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ECOPHYSIOLOGICAL RESPONSES OF TREE SPECIES TO ELEVATION GRADIENT IN THE SHOLA FORESTS OF KERALA

U.M. Chandrashekara

Kerala Forest Research Institute
(An Institution of Kerala State Council for Science, Technology and Environment)
Peechi- 680653, Thrissur, Kerala.

Abstract of Project Proposal

Code	KFRI RP 551/2008
Title	**Ecophysiological responses of tree species to elevation gradient in the shola forests of Kerala**
Activities undertaken	a) To compare and contrast ecophysiological features of trees of a given shola species growing in an elevation gradient, and b) To analyse physiological response to elevation by a set of co-dominant shola tree species
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CONTENTS

Abstract

This study describes changes in the structure and composition of tree community and growth and physiological properties of seven tree species in the shola forests, Anamudi Shola National Park, Kerala, over an altitude range of 1900 m- 2400m. A total of 61 tree species, belonging to 48 genera and 29 families were recorded. The total number of species per plot decreased as the altitude increased. Density of mature trees, saplings and seedlings and basal area of mature trees and saplings also declined with increase in elevation. Out of 61 tree species, seven species namely *Cinnamomum sulphuratum* (hereafter, *Cinnamomum), Litsea wightiana* (*Litsea*), *Neolitsea scorbiculata* (*Neolitsea*), *Persea macrantha (Persea*), *Phoebe lanceolata* (*Phoebe*), *Syzygium densiflorum* (*Syzygium*) and *Turpinia nepalensis* (*Turpinia*) were found in all in three tree phases in all elevations. These seven species were selected to compare and contrast their ecophysiological and growth properties along the elevation gradients. At each plot, growth (Relative Growth Rate; RGR) and physiological traits (photosynthetic rate; Pn, quantum use efficiency of photosynthetic system; Fv/Fm, stomatal conductance; Gs, and transpiration rate, E) varied among the seven species. In the lower altitude plot (P1: Altitude 1900 m above msl), *Cinnamomum* recorded significantly high RGR and Pn, when *Turpinia* recorded significantly high Gs and E. On the other hand, in the higher altitude plot (P3: Altitude 2400 m above msl) *Litsea, Neolitsea* and *Syzygium* recorded highest Gs while *Turpinia* recorded highest E. In the present study, strong and positive relationships between RGR, Pn and Gs observed in *Cinnmomum* indicated that in this species RGR is regulated both by Pn and Gs. Whereas, in species like *Persea, Syzygium* and *Turpinia* the Gs did not influence their RGR and Pn. A linear trend of increasing RGR and Pn in *Turpinia* and decreasing RGR and Pn in *Cinnamomum* with altitude was seen. However, the other five species showed least response to changing altitude and thus have the ability to acclimate to a wider range of environmental condition prevailing in shola forests. The study thus shows how a suite of inter-related ecophysiological and growth traits of different species can result in co-occurrence of several species in a shola forest.

1. Introduction

Shola forests of Kerala belong to the broad category of tropical montane forests represented in the continents of Asia, Africa and America. In Kerala, typical shola forests are distributed along the crest of the Western Ghats, where the altitude goes beyond 1,800 meters. These forests are structurally complex and harbor many plants endemic to the Western Ghats. Like in other tropical forest belts (Brown, 2001; Lomolino, 2001; Rahbek, 2005), in shola forests altitudinal gradient is one of the ecological factors, which influences structure, composition and diversity of plant community. This is due to the fact that with increasing altitude, temperature as well as the partial pressure of air, water vapour and CO_2 decrease, whereas solar radiation flux may increase (Ricklefs, 2004). Therefore, altitudinal gradients provide a most powerful `natural experimental set up' for testing ecological and evolutionary responses of biota to environmental changes (Qian and Ricklefs, 2004). A number of studies, particularly in low and midland tropical forests, have examined the plant community properties along altitudinal gradients (Beals, 1969; Liebermann et al., 1996; Brown, 2001; Lomolino, 2001) and such kind of studies are scanty in montane forests (Lovett *et al.*, 2006). At the same time, none of these studies have addressed the question does the elevational distribution of individual species in shola forests conform to the individualistic hypothesis or integrated hypothesis. The individualistic hypothesis postulates that each species has an independent, individualistic, distribution along the environmental gradient, whereas or to the integrated hypothesis predicts that each species is clustered into discrete communities with noticeable boundaries because the presence or absence of that species is largely governed by the presence or absence of other species.

The main geophysical drivers along altitudinal gradients from an ecological point of view are temperature, air pressure, precipitation and radiation. These geophysical drivers, apart from influencing the structure and functions of the plant community can also influence the leaf morphology and physiology of individual species (Letts *et al.*, 2010). Indeed, majority of the tropical tree species may maintain a regularly high level of growth-related activity through morphological, phenological and physiological changes in response to a wide range of environmental conditions prevailing along an altitudinal gradient (Cordell *et al.*, 1999). The main physiological traits that control the carbon uptake and water loss in plants and generally vary according to elevation are photosynthesis and stomatal conductance (Premoli and Brewer, 2007). In fact, majority of the studies on ecophysiology of tropical tree were aimed to compare among species of different successional status (Strauss-Debenedetti and Bazzaz, 1991;Thompson *et al.*, 1992; Sreejith *et al.*, 2008) and offered a great deal of information on ecophysiological growth differences between the extremes of the tree life history spectrum. However, studies to address the question of how species with similar ecologies or successional positions differ in their patterns of assimilation and allocation are scanty (Ashton, 1992; Davies, 1998). Fine-scale differences in ecophysiology and growth rate have been found to be important in influencing the distribution of some species with similar ecologies (Chazdon, 1986). However, studies to assess the degree to which variation among co-occurring species is reflected in their ecophysiological characteristics have not been addressed for the tropical montane forest tree species.

Tropical trees do show plasticity and ability to acclimatize to variable environmental conditions (Khurana and Singh, 2001). Physiological plasticity also helps the species to adjust to the composition of their communities, promoting co-existence and community diversity (Callaway *et al.*, 2003). The degree of plasticity across the elevation gradient may differ among species. It is also reported that variation in growth rates of seedlings of a species observed along the elevation gradients can be modulated by one or many physiological traits (Zhang *et al.*, 2005). However, certain questions still to be addressed include a) how the physiological properties and relative growth rates of a set of species alter along elevation gradients, b) what is the relationship among different physiological traits, and c) can physiological traits singly or in combination predict the growth of seedlings of a species.

The study was conducted in three sites along an altitudinal gradient in shola forests to make a comparative analysis of the functional response to gradients of elevation by a set of shola tree species. The specific objectives of the study were to a) compare and contrast growth and ecophysiological features of seedlings of a given shola species growing in an elevation gradient, and b) analyse growth and physiological response to elevation by a set of co-occurring shola tree species.

2. Study area and climate

The study was conducted in Anamudi Shola National Park (10° 05 ' N – 10° 20' N latitude and 77° 0' E – 77°10' E longitude) located in the Kerala part of Western Ghats, India. The total extent of the National Park is around 7.5 km^2. The climate is typically monsoonal and annual rainfall recorded is 4040 mm (Kallarackal and Somen, 1999) with maximum rainfall in July (1683 mm) and minimum in March (3 mm). Annual mean maximum temperature is 27.7^{0} C and the annual mean minimum temperature is 11.0^{0} C. During monsoon (June-September), mean temperature is 16.3^{0} C and it is 17.5^{0} C during dry season (October-May). May is the hottest with mean maximum temperature of 24.1^{0} C and January is the coldest mean minimum temperature of 15.3^{0} C. Relative humidity varies from 65-82%. Soil is loamy and acidic with high organic content. The pH varies from 5.2-5.6.

3. Methods

3.1. Selection of plots

Field surveys in the Anamudi Shola National Park were initiated during December, 2008 to select plots located along an elevation gradient. A Trimble GEOXT 2005 (TerasynTM Software) was used to stratify the study area into three altitudinal ranges with 200 m increment i.e., from 1900 m, 2100 m and 2300 m above msl respectively. Thus three distinct altitudinal gradients were selected and in each one of them a semi-permanent plot was established. While the plots at 1900 m (hereafter P1) and 2100 m (P2) were 1 ha (100 m x 100 m) in size, the plot at 2300 m (P3) above msl was 0.5 ha (50 m x 100 m) in size.

3.2. Vegetation analysis

Each plot was subdivided into 10 x10 m quadrats and all mature trees (gbh $\geq$30.1 cm; gbh measured with tape at 1.37 m above ground), saplings (gbh 10.1cm - 30.0 cm) and tree seedlings (girth<10.cm, height <1.0. m) were marked, identified and girth recorded. For the trees with large buttress, girth was measured just above the level of buttress. In the case of trees with multiple stems, each stem was measured separately. The data of the inventory were analyzed in accordance with published procedures (Kershaw, 1973). The density, basal area and frequency of distribution trees in the plot were analysed for relative density, relative dominance and relative frequency respectively. The sum of relative density, relative dominance and relative frequency represented Importance Value Index (IVI) of various species. Shannon index of general diversity and Simpson's index of dominance were calculated following Margalef (1968) and Simpson (1949) respectively.

3.3. Species selection

Seedlings of seven tree species present in all the three plots and in all three tree phases (mature tree, sapling and seedling) were selected. These were *Cinnamomum sulphuratum* (Kattukaruva), *Litsea wightiana* (Patrathali), *Neolitsea scorbiculata* (Velladan), *Persea macrantha* (Kula mavu), *Phoebe lanceolata, Syzygium densiflorum* (Pillanjaval) and *Turpinia nepalensis* (Pampara vetti).

3.4. Relative Growth Rate (RGR) measurement

Fifteen seedlings (seedling height ranging from 50 cm to 95 cm and collar girth 5.0-9.5 cm) of each species were harvested for developing allometric equations relating height, girth and shoot biomass. Increments in collar girth and height were recorded at six month intervals for two years (June 2009-2010) and the average biomass increments were calculated non-destructively with the help of regression equations, $\text{Log}_{10}\ Y= a+ b\ \text{Log}\ 10\ (d^2h)$, where Y is shoot biomass in gm and d is diameter in cm and h is height in cm.

Biomass increment of each of the five individuals of a given species in a given plot was calculated using the regression equation at six month intervals and then averaged to obtain one biomass increment value at a given time interval. RGR was then calculated as $RGR= (\ln W_2- \ln W_1)/(t_2-t_1)$, where W_1 and W_2 are initial and final biomass and t_1 and t_2 are initial and final time period, respectively.

3.5. Physiological trait measurement

Three physiological traits namely, photosynthetic rate (Pn), stomatal conductance (Gs) and transpiration rate (E) were studied at three plots during April 2010 and April 2011. Five seedlings per species were selected in each plot and labeled for measurement. The seedlings were approximately 70-80 cm height and collar girth ranged from 4.5 cm to 9.5 cm.

A Portable Photosynthesis System, LiCor-6400 (LiCor Instruments, USA) was used to measure photosynthetic rate (Pn), stomatal conductance (Gs) and transpiration rate (E). The measurement were taken for fully developed leaves of each of five seedlings of each species in each plot between 9.30 am and 11.30 am under cloud free condition for five days in each year during April 15 and April 21. The light intensity was 200-300 μ mol m^{-2} s^{-1}, as measured by LiCor-6400. There was no significant difference in light intensity between plots.

The chlorophyll fluorescence at ambient temperature was measured on fully developed leaves of five seedlings of each species in each plot using Portable Plant Efficiency Analyser (PEA, Hansatech, King's Lynn, UK). Before measurement, leaves were darkened with leaf clips at least for 20 minutes in order to make the photochemical and non-photochemical processes of the seedlings to relax. Later, the plant was illuminated with an extremely dim light (1 μ mol m^{-2} s^{-1}) for measuring F_0, the dark adapted yield of chlorophyll florescence. Subsequently, illumination with a brief pulse of extremely bright light (> 2000 μ mol m^{-2} s^{-1}) helped to saturate the electron transport through PSII and measure F_m, the maximum yield of chlorophyll fluorescence. The Fv/Fm ratio (F_v/F_m= 1- F_0/F_m) was used to estimate the quantum use efficiency of PSII.

3.6. Data analysis

Statistical analysis was performed using SPSS Software (Version 10.0, SPSS Inc., Chicago, IL, USA). Intra-species difference along the elevation gradients and inter-species difference in each plot in physiological and growth variables were determined using analysis of variance (ANOVA) and Tukey's post-hoc test.

4. Results and discussion

4.1. Distribution of life-stages of tree species across altitude gradients

The tree community of the elevational transects totaled 61 species in 48 genera and 29 families (Table 1). The total number of species in different phases of tree community varied with 58 species represented in mature tree phase, 46 in sapling phase and 50 in seedling phase. While 43 species were recorded in all three phases, 11 were seen only in tree phase, 4 were seen in tree and seedling phases and 3 in sapling and seedling phases.

In each tree phase, the total number of species per plot decreased as the altitude increased (Table 2; Appendix 1), paralleling a pattern seen in wet forests of Ecuador (Gentry, 1988) and Costa Rica (Lieberman et al., 1996). Three reasons can be drawn for the reduction in species richness with elevation in tropical forests. In tropical montane forests, the forest patches at high elevations are smaller in size and more isolated from similar habitats than those at low elevations, and thus support a lower equilibrium number of species. The second reason for the reduction in species richness with elevation in these forests could be elevational differences in nutrient availability, forest stratification and plant speciation. The greater availability of nutrients and moisture at lower elevations may reduce the whole-plant compensation points (Givnish, 1999) and thus permits more individuals and species to persist in the plot. The third reason could be the fact that at higher elevations cooler temperatures, decreased rate of nitrogen mineralization and nitrification (Heaney and Proctor, 1989; Tanner et al., 1990) and increased soil leaching (Vazquez and Givnish, 1998) prevailing at higher elevation may slow down the rate of plant growth resulting in diminishing the density-dependent forces that help a plant community to maintain high diversity.

The two adjacent plots such as P1 and P2 and P2 and P3 shared more number of common species than two plots located far away (P1 and P3) and this was also indicated by the similarity index values (Table 2). In order to assess the pattern of the species distributional limits, the ratio of number of species reaching an altitudinal limit (species recorded in a given plot and but absent in plot/s located at higher elevation; E) to the number of species not reaching such a limit (species present both in a given plot and in plot/s plots located at higher elevation; N) was calculated. For the mature tree community, both at altitudinal limits of 1900 m and 2100 m the E/N ratio was more than 1.0, indicating that comparatively more number of species are restricted within a given elevation limit. On the other hand, E/N ratio obtained for the sapling and seedling communities was less than 1.0 suggesting that in these two tree phases comparatively more number of species crosses a given elevation limit.

Table 1. Tree species recorded (+, present; - absent) in three tree phases (Mature trees; gbh > 30.1 cm, Saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three shola forests situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

No.	Species	Family	Mature trees	Saplings	Seedlings
1.	*Acronychia pedunculata* (L.) Miq.	Rutaceae	+	+	+
2.	*Actinodaphne bourdillonii* Gamble	Lauraceae	+	+	+
3.	*Aglaia elaegnoidea* (A. Juss.) Benth.	Meliaceae	+	-	-
4.	*Aidia densiflora* (Wall.) Masam.	Rubiaceae	+	-	-
5.	*Alseodaphne semecarpifolia* Nees.	Lauraceae	+	+	+
6.	*Aporosa fusiformis* Thw.	Euphorbiaceae	+	+	+
7.	*Ardisia rhomboidea* Wight	Myrsinaceae	-	+	+
8.	*Beilschmiedia wightii* (Nees) Benth.*ex* Hook. f.	Lauraceae	+	+	+
9.	*Bhesa indica* (Bedd.) Ding Hou	Celastracee	+	-	+
10.	*Canthium dicoccum* (Gaertn.) Teijsm. & Binn.	Rubiaceae	+	-	+
11.	*Celtis philippensis* Blanco var. wightii (Planch.) Soep.	Ulmaceae	+	+	+
12.	*Chionanthus ramiflorus* Roxb.	Euphorbiaceae	+	+	+
13.	*Cinnamomum malabatrum* (Burn.f.) Blume	Lauraceae	+	-	-
14.	*Cinnamomum sulphuratum* Nees	Lauraceae	+	+	+
15.	*Cinnamomum wightii* Meisner	Lauraceae	+	+	+
16.	*Clerodendrum viscosum* Vent.	Verbenaceae	+	+	+
17.	*Cryptocarya lawsonii* Gamble	Lauraceae	+	+	+
18.	*Cyathea nilgirensis* Holttum,	Cyatheaceae	+	+	+
19.	*Daphniphyllum neilgherrense* (Wight) K. Rosenth.	Euphorbiaceae	+	+	+
20.	*Derris brevipes* (Benth.) Baker	Fabacee	+	+	+
21.	*Elaeocarpus recurvatus* Corner	Elaeocarpaceae	+	+	+
22.	*Elaeocarpus serratus* L.	Elaeocarpaceae	+	-	-
23.	*Elaeocarpus tuberculatus* Roxb.	Elaeocarpaceae	+	-	+
24.	*Eugenia bracteata* (Willd.) Roxb. *ex* DC.	Myrtaceae	+	-	-
25.	*Eugenia calcadensis* Bedd.	Myrtaceae	+	-	-
26.	*Eurya nitida* Korth.	Theaceae	+	+	+
27.	*Glochidion neilgherrense* Wight	Euphorbiaceae	+	+	+
28.	*Gomphandra coriacea* Wight	Icacinaceae	+	+	+
29.	*Gymnacranthera canarica* (Bedd. *ex* King) Warb.	Myristicaceae	+	-	-
30.	*Hydnocarpus alpina* Wight	Flacourtiaceae	+	+	+
31.	*Ilex wightiana* Wall. *ex* Wight	Aquifoliaceae	+	+	+

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Table 1 (cont'd). Tree species recorded (+, present; - absent) in three tree phases (Mature trees; gbh > 30.1 cm, Saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three shola forests situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

No.	Species	Family	Mature trees	Saplings	Seedlings
32.	*Isonandra lanceolata* Wight	Sapotaceae	+	+	+
33.	*Isonandra stocksii* Clarke	Sapotaceae	+	+	+
34.	*Lasianthus acuminatus* Wight	Rubiaceae	-	+	+
35.	*Ligustrum perrottetii* A. DC.	Oleaceae	+	+	+
36.	*Litsea floribunda* (Blume) Gamble	Lauraceae	+	+	+
37.	*Litsea wightiana* Hook.f.	Lauraceae	+	+	+
38.	*Mahonia leschenaultii* (Wall. *ex* Wight & Arn.)	Berberidaceae	+	+	+
39.	*Mastixia arborea* (Wight) Bedd.	Cornaceae	+	+	+
40.	*Meliosma simplicifolia* (Roxb.) Walp.	Sabiaceae	+	+	+
41.	*Myrsine wightiana* Wall. *ex* DC.	Myrsinaceae	+	+	+
42.	*Neolitsea scrobiculata* (Meisner) Gamble	Lauraceae	+	+	+
43.	*Neolitsea zeylanica* (Nees) Merr.	Lauraceae	+	+	+
44.	*Persea macrantha* (Nees) Kosterm.	Lauraceae	+	+	+
45.	*Phoebe lanceolata* Nees	Lauraceae	+	+	+
46.	*Photinia integrifolia* Lindl.	Rosaceae	+	-	-
47.	*Prunus ceylanica* (Wight) Miq.	Rosaceae	+	-	-
48.	*Rhododendron nilagiricum* Zenk.	Ericaceae	+	+	+
49.	*Saprosma foetens* (Wight) K. Schum.	Rubiaceae	+	+	+
50.	*Schefflera racemosa* (Wight) Harms	Araliaceae	+	+	+
51.	*Symplocos cochinchinensis* (Lour.) Moore	Symplocaceae	+	+	+
52.	*Syzygium densiflorum* Wall. *ex* Wight & Arn.	Myrtaceae	+	+	+
53.	*Syzygium gardneri* Thw.	Myrtaceae	+	-	-
54.	*Syzygium hemisphericum* (Wight) Alston	Myrtaceae	+	+	+
55.	*Syzygium malabaricum* (Bedd.) Gamble	Myrtaceae	+	+	+
56.	*Syzygium montanum* (Wight) Gamble	Myrtaceae	+	+	+
57.	*Ternstroemia japonica* (Thunb.) Thunb.	Theaceae	+	-	+
58.	*Turpinia nepalensis* Wall. ex Wight & Arn.	Staphyleaceae	+	+	+
59.	*Vaccinium leschenaultii* Wight	Vacciniaceae	+	-	-
60.	*Viburnum coriaceum* Blume	Caprifoliaceae	+	+	+
61.	*Viburnum punctatum* Buch.-Ham. ex D. Don	Caprifoliaceae	-	+	+

Table 2. Inventory of species in three tree phases (mature trees; gbh > 30.1 cm, saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

Parameters	Mature trees	Saplings	Seedlings
Number of species in different plots			
P1	37	29	34
P2	29	28	26
P3	21	22	22
Number of species common to			
All three plots	8	7	18
P1 and P2	16	17	18
P2 and P3	12	15	13
P1 and P3	9	7	9
Similarity index			
Between P1 and P2	0.48	0.60	0.68
Between P2 and P3	0.48	0.60	0.54
Between P1 and P3	0.31	0.27	0.32
Number of species seen P1 and not in P2 or P3 (E1)	21	11	16
Number of species seen P1 and P2 or P3 (N1)	16	18	18
E1/N1	1.31	0.61	0.89
Number of species seen in P2 and not in P3 (E2)	17	13	13
Number of species seen in P2 and P3 (N2)	12	15	13
E2/N2	1.42	0.87	1.0

Density of mature trees, saplings and seedlings and basal area of mature trees and saplings decreased with increase in elevation (Table 3). The rate of decline in stem density from P1 to P2 in all three tree phases was less than that from P2 to P3. The similar trend in the rate of decline in basal area of mature trees and saplings with increase in elevation was recorded.

Dominant species in each tree phase at each elevation were defined as the three taxa with the highest SIVI. In the mature tree phase, the eight species thus identified were *Hydnocarpus alpina, Isonandra stocksii, Gomphandra coriacea, Litsea wightiana, Ilex wightiana, Alseodaphne semecarpifolia, Turpinia nepalensis* and *Syzygium malabaricum* (Table 3; Appendix 1). Among them *Hydnocarpus alpina, Isonandra stocksii* and *Gomphandra coriacea* were dominant species in P1, *Litsea wightiana, Ilex wightiana and Alseodaphne semecarpifolia* in P2 and *Turpinia nepalensis, Syzygium malabaricum* and *Litsea wightiana* in P3.

Table 3. Density, basal area, species diversity index and dominant species in three tree phases (Mature trees; gbh > 30.1 cm, Saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

Parameters	Mature trees	Saplings	Seedlings
Total tree density (individuals /ha)			
P1	645	712	2111
P2	552	602	598
P3	205	192	285
Rate of decline in density			
(P1-P2)*100/P1	14.4	15.4	71.7
(P2-P3)*100/P2	62.9	68.1	52.3
Total basal area (cm2 /ha)			
P1	505736	11759	Not calculated
P2	468098	11165	Not calculated
P3	175775	4181	Not calculated
Rate of decline in basal area			
(P1-P2)*100/P1	7.4	5.3	Not calculated
(P2-P3)*100/P2	62.4	62.6	Not calculated
Species diversity index (H)			
P1	2.739	1.885	2.401
P2	2.766	2.399	2.266
P3	2.545	2.445	2.428
Dominant species			
P1	*Hydnocarpus alpina, Isonandra stocksii, Gomphandra coriacea*	*Lasianthus acuminatus, Mastixia arborea, Hydnocarpus alpina*	*Lasianthus acuminatus, Mastixia arborea, Hydnocarpus alpina*
P2	*Litsea wightiana, Ilex wightiana, Alseodaphne semecarpifolia*	*Lasianthus acuminatus, Ardisia rhomboidea, Alseodaphne semicarpifolia*	*Lasianthus acuminatus, Ardisia rhomboidea, Litsea wightiana*
P3	*Turpinia nepalensis, Syzygium malabaricum, Litsea wightiana*	*Litsea wightiana, Syzygium malabaricum, Neolitsea scorbiculata*	*Litsea wightiana, Syzygium malabaricum, Syzygium densiflorum*

In seedling and sapling phases, *Lasianthus acuminatus*, a small tree was the first dominant species in P1 and P2. *Mastixia arborea* and *Hydnocarpus alpina* were the second and third dominant species in seedling and sapling phases of P1. On the other hand, in P2, *Ardisia rhomboidea* and *Alseodaphne semicarpifolia* in the sapling phase and *Ardisia rhomboidea* and *Litsea wightiana* in the seedling were the next two dominant species. *Litsea wightiana, Syzygium malabaricum* and *Neolitsea scrobiculata* were the dominant species both in seedling and sapling phases in P3.

Above observations indicated that in each tree phase, the dominant species possess distributional modes individualistically along the elevational gradient, with importance value declining more or less smoothly above or below the modal elevation in each case. It is also evident that the dominant species are likely to be each other's most important competitors and thus among the most important determinants of each other's distributions (Whittaker,1972).

In each tree phase and in each plot, at least 2 species were with their SIVI values more than 10% of the total IVI (i.e., SIVI >30.0) (Table 4). However, none of the species in the mature tree phase had IVI more than 20% of the total IVI. On the other hand, super-dominance of an understorey tree species *Lasianthus acuminatus* in P1 and P2 and *Litsea wightiana* in P3 can be seen in sapling and seedling phases where their individual contribution to total IVI was between 23-40%. It was also found that around 23-48% of total number of species in a given plot is represented with less than 1% of total IVI. The species diversity index values ranged from 1.885 to 2.766 with generally higher values in mature tree community than in sapling and seedling phases in each plot (Table 3).

Tree girth class distribution pattern in forest stands have been used as the indicator of forest stand quality. For instance, according to Richards (1996) a healthy forest stand will have a reversed J-shaped girth class distribution curve of trees with clear preponderance to lower girth classes. The tree girth class distribution curves obtained for all three plots followed this trend (Figure 1).

Table 4. Speices IVI distribution among species in three tree phases (mature trees; gbh > 30.1 cm, saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala. Species are ranked based on decreasing order of SIVI values.

	Mature trees		
No.	P1	P2	P3
1	55.1	46.8	49
2	39.3	32.2	46.7
3	25.6	24.6	31.2
4	25.3	21.4	26.9
5	23.7	19.7	24.7
6	20.8	19.5	24.3
7	12.6	16.3	19.8
8	12.3	14.3	18.5
9	9.7	13.1	15.0
10	9.1	13	10.8
11	8.7	12.8	7.2
12	7.2	11.7	4.1
13	6.0	9.9	4.0
14	5.2	8.9	3.9
15	4.2	7.3	2.9
16	4.1	5.3	2.9
17	3.9	3.7	2.3
18	3.8	2.6	2.3
19	3.8	2.4	1.2
20	2.2	2.2	1.2
21	1.7	2.1	1.1
22	1.6	1.9	
23	1.6	1.9	
24	1.3	1.4	
25	1.3	1.2	
26	1.3	1.0	
27	1.0	1.0	
28	1.0	1.0	
29	0.9	0.8	
30	0.9		
31	0.9		
32	0.8		
33	0.7		
34	0.7		
35	0.7		
36	0.6		
37	0.5		

	Saplings		
No.	P1	P2	P3
1	121.2	69.2	68.3
2	47.3	47.9	43.4
3	31	23.8	28
4	18.9	23.2	22.7
5	13	17.2	20.6
6	8.3	16.7	20.2
7	6.5	16.4	19.7
8	6.0	14.7	19.2
9	5.0	13.1	6.3
10	4.4	6.7	6.2
11	4.3	5.7	6.0
12	4.2	5.2	6.0
13	3.6	5.2	5.8
14	3.5	5	5.5
15	3.3	4.3	5.4
16	3.2	4.0	3.6
17	2.6	3.6	3.5
18	2.4	3.3	2.7
19	1.9	2.5	1.9
20	1.7	2.4	1.8
21	1.1	2.2	1.7
22	1.0	1.9	1.6
23	0.9	1.3	
24	0.8	1.2	
25	0.8	1.2	
26	0.8	1.1	
27	0.8	0.7	
28	0.8	0.6	
29	0.8		

	Seedlings		
No.	P1	P2	P3
1	88.8	79.6	71.1
2	26.3	57.9	38.4
3	21.9	20.7	33.2
4	19.6	17.7	25.6
5	18.3	14.7	19.5
6	17.2	14.2	19.0
7	16.6	13.1	16.7
8	9.7	11.5	16.5
9	9.6	9.7	10.7
10	8.1	8.3	9.9
11	7.0	7.9	9.6
12	5.8	6.7	5.7
13	5.8	6.6	3.9
14	5.4	5.6	3.1
15	5.1	4.0	2.9
16	4.9	4.0	2.8
17	4.5	3.5	2.5
18	4.3	3.1	2.5
19	3.5	3.0	1.8
20	2.9	2.9	1.6
21	2.2	1.9	1.6
22	1.8	0.8	1.2
23	1.8	0.8	
24	1.6	0.8	
25	1.6	0.6	
26	1.4	0.5	
27	1.2		
28	0.9		
29	0.7		
30	0.5		
31	0.4		
32	0.3		
33	0.3		
34	0.3		

Among 61 species recorded from the study plots, only *Cinnamomum sulphuratum, Litsea wightiana, Neolitsea scorbiculata, Persea macrantha, Phoebe lanceolata, Syzygium densiflorum* and *Turpinia nepalensis* were found in three plots and in all three tree phases. However, no clear trend in increase or decrease in their species diversity index value in relation to the elevation was noticed (Figure 2). These seven species were selected to compare and contrast their ecophysiological and growth properties along the elevation gradients.

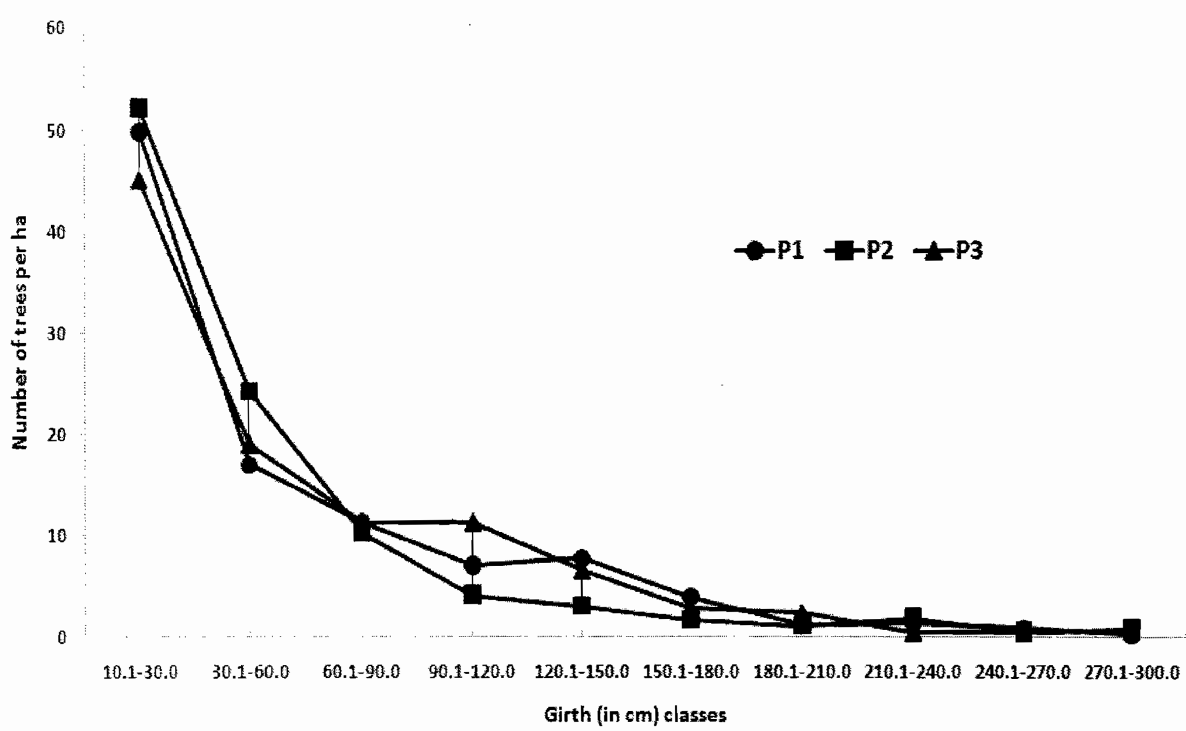


Figure 1. Girth class distribution of tree community in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

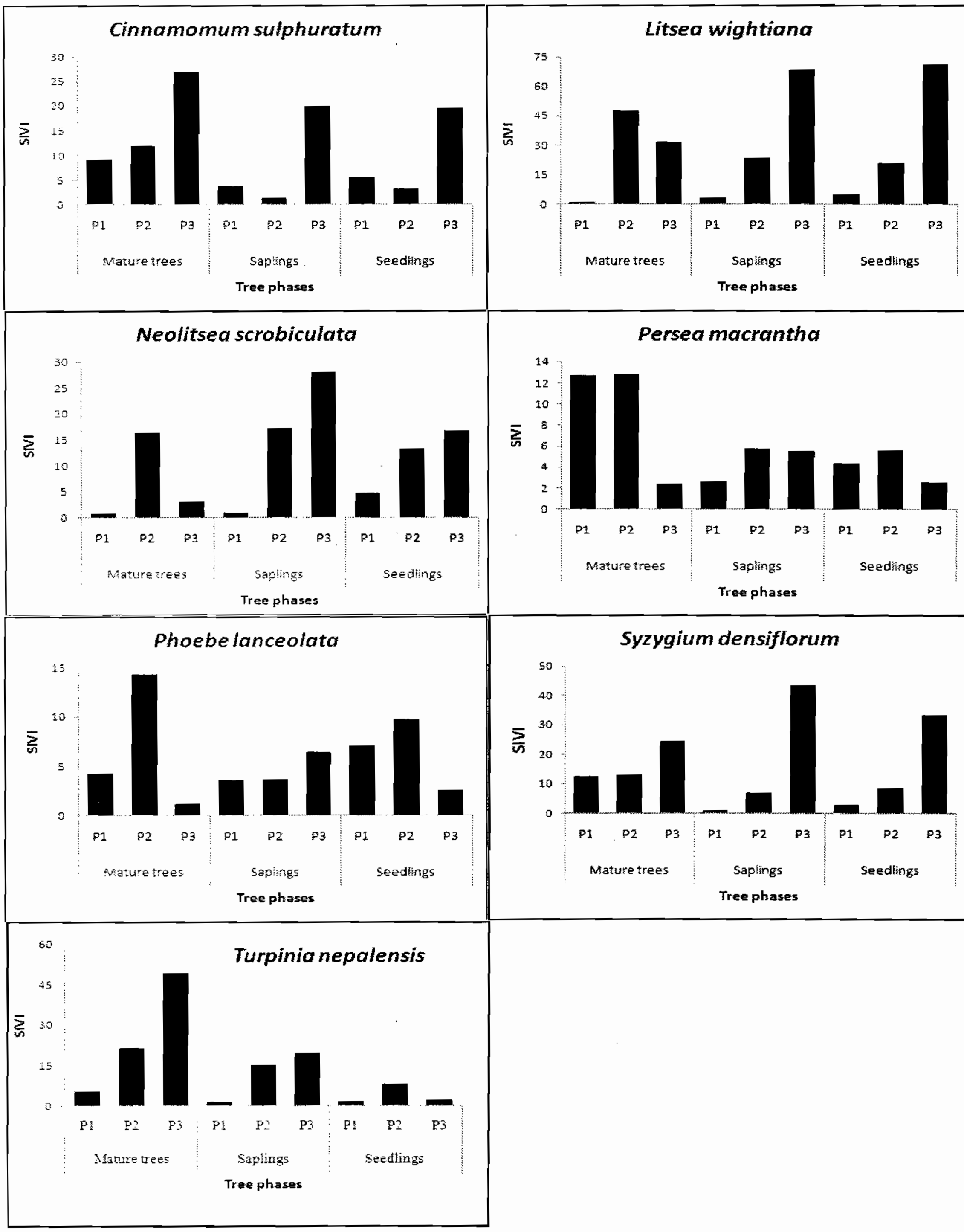


Figure 2. Species Importance index Value (SIVI) of seven tree species in three tree phases (mature trees; gbh > 30.1 cm, saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three shola forests situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

4.2. Growth rates and physiological functional traits of the tree species

In the tropics, natural forests are typically highly diverse in tree species and the associated species co-occur together with their differential functional strategies for either acquisitive use or conservative use of resources (Ellis *et al.*, 2000). A study conducted in a rainforest of Bolivia showed a high variability in leaf traits between 53 co-occurring tree species and demonstrated that leaf traits can be used to predict plant performance (Poorter and Bongers, 2006). It is also reported that a combination of some or all ecophysiological, growth and leaf nutrient traits may enable a species to survive, grow and become dominant in forest stand (Sales-Come and Holcher, 2010). In fact, there are lots of reports on ecophysiology of co-occurring plants in tropical low-land and mid-land forests (Reich *et al.*, 1991; Bonal *et al.*, 2007). However, studies to understand similar and dissimilar trend of a given functional trait in co-occurring tree species in a common environmental condition in tropical montane forests are lacking. The present study provides quantitative information on species-specific and inter-species variability of physiological and plant growth traits in a set of species of a tropical montane forest (shola) of India.

In the present study, the relative growth rates (RGR) of seedlings of the seven species differed by a factor of around 1.2 (Table 5). For instance, highest mean value for RGR was recorded by *Cinnamomum* in P1, *Phoebe* in P2 and *Turpinia* in P3. On the other hand, *Neolitsea* recorded the lowest mean value for the parameter in all the three plots. *Persea* and *Phoebe* in P1, *Neolitsea* and *Syzygium* in P2 and *Neolitsea, Litsea* and *Syzygium* in P3 did not show significant difference in their RGR ($P>0.05$).

Similar to the RGR, the photosynthetic rates (Pn) of the seven species varied considerably and significantly highest value for Pn was also recorded by *Cinnamomum*, *Phoebe* and *Turpinia* in P1, P2 and P3 respectively (Table 6). On the other hand, in all three plots, *Neolitsea* showed comparatively lowest value for Pn. According to Kitajima (1994), a species that shows greater abundance in a forest plot is also highly adapted physiologically to that locality by having higher photosynthetic rate. However, except for *Turpinia* in P3, no such relation between tree abundance and photosynthetic rate of a given species ($P>0.05$) was recorded.

Table 5. Relative Growth Rate (RGR; gm gm^{-1} yr^{-1}) of tree seedlings in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.Values are Mean ±SE, N=15 seedlings.

Species	Relative Growth rate (RGR; gm gm^{-1} yr^{-1})*		
	P1	P2	P3
Cinnamomum	$1.615±0.007^{a,A}$	$1.386±0.002^{a,B}$	$1.370±0.006^{a,C}$
Litsea	$1.384±0.005^{b,A}$	$1.426±0.007^{b,B}$	$1.285±0.004^{b,C}$
Neolitsea	$1.221±0.006^{c,A}$	$1.280±0.018^{c,A}$	$1.286±0.010b^{c,A}$
Persea	$1.418±0.005^{d,A}$	$1.421±0.003^{b,A}$	$1.315±0.019^{c,B}$
Phoebe	$1.430±0.004^{d,A}$	$1.481±0.004^{d,B}$	$1.327±0.012^{c,C}$
Syzygium	$1.298±0.004^{e,A}$	$1.304±0.006^{ce,A}$	$1.290±0.004^{bc,A}$
Turpinia	$1.282±0.002^{f,A}$	$1.325±0.012^{e,B}$	$1.423±0.006^{d,C}$

*, Within columns, species not sharing the same lowercase letters denote significant differences (P<0.05) among species for that plot. Within rows, plots not sharing the same uppercase letters denote significant differences (P<0.05) among plots for that species.

Table 6. Photosynthetic rate (Pn; μ mol m^{-2} s^{-1}) of tree seedlings in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.Values are Mean ±SE, N=15 seedlings.

	Photosynthetic rate (Pn; μ mol m^{-2} s^{-1})*		
	P1	P2	P3
Cinnamomum	$6.38±0.09^{a,A}$	$6.16±0.07^{a,AB}$	$6.10±0.07^{a,B}$
Litsea	$5.54±0.04^{b,A}$	$5.90±0.07^{b,B}$	$5.88±0.06^{b,B}$
Neolitsea	$4.44±0.05^{c,A}$	$4.82±0.04^{c,B}$	$4.78±0.04^{c,B}$
Persea	$5.90±0.07^{d,A}$	$5.80±0.07^{bd,A}$	$5.10±0.07^{d,B}$
Phoebe	$5.98±0.07^{d,A}$	$6.40±0.03^{e,B}$	$4.88±0.10^{c,C}$
Syzygium	$5.18±0.07^{e,A}$	$5.06±0.09^{f,A}$	$5.18±0.06^{d,A}$
Turpinia	$4.92±0.05^{f,A}$	$5.41±0.07^{g,B}$	$6.34±0.07^{e,C}$

*, Within columns, species not sharing the same lowercase letters denote significant differences (P<0.05) among species for that plot. Within rows, plots not sharing the same uppercase letters denote significant differences (P<0.05) among plots for that species.

The quantum use efficiency of photosynthetic system (Fv/Fm) was significantly high (P<0.05) in *Cinnamomum* and *Phoebe* in P1 and *Litsea* in P2 and P3 (Table 7). On the other hand significantly low (P<0.05) Fv/Fm was recorded by *Neolitsea* in P1, *Cinnamomum*, *Persea* and *Syzygium* in P2, and *Phoebe* P3. The present study indicate that in general the correlation between the quantum use efficiency of photosynthetic system (Fv/Fm) and the photosynthetic rate (Pn) of any given species is not significant (P>0.05).

In the Plot P1, among species studied, *Turpinia* had the highest stomatal conductance (Gs) while *Cinnamomum* and *Phoebe* had the lowest (Table 8). Both in P2 and P3, *Litsea*, *Neolitsea* and *Syzygium* recorded significantly high Gs. On the other hand, *Cinnamomum* in P2 and *Turpinia* in P3 had the lowest value for Gs. In all three plots, *Turpinia* and *Cinnamomum* recorded significantly maximum and minimum value for transpiration rate (E) respectively (Table 9). It was also recorded that the transpiration rates of *Cinnamomum* and *Phoebe* in P1, *Cinnamomum* and *Persea* in P2 and P3 and *Turpinia* and *Neolitsea* in P3 were not significantly different.

Table 7. Quantum use efficiency of photosynthetic system (Fv/Fm) of tree seedlings in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.Values are Mean ±SE, N=15 seedlings.

	Quantum use efficiency of photosynthetic system (Fv/Fm)*		
	P1	P2	P3
Cinnamomum	$0.7380 \pm 0.0057^{a,A}$	$0.5650 \pm 0.0053^{a,B}$	$0.6789 \pm 0.0169^{a,C}$
Litsea	$0.6343 \pm 0.0085^{b,A}$	$0.7520 \pm 0.0094^{b,B}$	$0.8877 \pm 0.0044^{b,C}$
Neolitsea	$0.4128 \pm 0.0055^{c,A}$	$0.7064 \pm 0.0036^{c,B}$	$0.5990 \pm 0.0071^{c,C}$
Persea	$0.6737 \pm 0.0083^{d,A}$	$0.5674 \pm 0.0047^{a,B}$	$0.5212 \pm 0.0049^{d,C}$
Phoebe	$0.7242 \pm 0.0078^{a,A}$	$0.6616 \pm 0.0044^{d,B}$	$0.4412 \pm 0.014^{e,C}$
Syzygium	$0.5402 \pm 0.0155^{e,A}$	$0.5655 \pm 0.0124^{a,A}$	$0.7842 \pm 0.0032^{f,B}$
Turpinia	$0.4288 \pm 0.0118^{f,A}$	$0.7035 \pm 0.0042^{ce,B}$	$0.6040 \pm 0.0037^{c,C}$

*, Within columns, species not sharing the same lowercase letters denote significant differences (P<0.05) among species for that plot. Within rows, plots not sharing the same uppercase letters denote significant differences (P<0.05) among plots for that species.

Table 8. Stomatal conductance (Gs; m mol m^{-2} s^{-1}) of tree seedlings in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.Values are Mean ±SE, N=15 seedlings.

	Stomatal conductance (Gs; m mol m^{-2} s^{-1})*		
	P1	P2	P3
Cinnamomum	$36.30±0.379^{a,A}$	$36.80±0.283^{a,A}$	$37.20±0.424^{a,A}$
Litsea	$45.76±0.611^{b,A}$	$47.20±0.228^{b,B}$	$48.30±0.277^{b,B}$
Neolitsea	$48.12±0.285^{c,A}$	$49.20±0.385^{b,B}$	$49.04±0.326^{b,B}$
Persea	$43.60±0.361^{bd,A}$	$42.68±0.340^{c,A}$	$40.30±0.292^{c,B}$
Phoebe	$38.20±0.361^{a,A}$	$41.60±0.158^{c,B}$	$39.14±0.216^{d,C}$
Syzygium	$46.24±0.282^{bce,A}$	$47.80±0.424^{b,B}$	$47.36±0.317^{b,B}$
Turpinia	$52.16±1.730^{f,A}$	$42.60±1.830^{c,B}$	$31.30±0.410^{e,C}$

*, Within columns, species not sharing the same lowercase letters denote significant differences (P<0.05) among species for that plot. Within rows, plots not sharing the same uppercase letters denote significant differences (P<0.05) among plots for that species.

Table 9. Transpiration rate (E; m mol m^{-2} s^{-1}) of tree seedlings in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala. Values are Mean ±SE, N=15 seedlings.

	Transpiration rate (E; m mol m^{-2} s^{-1})*		
	P1	P2	P3
Cinnamomum	$112.88±1.17^{a,A}$	$117.86±0.94^{a,AB}$	$120.76±1.39^{a,B}$
Litsea	$147.22±1.97^{b,A}$	$153.84±0.91^{b,B}$	$162.6±0.97^{b,C}$
Neolitsea	$173.72±1.02^{c,A}$	$184.46±1.44^{c,B}$	$180.74±2.76^{c,B}$
Persea	$136.80±1.13^{d,A}$	$125.06±0.99^{a,B}$	$121.62±0.88^{a,C}$
Phoebe	$120.30±1.14^{a,A}$	$137.78±0.61^{d,B}$	$127.9±0.71^{d,C}$
Syzygium	$157.76±0.97^{e,A}$	$164.62±1.47^{e,B}$	$166.38±1.58^{b,B}$
Turpinia	$267.02±8.87^{f,A}$	$218.22±9.37^{f,B}$	$183.28±1.23^{c,C}$

*, Within columns, species not sharing the same lowercase letters denote significant differences (P<0.05) among species for that plot. Within rows, plots not sharing the same uppercase letters denote significant differences (P<0.05) among plots for that species.

4.3. Correlations between growth rate and physiological traits of the tree species

As already indicated, seedlings of the seven species growing in a same plot differed in terms of their RGR (Table 5). For instance, in the plot P1, species can be arranged in the decreasing order of their RGR as follows

Cinnamomum> Phoebe≥ Persea> Litsea> Syzygium≥Turpinia≥Neolitsea

In order to understand the origin of variability in RGR among species, Pearson's correlation coefficients between RGR and physiological rates were calculated (Table 10). A positive significant ($P<0.05$) relationship between RGR and each of the four physiological rates (Pn, Fv/Fm, E and Gs) of *Cinnamomum* was recorded. In case of *Persea* and *Phoebe*, Pn and Fv/Fm were positively correlated with RGR ($P<0.05$), but the relationship between RGR and Gs in both the species was not significant ($P>0.05$) and between E and RGR in phoebe was negative ($P<0.05$). In case of *Litsea* and *Syzygium* also the relationships between RGR and Pn and Fv/Fm were positive and statistically significant ($P<0.05$) while between RGR and Gs and E were statistically significant ($P<0.05$) and negative in *Litsea*. On the other hand, in *Turpinia* a non-significant relation ($P>0.05$) between RGR and Pn and Fv/Fm and a positive relation ($P<0.05$) between RGR and E and Gs were recorded.

Table 10. Pearson Correlation coefficients between RGR and physiological rates for the 7 shola tree species in the plot P1 (Altitude 1900 m above msl) at Anamudi Shola National Park, Kerala. Numbers with asterisk in superscript indicate significant correlation at P=0.05.

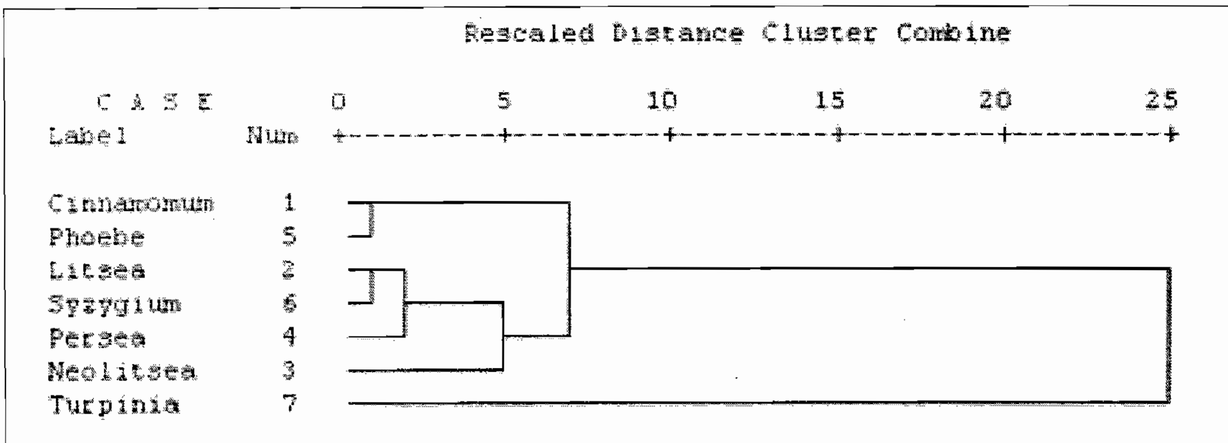
	Correlation coefficients between RGR and physiological rates			
	Pn	Fv/Fm	E	Gs
Cinnamomum	0.937*	0.843*	0.798*	0.788*
Litsea	0.834*	0.806*	-0.774*	-0.785*
Neolitsea	0.536	0.618*	-0.752	0.418
Persea	0.866*	0.811*	0.238	0.518
Phoebe	0.885*	0.837*	-0.751	0.428
Syzygium	0.763*	0.783*	0.318	0.633
Turpinia	0.438	0.514	0.882*	0.812*

It may be pointed out here that decrease in Pn and RGR among species in a plot showed a similar pattern and RGR is strongly related to Pn. According to Reich and others (2003), in a given species the Pn and Gs show strong and positive relationships and thus the RGR will be regulated both by Pn and Gs. However, in the present study, three different scenarios have been observed with respect to relationship between Pn and Gs of seven species growing in a given plot. *Cinnamomum*, which showed highest RGR in P1 showed a positive relationships between Pn and Gs. According to Wright and others (2004), the photosynthetic capacity can be influenced by Gs, carboxylation capacity and chlorophyll concentration of leaves. All these factors could be responsible for comparatively high photosynthetic rate recorded for *Cinnamomum* in P1. In the same plot, *Persea* and *Syzygium* which recorded comparatively a moderate RGR showed negative relationships between Pn and Gs. In these species, probably stomatal openings are restricted to lower their stomatal conductance and transpiration rate but comparatively high chlorophyll concentration in the leaf helped to show better carbon assimilation. The third scenario of comparatively low RGR and Pn and high Gs was recorded for *Turpinia* in P1. In this case, no significant relationship between Pn and Gs was also noticed. Thus it is clear that in case of *Turpinia*, high transpiration rate and stomatal conductance did not influence its photosynthetic rate and relative growth rate.

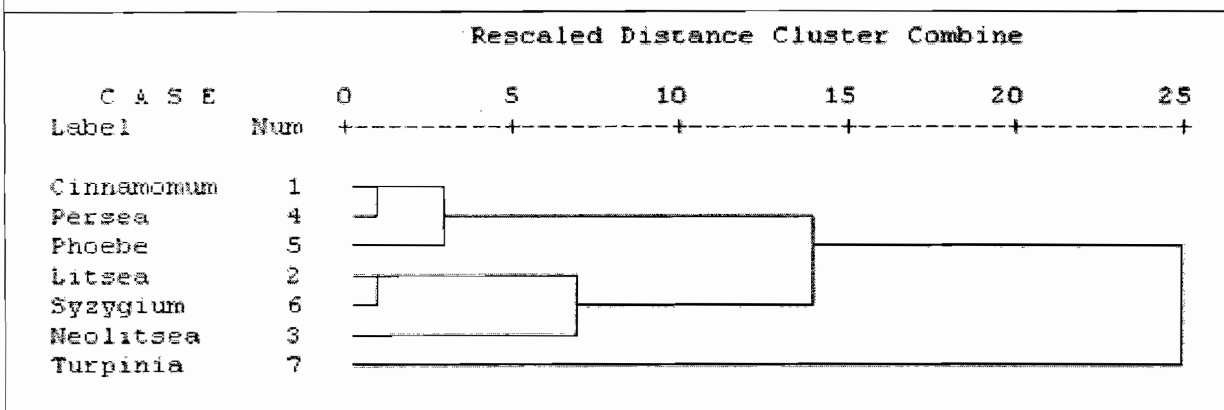
4.4. Clustering of species

A hierarchical cluster analysis was applied using the RGR, Pn, E, and Gs as variables. In the cluster analysis, the distance between the species in a given plot was assessed through Euclidean distance and clustering was done using the average link method. On the basis of cluster analysis the seven species were categorized into three clusters with different patterns in physiological and growth parameter (Figure 3). The different plots showed important variation in terms of species adaptability. In all three plots, *Turpinia* formed a separate cluster with exception being *Neolitsea* that clustered with *Turpinia* in P3. In P1, *Cinnamomum* and *Phoebe* formed a separate cluster, but in P2 and P3, *Persea* became a part of the same cluster.

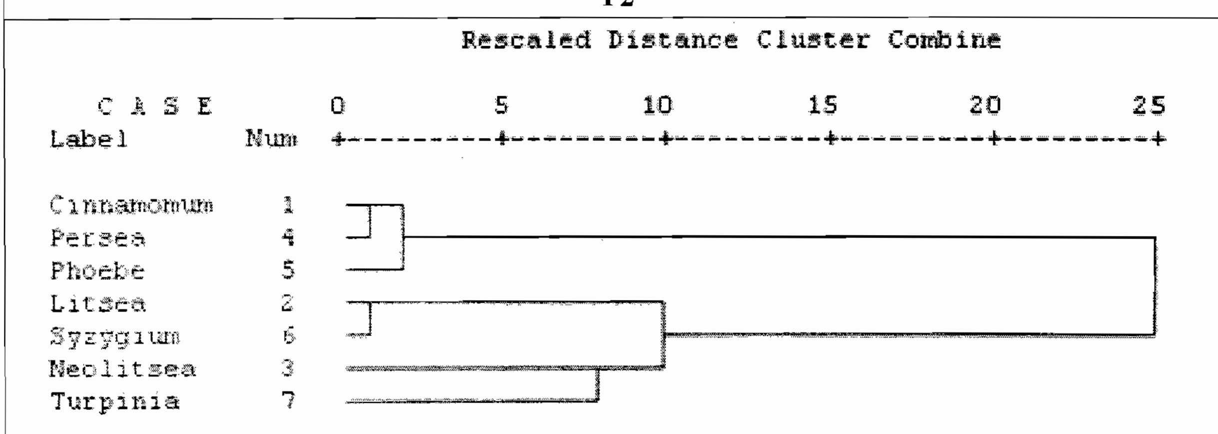
Table 3. Hierarchical classification of seven shola tree species using their physiological properties and growth rate as variables.



P1



P2



P3

4.5. Response of the species to elevation gradient

With the increase of altitude, the RGR and Pn increased significantly in *Turpinia* and decreased in *Cinnamomum* (Tables 5 and 6). In the case of *Persea*, values for both the parameters declined only in seedlings growing in P3. When *Phoebe* showed comparatively higher values for Pn and RGR in the mid-elevation plot (P2), *Syzygium* showed no significant variation in values for both the parameters in three plots. As observed in the present study for *Turpinia*, an increase in photosynthetic rate and growth rate of certain species with increase in elevation was also recorded by others (Woodward, 1986; Korner and Diemer, 1987). Genetic adaptation in these species to high elevation through maintenance of high nitrogen and chlorophyll content in leaves (Friend and Woodward, 1990), stomatal conductance and carboxylation efficiency (Kao and Chang, 2001) could be responsible for high values for photosynthetic rate and growth rate in high elevation plots. However, the reduction in photosynthetic rate (Pn) of *Cinnamomum* with increasing altitude reflects the pattern recorded for several tree species elsewhere in the tropics (Zhang *et al.*, 2005). The lower photosynthetic rates and relative growth rates at higher altitudes have been regarded to be caused by significant increase in thickness of leaf pubescence, lower stomatal conductance and leaf nitrogen content of plants in response to environmental conditions prevailing in the high elevation plots.

With increasing altitude, temperature as well as the partial pressure of air, water vapor and CO_2 decrease, whereas solar radiation flux and incidence of cloud cover may increase (Whiteman, 2000). Consequently, the mean values of stomatal conductance and transpiration rates are lower in plants growing in higher altitudes than in lower altitudes (Motser *et al.*, 2005). Among the seven species studied, only one species (*Turpinia*) showed significant reduction in its stomatal conductance and transpiration rates with increase in altitude (Tables 8 and 9). It is also reported that in some species, stomatal conductance and transpiration rates may decrease with increase in elevation but photosynthetic rate may increase due to increase in water use efficiency of plants with elevation (Korner et al., 1989). This could be the reason for significant decline in stomatal conductance and transpiration rates and increase in photosynthetic rate of *Turpinia* in high elevation plots. However, in the remaining six tree species no significant relation between E (or Gs) and elevation was noticed (Table 8 and 9). According to He and others (1994), with increasing altitude, in some species leaf traits such as leaf mass per unit area (LMA), thickness of leaf pubescence and stomatal size may increase but stomatal density may decrease. Changes in stomatal size and density in a species with increasing altitude might compensate for the reduction in CO_2 partial pressure, but stomatal conductance might not necessarily be related to stomatal density and size (Kao and Chang, 2001). Further studies are needed to determine the factors that are responsible for physiological plasticity shown by different species to contrasting environment prevailing in the elevation gradient.

5. Conclusions

In the present study, substantial differences in RGR and Pn among the seven tree species in shola forests were recorded. Species also varied in terms of growth and physiological traits in their response to altitudinal gradients. For example, RGR, Pn and Gs of *Litsea, Neolitsea, Persea, Phoebe* and *Syzygium* were least responsive to changing altitude, while *Cinnamomum* and *Turpinia* were most responsive. Thus it is clear that the species that show least response to changing altitude have the ability to acclimate to a wider range of environmental condition prevailing in the tropical montane forests of a region. Therefore, species level understanding of variation in physiological and growth rates and their interaction with altitude driven variables has implications for predicting plant responses to possible alteration in the microclimate triggered by climate change and anthropogenic disturbances. The shola forests of Kerala are a unique system and nearly one fifth of angiosperm species are endemic to the Western Ghats and one fourth of the species belong to different conservation categories. Further field research is necessary both to develop a coherent picture of physiological, leaf morphological, leaf nutrient and plant growth traits and for assessing possible consequences of human perturbations or global climate change on these species.

6. Acknowledgements

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Appendix 1. Tree species recorded in three tree phases (Mature trees; gbh > 30.1 cm, Saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

	Species	Species Importance Index Value (SIVI)								
		Mature trees			Saplings			Seedlings		
		Plots			Plots			Plots		
		P1	P2	P3	P1	P2	P3	P1	P2	P3
1.	*Acronychia pedunculata*	3.8	0	0	1	0	0	1.8	0	0
2.	*Actinodaphne bourdillonii*	9.7	1.4	0	13	0	0	19.6	0	0
3.	*Aglaia elaegnoidea*	0.7	0	0	0	0	0	2.4	0	0
4.	*Aidia densiflora*	0.5	0	0	0	0	0	0	0	0
5.	*Alseodaphne semecarpifolia*	4.1	24.6	0	0.8	23.8	0	0.3	14.2	0
6.	*Aporosa fusiformis*	0	8.9	0	0	4.3	0	0	0.8	0
7.	*Ardisia rhomboidea*	0	0	0	4.3	40.6	0	9.7	57.9	0
8.	*Beilschmiedia wightii*	20.8	19.5	0	5	16.7	0	18.3	14.7	0
9.	*Bhesa indica*	3.9	0	0	0	0	0	8.1	0	0
10.	*Canthium dicoccum*	1.3	0	0	0	0	0	1.8	0	0
11.	*Celtis philippensis*	1	1	0	0.8	0.7	0	0.5	0.5	0
12.	*Chionanthus ramiflorus*	25.3	0	0	18.9	0	0	17.2	0	0
13.	*Cinnamomum malabaricum*	0	1	0	0	0	0	0	0	0
14.	*Cinnamomum sulphuratum*	9.1	11.7	17.9	3.6	1.3	19.7	5.4	3.1	19.5
15.	*Cinnamomum wightii*	1.7	13.1	2.2	0	16.4	20.2	0	17.7	25.6
16.	*Clerodendron viscosum*	0.9	0	0	6	0	0	5.8	0	0
17.	*Cryptocarya lawosonii*	8.7	0	0	1.9	0	0	4.9	0	0
18.	*Cyathea neilgiriensis*	1.6	0	0	6.5	0	0	0.7	0	0
19.	*Daphniphyllum neilgherrense*	0	0	15.8	0	0	5.8	0	0	9.6
20.	*Derris brevipes*	0	3.7	0	0	2.4	0	0	0.8	0
21.	*Elaeocarpus recurvatus*	0	0	2.6	0	0	1.6	0	0	1.6
22.	*Elaeocarpus serratus*	1.6	0	0	0	0	0	0	0	0
23.	*Elaeocarpus tuberculatus*	1.3	0	0	0	0	0	0.3	0	0
24.	*Eugenia bracteata*	2.2	0	0	0	0	0	0	0	0
25.	*Eugenia calcadensis*	0	0.7	0	0	0	0	0	0	0
26.	*Eurya nitida*	1.3	0	0	3.3	0	0	2.2	0	0
27.	*Glochidion neilgherrense*	3.8	0	0	0.8	0.6	0	1.6	0.6	0
28.	*Gomphandra coriacea*	25.6	7.3	0	4.4	4	0	1.4	1.9	0
29.	*Gymnacranthera canarica*	0	1	0	0	0	0	0	0	0
30.	*Hydnocarpus alpina*	55.1	0	0	31	0	0	21.9	0	0

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Appendix 1(cont'd). Tree species recorded in three tree phases (Mature trees; gbh > 30.1 cm, Saplings; gbh 10.1 to 30.0 cm and seedlings; girth 1.0 to 10.0 cm and height <1 m) in three plots (P1; Altitude 1900 m above msl, P2; Altitude 2100 m above msl and P3; Altitude 2400 m above msl) situated along an altitudinal gradient in the Anamudi Shola National Park, Kerala.

	Species	Species Importance Index Value (SIVI)								
		Mature trees			Saplings			Seedlings		
		Plots			Plots			Plots		
		P1	P2	P3	P1	P2	P3	P1	P2	P3
31.	*Ilex wightiana*	0	32.2	46.1	0	3.3	6	0	4	10.7
32.	*Isonandra lanceolata*	0	2.4	9.8	0	7.3	5.2	0	1.1	1.2
33.	*Isonandra stocksii*	39.3	1.9	0	3.4	5	6.2	1.6	6.7	4.1
34.	Lasianthus acuminatus	0	0	0	121.2	69.2	0	88.8	79.6	0
35.	*Ligustrum perrottetii*	0	0	13.2	0	0	1.7	0	0	2.9
36.	*Litsea floribunda*	0.5	2.6	0	1.7	2.2	0	0.4	2.9	0
37.	*Litsea wightiana*	0.8	46.8	28.3	3.2	23.2	68.3	5.1	20.7	71.1
38.	*Mahonia leschenaultii*	0	0	14.4	0	0	20.6	0	0	16.5
39.	*Mastixia arborea*	23.7	5.3	0	47.3	1.9	0	26.3	3.5	0
40.	*Meliosma simplicifolia*	0	0	9.8	0	0	22.7	0	0	19
41.	*Myrsine wightiana*	0	1.9	6.4	0	1.1	3.5	0	0.8	1.6
42.	*Neolitsea scrobiculata*	0.7	16.3	2.6	0.8	17.2	26.4	4.5	13.1	16.7
43.	*Neolitsea zeylanica*	0	9.9	0	2.4	13.1	0	7.2	6.6	0
44.	*Persea macrantha*	12.6	12.8	2.2	2.6	5.7	5.5	4.3	5.6	2.5
45.	*Phoebe lanceolata*	3	14.3	1	3.5	3.6	6.3	7	9.7	2.5
46.	*Photinia integrifolia*	0.9	0	0	0	0	0	0	0	0
47.	*Prunus ceylanica*	0.7	0	0	0	0	0	0	0	0
48.	*Rhododendron nilagiricum*	0	0	19.7	0	0	2.7	0	0	3.9
49.	*Saprosma foetens*	7.2	0	0	8.3	0	0	13.6	0	0
50.	*Schefflera racemosa*	0.5	0	3.7	0	1.2	5.4	0	0	1.6
51.	*Symplocos cochinchinensis*	0	0	3.6	1.1	0	6	3.5	0	9.9
52.	*Syzigium densiflorum*	12.3	13	12.5	0.8	5.2	3.6	2.9	8.3	33.2
53.	*Syzigium gardneri*	4.6	0	0	0	0	0	0	0	0
54.	*Syzygium hemisphericum*	0	1.6	3.5	0	1.2	1.6	0	1.4	1.2
55.	*Syzygium malabaricum*	0	19.7	39.5	0.8	6.7	43.4	5.8	11.5	38.4
56.	*Syzygium montanum*	0	3.3	0	0	7.7	1.9	0	2.6	3.1
57.	*Ternstroemia japonica*	6	0	0	0	0	0	0.9	0	0
58.	*Turpinia nepalensis*	3	21.3	44.1	0.9	14.7	14	1.2	6.8	1.8
59.	*Vaccinium leschenaultti*	0	0.8	0	0	0	0	0	0	0
60.	*Viburnum coriaceum*	0	0	1.1	0	0	1.8	0	0	1.6
61.	*Viburnum punctatum*	0	0	0	0.8	0	0	0.3	0	0