

**BIODIVERSITY CHARACTERIZATION AND REGENERATION
ECOLOGY OF SOME IMPORTANT TREE SPECIES IN A
TROPICAL EVERGREEN SECONDARY FOREST IN NAMDAPHA
NATIONAL PARK, ARUNACHAL PRADESH**

ABSTRACT

By

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**THESIS SUBMITTED IN FULFILMENT OF THE DEGREE OF
DOCTOR OF PHILOSOPHY IN BOTANY**

**DEPARTMENT OF BOTANY
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Abstract

The present study was carried out in the secondary forests in and around Namdapha national park, in the Changlang district of Arunachal Pradesh. The secondary forests in and around Namdapha national park are regrowing on abandoned agricultural land, past human settlement areas and forest fallows and can be placed under post-extraction and post-abandonment categories. The major objectives of the present work were: (i) to characterize the vascular plant diversity in the secondary forests, (ii) to study the regeneration ecology of some of the important tree species and, (iii) to identify the factors affecting regeneration of some important tree species. While studying the above aspects, an attempt was made to address the following issues: (i) Whether the structure of secondary forests in and around Namdapha national park are significantly different from those of the primary forests? (ii) How differential landuse history has affected the present structure of the secondary forests? (iii) Whether tree regeneration process in the secondary forests is significantly different from the primary forests? (iv) Why some species are more successful in the secondary forest environment? (v) Whether the same species shows differential response to the primary and secondary forest environment? and (vi) Can the differential response of species during regeneration phase be an explanation of difference in species composition and structure of secondary forests?

Floristic diversity was higher in the secondary forests (180 species, 144 genera and 66 families) as compared to the primary forests (160 species, 117 genera and 62 families). Overall species similarity between the primary and secondary forests was 21.2%. The tree species exhibited 53.2% similarity, shrub species 21.8%, and herb and climber species exhibited 20.6% similarity. Similarity in canopy tree species between the primary

and secondary forests was 65%, while for middle and lower storied trees the similarity was 50% and 48%, respectively. Tree density between the primary and secondary forest did not differ significantly. Shrub density is significantly higher in the primary forest than the secondary forest and the density of herbs is greater in the secondary forests than the primary forests.

Mean tree basal area was higher in the primary forest ($67.14 \text{ m}^2 \text{ ha}^{-1}$) than that of the secondary forest stands ($31.65 \text{ m}^2 \text{ ha}^{-1}$). Species sharing most part of the basal area in the primary forests were *Altingia excelsa*, *Terminalia myriocarpa*, and *Mesua ferrea*, while in the secondary forests *Phoebe lanceolata*, *Dysoxylum reticulatum*, *Alangium chinense*, *Albizzia procera*, *Actinodaphne obovata* and *Dendrocalamus hamiltonii* had a major share.

More than 95 percent of the species exhibited clumped distribution both in primary and secondary forests. Only 3 to 4 percent exhibited random distribution. None of the species in the primary and secondary forest sites displayed regular distribution.

Amongst trees, *Ostodes paniculata*, *Saprosma ternatum* and *Altingia excelsa* were commonly encountered (>50% frequency) in the primary forests, whereas *Dysoxylum reticulatum* and *Alangium chinense* were frequently encountered in the secondary forest stands (>47% frequency). Amongst shrubs, high frequency was observed were for *Elatostemma platyphyllum*, *Sarcandra glabra*, *Phlogacanthus asperulus*, *Myrioneuron nutans* and *Psychrotia silhetensis* in the primary forests and in the secondary forests *Sida acuta*, *Debregeisia longifolia*, *Strobilanthes secundus*, *Leea compectiflora* and *Clerodendrum colebrookianum* were frequent. On the forest floor, *Adiantum caudatum*, *Forrestia mollissima*, *Dryopteris sparsa*, *Piper mullesua*, and *Commelina paludosa* were

frequent in the primary forests, while in the secondary forests the occurrence of *Ageratum conyzoides*, *Spilanthus paniculata*, *Oxalis corniculata*, and *Paspalum conjugatum* was frequent.

The α diversity for tree and shrubs was higher in primary forest than the secondary forest. For herbaceous species, the trend was reverse. Shannon-Weiner index for the tree species was higher in primary forests than the secondary forests. The reverse was true for shrubs and herbs. The Simpson's dominance index for trees, herbs and climbers was more in case of secondary forests than the primary forests. In shrubs, the dominance index was more in the primary forests as compared to secondary forests. Pielou's evenness index for trees was higher in the primary forests than the secondary forests. For shrubs and herbs the index was higher in the secondary forests than the primary forests. In general, the evenness index values were low indicating uneven distribution of different species. The β diversity was high between the secondary forest stands SF1 and SF3 (1.82), PF2 and SF3 (1.81) and PF1 and SF3 (1.80). PF1 and PF2 had the lowest β diversity value of 1.55.

The density-girth distribution pattern of trees shows that the secondary forests had more number of individuals in the lower girth classes' (i.e. 11-20 cm and 31-60 cm) than the primary forests. The number of individuals in the higher girth classes (>91cm) was more in the primary forests.

The secondary forests exhibited better tree regeneration than the primary forests. About 66% of the total regenerating species were in the secondary forests as compared to the latter, where only 50% species were regenerating. 41% of tree species in the secondary forests were not regenerating through seeds while in the primary forests such species constituted only 48%. Seedling populations in all the primary and secondary forest stands

showed marked differences between wet (June-July) and dry (November-December) seasons with more number of tree species in the seedling stage in the wet season.

Coppice regeneration was found only in the secondary forest stands and was predominant in SF3 with 50% of the species regenerating through coppicing. Stump girth size significantly affected sprouting in *Alangium chinense*, *Alstonia scholaris*, *Albizia procera* and *Melia azadiracht* ($p < 0.001$). Average number of sprouts was more in the girth classes of 90-120 cm and 121-150 cm. Density of coppice shoots had a significant effect over diameter and height of the shoots ($P < 0.05$ to $P < 0.001$) for all the selected species except *S. mukkorossi*. Average diameter and height of shoots was comparatively more in the stumps having less number of shoots. The number of stumps having sprout density ranging from 1-10 was more in case of *A. chinense*, *A. scholaris*, *M. azadiracht* and *S. mukkorossi*.

Flower and fruit production varied significantly across girth classes, stands and years. Flower and fruit production was higher in the secondary forests for *Alangium chinense*, *Sapindus mukkorossi* and *Spondias axillaris*, while for *Shorea assamica* and *Mesua ferrea* it was higher in the primary forest. In all the species, production was higher in the year 2004.

Seed dispersal in the selected species was primarily through gravity. But, height of release of samaras significantly affected settling time as well as dispersal distance in case of *Shorea assamica*. Pearsons' correlation coefficients showed significant negative relationship of seed weight with settling time and wing loading ($p < 0.05$; one-tailed), whilst significant positive relationships were established between wing area and settling time and seed weight, dispersal distance with settling time and wing area, and wing

loading with settling time, seed weight and wing area. Post-dispersal seed fate experiment showed that a large proportion of the seeds of *Spondias axillaris* and *Mesua ferrea* disappeared due to seed predation by ungulates and wild boar in the primary forests. In the secondary forests, most of the seeds of *Alangium chinense* and *Sapindus mukkorossi* lay dormant. Maximum seed germination was observed in case of *Shorea assamica*.

Seed viability of the selected species decreased consistently across a temporal scale. *Shorea assamica*, *Mesua ferrea* and *Spondias axillaris* recorded viability periods of 14 days, 48 days and 36 days respectively. Propagules of *Alangium chinense* and *Sapindus mukkorossi* maintained viability of 65 and 200 days respectively.

The *in situ* seed germination showed that stand quality characterised by canopy openness significantly affected seed germination in all the species ($P \leq 0.001$), whereas litter depth did not have any effect over seed germination in all the species studied. The *ex situ* seed germination experiment showed that the percentage of seed germination was more in case of the heavier seeds, as compared to the lighter ones in all the species but, statistically seed germination in all the study species was significantly affected by differences in light levels ($p < 0.05$ and $p < 0.005$) and not by seed weight (except *Shorea assamica* - $P < 0.05$).

Seedling recruitment for *Sapindus mukkorossi* and *Spondias axillaris* was higher in the secondary forests than in the primary forests. For *Shorea assamica*, seedling recruitment was higher in the primary forest. Year wise, the seedling recruitment for all the species was higher in the year 2004 than in the year 2003.

High seedling mortality of *Alangium chinense* and *Sapindus mukkorossi* occurred during first three months of germination. However, the seedling survivorship curves for *Mesua ferrea* and *Shorea assamica* showed a sharp reduction in the number of surviving

individuals after 3 months period and continued till the seedlings were one year old, after which the seedling population stabilized. The seedling mortality rate of *Alangium chinense* was negatively correlated with soil temperature ($p < 0.05$), while that of *Sapindus mukkorossi* it was correlated with light intensity ($p < 0.05$) in the secondary forest stand. The mortality rate for *Spondias axillaris* was positively correlated with light intensity ($p < 0.05$) and negatively correlated with soil moisture in the secondary forest. Seedling mortality for all the species was more under canopy of the parent tree than the peripheral area.

Relative growth rate in height and leaf area of *Sapindus mukkorossi* and *Spondias axillaris* was higher in the secondary forest as compared to the primary forest. On the other hand, for *Shorea assamica* the relative growth rate was more in the primary forest than the secondary forest. The relative growth rate in seedling height and leaf area reflected a strong seasonal influence with maximum growth in the rainy season (June-July) and least growth in the winter months (December-February).

The seedling size, seedling morphology and biomass accumulation of all the species varied significantly under different light and nutrient levels. Height, leaf area and collar diameter for *Alangium chinense* was highest at high light intensity (65%) while for *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* it was highest at intermediate light intensity (45%). All selected species responded vigorously to increased level of nutrients (30 and 35 gms of NPK) mostly under 45-65% light levels.

All the species exhibited similar patterns of biomass accumulation under different light and nutrient treatments with a general trend of increasing biomass allocation to stems, leaves and roots with increasing light. Root biomass decreased with increasing nutrient

concentration irrespective of light intensity in *Sapindus mukkorossi* and *Spondias axillaris*. In case of biomass allocation to leaves and stems an increasing trend was observed in all species with increasing nutrient concentration irrespective of light levels. In *Sapindus mukkorossi* and *Mesua ferrea*, maximum total plant biomass was obtained at 45% light; whilst in *Alangium chinense* total plant biomass was highest at high nutrient level (N₄) at 65% light. In *Sapindus mukkorossi* root biomass was highest at low nutrient level (N₁) while stem and leaf biomass was highest under high nutrient level (N₄). Root biomass in *Spondias axillaris* was highest at low nutrient level (N₁) whilst stem and leaf biomass was highest at higher nutrient level (N₄). For *Mesua ferrea* root, stem and leaf biomass were highest under high nutrient level (N₄). In *Shorea assamica* leaf and stem biomass values were highest at N₄ nutrient level while highest root biomass values were obtained at low nutrient level (N₁).

Relative growth rate in terms of height and leaf area increased consistently across light and fertilizer gradients. Relative growth rate in height increased along the fertilizer gradient and was highest at 65% light for all species while the relative growth rate in leaf area was highest under intermediate light intensity (45%) in all the species except *Alangium chinense*. Overall, LMR and SMR showed an increasing trend with increasing light and nutrient levels; but RMR, SLA and LAR exhibited a decreasing trend with corresponding levels of light and nutrient. Most of the derived growth parameters for all the selected species varied significantly within and between different fertility as well as light levels. But fertility level did not affect LAR in *Spondias axillaris*. Similarly RMR, LMR, SLA and LARMR were not affected significantly by light, nutrient or the

interactive effects of the two in case of *Mesua ferrea*. In case of *Shorea assamica* also variation in light levels did not have significant effect over SMR.

The β values in the multiple regression analysis shows that both light and nutrient have significant role in seedling growth in terms of relative growth rate in height and leaf area and total plant biomass accumulation. In case of *Alangium chinense*, *Sapindus mukkorossi* and *Shorea assamica* light intensity influenced RGRH, RGRLA and total plant mass more significantly than nutrient level. But in *Spondias axillaris* and *Mesua ferrea* nutrient levels more significantly influenced RGRLA and total plant mass than light levels respectively.

Considering the responses of various constituent species, it may be concluded that for faster recovery of secondary forests, manipulation of light and nutrient levels may be introduced. Based on the findings of the study following may be concluded:

1. The differential disturbance history had significant impact on the community structure, species composition and regeneration processes of the secondary forests.
2. The structure of primary and secondary forests significantly different, which was a function of prevailing microenvironment, nutrient availability and events during regeneration phases of the dominant species. All these factors, in turn, were also influenced by the community structure.
3. The secondary forests were species-rich and had better regeneration than the primary forests. However, due to past disturbance history, the community characteristics in these forests were relatively less complex than those of the matured primary forests.

4. The species had differential response to primary and secondary forest environments, which was both during adult as well as regenerating phases.
5. Based on the response of the species during the regenerating phase to two different forest environments, the future forest composition could be predicted.
6. Considering the species response to primary and secondary forest environment as well as the species characteristics, *Mesua ferrea* and *Shorea assamica* may be classified as primary species, *Alangium chinense* and *Spondias axillaris* as early successional species and *Sapindus mukorossi* as mid-successional species.

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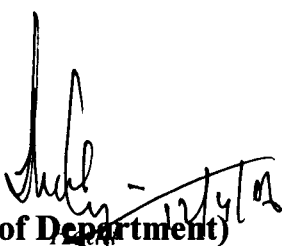
March, 2006

CERTIFICATE

I, Dibyendu Adhikari, hereby declare that the subject matter of this thesis entitled "*Biodiversity characterization and regeneration ecology of some important tree species in a tropical evergreen secondary forest in Namdapha national park, Arunachal Pradesh*" is the record of work done by me, that the contents of this thesis did not form basis of the award of any previous degree to me or to the best of my knowledge to anybody else, and that the thesis has not been submitted by me for any research degree in any other University/ Institute.

This is being submitted to the North-Eastern Hill University, Shillong for the award of the degree of Doctor of Philosophy in Botany.

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Chapter 1

General Introduction

Destruction of tropical rain forests for human habitation, agriculture and industry is one of the most pressing environmental concerns worldwide. This process has decreased substantial primary forest cover (Myers 1988) and has endangered a large number of species (Wilson 1992). Over-harvesting of NTFPs and logging have also added to the deterioration of primary forests. With the fast depletion of areas under primary forests, increasing attention is now being placed on the management of tropical secondary forests (Brown and Lugo 1990, Finegan 1992 and Corlett 1995). The management objectives of the secondary forests have largely been to meet the biomass needs of forest-dependent population, thereby reducing the pressure on the remaining undisturbed primary forests (Lammerts van Bueren and Duivenvoorden 1996, Guariguata and Ostertag 2001 and Bhat *et al.* 2001). The recognition of tropical secondary forests as the tropical forests of future has led to the rapid expansion in scientific works relating to these forests (Corlett 1994).

The tropical secondary forests have been defined in several ways. Definitions mostly cover all types of forests that have been affected in some way by anthropogenic disturbance. Such forests range from previously logged residual forests to successional forests undergoing recovery following disturbance (Brown and Lugo 1990, Weaver 1995). Definitions given to secondary forests by Finegan and Sabogal (1988), Lanly (1995), Corlett (1995) and Sips *et al.* (1997) mainly emphasize on reconstruction after complete removal of the original forest through natural and anthropogenic disturbances. However, in asian context, all the reconstructed forests arising out of the complete or partial removal of trees are referred to as secondary forests (Corlett 1995).

Chokkalingam and de Jong (2001) reviewed the contemporary definitions of secondary forests and have proposed a generalised working definition for secondary forests. The review says 'secondary forests are forests (could include land ≥ 0.5 ha in area and width of more than 20 m, with $> 10\%$ crown cover of trees and 5 m in height) regenerating largely through natural processes after significant human and/or natural disturbance of the original forest vegetation at a single point of time or over an extended period, and displaying a major difference in forest structure and/or canopy composition with respect to nearby primary forests or on similar sites'. Perhaps the best ecological definition that could be applied to secondary forests is those forests regenerating largely through a natural process after significant human disturbance of the original forest vegetation causing a major difference in forest ecosystem structure and function.

India has 2.5% of the world's land area and 1.8% of the global forest area. However, it supports 15.6% of the world's human population and 14% of the world's livestock population. In addition to a livestock population of about 300 million which graze in forests, India has a rural human population of nearly 700 million which is largely dependent on forests for meeting diverse biomass needs (Bhat *et al.* 2001). Because of the proximity to human settlements, forest products are easily extracted from the secondary forests and hence, economically more viable than the primary forests which are mostly found in inaccessible areas and far away from human habitations. Besides, the secondary forests help restore the productivity of the area, provide a variety of products like edible fruits, timber, medicinal plants and a host of NTFPs. Secondary forests may also function as buffer zones in protected areas by providing the habitat for the plants and animals, which are displaced from the primary forest in the core zone following

disturbance. Additionally, they also serve as better habitat for wildlife because they support higher animal production than mature forests (Brown and Lugo 1990). They are also potentially important for diverse ecological services such as soil and watershed conservation, flood control, and carbon sequestration (Bhat *et al.* 2001). Lugo and Brown (1992) have reported aboveground carbon (C) accumulations between 2 to 3.5×10^6 g C ha⁻¹year⁻¹ for young (less than 20 years old) tropical secondary forests, which is comparable with that of plantations of similar age (1.4 to 4.8×10^6 g C ha⁻¹ year⁻¹). The secondary forest could also play a significant role in ecosystem and biodiversity rehabilitation. This is particularly true, if an old growth secondary forest is allowed to remain for longtime which eventually lead to formation of primary forests. Brearley *et al.* (2004) showed that during the transition from secondary to primary forest, at least 70-80% structural recovery took place by 55 years. Thus, a substantial part of the primary forest could be taken over by the secondary forests. Several characteristics of secondary forests such as high biomass production rate, high density of economically important tree species and are more or less of similar age structure of tree populations (Finegan 1992) make their management more feasible than the primary forests. Therefore, the proper management of secondary forests could help in reducing the pressure on primary forests (Brown and Lugo 1990, Sips *et al.* 1997, Sips 1997, Bhat *et al.* 2001).

Secondary forests have been classified based on successional stages, vegetation types, ownership patterns, land use history, and nature of influence (Chokkalingam *et al.* 2000). In Asia, secondary forests have been classified based on landuse origin and nature of human influence. Accordingly, post-extraction secondary forests, swidden fallow

secondary forests, post-abandonment secondary forests, post-fire secondary forests and rehabilitated secondary forests exist in place (Chokkalingam *et al.* 2000).

The degradation of primary forests and formation of secondary forests in most south Asian countries have passed through three phases viz., (i) the pre-colonial period, when dependence on forest was less exhaustive with less impact on the forests; (ii) the colonial administration and post-colonial period, when the intensive use of forests had greater impact on forest vegetation that led to large-scale formation of post-extraction secondary forests; and (iii) the recent rehabilitated secondary forests on degraded lands due to dedicated efforts of regeneration (Bhat *et al.* 2001).

Most forests in India have been significantly affected by logging, clearfelling, grazing, fire, and collection of fuelwood, fodder and non-timber forest products. As a result, majority of the forests of India are secondary in nature, which are primarily post-extraction secondary forests. In India, secondary forests occupy about 32 million ha and constitute about 45.8% of the total forest area of the country (Chaturvedi 1992).

In northeastern India the main cause of deforestation is shifting cultivation and therefore, large tracts of forests found in secondary forest category are regenerating fallows belonging to swidden fallow secondary forest type. Secondly, more than 64% of the total forest area of the region either belongs to the communities or is owned by individuals. Because the livelihoods of the majority of population of north-eastern region are forest-dependent, most of these forests are over-extracted, thus giving way to the formation of post extraction secondary forests. Thirdly, large-scale plantation and rehabilitation programmes undertaken in the recent past in the region have resulted in an increase in the area of rehabilitated secondary forests.

Arunachal Pradesh, which is a part of Eastern Himalayas, is known for its rich biodiversity and undisturbed old-growth primary forest ecosystems. However, of late, due to increasing population pressure and diverse developmental activities, the areas under secondary forests are slowly increasing (FSI 2003).

Champion and Seth (1968) described 78 types of secondary forests in India based on physiognomy, structure, function, floristics, dynamics, habitat, physiography and history. Out of these, 25 types are in greater Assam (including NEFA, Nagaland, Sikkim and Bhutan) - part of the Eastern Himalayas, These are mainly: (i) Pioneer Euphorbiaceous scrub, (ii) Sub-Himalayan high alluvial semi-evergreen forest, (iii) *Syzygium* parkland, (iv) Eastern alluvial secondary semi-evergreen forest, (v) Sub-Himalayan secondary wet mixed forest, (vi) Secondary moist bamboo brakes, (vii) Moist sal savannah, (viii) Northern secondary moist mixed deciduous forest, (ix) Secondary Euphorbiaceous scrub, (x) Low alluvial savannah woodland, (xi) Eastern hollock forest, (xii) Sub-montane hill valley swamp forest, (xiii) Creeper swamp forest, (xiv) Tropical seasonal swamp forest, (xv) Eastern *wet alluvial* grassland, (xvi) Riparian fringing forest, (xvii) *Khair-sissu* forest, (xviii) Assam sub-tropical pine forest, (xix) Assam sub-tropical pine savannah, (xx) Montane bamboo brakes, (xxi) Alder forest, (xxii) Low-level blue-pine forest, (xxiii) *Hippophae/Myrica* scrub, (xxiv) Sub-alpine blue pine forest, and (xxv) Sub-alpine pasture. Kaul and Haridasan (1987) described two major types of secondary forests in Arunachal Pradesh viz., degraded forests and bamboo forests based on species composition. Considering the nature of origin of secondary forests of Arunachal Pradesh, following secondary forest types are recognized:

(i) *Swidden fallow secondary forest* - Shifting cultivation is among the major landuse practice in the northeastern states of India that has affected forest cover to the extent of 5476 km². Arunachal Pradesh (925 km²) is next to Nagaland (1011 km²) in terms of area affected by shifting cultivation (FSI 2003). The government has however realized the consequences of shifting agriculture, and introduced Jhum (Shifting Agriculture) Land Regulation Act 1974. The abandoned shifting cultivation areas undergo rapid regeneration resulting in the formation of swidden fallow secondary forests.

(ii) *Post extraction secondary forest* – Post extraction secondary forests include forest areas, which have undergone either clearfelling or selective felling or other extractive activities. This creates a very irregular forest structure, with numerous gaps filled with climbers. It is often represented by the dense stands of young trees. In the forest assessment by the FSI, such areas have been included under the open forest category. The area under open forest has increased from 14,113 km² in 2001 to 14,508 km² in 2003 thus increasing the area under post extracted secondary forests (FSI 2003).

(iii) *Rehabilitated secondary forests* – Tree plantations in degraded lands represent the rehabilitated secondary forests. Although forest plantation has remained a low key activity in Arunachal Pradesh due to rich forest, it started in early 1950s. The plantations started with native species such as *Terminalia myriocarpa*, *Bombax ceiba*, *Dipterocarpus macrocarpus* and some exotic species like *Tectona grandis*. At least 1600 km² of land area have been recorded under plantations in Arunachal Pradesh (FSI 1999) thus increasing the area under rehabilitated secondary forests.

Besides these three major categories of secondary forests, there are three other minor types of secondary forests found in Arunachal Pradesh. The latter have originated due to

various reasons and accordingly named as post fire secondary forests (forests regenerating after forest fires), post catastrophe secondary forests (forests regenerating after natural disasters like floods, landslides, earthquakes), and post abandoned secondary forests (forests regenerating after abandonment of human settlements or pastures).

Protected areas around the world are not free from human interferences and Namdapha national park is not an exception in this regard (Arunachalam *et al.* 2004, Adhikari *et al.* 2003). Secondary forests regrowing on abandoned agricultural land, past human settlement areas and forest fallows constitute an important component in the landscape matrix in and around Namdapha nature reserve. These secondary forests play an important role in meeting the biomass needs of the local population (Sarmah *et al.* 2003, Arunachalam *et al.* 2004). Earlier studies done in the National park mainly concentrated on characterizing the plant and animal diversity in the primary forest of the core zone. These include the botanical explorations in the core zone of Namdapha National Park conducted by Botanical Survey of India (Sharma *et al.* 1990, Chauhan *et al.* 1996), State Forest Research Institute (Arunachal Pradesh), and other agencies, which led to species inventorization in the primary forests. The present study has been carried out in the tropical evergreen secondary forests in and around Namdapha National Park, which are taxonomically and ecologically unexplained. The secondary forests are mainly confined to the buffer zone and can be placed under post-extraction and post-abandonment categories. No research has been conducted in these secondary forests for evolving better management strategies. In this study, in-depth plant diversity analysis has been carried out and the regeneration ecology of some selected tree species in the secondary forests have been studied. The results of the study can be used for developing an effective

management plan for the restoration and sustainable management of the tropical evergreen secondary forests of Namdapha National Park.

The specific objectives of the present study are to:

1. Characterize the plant diversity in secondary successional forest communities.
2. Study the regeneration ecology of a few important tree species, and to
3. Identify the factors influencing tree regeneration in secondary forests.

Chapter 2

Review of literature

Vast forest areas in the tropics have been cleared for expansion of agricultural activities, creating space for human habitation, Undertaking developmental projects and rapid urbanization. Over-harvesting of non-timber forest products (NTFPs) and logging have also added to the deterioration of the primary forests. The destruction of primary forests leads many species to the danger of extinction (Wilson 1992). Therefore, damage to primary forests of the tropics have been a matter of great concern both for the scientific community as well as the popular media. Simultaneously, there has been an increase in the areas under secondary forest as the deforested sites and abandoned lands get regenerated.

Realizing the socio-ecological and economic importance of the secondary forests, a lot of works have been carried out during the past one decade and there has been a lot of debate over the definition of secondary forest in the recent literature (Corlett 1994). Definitions mostly cover all types of forest that have been affected in some way by human disturbance, ranging from previously logged, residual forests, to successional forests that develop after complete clearance (Brown and Lugo 1990, Weaver 1995). Definitions given to “secondary forests” by Finegan and Sabogal (1988), Lanly (1995), Corlett (1995) and Sips *et al.* (1997) mainly emphasizes on ‘reconstruction after complete removal of the original forest through natural and/or human disturbance’. This definition when considered in the context of tropical secondary forests and their management in Africa, Asia and Latin America seems most appropriate to the Latin American context and to a lesser extent to Africa and Asia.

A secondary forest, created due to successional processes after a major disturbance is essentially a progressive modification in the structure and species composition of the vegetation (Grime 1979). Secondary forest succession can be visualized as a continuum from an early stage of ecosystem development, where the factors that govern colonization are most important, to later stages where competitive ability and tolerance to environmental conditions among species largely dictate patterns of species replacement over time (Walker and Chapin 1987). Succession has been a subject matter for research for a long time and several theories have been proposed to explain this phenomenon. These theories range from a holistic approach of Clements (1916), in which the vegetation was seen as an entity, moving in a predictable way towards a climax, to a more individualistic approach put forth by Gleason (1926), in which species enter into the system by chance and are found together with other species simply because their environmental requirements overlap. The floristic composition hypothesis proposed by Egler (1954) has been the basis for explaining the secondary forest succession in many tropical forests (Gomez-Pompa and Vasquez-Yanes 1981, Finegan 1984). It explains that species changes their ranks at different stages of succession depending on their life histories, growth rates and reproductive efficiency (Pena-Claros 2001). Species that dominate in the early stages of succession are called early successional species, while the species dominating in the consecutive successional stages have been referred to as mid- or late successional species (Bazzaz 1979). Secondary forest succession has been extensively studied throughout the lowland neotropics for many decades (Kenoyer 1929, Standley 1937, Budowski 1961). However, the mechanisms and patterns of forest

recovery still remain poorly understood (Brown and Lugo 1990, Lugo 1992, Finegan 1996, Brearley *et al.* 2004).

Several investigations on the community structure as well as species composition have been carried out in the disturbed and secondary forests in the tropics (Budowski 1961, Snedaker 1970, Tergas and Popnoe 1971, Knight 1975, Ewel 1971, 1976, Uhl *et al.* 1982, Uhl and Clark 1983, Aide *et al.* 1996, Fearnside and Guimaraes 1996, Guariguata *et al.* 1997, Hughes *et al.* 1999, Nicotra *et al.* 1999, Miller and Halpern 1998, Silver *et al.* 2000, Denslow and Guzman 2000, Lavertu *et al.* 1994, Sato *et al.* 1994, Herranz *et al.* 1997, Rikhari *et al.* 2000, Finegan and Delgado 2000, Andel 2001, Bellemare *et al.* 2002, Galindo-Jaimes *et al.* 2002, Kennard 2002, De Walt *et al.* 2003, Brearley *et al.* 2004).

The studies from India on disturbed and secondary forests mainly focused on the effect of varying degrees of disturbances on the forest structure and regeneration. The works on impact of disturbance on forest structure are those of Khan *et al.* 1987, Rao *et al.* 1990, Barik *et al.* 1996b, Arunachalam *et al.* 1997, Pandey and Shukla 1999, Pande 1999, Chittibabu and Parthasarathy 2000, Shukla and Pandey 2001, Bhuyan *et al.* 2001, 2003, Pandey and Shukla 2001 and Pandey and Shukla 2003. The tree regeneration as affected by cultural disturbance were studied by Shukla and Ramakrishnan 1986, Khan *et al.* 1987, Barik 1992, Barik *et al.* 1996a,b, Kikim and Yadava 1998, Pandey and Shukla 2001. Ramakrishnan and Toky 1981, Singh 1980, and Toky and Ramakrishnan 1983a,b studied the changes in species composition and community structure along a secondary successional path in the abandoned jhumlands. Bhat *et al.* (2001) analysed the underlying causes of secondary forest formation and recovery in India, particularly in the Western Ghats region of south India.

Guariguata and Ostertag (2001) reviewed the main biotic and abiotic factors that influence the patterns of neotropical secondary forest succession. They argued that the regenerative power of neotropical forest vegetation would be very high, if the propagules were found nearby and the intensity of land use was not severe before abandonment. The recovery of physical and biological properties of the forest ecosystem is dependent on the interactions between site-specific factors and land use pattern. Therefore, it is extremely difficult to predict successional trajectories in an anthropogenic setting. Bellemare *et al.* (2002) investigated the long-term effects of human disturbance on the species composition, structure and distribution of Rich Mesic Forests in western Massachusetts, USA. They found a persistent compositional difference between the vegetation of primary forests and post-agricultural secondary forests. This explains the distribution patterns of many plant species based on the past land use intensity i.e. agricultural activities. Finegan and Delgado (2000) studied the structural and floristic characteristics of a 30-year-old secondary forest developing on a 32.5 ha pasture land on a hilly terrain, abandoned after use of moderate intensity. They found that the tree species, including the dominants, were a mixture of those present in old-growth forest as well as those from adventives colonizing from agricultural land. Pena-Claros (2003) studied the changes in forest structure and species diversity during secondary succession using a series of chronosequenced forest stands (ranging in age from 2 to 40 years and mature forest stands) at two sites in the Bolivian Amazon and found that secondary forests rapidly attain a forest structure similar in many respects to mature forests with increase in canopy height and basal area. Webb and Sah (2003) studied the structure and diversity of natural and managed sal (*Shorea robusta*) forest in the Terai of Nepal and found that

successional sal forest recovered *ca.* 60% of species richness found in a natural sal forest stand in 20 years time. On the other hand, Brearley *et al.* (2004) through their study on the structure and floristics of a 55-year-old secondary rain forest in Central Kalimantan, Indonesia found that the forest recorded upto 82% in terms of biomass, upto 88% in terms of tree height and 74% in terms of biomass when compared with an adjacent primary forest. However, in terms of floristic and species richness, there remained a major gap. Kennard (2002) after characterizing the stand structure, species richness and population structure of tree species in 12 stands undergoing succession following slash-and-burn agriculture in a tropical dry forest in lowland Bolivia, revealed that tree species richness and canopy cover reached 75% of mature forest levels after 5 years of succession. This rapid recovery was attributed to a high percentage of sprouting tree species and high seed fall on the abandoned fields. In a study in Colombia, Faber-Langendoen (1991) estimated that after clearcutting tropical rain forest, 40 years would be required for the tree community to return to pre-cut diversity levels. China and Helmer (2003) investigated the diversity and composition of tropical secondary forests recovering from large-scale clearing in Puerto Rico and concluded that timing of abandonment, land use history and biophysical variables are of overwhelming importance in determining the species composition of recovering forests.

Numerous studies have shown a relationship between the distribution of tropical trees and soil fertility and/or moisture gradients at the landscape scale (Austin *et al.* 1972, Baillie *et al.* 1987, Swaine 1996). Miyamoto *et al.* (2003) studied the habitat differentiation among tree species in a tropical heath forest of Central Kalimantan in Indonesia and found that

edaphic and topographic factors, especially humus depth, contributed to spatial distribution of dominant tree species and floristic composition of the forest.

Condit *et al.* (1998) offered conclusive evidence to the fact that absence of juveniles suggests the population decline using data from a 50 ha census plot in Panama. Empirical evaluation of 216 tree populations showed that juvenile growth was the strongest predictor of size distribution. Size distribution did not have any correlation with population growth, but showed weaker relationship only in case of understory species. Their results also confirm that the demographic information is a better predictor of future population than the static information on size distribution.

The species-area and species-individual relationships are the foundations of modern ecological science (Connor and McCoy 1979, McGuinness 1984, Rosenzweig 1995, Durrett and Levin 1996) and have been central to community ecology for decades (Fisher *et al.* 1943, Preston 1948, 1962, MacArthur and Wilson 1967). They are fundamental components of conservation biology and are frequently used to formulate recommendations for species conservation and to predict extinction rates caused by habitat destruction (Diamond 1975, Schafer 1990, and Pimm *et al.* 1995). Condit *et al.* (1996) prepared the species accumulation curves for woody plants in three tropical forests viz. wet, old-growth forest in Peninsular Malaysia, in moist old-growth forest in Central Panama, and in dry previously logged forest in southern India. A total of 610000 stems were identified up to species level and were mapped to < 1m accuracy. Based on their study, they argued that species-individual curves are more useful for assessing and comparing diversity than species-area curves since species accumulate simply and predictably as a function of individuals counted, but not as a function of area. Previous

studies have also recognized that species-accumulation can be predicted better by counting individuals rather than area (Ashton 1977, Angermeier and Schlosser 1989).

Populations are always in a state of flux because of natality and mortality. Tree species populations differ in their modes of regeneration either through seeds or through vegetative means such as coppicing and root suckers. The process of regeneration through seeds involves various events in the plant life cycle such as flowering, seedling, seed dispersal, seed germination and seedling establishment. Each of these events is differentially affected by various biotic and abiotic factors. Many studies have been conducted in regeneration ecology of both unmodified and modified forests of different types located at different latitude, longitude and altitude (Brooks 1941, Ayliff 1952, Holmes 1956, Murray 1981, Kahn 1982, Heuvelink and Neumann 1983, Burschel *et al.* 1985, Venning 1985, Barik *et al.* 1996b, Khan and Tripathi 1987, Khan *et al.* 1986). Regeneration studies on selected species and specific categories of taxa are also available (Watt 1919, 1923, Barnard 1956, Khoon 1981, Newbold *et al.* 1981, Chaconsootelo 1983, Daly and Shankman 1985, Drapier 1985, Melnik 1985, Morin 1986, Szappanos 1986, Bernier 1987, Everard 1987). The shifts in the species composition during secondary succession have been explained based on the species response to disturbance during regeneration phase. However, it is indeed a difficult task to establish this hypothesis because of the long life of trees, where the response may be delayed for decades or possibly centuries. Direct observation is therefore only possible in exceptional cases. Ulft (2004) used computer models, based on ecological data, to simulate the long-term effects of disturbance on the species composition.

During the regeneration process, seedling establishment is the weakest link between the two successive generations as during this stage maximum selection pressures operate particularly in tropical forest species. In this stage, high rate of mortality occurs (Fenner 1987, Whitmore 1996), because of various density-dependent and density-independent factors. These factors include, pathogenic fungi (Augspurger 1988), herbivores (Janzen 1970, Clark and Clark 1984, Clark and Clark 1985), water stress (Poorter and Hayashida-Oliver 2000), nutrient (Whitmore 1996), and light limitation (Malcolm *et al.* 1996), and mechanical damage due to falling branches and leaves (Clark and Clark 1989, Clark and Clark 1991, Scariot 2000). Barik *et al.* (1996b) studied the effect of cultural disturbances on seed production, dispersal and germination of important tree species of north-east India viz. *Schima khasiana*, *Lithocarpus dealbatus* and *Quercus griffithi* and concluded that disturbance had conspicuous effects on the seed production, dispersal as well as germination of these species.

Coppicing is an important means of vegetative regeneration where large-scale disturbance occurs as a result of clearing, burning and extensive damage due to storm. Several workers have worked on coppice regeneration in cut dry forest (Ewel 1977, Murphy and Lugo 1986, Murphy *et al.* 1995) and in the wet tropics (Byer and Weaver 1977, Stocker 1981, Uhl *et al.* 1981, Putz and Brokaw 1989, Kauffman 1991, Bellingham *et al.* 1994).

Luoga *et al.* (2004) studied natural regeneration by coppicing of tree species in a forest reserve and more disturbed adjacent public lands in eastern Amazonian miombo woodlands. They found that 83% of the 30 harvested woody species in the forest reserve coppiced, while 90% of the 39 species in the public land sprouted. Mean number of

shoots per stump varied among the species, which was correlated with the plant size at the time of cutting, stump height and percentage of the stand removed.

Phenology is the study of the periodicity or timing of recurring biological events such as flowering, fruiting, leaf flushing and germination in plants (Sakai 2001) and plays an important role in survival and reproductive success of a plant. Off-season germination, flowering, and leaf production out of season causes low survivorship of seedlings (Tevis 1958), low seed production (Augspurger 1981), and a high predation rate (Aide 1992). Besides, the change in phenology can greatly affect animals that use young leaves, flowers, and mature and immature of the plants. Such changes in phenology have been attributed to temporal changes in plant resource availability (van Schaik *et al.* 1993). Excellent reviews on tree phenology are those of Primack (1987), and van Schaik *et al.* (1993). A brief review of flowering of tropical plants was made by Bawa (1983). Flowering phenology of many forest trees, have been studied in the evergreen forests of tropics (Holttum 1931, Holmes 1942a,b, Koelmeyer 1959, Pinto 1970, Medway 1972, Ng and Loh 1974, Cockburn 1975). The phenological studies conducted in forest ecosystems of Central Himalayas are those of Ralhan *et al.* (1985a,b), and Sundriyal (1990). Boojh and Ramakrishnan (1981), Shukla and Ramakrishnan (1982), Barik *et al.* (1996b), and Kikim and Yadava (2001) studied the phenology of forest trees in northeastern India. Most studies on plant phenology in tropical forests have tried to test the hypothesis that the species populations apportion various phonological events along different months of the year to optimize the use of resources by various species populations. In the process, it also helps the resource availability for consumer animals (Frankie *et al.* 1974, Croat 1975, Putz 1979, Opler *et al.* 1980, Foster 1982, Murali and Sukumar 1994).

Workers have developed different methods to study plant phenology, depending on the aim of the research, the type of plant and climatic conditions. These methods vary widely in terms of time required for data collection and the precision of the data. Sampling units may be single branches (Baker *et al.* 1982, Gill and Mahal 1986, Nilsen 1986, Negi and Singh 1992, Oliveira *et al.* 1994, Dhaila *et al.* 1995, Nitta and Ohsawa 1997) or whole plants (Frankie *et al.* 1974, Arroyo *et al.* 1981, Bertiller *et al.* 1991, Neeman 1999). The observation intervals vary from a few days (Estabrook *et al.* 1982, Shukla and Ramakrishnan 1984, Wright and Calderon 1995) to one month (Lowman 1992, Kaplan and Gutman 1999). Some authors just monitor one or a few individuals, which are considered as a prototype of the species or populations (Baker *et al.* 1982, Nilsen 1986, Orshan 1989, Nitta and Ohsawa 1997). Others select a representative number of samples to get the frequency of phenological stages across the population (Shukla and Ramakrishnan 1982, Kaplan and Gutman 1999).

Castro-Diez *et al.* (2003a) compared the phenological information gathered through different methods on the same population of *Halimum atriplicifolium* (Cistaceae), a Mediterranean evergreen shrub. The first method, called semi-quantitative (SQT), was based on a monthly estimation of each phenophase incidence through a visual inspection of ten whole plants. The second one, called quantitative (QT) was based on monthly monitoring of all the leaves, buds, flowers and fruits borne on five tagged branches throughout an annual cycle. They found that the QT method is most advisable for inconspicuous phenophases, such as leaf production by brachyblasts and the SQT is recommended for more conspicuous phenophases.

In the tropical regions, periodic change in rainfall caused by movements of the intertropical convergence zone often plays an important role as proximate and ultimate factors for plant phenology (van Schaik *et al.* 1993). Many studies have also shown correlation between tropical plant phenology and rainfall (Augspurger 1981, Borchert 1983, Reich and Borchert 1984). Most neotropical forest communities show flowering and fruiting peaks near the end of the dry season (Janzen 1967, Croat 1975, Foster 1982, Frankie *et al.* 1974, Hilty 1980, Opler *et al.* 1980, Bullock and Solis-Magallancs 1990, Justiniano and Fredericksen 2000). The pattern may be caused by high insolation and photosynthesis in dry seasons or by enhancement of germination and seedling survival by adjusting fruiting to precede the beginning of the wet season (van Schaik *et al.* 1993).

Seed dispersal has long been a topic of interest to naturalists, but only recently has the ecology of dispersal received concerted and rigorous scientific attention (Willson 1992). The probability of tree establishment in areas used for slash-and-burn agriculture and for human habitation is highly dependent on seed dispersal for the formation of secondary forests in these areas (Uhl 1987). This is due to the fact that the soil seed bank has been largely reduced during the burning and farming (Uhl *et al.* 1981, Uhl 1987) as well as disturbance to the area. Thus, seed arrival at the barren site either by primary (Howe and Smallwood, 1982, van der Pijl, 1982, Jurado *et al.* 1991, Peroni 1994, Muralikrishna and Chandrashekar 1997, Ganeshiah and Uma Shaanker 1991, Bhuyan *et al.* 2000, Osada *et al.* 2001) or secondary (Hammond *et al.* 1996, Hammond and Brown 1995, Hegde *et al.* 1991, Campos and Ojeda 1997, Dalling *et al.* 1998, Wenny 2000a,b) means is a prime importance for revegetation of the disturbed site. The primary modes of seed dispersal viz. dispersal by gravity have the limitation of clumping of seeds around the parent tree

leading to increased chances of density-dependent negativities for the tree species. Thus, post-dispersal seed removal may play an important role in determining the tree species composition and tree density of an area undergoing succession (De Steven 1991, Hammond 1995, Meiners and Stiles 1997, Myster and Pickett 1993, Uhl *et al.* 1988, Whelan *et al.* 1991, Pena-Claros 2001). The tree species composition can be influenced by seed removal rates if the seed removal agents have a preference for seeds of certain species over others (Meiners and Stiles 1997). The preferences could be nutritious, colorful as well as fleshy fruits to attract animal dispersers (Harper 1977, Schupp and Fuentes 1995, Nathan and Muller-Landau 2000) as well as seed characteristics such as seed size, nutrient content, local abundance, and handling time (Meiners and Stiles 1997). Some authors have found a negative relationship between seed removal rate and seed size (Nepstad *et al.* 1996, Uhl 1987), which implies that large seeded species would have a higher chance of being present in secondary forests than small seeded species. A few studies have found, however, no relationship exists between removal rate and seed size (Holl and Lulow 1997, Meiners and Stiles 1997, Myster and Pickett 1993).

Moreover, seed removal agents will finally determine how many dispersed seeds are actually available for germination (Uhl 1987). Several workers have studied seed removal rates in closed canopy forest in comparison to gaps, forest edges or pastures (e.g. Holl and Lulow 1997, Schupp 1988) and in secondary forests differing in successional stage (Hammond 1995, Uhl 1987, Pena-Claros 2003). Rodents and ants have been reported as the most important seed removal agents in areas undergoing succession (e.g. Whelan *et al.* 1991, Nepstad *et al.* 1996). Rodents seem to prefer habitats with more cover because cover provides them shelter from predators. Predation risk for rodents has been shown to

vary as a function of several environmental and stand characteristics, such as stand density, type of groundcover (Pena-Claros 2001), and amount of canopy cover (Lagos *et al.* 1995). There is little information available on the habitat preference of ants, although higher ant densities have been reported for younger successional stages than for older ones (e.g. Vasconcelos and Cherret 1995).

Overall, species can be classified depending on the basis of their requirements for germination and establishment into pioneer and primary species (Swaine and Whitmore 1988, Barik *et al.* 1996b), or into light demanding and shade tolerant species. In between these two extremes, there is also a large group of species that have intermediate characteristics (Budowski 1965, Denslow 1980) also termed as long-lived pioneer (Pena-Claros 2003). Long-lived pioneer tree species are thought to establish also in early successional stages but they have a considerably longer life-span than pioneer tree species (Budowski 1965, Finegan 1996).

Cruz *et al.* (2000) studied the germination and seedling survival of a few native tree species viz. *Cornus disciflora*, *Cornus excelsa*, *Drimys granadensis* var. *mexicana*, *Liquidamber styraciflua*, *Persea americana*, *Quercus laurina* and *Ternstroemia lineata* in nursery as well as in forest stands with varying dominance by pines in the central highlands of Chiapas. The nursery treatments included different composition of litter collected from replicated plots of three forest types viz. old-growth forest, mixed pine-oak forest and pine-dominated forest. They found that natural recruitment and germination of seeds were higher in old-growth forests and concluded that oak litter may favor germination and early establishment of the species.

Khan *et al.* (2002) observed the variation in fruit set and fruit size on sunlit and shaded parts of individual trees of *Mesua ferrea* and found that fruit set was significantly higher in parts of the individuals exposed to sunlight, though shaded parts produced heavier and larger fruits than sunlit parts. Seeds from four seeded fruits germinated earlier and their germination percentage was significantly higher than one-, two- and three-seeded fruits. On the other hand, seedlings emerging from one-seeded fruits survived and grew better (Arunachalam *et al.* 2003). Also, seedlings emerging from shaded parts showed better survival and growth than their counterparts from sunlit parts.

Seedling recruitment has been identified as an important factor limiting forest diversity by many authors (Grubb 1977, Pacala and Tilman 1994, Hubbell *et al.* 1999). Various processes which affect the spatial and temporal variation in seedling recruitment have been described by many workers which include synchronous temporal variation in seed production within populations (e.g. masting) (Godman and Mattson 1976, Graber and Leak 1992, Sork *et al.* 1993), highly localized seed dispersal in many tree species (Augsburger 1983, 1986, Hughes and Fahey 1988, Houle and Payette 1990), spatial and temporal variation in the abundance and foraging patterns of animal seed dispersers and consumers (Schupp 1988, Schupp *et al.* 1989), variation in climatic and microclimatic conditions that affect seed germination and early seedling survival, and spatial variation in substrate (seedbed) favorability and safe-site abundance (Bernsten 1955, Smith and Clark 1960, Eis 1967, Arnott *et al.* 1971, Minore 1972, Geier-Hayes 1987, Harmon and Franklin 1989, Anderson and Winterton 1996, LePage *et al.* 2000, Khurana and Singh 2000). Ibanez and Schupp (2002) assessed the effects of litter layer, soil surface conditions, and microhabitat on emergence of the tree *Cercocarpus ledifolius* and showed

that the role of litter layer varies during the first year of the life of this species, with litter inhibiting initial emergence but enhancing early seedling survival.

The establishment phase gives the biggest 'demographic squeeze' to the seedling population (Whitmore 1996) in the form of mortality. Seedling mortality across a spatial and temporal scale caused by factors such as light levels, understory shrubs, and resource limitation contributes to patterns of forest composition and species richness. Alvarez-Buylla and Martinez-Ramos (1992) showed the highest loss of population between seed germination and seedlings attaining 3mm stem diameter. Flores (1992) also found 50 percent mortality in the first year in two species studied in a Venezuelan cloud forest. Khurana and Singh (2000) pointed out that patterns of seed production, germination, survival and seedling development is affected by pronounced seasonality. Nevertheless, large number of workers have shown that high-light environments of disturbed forest sites may favor the germination and early establishment of some species in which growth is high and mortality low (Gerhardt 1993, 1996, Gerhardt and Fredriksson 1995, Morris *et al.* 2000, Rincon and Huante 1993), but dry-season conditions usually increase mortality rates among individuals (Gerhardt 1993, 1996 Gerhardt and Fredriksson 1995, Hammond 1995).

Meiners *et al.* (2002) examined the changes in seedling establishment of *Acer rubrum*, *Acer saccharum*, and *Quercus palustris*, along a forest–old field edge gradient and found that emergence increased with distance into the field for both *A. saccharum* and *Q. palustris*. Emergence for *A. rubrum* increased from forest to field, reaching a maximum near 20 m into the field, and then declined with further distance. Nearly all *A. rubrum* seedlings died shortly after emergence. Survival of *A. saccharum* increased with distance

into the old field, while survivorship of *Q. palustris* did not respond to the edge gradient. Establishment probabilities increased with distance into the old field for both *A. saccharum* and *Q. palustris*. Growth of *Q. palustris* and allocation patterns of *A. saccharum* also varied across the edge gradient. They concluded that edges have complex, species specific effects on tree establishment and growth that can influence the spatial pattern and species composition of regenerating forests.

McLaren and McDonald (2003a,c) studied the seedling dynamics after different intensities of human disturbance in a tropical dry limestone forest in Jamaica and found that the density of some species was affected by the environmental condition created by partial and clear cutting, and seasonal affects were more pronounced after disturbance. Also, biomass recovery by seedlings was negligible in comparison with coppice regrowth which offered considerable resilience to disturbance in the dry forest where successful regeneration by seed was highly susceptible to rainfall seasonality.

Litterfall has been demonstrated to be an important mechanism of seedling damage and mortality by several studies in tropical forests (Vandermeer 1977, Nunez-Farhan and Dirzo 1988, Clark and Clark 1989, Mack 1998, Scariot 2000, Drake and Pratt 2001) as well as in some temperate and boreal forests (Gregory 1966, Gillman and Ogden 2001). Gillman *et al.* (2003) studied the response of forest tree seedlings of *Corynocarpus laevegatus*, *Hedycara arborea*, *Nestegis cunninghamii*, *Knightia excelsa*, *Prumnopitys ferruginea*, *Nothofagus menziesii* and *Beilshmedia tawa* to stimulated litterfall damage and found that some species are more likely to survive in high-risk litterfall regimes than others. They also concluded that litterfall can contribute to regeneration niche differentiation. Holl (2002) studied the effect of shrubs on tree seedling establishment in

an abandoned tropical pasture and found that early successional shrubs have a net facilitative effect on the early stages of forest tree seedling establishment compared with areas without shrubs.

Eco-physiology of tree seedlings to a great extent determines the survival and growth of the seedlings in a given microenvironment. Plants adjust their allocation of carbon to shoots and roots in order to increase acquisition of limiting resources or survive periods of environmental stress. For example, shoot growth may increase if light is limiting, and root growth may be enhanced if water and nutrients are limiting (Long and Jones 1996). Studies have shown that elevation (Gunatilleke *et al.* 1998), interspecific variation in relative growth rate (Poorter *et al.* 1990, Ashton *et al.* 1995), gap size (Brown *et al.* 1999), nutrient availability (Lawrence 2001, Vincent and Davies 2003) and litter quality (Brearley *et al.* 2003) play important role in the overall seedling survival and growth.

Lawrence (2003) reviewed the recent literatures from Africa, Asia, Central or South America and Australia on the response of tropical tree seedlings to fertilization and found that a majority of the tree species exhibited a significant, positive response to fertilization. He also tested four common fallow tree species viz., *Melicope glabra*, *Macaranga*, *Persea romosa* and *Peronema canescens*, for a response to nitrogen and phosphorous fertilization and suggested that phosphorous rather than nitrogen, limits seedling performance and may ultimately influence tree diversity in young secondary tropical forests. Vincent and Davies (2003) tested the effects of nutrients (with and without NPK), mulching (with and without) and planting-hole sizes (12cm x 18cm and 20cm x 30cm) on early performance of *Dryobalanops aromatica* and *Shorea parviflora* planted in secondary forest in Sarawak, Malaysia over a period of 22 months. The

experiment was conducted in two sites to test for spatial variation in treatment effects. They found that nutrient addition had strongest effect on seedling growth of both the species. With the addition of nutrient, the growth rate was increased by >50%. Brearley *et al.* (2003) examined the potential role of nutrients contained within litter on the growth of dipterocarp seedlings by testing two hypotheses i.e. whether addition of leaf litter to the growth medium improves the growth of dipterocarp seedlings and whether litter addition affect the ectomycorrhizal colonization or community structure of dipterocarp seedlings. They found that nutrients obtained from leaf litter can improve the growth of dipterocarp seedlings.

Most of the works on forest ecology in northeast India have been done by the scholars from North Eastern Hill University (NEHU), Shillong. They mostly focused their study on community structure and dynamics, gap dynamics and regeneration ecology in sacred groves as well as tropical forests in Meghalaya, Manipur and Arunachal Pradesh. Ramakrishnan and co-workers focused their study on secondary successional stages following the abandonment of shifting cultivation areas. However, no significant work has been done on the community structure and tree regeneration of secondary forests. Adding to it, limited floristic survey has been conducted by the Botanical Survey of India (Itanagar) and State Forest Research Institute (Arunachal Pradesh) in the secondary forests in and around Namdapha national park. Therefore, this study aims at defining and characterizing the secondary forests in and around Namdapha national park, inventorying the species diversity in secondary forests and to identify the different ecological factors affecting their regeneration.

Chapter 3

Study site, climate and soil

The study sites were located in the buffer zone of Namdapha National Park in Changlang district of Arunachal Pradesh (Figure 3.1). The National Park lies between latitude 27°23'30"N and 27°39'40"N and longitude 96°15'2"E and 96°58'33"E surrounded by Myanmar in the east and south direction. In the north it has a common boundary with Kamlang wildlife sanctuary in the Lohit district of Arunachal Pradesh. Namdapha National Park is spread over an area of 1985 km² consisting of 1808 km² core zone and 177 km² of buffer zone. Two types of secondary forests were identified in the buffer zone of Namdapha national park viz., post extraction secondary forest (SF1 and SF3 - broadleaved forest) and post abandonment secondary forest (SF2 - mixed bamboo forest). Another two sites (PF1 and PF2) having primary forest in the buffer zone were selected for comparison. All the three types of forests had similar altitude (\approx 500 m above mean sea level).

History of Namdapha National Park

The National Park was originally a Reserved Forest under Assam Forest Regulation and was subsequently declared as a Wildlife Sanctuary in 1972 under Wildlife Protection Act, 1972. It was declared as a National Park in 1983 under the same Act. It has been a Tiger Reserve from 1983 under Project Tiger Scheme of Government of India. An area of 177.425 km² of Reserved Forest was added to the Tiger Reserve in 1986.

Biogeography

Namdapha falls within the Eastern Himalayas biogeographic province (2D) of the Himalayas biogeographic zone in Indian biogeographic region which covers the

Palaearctic Realm and the Indo-Malayan Realm (Rodgers and Panwar 1988). It is located at the junction of the Indian Sub-continent biogeographic region and the Indo-China biogeographic Region. As a result of this, high diversity of flora and fauna is observed in this belt (Table 3.1 and 3.2).

Table 3.1. Recorded floristic diversity of Namdapha national park (Chauhan *et al.* 1996)

Category	Dicots	Monocots	Lichens	Bryophytes	Pteridophytes	Gymnosperm
Families *215	119 (55.35)	19 (8.84)	17 (7.90)	21 (9.77)	36 (16.74)	3 (1.40)
Genera *639	403 (63)	111 (17.37)	34 (5.32)	33 (5.16)	54 (8.45)	4 (0.63)
Species *1119	674 (60.25)	196 (17.5)	73 (6.53)	59 (5.27)	112 (10)	5 (0.45)

* Total number families, genera and species; values in parentheses are percentage of total number

Table 3.2. Recorded faunal diversity of Namdapha national park (Singh *et al.* 2000)

Animals	Total number of species
Mammals	96
Birds	453
Reptiles	50
Amphibians	25
Fish	76
Butterflies and moth	140
Insects	430
Leech	5
Earthworm	10

Geology

The entire Eastern region is of recent origin and owes its formation to the upheaval of the Himalayas in Pleiocene period of the Tertiary age. The geological formations include a Tertiary and Quaternary sequence that is an extension from Nagaland and Upper Assam. Geologically it is bordered tectonic lineaments which remained active in various geological periods between upper cretaceous and Pleistocene times (Chauhan *et al.* 1996).

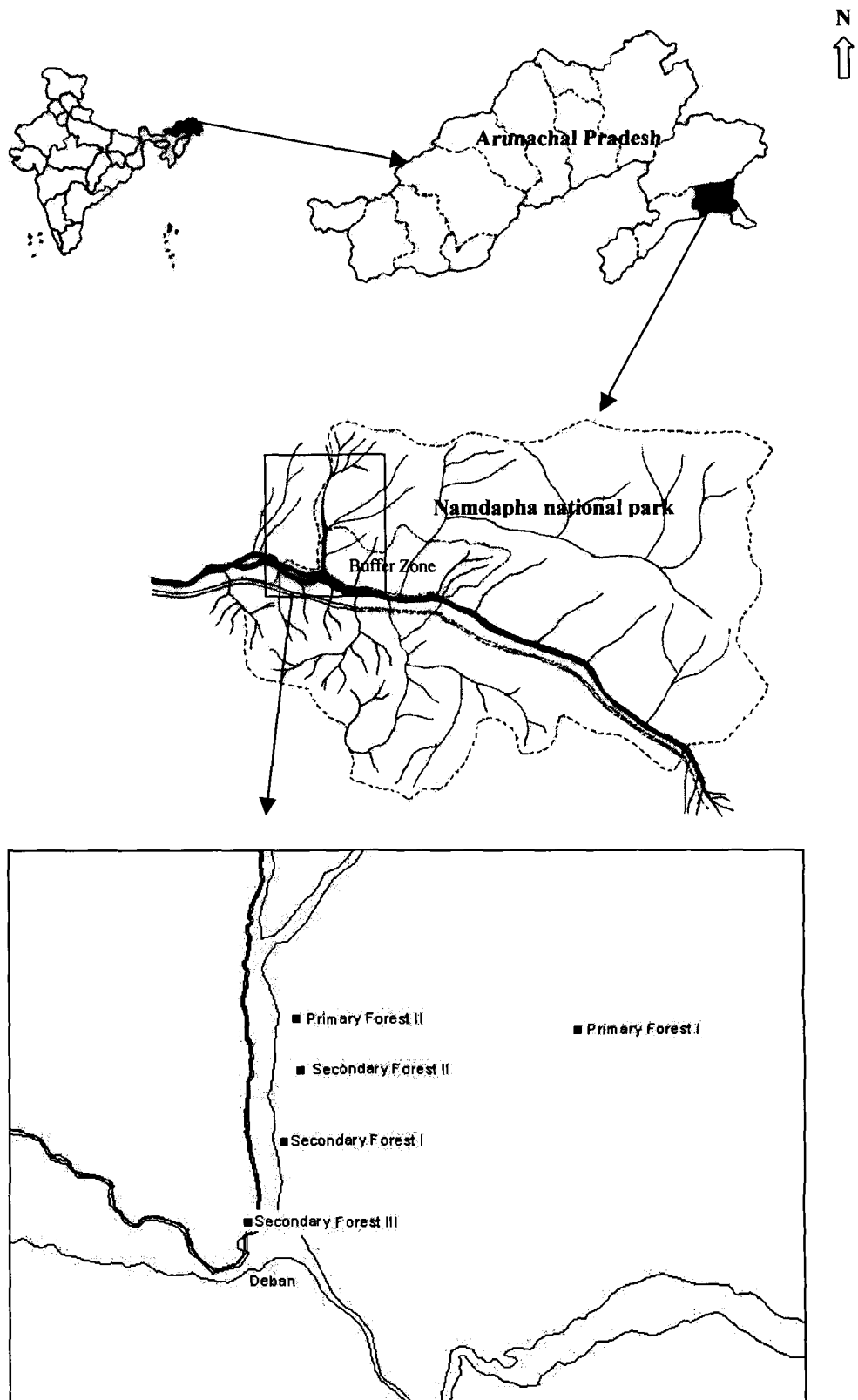


Figure 3.1. Map of Namdapha national park showing the primary and secondary forest sites





Plate 3.1. Secondary and primary forest sites in Namdapha national park.
[A] - Secondary forest 1, [B] - Secondary forest 2, [C] - Secondary forest 3, [D] - Primary forest 1, [E] - Primary forest 2

Climate

Being situated in 27° N of equator, the Namdapha National Park falls in tropical zone and enjoys the tropical climate. However, the climate of the area varies from place to place inside the PA due to altitudinal variation (200m to 4571m) and the area is also the zone of heavy rainfall (>1500 mm annum⁻¹). The mountainous part of the area enjoys a mountain type of climate while the low lying plains and valleys experience tropical climate. The seasons can be broadly divided into: winter (December to February), pre-monsoon (March to May), monsoon (June to September), and post-monsoon (October to November).

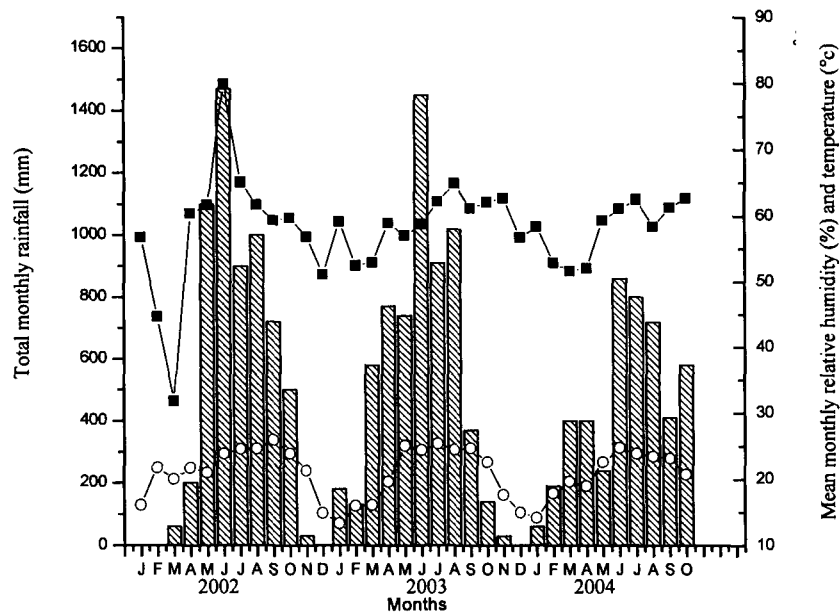


Figure 3.2 Climatogram of Namdapha national park showing total monthly rainfall (in bars), and mean relative humidity (dark boxes) and temperature (circles)

The area receives high rainfall, majority of which is received during June-August (Figure 3.2). The national park has an altitudinal range from 200 m to 4424 m (Dapha Bum peak) above mean sea level. The temperature varies with the altitudinal gradient. The

temperature in the foothill areas in December and January ranges from 5 °C to 20 °C (coldest month in the valley). In July and August (warmer month) temperature rises up to 37 °C. Relative humidity varies from a minimum of 47% to a maximum of 93%.

Landuse history

Since the declaration of Namdapha as a national park and tiger reserve in the year 1983, the area has been under the park administration and the then resident communities (Chakmas and Lamas) have been resettled outside the park boundary. More than 20 years of land abandonment as well as protection has helped in creation of different secondary forest types. But due to different land use history there are significant variations in the secondary forests in terms of floristic composition as well as community characteristics. The primary forests have no evidences of human disturbances. But the secondary forests have conspicuous evidences of past anthropogenic disturbances. SF1 and SF3 had a history of past extractions of timber and non-timber forest products. SF2 had a history of human settlements and settled cultivation. The three secondary forest sites have different canopy cover, tree basal area (m^2ha^{-1}), and tree density (stems ha^{-1}) (Table 3.3).

Soil

Soil physical and chemical properties (0-15 cm depth) of primary as well as secondary forest sites for wet (July-August) season was analysed using TSBF methodologies. Soil thermometer was used to measure soil temperature. Soil samples were collected from the primary and secondary forest stands using steel corer (5.5mm inner diameter) from (0-15 cm) depth. The soil samples were separated into two parts. One part of the sample was immediately sieved through 2 mm mesh and analysed for pH (using pH meter), moisture content, ammonium nitrogen (Indo-phenol blue method), nitrate nitrogen and available

phosphorous. The remaining air-dried soil was sieved through a 0.5mm mesh screen and used for the analysis of soil organic carbon, total nitrogen.

Table 3.3. Differentiation of secondary forests from primary forests in Namdapha national park

Parameters	Sites				
	Primary forest		Secondary forests		
	PF-1	PF-2	SF-1	SF-2	SF-3
Age (years)	Not known	Not known	20	20	20
Land use history	Nil	Nil	Selective timber and non-timber extractions	Human settlement and settled agriculture	Extraction of timber and settled agriculture
Canopy cover (%)	100	100	60-70	30-40	20-30
Basal area (m ² ha ⁻¹)	78.58	55.7	35.26	30.47	29.22

Soil texture was determined according to Bouyocous hydrometer method. Moisture content was determined by the gravimetric method after drying 10g of soil samples for 24 hours at 105⁰C in a hot-air oven. Bulk density was measured using a soil corer. Water holding capacity was measured by using Keen's boxes. Amongst chemical parameters, soil pH was measured in a soil and water mixture (1:2.5 w/v) using digital pH meter. Available phosphorus was determined by the molybdenum blue method (Jackson 1985) after an acid wet oxidation of 0.5g soil sample in nitric acid (HNO₃), sulphuric acid (H₂SO₄) and hypochloric acid (HClO₄). Organic-C, total-N, ammonium-N, nitrate-N, available-P and total-P of soil were determined by the complete oxidation, semi-micro Kjeldahl, indophenol blue, phenol disulphonic acid and molybdenum blue methods (Allen *et al.* 1974) respectively. Concentration of potassium was determined using flame photometer.

Percent of sand was more in the secondary forests but silt and clay percentage were more in the primary forests (Table 3.4). Overall, the textural class of soil was loamy sand in the primary forests and sandy loam in the secondary forests.

Table 3.4 Soil physico-chemical properties (0-15 cm) of the primary and secondary forests in and around Namdapha national park

Parameters	Primary forests		Secondary forests			ANOVA P value
	PF1	PF2	SF1	SF2	SF3	
Clay	16.60	13.34	12.17	7.20	2.90	-
Silt	13.02	10.06	9.38	9.10	8.60	-
Sand	70.38	76.60	78.45	83.70	88.50	-
Bulk density (g cm ⁻³)	0.55 ±0.03	0.54 ±0.01	0.68 ±0.02	0.77 ±0.04	0.89 ±0.02	0.001
Water holding capacity (%)	45.04 ±0.46	42.28 ±0.64	39.42 ±0.67	41.32 ±0.45	34.38 ±1.98	0.001
Soil moisture content (%)	25.77 ±1.30	25.40 ±0.85	24.40 ±0.67	24.80 ±2.96	21.50 ±1.33	0.010
pH	4.24 ±0.27	4.16 ±0.22	4.18 ±0.22	4.62 ±0.12	5.08 ±0.09	0.013
Soil organic carbon (%)	2.19 ±0.27	2.53 ±0.79	2.78 ±0.83	3.45 ±0.73	1.59 ±0.49	0.003
TKN (%)	0.52 ±0.14	0.42 ±0.16	0.55 ±0.10	0.31 ±0.08	0.26 ±0.09	0.026
NH ₄ -N (µg g ⁻¹)	6.49 ±0.02	6.43 ±0.03	8.01 ±0.08	9.57 ±0.15	5.64 ±0.13	0.003
NO ₃ -N (µg g ⁻¹)	7.19 ±0.03	6.25 ±0.05	10.18 ±0.06	9.32 ±0.08	7.22 ±0.06	0.010
PO ₄ -P (µg g ⁻¹)	11.22 ±0.04	9.94 ±0.10	7.18 ±0.03	8.32 ±0.04	5.97 ±0.05	0.001
K (mg 100gm ⁻¹)	0.35 ±0.01	0.31 ±0.02	0.39 ±0.01	0.45 ±0.01	0.32 ±0.01	0.010

Bulk density as well as water holding capacity (WHC) of soil varied significantly ($p < 0.001$) across sites. Bulk density was higher in the secondary forests than that of the primary forests. WHC of the primary forest soil was higher than that of the secondary forests and differed significantly ($p < 0.001$). Soil moisture content was higher in the primary forest soils as compared to that of the secondary forest and varied significantly across different sites ($p < 0.001$).

Soil pH ranged from 4.16 to 4.24 in the primary forest and from 4.18 to 5.02 in the secondary forest and varied significantly ($p < 0.01$). Soil organic carbon (SOC), available forms of nitrogen (NH₄-N and NO₃-N) and soil potassium was higher in the secondary forests as compared to the primary forests and varied significantly across the sites (Table 3.4).

Chapter 4

Plant species diversity and community structure

4.1 Introduction

The undisturbed forest ecosystems maintain their equilibrium along a temporal scale through homeostatic mechanism. These ecosystems do not show much temporal changes in species composition, biomass accumulation, productivity and nutrient cycling patterns due to their tremendous capacity of resistance and resilience. Today tropical forests around the world are subjected to a whole variety of disturbances ranging from recurrent localized events to less recurrent disturbances at landscape level. The impact on various ecosystem processes varies depending upon the kind, intensity and frequency of human disturbances. Although the occurrence of natural disturbances and parallel recovery are fundamental aspects of normal ecosystem behaviour (White 1979), human disturbances often become so severe and extensive that the forest ecosystems fail to recover. Deforestation due to shifting cultivation and timber extraction is the major human disturbance in the humid tropics. The destruction of large tracts of primary forests in the humid tropics has been attributed to these factors. Most of the primary forests failed to regenerate following the disturbance because of the severity and frequent occurrence of the disturbances. Since the species composition, community structure and its development subsequent to disturbance are strongly influenced by the nature and intensity of the stress (White 1979, Pandey and Singh 1985), most of the primary forest ecosystems end up with the formation of secondary forests.

Our understanding of the secondary forest ecosystems is extremely poor. The secondary forest ecosystem processes, structure and functions are not well studied in the Indian sub-

continent. Therefore, in the present chapter an attempt has been made to answer the following questions: (i) Whether the secondary forests are structurally different from the primary forests? (ii) How different is the secondary forest in terms of species composition and diversity in comparison to that of the primary forest? (iii) Whether there is a differential pattern of forest ecosystem recovery due to different disturbance history? These hypotheses have been tested in three tropical evergreen secondary forest stands in and around Namdapha national park, which have differential disturbance history such as (i) abandonment of human settlements, (ii) moderate intensity of timber and non-timber forest product extraction, and (iii) high intensity of forest product extraction.

4.2 Methodology

For studying the community structure of the secondary forest, three sites were selected based on landuse history viz., one post abandonment secondary forest having a history of past human habitations and two post extraction secondary forests having moderate and high intensity of extractions and tree felling. For comparison, two primary forest stands adjacent to the secondary forests were also selected viz., a mixed primary forest and a *Mesua*-dominated primary forest. Each of the three secondary forest stands was spread over an area of approximately 1 km². For spatial uniformity, the sampling in the two primary forests was done within demarcated area of 1 km² each.

Species composition

The species composition in each forest stand was studied by collecting the specimens and preparing the herbaria. The specimens were identified with the help of Flora of Namdapha (Chauhan *et al.* 1996), Flora of Arunachal Pradesh (Hajra *et al.* 1996) and Flora of Assam (Kanjilal *et al.* 1934-1940). Wherever necessary, the herbaria at State

Forest Research Institute, Itanagar and the Botanical Survey of India, Itanagar were consulted for correct identification of the specimens.

Community structure and plant diversity

One hundred quadrats were laid randomly at each site for sampling trees, shrubs, herbs and climbers. Quadrats of size 10m x 10m were used for sampling trees, 5m x 5m for sampling the shrubs, seedlings and woody climbers and 1m x 1m for sampling the herbs.

Various life forms in the forest vegetation were defined as follows: individuals having dbh \geq 30cm and having a distinct trunk and crown were considered as trees; saplings were characterized as individuals having a distinct crown whose dbh does not exceed 30cm; individuals belonging to tree species whose age does not exceed 1 year were considered as seedlings. Shrubs were distinguished from saplings and trees by the absence of a distinct trunk. Individuals not having persistent woody tissue in any of their parts were considered as herbs. The plant community structure in each of the stands was studied using the following analytical quantitative characters:

Dominance

The girth (g) of all trees and saplings occurring within the quadrats were measured at 1.37m above the ground level. Frequency, density, basal cover, abundance and importance value index (IVI) of the species were calculated following Misra (1968) and Muller-Dombois and Ellenberg (1974) with the data obtained from the enumeration of vegetation using quadrat method.

Basal area of each individual was calculated as $g^2/4\pi$. Basal cover (m^2ha^{-1}) for each species was calculated by adding up the basal area of all individuals occurring in all the 100 quadrats.

Importance Value Index (IVI) for trees and saplings was computed by summing up relative frequency, relative density and relative basal area. IVI for shrubs, climbers and herbs were calculated by adding up the relative values of frequency and density.

Diversity

Species richness

Number of species in the respective primary and secondary forest sites indicated species richness.

α and β diversity

α diversity was calculated following Whittaker (1960) as: $\alpha = S/\log N$, where 'S' is the total number of species and 'N' is the total number of individuals of all the species.

β diversity was calculated following Whittaker (1960) as: $\beta = (S/\alpha)-1$, where, 'S' is the total number of species encountered in the two sites counting each species only once and ' α ' is the mean species richness of two sites.

Shannon-Weiner diversity index

Species diversity was calculated using Shannon-Weiner index of diversity (Shannon and Wiener 1963) as: $H = - \sum (N_i / N) \ln (N_i / N)$ where, ' N_i ' is the IVI of i^{th} species and 'N' is the total IVI.

Simpson's dominance Index

Simpson's dominance Index (D) was estimated using Simpson index (Simpson 1949) and was calculated as: $D = \sum (N_i / N)^2$, where, ' N_i ' is the IVI of i^{th} species and 'N' is the total IVI of all species.

Sørensen's Similarity Index

Species similarity between the sites was studied using Sørensen's similarity index = $2c/(a+b) \times 100$, where, 'a' is the number of species at site a, 'b' is the number of species at site b and 'c' denotes the number of species common to stand a and stand b (Sørensen 1948).

Pielou's Evenness Index

Pielou's Evenness index 'e' (1969) was calculated as follows: $e = H / \ln S$, where H – Shannon -Weiner diversity index and S – Total number of species

Spatial distribution

Spatial distribution was determined following Whitford Index (1948) which is as follows: $WI = \text{Abundance/Frequency}$, if the ratio is <0.025 the species is considered to exhibit regular distribution, if the ratio is between 0.025-0.05 the species exhibits random distribution and if the ratio is >0.05 the species exhibit clumped distribution.

4.3 Results

Species per unit area

Species-accumulation curve for the tree species in all the forest stands reached asymptote around 0.9 km^2 (Figure 4.1). This suggests that a sampling area of approximately one square kilometer in the primary as well as secondary forest stands would represent majority of the tree species present. For shrubs and herbs, the curve flattened at 0.4 km^2 for the secondary forest stand SF3 and 0.5 km^2 for the primary forest stand PF1, respectively. For other primary and secondary forest stands the curve reached an asymptote around 0.3 km^2 (Figure 4.1).

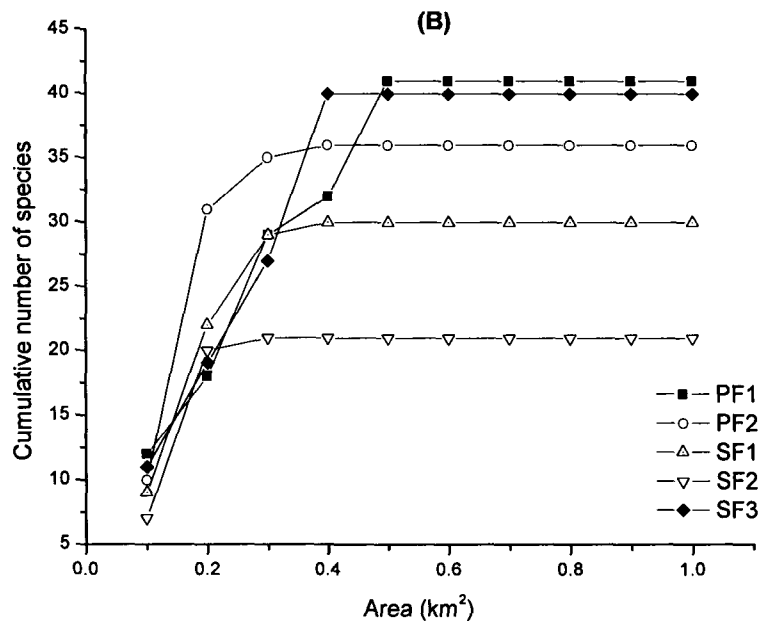
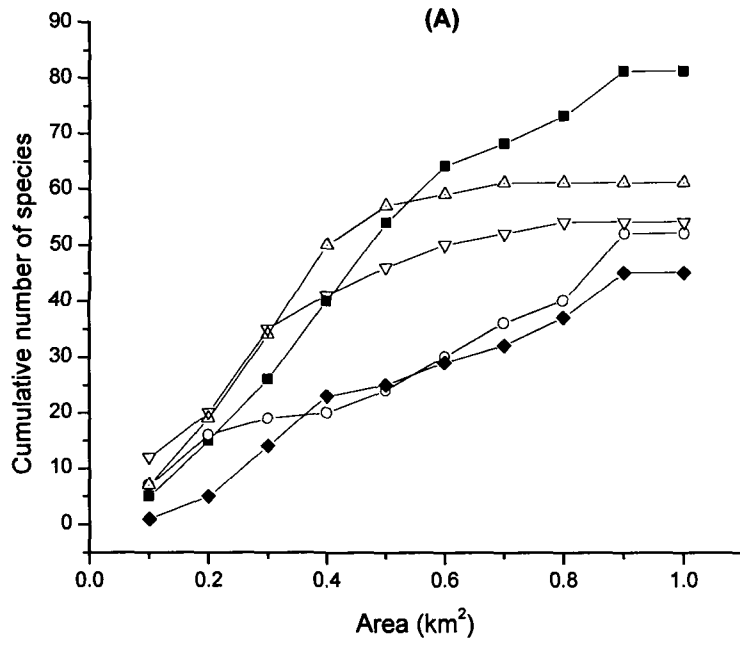


Figure 4.1. Species-accumulation curve for (A) trees and (B) shrubs & herbs in the primary and secondary forest stands

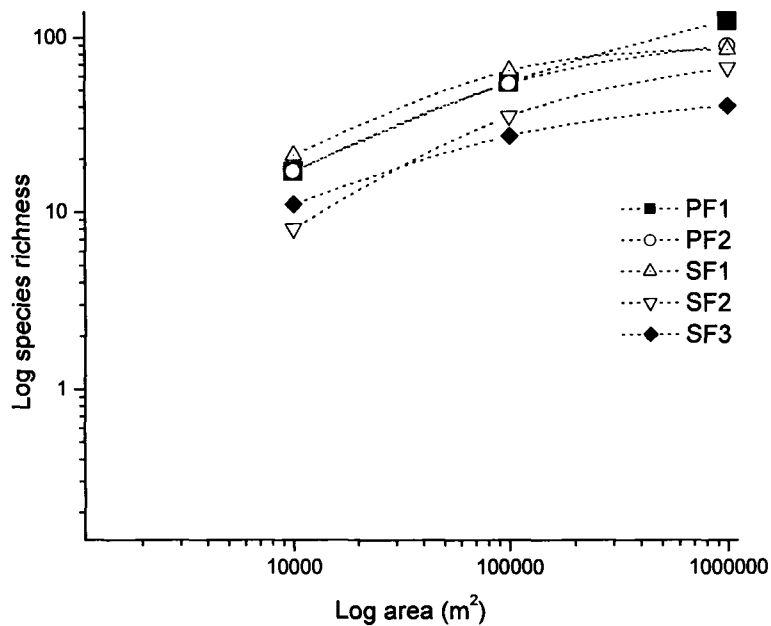


Figure 4.2. Species richness in the primary and secondary forests in three spatial scales

Species richness increased along a spatial scale of 1 ha, 10 ha and 100 ha in the primary and secondary forest stands. In the primary forest stands PF1 and PF2, the species richness increased from 17 each (ha^{-1}) to 55 and 54 (10 ha^{-1}), and to 122 and 88 (100 ha^{-1}). While in the secondary forest stands SF1, SF2 and SF3, the species richness increased from 21, 8 and 11 (ha^{-1}) to 64, 35 and 27 (10 ha^{-1}) to 84, 66 and 40 (100 ha^{-1}) (Figure 4.2).

Floristic diversity

The total number of species, genera and families in the secondary forests was higher than the primary forests (Table 4.1). The species: family ratio in the secondary forest was also higher compared to the primary forest. However, the primary forest stand (PF1) contained more number of species (123 km^{-2}), genera (96 km^{-2}) and family (55 km^{-2}) per

unit area than any other stand. Among the secondary forest stands, SF1 had maximum number of species i.e., 89 km⁻².

Table 4.1. Floristic characteristics of primary and secondary forest stands in and around Namdapha national park

Parameters	Primary forests			Secondary forests			
	PF1	PF2	Total	SF1	SF2	SF3	Total
Total no. of species	123	87	160	89	73	84	180
Total no. of genera	96	71	117	70	61	70	144
Total no. of families	55	40	62	42	42	43	66
Species/ family ratio	2.23	2.17	2.58	2.11	1.73	1.95	2.72

Members of Lauraceae were dominant both in the primary and secondary forest stands. Besides, members of Rubiaceae and Meliaceae were present in large numbers in the primary forest stands. In the secondary forest stands, members of Euphorbiaceae, Magnoliaceae and Meliaceae were present in large numbers in the SF1 and SF2 stands, while members of Asteraceae and Mimosaceae were co-dominated in the SF3 stand (Table 4.2).

Table 4.2. Five dominant families in the primary and secondary forests in Namdapha national park

Primary forests		Secondary forests		
PF1	PF2	SF1	SF2	SF3
Lauraceae (13)	Rubiaceae (11)	Lauraceae (10)	Lauraceae (6)	Asteraceae (12)
Rubiaceae (13)	Lauraceae (10)	Rubiaceae (6)	Meliaceae (4)	Lauraceae (6)
Meliaceae (8)	Meliaceae (5)	Meliaceae (6)	Magnoliaceae (4)	Urticaceae (5)
Magnoliaceae (6)	Euphorbiaceae (4)	Euphorbiaceae (6)	Verbenaceae (4)	Verbenaceae (5)
Euphorbiaceae (5)	Clusiaceae (4)	Moraceae (5)	Urticaceae (3)	Mimosaceae (5)

Values in parentheses show the number of species

Species composition

In the primary forests, the dominant tree species were, *Altingia excelsa*, *Terminalia chebula*, *Terminalia myriocarpa*, *Dipterocarpus macrocarpus*, *Anthocephalus chinense*, *Mesua ferrea*, *Ostodes paniculata*, *Saprosma ternatum*, *Litsea lancifolia* and *Baccaurea*

ramiflora. The dominant shrub species were, *Elatostemma platyphyllum*, *Camellia caudata*, *Psychrotia silhetensis*, *Sarcandra glabra*, *Leea indica*, *Myrioneuron nutans* and *Acanthus leucostachyus*. The important herbaceous species in the primary forests were *Adiantum caudatum*, *Carex baccans*, *Forrestia molissima*, *Pogostemon paniculatus* and *Commelina paludosa*. Amongst the climbers, *Piper sylvaticum*, *Tetrastigma bracteolatum* and *Tetrastigma obovatum* were important.

In SF1 and SF2 secondary forest stands, the dominant trees were, *Talauma hodgsonii*, *Chisocheton paniculatus*, *Dysoxylum reticulatum*, *Magnolia pterocarpa* along with a bamboo species, *Dendrocalamus hamiltonii* while in SF3 *Alangium chinense*, *Sapindus mukkorossi*, *Maesa indica*, *Albizia procera* were dominant. Among the shrubs, *Strobilanthes secundus*, *Diffflugosa colorata*, *Clerodendron colebrookianum*, *Clerodendron infortunatum*, *Leea compectiflora*, *Solanum torvum*, *Solanum nigrum*, *Sida acuta*, *Cassia alata* and *Pogostemon paniculatus* were dominant. *Bidens bitarnata*, *Selaginella semicordata*, *Ageratum conyzoides*, *Paspalum conjugatum*, *Oxalis corniculata*, *Borreria articularis*, *Dictyospermum scaberrimum* dominated the ground flora in the secondary forests. *Paderia foetida*, *Cayratia japonica* and *Cissus assamica* were important climbers in the secondary forests (Annexure 1).

The evergreen tree species dominated both the primary and secondary forests. In the primary forest stands, 94% of the trees were evergreen, while in the secondary forest stands it was only 80%. The proportion of deciduous trees was more in the secondary forests than the primary forests. Stand-wise comparison shows that the primary forest stand PF1 contained the highest proportion of evergreen trees (93.7%). Conversely, the

secondary forest stand SF3 contained the highest percentage (27%) of trees of deciduous nature (Table 4.3).

Table 4.3. Proportion (%) of evergreen and deciduous tree species in the primary and secondary forests of Namdapha national park

Functional types	Primary forests			Secondary forests			
	PF1	PF2	Total	SF1	SF2	SF3	Total
Evergreen species	93.7	92.3	94.7	91.7	86.5	72.7	80.9
Deciduous species	6.2	7.7	5.3	8.6	13.5	27.3	19.0

Species similarity

Overall species similarity between the primary and secondary forests was 21.2%. The tree species exhibited 53.2% similarity, shrub species 21.8%, and herb and climber species exhibited 20.6% similarity (Figure 4.3). Similarity in canopy tree species between the primary and secondary forests was 65%, while for middle and lower storied trees the similarity was 50% and 48%, respectively (Figure 4.4).

Across the five stands, species similarity was maximum between the primary forest stands PF1 and PF2 (45.7%), while the two secondary forest stands SF1 and SF3 had the least similarity (19.6%). Amongst the secondary forest stands SF1 and SF2 had maximum similarity (40.7%) (Table 4.4).

The tree species similarity was highest between stands PF2 and SF1 (52.7%) and least between stands PF1 and SF3 (29.0%). The tree species confined only to the primary forests were *Chickrassia tabularis*, *Dipterocarpus macrocarpus*, *Canarium strictum*, *Morus laevigata*, *Cinnamomum pauciflorum*, *Chisocheton cumingianus* while *Alangium chinense*, *Albizia procera*, *A. odoratissima*, *A. lucida*, *Alstonia scholaris*, *Bombax ceiba*, *Sterculia villosa*, *Trema orientalis*, *Erythrina indica* and *Callicarpa arborea* were present only in the secondary forest stands. *Spondias axillaris*, *Shorea assamica*, *Mesua ferrea*,

Dysoxylum procerum, *Cinnamomum tamala*, *Cinnamomum bejolghota*, *Aesculus assamica* were present both in the primary as well as the secondary forests.

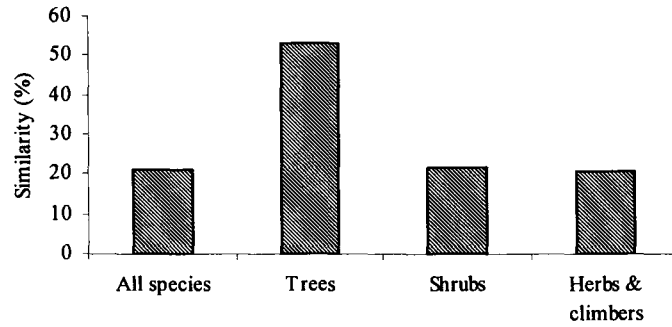


Figure 4.3. Similarity in species composition among different vegetation components between the primary and secondary forests in and around Namdapha national park

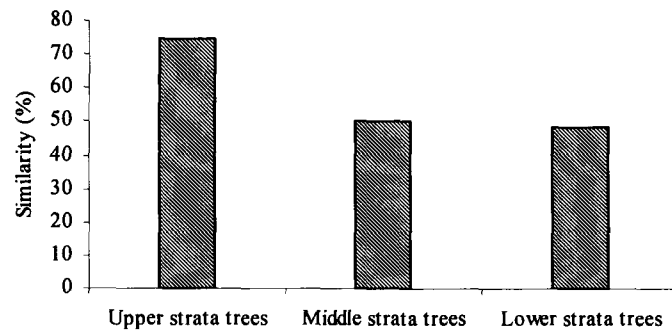


Figure 4.4. Similarity of tree species in different stratas between the primary and secondary forests in and around Namdapha national park

Table 4.4. Sorenson's similarity matrix for different components of the vegetation in primary and secondary forest stands in Namdapha national park

Sites	PF2						SF1						SF2						SF3					
	A	T	S	H	A	H	A	T	S	H	A	H	A	T	S	H	A	H	A	T	S	H		
PF1	A	45.71	-	-	35.84	-	-	-	-	-	31.63	-	-	-	-	-	21.25	-	-	-	-	-		
	T		50.00	-	-	40.57	-	-	-	-	-	40.90	-	-	-	-	-	-	29.03	-	-	-		
	S			29.78	-	-	-	30.00	-	-	-	-	5.71	-	-	-	-	-	10.25	-	-	-		
PF2	H				51.61	-	-	-	23.52	-	-	20.68	-	-	-	-	-	-	-	-	-	13.63		
	A					40.90	-	-	-	37.50	-	-	-	-	-	21.05	-	-	-	-	-	-		
	T						52.72	-	-	-	48.07	-	-	-	-	-	-	-	29.16	-	-	-		
	S							5.71	-	-	-	6.67	-	-	-	-	-	-	-	11.76	-	-		
SF1	H								32.25	-	-	30.76	-	-	-	-	-	-	-	-	-	14.63		
	A									40.74	-	-	-	-	-	19.65	-	-	-	-	-	-		
	T										50.90	-	-	-	-	-	29.41	-	-	-	-	-		
	S											8.69	-	-	-	-	-	-	0.00	-	-	-		
	H												27.58	-	-	-	-	-	-	-	-	13.63		
SF2	A															39.49	-	-	-	-	-	-		
	T																41.66	-	-	-	-	-		
	S																	54.55	-	-	-	-		
	H																		25.64	-	-	-		

A – All species, T – Trees, S – Shrubs, H – Herb, PF1 – Primary forest 1, PF2 – Primary forest 2, SF1 – Secondary forest 1, SF2 – Secondary forest 2 and SF3 – Secondary forest 3

For shrub species, SF2 and SF3 had maximum similarity (54.5%) whereas there was no similarity between SF1 and SF3. Shrubs such as *Acanthus leucostachys*, *Chloranthus elatior*, *Cissus assamica*, *Fissistigma wallichii*, and *Hogsonia macrocarpa* were present only in the primary forests, while *Eupatorium odoratum*, *Laportea terminalis*, *Leea compectiflora*, *Lantana camara*, *Pogostemon paniculatus* and *Clerodendrum infortunatum* were found only in the secondary forests.

The similarity in herbaceous species between PF1 and PF2 stands was maximum (51.6%), while there was least similarity between PF1, SF3 (13.6%) and SF1, SF3 (13.6%). Species such as *Adiantum caudatum*, *Begonia roxburghii*, *Globba clarkei* and *Psychrotia silhetensis* were restricted to primary forests only, while *Mikania micrantha*, *Ageratum conyzoides*, *Amaranthus spinosus*, *Bidens bitarnata*, *Bidens pilosa*, *Borreria hispida* were restricted to the secondary forest stands only.

Density

Overall tree density between the primary and secondary forest did not differ significantly. Shrub density is significantly higher in the primary forest than the secondary forest and the density of herbs is greater in the secondary forests than the primary forests (Table 4.5).

The tree density was highest in SF1 (1360 stems ha⁻¹) and lowest in SF2 (914 stems ha⁻¹) (Table 4.5). The species exhibiting maximum density in the primary forests were *Ostodes paniculata*, *Saprosma ternatum*, *Altingia excelsa*, *Litsea lancifolia*, *Mesua ferrea*, and *Baccaurea ramiflora*. In the secondary forests, *Dysoxylum reticulatum*, *Talauma hodgsonii*, *Randia cochinchinensis*, *Litsea cubeba*, *Dendrocalamus hamiltonii* and *Alangium chinense* had high density (Annexure I). The density of shrub was highest in

PF2 having 12620 individuals ha⁻¹ and lowest in SF2 having 2780 individuals ha⁻¹. The density of herbaceous species was greater in secondary forests than the primary forests, and SF3 in particular recorded 3,48,000 individuals ha⁻¹, while PF1 had only 42,200 individuals ha⁻¹ (Table 4.5).

Frequency

Amongst trees, *Ostodes paniculata*, *Saprosma ternatum* and *Altingia excelsa* were commonly encountered (>50% frequency) in the primary forests, whereas *Dysoxylum reticulatum* and *Alangium chinense* were frequently encountered in the secondary forest stands (>47% frequency). Amongst shrubs, high frequency was observed were for *Elatostemma platyphyllum*, *Sarcandra glabra*, *Phlogacanthus asperulus*, *Myrioneuron nutans* and *Psychrotia silhetensis* in the primary forests and in the secondary forests *Sida acuta*, *Debregesia longifolia*, *Strobilanthes secundus*, *Leea compectiflora* and *Clerodendrum colebrookianum* were frequent. On the forest floor, *Adiantum caudatum*, *Forrestia mollissima*, *Dryopteris sparsa*, *Piper mullesua*, and *Commelina paludosa* were frequent in the primary forests, while in the secondary forests the occurrence of *Ageratum conyzoides*, *Spilanthus paniculata*, *Oxalis corniculata*, and *Paspalum conjugatum* was frequent.

Tree basal area

Tree basal area was highest in the primary forest stands (PF1 - 78.58 m² ha⁻¹, PF2 - 55.7 m² ha⁻¹) and was lowest in SF3 (29.22 m² ha⁻¹) (Table 4.5). Species sharing most part of the basal area in the primary forests were *Altingia excelsa*, *Terminalia myriocarpa*, and *Mesua ferrea*, while in the secondary forests *Phoebe lanceolata*, *Dysoxylum reticulatum*,

Alangium chinense, *Albizia procera*, *Actinodaphne obovata* and *Dendrocalamus hamiltonii* had a major share.

Table 4.5. Species richness, density and basal area of trees, shrubs and herbs in the primary and secondary forest stands

Parameters	Primary forests			Secondary forests			
	PF1	PF2	Total	SF1	SF2	SF3	Total
Trees							
Species richness	80	52	99	58	52	45	104
Density (ha ⁻¹)	1207	986	1097	1360	914	983	1086
Basal area (m ² ha ⁻¹)	78.58	55.70	67.14	35.26	30.47	29.22	31.65
Shrubs							
Species richness	21	18	38	10	8	11	26
Density (ha ⁻¹)	6310	12620	9465	4540	2780	6060	4460
Herbs							
Species richness	17	14	19	17	12	27	45
Density (x 10 ⁴ ha ⁻¹)	4.22	9.97	7.09	16.88	9.34	34.8	20.34

Dominance

Altingia excelsa, *Ostodes paniculata*, *Mesua ferrea*, *Terminalia myriocarpa* and *Saprosma ternatum* shared more than 50% dominance in the primary forest stands. *Talauma hodgsonii*, *Alangium chinense* and *Dysoxylum reticulatum* were the dominant tree species in the secondary forest sites (Annexure I). Tree families scoring highest IVI were Rubiaceae (68.4), Euphorbiaceae (45.8), Clusiaceae (41.7) and Combretaceae (36.8) in the primary forests, and Alangiaceae (90.9) Lauraceae (58.3) and Meliaceae (50.8) in the secondary forests (Annexure 1).

Dominance-diversity curve for tree species showed that most of the IVI in case of the secondary forest stands SF2 and SF3 was concentrated in a single species viz. *Dendrocalamus hamiltonii* in SF2 and *Alangium chinense* in SF3. In the primary forest stands PF1 and PF2, and the secondary forest stand SF1, the IVI was distributed equitably among all the species (Figure 4.5).

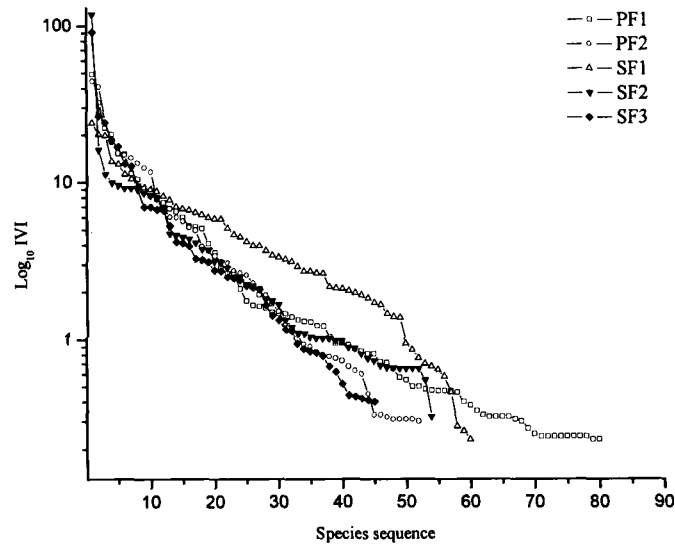


Figure 4.5. Dominance-diversity curve of tree species in the primary and secondary forest stands

Spatial distribution

More than 95 percent of the species exhibited clumped distribution both in primary and secondary forests. Only 3 to 4 percent exhibited random distribution (Figure 4.6). None of the species in the primary and secondary forest sites displayed regular distribution.

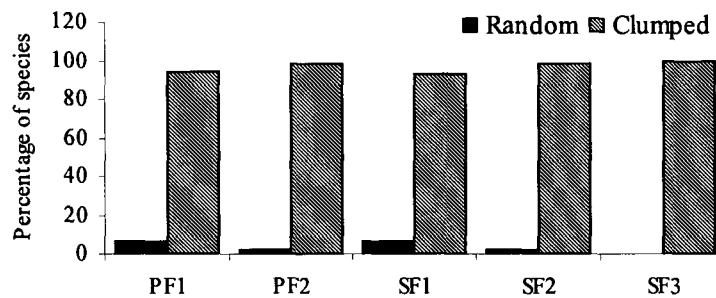


Figure 4.6. Species distribution pattern in primary and secondary forest stands

Species diversity

The α diversity for tree and shrubs was higher in primary forest than the secondary forest. For herbaceous species, the trend was reverse.

The α diversity values for trees and shrubs were significantly high in the primary forest stand PF1 than any other stand. The secondary forest stand SF3 had the lowest α diversity for trees. The α diversity of herbaceous species was highest in the secondary forest stand SF3 (Table 4.6).

Shannon-Weiner index for the tree species was higher in primary forests than the secondary forests. The reverse was true for shrubs and herbs.

Shannon-Weiner's index was highest in PF1 (3.33) followed by SF1 (3.15) and lowest in SF3 (0.81). Diversity of shrub species was greater in PF2 (2.42) and lowest in SF3 (1.72). On the contrary, Shannon-Weiner's index for herbaceous species was highest in SF3 (2.78) and lowest in SF1 (2.14) (Table 4.6).

The Simpson's dominance index for trees, herbs and climbers was more in case of secondary forests than the primary forests. In shrubs, the dominance index was more in the primary forests as compared to secondary forests.

Simpson's index of dominance for trees was highest in SF2 and lowest in SF1, while for shrubs it was highest in SF3 and lowest in SF1. For herbs, dominance index was maximum in SF1 and lowest in PF1 (Table 4.6).

Pielou's evenness index for trees was higher in the primary forests than the secondary forests. For shrubs and herbs the index was higher in the secondary forests than the primary forests. In general, the evenness index values were low indicating uneven distribution of different species (Table 4.6).

Table 4.6. General diversity patterns in the primary and secondary forest stands

Parameters	Primary forests			Secondary forests			
	PF1	PF2	Total	SF1	SF2	SF3	Total
Trees							
α diversity	24.61	17.39	29.64	18.53	17.56	15.05	29.62
Shannon's index	3.33	3.13	3.52	3.15	2.80	0.81	3.35
Simpson's index	0.06	0.06	0.05	0.03	0.17	0.12	0.11
Pielou's evenness index	0.76	0.79	0.76	0.77	0.70	0.21	0.72
Shrubs							
α diversity	6.88	6.42	8.89	4.25	3.73	4.40	6.31
Shannon's index	2.14	2.42	3.05	2.26	1.86	1.72	3.34
Simpson's index	0.16	0.13	0.06	0.11	0.17	0.29	0.04
Pielou's evenness index	0.70	0.83	0.82	0.98	0.89	0.71	0.94
Herbs and climbers							
α diversity	7.83	5.51	16.52	6.13	4.78	8.76	25.28
Shannon's index	2.61	2.25	2.78	2.14	2.38	2.78	3.49
Simpson's index	0.07	0.10	0.04	0.18	0.10	0.09	0.08
Pielou's evenness index	0.92	0.85	0.88	0.75	0.95	0.84	0.91

The β diversity was high between the secondary forest stands SF1 and SF3 (1.82), PF2 and SF3 (1.81) and PF1 and SF3 (1.80). PF1 and PF2 had the lowest β diversity value of 1.55 (Table 4.7).

Table 4.7. β diversity matrix for all species in the primary and secondary forest sites in Namdapha national park

Sites	PF2	SF1	SF2	SF3
PF1	1.55	1.65	1.70	1.80
PF2	1	1.60	1.64	1.81
SF1		1	1.61	1.82
SF2			1	1.62

Density-girth distribution of trees

The density-girth distribution pattern of trees shows that the secondary forests had more number of individuals in the lower girth classes' (i.e. 11-20 cm and 31-60 cm) than the primary forests. The number of individuals in the higher girth classes (>91cm) was more in the primary forests. In secondary forests, most of the higher girth classes remained unexplained, for instance, in SF2, there was no individual above the girth class of 121-150cm. Stem density decreased with increase in girth sizes in all the stands, except PF1

where the number of individuals in <180 cm girth class was higher than the previous girth classes i.e. 91-180 cm (Figure 4.7).

4.4 Discussion

The secondary forests had higher floristic diversity in terms of number of family, genera and species than the primary forests. This may be attributed to the distance of these forests from the nearby primary and secondary forests which act as potential seed sources. It is evident from the observations that the secondary forests in and around Namdapha national park contains a mixture of pioneers as well as primary species making them species rich. This is in conformity with Andel (2001) who found that the 60-year-old secondary forest plots had higher species diversity in northwest Guyana due to its close proximity to both older and younger forests. Similarly, Finegan and Delgado (2000) found that a 30-year-old secondary forest in Costa Rica had a mixture of tree species from the old-growth forest and newly colonizing species from agricultural land.

The primary forest stand PF1, in contrary was floristically much richer than any other individual forest stand. This could be due to the age of the stand, which is older than any other stand and has not experienced any other type of disturbances in recent past. The dominance of primary species, having lesser niche breadth, has contributed towards coexistence of majority of species in the stand (Beckage and Clark 2003, Webb and Peart 1999). On the other hand, in the secondary forest stands, which are of relatively recent origin, two or three species dominate leaving fewer resources for other species to exist, making the stands species-poor.

The α diversity for the herbaceous species was much higher in the secondary forests, indicating existence of more disturbed habitats for the latter. The higher value of

dominance index for the trees indicate that dominance increases as a function of stress and past damage caused due to disturbances preceding to the formation of secondary forests (Keel and Prance 1979). Therefore, the dense growth of the bamboo species *Dendrocalamus hamiltonii* in the secondary forest stand SF2 and *Alangium chinense* in secondary forest stand SF3 was observed.

β diversity, a measure of the degree of species replacement or biotic change along environmental gradients (Brokaw and Scheiner 1989, MacArthur 1965, Whittaker 1972, 1977, Wilson and Shmida 1984) showed a gradual increase from primary forest stands to the secondary forest stands indicating the increase in species turnover. This elucidates that previous landuse activities have resulted in creating variability in the habitat structure which in turn has effected the species composition.

The similarity in species composition between the primary and secondary forest stands was very low (21.2%). This indicates the significant difference in species composition between the two forests. Brearley *et al.* (2004) found major differences in the floristics and species diversity of a 55-year-old secondary rain forest compared to an adjacent primary forest. Similarly, Andel (2001) observed major differences in species composition between two primary and two late secondary forest stands.

As expected, the tree basal area of the primary forest was higher than that of the secondary forest which could be attributed to more number of individuals in the higher girth classes. The density-diameter distribution of tree populations has been used to understand regeneration, disturbances and future stability of tree species populations in the forest communities (Rao *et al.* 1990). The observed pattern of density-diameter

distribution in the secondary forests, follows the patterns of a forest regenerating after disturbance.

The tree species showed clumped distribution both in the primary and secondary forests. This is in conformity with several studies carried out in the tropics which have revealed that trees are more commonly clumped or randomly dispersed than being uniformly dispersed (Hubbell 1979, Thorington *et al.* 1982, Forman and Hahn 1980). Uniform distribution may be the consequence of direct competition of trees for water or allelopathy while aggregation of trees is brought about by the pattern of seed dispersal, soil nutrient status and other topographic factors (Thorington *et al.* 1982).

Although the three secondary forests have similar age, there are conspicuous differences in floristic diversity as well as community structure amongst them. This differential pattern could be attributed to the different landuse history. The high species richness, tree density and tree basal area in the secondary forest SF1 could be because of moderate intensity of past extractions and proximity to the primary forests. This is also supported by the intermediate disturbance hypothesis (Connell 1978) which says that diversity will be highest at moderate level of disturbance. Moreover, the presence of some remnant tree species like might have helped in preventing major variations in the forest microclimate. The secondary forest SF2 has a history of past human habitations. This site is characterised by the dominance of a bamboo *Dendrocalamus hamiltonii*, which is a characteristic feature of highly disturbed habitats brought about by shifting cultivation (Rao and Ramakrishnan 1987). This bamboo has taken up a large share (118) of the total IVI. Thus, a greater portion of the site resources is shared by this species of bamboo leaving a little for the others to grow and establish. As a result, the species richness is

lesser. Moreover, to make way for human habitations the big trees were clearfelled. This along with competition from the bamboo species has effected tree seedling establishment and growth. SF3 has lowest species diversity and tree basal area compared to all other primary and secondary forest sites. This site has undergone intensive extraction in the past and is presently subjected to recurrent anthropogenic disturbances. The people in the adjacent village depend mainly on this forest for fuelwood as well as other forest products. Moreover, this site also experiences grazing pressure.

From the above discussions, it is seen that there are considerable differences in floristic composition and community structure between the primary and the secondary forests. There are also differences in floristic composition between the three secondary forest stands though they have similar age of fallow. This reflects that the intensity of past land use has significantly effected the structure of the three secondary forest sites.

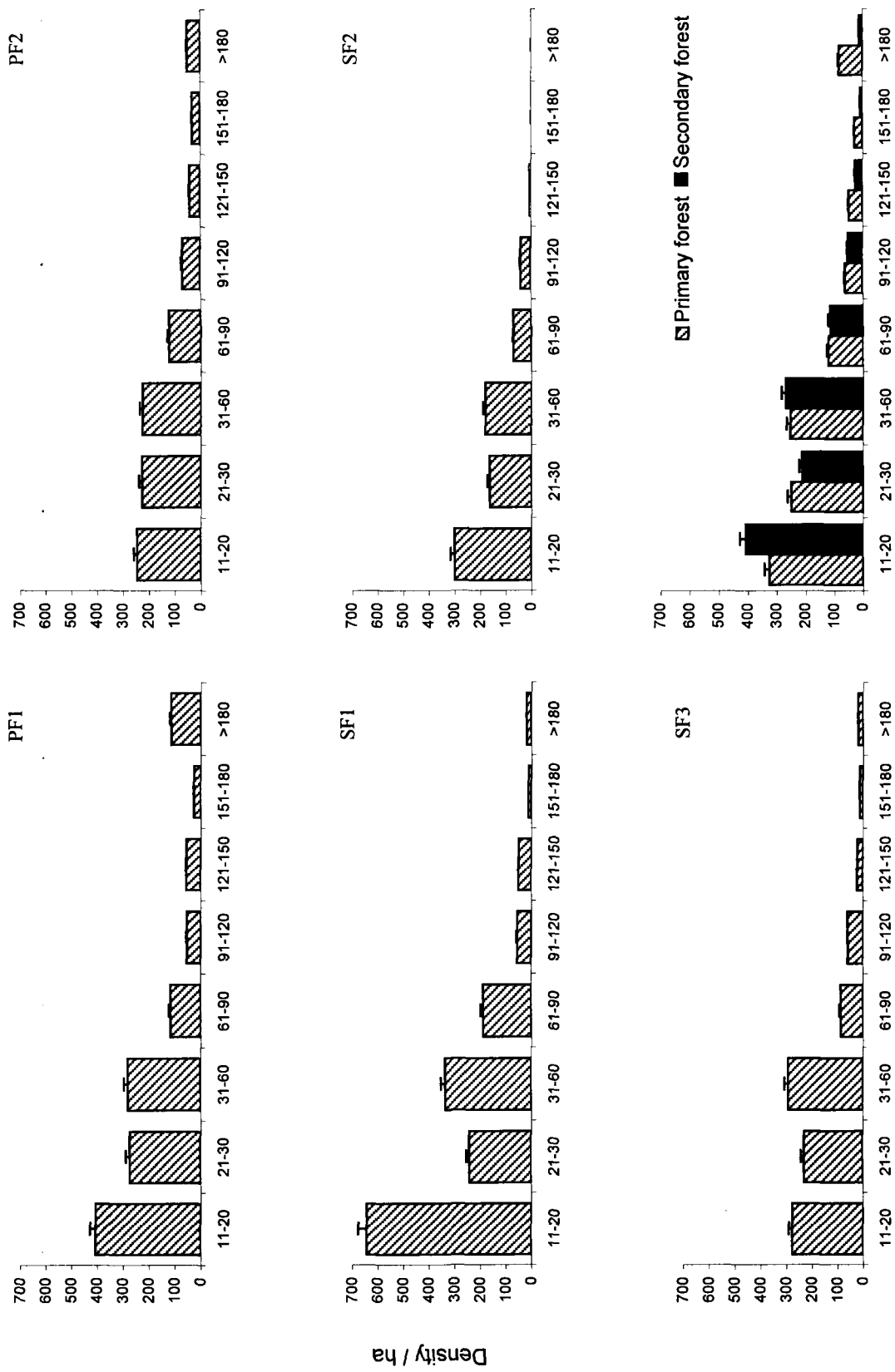


Figure 4.7. Density of tree species/ha in different girth classes in the primary and secondary forest stands in Namdapha national park
 PF1 - Primary forest 1, PF2 - Primary forest 2, SF1 - Secondary forest 1, SF2 - Secondary forest 2, SF3 - Secondary forest 3

Annexure 1. Density (ind ha⁻¹), basal area (m² ha⁻¹) and IVI of trees, shrubs, herbs and climbers in the primary and secondary forest stands

Name of species	Primary forest I			Primary forest II			Secondary forest I			Secondary forest II			Secondary forest III		
	Den.	BA	IVI	Den	BA	IVI	Den	BA	IVI	Den	BA	IVI	Den	BA	IVI
<i>Acanthopanax aculeatum</i> Seem.	0.08	0.01	1.71	-	-	-	-	-	-	-	-	-	-	-	-
<i>Actephila excelsa</i> (Dalz.) Muell.-Arg.	0.12	0.06	2.14	-	-	-	-	-	-	-	-	-	-	-	-
<i>Actinodaphne obovata</i> (Nees) Blume	-	-	-	0.14	0.62	4.95	0.03	0.00	0.64	0.35	3.17	8.27	0.02	0.27	1.41
<i>Aesculus assamica</i> Griffith.	0.02	0.01	0.48	0.03	0.11	0.90	0.16	0.40	3.42	0.22	0.39	3.74	0.10	0.24	2.72
<i>Ailanthus grandis</i> Prain	-	-	-	0.05	0.04	0.78	0.57	0.70	9.45	0.23	0.21	4.48	0.25	0.17	6.60
<i>Alangium chinense</i> (Lour.) Harms	-	-	-	-	-	-	-	-	-	-	-	-	4.39	7.01	90.91
<i>Albizia julibrissin</i> (Willd.) Durazz.	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.69	3.24
<i>Albizia lebeck</i> (L.) Benth.	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.39	2.12
<i>Albizia lucida</i> (Roxb.) Benth.	-	-	-	-	-	-	0.04	0.05	0.70	-	-	-	-	-	-
<i>Albizia odoratissima</i> (L.f.) Benth.	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.01	0.43
<i>Albizia procera</i> (Roxb.) Benth.	-	-	-	-	-	-	-	-	-	-	-	-	0.24	3.45	18.59
<i>Alstonia scholaris</i> Brown	-	-	-	-	-	-	-	-	-	-	-	-	0.05	0.03	2.07
<i>Altingia excelsa</i> Noronha	1.09	31.92	39.16	0.38	8.45	24.46	-	-	-	0.14	2.41	3.09	-	-	-
<i>Anthocephalus chinensis</i> (Lam.) A.Rich.ex Walp.	0.11	4.04	5.98	0.34	5.06	17.97	0.02	0.57	2.03	0.02	0.28	0.68	-	-	-
<i>Antidesma bunius</i> (L.) Sprengel	-	-	-	-	-	-	0.04	0.01	0.58	-	-	-	-	-	-
<i>Aphanamixis chitagona</i> (Miq.) Haridasan and Rao	-	-	-	0.01	0.24	0.73	-	-	-	-	-	-	0.86	1.89	26.48
<i>Aquilaria khasiana</i> Hall.	-	-	-	-	-	-	0.23	0.12	3.95	-	-	-	-	-	-
<i>Ardisia virens</i> Kurz.	-	-	-	-	-	-	-	-	-	0.40	0.57	8.53	-	-	-
<i>Artocarpus chaplasha</i> Roxb.	0.04	0.02	0.81	-	-	-	0.01	0.02	0.26	-	-	-	-	-	-
<i>Artocarpus heterophyllus</i> Lamk.	-	-	-	-	-	-	0.05	0.30	1.90	0.04	0.20	0.89	0.01	0.01	0.41
<i>Baccaurea ramiflora</i> Lour.	0.56	0.60	9.38	0.65	0.72	14.93	0.62	0.45	10.48	0.19	0.44	4.71	-	-	-
<i>Batispermum calycinum</i> Muell.-Arg.	-	-	-	-	-	-	0.02	0.01	0.46	-	-	-	-	-	-
<i>Betula alnoides</i> Buch.-Ham. Ex D. Don	0.02	0.03	0.35	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bischofia javanica</i> Bl.	-	-	-	0.01	0.01	0.31	0.16	1.26	6.40	0.02	0.14	0.66	0.16	0.80	6.95
<i>Blastus cochinchinensis</i> Lour.	0.02	1.63	2.09	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bombax ceiba</i> DC.	-	-	-	-	-	-	-	-	-	0.02	0.01	0.65	0.04	1.66	6.95
<i>Bridellia assamica</i> Hk. F	0.02	0.00	0.47	-	-	-	-	-	-	-	-	-	-	-	-
<i>Callicarpa arborea</i> Roxb.	-	-	-	-	-	-	-	-	-	0.02	0.00	0.65	-	-	-
<i>Cammelia caudata</i> Wallich	0.02	0.01	0.32	-	-	-	-	-	-	0.01	0.00	0.32	-	-	-
<i>Canarium strictum</i> Roxb.	0.04	1.70	2.62	0.01	0.25	0.76	-	-	-	-	-	-	-	-	-

Trees

<i>Garcinia</i> sp.	-	-	-	0.01	0.00	0.31	0.17	0.05	2.63	0.02	0.01	0.65	-	-	-
<i>Garcinia tinctoria</i> (DC.) W.F. Wight	-	-	-	-	-	-	0.50	1.38	13.06	-	-	-	-	-	-
<i>Glycosmis cyanocarpa</i> (Kurz)	0.04	0.01	0.94	-	-	-	-	-	-	-	-	-	0.05	0.12	2.37
<i>Glycosmis cymosa</i> (Kurz)	0.01	0.04	0.27	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gmelina arborea</i> Griffith.	0.02	0.07	0.38	0.02	0.04	0.67	-	-	-	0.08	0.14	1.75	0.18	0.19	3.93
<i>Grewia denticulata</i> Wallich ex Voigt.	-	-	-	-	-	-	-	-	-	-	-	-	0.03	0.04	1.32
<i>Grewia disperma</i> Rottb.	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.13	0.94
<i>Kayea assamica</i> K&P	0.01	0.00	0.24	0.01	0.00	0.31	0.17	0.44	2.91	-	-	-	-	-	-
<i>Knema angustifolia</i> (Roxb.) Warb.	0.02	0.03	0.50	-	-	-	-	-	-	-	-	-	-	-	-
<i>Knema cinerea</i> (Poiret) Warb.	0.02	0.00	0.32	-	-	-	-	-	-	-	-	-	-	-	-
<i>Kydia calycina</i> Roxb.	-	-	-	-	-	-	-	-	-	0.06	0.98	1.20	-	-	-
<i>Kydia calycina</i> Roxb. var. <i>glabrescens</i> (masters)	-	-	-	-	-	-	-	-	-	0.03	0.37	1.02	-	-	-
<i>Leea edgeworthii</i> Santapau	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.01	0.82
<i>Leportea pterostigma</i> Wedd.	0.01	0.00	0.24	-	-	-	0.25	0.16	4.49	0.12	0.87	2.49	0.62	0.30	13.12
<i>Lithocarpus dealbatus</i> (Hook.f.&Thomson ex Miq.)	-	-	-	-	-	-	-	0.20	5.94	-	-	-	-	-	-
<i>Litsea cubeba</i> (Lour.) Pers.	0.01	0.01	0.24	-	-	-	0.64	0.15	9.23	0.18	0.09	4.13	0.08	0.23	2.76
<i>Litsea lanceifolia</i> (Roxb. ex Nees) Hook.	0.95	0.56	5.17	-	-	-	-	-	-	-	-	-	-	-	-
<i>Litsea monopetala</i> (Roxb.) Pers.	0.08	0.03	1.29	-	-	-	0.06	0.02	0.76	-	-	-	-	-	-
<i>Litsea salicifolia</i> (Roxb. ex Nees) Hook.f.	0.01	0.00	0.23	-	-	-	0.12	0.13	2.61	0.24	0.09	4.36	0.01	0.01	0.44
<i>Litsea selsifera</i> Pers.	0.16	0.17	2.85	-	-	-	0.20	0.03	2.11	-	-	-	-	-	-
<i>Litsea</i> sp.	0.01	0.10	0.33	0.04	0.01	0.83	-	-	-	-	-	-	-	-	-
<i>Litsea</i> sp.	0.01	0.00	0.24	0.11	0.08	3.07	-	-	-	-	-	-	-	-	-
<i>Lyonia ovalifolia</i> (Wallich) Drude	-	-	-	-	-	-	-	-	-	0.08	0.67	1.81	-	-	-
<i>Macaranga denticulata</i> Muell.-Arg.	-	-	-	-	-	-	-	-	-	-	-	-	0.08	0.08	1.65
<i>Maesa indica</i> (Roxb.) A. DC.	-	-	-	-	-	-	-	-	-	-	-	-	0.64	0.74	16.85
<i>Mangifera sybatica</i> Roxb.	0.01	0.32	0.55	-	-	-	0.05	0.11	1.37	0.05	0.02	0.98	-	-	-
<i>Magnolia griffithii</i> Hk.f. & Th.	0.16	5.15	8.24	-	-	-	-	-	-	-	-	-	-	-	-
<i>Magnolia gustavi</i> King	0.03	0.93	1.62	-	-	-	-	-	-	-	-	-	-	-	-
<i>Magnolia pterocarpa</i> Roxb.	0.02	0.01	0.32	-	-	-	0.42	2.30	13.58	0.42	0.17	8.05	-	-	-
<i>Magnolia</i> sp.	0.02	0.00	0.47	0.01	0.01	0.33	0.02	0.09	0.67	-	-	-	-	-	-
<i>Melia azadirachta</i> L.	-	-	-	-	-	-	-	-	-	0.03	0.45	0.81	0.07	0.18	2.18
<i>Mesua ferrea</i> L.	0.05	0.04	1.21	1.31	9.96	40.82	0.34	0.20	6.63	0.11	0.03	2.50	-	-	-
<i>Meyna spinosa</i> Roxb. Ex Link	-	-	-	-	-	-	0.36	0.10	6.21	-	-	-	-	-	-
<i>Michelia baillonii</i> (Pierre) Finet Gagnepain	0.52	0.98	8.88	-	-	-	-	-	-	-	-	-	-	-	-
<i>Michelia</i> sp.	-	-	-	0.13	1.40	5.64	0.06	0.65	3.12	0.20	0.55	4.62	-	-	-
<i>Morus laevigata</i> Wall.	0.01	0.01	0.24	-	-	-	-	-	-	-	-	-	-	-	-
<i>Murraya paniculata</i> (L.) Jack.	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.08	0.67
<i>Naucllea griffithii</i> Hav.	-	-	-	0.05	0.81	2.57	-	-	-	-	-	-	-	-	-

<i>Lepotea crenulata</i> Gaud.	0.05	1.64	-	-	-	-	-	0.50	26.58	0.55	15.80
<i>Litsea lancifolia</i> (Roxb. ex Nees) Hook.	2.05	15.09	-	-	-	-	-	-	-	-	-
<i>Melia superbq</i> Roxb.	-	-	0.35	7.68	1.35	32.57	-	-	-	-	-
<i>Microtropis discolor</i> (Wallich) Arn.	-	-	-	-	-	-	-	-	-	-	-
<i>Mitusa globosa</i> (DC.) Panigr. & S.C. Misra	-	-	-	-	0.80	23.35	-	-	-	-	-
<i>Mitusa roxburghiana</i> (Wallich.) Hook. f. & Thomson	-	-	-	0.30	-	-	-	-	-	-	-
<i>Morinda angustifolia</i> Roxb.	1.65	11.87	-	-	-	-	-	-	-	-	-
<i>Mussaenda roxburghii</i> Hook. f.	-	-	0.80	-	-	-	-	-	-	-	-
<i>Myrtioneuron nutans</i> Kurz.	3.25	20.15	1.85	-	-	-	-	-	-	-	-
<i>Myxopyrum smilacifolium</i> (Wallich) Blume	-	-	0.50	-	-	-	-	-	-	-	-
<i>Paederia scandens</i> (Lour.) Merr	-	-	4.70	-	-	-	-	-	-	-	-
<i>Persicaria chinensis</i> (L.) H. Gross.	0.10	2.45	3.00	-	-	-	-	-	-	1.45	27.89
<i>Phlogacanthus asperulus</i> Nees in Wallich.	-	-	-	-	-	-	-	-	-	-	-
<i>Pogostemon paniculatus</i> Benth.	-	-	-	-	-	-	-	-	-	-	-
<i>Psychotria calocarpa</i> Kurtz.	0.30	4.47	-	-	-	-	-	-	-	7.60	92.50
<i>Psychotria silhetensis</i> Hook.	8.05	34.27	5.20	-	-	-	-	0.70	34.09	0.20	10.66
<i>Pycnarrhena pleniflora</i> Miers.	0.95	8.97	-	-	-	-	-	1.25	48.68	0.65	18.91
<i>Randia fasciculata</i> (Roxb.) DC.	0.05	1.64	-	-	0.85	23.97	-	0.65	32.26	0.65	17.92
<i>Rhamnus nepalensis</i> (Wallich) Lawson	0.30	4.47	0.30	5.92	-	-	-	-	-	-	-
<i>Sarcandra glabra</i> (Thun.) Makino	4.85	24.10	7.50	47.87	-	-	-	-	-	-	-
<i>Sida acuta</i> Burm. f.	-	-	-	-	-	-	-	-	-	-	-
Singpho pat (local name)	0.70	7.93	1.20	14.04	-	-	-	-	-	-	-
<i>Solanum nigrum</i> Linn.	-	-	-	-	-	-	-	-	-	-	-
<i>Solanum torvum</i> Swartz.	-	-	-	-	-	-	-	-	-	-	-
<i>Solanum xanthocarpum</i> Schrad & Wendl.	-	-	-	-	-	-	-	-	-	-	-
<i>Strobilanthes secundus</i> T. Anderson	0.75	7.32	-	-	1.20	30.18	-	-	-	-	-
<i>Tetrasigma bracteolatum</i> (Wallich) Planchon	0.25	3.99	-	-	0.40	15.86	-	-	-	-	-
<i>Tetrasigma obovatum</i> (Lawson) Gagnepan	0.20	3.62	-	-	0.15	9.66	-	-	-	-	-
<i>Toddalia asiatica</i> (L.) Lam.	0.05	1.64	-	-	-	-	-	-	-	-	-
<i>Vernonia volkamerifolia</i> DC.	-	-	0.25	5.46	-	-	-	-	-	-	-
Herbs and climbers											
<i>Dryopteris sparsa</i> (D. Don.) O. Ktze.	0.46	30.25	-	-	-	-	-	-	-	-	-
<i>Achyranthus aspera</i> L.	-	-	-	-	-	-	-	0.54	20.61	0.94	9.80
<i>Adiantum caudatum</i> L.	0.57	33.81	0.40	15.58	-	-	-	-	-	-	-
<i>Ageratum conyzoides</i> L.	-	-	-	-	-	-	-	-	-	-	-
<i>Amaranthus spinosus</i> L.	-	-	-	-	-	-	-	-	-	4.57	28.76
<i>Amblyanthus glandulosus</i> Roxb. DC.	0.29	18.54	-	-	-	-	-	-	-	0.23	4.22
<i>Amorophallus campanulatus</i> Roxb.	0.06	7.84	-	-	0.51	11.50	-	-	-	-	-

Chapter 5

Tree regeneration

5.1 Introduction

The regeneration of trees in a forest takes place either through seeds or through vegetative means like sprouting/coppicing or root suckers. The state of tree regeneration in a forest ecosystem can be envisaged from the tree population structure. A successful regeneration is predicted from the presence of adequate number of seedling, saplings and young trees in a given species population. The continued presence of a species in the community can be ensured only by the presence of adequate number of older plants, which act as the source of propagules for the future generation. In tree cut areas, in addition to seedling regeneration, regeneration by coppicing is an important regeneration mechanism, if the stems and roots of the past plants are left undisturbed (Ewel 1977, Murphy and Lugo 1986, Murphy *et al.* 1995). In the tropical forests, where large-scale disturbance occurs as a result of clearing, burning and extensive storm damage, regeneration from stem coppice is very important (Byer and Weaver 1977, Putz and Brokaw 1989, Bellingham *et al.* 1994). Thus, it is essential to know how far the coppicing species would be able to contribute to the resilience mechanism of the disturbed ecosystem. In this regard, stump size would play an important role in recuperation of the tree populations.

As already discussed, the areas in and around Namdapha national park have experienced varying degrees of anthropogenic disturbances (Adhikari *et al.* 2003, Arunachalam *et al.* 2004) due to forest clearance for settlement, agriculture and product extraction. Our understanding of regeneration mechanism and processes following a disturbance in

primary forest that lead to the formation of a secondary forest is inadequate. An understanding of the regeneration processes in the secondary forests is key to developing strategies for effective management of these forests. Therefore, it is important to know the regeneration mechanism of tree species of the secondary forests, particularly the species those are dominant, economically useful and culturally important. The regeneration mechanisms of these species together would help us predict the regeneration process of the secondary forests and would also help in predicting the future trends in species composition and forest community structure. The present chapter deals with the tree regeneration status and process of some selected tree species in primary and secondary forests. The findings of the study would therefore explain the differential regeneration process in the secondary and primary forests.

Five tree species viz., *Alangium chinense* (dominant species in successional environment), *Shorea assamica* (threatened category of species), *Sapindus mukkorossi* and *Spondias axillaris* (both are economic important) and *Mesua ferrea* (culturally important) were selected for detailed study. The species selected for coppice regeneration are *Alangium chinense*, *Alstonia scholaris*, *Albizia procera*, *Melia azadiracht* and *Sapindus mukkorossi*.

5.2 Methodology

Population structure of tree species

Population structure of the selected tree species was studied by classifying the individuals into four girth classes viz., seedling (0-10 cm), juvenile (11-30 cm), young (31-60 cm), elder (61-90) and mature (> 90 cm).

Regeneration status of tree species

Status of tree regeneration was determined based on the size of seedling and sapling populations (Bhuyan *et al.* 2003, Khan *et al.* 1987, Uma Shankar 2001) as well as coppice populations. Regeneration status was differentiated as follows: good regeneration, if seedlings > saplings > adults; fair regeneration, if seedlings \leq saplings \leq adults; poor regeneration, if the species exists only in sapling stage, but no seedlings (saplings may be <, > or = adults). If a species is present only in adult form it is considered as not regenerating. Species is considered as 'new' if the species has no adults but only seedlings or saplings.

Regeneration through coppice/sprouts and root suckers was also assessed by recording the number of individuals under different species in the forest stands.

Studies on coppicing

Regeneration through coppice was restricted to the secondary forest stand SF3. To study the effect of stump size on sprouting of selected species in SF3, 40 cut stumps of each species viz., *Alangium chinense*, *Alstonia scholaris*, *Albizia procera*, *Melia azadirachta* and *Sapindus mukhrosi* were marked with black paint. The stumps were categorized into different girth classes. The number of sprouts in each cut stump was recorded after one year (February, 2004). The total number of sprouts recorded in each girth classes was then calculated.

To assess the effects of diameter and height of the sampled stumps on the density of coppices, sprout density was divided into five categories viz., 1-5, 6-10, 11-15 and >15 shoots per stem.

Appropriate regression models were developed to establish the relationship between the stump sizes, height and diameter of sprouts and coppice number.

5.3 Results

Regeneration status of trees

The secondary forests exhibited better tree regeneration than the primary forests (Figure 5.1). About 66% of the total regenerating species were in the secondary forests as compared to the latter, where only 50% species were regenerating. 41% of tree species in the secondary forests were not regenerating through seeds while in the primary forests such species constituted only 48%.

Out of 80 species in PF1, only 45 species were found regenerating, 2 species of which had good regeneration, 13 species showed fair regeneration and 20 species showed poor regeneration (Figure 5.2, Annexure II). In PF2, out of 52 species, 22 species were found regenerating, of which 1 species had good regeneration, 6 showed fair regeneration and 15 had poor regeneration. Out of 58 species in SF1, 7 had good regeneration, 8 species had fair and 20 species had poor regeneration. In SF2, only 1 species had a good regeneration, 5 species had fair and 14 species had poor regeneration. In SF3, most species exhibited either poor or no seedling regeneration. At least 3 species in the stand had no adult trees. However, the number of such invading species was much more in SF1 (16) than any other stand. The proportion of newly colonizing and invading species was more in the secondary forests than the primary forests (Figure 5.3).

Seedling populations in all the primary and secondary forest stands showed marked differences between wet (June-July) and dry (November-December) seasons with more number of tree species in the seedling stage in the wet season.

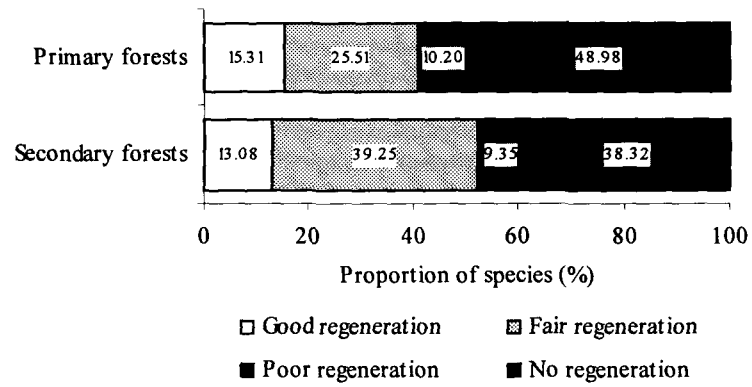


Figure 5.1. Regeneration status of trees in the primary and secondary forests (Values inside the figures are percent of total species)

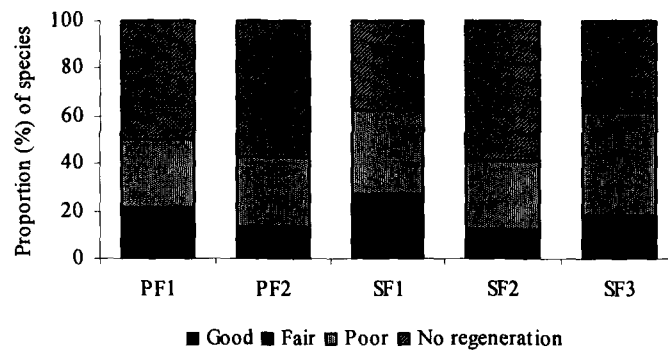


Figure 5.2. Regeneration status of trees in the primary and secondary forests stands

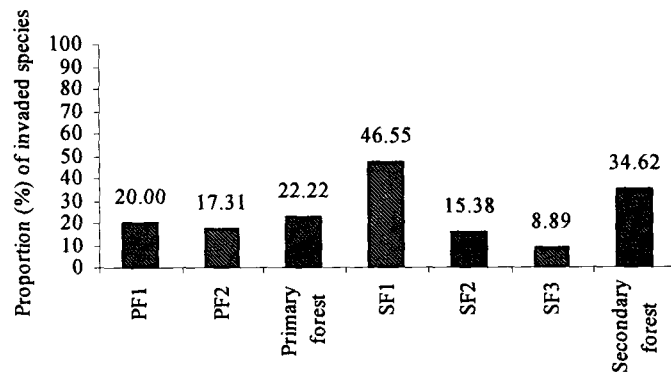


Figure 5.3. Proportion of invaded species in the primary and secondary forest stands (Values above the bars are percent of total tree species)

Coppice regeneration was found only in the secondary forest stands and was predominant in SF3 with 50% of the species regenerating through coppicing (Figure 5.4). *Alangium chinense* was a good coppicer, while *Sapindus mukkorossi* was a poor coppicer (Table 5.1). Species regenerating through root suckers such as *Actinodaphne obovata* were found only in SF2. Nearly 20% of the total tree species in SF1 showed signs of coppicing, whereas in SF2 nearly 45% of the total tree species showed signs of coppicing. No species in the two primary forests showed any sign of regeneration through coppices (Figure 5.4).

Table 5.1. Some coppicing species in the primary and secondary forests of Namdapha national park

Good coppicer	Moderate coppicer	Poor coppicer
<i>Alangium chinense</i>	<i>Talauma hodgsonii</i>	<i>Sapindus mukkorossi</i>
<i>Melia azediracht</i>	<i>Alstonia scholaris</i>	
<i>Albizzia procera</i>		
<i>A. odoratissima</i>		
<i>A. lebbeck</i>		

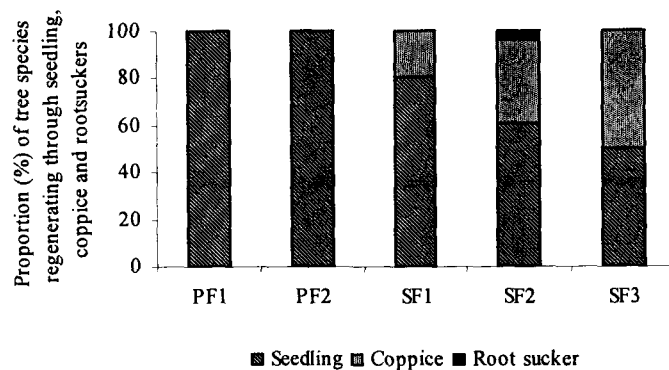


Figure 5.4. Proportion (%) of tree species regenerating through seedling, coppice and root suckers in primary and secondary forests

Population structure of regenerating tree species

Alangium chinense had a good population consisting of seedlings, juveniles and mature trees in the secondary forest, whereas in the primary forest only few seedlings were found. In case of *Sapindus mukkorossi* density of individuals was more in the seedling and juvenile stages in the secondary forests as compared to the primary forests. Individuals of *Spondias axillaris* were limited to young and adult stages only in the primary forest; and to seedling, juvenile and mature stages only in the secondary forest. *Mesua ferrea* had a good population in the primary forest with maximum number of individuals in the seedling and adult stages, with all other stages in between. But in the secondary forests it was found in seedling, juvenile and young stages. *Shorea assamica* was found in all the growth stages in the primary forest, while in the secondary forests only few mature trees and seedlings were encountered (Figure 5.5).

Effect of stump girth size on sprouting of selected species

Stump girth size significantly affected sprouting in *Alangium chinense*, *Alstonia scholaris*, *Albizia procera* and *Melia azadiracht* ($p < 0.001$). However, in case of

Sapindus mukkorossi, stump girth did not affect the sprouting intensity (Table 5.2).

Average number of sprouts was more in the girth classes of 90-120 cm and 121-150 cm.

Table 5.2. ANOVA for effect of stump size on sprouting intensity of some selected coppicers

Species	Stump girth (cm)	N	Levels	One-way ANOVA		
				F	P-value	df
<i>A. chinense</i>	30-150	40	4	19.795	0.001	3
<i>A. scholaris</i>	30-150	40	4	7.025	0.001	3
<i>A. procera</i>	30-150	40	4	16.935	0.001	3
<i>M. azediracht</i>	30-180	50	5	13.006	0.001	4
<i>S. mukkorossi</i>	30-150	40	4	0.632	0.599	3

Regression models for stump size *versus* number of sprouts showed significant linear relations for *A. chinense*, *M. azediracht*, *A. scholaris* and *A. procera* ($P = 0.001$) as shown in Table 5.3.

Table 5.3. Regression models showing the relationship between stump size and number of sprouts

Species	Regression model	N	r ²	P-value	Range of 'x'
<i>A. chinense</i>	$y = 0.09x + 0.22$	40	0.45	0.001	30-150
<i>A. scholaris</i>	$y = 0.06x + 1.34$	40	0.26	0.001	30-150
<i>A. procera</i>	$y = 0.08x + 0.90$	40	0.38	0.001	30-150
<i>M. azediracht</i>	$y = 0.06x + 1.48$	50	0.31	0.001	30-180
<i>S. mukkorossi</i>	$y = -0.0005x + 2.59$	40	0.001	ns	30-150

'N' - no. of observations, 'y' - no. of sprouts and 'x' - stump size

Effect of coppice density on diameter and height of coppice shoots

Density of coppice shoots had a significant effect over diameter and height of the shoots ($P < 0.05$ to $P < 0.001$) for all the selected species except *S. mukkorossi* (Table 5.4).

Average diameter and height of shoots was comparatively more in the stumps having less number of shoots. The number of stumps having sprout density ranging from 1-10 was more in case of *A. chinense*, *A. scholaris*, *M. azediracht* and *S. mukkorossi*.

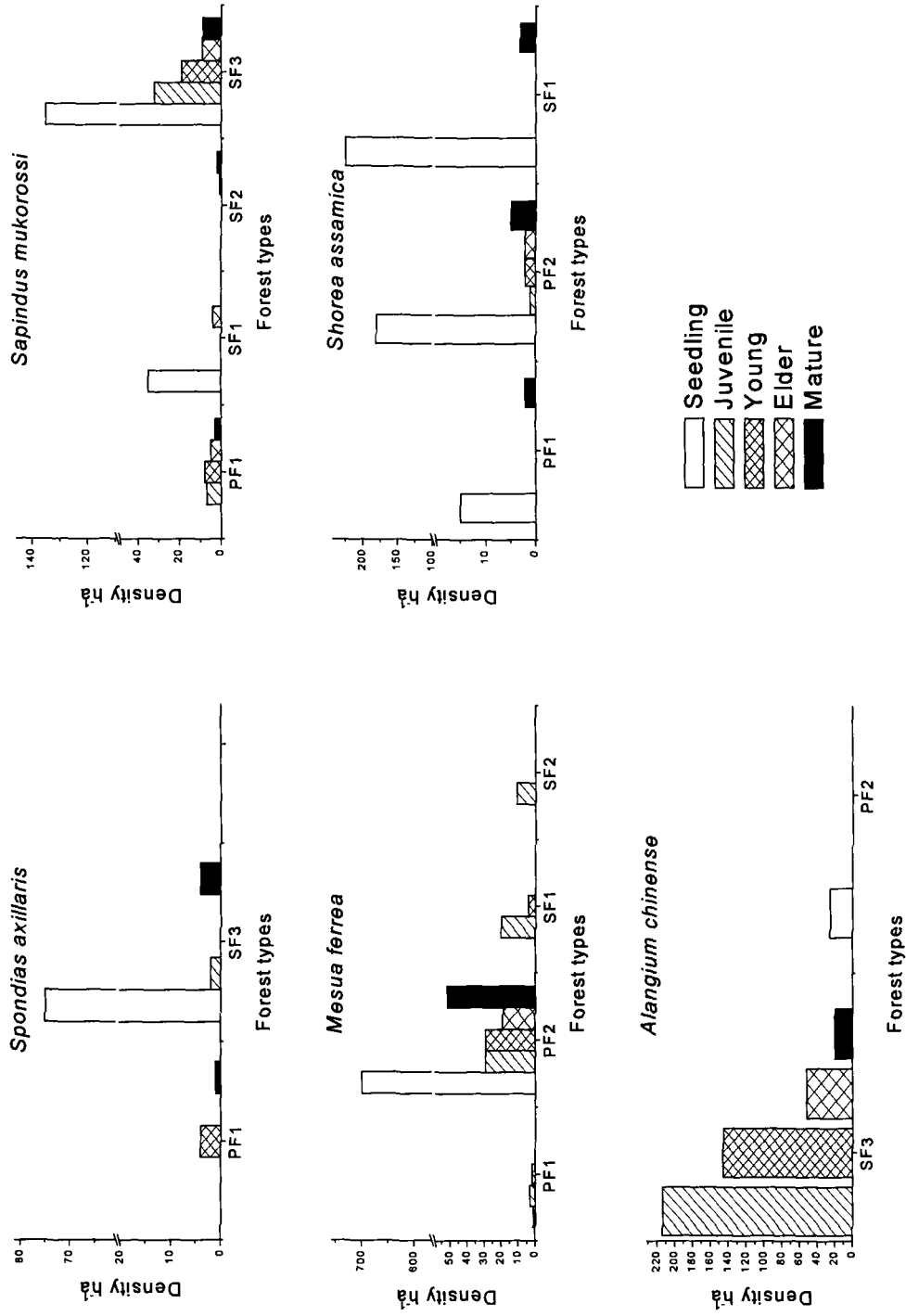


Figure 5.5. Population structure of some selected tree species in the primary and secondary forests of Namdapha national park (PF1 – Primary forest 1, PF2 – Primary forest 2, SF1 – Secondary forest 1, SF2 – Secondary forest 2, SF3 – Secondary forest 3)

Table 5.4. ANOVA on the effect of shoot density on average diameter and height of sampled shoots of some selected species

Species	Categories of shoot density/stump	Number of stumps	Average diameter of shoot (mm)	Average height of shoot (cm)	F-value	
					Diameter	Height
<i>A. chinense</i>	1-5	10	2.55	12.7	4.48**	16.12***
	6-10	15	1.50	12.4		
	11-15	10	1.50	12.4		
	>15	5	1.48	6.9		
<i>A. procera</i>	1-5	11	2.03	12.0	3.50*	10.56***
	6-10	9	1.52	11.5		
	11-15	19	1.60	7.6		
	>15	1	1.25	7.6		
<i>A. scholaris</i>	1-5	15	2.07	4.3	19.58***	8.03***
	6-10	12	1.36	4.1		
	11-15	13	1.18	3.9		
<i>M. azediracht</i>	1-5	16	4.95	11.1	22.63***	55.50***
	6-10	14	4.60	4.3		
	11-15	16	5.40	7.2		
	>15	4	2.67	2.9		
<i>S. mukkorossi</i>	1-5	39	2.27	2.4	2.80 ^{ns}	0.05 ^{ns}
	6-10	1	1.20	2.5		

***P<0.001, **P<0.005, *P<0.05, ns – not significant

5.4 Discussion

The regeneration status of trees was better in the secondary forests than the primary forests. This could be attributed to sufficient availability of light and nutrients in the secondary forests comparing to the primary forests. Presence of a number of remnant tree species like *Altingia excelsa*, *Talauma hodgsonii*, *Cinnamomum bejolghota*, and *Endospermum chinense* in the secondary forests has also boosted the recovery of the secondary forests to some extent by creating suitable microenvironment for the establishing seedlings. In this context, Guariguata and Ostertag (2001) advocated that presence of remnant tree species can strongly influence the rate of colonization through its effects on dispersal.

But, stand wise the number of species having poor regeneration was proportionately more in SF2 comparing to other primary and secondary forest sites. The reason could be heavy mortality of the tree species in the seedling stage and subsequently, difficulty in establishment in the forest environment that is exerting a pressure on the seedling population in these two sites. This could be presumably because of landuse history of the site. The site was earlier cleared for cultivation and presently harbors a mixed-bamboo forest. The presence of bamboo culms along with thick bamboo leaf litter and high density of herbaceous species could reduce seedling establishment thus reducing the seedling population. This observation is corroborated by the findings of Nishikami and Ishibashi (2000) who conducted a study to determine the regeneration characteristics for predicting stand growth of naturally regenerated broadleaved forests in the northern Kanto district of Honshu, Japan. The authors found that some topographic factors such as aspect and degree of slope caused differences in forest succession, and the presence of a dwarf bamboo species viz. *Sasa* sp. greatly influenced the growth of canopy tree saplings. In many logged over forest stands, poor natural regeneration has been attributed to dense growth of herbs which compete with the tree seedlings thus affecting their growth (Hough and Forbes 1943, Horsley 1977).

Species represented only through seedlings or saplings in the study stands were considered as 'new' species. Such species were more in SF1 and least in SF3. Invasions of newer species were more in SF1 presumably because this site provides ideal micro-environmental conditions for seed germination and seedling establishment of the species in question and provides ways for the opportunist species to germinate (Ohsawa *et al.* 1986). When such periods of opportunity are not available, the species not fit for the site

would not get any chance of getting established, as is the case in SF3. Proximity to the primary forests that act as promising seed sources for new species could be another cause behind more number of 'new' species in SF1 than in SF3.

Lower seedling populations in the primary and secondary forest sites during winter than in the rainy season could be due to the stress caused by reduction in soil moisture and unfavorable temperatures for the seedlings. Several other workers have also reported similar observations and results (Rao and Singh 1985, Kumar *et al.* 1994, Pereira and Kozłowski 1977, Khan *et al.* 1986).

Regeneration of some of the species i.e. *A. chinense*, *Sapindus mukkorossi* and *Spondias axillaris* selected for detailed study showed fair regeneration in the secondary forests, whereas in the primary forests they had poor regeneration. However in case of other selected species, *Mesua ferrea* and *Shorea assamica* regeneration was good in the primary forest, when compared to the secondary forest sites. The probable reasons could be the favorable niches that the present sites of active regeneration provide them. Whilst the selected species i.e. *Alangium chinense* and *Mesua ferrea* were found in populations in the primary and secondary forests, the other three species i.e. *Sapindus mukkorossi*, *Spondias axillaris* and *Shorea assamica* were sporadic in the stands. Thus, the spatial distribution of the parent trees also could have some role in the overall regeneration of the species in question. All the factors behind their present regeneration status in the primary and secondary forests have been investigated in detail in the foregoing chapters.

Tree regeneration in the primary and secondary forests has been affected by the different intensities of landuses. While seedlings were the chief mode of regeneration in the two primary forest stands, vegetative mode of regeneration through coppices/sprouts/root

suckers also has a role to play in the regeneration mechanisms along with seedlings in the secondary forest stands. Many workers have reported that sprouting contributes significantly to natural regeneration in tree cut forest stands (Beck 1980, McLaren and McDonald 2003b). Almost half of the tree species present in SF3 had capacity to regenerate through resprouting comparing to SF1 and SF2. The reason for the sites SF1 and SF2 having proportionately lesser number of vegetatively regenerating species could be less number of cut stumps. The sites SF1 and SF2 were cleared for human settlements and settled agriculture for which the cut stumps were almost removed. Subsequently, they were abandoned 20-25 years back. The remnant stumps that could not sprout lost their regenerative capacity due to rapid decay of the trunk base. Due to close proximity of the sites to the primary forest they were invaded by floristic elements of primary forests. Thus, the first two secondary forests (SF1 and SF2) had proportionately more number of species regenerating through seedlings comparing to sprouts/coppices. The above observations are corroborated by Ewel (1980) that trunk bases of trees in the wet tropics are subject to rapid decay comparing to dry tropics. So regeneration by vegetative means would likely to be more successful in the dry tropics than in the wet tropics.

Regeneration through sprouting and coppicing were more common in the secondary forests and especially in SF3 with 50% of the total species regenerating through vegetative means. Studies on the effect of stump size on sprouting of selected tree species (*Alangium chinense*, *Alstonia scholaris*, *Albizia procera* and *Melia azadirachta*) having good IVI ranking showed significant positive results. Average number of sprouts was also more in the higher girth classes of 90-120 cm and 121-150 cm. Bellingham (1993) reported that larger sized stems produced on an average more shoots and larger leading

shoots which might be as a result of larger sized stems having greater carbohydrate reserves that can be mobilized to facilitate higher levels of resprouting. The larger sized stems are bound to have a larger root biomass which will also be able to tap more of the resources needed to support growth. Conversely, Khan and Tripathi (1986) reported that in a disturbed sub-tropical wet hill forest of north-east India sprouting percentage of the stumps and number of sprouts per stump of *Alnus nepalensis*, *Quercus dealbata*, *Quercus griffithi* and *Schima khasiana* decreased with stump diameter. Also, the sprouts arising from the stumps of medium diameters (>15-30 and >30-45 cm) and heights (25-30 and 45-50 cm) survived better than those from the stumps of smaller or larger diameters and heights. This reduction in sprout numbers with increasing diameter has been attributed to the increasing bark thickness in the study species which provides mechanical hindrance while sprouting and physiological changes in tree species with advancement of age due to which the capability for rejuvenation by vegetative means decreases.

Coppice shoot density had a significant effect over diameter and height of the shoots ($P < 0.05$ to $P < 0.001$) for all the selected species except *S. mukkorossi*. Conversely, average diameter and height of shoots was comparatively more in the stumps having less number of shoots. Here, it could be said for the effect of shoot density on the average height and diameter of shoots, that high shoot density would result in increased competition among the shoots for available resources (McLaren and McDonald 2003b). Therefore, high shoot number may not be an indication of successful vegetative regeneration. While they may act as an indemnity against the death of one or a few leading shoots, but result in a significantly lower biomass recovery. Nonetheless, SF3 is relatively poor in terms of soil moisture content which could limit the growth of tree

seedlings, and it might be more so in the winter season. But McLaren and McDonald (2003b) reported that coppice regrowth offered a considerable resilience to disturbance in a disturbed tropical dry limestone forest in Jamaica where successful regeneration by seed is highly susceptible to rainfall seasonality. So, in this case regenerating through coppicing could help in recuperation of the third secondary forest (SF3).

From the above discussion it could be inferred that tree regeneration in the secondary forest sites have been markedly influenced by landuse history and the present levels of disturbances. The secondary forests SF1 and SF2 have more similarity with that of the primary forests and are likely to gain similar species composition earlier than that of the third secondary forest site (SF3) due to their proximity to the primary forests. Nevertheless, SF3 has also full potential to gather biomass due to current composition of strong coppicers like *Alangium chinense*, *Albizzia* spp., *Melia azadiracht* etc. But probably it cannot achieve similarity with that of the primary forests in terms of species composition.

Annexure II. Regeneration status of trees in the primary and secondary forests in Namdapha national park

Name of species	PF1			PF2			SF1			SF2			SF3		
	SE	SA	TR	Status	SE	SA	TR	Status	SE	SA	TR	Status	SE	SA	TR
<i>Acanthopanax aculeatum</i> Seem.	-	-	-	-	-	5	8	-	-	-	-	-	-	-	15
<i>Actephila excelsa</i> (Daltz.) Muell.-Arg.	-	-	-	-	-	-	6	6	-	-	-	-	-	-	-
<i>Actinodaphne obovata</i> (Nees) Blume	-	-	-	-	2	12	3	P	10	3	-	Nw	32.5	9	26
<i>Aesculus assamica</i> Griffith.	-	1	1	P	-	3	4	Nn	23	4	12	F	32.5	-	22
<i>Ailanthus grandis</i> Prain	-	-	-	-	1	4	18	P	35	18	39	F	17.5	12	11
<i>Alangium chinense</i> (Lour.) Harms	-	-	-	-	25	-	-	Nw	-	-	-	-	-	-	165
<i>Albizia julibrissin</i> (Willd.) Durazz.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	127
<i>Albizia lebeck</i> (L.) Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
<i>Albizia lucida</i> (Roxb.) Benth.	-	-	-	-	-	-	2	P	-	-	-	-	-	-	2
<i>Albizia odoratissima</i> (L.f.) Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Albizia procera</i> (Roxb.) Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Alstonia scholaris</i> Brown	-	-	-	-	-	5	-	Nw	-	-	-	-	-	-	15
<i>Altingia excelsa</i> Noronha	30	11	98	F	-	38	74	Nn	138	74	35	G	35	4	10
<i>Anthocephalus chinensis</i> (Lam.) A.Rich.ex Walp.	-	-	11	Nn	-	34	-	Nn	-	-	2	Nn	-	-	2
<i>Anitidesma bunius</i> (L.) Sprengel	-	-	-	-	-	-	4	Nw	-	-	-	-	-	-	-
<i>Aphanamixis chittagonga</i> (Miq.) Haridasan & Rao	-	-	-	-	-	1	-	Nn	-	-	-	-	-	-	-
<i>Aphanamixis polystachya</i> (Wallich) Parker	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aquilaria khasiana</i> Hall.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ardisia virens</i> Kurz.	-	-	-	-	-	-	12	P	-	-	11	P	-	-	-
<i>Artocarpus chaplasha</i> Roxb.	-	-	-	-	-	-	12	Nw	-	-	-	Nw	-	-	40
<i>Artocarpus heterophyllus</i> Lamk.	5	2	2	F	-	-	5	Nn	5	1	-	Nw	-	-	-
<i>Artocarpus ramiflora</i> Lour.	-	-	-	-	-	-	-	-	-	-	5	Nn	-	-	4
<i>Baccaurea ramiflora</i> Lour.	20	19	37	F	25	14	51	F	78	26	36	F	-	2	17
<i>Baliospermum calycinum</i> Muell.-Arg.	-	-	-	-	-	-	2	Nw	-	-	-	Nw	-	-	-
<i>Betula alnoides</i> Buch.-Ham. Ex D. Don	-	-	2	Nn	-	-	-	-	-	-	-	-	-	-	-
<i>Bischofia javanica</i> Bl.	-	-	-	-	-	1	16	Nn	15	-	-	P	-	-	4
<i>Blastus cochinchinensis</i> Lour.	-	-	2	Nn	-	-	-	-	-	-	-	-	-	-	-
<i>Boehmeria glomerulifera</i> Miq.	-	-	14	Nn	-	-	-	-	-	-	-	-	-	-	-
<i>Bombax ceiba</i> DC.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bridellia assamica</i> Hk. F	-	2	-	Nw	-	-	-	-	-	-	-	-	-	14	-
<i>Callicarpa arborea</i> Roxb.	-	-	-	-	-	-	14	-	-	-	-	Nw	-	-	2
<i>Camelia caudata</i> Wallich	-	1	1	P	-	-	-	Nn	-	-	90	Nn	-	-	1
<i>Canarium strictum</i> Roxb.	45	-	4	F	-	1	-	Nn	-	-	-	-	-	-	-
<i>Capparis multiflora</i> Hk. F and Th.	-	-	1	Nn	-	-	-	-	-	-	-	-	30	-	-

Chapter 6

Seed Ecology

6.1 Introduction

The successful regeneration of a tree species through seeds warrants sufficient seed production, long seed viability, wide seed dispersal, persistence in the soil seed bank and copious seed germination. Seed ecology thus engulfs a whole variety of issues relating to seed production, its dispersal, viability and subsequent germination as well as its persistence in the soil both at spatial and temporal scale. The interaction of a host of biotic and abiotic factors affecting each of these phenomenon during the regeneration phase also fall under the domain of seed ecology. The seed production shows spatial and temporal variation due to change in climate, nutrient availability, plant density, population structure, pollination rates, and level of defoliation. Therefore, mast seeding events in the alternate years are observed in many tropical tree species (Crawley 1992, Barik *et al.* 1996b). The production of seed follows wide dispersal that is very crucial for seed germination, seedling establishment and growth. Different workers have studied various facets of seed dispersal. Diverse modes of seed dispersal ranging from nutritious and colorful fruits to attract animal dispersers, to fruits that explode and shoot the seeds several metres away have been studied (Harper 1977, Schupp and Fuentes 1995, Nathan and Muller-Landau 2000). Others have also reported various mechanisms of secondary dispersal by animals and birds (Hammond *et al.* 1996, Hammond and Brown 1995, Hegde *et al.* 1991, Campos and Ojeda 1997, Dalling *et al.* 1998, Wenny 2000a,b) and primary dispersal by wind (Howe and Smallwood 1982, van der Pijl 1982, Jurado *et al.* 1991, Peroni 1994, Muralikrishna and Chandrashekar 1997, Ganeshaiyah and Uma Shaanker 1991, Bhuyan *et al.* 2000, Osada *et al.* 2001). The enormous amount of energy

spent on seed dispersal mechanism suggests that dispersal is of critical importance to the fitness of the resulting seedling. Two advantages of seed dispersal have been suggested: (i) seed dispersal increases the probability of encountering suitable sites for the establishment and subsequent development and, (ii) seed dispersal helps escape higher probability of mortality below the parent tree (Howe and Smallwood 1982). Connell (1971) and Janzen (1970) advocated that seed density should decrease with increasing distance from the tree.

After dispersal, the seed has to persist in the soil seed bank till it gets the favourable environmental conditions for germination. Seed germination and seedling emergence is affected by several physical factors such as litter (Santos and Valio 2002), soil surface conditions, microhabitat, soil physical and chemical characteristics and creation of gaps, that ameliorates the microenvironment for several species (Alvarez-Buylla and Martinez-Ramos 1990, Ellison *et al.* 1993, Kyereh *et al.* 1999, Pena-Claros 2001, Raich and Gong 1990, Rose 2000, van Rheenen *et al.* 2004). The biotic factors such as predation by mammals, insects and fungi may kill the seed before it germinates (Blate *et al.* 1998, Hammond *et al.* 1999, Notman and Gorchov 2001, Pena-Claros 2001, Zagt 1997). The regeneration of plants from seed depends on seeds being in the right place at the right time. They must also be in the right physiological state to germinate and establish seedlings, perhaps within a limited period when there is a good chance of regeneration. Thus, long seed viability period of a particular species increases its chances of survival. Several investigations reveal that in the disturbed tropical forests, the soil seed banks play a crucial role in regeneration following the disturbances (Bell 1970, Liew 1973, Hall and Swaine 1980, Hopkins and Graham 1983, Putz and Appanah 1987).

For studying seed ecology, 5 species were selected based on their ecological dominance (*Alangium chinense*), threatened and endemic category (*Shorea assamica*), economic importance (*Spondias axillaris*, *Sapindus mukkorossi*) and cultural importance (*Mesua ferrea*). *Alangium chinense* was found in secondary forest stand SF3; *Sapindus mukkorossi* in the primary forest stand PF1 and the secondary forest stands SF1 and SF3; *Spondias axillaris* in the primary forest stand PF1 and the secondary forest stand SF3; *Mesua ferrea* in the primary forest stand PF2 and *Shorea assamica* in the primary forest stands PF1, PF2 and the secondary forest stand SF1. Based on the findings, an attempt has been made to explain the poor regeneration of *Mesua ferrea* and *Shorea assamica*, and the better regeneration of *Alangium chinense*, *Spondias axillaris* and *Sapindus mukkorossi* in the secondary forests.

6.2 Methodology

Phenology of the study species

Ten individuals of each species were selected in the respective forest stands during January, 2003 for studying the phenological behaviour. Qualitative (time of active shoot growth, flowering, fruiting and leaf fall/leaf flush) and quantitative data (flower and fruit production) on vegetative and reproductive behaviour of the species were collected through periodical observations.

Estimation of flower and fruit production

For estimation of flower and fruit production, 5 fruiting trees of each species in different girth classes were selected and tagged. However, in case of *Spondias axillaris* and *Shorea assamica* the individuals could not be differentiated into different girth classes as they were having more or less uniform GBH. The numbers of flowers and fruits produced by

these marked trees were estimated for three consecutive years (2002-2004). Flower bud count was taken as a criterion to estimate the flower production. The fruits were counted on the tree itself just before maturity. Since dispersal of fruits starts during maturation on the tree itself, fruit production estimates made on the initial stage of maturation represented the total fruit production including those dispersed during the maturation phase.

The flower and fruit production for each tree of the selected species was estimated following Barik *et al.* (1996b). Total flower/fruit production = total number of branches x mean number of sub-branches per main branch x mean number of inflorescences per sub-branch x mean number of flower buds/fruits per inflorescence.

For each tree of the selected species, mean number of inflorescence per branch was calculated from a sample of 10 branches and mean number of flower buds/fruits per inflorescence was calculated from a sample of 50 inflorescences. The data were pooled for each GBH class, each stand and each year, and ANOVA was performed to test the effect of these factors on flower/fruit production. Flower abortion was estimated by subtracting the fruit production from flower production value in each case.

Average seed weight was determined from a composite sample of 500 fresh seeds collected from each of the marked trees. Seeds collected from different sites were subjected to Kolmogorov Smirnov's test for assessing normality of seed weight distributions.

Seed dispersal

Primary dispersal of seeds

For seed dispersal and predation studies, 5 sample fruiting trees of the selected species were marked in the respective stands where the species occurred. The trees marked for

this study were growing at least 100 m apart and no other individual of the same species was present in this distance range. Fruit dispersal was studied in concentric circles around each fruiting tree spaced at 5 m radial increments beyond the crown radius. The fruits falling under the tree crown were not taken into account in the fruit dispersal study. The first of the concentric circles had a radius of 5 m and the maximum radius considered was 45 m. The circles were visited at alternate days over a period of 20 days during the peak period of fruit-fall. During each visit, fruits in all circles were collected and counted separately. The dispersal was expressed as number of fruits per 100 m². Suitable regression models (Zar 1974) were developed to establish the relationship between dispersal distance and number of fruits dispersed.

Studying *in situ* seed dispersal for *Shorea assamica* was not possible as there were chances of experimental and execution error due to loss of marked seeds, because of anemochorous nature of the seed. So, marked samaras of different weights were released from heights of 15 m and 30 m respectively and observations on their settling time and dispersal distance was taken using a stop watch and a measuring tape. Along with it, the wind velocity was also recorded using an anemometer each time a seed was released. Observations were made on 180 seeds of different weights. Correlations were made to test inter-relationships between seed weight, vertical settling time, wing area, wing loading, dispersal distance and height. Wing loading was calculated as surface area of wings divided by the weight of the seed (Green 1980). Surface area of the wings was determined using a leaf area meter after the simulated experiment was over. A one-way ANOVA was made to see the effect of height on the dispersal distance keeping wind

velocity as a covariate. Pearsons' correlation was calculated to study the correlation amongst the variables.

Post-dispersal fate of seeds

Experimental assessment of the fractions of seed lost to predation and transport is very difficult (Van Tooren 1988). Thus, the term 'disappearance' used in this experiment includes the fruit loss due to predation as well as to transport and dispersal by animals and run-off (Barik *et al.* 1996b). Five 1 m × 1 m fruit traps made of nylon mesh of size 2 mm were laid at random under the tree crown of each of the 5 marked trees at the beginning of fruit-fall and were visited until the completion of fruit shedding. All the fruits in each trap were counted. The undamaged fruits were separated from those eaten by insects, rodents, ungulates, squirrels and birds. The difference between total fruit production and the undamaged fruits that fell beneath the tree crown represented the fraction of fruit population disappearing during the fruit-fall period. The fate of the undamaged fruits after fruit fall was studied by placing 50 fruits in each of the five 1 m x 1 m fruit traps beneath each tree. The plots were visited at 7-day intervals upto 35 days. On each observation date, the numbers of dormant/rotten/germinated fruits and those that had disappeared were noted. The percentage of fruits in each case was determined and the means (n = 5 trees) for respective stands was calculated.

Assessment of soil seed bank of selected species

To assess the fate of remaining seeds of *Alangium chinense*, *Spondias axillaris*, *Sapindus mukkorossi* and *Mesua ferrea* after dispersal/disappearance of fruits during the post-fruit fall period, seed banks were estimated beneath the five marked trees in the respective sites before the next seed fall. The seeds of the selected species usually remain above and

below the litter layer. However, not to miss any seeds in the soil seed bank, the seeds were searched upto 10 cm of soil depth. To study the seed bank, five 1 m x 1 m quadrats were randomly laid in each concentric circle with radii of 5, 10, 15, 20, 25, 30, 35, 40, 45 m from the base of the fruiting tree. The seeds were collected from each quadrat and total seed bank was computed for each marked tree during 2003 and 2004.

Seed viability

Seed viability of the species was determined using the tetrazolium (TTZ) assay (International Seed Testing Association 1993) and/or germination trials. For instance, the seeds of *Shorea assamica* and *Mesua ferrea* were tested for viability using TTZ test only. For the tetrazolium assay the embryo-cum-endosperm fractions of 15-20 seeds per species were extracted from the associated fruit/seed structures, and placed in a 1% aqueous solution of 2,3,5-triphenyl tetrazolium chloride for 48 hours at 25 °C. Embryos were scored as viable if stained red/pink. Germination trial was, however, used for *Alangium chinense*, *Spondias axillaris* and *Sapindus mukkorossi* due to their hard seed coat; and was conducted using samples of 15-20 whole seeds per species placed in a germination tray with 3-4 cm thick layer of garden soil moistened regularly with tap water. Trays for *Alangium chinense* were placed in 80% full sun due to their light demanding nature. Seeds were first tested for viability at 7-10 days intervals for first two months, and then at bi-monthly intervals for next 1 year.

Seed germination

In situ seed germination test was undertaken in November-December, 2003 (for *Alangium chinense* and *Mesua ferrea*) and February-March, 2004 (for *Sapindus mukkorossi*, *Spondias axillaris* and *Shorea assamica*) to study the effect of forest floor

(litter depth) and canopy condition on seed germination of selected species in the primary and secondary forest stands. Seeds of selected species were collected from the parent tree and un-damaged seeds were separated from the damaged ones by floatation method. 100 seeds of heavy weight category were selected and sown in each treatment i.e. above litter, under litter (3-4 cm depth) and in a cleared plot of size 5 x 5 m dimension. The plots were covered with nylon mesh of size 2 mm to avoid predation of the seeds but to allow light and air to pass through it. Seeds were considered germinated with the emergence of 2 mm radicle and the observations were made till the seed germination ceased.

Ex situ germination test in the nethouse was conducted to study the effect of seed weight and light intensity on seed germination of the selected species. Prior to that, seeds of the selected species were weighed using an electronic balance and graded into three weight categories i.e. light-, moderate- and heavy-weight. The seeds were sown under three light conditions in the nursery viz., low (25 %), medium (50 %) and high (75 %) light, to study the effect of different light intensities and seed weight categories on seed germination. The light conditions were created through shading with black and white cloths. Seeds were sown separately at 3-5 cm depth in polythene bags of 20 x 17 cm size, filled with garden soil. The texture was sandy loam with pH 4.9, 0.29% nitrogen and 4.2% organic matter. Each bag was supplied with 150 ml tap water at intervals of 3-4 days to prevent drying of the soil. Light intensity was measured using a lux meter. Germination was characterized as emergence of 1 mm long radicle.

Effect of animal grazing on seed germination: To study the effect of animal grazing on seed germination, regurgitated seeds of *Sapindus mukkorossi* and *Spondias axillaris* were collected from the primary and secondary forests. The seeds were then tested for viability

and germination in the nethouse. Seeds obtained from fruits not consumed by the animals were used as control.

6.3 Results

Ecological characteristics of selected tree species

The ecological characteristics such as shade tolerance, successional status, fruiting period, fruit type, colour in maturity, dispersal agents, seed weight and seed germination type are presented in Table 6.1.

Phenology of the study species

The various phenological events like dolichoblast vegetative growth (DVG), flower bud formation, flowering, fruit set, seed dispersal and leaf flushing have been depicted in Figure 6.1. *Alangium chinense* strictly followed a sequential order of one phenological event followed by the other with least overlapping between any two events. *Spondias axillaris* and *Sapindus mukkorossi* fruit setting overlapped with leaf flush, particularly during late winter. But in case of *Mesua ferrea*, there were two dolichoblast vegetative growth (DVG) phases in a year, one during February-April and another during August-October, and seed dispersal in October (Figure 6.1). Fruit set to fruit maturation takes much longer time in *Mesua ferrea* than the other study species. In *Shorea assamica*, DVG followed leaf flushing and also overlapped fruit set and seed dispersal during February-April.

Table 6.1. Ecological characteristics of the tree species selected for the study

Name of species	Shade tolerance	Successional status	Fruiting period	Fruit type	Colour in maturity	Dispersal agent(s)	Seed wt. (g)	Germination type
<i>Alangium chinense</i>	Low	Early	July-Sep	Drupe	Black	Birds	0.14±0.002	Hypogeal
<i>Sapindus mukorossi</i>	Medium	Intermediate	Nov-Mar	Drupe	Brown	Ungulate	2.36±0.02	Hypogeal
<i>Spondias axillaris</i>	High	Intermediate	Nov-Feb	Drupe	Yellow	Squirrels/ ungulates	2.46±0.03	Epigeal
<i>Shorea assamica</i>	High	Climax	Dec-Mar	Samara	Brown	Wind	1.60±0.04	Hypogeal
<i>Mesua ferrea</i>	High	Climax	Mar-Oct	Capsule	Brown	Gravity	4.69±0.38	Hypogeal

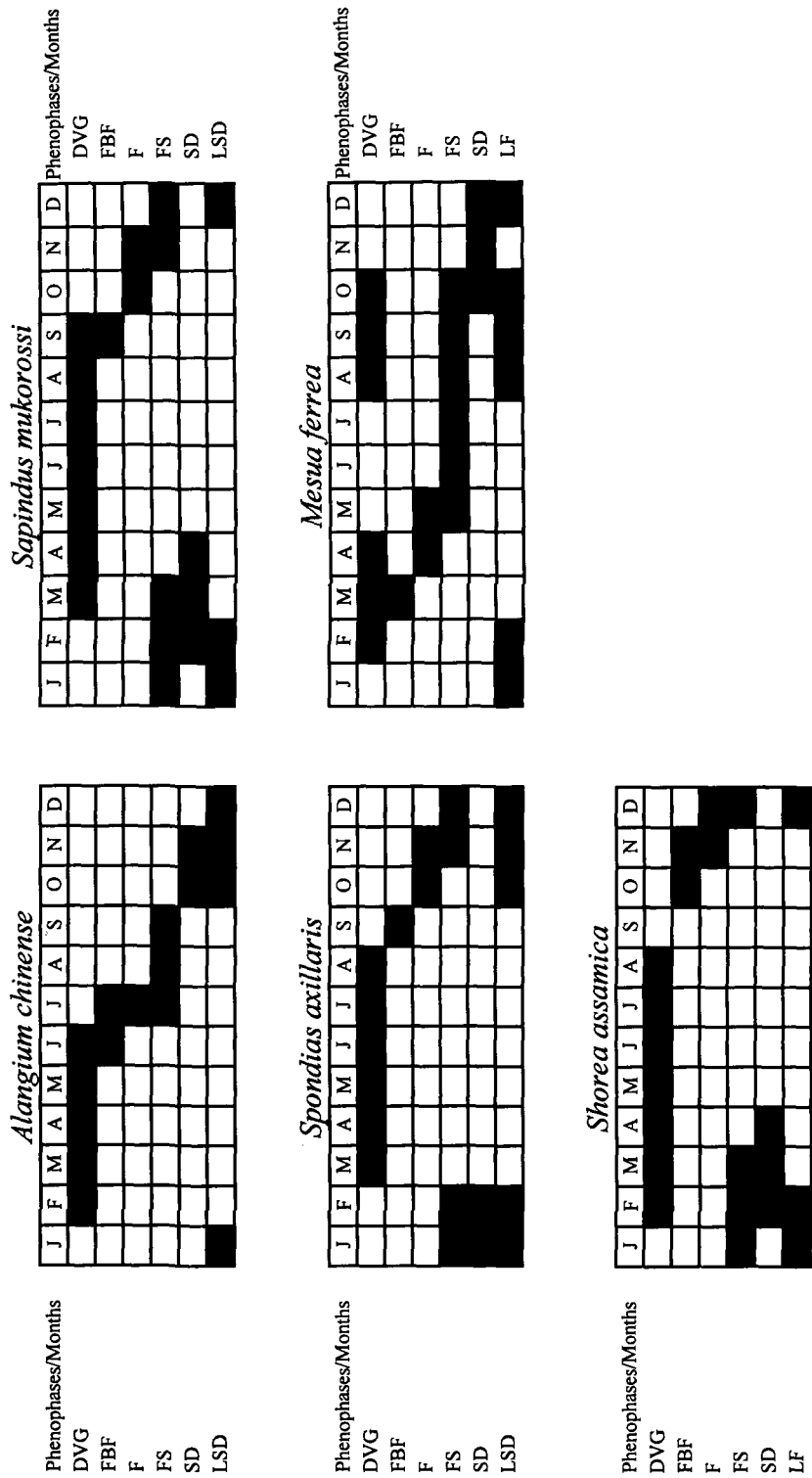


Figure 6.1. Phenological observations on the study species. DVG- dolichoblast vegetative growth, FBF- flower bud formation, F- flowering, FS- fruit setting, SD- seed dispersal, LSD- leaf shedding of dolichoblasts, LF- leaf flushing of dolichoblasts

Flower and fruit production

Table 6.2 shows the mean flower production, fruit production and flower abortion along with their variances across GBH, stands and years.

The number of flower and fruit produced in *Alangium chinense* was significantly higher ($P<0.05$) in the year 2003 than the years 2002 and 2004. The number of aborted flowers was the highest in the year 2004. Flower production varied significantly across girth classes ($P<0.001$).

The mean flower and fruit production was higher in the secondary forest stand compared to the primary forest stand for *Sapindus mukkorossi*. The percentage of flower abortion was higher (83%) in the primary forest stand than the secondary forest stands. Amongst the secondary forest stands, flower and fruit production was highest in the stand SF3. Fruit production varied significantly across GBH and stands, whereas flower production significantly varied only across GBH. But flower abortion varied significantly across both GBH and stands.

For *Spondias axillaris*, both flower and fruit production was higher in the secondary forest (SF3) as compared to the primary forest (PF1). The flower abortion was also high in the stand SF3. Fruit production varied significantly across stands ($P<0.05$).

In case of *Mesua ferrea*, both flower and fruit production was highest in the year 2003. The fruit production across the years varied significantly ($P<0.05$). The flower as well as fruit production across GBH classes also varied significantly ($P<0.001$).

In *Shorea assamica*, the flower and fruit production was significantly higher in the primary forest as compared to the secondary forests ($P<0.001$). Flower abortion was significantly higher ($P<0.05$) in the secondary forests (68-71%).

Table 6.2. Mean (\pm SD) of flower production, fruit production and flower abortion across stands and years irrespective of girth classes. F-ratios show their variances across GBH, stands and year

Name of species	Stands	2002			2003			2004			F-ratios
		No. of flowers	No. of fruits	Abortion (%)	No. of flowers	No. of fruits	Abortion (%)	No. of flowers	No. of fruits	Abortion (%)	
<i>Alangium chinense</i>	SF3	10120 \pm 4742	8260 \pm 4259	20	11695 \pm 5981	9681 \pm 5379	20	8547 \pm 4504	4423 \pm 2237	48	GBH: Fl - 122.0**, Fr - 24.1, Ab - 0.69ns Year: Fl - 0.8ns, Fr - 3.8*, Ab - 48.8**
	PF1	6526 \pm 3307	2697 \pm 1626	60	8545 \pm 3698	3045 \pm 1632	66	10100 \pm 4781	1520 \pm 642	83	GBH: Fl - 33.9**, Fr - 11.6**, Ab - 2.4* Stand: Fl - 2.2ns, Fr - 7.1*, Ab - 12.1** Year: Fl - 0.48ns, Fr - 0.02ns, Ab - 0.56ns
<i>Spondias axillaris</i>	SF1	8097 \pm 4647	3886 \pm 2231	52	11473 \pm 4740	4933 \pm 2038	57	10330 \pm 4748	5805 \pm 3070	43	Stand: Fl - 2.2ns, Fr - 7.1*, Ab - 12.1** Year: Fl - 0.48ns, Fr - 0.02ns, Ab - 0.56ns
	SF3	12659 \pm 5411	6076 \pm 2597	52	12921 \pm 5106	5424 \pm 2358	58	11919 \pm 4634	5648 \pm 1750	51	Stand: Fl - 1.3ns, Fr - 9.3*, Ab - 1.1ns Year: Fl - 2.0ns, Fr - 0.4ns, Ab - 2.3ns
<i>Mesua ferrea</i>	PF2	1020 \pm 551	842 \pm 484	18	1240 \pm 578	1057 \pm 514	16	1127 \pm 524	497 \pm 246	56	GBH: Fl - 300.3**, Fr - 26.0**, Ab - 0.1ns Year: Fl - 0.3ns, Fr - 3.9*, Ab - 126.0**
	PF1	17761 \pm 1249	9584 \pm 462	46	18924 \pm 721	10174 \pm 963	46	19576 \pm 2228	9933 \pm 77	49	Stand: Fl - 16.2**, Fr - 24.7**, Ab - 6.9* Year: Fl - 0.5ns, Fr - 2.1ns, Ab - 2.1ns
<i>Shorea assamica</i>	PF2	14436 \pm 2109	7458 \pm 1314	48	14425 \pm 3302	9387 \pm 506	32	13378 \pm 1038	7499 \pm 2036	43	Stand: Fl - 16.2**, Fr - 24.7**, Ab - 6.9* Year: Fl - 0.5ns, Fr - 2.1ns, Ab - 2.1ns
	SF1	13955 \pm 2124	4480 \pm 177	68	14869 \pm 3527	7442 \pm 310	48	10278 \pm 168	2993 \pm 657	71	Stand: Fl - 16.2**, Fr - 24.7**, Ab - 6.9* Year: Fl - 0.5ns, Fr - 2.1ns, Ab - 2.1ns

*P<0.05, **P<0.001, ns - not significant, Fl - Flowers, Fr - Fruits and Ab - Flower abortion

Seed dispersal

Primary seed dispersal

Primary seed dispersal was considered as the spatial distribution of the seeds around the parent tree due to gravity. Regression models for spatial distribution of seeds of *Alangium chinense* shows a logarithmic relationship of seed density (per 100m²) with increasing distance from the parent tree, while *Sapindus mukkorossi*, *Spondias axillaris* and *Mesua ferrea* exhibits significant polynomial relationship with distance as shown in Table 6.4.

Table 6.3. Regression models for primary seed dispersal of the selected species with seed density as a function of dispersal distance (n=10 for each species)

Species	Regression model	r	p	Range of 'x'
<i>Alangium chinense</i>	$Y = -408.05\ln(X) + 1450.9$	0.90	0.001	5-50
<i>Sapindus mukkorossi</i>	$Y = 0.28X^2 - 22.62X + 426.32$	0.98	0.001	5-50
<i>Spondias axillaris</i>	$Y = 0.14X^2 - 11.32X + 220.61$	0.97	0.001	5-50
<i>Mesua ferrea</i>	$Y = 0.14X^2 - 11.76X + 233.18$	0.97	0.001	5-50

'y' seed density per 100m² and 'x' dispersal distance

In the wind dispersed dipterocarp species *Shorea assamica*, height significantly affected settling time (F=32.62, N=180, P<0.001) as well as dispersal distance (F=56.89, N=180, P<0.001). Pearsons' correlation coefficients showed significant negative relationship of seed weight with settling time and wing loading (p<0.05; one-tailed), whilst significant positive relationships were established between wing area and settling time and seed weight, dispersal distance with settling time and wing area, and wing loading with settling time, seed weight and wing area (Table 6.4).

Table 6.4. Pearsons' correlation matrix for settling time (ST), seed weight (SW), wing area (WA), dispersal distance (DIS), wind velocity (WV) and wing loading (WL) for samaras of *Shorea assamica* (n=180)

	ST	SW	WA	DIS	WV
SW	-0.27*	1.00			
WA	0.20*	0.29*	1.00		
DIS	0.66*	-0.09	0.21*	1.00	
WV	-0.03	-0.05	-0.02	0.01	1.00
WL	0.38*	-0.76*	0.30*	0.18*	0.05

*P<0.05

Post-dispersal fate of seeds

In case of *Alangium chinense*, 44% of the seeds were dormant, while 36% disappeared. A small portion of the total seeds (8%) germinated. A large population of *S. mukkorossi* seeds (76%) in the secondary forest stands remained either dormant or disappeared or rotten. Only a small portion (4-24%) germinated. In the primary forest 83% of the fruits disappeared. The seed disappearance could be due to grazing of ungulates (*Cervus unicolor*) on the pulp of *S. mukkorossi*. In case of *Spondias axillaris*, 78-85% of the fruits disappeared, and 9-10% rotted, leaving only 5-9% for germination (Figure 6.2). Fruits of *Spondias axillaris* are consumed by squirrels (*Calloscilurus gerdoni*) in the tree itself, while fruits lying on the ground were predated by barking deer (*Muntiacus muntjac*) and sambhar (*Cervus unicolor*).

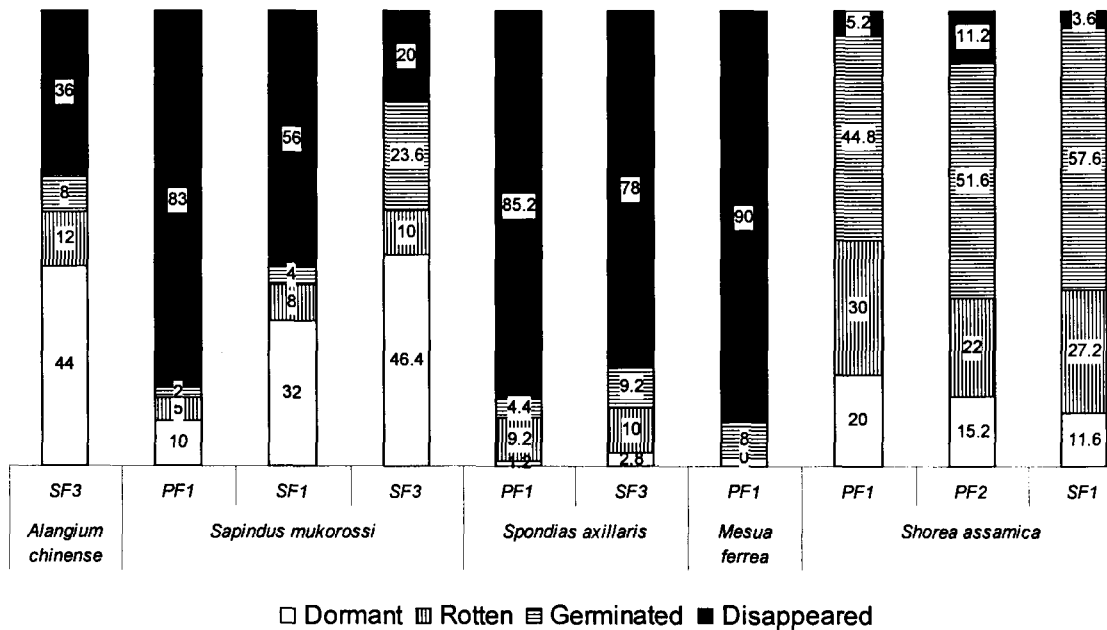


Figure 6.2. Seed fate of selected species in different forest stands (Values shown in bars are in percent)

About 90% of the seeds of *Mesua ferrea* were predated by wild boar and sambhar; whilst 8% germinated, the remaining 2% were dormant. In case of *Shorea assamica*, 45-58% of the seeds germinated, while 4-11% disappeared, 22-30% of the seeds rotted. About 12-20% however, remained dormant (Figure 6.2).

Soil seed bank

The size of soil seed bank for *Alangium chinense* varied significantly ($P < 0.001$) with the girth size (age). The soil seed bank in *Spondias axillaris* significantly varied along different stands and tree girth sizes (Table 6.5). The size of soil seed bank of *S. axillaris* was significantly higher in the secondary forest than the primary forest during the year 2004 (Figure 6.3). In *Mesua ferrea*, the seed bank varied significantly along different years only. The size of soil seed bank differed between species. The size of soil seed bank in *A. chinense* was (30-32) m^{-2} , for *S. mukkorossi* was (15-19) m^{-2} , for *S. axillaris* was (9-22) m^{-2} and for *M. ferrea* was (11-17) m^{-2} .

Table 6.5. ANOVA for variation in seed bank across tree girth size, stand and year

Source of variation	F-ratio			
	<i>A. chinense</i>	<i>S. mukkorossi</i>	<i>S. axillaris</i>	<i>M. ferrea</i>
Girth size	14.349***	2.940 ^{ns}	13.736***	0.979 ^{ns}
Stands	-	1.640 ^{ns}	8.196*	-
Year	0.421 ^{ns}	0.169 ^{ns}	3.563 ^{ns}	5.377*
Girth size x stand	-	1.770 ^{ns}	3.629*	-
Stand x year	-	5.051*	11.544***	-
Girth size x year	0.004 ^{ns}	2.836 ^{ns}	11.618***	2.128 ^{ns}
Girth size x stand x year	-	1.152 ^{ns}	3.744*	-

* $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$, ns – not significant

Seed viability

Seed viability of the selected species decreased consistently across a temporal scale. *Shorea assamica*, *Mesua ferrea* and *Spondias axillaris* recorded viability periods of 14 days, 48 days and 36 days respectively. Propagules of *Alangium chinense* and *Sapindus mukkorossi* maintained viability of 65 and 200 days respectively.

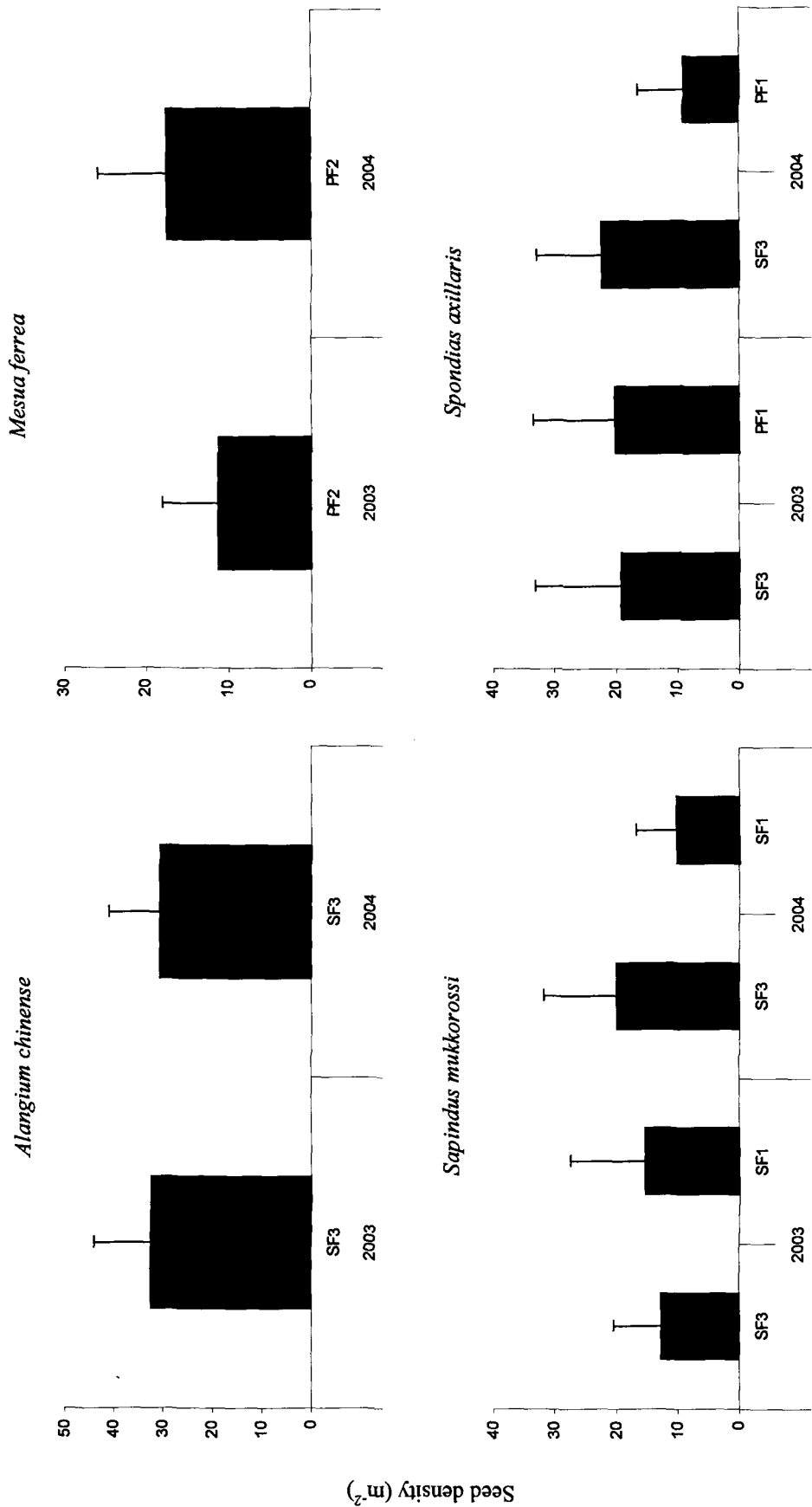


Figure 6.3. Density of seeds of the selected species in the soil seed bank in the primary and secondary forest stands (Mean and SD; n = 10)

Seed germination

In situ seed germination

Seeds of *Alangium chinense* and *Sapindus mukkorossi* germinated well in the secondary forests, but in case of *Mesua ferrea*, *Shorea assamica* and *Spondias axillaris*, germination was better in the primary forest (Figure 6.4). Stand quality characterised by canopy openness significantly affected seed germination in all the species ($P \leq 0.001$), whereas litter depth did not have any effect over seed germination in all the species studied (Table 6.6).

Table 6.6. ANOVA for the effects of stand quality and litter depth both on seed germination of selected species

Source of variation	F-values				
	<i>A. chinense</i>	<i>S. mukkorossi</i>	<i>S. axillaris</i>	<i>M. ferrea</i>	<i>S. assamica</i>
Stand quality	17.82***	22.18***	21.43***	101.94***	43.59***
Litter depth	2.38ns	3.23ns	3.24ns	0.63ns	1.52ns
Stand quality x Litter depth	31.04***	91.79***	141.62***	8.56**	105.08***

* $P < 0.05$, ** $P < 0.005$, *** $P < 0.001$, ns – not significant

Ex situ seed germination

The general trend showed that the percentage of seed germination was more in case of the heavier seeds, as compared to the lighter seeds (Figure 6.5) in all the species but, statistically seed germination in all the study species was significantly affected by differences in light levels ($p < 0.05$ and $p < 0.005$) and not by seed weight (except *Shorea assamica* - $P < 0.05$) (Table 6.7). Seeds of *Alangium chinense* revealed stronger preference for light. For instance, the germination was highest when exposed to 75% light.

Table 6.7. ANOVA for the effect of light intensity and seed weight on seed germination of the selected species

Source of Variation	F-values				
	<i>A. chinense</i>	<i>S. mukkorossi</i>	<i>S. axillaris</i>	<i>M. ferrea</i>	<i>S. assamica</i>
Light	19.80**	6.48*	5.21*	7.18*	0.46 ^{ns}
Seed weight	0.20 ^{ns}	0.84 ^{ns}	0.98 ^{ns}	1.50 ^{ns}	10.42*

* $P < 0.05$, ** $P < 0.005$, ns – not significant

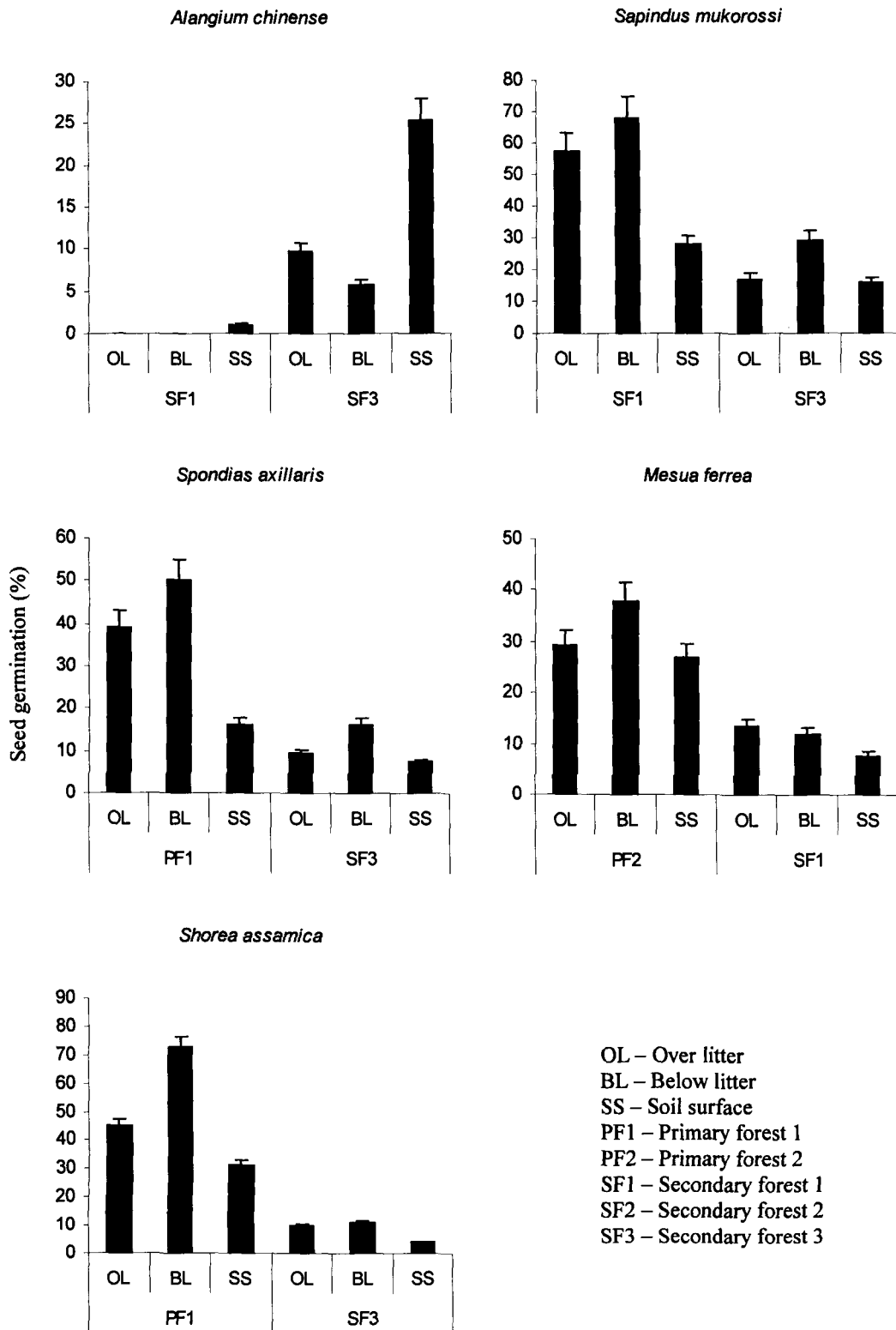


Figure 6.4. *In situ* seed germination under different treatments

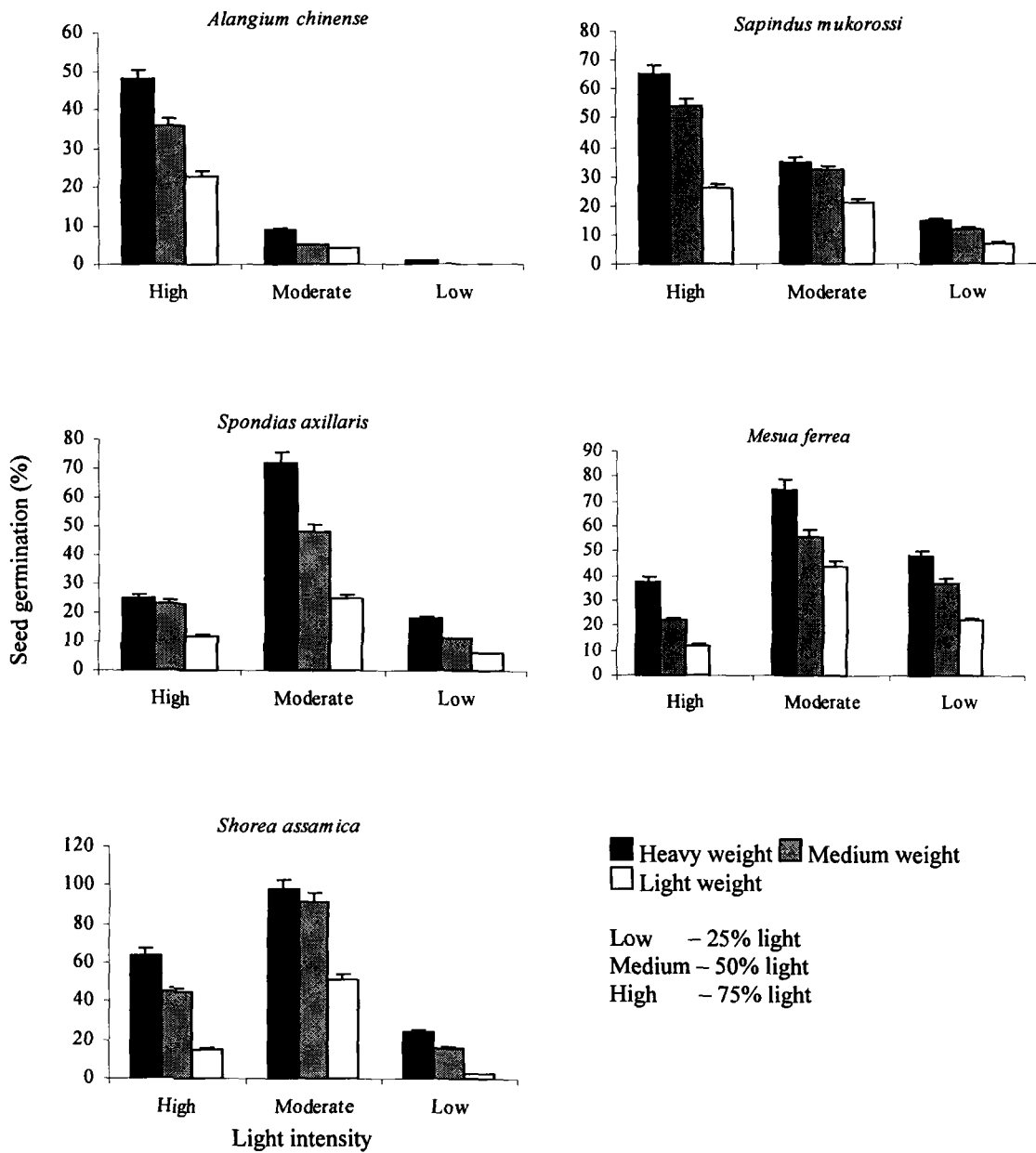


Figure 6.5. Seed germination of selected species across different light intensities and seed categories

Effect of animal grazing on seed germination

Seed germination of *Spondias axillaris* was significantly lower for regurgitated seeds as compared to the unregurgitated seeds. But in case of *Sapindus mukkorossi*, there was no significant difference in seed germination.

Table 6.8. Effect of animal grazing on seed germination

Name of species	Germination (%)	
	Regurgitated seeds	Un-regurgitated seeds
<i>Sapindus mukkorossi</i>	80	82
<i>Spondias axillaris</i>	5	75

6.4 Discussion

Phenological behaviour of the study species showed differences as well as similarities among each other in patterns of vegetative growth and reproductive development. Comparisons among the species show that the period of overlapping between primary shoot growth, flower bud formation and flowering increased with an increase in seed/fruit size. In this regard, *Alangium chinense* ($0.14 \pm 0.002\text{g}$) with different phenophases maintained a strict chronology of events; whereas in *Sapindus mukkorossi*, *Spondias axillaris* and *Shorea assamica* there were some overlapping in different phenophases (Figure 6.1). The phenological events of *Mesua ferrea* ($4.69 \pm 0.38\text{g}$) recorded greater overlapping i.e. vegetative phases coincided with reproductive development. In this regard it could be said that species growing in the unstable or harsh environments use the available resources faster to complete their reproductive cycle in a shorter period of time as compared to the species growing in more stable environments. In this process they spend less energy on biomass and shift more energy on producing more number of reproductive units. Similarly, Castro-Diez *et al.* (2003b) found in some woody species of the Mediterranean region that species with big fruits/seeds exhibit a high degree of

overlap between primary shoot growth, flower bud formation and flowering, which has been related to being negatively selected for by the risk of frosts, and by the internal competition with fruit maturation, respectively. The three phenophases would have been forced to occur simultaneously within a shorter period and to share the available resources. On the contrary, the shorter length of the fruit setting period in small-fruited species leaves a longer period to complete primary shoot growth, flower bud formation and flowering so that they can be protracted to reduce competition between them (Castro-Diez *et al.* 2003b).

In the present study, species with bigger reproductive organs (in *Mesua ferrea*) required longer periods to ripen compared to other species. On the contrary, *Mesua ferrea* had a shorter vegetative growth period compared to other species. Similar observations were made by Primack (1985) in trees of Florida, Eriksson and Ehrlen (1991) in north-European plants and by Castro-Diez *et al.* (2003b) among Mediterranean woody species. This could be tentatively explained following Castro-Diez *et al.* (2003b) that the carbon allocation shift from vegetative to reproductive meristem would occur earlier in species of bigger fruits or seeds, thus affecting the period of vegetative growth.

In the study species, flowering and fruiting occurred at the end of the dry season. This might be due to greater insolation and photosynthesis during dry season or by enhancement of germination and seedling survival by adjusting fruiting to precede the beginning of the wet season (van Schaik *et al.* 1993). But fruit maturation and dispersal in *Shorea assamica* occurred just before the onset of rainy season, which might be an adaptation of this species in compensating its low viability period. Based on the contention of Murali (1997), this could further be explained that species fruiting during

rainy season had lighter seeds and shorter viability periods comparing to species which fruit during the winter season. Such variations could well be adaptations to the time of dispersal, time of moisture availability in the habitat and seedling survival and thus explains the reproductive behaviour of *Shorea assamica*. Other species except *Alangium chinense* had heavier fruits and seeds and hence registered comparatively higher viability. It could be argued that the species due to its nature of occurring in the disturbed environment needs higher intensity of light (personal observation) for germination that is accomplished only in the dry season when forest canopy is relatively open and, increases the chances of survival.

Flower and fruit production varied significantly between girth classes for all the species studied. Overall, production increased with girth sizes. This could be attributed to the larger crown size of the individuals of higher girth classes (Bhuyan 2002). Further, flower and fruit production is very much affected by the climatic conditions like rainfall and insolation that guides the temporal variation *per se*. Stand factor significantly affected production in *Spondias axillaris* that had individuals producing more number of fruits/seeds in the secondary forests comparing to the primary forest. This is in conformity with Barik *et al.* (1996b) who attributed greater fruit production to increased availability of sunlight in the disturbed stands. For instance, high light intensity may elevate bud temperature, which may lead to increase in the concentrations of growth regulators particularly gibberellins (Pharis and Kuo 1977, Ross *et al.* 1983), stimulating flowering and fruiting. Moreover, light regime associated with temporary water stress in disturbed stands is known to stimulate bud initiation in some forest trees (Kozlowski 1981).

Seed dispersal regulates the spatial arrangement and physical environment of seeds from which the next cohort of seedlings is selected. More so, post-dispersal seed removal plays an important role in determining the composition and density of tree recruitment (De Steven 1991, Hammond 1995, Meiners and Stiles 1997, Myster and Pickett 1993, Uhl *et al.* 1988, Whelan *et al.* 1991), which is further influenced by seed characteristics such as seed size, nutrient content, local abundance and handling time (Meiners and Stiles 1997). The pulp of fleshy fruits, with the soft, edible, nutritive tissues surrounding the seeds, is a primary resource for many frugivorous animals (Howe 1986), who expectedly regurgitate, defecate, spit out or otherwise drop undamaged seeds away from the parent plants thus acting as a dynamic link between the fruiting plant and the seed or seedling bank in natural communities. In the present study, seeds of *Spondias axillaris* were discarded after consumption of the pulp by the black tailed squirrel (*Calloscilurus gerdoni*), while the seeds of *Sapindus mukkorossi* and *Spondias axillaris* were regurgitated by the barking deer (*Muntiacus muntjac*) and sambhar (*Cervus unicolor*) in the primary and secondary forest stands except in SF3 which is closer to human habitations. Fruits of *Alangium chinense* were observed to be consumed by birds but the regurgitated seeds could not be traced. Fruits of *Mesua ferrea* were observed to be predated by wild boar (*Sus scrofa*) leaving meagre number of seeds on the forest floor for germination. Seeds of *Shorea assamica* were actively dispersed through wind; seed predation by hornbill (*Buceros bicornis*) however has been observed. In all the species incidences of fruit predation was more frequently observed in the primary and secondary forest stands except SF3. This could have significant effect over the dispersal pattern and soil seed bank of the selected species. A study carried out on the effect of successional

stage on seed removal of tropical rain forest tree species in the Bolivian Amazon revealed that seed removal rate decreased with increase in the age of successional community (Pena-Claros and de Boo 2002). Seed removal varied from 50-100 % depending on the species and 74-90 % depending on successional stage. The lower dispersal rates in the older stands were related to abundance of removal agents. The active removal agents in the younger successional stands were the rodents. On the contrary, seed removal in the present study expressed in terms of disappearance was more in the stands nearer to the primary forests and the removal agents were mainly ungulates and other arboreal mammals like squirrels. Thus, it can be said that seed dispersal would depend on the species type.

The post-dispersal seed fate experiment demonstrated that the percentage of disappeared seeds (probably due to predation or secondary dispersal) was greater for *Spondias axillaris*, *Mesua ferrea* and *Sapindus mukkorossi* in both primary as well as secondary forest stands (Figure 6.3). Willson (1992) pointed out that plant propagules are critical food resources for a variety of animal species, and especially the fleshy-fruits engage in mutualism with their dispersal agents. Many vertebrate populations rely on pulp of fleshy fruits as food for migration, breeding and winter maintenance. Thus, the dispersal of the propagule of fleshy fruits may depend on the quantity of the pulp. In general, density of animal-dispersed fruits of *Spondias axillaris*, *Mesua ferrea*, *Sapindus mukkorossi* and *Alangium chinense* were abundant near the parent tree.

Tropical rain forests of Southeast Asia are characterized by the dominance of members belonging to Dipterocarpaceae (Osada *et al.* 2001), which mostly comprises of wind dispersed species. The fruits germinate without dormancy (Whitmore 1984). Thus,

distance of primary dispersal by wind is of critical importance for the distribution of most dipterocarp species (Suzuki and Ashton 1996). In the present study, simulated seed dispersal in *Shorea assamica* (a threatened dipterocarp) showed that height (with wind velocity as a covariate) significantly affected settling time. But wind velocity alone didn't seem to have significant effect on dispersal (horizontal distance travelled from the tower in metres). Incidentally there was no stronger wind during the course of the experiment. Nevertheless, dipterocarps in general have heights ranging from 40-60m (Whitmore 1984) and wind velocity is much higher in the emergent layer than in the canopy and understorey layers in a tropical rain forest (Aoki *et al.* 1978). Thus, wind dispersal could play an important role in the distribution of the species. Nonetheless, seed weight showed negative correlations with settling time and dispersal distance which also corroborates with Bhuyan and Khan (2000). Hence, it is likely that seeds of *Shorea assamica* having lighter weight would be dispersed more widely than its heavier counterparts. But, the relationship between seed weight and seedling fitness is well established (Ganeshaiah and Shaanker 1991, Muralikrishna and Chandrashekar 1997, Arunachalam *et al.* 2003). Thus, there must be a tradeoff between dispersal-efficiency and seedling fitness which could shape the seed size and subsequently increase the chances of survival for the species.

Soil seed banks play an important role in maintaining the ecological and genetic diversity of forest communities (Thompson and Grime 1979) and in assuring community regeneration following disturbance (Houle and Phillips 1988) which is more applicable in regenerating secondary forests (Guariguata and Ostertag 2001). But, as intensity of land use increases, the potential of secondary forests to regenerate from soil-stored seed banks concurrently diminishes. The state of affairs could be worsened if there are irregularities

in the phenological behaviour of the remnant trees or there are frequent instances of fruit/seed predation. In the present study, soil seed bank of the dominant successional species *Alangium chinense* varied significantly spatially. But year-wise variation in soil seed bank could not be established mainly due to the more or less uniform fruit production. Spatial variation could be attributed to disappearance of the seeds as a result of predation (presumably by rodents and birds).

Seed bank of *Spondias axillaris* displayed a significant spatial variation within as well as across forest stands with less seed density in the primary forest compared to the primary forest. As the fruits of *Spondias axillaris* are a good source of food for the animals, possibility of the fruits being consumed by them is always inevitable. However, some of the fruits get hidden under the litter layer thus preventing the frugivores from noticing it. *Mesua ferrea* seed bank dynamics could be attributed to similar reasons.

In situ seed germination of the selected species was significantly affected by stand quality characterized by open or closed canopy. Seed germination was better in the secondary forest for *Alangium chinense* and *Sapindus mukkorossi*, while germination percentage for *Mesua ferrea*, *Shorea assamica* and *Spondias axillaris* was higher in the primary forests. This is also supported by the *ex situ* seed germination experiment which shows that seed germination of *Alangium chinense* and *Sapindus mukkorossi* was higher at high light intensity. While germination was highest for *Mesua ferrea*, *Shorea assamica* and *Spondias axillaris* at intermediate light intensity. In case of *Shorea assamica*, seed weight had a significant effect over seed germination. This is corroborated by the findings of Khan and Uma Shankar (2001) in *Quercus semiserrata* and Tripathi and Khan (1990) in *Quercus dealbata* and *Quercus griffithi*. The general trend shows that seed germination

percentage was more in case of seeds placed below litter. This could be attributed to the moisture content inside the litter which has helped the seed in germination.

From the above discussion it could be generalized that disturbance significantly affects the seed production, seed dispersal, seed bank as well as seed germination by creating a heterogeneous milieu of abiotic factors (by changing the microclimate) along with the biotic factors (chiefly the animal components).

Chapter 7

Seedling ecology

7.1 Introduction

Regeneration patterns and species composition of a forest community are intimately related to recruitment, establishment, and growth of seedlings on the forest floor. Ironically, the greatest selection pressure is also exerted during the seedling stage of tropical forest tree species. During this stage a high rate of mortality occurs due to several factors such as pathogenic fungi (Augspurger 1988), herbivores (Janzen 1970, Clark and Clark 1985, Ceccon *et al.* 2004), water stress (Rao *et al.* 1997, Khurana and Singh 2001, Lawrence 2001), nutrient limitation (Whitmore 1996, Ceccon *et al.* 2004), light limitation (Malcolm *et al.* 1996, Poorter and Oliver 2000, Barik *et al.* 1996a), and mechanical damage due to falling branches and leaves (Clark and Clark 1991, Scariot 2000). All these factors regulate the seedling populations which in turn determine the forest community structure.

Nonetheless, seedlings of tropical tree species are not distributed randomly in space, but to a certain extent show some degree of clumping (Alvarez-Buylla and Martinez-Ramos 1992, Kitajima and Augspurger 1989, Itoh *et al.* 1997, Forget *et al.* 1999, Hubbell *et al.* 1999, Nicotra *et al.* 1999). Spatial distribution of seedlings depends on certain factors as distribution of parent trees and presence of favorable micro-environmental factors like light, moisture and nutrients (Ulft 2004). Factors that influence the survivorship and recruitment of seedlings and saplings in natural forests are particularly important as they largely determine the ultimate species composition of the canopy (Harper 1977). Seedling establishment forms an important phase in the developmental stages of a tree seedling

and significantly determines the successful regeneration of a tree species. The establishment of seedlings occurs sometimes in the autonomous stage, after the seedling is independent of seed reserves and has grown sufficiently to have a relatively high survivorship. Garwood (1996) concluded that seedlings persisting at their compensation point with no new net growth are not established. In most of the silvicultural studies tree life have been supposed to start at a dbh of 10cm, despite the fact that trees spend considerable time in the seedling or sapling stage (Poorter 1998). Even the seedlings may take 50-70 years to attain a height of 3 m as reported by Zagt (1997).

The pioneer and long-lived pioneer species reportedly have higher relative growth rate than shade tolerant species (Veneklaas and Poorter 1998, Agyeman *et al.* 1999, George and Bazzaz 1999, Walters and Reich 2000). The better performance of pioneer species over the shade tolerant ones have been attributed to their higher photosynthetic capacities and high leaf turnover rates in high light (Kitajima 1994, Ellsworth and Reich 1996, Strauss-Debenedetti and Bazzaz 1996) and higher leaf area ratio in low light (Osunkoya *et al.* 1993, Kitajima 1994, Veneklaas and Poorter 1998). Thus, understanding of seedling survival, mortality, establishment and seedling growth is crucial for interpreting the processes that sustain forest ecosystems.

While studying the patterns of seedling establishment of different species and the factors affecting the establishment, the following two hypotheses have been tested in the present chapter: (i) whether the same species have differential response to the primary and secondary forest environment during the seedling establishment stage, and (ii) whether such differential response during seedling establishment phase holds key to the

differential species composition and community structure as observed in a primary and secondary forest.

7.2 Methods

Individuals of tree species with a height up to 1 m were considered as seedlings in the present study.

Seedling recruitment and population dynamics

For studying mortality, seedlings were marked at the two-leaved stage after germination. Seedling recruitment for the selected species was studied for two consecutive years and was studied by marking all the new seedlings with aluminium labels. New seedlings were considered to belong to the same cohort of the year in which they were first encountered. Seedlings earlier than that were of mixed ages, and were not considered a cohort and therefore kept out while calculating recruitment. The first year's tagged seedlings were then monitored over a period of one year and the causes of mortality were noted down. Plants that were damaged and re-sprouted were not considered dead. The mortality rate of the seedling populations was calculated following Condit *et al.* (1995) as:

$$\frac{\ln(N_0) - \ln(N_t)}{t}$$

where N_0 is the number of initial seedlings, N_t is the number of seedlings remaining alive at time t (month) and $\ln(N)$ is the natural logarithm of N . Mortality rates were calculated for the periods March-June 2003, June-September 2003, September-December 2003, December-March 2004, March-June 2004, June-September 2004 and September-December 2004 for *Sapindus mukkorossi*, *Spondias axillaris* and *Shorea assamica*. For *Alangium chinense* and *Mesua ferrea* the mortality rates were calculated for the periods

Oct 2002 - Jan 2003, Jan-Apr 2003, Apr-Jul 2003, Jul-Oct 2003, Oct 2003-Jan 2004, Jan-Apr 2004 and Apr-Jul 2004.

Relationship between age-specific mortality rate (Q_x) of seedling populations and micro-environmental factors (viz. moisture, temperature, light intensity, soil temperature, air temperature, relative humidity etc.) was analysed for partial correlation analysis using STATISTICA 6.0.

To study the effect of intraspecific competition during seedling stage below the parent tree on seedling survival of the selected tree species, newly recruited seedlings of the selected species around as well as beneath the canopy of the selected species in the respective sites were tagged and observed for mortality as well as survivorship at intervals of three months.

***In situ* seedling growth**

For studying seedling growth of the selected species, an experimental area of 1ha was demarcated in each stand and 5 permanent quadrats of dimensions 10 m x 10 m were randomly laid for each species during mid March to April 2003. Measurements on micro-environmental variables i.e. light intensity, relative humidity, air temperature, soil moisture, and soil temperature were taken in each of the quadrats in the morning (7.00 to 7.30 AM), noon (12.00 to 12.30 AM) and evening (4.00 to 4.30 PM) hours during each sampling. Light intensity was measured using lux meter. Relative humidity (%) and air temperature ($^{\circ}\text{C}$) was measured at ground level using a thermohygrometer. Moisture content (%) of soil upto 10 cm depth was determined by oven drying 10gms of soil at 105 $^{\circ}\text{C}$. Soil thermometer was used to measure soil temperature upto 10 cm depth. Litter thickness was measured by line intercept method (Mueller-Dombois and Ellenberg

1974). The mean value of three readings i.e. morning, noon and evening for each micro-environmental variable was statistically analyzed using two-way ANOVA to test the variation due to forest stands and seasons.

10 individuals of first year seedlings of the selected species i.e. *Alangium chinense*, *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* belonging to same cohort were labelled with aluminium tags with serial numbers punched on them in the respective forest stands in the 10 m x 10 m quadrats. Seedling growth was monitored at three months interval for a period of one year. *Alangium chinense*, *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* were labelled during the months June 2003. Non- destructive measurements were made on the seedlings for basal diameter, total height and leaf area at intervals of three months. Dead seedlings were excluded from these measurements. Basal diameter and seedling height were measured using a digital caliper and a metre scale respectively and leaf area using a portable leaf area meter (LICOR 3000A). Relative growth rate of the tagged seedlings were calculated according to Hunt (1982). Relative growth rates of the individual seedlings in terms of height (RGRH) and total leaf area (RGRA) were calculated as:

$$RGR (t_{n-1} - t_n) = [\ln S(t_n) - \ln S(t_{n-1})] t_n - t_{n-1}^{-1}$$

Where, S = the plant size, i.e. height (cm) or total leaf area (cm²) and t = time (months). One- and two-way ANOVA was performed to test the effect of sites and seasons on seedling growth in terms of leaf area increment and total height growth. Data for seedling height and leaf area were first log transformed before performing ANOVA to reduce the effect of extreme values.

Effect of light and nutrients on growth of seedlings

Net house experiment was carried out between May 2004 and January 2005 to determine the response of seedlings of the selected species to different nutrient (NPK) and light levels. Seedlings of *Alangium chinense*, *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* were raised in the nursery after germination between December 2003 and April 2004. Seedlings of the selected species derived from heavyweight category of seeds were used to study the effect of light and nutrients on the overall growth. Species-wise, the seedlings used in the study belonged to the same cohort and were approximately of uniform growth attributes (height and leaf area) when the experiment was started.

Experimental design

Seedlings of the selected species were placed under three light levels (viz. L₁-15%, L₂-45% and L₃-65% light), created inside the net house using black and white muslin cloth. In each light regime, seedlings of the selected species were separated into four blocks containing 5 seedlings each and treated with four fertilization levels. To make a complete fertilizer of NPK for use in the present experiment, Urea (46%N), single superphosphate (16% P) and muriate of potash (60% K) were mixed in the ratio of 565g-438g-117g. The amount of nutrients used in preparing the mixture of NPK was ascertained from the minimum value of available soil nutrients *i.e.* N, P and K in the primary and secondary forests taken together. The seedlings received nutrients at four different concentrations viz. N₁ – 5gms, N₂ – 15gms, N₃ – 25gms and N₄ – 35gms per seedling. Full doses of NPK were mixed with the secondary forest soil as basal dressing one week before planting the seedlings. Second and third doses of NPK of the above concentrations were administered

in September 2004 and December 2004 as top dressing. The mass of soil in each polybag was ≈ 1.125 kg. Seedlings were watered periodically to avoid soil moisture stress.

Data collection and analysis

Initial reading on seedling height, collar diameter and leaf area were taken on May 2004 and final readings were taken on January 2005. Collar diameter and seedling height were measured using a digital caliper and a metre scale respectively and leaf area using a portable leaf area meter (LICOR 3000A). At the end of the experiment all the plants were harvested and washed under tap water to remove the soil adhered to roots. Plant parts were separated into leaves, stem and root and their weight were taken for measuring the biomass accumulation in different parts.

Relative growth rates of the individual seedlings in terms of height (RGRH) and total leaf area (RGRA) were calculated following Hunt (1982) as:

$$\text{RGR } (t_{n-1} - t_n) = [\ln S(t_n) - \ln S(t_{n-1})] / t_n - t_{n-1}$$

Where, S = the plant size, i.e. height (cm) or total leaf area (cm^2) and t = time (months).

From the primary data following variables were derived: root mass ratio (RMR; root mass/total plant mass, in g g^{-1}), stem mass ratio (SMR; stem + petiole mass/total plant mass, in g g^{-1}), leaf mass ratio (LMR; leaf mass/total plant mass, g g^{-1}), specific leaf area (SLA; leaf area/leaf mass, $\text{m}^2 \text{kg}^{-1}$), leaf area ratio (LAR; leaf area/total plant mass, in $\text{m}^2 \text{kg}^{-1}$), leaf area root mass ratio (LARMR; total leaf area/root mass, in $\text{m}^2 \text{kg}^{-1}$) (Poorter 1999).

One- and two-way ANOVA was performed to determine the effect of nutrient and light levels on height, collar diameter and leaf area of the selected species. Data for seedling height and leaf area were first transformed to its natural logarithm before performing

ANOVA to reduce the effect of extreme values. Multiple regression analysis was performed to identify the most significant factor affecting seedling growth amongst the treatments. All statistical analysis was done on STATISTICA Ver. 6.0.

7.3 Results

Seedling recruitment and population dynamics

Seedling recruitment for *Sapindus mukkorossi* and *Spondias axillaris* was higher in the secondary forests than in the primary forests. For *Shorea assamica*, seedling recruitment was higher in the primary forest. Year wise, the seedling recruitment for all the species was higher in the year 2004 than in the year 2003 (Table 7.1).

Table 7.1. Seedling recruitment and mortality of the selected species in the primary and secondary forest stands

Species	Sites	Recruitment 2003	Recruitment 2004	Mortality (dx)
<i>Alangium chinense</i>	SF3	280	396	65.71
<i>Sapindus mukorossi</i>	PF1	105	134	81.00
	SF1	137	162	90.51
	SF3	132	185	93.00
<i>Spondias axillaris</i>	PF1	115	136	66.00
	SF3	120	213	80.00
<i>Mesua ferrea</i>	PF2	285	327	88.00
<i>Shorea assamica</i>	PF1	292	350	78.00
	PF2	351	407	80.34
	SF1	255	346	87.33

High seedling mortality of *Alangium chinense* and *Sapindus mukkorossi* occurred during first three months of germination. However, the seedling survivorship curves for *Mesua ferrea* and *Shorea assamica* showed a sharp reduction in the number of surviving individuals after 3 months period and continued till the seedlings were one year old, after which the seedling population stabilized (Figure 7.1).

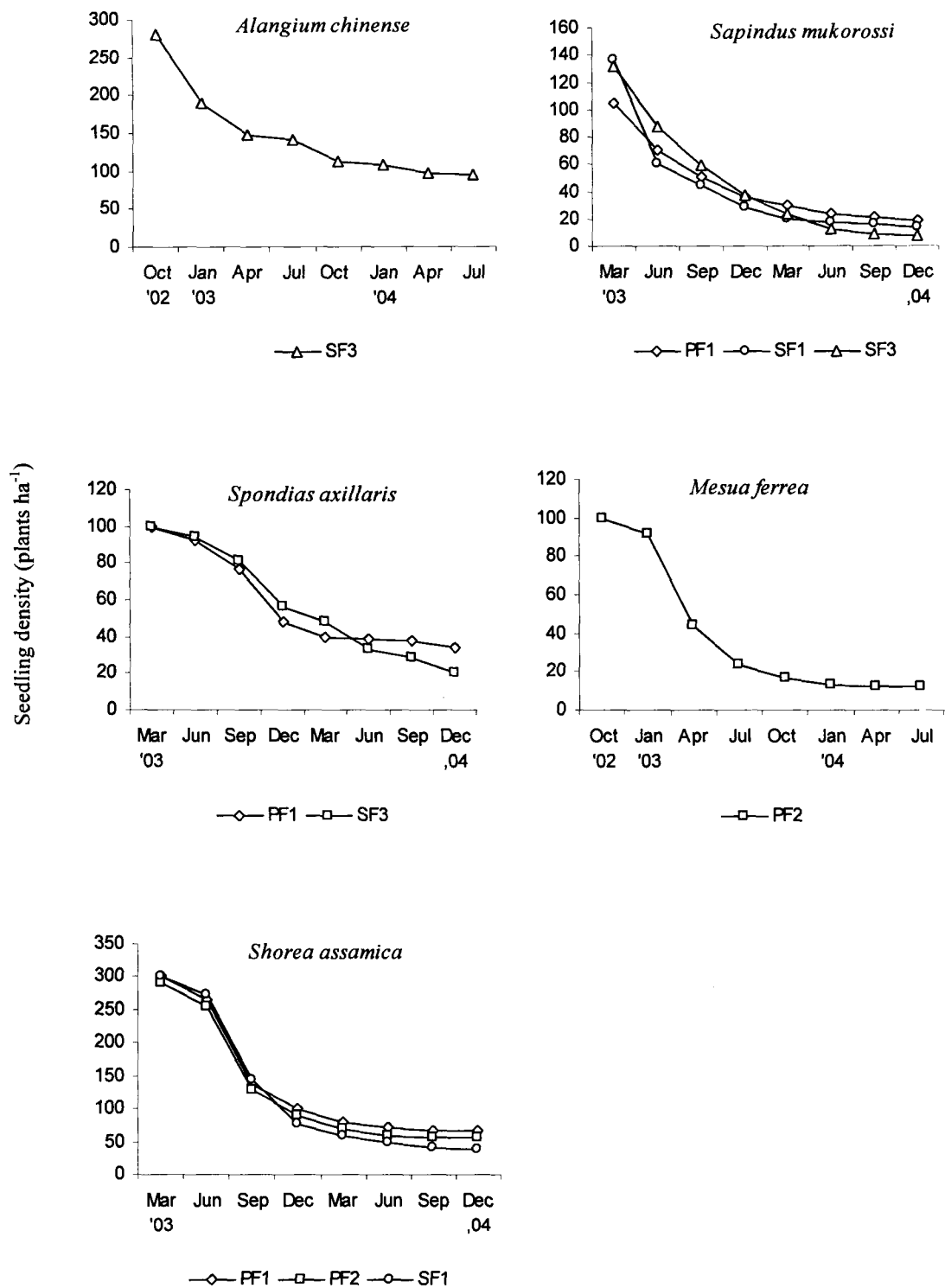


Figure 7.1. Seedling survivorship curves of the selected species in the primary and secondary forest stands

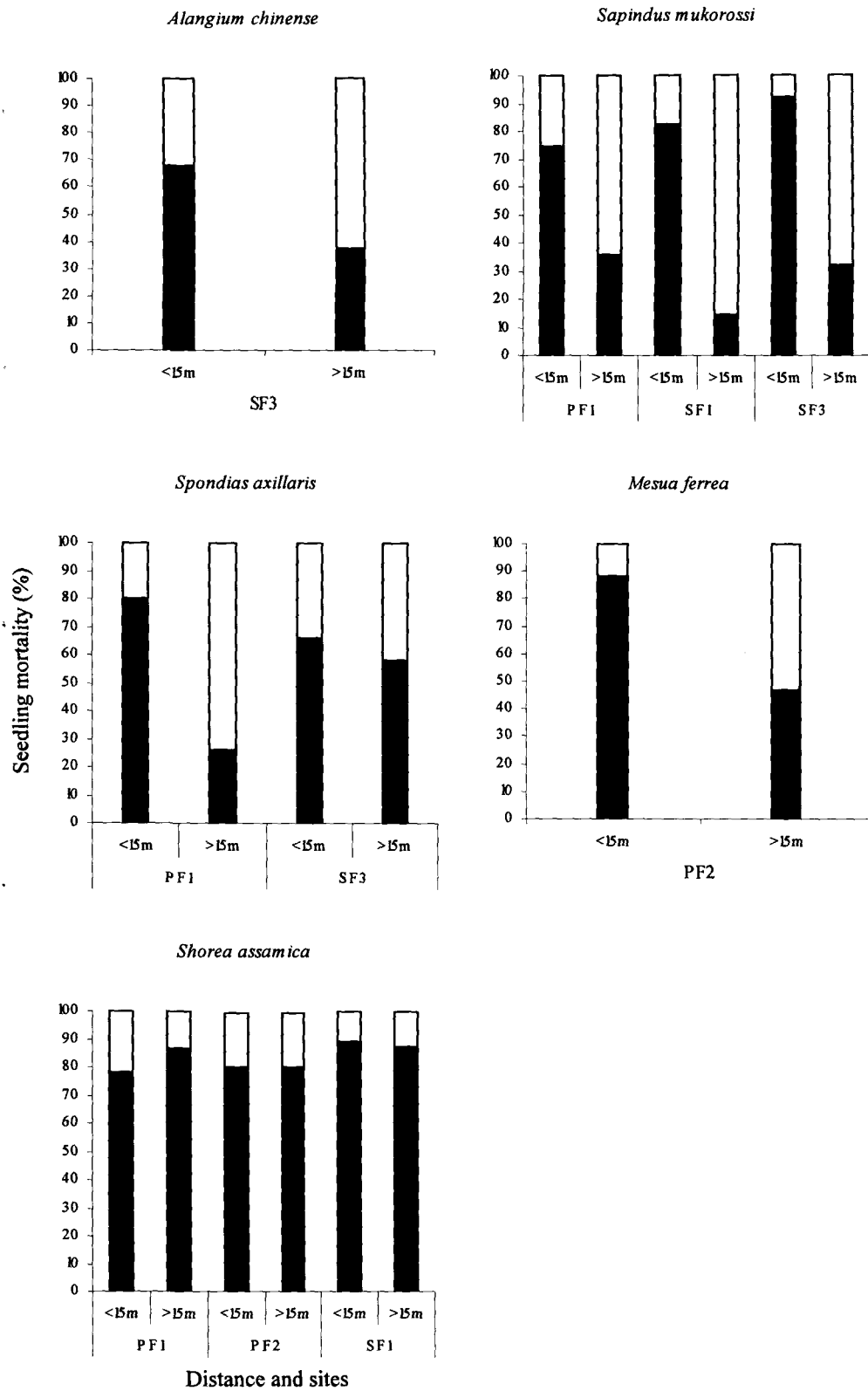


Figure 7.2. Seedling mortality as affected by the distance from the parent tree canopy in the primary and secondary forest stands (Shaded portion represents percent mortality)

The seedling mortality rate of *Alangium chinense* was negatively correlated with soil temperature ($p < 0.05$), while that of *Sapindus mukkorossi* it was correlated with light intensity ($p < 0.05$) in the secondary forest stand. The mortality rate for *Spondias axillaris* was positively correlated with light intensity ($p < 0.05$) and negatively correlated with soil moisture in the secondary forest (Table 7.3).

Seedling mortality for all the species was more under canopy of the parent tree than the peripheral area (Figure 7.2).

Table 7.2. Partial correlation coefficients of age-specific seedling mortality rate (Qx) with various environmental micro-environmental parameters (n=7)

Species / Sites	Forest stands	Microenvironmental parameters					
		Light intensity (Lux)	Relative humidity (%)	Air temperature (°C)	Soil temperature (°C)	Soil moisture (%)	Litter depth (cm)
<i>A. chinense</i>	SF3	-0.35	0.49	-0.70	-0.77*	0.44	-0.40
<i>S. mukkorossi</i>	PF1	0.57	-0.65	-0.53	0.54	-0.53	0.67
	SF1	-0.17	-0.70	-0.17	-0.25	-0.66	0.52
<i>S. axillaris</i>	SF3	0.88*	0.20	-0.20	-0.10	0.19	-0.03
	PF1	0.60	-0.65	-0.53	0.54	-0.53	0.67
	SF3	0.83*	-0.75	0.50	0.56	-0.78*	0.68
<i>M. ferrea</i>	PF2	0.33	0.22	-0.19	-0.07	-0.20	0.13
<i>S. assamica</i>	PF1	-0.14	0.34	0.15	-0.11	0.04	-0.36
	PF2	0.19	0.38	-0.18	0.06	-0.07	-0.03
	SF1	0.36	-0.07	-0.01	0.11	-0.49	-0.001

* $P < 0.05$

***In situ* seedling growth**

Relative growth rate in height and leaf area of *Sapindus mukkorossi* and *Spondias axillaris* was higher in the secondary forest as compared to the primary forest (Figure 7.3&7.4). On the other hand, for *Shorea assamica* the relative growth rate was more in the primary forest than the secondary forest (Figure 7.3). Relative growth rate in height in case of *Mesua ferrea* was quite low comparing to that of other species.

Relative growth rate in height as well as leaf area of all the selected species reflects strong seasonal influence with maximum growth in the rainy season (June-July) and least

growth in the winter months (December-February) (Table 7.2, Figure 7.3&7.4). The growth in basal diameter was significantly different among primary and secondary forest stands in case of *Sapindus mukkorossi* (Table 7.2).

Effect of light and nutrients on growth of seedlings

Seedling size and biomass accumulation

The seedling size, seedling morphology and biomass accumulation of all the species varied significantly under different light and nutrient levels (Table 7.4). Height, leaf area and collar diameter for *Alangium chinense* was highest at high light intensity (65%) while for *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* it was highest at intermediate light intensity (45%) (Table 7.5). *Shorea assamica* attained maximum height and collar diameter at 65% light. All selected species responded vigorously to increased level of nutrients (30 and 35 gms of NPK) mostly under 45-65% light levels.

Table 7.3. ANOVA for effect of sites, seasons and the interaction of the two on seedling growth of selected species

Species	Attributes	F-values		
		Sites	Seasons	Sites x Seasons
<i>Alangium chinense</i>	BD	-	551.47**	-
	TH	-	560.23**	-
	LA	-	1924.26**	-
<i>Sapindus mukkorossi</i>	BD	17.46**	52.79**	23.29**
	TH	1.79 ^{ns}	863.19**	157.49**
	LA	2.64 ^{ns}	80.90**	1.75 ^{ns}
<i>Spondias axillaris</i>	BD	1.08 ^{ns}	266.89**	40.33**
	TH	0.20 ^{ns}	1488.87**	15.38**
	LA	0.31 ^{ns}	80.42**	2.59 ^{ns}
<i>Mesua ferrea</i>	BD	-	33.46**	-
	TH	-	48.17**	-
	LA	-	18156.18**	-
<i>Shorea assamica</i>	BD	0.95 ^{ns}	610.42**	14.41**
	TH	0.25 ^{ns}	1261.65**	16.47**
	LA	0.09 ^{ns}	1345.98**	6.37**

**P<0.001, ns – not significant; BD – Basal diameter, TH – Total height, LA – Leaf area

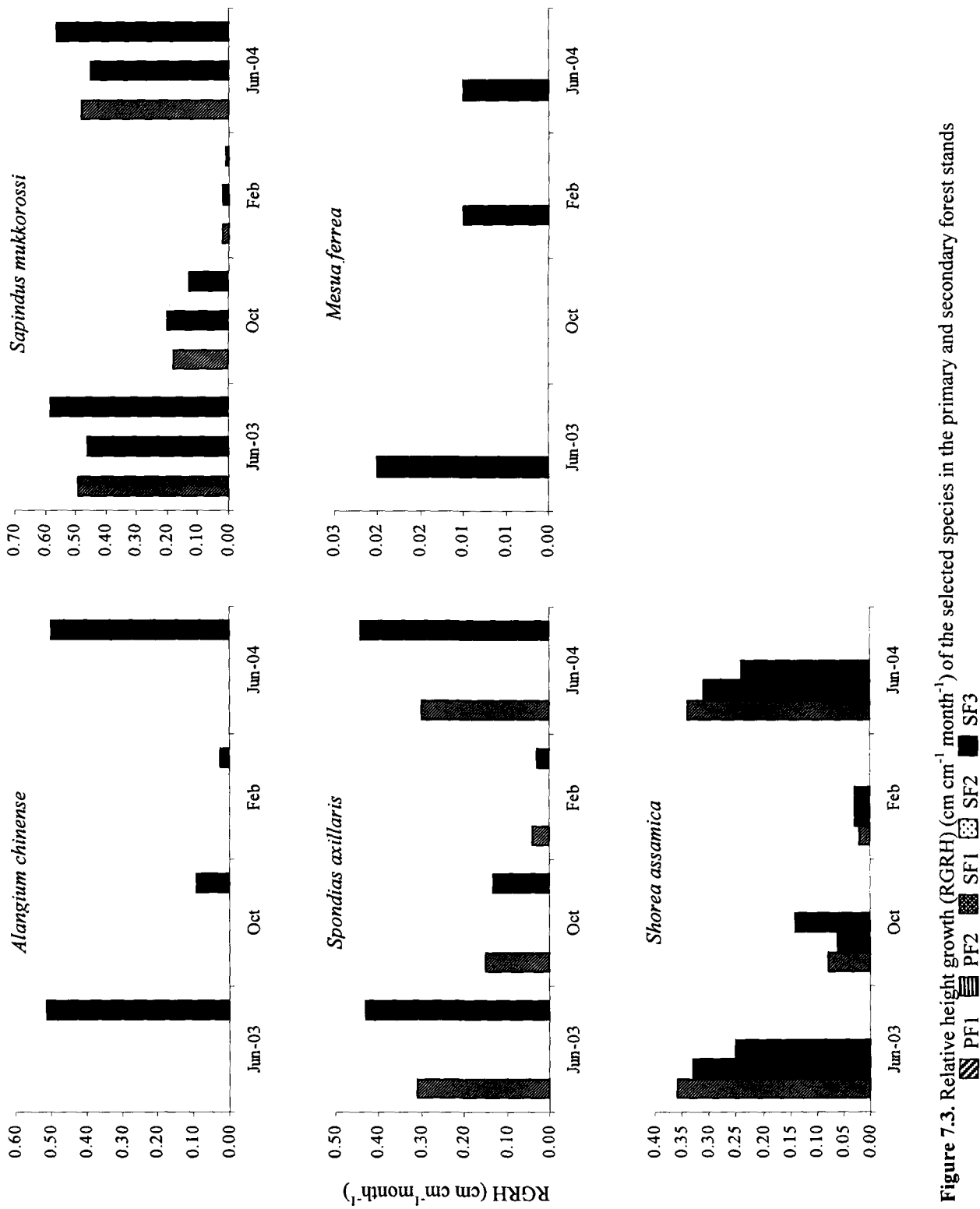


Figure 7.3. Relative height growth (RGRH) (cm cm⁻¹ month⁻¹) of the selected species in the primary and secondary forest stands

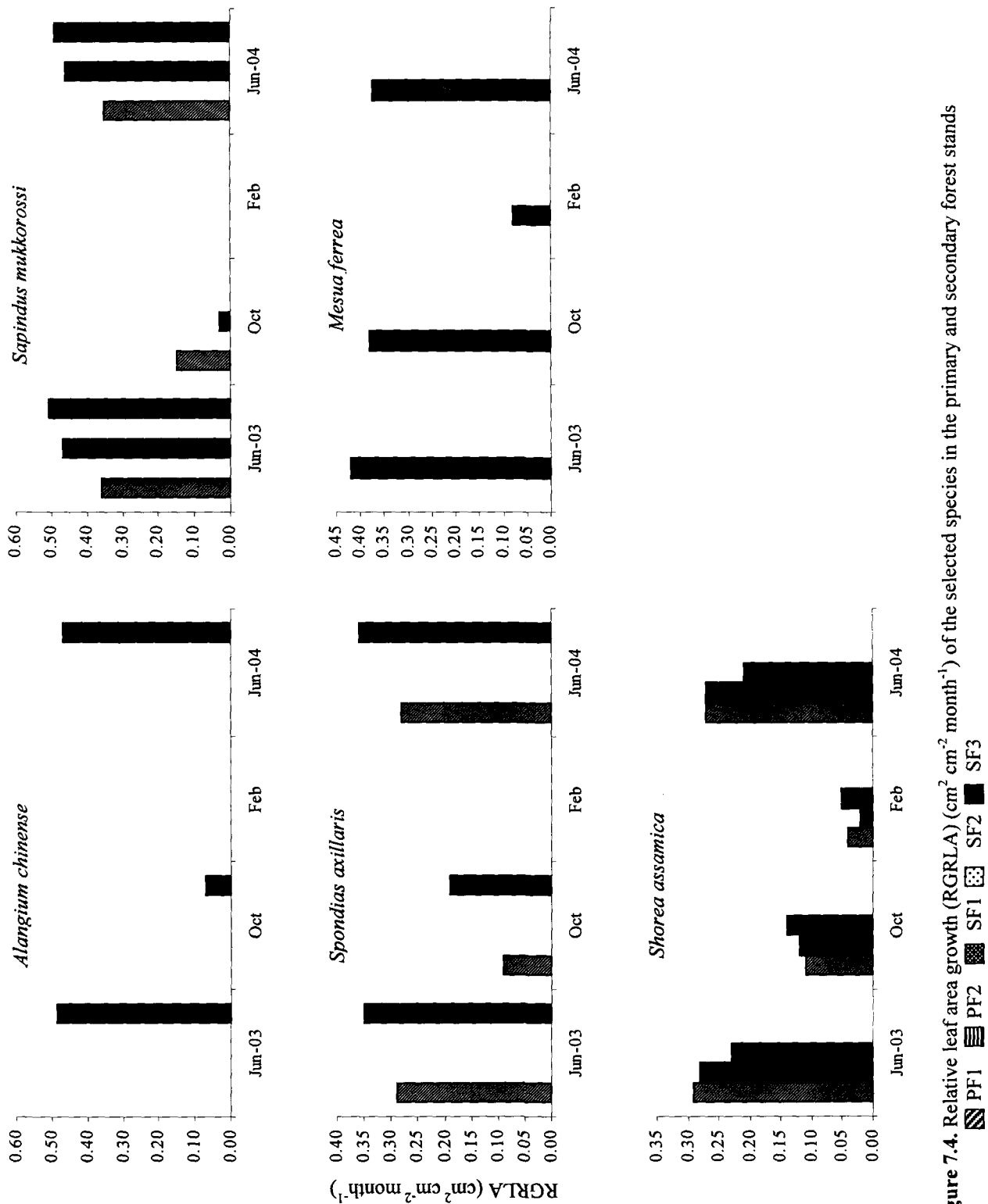


Figure 7.4. Relative leaf area growth (RGR)LA (cm² cm⁻² month⁻¹) of the selected species in the primary and secondary forest stands

All the species exhibited similar patterns of biomass accumulation under different light and nutrient treatments with a general trend of increasing biomass allocation to stems, leaves and roots with increasing light (Table 7.5). Root biomass decreased with increasing nutrient concentration irrespective of light intensity in *Sapindus mukkorossi* and *Spondias axillaris*. In case of biomass allocation to leaves and stems an increasing trend was observed in all species with increasing nutrient concentration irrespective of light levels.

In *Sapindus mukkorossi* and *Mesua ferrea*, maximum total plant biomass was obtained at 45% light; whilst in *Alangium chinense* total plant biomass was highest at high nutrient level (N₄) at 65% light. In *Sapindus mukkorossi* root biomass was highest at low nutrient level (N₁) while stem and leaf biomass was highest under high nutrient level (N₄). Root biomass in *Spondias axillaris* was highest at low nutrient level (N₁) whilst stem and leaf biomass was highest at higher nutrient level (N₄). For *Mesua ferrea* root, stem and leaf biomass were highest under high nutrient level (N₄) (Table 7.5). In *Shorea assamica* leaf and stem biomass values were highest at N₄ nutrient level while highest root biomass values were obtained at low nutrient level (N₁).

Relative growth rates in seedling height and leaf area

Relative growth rate in terms of height and leaf area increased consistently across light and fertilizer gradients (Figures 7.4 & 7.5). Relative growth rate in height increased along the fertilizer gradient and was highest at 65% light for all species while the relative growth rate in leaf area was highest under intermediate light intensity (45%) in all the species except *Alangium chinense* (Figure 7.5).

Overall, LMR and SMR showed an increasing trend with increasing light and nutrient levels; but RMR, SLA and LAR exhibited a decreasing trend with corresponding levels

of light and nutrient (Table 7.6). Most of the derived growth parameters for all the selected species varied significantly within and between different fertility as well as light levels. But fertility level did not affect LAR in *Spondias axillaris*. Similarly RMR, LMR, SLA and LARMR were not affected significantly by light, nutrient or the interactive effects of the two in case of *Mesua ferrea*. In case of *Shorea assamica* also variation in light levels did not have significant effect over SMR.

The β values in the multiple regression analysis shows that both light and nutrient have significant role in seedling growth in terms of relative growth rate in height and leaf area and total plant biomass accumulation. In case of *Alangium chinense*, *Sapindus mukkorossi* and *Shorea assamica* light intensity influenced RGRH, RGRLA and total plant mass more significantly than nutrient level (Table 7.7). But in *Spondias axillaris* and *Mesua ferrea* nutrient levels more significantly influenced RGRLA and total plant mass than light levels respectively.

Table 7.4. ANOVA for variables related to plant size, allocation and morphology of the selected species under different light and nutrient treatments
 (*P>0.05, ** P>0.005)

Species	Growth attributes	Variable	Source of variation			
			Light	Nutrient	Light x Nutrient	
<i>Alangium chinense</i>	Plant size	Height	474.30**	0.62ns	13.07**	
		Leaf area	655.95**	0.30ns	11.54**	
	Allocation	Collar diameter	258.85**	1.25ns	98.78**	
		Total plant biomass	1730.55**	625.46**	131.53**	
		RMR	88.97**	236.79**	28.69**	
		SMR	27.62**	48.41**	3.55*	
	Morphology	LMR	22.84**	40.96**	16.79**	
		SLA	15.73**	19.07**	4.09**	
		LAR	149.70**	71.25**	36.64**	
		LARMR	24.73**	12.85**	13.03**	
	<i>Sapindus mukkorossi</i>	Plant size	Height	6696.85**	257.73**	37.83**
			Leaf area	716.31**	56.83**	1.19ns
Allocation		Collar diameter	2299.23**	35.52**	13.84**	
		Total plant biomass	948.44**	42.10**	20.95**	
		RMR	1627.08**	202.99**	18.59**	
		SMR	61.74**	86.13**	5.52**	
Morphology		LMR	3.77*	93.35**	11.05**	
		SLA	87.56**	18.27**	13.60**	
		LAR	181.38**	22.54**	5.60**	
		LARMR	262.67**	102.19**	24.60**	
<i>Spondias axillaris</i>		Plant size	Height	915.51**	204.32**	34.12**
			Leaf area	1971.36**	1832.68**	442.35**
	Allocation	Collar diameter	2419.90**	666.90**	202.70**	
		Total plant biomass	263.97**	484.56**	19.24**	
		RMR	134.55**	554.12**	6.13**	
		SMR	24.87**	215.88**	4.51*	
	Morphology	LMR	10.91**	539.64**	4.58**	
		SLA	30.55**	515.93**	5.83**	
		LAR	463.15**	1.61ns	60.04**	
		LARMR	66.06**	102.40**	10.77**	

Species	Growth attributes	Variable	Source of variation			
			Light	Nutrient	Light x Nutrient	
<i>Mesua ferrea</i>	Plant size	Height	148.74**	48.68**	8.06**	
		Leaf area	68451.00**	1807.00**	1060.31**	
		Collar diameter	22.56**	10.43**	1.58ns	
	Allocation	Total plant biomass	65.66**	151.34**	2.90*	
		RMR	2.37ns	2.90*	2.13ns	
		SMR	8.60**	4.85*	3.10*	
	Morphology	LMR	172.79**	0.86ns	6.08**	
		SLA	1035.25**	112.88**	2.13ns	
		LAR	683.17**	57.53**	5.81**	
	LARMR	244.34**	7.00**	1.44ns		
	<i>Shorea assamica</i>	Plant size	Height	356.55**	86.84**	13.17**
			Leaf area	1268.20**	1674.50**	51.70**
Collar diameter			891.42**	239.78**	24.72**	
Allocation		Total plant biomass	1048.44**	229.30**	35.62**	
		RMR	22.38**	167.17**	13.32**	
		SMR	0.08ns	18.95**	3.09*	
Morphology		LMR	9.72**	20.90**	3.31*	
		SLA	130.07**	8.58**	3.72**	
		LAR	244.71**	6.73**	16.70**	
LARMR		45.38**	93.70**	23.08**		

RMR-Root mass ratio, SMR-Stem mass ratio, LMR-Leaf mass ratio, SLA-Specific leaf area, LAR-Leaf area ratio, LARMR-Leaf area root mass ratio

Table 7.5. The growth parameters of the transplanted seedlings under different levels of light and nutrient treatments measured after eight months i.e. at the end of the experiment (\pm SE)

Species /growth parameters	L1				L2				L3			
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4
<i>Alangium chinense</i>												
Height (cm)	18.42 \pm 0.29	17.67 \pm 0.46	21.93 \pm 0.54	21.51 \pm 1.21	29.85 \pm 0.28	34.41 \pm 0.74	35.46 \pm 0.62	35.84 \pm 0.48	47.71 \pm 0.74	59.50 \pm 1.45	57.62 \pm 0.54	59.81 \pm 0.58
Leaf area (cm ²)	110.38 \pm 4.59	116.38 \pm 5.38	122.25 \pm 6.34	131.42 \pm 3.69	111.82 \pm 8.10	127.36 \pm 5.01	166.99 \pm 3.60	176.60 \pm 6.39	345.04 \pm 4.37	331.25 \pm 4.07	365.80 \pm 4.97	332.79 \pm 4.29
Collar diameter (mm)	1.50 \pm 0.04	1.80 \pm 0.07	1.88 \pm 0.04	1.98 \pm 0.03	2.50 \pm 0.06	2.75 \pm 0.03	3.11 \pm 0.04	3.21 \pm 0.04	4.73 \pm 0.03	5.08 \pm 0.03	6.62 \pm 0.08	6.74 \pm 0.02
Root biomass (gm)	0.96 \pm 0.05	0.99 \pm 0.05	0.52 \pm 0.05	0.45 \pm 0.07	0.94 \pm 0.05	0.93 \pm 0.05	0.83 \pm 0.07	0.81 \pm 0.07	1.21 \pm 0.05	1.18 \pm 0.08	1.18 \pm 0.05	1.80 \pm 0.07
Stem biomass (gm)	0.37 \pm 0.04	0.65 \pm 0.03	0.82 \pm 0.05	0.90 \pm 0.07	0.95 \pm 0.01	0.90 \pm 0.02	1.94 \pm 0.01	2.26 \pm 0.08	0.90 \pm 0.04	1.86 \pm 0.03	3.23 \pm 0.06	3.23 \pm 0.04
Leaf biomass (gm)	0.31 \pm 0.06	0.65 \pm 0.02	0.75 \pm 0.06	1.19 \pm 0.01	1.05 \pm 0.04	1.04 \pm 0.05	2.22 \pm 0.04	2.19 \pm 0.04	0.93 \pm 0.04	1.72 \pm 0.05	2.53 \pm 0.06	2.49 \pm 0.07
Total plant biomass (gm)	1.64 \pm 0.10	2.28 \pm 0.12	2.09 \pm 0.09	2.54 \pm 0.10	2.94 \pm 0.08	2.86 \pm 0.11	4.99 \pm 0.10	5.25 \pm 0.15	3.04 \pm 0.13	4.76 \pm 0.15	6.94 \pm 0.09	7.52 \pm 0.18
<i>Sapindus mukorossi</i>												
Height (cm)	15.35 \pm 0.63	15.97 \pm 0.66	19.27 \pm 0.39	28.39 \pm 0.42	29.59 \pm 0.36	30.13 \pm 0.34	31.92 \pm 0.16	32.87 \pm 0.30	47.94 \pm 0.11	48.61 \pm 0.13	51.33 \pm 0.28	55.04 \pm 0.37
Leaf area (cm ²)	127.29 \pm 12.12	122.26 \pm 10.04	190.90 \pm 7.35	192.57 \pm 14.21	378.45 \pm 7.69	400.37 \pm 10.96	450.19 \pm 12.24	488.13 \pm 11.19	196.00 \pm 9.15	224.53 \pm 5.82	282.11 \pm 10.19	299.28 \pm 9.66
Collar diameter (mm)	2.79 \pm 0.08	3.56 \pm 0.04	3.51 \pm 0.05	3.71 \pm 0.04	3.96 \pm 0.06	3.95 \pm 0.05	4.07 \pm 0.05	4.36 \pm 0.04	5.96 \pm 0.07	6.05 \pm 0.07	6.14 \pm 0.07	6.06 \pm 0.06
Root biomass (gm)	2.43 \pm 0.04	1.69 \pm 0.09	1.40 \pm 0.13	1.01 \pm 0.06	3.62 \pm 0.09	3.13 \pm 0.04	2.96 \pm 0.06	2.75 \pm 0.05	4.19 \pm 0.07	3.51 \pm 0.03	3.18 \pm 0.07	2.76 \pm 0.10
Stem biomass (gm)	1.38 \pm 0.04	1.35 \pm 0.09	1.71 \pm 0.09	2.54 \pm 0.09	1.54 \pm 0.05	2.40 \pm 0.02	2.51 \pm 0.07	2.84 \pm 0.09	1.32 \pm 0.07	2.19 \pm 0.06	2.22 \pm 0.03	2.79 \pm 0.06
Leaf biomass (gm)	1.05 \pm 0.09	1.36 \pm 0.05	1.02 \pm 0.03	1.83 \pm 0.03	1.42 \pm 0.06	2.25 \pm 0.10	2.47 \pm 0.06	2.84 \pm 0.04	1.69 \pm 0.07	2.29 \pm 0.05	2.14 \pm 0.04	2.26 \pm 0.05
Total plant biomass (gm)	4.86 \pm 0.14	4.40 \pm 0.19	4.13 \pm 0.21	5.38 \pm 0.15	6.58 \pm 0.16	7.77 \pm 0.19	7.94 \pm 0.21	8.43 \pm 0.18	7.20 \pm 0.20	8.00 \pm 0.14	7.54 \pm 0.14	7.82 \pm 0.22

Continued

Species /growth parameters	L1				L2				L3			
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4
<i>Spondias axillaris</i>												
Height (cm)	27.79 ±0.85	31.54 ±0.21	41.58 ±0.53	47.90 ±0.51	44.08 ±0.43	57.99 ±0.58	56.59 ±1.08	66.31 ±0.71	56.82 ±0.86	58.76 ±0.56	61.28 ±0.60	61.57 ±1.66
Leaf area (cm ²)	113.70 ±1.67	188.92 ±0.61	185.30 ±0.99	198.01 ±1.36	120.07 ±1.75	170.52 ±1.20	339.93 ±2.65	358.16 ±1.89	89.21 ±3.37	133.18 ±3.38	164.66 ±3.64	166.56 ±4.31
Collar diameter (mm)	3.46 ±0.06	3.61 ±0.04	4.58 ±0.03	3.76 ±0.02	4.46 ±0.07	4.85 ±0.05	6.23 ±0.05	7.63 ±0.03	5.60 ±0.07	5.84 ±0.04	6.09 ±0.04	6.88 ±0.07
Root biomass (gm)	1.93 ±0.07	1.14 ±0.03	0.87 ±0.02	0.54 ±0.06	2.15 ±0.06	2.05 ±0.03	1.49 ±0.05	1.13 ±0.06	2.89 ±0.06	2.88 ±0.08	2.18 ±0.04	1.72 ±0.04
Stem biomass (gm)	0.89 ±0.05	1.23 ±0.13	2.78 ±0.12	3.07 ±0.06	0.87 ±0.08	1.29 ±0.03	3.70 ±0.06	4.06 ±0.10	0.58 ±0.16	1.27 ±0.11	4.03 ±0.15	4.88 ±0.12
Leaf biomass (gm)	0.17 ±0.01	1.52 ±0.08	2.30 ±0.17	2.31 ±0.11	0.18 ±0.01	2.29 ±0.17	2.24 ±0.08	2.51 ±0.07	0.19 ±0.01	2.69 ±0.05	2.85 ±0.12	3.35 ±0.13
Total plant biomass (gm)	2.98 ±0.14	3.89 ±0.21	5.94 ±0.28	5.91 ±0.24	3.20 ±0.18	5.63 ±0.23	7.43 ±0.21	7.70 ±0.22	3.65 ±0.24	6.84 ±0.26	9.06 ±0.29	9.96 ±0.29
<i>Mesua ferrea</i>												
Height (cm)	24.28 ±1.09	23.66 ±1.00	26.67 ±0.96	25.85 ±0.27	27.23 ±0.62	32.66 ±0.52	37.42 ±0.75	34.86 ±0.51	27.10 ±0.54	34.08 ±0.49	34.64 ±0.79	35.32 ±0.85
Leaf area (cm ²)	207.05 ±1.27	213.45 ±1.08	218.11 ±0.46	239.10 ±1.45	346.48 ±0.77	440.29 ±0.31	456.46 ±1.18	454.04 ±1.08	402.61 ±0.38	407.56 ±0.21	408.16 ±0.29	403.59 ±0.62
Collar diameter (mm)	3.58 ±0.08	3.74 ±0.09	3.93 ±0.16	4.15 ±0.09	4.04 ±0.19	4.21 ±0.14	4.53 ±0.12	4.89 ±0.13	4.12 ±0.13	4.24 ±0.12	4.32 ±0.05	4.29 ±0.10
Root biomass (gm)	1.41 ±0.04	1.77 ±0.03	1.85 ±0.05	2.06 ±0.01	1.84 ±0.03	2.10 ±0.08	2.05 ±0.04	1.98 ±0.03	1.52 ±0.11	1.87 ±0.05	2.11 ±0.02	2.13 ±0.03
Stem biomass (gm)	1.41 ±0.14	1.99 ±0.07	2.33 ±0.09	2.39 ±0.09	1.50 ±0.05	2.17 ±0.10	2.41 ±0.07	2.57 ±0.05	1.89 ±0.07	2.11 ±0.11	2.20 ±0.10	2.37 ±0.16
Leaf biomass (gm)	0.92 ±0.02	1.07 ±0.01	1.22 ±0.02	1.31 ±0.02	1.02 ±0.02	1.45 ±0.01	1.57 ±0.01	1.59 ±0.01	1.55 ±0.03	1.69 ±0.01	1.80 ±0.02	1.83 ±0.03
Total plant biomass (gm)	3.75 ±0.18	4.83 ±0.15	5.40 ±0.16	5.76 ±0.11	4.35 ±0.10	5.72 ±0.19	6.03 ±0.13	6.15 ±0.10	4.97 ±0.19	5.68 ±0.17	6.12 ±0.14	6.33 ±0.21

Continued

Species /growth parameters	L1				L2				L3			
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4
<i>Shorea assamica</i>												
Height (cm)	18.41 ±0.35	20.62 ±0.64	20.29 ±0.39	20.55 ±0.22	21.52 ±0.51	28.12 ±0.31	28.10 ±0.47	27.31 ±0.39	23.14 ±0.69	34.32 ±0.82	33.40 ±0.62	33.37 ±1.10
Leaf area (cm ²)	187.34 ±1.04	263.66 ±1.13	284.62 ±1.38	311.78 ±1.93	223.02 ±0.47	365.71 ±1.50	410.29 ±1.48	395.20 ±1.70	256.68 ±0.91	368.06 ±6.79	382.26 ±4.64	385.12 ±3.22
Collar diameter (mm)	2.89 ±0.04	3.27 ±0.09	3.46 ±0.03	4.31 ±0.02	3.89 ±0.04	4.52 ±0.05	4.76 ±0.05	4.96 ±0.04	4.44 ±0.04	4.90 ±0.04	4.97 ±0.04	5.00 ±0.06
Root biomass (gm)	0.51 ±0.03	0.40 ±0.03	0.36 ±0.02	0.19 ±0.02	0.51 ±0.01	0.54 ±0.01	0.42 ±0.02	0.30 ±0.01	0.58 ±0.02	0.66 ±0.02	0.67 ±0.02	0.70 ±0.03
Stem biomass (gm)	0.40 ±0.03	0.64 ±0.03	0.73 ±0.03	0.65 ±0.04	0.47 ±0.04	0.94 ±0.05	1.13 ±0.08	1.27 ±0.06	0.82 ±0.06	1.56 ±0.06	1.76 ±0.08	1.58 ±0.06
Leaf biomass (gm)	0.46 ±0.02	0.63 ±0.03	0.76 ±0.07	0.76 ±0.04	0.56 ±0.04	1.31 ±0.04	1.25 ±0.05	1.33 ±0.01	0.96 ±0.03	1.99 ±0.04	1.92 ±0.02	1.95 ±0.03
Total plant biomass (gm)	1.38 ±0.10	1.67 ±0.10	1.85 ±0.12	1.60 ±0.10	1.55 ±0.10	2.80 ±0.11	2.80 ±0.15	2.91 ±0.08	2.37 ±0.11	4.21 0.11	4.34 ±0.12	4.23 ±0.12

L1 – 15% light, L2 – 45% light, L3 – 65% light, N1 – 5gm NPK, N2 – 15gm NPK, N3 – 25gm NPK, N4 – 35gm NPK

Table 7.6. Derived seedling growth parameters of the selected species under different light and nutrient treatments

Species/Parameters	L1			L2			L3					
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4
<i>Alangium chinense</i>												
RMR	0.58	0.43	0.25	0.17	0.32	0.33	0.17	0.15	0.40	0.25	0.17	0.24
SMR	0.23	0.28	0.39	0.35	0.32	0.31	0.39	0.43	0.30	0.39	0.47	0.43
LMR	0.19	0.29	0.36	0.47	0.36	0.36	0.44	0.42	0.31	0.36	0.36	0.33
SLA	431.88	178.90	168.53	110.12	107.67	124.65	75.41	81.10	374.23	193.47	144.78	134.43
LAR	67.95	51.01	58.70	52.20	38.29	44.66	33.50	33.74	113.66	69.85	52.77	44.27
LARMR	116.55	118.92	246.97	316.80	120.95	138.76	206.61	223.13	286.67	287.78	314.18	186.08
<i>Sapindus mukkorossi</i>												
RMR	0.86	0.80	0.77	0.51	0.55	0.40	0.37	0.33	0.34	0.21	0.19	0.13
SMR	0.28	0.31	0.41	0.47	0.20	0.28	0.28	0.33	0.21	0.30	0.33	0.36
LMR	0.22	0.31	0.25	0.34	0.22	0.29	0.31	0.34	0.23	0.29	0.28	0.29
SLA	127.43	90.38	188.46	104.85	267.38	180.62	182.56	172.38	117.64	97.97	132.02	132.24
LAR	26.31	27.93	46.34	35.77	57.62	51.72	56.80	58.03	27.27	28.08	37.46	38.29
LARMR	30.44	34.83	60.25	70.75	104.78	128.31	152.39	177.77	80.57	134.50	206.46	301.63
<i>Spondias axillaris</i>												
RMR	12.08	13.43	21.63	26.88	36.40	45.17	53.14	61.09	28.41	47.86	74.26	107.42
SMR	5.05	5.42	8.12	11.44	13.16	16.67	19.44	21.52	10.56	18.75	29.72	42.30
LMR	4.29	4.72	7.45	9.59	12.40	15.47	18.15	20.66	9.76	16.66	26.00	37.43
SLA	1.87	2.04	3.12	4.21	5.13	6.44	7.52	8.44	4.08	7.09	11.15	15.95
LAR	6.18	2.76	3.37	3.55	15.37	5.65	6.13	6.53	6.95	4.99	7.90	11.06
LARMR	6.77	2.76	2.71	2.54	16.15	3.90	3.83	3.88	6.70	2.73	4.37	5.88

Continued

Species/Parameters	L1			L2			L3					
	N1	N2	N3	N4	N1	N2	N3	N4	N1	N2	N3	N4
<i>Mesua ferrea</i>												
RMR	3.37	2.86	2.97	17.66	6.06	2.28	2.78	3.32	3.10	1.74	3.55	5.25
SMR	1.89	2.24	2.80	22.36	2.38	1.40	2.26	2.84	1.36	1.30	3.13	4.89
LMR	1.32	1.28	1.45	10.01	2.12	0.93	1.26	1.54	1.12	0.77	1.68	2.54
SLA	0.65	0.71	0.85	6.48	0.91	0.47	0.71	0.88	0.50	0.42	0.97	1.49
LAR	1.49	0.78	0.94	3.93	1.70	0.77	1.04	1.03	1.19	0.62	0.94	1.49
LARMR	1.93	0.82	1.03	2.83	1.74	1.03	1.14	1.04	1.57	0.89	1.05	1.57
<i>Shorea assamica</i>												
RMR	2.35	1.26	1.79	1.53	7.14	2.92	1.11	1.59	2.21	3.38	2.22	2.20
SMR	1.80	1.18	1.73	0.90	8.74	3.05	0.84	1.59	1.80	3.69	2.19	1.92
LMR	1.05	0.62	0.89	0.62	3.98	1.50	0.50	0.80	1.01	1.77	1.11	1.03
SLA	0.58	0.37	0.53	0.31	2.56	0.91	0.28	0.48	0.57	1.10	0.66	0.60
LAR	3.59	4.84	7.00	3.84	7.11	2.50	3.09	0.65	2.01	1.59	1.06	1.07
LARMR	4.92	6.95	9.31	6.08	8.71	3.18	4.39	1.16	2.94	2.08	1.44	1.54

L1 – 15% light, L2 – 45% light, L3 – 65% light, N1 – 5gm NPK, N2 – 15gm NPK, N3 – 25gm NPK, N4 – 35gm NPK, RMR-Root mass ratio, SMR-Stem mass ratio, LMR-Leaf mass ratio, SLA-Specific leaf area, LAR-Leaf area ratio, LARMR-Leaf area root mass ratio

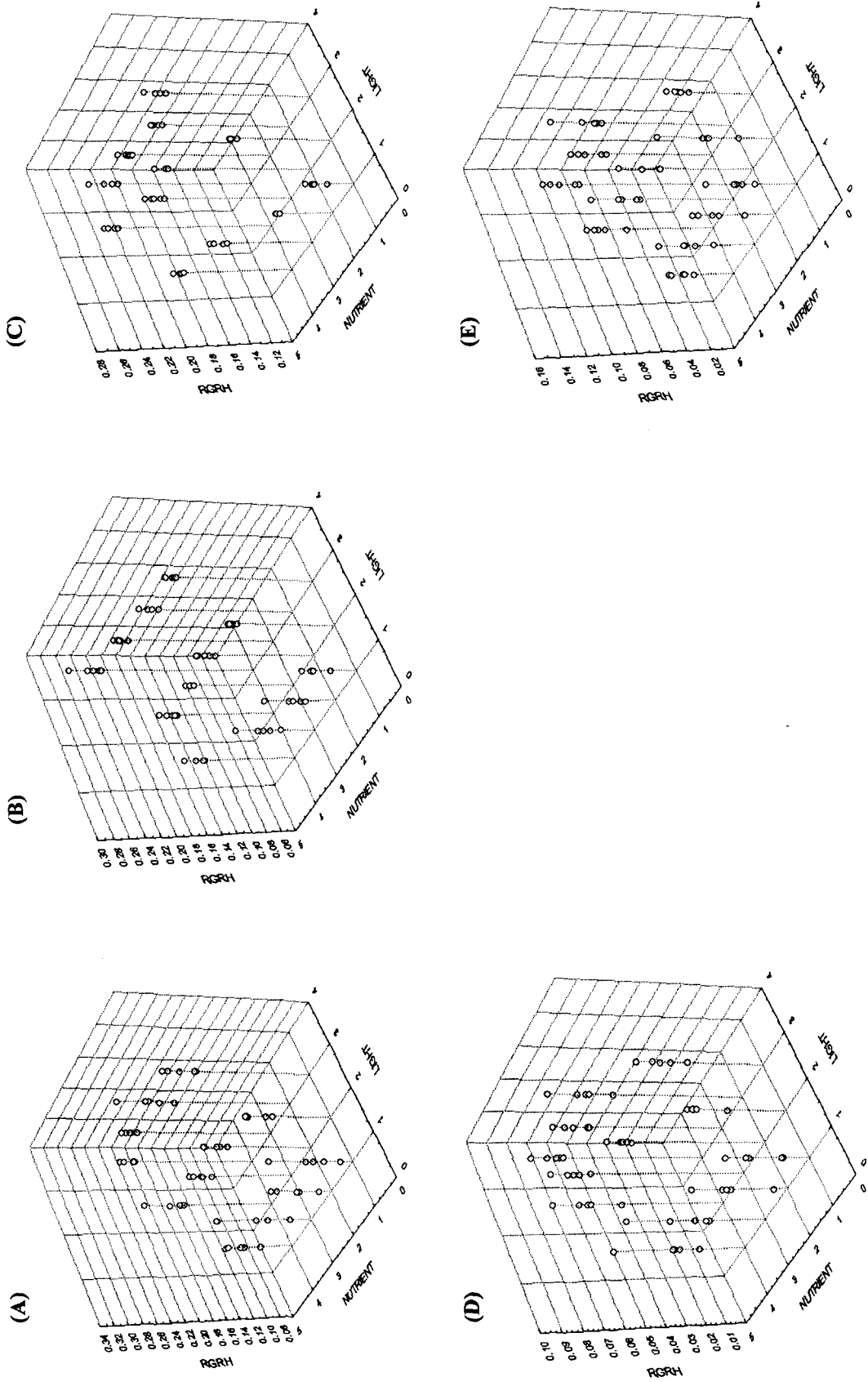


Figure 7.4. 3D scatterplot for relative height growth rate for the selected species under different light and nutrient levels (A) *Alangium chinense*, (B) *Sapindus mukkorossi*, (C) *Spondias axillaris*, (D) *Mesua ferrea* and (E) *Shorea assamica*

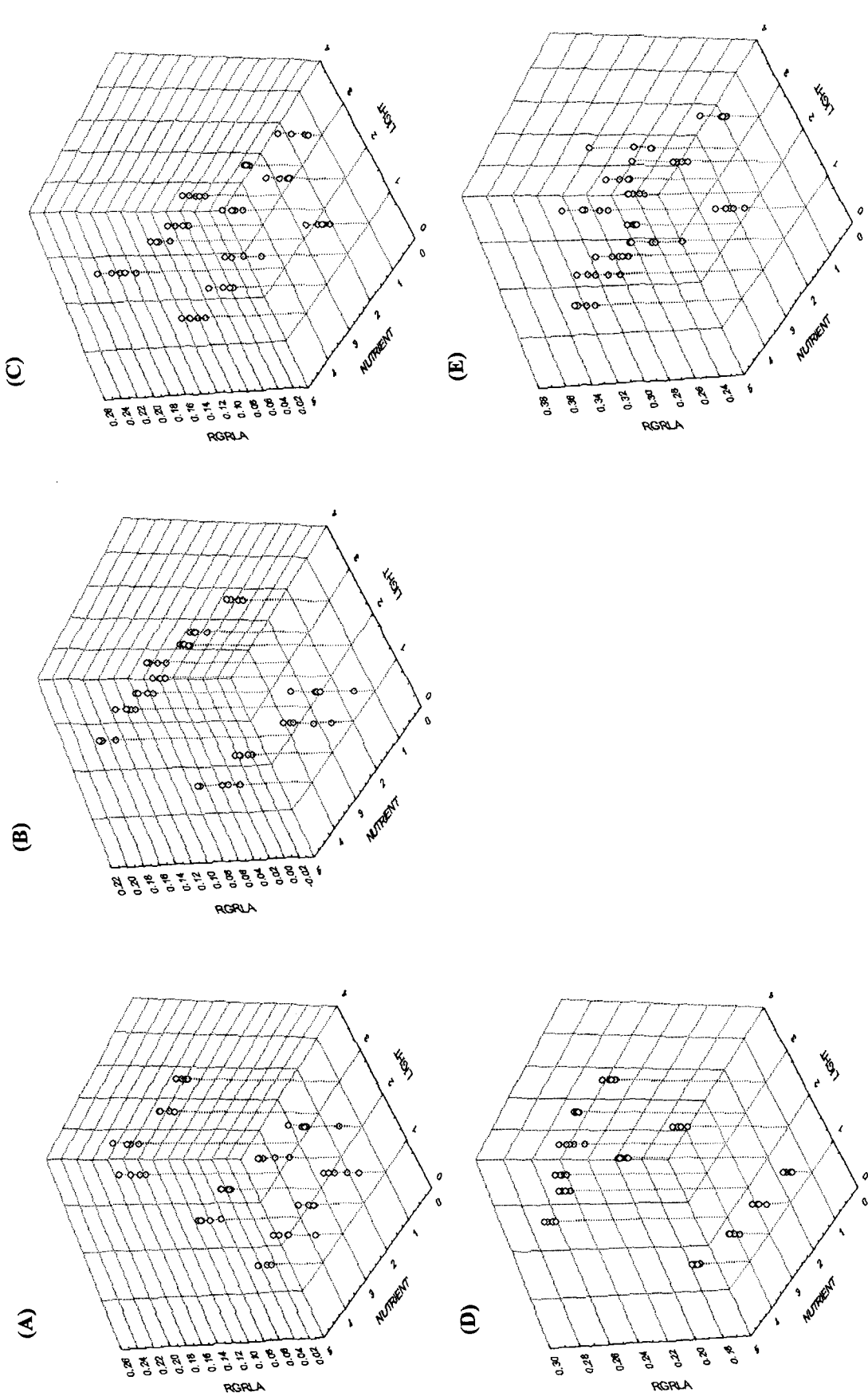


Figure 7.5. 3D scatterplot for relative leaf area growth rate for the selected species under different light and nutrient levels. (A) *Alangium chinense*, (B) *Sapindus mukorossi*, (C) *Spondias axillaris*, (D) *Mesua ferrea* and (E) *Shorea assamica*

Table 7.7. Results of multiple regression analysis for effect of light and nutrients on relative growth rate in height and leaf area and total plant mass for the selected seedlings

Name of species	Dependent variable	No. of cases	R ²	F-value	df	Intercept	β-values
<i>Alangium chinense</i>	RGRH	60	0.79	117.29	(2, 57)	0.05	Light = 0.88* Nutrient = 0.11
	RGRLA	60	0.82	155.44	(2, 57)	-0.02	Light = 0.90* Nutrient = 0.15*
	Plant mass	60	0.84	164.39	(2, 57)	-1.78	Light = 0.74* Nutrient = 0.54*
<i>Sapindus mukkorossi</i>	RGRH	60	0.88	241.61	(2, 57)	0.03	Light = 0.91* Nutrient = 0.23*
	RGRLA	60	0.25	9.95	(2, 57)	0.01	Light = 0.40* Nutrient = 0.30*
	Plant mass	60	0.67	61.09	(2, 57)	3.02	Light = 0.79* Nutrient = 0.20*
<i>Spondias axillaris</i>	RGRH	60	0.72	79.91	(2, 57)	0.11	Light = 0.74* Nutrient = 0.42*
	RGRLA	60	0.60	46.86	(2, 57)	0.07	Light = -0.30* Nutrient = 0.72*
	Plant mass	60	0.86	203.62	(2, 57)	-0.61	Light = 0.49* Nutrient = 0.79*
<i>Mesua ferrea</i>	RGRH	60	0.56	37.05	(2, 57)	0.01	Light = 0.66* Nutrient = 0.35*
	RGRLA	60	0.72	76.41	(2, 57)	0.13	Light = 0.83* Nutrient = 0.19*
	Plant mass	60	0.81	124.04	(2, 57)	3.18	Light = 0.43* Nutrient = 0.79*
<i>Shorea assamica</i>	RGRH	60	0.56	36.73	(2, 57)	0.01	Light = 0.69* Nutrient = 0.29*
	RGRLA	60	0.50	29.67	(2, 57)	0.31	Light = -0.51* Nutrient = 0.49*
	Plant mass	60	0.81	128.93	(2, 57)	-0.40	Light = 0.82* Nutrient = 0.37*

Values with asterix mark are significant

7.4 Discussion

The forest microenvironment played a significant role in seedling mortality of *Alangium chinense*, *Sapindus mukkorossi* and *Spondias axillaris*. But, in case of *Mesua ferrea* and *Shorea assamica* partial correlation analysis did not show significant role of microenvironment in their overall seedling mortality. This could be attributed to lesser fluctuations in the forest microenvironment in the primary forest stands due to presence of canopy cover. Besides microenvironmental factors, the seedling mortality of the species in the primary and secondary forest stands was also due to various endogenous (viz. litterfall and drought) as well as exogenous (viz. herbivory by animals as well as insects) factors, though their roles were much lesser in comparison to microenvironment. Studies have shown that different microenvironments that exist across the groundstorey of the canopy opening e.g. soil moisture, nutrient status, solar radiation quality and quantity (Ashton 1992, Chazdon and Fetcher 1984) influence regeneration, survival and growth of tree species within the opening itself (Brandani *et al.* 1988, Brown and Whitmore 1992, Uhl *et al.* 1988). Seedling mortality was greater in the dry winter months than in the wet summer month, which is mainly due to soil moisture stress. Several workers have reported the damaging effect of soil moisture stress on the survival of tree seedlings (Khan *et al.* 1986, Khan and Tripathi 1991, Kumar *et al.* 1994, Kikim 1999, McLead and Murphy 1977, Mueller-Dombois *et al.* 1980, Pereira and Kozlowski 1977, Rao and Singh 1985, Rao *et al.* 1997, Schulte and Marshall 1983).

The mortality rate of *Alangium chinense* - a successional species in the secondary forest (SF3) showed significant negative correlations with air temperature which shows that the species needs a disturbed area with an open canopy with a lot of sunlight for its growth

and survival. Similarly, mortality rate of *Sapindus mukkorossi* and *Spondias axillaris* had significant positive correlations with light intensity, indicating the vulnerability of both the species to over-exposure to light in the prevailing canopy condition of the secondary forests.

Seedling mortality rate in *Mesua ferrea* and *Shorea assamica* didn't show any significant correlations with the micro-environmental factors in the primary and secondary forest stands. Seedling mortality in *Shorea assamica* was high in the early stages (first three months), which could be attributed mainly to herbivory by an unidentified insect larva. There are evidences that nutrient content in tropical forests influences the levels of herbivory and have been obtained from studies of nitrogen concentration in leaves of rain-forest plants (Coley and Kursar 1996). Low leaf nitrogen is associated with reduced preference by insects due to reduction in nutritional value (Moran and Hamilton 1980); likewise, changes that reduce the nitrogen concentration in tropical rainforest leaves reduce the rates of herbivory in the field (Kursar and Coley 1991). Another probable reason could be depletion of food reserve of the selected species associated with the pressure of sibling competition for the available resources (viz. light and moisture). Milberg and Lamont (1997) argued that seed size plays an important role in the early establishment of tree seedlings.

The seedling mortality of *Spondias axillaris* was negatively correlated with soil moisture indicating the importance of the same. The role of soil moisture in seedling establishment has been studied by Mueller-Dombois *et al.* 1980, Khan and Tripathi 1989, and Ashton *et al.* 1995.

In the present study, besides microenvironmental factors, foliage herbivory by insect larvae was more common in case of *Alangium chinense* and *Shorea assamica*. At Pasoh, Malaya, seedling populations of the shade-tolerant dipterocarp *Shorea maxwelliana* showed much lower mortality over 2 years than the light-demander *S. leprosula*, 16 and 27 percent yr⁻¹ respectively (Becker 1983), and had less leaf damage by insects and fewer insect species feeding on them (Becker 1981). Moreover, there are evidences that nutrient content in tropical forests influences the levels of herbivory and have been obtained from studies of nitrogen concentration in leaves of rain-forest plants (Coley and Kursar 1996). Low leaf nitrogen is associated with reduced preference by insects due to reduction in nutritional value (Moran and Hamilton 1980); likewise, changes that reduce the nitrogen concentration in tropical rainforest leaves reduce the rates of herbivory in the field (Kursar and Coley 1991). In addition, other factors like litterfall and seasonal drought have also caused mortality of tree seedlings of the selected species with the second factor being more common in the secondary forest stands.

Seedling mortality was more in the first 15 metres from the respective parent tree of the selected species. This is in conformity with the findings of Clark and Clark (1984). Such seedling mortality of the selected species in the primary and secondary forest stands could be attributed to density effects, damage due to branch falls and trampling by herbivores.

Overall seedling growth in terms of increment in basal diameter, total height and leaf area of all species varied significantly across seasons as well as across species. Among species differences in relative growth rates are caused by morphological parameters, while temporal changes are caused by physiological parameters (Isabel *et al.* 2001). There was

no significant effect of site over the overall growth rate except *Sapindus mukkorossi*, in which the basal diameter showed significant variation across sites.

Seedlings of all the study species showed low relative growth rates during the winter months, which could be attributed to soil moisture stress due to low rainfall as well as leaf shedding in *Alangium chinense*, *Spondias axillaris* and *Sapindus mukkorossi*. Many workers have studied the role of soil moisture in influencing growth of seedlings (McLead and Murphy 1977, Mueller-Dombois *et al.* 1980). The high relative growth rate in the rainy months could be attributed to the increased availability of nutrients due to rapid decomposition of litter on the forest floor and also to the higher moisture content of the soil.

Overall, the selected seedlings responded positively to increased fertilization as well as light levels. This is corroborated by Lawrence (2003) who reviewed the recent literatures from Africa, Asia, Central or South America and Australia on the response of tropical tree seedlings to fertilization and found that a majority of the tree species demonstrated a significant, positive response of biomass to fertilization. Maximum height and leaf area attained by *Alangium chinense*, *Sapindus mukkorossi* and *Shorea assamica* at enhanced nutrient concentrations (N₃ & N₄) under 65% light is corroborated by the findings of several workers (Burslem *et al.* 1994, Fetcher *et al.* 1996, Turner 1991 and Veenendaal *et al.* 1996) that light-demanding species tested throughout the tropics respond positively to enhanced nutrient availability. *Mesua ferrea* and *Spondias axillaris* attained maximum height growth and leaf area at better nutrient availability (N₃ & N₄) at moderate (45%) light.

Biomass accumulation in the plant parts have also been highly influenced by increasing light as well as nutrient levels except in *Sapindus mukkorossi* and *Mesua ferrea* in which maximum plant biomass was accumulated at 45% light. This is partly explained by the study made by Poorter (1999) on growth responses of 15 rain-forest tree species to a light gradient with special emphasis on the relative importance of morphological and physiological traits which says that plants attained the highest biomass under intermediate light conditions (12-25% light).

Root biomass for *Sapindus mukkorossi* and *Spondias axillaris* was highest at low fertility level (N₁) which follow descriptions of Chapin (1980) and predictions of Tilman (1988) and has been found by Kolb *et al.* (1990) for northern red oak (*Quercus rubra* L.) and Minotta and Pinzauti (1996) for beech (*Fagus sylvatica* L.) seedling growth. Moreover, Hall *et al.* (2003a) while studying the seedling performance of four sympatric African mahoganies (viz. *Entandrophragma angolense*, *Entandrophragma candollei*, *Entandrophragma cylindricum* and *Entandrophragma utile*) in relation to soil nutrient and moisture status in a shade-house experiment and found that in naturally occurring forest soils, *Entandrophragma cylindricum* and *Entandrophragma utile* exhibited decreased root mass ratio (RMR) with an increase in soil fertility while *Entandrophragma angolense* and *Entandrophragma candollei* did not. For *Mesua ferrea* root biomass was highest under increased soil fertility (N₄) as well as light level which could be partly explained based on Poorter (1999) that plants in high light are faced with high radiation loads which lead to more investment in root mass, in a way that compensates for higher transpiration losses by water uptake. Lawrence (2001) also advocated that shade-tolerant plants, unlike shade-intolerant plants, have a tendency to

capture and store more nutrients in their tissue for future use and production of higher root biomass points towards this fact.

Some evidences suggested that dipterocarp seedlings respond by changes in growth at very low nutrient levels (Turner *et al.* 1993). But, in the present study, biomass of different plant components viz. leaf, stem and root in case of *Shorea assamica* peaked at different nutrient levels (Table 8.3). Here interaction of light with nutrients could be playing a major role in differential allocation of biomass to different plant components. Interestingly, Hall *et al.* (2003b) studied seedling growth of three co-occurring *Entandrophragma* species (Meliaceae) under three light regimes (shade, light shade and full sunlight) and found that all the three species viz. *Entandrophragma angolense*, *Entandrophragma cylindricum* and *Entandrophragma utile* exhibited similar patterns in biomass allocation between light treatments with a general pattern of increasing allocation to leaves with decreasing light, and increasing allocation to both stems and roots with increasing light. But in this case the role of nutrient has not been discussed elaborately, pointing at the possibility of the existence of an interaction between light levels as well as nutrients which could effect plant growth.

Most of the derived growth parameters for the selected species varied significantly within and between different fertility as well as light levels. But fertility level did not affect LAR in *Spondias axillaris*. Similarly, RMR, LMR, SLA and LARMR were not affected significantly by light, nutrient or the interactive effects of the two in case of *Mesua ferrea*. In case of *Shorea assamica* also variation in light levels did not have significant effect over SMR. Poorter (1999) found a decrease in LMR and an increase in RMR with increased light in a study on the growth responses of 15 rain-forest tree species to a light

gradient. However, LMR and SMR increased with light and fertility levels; but RMR, SLA and LAR exhibited a decreasing trend with corresponding levels of light and nutrient which could be due to the interactive effect of light as well as fertility levels.

β values in the multiple regression analysis also show that both light and nutrient have significant role in seedling growth in terms of relative growth rate in height & leaf area and total plant biomass accumulation. In case of *Alangium chinense*, *Sapindus mukkorossi* and *Shorea assamica* light intensity influenced RGRH, RGRLA and total plant mass more significantly than nutrient level. But *Alangium chinense* did not show significant responses to increased nutrient supply which is corroborated by Lawrence (2001) who found in his study on four fallow tree species that *Peronema*, the smallest-seeded, demonstrated the most rapid growth but failed to show any response to nutrient enrichment. In this regard Huante *et al.* (1995a,b) showed a negative correlation between seed size and both relative growth rate and growth response to phosphorous.

The seedling survival of the selected species in the primary and secondary forest stands in Namdapha national park is governed by both endogenous as well as exogenous factors; the endogenous factors being more common in the primary forests and the exogenous one being more common in the secondary forest stand. Nevertheless, seedling growth rate of the selected species is strongly controlled by seasonal factors as well. From the present study it could be inferred that seedling growth of the selected species is more importantly governed by light than nutrient levels, and manipulation of light levels is warranted along with application of nutrient (NPK) for healthy growth of the seedlings in the secondary forest sites. For *Alangium chinense*, *Sapindus mukkorossi* and *Shorea assamica*, availability of sufficient light along with nutrient is important for its healthy growth. In

case of *Spondias axillaris* and *Mesua ferrea*, high intensity of light causes leaf damage as well as stunted growth irrespective of presence of high amount of nutrient.

Chapter 8

General Discussion

Secondary forests are becoming more common following different anthropogenic and natural disturbances in the forested landscapes in the tropics. They have been classified based on successional stages, vegetation types, ownership patterns, land use history, and nature of influence (Chokkalingam *et al.* 2000). In Asia, secondary forests have been classified based on landuse origin and nature of human influence. Accordingly, post-extraction secondary forests, swidden fallow secondary forests, post-abandonment secondary forests, post-fire secondary forests and rehabilitated secondary forests exist in asian countries (Chokkalingam *et al.* 2000). Champion and Seth (1968) described 78 types of secondary forests in India based on physiognomy, structure, function, floristics, dynamics, habitat, physiography and history of forests. Kaul and Haridasan (1987) described two major types of secondary forests in Arunachal Pradesh viz., degraded forests and bamboo forests based on species composition. But, considering the nature of origin of secondary forests of Arunachal Pradesh, following secondary forest types are recognized: (i) Swidden fallow secondary forest, (ii) Post-extraction secondary forest, (iii) Rehabilitated secondary forest, (iv) post fire secondary forests (forests regenerating after forest fires), (v) post catastrophe secondary forests (forests regenerating after natural disasters like floods, landslides, earthquakes), and (vi) post-abandonment secondary forests (forests regenerating after abandonment of human settlements or pastures).

Because of their immense ecological, economical, cultural and aesthetic importance, scientific studies on structure and function of these forests have been intensified in recent times. The present research was conducted in the secondary forests in and around

Namdapha national park which are regrowing on abandoned agricultural land, past human settlement areas and forest fallows. These secondary forests can be placed under post-extraction and post-abandonment categories.

The detailed vegetation analysis as well as regeneration studies undertaken during the preparation of this thesis have helped in understanding the ecology of these secondary forests. The issues which have been addressed are: (i) Whether the structure of secondary forests in and around Namdapha national park are significantly different from those of the primary forests? (ii) How differential landuse history has affected the present structure of the secondary forests? (iii) Whether tree regeneration process in the secondary forests is significantly different from the primary forests? (iv) Why some species are more successful in the secondary forest environment? (v) Whether the same species shows differential response to the primary and secondary forest environment? and (vi) Can the differential response of species during regeneration phase be an explanation of difference in species composition and structure of secondary forests?

The secondary forests showed significant differences in species composition and community characteristics from that of the primary forests. The total number of species, genera and families in the secondary forests was higher than the primary forests (Chapter 4, Table 4.1). This could be attributed to the floristic mixture of both pioneers as well as primary species in the secondary forests which makes it more heterogeneous. Adding to it, wider spatial heterogeneity that exists in these forests than the primary forests enhance the chance of colonization of new species through locating more response of favorable microsites for their establishment. Nevertheless, the primary forests were richer in endemic and threatened categories of species, although the secondary forests did support

some of the rare, endangered and endemic species like *Sapria himalayana*, *Musa velutina*, *Zalacca secunda* etc (Table 8.1).

Shannon Weiner diversity index for herbs was significantly higher in secondary forest than the primary forest. For trees and shrub species, the trend was reverse. The density of herbaceous species was high in case of the secondary forests (Chapter 4, Table 4.5). This could be due to the open canopy of the secondary forests (Chapter 3). Conversely, the Simpson's dominance index was higher for all the components in the secondary forests than the primary forests which could be attributed to the recent history of disturbance. Such findings are in conformity with the established fact that dominance increases as a function of stress (Keel and Prance 1979). Pielou's evenness index for trees was higher in the primary forests than the secondary forests, indicating greater stability of primary forests. For shrubs and herbs the index was higher in the secondary forests than the primary forests. In general, the evenness index values were low indicating uneven distribution of different species (Table 4.6).

Though, α diversity and density values of trees between the primary and secondary forest did not differ significantly, the tree species exhibited only 53% similarity. But there was 65% similarity between the primary and secondary forests for canopy tree species, which decreased to 50% and 48% respectively for the middle and lower storied trees (Figure 4.4). Shrubs, herbs and climbers showed only about 20% similarity (Figure 4.3). Overall species similarity between the primary and secondary forests was only 21%.

Tree basal area was higher in the primary forest ($67.14 \text{ m}^2 \text{ ha}^{-1}$) than the secondary forest ($31.65 \text{ m}^2 \text{ ha}^{-1}$) (Table 4.5). This could be attributed to the presence of more number of individuals in the higher girth classes which is observed from the density-girth

distribution pattern of trees. It shows that the primary forests have more number of individuals in the higher girth classes (>91cm) than the secondary forests.

More than 95 percent of the species exhibited clumped distribution both in primary and secondary forests. Only 3 to 4 percent exhibited random distribution (Figure 4.6). None of the species in the primary and secondary forest sites displayed regular distribution.

The β diversity was higher between the secondary forest stands than that between the primary forest stands (Table 4.7) depicting the existence of higher habitat heterogeneity in the secondary forests.

Table 8.1. Rare, endangered, threatened and endemic species in the primary and secondary forests in Namdapha national park

Category	Primary forests		Secondary forests		
	PF1	PF2	SF1	SF2	SF3
Rare species					
Trees	19	13	3	1	9
Shrubs	6	2	2	1	2
Herbs	3	1	2	1	1
Climbers	2	-	2	-	-
Endemic species					
Trees	9	5	3	2	2
Shrubs	-	1	-	-	-
Herbs	-	-	3	-	-
Climbers	1	-	1	-	-
Endangered/threatened species					
Trees	2	1	1	-	-
Shrubs	-	-	-	-	-
Herbs	1	-	1	-	-
Climbers	-	-	-	-	-

The landuse history has affected the successional trajectory in different secondary forest stands in Namdapha national park. Amongst the secondary forests, SF1 is floristically much diverse in terms of number of species than the other two secondary forests *i.e.* SF2 and SF3. The probable reason for this might be the moderate intensity of previous landuse and proximity of the site to the primary forests. The site is also in close proximity

to the other two secondary forest stands. Thus, there are floristic elements of both the primary as well as secondary forests at this site. The secondary forest stand SF2 had a lower diversity compared to the two primary forest stands and the secondary forest SF1. This is because, the stand had undergone an arrested succession by a bamboo species, *Dendrocalamus hamiltonii*, which is a characteristic feature in many abandoned jhum lands of northeastern India (Rao and Ramakrishnan 1987). This bamboo has taken up a larger share (118) of the total IVI. Thus, a greater portion of the site resources is shared by this species of bamboo leaving a little for the others to grow and establish. The secondary forest stand SF3 had lowest diversity comparing to other secondary forest stands. This could be because of the fact that this stand is subjected to recurrent disturbances that included both natural as well as anthropogenic. The people in the adjacent village depend mainly on this forest for fuelwood as well as for other forest products. Moreover, this site also experiences grazing.

The secondary forests exhibited better tree regeneration than the primary forests (Chapter 5). About 66% of the total tree species were regenerating in the secondary forests as compared to the latter, where only 50% species were regenerating. This could be attributed to sufficient availability of light and nutrients in the secondary forests as compared to the primary forests. Moreover, a number of remnant individual trees belonging to species *Altingia excelsa*, *Talauma hodgsonii*, *Cinnamomum bejolghota*, and *Endospermum chinense* were present in the secondary forests which acted as propagule sources. Guariguata and Ostertag (2001) advocated that presence of remnant tree species can strongly influence the rate of colonization through its effects on dispersal thus increasing the rate of recovery of both diversity as well as density of species.

Along with seedlings, the regeneration processes in the secondary forests were also through vegetative means like sprouting/ coppicing. Number of species regenerating through coppicing is more in the secondary forest stand SF3 where almost 50% of the species exhibited coppice regeneration (Chapter 5). This is because the stand is comparatively drier than the other two secondary forest stands. The cut stumps in the other two secondary forests might have been decomposed as a result of which the stumps lost its regenerative potential. Ewel (1980) also reported that trunk bases of trees in the wet tropics are subject to rapid decay comparing to dry tropics. So, regeneration by vegetative means would likely to be more successful in the dry tropics than in the wet tropics. However, there were species like *Talauma hodgsonii* and *Actinodaphne obovata* in the two secondary forest stands which were regenerating through coppicing

Nevertheless, the success of coppice regeneration in gathering biomass is dependent on the intensity of coppicing by the species present there. Studies on the effect of stump size on sprouting of selected dominant tree species (*Alangium chinense*, *Alstonia scholaris*, *Albizzia procera* and *Melia azadirachta*) (Chapter 4, Annexure I) showed that average number of sprouts was more in the higher girth classes. Bellingham (1993) also reported that larger sized stems produced more shoots and larger leading shoots. This could be due to the availability of greater carbohydrate reserves in large size stems that can be mobilized to facilitate higher levels of sprouting. The larger sized stems are bound to have a larger root biomass which will also be able to tap more of the resources needed to support growth. Conversely, Khan and Tripathi (1986) reported that sprouting percentage of the stumps and number of sprouts per stump of *Alnus nepalensis*, *Quercus dealbata*, *Quercus griffithi* and *Schima khasiana* decreased with stump diameter. Also, the sprouts

arising from the stumps of medium diameters (>15-30 and >30-45 cm) and heights (25-30 and 45-50 cm) survived better than those from the stumps of smaller or larger diameters and heights. This reduction in sprout numbers with increasing diameter has been attributed to the increasing bark thickness in the study species which provides mechanical hindrance while sprouting. The other cause of such reduction is certain physiological changes in tree species with advancement of age due to which the capability for rejuvenation by vegetative means decreases.

Coppice shoot density had a significant effect over diameter and height of the shoots for all the species except *Sapindus mukkorossi*. The growth of diameter and height of shoots was comparatively better in the stumps having less number of shoots. The poor growth of shoots at high shoot density is attributed to increased competition among the shoots for available resources (McLaren and McDonald 2003b). Therefore, high shoot number may not be an indication of successful vegetative regeneration. Although they may act as an indemnity against the death of one or a few leading shoots, higher shoot density results in a significantly lower biomass recovery. The seedling populations in all the primary and secondary forest stands showed marked differences between wet (June-July) and dry (November-December) seasons with less number of tree seedlings in the dry season (Chapter 5). Thus, regenerating through coppicing could help in recuperation of the secondary forest stands.

Successful regeneration of a species is intimately related to greater seed production, long viability period, copious germination, mass recruitment, healthy growth, good survivorship and early establishment of seedlings on the forest floor. A spectrum of abiotic as well as biotic factors affect these processes thus putting a selection pressure on

any of these stages. Five species viz., *Alangium chinense*, *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* were studied for their seed and seedling ecology. Amongst them *Alangium chinense*, *Sapindus mukkorossi* and *Spondias axillaris* were more successful in the secondary forests. *M. ferrea* and *S. assamica* had poor regeneration in these forests.

Alangium chinense had a higher number of individuals in the seedling, juvenile and young stages than mature individuals in the secondary forest, whereas in the primary forest only a few seedlings were present. The primary forest did not have any mature individuals of this species. This signifies that the species, due to its light demanding nature, would have difficulty in establishing in the primary forest environment. This is evident from the fact that the species demands a high light environment for its germination (Chapter 6).

The density of seedlings and juveniles of *Sapindus mukkorossi* and *Spondias axillaris* was more in the secondary forests than the primary forests. This could be attributed to lesser seed production, more flower abortion and high seed predation by the ungulates and squirrels in the primary forests. In the secondary forests the production was high and the frequency of seed predation was comparatively less. Most seeds of *S. mukkorossi* were dormant in the secondary forests. But the viability period of the seed is about 200 days. So, there is always a chance of seed germination when ideal conditions come in place.

Mesua ferrea had a good population in the primary forest with maximum number of individuals in the seedling and adult stages. However, in the secondary forests it was found only in seedling and juvenile stages. Dispersal of seeds of *Mesua ferrea* is

mediated by such animals as wild boar, which predate on the seeds. However, very few intact seeds are left there after consumption by wild boar. The absence of parent tree in the secondary forest stands and poor seed dispersal mechanism of the species contributed to its poor regeneration in the secondary forest. New recruitment of seedlings in the secondary forests is attributed to other dispersal agents like human beings, which are occasional.

Shorea assamica was found in all the growth stages in the primary forest, while in the secondary forest the species occurred mostly in seedling stages. The absence of individuals above the seedling stage in the secondary forests could be due to higher mortality and poor seedling recruitment as compared to the primary forests. Seed production in the primary forests was also much more than the secondary forests, perhaps because of higher rate of flower abortion in the latter. Moreover, due to recalcitrant nature of the seeds of this species, seeds lose viability quickly, i.e. within 10 days of seed fall. An inefficient seed dispersal mechanism associated with unavailability of suitable habitat for germination in the dry and open environment of the secondary forest, with short seed viability period results in low recruitment of *Shorea assamica* seedlings in the secondary forests.

Flower and fruit production showed inter-species and intra-species as well as spatio-temporal variations. These variations could either be the result of external variables like light, moisture, nutrient, rainfall or such internal mechanism of the species as masting which has been evolved to adapt the changing environment. In the present study, flower and fruit production varied significantly across different girth classes, stands as well as years. The flower and fruit production was higher for *Alangium chinense*, *Sapindus*

mukkorossi and *Spondias axillaris* in the secondary forest, whereas for *Shorea assamica* and *Mesua ferrea* the production was higher in the primary forest. Higher production in the secondary forest could be attributed to increased availability of sunlight (Barik *et al.* 1996a). High light intensity may elevate bud temperature, which may lead to increase in the concentrations of growth regulators particularly gibberellins (Pharis and Kuo 1977, Ross *et al.* 1983), stimulating flowering and fruiting. Moreover, light regime associated with temporary water stress in disturbed stands is known to stimulate bud initiation in some forest trees (Kozlowski 1981). Greater seed production in the higher girth classes could be attributed to bigger crown size as studied by Bhuyan (2002).

Seed germination in *A. chinense*, *S. mukkorossi*, *S. axillaris*, *M. ferrea* and *S. assamica* was significantly affected by stand quality ($P \leq 0.001$) (Chapter 6). *In situ* germination of *Alangium chinense* seeds was maximum (25%) on the soil surface without canopy cover and was very poor with canopy cover (1-2%). Seeds of *Sapindus mukkorossi*, *Spondias axillaris* and *Shorea assamica* germinated well under intermediate canopy cover in the secondary forest. Similar trends were also observed in the *ex situ* seed germination in the nethouse (Chapter 6). The general trend showed that the percentage of seed germination was more in case of the heavier seeds, as compared to the lighter ones (Figure 6.6) in all the species. Milberg and Lamont (1997) argued that seed size plays an important role in the early establishment of tree seedlings. They experimentally removed the cotyledons from seedlings of *Eucalyptus loxophleba* (small seeded species) and *Hakea psilorrhyncha* (large seeded species) in southwestern Australia and found increased mortality and reduced root-penetration, growth rate and weight of plants after 12 weeks, in proportion to seed size. Grime and Jeffrey (1965) and Rabinowitz (1978) also showed that seed mass

was positively correlated with the ability to survive in shady environments. On the contrary, Augspurger (1984) and Boot (1996) argued that survival was not related to initial seed mass. Nevertheless, tiny seedlings suffer the heaviest mortality as reported by Lieberman (1996) and Alvarez-Buylla and Martinez-Ramos (1992) which is yet another function of seed size (Khan *et al.* 2002). Progressively lower mortality with increasing seed size has been shown in Penang by Turner (1990), for dipterocarps by Brown and Whitmore (1992), and Swaine (1990). Still (1996) reported that a mortality rate of dipterocarp seedlings at Danum was much higher in species regarded as light-demanders compared to shade-tolerant species.

But, seed size did not significantly affect seed germination of the study species except *Shorea assamica*. In all other species, germination was significantly affected by differences in light levels (Table 6.7). This indicates the role of canopy opening in seed germination.

Although significant correlation between litter depth and seed germination was not obtained, all the species except *Alangium chinense* did exhibit positive correlation between the two variables. This could be due to the absence of moisture in the litter. Plant litter can influence patterns of seedling regeneration in tropical rain forests through a number of processes affecting both the physical and chemical environment (Facelli and Pickett 1991). At the seed germination stage, litter can intercept light, which will inhibit germination by altering the red/far-red ratio (Vazquez-Yanes *et al.* 1990); it can act as a physical barrier to seedling emergence (Molofsky and Augspurger 1992), especially for small-seeded species which do not have a large supply of resources (Metcalf and Turner

1998), and may prevent newly germinated radicles from reaching the soil (Brearley *et al.* 2003).

Seedling recruitment of the selected species also differed in the primary and the secondary forest stands. Seedling recruitment for *Alangium chinense*, *Sapindus mukkorossi* and *Spondias axillaris* was higher in the secondary forests than in the primary forests. Conversely, seedling recruitment for *Mesua ferrea* and *Shorea assamica* was higher in the latter than the former. Year-wise, the seedling recruitment for all the species was higher in the year 2004 than in the year 2003, indicating the occurrence of mast fruiting events in all the species studied. The high seedling mortality of *Alangium chinense* and *Sapindus mukkorossi* occurred during the early months of germination, which was correlated with soil temperature and light intensity, respectively (Chapter 7, Table 7.3). Seedling mortality in case of *Spondias axillaris* was positively correlated with light intensity and negatively correlated with soil moisture. However, the seedling survivorship curves for *Mesua ferrea* and *Shorea assamica* showed a sharp reduction in the number of surviving individuals after 3 months period and continued till the seedlings attained one year age, after which the seedling populations stabilized (Chapter 7, Figure 7.1). Mortality in this case could be attributed to such exogenous factors as herbivory and falling of plant parts. In general, seedling mortality for all the species was more under canopy of the parent tree than the peripheral area (Chapter 7, Figure 7.2), supporting the “escape hypothesis”. This could be due to trampling by animals and competition amongst the seedlings, whose density below the parent tree was invariably high.

In general, the relative growth rate in height as well as leaf area of all the selected species was strongly influenced by seasonal changes with maximum growth in the rainy season

(June-July) and least growth in the winter months (December-February) (Table 7.2, Figure 7.3 and Figure 7.4). Seedling growth rate in terms of height and leaf area was higher in the secondary forests for *Alangium chinense*, *Sapindus mukkorossi* and *Spondias axillaris*. For *Shorea assamica* and *Mesua ferrea*, the relative growth rate was more in the primary forest than the secondary forest (Figure 7.3 and Figure 7.4). These variations could be either due to variation in light or availability of nutrients.

Seedlings were grown *in situ* condition in the nethouse under three light levels and four fertility gradients to know which factor was causing significant variation in seedling growth. The study showed that the seedling size, seedling morphology and biomass accumulation of all the species varied significantly under different light and nutrient levels (Table 7.4). But height, leaf area and collar diameter for *Alangium chinense* was highest at high light intensity (65%) while for *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* it was highest at intermediate light intensity (45%) (Chapter 7, Table 7.5). *Shorea assamica* attained maximum height and collar diameter at 65% light. All the selected species responded positively to increased level of nutrients (30 and 35 gm of NPK) mostly under 45-65% light levels.

All the species exhibited similar patterns of biomass accumulation under different light and nutrient treatments with a general trend of increasing biomass allocation to stems, leaves and roots with increasing light (Chapter 7, Table 7.5). Root biomass decreased with increasing nutrient concentration irrespective of light intensity in *Sapindus mukkorossi* and *Spondias axillaris*. With increasing nutrient concentration, irrespective of light levels, biomass allocation to leaves and stems increased in all species.

In *Sapindus mukkorossi* and *Mesua ferrea*, maximum total plant biomass was obtained at 45% light; whilst in *Alangium chinense* total plant biomass was highest at high nutrient level (N₄) at 65% light. In *Sapindus mukkorossi* root biomass was highest at low nutrient level (N₁) while stem and leaf biomass was highest under high nutrient level (N₄). Root biomass in *Spondias axillaris* was highest at low nutrient level (N₁) whilst stem and leaf biomass was highest at higher nutrient level (N₄). For *Mesua ferrea* root, stem and leaf biomass were highest under high nutrient level (N₄) (Table 7.5). In *Shorea assamica* leaf and stem biomass values were highest at N₄ nutrient level while highest root biomass values were obtained at low nutrient level (N₁). Similar trend of decreased root biomass with increase in nutrient levels was reported by several workers (Gleeson 1993, Hilbert 1990, Kachi and Rorison 1989). A similar pattern was found empirically by Wilson (1988) in a review of experimental studies on biomass allocation.

Relative growth rate in terms of height and leaf area increased consistently across light and fertilizer gradients (Chapter 7, Figures 7.4 & 7.5). Relative growth rate in height increased along the fertilizer gradient and was highest at 65% light for all species while the relative growth rate in leaf area was highest under intermediate light intensity (45%) in all the species except *Alangium chinense* (Chapter 7, Figure 7.5).

Overall, LMR and SMR showed an increasing trend with increasing light and nutrient levels; but RMR, SLA and LAR exhibited a decreasing trend with corresponding levels of light and nutrient (Chapter 7, Table 7.6). Most of the derived growth parameters for all the selected species varied significantly within and between different fertility as well as light levels. But fertility level did not affect LAR in *Spondias axillaris*. Similarly RMR, LMR, SLA and LARMR were not affected significantly by light, nutrient or the

interactive effects of the two in case of *Mesua ferrea*. In case of *Shorea assamica* also variation in light levels did not have significant effect over SMR. Conversely, Poorter (1999) and reported decrease in SLA and LAR, and increase in RMR with increased irradiance in 15 rain forest-tree species along a light gradient. But, in his studies, he did not take into consideration the different nutrient levels which could also have some effect on seedling growth. In the present study, both light and nutrient had significant role in seedling growth in terms of relative growth rate in height and leaf area and total plant biomass accumulation (Chapter 7, Table 7.5). Thus, in case of *Alangium chinense*, *Sapindus mukkorossi* and *Shorea assamica* light intensity influenced RGRH, RGRLA and total plant mass more significantly than nutrient level (Chapter 7, Table 7.7). But in *Spondias axillaris* and *Mesua ferrea*, nutrient levels more significantly influenced RGRLA and total plant mass than light levels. Thus, it could be said that both light as well as nutrients have significant roles to play in the overall seedling growth.

Alangium chinense, *Sapindus mukkorossi* and *Spondias axillaris* were performing better in the secondary forest, while *Mesua ferrea* and *Shorea assamica* have better regeneration in the primary forests (Table 8.1). Based observations as well as different evidences from literature *Alangium chinense*, *Sapindus mukkorossi* and *Spondias axillaris* could be considered as successional species and *Mesua ferrea* and *Shorea assamica* could be placed under primary species.

Table 8.2. Species response to the primary and secondary forest environments

Species	Parameters	Response	
		Primary forests	Secondary forests
<i>A. chinense</i>	Population density	Nil	High
	Seed production	Nil	High
	Seedling population	Low	High
	Seedling growth	Poor	Good
	Coppice density	Nil	High
<i>S. mukkorossi</i>	Population density	Low	Moderate
	Seed production	Average	High
	Seedling population	Average	High
	Seedling growth	Average	Good
	Coppice density	Nil	Average
<i>S. axillaris</i>	Population density	Low	High
	Seed production	Average	High
	Seedling population	Average	High
	Seedling growth	Poor	Average
	Coppice density	Nil	Nil
<i>M. ferrea</i>	Population density	High	Low
	Seed production	High	Nil
	Seedling population	High	Low
	Seedling growth	Average	Poor
	Coppice density	Nil	Nil
<i>S. assamica</i>	Population density	Moderate	Low
	Seed production	High	Average
	Seedling population	High	Average
	Seedling growth	Good	Poor
	Coppice density	Nil	Nil

Table 8.3. Characters of tree species studied and used for classifying pioneer tree species in Namdapha national park

Features	Evidences	Species displaying the characters
Diagnostic	Seeds only germinate in canopy gaps open to the sky	<i>A. chinense</i> , <i>S. mukkorossi</i>
Reproduction	Seeds small and often orthodox Reproductive effort high; seeds produced in large numbers	<i>A. chinense</i> , <i>S. mukkorossi</i> <i>A. chinense</i>
Demography	Seeds abundant in soil seed bank Juvenile mortality high	<i>A. chinense</i> <i>A. chinense</i> , <i>S. axillaris</i>
Growth and form	Growth rapid Wood pale and low density Leaves generally large Leaves short-lived (with high turn over)	<i>A. chinense</i> , <i>S. mukkorossi</i> , <i>S. axillaris</i> <i>A. chinense</i> , <i>S. axillaris</i> <i>A. chinense</i> <i>A. chinense</i> , <i>S. axillaris</i>
General	Strongly associated with disturbance	<i>A. chinense</i>

Considering the responses of various constituent species, it may be concluded that for faster recovery of secondary forests, manipulation of light and nutrient levels may be introduced. Based on the findings of the study following may be concluded:

1. The differential disturbance history had significant impact on the community structure, species composition and regeneration processes of the secondary forests.
2. The structure of primary and secondary forests significantly different, which was a function of prevailing microenvironment, nutrient availability and events during regeneration phases of the dominant species. All these factors, in turn, were also influenced by the community structure.
3. The secondary forests were species-rich and had better regeneration than the primary forests. However, due to past disturbance history, the community characteristics in these forests were relatively less complex than those of the matured primary forests.
4. The species had differential response to primary and secondary forest environments, which was both during adult as well as regenerating phases.
5. Based on the response of the species during the regenerating phase to two different forest environments, the future forest composition could be predicted.
6. Considering the species response to primary and secondary forest environment (Table 8.2) as well as the species characteristics (Table 8.3), *Mesua ferrea* and *Shorea assamica* may be classified as primary species, *Alangium chinense* and *Spondias axillaris* as early successional species and *Sapindus mukorossi* as mid-successional species.

Summary

Secondary forests are becoming an integral component of the tropical forest landscapes. Due to their role in providing ecological services, economical returns, cultural values and aesthetic importance, scientific studies on these forests is gaining momentum. Secondary forests can be defined as 'forests regenerating after partial or complete removal of tree component due to anthropogenic factors e.g. logging, shifting cultivation, clearance for settled agriculture and human settlements etc., which significantly alters the overall community structure as well as the species composition'. They have been classified based successional stages, vegetation types, ownership patterns, land use history, and nature of influence.

The present study was carried out in the secondary forests in and around Namdapha national park, in the Changlang district of Arunachal Pradesh. They are regrowing on abandoned agricultural land, past human settlement areas and forest fallows and can be placed under post-extraction and post-abandonment categories.

The major objectives of the present work were to: (i) characterize the vascular plant diversity in the secondary forests, (ii) study the regeneration ecology of some of the important tree species and, (iii) identify the factors affecting regeneration of some important tree species. The major findings have been summarized in the foregoing sections.

- Floristic diversity was higher in the secondary forests (180 species, 144 genera and 66 families) as compared to the primary forests (160 species, 117 genera and 62 families).

- Overall species similarity between the primary and secondary forests was 21.2%. The tree species exhibited 53.2% similarity, shrub species 21.8%, and herb and climber species exhibited 20.6% similarity. Similarity in canopy tree species between the primary and secondary forests was 65%, while for middle and lower storied trees the similarity was 50% and 48%, respectively.
- Tree density between the primary and secondary forest did not differ significantly. Shrub density is significantly higher in the primary forest than the secondary forest and the density of herbs is greater in the secondary forests than the primary forests.
- Amongst trees, *Ostodes paniculata*, *Saprosma ternatum* and *Altingia excelsa* were commonly encountered (>50% frequency) in the primary forests, whereas *Dysoxylum reticulatum* and *Alangium chinense* were frequently encountered in the secondary forest stands (>47% frequency). Amongst shrubs, high frequency was observed were for *Elatostemma platyphyllum*, *Sarcandra glabra*, *Phlogacanthus asperulus*, *Myrioneuron nutans* and *Psychrotia silhetensis* in the primary forests and in the secondary forests *Sida acuta*, *Debregesia longifolia*, *Strobilanthes secundus*, *Leea compectiflora* and *Clerodendrum colebrookianum* were frequent. On the forest floor, *Adiantum caudatum*, *Forrestia mollissima*, *Dryopteris sparsa*, *Piper mullesua*, and *Commelina paludosa* were frequent in the primary forests, while in the secondary forests the occurrence of *Ageratum conyzoides*, *Spilanthus paniculata*, *Oxalis corniculata*, and *Paspalum conjugatum* was frequent.
- Tree basal area was higher in the primary forest stands (55.7 - 78.58 m² ha⁻¹) than that of the secondary forest stands (29.22 – 35.26 m² ha⁻¹). Species sharing most part of the basal area in the primary forests were *Altingia excelsa*, *Terminalia myriocarpa*,

and *Mesua ferrea*, while in the secondary forests *Phoebe lanceolata*, *Dysoxylum reticulatum*, *Alangium chinense*, *Albizia procera*, *Actinodaphne obovata* and *Dendrocalamus hamiltonii* had a major share.

- Both the primary as well as secondary forests displayed more than 95 percent clumped distribution of species. Only 3 to 4 percent exhibited random distribution. None of the species in the primary and secondary forest sites displayed regular distribution.
- The α diversity for tree and shrubs was higher in primary forest than the secondary forest. For herbaceous species, the trend was reverse. Shannon-Weiner index for the tree species was higher in primary forests than the secondary forests. The reverse was true for shrubs and herbs. The Simpson's dominance index for trees, herbs and climbers was more in case of secondary forests than the primary forests. In shrubs, the dominance index was more in the primary forests as compared to secondary forests. Pielou's evenness index for trees was higher in the primary forests than the secondary forests. For shrubs and herbs the index was higher in the secondary forests than the primary forests. In general, the evenness index values were low indicating uneven distribution of different species.
- The secondary forests showed more habitat variability than the primary forests, which is characterized by high β diversity between the stands SF1 and SF3 (1.82), PF2 and SF3 (1.81) and PF1 and SF3 (1.80). PF1 and PF2 had the lowest β diversity value of 1.55.
- The density-girth distribution pattern of trees shows that the secondary forests had more number of individuals in the lower girth classes' (i.e. 11-20 cm and 31-60 cm)

than the primary forests. The number of individuals in the higher girth classes (>91 cm) was more in the primary forests.

- The secondary forests exhibited better tree regeneration than the primary forests. About 66% of the total regenerating species were in the secondary forests as compared to the latter, where only 50% species were regenerating. 41% of tree species in the secondary forests were not regenerating through seeds while in the primary forests such species constituted only 48%.
- Seedling populations in all the primary and secondary forest stands showed marked differences between wet (June-July) and dry (November-December) seasons with more number of tree species in the seedling stage in the wet season.
- Coppice regeneration was found only in the secondary forest stands and was predominant in SF3 with 50% of the species regenerating through coppicing.
- Stump girth size significantly affected sprouting in *Alangium chinense*, *Alstonia scholaris*, *Albizia procera* and *Melia azadiracht* ($p < 0.001$). Average number of sprouts was more in the girth classes of 90-120 cm and 121-150 cm.
- Density of coppice shoots had a significant effect over diameter and height of the shoots ($P < 0.05$ to $P < 0.001$) for all the selected species except *S. mukkorossi*. Average diameter and height of shoots was comparatively more in the stumps having less number of shoots. The number of stumps having sprout density ranging from 1-10 was more in case of *A. chinense*, *A. scholaris*, *M. azadiracht* and *S. mukkorossi*.
- Flower and fruit production varied significantly across girth classes, stands and years. Flower and fruit production was higher in the secondary forests for *Alangium chinense*, *Sapindus mukkorossi* and *Spondias axillaris*, while for *Shorea assamica*

and *Mesua ferrea* it was higher in the primary forest. In all the species, production was higher in the year 2004.

- Seed dispersal in the selected species was primarily through gravity. But, height of release of samaras significantly affected settling time as well as dispersal distance in case of *Shorea assamica*. Pearsons' correlation coefficients showed significant negative relationship of seed weight with settling time and wing loading ($p < 0.05$; one-tailed), whilst significant positive relationships were established between wing area and settling time and seed weight, dispersal distance with settling time and wing area, and wing loading with settling time, seed weight and wing area.
- Post-dispersal seed fate experiment showed that a large proportion of the seeds of *Spondias axillaris* and *Mesua ferrea* disappeared due to seed predation by ungulates and wild boar in the primary forests. In the secondary forests, most of the seeds of *Alangium chinense* and *Sapindus mukkorossi* lay dormant. Maximum seed germination was observed in case of *Shorea assamica*.
- Seed viability of the selected species decreased consistently across a temporal scale. *Shorea assamica*, *Mesua ferrea* and *Spondias axillaris* recorded viability periods of 10 days, 48 days and 36 days respectively. Propagules of *Alangium chinense* and *Sapindus mukkorossi* maintained viability of 65 and 200 days respectively.
- The *in situ* seed germination showed that stand quality characterised by canopy openness significantly affected seed germination in all the species ($P \leq 0.001$), whereas litter depth did not have any effect over seed germination in all the species studied.
- The *ex situ* seed germination experiment showed that the percentage of seed germination was more in case of the heavier seeds, as compared to the lighter ones in

all the species but, statistically seed germination in all the study species was significantly affected by differences in light levels ($p < 0.05$ and $p < 0.005$) and not by seed weight (except *Shorea assamica* - $P < 0.05$).

- Seedling recruitment for *Sapindus mukkorossi* and *Spondias axillaris* was higher in the secondary forests than in the primary forests. For *Shorea assamica*, seedling recruitment was higher in the primary forest. Year wise, the seedling recruitment for all the species was higher in the year 2004 than in the year 2003.
- High seedling mortality of *Alangium chinense* and *Sapindus mukkorossi* occurred during first three months of germination. However, the seedling survivorship curves for *Mesua ferrea* and *Shorea assamica* showed a sharp reduction in the number of surviving individuals after 3 months period and continued till the seedlings were one year old, after which the seedling population stabilized.
- The seedling mortality rate of *Alangium chinense* was negatively correlated with soil temperature ($p < 0.05$), while that of *Sapindus mukkorossi* it was correlated with light intensity ($p < 0.05$) in the secondary forest stand. The mortality rate for *Spondias axillaris* was positively correlated with light intensity ($p < 0.05$) and negatively correlated with soil moisture in the secondary forest. Seedling mortality for all the species was more under canopy of the parent tree than the peripheral area.
- Relative growth rate in height and leaf area of *Sapindus mukkorossi* and *Spondias axillaris* was higher in the secondary forest as compared to the primary forest. On the other hand, for *Shorea assamica* the relative growth rate was more in the primary forest than the secondary forest. The relative growth rate in seedling height and leaf

area reflected a strong seasonal influence with maximum growth in the rainy season (June-July) and least growth in the winter months (December-February).

- The seedling size, seedling morphology and biomass accumulation of all the species varied significantly under different light and nutrient levels. Height, leaf area and collar diameter for *Alangium chinense* was highest at high light intensity (65%) while for *Sapindus mukkorossi*, *Spondias axillaris*, *Mesua ferrea* and *Shorea assamica* it was highest at intermediate light intensity (45%). All selected species responded vigorously to increased level of nutrients (30 and 35 gms of NPK) mostly under 45-65% light levels.
- All the species exhibited similar patterns of biomass accumulation under different light and nutrient treatments with a general trend of increasing biomass allocation to stems, leaves and roots with increasing light. Root biomass decreased with increasing nutrient concentration irrespective of light intensity in *Sapindus mukkorossi* and *Spondias axillaris*. In case of biomass allocation to leaves and stems an increasing trend was observed in all species with increasing nutrient concentration irrespective of light levels.
- In *Sapindus mukkorossi* and *Mesua ferrea*, maximum total plant biomass was obtained at 45% light; whilst in *Alangium chinense* total plant biomass was highest at high nutrient level (N₄) at 65% light. In *Sapindus mukkorossi* root biomass was highest at low nutrient level (N₁) while stem and leaf biomass was highest under high nutrient level (N₄). Root biomass in *Spondias axillaris* was highest at low nutrient level (N₁) whilst stem and leaf biomass was highest at higher nutrient level (N₄). For *Mesua ferrea* root, stem and leaf biomass were highest under high nutrient level (N₄).

In *Shorea assamica* leaf and stem biomass values were highest at N₄ nutrient level while highest root biomass values were obtained at low nutrient level (N₁).

- Relative growth rate in terms of height and leaf area increased consistently across light and fertilizer gradients. Relative growth rate in height increased along the fertilizer gradient and was highest at 65% light for all species while the relative growth rate in leaf area was highest under intermediate light intensity (45%) in all the species except *Alangium chinense*.
- Overall, LMR and SMR showed an increasing trend with increasing light and nutrient levels; but RMR, SLA and LAR exhibited a decreasing trend with corresponding levels of light and nutrient. Most of the derived growth parameters for all the selected species varied significantly within and between different fertility as well as light levels. But fertility level did not affect LAR in *Spondias axillaris*. Similarly RMR, LMR, SLA and LARMR were not affected significantly by light, nutrient or the interactive effects of the two in case of *Mesua ferrea*. In case of *Shorea assamica* also variation in light levels did not have significant effect over SMR.
- The β values in the multiple regression analysis shows that both light and nutrient have significant role in seedling growth in terms of relative growth rate in height and leaf area and total plant biomass accumulation. In case of *Alangium chinense*, *Sapindus mukkorossi* and *Shorea assamica* light intensity influenced RGRH, RGRLA and total plant mass more significantly than nutrient level. But in *Spondias axillaris* and *Mesua ferrea* nutrient levels more significantly influenced RGRLA and total plant mass than light levels respectively.

Considering the responses of various constituent species, it may be concluded that for faster recovery of secondary forests, manipulation of light and nutrient levels may be introduced. Based on the findings of the study following may be concluded:

- The differential disturbance history had significant impact on the community structure, species composition and regeneration processes of the secondary forests.
- The structure of primary and secondary forests significantly different, which was a function of prevailing microenvironment, nutrient availability and events during regeneration phases of the dominant species. All these factors, in turn, were also influenced by the community structure.
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- The species had differential response to primary and secondary forest environments, which was both during adult as well as regenerating phases.
- Based on the response of the species during the regenerating phase to two different forest environments, the future forest composition could be predicted.
- Considering the species response to primary and secondary forest environment as well as the species characteristics, *Mesua ferrea* and *Shorea assamica* may be classified as primary species, *Alangium chinense* and *Spondias axillaris* as early successional species and *Sapindus mukorossi* as mid-successional species.

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