HUMAN USE, REPRODUCTIVE ECOLOGY, AND LIFE HISTORY OF
GARCINIA GUMMI-GATTA, A NON TIMBER FOREST PRODUCT,
IN THE WESTERN GHATS, INDIA

A Thesis in
Biology
by
Nitin Devdas Rai

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The thesis of Nitin Devdas Rai has been reviewed and approved* by the following:

Christopher F. Uhl
Professor of Biology
Thesis Adviser

Andrew G. Stephenson
Professor of Biology

James H. Marden
Associate Professor of Biology

Stephen M. Smith
Professor of Agricultural Economics

Douglas R. Cavener
Professor of Biology
Head of the Department of Biology

*Signatures are on file in the graduate school
ABSTRACT

The harvest and sale of Non timber forest products (NTFP) by local communities has been suggested as a possible solution to the often observed conflict between forest use and forest conservation, due to the lower impact of NTFP harvest as compared to timber harvest. Recent studies have however suggested that the economic rewards might not be constant, and that ecological effects of harvest might be higher than previously believed. In India, the trade in NTFPs has a long history but few studies have explored both the ecological and socio-economic aspects of harvest. I report here, the results of a socio-economic and ecological study on the harvest of fruits from a rain-forest tree, *Garcinia gummi-gatta*, which occurs in the tropical forests of the Western Ghats. I studied the characteristics of *G. gummi-gatta* fruit harvest, socio-economic factors that influence harvest, and the ecological effect of fruit harvest.

The socio-economic study revealed that 1) Brahmin households had significantly higher income than non-Brahmin households and high income households harvested significantly more *G. gummi-gatta* rind than low income households, 2) the harvest of *G. gummi-gatta* fruits varied with forest tenure: harvest of unripe fruits and associated damage to trees in the ‘open access’ forest, and ripe fruit harvest in private forests, 3) *G. gummi-gatta* seedling density is higher in private forest than in ‘open access’ forest suggesting that security of tenure might result in stable populations of *G. gummi-gatta*, 4) a sharp fall in the price of *G. gummi-gatta* rind, due to market instability, resulted in a large decrease in the income of harvester households. My findings thus suggest that dependence on NTFP harvest by local communities might be problematic due to market
instability, patchy resource distribution, inequitable access to forest resources within the village, and the lack of security of tenure.

The genus *Garcinia*, which is well represented in the Asian flora, is dioecious, and some species are apomictic. I studied the occurrence of apomixy, the mode of pollination, flowering phenology, flower production, and fruit set in a *G. gummi-gatta* population. *G. gummi-gatta* is dioecious and both male and female trees flower in the dry season. I found some evidence of facultative apomixy, possibly due to isolated trees occurring far from pollen pools. Female flowers offer no floral reward and are pollinated by ‘mistake’ by weevils of the genus *Deleromus*. I suggest that the correspondence between pollination by small insects and the occurrence of fleshy fruits in dioecious species is due to the trade off between the cost of elaborate floral displays and benefit accrued from increased gene flow due to seed dispersal by animals.

In order to understand the life history of *G. gummi-gatta*, I studied fruit production, seed dispersal, seed predation, seedling growth, seedling survival, spatial distribution of seedlings, juveniles, and adults, and adult tree growth. I found low inter-annual variability in fruit production at the population level. The degree of participation of individual trees in fruit production however varies from year to year. There is a significant positive relationship between tree size and fruit production. However, trees in the largest size class show decreased fruit production. In the study area, seeds of *G. gummi-gatta* are dispersed by two species of primates and endozoochorously by two species of civets. The average post dispersal seed predation was 86% at the end of 10 months. Seeds dispersed into sites far from parent trees showed significantly higher survival than seeds dispersed near adult trees. Seedlings in high density patches and near
adult trees showed a higher probability of mortality than seedlings in low density patches and far from adult trees. The spatial distribution of *G. gummi-gatta* saplings and adult female trees shows that significantly fewer than expected saplings occur between 5 and 12m of an adult tree suggesting greater probability of seedling establishment with increasing distance from adult trees.

Seedlings in canopy gaps showed significantly higher growth than seedlings in shade. Canopy cover however did not significantly affect seedling mortality. Larger trees whose crowns were in the canopy showed higher growth rates than smaller trees whose crowns were located below the canopy, suggesting that tree growth is influenced by light. I found no difference in *G. gummi-gatta* seedling density between high intensity and low intensity harvest sites suggesting that harvest of *G. gummi-gatta* fruits might have no affect on seedling recruitment.

The analysis of population growth using a stage structured matrix model showed that the rate of *G. gummi-gatta* population growth was stable over the two year study period. A simulation of the effects of seed removal on population growth rate resulted in $\lambda$ decreasing in small increments up to 90% seed removal, while greater than 90% seed removal resulted in a larger decrease in $\lambda$. High rates of adult tree mortality were observed in open access areas due to damage during fruit harvest. Simulation of population growth rate using these estimates of adult tree mortality showed a large decrease in $\lambda$. Population growth is more sensitive to adult tree mortality than fruit harvest. My results agree with other studies on rain forest tree species that have shown that population growth is not sensitive to seed removal. My findings suggest that due to stable fruit production, seed dispersal by animals, persistence of seedlings in shade, and
adequate seedling recruitment under high fruit harvest, fruits of *G. gummi-gatta* might be harvested with few adverse demographic effects.

Overall my study indicates that the ecological effects of fruit harvest are strongly influenced by the prevalent socio-economic conditions. The paradigm of ‘good extractivism’ that has fuelled much of the interest in NTFPs therefore needs to be re-evaluated in the light of increasing evidence that a complex interplay of factors, such as forest access, intra-community social dynamics, and fluctuating markets influence the ecology and use of NTFPs.
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CHAPTER 1

INTRODUCTION
Driven by the question of how forest biomass extraction by local farmers affects forest productivity, I visited the heavily forested district of Uttara Kannada for the first time in 1997. During preliminary fieldwork I found it increasingly difficult to recruit local people to assist me in establishing vegetation sampling plots. It was not long before I determined the reason; the harvesting of the fruits of the locally abundant forest tree, *Garcinia gummi-gatta*, was consuming the efforts of most villagers. The dried rind of the fruit was being sold for a price high enough to make my wage offer unattractive. My interest in studying the effect of biomass extraction was largely due to my desire to help find solutions to the long standing conflict between the state, which owns most forest land, and forest dwellers, who depend on the forest for various wood and non-wood products. While local people have demanded more rights of access to forests, the state continues to deny them these rights. I was therefore attracted by the increasing economic importance of *G. gummi-gatta* fruit harvest, and its possible role in reducing the conflict between forest use and conservation.

I studied the characteristics of *G. gummi-gatta* fruit harvest, the socio-economic landscape of the village, and the effect of *G. gummi-gatta* fruit harvest on the ecology of the species. Most studies on the effect of Non timber forest products (NTFP) extraction in India have been conducted in the dry forest (Murali et al. 1996, Sinha 2000) where, due to the lower diversity of species, abundance of the target species is often higher and economic rewards therefore greater than from NTFP harvest in wet forest (Narendran et al. 2001).
NTFP use, forest conservation, and livelihoods

The sale of NTFPs by local communities has been suggested as a possible solution to the often observed conflict between forest use and forest conservation, especially as forests are being harvested for timber which has high ecological impacts (Peters et al. 1989, Panayatou and Ashton 1992, Grimes et al. 1994). The harvest and marketing of NTFPs instead of the extraction of timber has been called ‘conservation by commercialisation’ (Evans 1993) and ‘good extractivism’ (Almeida 1996). This approach influenced many conservation and funding initiatives during the 1990s. Although initial findings suggested high economic returns and low ecological impacts of NTFP extraction (Peters et al. 1989), recent studies have provided a more realistic picture of the economic benefits (Browder 1992, Homma 1992, Dove 1993, Godoy and Bawa 1993, Godoy et al. 1995, Hegde et al. 1996, Godoy et al. 2000,) and ecological impacts (Ratsirarson et al. 1995, Pollak et al. 1995, Murali et al. 1996, Hall and Bawa 1996, Peters 1996, Uma Shankar et al. 1998, Sinha 2000). These studies tempered the initial enthusiasm for NTFP, with some studies even suggesting that dependence on NTFP might contribute to the maintenance of poverty (Byron and Arnold 1999). Sheil and Wunder (2002) have cautioned that it might be premature to dismiss the role of NTFPs in income generation or forest conservation, and that a more nuanced understanding of individual case studies is required. A recent analysis of data from 61 NTFP cases from around the world suggests that economic outcomes of NTFP use for local communities will depend on such diverse variables as government trade policies, transport infrastructure, and forest tenure (Manuel Ruiz-Perez et al. 2003, unpublished manuscript). The study of NTFP harvest and impact therefore demands a
multidisciplinary approach to unravel the ecological, social, and economic issues relevant to NTFP use (Andersen 1998).

**The Western Ghats**

I was born on the western coast of south India, and raised in an inland city, which meant that as a child, on my way from the city of my upbringing to the city of my birth, I travelled over and across the Western Ghats. The winding roads and surrounding forests of the Ghats kept me awake on the bus, through the night. It was when I took the train that I realised that the forests that seemed dark and forbidding at night, were magnificent in the light of the rising sun as the train crested the slope and crept in and out of the many tunnels that perforated the hillside. Over the years the forests and hill slopes of the Western Ghats have attracted many people: tourists, pilgrims, hikers, ecologists, timber merchants, coffee growers, and iron ore miners, often with dire results. The recent rapid increase in the rate of deforestation largely due to iron ore mining, conversion of forest to coffee plantations (Lélé, S. M. personal communication), and submergence of forests due to hydro-electric power generation projects (Nadkarni et al. 1989) is threatening a region that has been inhabited for nearly 5000 years (Chandran 1997). The high rates of deforestation and forest fragmentation have attracted national and global concern (Nair 1985, Bhat et al. 1986, Myers 1990). More recently, Myers et al. (2000) identified the forests of the Western Ghats as one of ten global ‘hottest hotspots’ of biological diversity.

The Western Ghats extend from 8° N to 22° N, a length of about 1600 km, and parallel to the western coast of India. The hills rise sharply from the coast to varying heights, about 2400m at their highest, and recede gradually towards the east. The western escarpment catches the moisture laden monsoon winds that sweep in from the
Indian Ocean during the months of June to October. There is a north-south gradient in rainfall with both the amount of rain and number of wet months decreasing with increasing latitude. The altitudinal and rainfall gradient have resulted in a diversity of habitats and high levels of endemicity of plant and animal species (Bhat et al. 1986, Daniels 1991).

I conducted this study in the forests surrounding Kelaginkeri village (14° 30' N and 74° 45' E) in Uttara Kannada district of Karnataka state. The forests belong to the Wet Tropical Forest of the Holdridge classification system. The forests occurring on the hill top and western slopes of the Western Ghats in Uttara Kannada district belong to the Persea macrantha - Diospyros spp.-Holigarna spp. type (Pascal 1988). The annual rainfall in the study area averages about 3700mm and is largely restricted to the monsoon months of June to October, resulting in a dry season that lasts 7 months. The average altitude of the study area is 580 m. The landscape, which is typical of the Western Ghats, is a matrix of forest, agricultural fields, and palm plantations, with 79% of the area being classified as forest (Nadkarni et al. 1989). However the condition of the forest varies from site to site within the study area depending on human use.

The soils of the study area belong to Archaean rock derived Dharwar schists, which are largely ferralitic soils belonging to the Udalf group (Order Alfisols in a high moisture regime) and the Tropepts group (Order Inceptisols) (Bourgeon 1989).

**Overview of forest use in the Western Ghats**

During the 19th and 20th century, the British used wood obtained from the forests of the Western Ghats to build ships and railway tracks (Buchy 1996). To ensure a steady supply of timber, the British government established in 1878 Reserved and Protected
forests and assumed control over all forests (Gadgil and Guha 1992). This state control of forests continues to this day (Nadkarni et al. 1989, Lélé and Srinidhi 2000). The Forest Act of 1927 further intensified state control of forests. The demands by local communities and by the Indian environmental movement that local people be involved in forest product use and management resulted in the establishment of the Joint Forest Management (JFM) program by the state. Under JFM, local villagers and the state Forest Department participate in regenerating degraded forests, for which villagers are paid wages. The scheme has largely concentrated on afforestation of degraded minor forests with fast growing, commercial pulp wood species such as *Acacia auriculiformis*. The JFM effort has been criticized as attempts by the state to co-opt local initiatives (Dove 1995). JFM efforts in Uttara Kannada have been concentrated in degraded areas, thus enabling the forest department to obtain international donor support and yet retain control over resources in the intact forest (Correa 1999, Saxena and Sarin 1999).

The National Forest Policy of 1988 was aimed at ‘conserving the natural heritage of the country by preserving the remaining natural forests with the variety of flora and fauna, which represent the remarkable biological diversity and genetic resources of the country’ (Government of India, 1988). The policy however says little about the people who live in and around protected areas. In actuality, the creation of a protected area is a great hindrance to resource use by local communities. Although the forests of Uttara Kannada have been harvested for NTFP for centuries (Chandran 1997), there are no village level forest access laws. As no concrete state or local policy governs NTFP use, most NTFP extraction occurs rampantly with little monitoring of the impact of harvest.
The absence of local institutions governing the use of forest resource has severely hindered any attempt at achieving resource sustainability.

**Human population and land use in the Western Ghats**

The human population in the hilly tracts of the Western Ghats occurs at lower densities (54 humans per sq km) than either on the coast or on the eastern plains. The major source of income is from agriculture. In Uttara Kannada district the main crop is the *Areca catechu* palm. The palms are largely grown in the valleys that are well watered by the several streams that drain the forests. The palm plantations have largely replaced the *Myristica* swamp forests that were found in the valleys and that are now a highly threatened habitat (Chandran 1993). As a result of the conversion of forests in the valley into plantations, forests are restricted to the tops of hills. The forests surrounding the plantations are used for the collection of mulch, fuel wood, and NTFPs.

As is typical for the rest of India the village community in Uttara Kannada district is divided along the basis of caste and religion. This division has resulted in great inequity in access to forest resources. A study of the use of forest resources by local people can not therefore ignore the issue of social discrimination and skewed resource distribution that is such a large part of the human dynamic of the region. The sale of NTFPs has been linked to empowerment of local people (Arnold and Ruiz Pérez 1998). Socio-economic and ecological information on forest resource use might thus help local communitites find ways to increase incomes from NTFP and better manage the resource.

Local people have harvested such forest products as Black pepper (*Piper nigrum*), Cardamom (*Elettaria cardamom*), and Cinnamon (*Cinnamomum zeylanicum*) from the wet tropical forests of the Western Ghats, which have provisioned Arabian kitchens from
the 9th century and European larders from the 15th century. These NTFPs were domesticated and are now almost completely obtained from cultivated lands. However, several NTFPs continue to be harvested from Western Ghats forests and are traded both locally and globally. One such species is *G. gummi-gatta*, an understory rain forest tree and endemic to the Western Ghats and Sri Lanka (Ramesh and Pascal 1997). Local people harvest the fruit of *G. gummi-gatta*, and the dried rind is sold to factories where Hydroxy-citric acid is extracted and exported to Europe and the U.S.A. Hydroxy-citric acid has been reported to reduce human body weight (Sergio 1988).

**The natural history of *G. gummi-gatta***

*G. gummi-gatta* is common in evergreen and lower shola forests up to a height of 1000 m (Tissot et al. 1994). There is scant information on the density of *G. gummi-gatta* in various parts of its range. Available information suggests that *G. gummi-gatta* densities are the highest in Uttara Kannada district which is the northern part of the range of *G. gummi-gatta*. The relative density of *G. gummi-gatta* (proportion individuals of a species to the total number of stems in the sample) has been reported to be 0.25% for a wet forest plot in southern Karnataka (Claire Elouard, *personal communication*) compared to the relative density of 7.2% in Uttara Kannada (N. Rai, *unpublished data*).

*G. gummi-gatta* trees have a dark, smooth bark with an average thickness of 5.3 mm (Hegde et al. 1998). The trees grow to an average height of 18m and attain diameters of up to 70 cm. *G. gummi-gatta* trees are dioecious, with a male to female sex ratio of 1:1 (N. Rai, *unpublished data*). Trees of both the sexes usually commence flower production when they are about 14 cm in diameter. Male and female trees produce flowers from early February to April, and the fist sized fruits which weigh about 80 g, ripen from June...
to August. While unripe *G. gummi-gatta* fruits are green, the ripe fruit is a bright yellow, a color associated with many monkey dispersed fruits (Janson 1983, Terborgh 1986). In the study area, the pulp of *G. gummi-gatta* fruits is consumed by two primate species (*Presbytus entellus* and *Macaca radiata*) and two species of civets (*Paradoxorus hermaphroditus* and *P. jerdonii*). The seeds are consumed by two species of arboreal squirrels (*Ratufa indica* and *Funambulus palmaram*). *G. gummi-gatta* seeds are about 5 cm long and 2 cm wide and weigh about 1 g. Seeds lie dormant for 8 months (Mathew and George 1995, Chacko and Pillai 1997), which coincides with the amount of time between the cessation and onset of annual rainfall.

**The thesis format**

The dissertation consists of three chapters each of which has been prepared as a separate manuscript for publication in peer reviewed journals. In the first paper (Chapter 2) I examine the role of *G. gummi-gatta* fruit trade in the economic and social landscape of a forest village in the Western Ghats. Specifically, I examine the the effect of forest tenure and household income on the dependence by households on *G. gummi-gatta* fruit harvest. I use the case of *G. gummi-gatta* fruit harvest, to critique the approach by some conservation organizations which promote, without a nuanced understanding of local social conditions, the dependence on NTFPs by local communities. In the second paper (Chapter 3) I report the findings of a study on the reproductive ecology of *G. gummi-gatta*. The genus *Garcinia* which is well represented in the Asian flora is dioecious, and sometimes apomictic. I studied the occurrence of apomixy, the mode of pollination, flowering phenology, flower production, and fruit set in a *G. gummi-gatta* population. Understanding the pollination ecology of a species whose fruits are a major forest
product is important, as fruit production is a direct result of flower pollination and fertilisation. The third paper (Chapter 4) is on the study of the life history of *G. gummi-gatta*. I studied the fruit production, seed dispersal, seed predation, seedling growth, seedling survival, spatial distribution of seedlings, juveniles and adults, and adult tree growth of *G. gummi-gatta*. I used the life history information to study the demography of *G. gummi-gatta* and determine the pattern of population growth.
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CHAPTER 2

NON-TIMBER FOREST PRODUCT USE, FOREST CONSERVATION, AND LIVELIHOODS: THE CASE OF UPPAGE (Garcinia gummi-gatta) FRUIT HARVEST IN THE WESTERN GHATS, INDIA
Introduction

Humans have historically depended on tropical forests for a variety of plant and animal products (Posey 1982), and have converted forests to both permanent and swidden agriculture (Ramakrishnan 1993). The notion that natural forests have been largely untouched by human use is false (Deneven 1992). Although tropical forests have experienced centuries of human use, recent demand for timber and the expansion of agricultural activities has resulted in an increased rate of loss of tropical forests. The rapid and large scale loss and conversion of forests encouraged several countries, including India, to set aside land with the aim of conserving forests. Consequently, local people living in these forests were denied use of forests to which they have had historical access (Gadgil and Guha 1992). Despite evidence that tropical forests have been used and modified by humans for centuries (Fairhead and Leach 1997, Posey 1982, Moegenburg 2002) conservationists maintain that human use of forests is detrimental to biodiversity conservation (Noss 2002). The premise that human use is inimical to biodiversity has dictated forest policy in India since the 19th century (Saberwal 1998) and resulted in the exclusion of local people from their resource base. The ideological and sometimes physical conflict between the state and local communities over forest use has thus hindered both conservation efforts and livelihood enhancement initiatives (Kothari et al. 1998).

Following an influential study on the potential high economic value of tropical forest to indigenous communities (Peters et al. 1989, see Sheil and Wunder 2002 for a critique), the extraction of non-timber forest products (NTFPs) by local communities was widely proposed as a strategy to conserve forest and enhance livelihoods (Nepstad and
Schwartzman 1992, Panayatou and Ashton 1992). This approach to forest resource use had its critics, especially among preservationists (Bodmer et al. 1990). It has however spawned much interest and research on the extraction of NTFPs, and their role in forest conservation (Peters 1996) and livelihoods (Godoy et al. 1995). Social scientists have suggested that this conservation-livelihood approach be broadened to include social and political issues (Zerner 2000) because of the inequity in resource access within communities (Ribot 2000) due to the fractious nature of most communities (Agrawal and Gibson 1999). The assumption that the harvest of NTFPs is beneficial to all sections of the community has to be therefore reevaluated.

An emphasis on NTFP as a major source of income for forest communities might be problematic for several reasons: markets are frequently unstable (Padoch 1992); trade is often controlled by the elite, both locally and regionally (Ribot 2000); access to NTFPs is socially mediated and inequitable (Kumar 2002); lack of security of tenure often results in adverse ecological impact such as damage during harvest (Momberg et al. 2000) or suppressed regeneration; most NTFPs occur at low densities (LaFrankie 1994); and the potential for trade is usually low, with only few species being traded (Saw et al. 1991). There is increasing evidence that NTFP harvest in practice often does not follow the concept of ‘good extractivism’, a strategy that ‘preserves natural resources while enhancing income’ (Almeida 1996). Ecological effects have been shown to be higher than expected (Padoch 1992) and economic returns are low (Godoy et al. 2000).

Using the case of Uppage, a rain forest tree valued for its fruit, I investigated the potential of NTFP harvest in livelihood enhancement and the ecological impacts of harvest, under the current trade and resource use policies. Specifically, I asked the
following questions: What is the social structure of the village community? Are low income households more dependent on Uppage than high income households? Does the position of a household within the social structure of the village determine access to Uppage trees and income from Uppage rind? Does security of forest tenure affect harvest behavior?

The paper begins with a profile of the product, its uses, and a description of the study area and land uses. This will be followed by a description of the Kelaginkeri village community, and an overview of the NTFP trade regime, forest use policy, and tenurial rights regimes, and the ways in which they influence NTFP extraction. A description of the methods used to answer the research questions will precede an analysis of the socio-economic and ecological data obtained during the study. In the concluding section, I will present the research findings in the context of what is known about NTFP harvest, and consider if lessons from the Uppage case can be applied to other NTFPs in the region.

The forest product

Uppage is the Kannada name for Garcinia gummi-gatta (L.) Robson, (Family Guttiferae), an understory rainforest tree, restricted to the moist forests of the Western Ghats and Sri Lanka (Ramesh and Pascal 1997). The fruit of the tree is harvested by villagers, who after removing the seeds and pulp, sell the dried rind to traders. The rind of the Uppage fruit has been traditionally used in Kerala and Sri Lanka as a culinary additive and fish preservative (Samarajeewa and Shanmugapirabu 1983). The long history of use has resulted in the species being domesticated in home gardens in Kerala for centuries.
The domestic demand for the rind in Kerala kept the price at a steady but low level until the early 1990s (Figure 2.6). In the late eighties, some studies showed that Hydroxy citric acid (HCA), a secondary compound present in the rind of Uppage fruit, might be effective in weight loss (Sergio 1988). This finding interested drug manufacturers in the United States of America who touted the drug as a natural solution to obesity (Majeed et al. 1994). Drugs such as Citrin® and Citrimax® were widely sold over the counter. These neutraceuticals, as drugs derived from natural products came to be called, were aggressively advertised despite a lack of rigorous studies on its efficacy. As a result of the increased demand for these products in Western markets, the price of Uppage rind increased rapidly in India. The aggressive advertisement campaign did not go undetected by regulatory authorities. The Food and Drug Administration in the U.S.A. fined Home Television Network for making unsubstantiated claims regarding the product. The biggest blow however, was delivered by a team of researchers from the Roosevelt Obesity Center, New York. The results of their randomized clinical trial showed that the control group, which was given a placebo lost more weight than the treatment group that was given Hydroxy Citric Acid (Heymsfield et al. 1998). As the results of this study were disseminated widely, primarily on the internet, the demand for the product declined. The effect on the price of rind in India was dramatic. The price fell from an average of Rs. 60/kg ($1.43/kg) in 1999 to Rs. 28/kg ($0.66/kg) in 2000, and the price of HCA exported to the US fell from $30/kg in 1999 to $8.50/kg in 2000. Subsequent warnings by various other agencies regarding the continued usage of the drug have further debilitated demand (www.goaskalice.columbia.edu).
Study area

The Western Ghats in southern India are a 1600 km long north-south oriented hill range, traversing the states of Maharashtra, Karnataka, Tamil Nadu, and Kerala. This study was conducted in an area of approximately 49 sq km in the environs of Kelaginkeri village, Uttara Kannada district, Karnataka (Figures 2.1 and 2.2). Kelaginkeri village is situated at an altitude of 620 m. The average precipitation of about 3600 mm is largely restricted to the monsoon months of June to October. The tropical wet forests along the crestline and the western slopes, have high levels of endemicity: 12% for birds and 60% for amphibians (Daniels 1991, 1996). The Western Ghats have been identified by Myers (1990) as one of eighteen hot-spots of global biological diversity and more recently as one of eight global ‘hottest’ hot-spots (Myers et al. 2000). The proportion of the area in forest is 79%, which is remarkably high for any district in India.

Human habitation in the Western Ghats dates back to the Mesolithic age, about 5,000 years ago. The agricultural practices of today probably commenced about 1,500 years ago (Chandran 1997). Areca palm (*Areca catechu*), black pepper (*Piper nigrum*), betel leaf (*Piper betle*), cardamom (*Elettaria cardamom*), and Banana (*Musa sapientum*) were grown in multi-crop orchards, known as ‘Areca - Spice’ gardens. The nut of the Areca palm is a traditional stimulant that is chewed along with betel leaves. Spices, especially pepper, have been traded with Arabia since 50 AD and with Europe since the 16th century (Achaya 1998). Pepper, destined for markets in Europe, came from the orchards and the forests surrounding the orchards, where vines were trained on forest
trees. However in the study area Areca palm cultivation was probably established about 400 years ago.

Areca palm plantations, rice paddies, and human habitations occur in the montane valleys, thus restricting forests to the hilltops. The valleys, with their perennial streams and shade offer the best sites for Areca plantations. Forest occur on the hill slopes and canopy openness depends on use, which ranges from fuelwood collection, green leaf harvest for use as green manure, to fruit and honey collection.

The area of Kelaginkleri village and forests within the village boundary is 1503 ha. Ninety three percent of the area is forest land including *soppinabetta* (Census of India 1991). The 1991 National Census lists 50 households in the village with a total population of 316 (169 males, 147 females). However, a survey of households in 1999 showed that the number had increased to 82 households as a result of division of land among male siblings, and recent settlers.

One hundred and thirty species of NTFPs are used to varying extents by villagers in Uttara Kannada district (Hegde et al. 2000). The extent of dependence on the forest among households varies. Farmers growing Areca, the major land use of the region, use leaves obtained from the forest as mulch; meat-eating non-Brahmins obtain wild game and mushrooms; Brahmins harvest herbs and other plant products for food; and low income households trade various NTFPs even if only marginally lucrative. However, high-value NTFPs such as *Uppage* are attractive to all segments of the community. In Uttara Kannada district, the oil extracted from seeds of the *Uppage* fruit has been used

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1 Buchanan (1802) (cf Nadkarni et al, 1989) records the arrival, in the 16th century, of a Mahratta Brahmin from the coastal zone, who was given land by the then king for the cultivation of Areca.

2 *Soppinabetta*, a Kannada word translates as ‘leaf forest’. These forest patches, are adjacent to plantations and have been leased to Areca farmers for the harvest of leaves that are applied to the base of Areca trees as mulch.
traditionally in cooking. The seed has high oil content of 50 percent (Mannan et al. 1986). Though the oil is no longer used as much as in the past, it has ensured that Uppage trees in soppinabetta were maintained, and thus available to be harvested by soppinabetta owners when the market for the rind developed in the mid 1990s.

The human population density of 54 per sq km in Uttara Kannada district is among the lowest in the country (Census of India 1991). The average annual household cash income in the district (US$ 861, Hegde et al. 2000) is 1.2 times the national average (US$ 687, Bhandare and Mukhopadhyay 1998). The higher average income in the district is due largely to the cultivation of Areca nut. In the last fifteen years Areca has experienced a steep increase in value as a result of the aggressive marketing of Ghutka, a tobacco coated areca product, to which a large number of people, especially youth, have become addicted. Recently the state governments of Maharashtra and Uttar Pradesh, the largest consumers of Ghutka, have announced a ban on the sale of Ghutka. The possibility exists that other states will follow suit (Vijapurkar 2002). These recent legislations have the potential for greatly altering the economic and social environment of Areca nut producing areas, should Areca prices decline.

The structure of the village community

The social structure of the Kelaginkeri village community is strongly hierarchical. At the top of this traditional hierarchy is the Havyaka Brahmin community, which is the richest and most politically influential. Havyakas constitute 54% of the 82 households in the village. The non-Brahmins in the village are socially lower in the order and are to varying degrees considered by the Brahmins to be ‘untouchable’ depending on their caste. These castes are Kare-vokkaliga (15% of the households in Kelaginkeri), Naik
(15%), Siddi (8%), Marathi (7%), and Mahalaya (1%). The practice of social
discrimination (untouchability and caste-based discrimination) continues here as it does
in the rest of the country, despite the state having declared it unconstitutional and illegal.
Brahmins in Kelaginkeru discriminate against non-Brahmins by amongst other things,
preventing the entry of non-Brahmins into Brahmin houses (personal observation).
Brahmins, in the role of the clergy, have for centuries controlled the affairs of the village,
effectively stifling participation of other communities in village-level decision making.

The majority of Areca plantations are owned by Brahmins. Non-brahmins who do
not own Areca plantations usually work in the plantations of the Brahmins as laborers,
and cultivate their often small rice paddies in the monsoon when water is available. Areca
plantations are the most resource intensive and economically profitable land use in the
district. The price of Areca nut increased appreciably in the mid 1980s. The increased
earnings further concentrated power in the hands of the Brahmins. The lure of greater
earnings from Areca resulted in many poorer farmers and plantation workers establishing
Areca plantations by illegally cutting down state controlled forests. Havyaka Brahmins
increased their Areca holdings by expanding into adjacent valleys. Farmers with recently
established Areca plantations however continued to work in the plantations of the richer
farmers, as Areca palms take 8 to 10 years to yield. Recent forest conversions to Areca
plantations however do not have access rights to the forest for the collection of green
mulch, as the practice of granting soppinabetta to Areca farmers was abolished in 1975
(Nadkarni et al. 1989). This has resulted in illegal expansion into Reserve forests by
farmers who have recently established plantations, and the intensification of use of
existing soppinabetta.
**Forest access laws and property rights regimes**

In 1878, Reserved and Protected forests were set up by the then British government, in order to assume control over most forests in India, resulting in the loss of local control and access to resources. The Forest Act of 1927 further intensified and expanded state control of forests. Though India became independent in 1947, these forest laws continue to operate. The Wild Life (Protection) Act of 1972 led to the creation of protected areas such as sanctuaries and national parks. In many cases the establishment of a national park resulted in the eviction of people living within its boundaries (Kothari *et al.* 1998). In response to demands by communities, and with mounting pressure from the Indian environmental movement, the government of India encouraged state governments to involve village communities in the management of forests through benefit-sharing initiatives. One such initiative is Joint Forest Management (JFM) (Jeffery and Sundar 1999), in which local villagers and the forest department participate in regenerating degraded forests, for which villagers are paid wages.

There are as yet no clear policies governing NTFP harvest. However, some steps are being taken towards the formulation of a NTFP harvest policy. In a recent report the forest department of Karnataka State outlined some objectives for NTFP use and management (Karnataka Forest Department 1999) which are yet to be instituted: 1) to ensure the sustainable use of forest resources; 2) local collectors have first rights on available forest produce; 3) the resource should be managed through local bodies such as NTFP societies where possible; 4) forest dependent communities should be motivated and trained in the management, harvest, and marketing of NTFPs, including processing and marketing of value added products. However, currently much of the extraction occurs
rampantly with little monitoring of the impact of harvest. The absence of local institutions has hobbled attempts at achieving resource sustainability.

The rights regimes (\textit{sensu} Srinidhi and Lélé 2000) that exist in the forests of the study area are Reserve forest, Minor forest$^3$, and \textit{Soppinabetta}. Though all forest is owned by the state, each category has different usufruct rights. Reserve forest is the largest of the three categories and the state has the greatest control over these lands. In Reserve forests most silvicultural operations, such as selection felling, thinning, replanting, and extraction of dead wood for subsequent sale as fuel wood are conducted by the state. Limited collection of fuel wood and fodder is granted to local communities, but the granting of these rights is at the discretion of forest officials. The forest department auctions the rights to extraction and trade of NTFPs to private contractors. The absence of usufruct rights in the Reserve forest results in an ‘open access’ situation for NTFP collection, where NTFPs can be harvested by anyone, as and when they are available.

\textit{Soppinabetta} is private access forest that occurs only in the three hill \textit{talukas}$^4$ of the state: Sirsi, Siddapur, and Yellapur. In the 1890s, the then British administration leased 9 ha of surrounding forest for every hectare of orchard owned (Buchy 1996, Nadkarni \textit{et al.} 1989). This was to allow farmers to harvest leaves from forest trees biomass which is used as mulch for Areca palm trees. Farmers have complete control over the extraction of fuel wood, fodder, soil, and green leaves. NTFPs can however only be sold to the contractor appointed by the forest department. In terms of NTFP harvest,

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$^3$ Minor Forest is forest land given to the entire village in the ratio of 1 hectare of land for every head of cattle. This enabled local communities to meet their subsistence needs of fuel-wood, fodder, and leaf mulch. The harvesting of resources, including NTFPs, for commercial purposes is not allowed. After decades of intense use, the vegetation in minor forest is mostly scrub and stunted trees.

$^4$ A \textit{taluka} is an administrative subdivision of a district. Utarra Kannada district has a total of nine \textit{talukas}.\normalsize
while *soppinabetta* ensures security of tenure to farmers, Reserve forests are open access. In the forest range in which Kelaginkeri village is located, 56 percent of the forest area is Reserve forest and 23 percent is *soppinabetta* (Karnataka Forest Department 1999).

**Harvest and trade scenario**

*Uppage* is harvested from Reserve forests, and from *soppinabetta*. Due to the ‘open access’ in Reserve forests, collectors are driven by necessity to harvest *Uppage* before others. The early harvest results in low quality *Uppage* rind as fruits are not fully developed and rind obtained from unripe fruit weighs less than rind from ripe fruit. The harvested fruits are taken to the households of the collectors where they are processed and seeds are discarded. Due to the difficulty in deseeding unripe fruits, harvesters often dry the undeveloped seeds along with the rind. Reserve forest patches, in some cases having as many as 100 *Uppage* trees per hectare, attract collectors from distant villages. There is therefore a conflict of interest between migrant harvesters and local villagers who are also involved in *Uppage* collection. Under the current rights regime local villagers are unable to prevent migrant harvesters from collecting in the Reserve forests surrounding their village. My surveys in forests frequented by migrant harvesters have shown that branches were cut in over 50 percent of adult fruiting *Uppage* trees. The cutting of branches makes the harvest of fruits easier than picking individual fruits from the tree. Often the largest branches are cut, as fruits at the tips of these branches are the most inaccessible. As most harvest occurs early in the season, unripe fruits are more difficult to dislodge, thus encouraging the cutting of branches to the ground where they are then picked clean.
The harvest practice in *soppinabetta* is different. *Soppinabetta* owners wait for *Uppage* fruits to ripen before harvesting. They usually harvest fruit that has fallen to the ground after ripening or after primates have eaten the pulp and discarded the rind. This results in better quality rind. Fruits are brought to the homes of the collectors where they are deseeded and the rind is dried in a wood-fired oven, which is usually comprised of a metal mesh suspended over burning logs. The rind has to be dried within a day of harvest as the rind tends to spoil quickly in the humid climate.

The forest department auctions the rights to the harvest and trade of NTFPs bi-annually. Trade rights for major NTFPs like *G. gummi-gatta* are auctioned separately, while the auctioning of cheaper and less abundant NTFPs are combined. Auctioning of the rights to NTFP trade has been a practice for several decades. Rights are auctioned for each forest Range, which is the basic administrative unit of forest, measuring about 250 km². Fifty seven percent of the total revenue earned by the Karnataka forest department from all NTFP auctions in 1995-97 was from *Uppage* alone, illustrating the prominence of *Uppage* in the NTFP trade scenario of the region at that time. However, revenue earned by the Karnataka forest department from NTFPs in the district is less than 1% of their total revenue (Gaonkar *et al*. 1998). The meager revenue accounts for a general lack of interest in NTFP trade. Not surprisingly, the Department has raised concerns about the harvest from the Reserve forest of fuel wood used to dry *Uppage* rind, and argued that the revenue earned from auctioning trade rights is not commensurate with the loss of biomass (Saibaba *et al*. 1996).

The winning bidder assumes complete control of the trade of *Uppage* for the range. These contracts, usually won by affluent business people from outside the area,
give individuals, henceforth called contractors, marketing rights to all extracted *Uppage* fruit. The harvest of the fruit itself is done by local people. The contract regulations require contractors to harvest fruits themselves, effectively marginalizing the local community. The task of collecting *Uppage* fruit from vast areas of forest by the contractor, even by employing people for that purpose is impossible. Contractors therefore announce that they will issue passes to local people and suggest a date for the commencement of harvest. Seldom however is a pass issued or a date announced. The short lease period of two years gives contractors little incentive to ensure that NTFP harvest is conducted with minimum impact to the resource base.

Harvesters sell the dried rind to a contractor-appointed agent at a price determined by the contractor. The agent gets a commission for each kilogram bought. The contractor collects the rind from the agent at regular intervals. Apart from the agent, there are other buyers who acquire and sell small quantities of rind. These village traders sell *Uppage* to either the legal contractor or to other traders who operate on the black market. The occurrence of a black market ensures that prices are higher than if the contractor was the sole buyer of the rind. The contractor attempts to curtail this illegal trade by recruiting people to patrol the borders of the range to ensure that *Uppage* is not purloined to a neighboring range, the jurisdiction of different contractor, where prices may be higher, even if marginally. There is however little support for such monitoring either from villagers, who stand to benefit from the higher prices and greater options, or from the Forest Department, which having auctioned off the contract does not interest itself in the operational details of harvest and trade. Tensions between traders, and between collectors and the contractor therefore run high during the harvest season.
The contractor stores the dried rind in large sheds in the nearby town of Sirsi, where it is sorted, graded, and sometimes adulterated with common salt and charcoal to increase weight. The rind is then sold to HCA processing firms, which are usually located in cities, and are capital-intensive industrial units with the necessary technological expertise to extract HCA from rind for subsequent export. A majority of these firms produce products from a variety of plant species which enables them to withstand, for a certain period of time, the fluctuations in market demand of any single product. These processing firms directly export HCA to buyers in the US and Europe. Thus, factors such as access to global markets, previous experience in plant product extraction, and existing infrastructure determines the participants in the HCA processing and export business (Figure 2.3).

There are about 35 processing firms involved in the extraction of HCA in India. Sami Chemicals, situated in Bangalore, a subsidiary of Sabinsa Corporation, USA, the initial promoters of HCA, was the first Uppage processor and continues to be the largest. Due to the sudden drop in demand for rind, as a result of studies in the U.S.A. that questioned the efficacy of HCA in weight loss programs, Sami Chemicals bought no rind in 2000. As a consequence, price of Uppage dropped from Rs 60/kg ($1.43/kg) to Rs 28/kg ($0.66/kg). Exporters also attribute the drop in price to a steep increase in the number of processors and a subsequent spurt in supply. Other reasons cited for the drop in prices are low rind quality due to the harvest of unripe fruit, and the import of Uppage fruit from Sri Lanka at lower prices (Suresh Kumar, Sami Chemicals, Bangalore personal communication).
Methods

Socio-economic profile of Kelaginkeri village

How important is *Uppage* to the household economy of Kelaginkeri village? I determined the effect of participation in *Uppage* harvest on the income of rich and poor, Brahmin and non-Brahmin households, and the level of dependence of households on *Uppage* collection. Information on the socio-economic characteristics of households in Kelaginkeri village was obtained from interviews in May and June, 2001. Interviews were conducted at the end of a three year stay in the village. Fifty one of the eighty two households in the village were interviewed. Households were selected to ensure that all castes and income classes were represented. During the interviews I gathered information on 1) Household structure and income: number of people in the household; income from agriculture, NTFPs, and wage labor; size of landholding and land use, 2) NTFP collection: number of species collected, quantity collected in 1999 and 2000, 3) *Uppage* harvest: number of kilos of *Uppage* collected in 1999 and 2000; number of years of *Uppage* collection; number of household members involved in *Uppage* collection; time spent on *Uppage* collection and processing; amount of fuel wood used per day in drying *Uppage*, 4) Trade and access: amount of *Uppage* sold to contractor and on the black market; presence of informal tenurial arrangements; barriers to involvement in *Uppage* harvest, 5) Harvest practice: preference of harvest mode– climb and harvest or collection of fallen rind; proportion of *Uppage* obtained from *soppinabetta*, proportion of fruits left on the trees.
**Resource access and trade**

To obtain a description of the policy governing forest resource access and NTFP trade I interviewed forest officials, traders, and conservation activists in the town of Sirsi, Uttara Kannada district. Two contractors in Sirsi and Siddapur were interviewed for their perceptions on NTFP trade, quantity of *Uppage* obtained, final markets, and profit margins. For an estimate of the significance of the black market trade a trader operating on the black market was interviewed. In 1988, prior to the establishment of overseas markets, and the boom in *Uppage* prices, the Bakkala village co-operative located about 25 km from the town of Sirsi, held the contract for trade in *Uppage* rind. I talked to the secretary of the Bakkala village co-operative to evaluate the potential for such village co-operatives being involved in NTFP trade. I interviewed representatives of five HCA extraction firms in Bangalore and Ankola to obtain information on the quantity of rind acquired per year, the price of *Uppage*, the sources of *Uppage*, the price of the finished product, size of the export market, and fluctuations in demand.

**Ecology**

The ecological study was part of a larger study on the ecology of Uppage and effect of harvest. To determine the density and distribution of *Uppage* in the study area, trees greater than 10 cm diameter at breast height were enumerated in sample plots established in the forests of Kelaginkeri village. The total area sampled was 30.5 ha. The pattern of distribution of *Uppage* in Kelaginkeri was determined by sampling along a 20 m wide, 11.8 km long transect. The belt transect was subdivided into 50 m continuous sections and the number of *Uppage* trees in each section was recorded. The number of
trees in each 50m section was analysed using a non parametric Runs test to determine if the occurrence of *Uppage* along the 11.8 km transect was random or clumped.

To determine if the impact of harvest practices varies between the two regimes, Reserve forest and *soppinabetta*, I laid two 1 ha plots in *soppinabetta* (Map 2, S1 and S2) and six 1 ha plots in Reserve forest. In the Reserve forest, two plots (plots R1 and R2, Map 2) were in sites harvested by migrant collectors and hence assumed to experience a high intensity of fruit harvest. Two Reserve forest plots (plots R3 and R4, Map 2) were considered medium-intensity sites due to their close proximity to many households. Two other Reserve forest plots (plot R5 and R6, Map 2) were considered low-intensity sites as each was harvested by one household, due to an informal tenurial agreement.

The greater security of tenure in *soppinabetta* helps ensure that harvesters allow fruits to ripen on trees, increasing the probability of seeds being locally dispersed by primates. While in the Reserve forest, fruits are picked when unripe before seeds are fully developed and fruits along with seeds are taken to the households of collectors for processing and drying. I tested the hypothesis that a higher number of seeds are dispersed in *soppinabetta*, than in Reserve forest where seeds are removed along with fruits during harvest, by comparing the ratio of seedlings (less than 0.5m height) to trees greater than 20 cm diameter at breast height in *soppinabetta* and Reserve forest plots. A higher ratio would suggest that more seeds are germinating per adult tree. I used only seedling number as I observed that saplings (plants greater than 0.5 m in height) were periodically cut in *soppinabetta* during biomass harvest.

Damage caused to trees during harvest was assessed in the six forest plots. If damage to trees was observed in plots, I selected additional trees outside the plots along
transects of variable lengths to ensure adequate sample size and recorded percent damage for each tree encountered along the transect. Damage was observed in the high-intensity Reserve forest sites RF1 and RF2 where 187 female trees were assessed for damage. The proportion of branches cut was recorded as percent damage. Stumps of felled *Uppage* trees were enumerated in the plots and along the transect.

**Results**

Role of *Uppage* in income generation:

The average annual household income of the 51 households was Rs 104,229 (US$ 2,316), which is higher than the average annual household income of Uttara Kannada district (US$ 861, Hegde *et al.* 2000) or the country (US$ 687, Statistical outline of India 1998). A comparison of Brahmin and non-Brahmin household incomes shows a significant difference indicating that the distribution of income within the village is not equitable (*t* test, *p* < 0.001; Average Brahmin US$ 3,218, *n*=26; Average non-Brahmin Rs 1,347, *n*=25). The income disparity between Brahmin and non-Brahmin households does not however result in differential dependence on *Uppage*, as the relative contribution of *Uppage* to Brahmin (7.7% of household income from *Uppage*) and Non-Brahmin (11.6%) households is not significantly differently (Mann-Whitney U, *p*=.39).

I tested the hypothesis that low income households collect more *Uppage* than high income households. Households were divided into those with incomes less than Rs.50,000 (*n*=16) and greater than Rs. 100,000 (*n*=16). In 2000, low income households collected 85 ± 124 kg which is significantly lower than rind collected by high income households, who collected 398 ± 432 kg of *Uppage* (*t* test, *p* = 0.01). Moreover, the average *Uppage* harvest by low income households decreased from 122 kg/household in
1999 to 85 kg/household in 2000, while that of high income households increased from 277 kg/household to 398 kg/household (Figure 2.4). In 2000, households with access to *soppinabetta* collected 62% of their *Uppage* from *soppinabetta*. 

It has been hypothesized that with increase in income, households extract fewer NTFPs (Godoy et al. 1995). I compared the number of NTFPs used by households with incomes greater than Rs 100,000 (n = 16) with the number of NTFPs used by households with incomes less than Rs 50,000 (n = 16). There was no significant difference in the number of products extracted by these two groups (Mann Whitney U, p=.28). Contrary to expectations, richer households harvested on the average a higher number of products (2.4 products) than poorer households (1.9 products), but not significantly so. *Uppage* constituted 83 percent of the total household income in 2000 obtained from NTFPs by 51 households, suggesting that households depend on one, or few, high value products and when they become attractive (Table 2.1). 

The drop in demand for HCA in overseas markets resulted in a steep decrease in price of *Uppage* rind. To illustrate the effect of the fickle price regime on income generation, I compared income from *Uppage* for the years 1999 and 2000, during which time prices fell from Rs. 62 per kg to Rs. 28 per kg. Though the quantity of *Uppage* collected by 51 households increased marginally from 1999 to 2000 (12,611 kg to 14,622 kg), the reduction in price resulted in the total earnings from *Uppage* dropping from Rs. 800,969 in 1999 to Rs. 436,233 in 2000. The vagaries of external markets and demand could thus be debilitating to the economy of harvester households.
Species ecology and impact of harvest

Ecology: *Uppage* grows in the understory of wet tropical forests and is dioecious, with separate male and female trees. Both sexes flower from February to April and fruits ripen from July to September, which coincides with the rainy season. The flowers are probably pollinated by weevils that also pollinate Areca palms. Fruits on an *Uppage* tree do not all ripen at the same time. The staggered fruiting ensures that most fruits are probably eaten by animals, thus ensuring that a large proportion of the seeds are dispersed (Lee 1988). *Uppage* is an important food resource for the Common langur, Bonnet macaque, Common palm civet, and the endangered Brown palm civet all of which feed on the pulp. These animals play an important role in the ecology of *Uppage* by dispersing seeds away from parent trees, thereby increasing the probability of survival of seeds and seedlings (N. Rai, unpublished data). Animals discard *Uppage* rind to the ground, after eating the pulp. Collection of fallen rind, after it has been thus discarded, has no overt adverse impact on the ecology of *Uppage*.

Harvest behavior: Collectors pick rind from the ground only in forests that have secure tenurial arrangements, as in soppinabetta. Picking rind might be more time consuming than climbing and harvesting trees, but the economic returns are higher as only ripe fruits are obtained when harvested in this fashion in contrast to a mixture of ripe and unripe fruits that are obtained when the entire tree is harvested at once, as fruits do not all ripen at the same time. Rind from ripe fruit weighs more than unripe fruits and sells for about Rs 5 to 10 more per kg than rind from unripe fruit. Sixty seven percent of the 42 harvesters interviewed preferred to pick fallen fruit than climb trees. They offered such reasons as lesser effort, less dangerous harvest practice, measured pace of work,
decreased processing time as ripe fruits are easier to deseed, and better quality rind for their decision. Only twenty six percent of the households preferred to climb trees, as that allowed the harvest of fruits from trees in remote areas that might not be possible to be visited on a regular basis or in areas that are harvested by several people.

**Population structure:** The density of *Uppage* trees ranged from 4 trees/ha to 123 trees/ha, and an average of 29 trees/ha. The result of the Runs test was significant at *p*<0.001, showing that *Uppage* trees are not evenly distributed in the forests of Kelaginkeri. A comparison of the *soppinabetta* and Reserve forest sites shows that there are few juveniles (0.5 – 2m height) and young adults (1-20 cm dbh) in *soppinabetta* (Figure 2.10), due to the clearing of undergrowth periodically for fodder and mulch collection. There is however adequate number of seedlings for adult populations of establishing if the existing young trees are allowed to grow. The ratio of seedlings to mature trees is higher in *soppinabetta* than in Reserve forest with the exception of the Reserve forest site RF2. The generally high proportion of seedlings in *soppinabetta* suggests that the practice of collecting fallen rind results in greater seedling to adult ratios. This suggests that picking rind is a more ecologically sustainable harvest behavior than harvesting fruits directly from the tree. However, such factors as greater mortality of seedlings in intact forest, and high rates of seed predation in diverse forest (N. Rai, **unpublished data**) might also be responsible for the lower seedling ratios in Reserve forest.

**Damage due to harvest:** The cutting of lateral limbs of *Uppage* trees during harvest was observed in areas that are heavily used. In the two sites, RF1 and RF2, branches were cut on fifty seven percent of trees, all branches on 8% of the trees were
cut, and 11 trees (6%) were cut at the trunk at a height of 1m with the bole of the tree lying near the stump (Figure 2.8). Due to the short history of fruit harvest extreme impacts such as the cutting of branches and trees are currently confined to the forest patches that are close to high density villages below the Western Ghats from where migrant harvesters originate. An increase in the price of *Uppage* could result in these impacts rapidly spreading to larger areas, if local villagers are not given more control and access rights to *Uppage* trees.

**Rind production:** I estimated the *Uppage* rind production from the forests of Sirsi division. The data used in this analysis comes from a larger ecological study (N. Rai *unpublished data*). The average yield per year for a female tree in closed canopy forest is 904 fruits (n=124 trees, 4 years). Based on my observations of harvest (167 trees over four years) and from my interviews with harvesters I determined that collectors obtain more than 95% of the fruits on a tree during harvest. The average wet weight of a fruit is 31g (n = 7954 fruits). Average weight of rind after processing and drying is 10% the wet weight of the fruit, therefore weight of dry rind obtained per fruit is 3.1 g. Hence dry rind yield for a tree in closed canopy forest = 904*3.1 = 2804 g. The average density of *Uppage* trees obtained from the belt transect with sampled area of 23.9 ha was 27 trees ha⁻¹. Given the male to female tree ratio of 1:1 (N. Rai, *unpublished data*) I estimated the density of female *Uppage* trees in the Kelaginkeri village-forest complex at 13.5 trees ha⁻¹. Dry rind production ha⁻¹ is therefore = 13.5 x 2804 = 37,854 g or 37.9 kg ha⁻¹ yr⁻¹. The area under forest in Sirsi Division is 79,798 ha (compiled from Census of India 1991). Assuming that the density of *Uppage* trees in the study area is representative of the district, the annual *Uppage* production for Sirsi division is 30,20,673 kg. The official
estimate provided by the forest department for the period 1997-99 is 16,31,500 kg year\(^{-1}\) (Figure 2.5), or 54% the estimated quantity. This disparity in estimates might be due to *Uppage* rind being traded on the black market and under-reporting by contractors.

**Impact of fuelwood collection:** The drying of *Uppage* rind requires fuel wood which is collected from the forest. The Karnataka forest department estimated that 25 kg of wood is required to obtain 1 kg of dried rind (Saibaba *et al.* 1996). I estimated the amount of fuel wood used, by weighing the wood required to dry known amounts of rind. I estimated that 10.5 kg of wood is used to obtain 1 kg of dried rind. This was within the range of values provided by harvesters during the interviews. Lélé (1993) estimated the total above-ground wood production in the area to be 1100 to 3100 kg ha\(^{-1}\) yr\(^{-1}\). The estimate of dry rind produced per ha in the study area is 37.9 kg ha\(^{-1}\). Thus the estimated fuel wood consumption is 398 kg ha\(^{-1}\) yr\(^{-1}\), which is less than half the lower range of the estimated above-ground wood production in these forests. Although lesser wood is extracted than total production, it is removed from a smaller area of forest, often close to the harvester household. This might result in an unacceptably high level of impact on smaller areas of forest.

**Discussion**

*There is significant disparity in the income of upper class (Brahmin) and lower class (non-Brahmin) households in Kelaginkeri.* There is variability in household incomes within the village and income distribution is related to the social stratification within the village. It has been shown that most village communities are highly stratified (Agrawal and Gibson 1999). Under the existing social structure, access to resources is biased towards the upper-class households. To ensure equitable resource access ‘…
negotiations that can modify the effects of alienation, hierarchy, and domination’ (Agrawal 1999) are necessary.

Higher income households collect significantly more Uppage, and a marginally higher number of NTFP species than poor households. High income households increased the quantity of Uppage collected from 1999 to 2000, while low income households either ceased or reduced collection. This finding contradicts studies that have shown that households with low income are more dependent on NTFPs than high income households (Gunatilake et al. 1993). However, Kumar (2002) has shown that in the dry forest of Central India, high income households benefit more from the extraction of NTFPs than low income households. Godoy et al. (1995) have also shown that in a Nicaraguan village, an increase in household income does not encourage households to specialize on fewer forest products or reduce their dependence on forests. The significantly higher quantities of Uppage collected by high income households is probably a result of the greater access to Uppage trees in soppinabetta. In addition, their greater wealth enables them to employ people from Kelaginkeri and from far away villages to collect rind from the Reserve forest. Trees growing in the open canopy soppinabetta, due to their larger size, produce more fruit than those growing in the dense canopy forest (N. Rai, unpublished data). The greater tenurial security enjoyed by soppinabetta owners enables them to collect ripe fruits, resulting in greater economic returns as ripe fruits fetch higher prices. The lower quantities collected by poorer households might be due to their being involved in labor duties in Areca plantations or in their own rice fields which are cultivable only in the monsoons when water is available, which coincides with the peak fruiting season of Uppage trees.
Price of Uppage rind fell sharply, resulting in a large decrease in household income. NTFPs often show boom-bust scenarios, with significant effects on local incomes. Collectors make the decision to harvest based on limited market information, and often suffer the consequences of market collapse. Padoch (1992) describes a boom and bust scenario in the extraction of Aguaje (*Mauritia flexuosa*) in the Amazon. Prices in local markets showed a 6-fold price increase in a week which then spurred a massive increase in palm fruit harvest, causing a subsequent crash in the price to, or below, the pre-boom value. If local communities are to rely on NTFPs there has to be greater market stability, a scenario that is complicated by an increasingly global trade regime as illustrated in this case study. There is however a stable, albeit less lucrative, domestic market for Uppage rind in the state of Kerala. Interviews with traders suggest that about 20% of the rind from Sirsi district, even during peak international export, was being directed to markets in Kerala state. The existence of multiple uses and markets for the rind is encouraging for the continued marketability of Uppage.

Households in Kelaginkeri specialize on a few, high value NTFPs. Despite the diversity of NTFPs in the forest (Hegde *et al*. 2000), households engage in the collection and trade of only a few NTFPs (Figure 2.7) which constitutes 14% of the average total household income, a large portion of which (83%, Table 2.1) is from Uppage rind alone. Most NTFPs that occur in the forests around Kelaginkeri are either financially unattractive (Table 2.1), or are at low densities (N. Rai, *unpublished data*). Saw *et al*. (1991) have shown that only one species (*Parkia speciosa*) out of 76 edible fruit bearing species (9% of total tree species) in a 50 ha forest plot in Malaysia, was harvested for sale. Thus an emphasis on forest products as a major source of income, as many
conservation and development agencies have suggested, might not improve the economic situation of forest dependent communities. This, therefore, casts doubts over the role of NTFPs as a primary income source for forest dwelling communities.

Seedling regeneration is higher in soppinabetta, indicating that security of tenure might result in stable populations of Uppage. Security of tenure rights has been cited as an important factor that ensures sustainable harvest of forest resources (Momberg et al. 2000). The practice of delayed harvest of Uppage fruits is seen often in soppinabetta, a more secure tenurial regime, and rarely in Reserve forest. Harvesters who lack secure rights of access are tempted to harvest fruits before other collectors, resulting in seeds not being dispersed and a probable reduction in seedling regeneration. Greater security of tenure will ensure that fruits are harvested later in the season, and thus picked from the ground instead of being plucked from the tree. Collectors who use this mode of harvest can not however harvest over large areas, as Uppage fruits can lie on the ground for only one to two days before rotting in the heavy rain that falls during the fruiting season, thus requiring frequent visits to fruiting trees. Lack of tenure security has also resulted in a high incidence of damage to trees during collection. More than half the number of Uppage trees in the intense harvest sites was intentionally damaged during harvest. Local control of resources by villagers and ecological monitoring of the Uppage population might ensure that damage to trees, usually caused by migrant harvesters, is minimized and that seedling regeneration is adequate.

There have been precedents for the local control of forests in India through the granting of rights of forest use to the entire village, and regulated through a village council (Kothari et al. 1998). In Karnataka state, village forest councils (VFCs) exist in
several villages, but at present their scope is limited to the management of degraded forest, and rarely extends to Reserved forest. Increasing the authority of VFCs and granting rights of NTFP harvest within prescribed village boundaries will greatly enhance the access rights of local communities.

Granting of private tenure rights will however have to take into account the possibility that the condition of the forest might change. It has been suggested that resource extraction might be a transitional phase between forest and agriculture (Almeida 1996). The case of *soppinabetta* in Uttara Kannada is illustrative in this context. The original leasing of forest land for the harvest of leaves has resulted in the transformation of the original closed canopy evergreen forest to open, predominantly deciduous woodland (Lélé 1993, N. Rai, *unpublished data*). Farmers, however, perceive *soppinabetta* to be extensions of their gardens (*personal observation*), and not as biologically diverse forests, demonstrating that the transition from forest to agro-forest has occurred as hypothesized.

*Uppage trees are not evenly distributed in the forest.* How then are resources to be divided amongst the members of a heterogeneous community? Important and empowering as securing rights of tenure is, some questions regarding the process of granting tenure remain. As many NTFPs are patchily distributed, drawing boundaries around households might not result in an equitable distribution of forest products. Nor can it be assumed that granting property rights alone will ensure that the larger issues of access to markets, involvement in policy decisions, and effective resource management will be addressed (Zerner 2000). Such issues of resource sharing are best addressed by
community members and stakeholders themselves, through negotiations facilitated by the establishment of local institutions (Martin and Lemon 2001).

Middle traders are important to NTFP product trade. Gaonkar et al. (1998) have suggested that the current contractual system be replaced by a village-level NTFP cooperative that undertakes the trade of the product directly, eschewing the contractor and other middle traders. The current system is unfavorable to collectors as the price is set by the contractor, and harvesters get a proportionally small share of the final profits. However due to their experience and contacts with the external markets, traders are more adept at finding markets and absorbing the risk of market collapse. This was corroborated by the experience of a village sales cooperative that had won the contract for Uppage trade in 1988 (S. M. Hegde, personal communication). As a result of their inability to effectively market the rind, they lost money over the two years that they had the contract.

I found that the reported estimates of Uppage rind bought and traded by contractors might have been underestimated. Contractors might under report quantities in order to drive down auction prices, and deflate profit estimates in order to offer lower prices to collectors. This has been possible due to the lack of monitoring by the Forest department, and the lack of transparency in trade. Information on actual quantities will enable a better understanding of the impact of NTFP harvest on village household income, size of the trade, and the impact on the ecosystem of fuel wood collection. My results show that the amount of fuel wood required for drying rind is lower than previously published estimates (Saibaba 1996). However the impact of biomass removal on forest patches might be high, as wood is extracted from areas close to households thus focusing fuel wood extraction on small areas.
In a review of the *Uppage* marketing regime in the district, Saxena *et al.* (1996) have argued that although monopolistic NTFP trade regimes may not be conducive to local income augmentation, the ecological effects of such a trade regime are benign due to depressed prices and a quasi-regulated harvest regime. There is however little information on the impact of the trade regime on the ecology of NTFP species. The case of nutmeg (*Myristica malabaricum*) is illustrative of an NTFP that despite being traded under the contractual system was overexploited to the point where harvest and trade was banned by the Karnataka forest department (Saibaba *et al.* 1996) due to extensive tree damage. There is therefore little evidence to suggest that changes in the trade regime will result in more benign harvest.

**Conclusion**

My study shows that greater local control over forest resources will increase the probability of sustainable *Uppage* harvest, mainly through the harvest of ripe fruits and decreased tree damage during harvest. Transparency in trade and decision making at all levels (state, contractor and harvester) will ensure faster response by all stakeholders to variability in market demand and resource condition. I found a large disparity in access to forest resource within the village. This heterogeneity can be reduced through the representation of non-brahmins in local institutions thus giving them a greater voice in resource use decisions. In cases where these structures have been initiated, it has been largely through the efforts of local non-governmental agencies (Jeffrey and Sundar 1999), suggesting that the role of external agencies is critical in ensuring sustainable harvest and equitable distribution of rewards. If communities are to become more dependent on
NTFPs, a greater involvement by the state and by non-governmental agencies is necessary.

The *Uppage* case shows that NTFP use is dependent on more than just the direct interaction of markets, forests, and livelihoods. The paradigm of ‘good extractivism’ that has fuelled much of the interest in NTFPs needs to be re-evaluated in the light of increasing evidence that a complex interplay of factors such as regulation of forest access, social dynamics within the community, unstable trade due to fluctuating market demand, and local and global economic scenarios influence NTFP use. Although strategies evolved for one area can seldom be used in other areas due to differences in the prevailing economic, social, and ecological scenarios (Sheil and Wunder 2002), basic aspects such as greater local control, ecological monitoring, and transparency in trade appear to be important for NTFP harvest to be sustainable. The skewed distribution of resources and opportunities such as land, income, and social status, is a characteristic of most villages in India (Kumar 2002), and possibly many other countries. It is therefore critical that the basic issue of social justice be addressed in order for biodiversity conservation and poverty alleviation programs to succeed.
References


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<table>
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<th>Non timber forest product</th>
<th>Value in 2000 (US$/kg)</th>
<th>Number of households involved</th>
<th>Quantity collected (kg)</th>
<th>Income (US$) (% of total)</th>
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<tr>
<td>Uppage (G. gummi-gatta)</td>
<td>0.69</td>
<td>42</td>
<td>14,622</td>
<td>10096 (82.6)</td>
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<td>Wante (Artocarpus locucha)</td>
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<td>17</td>
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<td>Rampathre (Myristica malabaricum)</td>
<td>3.10</td>
<td>11</td>
<td>148</td>
<td>459 (3.8)</td>
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<td>Muruglu (G. indica)</td>
<td>0.60</td>
<td>16</td>
<td>725</td>
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<tr>
<td>Lavanga (Cinnamomum zeylanicum) flower</td>
<td>2.74</td>
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<td>67</td>
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<td>Anilekai (Terminalia chebula)</td>
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<td>Honey</td>
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<tr>
<td>Suragi (Ochrocarpus longifolius)</td>
<td>4.05</td>
<td>1</td>
<td>15</td>
<td>61 (0.5)</td>
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Table 2.1. NTFPs traded and income earned by fifty one households in 2000 in Kelaginkeri village, India.
Figure 2.1. Map of A) India showing Karnataka state and Uttara Kannada district, and B) location of Kelaginski village and the 450m contour of the Western Ghats.
Figure 2.2. Map of Kelagakari village showing location of households and sample plots. Plot RF3 is not shown due to its distance from the village.
Figure 2.3. The *Uppage* trade network from harvester to overseas market.
Figure 2.4. *Uppage* collection by low and high income households in 1999 and 2000 in Kelaginkeri village, India. The mid line inside the box indicates the median value, and the edges are the first and the third quartiles. The whiskers extend to the adjacent values outside the box. Asterisk indicates an outlier.
Figure 2.5. *Uppage* production and auction amount in Sirsi forest division, India. The two-year period reflects the length of the contract. Data for 1989-95 from the Forest department (Gaonkar *et al.* 1998).

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<td><strong>Uppage</strong> Rind (kg)</td>
<td>258,060</td>
<td>290,000</td>
<td>417,000</td>
<td>1,111,000</td>
<td>3,263,000</td>
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<td><strong>Auction amount (Rs)</strong></td>
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<td>384,500</td>
<td>900,900</td>
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<td>1,750,000</td>
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*Data from Range forest office records maintained by the Forest department.*
Figure 2.6. The trend in price paid to *Uppage* collectors and in household participation in *Uppage* trade (n=51) from 1978 to 2002, in Kelaginkeri village, India.
Figure 2.7. The number of NTFP traded by households in 2000 in Kelaginki village, India, including Uppage which was sold by 42 of the 51 households interviewed.
Figure 2.8. Percent damage to *Uppage* trees in the Reserve forest surrounding Kelaginkeri village, India. Damage is expressed as percent of branches cut.
Figure 2.9. Ratio of Uppage seedlings (<0.5m in height) to trees (> 20 cm diameter) in soppinabetta and Reserve forest in Kelaginkeri. RF1- RF6 are Reserve forest plots and SB1 and SB2 are soppinabetta plots.
Figure 2.10. Size class distribution of *Uppage* in *soppinabatta* and Reserve forest plots near Kelaginkeri village, Western Ghats. a. SB1 b. SB2. c. RF1 d. RF2. e. RF5 f. RF6
CHAPTER 3

THE REPRODUCTIVE ECOLOGY OF A DIOECIOUS, TROPICAL

UNDERSTORY TREE, *Garcinia gummi-gatta*
Introduction

The selective pressure for out-crossing in self-compatible plant species has been suggested as a probable pathway for the evolution of dioecy (Baker 1959, Bawa 1980a). However, unisexuality, or single sex flowers, might result in decreased visitation by pollinators to female flowers unless species invest in costly floral rewards to attract pollinators (Givnish 1980). Kaplan and Mulcahy (1971) suggested that in species that do not offer rewards in female flowers, pollinator discrimination against female flowers might result in decreased visitation to female flowers, thus encouraging the evolution of wind pollination. This might explain the observed correspondence between dioecious species, which usually have nondescript flowers, and ‘mistake’ pollination by insects (Baker 1976); small, generalist insect pollination (Bawa and Opler 1975); wind pollination (Charlesworth 1993); and pollination by both insects and wind (Culley et al. 2002). Further, Bierzychudek (1987) has suggested that pollinator discrimination and the resulting avoidance of female flowers, especially in stressful environments, might result in species producing seeds through apomixis. I explore the occurrence of these reproductive processes and attributes in a tropical dioecious tree species, *Garcinia gummi-gatta*.

Gadgil and Bossert (1970) postulated that there is a trade off between the profit function of increased reproduction and the cost function of greater effort due to reproduction, and that overall fitness would be optimized by the adjustment of reproductive effort through natural selection. These theoretical considerations can be explored in dioecious species as the cost of reproduction varies intraspecifically, and the two sexes can be compared in a multitude of ways. The predictions of the Gadgil-Bossert
model have been demonstrated in many dioecious species, with female trees showing
greater costs of reproduction and hence increased mortality and lower growth (Lloyd and
Webb 1977, also see Delph 1997 for an extensive review). The intraspecific variation in
life history traits could affect the sex ratio of a species through differential mortality of
the sexes. Thus sex ratio is often male-biased, explained by the greater mortality of
females due to differential investment in reproduction (Lloyd and Webb 1977) and in
defense against herbivory (Jing and Coley 1990). However several studies have reported
a 1:1 sex ratio for many dioecious species (Opler and Bawa 1978, Bullock and Bawa

Dioecy is common in the flora of tropical forests (an estimated 26% of tree
species in Sarawak, Ashton 1969; 28% of tree species in Pasoh, Thomas and LaFrankie
1993; 15% of angiosperms in Hawaii, Sakai et al. 1995). Estimates of dioecy in the
worldwide flora range from 3-4% (Yampolsky and Yampolsky 1922) to 6% (Renner and
Ricklefs 1995). Dioecious tree species often occur in the forest understory (Muenchow
1987), are pollinated by small generalist insect species (Bawa and Opler 1975, Armstrong
and Irvine 1989a), and commonly have fleshy fruits (Givnish 1980). Although a causal
relationship between dioecy and several ecological factors have been suggested, there is
debate on the generality of these patterns (Sakai and Weller 1997). For example, recent
studies reveal that a range of pollination syndromes might occur in dioecious species:
wind (Charlesworth 1993), ambophilly (both wind and insect pollinated, Bullock 1994,
Culley et al. 2002), generalist pollinators (Bawa and Opler 1975), and specialized
pollinators (Renner and Feil 1993, but see Bawa 1994).
The genus *Garcinia* (Clusiaceae) is widespread in the paleotropics with about 400 species occurring in Asia alone (Whitmore 1973). The genus contains several important economic species such as *G. mangostana* (mangosteen), *G. cowa*, and *G. gummi-gatta*. Most reports of apomixy in the paleotropics have been restricted to the families Clusiaceae and Dipterocarpaceae (Richards 1990a). The incidence of apomixy in *Garcinia* has been shown to be high (*G. parviflora* Ha et al. 1988, *G. mangostana* Kaur et al. 1978, *G. stortechtinii* Thomas 1997, *G. hombroniana* Richards 1990b, *G. livingstonii* Puri 1939). Of the *Garcinia* species investigated, only *G. cantleyana* has been shown to lack apomixy, and Richards (1997) claims that hundreds of *Garcinia* species might be apomictic. In addition to reports of apomixy, many *Garcinia* species have female biased sex ratios, especially in South East Asian forests (Thomas 1997). Michaels and Bazzaz (1986) have shown that in *Antennaria parlinii*, apomictic individuals have lower competitive abilities than sexual forms. Kaur *et al.* (1978) have suggested that due to reduced genetic vigor apomictic individuals might be at a competitive disadvantage in diverse species assemblages. Although thirty one species of *Garcinia* occur in India (Maheshwari 1974) there is little information on the breeding systems of any of these species.

This study on the reproductive biology of *G. gummi-gatta* was conducted as part of a larger study on the impacts of fruit harvest on the biology of the species. Some of the questions I asked were a) Is *G. gummi-gatta* an apomictic species, as are several *Garcinia* in South East Asia? b) What is the mating system of *G. gummi-gatta*? c) How are *G. gummi-gatta* flowers pollinated? d) What is the flowering phenology and magnitude of flower production of male and female trees? e) Do sexes differ in their spatial
distribution, growth rate, and population structure? f) Do sex ratios deviate from 1:1, as they do in several tropical dioecious species?

**Study area and Methods**

The study was conducted in the forests surrounding Kelaginkeri village, within an area of approximately 45 sq km, situated in the Western Ghats, southern India. The forest belongs to the *Persea macrantha* - *Diospyros* spp.-*Holigarna* spp. type of Pascal (1988). The annual rainfall in the study area averages about 3700mm and is concentrated in the months of June to October. The altitude of the study area is 580 m. The landscape, which is typical of the Western Ghats, is a matrix of forest and farms. The soils of the study area are derived from Archaean rock, thus largely ferralitic, and belong to the Udalf group (Order Alfisols, in a high moisture regime) and the Tropepts group (Order Inceptisols) (Bourgeon 1989). A total of sixty six species of trees above 10 cm dbh were enumerated in three 1 hectare plots established in mature forests at different locations within the study region. This study was conducted at two sites: Nellithotta (NT) and Arekattu (AK), which are about three km apart. One hundred and seventy two *G. gummi-gatta* trees (> 10 cm DBH) were marked with numbered tags, and the diameter at breast height of each tree was measured in an area of approximately 2 ha in NT. In AK, all reproductive *G. gummi-gatta* individuals were mapped, tagged, and measured in a 100 x 100 m plot. In both sites the sex of each reproductive tree was recorded during flowering.

**Phenology and flower production:**

I visited 111 tagged reproductive *G. gummi-gatta* trees, once a week, to record if trees were in flower, fruit, or non-reproductive. A pair of binoculars was used to scan the canopy and determine flowering stage and sex. The abundance of flowers on each tree
was not estimated as the dense canopy made this estimation impossible. I followed the fates of 100 pistillate flowers on 4 trees to estimate time of anthesis, duration of receptivity, and time to flower abscission. To estimate flower production and timing I set up free-draining litter fall traps under three males (59, 48, and 22 cm dbh) and four females (55, 27, 37, and 42 cm dbh) in NT. Trees were chosen to represent the various size classes. Three traps, each measuring 1 m², were set up under the canopy of each tree. The trap consisted of a fine mesh cloth attached to a 1 m² metal grid, elevated 75 cm above the forest floor. Traps were positioned randomly under the canopy of the tree, the position chosen by the second hand of a watch. I collected the contents of the traps every ten days, and recorded the number of buds, petals, flowers, and fruits in each trap. To estimate the extent of the canopy I took measurements from the trunk of the tree to the outermost leaves in the four cardinal directions. Using the average of these four measurements as the radius, I estimated the area of the circle circumscribed by this radius and thus arrived at an estimate of the area under the canopy. Total flower production was subsequently calculated by extrapolating the sample from the litter fall traps to the area under the canopy. The total flower production of female trees was obtained by counting all fruits at the end of the fruiting season and adding it to the estimated total flower counts. Fruit set percentages were then obtained from the estimates of fruit and flower production thus derived. Using the estimates of total flower production I obtained the floral sex ratio, the ratio of functional female flowers to functional male flowers (Sutherland 1986).

Stephenson (1980) has shown that in Catalpa speciosa individual branches produce the energy required to mature the fruits they bear. Branches might therefore be
selected as units to determine fruit set and inter-annual variability. I counted all flowers on 5 branches of two female trees that were not used in the litter fall experiment (diameter at breast height of 27.2 and 40 cm). The number of fruits on the same branches was obtained after flowering ceased. The flower and fruit counts on these branches were repeated the following year to determine variability in flower production and fruit set. Data from the litter fall traps and the total branch flower counts were used to test the hypothesis that there is an inverse relationship between number of flowers produced and percentage fruit set (Stephenson 1980).

**Observations at flowering trees**

I observed male and female flowers for visitation by insects. I recorded the time of anthesis of male and female flowers, and the occurrence of visitation by insects to flowers. All observations were made on flowers close to the ground on 3 female and 3 male trees. Flowers were observed at a distance of 5m for visitation by bees and other mid to large sized insects and at 0.5 m for small insects. About 40 hours of observations were made between 1700 and 1900 hours in February and March, in 1998 and 1999. Insects collected from female flowers were immersed in a bath of Acetocarmine. The acetocarmine wash was then observed under a compound microscope for pollen.

**Pollinator exclusion experiment**

To determine if G. gummi-gatta is apomictic, I excluded pollen from the stigmatic surfaces of female flowers by covering flowers in fine nylon mesh bags. Flowers selected for the bagging treatments were located on the lower branches that could be reached from the ground. I have assumed that the position of the flower in the canopy does not influence results significantly. Flowers were bagged before they opened and the bags
were kept on until long after flowers senesced or fruits were produced. In 1998, 139 flowers in 30 bags, on five trees were thus enclosed. As a control, I tagged 134 flowers on the same five trees. In 1999, 187 flowers in 28 bags, on 8 trees were bagged. The number of fruit produced inside the bags was recorded after the flowering season. Based on the results obtained in 1998, I determined if isolated trees were more likely to be apomorphic. I chose four isolated female trees and enclosed 119 flowers in 16 nylon mesh bags and observed fruit set.

Wind pollination

To determine if pollination occurs by wind, I enclosed 155 flowers in 32 nylon mesh bags on 8 trees and estimated fruit set. The bags might allow the entry of pollen but not of insect pollinators. In a second experiment, I suspended thirty clear plastic tags, each measuring 5x2 cm, from the branches of two female trees. Each tag was coated with a thin film of Vaseline® to trap wind laden pollen. The tags were left in place for 48 hours and then observed under a microscope for the presence of pollen.

Time of fertilization

To determine the most likely time of fertilization, I covered one set of flowers with a fine nylon mesh to prevent visitation or pollen entry during the day and uncovered them at night, while another set of flowers were covered during the day and uncovered at night. While one set of flowers was bagged from 0600 to 1800 hrs, the other set was bagged from 1800 to 0600 hrs. This was repeated until the flowers either senesced or set fruit. Eight mesh bags were used for each treatment. Twelve flowers from 4 trees were selected for each treatment.
Intersexual differences in frequency, distribution, growth, and population structure

I obtained the sex ratio of adult trees in five sites within the study area: Arekattu (n=104), Nellithotta (n=135), Asolli (n=42), Sawle (n=30), and Hosalli (n=25). A total of 340 flowering *G. gummi-gatta* trees were observed and the sex of each tree was determined. A Replicated Goodness of Fit test (G₁ for homogeneity of populations, and Gₚ for total population) was used to test if male to female ratios were at parity (Sokal and Rohlf, 1995). The spatial distribution of male and female trees was determined in the 1 ha plot in Arekattu. The plot was divided into 10 m grids and X-Y coordinates for *G. gummi-gatta* trees was determined. The spatial pattern of male and female trees was analyzed using Ripley’s K estimate (for a detailed description see Duncan 1991, Haase 1995). This spatial point pattern analysis uses all plant to plant distances within a plot and the variance of these distances is used to estimate the degree of spatial distribution. The bivariate function $L_{12}(t)$, where $t$ is distance, estimates the spatial relationship of any two groups. To determine the degree of randomness, $L_{12}(t)$ was plotted against $t$. If $L_{12}t = 0$, the distribution is random, $L_{12}(t) > 0$ suggests association and $L_{12}(t) < 0$ indicates repulsion. The DOS program Spatial Analysis Programmes by Duncan (1990) was used to estimate $K_{12}$. $L_{12}(t)$ was then calculated using $L_{12}(t) = \sqrt{(K_{12}(t)/\pi)}-t$. To test if the deviation from random is significant, 95% confidence intervals were generated using Monte Carlo simulations. To determine the differences in the size-class distribution of male and female trees, I obtained the DBH of all reproductive individuals in the two populations. A Kolmogorov-Smirnov test was used to evaluate if size class distributions differed between sexes. Growth rates of male and female trees were estimated by obtaining three diameter measurements at three fixed points, 10cm apart, above the
buttress for each tree. The average of the three measures was recorded as the diameter for the current year. The procedure was repeated at the same three points a year later. The difference between the two measures estimates the annual growth increment. Three year growth increments were obtained for 9 male and 13 female trees in Nellithotta, and one year increment was obtained for 6 male and 13 female trees in Arekattu. A Mann-Whitney U test was used to determine if male and female trees differed in their growth rates.

Results

Floral morphology

Male and female flowers of *G. gummi-gatta* are remarkably similar in outward appearance, color, and size. Both flower types are usually red, but trees with yellow flowers are also observed. Male flowers occur in clusters of 15 to 20 flowers. Flowers have 4 petals and are about 12 mm wide, and 11 mm long. Anthers are attached to a pistillode with a non-functional stigma. Pollen is easily picked up by wind when flowers are tapped lightly. The exine of the pollen is reticulated and 4 colporate (Tissot *et al.* 1994). Female flowers occur singly or in clusters of up to 4 flowers. Female flowers are the same size as males, but they differ in the internal structure, with an enlarged stigmatic surface and no style. Pistillate flowers have rudimentary and nonfunctional staminodes. Neither male nor female flowers produce nectar.

Phenology and flower production

*G. gummi-gatta* trees flower during the dry months of February to May (Figure 3.1) although there is interannual variation in initiation and duration of flowering. While flowering in males was first observed on 5th March in 1998, flowering commenced on the
20th February in 1999. In any year, male trees commence flowering earlier than females (Figure 3.1). The flowering in both sexes lasts about 90 days. Male and female flowers within an inflorescence show staggered anthesis, with only one or few flowers opening on any day. Male flowers open between 1730 and 1830 hrs, while female flowers open between 1800 and 1900 hrs. Staminate flowers have a short life, changing color and wilting within 12 hours, while abscission occurs within 24 to 36 hours. Pistillate flowers open approximately 30 minutes after staminate flowers. Petals begin to drop at 1.85 days (SD= 0.67, range 1-3, n=67) after anthesis. The time to flower abscission for unfertilized flowers is 5.25 days (SD=2.14, range 2-11, n=47). Male flowers had shorter lives, averaging 1 day (SD= 0, n=55). Flower production by male trees (average 1505 ± 176 flowers m⁻²) is about eight times higher than that of female trees (average 188 ± 25 flowers m⁻²) (t test, p=0.000; Figure 3.2). The floral sex ratio, obtained from the average flower production of 4 female and 3 male trees, is 0.13 female flowers to 1 male flower. This estimate is at the lower end of the range of reported values for 31 dioecious species (Range 0.021 - 1.799, Mean 0.38 ± .125, Sutherland 1986).

**Fruit set**

The percentage of aborted fruits collected from litter fall traps for the four female trees were 35.3%, 6.2%, 7.5%, and 12% (Table 3.1). Fruit set percentages of around 25% was observed for three trees out of four trees (Table 3.1). The tree producing the largest number of flowers showed the lowest fruit set of 12.6%. This finding is corroborated by the flower counts on branches. A plot of the number of flowers on a branch and percent fruit set showed an inverse relationship, that larger flower yields result in lower fruit set (Figure 3.3)(Spearman’s correlation coefficient rₛ = -1.0, p < 0.01). Fruit set estimated
from the tagging of 134 control flowers on five other trees ranges from 15% to 45%. An inverse relationship is observed between fruit set and total fruit yield and tree size (Figure 3.4).

Pollinator exclusion

In 1998 only one of the five trees (ISOL 1) showed fruit set in mesh bags (Table 3.2). Thirty eight percent of enclosed flowers set fruit, while 35 % of control flowers set fruit, suggesting agamospermy in this tree. ISOL 1 is an isolated individual, removed from the nearest male by more than 50m. However, flowers that were bagged on this individual and other isolated individuals (ISOL 2-4) the following year, showed no fruit set (Table 3.2). Eight percent of flowers enclosed in pollen entry bags in 4 of the 6 trees set fruit, while only one of the 187 flowers in pollen exclusion bags set fruit (Table 3.2).

Time of fertilization

The night and day bagging experiment revealed that flowers are mostly pollinated at night, as none of the flowers whose stigmatic surfaces were exposed during the day showed any fruit set, while 2 of the 12 flowers exposed at night were pollinated and set fruit. This corroborates observational evidence such as the synchrony of anthesis of male and female, and the timing of anthesis.

Observations at flowering trees

Observations at flowers revealed that stingless bees belonging to the genus Trigona exclusively visited male flowers to collect pollen and were seen with full corbiculae. No Trigona were seen at female flowers. Hence Trigona discriminated between male and female flowers. Large bees of the genus Xylocopa were often seen around flowering trees, but not seen visiting either male or female flowers. Other visitors
at male flowers, feeding on the pollen were ants and thrips, while these insects were not seen to visit female flowers. Weevils (*Derelomus* sp) (Coleoptera: Curculionidae) were the only visitors that were observed on both male and female flowers.

Examination of Acetocarmine wash of thirty weevils collected from female flowers did not show any pollen. Although I found no clear evidence of pollen carriage, weevils collected from male flowers had pollen grains adhering to their bodies, suggesting that these weevils might be the primary pollinators of *G. gummi-gatta*. Observations under a microscope revealed that the pollen exine is reticulate, a morphology that is not atypical of wind pollinated species (Bullock 1994, Faegri *et al.* 1989). However, Vaseline® smeared tags suspended below female flowers did not capture any pollen.

**Intersexual differences in frequency, distribution, growth, and population structure**

The sex ratios of *G. gummi-gatta* in five sites are given in Table 3.3. A replicated goodness of fit test showed that sex ratios in the five sites were homogeneous ($G_H = 1.45, df = 4, p = 0.18$) and did not differ from a 1:1 female to male ratio ($G_T = 1.86, df = 5, p=0.13$). Male and female trees are randomly distributed at all distances ($p > .05$, Figure 3.5). A Kolmogorov-Smirnov test of size class distribution of male and female trees in the Nellithotta and Arekattu plots showed no significant difference (NT, $p=.893$; AK, $p=.699$; Figure 3.6). A comparison of male and female trees in the larger size classes (>50 dbh in NT, > 40 dbh in AK) showed significant difference in Nellithotta with a greater number of males in the 50-59.9 cm size class and no males in the >60 cm size class ($\chi^2 = 6.62, p = .01$), while in Arekattu the difference is not significant ($\chi^2 = 1.92, p = .16$). The decrease in number of individuals from the 40 - 49.9 size-class to the 50-59.9
size-class is 13% for males and 63% for females in NT, and 16% for males and 80% for females in AK, suggesting higher mortality of females in both sites in the larger size classes. The annual growth increment of male and female trees in two populations showed no difference in both populations (Mann Whitney U test; NT: p= 0.40; annual increment: male = 39.7 ± 29.6 mm, female = 27.1 ± 17.6 mm; AK: p= 0.69; annual increment: male = 24.0 ± 14.9 mm, female = 12.9 ± 47.4 mm).

Discussion
Flowering and fruiting phenology

*G. gummi-gatta*, which grows in seasonal wet forests and is animal dispersed, shows a phenological pattern of dry season flowering and wet season fruiting. Several species in the seasonal tropical forests of India flower in the dry months (Murali and Sukumar 1994, Murali 1997). This interspecific synchrony in flowering is coincident with high insect densities which might in turn be responding to the availability of floral resources. Frankie *et al.* (1974) found that twice as many tree species flower in the dry season as in the wet season. Janzen (1967) suggests that trees flower in the dry season as that is when there is least interference with vegetative processes as trees would have built up reserves during the wet growing period, and due to the optimization of pollinating agents. In a study of the phenology of 54 species in two sites differing in soil moisture content in a seasonal tropical forest in India, Murali and Sukumar (1994) found that flowering in the moister site peaked in the dry season and flowering in the drier site peaked in the wet season. Animal dispersed species on the moist site flowered in the dry season and fruited in the wet season. For species that are dependent on generalist pollinators, the critical factor in the evolution of flowering seasonality might be fruit
development and seed dispersal rather than pollinator availability per se. Borchert (1983) has suggested that flowering in tropical trees is controlled by internal physiological factors such as tree water status rather than by the selection of optimal tree-pollinator interaction. In sites that experience strong seasonality, female trees might be dependent on rainfall during a resource demanding period such as fruit development and for the requirement of moisture to maintain turgor pressure (Smythe 1970). The increased probability of pollination in the dry season, and optimum fruit development during the wet season might explain why *G. gummi-gatta*, which appears to be pollinated by generalist small beetles, flowers in the dry and fruits in the wet season.

Synchronous flowering of male and female flowers has been shown to increase pollinator visitation rates and fruit set in a tropical shrub *Hybanthus prunifolius* (Augspurger 1980, 1981). However Stephenson (1982) has shown that rates of outcrossing in *Catalpa speciosa* were highest towards the end of the flowering season when the ratio of male to female flowers is low. Female *G. gummi-gatta* trees attain peak flowering well after male trees. I have observed that female *G. gummi-gatta* flowers which offer no rewards to pollinators, attract small insects due to their similarity to male flowers. By delaying flowering, female trees might increase the probability of visitation by pollinators.

In a review of literature on flower longevity, Primack (1985) found that flower life spans of 1 to 1.3 days for 81 species in tropical forest. It has also been found that in dioecious species, male flowers have significantly shorter life spans than females (Primack 1985). *G. gummi-gatta* female flowers have a mean longevity of 1.85 days and that of males is 1 day, which compares well with the average for tropical species. There is
however no information on whether stigmatic surfaces of *G. gummi-gatta* flowers stay receptive after flowers have lost their corolla and color.

**Intersexual differences**

Dioecious species have been reported to have a male bias due to females experiencing higher mortality because of the greater cost of reproduction, and flowering at an earlier age by males (Lloyd and Webb 1977, Thomas and LaFrankie 1993). Males have been shown to have higher rates of growth and longer survivorship than females (Lloyd and Webb 1977, Putwain and Harper 1972). Males however expend greater energy than females before fertilization due to the larger number of flowers produced (Bawa and Opler 1977). The greater mortality of female *G. gummi-gatta* trees in the larger size classes does not seem to affect the sex ratio, assuming that the populations are in equilibrium. Moreover I did not find more males flowering in the smaller size classes suggesting that males and females do not differ in time to first reproduction, neither did males grow faster than females. Male biased sex ratio as seen in several dioecious species is not apparent in *G. gummi-gatta*. This parity in sex ratio, despite higher female mortality, might be due to the presence of apomixy. The pollen exclusion study suggests that *G. gummi-gatta* might be a facultative apomict. Seeds produced by apomixy produce female seedlings (Richards 1997), which might skew the sex ratio of juveniles towards females, thus swamping the male bias that might be produced by a purely outcrossing dioecious species. I have observed that *G. gummi-gatta* also reproduces from root suckers but the extent of sprouting from root suckers is unknown. However the spatial distribution of male and female trees gives no indication of vegetative propagation. Large seed dispersal distances might ensure that seeds of apomictic individuals are not
clumped, thus low levels of apomixy might not be revealed by the spatial pattern of the sexes. The similarity in growth rates of male and female trees might be due to lack of resource constraints in the habitat, thereby the greater resources required for reproduction might be readily available (Wallace and Rundel 1979), similar investment in reproduction by males and females, or inter-annual variation in flower production (Delph 1997).

**Apomixy**

Apomixy might be indicated if the species shows very consistent fruit crop sizes (Turner 2001) and polyembryony, the occurrence of multiple seedlings from a single seed (Kaur *et al.* 1979, but see Ganeshaiah *et al.* 1991 for arguments against equating polyembryony with asexual reproduction). While my studies on fruit yield variation showed that trees produced fruit annually there was little evidence of constant production. Three year data on fruit production for 11 trees showed significant variation in fruit yield (*personal observation*). Out of the 1767 seedlings enumerated in a .4 ha plot I found only three instances of polyembryony. Richards (1990b) has shown that isolated female *G. hombroniana* trees will set fruit by agamospermy. Preliminary observations indicate that *G. gummi-gatta* females might switch to apomixy when they find themselves far from pollen pools, and that the switching might even be temporal, as I did not observe apomictic fruit set the following year.

**Sexual mimicry and insect pollination**

The similarity in the structure of male and female flowers might be due to the evolution of intersexual mimicry to induce ‘mistake’ visitation by insects (Baker 1976, Bawa 1980, Willson and Ågren 1989). Renner and Feil (1993) report that in a third of the species they surveyed, the female flower offered no reward to pollinators. ‘Mistake’
pollination has been reported for several species (Baker 1976, Ågren and Schemske 1991, Armstrong and Irvine 1989b). In the old world flora female flowers of many species do not offer any rewards to insects and are mistakenly pollinated by generalist small beetles (Armstrong and Irvine 1989a, Armstrong and Drummond 1986). G. gummi-gatta appears to be pollinated in the study area by a small weevil in the genus Deleromus (Curculionidae). The pantropical genus Deleromus in which 23 species have been identified, are pollinators of palms (Areccaceae) (Anstett 1999). Dufaÿ et al. (2003) have shown that in Australia, the leaves of the palm Chamaerops humilis produce an aromatic exudate that attracts the weevil, Deleromus chamaeropsis, which is the sole pollinator of the species. The main cash crop of the study area is the palm, Areca catechu, which suggests that the weevil is not exclusive to G. gummi-gatta. It is likely that in other parts of the range of G. gummi-gatta the suite of pollinators might be different, and varied, depending on the insect diversity at the site. In a survey of pollination systems in an Asian tropical forest, Momose et al. (1998) found that 56 out of 270 tree species studied (21%) were beetle pollinated. Characteristics of flowers that are beetle pollinated include yellow to red flower color, strong fragrance during anthesis, and lack of nectaries in the female flower (Armstrong and Drummond 1986), all of which are characteristics of G. gummi-gatta flowers. The pollination system in G. gummi-gatta lends credence to the ‘Bawa hypothesis’ (Renner and Feil 1993) that dioecious species are mostly pollinated by small, unspecialized pollinators.

Weevils are probably attracted to the olfactory cues exuded by both male and female flowers. Weevils feed on pollen that is available only in male flowers. Pollen is also rapidly harvested by bees belonging to the genus Trigona as soon as flowers open.
This competition for pollen might force beetles to fly in search of flowers on neighboring trees. The delayed anthesis of female flowers further encourages ‘mistake’ visitation when pollen from male flowers is exhausted. For a deceit pollinated species, the end of the flowering season is critical as the ratio of male to female flowers decreases due to the decline in male flowering and continued flowering by females, resulting in a greater frequency of visits by insects to female flowers (Stephenson 1982). Weevils (Curculionidae) are known to fly some 20 m between trees (Armstrong and Irvine 1989b). The smell of female flowers may attract weevils, and pollen adhering to the body of weevils may be deposited on the sticky stigmatic exudate. While the actual pollination is probably by weevils, larger bees feed on the pollen without aiding in pollination.

Hymenoptera such as honey bees have been shown to discriminate between the sexes of flowers (Kay 1982, Kay et al. 1984). Roubik (1989) has listed several dioecious species in Panama that are visited by honey bees for pollen but are not pollinated by them. Charlesworth (1993) states that discrimination by pollinators in many plant species is a disadvantage for female flowers and that this could result in such costs as reduced visitation and fertility. It is interesting to note here that George et al. (1992) have reported the presence of sterile and low viability pollen in the female flowers of southern populations of G. gummi-gatta, in Kerala, India. This suggests that female flowers in certain G. gummi-gatta populations might offer pollen as a reward, and thus be pollinated by bees. However there is no information on the pollinators of these populations, and it is not known if female flowers are visited by Trigona as is the case in many Garcinia species in S.E. Asia (Richards 1997).
Studies have shown that many dioecious species are ambophilous, both animal and wind pollinated (Culley et al. 2002). There is some indication, however tenuous, that pollination in *G. gummi-gatta* might be ambophilous. The relatively high percentage of fruit set inside pollen entry bags (8.4%), the presence of dry, non sticky pollen, small pollen size (22-29 µm, Tissot et al. 1994), and dry season flowering indicates the possibility of wind pollination. The exine is reticulate and not heavily sculpted, suggesting that it could be dispersed by wind (Fægri et al. 1989). Activity of *Trigona* bees in and near male flowers might help disperse the dry pollen in the wind (Fægri and van der Pijl 1979).

**Conclusion**

Bawa (1980) posits that there is high maternal investment in fruit and seed so as to enable the developing seedling to survive low light conditions on the tropical forest floor, by providing seed reserves, and that dioecy, through the segregation of male and female functions, and through genetic vigor provided by outcrossing, enables the production of larger seeds. Muenchow (1987) however suggests that the relationship between fleshy fruit and dioecy might be indirect, and that they might both be related to the understory habitat of most dioecious species. *G. gummi-gatta*, an understory species, has a fleshy fruit with large seeds (1.14 ± 0.24 g, n=301) with long dormancy, and is dispersed zoochorously by Bonnet macaque (*Macaca radiata*) and Common langur (*Presbytis entellus*), and endozoochorously (passage through the gut) by Palm civets (*Paradoxorus hermaphroditus*) (N. Rai, *unpublished data*). Langurs disperse seeds under the canopy or a few meters away from the tree, while macaques often fill their cheek pouches with the pulp and seeds, carry it to a safe feeding post, often a high canopy tree.
several tens of meters away, where the seeds are discarded and the pulp consumed. The civet disperses seeds the farthest by swallowing the pulp and seeds whole, and passing seeds through the digestive tract. The large home range of civets, which are omnivorous, ensures that seeds are dispersed over great distances.

I suggest that the evolution of fleshy fruits in dioecious species, especially in species that are pollinated by small insects, might be due to the dynamics of gene flow. In a species pollinated by beetles and small insects, pollen mediated gene flow might be limited due to the small distances flown by small insects and hence distances of pollen travel are short (Nason and Hamrick 1997). Seeds of fleshy fruits are dispersed farther by large animals, hence gene flow through seed dispersal is higher than pollen mediated gene flow. The correspondence between generalist insect pollinated flowers and the presence of fleshy fruits in dioecious species might be explained by the advantages accrued to a species that increases gene flow. The reduced pollen mediated gene flow is compensated for by better seed dispersal while the ecological benefits of larger seeds, such as improved probability of establishment, and colonization of safe sites far from adults, are immense (Leishman and Westoby 1994). All this while decreasing the cost of elaborate floral displays, provision of nectar, and longer flower longevities that might attract larger pollinators, but place demands on resource acquisition at a time when resources are limiting, as during the dry season when many dioecious species are flowering. This hypothesis could be tested for a range of species differing in their pollination and dispersal syndromes.
References


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<td><strong>Total flower production</strong></td>
<td><strong>36727</strong></td>
<td><strong>13009</strong></td>
</tr>
<tr>
<td>No. of aborted fruits (%)</td>
<td>256(35)</td>
<td>41(6.3)</td>
</tr>
<tr>
<td>Percent fruit set</td>
<td>12.6</td>
<td>24.8</td>
</tr>
</tbody>
</table>

Table 3.1. Litter fall trap data for four female and three male *G. gummi-gatta* trees in the Western Ghats, India. a Average ±SE (of three 1x1m traps per tree). b Litter fall trap data extrapolated to the canopy extent = (a* canopy area). c Yield obtained by complete count of fruits after fruit harvest. d Estimated from a regression of DBH vs. yield of 51 trees in closed canopy forest in 1998. e Fruit yield + b. f No. of aborted fruits in 3 m² litter fall trap, percentage is that of number of flowers collected in 3 m², = (a*3). g Fruit set = Fruit yield / Total flower production.
<table>
<thead>
<tr>
<th>Year</th>
<th>Tree #</th>
<th>No. flowers bagged</th>
<th>Fruit set (%)</th>
<th>Control – flowers tagged</th>
<th>Control – fruit set (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>SB2</td>
<td>17</td>
<td>0 (0)</td>
<td>20</td>
<td>9 (45)</td>
</tr>
<tr>
<td></td>
<td>SB3</td>
<td>25</td>
<td>0 (0)</td>
<td>33</td>
<td>5 (16)</td>
</tr>
<tr>
<td></td>
<td>SB4</td>
<td>32</td>
<td>0 (0)</td>
<td>27</td>
<td>4 (15)</td>
</tr>
<tr>
<td></td>
<td>SB5</td>
<td>33</td>
<td>0 (0)</td>
<td>20</td>
<td>4 (20)</td>
</tr>
<tr>
<td></td>
<td>ISOL1</td>
<td>32</td>
<td>12 (38)</td>
<td>34</td>
<td>12 (35)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>139</td>
<td>12 (9)</td>
<td>134</td>
<td>34 (25)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Tree #</th>
<th>No. flowers</th>
<th>No. fruit set</th>
<th>Insect and Pollen exclusion</th>
<th>Insect exclusion/Pollen entry</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999</td>
<td>ISOL1</td>
<td>34</td>
<td>0</td>
<td>24</td>
<td>6 (25)</td>
</tr>
<tr>
<td></td>
<td>ISOL2</td>
<td>31</td>
<td>0</td>
<td>31</td>
<td>1 (3)</td>
</tr>
<tr>
<td></td>
<td>ISOL3</td>
<td>32</td>
<td>0</td>
<td>22</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>ISOL4</td>
<td>22</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>KDGM</td>
<td>30</td>
<td>0</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>SB2</td>
<td>17</td>
<td>0</td>
<td>30</td>
<td>5 (17)</td>
</tr>
<tr>
<td></td>
<td>SB3</td>
<td>7</td>
<td>1</td>
<td>20</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>SB5</td>
<td>14</td>
<td>0</td>
<td>28</td>
<td>1 (4)</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>187</td>
<td>1</td>
<td>155</td>
<td>13 (8)</td>
</tr>
</tbody>
</table>

Table 3.2. Fruit set in G. gummi-gatta flowers enclosed in mesh bags to exclude insect and pollen.
<table>
<thead>
<tr>
<th>Site</th>
<th>Male trees</th>
<th>Female trees</th>
<th>Ratio (M / F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arekattu</td>
<td>50</td>
<td>54</td>
<td>0.93</td>
</tr>
<tr>
<td>Nellithotta</td>
<td>74</td>
<td>61</td>
<td>1.21</td>
</tr>
<tr>
<td>Asolli</td>
<td>21</td>
<td>21</td>
<td>1.00</td>
</tr>
<tr>
<td>Sawle</td>
<td>16</td>
<td>14</td>
<td>1.14</td>
</tr>
<tr>
<td>Hosalli</td>
<td>12</td>
<td>13</td>
<td>0.92</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>173</strong></td>
<td><strong>163</strong></td>
<td><strong>1.06</strong></td>
</tr>
</tbody>
</table>

Table 3.3. Sex ratio of *G. gummi-gatta* trees at five sites around Kelaginkeri, Western Ghats. Ratio is number of male trees to one female.
Figure 3.1. The flowering phenology of male and female *G. gummi-gatta* trees in Kelaginkeri, Western Ghats.
Figure 3.2. Flower production in 3 male and 4 female *G. gummi-gatta* trees in Kelaginkeri, Western Ghats. Data is from litter fall trap samples of 3m² under the canopy of each tree.
Figure 3.3. Flower production and fruit set of selected branches of two female *G. gummi-gatta* trees in Kelaginkeri, Western Ghats. Data from 1998 and 1999.

![Graph showing flower production and fruit set](image)

\[ y = -0.01x + 43.77 \]

\[ R^2 = 0.97 \]

<table>
<thead>
<tr>
<th>Tree #</th>
<th>Branch #</th>
<th>Branch diameter (mm)</th>
<th>1998</th>
<th>1999</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td># of flowers</td>
<td>Percent fruit set</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>44.1</td>
<td>73</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>56.6</td>
<td>144</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>98.7</td>
<td>1831</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>2048</td>
<td>14</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>130.2</td>
<td>336</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>92.0</td>
<td>117</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>453</td>
<td>35</td>
</tr>
</tbody>
</table>

Figure 3.4. Percent fruit set as a function of tree size (A) and total fruit yield (B) for 6 G. gummi-gatta trees in open canopy forest in Kelaginkeri, Western Ghats. Fruit set estimated from litter fall trap data for three trees, and by complete counts of flowers and fruits on selected branches of 2 trees, and tagging of control flowers on one tree. Fruit yield estimated by obtaining total counts of fruits by harvesting ripe fruits.

\[ y = -1.45x + 93.58 \]

\[ R^2 = 0.96 \]

\[ y = -0.01x + 72.69 \]

\[ R^2 = 0.89 \]
Figure 3.5. A) Spatial distribution of adult male and female *G. gummi-gatta* trees > 10 cm DBH, in 1 ha in Uttara Kannada, Western Ghats. B) Ripley’s K plot of association between male and female trees in AK. Dashed lines are 95% confidence interval.
Figure 3.6. Distribution of male and female *G. gummi-gatta* trees in dbh size classes in Nellithotta (A) and Arekattu (B) in the Western Ghats.
CHAPTER 4

FRUIT PRODUCTION, SEED PREDATION, SEEDLING RECRUITMENT, AND POPULATION ECOLOGY OF A NON-TIMBER FOREST PRODUCT, *Garcinia gummi-Gatta*, IN THE WESTERN GHATS, INDIA.
Introduction

Peters et al. (1989) suggested that the harvest of non-timber forest products (NTFP) by local communities, instead of the extraction of timber, might decrease rates of tropical forest loss. However, the impact of NTFP extraction on the ecology of harvested species can be significant (Padoch 1992, Hall and Bawa 1993, Pollak et al. 1995, Peters 1996a). In India, non-timber forest products are extensively harvested from such forest tree species as Phyllanthus emblica (fruits), Madhuca indica (flowers), Diopyros melanoxylon (leaves), Cinnamomum zeylanicum (bark), and Vateria indica (resin). There is however little information on the ecological effects of NTFP harvest from forests in India (but see Murali et al. 1996, Uma Shankar et al. 1996, Sinha 2000 all on Phyllanthus emblica in dry forest).

Schupp and Fuentes (1995) suggested that in order to understand the ecology of a plant species, studies of the different life history stages should be integrated. Due to mortality of individuals at each stage of the life history of a tree species, an extremely small fraction of seeds become adults. Peters (1990a) estimated that approximately 1 out of 1.5 million seeds of the rain forest tree Brosimum alicastrum makes it to the adult stage. Plant populations are influenced by such factors as seed size (Harper et al. 1970), seed resources (Leishman and Westoby 1994), seed dormancy (Vazquez-Yanes and Orozco-Segovia 1986), persistence of seedling in shade (Popma and Bongers 1988), seedling morphology (Garwood 1996), and response of seedlings to light (Brown et al. 1999). In addition, the harvest by humans of animal-dispersed fruits might affect seed dispersal and thus the arrival of seeds at ‘safe sites’ (Harper 1977). The study of the
ecology of seed production, seed dispersal, and seedling establishment is therefore essential for an understanding of the life history of a harvested species.

I studied a tropical tree, *Garcinia gummi-gatta*, whose fruits are harvested by local people in the wet forests of the Western Ghats, India. I investigated aspects of fruit production, seed dispersal, seed predation, seedling growth, seedling survival, tree growth, and size class distribution. The principle questions I addressed were: Is there variation in annual fruit production by *G. gummi-gatta* trees? Is there a relationship between tree size and fruit production? How are *G. gummi-gatta* seeds dispersed? What are the rates of *G. gummi-gatta* seed predation? What is the pattern of seedling growth and survival in shade and canopy gaps? What is the spatial distribution of seedlings, saplings, and adult female trees? What is the rate of growth of *G. gummi-gatta* trees? What is the density, size class distribution and population growth rate of *G. gummi-gatta*?

**Natural history of *G. gummi-gatta***

*G. gummi-gatta* grows on the humid slopes of the Western Ghats, up to an altitude of 1000 m (Tissot *et al.* 1994). The species occurs in the understory of high canopy forests in the Western Ghats of India and in Sri Lanka (Ramesh and Pascal 1997). In forests were the canopy is low, probably as a result of shallow soils (Burgeon 1989), *G. gummi-gatta* occurs in the canopy (Pascal 1988, Ramesh and Pascal 1997). The tree has a dark, smooth bark with an average thickness of 5.3 mm (Hegde *et al.* 1998). Trees grow to an average height of 18m and the largest *G. gummi-gatta* trees in closed canopy forest were around 60 cm diameter. In some cases trees in open canopy forest attained diameters of 80 cm and heights of up to 29m. I estimated the canopy radius of an aduly
G. gummi-gatta tree to be 4.6 m (S.D. = 1.2 m, n = 7 trees). The specific gravity of the wood of adult G. gummi-gatta trees is 0.76 (Rai and Proctor 1986).

G. gummi-gatta trees are dioecious, with a male to female sex ratio of 1:1 (N. Rai, unpublished data). Trees of both the sexes usually commence flower production when they are about 14 cm in diameter. Male and female trees produce flowers from early February to April, and the fist-sized fruits which weigh about 80 g, ripen from June to August. While unripe G. gummi-gatta fruits are green; the ripe fruit is bright yellow, a color associated with many monkey dispersed fruits (Janson 1983, Terborgh 1986). In the study area, the pulp of G. gummi-gatta fruits is consumed by two primate species (Presbytus entellus and Macaca radiata) and two species of civets (Paradoxurus hermaphroditus and P. jerdonii). The seeds are consumed by two species of arboreal squirrels (Ratufa indica and Funambulus palmarum).

Local people harvest the fruit of G. gummi-gatta, and the dried rind is sold to factories where Hydroxy-citric acid is extracted and exported. Hydroxy-citric acid has been reported to reduce human body weight (Sergio 1988) and is widely used in the U.S.A. G. gummi-gatta seeds are about 5 cm long and 2 cm wide and weigh about 1.1 g. Seeds lie dormant for 8 months (Mathew and George 1995, Chacko and Pillai 1997), which coincides with the amount of time between the cessation and onset of annual rainfall.

The Study area

The Western Ghats of India has been identified as one of twenty five global biodiversity ‘hotspots’, and one of eight ‘hottest hotspots’ (Myers 1990, Myers et al. 2000, due to high levels of endemic plant and animal species, and the high risk of species extinction largely due to forest fragmentation (Ramesh et al. 1997). The Western Ghats
are a hill range that extends from 8° N to 22° N, a length of about 1600 km, and parallel to the western coast of India. I conducted the study in the forests surrounding Kelaginkeri village (14° 30' N and 74° 45' E) in Uttara Kannada district of Karnataka state. The forests belong to the Wet Tropical Forest of the Holdridge classification system. The forests occurring on the hill top and western slopes of the Western Ghats in Uttara Kannada district belong to the Persea macrantha - Diospyros spp.-Holigarna spp. type (Pascal 1988). The annual rainfall in the study area averages about 3700mm and is largely restricted to the monsoon months of June to October, resulting in a dry season that lasts 7 months. The average altitude of the study area is 580 m. The landscape, which is typical of the Western Ghats, is a matrix of forest and cultivated land, with 79% of the area being classified as forest (Nadkarni et al. 1989).

The soils of the study area belong to Archaean rock-derived, Dharwar schists, which are largely ferralitic soils belonging to the Udalf group (Order Alfisols in a high moisture regime) and the Tropepts group (Order Inceptisols) (Bourgeon 1989). The soil profile is characterized by unweathered rocks and the nutrients are concentrated in the humus layer.

**Methods**

**Fruit production**

I estimated the fruit yield of *G. gummi-gatta* trees during fruit harvest, after fruits were felled to the ground by collectors. Yield estimates for a total of 169 different *G. gummi-gatta* trees were obtained from 1998 to 2001. The number of trees sampled each year over the four year period was 81, 56, 87, and 23 trees. Continuous data for three years was obtained for 11 trees. The diameter of each tree was measured. The forest type
was subjectively recorded as either being closed canopy or open canopy forest based on if the canopy layer was contiguous or if *G. gummi-gatta* trees were isolated from other trees.

Population-level variation in inter-annual yield of *G. gummi-gatta* trees was determined by estimating the coefficient of variation (CV) of the average annual fruit production following Herrera (1998b). Average fruit yield per tree was obtained for each of the 4 years and the CV of the yearly averages estimated the population CV (henceforth CV-p). CV-p was calculated for trees in closed canopy forest (n=124), trees in open canopy forest (n=39), and for the pooled sample (n = 163).

Within plant variance in yield was obtained over a three-year period for 11 trees for which continuous three year data were available. The coefficient of variation was estimated for each tree and then averaged to obtain the average CV of individual trees (henceforth CV-i). To determine if there was synchrony in inter annual fruit production of *G. gummi-gatta* trees I obtained the Kendall’s coefficient of concordance for the fruit yield estimates of 11 trees over the three years.

I used tree diameter as a surrogate for tree size, and determined if there is a relationship between tree size and fruit yield. I obtained the linear regression between diameter and fruit yield for trees in open and closed canopy forests for the years 1998 to 2001. Trees with diameter greater than 60cm were removed as exploratory data analysis showed that larger trees produced fewer fruits suggesting that fruit production decreased after a threshold tree size probably due to senescence. I compared total fruit production in open and closed canopy forests for each year. I controlled for tree size by dividing the
number of fruits produced by the basal area of *G. gummi-gatta* trees to obtain the number of fruits produced per cm$^3$ of wood.

To determine if there was a significant curvilinear relationship between tree size and average annual fruit yield, I used the estimates of fruit yield of *G. gummi-gatta* trees for which two or more year data was obtained (n= 57). I included trees with diameter greater than 60 cm in this analysis. The yield estimates were log transformed as the plot of residuals versus fitted values showed uneven variance. A polynomial regression between dbh and log$_{10}$(fruit yield) was then obtained.

The weights of rind, pulp, and seeds were obtained from 56 fruits from 6 randomly selected trees. The rind was oven dried in the lab and the weight was obtained. Average seed wet weight was obtained from a sample of 300 seeds taken from the randomly selected fruits of the above 6 trees. Two hundred seeds were weighed after removing the thick seed coat to obtain the weight of cotyledon and embryo.

**Seed dispersal**

To identify the possible seed dispersers of *G. gummi-gatta*, I compiled a list of possible frugivores that occur in the study area from Prater (1998). The list includes two primates (*Presbytus entellus, Macaca radiata*), one squirrel (*Ratufa indica*), two civets (*Paradoxurus hermaphroditus, P. jerdonii*), and three species of bats (*Cynopterus sphinx*), and one species of deer (*Cervus unicolor*). I conducted feeding trials at the Karnataka Forest Department Zoo in Sirsi, Uttara Kannada, to determine the mode of feeding of some of these species. Two individuals each of *P. entellus*, and *M. radiata*, one individual of *P. hermaphroditus*, and twelve individuals of *C. unicolor* were fed ripe *G. gummi-gatta* fruits and their behavior observed. Seeds that were ingested were
collected after passage through the gut. To determine if bats consumed *G. gummi-gatta* fruits, I observed two fruiting trees for two hours each night for four consecutive nights.

Population ecology

I established a permanent 100x100m plot (henceforth denominated as the permanent plot) in closed canopy forest for the long-term monitoring of *G. gummi-gatta* individuals. The plot was established on a horizontal plane to correct for the uneven topography, and subdivided into 10x10m plots. All *G. gummi-gatta* individuals greater than 0.5m height were mapped to the nearest 0.1m by obtaining the slope, angle, and distance to the base of the stem from the north-west corner of each 10x10m subplot. All stems were tagged, and the diameter at 1.3 m height (henceforth diameter) was measured. The first enumeration was in March - April 1999, and individuals were recensused in April 2000 and April 2001.

I established a 40 x 100m plot within this permanent plot and mapped the location of all *G. gummi-gatta* seedlings (< 0.5 m height). The plot was subdivided into 2x2 m plots. I estimated the canopy cover for each 2x2m plot using a spherical densiometer. I determined the occurrence, growth, and mortality of *G. gummi-gatta* seedlings within this plot from 1999 to 2001. At each census, I measured the height, collar girth, and number of leaves of each *G. gummi-gatta* seedling. The first enumeration was conducted in May 1999. In December 1999, eighteen of the forty 10x10m plots were enumerated to determine the number of *G. gummi-gatta* seedlings that germinated during the monsoon rains. The entire 0.4 ha plot was re-censused in May 2000 and May 2001.

In an open canopy forest site I enumerated and tagged 172 *G. gummi-gatta* trees greater than 10 cm diameter. I selected *G. gummi-gatta* trees from this sample for the
estimation of growth rates and fruit production. The open canopy forest is private forest that is used by local households for the extraction of fuel wood, green leaves, and litter. In addition to the removal of a few trees for timber, the undergrowth is periodically cleared to obtain mulch for *Areca catechu* palm plantations.

**Seed predation**

I tested the hypothesis that seeds dispersed under parent trees experience higher rates of predation than seeds dispersed away from parent trees (Janzen 1970) in the permanent plot. As all *G. gummi-gatta* individuals in the permanent plot were mapped, I chose eleven points within the plot that were identified as being greater than 10m from a fruiting female *G. gummi-gatta* tree, and established one 0.5 x 0.5m plot at each point. In each plot I provisioned 16 seeds for a total of 176 seeds. Nine reproductive female *G. gummi-gatta* trees were randomly selected and a single 0.5 x 0.5 m plot was located below the canopy of each for a total of 144 seeds. To prevent seeds from being washed away in the characteristic heavy rain, and to ensure relocation, all seeds were attached to stakes inserted into the ground, using 0.5m thin black string which was tied around the middle of the seed.

Grubb (1996b) suggested that sites with higher tree species richness have higher rates of seed predation than sites with lower tree species richness. I tested this hypothesis by selecting two sites. In addition to the above permanent plot site I selected a site with a higher tree species diversity. Site 1 (the less diverse site) in the permanent plot, had a floristic composition of 35 tree species ha\(^{-1}\) (>10 cm diameter) and Site 2 (the more diverse site) contained 46 tree species ha\(^{-1}\) (>10 cm diameter). In Site 2, I provisioned 370 seeds in clusters of ten, at distances between 0 and 10m from the stems of three
female *G. gummi-gatta* trees. Each cluster consisted of ten seeds placed within a 0.5 x 0.5m plot. I pooled data from the below canopy and away from canopy plots in Site 1 for the analysis of differences in seed mortality between diverse and less diverse sites.

In a separate experiment I determined if seeds were being cached by rodents. I attached 1m long fine string to 100 seeds. A small piece of orange flagging tape was then attached to the end of the string to enable locating seeds in case seeds were moved from the original location by seed caching animals. If seeds were moved by predators, the numbered seed flags were recovered and distance from the original location recorded. Twenty clusters of 5 seeds each were placed at varying distances of 0 to 10m from the trunk of two adult female *G. gummi-gatta* trees.

All seed predation plots at both sites were established during peak fruit production and monitored for 10 months. The plots were visited on days 1, 2, and 4 of the first week, once a week for the first month, once every two weeks for the second and third month, and subsequently at four, seven and ten months.

The mortality of seeds in diverse versus non-diverse forest, and the below canopy versus far from canopy seed plots were compared using the nonparametric log rank test (Pyke and Thomas 1986). For the between-site comparisons, data from all plots within a site were pooled. Census dates were used as the time to mortality of eaten or missing seeds. The data were considered to be censored as not all seeds were eaten or missing by the end of the study. The statistical package Minitab was used to generate survivorship curves and Kaplan-Meir survival estimates?
Seedling growth

All *G. gummi-gatta* seedling data was obtained from the 0.4 ha subplot within the permanent plot. I determined if there was relationship between the height increment of *G. gummi-gatta* seedlings and canopy cover above seedlings. The annual increment in height of seedlings was determined from the difference in height between census dates. As most seedlings in the 0.4 ha seedling plot were under a canopy cover of >85%, I increased the sample of seedlings growing in more open canopy cover by sampling in two tree fall gaps outside the 0.4 ha seedling plot but within the 1 ha permanent plot. All *G. gummi-gatta* seedlings within the gaps were enumerated and measured in 2000 and 2001. The effect of canopy cover on seedling growth was estimated by comparing the annual height increment of seedlings in the > 95% canopy cover class with seedlings in the 65 - 80% canopy cover class. Seedlings that showed negative height increment were assumed to have been measured incorrectly or to have sustained damage, and were therefore removed from the analysis.

Seedling survival

I investigated the effect of canopy cover, distance from parent trees, and conspecific seedling density on the survival of *G. gummi-gatta* seedlings in the 0.4 ha seedling plot. Recruits in the year 2000 were mapped and re-censused in May 2001. I hypothesized that *G. gummi-gatta* seedlings close to parent trees would show higher mortality than seedlings that were farther away. I estimated the distance to nearest female tree of each seedling using the mapped spatial coordinates of seedlings and adult trees. An ANOVA was used to test if distance from adult trees differed between dead and surviving seedlings. The canopy cover above dead and surviving seedlings was tested for
significant differences using a t test. The effect of seedling density on *G. gummi-gatta* seedling survival was determined by tagging recruited seedlings in 2x2m plots with high *G. gummi-gatta* seedling density (> 2 seedlings m\(^{-2}\), n = 50 seedlings in 23 plots) and in plots with low *G. gummi-gatta* seedling density (< 0.75 seedlings m\(^{-2}\), n = 37 seedlings in 33 plots). I ensured that low density plots located next to high density plots were not included in the analysis. I used a chi-square test to test for an association between seedling survival and *G. gummi-gatta* seedling density.

**Spatial pattern**

I determined the spatial distribution of *G. gummi-gatta* seedlings (< .5m height), saplings (2 to 5cm diameter), and adult female trees (>20cm diameter) in the permanent plot. I used the Ripley’s K function which is an analysis of point patterns in a two dimensional space to obtain the spatial pattern for seedlings; and for saplings and adult female trees (Duncan 1991, Haase 1995). This spatial point pattern analysis uses all plant to plant distances within a plot and the variance of these distances is used to estimate the degree of spatial distribution. The univariate function \( L(t) \), where \( t \) is distance, estimates the spatial relationship of individuals within one group and was thus used for the analysis of seedling distribution. The bivariate function \( L_{12}(t) \), estimates the spatial relationship between individuals of two groups was thus used for the analysis of saplings and adult trees. \( L(t) \) and \( L_{12}(t) \) were estimated using \( L(t) = \sqrt{(K(t)/ \pi )} - t \), and \( L_{12}(t) = \sqrt{(K_{12}(t)/ \pi )} - t \). To determine the degree of randomness, \( L(t) \) and \( L_{12}(t) \) were plotted against \( t \). If \( L(t) \) or \( L_{12}(t) = 0 \), the distribution is random, \( L(t) \) or \( L_{12}(t) > 0 \) suggests association and \( L(t) \) or \( L_{12}(t) < 0 \) indicates repulsion. To test if the deviation from random is significant, 95%
confidence intervals were generated using Monte Carlo simulations. The DOS program Spatial Analysis Programmes by Duncan (1990) was used to estimate K and $K_{12}$.

**Growth rate**

I estimated the growth rate of *G. gummi-gatta* individuals in two sites: open canopy forest and in the closed canopy permanent plot. In both sites trees were selected to represent the range of diameter size classes. Growth rate was estimated by obtaining three diameter measurements at three fixed points, 10cm apart, at a point. To mark the exact spot at which subsequent measurements would be taken, I affixed an aluminum nail at a point above the buttress where the bole of the tree was relatively uniform. During the measurement I hung a metal strip marked at 10cm distances. The first measurement was taken 10 cm below the nail. The average of the three measures was recorded as the diameter for the current year. The procedure was repeated at the same three points a year later. Twenty four *G. gummi-gatta* individuals were measured in the open forest over a three year period. In the closed canopy forest, the diameter increments of 52 trees were measured over one year. I tested for differences in annual growth rates of trees in the open and closed forest by using a t test.

**Density and size class distribution**

In addition to the permanent plot I established 5 other plots in closed canopy forest within the study area to obtain the size class distribution of *G. gummi-gatta* (Table 4.1). Each plot consisted of 3 to 5 parallel subplots of size 20 x 100m, separated from each other by 100 m. Within each subplot the diameter of all *G. gummi-gatta* trees (> 10 cm diameter) was measured. Within each 20x100 subplot, I sampled saplings (0.5m to
2m height) in a nested 5 x 100m plot, and, and seedlings (< 0.5m height) in a nested 2x100m plot.

The density of *G. gummi-gatta* trees (>10 cm diameter) in the study region was estimated from the 6 sample plots (sampled area of 0.6 to 1 ha ) that were established across the study region (Table 4.1). I recorded if branches of *G. gummi-gatta* trees were cut by collectors during fruit harvest. The percentage of total trees damaged, and the approximate number of households harvesting *G. gummi-gatta* fruits in that site was used as used as a surrogate for fruit harvest intensity. To determine if size class distributions differed among the 6 sites, a Friedman’s two way analysis of variance was used (treatment = sites; blocks = size classes). The seven size classes were seedlings (<.5m ht), saplings (.5-2m ht), juveniles (<9.9 cm dbh), 10-19.9 cm dbh, 20-29.9 cm dbh, 30-39.9 cm dbh, > 40 cm dbh.

**Population growth**

I used a stage-structured matrix model (Caswell 2001) to estimate population growth rate. *G. gummi-gatta* individuals in the permanent plot were classified into six size classes: seedlings (<0.5m height), <5 cm diameter, 5-9.9, 10-19.9, and >20 cm diameter. Transition rates, the probability of an individual in one size class moving to the next class from one year to the next, or of staying in the same size class, were estimated for the combined two year period. I combined the data from 1999 to 2001 as *G. gummi-gatta* individuals failed to transition from one stage to the next in the two one-year periods, thus affecting the results. I used the Poptools statistical package (Hood 2002) to estimate the population growth rate (λ), and the intrinsic growth rate (r). The impact of
fruit harvest on the population growth rate ($\lambda$) was assessed by varying the estimate of seed production and recalculating $\lambda$.

**Results**

**Fruiting ecology**

My observations of the phenology of female *G. gummi-gatta* trees revealed that fruits ripen between June and August. While unripe fruits are green, ripe fruits are usually bright yellow. Fruits on a tree do not ripen synchronously. At any given time only a proportion of fruits are ripe with the ratio of ripe to unripe fruits increasing as the fruiting season progresses. All female *G. gummi-gatta* trees produced fruits every year though the amount of fruit production varied from year to year.

The average weight of a ripe *G. gummi-gatta* fruit is 84g, 73% of which is comprised of rind, 20% pulp, and 7% seeds (Table 4.2). Each fruit contains on average 6 seeds. Seeds are about 5 cm long and 2cm wide, with a fresh weight of $1.1 \pm 0.3$ g per seed. The average weight of the fibrous seed coat is $0.5 \pm 0.1$g, and cotyledons and embryo together weigh $0.6 \pm 0.2$ g (Table 4.2).

The average fruit yield of *G. gummi-gatta* trees in the open-canopy forest was significantly higher than in closed canopy forest for three out of four years, and the average diameter of the sampled *G. gummi-gatta* trees was also significantly higher in the open-canopy forest for the same three years (Table 4.3). The number of fruits produced per cm$^2$ of wood in open and closed canopy forest was significantly different for only one of the four years (Table 4.3).

The polynomial regression between tree diameter and average multi-year fruit production for all trees was significant (Figure 4.1), showing that trees larger than 60cm
diameter produce less fruits than trees in the 30 – 50 cm size class, probably due to senescence. The linear regression of tree diameter with fruit yield showed significant relationship for all years in the closed canopy forest and for two of four years for trees in the open canopy forest (Table 4.4). When trees in open and closed canopy forest were pooled for all years I obtained a significant positive relationship for three years (Figure 4.2).

Over the four year study period, the annual average fruit yield of trees in the open-canopy forest ranged from 450 to 2500 fruits per tree, while the average annual yield of trees in the closed canopy forest ranged from 625 to 1150 fruits per tree (Table 4.3). The inter-annual variability in fruit production as estimated by the CV-p of annual fruit production was 42.8% for all trees (n=76, 56, 87, and 23 trees for 1998, 1999, 2000, and 2001 respectively). The CV-p for closed-canopy forest trees was 30.2% (n= 53, 39, 67, and 15 trees for 1998, 1999, 2000, and 2001 respectively) and CV-p for open-canopy was 68.4% (n= 23, 17, 20, and 8 trees for 1998, 1999, 2000, and 2001 respectively). The lower CV-p for closed canopy trees suggests a more consistent inter-annual fruit production than trees in the open canopy. The average CV of within individual fruit production (CV-i) of 11 trees for three years was 57.1% and the Kendall degree of concordance was 0.4 (n= 11 trees, 3 years, Table 4.5). The Kendall degree of concordance statistic ranges between 0 and 1. A value of 0 denotes no synchrony in fruit production and 1 denotes high concordance. A value of 0.4 suggests that there is some variation in the degree of participation of individual trees in inter-annual fruit production.
Seed dispersal:

The feeding trials performed at the zoo, and observations at fruiting trees showed that primates *P. entellus* and *M. radiata* consume the pulp and discard the rind and seeds. Feeding trials with the Common palm civet, *P. hermaphroditus* showed that these nocturnal arboreal frugivores consume the seeds along with the pulp, and egest seeds whole after passage through the gut. The passage of seeds through the gut took about 8 hours. The egested seeds showed no scarification. I found *G. gummi-gatta* seeds in the feces of *P. hermaphroditus* deposited on the trunks of fallen trees in the closed canopy forest. Only one of the twelve Sambar deer, *C. unicolor* that were offered *G. gummi-gatta* fruits at the zoo consumed fruit. Fruits were consumed whole and no regurgitation of the seeds was observed. No bats were observed at fruiting trees, although I observed the Short-nosed fruit bat *Cynopterus sphinx* feeding on the fruits of a nearby cultivated *Manilkara achras* tree. The only arboreal seed predation observed was by the Malabar Giant Squirrel, *Ratufa indica*, a diurnal arboreal granivore, which fed on the oil rich cotyledon, after removing the resinous seed coat.

Seed predation

*G. gummi-gatta* seeds were consumed by insects and mammals through out the ten month seed monitoring period. After ten months 93% of *G. gummi-gatta* seeds provisioned in both sites were eaten by seed predators. The rate of seed predation in diverse forest was significantly higher than in the less-diverse forest site (Log rank test, p<0.001, Figure 4.3). The Kaplan-Meier survival estimate showed that 87% of the seeds persisted beyond 25 days in the diverse forest, while in the less-diverse forest the same percentage of seeds persisted beyond 50 days.
After 160 days 84% of seeds were eaten under the canopy of *G. gummi-gatta* trees while only 62% of seeds were eaten in plots located far from adult trees. Percentage seed predation at the end of the ten month seed monitoring period was 87% and 85% in plots below canopy and far from adult trees respectively. The Log rank test showed that the pattern of seed mortality was significantly different between below canopy and away from adult *G. gummi-gatta* trees in the permanent plot (p< 0.01, Figure 4.3).

None of the 100 seeds that were tagged with orange flagging to determine if seeds are being cached survived past the ten-month monitoring period. Only two seeds were moved to a distance of 3m from the original location and were eaten. There was therefore no evidence of secondary dispersal of *G. gummi-gatta* seeds.

**Seedling survival and growth**

The canopy cover in the intensive 0.4 ha seedling plot and the sampled canopy gaps varied between 65% and 99%. I found that canopy cover significantly affects *G. gummi-gatta* seedling height growth (One way ANOVA, 60-80% CC: mean = 2.3 ± 2.3 cm year\(^{-1}\); >95%CC: mean = 0.1 ± 0.1 cm year\(^{-1}\), p<.001, Figure 4.4). Canopy cover above *G. gummi-gatta* seedlings however did not affect seedling survival. The canopy cover above seedlings that survived to the end of the first year and above those that died was not significantly different (surviving seedlings: n = 78, Mean canopy cover = 92.8 ± 3.5%; dead seedlings: n = 107, Mean canopy cover = 92.2 ± 3.6%, t test, p = 0.5).

Seedling mortality was highest in the first year after germination (Figure 4.5). Out of the 246 *G. gummi-gatta* seedlings that were enumerated in 18 of the forty 10 m\(^2\) plots 3 months after germination, 124 (50%) were alive 6 months later, and only 28% were alive 18 months later. Forty one percent of one-year old seedlings in 2000 were dead a
year later suggesting that mortality of *G. gummi-gatta* continues to be high during the second year. For a mixed aged group of 1078 seedlings enumerated in 1999, 21% of the seedlings died between 1999 and 2000, and 19% of the 1078 seedlings died between 2000 and 2001 (Figure 4.6).

Distance to adult *G. gummi-gatta* trees appears to affect seedling survival. The distance of *G. gummi-gatta* seedlings to nearest adult female *G. gummi-gatta* tree was significantly greater for seedlings that survived than for seedlings that died (ANOVA, p = 0.006, Mean distance of surviving seedlings from adult female = 5.5 ± 4.1 m, n = 108, mean distance of dead seedlings from adult female = 3.9 ± 3.1 m, n = 78). The average canopy radius of *G. gummi-gatta* trees was found to be 4.6 m, suggesting that seedlings that survived were often located beyond the canopy of adult *G. gummi-gatta* trees, while seedlings that died were often below the canopy.

*G. gummi-gatta* seedling density showed a significant effect on conspecific seedling survival. Eighteen of the 50 seedlings recruited into high *G. gummi-gatta* seedling density plots in 2000 died in 2001, while only six out the 36 recruited *G. gummi-gatta* seedlings died in low *G. gummi-gatta* seedling density plots. The mortality of *G. gummi-gatta* seedlings in high density plots was significantly greater than seedling mortality in low density plots ($\chi^2 = 4.1$, df = 1, p < .05).

I estimated the probability of survival of seeds and seedlings obtained from seed predation experiments and seedling monitoring in the permanent plot (Figure 4.5). The number of seeds produced by *G. gummi-gatta* trees was estimated from the annual fruit production of trees in the permanent plot (1084 fruits per tree), number of female trees > 15 cm diameter (45 trees ha$^{-1}$), number of seeds per fruit (5.35 seeds, Table 4.2). The
seed predation experiment showed that 14% seeds survived for one year, and 4% germinated. I thus estimated that about 4200 seedlings germinated in the 0.4 ha intensive study plot. Using the number of recruits that survived to the first year (174 seedlings) and subsequent survival of these recruits to the second year (101 seedlings), I estimated that the probability of a seed reaching the one-year seedling stage is 0.002 and of reaching the two year stage is 0.001. Hence only 1 out of 1035 seeds that fall to the forest floor grows to the two-year seedling stage.

Spatial pattern

*G. gummi-gatta* seedlings appear to be clumped either around adult female trees or in clusters far from adults probably due to directed dispersal by animals (Figure 4.7). The canopy width of *G. gummi-gatta* trees is about 4.6 ± 1.2 m. The Ripley’s K plot shows that seedlings are significantly clumped at distances of 1 to 12 m (p < .05, Figure 4.9). The spatial distribution of *G. gummi-gatta* saplings (2 to 5 cm dbh) and adult female trees (>20 cm dbh) in the permanent plot shows that there is spatial separation between the two size classes (Figure 4.8). This pattern is confirmed by the Ripley’s K plot for saplings and adult female trees which shows significant repulsion (p < .05) at distances between 5 and 12m (Figure 4.9) demonstrating that significantly fewer than expected saplings occur between 5 and 12m of an adult tree. At distances less than 5m and greater than 12m there is a random association between saplings and adults. While seedlings tend to be clumped around adult trees, saplings are located far from adults suggesting that the probability of sapling establishment increases with distance from adult female trees.
Growth rate of trees

The growth rate of *G. gummi-gatta* trees is significantly different between the open and closed canopy forest for trees in smaller sizes class (<15 cm), while trees in the larger size classes do not show significant difference (Figure 4.11). The overall growth rates of *G. gummi-gatta* individuals in closed and open canopy were significantly different, with open canopy trees showing higher growth than closed canopy trees (t test, p<.001, Mean annual increment: Open forest: 0.36 ± 0.26 cm; closed forest: 0.12 ± 0.28 cm). The scatter plot of tree diameter versus annual growth increment shows a significant negative relationship ($R^2 = 0.31$, p=.005) between initial tree size and growth of open canopy trees. In the closed canopy forest, a significant positive relationship is obtained ($R^2 = 0.15$, p = .006) when an anomalous observation is removed (dbh 31.8 cm, increment = -1.26 cm, when included in the analysis: $R^2 = .03$, p= 0.18) (Figure 4.10).

Population structure and density

The density of *G. gummi-gatta* trees (> 10 cm dbh) in the study area, estimated from Plots 1 to 6 was 69 ± 39 trees (> 10 cm diameter) ha$^{-1}$ (Table 4.1). The size class distribution of individuals in Plots 1 to 6 showed the ‘reverse J’ pattern typical of stable plant populations (Figure 4.12). Size class distributions showed significant difference among sites (Friedman’s two way analysis of variance, $\chi^2$=12.05, df = 5, p = .03). The sum of ranks suggests the organization of cases into three clusters: Plot 5 (sum of ranks = 35) and Plot 6 (32); Plot 2 (25.5); and Plot 3 (20), Plot 1 (18) and Plot 4 (16.5). This clustering corresponds to the fruit harvest intensity gradient along which these sites were located. Plots 5 and 6 were the least harvested, while Plots 1 to 4 experienced mid to high fruit harvest. Size-class distributions of the pooled low intensity (Plots 5 and 6) and high
intensity plots (Plots 1 – 4) showed no significant difference (Kolmogorov-Smirnov test, p=.94, Figure 4.13).

Population growth

The transition matrix for the *G. gummi-gatta* individuals in the permanent plot for the period 1999 to 2001 is shown in Figure 4.13. The element in the matrix $a_{ij}$, is the probability of an individual moving from stage $i$ to stage $j$ in year $t$ to $t+1$. In the matrix each of the transition probabilities along the lower sub-diagonal is the probability of moving to the larger size class, while the probability of staying in the same size class is shown by the element $a_{ii}$ which is along the diagonal. The elements along the upper sub-diagonal denote the probability of moving to a smaller size class. The top row of the matrix contains the annual seed production of each size class, except for the first element which is the probability of a seed remaining dormant. The low transition rates of *G. gummi-gatta* individuals in each of the two years (1999 - 2000 and 2000 - 2001), shows that annual population growth is slow and that few individuals grew to the next stage in either period. Seedlings transitioned to the $<5$ cm stage in only one of the two years. Some adult trees decreased in size and transitioned to a smaller size class. The estimated $\lambda$ is 1.006 for the combined two year period, which suggests a stable *G. gummi-gatta* population. The population growth rate drops below 1.0 when more than 50% of the seeds are removed (Figure 4.15).
Discussion

Fruit production

Plant seedling recruitment and establishment is dependent on the number of seeds produced by adult trees and the temporal variability of that production (Schupp 1990). Adult female *G. gummi-gatta* trees of diameter greater than about 14 cm dbh fruit annually. The inter-annual variation in total fruit production of *G. gummi-gatta* trees (CV-p = 30.2%) in the closed canopy forest lies near the lower limit of the range of values estimated for 144 species by Herrera *et al.* (1998). Only 4 plant species in Herrera *et al.* (1998) had CV values that were lower than the observed value for *G. gummi-gatta*. However De Steven and Wright (2002) argue that, as most studies on endozoochorously dispersed species have been of a short duration (< 6 years) they might have missed peaks in fruit production. Long-term studies (~ 10 years) of animal dispersed species show higher population coefficients of variation (average of 120% in Herrera *et al.* 1998) than short term studies (De Steven and Wright 2002). As my study is of a short duration (4 years) the finding that *G. gummi-gatta* has relatively constant fruit production is therefore tentative.

There are few multi-year studies of fruit production of tropical trees (Janzen 1978, Herrera 1998), although temperate trees have been fairly well studied (Sork 1993, Houle 1999). Studies of fruit production by tropical trees have focused on the phenomenon of ‘masting’ a fruiting strategy hypothesized to have evolved to satiate seed predators (Janzen 1970, Curran and Webb 2000) and optimize resource allocation (Sork 1993), and the demographic consequences of ‘masting’ (Connell and Green 2000). Tropical tree species that show constant fruiting have not received much attention (Kelly 1994).
However in a survey of fruit production in 144 plant species, Herrera et al. (1998) found a continuum between the plant strategies of constant fruiting and ‘masting’, instead of a bimodal distribution as previously hypothesized (Janzen 1978).

It has been argued that steady seed production might sustain a high number of seed predators from one seed producing season to the next, therefore increasing the rate of seed predation (Janzen 1970). However the occurrence of *G. gummi-gatta* seed dispersal by animals that forage over a large area might ensure that a certain proportion of seeds reach sites that are safe from seed predators and far from parent trees. The genetic advantages of increased gene flow (Nason and Hamrick 1997) and the demographic benefits of dispersal (Howe and Miriti 2000) might outweigh the costs of increased seed predation which is usually associated with steady seed production, large seed size, and high seed resources. My findings, as well as those from other studies (Howe 1993, Harms et al. 2000, Nathan and Muller-Landau 2000) show that rates of seed predation are lower with increasing distances from parent trees suggesting an increased demographic advantage of seed dispersal (Howe and Miriti 2000).

Animal dispersed species have been shown to have low inter-annual variation in fruit yield (Herrera et al. 1998), probably due to the stable inter-annual population sizes of mammal frugivore communities. McKey (1975) suggested a mutualistic association between frugivores and plants, with plants provisioning fruits with nutrients to attract animals to ensure seed dispersal. However, in a long-term study of Mediterranean plant-frugivore interactions, Herrera (1998a) found no relationship between frugivore density and fruit production, and suggested that fruit production might be more a result of physical constraints than a selection for increased seed dispersal.
Variability in fruit production might also be a function of pollinator limitation as has been observed for a large number of plant species (Burd 1994). Moreover it has been shown that the resource allocation by plants in reproduction is around 5% and maybe as low as 2% (Kira 1978), thus enabling plants to produce excess flowers that might compensate for such variable factors as pollen availability, fruit and seed predation, and unpredictable physical environment (Stephenson 1981, Lee 1988).

Reproductive output has also been shown to be a function of plant size (Harper 1977, Garwood and Horvitz 1985). There was a significant relationship between *G. gummi-gatta* tree diameter and number of fruits in the closed forest in all 4 years, confirming that reproductive output is related to tree size. However trees greater than ~60 cm diameter showed a decrease in the number of fruits probably as a result of senescence.

*G. gummi-gatta* trees in the open canopy forest have a greater average size and also produce a significantly higher number of fruits than the trees in the closed canopy forest. However the significantly higher fruit yield by *G. gummi-gatta* trees in the open canopy forest disappeared when I controlled for tree size. The difference in yields might therefore be largely due to to difference in basal area between open and closed canopy forest. Bazzaz *et al.* (2000) have similarly shown that difference in reproductive output between populations is due to differences in size of individuals.

**Seed dispersal**

Seed dispersal is the ‘demographic bridge’ that connects the reproductive phase of adult trees with the seedling stage (Wang and Smith 2002). Hubbell and Foster (1986) emphasized the role of dispersal in determining the species assemblage at a site at the moment of gap formation, and suggested that the ability to reach sites is more important
than the ability to out-compete other species in gaps. The occurrence of seedling in sites before gap formation in some instances determines the composition of the future plant community (Uhl et al. 1988, Connell 1989). Webb and Peart (2001) have estimated that about 60% of seedlings in a South-east Asian tropical forest were germinated from dispersed seeds, emphasizing the importance of seed dispersal in tropical forest.

Twenty percent of the fresh weight of *G. gummi-gatta* fruit consists of pulp indicating that there might be selection for dispersal of fruits by large mammals (Mckey 1975). *G. gummi-gatta* fruits are not ripened synchronously on the tree but differentially matured throughout the three month fruiting season. Differential maturation of fruits has been suggested to be a plant strategy to ensure seed dispersal (Lee 1988). By ripening fruits differentially and preventing the satiation of frugivores, the probability that all fruits are consumed by frugivores is increased. Differential maturation in *G. gummi-gatta* might ensure that seeds are ingested and moved far from the parent tree, thus increasing seed survivorship, as dispersed seeds tend to have a higher chance of survival than undispersed seeds (Nathan and Muller-Landau 2000).

The two primate species in the study area are *P. entellus*, which is primarily a folivore though it eats fruits when available, and *M. radiata*, which is a frugivore (Prater 1998). *P. entellus* and *M. radiata* discarded seeds and rind after feeding on the pulp that surrounds the seeds. Most seeds from fruits consumed in this fashion were discarded near the adult tree. In some cases *M. radiata* carried the pulp and seeds in cheek pouches to nearby tall trees, where the pulp was consumed and seeds discarded thus affecting an intermediate level of dispersal. Although I did not find evidence that the large deer *C.*
unicolor disperse G. gummi-gatta seeds, it has been observed to consume fruits of Phyllanthus emblica and regurgitate the hard seeds (Murali et al. 1996).

In addition to primates, the Palm civet, Paradoxorus hermaphroditus consumes G. gummi-gatta fruit. In a survey of dispersal modes of rainforest species in the southern Western Ghats, Ganesh and Davidar (2001) found that civets (genus Paradoxorus) play a larger role in seed dispersal than primates. Two species of civets occur in the study area: Paradoxorus hermaphroditus, and the larger, but rarer species, Paradoxorus jerdonii. Both species are primarily fruit eaters and disperse seeds endozoochorously (Ganesh et al. 1995). I found that civets defecate on fallen trees, a probable territory marking behavior, which might result in seeds being dispersed into gaps, a possible case of ‘directed dispersal’ (Wenny and Levey 1998, Wenny 2001). The occurrence of dense seedling clusters of varying ages far from adult trees (Figure 4.7) suggests that seeds are being repeatedly dispersed to specific areas of the forest. The cluster of seedlings found in the 0.4 ha seedling plot far from female adult G. gummi-gatta trees was directly below a dead Syzigium cuminii tree. S. cuminii due to their large lateral branches are known to be frequented by arboreal mammals such as civets and primates (Prater 1998). The seedlings in this isolated cluster might have germinated from seeds that were dispersed into this site repeatedly.

G. gummi-gatta seeds collected from the feces of palm civets did not show any scarification. Lieberman and Lieberman (1986) and Vazquez-Yanes and Orozco-Segovia (1986) found no difference between the germination of seeds that were taken directly from fruits and those taken from animal feces. However, seeds of four species of plants collected from the feces of a civet, Paradoxorus philippinensis, were shown to have
significantly shorter times to germination (Gruezo and Soligam 1990). It is clear therefore that the study of the ecology of the animal dispersers is critical for a better understanding of plant population dynamics (Howe 1989, Herrera 1995) especially as several studies are demonstrating that plant populations might be dispersal limited (Dalling et al. 1998, Brown et al. 1999).

The seed weight of *G. gummi-gatta* (cotyledon and embryo weight of 0.6 ± 0.2g) is higher than the average seed weight of thirty six animal dispersed seeds studied by Lokesha et al. (1992). Animal dispersed fruits have significantly larger seeds than wind dispersed or passively dispersed seeds (Lokesha et al. 1992, Grubb 1996a). A large seed size has been shown to enable germinating seedlings to establish in poor soils (Grubb 1996b), persist in shade (Leishman and Westoby 1994, Saverimuttu and Westoby 1996), withstand seed predation by insects (Dalling and Harms 1999), and tolerate herbivory of seedlings (Dalling et al. 1997).

Animal dispersed seeds tend to have a higher percentage of fat than passively dispersed seeds as fat reduces seed weight while maintaining energy content (Lokesha et al. 1992). With a high fat content of 50.2% (Mannan et al. 1986), which is one standard deviation above the mean seed fat content of 36 animal dispersed species (Lokesha et al. 1992), *G. gummi-gatta* seeds corroborate the relationship between fat content and animal dispersal. However animal dispersed seeds, probably due to their higher reserve of fatty oils experience higher rates of seed predation by ants than wind dispersed seeds (Dalling et al. 2002). During an attempted germination experiment, in which I planted 1000 seeds evenly spaced out in a 5 x 10 m garden plot, I found that 90% of seeds were damaged by ants within 5 days suggesting that *G. gummi-gatta* seeds are highly attractive to ants.
Seed predation

Seed predation greatly influences the number of seeds that are able to germinate. The long dormancy, the large seed size, and high fat content makes *G. gummi-gatta* seeds highly prone to seed predation: 99.7% in the diverse site and 86% in the permanent plot 10 months after dispersal. Similarly high rates of seed predation have been shown for other tropical species such as *Astrocaryum mexicanum* (Sarukhan 1978) and *Gustavia superba* (Sork 1987).

The spatial pattern of seed dispersal plays an important role in determining the fate of *G. gummi-gatta* seeds. I found that seeds that are dispersed far from adults have a significantly higher probability of survival than seeds that fall under the canopy where natural seed densities are higher. This pattern of higher seed mortality near adults has been conclusively demonstrated for several species in a tropical forest in Panama (Harms *et al.* 2000). Thus seeds that are dispersed far from adults have greater survival than those that fall close to adults. The increasing empirical evidence for the Janzen (1970) and Connell (1971) model of seed mortality and seedling establishment presents the opportunity to use this pattern of seedling establishment increase tree species density in intact forests (Howe and Miriti 2000). This has implications for the management of *G. gummi-gatta* and other harvested tree species. As most seeds that fall close to adults are at a higher risk of predation, the directed dispersal of seeds into areas that are far from adults might increase the population density of the target species.

*G. gummi-gatta* seed mortality in the diverse forest site was higher than in the less-diverse site. Grubb (1996b) has suggested that sites with higher plant species richness have higher rates of seed predation due to a more diverse generalist seed
predator community. Over the duration of the study (three years) I encountered small mammal seed predators such as Palm squirrels (*Funambulus palmaram*) and Malabar giant squirrels (*Ratufa indica*), more often in the high diverse site than in the low diverse site. The greater foliar heterogeneity, and the denser undergrowth, suggests that the diverse site had greater faunal diversity which might explain the greater rate of *G. gummi-gatta* seed predation.

**Seed germination**

*G. gummi-gatta* seedlings belong to the Crypto-coty lar hypogeal reserve type (CHR) (Hladik and Miguel 1990). There appears to be a correspondence between hypogeal seedling morphology and seed dormancy. A significant proportion (61%) of 31 plant species belonging to the CHR seedling type in a Malaysian forest showed delayed (>12 weeks) germination (Garwood 1996, using data from Ng 1978). The length of time to germination increases the probability of seeds being buried under litter, thus emerging seedlings have to push through a layer of litter, a process more easily accomplished by hypogeal seedlings (Harper *et al*. 1970).

As *G. gummi-gatta* seeds are dispersed during the season of heavy rainfall, the probability of burial of uneaten seeds under falling leaves and debris is high. Seeds that escape predation might thus stay dormant under litter awaiting optimum germination conditions (Molofsky and Augspurger 1992, Pearson *et al*. 2002). Seed dormancy, either induced or innate, imparts seeds with such advantages as optimization of environmental conditions for germination (Vazquez-Yanes and Orozco-Segovia, 1993). In an exploration of the patterns of occurrence and the possible evolutionary reasons for dormancy, Rees (1997) hypothesized that a) plants with efficient seed dispersal systems
are likely to have less dormancy, and b) larger seeded plants will have reduced dormancy. Vazquez-Yanes and Orozco-Segovia (1993) suggest that light demanding species are more likely to have dormant seeds, and species that establish under forest canopy have less dormancy. My observations however show that *G. gummi-gatta*, which is large seeded, animal dispersed, and shade tolerant, does not fit the relationship between dormancy and seed size, dispersal mode, and regeneration strategy.

Horvitz and Schemske (1994) have suggested that plant species with dormant seeds might show greater variability in seedling emergence than in seed production. Using data from the 0.4 ha seedling plot, I found that 174 *G. gummi-gatta* seedlings survived to the end of the first year in 2000 and 365 seedlings survived to the end of the first year in 2001. Fruit production of *G. gummi-gatta* trees for 1998 and 1999 (the years in which these germinated seeds were most probably produced) was obtained by regressing DBH and actual yield of *G. gummi-gatta* trees. The regression equation was then used to estimate fruit production of the specific tree sizes that occurred on the 0.4 ha plot. I thus obtained estimates of 449 and 489 fruits per tree in 1998 and 1999 respectively. The significant relationship between tree diameter and fruit production suggests that the annual estimates of fruit production thus derived are valid. *G. gummi-gatta* seedling emergence is therefore more variable than seed production by adult *G. gummi-gatta* trees. In contrast, a high correspondence between seed production and seedling recruitment has been demonstrated for three tree species with non-dormant seeds in Panama (De Steven and Wright 2002).
Seedling survival and growth

*G. gummi-gatta* seeds germinated during the monsoon rains, after being subjected to a period of drying. The waxy water-impermeable layer between the seed coat and the cotyledon breaks down during the drying that might occur during the dry season, thus permitting the entry of moisture and subsequent germination during the rains. In the permanent plot, I only observed recruits after the onset of the rains. Out of the 246 newly germinated *G. gummi-gatta* seedlings that were enumerated in eighteen of the forty 10 m² plots 3 months after germination, 124 (50%) survived to 6 months and 69 (28%) survived to 18 months. Six month survival rates for tropical species range from 0% for *Cecropia obtusiflia* (Alvarez-Buyla and Martinez-Ramos 1992), 21.4 to 86.1 % for eight neotropical tree species (Sarukhan 1980), and 94.3 % for *Gustavia superba* (Sork 1985). The survival of *G. gummi-gatta* seedlings is around the median value obtained for tropical trees.

I estimated that the ratio of seedlings germinating for every *G. gummi-gatta* seed that falls to the forest floor is 0.04. This is within the range of recruitment estimates found for tropical species (0.15 for *Phytelephas seemanii*, Bernal 1998, 0.1 for *Faramea occidentalis* Schupp 1990, 0.049 for *Euterpe globosa*, Van Valen 1975, 0.005 for *Hymenaea courbaril*, Janzen 1978, 0.038-0.35 for *Platypodium elegans*, Augspurger 1983, 0.072 for *Astrocaryum mexicanum*, Pinero et al. 1984). Twenty nine percent of the surviving *G. gummi-gatta* seeds germinated at the end of 10 months. It is possible that the recruitment estimate might be higher if seed fates are followed until all viable seeds are germinated. However as the estimate is from a forest site that experienced lower seed predation than a more species diverse site, it might lie at the upper end of the variation in
recruitment rates. Due to the apparent variability in seed predation rates there might be high variation in recruitment across habitats.

Mortality of *G. gummi-gatta* seedlings was higher close to adult female trees and in plots with high conspecific seedling density suggesting that *G. gummi-gatta* seedling survival is density dependent. Plant seedlings are susceptible to mortality due to predation by insects (Terborgh *et al.* 1993), pathogens (Augspurger 1983a), and herbivory by mammals (Howe 1990). Seedlings in clusters, usually around the parent tree, often suffer higher rates of mortality than seedlings that are far from conspecific aggregations (Augspurger 1983b).

The spatial distribution of seedlings, as seen from the plots of the Ripley’s K function, shows that seedlings are significantly clumped at distances of up to 12 meters. The spatial distribution of saplings and adult trees however showed significant repulsion at distances between 5 and 12 meters. This spatial separation is further evidence of a strong density dependent pattern of sapling recruitment. Similar spatial patterns have been obtained for the seedlings of a neotropical tree, *Platypodium elegans* (Augspurger 1983b). Distance of seedlings from adults increased with time showing density dependent mortality. Distance of parents to seedlings was less than the distance of parents to 3 month old plants, and older saplings were farther away from parents than 1 year old plants (Augspurger 1983b).

After seeds are dispersed into sites, escape predation, and germinate, their subsequent growth is dependent on the amount of light they receive (Swaine and Whitmore 1988, Brown *et al.* 1999, Osunkaya *et al.* 1993). The growth of *G. gummi-gatta* seedlings was low in shade (>95% cover cover) but significantly higher under
greater canopy openness (60 - 80% canopy cover). The presence of substantial seed resources might enable *G. gummi-gatta* seedlings to survive the low light conditions under the forest canopy (Saverimutu and Westoby 1996). The occurrence and the small but positive growth of seedlings in shade suggests that *G. gummi-gatta* is a shade tolerant species which responds to increases in sunlight by significantly increasing height. Seedling growth below the canopy has been shown to be strongly correlated with even small levels of canopy openness (Turner 1990) probably due to the occurrence of sun flecks which have been shown to significantly affect seedling growth (Pearcy *et al.* 1987, Chazdon 1988).

Adult wood density has been shown to be positively correlated with shade tolerance (Augspurger 1984). The average specific gravity for trees in a secondary forest in Borneo was found to be 0.31, which was lower than the average specific gravity of trees in a nearby primary forest, which was 0.58 (Suzuki 1999). If specific gravity can be therefore assumed to be an indicator of shade tolerance, the value of 0.76 for *G. gummi-gatta* (Rai and Proctor 1986) suggests that *G. gummi-gatta* is a shade tolerant species, as is also shown by the persistence of seedlings in shade, and the occurrence of adult trees in the under-story (Pascal 1988).

**Growth rate of trees**

Once established, plants increase their biomass at rates determined by the amount of light received by the crown of the individual plant. Clark and Clark (1992) have shown that higher light levels resulted in greater tree growth rates for 6 species in Costa Rica. I found that the pattern of annual diameter growth rate of the various tree sizes of *G. gummi-gatta* differed between open and closed canopy forest. The growth rate of larger
individuals was greater than that of smaller trees in the closed canopy forest, while smaller sized individuals showed higher growth rates than larger individuals in the open forest. The pattern is probably due to the different light regimes of individual *G. gummi-gatta* trees at the two sites. In the open canopy forest, due to the greater amount of light reaching the understory, smaller trees grow rapidly, while small trees in the closed canopy forest occurred in the shade and thus showed slow growth rates.

There was no difference between the growth rate of adult trees (>15cm diameter) in open and closed canopy forest due to the crowns of adult *G. gummi-gatta* trees occurring in the canopy at both sites. In the closed canopy forest, the crowns of adult *G. gummi-gatta* trees were often in the canopy due to the low stature of the forest. For twenty four tree species in the Western Ghats, individuals whose crowns were in or above the canopy showed the fastest growth rates (Pellisier and Pascal 2000). I found that the growth rate of large *G. gummi-gatta* trees in open and closed forest showed a decrease indicating that there is a size-dependent threshold for growth. Clark and Clark (1999) however found that growth rate did not decline in the larger size classes for most tree species that were studied in a neotropical forest.

**The effect of fruit harvest**

The fruits of *G. gummi-gatta* are harvested intensively from the forests of the study area. By observing the actual harvest of fruits by collectors, I estimated that between 90 to 95% of fruits are removed from individual trees in the high harvest areas, where fruits along with seeds are removed. Such high seed removal rates have been recorded for *Bertholletia excelsa* (Zuidema and Boot 2002). In areas that experience low intensity of fruit harvest (lesser number of harvesters per unit area) *G. gummi-gatta* fruits
are removed later in the fruiting season thereby allowing animal dispersers to forage and disperse seeds. In addition, smaller sized trees that do not produce many fruits or are difficult to climb are often not harvested in the low harvest intensity sites.

I hypothesized that the proximal effect of fruit removal will be a reduction in the number of seedlings. Seedling density in 6 sites was adequate (minimum density of 1625 seedlings ha\(^{-1}\), median = 2563 seedlings ha\(^{-1}\)). The highest seedling density (9013 seedling ha\(^{-1}\)) was observed in a site that experienced high levels of fruit harvest, suggesting that current levels of fruit harvest might not be high enough to reduce recruitment of *G. gummi-gatta* seedlings. Zuidema and Boot (2002) have similarly demonstrated that even with 93% seed removal there was adequate seedling recruitment in *Bertholletia excelsa*. The effect of fruit harvest on the demography of *Grias peruviana* trees has also been shown to be low (Peters 1990b).

The significant difference in the size class distribution of *G. gummi-gatta* at at least one site was probably due to the greater density of adult stems in some of the sites and less due to the effect of harvest. The demographic effect of harvest might not yet be reflected in the size class distribution due to the recent history of fruit harvest (about 5 years). The long seed dormancy and the slow growth of *G. gummi-gatta* seedlings and juveniles suggest that the effect of *G. gummi-gatta* seed removal on adult plant abundance might not be perceived for several years.

The use of matrix models has been proposed as a method for understanding the effect of human use on the demography of plant populations (Caswell 2001, Peters 1996b). The rate of population growth (\(\lambda\)) for the *G. gummi-gatta* population was 1.006, suggesting that the population is stable. Despite the *G. gummi-gatta* population in the
permanent plot having the highest tree density of all sampled sites, low seed predation rates, and a low intensity of fruit harvest, the population growth analysis showed a non-increasing population under the current fruit harvest regime. My analyses show that the removal of 50% of the seeds of *G. gummi-gatta* results in the population growth rate dropping below 1.0. However, even when no seeds are harvested the rate of population growth is marginally above 1.0, and decreases in small increments up to 90% seed removal. The largest decrease in lambda is between 90 and 100% seed removal, suggesting that if the initial rate of population growth is high, about 90% of seeds can be removed from the population without a large effect on population growth.

The low transition and growth rates of *G. gummi-gatta* means that longer term data is needed to arrive at definitive results. It is not surprising therefore that population models have largely been used for such easily aged or fast growing taxa as tropical palms (Svenning and Macia 2002, Bernal 1998, Pinero *et al.* 1984, Ratsirarson *et al.* 1996, Silva-Matos *et al.* 1999, Pinard 1993, Olmsted and Alvarez-Buylla 1995), pioneer species (Alvarez-Buylla 1994, Martinez-Ramos *et al.* 1989), shrubs (Shea and Kelly 1998, Pascarella and Horvitz 1998), understory herbs (Horvitz and Schemske 1995, Bierzychudek 1982), and bromeliads (Ticktin *et al.* 2002). In one of the few applications of population matrix models to tropical canopy tree demography, Zuidema and Boot (2000) concluded that matrix models are insensitive to changes in reproduction, but sensitive to the survival of the larger individuals. Peters (1990b) and Bernal (1998) have similarly shown that simulated changes in seed production results in extremely small changes in population growth.
Due to the slow growth of tropical shade-tolerant understory species, results of matrix model simulations based on short term data have to be viewed with caution (Zagt and Boot 1997). Thus in the absence of long term data on slow growing tree species, it might be more appropriate to use such indicators of fruit harvest as seedling and juvenile abundance rather than matrix population models.

Conclusion

*G. gummi-gatta* fruits are an important resource for several animals, and for the human population in the forests of the Western Ghats. My findings show that due to stable fruit production, seed dispersal by animals, persistence of seedlings in shade, and adequate seedling recruitment under high fruit harvest, fruits of *G. gummi-gatta* might be harvested with few adverse demographic effects. The ecological information on seed predation and seedling establishment provides an opportunity for the management and continued harvest of *G. gummi-gatta* fruits. The greater survival of seeds far from adult trees and the increased growth of *G. gummi-gatta* seedlings in the open suggest that the active dispersal of seeds far from adult *G. gummi-gatta* trees and into tree fall gaps might significantly increase *G. gummi-gatta* abundance. My findings of the effects of fruit harvest might apply to similar animal-dispersed, fleshy-fruited tree species in the forests of Western Ghats, but more studies are required before arriving at definitive conclusions on the effect of fruit harvest on tropical tree species.
References


<table>
<thead>
<tr>
<th>Sample site</th>
<th>Trees (&gt;10 cm diameter)</th>
<th>Trees (0-9.9 cm diameter)</th>
<th>Juveniles (0.5-2 m ht)</th>
<th>Seedlings (&gt;0.5 m ht)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Area sampled (ha)</td>
<td>Density (# ha⁻¹)</td>
<td>Damaged trees (%)</td>
<td>Area sampled (ha)</td>
</tr>
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<td>Plot 1</td>
<td>1.0</td>
<td>45</td>
<td>64</td>
<td>1.0</td>
</tr>
<tr>
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<td>35</td>
<td>1.0</td>
</tr>
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<td>70</td>
<td>0</td>
<td>0.6</td>
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<tr>
<td>Plot 4</td>
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<td>1.0</td>
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<td>0.8</td>
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<td>Plot 6 (Permanent plot)</td>
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<td>0</td>
<td>1.0</td>
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<td>Total</td>
<td><strong>5.4</strong></td>
<td><strong>69 ± 39</strong></td>
<td><strong>9</strong></td>
<td><strong>5.4</strong></td>
</tr>
</tbody>
</table>

Table 4.1. Density of *G. gummi-gatta* seedling, juvenile, and trees in the Western Ghats, India. Density is mean ± 1 S.D. Harvest damage is percentage of adult female *G. gummi-gatta* trees (>10 cm diameter) with cut branches or stems.
<table>
<thead>
<tr>
<th></th>
<th>Whole fruit weight</th>
<th>Rind weight (%)</th>
<th>Pulp weight (%)</th>
<th>Seeds weight (g) (%)</th>
<th>No. of seeds/fruit</th>
<th>No. of aborted seeds/fruit</th>
<th>Whole seed weight</th>
<th>Seed coat weight</th>
<th>Seed weight</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean</strong></td>
<td>83.57</td>
<td>60.91 (73)</td>
<td>16.9 (20)</td>
<td>5.7 (7)</td>
<td>7.25</td>
<td>1.27</td>
<td>1.14</td>
<td>0.54</td>
<td>0.60</td>
</tr>
<tr>
<td><strong>S.D.</strong></td>
<td>29.98</td>
<td>23.88</td>
<td>5.89</td>
<td>2.40</td>
<td>0.88</td>
<td>1.70</td>
<td>0.26</td>
<td>0.09</td>
<td>0.24</td>
</tr>
<tr>
<td><strong>N</strong></td>
<td>55</td>
<td>55</td>
<td>55</td>
<td>55</td>
<td>55</td>
<td>55</td>
<td>300</td>
<td>200</td>
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</tr>
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Table 4.2. Wet weight in grams of constituent parts of *G. gummi-gatta* fruits and seeds, and the number of seeds and aborted seeds per *G. gummi-gatta* fruit in the Western Ghats, India.
Table 4.3. Fruit production by *G. gummi-gatta* trees, average diameter, and number of fruits per cm$^{-2}$ in open and closed canopy forest over four years in the Western Ghats, India. Different superscripts indicate significant difference between open and closed forest trees within each year (Mann Whitney U test, p < 0.5).

<table>
<thead>
<tr>
<th></th>
<th>1998</th>
<th>1999</th>
<th>2000</th>
<th>2001</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Open</td>
<td>Closed</td>
<td>Open</td>
<td>Closed</td>
</tr>
<tr>
<td>N</td>
<td>23</td>
<td>53</td>
<td>17</td>
<td>39</td>
</tr>
<tr>
<td>Mean no. fruits</td>
<td>2539$^a$</td>
<td>708$^b$</td>
<td>2080$^a$</td>
<td>1117$^b$</td>
</tr>
<tr>
<td>S.D.</td>
<td>1974</td>
<td>680</td>
<td>1665</td>
<td>967</td>
</tr>
<tr>
<td>Mean dbh (cm)</td>
<td>35.4$^a$</td>
<td>27.6$^b$</td>
<td>36.1$^a$</td>
<td>29.9$^b$</td>
</tr>
<tr>
<td>S.D.</td>
<td>6.6</td>
<td>9.6</td>
<td>13.2</td>
<td>8.2</td>
</tr>
<tr>
<td>Yield/Basal area (fruits cm$^{-2}$)</td>
<td>2.4$^a$</td>
<td>1.1$^b$</td>
<td>2.3$^a$</td>
<td>1.5$^a$</td>
</tr>
<tr>
<td>S.D.</td>
<td>1.5</td>
<td>0.9</td>
<td>1.5</td>
<td>1.2</td>
</tr>
<tr>
<td>Year</td>
<td>Open canopy forest</td>
<td>Closed canopy forest</td>
<td></td>
<td></td>
</tr>
<tr>
<td>------</td>
<td>--------------------</td>
<td>----------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>$R^2 = 0.44$</td>
<td>$R^2 = 0.25$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p = .001$</td>
<td>$p &lt; .001$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1999</td>
<td>$R^2 = 0.28$</td>
<td>$R^2 = 0.36$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p = 0.04$</td>
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<td></td>
<td></td>
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<tr>
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<td>$R^2 = 0.16$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p = 0.4$</td>
<td>$p = .001$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2001</td>
<td>$R^2 = 0.01$</td>
<td>$R^2 = 0.51$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$p = .9$</td>
<td>$p = .007$</td>
<td></td>
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Table 4.4. Results of the linear regression analysis of *G. gummi-gutta* fruit yield against tree diameter for four years in open and closed canopy forest.
<table>
<thead>
<tr>
<th></th>
<th>Population CV&lt;sup&gt;a&lt;/sup&gt; (4 years)</th>
<th>Average CV of individual trees&lt;sup&gt;b&lt;/sup&gt; (3 years, 11 trees)</th>
<th>Kendall’s degree of Concordance (3 years, 11 trees)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed canopy forest</td>
<td>30.2 (124 trees)</td>
<td>48.8</td>
<td>0.63</td>
</tr>
<tr>
<td>Open canopy forest</td>
<td>68.4 (39 trees)</td>
<td>71.4</td>
<td>0.25</td>
</tr>
<tr>
<td>All trees</td>
<td>42.8 (163 trees)</td>
<td>57.1</td>
<td>0.40</td>
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</table>

Table 4.5. Variation and concordance in *G. gummi-gatta* fruit production in open canopy, closed canopy, and pooled forest trees in the Western Ghats, India. <sup>a</sup> CV of the annual fruit yields of all trees for four years; <sup>b</sup> within tree variation for 11 trees averaged across years.
Figure 4.1. Non-linear regression of average fruit yield and diameter of *G. gummi-gatta* trees in the Western Ghats, India. Yield estimates for individual trees are averages of two or more years. The number of fruits per tree was log transformed to reduce the variance of residuals.
1998: $y = 88.9x - 1462.6; R^2 = 0.33; n=81$
1999: $y = 58x - 427.6; R^2 = 0.21; n=54$
2000: $y = 62.9x - 166.6; R^2 = 0.11; n=84$
2001: $y = 4.65x + 388.5; R^2 = 0.01; n=22$

Figure 4.2. Regression plot of annual fruit production and diameter of *G. gummi-gutta* trees from 1998 to 2001 in the Western Ghats, India.
Figure 4.3. Survival probabilities of *G. gummi-gatta* seeds in A) below canopy and far from adults, and B) diverse and less diverse forest in the Western Ghats, India.
Figure 4.4. Mean annual growth in cm of *G. gummi-gatta* seedlings in two canopy cover (CC) classes and of juveniles (<2m height) in the Western Ghats, India. Error bars are ± 1 standard deviation.
Figure 4.5. Probability of survival of *G. gummi-gutta* from seed stage to two-year seedling stage in a 0.4 ha plot in the Western Ghats, India.
Figure 4.6. Total number and survival of *G. gummi-gatta* seedlings from 1999 to 2001, and the annual seedling recruitment and mortality in 2000 and 2001 in the 0.4 ha intensive seedling plot in the Western Ghats, India.
Figure 4.7. A) Number of *G. gummi-gatta* seedlings in 2x2m subplots and B) distribution of seedlings and adult female trees of *G. gummi-gatta* in a 0.4 ha plot in the Western Ghats of India.
Figure 4.8. The spatial distribution of adult female trees (>20 cm dbh) and juveniles (2 to 5 cm dbh) of *G. gummi-gutta* in a 1 ha plot in the Western Ghats of India.
Figure 4.9. Ripley’s K plot of the spatial distribution of A) saplings (2-5 cm dbh) and adult female *G. gummi-gutta* trees (>20 cm dbh) in 1 ha permanent plot, and B) seedlings in the 0.4 ha intensive study plot in the Western Ghats, India. The derived statistic L12 and L are plotted against distance. Values of L or L12 > 0 indicate association between individuals, and < 0 indicate repulsion. Values of L and L12 above or below the 95% confidence intervals (dashed lines) suggest significant association or repulsion respectively.
Figure 4.10. Growth rate of *G. gummi-gutta* trees in A) open canopy and B) closed canopy forest. Mean of 3 year increments for trees in open canopy forest, error bars are 1 S.D. One year increment for closed canopy forest trees.
Figure 4.11. Average growth rate (mm/year) of *G. gummi-gatta* trees in three size classes in open and closed canopy forest in the Western Ghats, India. Error bars are ±1 standard error. Different letters denote significant differences (Mann-Whitney U, p<0.05).
Figure 4.12. Size class distribution of *G. gummi-gatta* in six sites in the Western Ghats, India. High intensity harvest: Plots 1, 2, 3, 4. Low intensity harvest: Plots 5 and 6.
Figure 4.13. Average size class distribution of *G. gummi-gatta* in the pooled high intensity (n=4) and low intensity (n=2) fruit harvest sites in the Western Ghats, India.
### A.

<table>
<thead>
<tr>
<th>Seeds</th>
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<th>&lt; 5</th>
<th>5-9.9</th>
<th>10-19.9</th>
<th>&gt; 20</th>
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</thead>
<tbody>
<tr>
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<tr>
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### B.

<table>
<thead>
<tr>
<th>Seeds</th>
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<th>5-9.9</th>
<th>10-19.9</th>
<th>&gt;20</th>
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</tbody>
</table>
Figure 4.14. The life cycle and transition rates of *G. gummi-gutta* for the periods A) 1999-2000, B) 2000-2001, and C) the combined two year period 1999-2001, obtained from a 1 ha plot in the Western Ghats, India. Short arrows denote transition from one size class to the next or staying in the same size class for a given period. Long arrows denote seed production by adults. Values along the diagonal (shaded) are the probabilities of individuals remaining in the same stage. The values below the diagonal are probabilities of individuals moving to the larger size class, and values above the diagonal are probabilities of individuals moving to a smaller size class. The numbers of seeds produced by the adults (>10 cm) is in the first row of each adult size class stage.
Figure 4.15. The effect of seed removal on $G. \text{gummi-gatta}$ population growth rate ($\lambda$) in a 1 ha. sample plot in the Western Ghats, India.
CHAPTER 5

CONCLUSION
The demand in the United States of America for Hydroxy-citric acid, a product with professed body weight reducing properties, resulted in the intensive harvest of *Garcinia gummi-gatta* fruit by local communities in the Western Ghats of India. The initial increase in the price of the rind in the year 1994 was followed by a sharp decrease in 2000, as a result of a collapse in the export market. This boom and bust scenario provided me with an opportunity to study a) the role of NTFPs in the economy of forest dependent households, b) the effect of rind collection on the income of harvester households, and c) the impact of *G. gummi-gatta* fruit harvest on the ecology of the species. The main hypotheses I tested in the study were a) low income households are more dependent on *G. gummi-gatta* than high income households, b) greater tenurial security to forest resources will ensure seedling regeneration and lesser tree damage, and c) the harvest of fruits and concomitant removal of seeds decreases the rate of *G. gummi-gatta* population growth. In this section I present the main findings of my socio-economic and ecological investigations and suggest a framework for the continued harvest of *G. gummi-gatta* from the forests of the Western Ghats.

**Socio-economic outcomes:** I found that the social and economic distribution of households within Kelaginkeri village was skewed. Brahmin households had greater access to forest resources, agricultural land, and significantly higher incomes than non-brahmin households. Contrary to expectations, I found that high income households harvested significantly higher quantities of *G. gummi-gatta* fruit rind than low income households, due, at least in part, to high income households having greater access to *G. gummi-gatta* trees in private forest holdings. The economic returns from *G. gummi-gatta* collection are thus dependent on the social status of the harvester household. Elsewhere
in India, Kumar (2002) has similarly observed that the benefits of forest use are disproportionately distributed, with a large portion of the benefits accruing to elites.

I found the proportion of unripe fruit harvested was largely defined by whether households have tenurial security over G. gummi-gatta trees. The greater the security the higher the proportion of ripe fruits that were harvested, therefore increasing income (as ripe fruits weighed more and fetched higher prices), and increasing the probability that seeds would be consumed by frugivores, subsequently dispersed, and seedlings recruited into the population. I therefore suggest that the granting of access rights to local communities might result in more ecologically benign and economically beneficial harvest. Security of tenure encourages collectors to harvest ripe fruits, instead of the current harvest of unripe fruit in ‘open access’ areas. Moreover, I found that in forest areas in which collectors had some level of tenurial security, damage to trees was minimal.

**Ecological impacts:** To assess the ecological effects of G. gummi-gatta fruit harvest and identify the life history stages that are most sensitive to fruit harvest, I evaluated three management scenarios: **Scenario 1** - no fruit harvest; **Scenario 2** - harvest of fruit without tree damage; and **Scenario 3** - harvest of fruit with associated tree damage. I used stage structured matrix modeling to simulate the effects of fruit harvest and tree damage on the population growth rate under these harvest scenarios (Caswell 2001).

**Scenario 1:** This scenario was not observed in the study area as the high value of rind ensured that all G. gummi-gatta trees within the study area were harvested. I will use the results from this simulation to assess the relative impact of fruit harvest and tree
damage. Using estimates of fruit production by trees in reserve forest, I obtained the rate of population growth when no fruits are harvested to be 1.006. A value of 1.0 indicates a stable population growth rate, thus the obtained estimate indicates a marginally increasing population. The low population growth rate of the sampled *G. gummi-gatta* population might be due to the slow growth of *G. gummi-gatta* individuals (Chapter 4).

**Scenario 2**: The scenario of fruit harvest and no associated tree damage was observed in forest areas with low to medium human density and in forest areas that had some form of tenurial arrangement. From personal observation and from interviews, I estimated that about 90% to 95% of the fruits are removed during fruit harvest in the Reserve forest. Using an estimate of 90% fruit harvest I calculated the rate population growth to be 0.987, which is marginally below stable population growth. Thus population growth rate does not appear to be strongly affected by fruit harvest.

**Scenario 3**: Fruit harvest and associated tree damage were observed in areas where human density was high. Tree damage in such areas includes the cutting of branches and the felling of trees. Using an estimate of the number of trees felled (mortality) from a sample of 187 trees, I obtained a value of 0.969 for the rate of population growth, suggesting that population growth rate is sensitive to adult tree mortality.

The results of the simulations indicate that damage to trees during harvest has the largest impact on the rate of population growth, while fruit harvest of up to 90% does not greatly decrease the rate of population growth. These results have implications for the management of the species. As the most sensitive life history stage is the adult tree, felling of adult trees during harvest should be prevented. When confronted with
incidences of high tree damage during *Myristica malabaricum* fruit harvest, the state banned the harvest of *M. malabaricum* (Saxena *et al*. 1997) rather than address factors that cause tree damage, such as the lack of local access rights and the lack of periodic monitoring of resource condition.

The incidence of cutting of branches and felling of *G. gummi-gatta* trees in ‘open access’ areas has an impact on future fruit production. I assessed the damage in percent branches cut and trees felled for a sample of 187 female *G. gummi-gatta* trees. Using size-specific fruit production values, I estimated the reduction in fruit yield for each tree. The total reduction in future fruit production of 187 trees, as a result of cutting of branches and of whole trees, was found to be about 40%. Thus, in addition to reduced population growth rate, tree damage during harvest has an economic impact of decreased fruit production.

My study indicates that the harvest of ripe fruits (as in private forest) might not adversely affect the dispersal of seeds and the subsequent recruitment of seedlings. *G. gummi-gatta* fruit are consumed by several frugivore species which disperse seeds far from adult trees. Seeds of unconsumed fruit that fall under the adult tree tend to experience high rates of predation. Seeds that escape predation and germinate close to adult trees have a lower probability of survival, due to density dependent mortality. Thus the probability of survival of seeds from fruits that are not consumed by frugivores is low. Allowing fruits to ripen on trees results in the consumption of fruits by frugivores and increases the chance of seedling recruitment. The discarded rind and fallen fruit might then be harvested by collectors, resulting in the ecological benefit of seed dispersal and the economic benefit of rind harvest.
Recommendations: The control of forests in India is vested with the state, and local communities only have *de facto* rights of access to forest resources (Shrinidhi and Lélé 2000). As a result of the lack of security of tenure there is little incentive for local communities to ensure that forest resources are harvested in a benign manner. I suggest therefore that local communities be accorded stronger access rights to forest resources. The granting of rights should however be at the level of the village rather than at the level of the household. Experience with granting forest tenure at the household level (e.g. *soppinabetta* in Uttara Kannada) has shown that closed canopy forests are often converted to woodland as a result of extraction of biomass (Nadkarni *et al*. 1989).

The granting of access rights at the level of the village might be accomplished through the establishment of village forest councils (VFC). Although collectors might continue to be tempted to harvest fruits from the forest before others, a set of regulations such as the harvest of only ripe fruits and penalizing harvesters who damage trees, might ensure a more sustainable harvest scenario. As most of the tree damage is currently caused by harvesters who migrate from other villages and nearby towns, local control will effectively hinder the ability of migrant harvesters from harvesting in village forests. It has been shown that village-level resource use regimes have succeeded in ensuring sustainable resource use in several parts of India (Kothari *et al*. 1998). Other studies have also suggested that forest resource use can be sustainable if local communities are given more control over forest resources (Jeffrey and Sundar 1999, Momberg *et al*. 2000).

My study of *G. gummi-gatta* shows that the pattern of fruit production, seed predation, seedling survival and tree growth are similar to those observed in other tropical tree species that have fleshy fruits, are animal dispersed, and grow in the understory. This
suggests that the results of this study could be applied to the management of tree species in the Western Ghats with similar ecological attributes such as such as *M. malabaricum, and G. indica*. The present study adds to the increasing body of knowledge that suggests that the harvest of fruits might not have significant impact on the rate of population growth, and that the rate of population growth is more sensitive to adult mortality than to fruit harvest (Peters 1990, Zuidema and Boot 2002). My finding that *G. gummi-gatta* seeds that are dispersed far from adult trees have a higher chance of survival suggests that *G. gummi-gatta* population density might be increased by introducing seeds into sites with low density of *G. gummi-gatta* trees. The timing of such dispersal is also important due to prolonged seed dormancy. Seeds should therefore be dispersed before the onset of the rains to prevent seed predation and enable germination.

I have argued that dependence by households on NTFPs might be problematic due to social (inequitable access within a village), economic (highly unstable markets), and ecological (variable distribution and seasonality) factors. There is however potential for NTFPs to augment household income, as was attested by a harvester who legalised his recently settled land with the spurt in income from *G. gummi-gatta*, but claimed that he would not however depend on NTFPs for a steady income (Ramachandra Siddi, personal communication). Through the granting of tenurial security and the monitoring of the ecological condition of NTFPs, such as assessing damage to trees and taking measures to ensure seedling regeneration, the harvest of NTFPs might play a useful role in augmenting household income without adversely affecting the species.
References


CURRICULUM VITAE
Nitin Devdas Rai

Education:
2003: Ph. D., Department of Biology, Pennsylvania State University.
1987: B.Sc., Environmental Science, Chemistry, and Zoology, Bangalore University.

Other:
February 1993 - September 1993: Research Assistant, Small carnivore project, Wildlife Institute of India. Survey of small carnivores in Mizoram and Sikkim, India.

Awards and Fellowships:
1999: Research grant from Conservation, Food, and Health Foundation, USA.
2001: Ben Hill Award for Plant Ecology Research, Pennsylvania State University.

Publications

Technical reports