.17 |
| Total new arrivals (e) | 52 | 43 | 55 |
| Total mortality (f) | 12 | 39 | 19 |
| Total plants recorded (g) | 223 | 254 | 270 |
| Percentage annual death ( $h = \frac{f}{g} \times 100$ ) | 5.38 | 15.35 | 7.04 |
| Percentage annual recruitment ( $(i = \frac{e}{g} \times 100)$ | 23.32 | 16.93 | 20.37 |

***Calamus vattayila***

In the initial observation of *C. vattayila*, there were 14 plants which increased to 24 at the end of the first year. In the second year there were 30 individuals and in the third year it decreased to 20. In the first year, new arrivals were 11 and total death was 1. The rate of increase was 1.71. In the second year new arrivals were 11 and the mortality was 5. So the rate of increment was 1.25. In the third year rate of increase was 0.67. The rate of increase was going down from first year to second year and became unstable in third year. Percentage of annual death increased from first year to third year. In the third year it reached a very high value 33.33. Moreover the percentage of recruitment decreased from 44 to 0 during the three-year duration. As the annual death increases drastically and annual recruitment decreases from year to year growth of population of *C. vattayila* is getting decreased (Table 30).

Table 30. Population flux of *Calamus vattayila*

| | First year | Second year | Third year |
|---|---|---|---|
| No. of plants in the initial observation (a) | 14 | 24 | 30 |
| No. of plants in the final observation (b) | 24 | 30 | 20 |
| Net change (c=b-a) | 10 | 6 | -10 |
| Rae of increase (d) | 1.71 | 1.25 | 0.67 |
| Total new arrivals (e) | 11 | 11 | 0 |
| Total mortality (f) | 1 | 5 | 10 |
| Total plants recorded (g) | 25 | 35 | 30 |
| Percentage annual death ( $h = \frac{f}{g} \times 100$ ) | 4.00 | 14.29 | 33.33 |
| Percentage annual recruitment ( $(i = \frac{e}{g} \times 100)$ | 44.00 | 31.43 | 0.00 |

***Calamus delessertianus***

Total number of plants in the initial observation of *C. delessertianus* was 187. This increased to 404 at the end of first year. In the second year it decreased into 369 and in the third year it again decreased to 335. In the first year, new arrivals were 275 and the mortality was 58. The rate of increase was 2.16. In the second year, new arrivals were 74 and the mortality was 109.

Table 31. Population flux of *Calamus delessertianus*

| | First year | Second year | Third year |
|---|---|---|---|
| No. of plants in the initial observation (a) | 187 | 404 | 369 |
| No. of plants in the final observation (b) | 404 | 369 | 335 |
| Net change (c=b-a) | 217 | -35 | -34 |
| Rae of increase (d) | 2.16 | 0.91 | 0.91 |
| Total new arrivals (e) | 275 | 74 | 38 |
| Total mortality (f) | 58 | 109 | 72 |
| Total plants recorded (g) | 462 | 478 | 407 |
| Percentage annual death ($h = \frac{f}{g} \times 100$) | 12.55 | 22.80 | 17.69 |
| Percentage annual recruitment ($((i = \frac{e}{g} \times 100)$) | 59.52 | 15.48 | 9.34 |

So the rate of increase became less than one (0.91). In the third year, also the rate of increase was 0.91. Percentage of death was greater in second and third year than the first year. Moreover recruitment percentage decreased from 59.52 to 9.34 during the three years of study. So in this case also the population growth is decreasing (Table 31).

# DISCUSSION

# DISCUSSION

## Stage duration

Four species were selected from the Western Ghats region for the study. Of these two species, *C. thwaitesii* and *C. hookerianus*, were seen together in a moist deciduous forest and other two, *C. delessertianus* and *C. vattayila* were growing in an evergreen forest area. Even though, all the biotic and abiotic conditions affecting the populatios were same, the species growing in the same area were responding differently. *C. thwaitesii* was growing faster than *C. hookerianus* and *C. delessertianus* was growing faster than *C. vattayila*.

A species, in its different life stages shows different affinity towards the light (Siebert, 1993). In a single environmental condition two species behaved differently which indicates that fast growing species (*C. thwaitesii*) is totally adapted to this environmental condition. *C. thwaitesii* is very much adapted to moist deciduous forest with open canopy. But *C. hookerainus* is not that much adapted to the conditions of moist deciduous forest. Similarly *C. delessertianus* is more adapted to the environmental condition in which it grows when compared to *C. vattayila*. In the seedling stage *C. hookerianus* is very slow growing when compared to *C. thwaitesii*. In all other life stages also the stage duration is longer for *C. hookerianus*.

*C. vattayila* has longer stage durations in all the life stages except adult stage when compared to *C. delessertianus.* The basal diameter of *C. vattayila* is only 1.5 cm and the basal internodal length is 2.5 cm. In *C. delessertianus* the diameter is 9 - 12 cm and the internodal length is 4.5 cm. Similarly *C. thwaitesii* is a larger diameter cane when compared to *C. hookerianus.* Generally large diameter rattans grow slower when compared to small diameter rattans (Kiew, 1972). In this study, this growth rate does not agree with this observation.

In *C. vattayila* reversal of juvenile to seedling is very high. It has no effect on transition but more influence on stage duration. A similar observation is reported in Malassian rattans (Bøgh, 1995). Low light penetration from the closed canopy is preferred by *C. delessertianus* but it inversely affects the juvenile stage growth rate of *C. vattayila.* Reversal of juvenile to seedling is very little in the case of *C.delessertianus.* Short inter nodes at the base is the indicator of deficiency of light.

Very predominant sub-adult stage duration is exhibited by *C. vattayila.* All the other three species show shorter sub-adult stage duration. *C. vattayila* takes a very long time to reach the reproductive stage.

Very long adult stage duration is exhibited by *C.hookerainus* when compared to *C. thwaitesii.* In *C. hookerianus,* vegetative fecundity exhibited is much greater than that of *C. thwaitesii.* So the competition among the individual is very high, which inversely affects the growth rate.

The sum of the stage durations are estimates of the longevities of the plant. Hence *C. vattayila* is having the longest life duration followed by *C. hookerianus* and *C. delessertianus*. *C. thwaitesii* is having the shortest life duration.

### Yearly production of stem

In *C.vattayila* and *C. delessertianus,* the number of individuals is limited due to solitary nature of stem. The low annual stem production is due to the low number of individuals and long developmental period. Because of the clustered nature *C. thwaitesii* and *C. hookerianus* can produce large amount of individual plants, most successfully.

### Population matrix

Matrix population models have become standard tools for the study of life history and population dynamics of age or stage structured populations (Caswell, 1989, 2001; Slade, 1990; Tuljapurkar and Caswell, 1997; van Tienderen, 2000).

The $\lambda$ is an estimator of the population growth rate. Population size is constant when $\lambda$ equals one, increase when $\lambda$ is greater than one and declines when it is less than one.

In this study $\lambda$ value is greater than one for *C. thwaitesii* (1.01), *C. hookerianus* (1.05) and *C.delessertianus* (1.21) which denotes that the population size is increasing. But in *C. vattayila* the $\lambda$ value is less than one (0.94), which shows that the population is decreasing. Enright and Watson

(1992), Pinard (1993), Piñero *et al.* (1984) and Bøgh (1995) reported increasing populations for four palm species. A population of *Iriartea deltoidea* studied by Svenning and Balslev (1999) was reported to be decreasing. A similar result is reported here in the case of *C. vattayila* (0.94).

The longevity of the sub-adult stage of the *C. vattayila* and *C. delessertianus* resulted in few adult plants. *C. delessertianus* shows very high value of sexual fecundity other than the other three species.

Short transition period of seedling to juvenile and comparatively long stage duration of juveniles become the selective forces behind the most predominant life period (juvenile). Clustering species show above 50 per cent recruitment of adult from sub-adult, where as, in solitary species it is less than 50 per cent.

In population studies, a decrease in adult survival rate is considered as detrimental to population growth. Life history strategies are inexorably linked to vital rates (Heppel *et al.* 2000). In *C. vattayila,* there is a decrease in adult population. Hence this species can be considered as threatened.

Stearns (1976), states that environmental conditions are a major factor in shaping the life history of a species in the field but the conditions are usually not taken into account in the models. The finite rate of population $\lambda$ is 1.21 for *C. delessertianus*, which shows that it is the most successful species to its habitat. But its co-existing species *C. vattayila* shows decline in population rates (0.93). This difference in performance of different species in the same habitat can be explained on the basis of tolerance to environmental factors.

*C. thwaitesii* grow faster than *C. hookerianus* which has shorter life stage duration. The growth rate is controlled by characters like clustering growth habit, vegetative reproduction capabilities, light availability, the photosynthetic efficiency of a plant etc.

Commonly the seedling is the most vulnerable vegetative stage (Harper, 1977). In general, *Calamus* seedlings show low light preferences. In the evergreen forests, there is a low mortality rate when compared to that in moist deciduous forests. Adult stage of these species demand more light and hence the adult stage recruitment is very high in moist deciduous forests and very low in evergreen forests.

Because of the integrated nature of $\lambda$, the internal mechanism with in the species is more or less obscure (Werner and Caswell, 1977). To avoid such a defect in $\lambda$, in this work the population dynamics and flux of these species also were analysed.

**Elasticity**

Elasticity analysis is a useful tool in conservation biology. Elasticity analysis can be a quantitative guide for research and management particularly for poor known species and a useful first step in a larger modeling effort to determine population viability. An elasticity pattern is composed of the relative contribution of matrix entries to population growth that are grouped biologically meaningful ways for comparative analysis (Silvertown *et al.*, 1993, 1996).

When P values were analyzed for the four species, it was observed that the adult and sub-adult stages were commonly critical in changing the $\lambda$ value in three species except in *C. vattayila*. In *C. vattayila* juvenile and adult stages influence the $\lambda$ value. In a stable population, the growth rate increase mainly depends on the adult surviving probability. But in the case of declining population the juvenile stage is more important and critical than the other life stages. Population growth rate does change in response to changes in the survival of juveniles regardless of time of reproduction (Oli and Zinner, 2001). One per cent change in the juvenile stage of *C. vattayila* makes a change of 0.453 in the $\lambda$ value. Hence in the of conservation programmes for *C. vattayila* the juvenile stage is more important. But in the case of other three species adult and sub-adult stages are more important.

High $P_2$ value indicates the unstable population. *C. delessertianus* is having a stable population growth due to high selection pressure.

In the present study, the survival probability is the most important parameter in determining the population growth rate (Figures 5 - 8). Although the largest values in the transition matrices (Tables 12 - 15) are the sexual fecundities, they have very little influence on finite rate of population increase. But the high elasticity of vegetative fecundity values of *C. hookerianus* has much influence on population growth rate. This result indicates that genet level study of *Calamus* demography support the view that vegetative reproduction is part of an integral growth process that enhances genet fitness and reproductive value. (Caswell, 1985; Cook, 1985).

### $\chi^2$ Test

The result indicated (Table 19) that most of the cases the assumption was violated except *C. vattayila.* In the case of *C. vattayila* $\chi^2$ test results agree the assumption was correct. It was due to decreased number of individuals in each stage. In reality the growth and survival rates vary. As pointed out by Van Valen (1975), it seems likely that the mortality is highest among the slowest growing individuals. If this is true, the average growth rates underestimate the growth rates of surviving individuals. Thus, the $G_i$ values may be underestimated, especially in the seedling stage where the mortality is highest. However, the elasticity analyses indicate that the effects on the population growth rates of changes in $G_i$ are relatively small. Without knowledge of the actual within stage distributions the overall effects of such violations of the assumption on the population growth rate is unknown.

### Population dynamics

#### ***Calamus thwaitesii* and *C. hookerianus***

*C. thwaitesii* produces a large number of seedlings. There is a gradual decrease in number of individuals in each stage from seedling to adult which indicates that the selection pressure on that population is normal and this is the normal life cycle pattern of a population with a regular transition from seedling to adult (Table 11). This is a cluster forming species and male plants are closely clustered than female plants.

In *C. hookerianus* seedling number is lower than juveniles. The ramet (sucker) production contributes to the juvenile population, hence the increase in number. The increasing shoot density lead to increased competition between shoots and a good number of shoots die when surviving shoots grow faster (Sarukhan and Harper, 1973; Harper, 1977; Noble *et al.,*1979; Bartlett and Noble, 1985; Dickerman and Wetzel, 1985; Cain, 1990). Clustering is more compact in *C. hookerianus* than in *C. thwaitesii*. So there will be more competition for food among the new shoots in *C. hookerianus.*

***Calamus vattayila* and *C. delessertianus***

There were only very limited number of adult plants for both *C. vattayila* and *C. delessertianus*. This resulted in low recruitment rates.

In C. *vattayila,* the duration of juvenile and sub-adult stages were longer. This may be due to the inadequacy of light. In C. *delessertianus* also seedling production is not a continuous process because of the limited number of adult plants. In *C. vattayila,* large number of fruits is pre maturely eaten by small mammals and birds. These fruits may not germinate at all. Single stemmed nature is a limiting condition in both these species, because once the growing apical meristem is damaged, that plant will die.

**Birth and death rates**

The balancing of birth rate and death rate determines increase and decrease of population. All the stages of *C. thwaitesii* show a positive trend towards growth due to the balancing of mortality by new recruitment and transition. In *C. hookerianus* low rate of new recruitment from seeds affected the transition rate to sub-adult and adult stages. High vegetative fecundity rates compensate the low sexual reproduction values and round up the increments in individual's number from juvenile onwards (Figures 11 - 15).

Fully adapted species in a perticular habitat exhibit maximum birth rate and minimum death rate. Any change in the ratio of birth/death would result in vanishing of the population. Among the four species studied *C. thwaitesii* from moist deciduous habitat and *C. delessertianus* from evergreen habitat shows maximum birth rate. So these two species are very much adapted to their habitats.

In *C. vattayila* the death rate is greater when compared to other three species. Moreover, the number of adults also is very limited. This may be due to the fact that this species is not well adapted to the present habitat.

**Seasonal variations in recruitment and death rates**

There are no obvious seasonal variations in the recruitment and death of the species studied. Slow growth and delayed germination are common in family Arecaceae. Due to this, the four studied species show high birth rate during September to January. Besides these months other observational months also showed new birth due to extended fruiting period and delayed germination. Moreover failure of fruiting or intermittent sexual fecundity made the seasonal birth recruitment vague. In general, *C. vattayila* and *C.*

*delessertianus*, the maximum number of seedlings appeared in January, and in the other two species, in September and January (Table 4 - 7). The mortality rates also were higher during September and January, for all the species. Seedling mortality is directly proportional to number of seedlings produced. In the case of *C. thwaitesii* and *C. delessertianus,* the high rate of seedling mortality is due to the bulk seedling production and resulting competition among them for survival. Poorly rooted exhausted seedlings easily become dead. Topography, soil erosion and leaf litter multiplies the number of death. Open canopy and draught are identified as death factor in moist deciduous forest. These factors accelerate death rate along with biotic factors.

In the case of evergreen species, excess moisture content made the fungus attack to seedling during rainy season. Draught also played a minor role in death. In the case of *C. vattayila*, the height of seedling is also become a death factor. In this species transition from seedling to adult through juvenile and sub-adult is very slow due to very long developmental period, especially in the sub-adult stage. So the adult individual's number is reduced to threatened population range. In all four studied species, death and its factors varied with varying observation. So the seasonal variation in the death rate also became vague (Figure 14).

### Regression

The increasing trend was observed in most of the cases. This is only with increased transition rates but also with decreased mortality rate. High recruitment value and lower mortality rate gives an increasing trend in the total numbers of individual. It determines the species fitness. Increased $R^2$ value indicates the highly fittest condition of species. Juvenile and sub-adult stages of *C. thwaitesii* are the fittest than adult stage. Juvenile and adult stages are fittest than seedling stage in *C. hookerianus*. Juvenile stage of *C. vattayila* and *C. delessertianus* is the fittest than other three stages of each species (Table 24 - 27).

Trend showing stages indicate the dominance of transition than death rates. Generally seedlings show trend in the case of regularly annual flowering plants. But intermittent flowering of low numbered adult plants of evergreen species shows no trend in seedlings. Stable population growth rate can produce trend in number of individuals along the duration. Number of adult plants is much greater in, *C. thwaitesii* and *C. hookerianus,* so the intermittent flowering will not affect the seedling trend in these species.

### Population flux.

#### ***Calamus thwaitesii***

In *C. thwaitesii*, the rate of increase in population was more than one through out the three year duration. It is a stable population value. This shows that the population is very much adapted to micro climate of the habitat (Table 28). Annual death rate decreased from first year to third year. Annual recruitment decreased in second year and showed maximum in third year.

Both population matrix and population flux show a stable population increase in *C. thwaitesii.*

### *Calamus hookerianus*

Here the rate of increase in population is slightly greater than one and is a stable population growth rate. Annual death rate of this species is lowest in first year, maximum in second year and medium in third year. Both *C. hookerianus* and *C. thwaitesii* show minimum annual recruitment in second year. Annual recruitment rate is maximum in first year and medium in third year (Table 29). This species also shows stable population increase in matrix and population flux.

### *Calamus vattayila*

In *C. vattayila* the rate of increase in population is more than one in first two years but less than one in third year. Annual death rate increased during the study period, and annual recruitment decreased (Table 30). Growth rates of population matrix and population flux show a population decrease during the study period. This condition, if continued in future with out any management programme, will lead to population collapse and the species will become extinct in the near future.

### *Calamus delessertianus*

There is also a gradual increase in annual recruitment rate of population from first year to second year (Table 31). Rate of increase in population is more than two in first year and lower than one in second and third years. This species also show a tendency to unstable population but the $\lambda$ value of this species is greater than one (1.2) which denotes that the population size is increasing. In matrix study of *C. delessertianus* the population growth rate is much more robust when compared to other three species. Even though large amount of individuals are present in juveniles and seedlings, its benefits are not seen in sub-adult stage due to low selection pressure.

**Demographic factors affecting the population**

It includes biotic and abiotic factors. Abiotic factors include slop of the terrain and drought condition. Drought condition mainly affects the moist deciduous forest. Slop of the terrain affects both evergreen and moist deciduous forests. The seedling populations of all the four species are affected by this factor. The seedlings, standing on the slop will be washed away during heavy rain. Heavy drought adversely affects the seedling population of *C. thwaitesii* and *C. hookerianus.*

Biotic factors affecting the population include man, animals, insect and micro-organisms. In case of *C. delessertianus,* it is noted that a large number of seedlings appear in a small area. This type of population is easily affected with fungal attack (Mohanan, 1994). Root rot was noticed in this species during this study.

An insect which attack the shoot tip of *Calamus* species was noticed in the field (Varma *et al.*, 2003). This type of attack which destroys the growing meristem of the stem affects the population size negatively. Wild animals like deer, rodents etc. eat the leaves of the seedlings and juveniles thus destroying the plants causing a decrease in population size. Large mammals like elephants stamp over the seedlings, killing them. Human beings cut and remove the stem without any scientific management and this drastically reduces the adult population.

**Conservation strategies**

Quantitative analysis of extinction risk is one of the criteria for risk categorization (IUCN - 1997). Most species are classified by population size, as well as by observed rates of decline of habitat (IUCN - 1996). Matrix and elasticity analysis are very useful in resource management planning.

In the four species of *Calamus* studied, *C. vattayila* and *C. delessertianus* of evergreen forest are really threatened due to inability of clustering (solitary) nature. Conservation and utilization of *Calamus* species is gaining importance in the current context when forest wealth of the state as a whole has been on decline. In the absence of concrete efforts towards their replenishment, all the four *Calamus* species studied; are likely to face the threat of extinction in the near future.

The hidden internal factors of decreased adult transition rate in *C. vattayila* and *C. delessertians* are more deleterious. Due to their solitary stem and their decreased adult population these *Calamus* species need to be protected very carefully. The $\lambda$ value of *C. vattayila* indicates its declining population rate. If this trend is allowed to continue without any conservation strategies, the species will face extinction in the near future.

From the study of the current status of the selected species, it is noted that the most vulnerable species is *C. vattayila.* Hence drastic conservation measures should be taken for this species. The stem is most vulnerable to any kind of damage. Discontinuous seedling production, low seed germination and large stage duration of juvenile stage are also the reasons for the declined population. The elasticity values indicates the most important protective stage of this population is juvenile. In the juvenile stage competition from under growth species and herbivory are probably important causes of death. A reduction of these factors would also cause increased growth rates of juveniles. The conservation strategy has to be developed considering all these aspects. At the same time over exploitation and habitat destruction is very harmful to these species. Heavy shading by shrubs and high levels of competition by herbaceous dicots are probably responsible for the low growth rates of this species. This species shows increased developmental period which give greater chance to death.

Population studies of *C. delessertianus* indicate that the population rate is unstable. It is mainly due to the low adult population. Seedling death due to fungal attack and animal disturbances also decreases the population growth. The elasticity study of this species indicates the adult stage is more critical than the other three stages.

Juvenile nursery practices and augment plantation should focus on threatened species. Harvesting should be prevented and repeated plantation should arise for threatened species. The efficiency of juvenile stage in plantations can be significantly improved by regular clearing of competing under growth.

In the case of *C. thwaitesii* and *C. hookerianus* death is common in four stages of these species. Draught and human interference are two major factors controlling population growth. In this study their population growth is stable in nature when the demographic factors remain constant. In *C. hookerianus* the competition among the suckers leads to more developmental period for this species. The elasticity studies showed that sub-adult stage of *C. thwaitesii* and adult stage of *C. hookerianus* are more important for conservation.

In all the four *Calamus* species studied, human activity and grazing contributed to the high mortality rate of the seedling. The control of the above two factors will promote stability of populations. To promote seed germination capacity, raise large seedling collection with improved nursery techniques. Tissue culture techniques can also be employed to produce enough number of seedlings in the case of threatened species (*C. vattayila*).

In *Calamus* species the life span of individuals is very long and the mortality is very high in the initial stages. New recruitment is seasonal. So the protection of young seedlings will help for stable growth rate.

Climatic factors have more influence in *Calamus* species. The light availability will influence the photosynthetic and reproductive efficiency. Canopy manipulation will help to maintain proper growth rate in plantations.

Other than *in situ* conservation methods like augment plantation, *ex situ* methods also should be initiated. Raising plantations is the best *ex situ* conservation method for these species.

# SUMMARY

# SUMMARY

Demography is the study of population changes and their causes throughout the life cycle. During the past three decades, the exploitation of rattans from the Western Ghats was very extensive resulting in the disappearance of rattans from all the accessible areas. Large scale destruction and fragmentation of the forest have further aggrevated the situation. In Kerala part of Western Ghats, rattans are restricted mostly to remote areas in the forests and some species are on the verge of extinction. Hence conservation measures have to be initiated urgently to protect this valuable natural resource.

Demographic and population ecological studies will help to analyse the changes that is taking place with in a population and to understand their regulating mechanisms. This understanding will lead to formulation of the management criteria for the species under study. Four commercially important species were selected for the present study, *viz*, *C. thwaitesii, C. hookerianus, C. vattayila and C. delessetianus.*

The main objectives were:

a) To study the population structure and the changes taking place in it over a period of time and

b) To develop conservation strategies for the species selected.

The study plots were selected in the natural forest areas in the Western Ghats at Athirapilly under Vazhachal Forest Division in Central Circle (Thrissur district) and at Nelliyampathy under Nemmara Forest Division in Olavakkode Circle (Palakkad district). Two rattan species, *C. thwaitesii* and *C.delessertianus* were common at Athirappilly forest areas with moist deciduous forests. At Nelliampathy, *C.vattayila* and *C.delessertianus* were common. The forest type was evergreen.

The number of individuals coming under different life stages namely seedling, juveniles, sub-adults and adults were taken periodically at four months interval for three years. The height, girth, number of individuals in each clump, production of new leaves, suckers etc were noted. Average internodal lengths of each species also were measured.

For each of the life stage, yearly transition probabilities $G_{i,}$ yearly probabilities of surviving in the same stage, $P_{i,}$ average yearly fecundities, $F_{ij}$ were calculated. These parameters were used to construct transition matrices and from these matrices, the finite rate of population increase $\lambda$ were calculated as the dominant eigen values and the stage distributions 'w', were given by the corresponding right eigen vectors. The elasticity values for the matrix coefficients were also calculated.

In order to study the population dynamics, recruitment and death rates were found out and population flux was calculated. Of the two species selected from a single forest type, even though the environmental conditions were the same, one species registered faster growth. *C. thwaitesii* from moist deciduous forest and *C.delessertianus* from evergreen forest were growing faster when compared to *C. hookerianus* and *C. vattayila* respectively. *C.thwaitesii* and *C.delessertianus* are large diameter rattans, and actually they need more time for elongation than the medium diameter rattans. But the shorter stage durations for *C. thwaitesii* and *C.delessertianus* shows that these two species are well adapted to the environment in which they grow. *C. vattayila* show short internodes at the basal region and this suggests a deficiency of light. In this species, a reversal of juvenile to seedling is very high which has no effect on transition but more influence on stage duration. The sub adult stage duration is very long here. *C.delessertianus* shows very high value of sexual fecundity when compared to other species.

*C. vattayila* is having the longest life duration followed by *C. hookerianus* and *C.delessertianus. C. thwaitesii* is having the shortest life duration.

In the matrix models, $\lambda$ is the dominant eigen value, which indicates population growth rate. All the selected species except *C. vattayila* show a tendency towards increase in growth rate. The $\lambda$ value of *C. vattayila* is less than one (0.94) which indicates a decline in population. In population studies, a decrease in adult survival rate is detrimental to population growth. In *C. vattayila,* there is a decrease in adult population. Hence this species can be considered as threatened.

The $\lambda$ value is 1.21 for *C. delessertianus* which shows that it is the most successful species in its habitat.

Seedling mortality rate is high among the species seen in the moist deciduous forests when compared to the species in the evergreen forests. This shows that the seedling is shade demanders. The rate of adult recruitment is very high among the species seen in moist deciduous forests which shows that adult plants are light demanders.

When yearly probabilities of surviving and remaining in the same state (P values) were analysed for the four species studied, it was seen that the adult and the sub-adult stages were commonly critical in changing the finite rate of the population increase in the three species except *C. vattayila*. In *C. vattayila,* juvenile and adult stages influence the value.

Although sexual fecundity values of all species are higher, they have very little influence on finite rate of population increase. But the high elasticity of vegetative fecundity values of *C. hookerianus* has much influence on its population growth.

*C. thwaitesii* shows a normal life cycle pattern with regular transition from seedlings to adults. In *C.hookerianus* juveniles are the major population. Other than seedlings, suckers also contribute to juvenile population. But increased shoot density in a clump leads to competition which results in the death of a number of shoots reducing the number of sub-adults.

In case of *C. vattayila* and *C.delessertianus,* there were only limited number of adult plants which resulted in low recruitment rates. In *C. vattayila,* immature fruits are eaten by small mammals and birds. Single stemmed nature of these two species also is detrimental to the population.

The balancing of birth and death rate determines the size of the population. *C. thwaitesii* and *C. delessertianus* show maximum birth rate, but in *C. vattayila* the death rate is greater. There is no obvious seasonal variation in the recruitment and death of the species studied.

The regression reveals that in *C. thwaitesii* juvenile and sub-adult stages are more fitted for lineartrend among life stages in the population where as it is the juveniles and adult stages in *C. hookerianus*. In *C. vattayila* and *C. delessertianus* number of juveniles shows a linear trend.

In *C. thwaitesii,* the rate of increase in population is more than one which is an indication of the stable nature of the population. This shows that the population is very much adapted to its habitat.

In *C. hookerianus,* also the rate of increase in population is slightly greater than one indicating a stable population.

In *C. vattayila,* the rate of increase in population was less than one towards the end of the study period. This condition, if continued without any management programme, will lead to the population collapse and the species will become extinct in the near future.

*C. delessertianus* also shows a tendency to unstable population. But the population growth rate $\lambda$ greater than one (1.2) in this species which shows that the population is actually increasing.

Both biotic and abiotic factors influence the population growth. The major abiotic factors are man, animals including insects and micro organisms.

In the present study, *C. vattayila* shows a declining population rate and very low survival probability. Hence drastic conservation measures should be taken for this species. In *in situ* conservation the juvenile stage of this species should be protected. Raising plantations is the best *ex situ* conservation method for this species. Since availability of mature seeds is a problem here, tissue culture techniques can be made use of to produce sufficient number of seedlings.

*C. delessertianus* also requires conservation strategies. Here the adult stage is to be protected. Since this is large diameter rattan this is extracted heavily. Here also *ex situ* conservation is a must.

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