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Determination of the Biomass Production and Carbon Sequestration Capacity of Selected Forest Types of Sri Lanka

By

Professor W.A.J.M. De Costa
Department of Crop Science, Faculty of Agriculture
University of Peradeniya

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(Submitted simultaneously to the National Science Foundation of Sri Lanka and the Forest Department of Sri Lanka)

Contents

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- Forest Department staff of the Sinharaja MAB forest reserve and the Kanneliya-Dediyagala-Nakiyadeniya forest complex.

Section 1:

Information regarding Project/Project Personnel:

i. Contract Number: RG/2003/FR/01

ii. Title of the Project:

Determination of the biomass production and carbon sequestration capacity of selected forest types of Sri Lanka

iii. Principal Investigator:

Prof. W.A.J.M. De Costa,
Department of Crop Science, Faculty of Agriculture, University of Peradeniya

iv. Co-Investigators:

None.

Prof. D.M.S.H.K. Ranasinghe (Department of Forestry and Environmental Sciences, University of Sri Jayewardenepura) was listed as a co-investigator in the project proposal. However, during the execution of the project, the contribution of Prof. Ranasinghe has been minimal (i.e. less than 1% of the work done in the project).

v. Institute(s) where research was being carried out:

Department of Crop Science, Faculty of Agriculture, University of Peradeniya

vi. Date of award:

vii. Date of completion of project:

viii. Total allocation of funds:

ix. Total spent:

x. Number of research students employed: Two (02).

From May 2004 to April 2007: Mr. W.M.P.S.B. Wahala

From May 2007 to September 2008: Mr. H.R. Suranga

xi. Postgraduate degrees completed with dates:

None.

Mr. W.M.P.S.B. Wahala registered for a PhD degree (by research) at the University of Sri Jayewardenepura. However, this has not been completed. Mr. Wahala has not been able to engage in the project since his departure to the Sabaragamuwa University in April 2007. However, he is planning to resume work on his PhD from April, 2010 onwards after obtaining study leave from his university position.

xii. Number of Technical Assistants and/or labourers employed and period of service:

None.

xiii. Publications/Communications arising from the project during the reporting period:

Published as peer-reviewed abstracts:

Wahala, W.M.P.S.B., De Costa, W.A.J.M. and Ranasinghe, D.M.S.H.K. (2006). Current status of the forest canopy and its understorey light environment in selected areas of Sinharaja, Kanneliya and Knuckles Forest Reserves in Sri Lanka. Proceedings of the International Conference on Humid Tropical Ecosystems: Changes, Challenges and Opportunities. 04 – 09 December, 2006, Kandy, Sri Lanka. pp. 8.

Wahala, W.M.P.S.B., De Costa, W.A.J.M., Ratnayake, R.M.D.D. and Ranasinghe, D.M.S.H.K. (2006). Mitigating the impacts of climate change – Carbon sequestration capacity of selected natural forests in the humid zones of Sri Lanka. Proceedings of the International Conference on Humid Tropical Ecosystems: Changes, Challenges and Opportunities. 04 – 09 December, 2006, Kandy, Sri Lanka. pp. 73.

De Costa, W.A.J.M., Suranga, H.R. and Ranasinghe, D.M.S.H.K. (2009). Estimation of carbon stocks in the forest plantations of Sri Lanka. Proceedings of the National Forestry Research Symposium, 12 – 13 March, 2009, Kandy, Sri Lanka. pp. 12-13.

Suranga, H.R. and De Costa, W.A.J.M. (2009). Photosynthetic light response of selected plant species occupying different vertical strata of lowland wet evergreen forests in Sri Lanka. Proceedings of the 14th International Forestry and Environment Symposium, 18 – 19 December, 2009, University of Sri Jayewardenepura, Sri Lanka.

Full-length research article submitted for publication:

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Section 2:

Executive Summary of the Project

Forests constitute a highly important form of vegetation in Sri Lanka. Exponentially increasing atmospheric carbon dioxide concentrations has been the key factor responsible for global warming and long-term climate change. Forests have the capacity to mitigate climate change by absorbing and storing (i.e. sequestering) substantial amounts of atmospheric carbon via photosynthesis and biomass production. Therefore, the objective of the present project was to determine the biomass production and carbon sequestration capacity of major natural forests and forest plantations of Sri Lanka.

The project was carried out as two separate components, one on natural forests and the other on forest plantations. In the first component, we developed a novel combination of methodology to quantify the carbon sequestration capacity of natural forests, which is a highly complex ecosystem with high species density and diversity. One component of this methodology consisted of canopy hemispherical photography to characterize the forest canopy and estimate its radiation interception capacity. Conversion of intercepted radiation to forest biomass carbon through photosynthesis was quantified by developing a multi-layered canopy photosynthesis model. Long-term carbon sequestration was computed by adding a further component to the model to estimate heterotrophic respiration. Using this methodology, both medium-term carbon sequestration rate (C_{seq}) in terms of net primary productivity (NPP) and long-term carbon sequestration rate (C_{seqL}) in terms of net ecosystem productivity (NEP) were computed for the two major lowland wet evergreen forest ecosystems in Sri Lanka, the Sinharja Man and Biosphere Forest Reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) Forest Complex. The computations were based on 343 canopy hemispherical photographs representing different forest regions and elevation zones and photosynthetic light response curves of 14 forest tree/plant species occupying different vertical strata of the forest canopy.

The estimated C_{seq} rates of Sinharaja and KDN forest complexes are 7.403 (± 0.094) and 8.953 (± 0.133) mt C ha^{-1} yr^{-1} respectively. Through these carbon sequestration rates, Sinharaja and KDN forest complexes absorb 2.52% and 3.26% of the current annual CO_2 emissions of Sri Lanka. Considering the fact that Sinharaja and KDN forest complexes occupy only 0.13% and 0.18% of the total land area of Sri Lanka, the above values of their percentage absorption of national CO_2 emissions indicate that these two tropical rainforests are extremely efficient carbon sinks. The residence times of this initially sequestered carbon were estimated to be 42.2 and 35.5 years for Sinharaja and KDN respectively. Accordingly, long-term C_{seqL} rates of Sinharaja and KDN are 0.371 (± 0.003) and 0.378 (± 0.003) mt C ha^{-1} yr^{-1}. In addition to these estimates of carbon sequestration, a comprehensive analysis was carried out on canopy and photosynthetic properties of these two natural forests to elucidate their role in controlling the carbon sequestration rates. A comparative analysis was also done to compare our estimates with published carbon sequestration rates of similar lowland tropical forest ecosystems such as the Amazon.

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In the second component of the project, the total carbon stocks of all forest plantations maintained by the Forest Department of Sri Lanka were estimated using the basic forest inventory data in the FORDATA database. The total estimated monoculture C stock in 2008 amounted to 4.23 million metric tons in an area of 57618.8 ha. Around 89% of this total C stock in monocultures is contributed by five tree species, namely, *Pinus caribaea* (44%), *Tectona grandis* (21%), *Eucalyptus grandis* (11%), *Eucalyptus camaldulensis* (7%) and *Swietenia macrophylla* (6%), occupying 92% of the area. Total C stock in mixed cultures in 2008 amounted to 0.681 million tons in 5949.6 ha. Five mixed cultures, i.e. *Eucalyptus robusta & E. grandis* (17%), *Pinus* mixed (13%), *E. grandis & E. microcorys* (12.5%), *Eucalyptus* mixed (7%) and *Acacia mangium & A. auriculiformis* (5%), contributed 55% of this C stock.

Our estimates of per ha C stocks of Sri Lankan forest plantations were compared with the global standards for comparable climatic zones. The maximum per ha C stocks observed from some of the Sri Lankan forest plantations in different climatic zones were either on par or above the benchmark average C stock values specified by the Intergovernmental Panel for Climate Change (IPCC) for the respective climatic zones.

The average medium-term carbon sequestration rate (i.e. C_{seq} in terms of NPP) of the forest plantations is 2.575 mt C ha^{-1} yr^{-1} with an average residence time of 30 years. Through this carbon sequestration, forest plantations absorb 4.95% of the annual CO_2 emissions of Sri Lanka. Here again, in view of the fact that the forest plantations occupy only 1% of the total land area of Sri Lanka, the nearly 5% absorption of national CO_2 emissions by the forest plantations indicate their role in climate change mitigation as highly efficient carbon sinks.

A quantitative index of the efficiency of the respective carbon sinks showed that Sinharaja and KDN forest complexes have greater efficiencies as carbon sinks than even the most productive forest plantations in Sri Lanka.

The above-described quantitative information on the carbon sequestration capacity of both natural and plantation forests of Sri Lanka has been generated in this project for the first time in Sri Lanka. They will be extremely useful in the formulation of policies and strategies for climate change mitigation in Sri Lanka.

We strongly propose that the new combination of methodology that has been developed in this study be employed in a second phase of this research project in the future, to estimate the carbon sequestration rates of the rest of the forest types of Sri Lanka, which include the Knuckles forest reserve, Peak Wilderness forest reserve, the Montane forests in the Horton Plains and the dry zone forests.

Section 3:

Report in detail

This part of the report has been prepared in two separate sections:

Section 3.I: Determination of the biomass production and carbon sequestration capacity of the Sinharaja Man and Biosphere (MAB) Forest Reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) Forest Complex

Work described in this section estimated the rates of biomass production and carbon sequestration rates of the Sinharaja Man and Biosphere (MAB) Forest Reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) Forest Complex.

Section 3.II: Estimation of carbon stocks in the forest plantations of Sri Lanka

Work described in this section estimated the total carbon stocks of all forest plantations of Sri Lanka.

This section is presented in the form of a research article that has been submitted for possible publication in the Journal of the National Science Foundation of Sri Lanka. The manuscript was submitted in August 2009 and is still under review.

Section 3.I:

Determination of the biomass production and carbon sequestration capacity of the Sinharaja Man and Biosphere (MAB) Forest Reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) Forest Complex

Summary

Carbon dioxide is one of the principal greenhouse gases that cause global warming. Forests can play a major role in mitigating the impacts of climate change by absorbing substantial quantities of atmospheric CO_2 for photosynthesis. Most available methods for estimating forest carbon sequestration are empirical. The objective of this study was to determine the carbon sequestration capacity of the two major lowland wet evergreen forest ecosystems in Sri Lanka, the Sinharja Man and Biosphere Forest Reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) Forest Complex through a new, process-based method.

We developed a novel combination of methodology to quantify the carbon sequestration capacity of natural forests, which is a highly complex ecosystem with high species density and diversity. One component of this methodology consisted of canopy hemispherical photography to characterize the forest canopy and estimate its radiation interception capacity. Conversion of intercepted radiation to forest biomass carbon through photosynthesis was quantified by developing a multi-layered canopy photosynthesis model. Long-term carbon sequestration was computed by adding a further component to the model to estimate heterotrophic respiration. Using this methodology, both medium-term carbon sequestration rate (C_{seq}) in terms of net primary productivity (NPP) and long-term carbon sequestration rate (C_{seqL}) in terms of net ecosystem productivity (NEP) were computed for Sinharaja and KDN forest complexes. The computations were based on 343 canopy hemispherical photographs representing different forest regions and elevation zones and photosynthetic light response curves of 14 forest tree/plant species occupying different vertical strata of the forest canopy.

The estimated C_{seq} rates of Sinharaja and KDN forest complexes are 7.403 (± 0.094) and 8.953 (± 0.133) mt C ha^{-1} yr^{-1} respectively. Through these carbon sequestration rates, Sinharaja and KDN forest complexes absorb 2.52% and 3.26% of the current annual CO_2 emissions of Sri Lanka. Considering the fact that Sinharaja and KDN forest complexes occupy only 0.13% and 0.18% of the total land area of Sri Lanka, the above values of their percentage absorption of national CO_2 emissions indicate that these two tropical rainforests are extremely efficient carbon sinks. The residence times of this initially sequestered carbon were estimated to be 42.2 and 35.5 years for Sinharaja and KDN respectively. Accordingly, long-term C_{seqL} rates of Sinharaja and KDN are 0.371 (± 0.003) and 0.378 (± 0.003) mt C ha^{-1} yr^{-1}. In addition to these estimates of carbon sequestration, a comprehensive analysis was carried out on canopy and photosynthetic properties of these two natural forests to elucidate their role in controlling the carbon sequestration rates. A comparative analysis was also done to compare our estimates with published carbon sequestration rates of similar lowland tropical forest ecosystems such as the Amazon.

1. Introduction

1.1 Tropical forests and their importance in the global carbon cycle

Tropical forests can be broadly defined as the forests located around the equator up to the tropics of Cancer and Capricorn (Lewis, 2006) and include a range of distinct forest types such as lowland evergreen rain forests, moist deciduous forests, dry deciduous forests, hill and montane forests, savannahs and mangroves. Tropical forests and woody savannahs account for 50% of the global forest area (Malhi and Grace, 2000). Tropical forests form a key component in the global carbon cycling (Dixon et al., 1994; Malhi and Grace, 2000; Grace, 2004) and thereby have the capacity to exert a significant influence on the global climate (Lewis et al., 2006). Although tropical forests occupy only about 7 - 10% of the earth's land surface area, they annually process a large pool of carbon through photosynthesis and respiration, which is six-times the annual anthropogenic carbon emission from fossil fuel use (Malhi and Grace, 2000). About 40 – 60% of carbon in terrestrial vegetation is stored in tropical forests (Dixon et al., 1994; Malhi and Grace, 2000; Lewis et al., 2006), which are also responsible for 30 – 50% of terrestrial net primary production (Melillo et al., 1993; Field et al., 1998; Grace et al., 2001). Furthermore, tropical forests are the major seats of a large fraction of global biodiversity, as they hold more than one-half to two-thirds of species of the world (Groombridge and Jenkins, 2003). In addition, tropical forests are valuable for protection of watersheds and their scenic beauty (Daily et al., 2000). In terms of land area, about 65% of the tropical forests consist of tropical rain forests, which are also termed humid or moist tropical forests or tropical wet evergreen forests (De Rosayro, 1950; Holmes, 1956; Koelmeyer, 1957). The present study focuses on the carbon sequestration rates of two tropical wet evergreen forest complexes located in the South-West of Sri Lanka.

1.2 Tropical forests and global climate change

There has been considerable debate over whether tropical forests are a net carbon sink or a source especially in view of long-term changes in the global climate such as increasing atmospheric carbon dioxide concentrations and temperatures (Körner, 1998; Clark, 2004a & b; Grace, 2004). While atmospheric CO_2 is absorbed during photosynthesis of the forest vegetation, a range of processes release carbon dioxide from the forest ecosystem to the atmosphere. These include natural biological processes such as autotrophic and heterotrophic respiration, natural physical processes such as forest fires and anthropogenic processes such as deforestation (Achard et al., 2002 & 2004; De Fries et al., 2002). As increasing atmospheric carbon dioxide concentrations are responsible for 60% of the observed global warming (Grace, 2004) through the enhanced greenhouse effect, tropical forests can play a substantial role in mitigating future climate change. In addition to the already-understood enhanced greenhouse effect (Houghton, 2009), CO_2 emissions from tropical forests can induce global climate change through processes, which are yet to be completely understood. For example, numerous organic compounds produced from biomass burning can increase the concentrations of aerosol and cloud condensation nuclei, which can have significant impacts on cloud microphysics, rainfall generation mechanisms and large-scale climate dynamics (Andreae et al., 2002). Andreae et al. (2004) have further showed that forest fires in the Amazon reduce the cloud droplet size and delay the onset of precipitation. The processes set in motion by the released smoke from forest fires can have profound radiative impacts on the climate system influencing the regional and global circulation patterns. Global climate can be changed by changes in the earth's surface albedo (i.e. the fraction of incoming radiation reflected back by the earth's surface) caused by deposition of substantial amounts of black carbon from forest fires and biomass burning following deforestation. Changes in the earth's surface albedo caused by deposition on snow of substantial amounts of black carbon from forest fires and biomass burning following deforestation can contribute to global climate change. Released black carbon also increases the atmospheric aerosol content and influences the global radiation and energy balances. Climate models have shown that deforestation in the Amazonia impacts the local and regional energy balance, causing a warmer and a drier climate (Grace, 2004). Moreover, these impacts can propagate thousands of kilometres beyond the Amazon.

1.3 Focus of the present study

Forests constitute a highly important form of vegetation in Sri Lanka. The present study seeks to quantify the carbon sequestration potential of two important lowland wet evergreen forest complexes, namely the Sinharaja Man and Biosphere Forest Reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) forest complex, located in the wet zone of Sri Lanka. These two forest complexes are located in zones of extremely high floristic richness (Ashton and Gunatilleke, 1987; Gunatilleke and Gunatilleke, 1990). As valid estimates of the carbon sequestration potential of Sri Lankan forests are not available at present, results of this study will provide important information for valuation of Sri Lankan forests, especially as a carbon sink for mitigation of impacts of climate change.

1.4 Estimated carbon fluxes in tropical forests using different methods of assessment

1.4.1 Eddy covariance

Quantitative estimates of components of the carbon balance of tropical forests are highly variable because of incomplete understanding of the processes involved and the inadequacies, weaknesses and uncertainties of the methods used (Baldocchi et al., 1996; Houghton, 2005; Lewis et al., 2009). The eddy covariance method measures the net carbon flux over an area of the forest ranging from 0.1 to 1 km^2 (Baldocchi, 2003; Grace, 2004). This measures the net ecosystem exchange (NEE) or net ecosystem productivity (NEP), which is the difference between gross photosynthetic rate of the forest plants (P_g) and the sum of respiration by forest plants (R_p) and heterotrophs such as soil microbes and animals (R_h). When measured over a prolonged period of time, the NEE provides a measurement of long-term carbon sequestration by the forest ecosystem. Disturbances such as deforestation and fire can reduce a positive NEE by reducing P_g and releasing CO_2 in to the atmosphere.

Using measurements of carbon dioxide fluxes over extensive areas of forests by the eddy covariance method, Grace et al. (1995), Malhi et al. (1998) and Andreae et al. (2002) showed that undisturbed tropical forests, which were believed to be in the climax stage, in selected parts of the Amazon were net carbon sinks. In contrast, using eddy covariance as well as ground-based forest inventory measurements, Saleska et al. (2003) showed a net carbon loss from an old-growth tropical moist forest in the Amazon. However, they implied that it was a transient effect of recent disturbances, which were superimposed on the long-term balance.

An inadequacy in the eddy covariance method is its inability to account carbon losses by the emission of volatile organic compounds (VOCs) by the forest vegetation (Grace, 2004). Carbon initially fixed in plant biomass and soil could be released again through respiration and soil organic matter decomposition. Therefore, true long-term carbon sequestration may be equal to the rate at which carbon accumulates in the soil and in long-lived forest products such as structural timber (Grace, 2004).

1.4.2 Atmospheric sampling

Precise measurement of concentrations of carbon, oxygen and their isotopes in atmospheric samples taken over large landscapes in combination with atmospheric transport models allow quantification of carbon sinks and sources over different geographical regions or different biome types (Keeling et al., 1996; Styles et al., 2002; Gurney et al., 2002). Rödenbeck et al. (2003), using atmospheric measurements of CO_2, CH_4 and CO along with atmospheric transport models and after taking the carbon release due to tropical deforestation in to account, showed that the tropical zone, as well as temperate and boreal zones, is a net carbon sink. Although atmosphere-based estimates of carbon sinks have been shown to be consistent with land-based estimates such as eddy covariance, both methods have wide uncertainties (Goulden et al., 1996; Grace, 2004). The atmosphere-based estimates may be limited by the number of measurement sites (Bousquet et al., 2000). It has been suggested that eddy covariance measurements may be biased towards forest areas which are accumulating biomass (Keller et al., 1996) and may not measure accurately the night-time CO_2 efflux from forest to the atmosphere (Moncrief et al., 1996; Phillips et al., 2002). Therefore, it is critically important that eddy covariance measurements and ground-based measurements are carried out concurrently at a set of benchmark sites to improve our current understanding of carbon sequestration rates of forests and their controlling factors.

1.4.3 Ground-based forest inventory in permanent sampling plots

Several groups of scientists (Phillips et al., 1998; Chave et al., 2003; Baker et al., 2004; Chave et al., 2008; Phillips et al., 2008; Lewis et al., 2009) have resorted to ground-based forest inventory on permanent sampling plots (PSPs) to overcome the uncertainties involved in micrometeorological (e.g. eddy covariance) and atmospheric methods. PSPs monitor tree growth by conventional forest inventory methods (Brown et al., 1989; Brown, 1997; Clark et al., 2001a) such as measurement of diameter at breast height (dbh) from which existing above-ground tree biomass is calculated using allometric relationships. Repeated measurements at adequate time intervals along with records of tree mortality provide estimates of changes in above-ground tree biomass. Only trees having a dbh greater than a certain value, e.g. 10 cm (Phillips et al., 1998; Baker et al., 2004) or 1 cm (Chave et al., 2008), are measured. Correction factors are used to account for biomass of smaller trees (e.g. < 10 cm dbh) and lianas. Below-ground biomass change is estimated as a ratio of that above-ground (e.g. 1:3 in Phillips et al., 1998). Combination of above-ground and below-ground changes in biomass change gives an estimate, which may be considered as approximating the long-term carbon sequestration rate (C_{seqL}) in terms of net ecosystem productivity (NEP).

Phillips et al. (1998) reported an overall total C gain (C_{seqL}) of 0.385 ± 0.22 mt ha^{-1} yr^{-1} for 478 PSPs in 68 pantropical sites covering humid tropics, humid Neotropics, humid lowland Neotropics and Amazonia. Baker et al. (2004) estimated a weighted average total C_{seqL} rate 0.62 ± 0.23 mt ha^{-1} yr^{-1} across 59 sites in old growth Amazonian forests. It is notable that the above-ground C_{seqL} rates of individual plots of Baker et al. (2004) ranged from -4.14 to 5.40 mt ha^{-1} yr^{-1} (i.e. total C_{seq} ranging from -5.52 to 7.20 mt ha^{-1} yr^{-1}). Phillips et al. (2008) continued measurements in old-growth Amazonian forests, which included some of the plots used by Baker et al. (2004), and reported a mean C_{seqL} rate of 1.016 ± 0.369 mt ha^{-1} yr^{-1}. Lewis et al. (2009) estimated an average above-ground carbon sequestration rate of 0.63 (95% confidence interval of 0.22 – 0.94) mt ha^{-1} yr^{-1} across 79 plots of tropical African forests during the period from 1968 to 2007. Lewis et al. (2009) further estimated a mean above-ground C_{seqL} rate of 0.49 (95% CI 0.29 – 0.66) mt ha^{-1} yr^{-1} for all standardized inventory data from 156 plots in tropical Africa, America and Asia (Phillips et al., 1998; Baker et al., 2004; Chave et al., 2008). These above-ground C_{seqL} rates translate in to total C_{seqL} rates of 0.84 and 0.65 mt ha^{-1} yr^{-1} respectively for tropical African forests and for tropical forests in Africa, America and Asia.

Using repeated forest inventory data from ten large (16 – 52 ha) PSPs of undisturbed tropical forests over a period of 20 years, Chave et al. (2008) found a statistically significant average above-ground carbon gain of 0.24 mt ha^{-1} yr^{-1}. Interestingly, one of the ten PSPs was from the Sinharaja MAB reserve, which showed a statistically non-significant, mean above-ground carbon loss of 0.98 mt ha^{-1} yr^{-1}, with a bootstrapped 95% confidence interval from -2.48 to 0.40 mt ha^{-1} yr^{-1}. This was primarily because of substantial tree mortality of the shade-tolerant canopy species, *Mesua nagasarium* (Gunatilleke et al., 2004). Therefore, when the Sinharaja plot was excluded, the other PSPs showed an average above-ground carbon gain of 0.32 mt ha^{-1} yr^{-1}, with a 95% confidence interval from 0.15 to 0.48 mt ha^{-1} yr^{-1}. At the ratio of 3:1 for the above- to below-ground biomass, this translates in to a total C_{seqL} rate of 0.43 mt ha^{-1} yr^{-1}. Through repeated forest inventory data at five-year intervals over 15 years, Chave et al. (2003) found an average above-ground carbon gain of 0.10 mt ha^{-1} yr^{-1} (total C_{seq} rate of 0.13 mt ha^{-1} yr^{-1}) in a 50 ha PSP in a moist tropical forest on Barro Colorado Island in Panama. Both Chave et al. (2003) and Chave et al. (2008) showed that carbon gain or loss in a given forest varied between successive census intervals.

Estimations of C_{seqL} rates from PSPs can have several potential sources of error (Clark et al., 2001a; Clark, 2002; Phillips et al., 2002). These include biased site selection (i.e. selection of mature-phase, gap-free sites or immature successional forests, selection of easily accessible fragmented forests with significant edge effects), field measurement errors (i.e. dbh measurements around buttresses, incomplete census by missing new recruits or existing trees), bias in post-measurement data checking and filtering (i.e. reducing extreme increments, rounding-up negative increments) and bias due to research intervention (i.e. soil compaction, tree damage), which could either underestimate or overestimate C_{seqL} rates. Clark (2002) specifically cited the estimated above-ground carbon gains reported by Phillips et al. (1998) to be overestimates because of erroneous dbh measurements in buttressed trees and selection of sites located on recent floodplains, which may be gaining biomass due to primary succession. In response to Clark (2002)'s critique, an in-depth analysis of the magnitudes of the above sources of error and potential bias for overestimation of C_{seqL} rates by Phillips et al. (2002) concluded that they are unlikely to have introduced significant and systematic errors.

The use of common allometric equations to estimates above-ground tree mass of a large number of different tree species from measurements of the respective dbh and wood densities can introduce errors in to the biomass calculation. However, after a comparison of different allometric equations, Chambers et al. (2001) and Chave et al. (2005) concluded that carefully-chosen allometric equations can be used to estimate above-ground biomass of a broad range of tropical forests. However, a comparison of estimates of 14 allometric equations with actual harvested biomass data from the Amazon showed that some allometric equations overestimated biomass as much as 318% (Araujo et al., 1999). Particularly, according to Brown and Lugo (1992) and Brown et al. (1995), substantial errors can occur in the estimation of biomass of large trees (dbh > 70 cm) if the allometric equation was not developed on harvest data which included large trees as well. Furthermore, biomass increments of certain plant groups such as palms, hemiepiphytes and lianas may not fit in to many common allometric equations. Also, lianas and hemiepiphytes, which do not reach the ground level are not accounted in censuses. This could lead to significant underestimation of C_{seqL} rates of rainforests in the humid tropics, which are rich in these life forms, with lianas contributing to 30% of leaf area in some tropical forests (Putz, 1983).

It is notable that the estimated mean C_{seqL}, rates from a smaller number of large PSPs (Chave et al., 2005 and 2008) tend to be smaller than the estimates from a large number of smaller PSPs (Phillips et al., 1998; Baker et al., 2004; Lewis et al., 2009). Chave et al. (2008) argue that large PSPs subsume the micro-scale variation created by tree fall and canopy gaps that are present in smaller PSPs and therefore provide more representative estimates of carbon fluxes. However, Chave et al. (2008) tend to agree with the contention of Clark (2002) that the smaller number of large PSPs may not adequately represent the landscape-scale heterogeneity in tropical forests. On the other hand, the larger number of smaller PSPs can capture the wide range of geographical, spatial and environmental heterogeneity in tropical forest ecosystems. Keller et al. (2001) showed that at least 21 0.25 ha sampling plots are needed to estimate the above-ground biomass of a given forest type to within 20% with 95% confidence. Chave et al. (2003) point out that only seven sites in Phillips et al. (1998)'s study meet the above requirement.

Another important limitation in estimating total C_{seqL} rates using forest inventory methods in PSPs is the inability to measure several important components in the carbon cycle that determine net ecosystem productivity (NEP) (Clark et al., 2001a & b). These include below-ground carbon sequestration in roots and soil carbon pool and carbon stocks and fluxes in litter and coarse woody debris (i.e. fallen and broken trees, broken branches etc.). For example, Chambers et al. (2001) estimated that tree damage could lead to a litter production of 0.45 mt C ha^{-1} yr^{-1} in selected PSPs in the Central Amazon and branch fall can range from 0.1 to 2.9 mt C ha^{-1} yr^{-1} (Clark et al., 2001b). Furthermore, carbon fluxes in seedlings, lianas, rattans, non-woody monocots, twigs, leaves and reproductive organs are also excluded from inventory in PSPs (Chave et al., 2008). Therefore, Clark et al. (2001a) contend that the existing field-based estimates of forest C_{seqL} rates are likely to be significant underestimates.

1.5 Estimation of net primary productivity

Estimation of net primary productivity (NPP) by various methods (Cramer et al., 1999; Clark et al., 2001b) can also yield estimates of carbon sequestration (C_{seq}) rates by tropical forests. Although NPP is defined as the difference between total gross photosynthesis (P_g) and total autotrophic (i.e. plant) respiration (R_p), Clark et al. (2001a) defined NPP as the total new organic matter produced during a specified time interval. This is because both P_g and R_p of forests cannot be quantified accurately at the ecosystem level (Waring and Schlesingher, 1985; Clark et al., 2001a; Chapin et al., 2002) and because of transformations (e.g. litter fall, branch fall, tree mortality, herbivory, decomposition and exudation as volatile organic compounds and root exudates) that the initially fixed carbon undergo during the measurement period. Clark et al. (2001a) defined the quantity NPP*, which was called the field-measurement based, operational estimate of actual NPP. With respect to a given measurement interval (e.g. the interval between two successive censuses in PSPs), NPP* of a forest ecosystem was defined as the sum of organic matter (i.e. biomass) that is retained by standing vegetation during the interval and the organic matter that is produced and lost during the same interval. Hence, the components of NPP* of a forest ecosystem are, above-ground biomass increment, net increments in coarse and fine roots, net increases in stores of non-structural carbohydrates, fine litter fall, above-ground losses to consumers (e.g. herbivores, seed and fruit predators), emissions of biogenic volatile organic compounds (BVOCs), above-ground losses of leached organic compounds, root losses to consumers, root exudates, carbohydrates exported by plants to their mycorrhizal or nodule symbionts (Clark et al., 2001a & b). Clark et al. (2001a) argued that in most studies estimating NPP, only a few of the above components are quantified, thereby making many of the existing estimated NPP values underestimates of actual NPP. Clark et al. (2001a & b) also estimated the potential errors associated with measuring or ignoring the above components of the NPP* for one example tropical moist forests and showed that NPP can be underestimated by as much as > 200%.

In order to estimate C_{seq} rate of a tropical forest, its NPP measurements need to be supplemented with estimations of heterotrophic respiration, which would enable computation of the net ecosystem exchange (NEE). Heterotrophic respiration (R_h) is respiration by organisms such as soil micro-organisms and animals, which use organic matter of plant or animal origin to generate their energy requirement. Clark et al. (2001a) argues that like NPP, R_h in forest ecosystems also cannot be measured with a sufficient degree of precision to estimate NEE to the required level of precision. As NEE is the difference between two imperfectly estimated carbon fluxes, errors in measurement of NPP and/or R_h could introduce substantial errors in to an estimate of NEE.

Grace (2004) estimated NEP of different biomes of the earth by using a simple model based on the net primary productivity, NPP, (i.e. P_g - R_p) estimates of Saugier et al. (2001) and a method developed by Taylor and Lloyd (1992) to estimate R_h. According to these estimates, Grace (2004) showed a global terrestrial carbon sink of 2 – 3 Gt C yr^{-1}, to which tropical forests made the highest contribution (i.e. 0.66 Gt C yr^{-1}) followed by tropical savannah and grasslands (0.39 Gt C yr^{-1}), suggesting a strong carbon sink in the tropical regions. In this analysis, the average annual per hectare long-term carbon sequestration rate of tropical forests was estimated to be 0.37 mt ha^{-1} yr^{-1}.

Clark et al. (2001b) attempted to estimate as much components of the NPP as possible in 39 tropical forest sites covering a broad range of precipitation, temperature and elevation. They were able to develop logarithmic relationships between above-ground biomass increment and fine litterfall and between standing above-ground biomass and above-ground biomass increment. In addition, Clark et al. (2001b) estimated above-ground losses to consumers and volatile organic compounds and computed the total above-ground NPP, which ranged from 1.4 to 9.9 mt ha^{-1} yr^{-1}, when an extremely high value of 14.3 mt ha^{-1} yr^{-1} was excluded. Thereafter, Clark et al. (2001b) calculated lower- and upper-bounds of below-ground NPP based on fractions of 0.2 and 1.2 of above-ground NPP obtained from literature. Accordingly, lower- and upper-bound total NPP values were estimated. The estimated lower-bound total NPP values ranged from 1.7 to 11.8 mt ha^{-1} yr^{-1} while the upper-bound total NPP ranged from 3.1 to 21.7 mt ha^{-1} yr^{-1}. However, Clark et al. (2001b) also noted that the above ranges could be overestimates as 32 of the 39 studies were based on plots of less than 1 ha with the median at 0.25 ha, where estimates could be biased by the presence of large trees.

Cramer et al. (1999) estimated the annual fluxes of NPP of the land biosphere using 17 different terrestrial biogeochemical models, which included models based on remote sensing as well as those simulating the vegetation structure and carbon fluxes via photosynthesis and respiration. When the outputs from all 17 models were averaged, the highest annual NPP was observed in the humid tropics, which covered the Amazonia, Central Africa and South-East Asia including the wet zone of Sri Lanka (Fig. 1 of Cramer et al., 1999). The estimated average annual NPP, in terms of C flux, was in the range of 10 – 12 mt ha^{-1} yr^{-1}.

1.6 Different models for estimating NPP

Some of the models used in Cramer et al. (1999)'s study estimated NPP directly by relating it to vegetation characteristics and environmental variables (e.g. Potter et al., 1993). The others estimated NPP as the difference between gross primary productivity (GPP) and autotrophic respiration (R_a), which were estimated separately from vegetation structural characteristics and environmental variables. In either of the two model types, the vegetation may be characterized through satellite-based remote sensing (Potter et al., 1993; Prince and Goward, 1995), direct ground-based measurements (Kindermann et al., 1993; Running and Hunt, 1993; Warnant et al., 1994) or through a sub-model simulating canopy growth and phenology (Woodward et al., 1995; Haxeltine and Prentice, 1996; Friend et al., 1997).

The satellite-based measurements, which are various combinations of red and near infrared wavebands, e.g. NDVI (Sellers et al., 1994), are related to the fraction of photosynthetically-active radiation (F_{PAR}) absorbed by the vegetation canopy (Goward and Huemmrich, 1992). F_{PAR} is then used to estimate biomass production by using the concept of radiation use efficiency (RUE) as proposed by Monteith (1977). RUE is defined as the amount of biomass produced per unit of radiation (PAR) absorbed. Therefore, NPP can be estimated as,

$$NPP = F_{PAR} \text{ x } RUE \text{ x } 0.5$$

where, the factor 0.5 is used to convert biomass production to carbon sequestration in NPP by assuming that the carbon content of plant biomass is 50%. RUE is a measurement of the efficiency of conversion of absorbed PAR in to biomass through the balance between gross photosynthesis and autotrophic respiration. When applied to a heterogeneous and highly diverse forest ecosystem such as tropical lowland wet evergreen forests, RUE gives an overall composite measurement of the efficiency of radiation conversion by the ecosystem as a whole. RUE is considered to be an approximately constant parameter under optimum environmental and growing conditions (Monteith, 1977; Landsberg, 1986). However, both photosynthesis and respiration of forest ecosystems are highly sensitive to variations in the growing environment, canopy structure and other plant characteristics such as the photosynthetic pathway (i.e. C_3, C_4 or

CAM) (Jarvis and Leverenz, 1983). Therefore, when RUE is used to estimate biomass production and carbon sequestration of tropical forests, RUE of the forest ecosystem in question and its variation have to be either measured empirically or estimated using a process-based sub-model. Some of the models that have used the RUE concept to estimate forest carbon sequestration include Potter et al. (1993), Knorr and Heimann (1995) and Ruimy et al. (1996).

1.7 Objectives of the present work

Despite the recognized potential of forests as an important sink to sequester carbon (Phillips et al., 1998; Malhi and Grace, 2000; Baker et al., 2004; Lewis et al., 2009), accurate estimates of the carbon sequestration potential of different forest types in Sri Lanka are not available. Therefore, there is an urgent need to carry out systematic studies to quantify, the actual amounts of carbon sequestered at present by Sri Lankan forests, especially the floristically rich lowland wet evergreen forests, which are located in the wet zone where biomass production and carbon sequestration potential is largely unrestricted by environmental stresses. Therefore, the specific objectives of the study were:

1. To characterize the canopy properties of the Sinharaja MAB forest reserve and the KDN forest complex and thereby estimate the fraction of incident PAR intercepted by the respective forest canopies;
2. To estimate the radiation use efficiency (RUE) of the respective forest canopies by a layered canopy photosynthesis model;

3. To determine the annual carbon sequestration rates of the two forest complexes in terms of both net primary productivity (NPP) and net ecosystem productivity (NEP);
4. To quantify the within-forest variation in canopy structure, radiation interception and carbon sequestration capacities of the two forest complexes.

2. Methodology

Estimation of carbon sequestration in natural forests formed the first component of this project. The estimation methodology was based on canopy hemispherical photography, leaf photosynthesis measurements and modelling of canopy photosynthesis. Details of each of the above methodologies are given below.

2.1 Study sites – Physical Features and Climate

Measurements were carried out in the Sinharaja Man and Biosphere Forest Reserve (described hereafter as the 'Sinharaja MAB forest reserve') and the Kanneliya-Dediyagala-Nakiyadeniya forest complex (described hereafter as the 'KDN forest complex'). Both these forest complexes belong to the lowland rainforest formation and have been classified as Wet Evergreen Forest Climax (De Rosayro, 1950), as Wet Tropical Evergreen Forests (Holmes, 1956; Koelmeyer, 1957) and as *Doona-Dipterocarpus-Mesua* Series (Gaussen et al., 1964). These are the two major tropical wet evergreen primary rainforests remaining in Sri Lanka. Both forests complexes are located in the South-Western slopes of the humid tropical zone (known locally as the 'Wet Zone') of Sri Lanka (Fig. 2.1). It is highly likely that Sinharaja and KDN forests

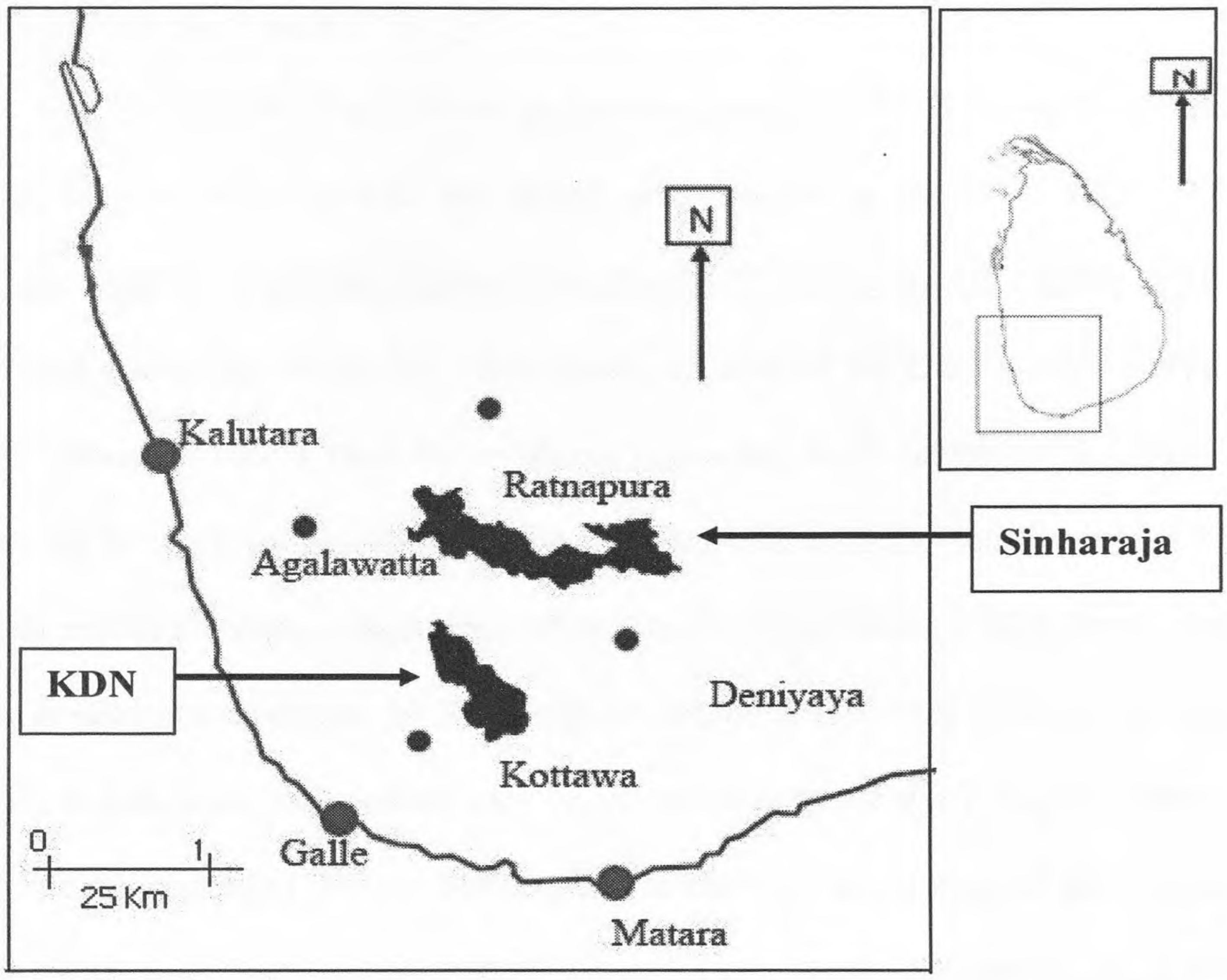


Figure 2.1: Locations of the Sinharaja Man-and-Biosphere Forest Reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) forest complex.

were parts of a larger continuous primary forest that existed in the past covering most of the south west of Sri Lanka.

The Sinharaja MAB forest reserve occupies approximately 8564 ha with its North-West corner at 6.35° – 6.43° N and the South-West corner at 80.35° – 80.57°E latitudes (http://whc.unesco.org/archive/periodicreporting/APA/cycle01/section2/405.pdf). The whole forest including the buffer zone covers an area of 11,250 ha. The forest reserve spans an elevation range from 90 m above mean sea level (amsl) in the moist coastal lowlands up to 1170 m amsl in the lower montane hills in the south western and south eastern slopes of the central highlands of Sri Lanka (Gunatilleke and Ashton, 1987). The average annual precipitation in Sinharaja is around 5000 mm (Ashton et al., 2006). However, it has been reported to vary in different parts of the forest reserve, with the western region receiving 3750 – 6000 mm and the high elevations of the eastern region receiving 3000 mm (Ashton, 1992; Gunatilleke et al., 1998). Similarly, while the annual average temperature is 25° – 27°C with a diurnal fluctuation of ± 4°C, it could vary from 18°C at high elevations in the eastern region to 24°C in the western region.

The KDN forest complex is located to the south west of Sinharaja and occupies an area of 12,050 ha between 6.15° and 6.60° N and 80.32° and 80.45°E. The elevation ranges from 60 m to 425 m amsl. According to Nisbet (1961) and Singhakumara (1995), the Kanneliya forest reserve (in Galle district) consists of several parallel ridges and valleys aligned along the north-west to south-east direction. The ridges in Nakiyadeniya (Galle district) and Dediyagala (Matara district) forest reserves are lower in elevation (i.e. approximately 230 m amsl) and are broken in to several isolated, rounded hills. The annual precipitation of Kanneliya is around 4445 mm, which is greater than that of

Dediyagala (3125 mm) and Nakiyadeniya (3750 mm) (Nisbet, 1961; Singhakumara, 1995). Variations in topography, aspect and relief of land have been identified as the probable causes of the above variation in precipitation (Singhakumara, 1995).

The topography is undulating from valley to ridge. While the soils are deep in the valleys, they can be shallow in the ridges. The soils of both forests are dominated by largely well-drained Ultisols (USDA, 1975; Mapa et al., 1999), with udults (with a loose litter layer but little or no organic horizon) on the low-lying valley bottoms and humults (2 – 3 cm thick organic horizon with a fibrous root mat) on the ridges (Ashton et al., 2006). The soils are derived from bedrocks of metamorphic khondalitic and charnokitic gneiss and schist of the Highland Geological Series (Cooray, 1967).

2.2 Study sites – Vegetation

Four different associations of tree species (known as forest communities) have been identified in the lowland wet evergreen forests in Sinharaja and KDN forest complexes based on the dominant tree species (De Rosayro, 1942). These include the two primary communities known as the 'Dipterocarpus community' and the '*Mesua-Shorea* community' and their two early successional composites known as the '*Campnosperma* and other species community' and the '*Vitex-Wormia (Dillenia)-Chaetocarpus-Anisophyllea* community' (Gunatilleke and Ashton, 1987). Some areas of both forest complexes have been selectively logged in the past, with the KDN forest complex being subjected to heavier logging than Sinharaja. Therefore, both the two primary communities and the two secondary communities are found in both forest complexes with the secondary communities being more prevalent in KDN.

In Sinharaja, the dominant families are Clusiaceae, Dipterocarpaceae, Bombacaceae, Sapotaceae and Myrtaceae (Gunatilleke and Gunatilleke, 1985). Different mixtures of tree species have been reported to occur at different elevation ranges (Gunatilleke and Gunatilleke, 1981, 1985; Gunatilleke and Ashton, 1987). The lower slopes and valleys at elevations below 300 m amsl are occupied by the *Dipterocarpus* community (Gunatilleke and Ashton, 1987) and *Shorea megistophylla-Mesua ferrea* association (Ashton, 1990 as cited by Singhakumara, 1995). Steep upper slopes and mid-elevations from 300 to 900 m amsl are occupied by the *Mesua-Shorea* community (Gunatilleke and Ashton, 1987) and the *Shorea trapezifolia-Shorea disticha* association (Ashton, 1990 as cited by Singhakumara, 1995). According to Gunatilleke and Ashton (1987), the *Mesua-Shorea* community extends down to low elevations when the soils are shallow. Gunatilleke and Gunatilleke (1981, 1985) observed that eight out of nine *Shorea* section *Doona* species of the family Dipterocarpaceae can occur in the 300 – 900 m amsl elevation zone. The elevations above 900 m amsl are dominated solely by *Shorea gardneri* (Thw.) Ashton, or its mixtures with other families (Gunatilleke and Ashton, 1987). Steep slopes and rocky ridges with shallow soil are restricted to the *Shorea worthingtoni-Mesua nagassarium* association (Ashton, 1990 as cited by Singhakumara, 1995).

In the KDN forest complex, the dominant families are Clusiaceae (dominant in Kanneliya only), Anacardiaceae (dominant in K, D and N), Dipterocarpaceae (K and N only), Euphorbiaceae (K, D and N), Sapotaceae (K and D only) , Dilleniaceae (D and N only), Anisophylleaceae (D only) and Annonaceae (N only) (Singhakumara, 1995). According to Peiris (1975), KDN forests have the *Mesua-Doona (Shorea)* community of De Rosayro (1942). In 1975, the leading dominant species in Kanneliya were *Mesua* *nagassarium*, *Cullenia zeylanica* and *Shorea worthingtoni* (Peiris, 1975). In his more recent study in 1995, Singhakumara (1995) identified 15 dominant genera for Kanneliya, Dediyagala and Nakiyadeniya forests based on the Importance Value Index (IVI) with Shorea, Semecarpus and Dillenia being among the top five in all three forests. Other genera which came within the top five dominants were Palaquium (in Kanneliya only), Anisophyllea (in Kanneliya and Dediyagala only) and Xylopia and Hydnocarpus (in Nakiyadeniya only). Based on the IVI, the species within the top five dominants were *Anisophyllea cinnamomoides*, (in K and D only), *Cullenia rosayroana* (in K and N only), *Gyrinops walla* (in K and D only), *Dillenia retusa* and *Xylopia championii* (in K, D and N), *Chaetocarpus castanocarpus* (in D only) and *Hydnocarpus octandra* and *Diospyros* spp. (in N only) (Singhakumara, 1995).

Vertical stratification of vegetation can be observed in most of the undisturbed regions of both Sinharaja and KDN forest complexes (De Rosayro, 1950). Usually, four strata can be identified. The main canopy reaches 30 – 40 m above ground, while the sub-canopy reaches a height of 15 – 30 m. The understorey tree stratum is 5 – 15 m tall while the bottom-most stratum consists of a sparsely-distributed shrub layer and ground vegetation.

2.3 Stepwise procedure to estimate the rates of carbon sequestration by natural forests

An overview of the entire calculation procedure is given in the flow diagram of Fig. 2.2. The present study utilized the well-established relationship between biomass production and radiation interception (Monteith, 1977) to estimate the carbon sequestration capacity

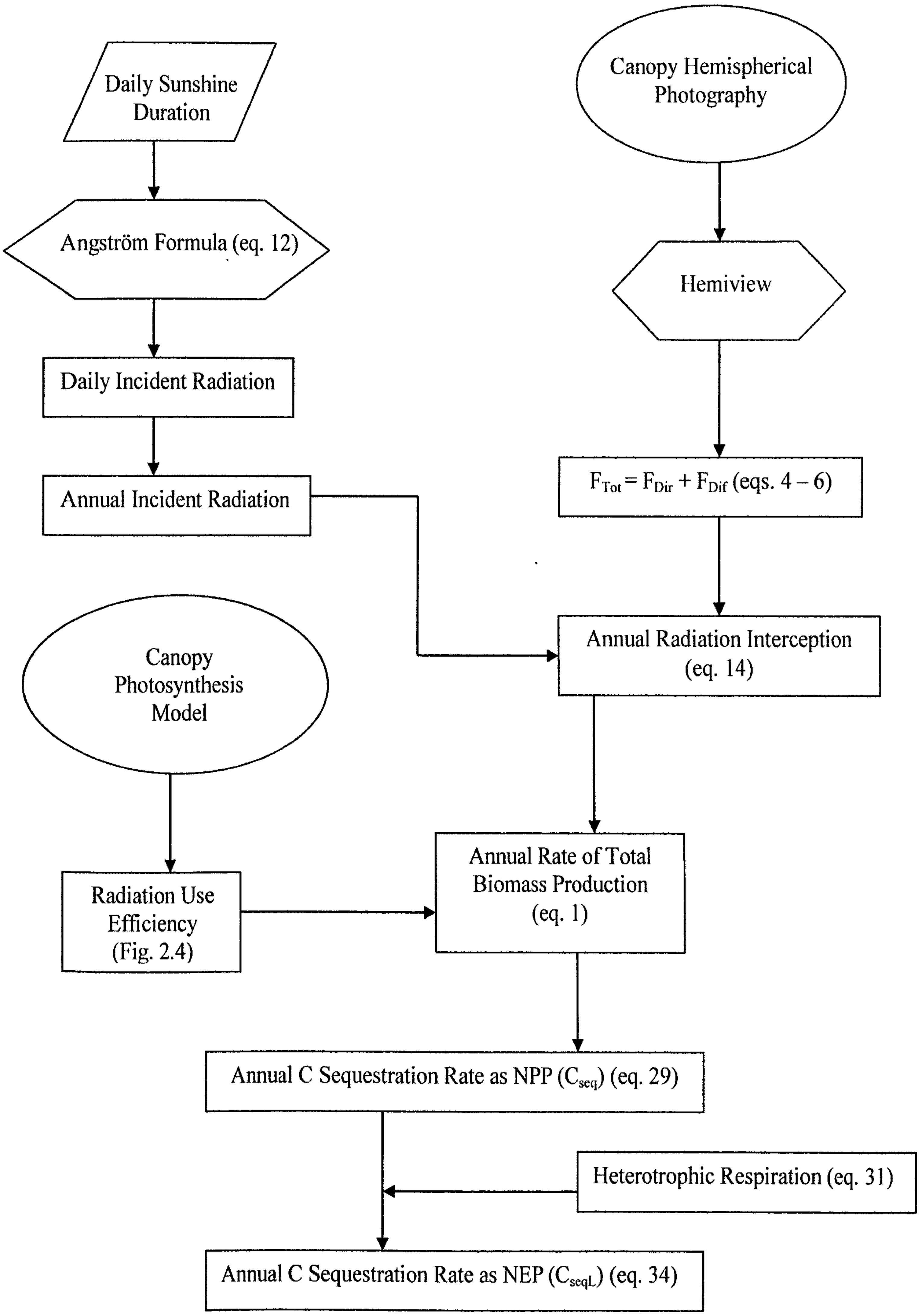


Figure 2.2: Overview of the entire procedure for calculation of carbon sequestration rate of Sinharaja and KDN forest complexes. The canopy photosynthesis model is given in Fig. 2.4.

of the Sinharaja MAB forest reserve and the KDN forest complex. Monteith (1977)'s relationship can be given as,

$$W = R_I \times RUE \qquad \text{(eq. 1)}$$

where, W is the rate of biomass production of a given vegetation system (i.e. natural forests in the present study) in terms of weight of biomass produced per unit land area per unit time and R_I, the rate of radiation interception by the foliage canopy in terms of radiation energy intercepted per unit land area per unit time. RUE is radiation use efficiency, defined as the weight of biomass produced per unit of intercepted radiation. RUE is a measurement of the efficiency with which intercepted radiation is converted to biomass through photosynthesis and subsequent biosynthesis pathways. In the present study, R_I was estimated using canopy hemispherical photography and RUE was estimated using a layered canopy photosynthesis model.

2.3.1 Estimation of intercepted radiation by canopy hemispherical photography

Canopy hemispherical photography (CHP) was used to analyze the canopy structure of the two selected natural forest complexes and to estimate the radiation interception by their canopies. CHP involves taking an upward-looking photograph of the forest canopy from the ground level using a superwide-angle, 180^0 hemispherical (fish-eye) lens pointed upwards. Hence, it is a kind of 'upside down' remote sensing. The photograph so obtained (Plate 2.1: An example of a canopy hemispherical photograph) consists of the visible sky through canopy gaps and obstructions such as leaves, branches and stems

Plate 2.1: Example of a canopy hemispherical photograph taken from Sinharaja MAB forest reserve.

across a hemisphere above the ground level with its centre at the place from which the photograph is taken. Image analysis of hemispherical photographs using the information on the direction of incoming solar radiation, geographical co-ordinates (i.e. latitude and longitude) of the location and the relevant meteorological relationships yields a wealth of information on properties of the forest canopy and enables calculation of radiation interception by the canopy (Evans and Coombe, 1959; Anderson, 1964a, 1970, 1971). Hence, CHP is ideally suited to examine the spatial variability of canopy properties and radiation interception of highly heterogeneous natural forests such as Sinharaja and KDN. In the Sinharaja MAB forest reserve, CHP was carried out in three different forest regions as defined by the respective entry points to the forest, namely, Kudawa, Pitadeniya and Morningside. In the KDN forest complex, CHP was done in Kanneliya and Dediyagala forest regions. In both forest complexes, hemispherical photographs were taken along 1 km line transects along contours at 100 m intervals. Because of the expected significant variation in canopy properties of the forest at different topographic positions (i.e. valley, mid-slope and ridge-top) (Ediriweera et al., 2008), transects were laid along all topographic classes (Table 2.1).

Table 2.1: Locations of canopy hemispherical photography

Forest	Forest region	Topographic class	No. of transects	No. of sampling points[†]
Sinharaja MAB forest reserve	Kudawa	Valley	5	40
		Mid-slope	4	42
		Ridge-top	8	46
	Pitadeniya	Valley	1	20
		Mid-slope	1	14
		Ridge-top	2	17
	Morningside	Valley	2	7
		Mid-slope	2	3
		Ridge-top	2	13
	Sub-total		*27*	*202*
KDN forest complex	Kanneliya	Valley	5	42
		Mid-slope	4	37
		Ridge-top	3	19
	Dediyagala	Valley	2	12
		Mid-slope	2	17
		Ridge-top	2	14
	Sub-total		*18*	*141*
	Total		45	343

[†] Each sampling point represents one location at which a canopy hemispherical photograph was taken.

The Magellan meridian (Version 5.38) Global Positioning System was used to mark transects. The 180°-angled (Fish eye) lens (Delta-T Devices, UK) was used to capture the hemispherical photographs by using a Nikon 32 mm coolpix digital camera fixed on a tripod at a height of 1 m above the ground level. The camera was mounted on an upward-facing self-levelling device. These photographs were taken on the high quality fine mode after making the correct orientation for the north using the compass inset attached to the self-levelling device. The latitude and longitude of each sample point and sampled date and time were recorded after each capturing. In addition to these, cloudiness of the sky and slope of the land at the sample point were recorded as information of possible use during analysis of photographs. Sampling locations were selected after avoiding possible obstacles such as large boulders.

2.3.2 Image analysis of canopy hemispherical photographs

The captured hemispherical photographs were developed by using the Adobe Photoshop (version 7.0) photo-editing package to remove distinguishable stems and any other objects which are in the canopy free, blank area of the picture. Then the well-developed hemispherical photographs were analyzed with the Hemiview (Version 2.1, Delta-T Devices, UK) canopy analysis software. Brightness and contrast were adjusted and the threshold method was used to enable Hemiview to distinguish areas of the photograph which show the open sky (i.e. canopy gaps) from those covered by the forest canopy. The threshold method involves dividing the photograph in to a series of sky sectors (as defined by a series of zenith and azimuth angles) and determining a threshold light intensity (i.e. as indicated by the brightness on the photograph) value, above which a given segment is classified as open (i.e. a canopy gap) and below which is classified as obscure (i.e. covered with foliage). The 'Gap Fraction' is calculated as the proportion of visible sky (i.e. canopy opening) within a given sky sector. Hence, a Gap Fraction of zero indicates complete canopy cover whereas a value of one indicates complete light penetration because of a canopy gap.

Images (i.e. hemispherical photographs) classified as above, are overlain with a Sunmap (Plate 2.2a. An image with the Sunmap overlain) and a Skymap (Plate 2.2b. An image with the Skymap overlain) as determined by the latitude and longitude of the location and day of the year on which the photograph was taken. The Sunmap defines the paths of the

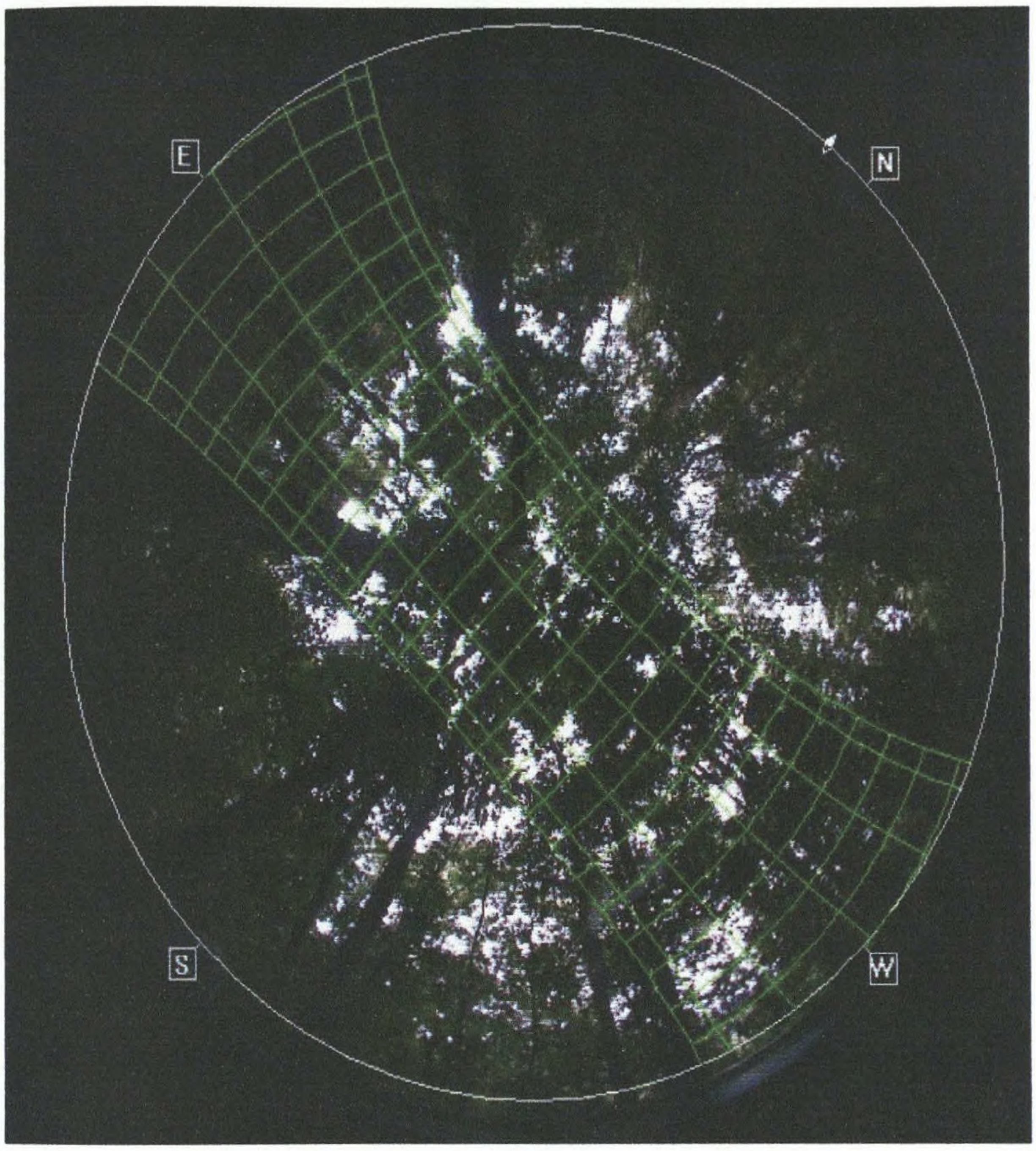


Plate 2.2.a: A canopy hemispherical photograph with the sunmap overlain on it.

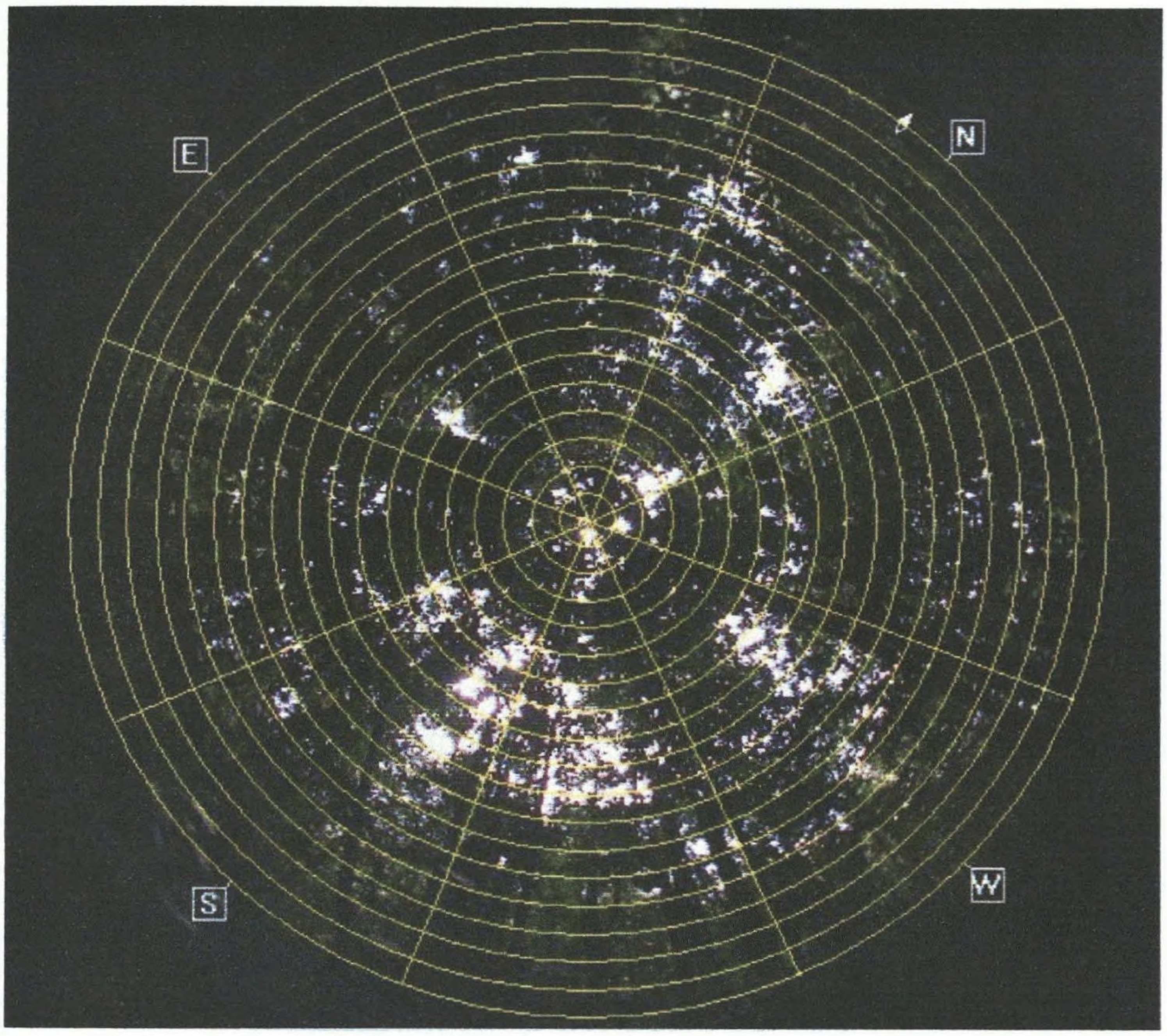


Plate 2.2.b: A canopy hemispherical photograph with the skymap overlain on it.

sun over the location at different times of the year as determined by the latitude of the location. The solar tracks for a given latitude and day of the year are derived using the following relationships:

$$\sin \alpha = \sin \psi \sin \delta + \cos \psi \cos \delta \cos \eta \qquad \text{(eq. 2)}$$

$$\sin \beta = - \cos \delta (\sin \eta / \cos \alpha) \qquad \text{(eq. 3)}$$

where α is the solar altitude or the angular elevation above the horizon, β is the solar azimuth, δ is the solar declination at the respective date, ψ is the latitude and η is the hour angle. The hour angle is equal to $\pi/180\ (H - 12)\ 15$, where H is the mean solar time in hours. All angles are expressed in radians. The gap fraction along the path of the sun gives an estimation of the proportion of sky visible in each sky sector (Anderson, 1971; Anon., 1999a). The Sunmap matches the track of the sun throughout the day, and through the year and hence divides the hemispherical photograph in to areas representing time. Therefore, gap fractions of the respective sky sectors obtained by overlaying the Sunmap on the hemispherical photograph, after correcting for angle of incidence, provide an estimation of the fraction of incident direct radiation (i.e. the radiation that comes directly from the solar disc and reaches the top of the forest canopy without any interruption) reaching the sampling location by transmission through the forest canopy. Based on these estimates, Hemiview calculates the Direct Site Factor (DSF) as the proportion of direct solar radiation reaching a given sampling location, relative to that in a location with no sky obstructions (Anon., 1999a). The angle of incidence is the angle between a surface and incoming radiation reaching the surface, measured relative to the direction normal to the surface (Anon., 1999a).

The Skymap, which has been constructed according to instructions given by Anderson (1964b), divides the hemispherical photograph in to areas representing different directions of the sky. Gap fractions of the respective Skymap sectors obtained by overlaying the Skymap on the hemispherical photograph, after correcting for the angle of incidence, provides an estimation of the fraction of incident diffuse radiation (i.e. solar radiation, which comes from all angles of the sky after being scattered and reflected downwards) on to the sampling location by transmission through the forest canopy. Based on these estimates, Hemiview calculates the Indirect Site Factor (ISF), also called the Diffuse Site Factor (Anderson, 1964b), as the proportion of diffuse solar radiation reaching a given sampling location, relative to that in a location with no sky obstructions (Anon., 1999a). The Global Site Factor, also called the Total Site Factor (Anderson, 1964b), is defined as the proportion of global radiation (i.e. direct plus diffuse) beneath the forest canopy at a given sampling location relative to that in the open.

2.3.3 Calculation of intercepted fractions of direct, diffuse and total radiation

After analysis of each image by Hemiview, intercepted fractions of incident direct (F_{Dir}), diffuse (F_{Dif}) and total (F_{Tot}) radiations were calculated as following:

$$F_{Dir} = (Dir_{Ab} - Dir_{Be})/Dir_{Ab} = 1 - DSF \qquad \text{(eq. 4)}$$

$$F_{Dif} = (Dif_{Ab} - Dif_{Be})/Dif_{Ab} = 1 - ISF \qquad \text{(eq. 5)}$$

$$F_{Tot} = [(Dir_{Ab} + Dif_{Ab}) - (Dir_{Be} + Dif_{Be})]/(Dir_{Ab} + Dif_{Ab}) = 1 - GSF \qquad \text{(eq. 6)}$$

where, Dir_{Ab} and Dir_{Be} are respectively the estimated amounts of direct radiation above and below the forest canopy and Dif_{Ab} and Dif_{Be} are respectively the estimated amounts of diffuse radiation above and below the forest canopy. DSF, ISF and GSF are the direct, indirect and global site factors as defined earlier.

2.3.4 Calculation of canopy properties

Leaf area index (LAI), defined as half of the total leaf area per unit ground surface area (Lang et al., 1991; Chen and Black, 1992), is calculated by Hemiview using an inversion of the Beer's Law for transfer of energy across a medium (Monteith and Unsworth, 1990). The Beer's Law, as applied to the present situation, can be given as,

$$G(\theta) = e^{-k(\theta)\,LAI} \qquad \text{(eq. 7)}$$

where G (θ) and k (θ) are the Gap Fraction and light extinction coefficient at a given solar zenith angle (θ). Hemiview estimates LAI by inversion of eq. 7 (eq. 8) by an iteration procedure as the inverted equation cannot be solved analytically.

$$LAI(\theta) = -\ln[G(\theta)]/k(\theta) \qquad \text{(eq. 8)}$$

This calculation of LAI assumes a random distribution of completely black (i.e. complete absorption of intercepted radiation) leaf elements along any given horizontal plane within the canopy. As the clumping of leaf elements is low in broad-leaved tree canopies (unlike in conifers which show significant clumping), this assumption does not introduce a significant error to the LAI calculation (Chen et al., 1991; Chen and Black, 1992; Chen and Cihlar, 1995; Anon., 1999a).

k (θ) is estimated based on the Ellipsoidal Leaf Angle Distribution (ELADP) as defined by Campbell (1986), who derived an equation for k (θ) for a canopy with its leaf elements distributed in the same proportions and orientation as the surface of an ellipsoid of revolution, symmetrical about a vertical axis (Fig. 2.3). ELADP is defined as,

$$\text{ELADP} = x = b/a \qquad \text{(eq. 9)}$$

where, a and b are the semi-vertical and semi-horizontal axes of the ellipsoid (Fig. 2.3). It follows that an ELADP of greater than one indicates a flatter canopy with more horizontally-oriented leaves. In contrast, an ELADP of less than one indicates a deeper canopy with more vertically-oriented leaves.

In the iteration procedure to calculate LAI, Hemiview initially calculates initial values of LAI and ELADP for a theoretical canopy with an ellipsoidal distribution of leaf elements that give the best fits to the measured Gap Fraction of the hemispherical photograph. These initial best fit values of LAI and ELADP are used in the subsequent iterations until they converge on a minimum error sum of squares.

Mean leaf angle (MLA), defined as the average angle of canopy leaf elements to the horizontal, for an ellipsoidally-distributed canopy is calculated by Hemiview using the following integral,

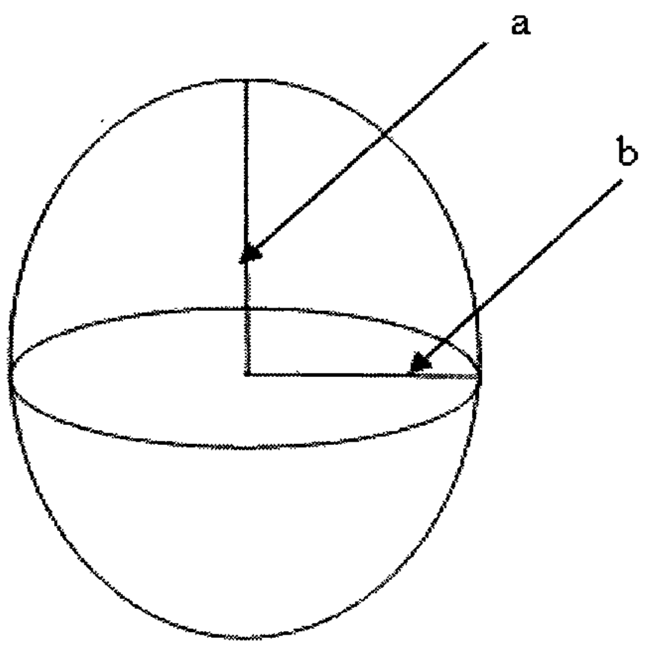


Figure 2.3: Semi-vertical and semi-horizontal axes for defining Ellipsoidal Leaf Angle Distribution (ELADP).

$$MLA(x) = \frac{\int_0^{\frac{x}{2}} \sqrt{\sin(\alpha)^2 + x^2.\cos(\alpha)^2}.a\tan\frac{\tan(\alpha)}{x}.\sin(\alpha).d\alpha}{\int_0^{\frac{x}{2}} \sqrt{\sin(\alpha)^2 + x^2.\cos(\alpha)^2}.\sin(\alpha).d\alpha} \qquad \text{(eq. 10)}$$

where, x is ELADP and α is the solar inclination angle, i.e. the angle between the plane of the canopy element and the horizontal (Anon., 1999a). A close approximation of the above integral is,

$$MLA(x) = \frac{150}{\left(x^{1.2} + \frac{5}{3}\right)} \qquad \text{(eq..11)}$$

2.3.5 Calculation of incident radiation

Daily incident total solar radiation energy on the forest canopy (in MJ m^{-2} d^{-1}) was calculated by converting the daily sunshine duration (h d^{-1}) data from nearby meteorological stations (Table 2.2) using the Angström Formula (Angström, 1924),

$$S = S_0\,[a + b\,(H/Z)] \qquad \text{(eq. 12)}$$

where, S is the daily incident solar radiation (MJ m^{-2} d^{-1}) on a horizontal surface on the earth and S_0 is the corresponding value at the top of the atmosphere. H is the daily sunshine duration (h d^{-1}) and Z is the day length (h d^{-1}). S_0 and Z were calculated using a set of standard meteorological equations (List, 1968).

Table 2.2: Meteorological stations from which sunshine duration data were used to calculate daily incident radiation on the forest canopy

Location	Latitude & Longitude	Mean annual day length (h d^{-1})	Coefficients of the Angström Formula	
			a	b
Ratnapura	6.683°N, 80.399°E	12.1233	0.25	0.44
Agalawatta	6.542°N, 80.158°E	12.1231	0.22	0.50
Deniyaya	6.317°N, 80.567°E	12.1228	0.23	0.47
Kottawa	6.083°N, 80.336°E	12.1226	0.25	0.45

Values of coefficients of the Angström Formula for Ratnapura and Agalawatta were obtained from Samuel (1991) while those for Deniyaya and Kottawa were estimated by linear interpolation. At Ratnapura and Agalawatta, sunshine duration data for the 31-year period from 1978 to 2008 were used. At Deniyaya, sunshine duration data were available for a nine-year period (i.e. 1990-4, 1996, 2001-2, 2004) whereas at Kottawa data were available for only two years (i.e. 2007-8). Mean incident total solar radiation values for each location were obtained by taking the arithmetic average over the above periods.

Mean incident radiation within the photosynthetically-active radiation (PAR) range (i.e. 0.4 – 0.7 μm wavelength range) was calculated by multiplying the mean incident total solar radiation (i.e. 0.3 – 3 μm) by 0.5. This assumes that 50% of energy in total solar radiation is within the PAR range (Monteith and Unsworth, 1990). For subsequent calculations of photosynthesis, incident PAR in energy units were converted to incident PAR in molar units as,

$1 \text{ J PAR} \approx 4.6 \ \mu\text{mol PAR}$ (eq. 13) (Salisbury, 1996)

Mean instantaneous photosynthetic photon flux densities (PPFD) were calculated by dividing the relevant mean daily values by the respective mean day lengths of the different locations.

Based on the geographical co-ordinates of the two forest complexes and the locations from which the sunshine duration data were collected (Fig. 2.1), mean incident solar radiation on the forest canopy of Sinharaja was obtained by averaging the data from Ratnapura, Agalawatta and Deniyaya. Likewise, the mean incident solar radiation on the KDN forest complex was obtained by taking the average of data from Deniyaya and Kottawa.

2.3.6 Calculation of intercepted radiation (R_I)

Total intercepted radiation by the forest canopy (R_I in MJ m^{-2} d^{-1}) at each sampling point of hemispherical photography was calculated as the product between the fraction of incident total (global) radiation intercepted (F_{Tot}) and average daily incident radiation (S in MJ m^{-2} d^{-1}) of the respective forest complexes;

$$R_I = F_{Tot} \, . \, S \qquad \text{(eq. 14)}$$

As explained above, F_{Tot} was estimated from canopy hemispherical photography and S was calculated from meteorological data.

2.3.7 Estimation of Radiation Use Efficiency (RUE) by a layered canopy photosynthesis model

Estimation of RUE requires the simultaneous estimation of biomass increase and radiation interception during a fixed period of time. However, direct measurement of biomass production is not possible in a natural forest, which consists of a mixture of a large number of tree/plant species with their foliage canopies in different vertical strata. Therefore, a canopy photosynthesis model (Fig. 2.4) was developed to estimate daily biomass production by the natural forest. The model involved dividing the forest canopy in to three different strata (i.e. canopy, sub-canopy and understorey) and estimating the canopy photosynthesis rate of each stratum.

2.3.8 Measurement of photosynthetic light response curves

In order to estimate the photosynthesis rate from each canopy stratum, photosynthetic light response curves were measured in 14 tree/plant species representing different strata of the forest canopy (Table 2.3). Measurements were done on potted seedlings raised in the nursery in the Kanneliya forest reserve and kept in a partially-shaded plant house at the University of Peradeniya. The LICOR6400 portable photosynthesis measurement system (LI-COR Inc., Lincoln, NE, USA) was used to obtain light response curves on a series of cloudless sunny days. Leaf net photosynthetic rate (P_n) was measured on the youngest fully expanded leaves under natural light. Intensity of light incident on the leaf chamber was varied by using layers of white-coloured gauze cloth. After taking measurements at full sunlight, a series of lower light intensities were achieved by varying the number of cloth layers. Levels of incident light intensity were varied in a random

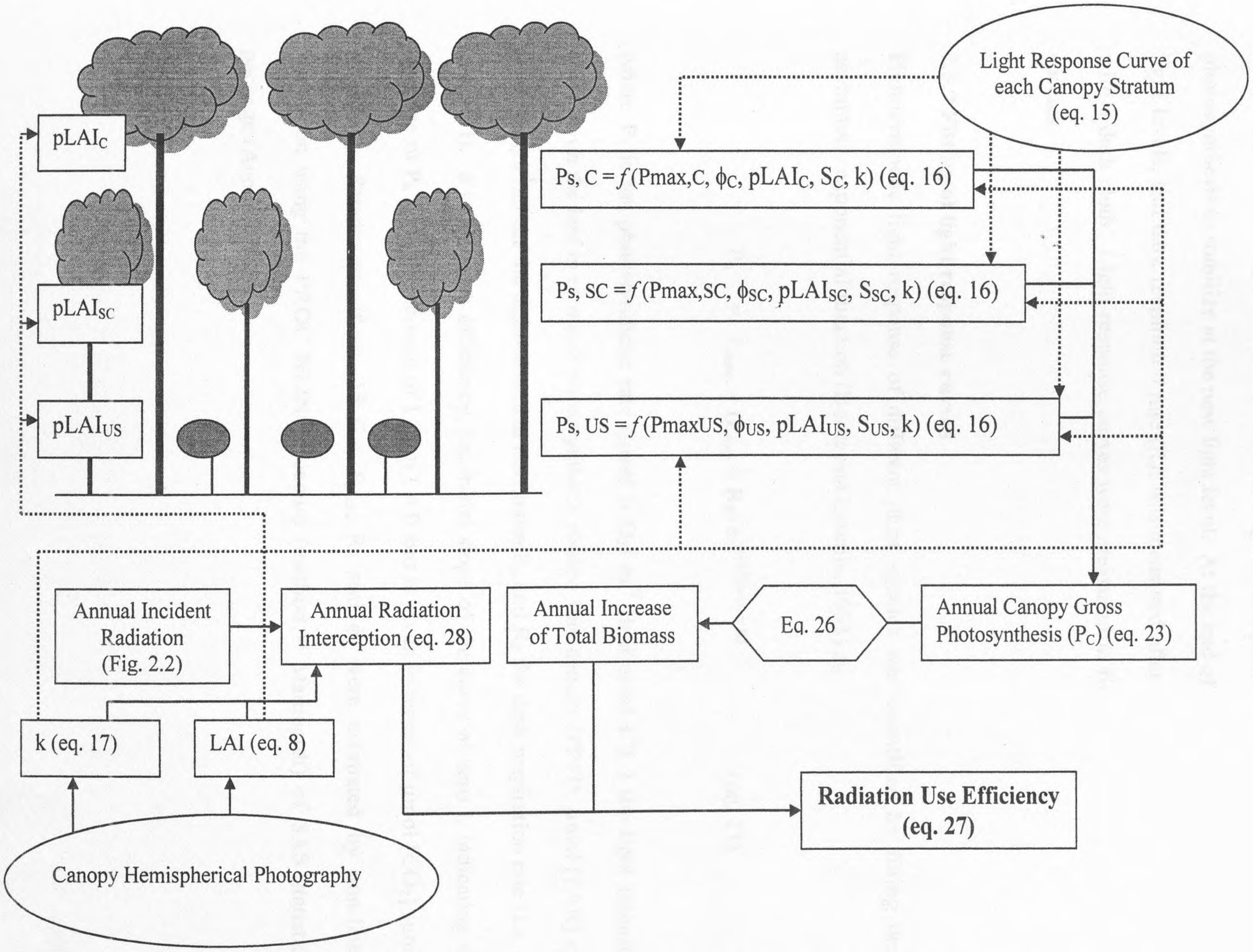


Figure 2.4: Flow diagram of the canopy photosynthesis model to calculate radiation use efficiency (RUE).

manner. When light intensity was changed, adequate time was allowed for photosynthesis to stabilize at the new light level. At the end of measurements at different light levels, leaf dark respiration rate (R_d) was measured after covering the leaf chamber with a dark cloth. Light response curves were measured in five replicate leaves in each species.

2.3.9 Fitting of light response curves

Photosynthetic light response of different plant species was quantified by fitting the asymptotic exponential function (Boote and Loomis, 1991) as,

$$P_n = P_{max} - (P_{max} + R_d)\, e^{-\phi I/(Pmax + R)} \qquad \text{(eq. 15)}$$

where P_n is net photosynthetic rate (μmol [CO_2] m^{-2} [leaf area] s^{-1}), I the light intensity incident on the leaf in terms of photosynthetic photon flux density (PPFD, μmol [PAR] m^{-2} [leaf area] s^{-1}), P_{max} the light-saturated maximum P_n and R_d the dark respiration rate (i.e. P_n at zero I). ϕ is quantum efficiency, i.e. initial slope of the curve at zero I, indicating the increase of P_n per unit increase of I from I = 0 and is given in terms of μmol [CO_2] (μmol [PAR]$)^{-1}$. Parameters of eq. 15 (i.e. P_{max}, R_d and ϕ) were estimated by non-linear regression using the PROC NLIN procedure (method = Marquardt) of SAS statistical package (Anon., 1999b).

Table 2.3: List of tree/plant species that were used to develop light response curves for different vertical canopy strata

No.	Species	Family	Stratum occupied in the forest vertical profile
1	*Shorea congestiflora*	Dipterocarpaceae	Canopy
2	*Vateria copallifera*	Dipterocarpaceae	Canopy
3	*Shorea stipularis*	Dipterocarpaceae	Canopy
4	*Dipterocarpus zeylanicus*	Dipterocarpaceae	Canopy
5	*Shorea disticha*	Dipterocarpaceae	Canopy
6	*Calophyllum bracteatum*	Clusiaceae	Sub canopy
7	*Mesua ferrea*	Clusiaceae	Sub canopy
8	*Dillenia triquetra*	Dilleniaceae	Sub canopy
9	*Stemonoporus kanneliyensis*	Dipterocarpaceae	Sub canopy
10	*Garcinia quaesita*	Clusiaceae	Sub canopy
11	*Calophyllum calaba*	Clusiaceae	Sub canopy
12	*Agrostistachys coriacea*	Euphorbiaceae	Understorey
13	*Aporusa cardiosperma*	Euphorbiaceae	Understorey
14	*Schumacheria castaneifolia*	Dilleniaceae	Understorey

Curves were first fitted for each species separately after pooling the data from different replicate leaves. Utilizing the estimated parameters of individual tree/plant species in building the canopy photosynthesis model requires information about the contribution from each individual species to the total canopy area of the forest. Although there have been comprehensive studies on the phytosociology of both Sinharaja (Gunatilleke and Gunatilleke, 1981, 1985; Gunatilleke and Ashton, 1987) and KDN (Singhakumara, 1995), such detailed information on the forest canopy and its vertical stratification was not available. Therefore, the photosynthetic light response data from tree/plant species representing each vertical stratum were pooled to obtain a pooled light response curve for each stratum.

2.3.10 Calculation of canopy photosynthesis

Canopy gross photosynthesis (P_c) of each sampling location (i.e. locations at which canopy hemispherical photographs were taken, Table 2.1) was computed as the sum of photosynthesis of the three canopy strata at the respective sampling location. Daily gross photosynthesis of a given canopy stratum i ($P_{s,i}$) (μmol [CO_2] m^{-2} [Ground Area] d^{-1}) was computed using an equation given by Charles-Edwards (1982) as,

$$P_{s,i} = \frac{\phi_i .S_i .h.P_{\max,i}[1 - e^{-k.pLAI_i}]}{\phi_i .k.S_i + h.P_{\max,i}} \qquad \text{(eq. 16)}$$

where, ϕ_i is the quantum (photochemical) efficiency (μmol [CO_2] μmol [PAR]$^{-1}$), $P_{max,i}$ the maximum light saturated net photosynthetic rate (μmol [CO_2] m^{-2} [Leaf Area] s^{-1}) and L_i the partial leaf area index of canopy stratum i. S_i is mean daily incident radiation (μmol [PAR] m^{-2} [Ground Area] d^{-1}) on canopy stratum i and h is mean day length (s d^{-1}) as specified earlier for the two forest complexes. k is the canopy light extinction coefficient of the forest at each sampling location.

The overall canopy light extinction coefficient (k) at each sampling point was calculated by inverting the Beer's Law as,

$$k = - \ln (V_{sky})/LAI \qquad \text{(eq. 17)}$$

where, V_{sky} is the overall proportion of the sky hemisphere that is visible and LAI the total canopy LAI at the sampling point.

Calculation of partial LAI of a given stratum requires division of the total canopy LAI in to the three strata. As direct measurement of LAI in the different canopy strata was not possible practically, it was estimated based on radiation penetration in to different vertical strata of the canopy. This estimation was based on the assumption that partial LAI of a given canopy stratum is determined by the amount of radiation reaching that stratum, with greater light penetration allowing the development of a larger leaf area in the stratum. Ashton et al. (2006) specified the photosynthetic photon flux densities incident at the canopy top (F) and under bright shade (B), medium shade (M) and deep shade (D) as 1600, 700 (44% of full sunlight), 350 (22%) and 50 (3.1%) μmol [PAR] m^{-2} s^{-1}. The respective daily photon flux densities under the same conditions were 38.1, 16.3 (43% of full sunlight), 6.0 (16%) and 1.2 (3.2%) mol [PAR] m^{-2} s^{-1}. Based on these values, in the present study, the radiation receipt at the sub-canopy level was estimated as 31% of full sunlight, which is the average of percentage light penetration values of bright and medium shade of Ashton et al. (2006) (i.e. mean of 44% and 22% based on maximum instantaneous photon flux density and 43% and 16% based on maximum daily photon flux density on clear sunny days – Table 1 of Ashton, 2006). Similarly, the radiation receipt at the understorey level was estimated as 11% of full sunlight, which is the average of percentage light penetration values of medium and deep shade of Ashton et al. (2006) (i.e. mean of 22% and 3.1% based on maximum instantaneous PFD and 16% and 3.2% based on maximum daily PFD on clear sunny days). Based on these fractional light penetrations at the sub-canopy and understorey, the cumulative LAIs that penetrating radiation has to pass through to reach the sub-canopy ($cLAI_{SC}$) and understorey ($cLAI_{US}$) levels (Fig. 2.5) were estimated as,

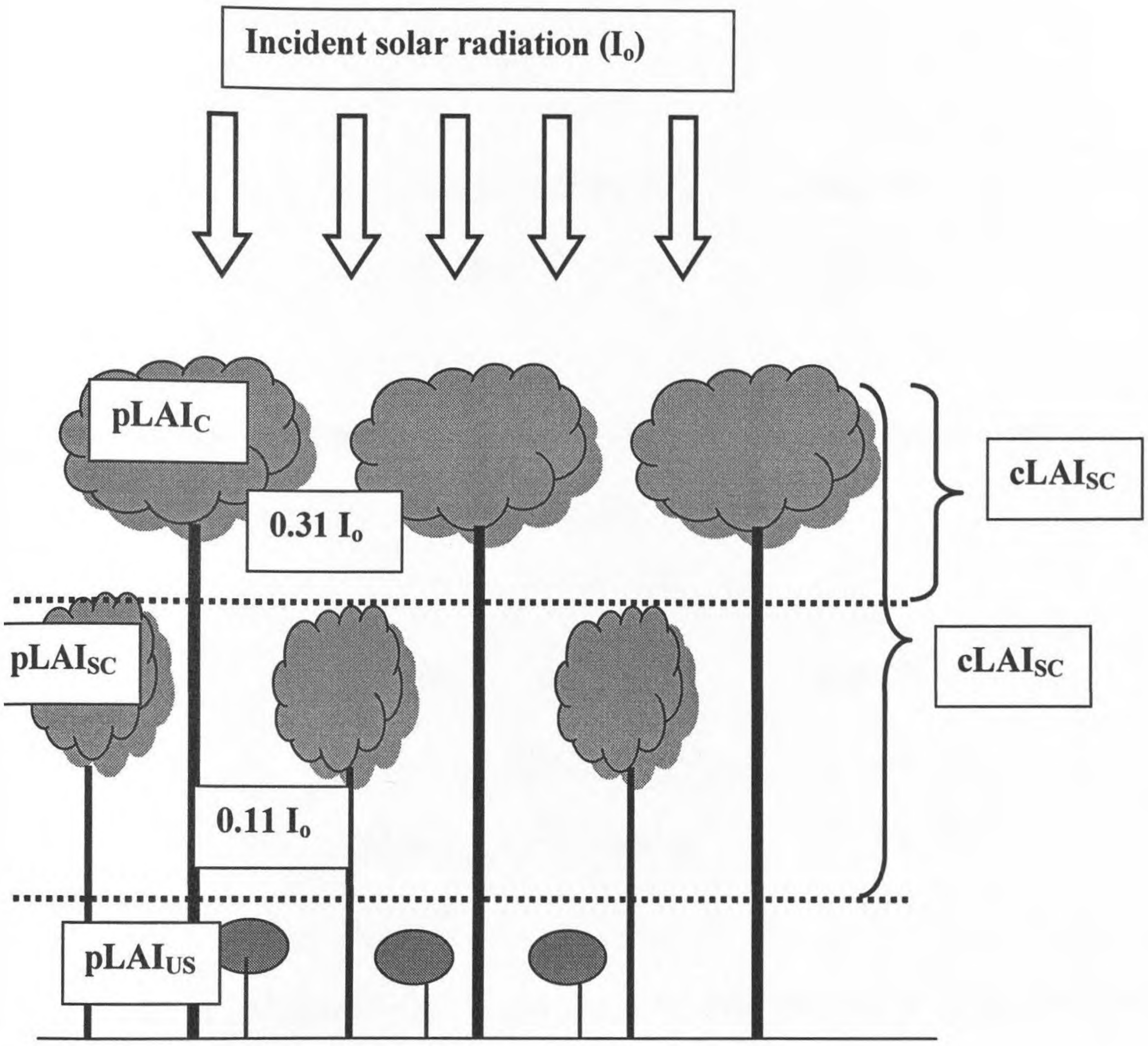


Figure 2.5: Radiation interception model for the Sinharaja and KDN forest complexes. $pLAI_C$, $pLAI_{SC}$ and $pLAI_{US}$ are the respective partial leaf area indices of the canopy, sub-canopy and understorey strata. $cLAI_{SC}$ and $cLAI_{US}$ are the respective cumulative leaf area indices that the radiation has to be pass through to reach the sub-canopy and understorey strata.

$$cLAI_{SC} = -\ln(0.31)/k \qquad \text{(eq. 18)}$$

$$cLAI_{US} = -\ln(0.11)/k \qquad \text{(eq. 19)}$$

Accordingly, the respective partial LAIs, of the canopy ($pLAI_C$), sub-canopy ($pLAI_{SC}$) and understorey ($pLAI_{US}$) were calculated as,

$$pLAI_C = cLAI_{SC} \qquad \text{(eq. 20)}$$

$$pLAI_{SC} = cLAI_{US} - cLAI_{SC} \qquad \text{(eq. 21)}$$

$$pLAI_{US} = LAI - cLAI_{US} \qquad \text{(eq. 22)}$$

The partial LAIs calculated as above were inserted in to eq. 16 along with the respective parameters of the light response curves (i.e. P_{max} and ϕ), incident radiation (S) and day length (h) and the canopy light extinction coefficient (k) to calculate the daily gross photosynthesis of each canopy stratum ($P_{s,i}$) (μmol [CO_2] m^{-2} [Ground Area] d^{-1}). $P_{s,I}$ values from three strata were added to obtain the total daily canopy photosynthesis (P_c) as,

$$P_c = P_{s,C} + P_{s,SC} + P_{s,US} \qquad \text{(eq. 23)}$$

where, $P_{s,C}$, $P_{s,SC}$ and $P_{s,US}$ were the respective daily gross photosynthetic rates of the canopy, sub-canopy and understorey strata.

2.3.11 Conversion of canopy gross photosynthesis to tree biomass

The CO_2 that is absorbed during photosynthesis is assimilated in to biomass. During this process, part of the assimilated CO_2 is used for respiration, which is the process of generating energy for all metabolic processes in plants. Respiratory energy is utilized for synthesis of different components of plant biomass (i.e. carbohydrates such as cellulose, lignin etc., amino acids, proteins, lipids, nucleic acids, secondary metabolites etc.) (known as growth respiration, R_g) and to maintain the existing biomass (known as maintenance respiration, R_m). McCree (1970, 1974) expressed the growth- and maintenance components of total respiration (R) in terms of two coefficients as,

$$R = R_g + R_m = a\ P_c + b\ W \qquad \text{(eq. 24)}$$

where, a is the proportion of gross photosynthesis used for synthesis of new biomass and b the proportion of standing biomass used for cellular maintenance processes on a daily basis. However, this equation cannot be applied to calculate the respiration rate of forests because the two coefficients *a* and *b* have not been determined for any of the tree species. McCree (1970) initially developed the equation for herbaceous plants. Therefore, although theoretically sound, it is doubtful whether this equation can be applied to tree species or forests. Even in the experimental determination of the two respiratory coefficients, there are major difficulties, especially in the estimation of R_m. R_m is the respiratory cost of metabolic processes required for tissue maintenance and was therefore considered by McCree (1970, 1974) to be proportional to the standing biomass (W). However, tree biomass contains a large fraction of woody, metabolically inactive tissues, which are unlikely to demand respiratory energy for their maintenance. Therefore, in addition to the estimation of the maintenance respiration coefficient b, estimation of R_m requires knowing the proportion of metabolically active biomass in the total standing tree biomass.

The method recommended by McCree (1970, 1974) to measure R_m is to measure the dark respiration of a plant after keeping it in the dark for more than 24 hours. This is aimed at exhausting all newly formed respiratory substrate, glucose, from gross photosynthesis and thereby decreasing R_g to zero. Hence, any respiration that would be observed after keeping the plant in the dark for a prolonged period would be R_m. However, Butler and Landsberg (1981) could not observe any stabilization or a reduction in the CO_2 efflux from apple trees even after keeping them in the dark for up to 36 hours. Hence, they concluded that they were not able to separate R_g and R_m in large woody plants.

Because of the difficulty of using the McCree (1970, 1974)'s mechanistic relationship to estimate total respiration, in the present study, canopy gross photosynthesis (P_c) was converted to plant biomass by using a conversion factor of 0.0285 kg of biomass per mol^{-1} of CO_2 absorbed for gross photosynthesis as given by Landsberg (1986). This value has a mechanistic basis as it varies with the chemical composition of biomass (i.e. proportions of carbohydrates, proteins and lipids etc..), which means that it takes R_g in to account. Although Landsberg (1986) does not mention anything about the above factor taking R_m also in to account, it is highly likely that R_m is also accounted for. Thornley (1977) and Barnes and Hole (1978) argued that R_m can be more realistically related to the amount of proteinaceous material in the plant as protein turnover is a major maintenance activity requiring respiratory energy. As the amount of proteinaceous material is directly proportional to the nitrogen content of plant tissue (N), Charles-Edwards et al. (1986) modified eq. 24 as,

$$R = R_g + R_m = a\, P_c + b_o\, N \qquad \text{(eq. 25)}$$

where, b_o is the maintenance respiratory coefficient in terms of plant nitrogen. As the plant nitrogen content does not change appreciably over a day, b_o N in eq. 25 can be considered constant. Therefore, R can be expected to be linearly related to P_c (Charles-Edwards et al., 1986). This is the mechanistic basis of the conversion factor of 0.0285 kg of biomass per mol^{-1} of CO_2 absorbed for gross photosynthesis that will be used in eq. 26. Accordingly, the annual rate of biomass production by the forest (ΔW) was estimated as,

$$\Delta W = P_c \times 0.0285 \times 10^{-5} \qquad \text{(eq. 26)}$$

where, P_c is given in µmol [CO_2] m^{-2} [Ground Area] d^{-1} and ΔW is calculated in metric tons [Biomass] ha^{-1} [Ground Area] yr^{-1}. ΔW was calculated for each sampling point of hemispherical photography.

2.3.12 Calculation of Radiation Use Efficiency (RUE)

Radiation use efficiency of the forest canopy at each sampling point of hemispherical photography was calculated as the ratio between simultaneously estimated annual forest biomass increment (ΔW) and annual intercepted radiation by the forest canopy (ΔR_I).

$$RUE = \Delta W / \Delta R_I \qquad \text{(eq. 27)}$$

For the calculation of RUE, ΔR_I was estimated from the Beer's Law as,

$$\Delta R_I = S.\,(1 - e^{-k\,LAI}) \qquad \text{(eq. 28)}$$

ΔR_I estimated in this way is slightly different from that estimated by canopy hemispherical photography (eq. 14). This is because of the slightly different ways in which Hemiview calculates the V_{sky}, on which the overall canopy light extinction coefficient (k) is based (eq. 17), and G (θ), which is used to calculate F_{Tot} (eqs. 7, 8 and 14).

2.3.13 Calculation of carbon sequestration rate (C_{seq}) by the respective forests

Annual biomass production rate (W, given in mt ha^{-1} yr^{-1}) was estimated using eq. 1 as,

$$W = R_I \times RUE \qquad \text{(eq. 1)}$$

R_I was estimated from eq. 14 and RUE was estimated from eq. 27.

Annual carbon sequestration rate (C_{seq}, given in mt C ha^{-1} yr^{-1}) was calculated from annual biomass production rate assuming a carbon content of 50% in biomass (Sampson, 1992; Houghton et al., 2001; Chave et al., 2005).

$$C_{seq} = 0.5 \times W \qquad \text{(eq. 29)}$$

The carbon sequestration rate calculated from eq. 29 is equivalent to the net primary productivity (NPP), which is the difference between gross photosynthesis by the entire forest ecosystem and the total autotrophic respiration by the vegetation of the forest ecosystem (Clark et al., 2001a & b; Grace, 2004). This represents the amount of carbon absorbed from the atmosphere during the primary production process of the forest ecosystem. At the ecosystem level, this represents the absorption of CO_2 from the atmosphere during the process of biomass production (i.e. primary production) by the forest. However, over time, part of this absorbed carbon is released back to the atmosphere through heterotrophic respiration (R_h). One significant component of R_h is the carbon that is released to the atmosphere through decomposition of dead plant matter in the form of microbial respiration (Chapin et al., 2002). Respiration by animals which had consumed some of the initially produced biomass, either as herbivores or carnivores, is the other component of R_h.

Therefore, estimation of long-term carbon sequestration rate (C_{seqL}) requires the calculation of net ecosystem productivity (NEP) (also termed net ecosystem exchange, NEE), which is the difference between NPP and R_h.

$$C_{seqL} = NEP = NPP - R_h = C_{seq} - R_h \qquad \text{(eq. 30)}$$

It is difficult to measure R_h directly at the ecosystem level (Schlesinger, 1977; Cramer et al., 1999; Clark et al., 2001a; Grace, 2004). Therefore, in the present study, a method used by Lloyd and Taylor (1994) and Saugier et al. (2001) was used to estimate R_h. This estimation of R_h is based on the fact that it is the carbon that is initially fixed during primary production (i.e. NPP) that provides the substrate for R_h. Hence, R_h should be directly proportional to NPP. However, R_h lags behind NPP because of the residence time of initially fixed carbon in standing biomass. Therefore, Lloyd and Taylor (1994) and Saugier et al. (2001) assumed that R_h at time t is equal to NPP at time $t - t_r$ where t_r is the residence time. Hence,

$$R_h = NPP\ (t - t_r) \qquad \text{(eq. 31)}$$

Based on the above estimate of R_h, NEP was estimated by a method used by Grace (2004) and Grace et al. (2006), which is built on the method of Lloyd and Taylor (1994) and Saugier et al. (2001). Based on a large body of published literature on the response of plants to increasing atmospheric CO_2 concentrations (C_a), Grace (2004) assumed that NPP would increase with time because of increasing C_a and increased deposition of active nitrogen with time. This follows that R_h would also increase because of its direct relationship to NPP and because of its dependence on temperature (Chapin et al., 2002), which is also increasing with increasing atmospheric CO_2 (Houghton, 2009). Assuming a linear increase of NPP with time, NPP after time *t* (in years), NPP (t), can be given as,

$$NPP\ (t) = NPP_o\ (1 + a\ t) \qquad \text{(eq. 32)}$$

where, NPP_o is NPP at t = 0 (i.e. current NPP) and *a* the rate of increase of NPP per year. Experiments on woody plants grown at doubled C_a have shown a 30% increase of NPP

(Wullschleger et al., 1995; Idso, 1999). Taking the current rate of increase of C_a as 0.4% per year (IPCC, 2007), the annual proportional increase of NPP, (i.e. *a* in eq. 32), would be 0.0012 yr^{-1}. Therefore, NEP can be calculated as,

$$NEP = NPP\ (t) - R_h \qquad \text{(eq. 33)}$$

Combining eqs. 31 - 33

$$NEP = NPP\ (t) - NPP\ (t - t_r) = NPP_o\ a\ t_r \qquad \text{(eq. 34)}$$

Residence time (t_r) was calculated as the ratio between the total carbon stock in standing total biomass (C_{TBM}) and current NPP.

$$t_r = C_{TBM} / NPP_o \qquad \text{(eq. 35)}$$

To estimate the standing biomass, we developed a relationship between leaf area index and carbon stock in above-ground biomass (AGB) based on a recent study by Pathinayake (2009) to estimate AGB of the Sinharaja MAB forest reserve using remote sensing and ground-based forest inventory. The developed relationship was,

$$C_{AGB} = 111.25\ Log_e\ (LAI) + 126.87 \quad \text{(with } R^2 = 0.86) \qquad \text{(eq. 36)}$$

where, C_{AGB} is the carbon stock in above-ground biomass (mt ha^{-1} yr^{-1}). Therefore, C_{AGB} was estimated for each sampling point using the LAI values estimated from canopy hemispherical photography. C_{AGB} was converted to C_{TBM} by assuming the above-ground to below-ground biomass ratio to be 3:1 (Phillips et al., 1998).

2.4 Data analysis

All calculations of radiation interception and carbon sequestration were done separately for each sampling point. Significance of variation in the measured parameters between different transects was analyzed using analysis of variance (ANOVA). Here, each transect was taken as a 'treatment' and each sampling point within that transect was taken as a replicate measurement. Thereafter, sampling points were classified in to different forest regions (i.e. Kanneliya and Dediyagala in the KDN forest complex and Kudawa, Pitadeniya and Morningside in the Sinharaja MAB reserve) and elevation zones. Significance of the variation of measured and calculated parameters between different forest regions and elevation zones was tested by ANOVA. Here, the forest regions and elevation zones were treated as two factors in a two-factor factorial treatment structure. Radiation interception, radiation use efficiency and carbon sequestration rates of the two forest complexes were compared by ANOVA of the respective transect means from each forest. Here, each forest complex was taken as a 'treatment' and each transect mean within a forest complex was considered as a replicate. Mean separation was carried out by the Duncan's New Multiple Range Test (DNMRT) at $\alpha = 0.05$.

Interrelationships between different parameters were initially tested using linear correlation analysis. For non-linear relationships, appropriate non-linear functions were fitted using non-linear regression. Initially, correlation and regression analyses were done after pooling the data for all sampling points from each forest complex. Thereafter, the sampling points within each forest complex were classified in to different forest regions and elevation zones. Relevant correlation and regression analyses were performed separately for different forest regions and elevation zones.

SAS statistical package (Anon., 1999b) and curve fitting facility of Excel (MS-Office) were used in all statistical analyses.

3. Results

3.1 Kanneliya-Dediyagala-Nakiyadeniya (KDN) Forest Complex

3.1.1 Properties of the forest canopy – Variation between different transects

Altogether 141 hemi-spherical photographs across 18 transects were taken from the KDN forest complex. These included 98 photographs across 12 transects from Kanneliya and 43 photographs across 6 transects from Dediyagala. Both canopy leaf area index (LAI) and mean leaf angle (MLA) of different transects showed highly significant ($p=0.0004$ and 0.0144 for LAI and MLA respectively) variation between different transects (Figs. 3.1 and 3.2). LAI ranged from 2.18 to 3.68 while MLA ranged from 9.02° (i.e. almost horizontal leaves) to 49.00°. The significant variation of canopy properties between transects demonstrates the high heterogeneity in the forest canopy within the KDN complex. As a result of this heterogeneity in the forest canopy, the mean fraction of ground cover (F_{GCov}) of different transects varied from 0.77 to 0.88. (Fig. 3.3). It is notable that the variability of MLA, which had a coefficient of variation of 53%, was greater than those of LAI and F_{GCov}, which had CVs of 19% and 13% respectively. As

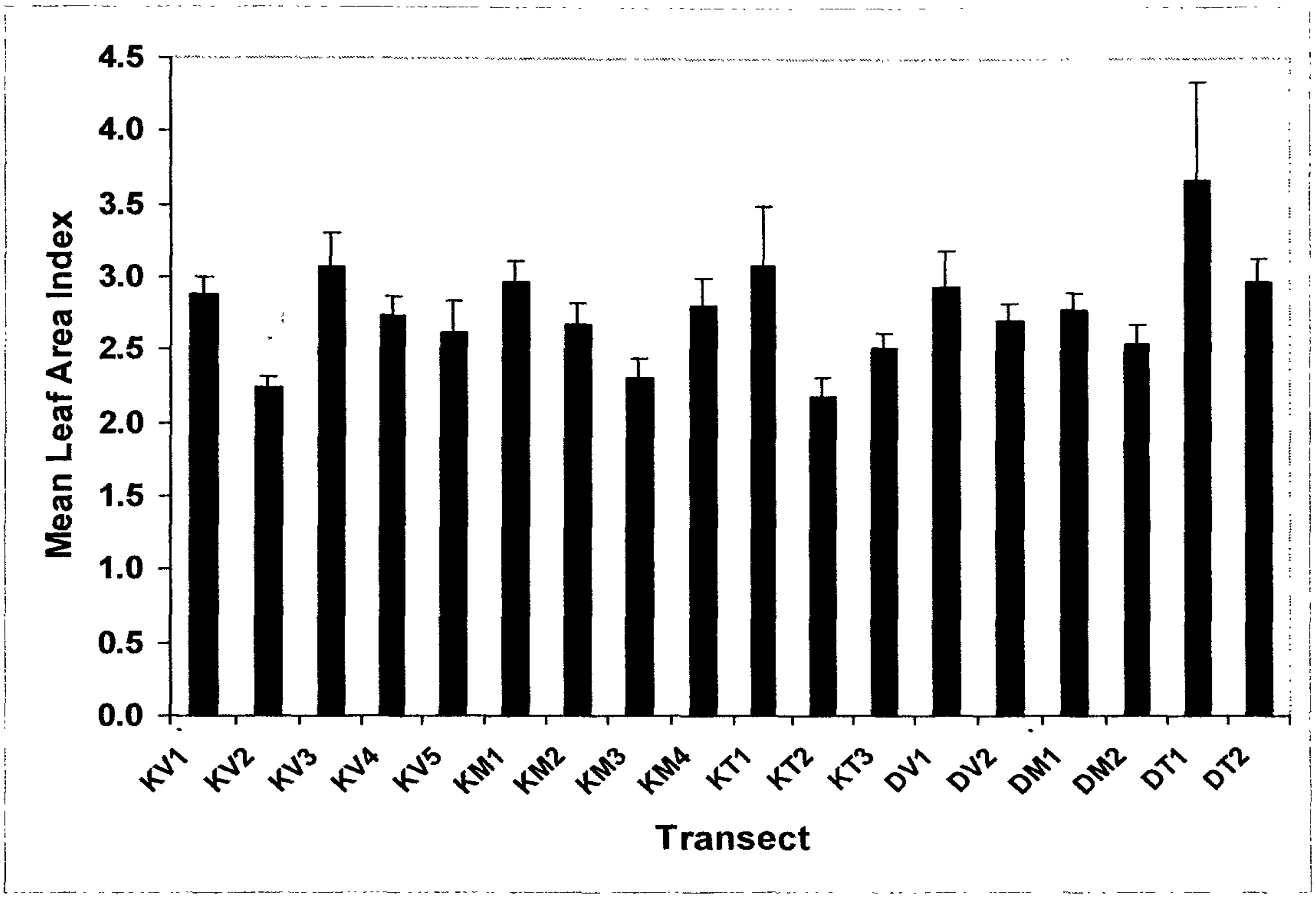


Figure 3.1: Variation of mean canopy leaf area index between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

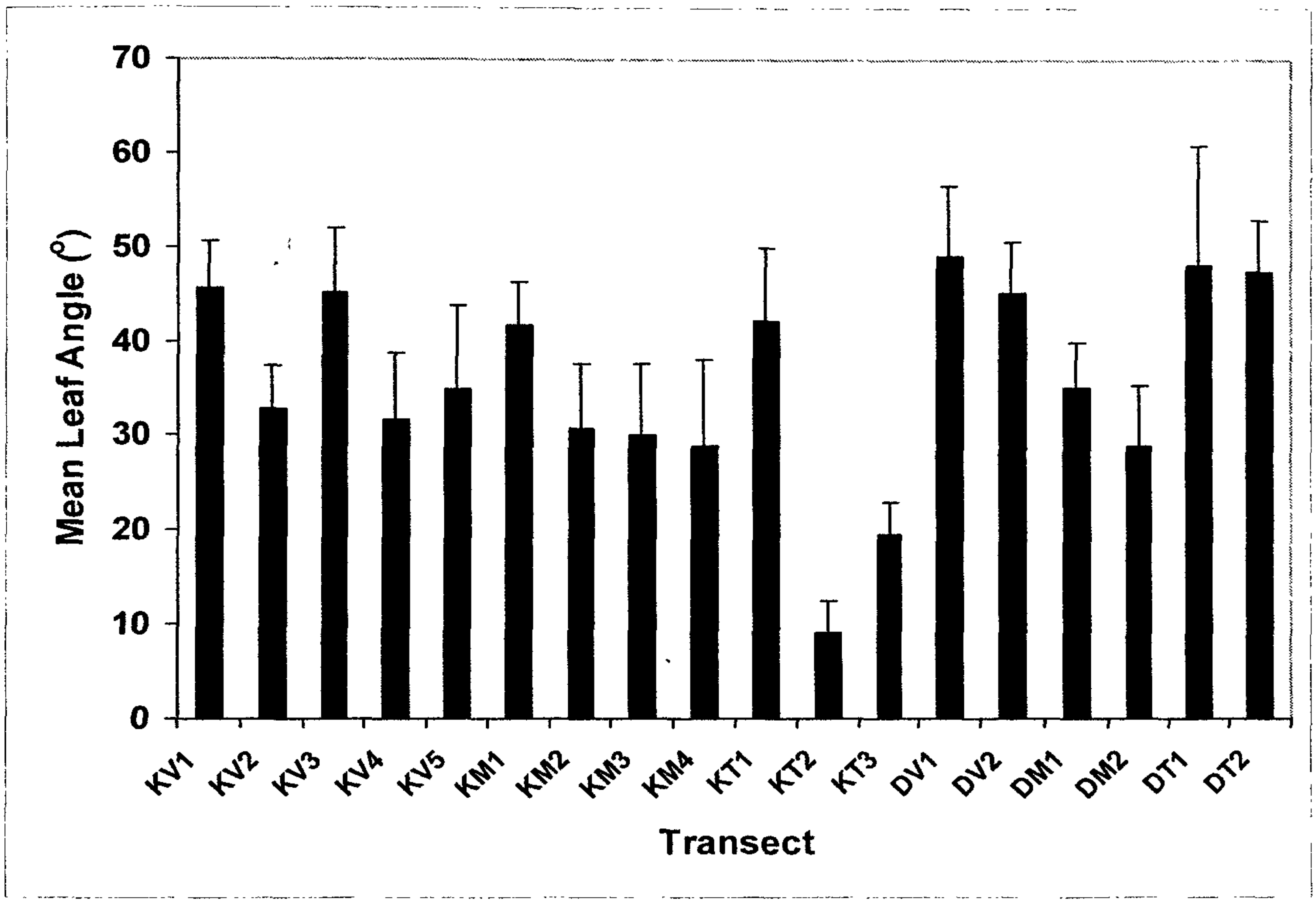


Figure 3.2: Variation of mean leaf angle between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

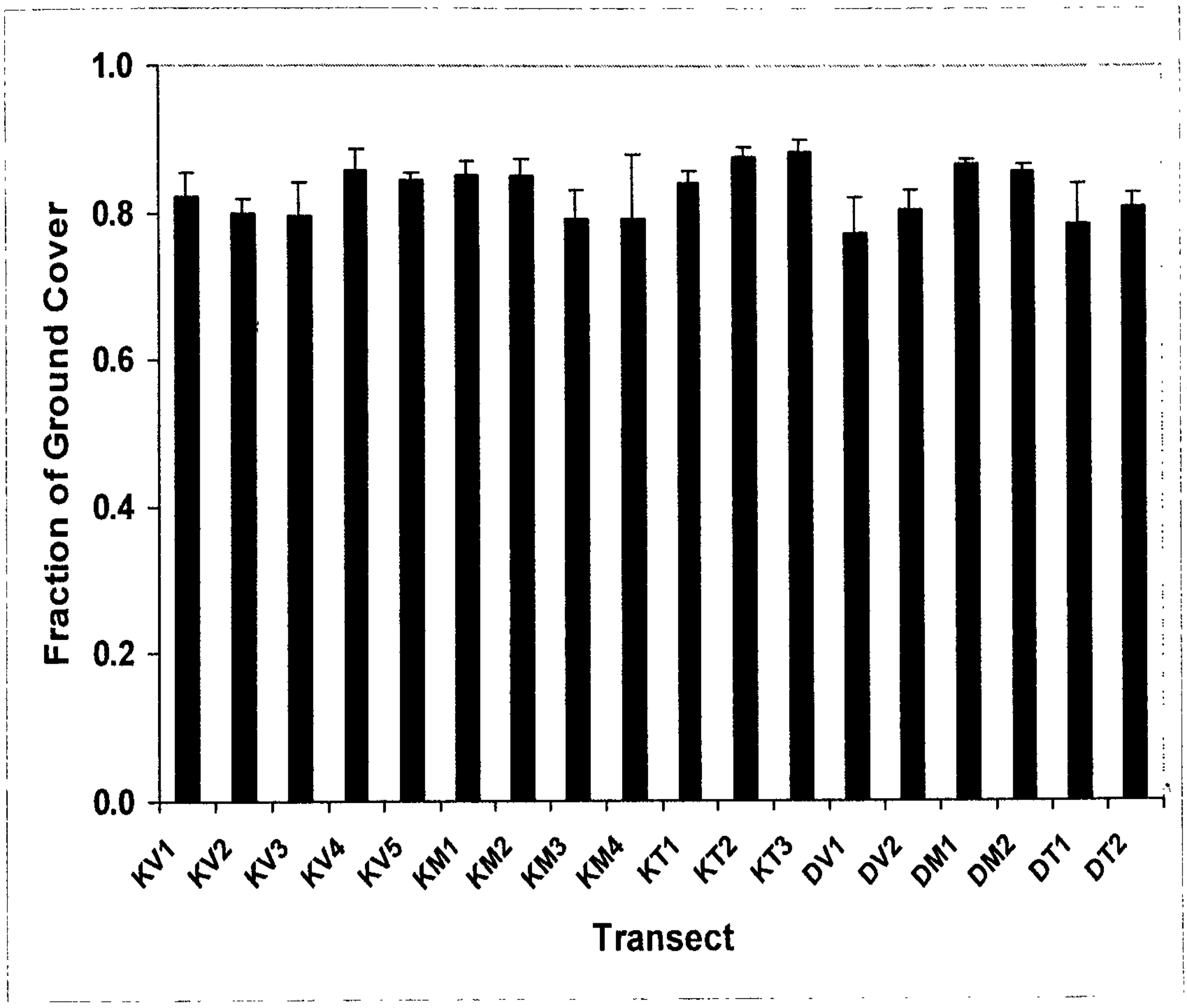


Figure 3.3: Variation of fractional ground cover between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

expected, there was a highly significant negative correlation between MLA and F_{GCov} (linear correlation coefficient, r, = -0.739 with $p<0.0001$). This meant that fractional ground cover increased when the leaves became relatively more horizontal (i.e. decreasing MLA). Interestingly, there was a highly significant positive relationship between LAI and MLA ($r = 0.769$, $p<0.0001$ Fig. 3.4), which meant that the leaf area index was higher when the leaves were relatively more vertical (i.e. higher MLA). There was also a highly significant negative correlation ($r = -0.539$, $p<0.0001$) between LAI and F_{GCov}, which is contrary to what would normally be expected as increasing leaf area would be expected to increase ground cover. The fractional ground cover by the forest canopy would be determined by the combined effects of canopy leaf area (as quantified by the LAI) and leaf angle. The significant negative correlation between LAI and F_{GCov} indicated that leaf angle had a greater influence than LAI in determining ground cover in the KDN forest complex.

3.1.2 Fractions of incident radiation intercepted – Variation between different transects

There was highly significant variation between transects in the intercepted fractions of total ($p<0.0001$), direct ($p=0.0006$) and diffuse ($p<0.0001$) radiations (Fig. 3.5). The respective ranges of different fractional interceptions were 0.82 – 0.89 (total), 0.83 – 0.89 (direct) and 0.86 – 0.91 (diffuse). It is notable that the fractional interception of diffuse radiation (F_{Dif}) was greater than that of direct radiation (F_{Dir}) in all transects. As diffuse radiation comes from all directions of the sky, it has a greater probability of being

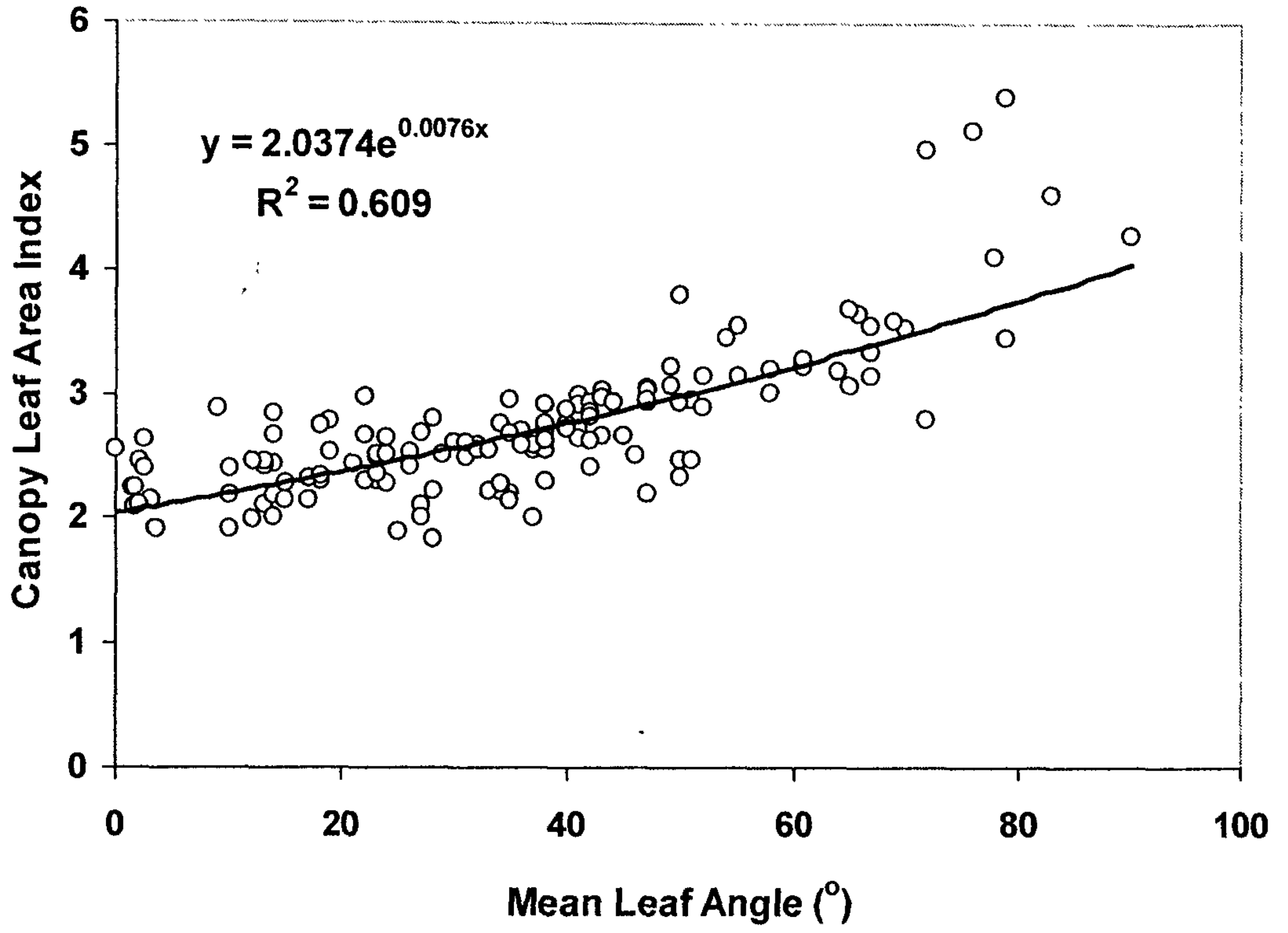


Figure 3.4: Variation of canopy leaf area index with mean leaf angle in the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The data points represent 141 sampling points across 18 transects of the forest.

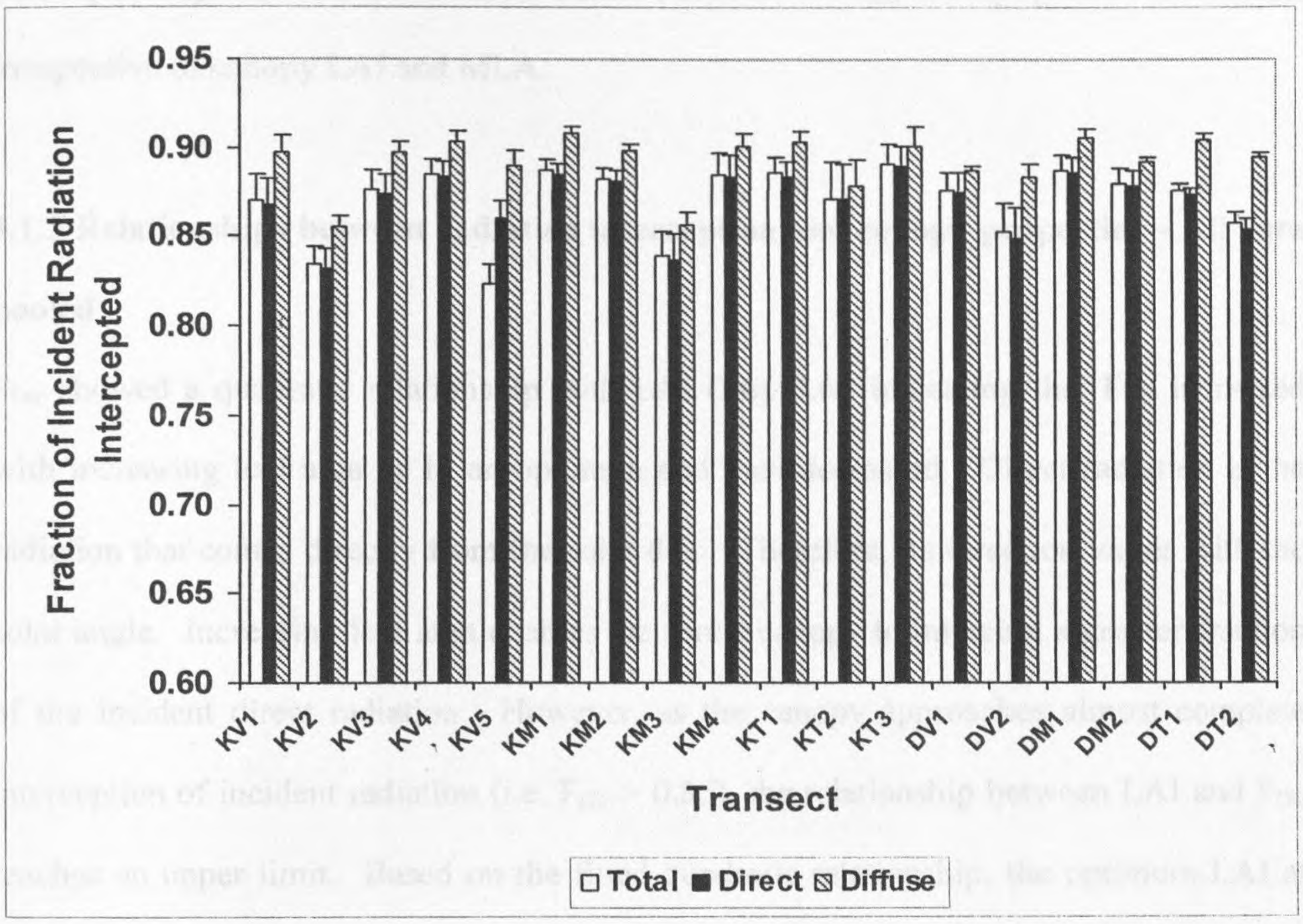


Figure 3.5: Variation of intercepted fractions of direct, diffuse and total incident radiation between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top. Note the bottom-truncated y-axis to highlight the differences in intercepted fractions.

intercepted by the forest canopy, which resulted in F_{Dif} being greater than F_{Dir}, irrespective of canopy LAI and MLA.

3.1.3 Relationships between radiation interception and canopy properties – All data pooled

F_{Dir} showed a quadratic relationship with LAI (Fig. 3.6), indicating that F_{Dir} increased with increasing leaf area up to an optimum and then decreased. Direct radiation is the radiation that comes directly from the solar disc. Therefore, its direction varies with the solar angle. Increasing leaf area enables the forest canopy to intercept a greater fraction of the incident direct radiation. However, as the canopy approaches almost complete interception of incident radiation (i.e. $F_{Dir} > 0.85$), the relationship between LAI and F_{Dir} reaches an upper limit. Based on the fitted quadratic relationship, the optimum LAI at which maximum F_{Dir} was achieved was estimated to be 3.60 for the KDN forest complex. F_{Dir} showed a slight decline at LAIs beyond the optimum. Because of variation in the direction of incident direct radiation, mutual shading can occur at some combinations of the angle of incidence of direction radiation and MLA at higher LAI, thus causing the slight decline in F_{Dir} at LAIs above the optimum (Fig. 3.6). The R^2 value of 0.17 for this quadratic relationship is because of the considerable scatter of data points, which is another indication of the extreme heterogeneity of the forest canopy between different sampling points.

F_{Dir} showed a significant negative correlation with mean leaf angle ($r = -0.465$, $p<0.0001$ Fig. 3.7), indicating that interception of direct radiation decreased when leaves become more vertically oriented (i.e. increased leaf angle). This is also an indication that a major

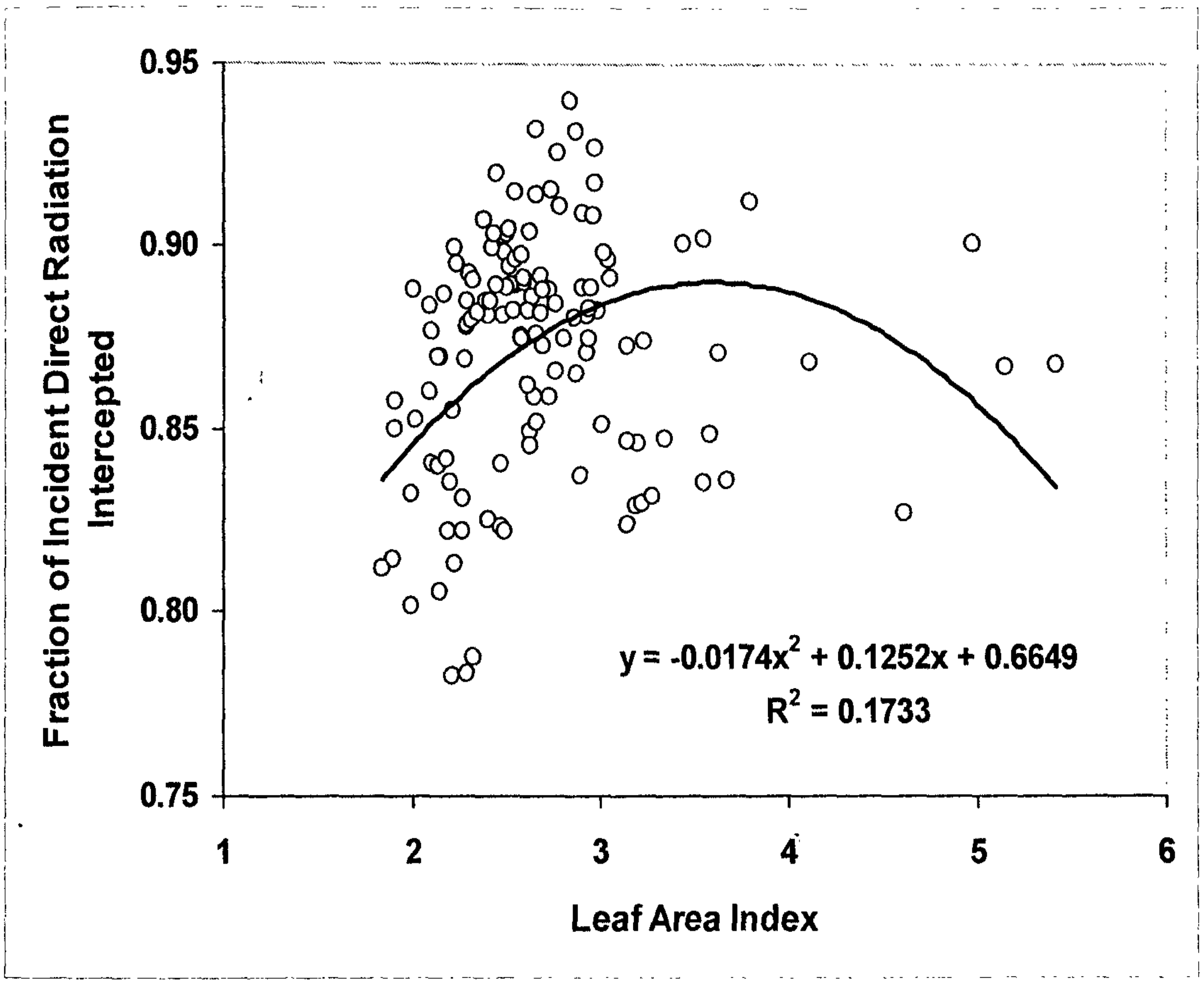


Figure 3.6: Variation of the fraction of direct radiation intercepted with canopy leaf area index in the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The data points represent 141 sampling points across 18 transects of the forest.

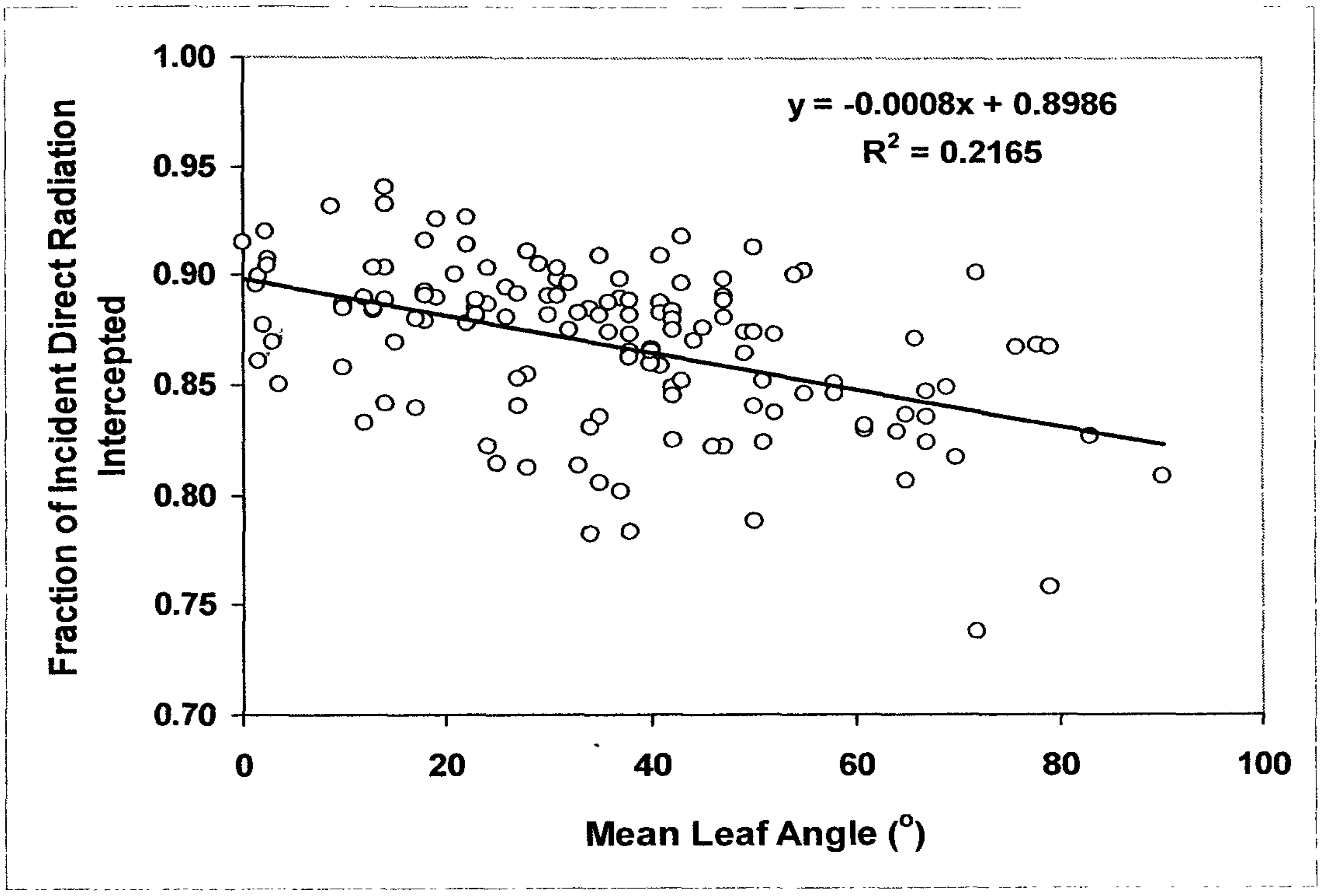


Figure 3.7: Variation of the fraction of direct radiation intercepted with mean leaf angle in the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The data points represent 141 sampling points across 18 transects of the forest.

portion of direct radiation comes at an approximately vertical angle (i.e. closer to 90^o) relative to the horizontal plane.

While F_{Dir} showed significant relationships with both LAI and MLA, F_{Dif} showed a significant relationship with only LAI (Fig. 3.8). There was no significant relationship or correlation between F_{Dif} and MLA. This is because of the absence of a directional property in diffuse radiation, which makes its interception independent from the leaf angle. Even though diffuse radiation comes from all directions of the sky, its fractional interception would still be dependent on the canopy leaf area. Similar to the relationship between F_{Dir} and LAI, that between F_{Dif} and LAI was also a quadratic relationship, with an optimum LAI of 3.86 for the KDN forest complex. This is because interception of diffuse radiation also would increase with increasing leaf area up to an optimum beyond which interception would decrease because of mutual shading. It is notable that the optimum LAI for maximum interception of diffuse radiation (i.e. 3.86) was slightly greater than that for interception of direct radiation (i.e. 3.60). This is again because of the difference in the directional property of these two components of incident radiation. The forest canopy would require a greater leaf area to achieve maximum interception of diffuse radiation which comes from all directions at all times of the day as compared the canopy leaf area required to achieve maximum interception of direct radiation which comes from a specific direction at any given time.

The fractional interception of total incident radiation (F_{Tot}) also showed a quadratic relationship with LAI (Fig. 3.9), which was similar to those shown by F_{Dir} (Fig. 3.6) and F_{Dif} (Fig. 3.8). The optimum LAI for maximum interception of total solar radiation in the KDN forest complex was 3.64, which was approximately similar to the corresponding

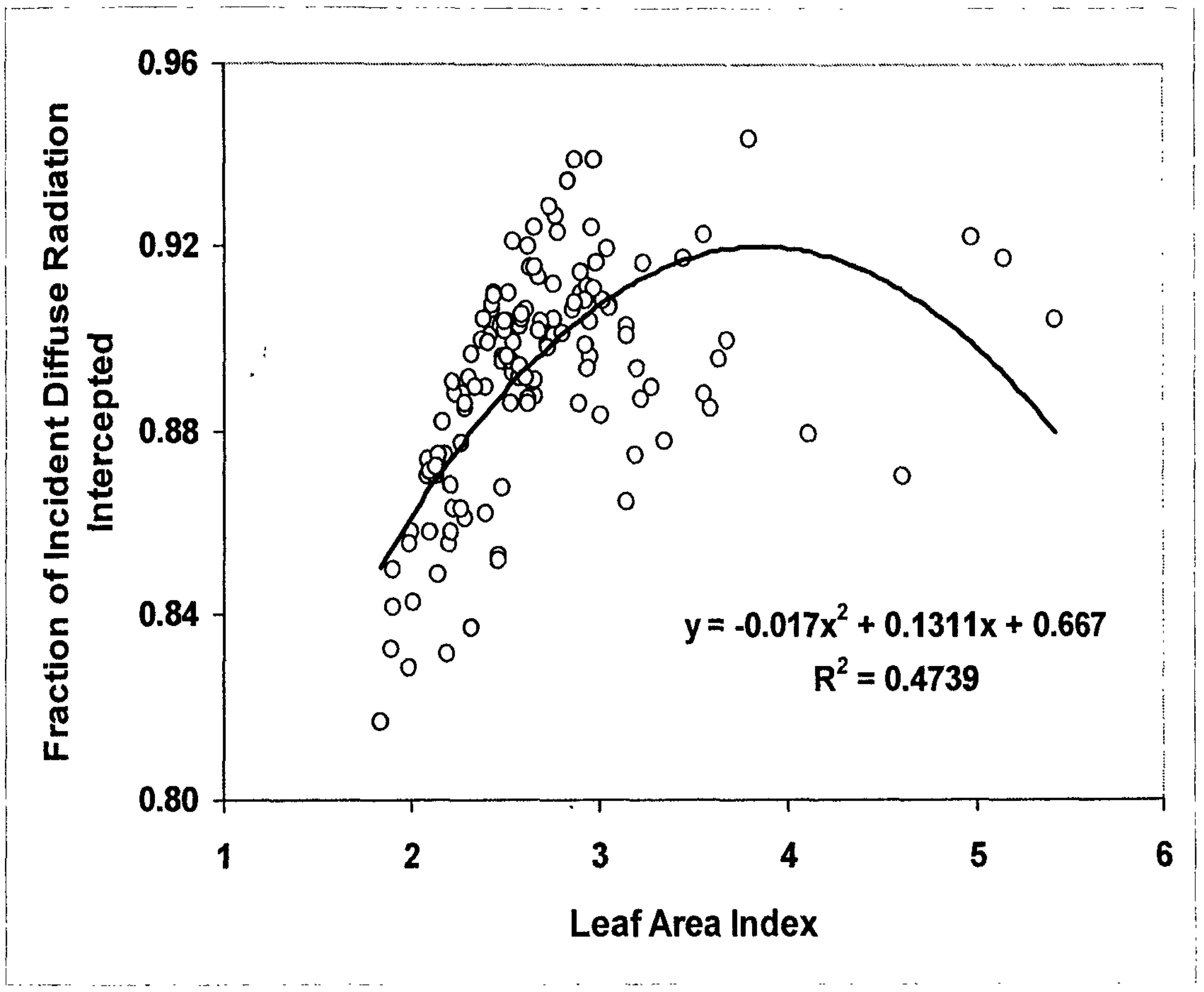


Figure 3.8: Variation of the fraction of diffuse radiation intercepted with canopy leaf area index in the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The data points represent 141 sampling points across 18 transects of the forest.

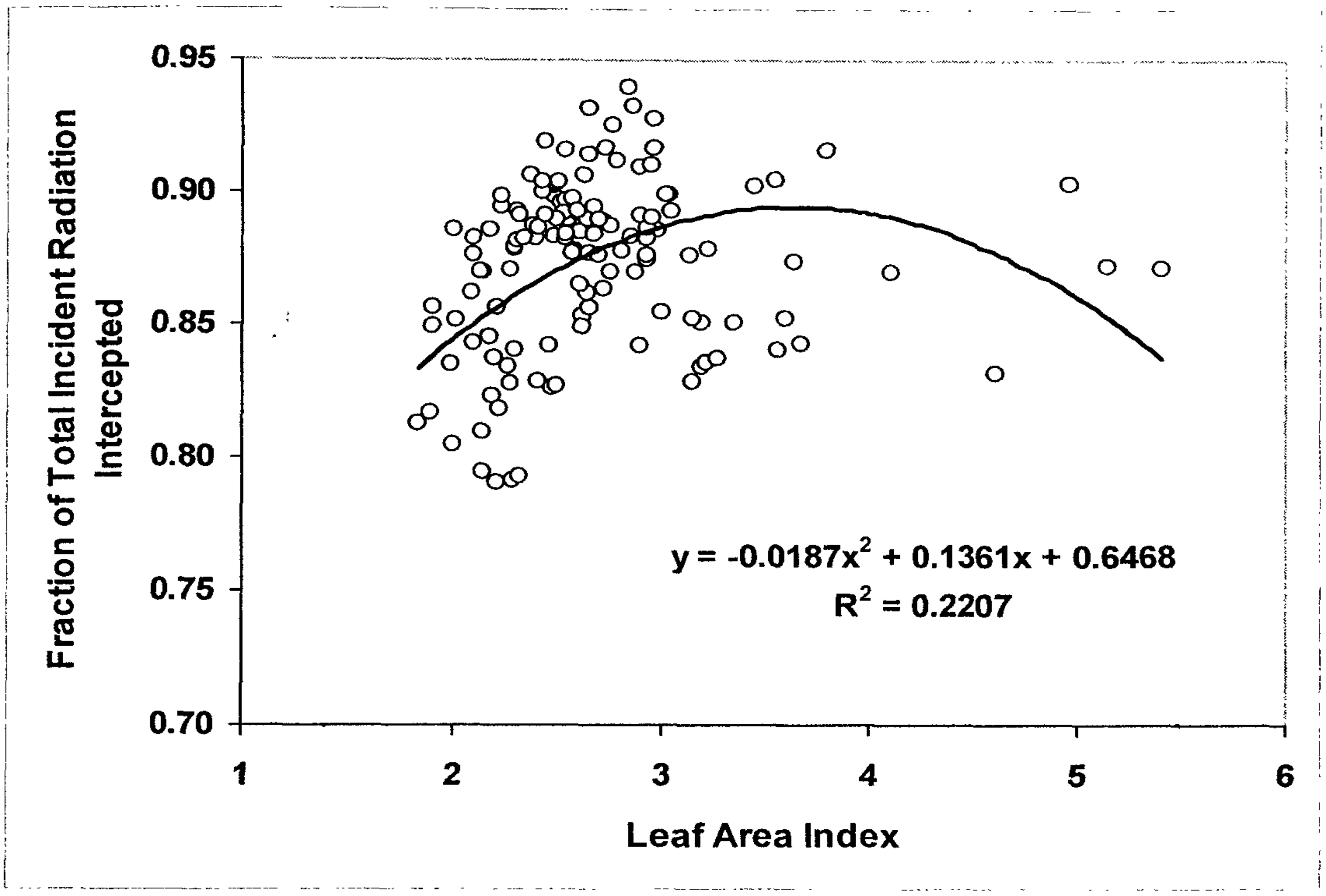


Figure 3.9: Variation of the fraction of total radiation intercepted with canopy leaf area index in the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The data points represent 141 sampling points across 18 transects of the forest.

optimum for F_{Dir} (3.60) and slightly lower than the optimum LAI for F_{Dif} (3.81). F_{Tot} showed a negative relationship with MLA (Fig. 3.10), which was similar to that observed between F_{Dir} and MLA (Fig. 3.7).

3.1.4 Properties of the forest canopy – Variation between different regions of the forest and between different elevation zones

Analysis of variance showed that both LAI and MLA differed highly significantly between the two regions of the forest and between different elevation zones (Table 3.1). The region x elevation zones interaction effects were not significant for either LAI or MLA. The high coefficients of variation (CV) indicated that both these canopy characters showed a high degree of variability even within a given region x elevation zone environment. In contrast to LAI and MLA, the fraction of ground cover (F_{GCov}) showed a significant region x elevation zone ($p=0.021$) interaction and a lower CV. Within each region of the KDN forest complex, LAI did not show significant variation between different elevation zones. However, MLA showed significant ($p<0.05$) variation between elevation zones in Dediyagala, but not in Kanneliya.

The significant regional variation in LAI that was shown in the overall ANOVA, was primarily because of the higher LAI values of the valley and the ridge-top in Dediyagala, which were 5.5% and 22% greater than the corresponding values in Kanneliya (Fig. 3.11). In Kanneliya, mean LAI of all elevation zones varied within the 2.6 – 2.7 range. In contrast, mean LAI of the ridge-top in Dediyagala (3.22) was 17% greater than the average LAI of the valley and mid-slope (2.75).

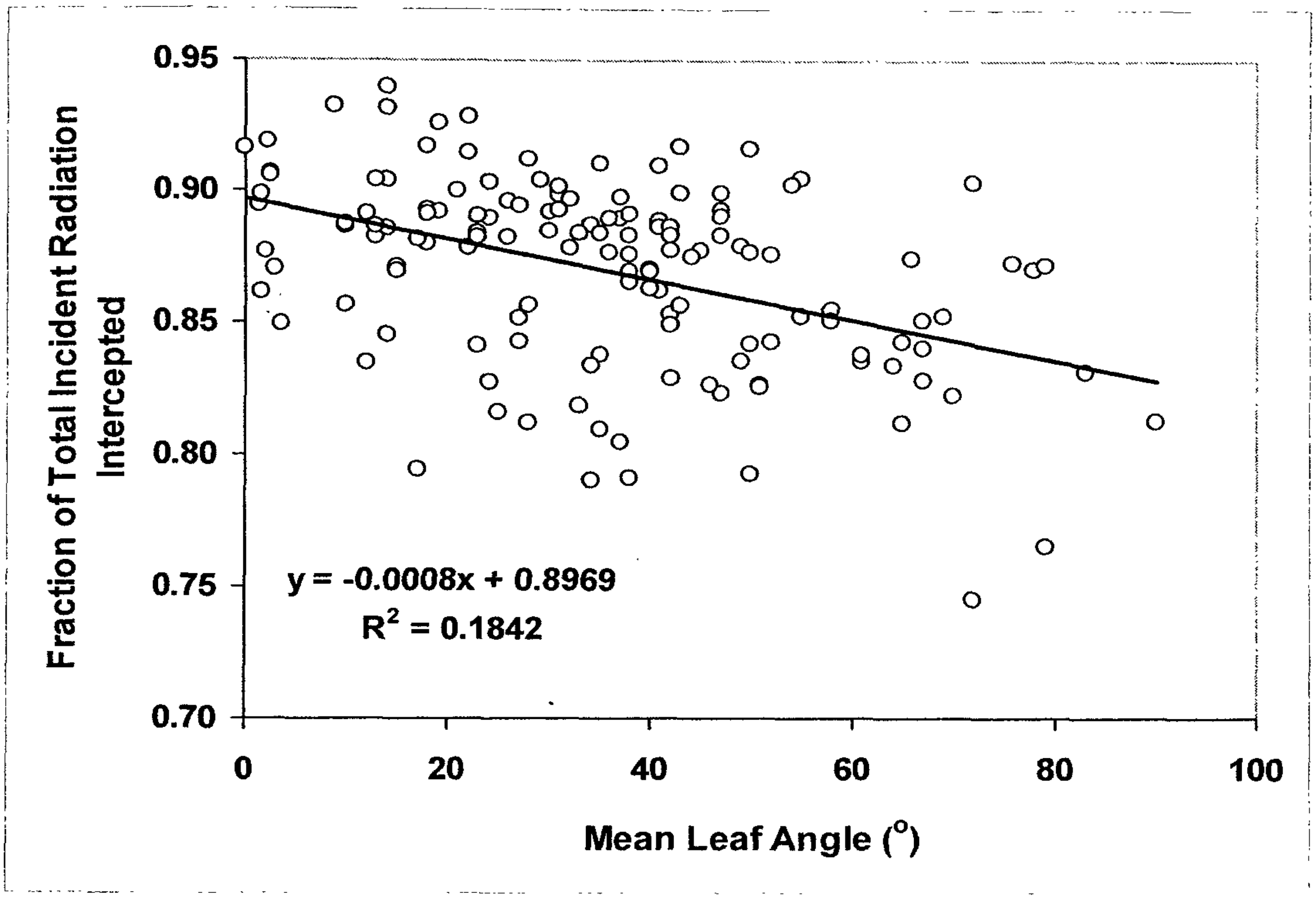


Figure 3.10: Variation of the fraction of total incident radiation intercepted with mean leaf angle in the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The data points represent 141 sampling points across 18 transects of the forest.

Table 3.1: Probabilities of significance of differences† in forest canopy and radiation interception properties between different regions of the KDN forest complex and between different elevation zones

ANOVA with regions and elevation zones analyzed together

Sources of variation	Leaf area index	Mean leaf angle	F_{GCov}	F_{Tot}	F_{Dir}	F_{Dif}
Region	0.0005	0.0008	n.s.	0.0591	n.s.	<0.0001
Elevation zone	0.0344	0.0379	n.s.	0.0017	0.0088	0.0002
Region x Elev. Zone	n.s.	n.s.	0.0210	0.0004	0.0011	0.0356
CV (%)	21.75	53.55	12.70	3.36	3.49	2.28
ANOVA for Kanneliya separately						
Elev. zone	n.s.	n.s.	0.1031	<0.0001	<0.0001	<0.0001
CV (%)	21.83	61.72	14.51	3.55	3.63	2.52
ANOVA for Dediyagala separately						
Elev. zone	n.s.	0.0350	0.0069	0.0522	0.0527	0.0138
CV (%)	21.52	42.16	8.09	3.03	3.26	1.45
ANOVA for Valley separately						
Region	0.0059	0.0360	n.s.	0.0961	0.1194	0.0029
CV (%)	14.55	34.33	19.32	4.56	4.89	2.17
ANOVA for Mid-slope separately						
Region	n.s.	n.s.	n.s.	0.0172	0.0215	0.0045
CV (%)	20.89	74.64	9.95	3.48	3.67	2.52
ANOVA for Ridge-top separately						
Region	0.1337	0.0093	0.0155	0.0044	0.0033	n.s.
CV (%)	27.32	57.50	8.26	2.35	2.46	1.89

†Probability of the variation due to the respective factor occurring as a result of random variation. F_{GCov} – Fraction of ground cover; F_{Tot}, F_{Dir} and F_{Dif} – Fractions of incident total, direct and diffuse radiations intercepted respectively.

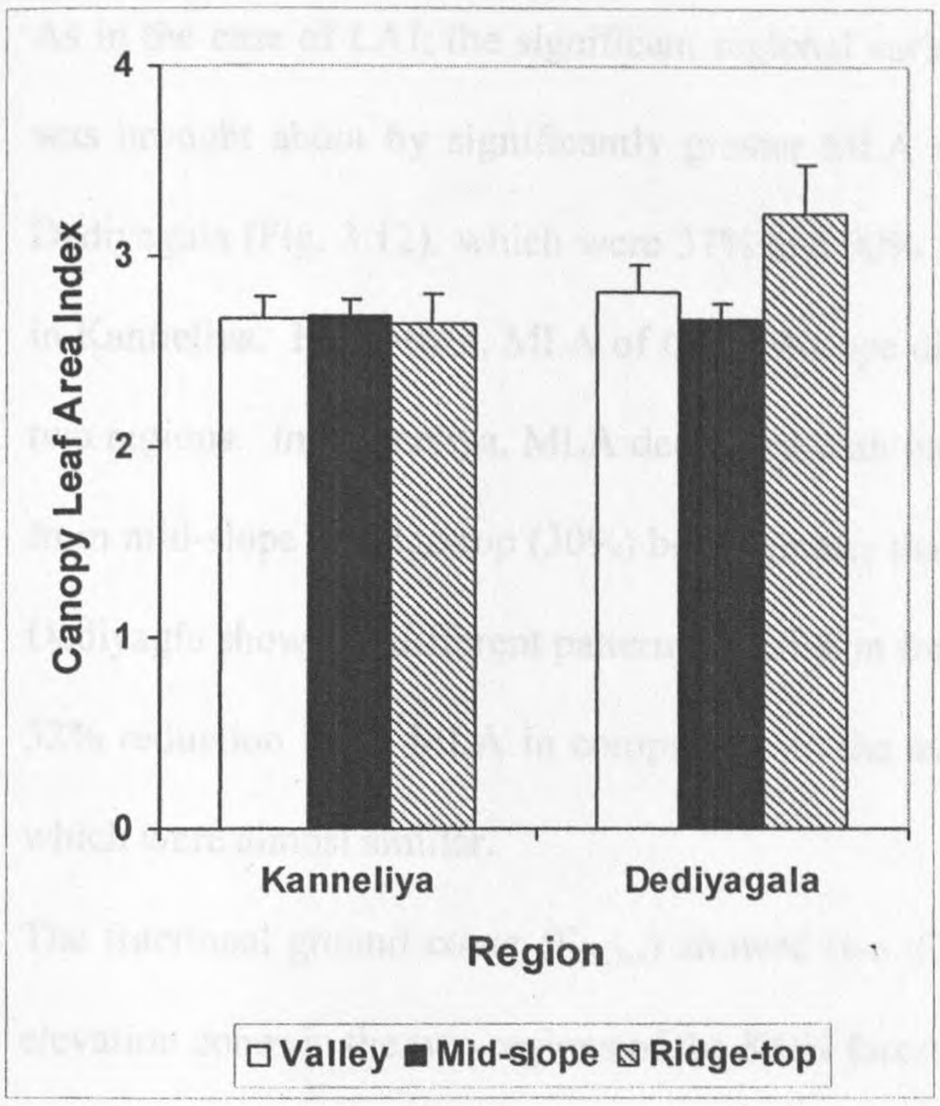


Figure 3.11: Variation of canopy leaf area index between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

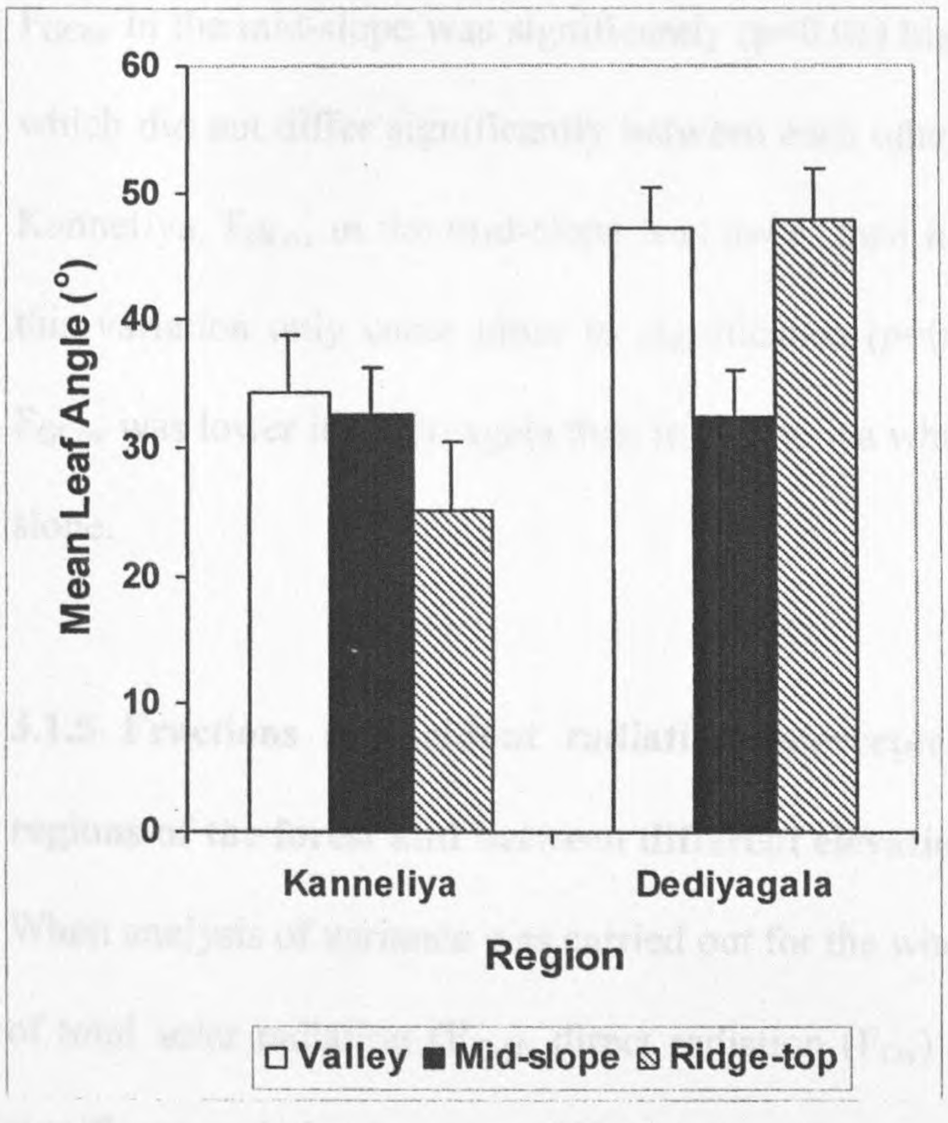


Figure 3.12: Variation of mean leaf angle between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

As in the case of LAI, the significant regional variation of MLA in the overall ANOVA was brought about by significantly greater MLA values in the valley and ridge-top in Dediyagala (Fig. 3.12), which were 37% and 90% greater than the corresponding values in Kanneliya. In contrast, MLA of the mid-slope did not differ significantly between the two regions. In Kanneliya, MLA decreased with increasing elevation, with the reduction from mid-slope to ridge-top (30%) being greater than that from valley to mid-slope (6%). Dediyagla showed a different pattern of variation for MLA, with the mid-slope showing a 32% reduction in its MLA in comparison to the average value of valley and ridge-top, which were almost similar.

The fractional ground cover (F_{GCov}) showed two different patterns of variation between elevation zones in the two regions of the KDN forest complex (Fig. 3.13). In Dediyagala, F_{GCov} in the mid-slope was significantly ($p<0.01$) higher than in the valley and ridge-top, which did not differ significantly between each other (Table 3.1). On the other hand, in Kanneliya, F_{GCov} in the mid-slope was lower than in the other two elevation zones, and this variation only came close to significance ($p=0.103$). In the valley and ridge-top, F_{GCov} was lower in Dediyagala than in Kanneliya whereas it was the opposite for the mid-slope.

3.1.5 Fractions of incident radiation intercepted – Variation between different regions of the forest and between different elevation zones

When analysis of variance was carried out for the whole data set, the intercepted fractions of total solar radiation (F_{Tot}), direct radiation (F_{Dir}) and diffuse radiation (F_{Dif}) showed significant variation between different elevation classes (Table 3.1). However, only F_{Tot}

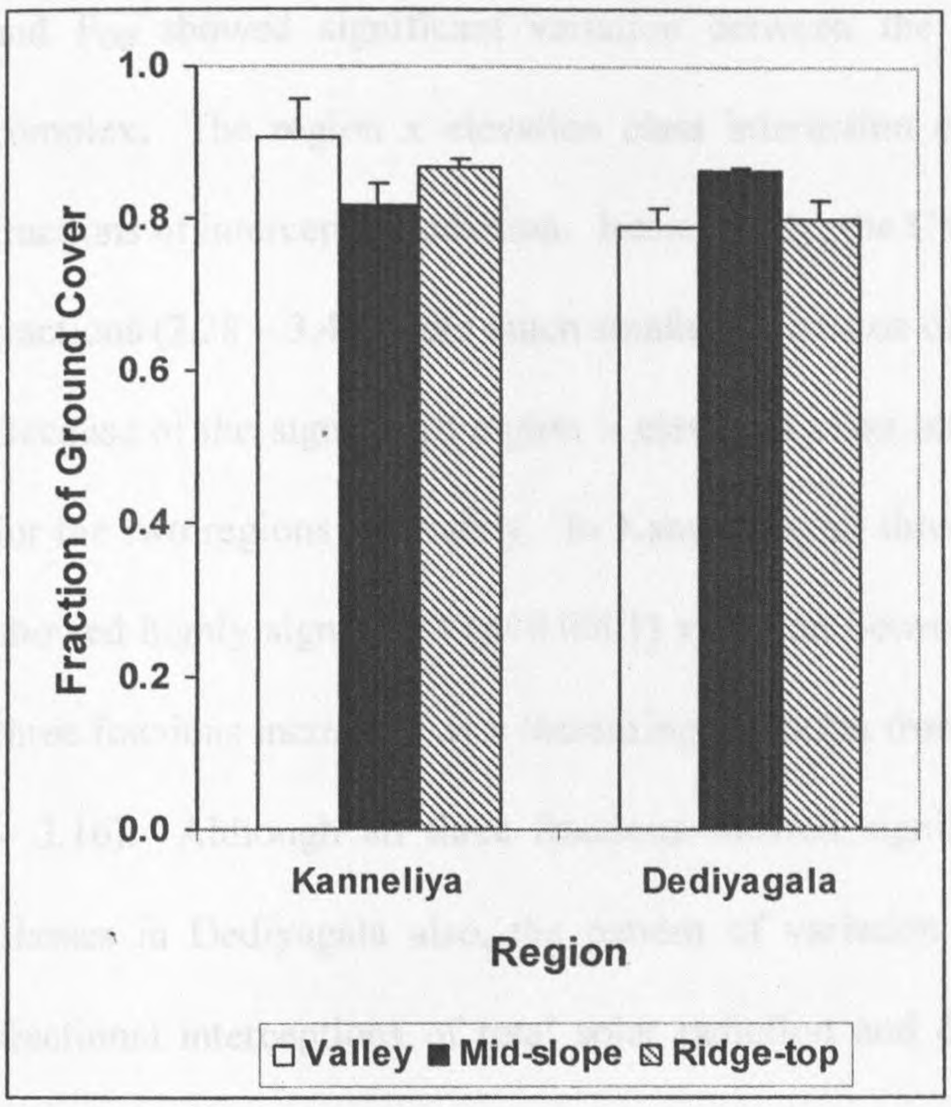


Figure 3.13: Variation of mean fraction of ground cover (F_{GCov}) between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

and F_{Dif} showed significant variation between the two regions of the KDN forest complex. The region x elevation class interaction effect was significant for all three fractions of intercepted radiation. Interestingly, the CVs of all three intercepted radiation fractions (2.28 – 3.49) were much smaller than those of LAI and MLA.

Because of the significant region x elevation class interaction, ANOVA was performed for the two regions separately. In Kanneliya, all three fractions of intercepted radiation showed highly significant ($p<0.0001$) variation between different elevation classes. All three fractions increased with increasing elevation from valley to the ridge-top (Figs. 3.14 – 3.16). Although all three fractions showed significant variation between elevation classes in Dediyagala also, the pattern of variation was different. Here, the highest fractional interceptions of total solar radiation and direct radiation were shown in the mid-slope, while the respective values of the valley and ridge-top were not significantly different from each other. F_{Dif} of the valley in Dediyagala was significantly lower than those of the mid-slope and ridge-top which did not differ significantly from each other.

3.1.6 Relationships between radiation interception and canopy properties – Variation between different regions and elevation zones

The highly significant ($p<0.0001$) positive correlation that was shown in the overall data set between LAI and mean leaf angle (MLA) was shown in the two regions of the KDN forest complex and also in the three elevation zones (Table 3.2). This showed that irrespective of the region or elevation zone, increasing leaf angle (i.e. more vertical leaves) increased the canopy leaf area index. The intercepted fractions of total and direct

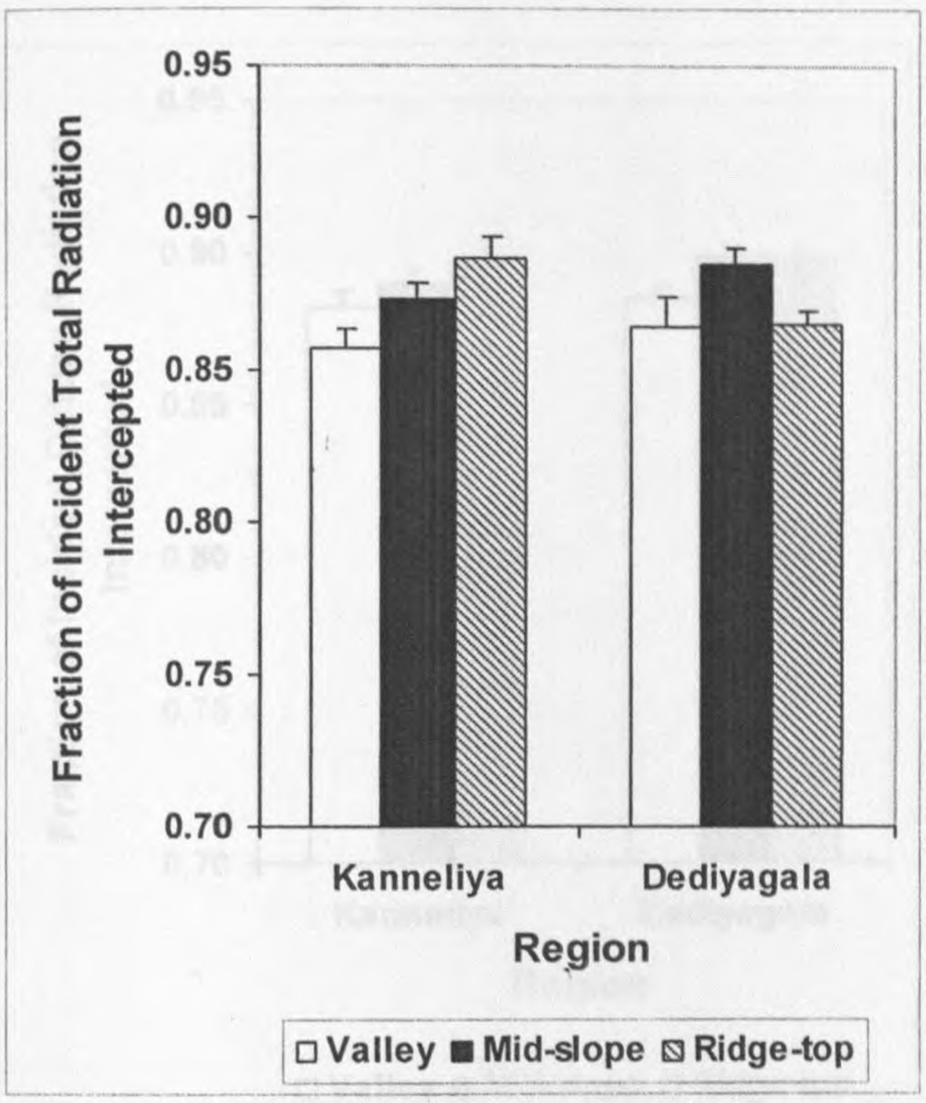


Figure 3.14: Variation of mean fraction of incident total solar radiation intercepted (F_{Tot}) between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

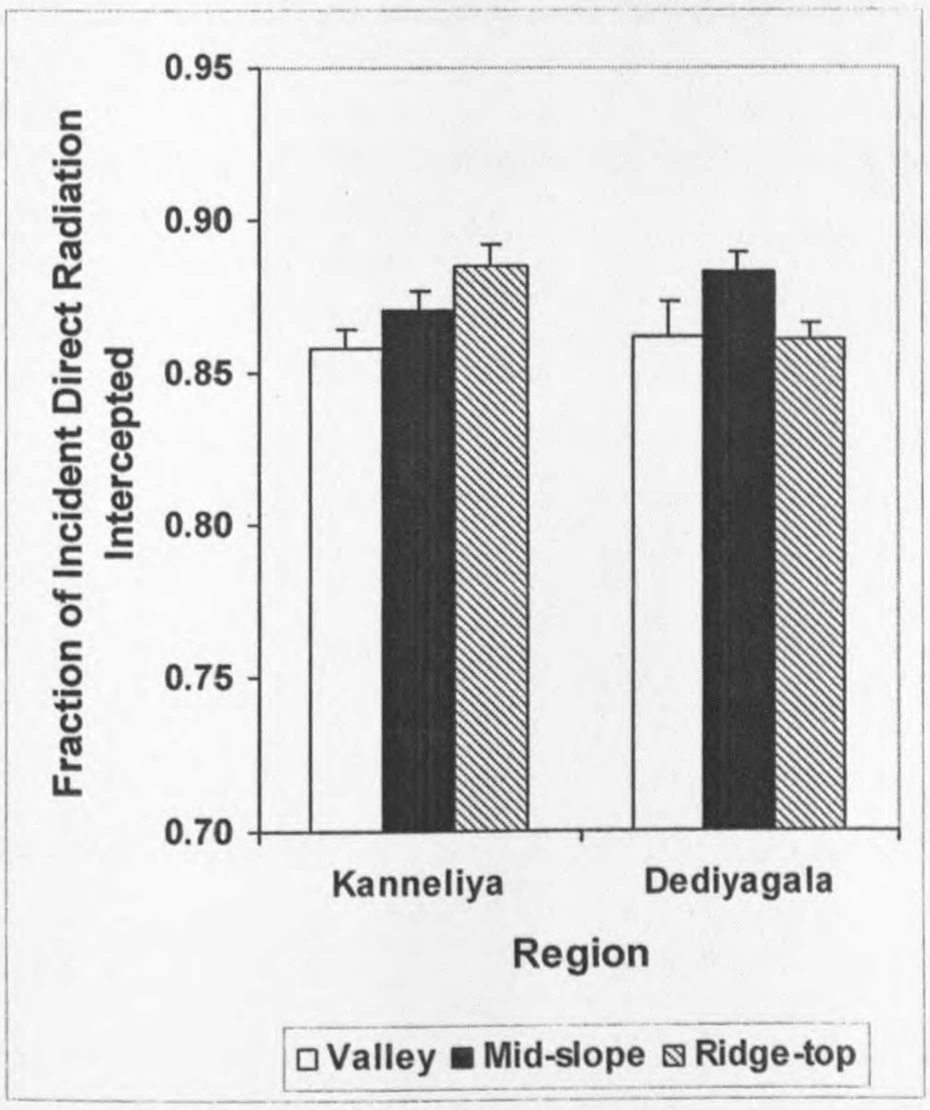


Figure 3.15: Variation of mean fraction of incident direct solar radiation intercepted (F_{Dir}) between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

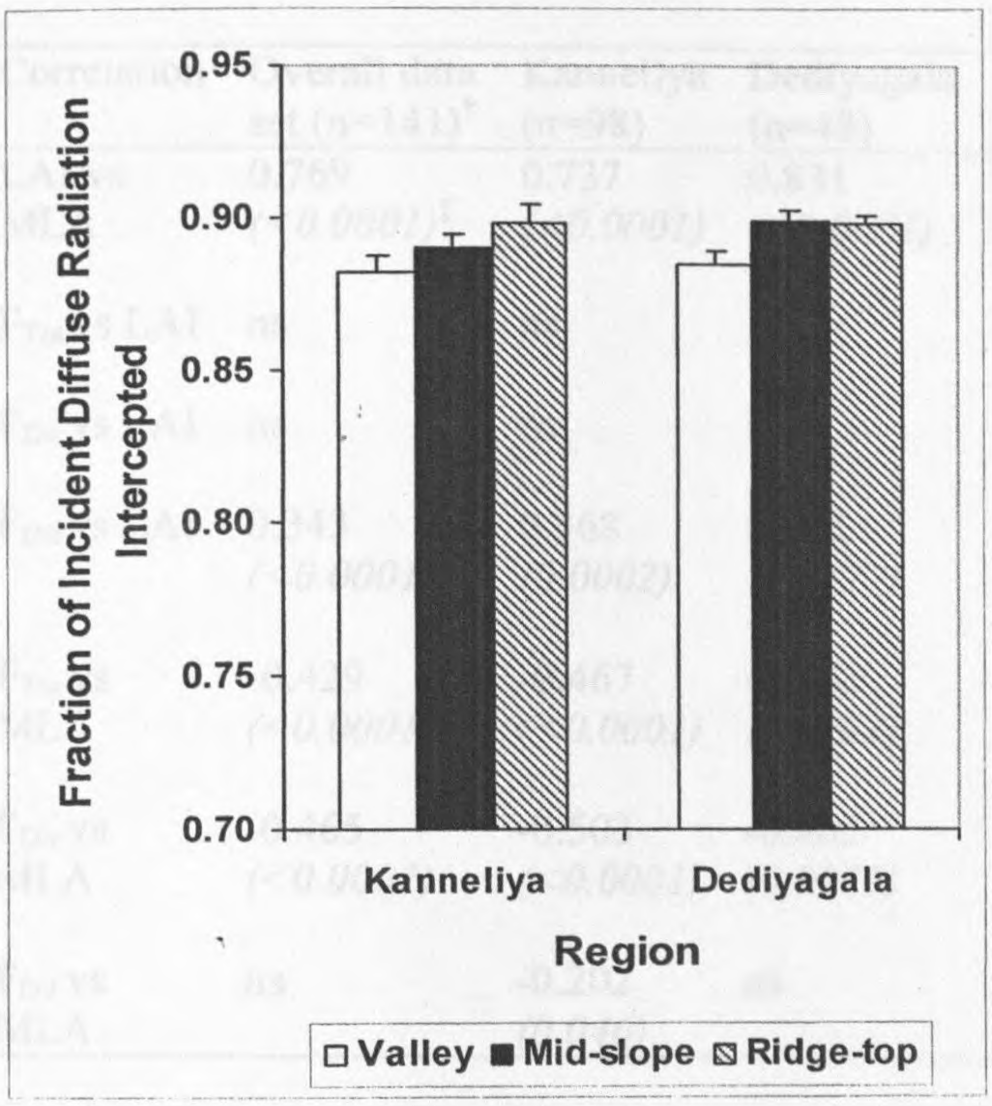


Figure 3.16: Variation of mean fraction of incident diffuse solar radiation intercepted (F_{Dif}) between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

Table 3.2: Linear correlation coefficients of correlations between canopy properties and fractions of radiation intercepted in the KDN-forest complex

Correlation	Overall data set (n=141)[†]	Kanneliya (n=98)	Dediyagala (n=43)	Valley (n=54)	Mid-slope (n=54)	Ridge-top (n=33)
LAI vs MLA	0.769 *(<0.0001)*[‡]	0.737 *(<0.0001)*	0.831 *(<0.0001)*	0.783 *(<0.0001)*	0.823 *(<0.0001)*	0.822 *(<0.0001)*
F_{Tot} vs LAI	ns	ns	ns	ns	ns	ns
F_{Dir} vs LAI	ns	ns	ns	ns	ns	ns
F_{Dif} vs LAI	0.343 *(<0.0001)*	0.368 *(0.0002)*	0.292 *(0.0577)*	0.347 *(0.0102)*	0.242 *(0.078)*	0.446 *(0.0093)*
F_{Tot} vs MLA	-0.429 *(<0.0001)*	-0.467 *(<0.0001)*	-0.388 *(0.0102)*	-0.355 *(0.0084)*	-0.502 *(0.0001)*	-0.372 *(0.033)*
F_{Dir} vs MLA	-0.465 *(<0.0001)*	-0.503 *(<0.0001)*	-0.402 *(0.0075)*	-0.414 *(0.0018)*	-0.521 *(<0.0001)*	-0.407 *(0.019)*
F_{Dif} vs MLA	ns	-0.202 *(0.046)*	ns	ns	ns	ns

[†] Number of data points in the correlation

[‡] Probability of the correlation coefficient being not significantly different from zero.

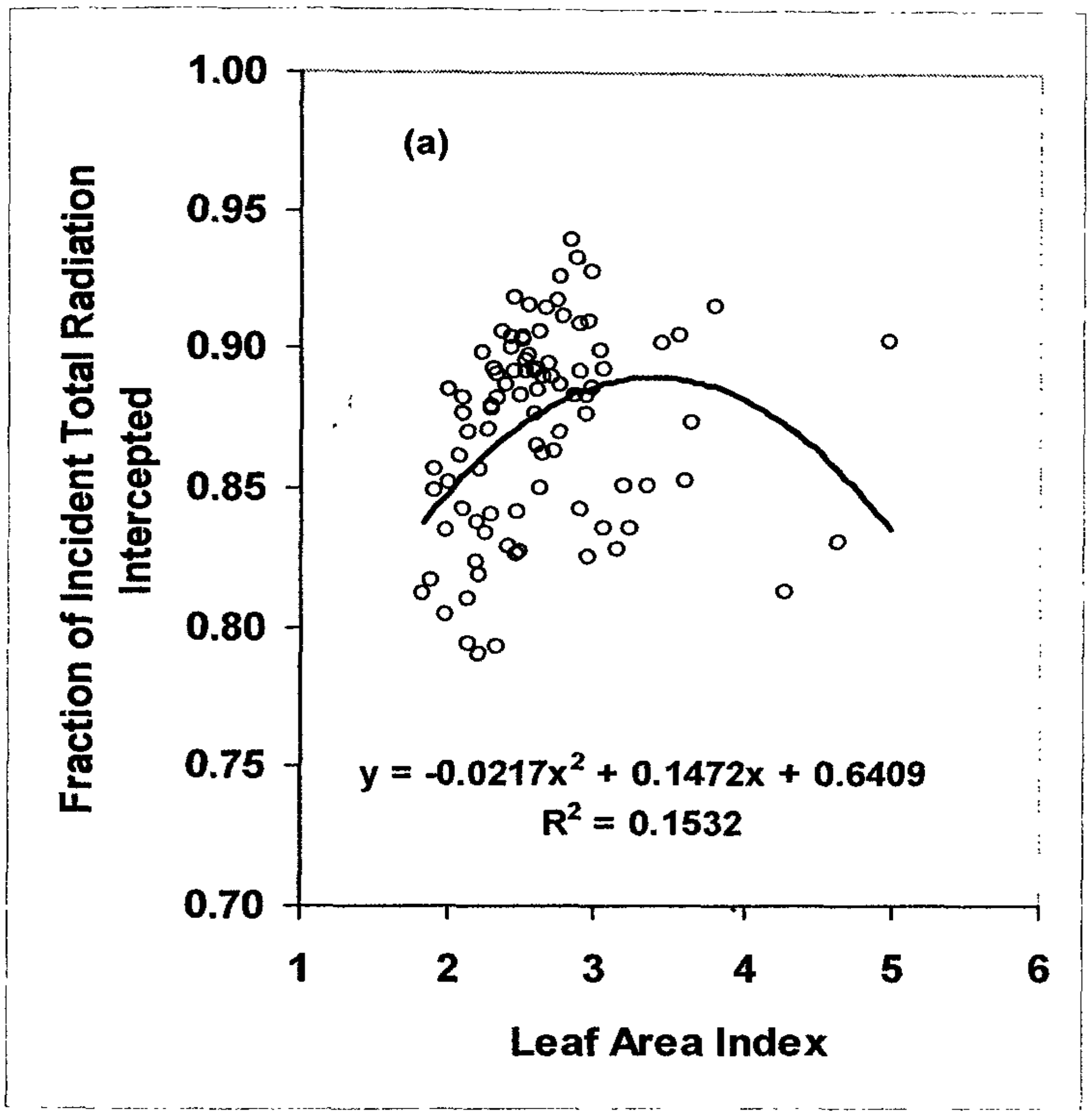
F_{Tot}, F_{Dir} and F_{Dif} – Fractions of incident total, direct and diffuse radiation intercepted

LAI – Canopy leaf area index

MLA – Mean leaf angle

radiation (i.e. F_{Tot} and F_{Dir}) had highly significant negative correlations with MLA in the overall data set as well as in different regions and elevation zones. This meant that increasing leaf angle decreased the fractional interception of direct radiation, which comes vertically downwards during a major part of the day. Because of the greater proportion of direct radiation in the total incident solar radiation, fractional interception of total solar radiation also showed a similar negative correlation with leaf angle. However, neither F_{Tot} nor F_{Dir} showed significant linear correlations with LAI. This is primarily because, as shown in Figs. 3.6 and 3.9 for the overall data set, the respective relationships between F_{Tot}, F_{Dir} and LAI were curvilinear. In Kanneliya, both F_{Tot} and F_{Dir} showed quadratic relationships with LAI (Fig. 3.17), with respective optimum LAIs for maximum F_{Tot} and F_{Dir} being 3.39 and 3.36 respectively (Table 3.3). However, notably, no such relationships could be detected in Dediyagala (Fig. 3.18). Significant quadratic relationships could be observed between F_{Tot}, F_{Dir} and LAI in all three elevation zones (Figs. 3.19 – 3.21). Interestingly, the respective optimum LAIs in the mid-slope (i.e. 2.90 and 2.88 for F_{Tot} and F_{Dir} respectively) were lower than those in the valley (3.28 and 3.24) and ridge-top (3.85 and 3.82) (Table 3.3).

Similar to what was observed for the whole data set (Fig. 3.8), the intercepted fraction of incident diffuse radiation (F_{Dif}) showed significant quadratic relationships with LAI in both Kanneliya and Dediyagala (Fig. 3.22) and also in all three elevation zones (Fig. 3.23). The respective optimum LAIs for maximum interception of diffuse radiation were 3.52 and 4.43 for Kanneliya and Dediyagala (Table 3.3). The respective optimum LAIs for the three elevation zones were 3.39, 3.08 and 4.01 respectively for the valley, mid-slope and ridge-top. It is notable that similar to what was observed for F_{Tot} and F_{Dir}, the



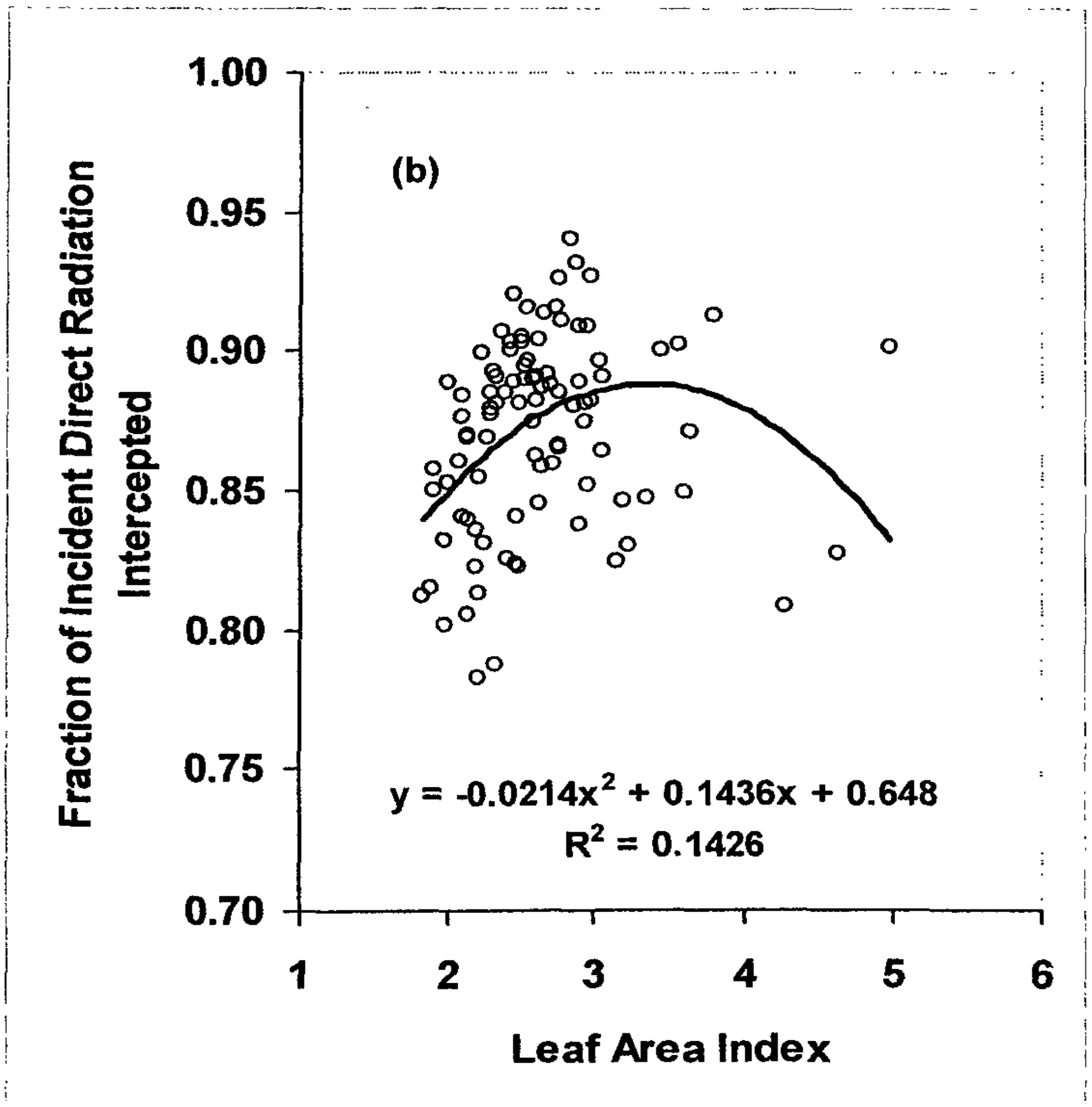


Figure 3.17: Variation of the fraction of total (a) and direct (b) radiation intercepted with canopy leaf area index in Kanneliya region of the KDN forest complex. The data points represent 98 sampling points across 12 transects of the forest.

Table 3.3: Estimated optimum canopy leaf area indices for maximum fractional interception of incident total (F_{Tot}), direct (F_{Dir}) and diffuse (F_{Dif}) radiation for different regions and elevation classes in the KDN-forest complex

	Kanneliya	Dediyagala	Valley	Mid-slope	Ridge-top
F_{Tot}	3.39	†	3.28	2.99	3.85
F_{Dir}	3.36	†	3.24	2.88	3.82
F_{Dif}	3.52	4.43	3.39	3.08	4.01

† - The data did not fit a second-order polynomial function so that an optimum LAI could not be estimated.

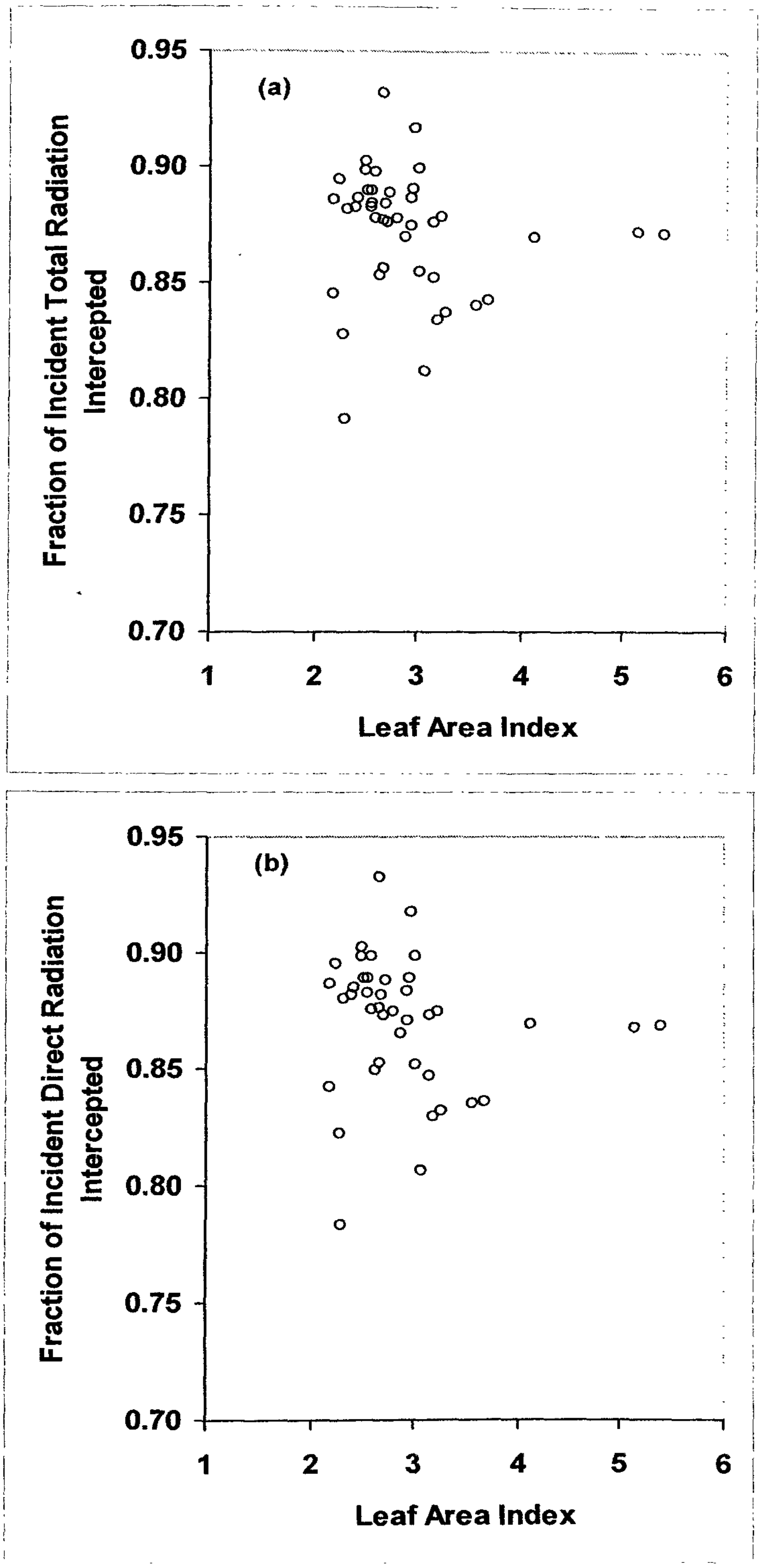


Figure 3.18: Variation of the fraction of total (a) and direct (b) radiation intercepted with canopy leaf area index in Dediyagala region of the KDN forest complex. The data points represent 43 sampling points across 6 transects of the forest.

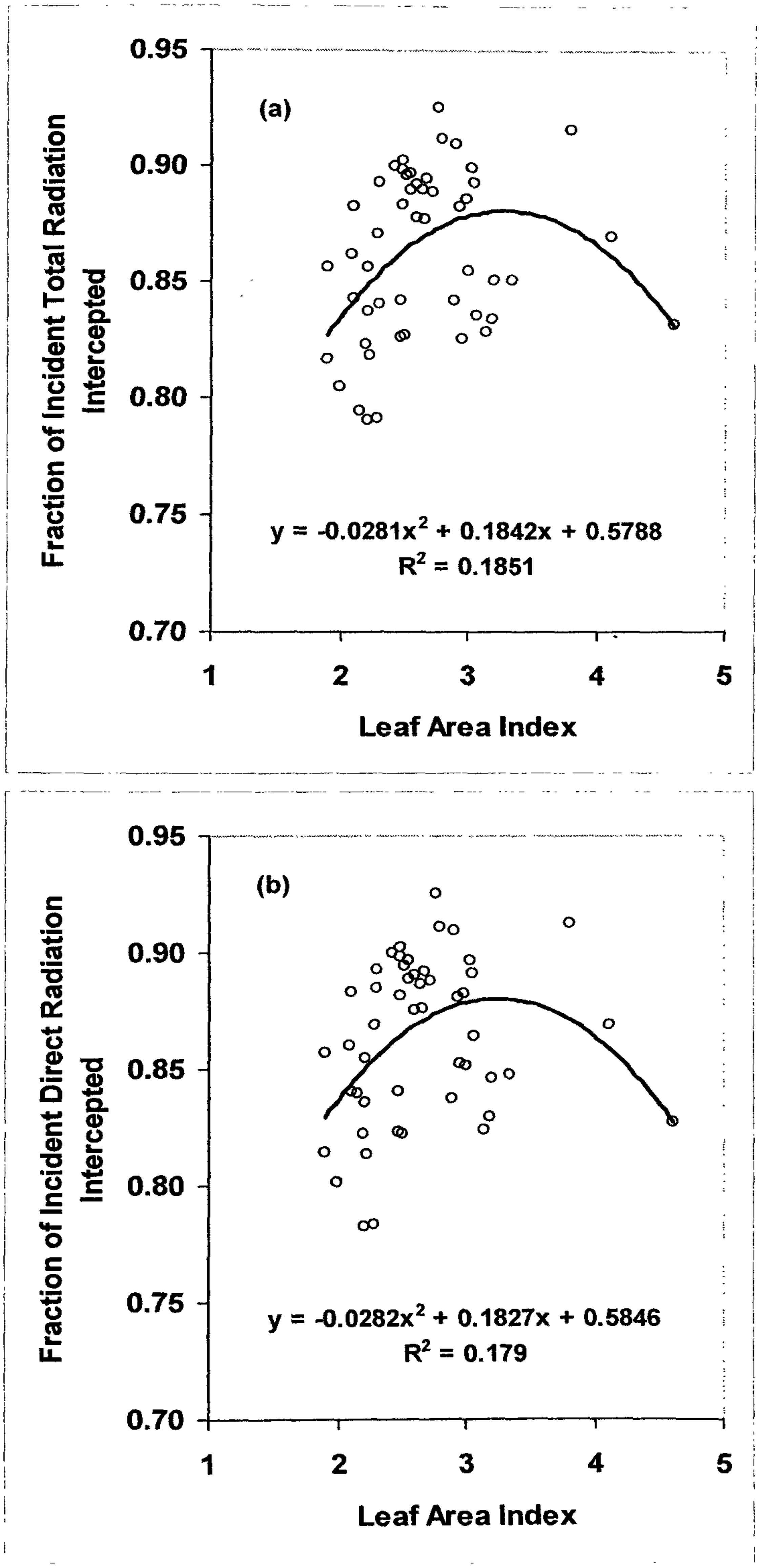


Figure 3.19: Variation of the fraction of total (a) and direct (b) radiation intercepted with canopy leaf area index in the valley of the KDN forest complex. The data points represent 54 sampling points across 7 transects of the forest.

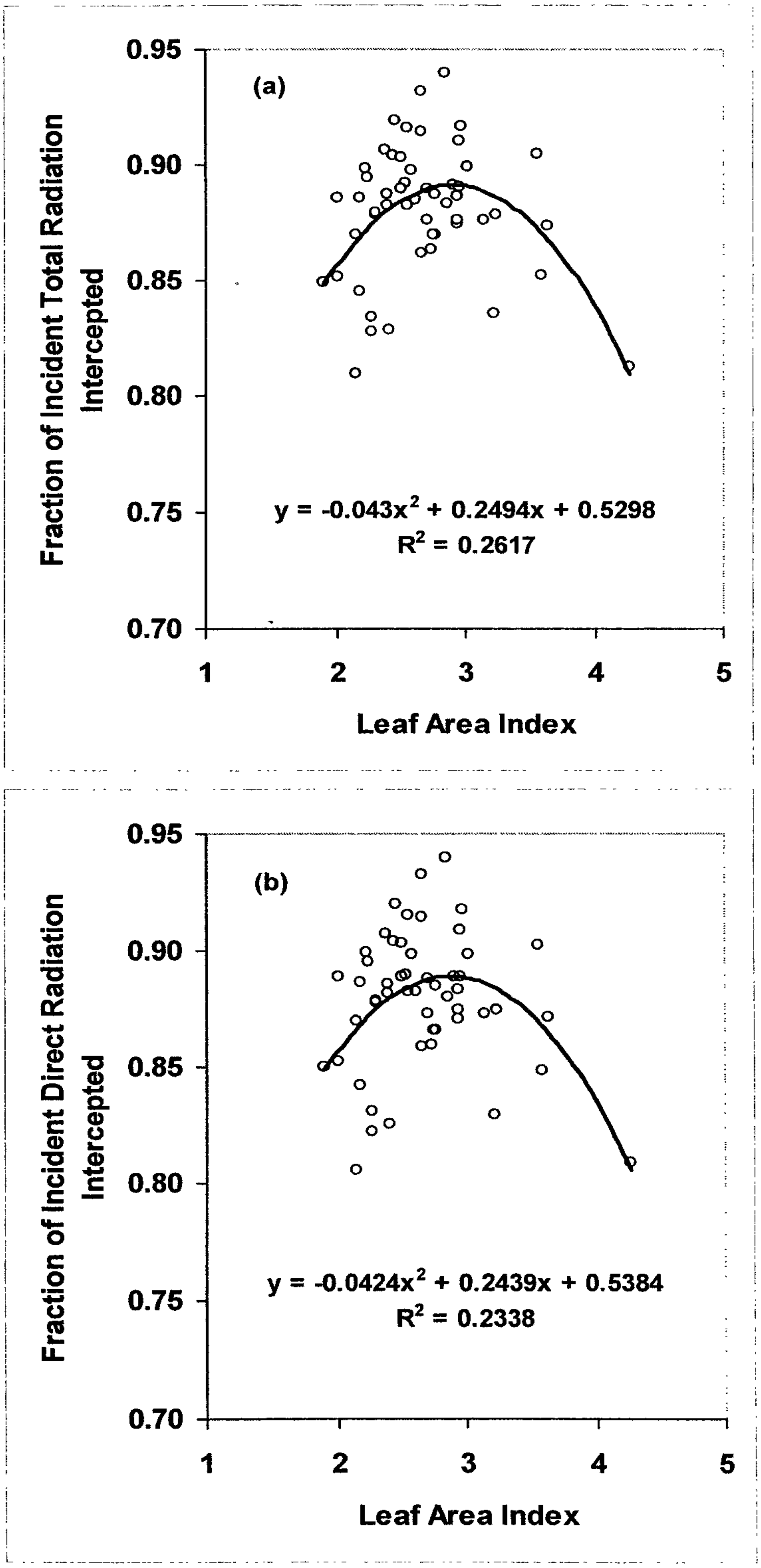


Figure 3.20: Variation of the fraction of total (a) and direct (b) radiation intercepted with canopy leaf area index in the mid-slope of the KDN forest complex. The data points represent 54 sampling points across 6 transects of the forest.

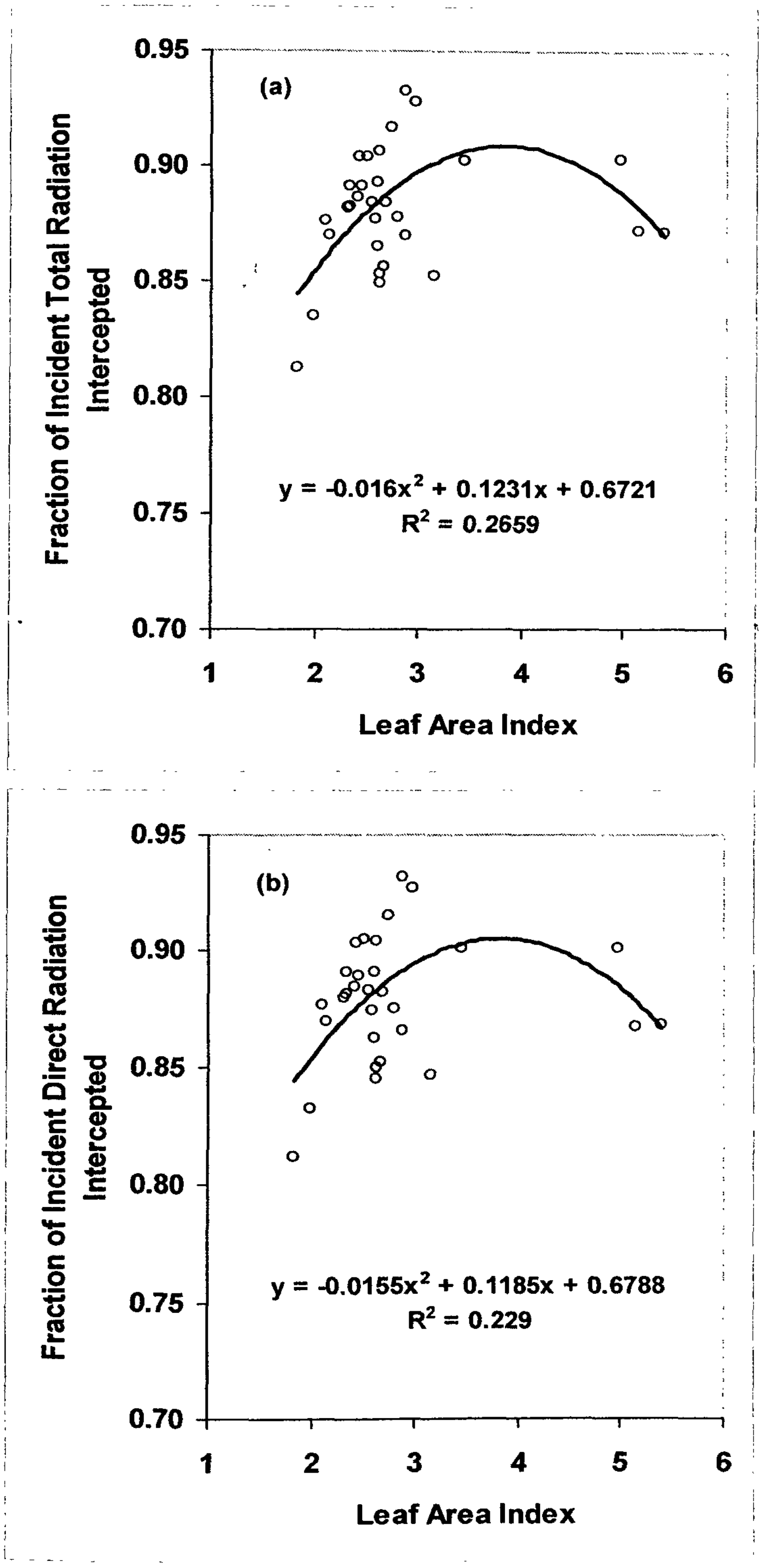


Figure 3.21: Variation of the fraction of total (a) and direct (b) radiation intercepted with canopy leaf area index in the ridge-top of the KDN forest complex. The data points represent 33 sampling points across 5 transects of the forest.

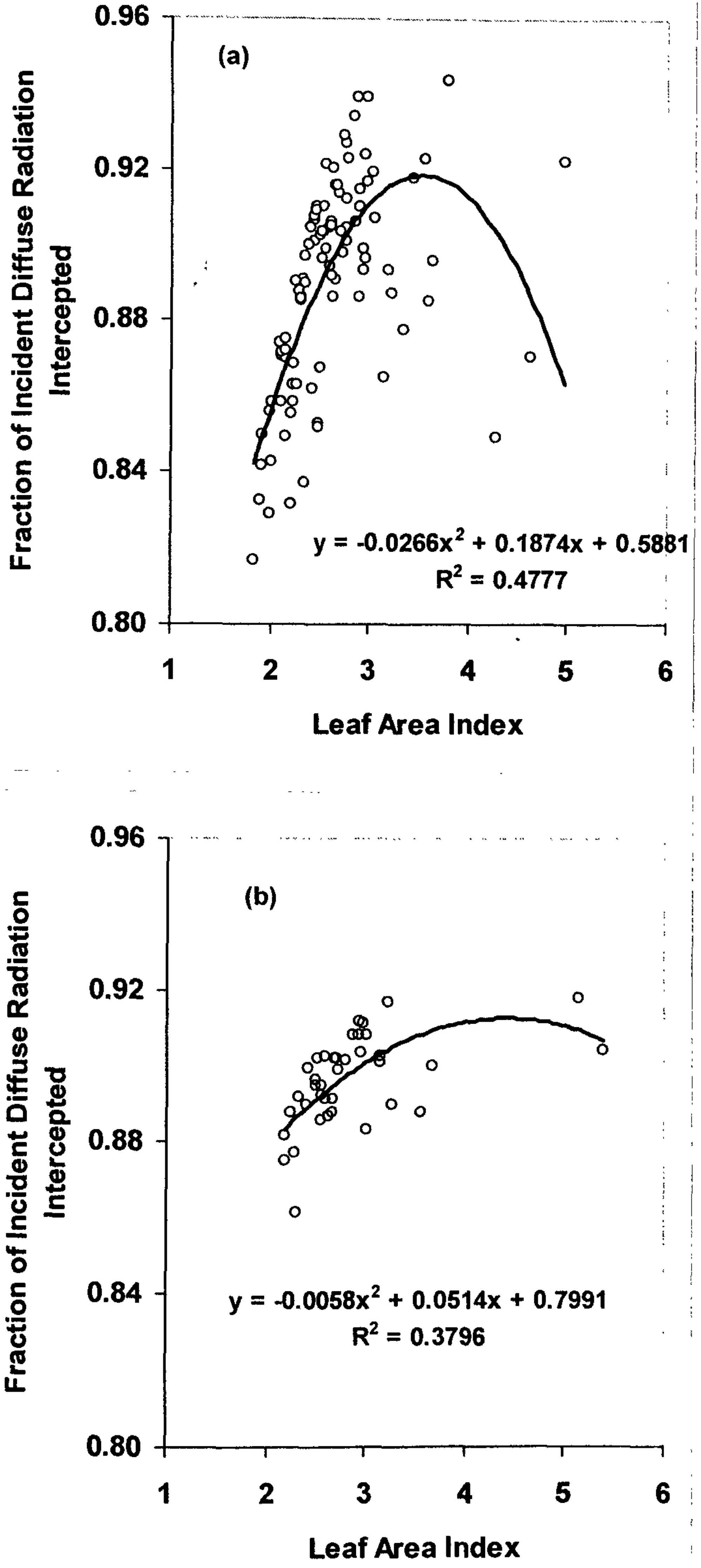


Figure 3.22: Variation of the fraction of diffuse radiation intercepted with canopy leaf area index in Kanneliya (a) and Dediyagala (b) of the KDN forest complex. The data points in Kanneliya represent 98 sampling points across 12 transects while those in Dediyagala represent 43 sampling points across 6 transects.

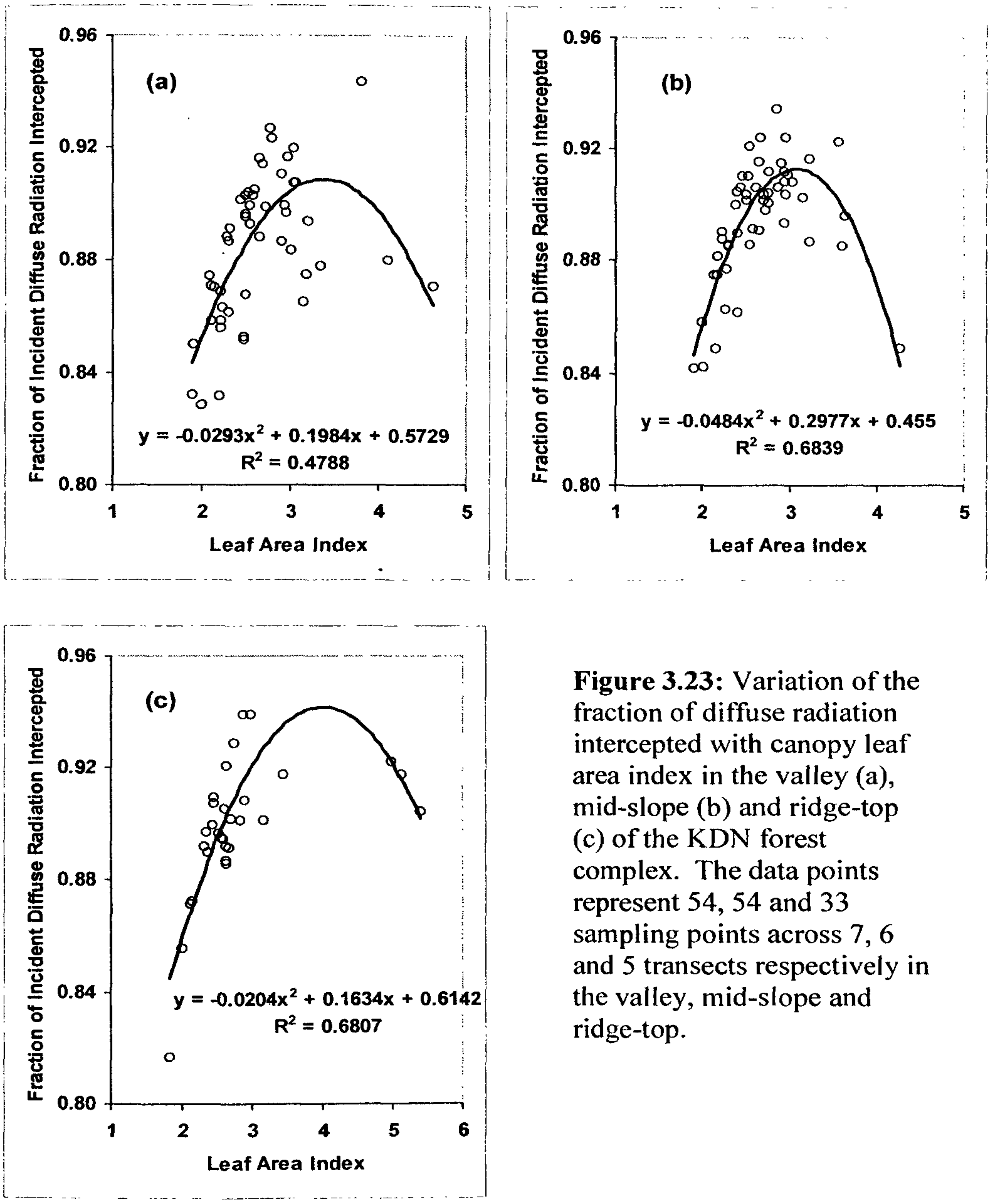


Figure 3.23: Variation of the fraction of diffuse radiation intercepted with canopy leaf area index in the valley (a), mid-slope (b) and ridge-top (c) of the KDN forest complex. The data points represent 54, 54 and 33 sampling points across 7, 6 and 5 transects respectively in the valley, mid-slope and ridge-top.

optimum LAI for maximum F_{Dif} in the mid-slope was lower than those of the valley and ridge-top. Similarly, the highest optimum LAI was observed in the ridge-top. It is notable that the R^2 values of the relationships for F_{Dif} were higher than those for F_{Tot} and F_{Dir}. This is probably because F_{Dif} is determined primarily by canopy size (as quantified by the LAI), with leaf angle not having a significant influence. In contrast, F_{Tot} and F_{Dir} is determined by both canopy size and leaf angle.

3.2 Sinharaja MAB forest reserve

3.2.1 Properties of the forest canopy – Variation between different transects

Hemispherical photography was done in three regions of the Sinharaja MAB forest reserve. These regions are designated according to their points of entry in to the forest as Kudawa, Pitadeniya and Morningside. A total of 202 hemispherical photographs were taken across 27 transects in all three regions. These included 128 photographs over 17 transects in Kudawa, 51 photographs across 6 transects in Pitadeniya and 23 photographs across 4 transects in Morningside. The two main canopy properties, the leaf area index (LAI) and mean leaf angle (MLA) showed significant ($p<0.05$) variation between different transects across the three regions (Figs. 3.24 and 3.25). Transect means of LAI ranged from 1.85 to 3.50 while those of MLA ranged from 2.95° and 56.80°. Both these ranges were slightly wider than the corresponding ranges of transect means that were observed for the KDN forest complex, i.e. 2.18 – 3.68 and 9.02° – 49.00° (Figs. 3.1 and 3.2). Accordingly, the fractional ground cover (F_{GCov}) in Sinharaja also showed a wider range, i.e. 0.64 – 0.91, (Fig. 3.26) than that in the KDN, i.e. 0.77 – 0.88 (Fig. 3.3). Similar to what was observed in KDN, in Sinharaja also, MLA showed greater variability

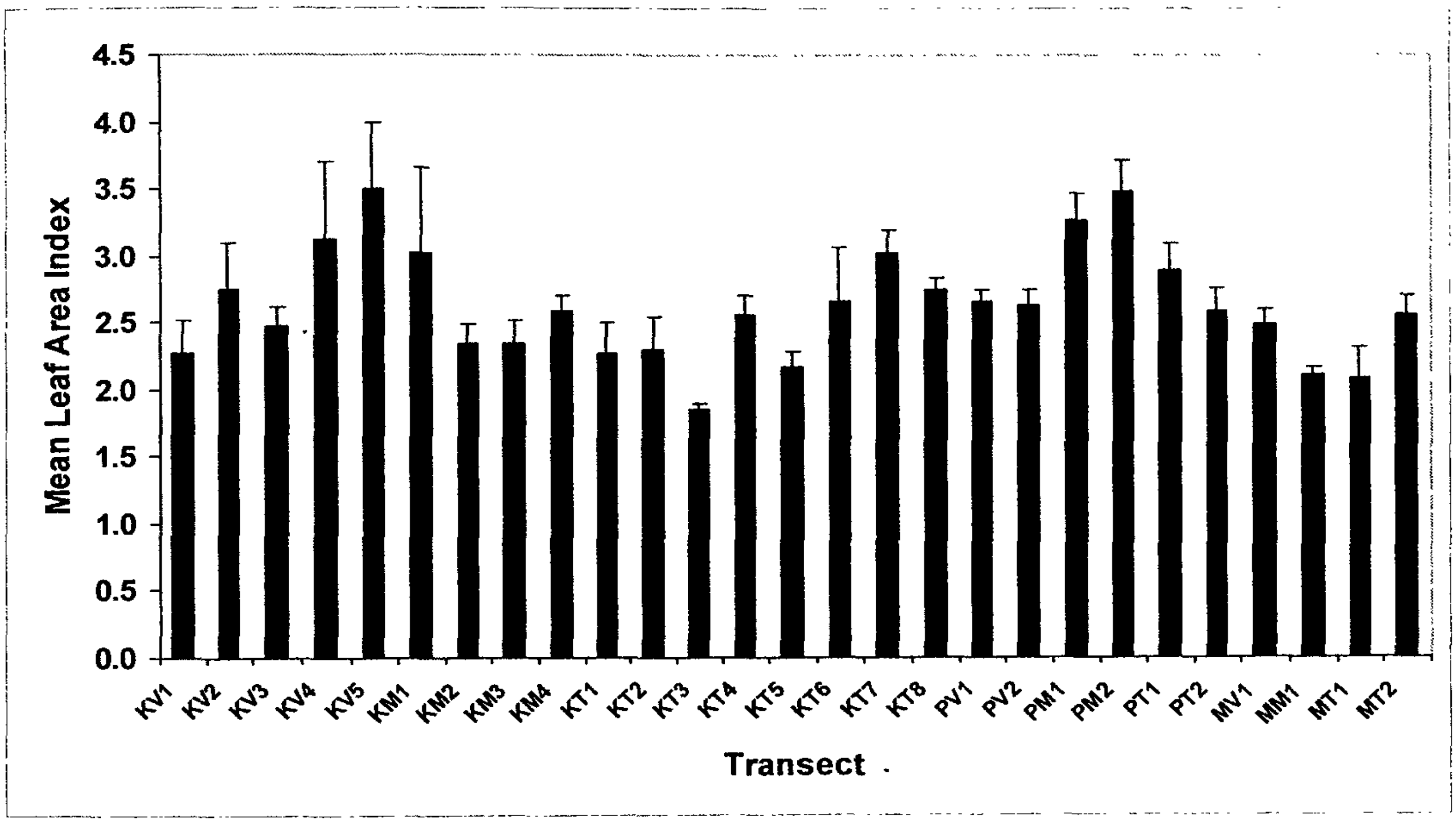


Figure 3.24: Variation of mean canopy leaf area index between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

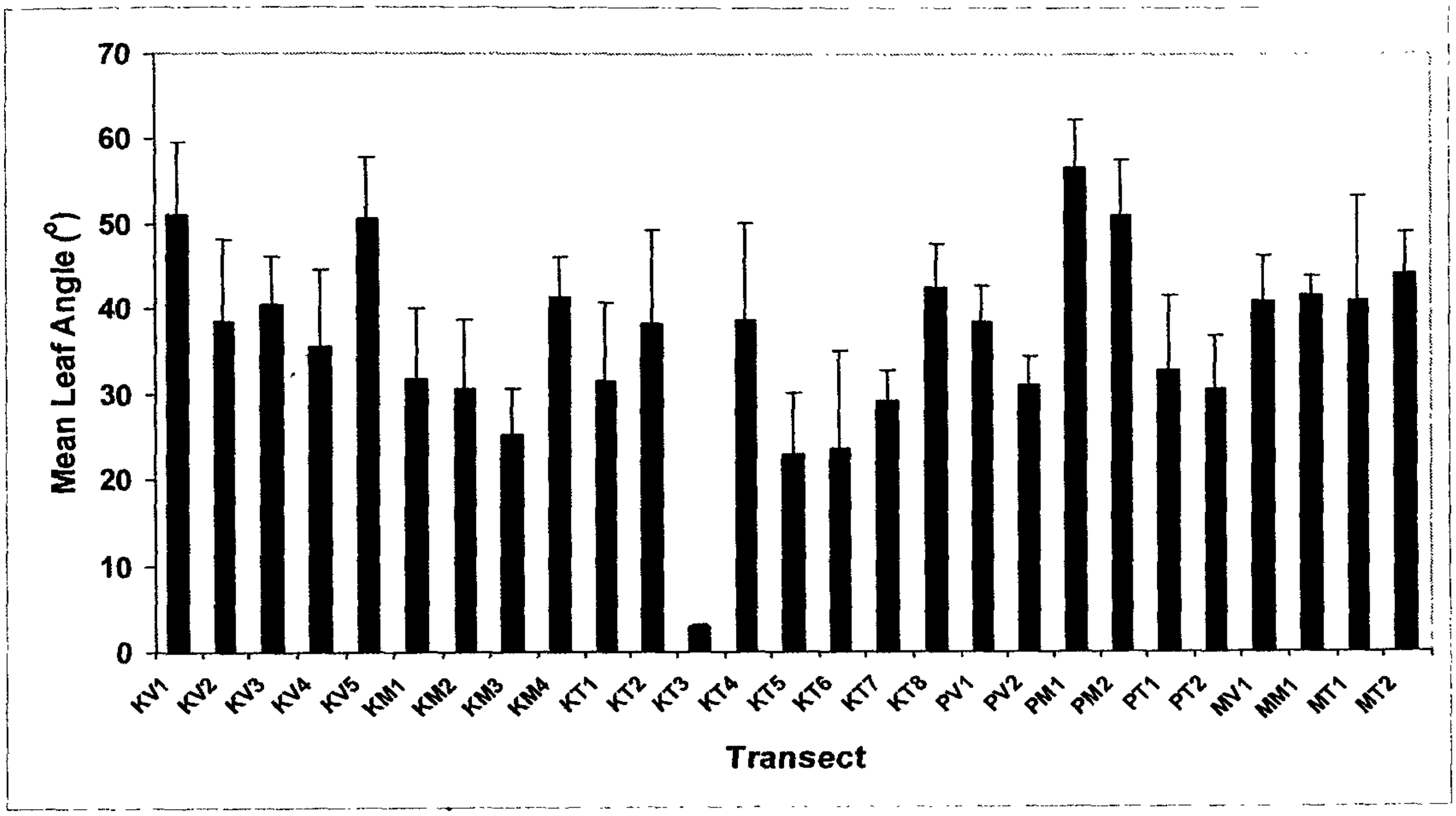


Figure 3.25: Variation of mean leaf angle between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

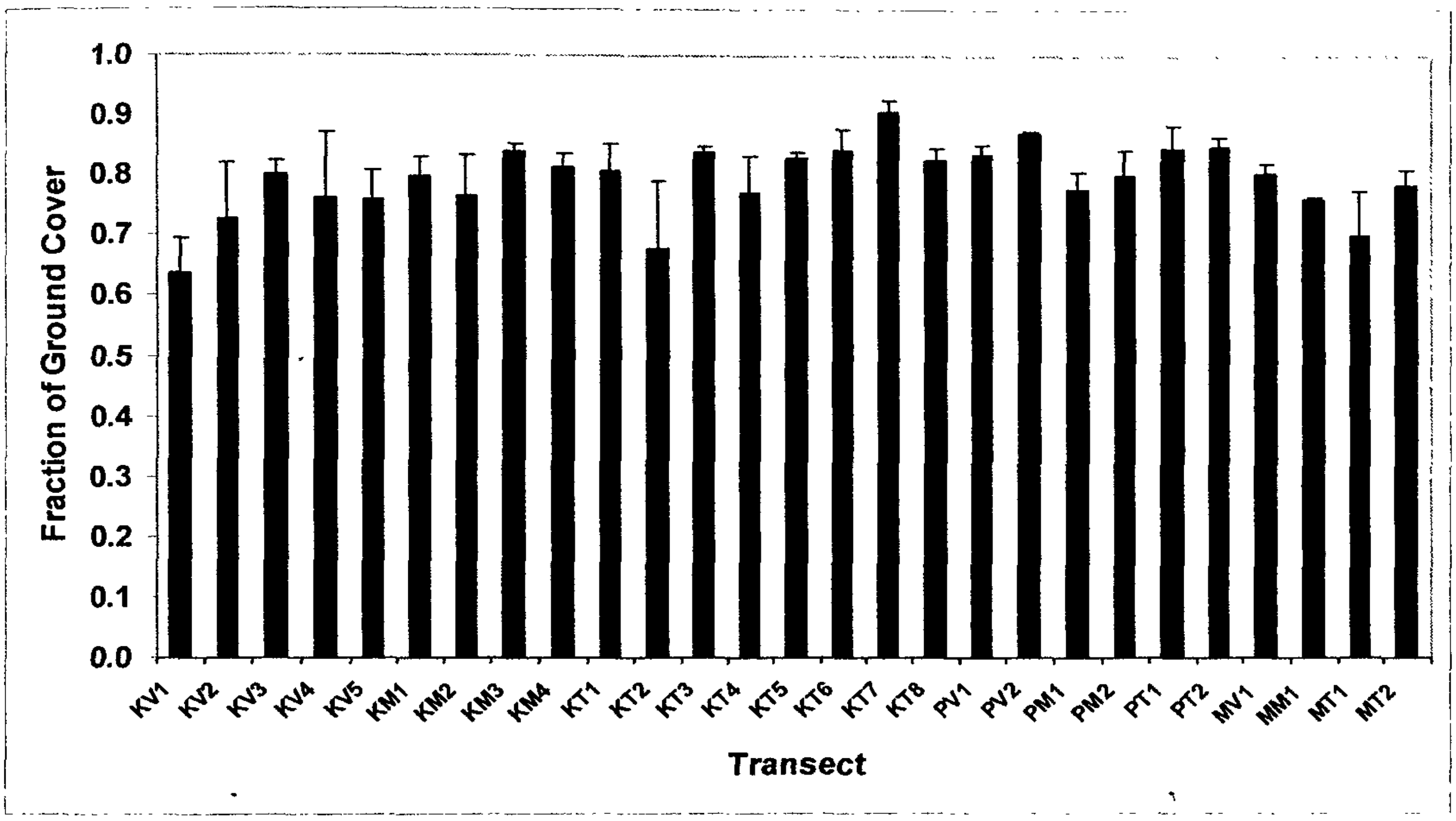


Figure 3.26: Variation of fractional ground cover between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

(i.e. CV of 57%) than LAI (CV=33%) and F_{GCov} (CV=18%). All three canopy characteristics had greater CV values in Sinharaja as compared to KDN.

There were significant correlations between different canopy properties in Sinharaja, with a significant positive correlation between LAI and MLA ($r = 0.651$ at $p<0.0001$, Fig. 3.27) and significant negative correlations between MLA and F_{GCov} ($r = -0.729$ at $p<0.0001$) and between LAI and F_{GCov} ($r = -0.494$ at $p<0.0001$). These correlations were similar to those observed in KDN. However, strengths of the correlations, as quantified by the correlation coefficient, r, were slightly lower in Sinharaja, again indicating its greater variability in canopy properties as compared to KDN. As in KDN, in Sinharaja also, canopy architecture, as quantified by the mean leaf angle, had a greater influence than canopy size, as quantified by the leaf area index, in determining the fractional ground cover by the forest canopy.

Comparison of the relationship between MLA and LAI in Sinharaja and KDN (Figs. 3.4 and 3.27) show some interesting differences in their canopy properties. The y-axis intercept of these relationships, which may be called the 'base LAI' indicates the LAI when the leaves are perfectly horizontal (i.e. MLA=0). KDN had a higher base LAI than KDN. On the other hand, LAI of Sinharaja showed a faster increase with increasing MLA than that of KDN. The leaf area index is defined as the total leaf area per unit ground area. It is determined by the total leaf area and how that leaf area is distributed in the canopy. The vertical stratification of the forest canopy, which is a characteristic feature of the canopies of tropical rainforests, influences the LAI in a complex manner. Theoretically, LAI also indicates the number of leaf layers when leaves are perfectly horizontal. The slightly higher base LAI of KDN indicates that its vertical stratification

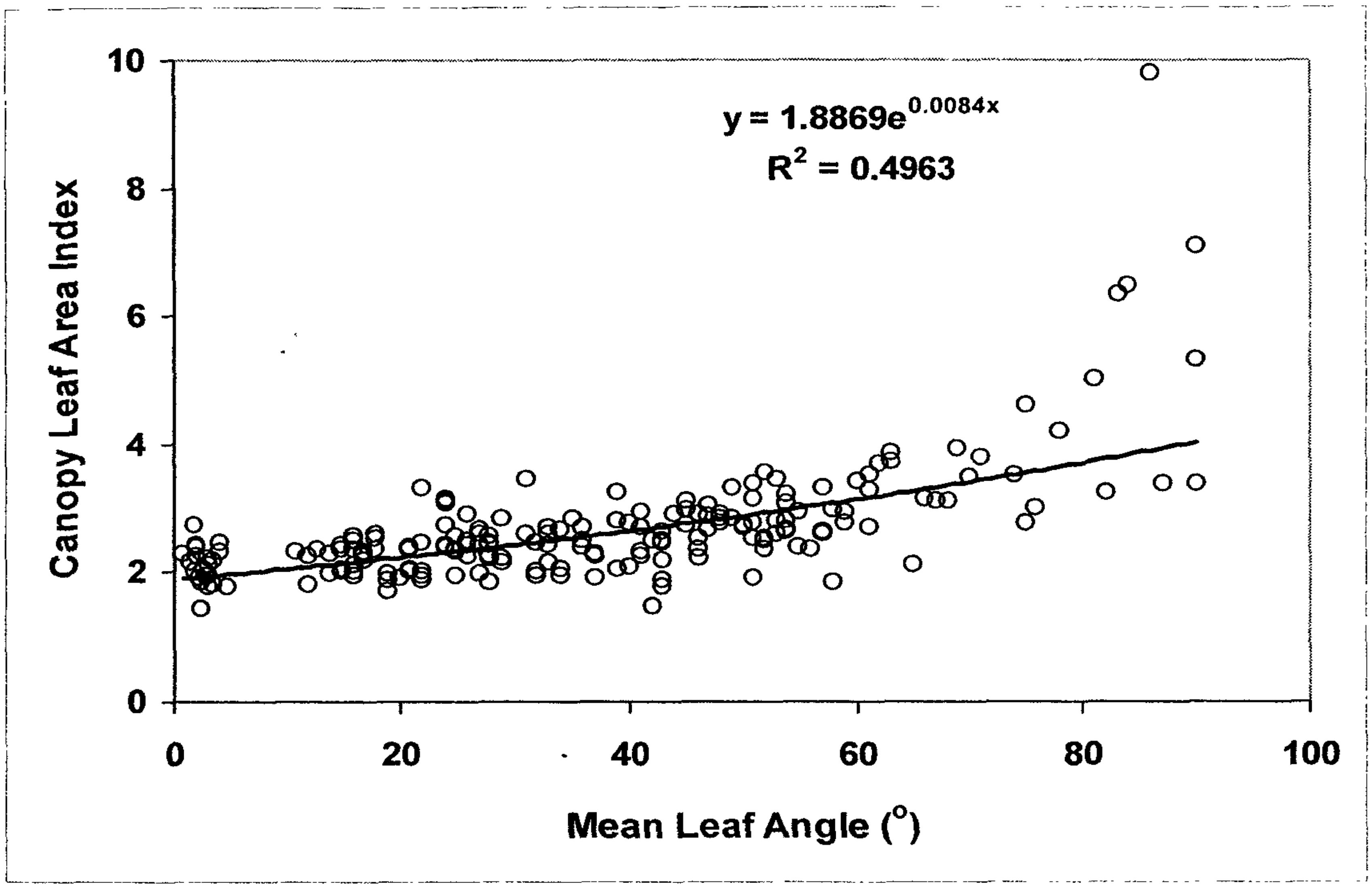


Figure 3.27: Variation of canopy leaf area index with mean leaf angle in the Sinharaja MAB forest reserve. The data points represent 202 sampling points across 27 transects of the forest.

is slightly higher than that of Sinharaja, when the mean leaf angle is close to zero. When the leaves are perfectly horizontal their interception of vertically-incident radiation is maximum because each leaf is perfectly normal to the direction of incoming radiation. At the same time, radiation penetration in to the lower layers of the canopy is minimum when the leaves are perfectly horizontal. The resulting limitation of light minimizes the overall canopy size and the number of leaf layers that the forest canopy can sustain. Accordingly, the lower base LAI of Sinharaja indicates lower light penetration when the leaves are perfectly horizontal in comparison to KDN. Light penetration, when the leaves are perfectly horizontal, is largely determined by the canopy gaps, with greater light penetration with increasing canopy gaps. Therefore, the lower base LAI in Sinharaja is an indication that its forest canopy has a lesser amount of gaps (i.e. more dense in common parlance) than the canopy of KDN.

As the leaf angle increases, the leaves become more and more inclined towards the vertical. This opens up the canopy allowing greater penetration of incident radiation in it. The greater availability of light within the canopy also allows the development of a higher number of leaf layers, thus increasing the LAI. The rate at which LAI increases with increasing MLA is an indicator of the extent to which canopy can respond to the opening up of its architecture by developing more leaf layers. Figs. 4 and 27 show a similar range of MLA in both forests. However, the canopy at Sinharaja shows a much greater range of LAI than that of KDN. The greater increase of LAI in response to increasing MLA in Sinharaja showed that it has a greater capacity to increase its canopy size in response to opening up of its canopy architecture. The greater range of LAI in Sinharaja, especially at higher leaf angles indicates that the vertical stratification and complexity is greater in the forest canopy in Sinharaja as compared to that in KDN. Moreover, the lower base LAI in Sinharaja indicated a denser canopy with lower gaps. Opening up of the canopy architecture by increasing leaf angle increases the light penetration in to deeper canopy layers. This would happen to a greater extent in a denser canopy with less canopy gaps as compared to a canopy with more gaps where canopy gaps would allow a certain degree of light penetration even at lower leaf angles. Therefore, the greater response of the forest canopy in Sinharaja to increasing leaf angle provides further evidence of a denser canopy as compared to the forest canopy in KDN. The denser forest canopy of Sinharaja and its greater capacity to increase in size with increasing leaf angle may be because of a greater plant/tree density in Sinharaja than in KDN.

3.2.2 Fractions of incident radiation intercepted – Variation between different transects

As in KDN, in Sinharaja also, all fractional interception of total (F_{Tot}), direct (F_{Dir}) and diffuse (F_{Dif}) radiations showed highly significant ($p<0.0001$) variation between different transects (Figs. 3.28 – 3.30). However, the respective ranges of the different fractional interceptions, i.e. 0.75 – 0.92 for F_{Tot}, 0.75 – 0.91 for F_{Dir} and 0.80 – 0.93 for F_{Dif}, were greater than the corresponding ranges in KDN (Fig. 3.4). In all transects, fractional interception of diffuse radiation was slightly greater than those of total and direct radiation. This was because diffuse radiation was coming from all directions as opposed to direct radiation which comes from one direction only at a given time.

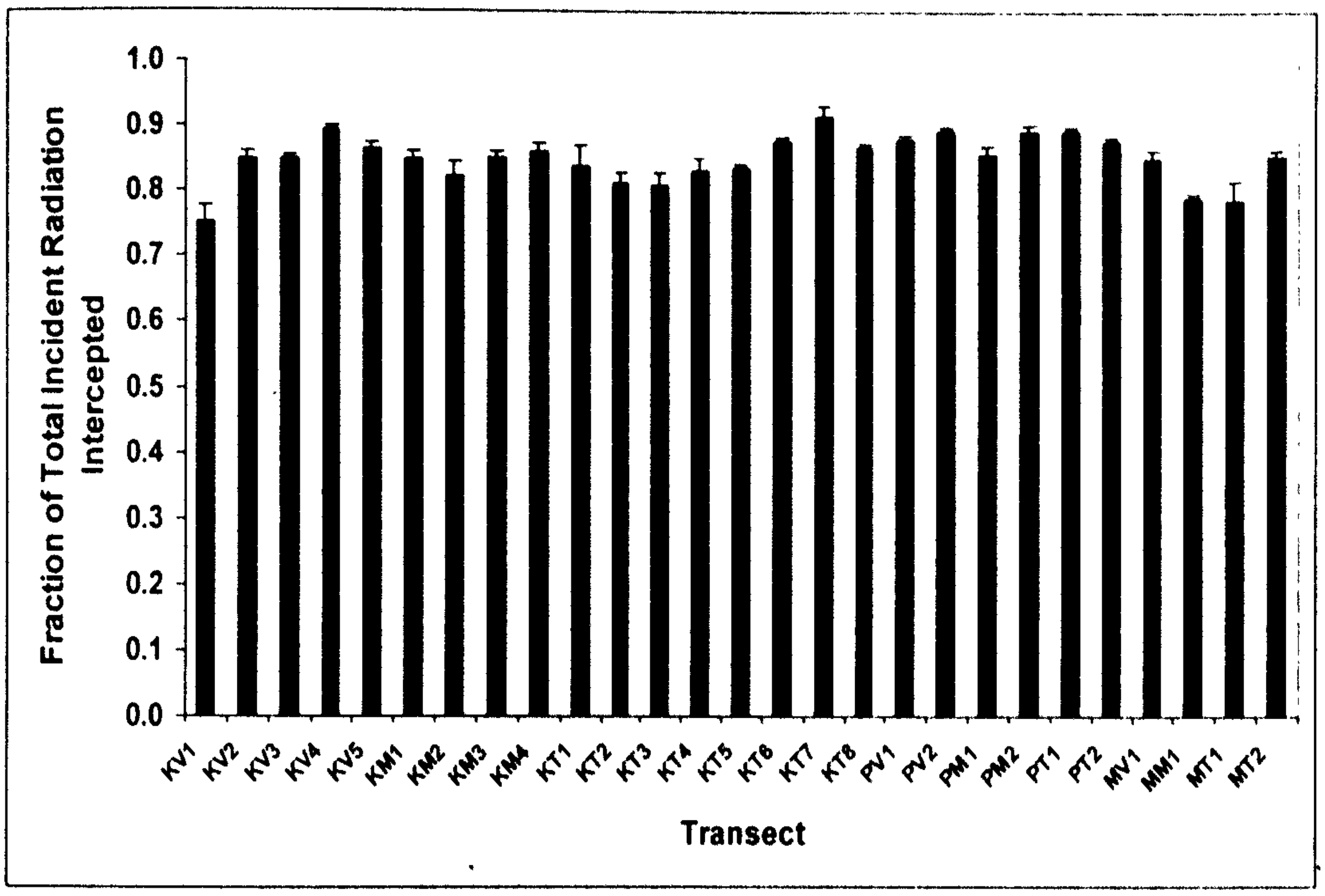


Figure 3.28: Variation of the fraction of total incident radiation intercepted between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

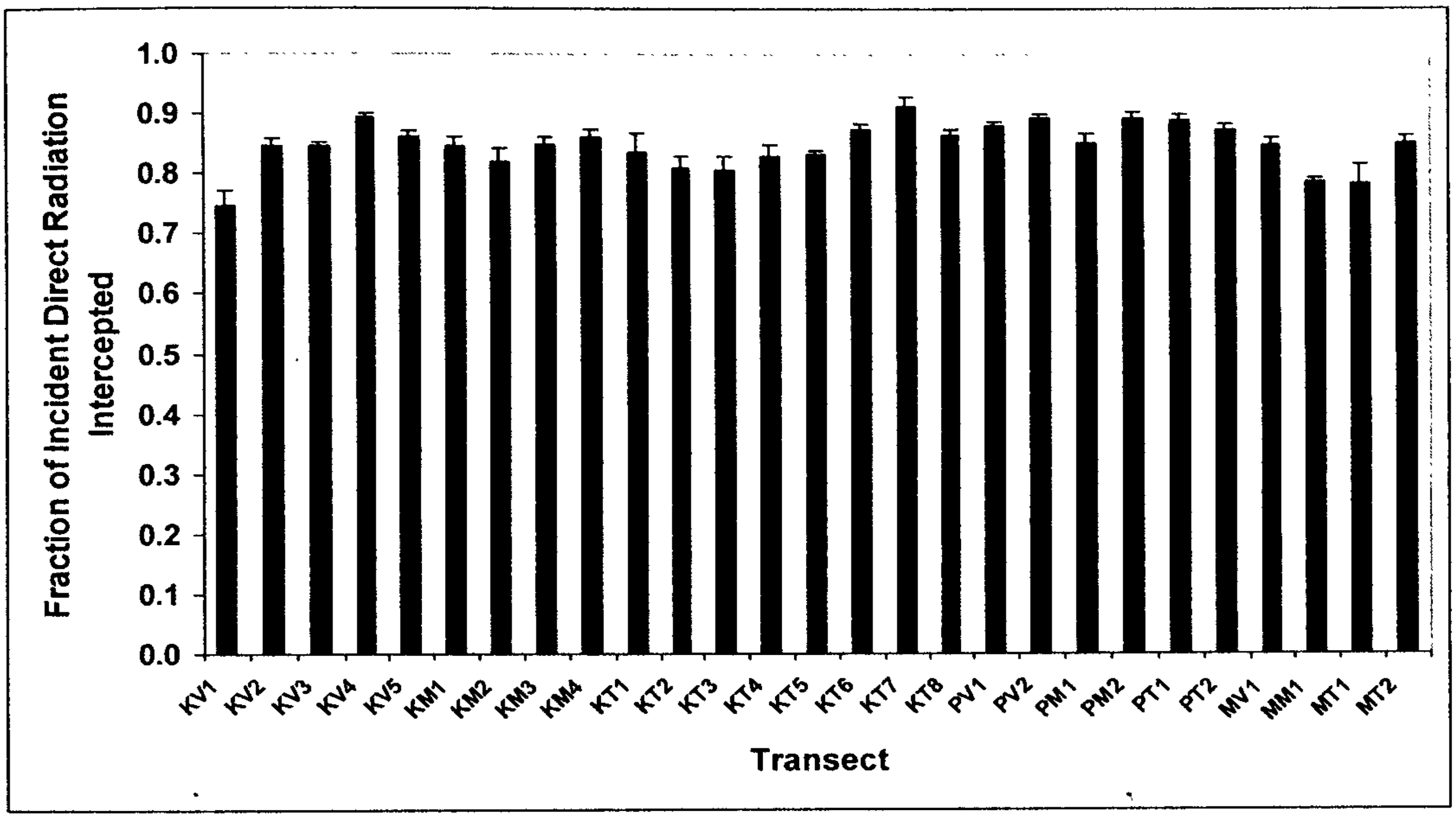


Figure 3.29: Variation of the fraction of incident direct radiation intercepted between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

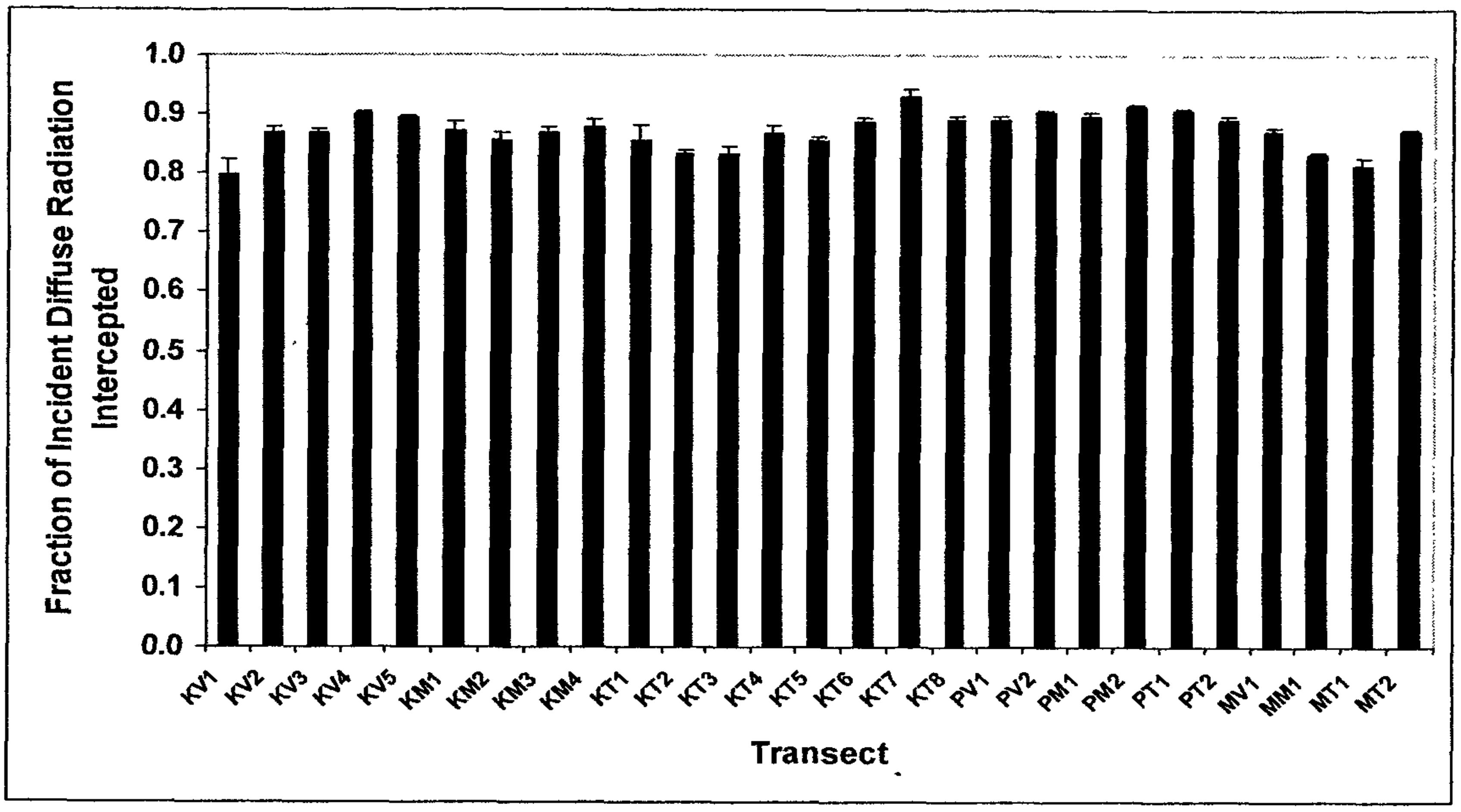


Figure 3.30: Variation of the fraction of incident diffuse radiation intercepted between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

3.2.3 Relationships between radiation interception and canopy properties – All data pooled

Relationships between radiation interception and canopy properties at Sinharaja were more complex than in KDN because of the greater variability shown in the canopy properties and the fractions of radiation intercepted in Sinharaja. Especially, there is one data point with an extremely high LAI value of 9.80. This was considered an outlier because the next highest LAI value was 7.09. However, outliers are also important because they provide valuable information about responses outside the normal range of conditions. In this case, it provides information about how radiation interception properties of the forest canopy have responded to LAI values which are outside the normal range of LAI of the canopies of tropical rainforests. Therefore, relationships between radiation interception and canopy properties are presented both with- and without the outlier.

When the whole data set was used in the regression, the variation of F_{Dir} with LAI followed both a second-order polynomial- (i.e. quadratic) relationship and a logarithmic relationship (Fig. 3.31.a). The logarithmic relationship showed a slightly better fit, with a marginally higher R^2 value, than the quadratic relationship. According to the quadratic relationship, maximum F_{Dir} was achieved at an optimum LAI (L_{Opt}) of 6.15. The quadratic relationship indicates that F_{Dir} would show a slight decrease when the LAI increases beyond the optimum because of mutual shading. On the other hand, when the outlying LAI value is taken in to account, the logarithmic relationship shows that F_{Dir} increases very slowly even beyond L_{Opt}. At L_{Opt}, the increase of F_{Dir} per unit increase of

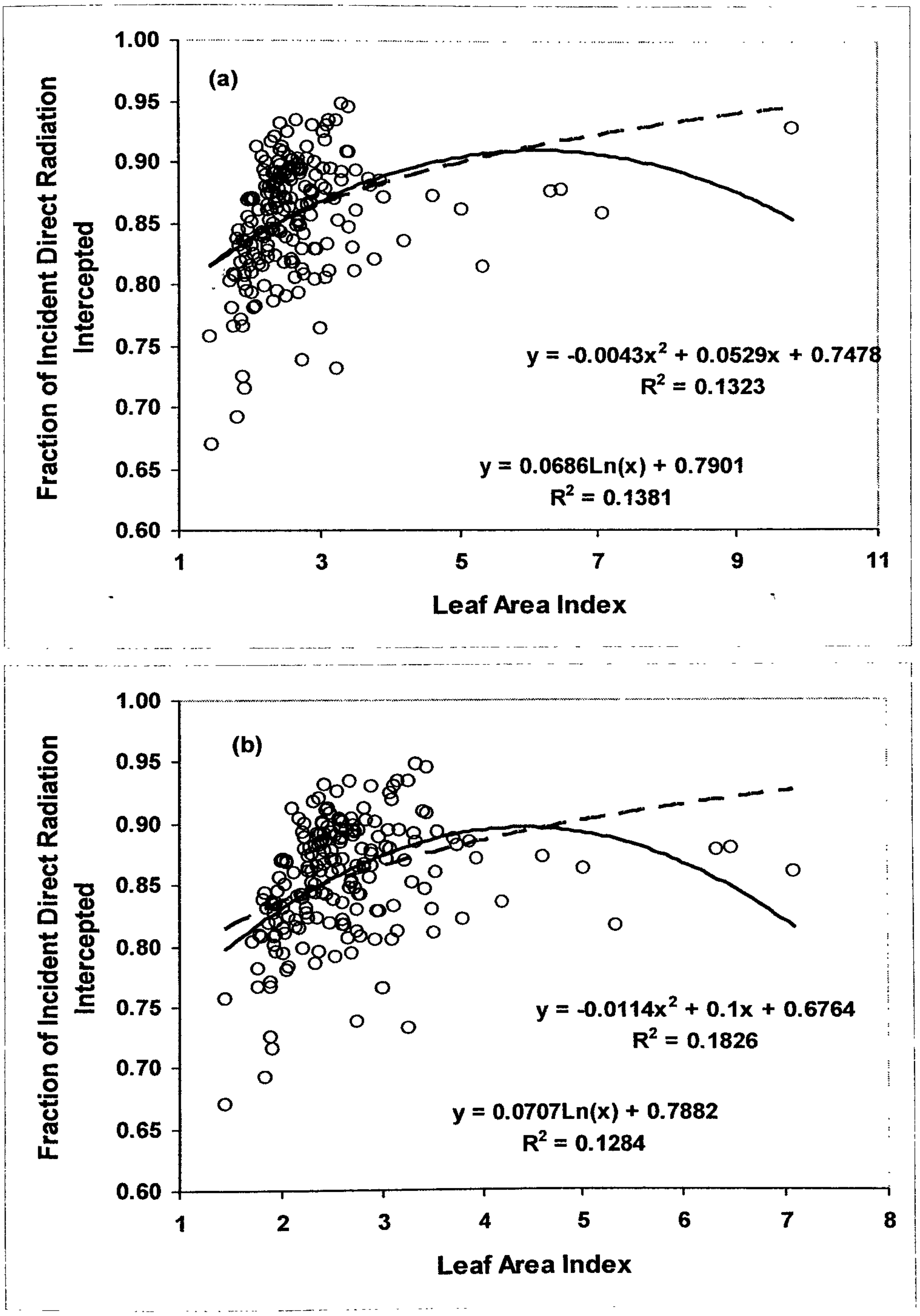


Figure 3.31: Variation of the fraction of direct radiation intercepted with canopy leaf area index in the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The full data set represents 202 sampling points across 27 transects of the forest.

LAI, as given by the slope of the logarithmic curve, is 0.011 (i.e. a 1.1% increase in interception of direct radiation per unit increase of LAI above L_{Opt}).

In contrast, when the outlying LAI value is disregarded in the regression, the variation of F_{Dir} with increasing LAI (Fig. 3.31.b) was described better by the quadratic relationship (R^2 = 0.20) than by the logarithmic relationship (R^2 = 0.15). The estimated L_{Opt} was 4.39, which was lower than that estimated when the outlier was also considered. Both L_{Opt} values estimated for maximum interception of direct radiation by the forest canopy in Sinharaja were higher than the corresponding L_{Opt} of 3.60 estimated for KDN (Fig. 3.6).

Similar to KDN, in Sinharaja also, F_{Dir} showed a significant negative correlation ($r = -0.296$, $p<0.0001$) with MLA (Fig. 3.31.c). However, strength of the correlation, as indicated by the correlation coefficient, r, was lower in Sinharaja, probably because of the greater heterogeneity in its forest canopy. F_{Dir} of Sinharaja showed a slower rate of decline with increasing MLA than that of KDN (Fig. 3.7). As explained earlier, F_{Dir} declines with increasing leaf angle (i.e. leaves becoming more vertical) because direct radiation comes vertically downwards for most part of the day. The lower rate of reduction of F_{Dir} with increasing MLA in Sinharaja again shows evidence of greater vertical stratification in its canopy. This is because the greater number of layers in the canopy in Sinharaja could capture the increased fraction of direct radiation that would penetrate in to the canopy as the leaf angle increases to a greater extent than the canopy in KDN, which has a lower number of layers. Hence, F_{Dir} in Sinharaja would decrease more slowly with increasing MLA than the F_{Dir} in KDN.

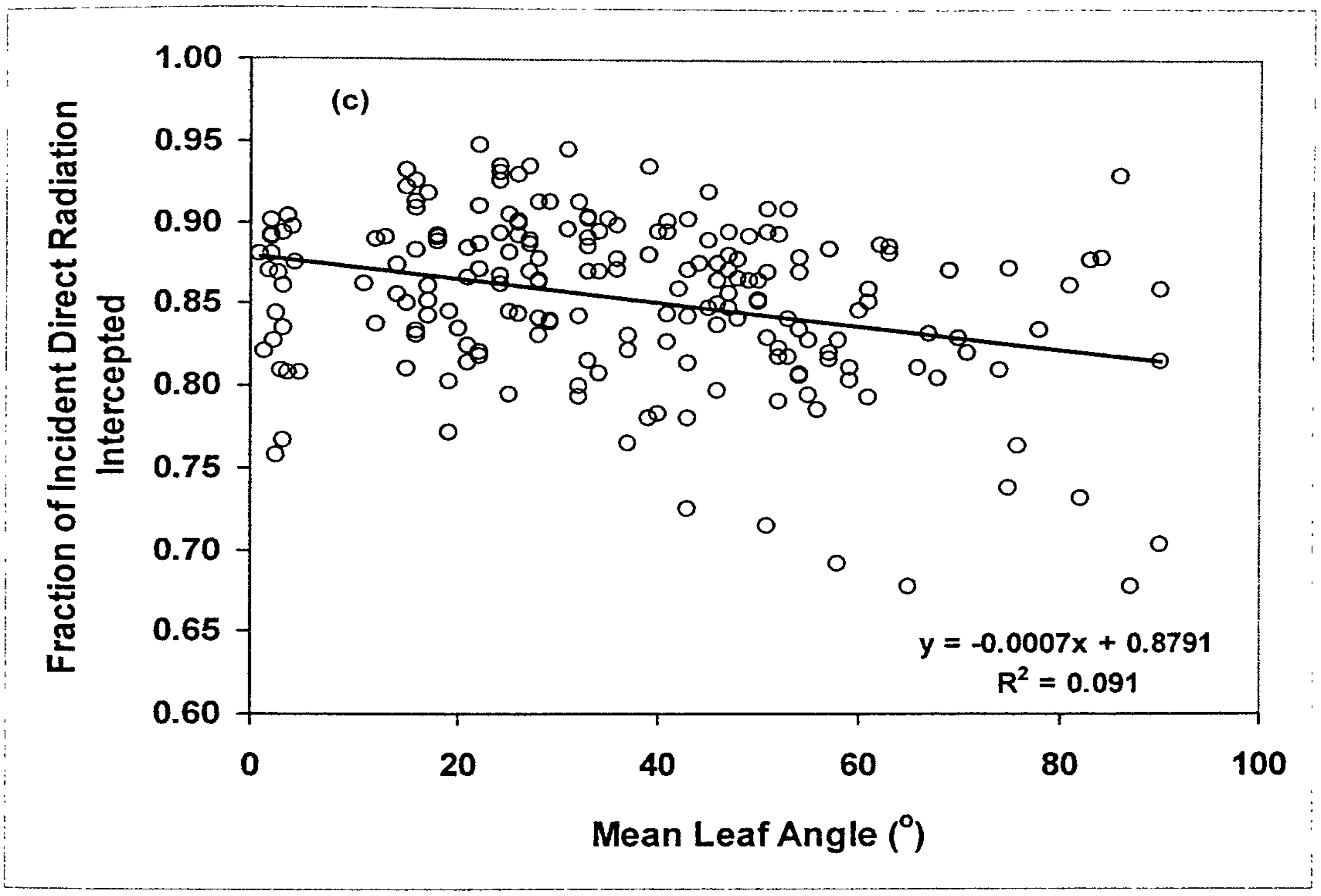
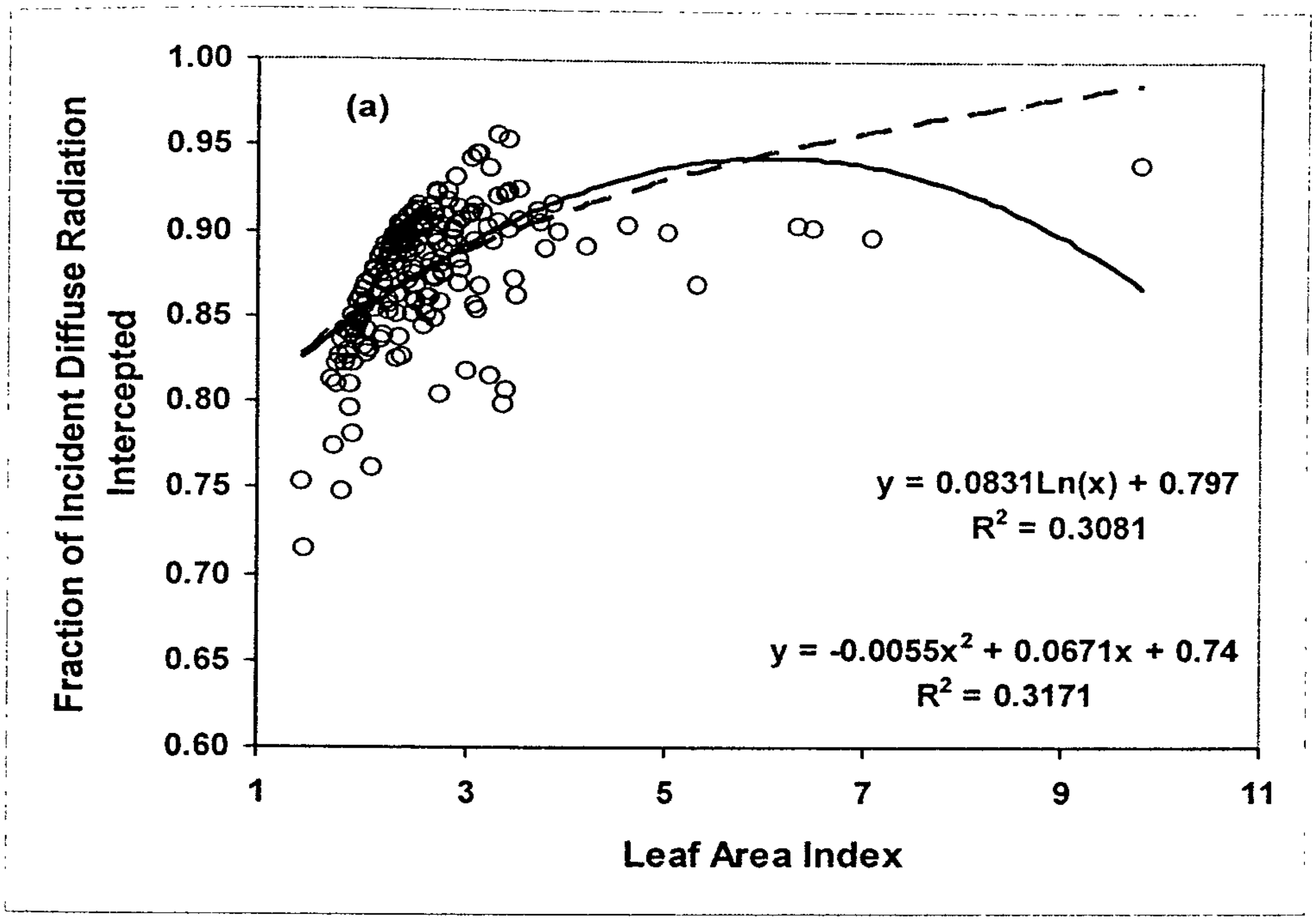


Figure 3.31.c: Variation of the fraction of direct radiation intercepted with mean leaf angle in the Sinharaja MAB forest reserve. The data points represent 202 sampling points across 27 transects of the forest.

When the full data set was used in the regression, variation of the fraction of incident diffuse radiation intercepted (F_{Dif}) could be described by both a quadratic relationship and a logarithmic relationship (Fig. 3.32.a). Here, the quadratic relationship gave a marginally better fit than the logarithmic relationship. The quadratic relationship showed an optimum LAI of 6.1. At this L_{Opt}, the logarithmic relationship showed that F_{Dif} increased marginally at a rate of 0.014 per unit increase of LAI. When the outlying LAI value was excluded from the regression (Fig. 3.32.b), the quadratic relationship showed a better fit than the logarithmic relationship, with an optimum of 4.58. Both L_{Opt} values for maximum F_{Dif} in Sinharaja were greater than the corresponding value of 3.86 in KDN (Fig. 3.8). It is difficult to exactly pinpoint reasons for the higher L_{Opt} values for F_{Dif} in Sinharaja. Unlike direct radiation, diffuse radiation comes from all directions of the sky at all times. Therefore, a greater L_{Opt} means that diffuse radiation is able to penetrate deeper in to the forest canopy in Sinharaja than in KDN. Deeper penetration of radiation, whether direct or diffuse, requires canopy gaps. For greater penetration of direct radiation, which comes vertically downwards for most of the day, a greater amount canopy gaps on the horizontal plane (i.e. gaps visible when the canopy is viewed from the top) is needed. On the other hand, for greater penetration of diffuse radiation, a greater amount of canopy gaps is needed on both the vertical and horizontal planes. The foregoing discussion of the respective relationships between LAI and MLA (Figs. 3.4 and 3.27), F_{Dir} and LAI (Figs. 3.6 and 3.31) and F_{Dir} and MLA (Figs. 3.7 and 3.31.c) showed evidence that there are less canopy gaps on the horizontal plane in Sinharaja as compared to KDN. Therefore, it is likely that the greater L_{Opt} for F_{Dif} indicates greater canopy gaps in the vertical plane at Sinharaja. This is possible if the forest canopy has greater vertical



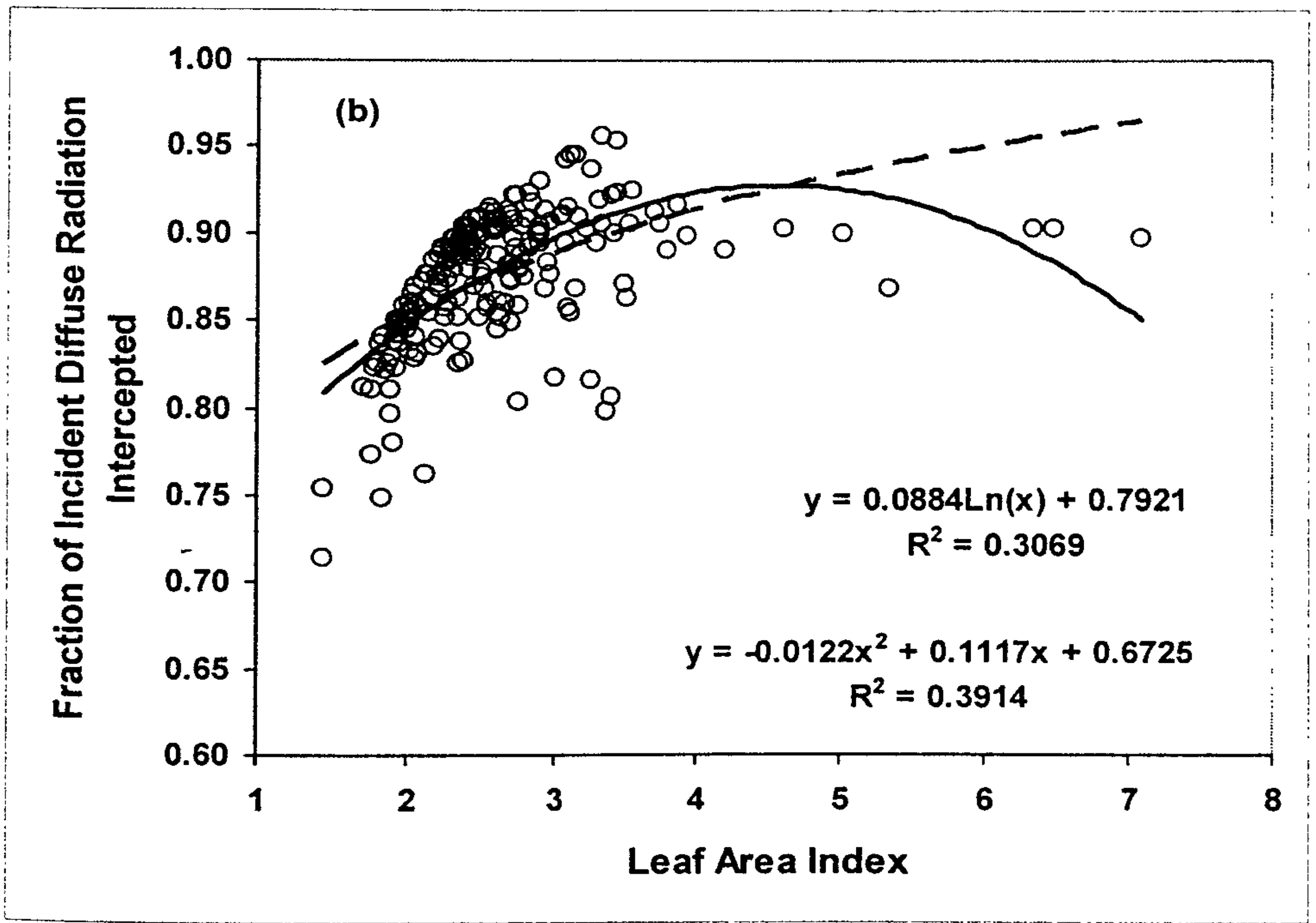


Figure 3.32: Variation of the fraction of diffuse radiation intercepted with canopy leaf area index in the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The full data set represents 202 sampling points across 27 transects of the forest.

stratification. Hence, it is probable that the greater L_{Opt} for F_{Dif} also provides further evidence for greater vertical stratification of the forest canopy in Sinharaja in comparison to KDN. The respective relationships between F_{Dif} and LAI in Sinharaja showed greater variability than in KDN, with lower R^2 values also is a consequence of the greater heterogeneity of the forest canopy in Sinharaja. As in KDN, there was no significant relationship or correlation between F_{Dif} and MLA in Sinharaja as well.

The respective relationships between the fractional interception of total incident radiation (F_{Tot}) and LAI, for both the full data set (Fig. 3.33.a) and for the data set without the outlier (Fig. 3.33.b), differed only marginally from the corresponding relationships between F_{Dir} and LAI (Figs. 3.31.a and b). Based on the quadratic relationship, the respective L_{Opt} values for maximum F_{Tot} were estimated to be 6.17 and 4.44 respectively. As was observed in KDN, L_{Opt} for maximum F_{Tot} were slightly higher than the corresponding values for maximum F_{Dir}. Similar to what was observed for F_{Dir}, the L_{Opt} values for F_{Tot} were greater in Sinharaja than those in KDN. As explained earlier, this indicates a denser forest canopy with greater vertical stratification in Sinharaja as compared to KDN.

F_{Tot} showed a significant negative correlation ($r = -0.281$, $p<0.0001$) with MLA (Fig. 3.34). A similar negative correlation ($r = -0.429$, $p<0.0001$) was observed in KDN as well (Fig. 3.10). The lower correlation coefficient in Sinharaja, once again, showed the greater heterogeneity in its forest canopy. As was argued earlier for the relationship between F_{Dir} and MLA, the lower rate of reduction of F_{Tot} with increasing leaf angle showed evidence of greater vertical stratification in the forest canopy in Sinharaja.

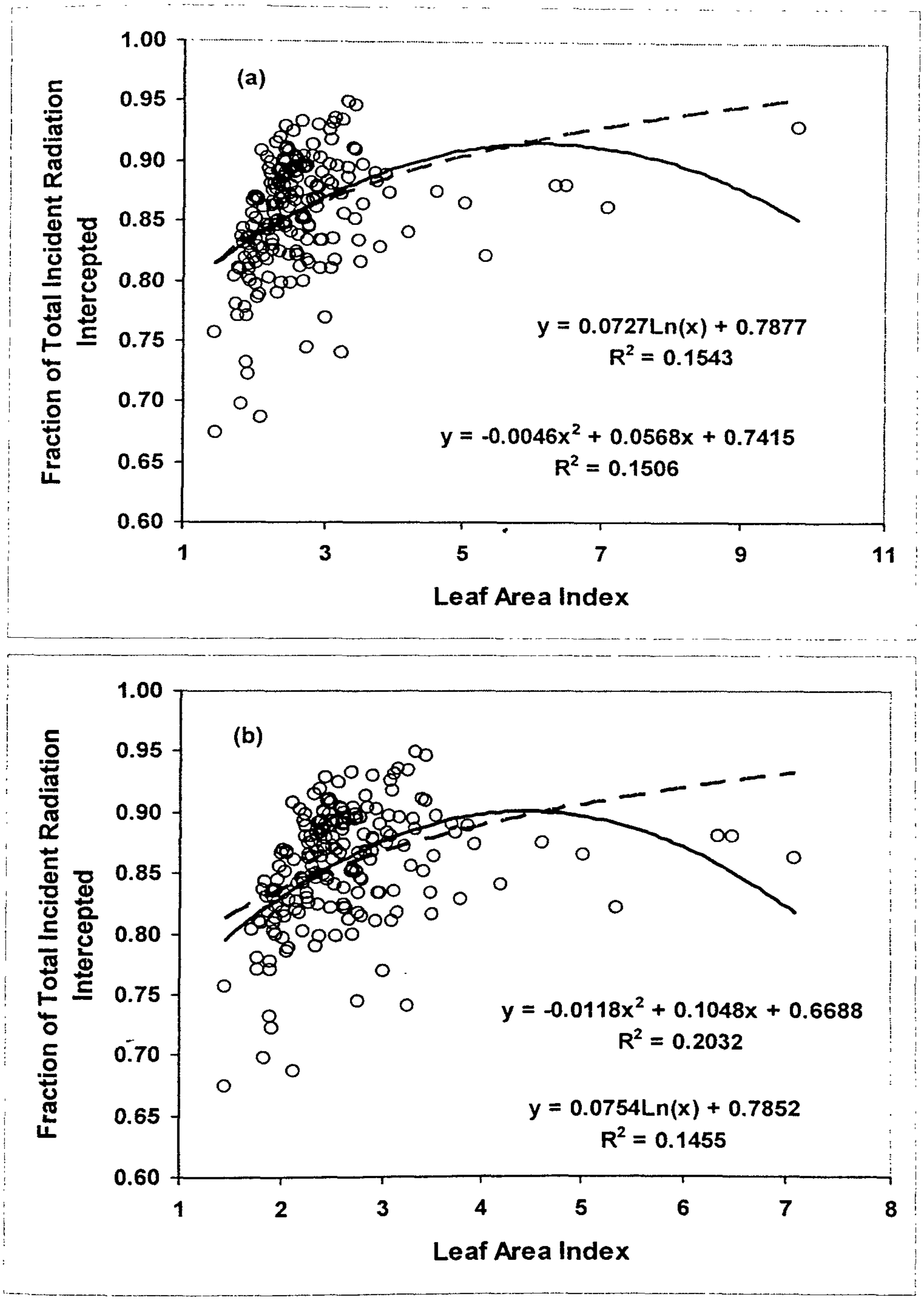


Figure 3.33: Variation of the fraction of total incident radiation intercepted with canopy leaf area index in the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The full data set represents 202 sampling points across 27 transects of the forest.

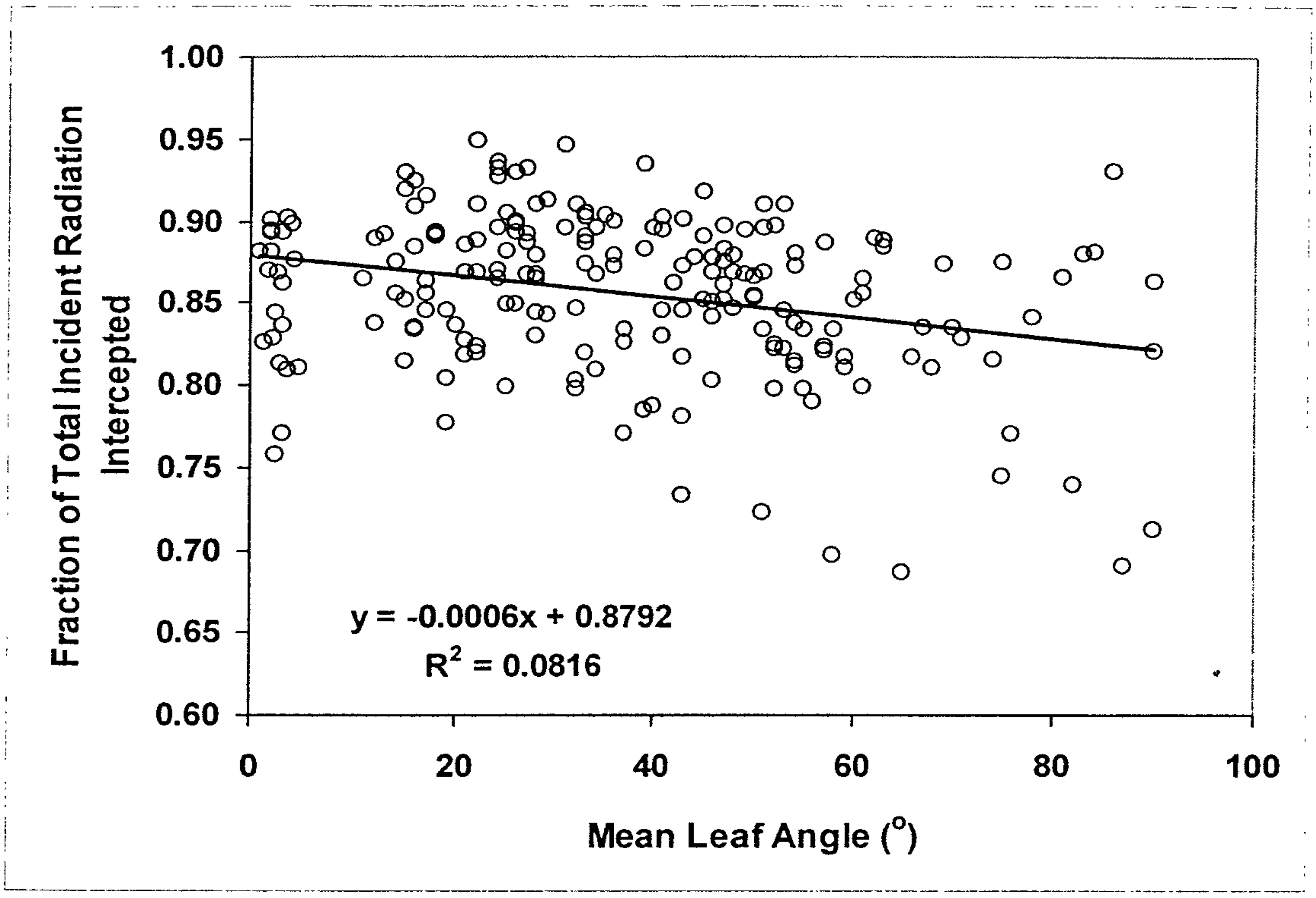


Figure 3.34: Variation of the fraction of total incident radiation intercepted with mean leaf angle in the Sinharaja MAB forest reserve. The data points represent 202 sampling points across 27 transects of the forest.

3.2.4 Properties of the forest canopy – Variation between different regions of the forest and between different elevation zones

Analysis of variance with the full data showed that LAI differed significantly ($p<0.05$) between different regions of the Sinharaja forest reserve (Table 3.4). However, the there was no significant variation in LAI between different elevation zones and the region x elevation zone interaction effect was not significant as well. When averaged across different elevation zones, mean LAI in Pitadeniya was 14% greater than those in Kudawa and Morningside, which did not differ significantly at $p=0.05$ (Fig. 3.35.a). Within each forest region, only Pitadeniya showed significant ($p<0.001$) variation in LAI between different elevation zones (Table 3.4), with 26% greater LAI in the mid-slope as compared to the valley and ridge-top (Fig. 3.35.a). When ANOVA was done for different elevation zones, only the ridge-top showed significant ($p=0.0529$) variation in LAI between different regions, with Pitadeniya showing 11% higher LAI than the rest.

When the extremely high LAI value (i.e. 9.795 at one sampling point in Kudawa in the mid-slope) was excluded from the ANOVA, the coefficient of variation (CV) was reduced from the 34% in the full data set to 27% for the data set without the outlier. As a result, in addition to the increased significance ($p<0.001$) level for the variation in LAI between regions, the region x elevation interaction effect on LAI also became highly significant ($p<0.01$). This meant that the variation in LAI between different elevation zones varied significantly in the different forest regions of the Sinharaja forest reserve (Fig. 3.35.b). At Kudawa, the LAI in the valley was significantly greater than those in the mid-slope and ridge-top. In contrast, LAI in the mid-slope was the highest and lowest among the three elevation zones in Pitadeniya and Morningside respectively.

Table 3.4: Probabilities of significance of differences[†] in forest canopy and radiation interception properties between different regions of the Sinharaja MAB forest reserve and between different elevation zones

Sources of variation	Leaf area index	Mean leaf angle	F_{GCov}	F_{Tot}	F_{Dir}	F_{Dif}
ANOVA with regions and elevation zones analyzed together						
Region	0.0422 *(0.0003)*[‡]	n.s.	0.0192	<0.0001	<0.0001	<0.0001
Elevation zone	n.s. *(n.s.)*	n.s.	n.s.	n.s.	n.s.	n.s.
Region x Elev. Zone	n.s. *(0.0022)*	0.0084	n.s.	n.s.	n.s.	n.s.
CV (%)	34.34 *(26.99)*	57.16	17.96	5.23	5.43	3.94
ANOVA for Kudawa separately						
Elev. zone	n.s. *(0.0309)*	0.0076	0.0932	n.s.	n.s.	n.s.
CV (%)	40.87 *(32.89)*	63.41	21.46	6.40	6.63	4.78
ANOVA for Pitadeniya separately						
Elev. zone	0.0003	0.0021	0.0839	n.s.	n.s.	n.s.
CV (%)	16.45	41.32	8.94	2.97	3.14	1.92
ANOVA for Morningside separately						
Elev. zone	n.s.	n.s.	0.0575	0.0829	0.0959	0.0173
CV (%)	14.37	22.46	8.46	4.32	4.65	2.16
ANOVA for Valley separately						
Region	n.s.	n.s.	0.0108	0.0001	0.0001	0.0004
CV (%)	19.44	49.15	18.24	5.75	5.94	4.56
ANOVA for Mid-slope separately						
Region	n.s. *(<0.0001)*	0.0279	n.s.	0.0089	0.0096	0.0066
CV (%)	54.26 *(16.32)*	54.51	12.21	4.65	4.75	4.02
ANOVA for Ridge-top separately						
Region	0.0529	n.s.	n.s.	0.0001	0.0002	<0.0001
CV (%)	21.33	65.57	18.61	4.62	4.84	3.27

[†] Probability of the variation due to the respective factor occurring as a result of random variation. F_{GCov} – Fraction of ground cover; F_{Tot}, F_{Dir} and F_{Dif} – Fractions of incident total, direct and diffuse radiations intercepted respectively. [‡] For ANOVA done without the extremely high LAI value.

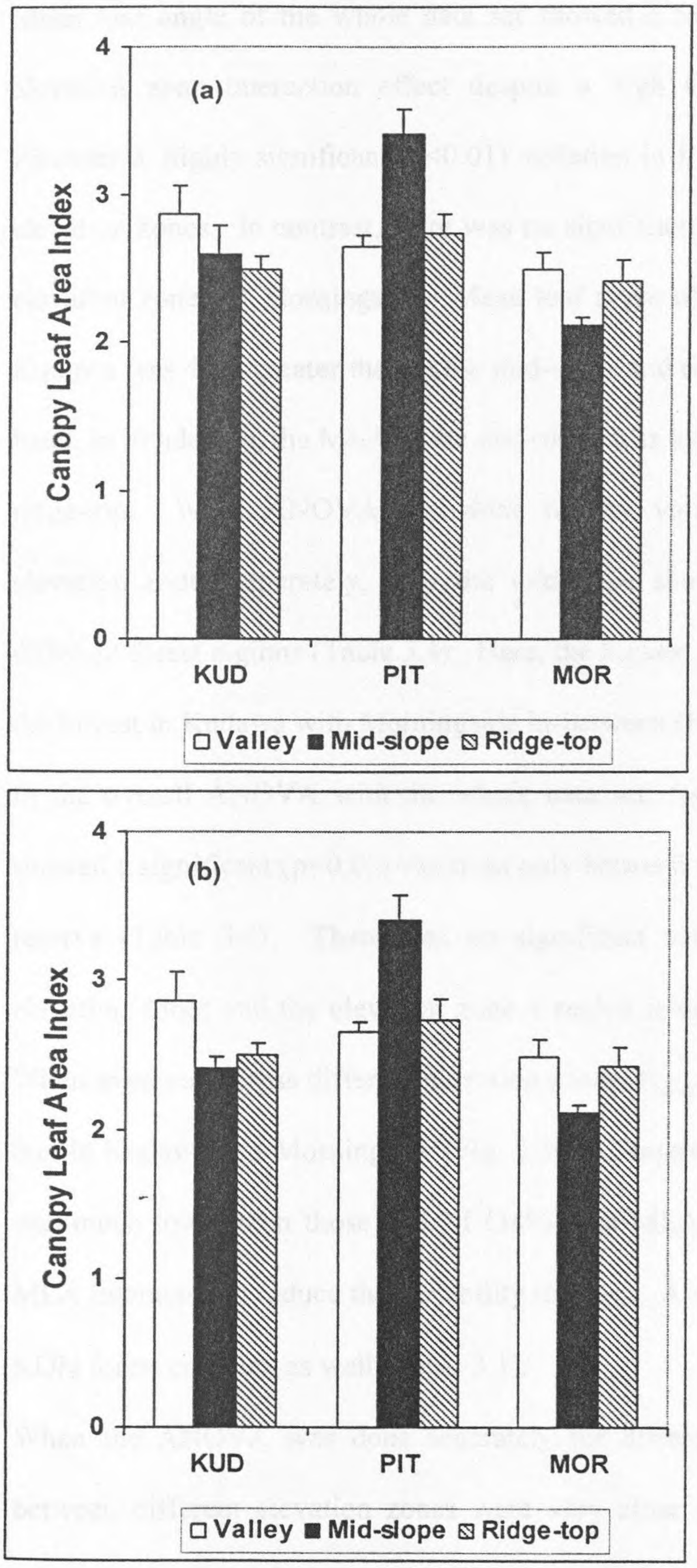


Figure 3.35: Variation of canopy leaf area index between different regions and elevation classes in the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The error bars indicate the standard error of mean. KUD-Kudawa; PIT-Pitadeniya; MOR-Morningside.

Mean leaf angle of the whole data set showed a highly significant ($p<0.01$) region x elevation zone interaction effect despite a high CV (i.e. 57%). At Kudawa and Pitadeniya, highly significant ($p<0.01$) variation in LAI was observed between different elevation zones. In contrast, there was no significant variation in LAI between different elevation zones of Morningside. Mean leaf angle of the forest canopy in the valley of Kudawa was 41% greater than in the mid-slope and ridge-top (Fig. 3.36.a). On the other hand, in Pitadeniya, the MLA of the mid-slope was 63% greater than in the valley and the ridge-top. When ANOVA was done for the variation of MLA between different elevation zones separately, only the mid-slope showed significant variation between different forest regions (Table 3.4). Here, the highest MLA was shown in Pitadeniya and the lowest in Kudawa with Morningside in-between (Fig. 3.36.a).

In the overall ANOVA with the whole data set, the fraction of ground cover (F_{GCov}) showed a significant ($p<0.05$) variation only between different regions of Sinharaja forest reserve (Table 3.4). There was no significant variation in F_{GCov} between different elevation zones and the elevation zone x region interaction was not significant as well. When averaged across different elevation zones, F_{GCov} in Pitadeniya was 7% greater than that in Kudawa and Morningside (Fig. 3.36.b). Interestingly, the CV of F_{GCov} (i.e. 18%) was much lower than those of LAI (34%) and MLA (57%), showing that the LAI and MLA interacted to reduce the variability in F_{GCov}. A similar observation was made in the KDN forest complex as well (Table 3.1).

When the ANOVA was done separately for different regions, the variation in F_{GCov} between different elevation zones were very close to being statistically significant at $p=0.05$ with the relevant probability values ranging from 0.06 to 0.09 (Table 3.3).

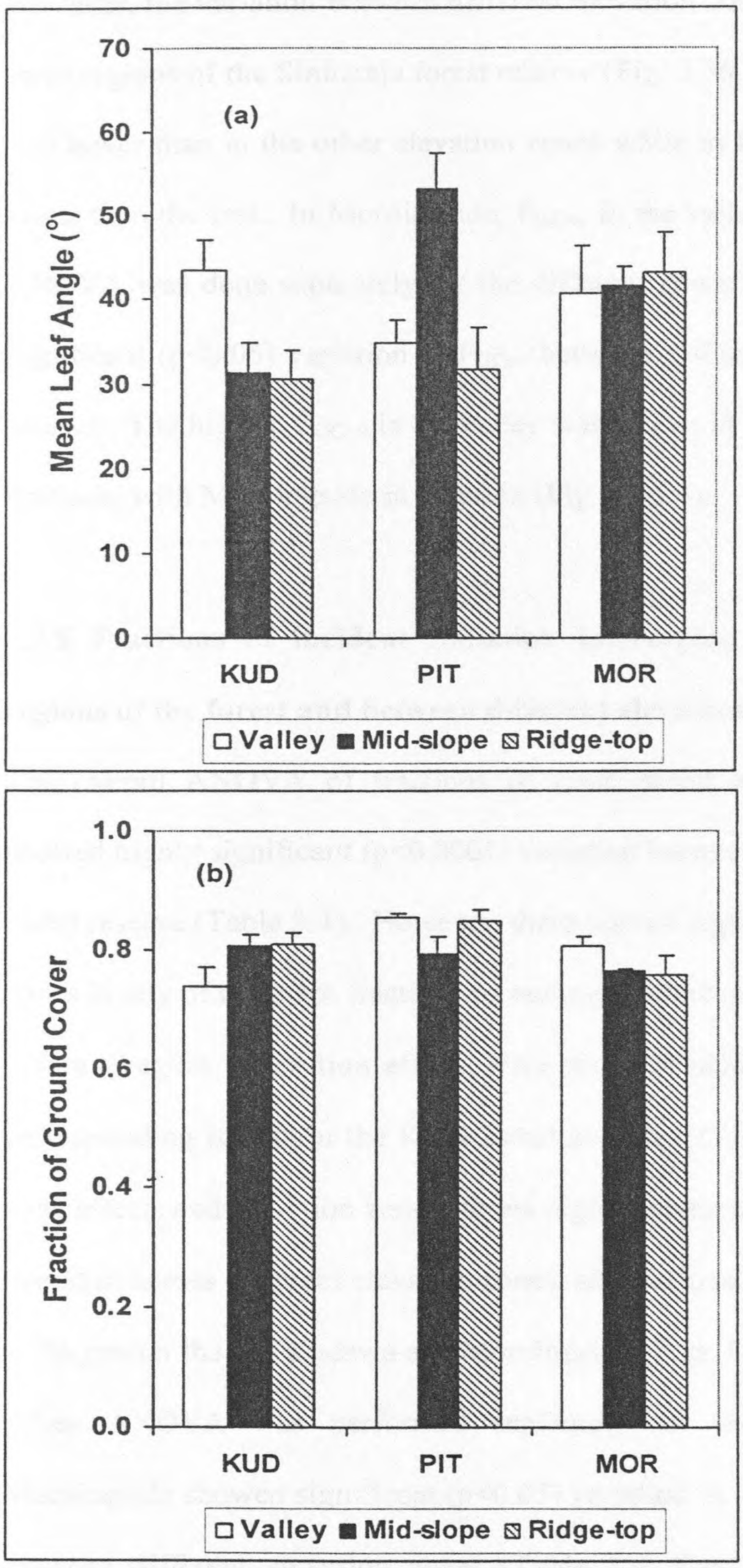


Figure 3.36: Variation of mean leaf angle (a) and fraction of ground cover (b) between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. KUD-Kudawa; PIT-Pitadeniya; MOR-Morningside.

However, the variation between different elevation zones was not consistent between the three regions of the Sinharaja forest reserve (Fig. 3.36.b). In Kudawa, F_{GCov} in the valley was lower than in the other elevation zones while in Pitadeniya, F_{GCov} in mid-slope was lower than the rest. In Morningside, F_{GCov} in the valley was higher than the rest. When ANOVA was done separately for the different elevation zones, only the valley showed significant ($p<0.05$) variation in F_{GCov} between different regions of the Sinharaja forest reserve. The highest F_{GCov} in the valley was shown in Pitadeniya while the lowest was in Kudawa, with Morningside in between (Fig. 3.36.b).

3.2.5 Fractions of incident radiation intercepted – Variation between different regions of the forest and between different elevation zones

The overall ANOVA of fractions of total, direct and diffuse radiations intercepted showed highly significant ($p<0.0001$) variation between different regions of the Sinharaja forest reserve (Table 3.4). However, there was no significant variation between elevation zones in any of the three fractions of radiation interception. Likewise, the elevation zone x forest region interaction effects were also not significant. This contrasted with the corresponding results in the KDN forest complex (Table 3.1), where both the elevation zone effects and elevation zone x forest region interaction effects were significant. When averaged across different elevation zones, all fractional interceptions in Pitadeniya were 4 – 5% greater than in Kudawa and Morningside (Figs. 3.37-3.39).

When ANOVA was performed separately for the different forest regions, only Morningside showed significant ($p<0.05$) variation in its fractional radiation interceptions between different elevation zones (Table 3.4, Figs. 3.37-3.39). Here, all fractional

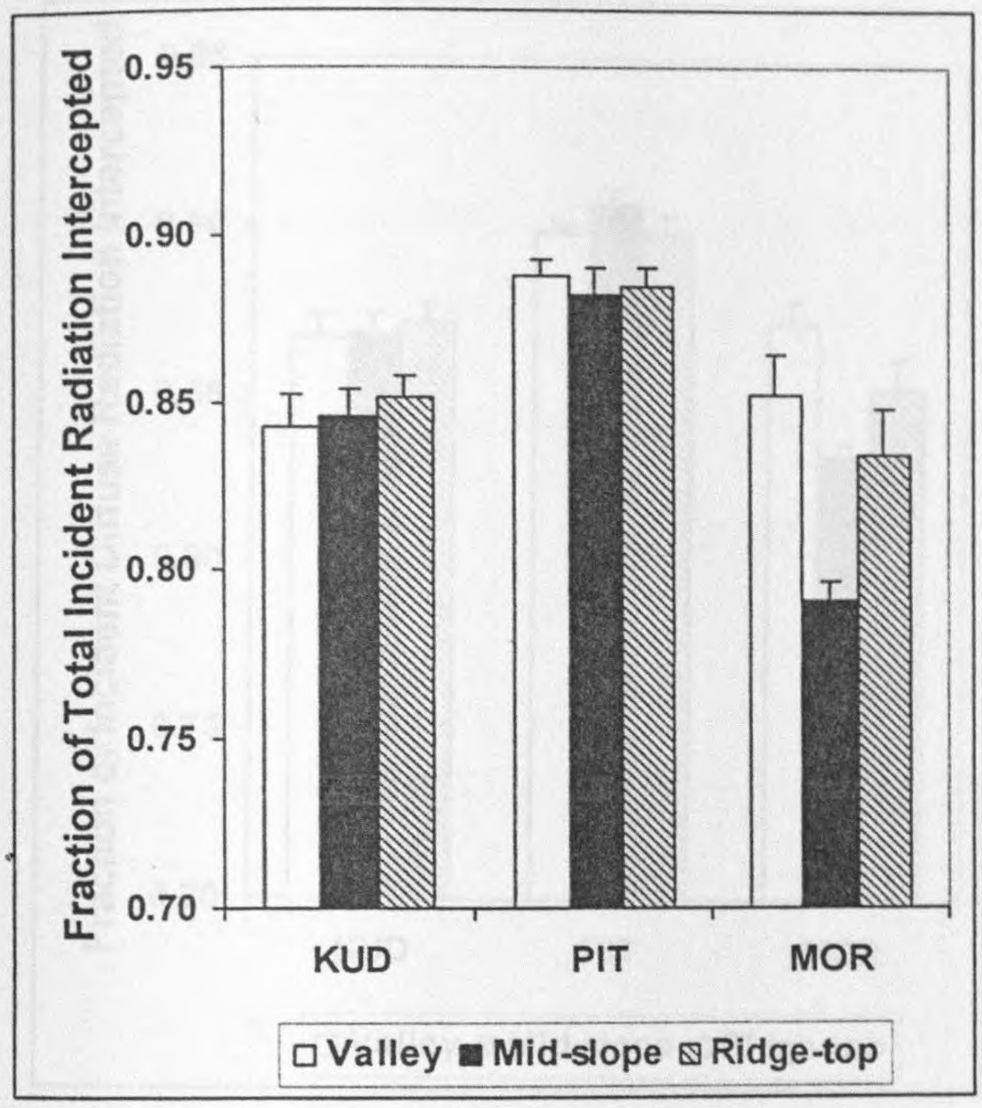


Figure 3.37: Variation of mean fraction of incident total solar radiation intercepted (F_{Tot}) between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. KUD-Kudawa; PIT-Pitadeniya; MOR-Morningside.

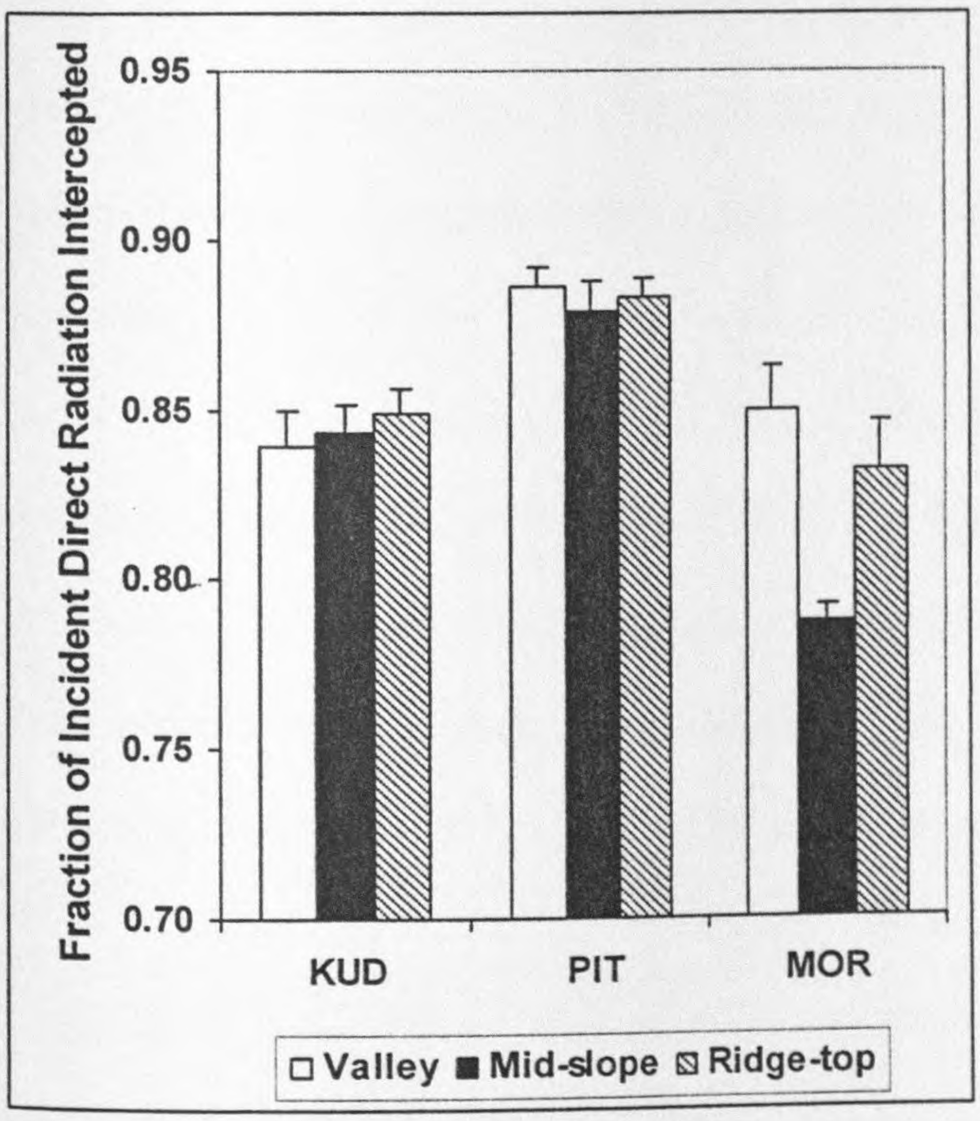


Figure 3.38: Variation of mean fraction of incident direct radiation intercepted (F_{Dir}) between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. KUD-Kudawa; PIT-Pitadeniya; MOR-Morningside.

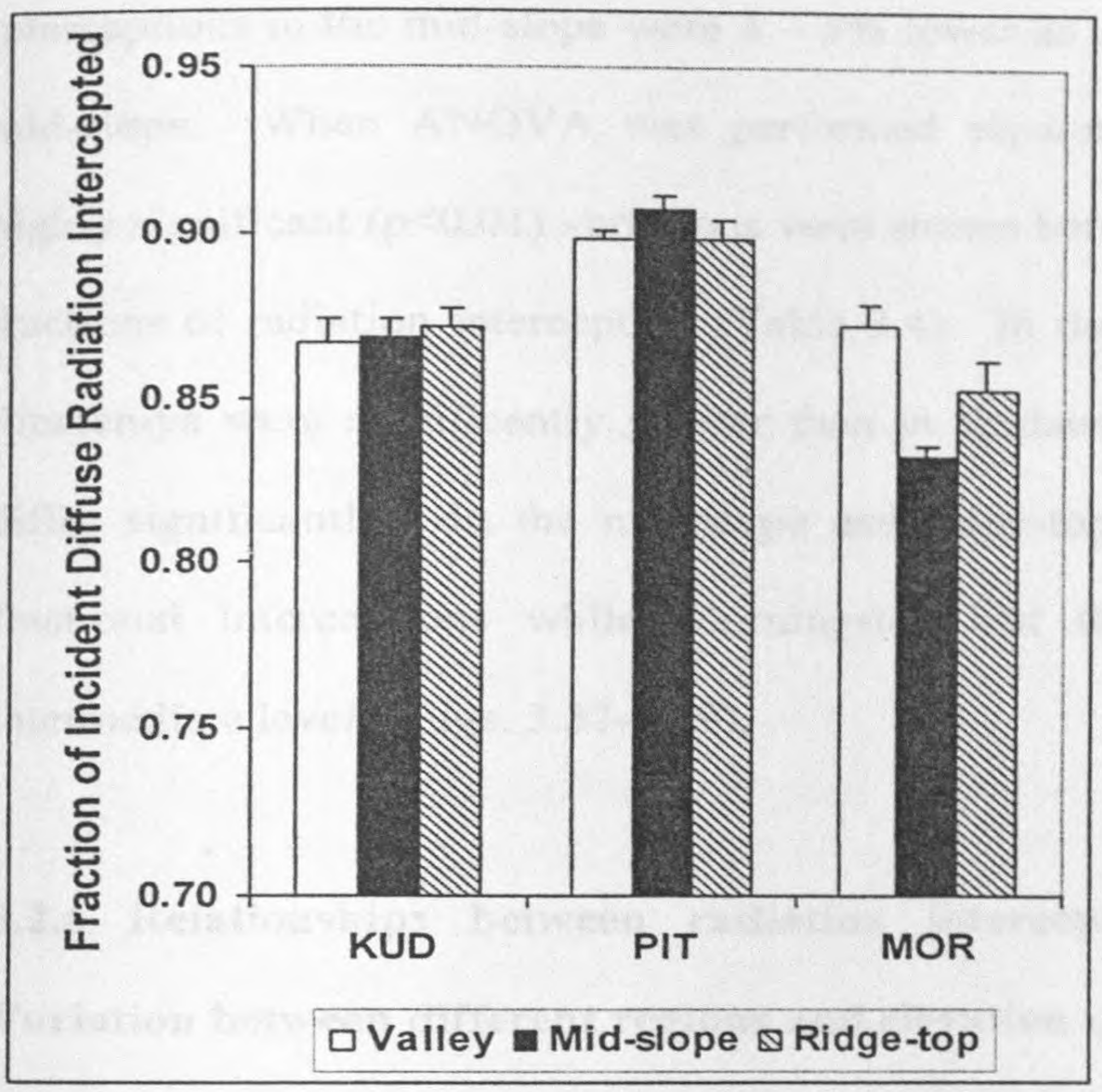


Figure 3.39: Variation of mean fraction of incident diffuse radiation intercepted (F_{Dif}) between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. KUD-Kudawa; PIT-Pitadeniya; MOR-Morningside.

interceptions in the mid-slope were 4 – 5% lower as compared to those in the valley and mid-slope. When ANOVA was performed separately for different elevation zones, highly significant ($p<0.01$) variations were shown between different forest regions for all fractions of radiation interception (Table 3.4). In the valley, fractional interceptions in Pitadeniya were significantly greater than in Kudawa and Morningside, which did not differ significantly. In the mid-slope and ridge-top also, Pitadeniya had the highest fractional interceptions while Morningside had the lowest, with Kudawa having intermediate levels (Figs. 3.37-3.39).

3.2.6 Relationships between radiation interception and canopy properties – Variation between different regions and elevation zones

There was a highly significant ($p<0.0001$) positive correlation between LAI and MLA in the overall data set as well as for different forest regions and elevation zones (Table 3.5). This was similar to what was observed in the KDN forest complex (Table 3.2). While all correlations had correlation coefficients (r) greater than 0.6, those for Pitadeniya ($r=0.878$) and Morningside ($r=0.793$) were appreciably higher than the rest, indicating greater strength in the relationship between LAI and MLA in these regions.

Fractions of interception of all three radiation components showed significant second-order polynomial (i.e. quadratic) relationships with LAI for the different regions of the Sinharaja forest reserve (Figs. 3.40 - 3.43 and 3.48) and also for different elevation zones (Figs. 3.44 - 3.47 and 3.49). As was observed for the KDN forest complex (Figs. 3.17 – 3.23), the R^2 values of the fitted quadratic relationships for the Sinharaja forest reserve were greater for F_{Dif} than for F_{Tot} and F_{Dir}, confirming the greater dependence of diffuse

Table 3.5: Linear correlation coefficients of correlations between canopy properties and fractions of radiation intercepted in the Sinharaja MAB forest reserve

Correlation	Overall data set (n=202)†	Kudawa (n=128)	Pitadeniya (n=51)	Moringside (n=23)	Valley (n=69)	Mid-slope (n=57)	Ridge-top (n=76)
LAI vs MLA	0.651 *(<0.0001)*‡	0.632 *(<0.0001)*	0.878 *(<0.0001)*	0.793 *(<0.0001)*	0.664 *(<0.0001)*	0.660 *(<0.0001)*	0.701 *(<0.0001)*
F_{Tot} vs LAI	0.261 *(0.0002)*	0.280 *(0.0014)*	ns	ns	ns	0.392 *(0.0026)*	0.267 *(0.0198)*
F_{Dir} vs LAI	0.245 *(0.0004)*	0.245 *(0.0025)*	ns	ns	ns	0.377 *(0.0039)*	0.243 *(0.0346)*
F_{Dif} vs LAI	0.432 *(<0.0001)*	0.422 *(<0.0001)*	0.304 *(0.0299)*	0.486 *(0.0188)*	0.326 *(0.0063)*	0.529 *(<0.0001)*	0.524 *(<0.0001)*
F_{Tot} vs MLA	-0.281 *(<0.0001)*	-0.296 *(0.0007)*	-0.420 *(0.0022)*	-0.413 *(0.0502)*	-0.435 *(0.0002)*	ns	-0.334 *(0.0032)*
F_{Dir} vs MLA	-0.296 *(<0.0001)*	-0.311 *(0.0004)*	-0.440 *(0.0013)*	-0.430 *(0.0405)*	-0.447 *(0.0001)*	ns	-0.351 *(0.0019)*
F_{Dif} vs MLA	ns	ns	ns	ns	-0.259 *(0.0318)*	ns	ns

†Number of data points in the correlation

‡Probability of the correlation coefficient being not significantly different from zero.

F_{Tot}, F_{Dir} and F_{Dif} – Fractions of incident total, direct and diffuse radiation intercepted

LAI – Canopy leaf area index

MLA – Mean leaf angle

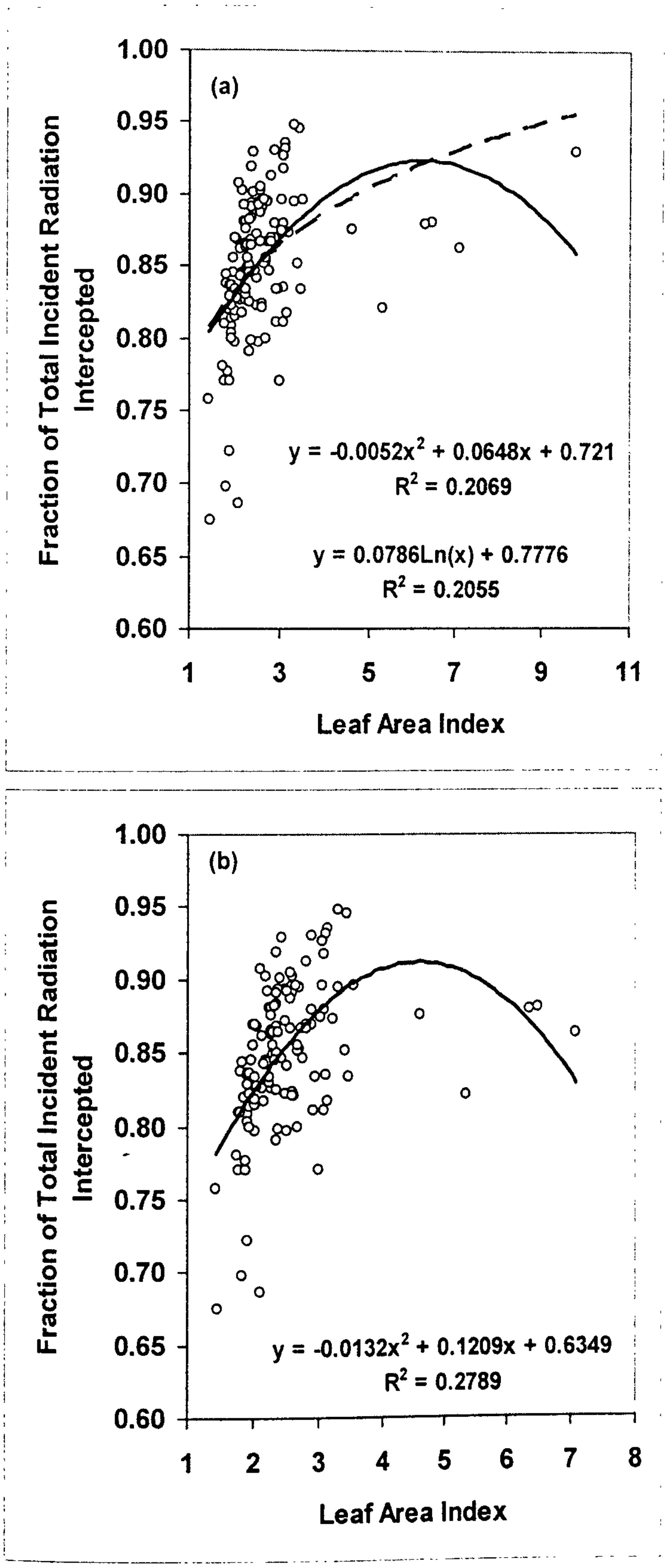


Figure 3.40: Variation of the fraction of incident total radiation intercepted with canopy leaf area index in Kudawa region of the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The data points represent 128 sampling points across 17 transects of the forest.

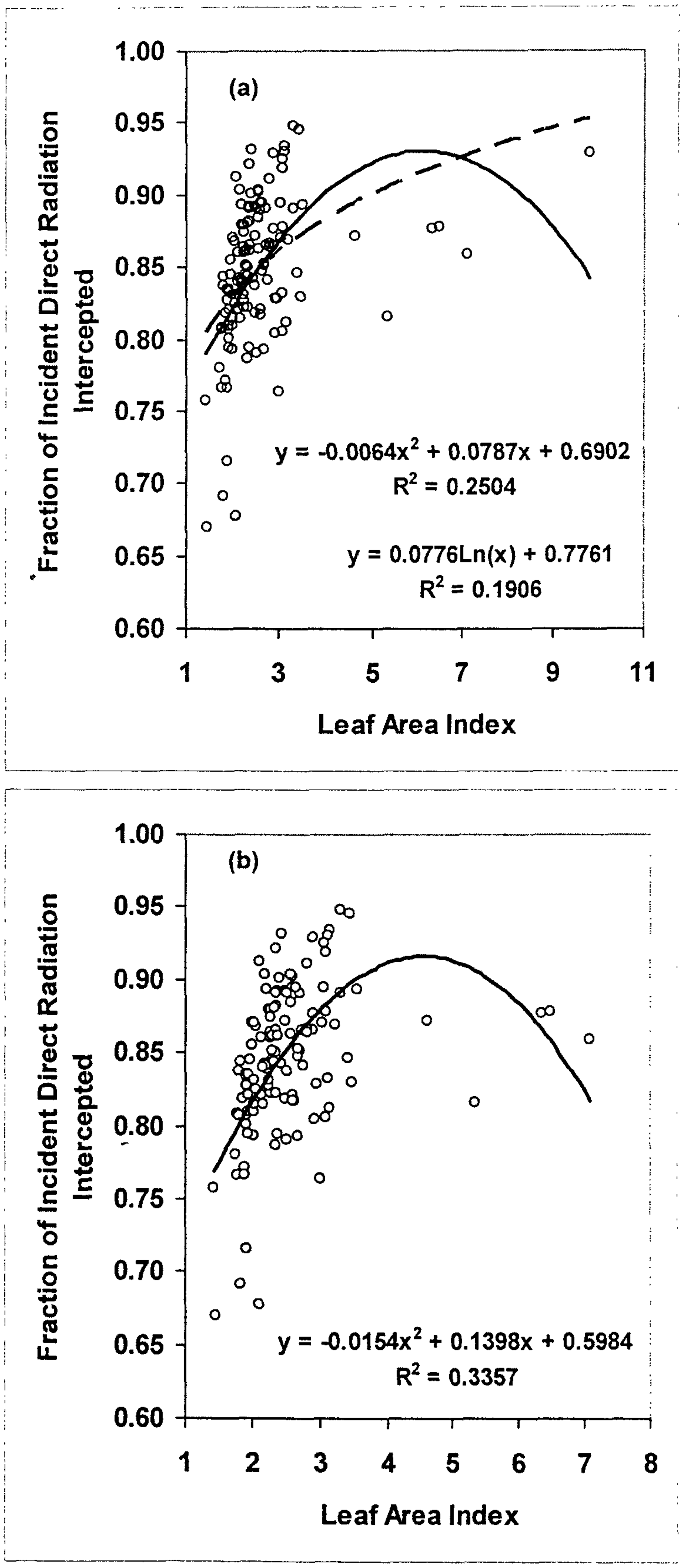


Figure 3.41: Variation of the fraction of incident direct radiation intercepted with canopy leaf area index in Kudawa region of the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The data points represent 128 sampling points across 17 transects of the forest.

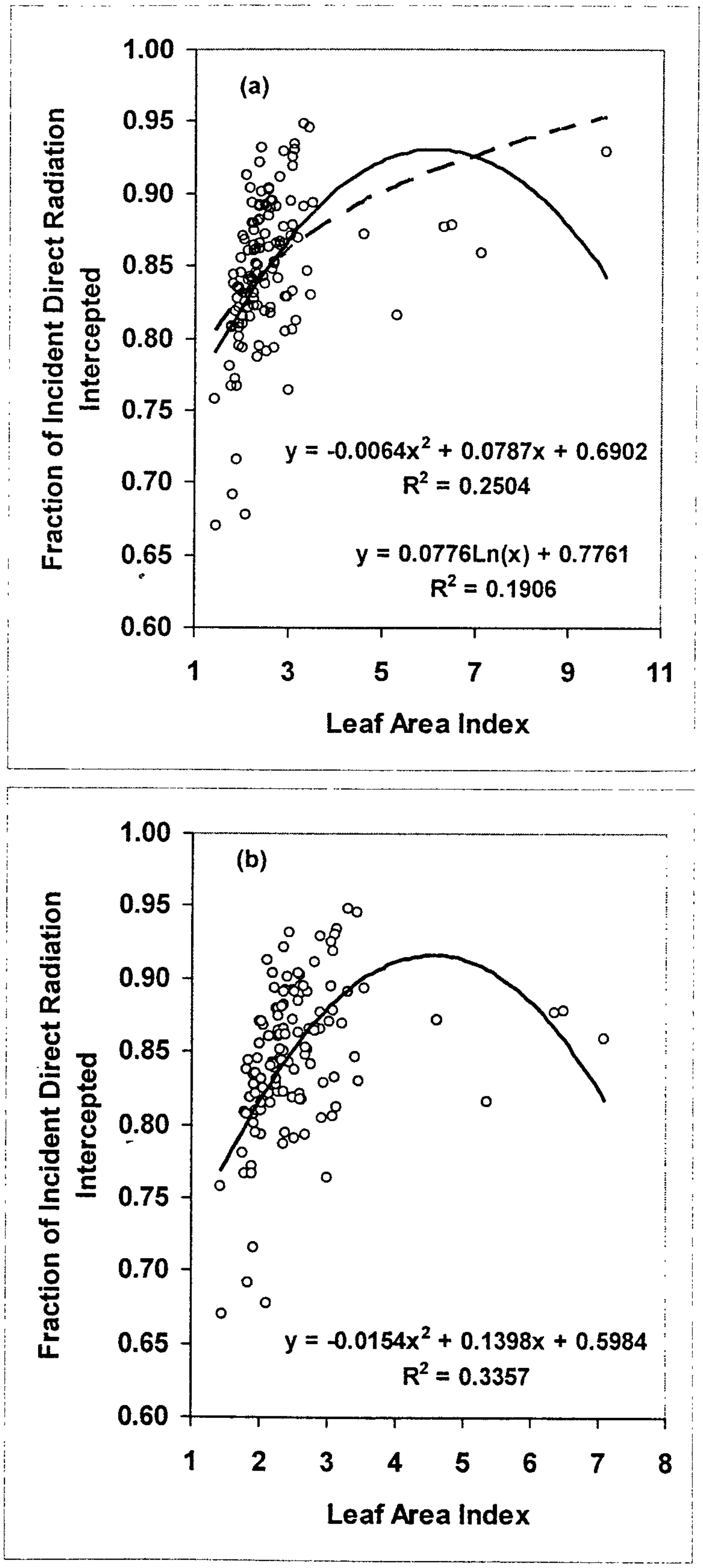


Figure 3.41: Variation of the fraction of incident direct radiation intercepted with canopy leaf area index in Kudawa region of the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The data points represent 128 sampling points across 17 transects of the forest.

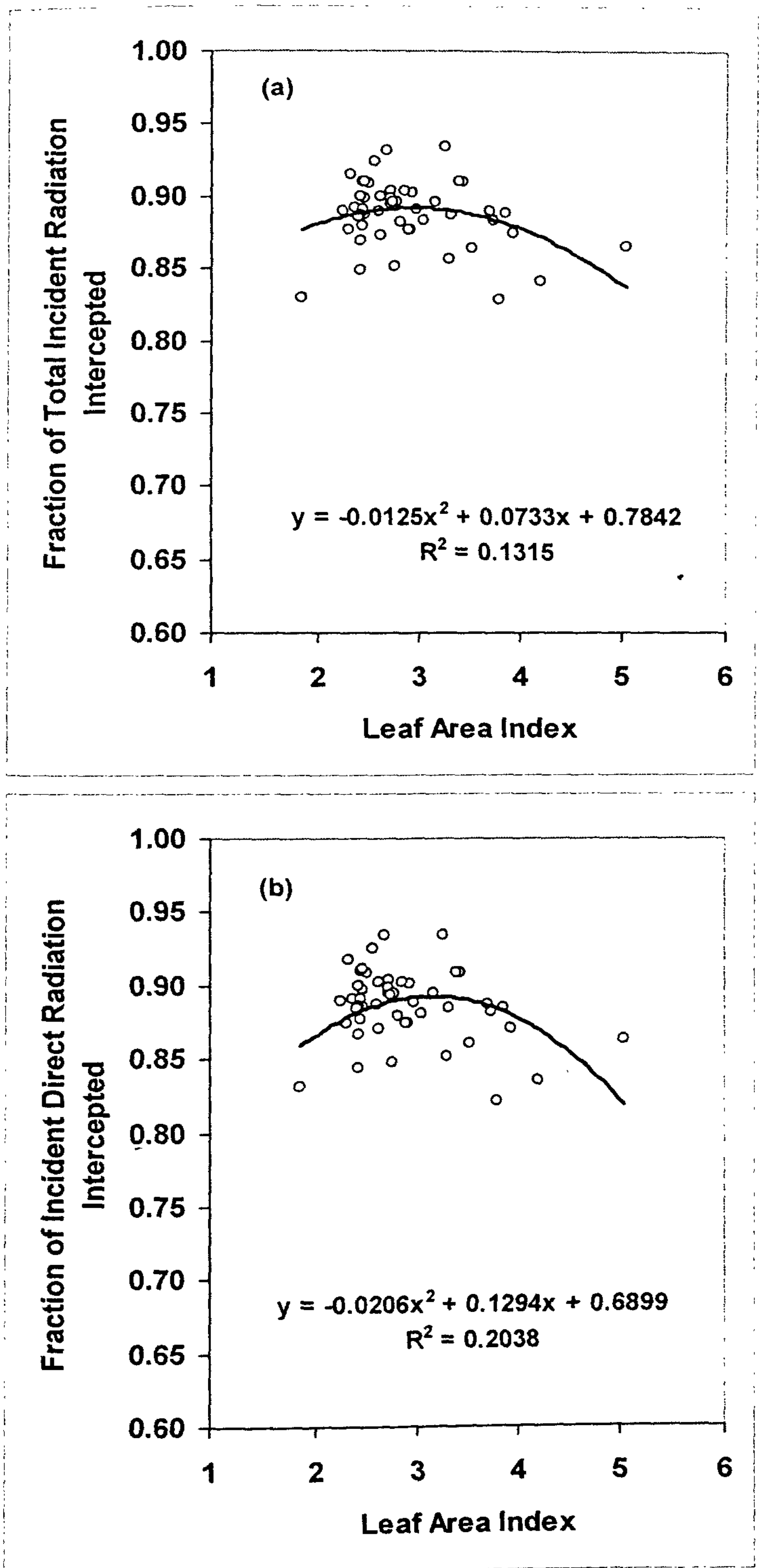


Figure 3.42: Variation of the fraction of incident total (a) and direct (b) radiation intercepted with canopy leaf area index in Pitadeniya region of the Sinharaja MAB forest reserve. The data points represent 51 sampling points across 6 transects of the forest.

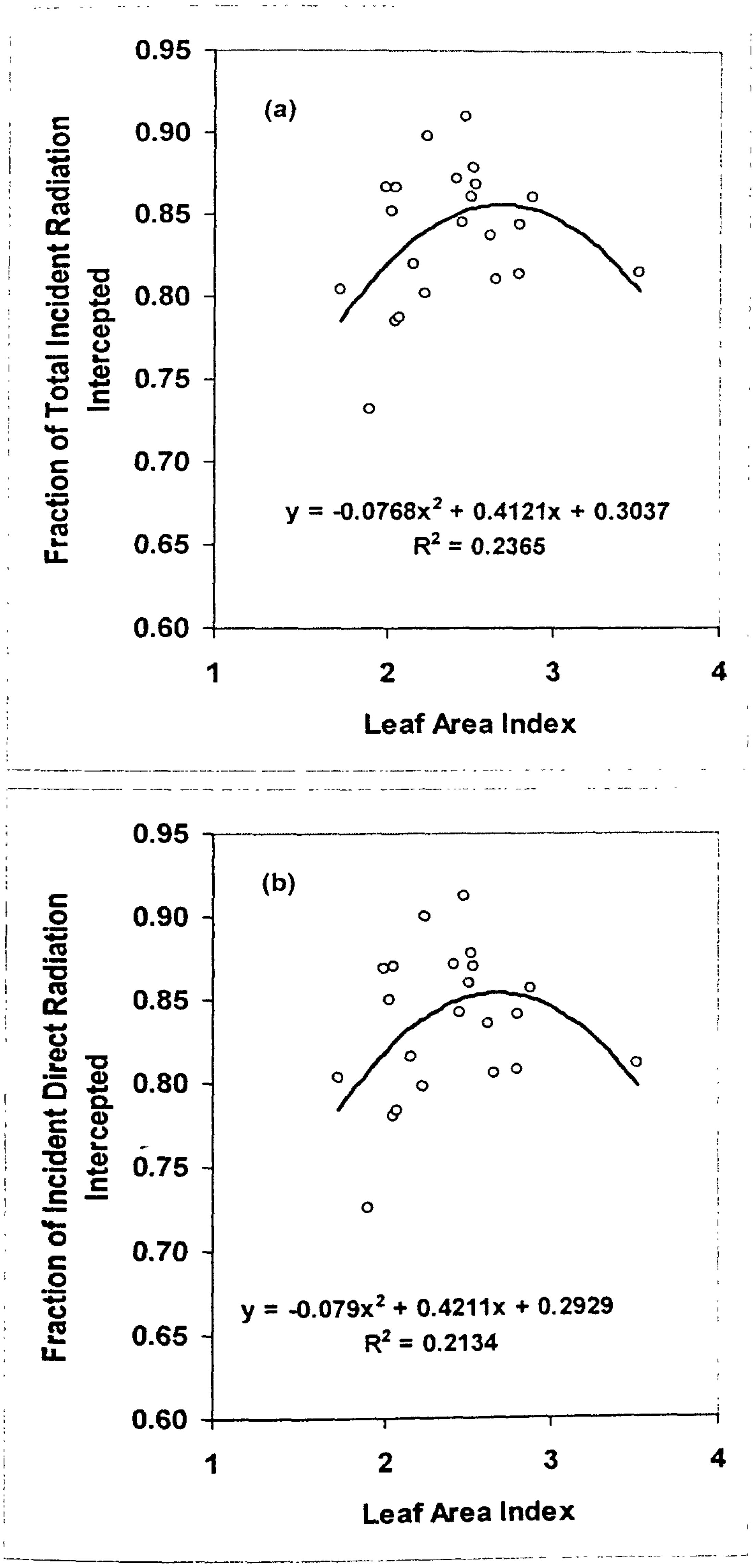


Figure 3.43: Variation of the fraction of incident total (a) and direct (b) radiation intercepted with canopy leaf area index in Morningside region of the Sinharaja MAB forest reserve. The data points represent 23 sampling points across 4 transects of the forest.

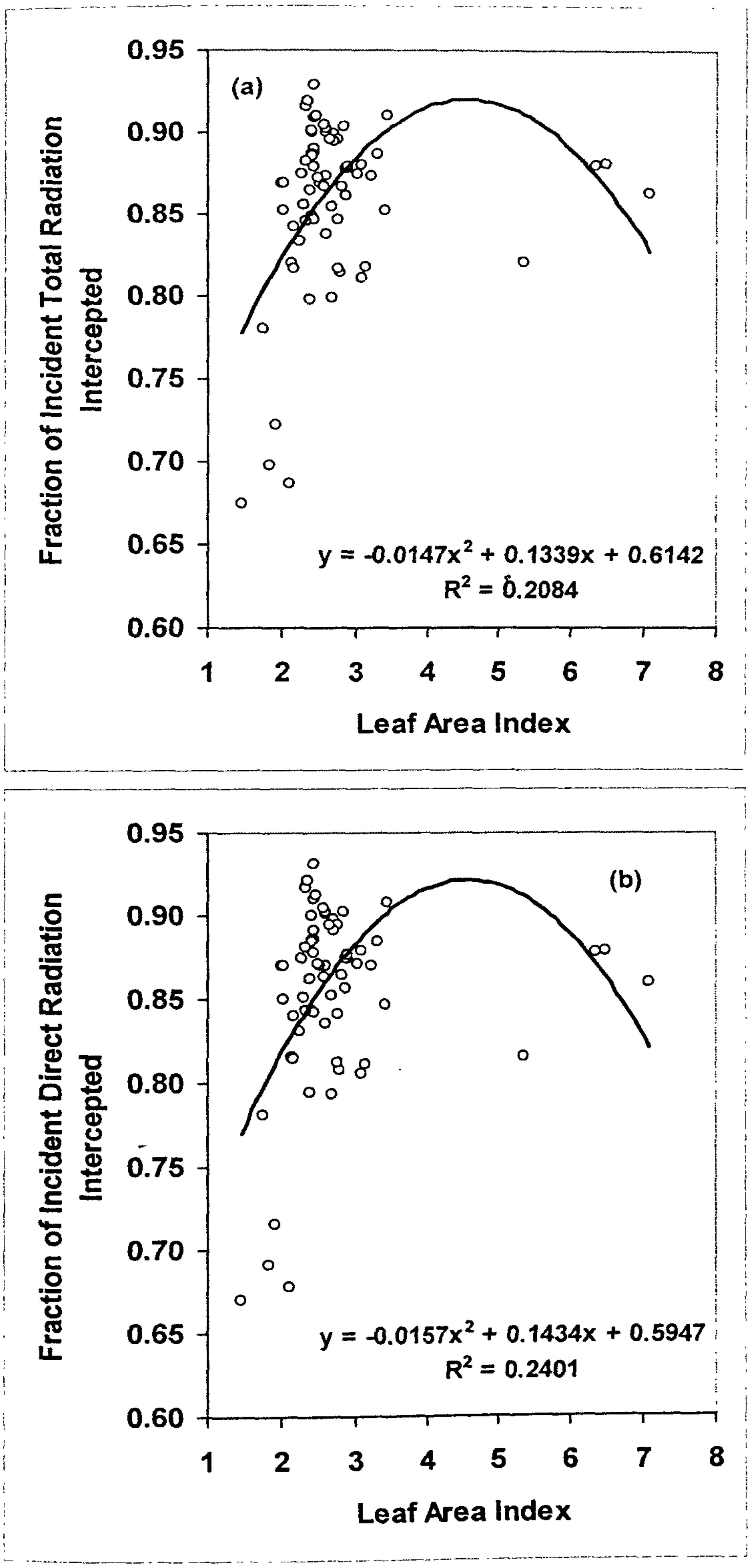


Figure 3.44: Variation of the fraction of incident total (a) and direct (b) radiation intercepted with canopy leaf area index in the valley of the Sinharaja MAB forest reserve. The data points represent 69 sampling points across 8 transects of the forest.

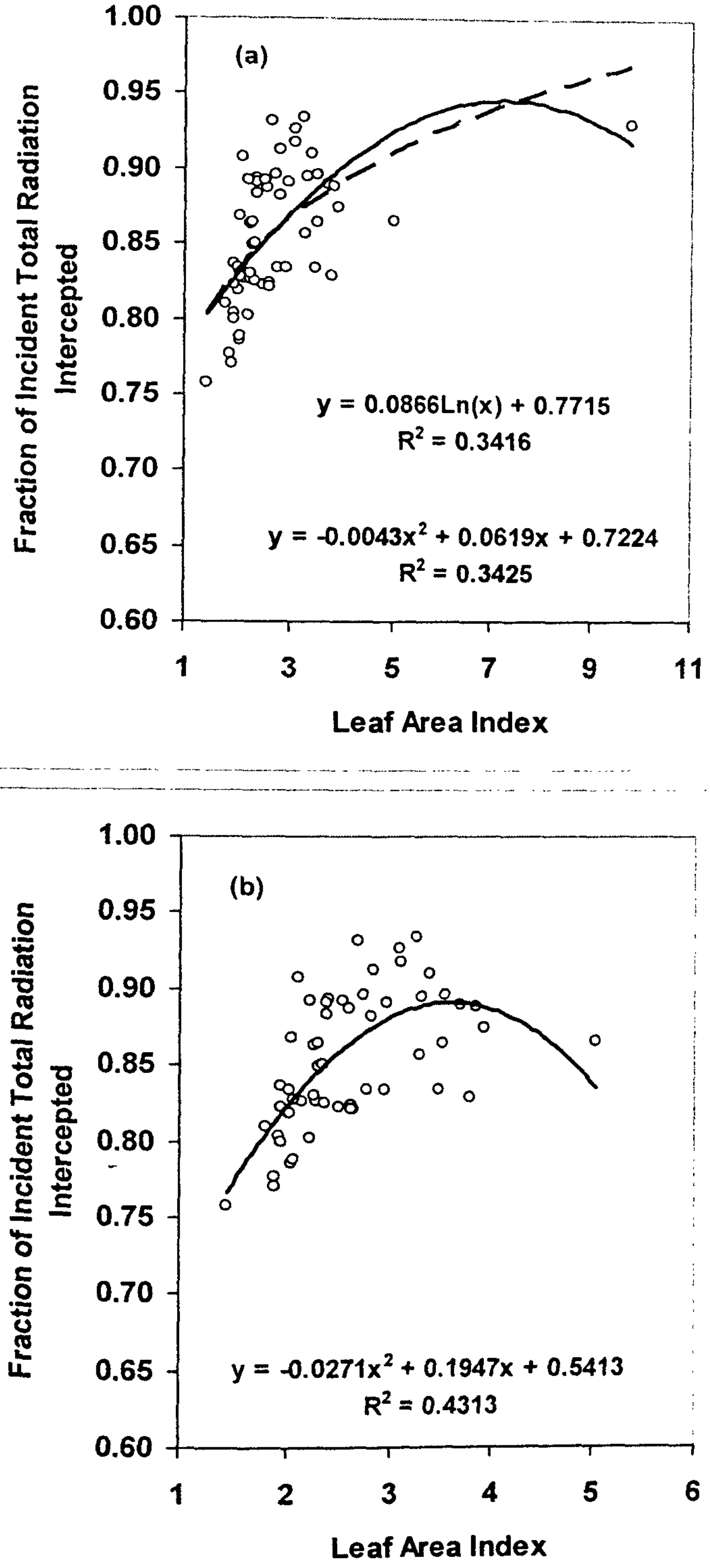


Figure 3.45: Variation of the fraction of incident total radiation intercepted with canopy leaf area index in the mid-slope of the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The full data set represents 57 sampling points across 7 transects of the forest.

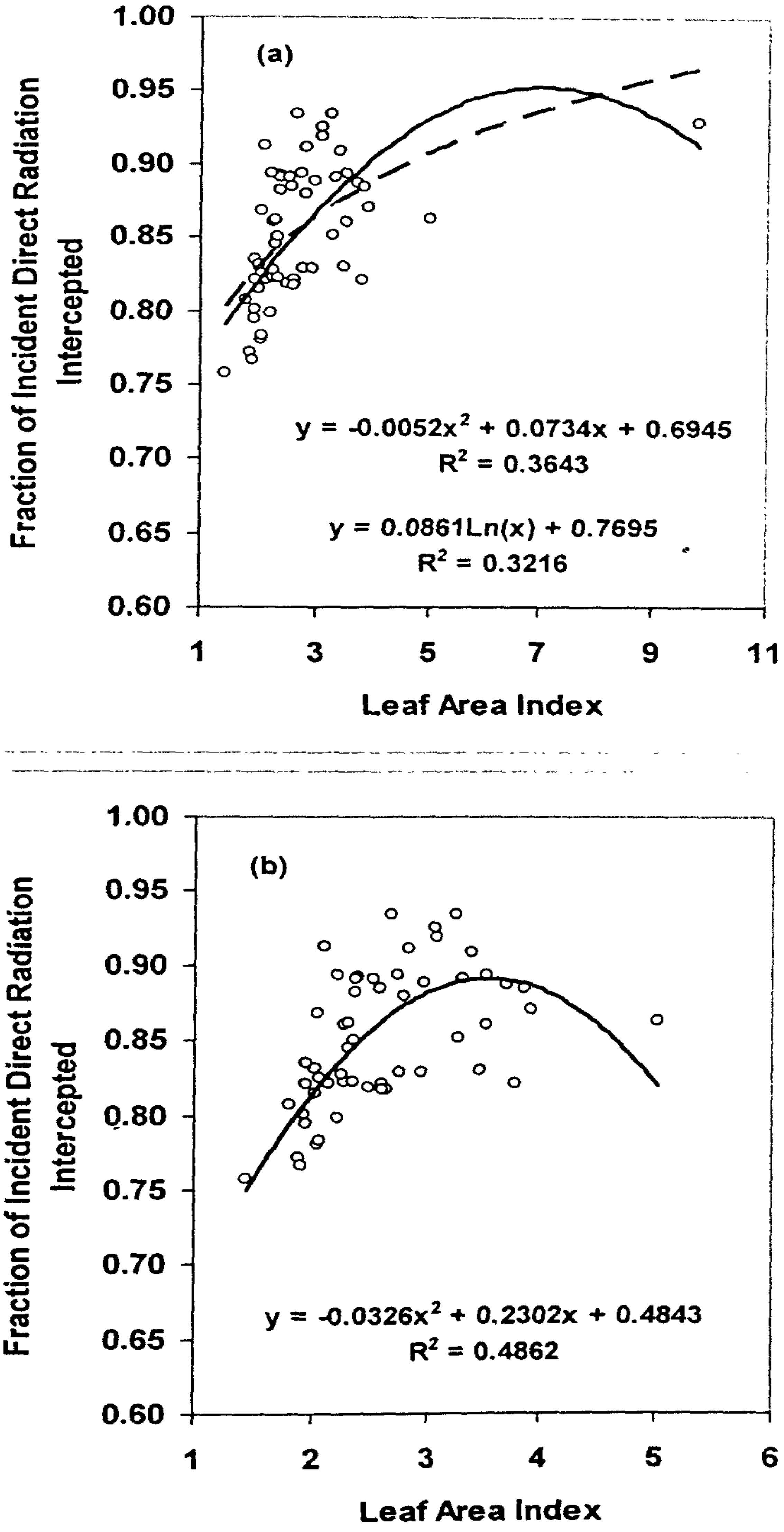


Figure 3.46: Variation of the fraction of incident direct radiation intercepted with canopy leaf area index in the mid-slope of the Sinharaja MAB forest reserve for the full data set (a) and without the outlier (b). The full data set represents 76 sampling points across 12 transects of the forest.

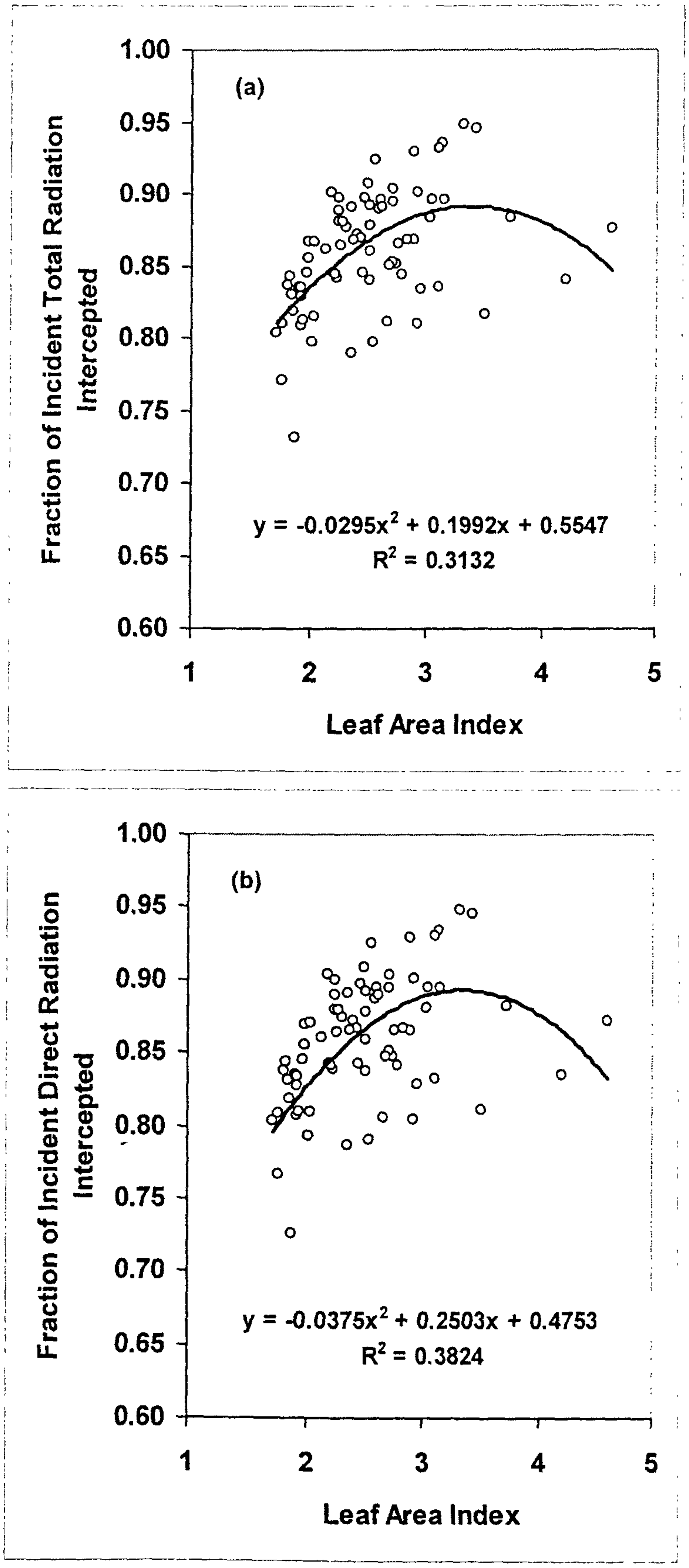


Figure 3.47: Variation of the fraction of incident total (a) and direct (b) radiation intercepted with canopy leaf area index in the ridge-top of the Sinharaja MAB forest reserve. The data points represent 76 sampling points across 12 transects of the forest.

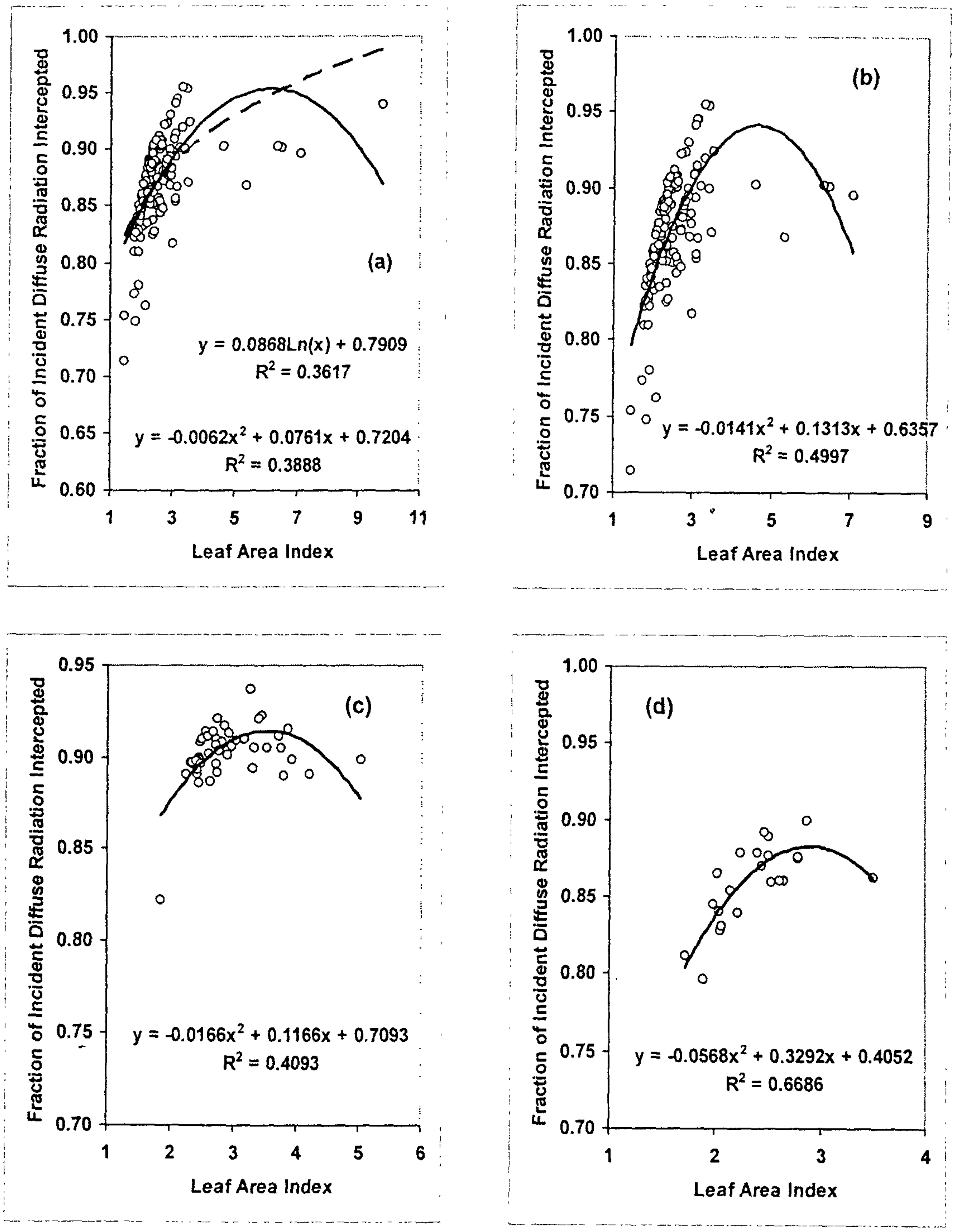


Figure 3.48: Variation of the fraction of diffuse radiation intercepted with canopy leaf area index in Kudawa with full data set (a) and without the outlier (b), Pitadeniya (c) and Morningside (d) regions of the Sinharaja MAB forest reserve. The data points represent 128 (full data set), 51 and 23 sampling points across 17, 6 and 4 transects respectively in Kudawa, Pitadeniya and Morningside.

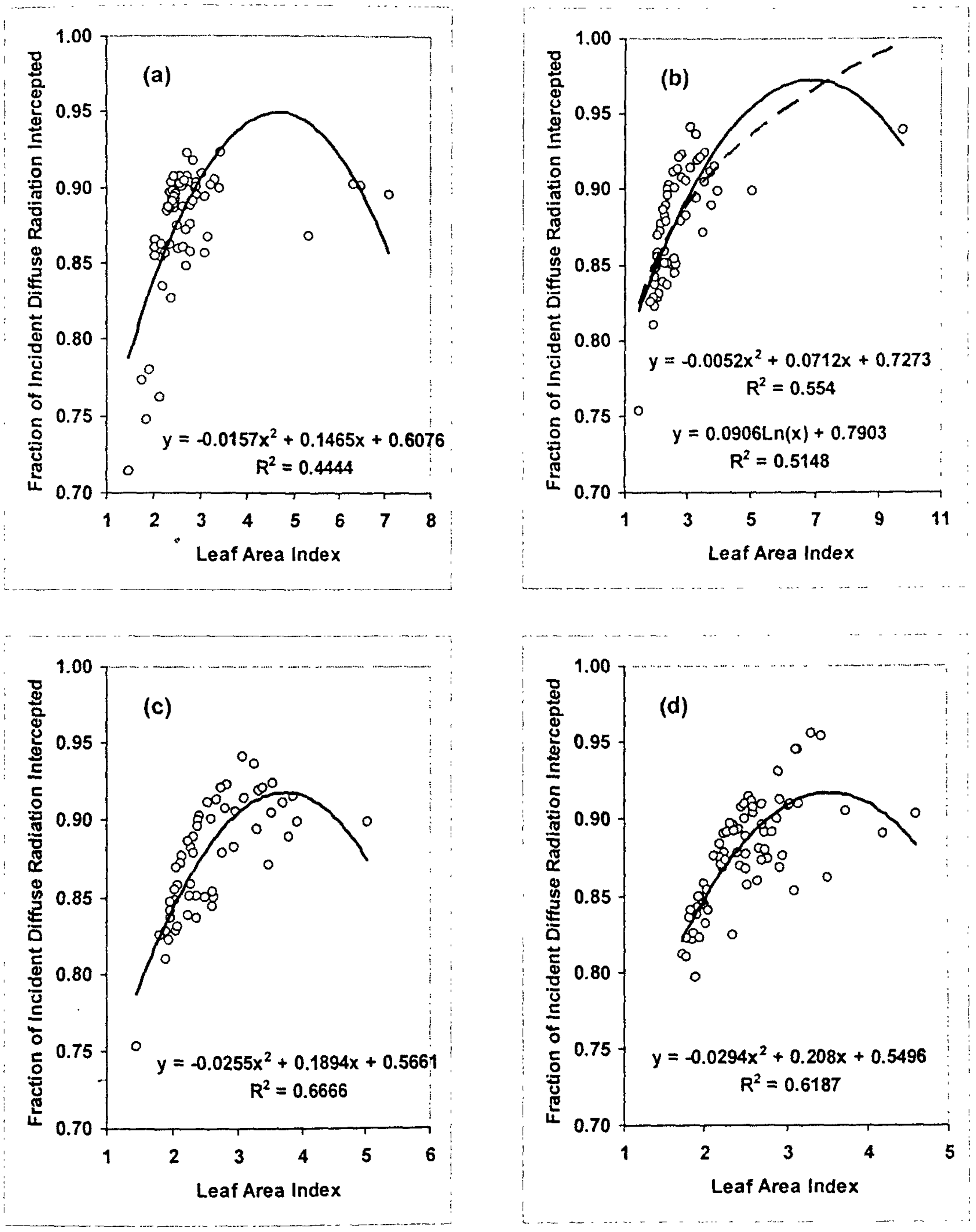


Figure 3.49: Variation of the fraction of diffuse radiation intercepted with canopy leaf area index in the valley (a), mid-slope with full data set (b) and without the outlier (c) and ridge-top (d) regions of the Sinharaja MAB forest reserve. The data points represent 69, 57 (full data set) and 76 sampling points across 8, 7 and 12 transects respectively in the valley, mid-slope and ridge-top.

radiation on a higher canopy surface area for its maximum interception. The estimated optimum LAIs for maximum fractional interceptions were substantially greater in Kudawa than in Pitadeniya and Morningside (Table 3.6). This was true irrespective of whether the outlying LAI value in Kudawa was considered or not. When the optimum LAIs in Pitadeniya and Morningside were compared Pitadeniya had higher values for all three fractional interceptions. The optimum LAIs for maximum F_{Tot} and F_{Dir} in Kanneliya (Fig. 3.17) (i.e. 3.39 and 3.36 respectively) were lower than the corresponding values in Kudawa, but were greater than those in Pitadeniya and Morningside. The optimum LAI for maximum F_{Dif} in Kanneliya (Fig. 3.22.a) (i.e. 3.52) was lower than that in Kudawa but was similar to that in Pitadeniya and higher than that in Morningside. On the other hand, the optimum LAI for maximum F_{Dif} in Dediyagala (Fig. 3.22.b) (i.e. 4.43) was higher than those in Pitadeniya and Morningside but still lower than that in Kudawa. When the optimum LAIs in the different elevation zones were compared the comparative variation differed whether the outlying LAI value in the mid-slope was considered or not. If the outlier was considered, the mid-slope had, by far, the highest optimum LAIs for all three fractional interceptions than in the valley and the ridge-top (Table 3.6). However, when the outlier was disregarded, the valley had the highest optimum LAIs for all three fractional interceptions (Table 3.6). The optimum LAIs were lowest in the ridge-top. This contrasted with observations in the KDN forest complex, where the highest optimum LAIs were observed in the ridge-top. When the optimum LAIs for the corresponding elevation zones in the two forests were compared Sinharaja MAB forest reserve had higher optimum LAIs in the valley and in mid-slope while the KDN forest complex had higher optimum LAIs in the ridge-top.

Table 3.6: Estimated optimum canopy leaf area indices for maximum fractional interception of incident total (F_{Tot}), direct (F_{Dir}) and diffuse (F_{Dif}) radiation for different regions and elevation classes in the Sinharaja MAB forest reserve

	Kudawa		Pitadeniya	Moring-side	Valley	Mid-slope		Ridge-top
	Full data set	Without Outlier				Full data set	Without Outlier	
F_{Tot}	6.23	4.58	2.93	2.68	4.55	7.20	3.59	3.38
F_{Dir}	6.15	4.54	3.14	2.67	4.57	7.06	3.53	3.34
F_{Dif}	6.14	4.66	3.51	2.90	4.67	6.85	3.71	3.54

Similar to the observations in the KDN forest complex, negative correlations were shown between MLA and the fractional interceptions of total (F_{Tot}) and direct (F_{Dir}) radiations in all regions and elevation zones except the mid-slope of the Sinharaja forest reserve (Table 3.5). Among the different forest regions of Sinharaja, strengths of the respective correlations in Kudawa were lower than those in Pitadeniya and Morningside. Among the different elevation zones, strengths of correlations in the valley were greater than those in the ridge-top. Although the overall correlations between MLA, F_{Tot} and F_{Dir} in Sinharaja were less strong than in KDN (Tables 3.2 and 3.5), there was no consistent variation between the two forests at the forest region or elevation zone level. With the exception of the valley in Sinharaja, there were no significant correlations between MLA and the fractional interception of diffuse radiation (F_{Dif}).

3.3 Incident radiation at different locations

Incident solar radiation and PAR levels (Table 3.7) of the four locations around the Sinharaja and KDN forest complexes did not show significant ($p<0.05$) variation between different locations. Therefore, it was possible to average across incident solar radiation values of Ratnapura, Deniyaya and Agalawatta were averaged to obtain the mean value for Sinharaja. Similarly, mean incident solar radiation for KDN was obtained by averaging across Deniyaya and Kottawa. The mean daily solar radiation incident on the KDN forest complex was slightly greater than that on the Sinharaja MAB reserve. These values were within the range of values reported by Samuel (1991) for Ratnapura and Agalawatta.

Table 3.7: Incident solar radiation levels of selected locations around the Sinharaja MAB reserve and the KDN forest complex

Location	No. of years	Daily total solar radiation ± Std. error ($MJ\ m^{-2}\ d^{-1}$)	Daily total PAR ± Std. error ($mol\ [PAR]\ m^{-2}\ d^{-1}$)	Mean instantaneous photon flux density ± Std. error ($\mu mol\ [PAR]\ m^{-2}\ s^{-1}$)
Agalawatta	31	15.719[*] ± 0.136	36.153 ± 0.312	828.382 ± 7.149
Deniyaya	9	16.410 ± 0.135	37.743 ± 0.310	864.835 ± 7.104
Kottawa	2	17.164 ± 0.379	39.478 ± 0.873	904.598 ± 19.997
Ratnapura	31	15.805 ± 0.171	36.352 ± 0.393	832.920 ± 8.997
Sinharaja[†]	71	15.844 ± 0.099	36.442 ± 0.228	834.984 ± 5.230
KDN[‡]	11	16.547 ± 0.152	38.059 ± 0.349	872.065 ± 7.989

[*] Mean values were obtained by averaging the daily incident solar radiation values of 365 days of the number of years indicated in column 2.

[†] Means of Ratnapura, Deniyaya and Agalawatta

[‡] Means of Deniyaya and Kottawa

3.4 Light response curves

Fitted light response curves of the selected species are shown in Fig. 3.50. Parameters of the light response curves fitted for individual species are given in Tables 3.8 and 3.9. Out of the curves fitted to the 14 species, 12 curves had R^2 values greater 0.80 (Table 3.8) thus indicating that the asymptotic exponential function was an appropriate model to be used for light response curves. Estimated values of all five parameters of the light response curves showed significant variation between different plant species. The highest and lowest maximum light-saturated net photosynthetic rates (P_{max}) were observed in the canopy tree *Shorea stipularis* and the understorey plant *Schumacheria castaneifolia* respectively. There was a more than four-fold different between the highest and lowest P_{max} values. On the other hand, the canopy tree *Shorea congestiflora* had the lowest quantum efficiency (ϕ) while the highest was found in the sub-canopy plant *Calophyllum calaba*, which was more than three-fold of the lowest ϕ. The highest and lowest leaf dark respiration (R_d) values were shown by the sub-canopy plant *Calophyllum calaba* and the canopy tree *Vateria copallifera*. The difference between the highest and lowest R_d values was more than seven-fold. Apart from *Vateria copallifera*, the understorey plant *Agrostistachys coriacea* and the sub-canopy plant *Mesua ferrea* also showed lower R_d values. The ratio between R_d and P_{max} was lowest in *Vateria copallifera* (a canopy species) and highest in *Schumacheria castaneifolia* (an understorey species). The canopy species *Dipterocarpus zeylanicus* showed the highest values for both light saturation point (LSP) and light compensation point (LCP). Three species showed the lowest range of values for LSP and LCP. These were *Vateria copallifera* (a

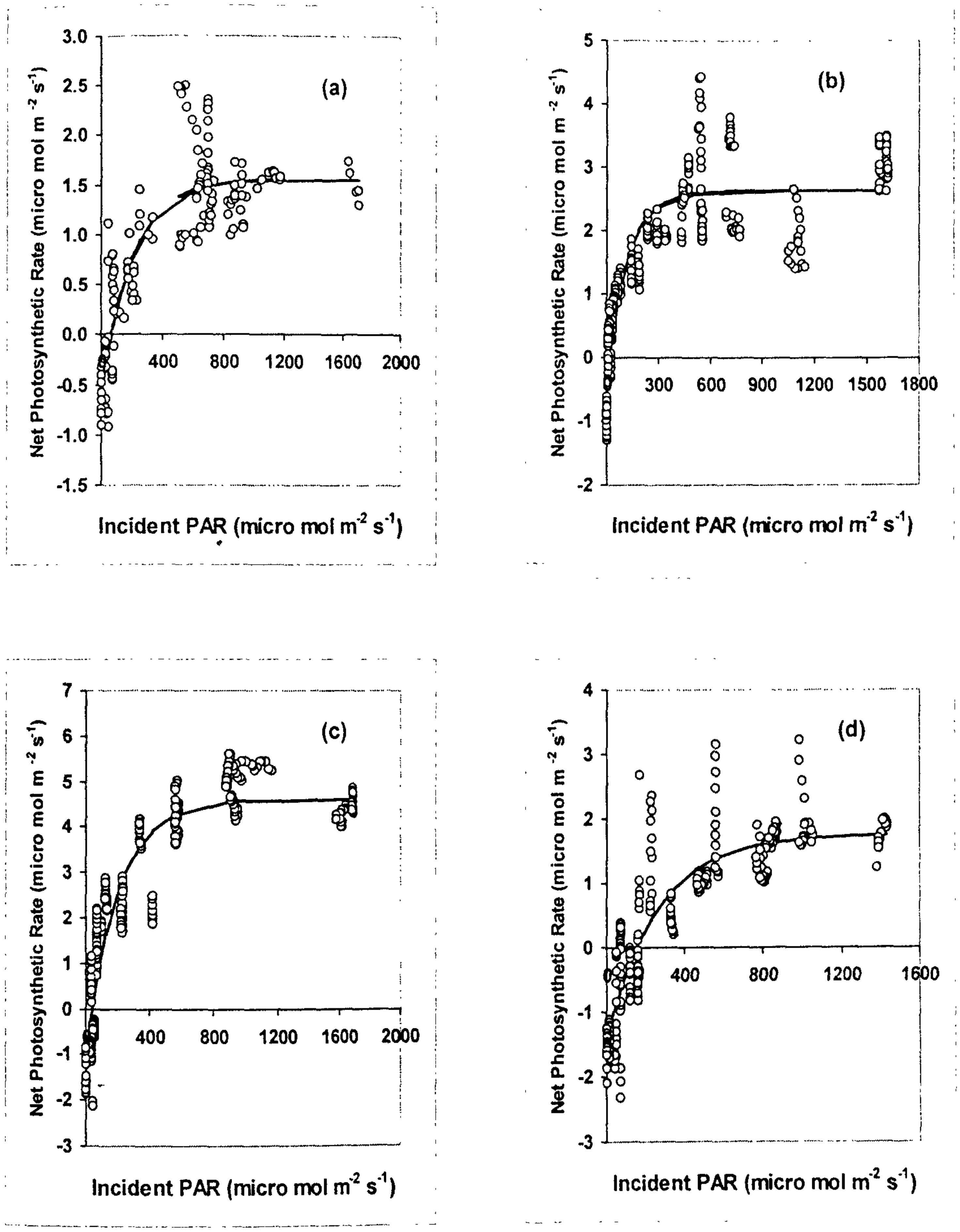


Figure 3.50: Light response curves of *Shorea congestiflora* (a), *Vateria copallifera* (b), *Shorea stipularis* (c) and *Dipterocarpus zeylanicus* (d).

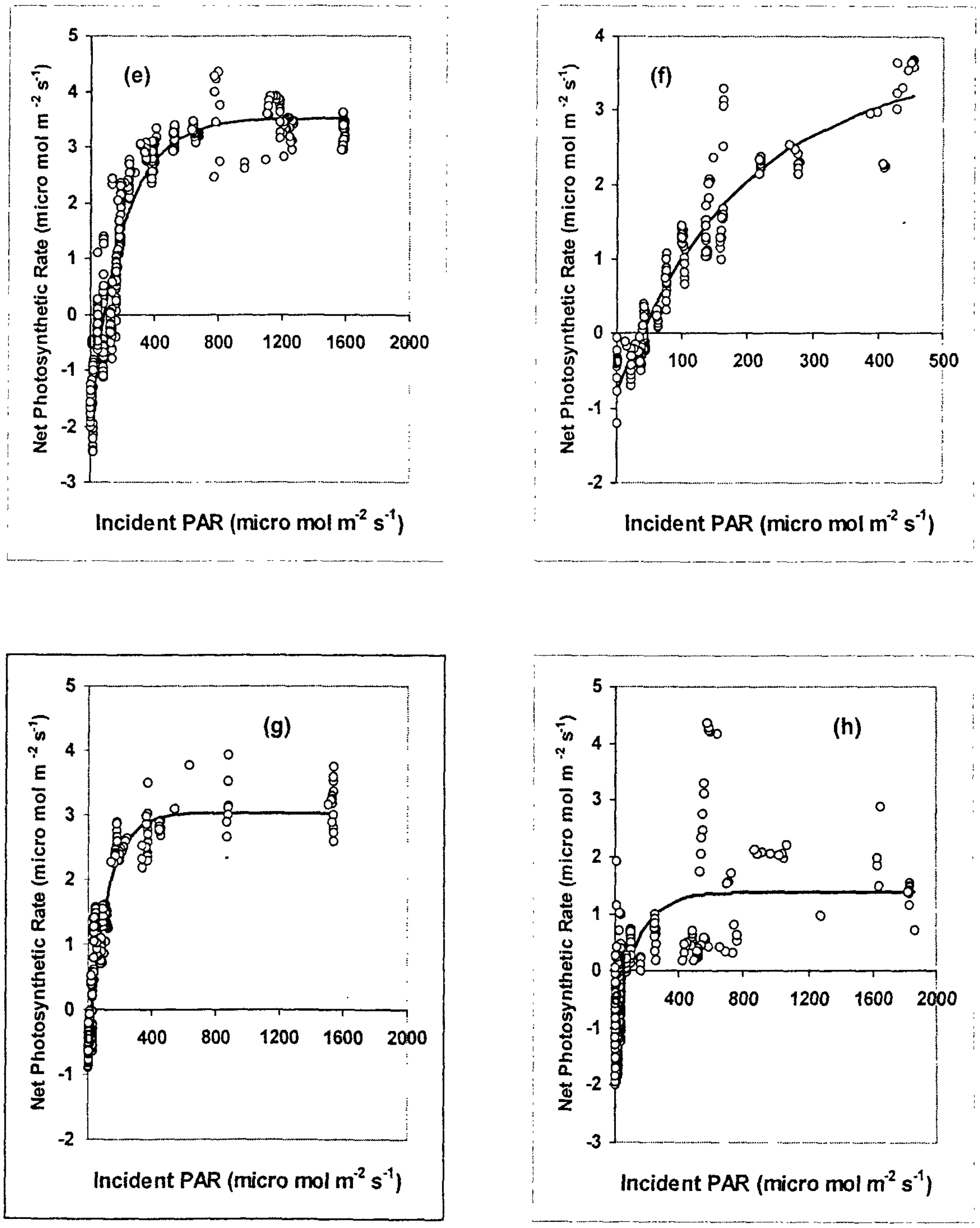


Figure 3.50 *(continued)*: Light response curves of *Shorea disticha* (e), *Calophyllum bracteatum* (f), *Mesua ferrea* (g) and *Dillenia triquetra* (h).

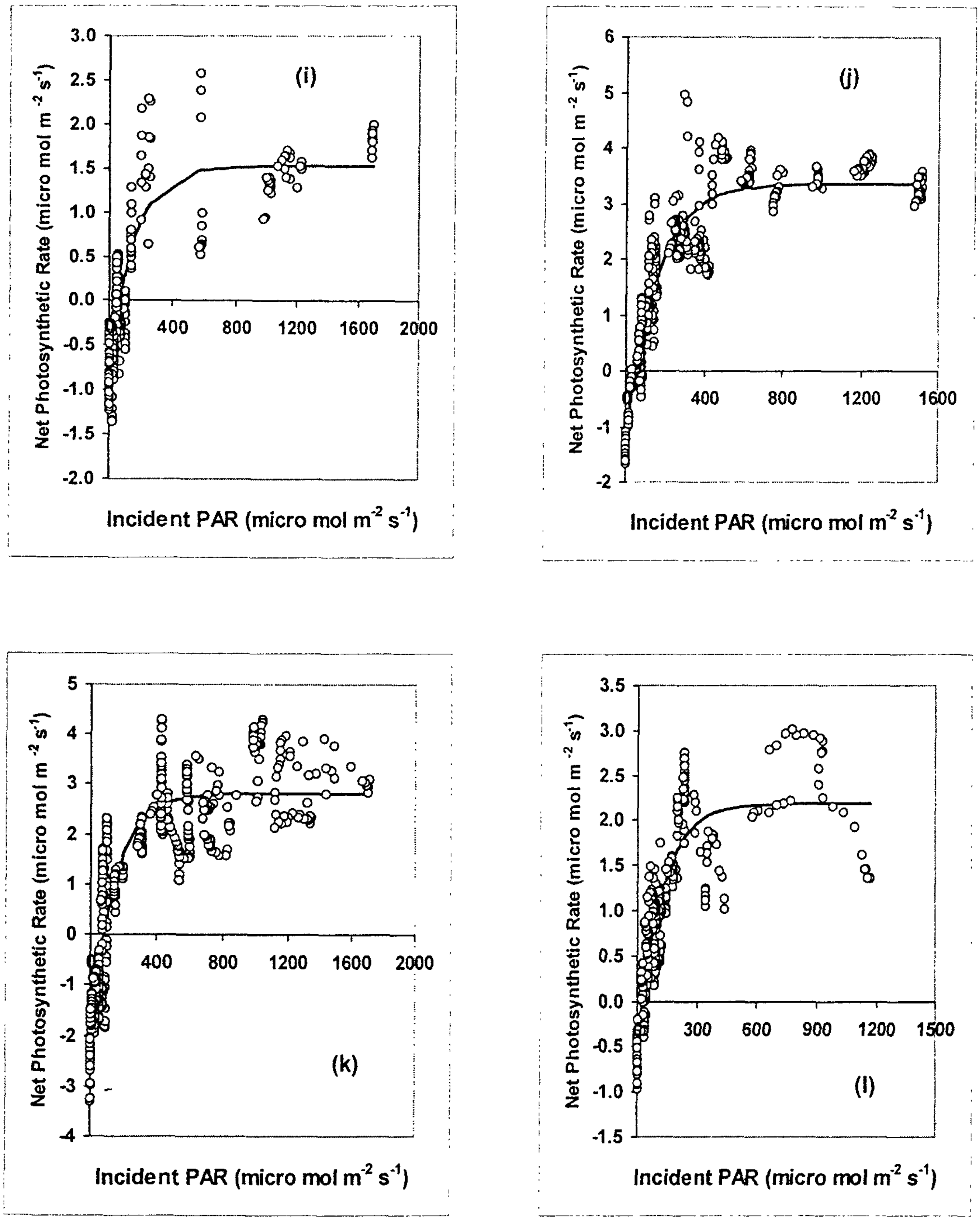


Figure 3.50 ***(continued)***: Light response curves of *Stemonoporus kanneliyensis* (i), *Garcinia quaesita* (j), *Calophyllum calaba* (k) and *Agrostistachys coriacea* (l).

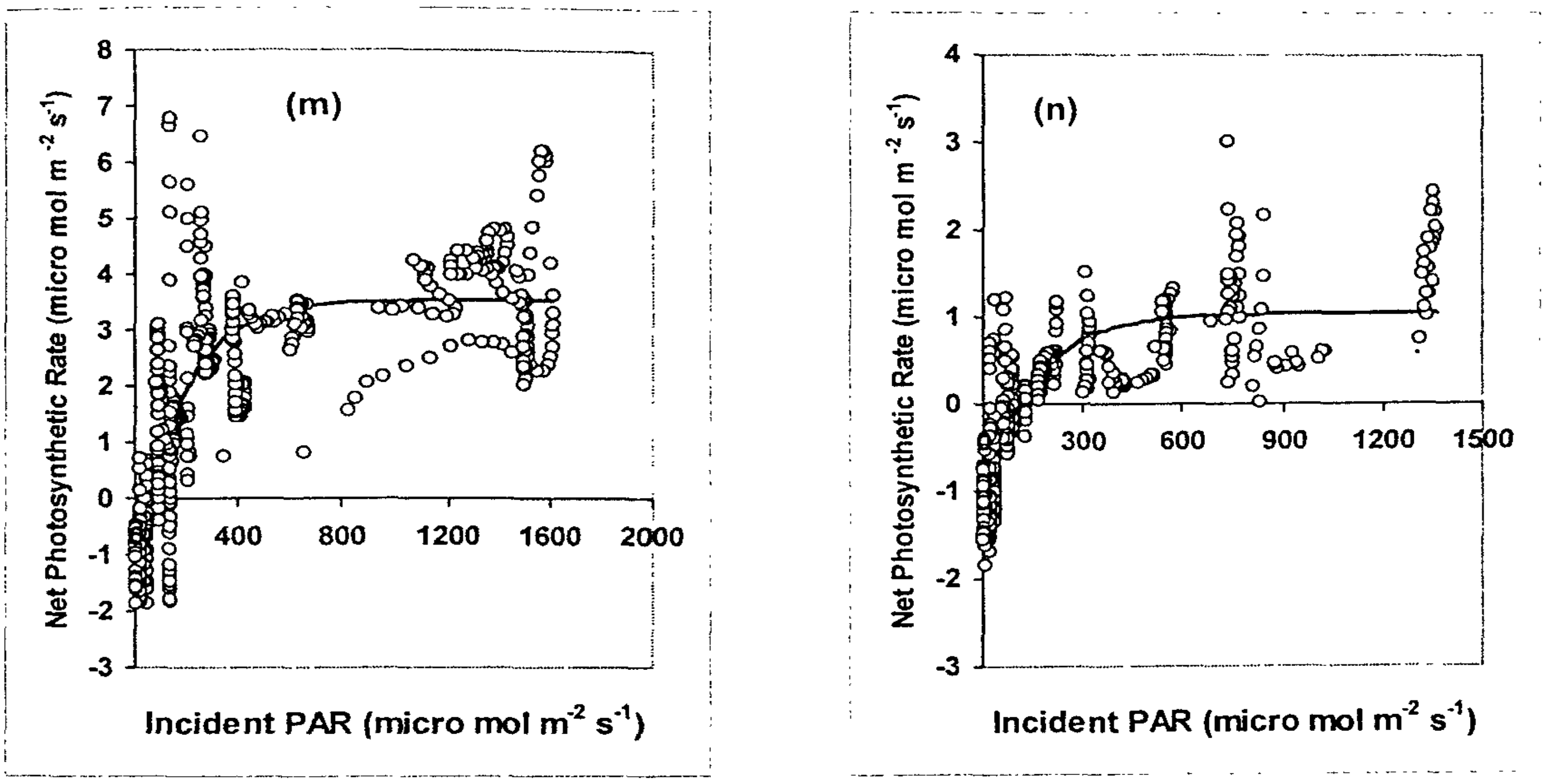


Figure 3.50 ***(continued)***: Light response curves of *Aporusa cardiosperma* (m) and *Schumacheria castaneifolia* (n).

Table 3.8: Estimated parameters of the light response curves of different plant species from different canopy strata of lowland wet evergreen forests of Sri Lanka

Species	Strat.	P_{max}	Std. Err.	ϕ	Std. Err.	R_d	Std. Err.	R^2
Shorea congestiflora	C	1.561	0.061	0.0106	0.0016	0.600	0.101	0.89
Vateria copallifera	C	2.639	0.051	0.0239	0.0024	0.292	0.072	0.92
Shorea stipularis	C	4.596	0.070	0.0287	0.0016	1.068	0.090	0.95
Dipterocarpus zeylanicus	C	1.756	0.077	0.0122	0.0010	1.437	0.076	0.81
Shorea disticha	C	3.514	0.056	0.0254	0.0010	1.747	0.067	0.95
Calophyllum bracteatum	SC	3.621	0.189	0.0225	0.0015	0.764	0.068	0.94
Mesua ferrea	SC	3.032	0.055	0.0316	0.0015	0.598	0.042	0.95
Dillenia triquetra	SC	1.373	0.091	0.0172	0.0025	0.949	0.069	0.59
Stemonoporus kanneliyensis	SC	1.535	0.057	0.0151	0.0014	0.801	0.052	0.82
Garcinia quaesita	SC	3.355	0.050	0.0296	0.0013	1.219	0.068	0.95
Calophyllum calaba	SC	2.812	0.061	0.0350	0.0022	2.128	0.083	0.88
Agrostistachys coriacea	US	2.185	0.064	0.0233	0.0017	0.558	0.068	0.91
Aporusa cardiosperma	US	3.532	0.087	0.0272	0.0019	1.329	0.116	0.83
Schumacheria castaneifolia	US	1.045	0.049	0.0131	0.0012	1.014	0.052	0.70

Strat. – Canopy stratum; C – Canopy; SC – Sub-canopy; US – Understorey; P_{max} – Maximum light-saturated net photosynthetic rate (μmol [CO_2] m^{-2} s^{-1}); ϕ – Quantum efficiency of photosynthesis (μmol [CO_2] (μmol [PAR]$)^{-1}$); R_d – Leaf dark respiration rate (μmol [CO_2] m^{-2} s^{-1}).

Table 3.9: Estimated parameters of the light response curves of different plant species from different canopy strata of lowland wet evergreen forests of Sri Lanka *(continued)*

Species	Stratum	LSP	LCP	R_d/P_{max}
Shorea congestiflora	C	677.09	66.33	0.38
Vateria copallifera	C	380.24	12.88	0.11
Shorea stipularis	C	632.37	41.23	0.23
Dipterocarpus zeylanicus	C	940.54	156.49	0.82
Shorea disticha	C	704.08	83.60	0.50
Calophyllum bracteatum	SC	621.15	37.32	0.21
Mesua ferrea	SC	364.82	20.69	0.20
Dillenia triquetra	SC	475.35	70.92	0.69
Stemonoporus kanneliyensis	SC	528.30	64.93	0.52
Garcinia quaesita	SC	510.77	47.89	0.36
Calophyllum calaba	SC	502.31	79.52	0.76
Agrostistachys coriacea	US	379.38	26.77	0.26
Aporusa cardiosperma	US	592.46	57.09	0.38
Schumacheria castaneifolia	US	577.27	106.55	0.97

LSP – Light saturation point (μmol [PAR] m^{-2} s^{-1}); LCP – Light compensation point (μmol [PAR] m^{-2} s^{-1}); R_d/P_{max} – Ratio between dark respiration and maximum light-saturated net photosynthetic rates.

canopy species), *Mesua ferrea* (a sub-canopy species) and *Agrostistachys coriacea* (an understorey species).

Although all parameters of the light response curves showed substantial variation between individual species, this variation was not correlated with their position in the vertical stratification of the forest canopy (Tables 3.8 and 3.9). For example, species with comparatively higher P_{max} values (i.e. > 3 (μmol [CO_2] m^{-2} s^{-1}) could be found among all canopy strata. Likewise, all canopy strata contained species with comparatively lower P_{max} values (i.e. < 2 (μmol [CO_2] m^{-2} s^{-1}) as well. The same could be observed for other parameters of the light response curves. However, there were several significant ($p < 0.10$) correlations between different parameters across the canopy strata (Table 3.10). For example, there were highly significant ($p < 0.01$) positive correlations between P_{max} and ϕ, between R_d/P_{max} and LCP and between LSP and LCP. As expected, R_d/P_{max} was significantly ($p<0.05$) negatively correlated with P_{max} and significantly positively correlated with R_d. In addition, ϕ showed negative correlations with both LCP ($p=0.0589$) and LSP ($p=0.103$) and R_d also showed positive correlations with both LCP ($p=0.0311$) and LSP ($p=0.1099$).

Pooled light response curves for the three strata, which were obtained by pooling the data from all species within a given stratum and fitting a common curve, are shown in Fig. 3.51. Parameters of the fitted curves are shown in Table 3.11. The canopy layer had a significantly greater P_{max} value and significantly lower R_d and ϕ values than the sub-canopy and understorey. The sub-canopy had significantly greater P_{max} and ϕ values than the understorey. R_d did not differ significantly between the sub-canopy and the understorey. The LSP of the canopy stratum (i.e. 741 μmol [PAR] m^{-2} s^{-1}) was

Table 3.10: Linear correlation coefficients for correlations between estimated parameters of the light response curves of different plant species from different canopy strata of lowland wet evergreen forests of Sri Lanka

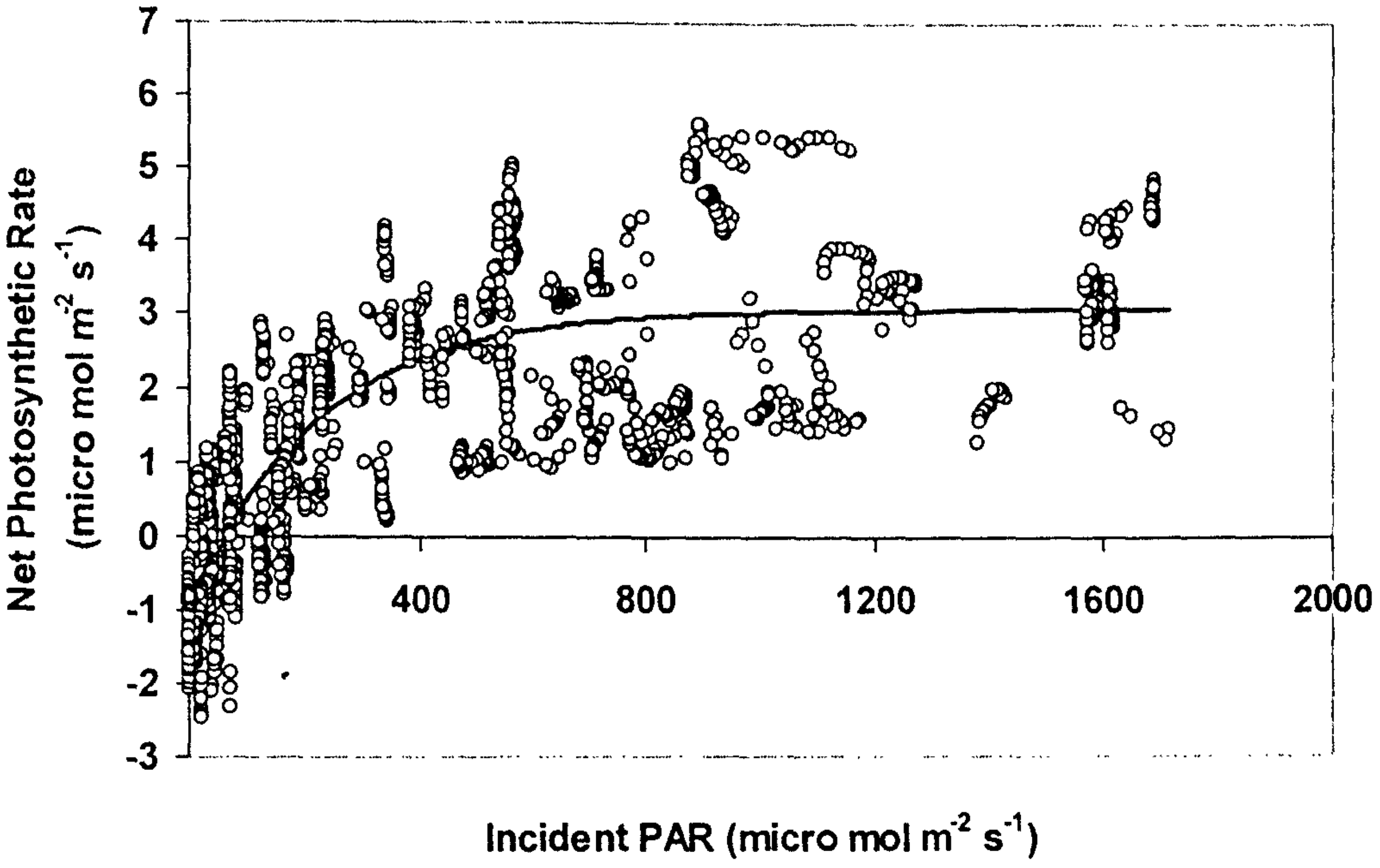
	ϕ	R_d	R_d/P_{max}	LSP	LCP
P_{max}	0.761 *(0.0016)*†	0.226^{ns}	-0.599 *(0.0237)*	-0.0140^{ns}	-0.447 *(0.1094)*
ϕ	-	0.329^{ns}	-0.414^{ns}	-0.454 *(0.103)*	-0.516 *(0.0589)*
R_d	-	-	0.565 *(0.0354)*	0.446 *(0.1099)*	0.576 *(0.0311)*
R_d/P_{max}	-	-	-	0.427^{ns}	0.871 *(<.0001)*
LSP	-	-	-	-	0.789 *(0.0008)*

†Probability of each correlation coefficient not being significantly greater than zero.

^{ns}Correlation coefficient is not significantly different from zero at p=0.10.

The number of data points was 14 for each correlation.

(a) Canopy



(b) Sub Canopy

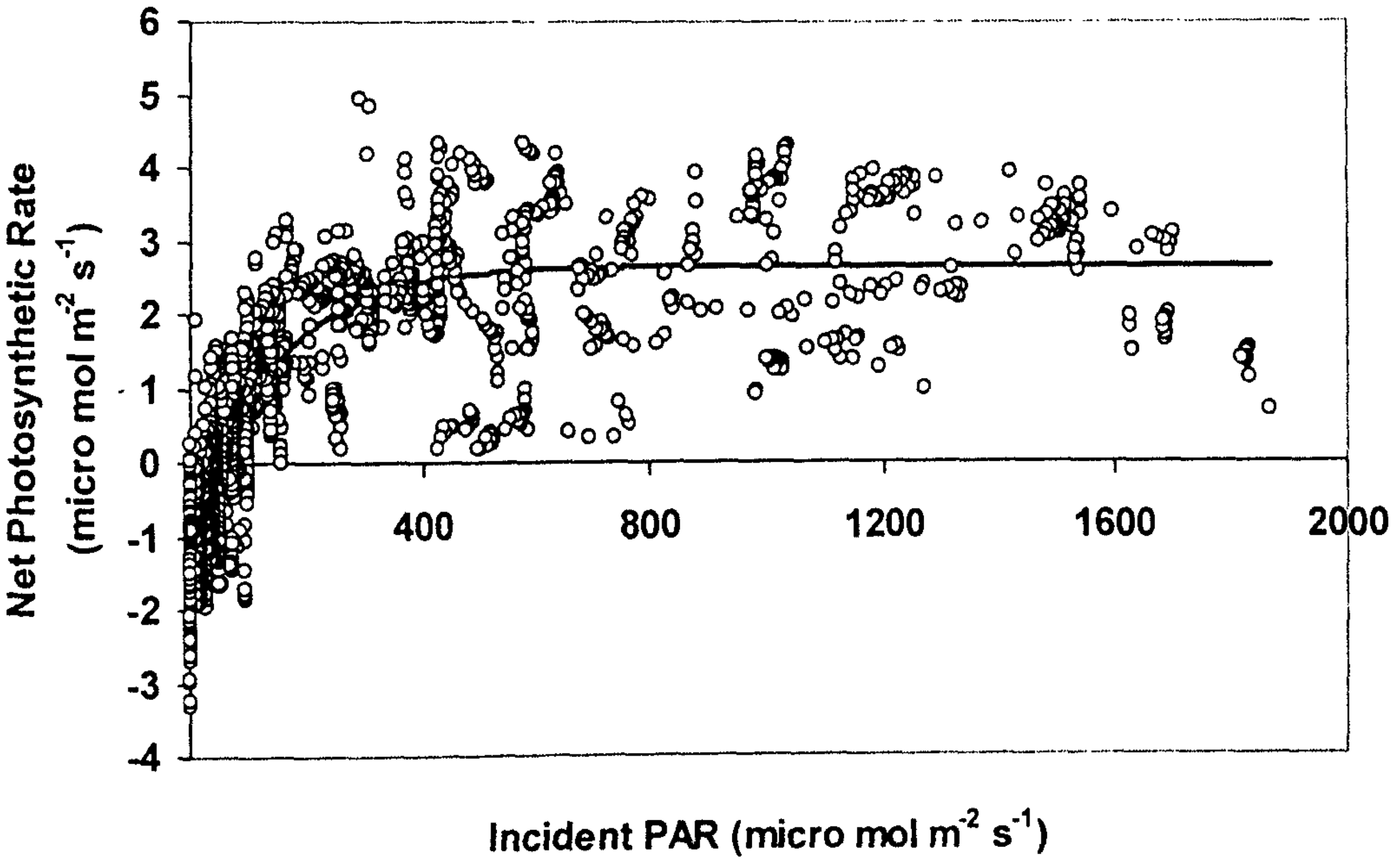


Figure 3.51: Pooled light responses curves for canopy (a) and sub-canopy (b) species.

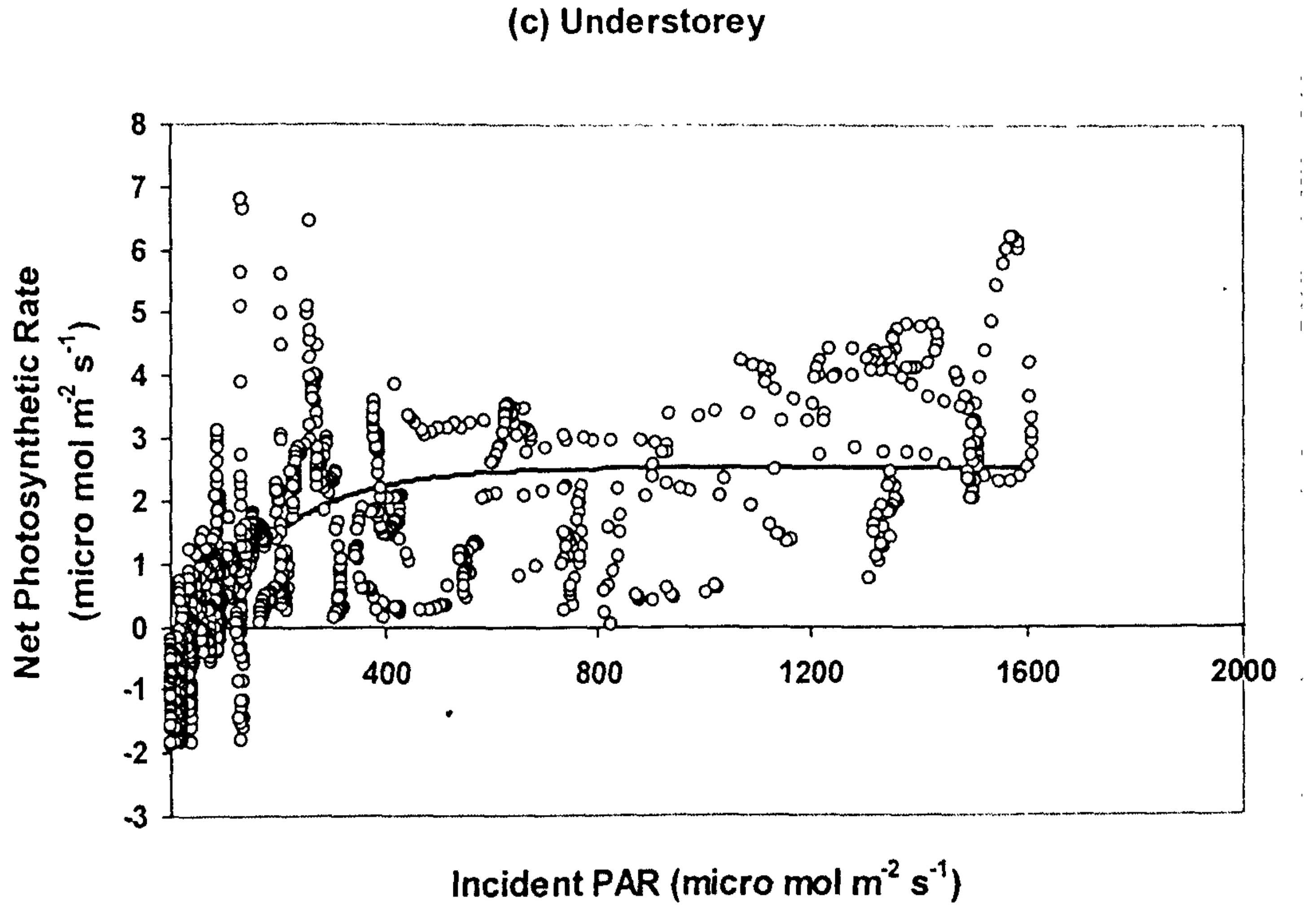


Figure 3.51 *(Continued)*: Pooled light responses curves for canopy (a), sub-canopy (b) and understorey (c) species.

Table 3.11: Estimated parameters of pooled light response curves of different canopy strata of lowland wet evergreen forests of Sri Lanka

Str.	P_{max}	Std. Err.	ϕ	Std. Err.	R_d	Std. Err.	LSP	LCP	Rd/Pmax	R^2
C	3.080	0.056	0.0175	0.0009	0.905	0.061	740.95	58.67	0.294	0.78
SC	2.653	0.038	0.0278	0.0010	1.169	0.038	462.06	50.21	0.441	0.80
US	2.544	0.062	0.0225	0.0014	1.065	0.071	536.58	56.07	0.418	0.69

Stra. – Canopy stratum; C – Canopy; SC – Sub-canopy; US – Understorey.

substantially greater than those of sub-canopy and understorey strata (462 and 537 μmol [PAR] m^{-2} s^{-1} respectively). However, there was no appreciable variation between the three canopy strata in LCP, which varied between 50 and 59 μmol [PAR] m^{-2} s^{-1}. The ratio between R_d and P_{max} was lower in the canopy stratum (0.29) as compared to the sub-canopy (0.44 and 0.42) and understorey strata.

3.5 Distribution of LAI in different canopy strata

3.5.1 KDN forest complex

Distribution of LAI in different canopy strata and its variation between transects of the KDN forest complex is given in Fig. 3.52. Partial LAI values of the canopy ($pLAI_C$) and sub-canopy ($pLAI_{SC}$) strata did not differ significantly ($p=0.05$) between different transects (Fig. 3.52.a). However, their percentage contributions to the total canopy LAI showed highly significant ($p<0.0001$) variation between transects (Fig. 3.52.b). Partial LAI of the understorey ($pLAI_{US}$) and its percentage contribution to the total canopy LAI showed highly significant ($p<0.0001$) variation between transects. Partial LAI in the canopy stratum contributed 43 – 54% while those in the sub-canopy and understorey contributed 38 – 48% and 1.4 – 19% respectively.

Variation of partial LAIs and their percentage contributions to the total LAI with different forest regions and elevation zones in the KDN forest complex is shown in Figs. 3.53 and 3.54. Partial LAIs the canopy and sub-canopy strata did not differ significantly between forest regions or elevation zones. However, partial LAI of the understorey showed highly significant variation between forest regions ($p<0.0001$) and elevation zones ($p=0.0023$). $pLAI_{US}$ of Dediyagala was significantly greater than that of Kanneliya

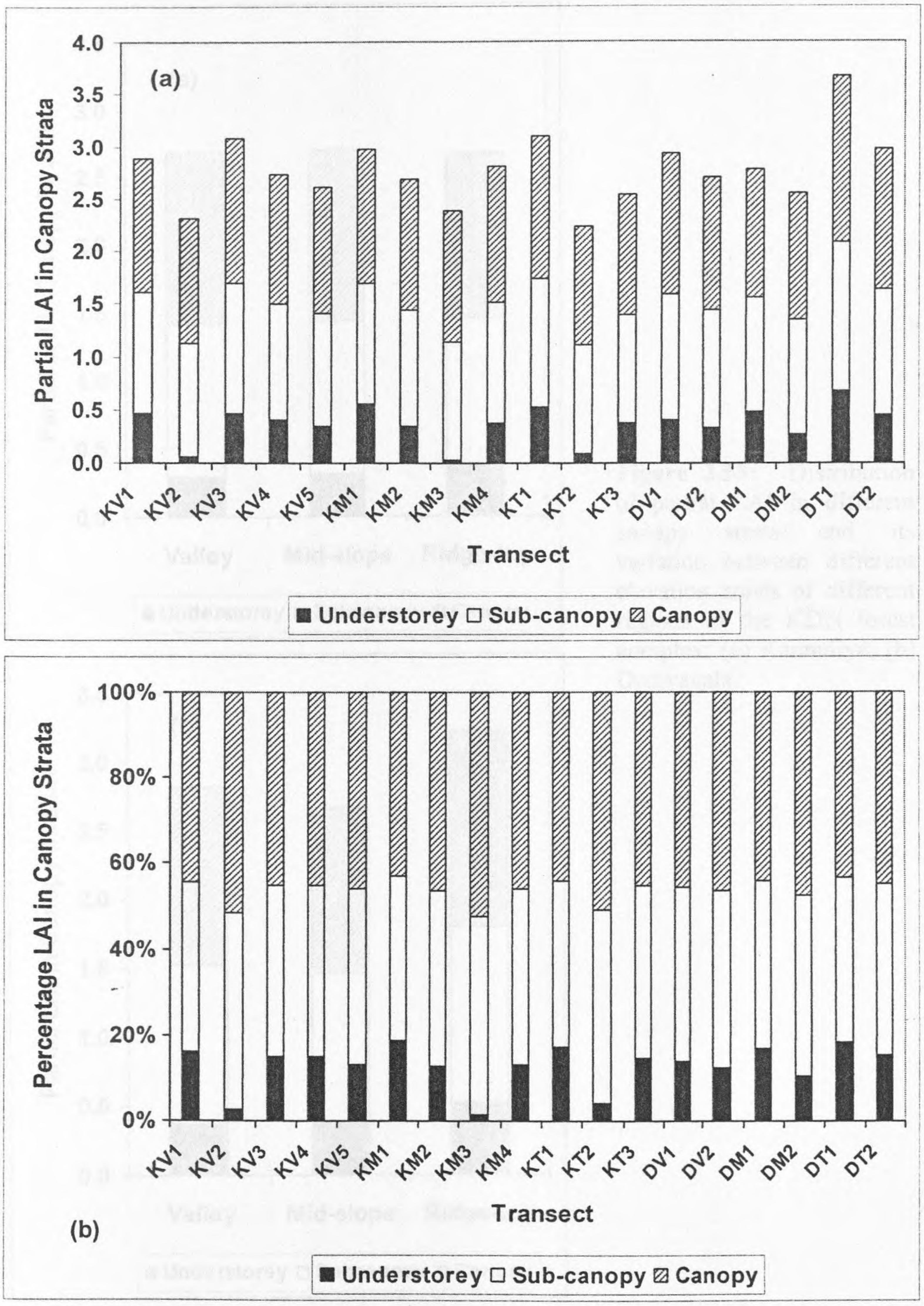


Figure 3.52: Distribution of partial LAI and percentage LAI in different canopy strata and its variation between different transects of the KDN forest complex. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

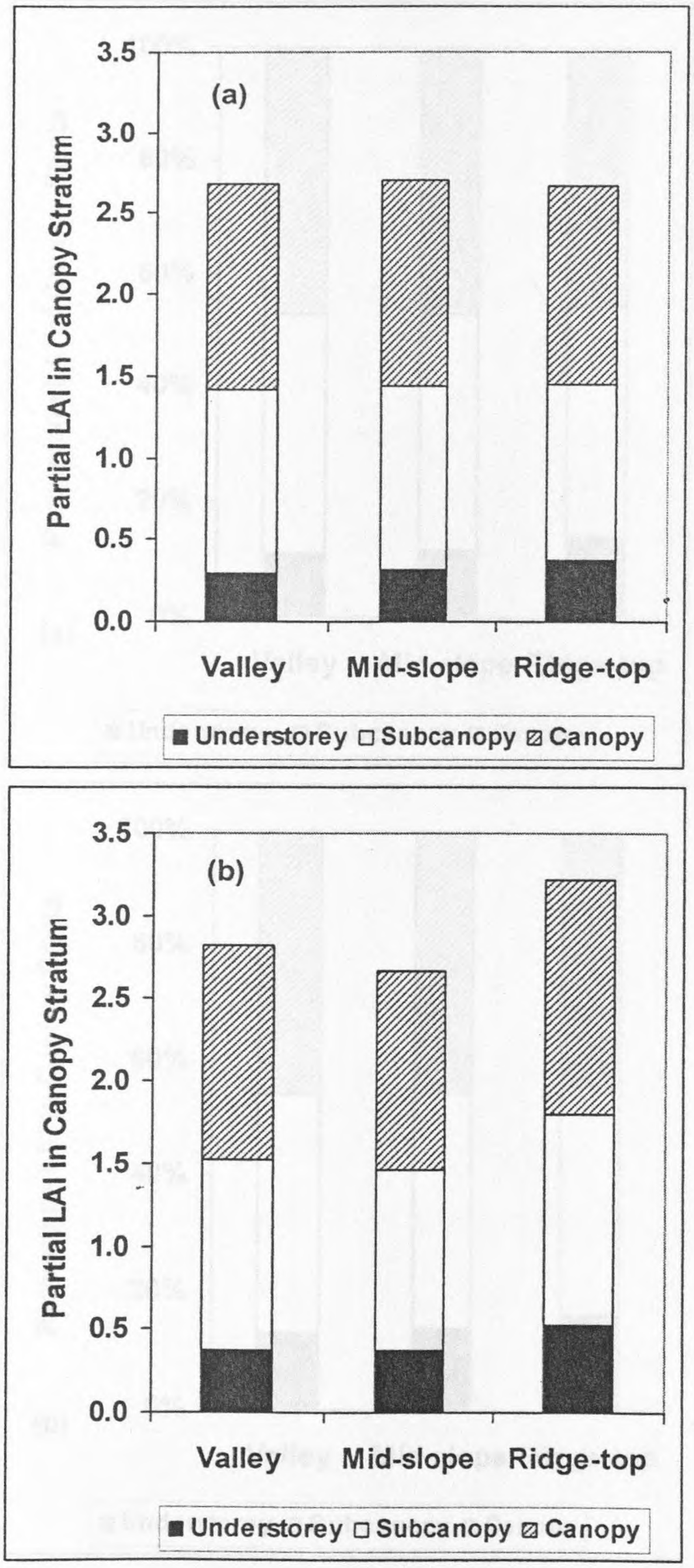


Figure 3.53: Distribution of partial LAI in different canopy strata and its variation between different elevation zones of different regions of the KDN forest complex: (a) Kanneliya; (b) Dediyagala.

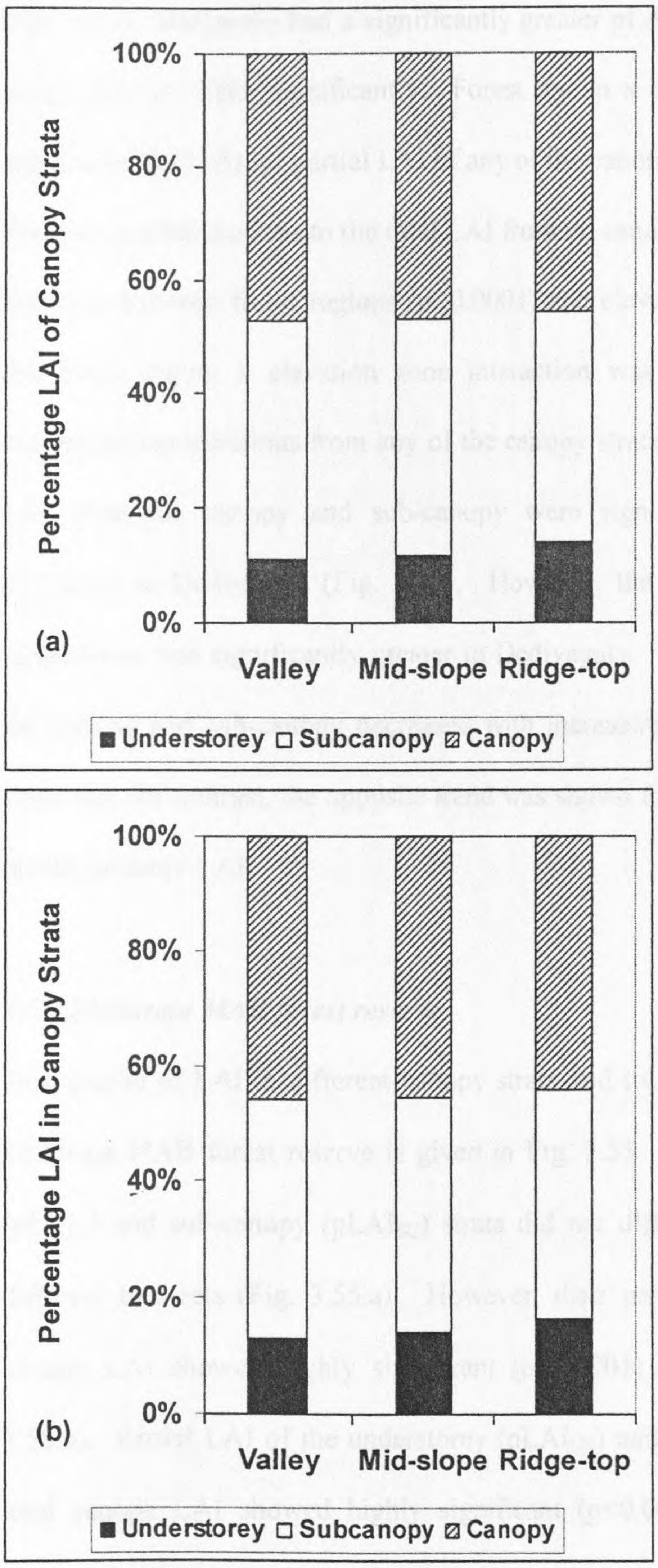


Figure 3.54: Distribution of percentage LAI in different canopy strata and its variation between different elevation zones of different regions of the KDN forest complex: (a) Kanneliya; (b) Dediyagala.

(Fig. 3.53). Ridge-top had a significantly greater $pLAI_{US}$ than the mid-slope and valley, which did not differ significantly. Forest region x elevation zone interaction was not significant ($p=0.05$) for partial LAI of any of the canopy strata.

Percentage contributions to the total LAI from all canopy strata showed highly significant variation between forest regions ($p<0.0001$) and elevation zones ($p=0.0105$). However, the forest region x elevation zone interaction was not significant ($p=0.05$) for the percentage contributions from any of the canopy strata. Percentage contributions to total LAI from the canopy and sub-canopy were significantly greater in Kanneliya as compared to Dediyagala (Fig. 3.54). However, the percentage contribution from the understorey was significantly greater in Dediyagala. The percentage contributions from the canopy and sub-canopy decreased with increasing elevation from the valley to the ridge-top. In contrast, the opposite trend was shown for the percentage contribution from the understorey LAI.

3.5.2 Sinharaja MAB forest reserve

Distribution of LAI in different canopy strata and its variation between transects of the Sinharaja MAB forest reserve is given in Fig. 3.55. Partial LAI values of the canopy ($pLAI_C$) and sub-canopy ($pLAI_{SC}$) strata did not differ significantly ($p=0.05$) between different transects (Fig. 3.55.a). However, their percentage contributions to the total canopy LAI showed highly significant ($p<0.0001$) variation between transects (Fig. 3.55.b). Partial LAI of the understorey ($pLAI_{US}$) and its percentage contribution to the total canopy LAI showed highly significant ($p<0.0001$) variation between transects.

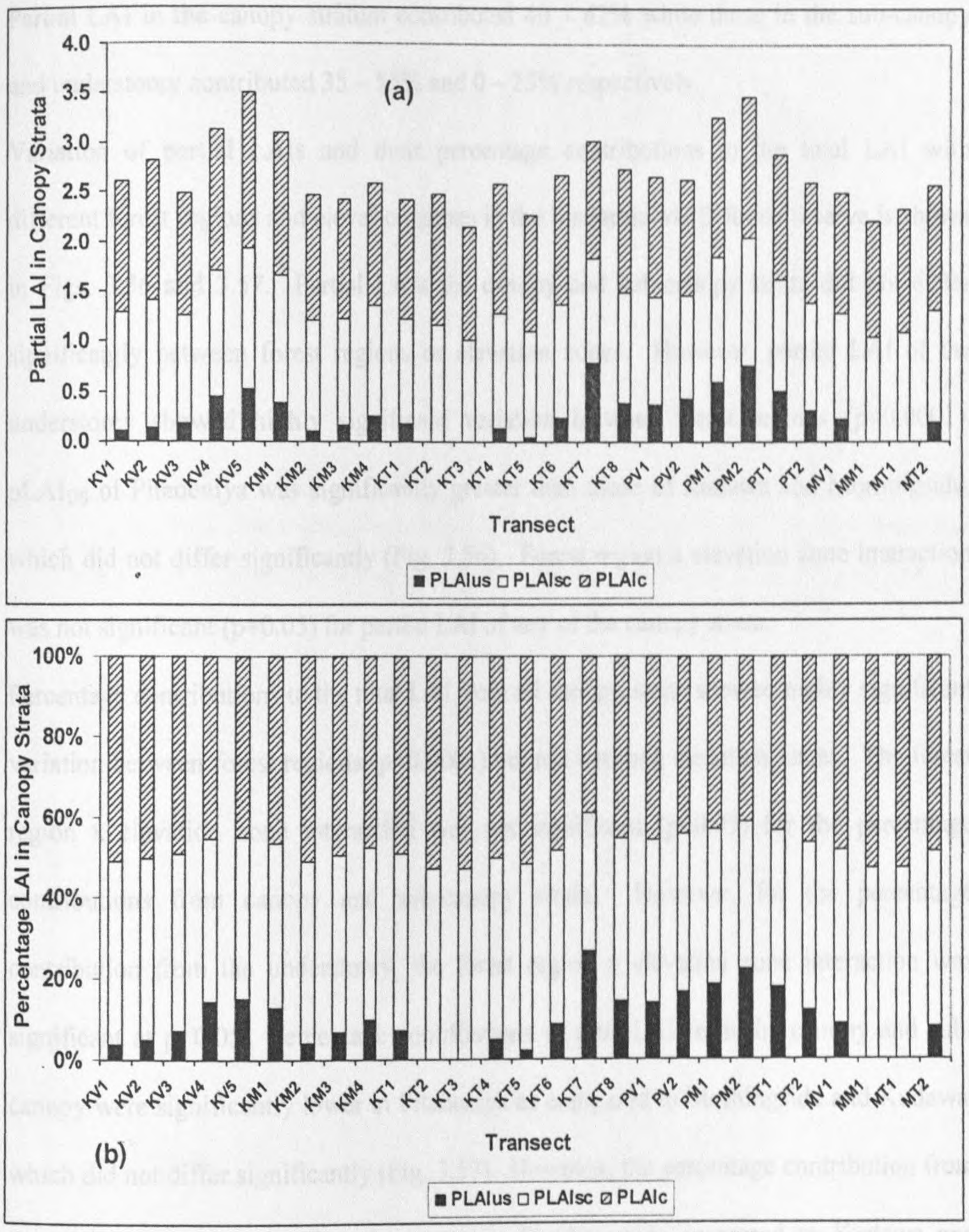


Figure 3.55: Distribution of partial LAI and percentage LAI in different canopy strata and its variation between different transects of the Sinharaja MAB forest reserve. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

Partial LAI in the canopy stratum contributed 40 – 62% while those in the sub-canopy and understorey contributed 35 – 55% and 0 – 25% respectively.

Variation of partial LAIs and their percentage contributions to the total LAI with different forest regions and elevation zones in the Sinharaja MAB forest reserve is shown in Figs. 3.56 and 3.57. Partial LAIs the canopy and sub-canopy strata did not differ significantly between forest regions or elevation zones. However, partial LAI of the understorey showed highly significant variation between forest regions ($p<0.0001$). $pLAI_{US}$ of Pitadeniya was significantly greater than those of Kudawa and Morningside, which did not differ significantly (Fig. 3.56). Forest region x elevation zone interaction was not significant ($p=0.05$) for partial LAI of any of the canopy strata.

Percentage contributions to the total LAI from all canopy strata showed highly significant variation between forest regions ($p<0.0001$) but not between elevation zones. The forest region x elevation zone interaction was not significant ($p=0.05$) for the percentage contributions from canopy and sub-canopy strata. However, for the percentage contribution from the understorey, the forest region x elevation zone interaction was significant at $p<0.05$. Percentage contributions to total LAI from the canopy and sub-canopy were significantly lower in Pitadeniya as compared to Morningside and Kudawa, which did not differ significantly (Fig. 3.57). However, the percentage contribution from the understorey was significantly greater in Pitadeniya as compared to Kudawa and Morningside, which did not differ significantly. Percentage contribution from the understorey in the mid-slope was the highest among the three elevation zones at Pitadeniya (Fig. 3.57.b). However, at Morningside, the corresponding contribution was the lowest (Fig. 3.57.c). This variation was mainly responsible for the significant forest

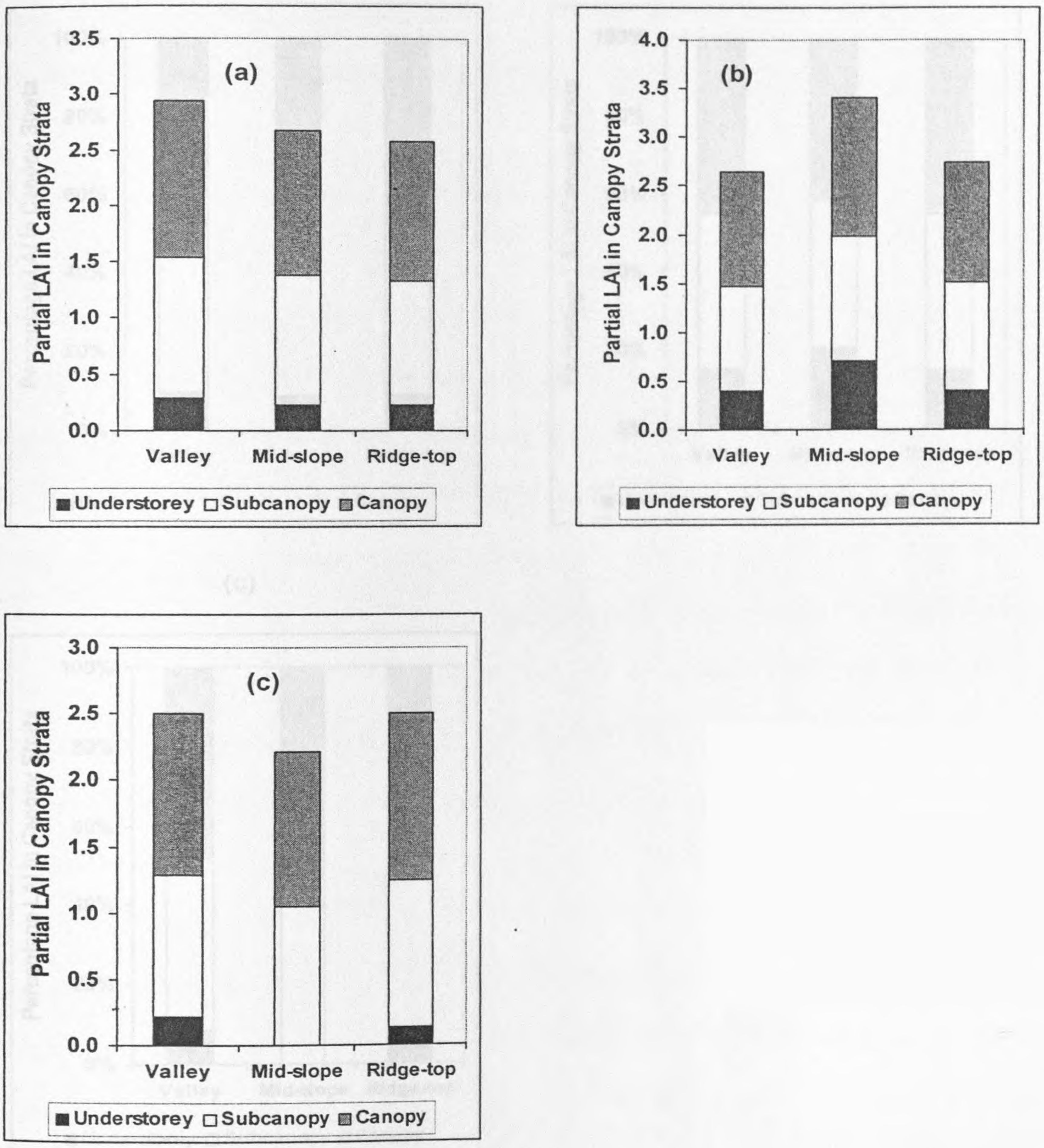


Figure 3.56: Distribution of partial LAI in different canopy strata and its variation between different elevation zones of different regions of the Sinharaja MAB forest reserve: (a) Kudawa; (b) Pitadeniya; (c) Morningside.

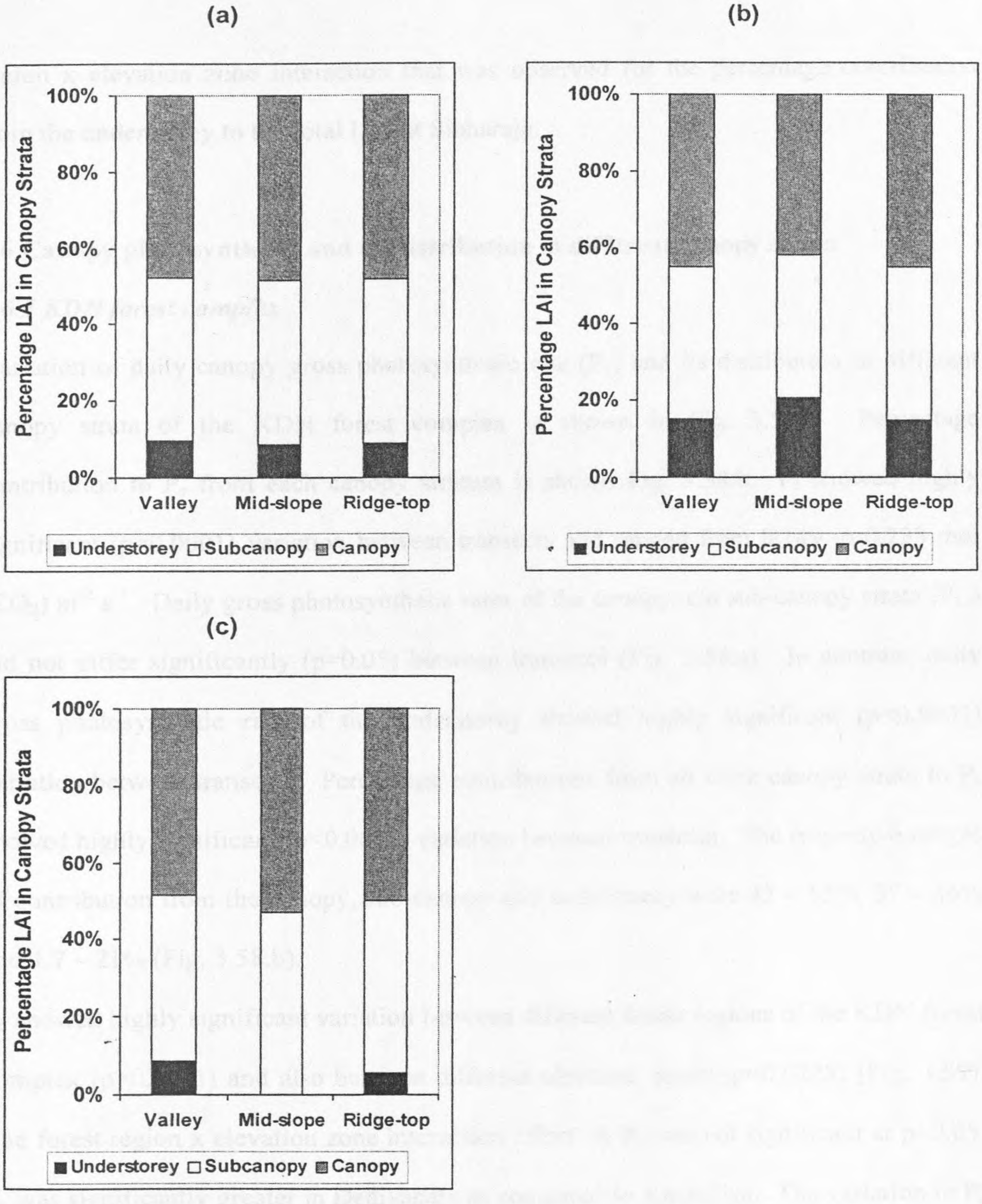


Figure 3.57: Distribution of percentage LAI in different canopy strata and its variation between different elevation zones of different regions of the Sinharaja MAB forest reserve: (a) Kudawa; (b) Pitadeniya; (c) Morningside.

region x elevation zone interaction that was observed for the percentage contribution from the understorey to the total LAI at Sinharaja.

3.6 Canopy photosynthesis and its distribution in different canopy strata

3.6.1 KDN forest complex

Variation of daily canopy gross photosynthetic rate (P_c) and its distribution in different canopy strata of the KDN forest complex is shown in Fig. 3.58.a. Percentage contribution to P_c from each canopy stratum is shown Fig. 3.58.b. P_c showed highly significant (p=0.0001) variation between transects and ranged from 0.149 to 0.233 mol (CO₂) m^{-2} s^{-1}. Daily gross photosynthetic rates of the canopy and sub-canopy strata ($P_{s,i}$) did not differ significantly (p=0.05) between transects (Fig. 3.58.a). In contrast, daily gross photosynthetic rate of the understorey showed highly significant (p<0.0001) variation between transects. Percentage contributions from all three canopy strata to P_c showed highly significant (p<0.0001) variation between transects. The respective ranges of contribution from the canopy, sub-canopy and understorey were 42 – 52%, 37 – 46% and 1.7 – 21% (Fig. 3.58.b).

P_c showed highly significant variation between different forest regions of the KDN forest complex (p>0.0001) and also between different elevation zones (p=0.0223) (Fig. 3.59). The forest region x elevation zone interaction effect on P_c was not significant at p=0.05. P_c was significantly greater in Dediyagala as compared to Kanneliya. The variation in P_c between elevation zones was more prominent in Dediyagala and than in Kanneliya. Ridge top had a significantly greater P_c than the valley and mid-slope, which did not differ significantly. $P_{s,i}$ of the canopy and sub-canopy strata did not show significant

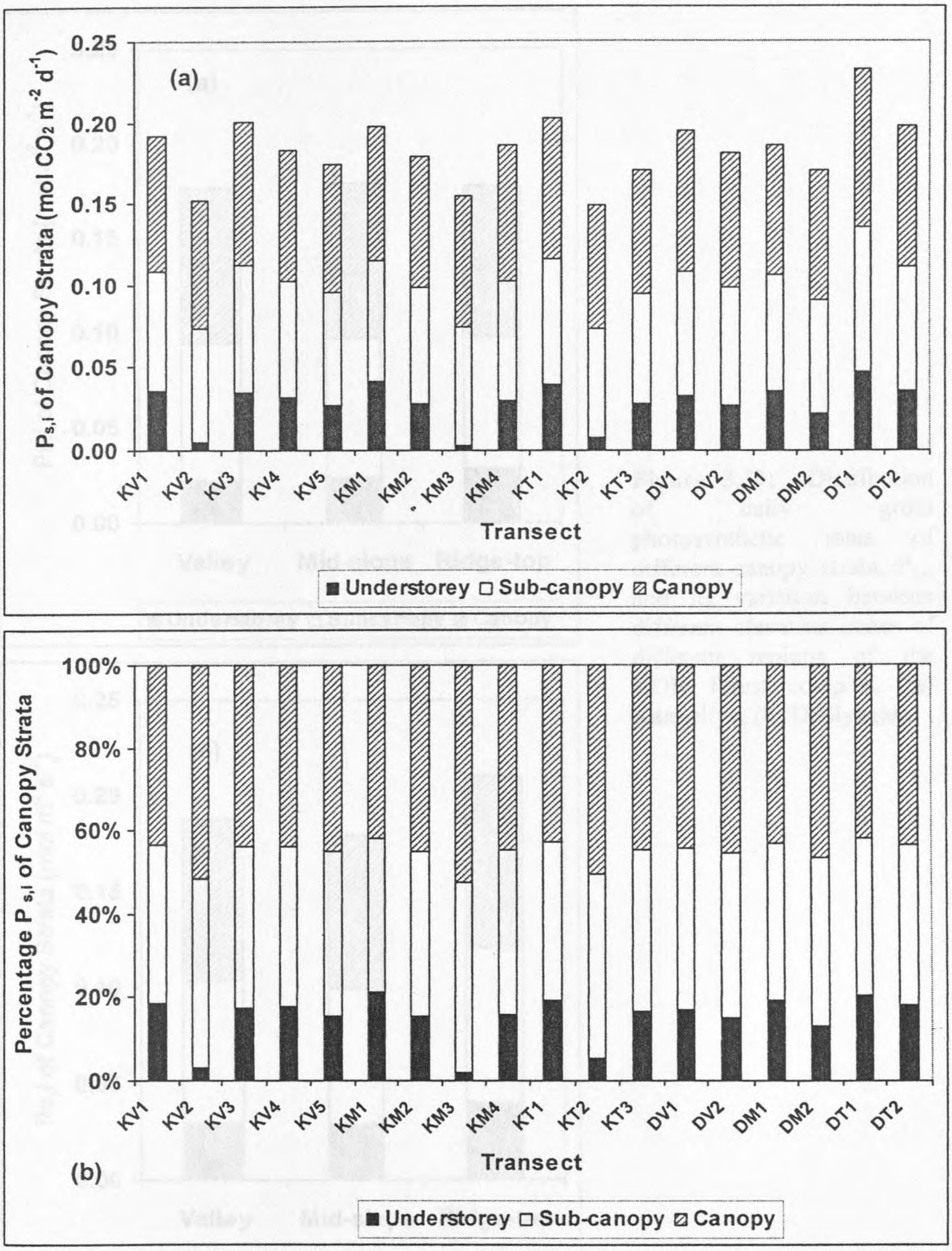


Figure 3.58: Distribution of daily gross photosynthetic rates of different canopy strata, $P_{s,i}$, (a), their % contribution to the daily canopy gross photosynthetic rate, P_c, (b) and their variation between different transects of the KDN forest complex. P_c is given by the whole bar in (a). Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

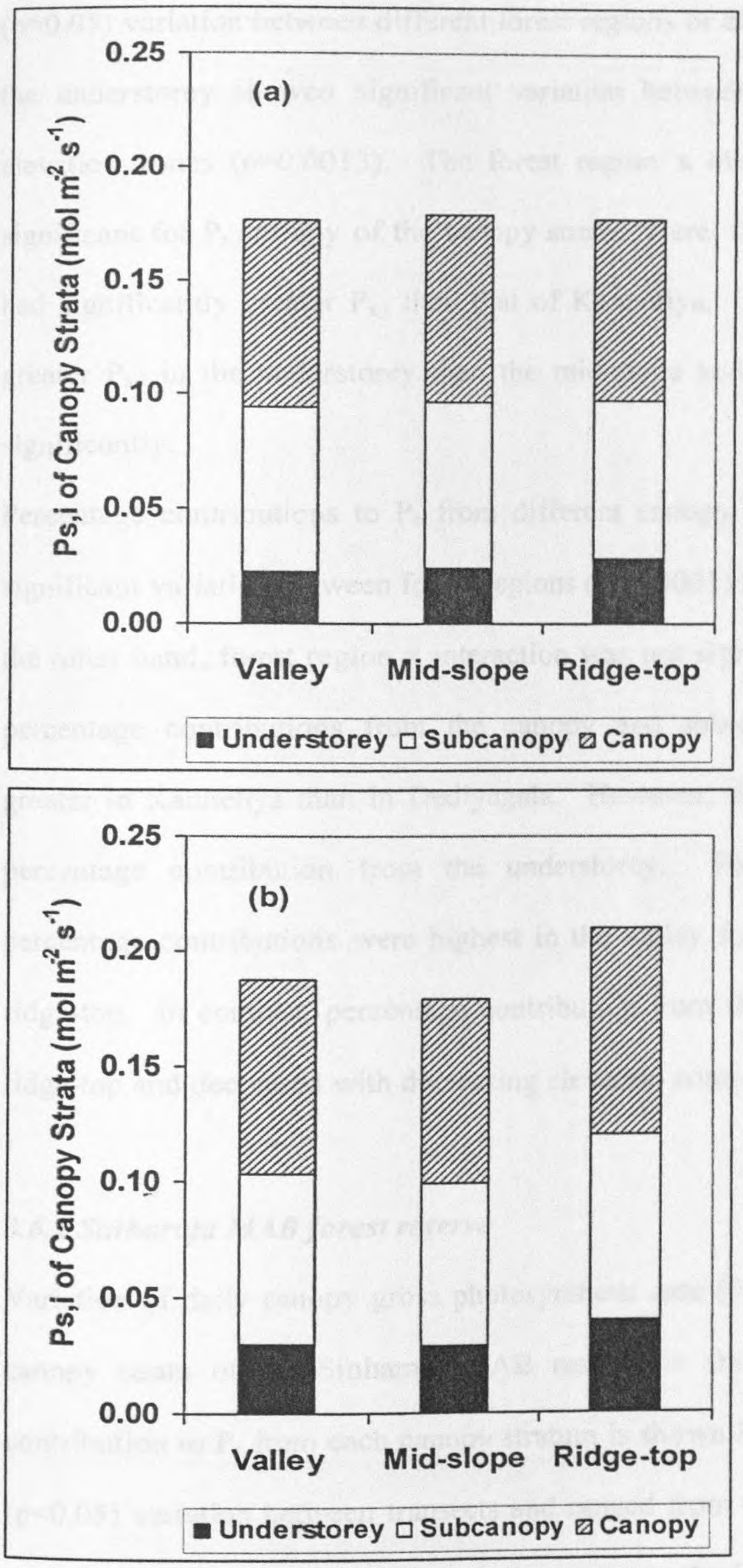


Figure 3.59: Distribution of daily gross photosynthetic rates of different canopy strata, $P_{s,i}$, and its variation between different elevation zones of different regions of the KDN forest complex: (a) Kanneliya; (b) Dediyagala.

($p=0.05$) variation between different forest regions or elevation zones. In contrast, $P_{s,i}$ of the understorey showed significant variation between forest regions ($p<0.0001$) and elevation zones ($p=0.0013$). The forest region x elevation zone interaction was not significant for $P_{s,i}$ of any of the canopy strata. Here, the understorey of the Dediyagala had significantly greater $P_{s,i}$ than that of Kanneliya. Furthermore, the ridge-top had a greater $P_{s,i}$ in the understorey than the mid-slope and the valley which did not differ significantly.

Percentage contributions to P_c from different canopy strata (Fig. 3.60) showed highly significant variation between forest regions ($p<0.0001$) and elevation zones ($p<0.01$). On the other hand, forest region x interaction was not significant at $p=0.05$. Interestingly, percentage contributions from the canopy and sub-canopy strata were significantly greater in Kanneliya than in Dediyagala. However, the opposite was observed for the percentage contribution from the understorey. For the canopy and sub-canopy, percentage contributions were highest in the valley followed by the mid-slope and the ridge-top. In contrast, percentage contribution from the understorey was highest at the ridge-top and decreased with decreasing elevation zone.

3.6.2 Sinharaja MAB forest reserve

Variation of daily canopy gross photosynthetic rate (P_c) and its distribution in different canopy strata of the Sinharaja MAB reserve is shown in Fig. 3.61.a. Percentage contribution to P_c from each canopy stratum is shown Fig. 3.61.b. P_c showed significant ($p<0.05$) variation between transects and ranged from 0.129 to 0.177 mol (CO_2) m^{-2} s^{-1}, which was lower than the corresponding range in the KDN forest complex (Fig. 3.58.a).

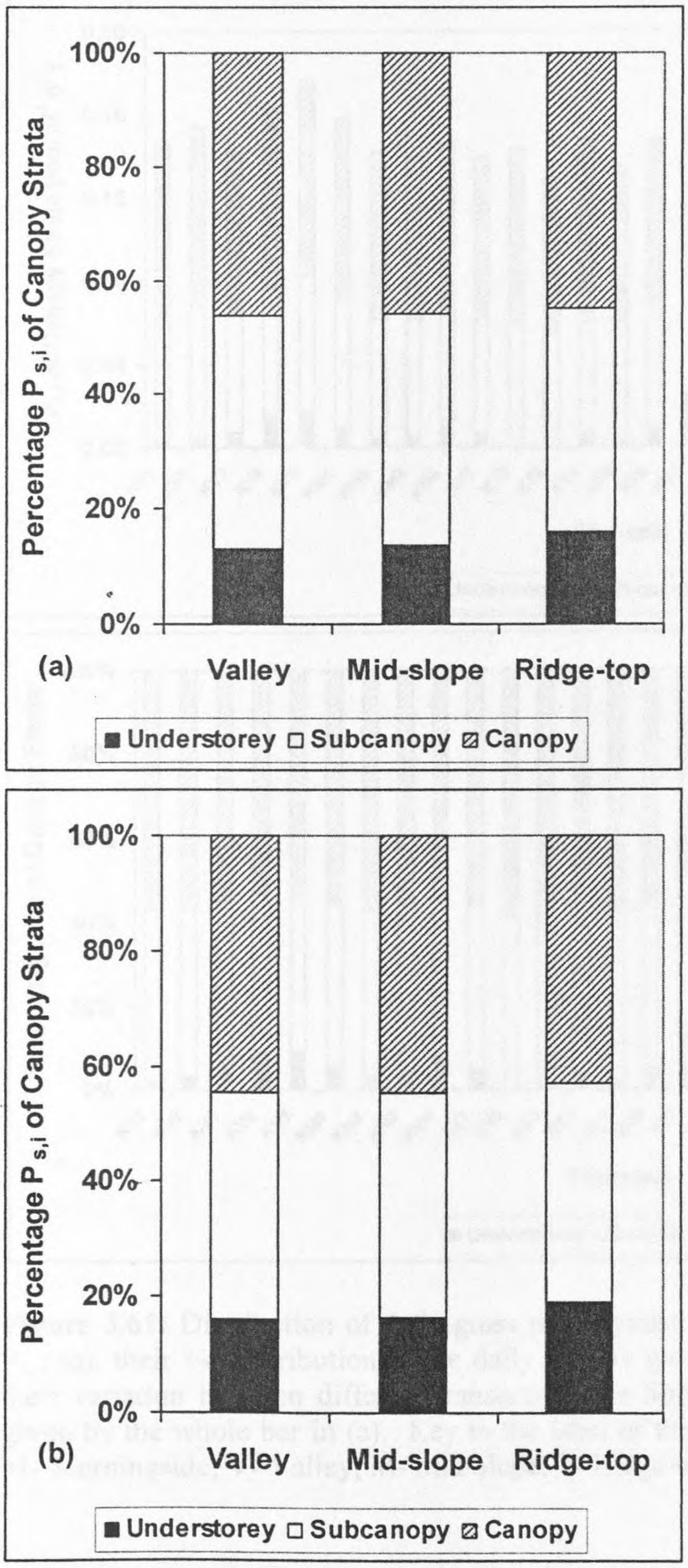


Figure 3.60: Percentage contribution to the daily canopy gross photosynthetic rate, P_c, from different canopy strata and its variation between different elevation zones of different regions of the KDN forest complex: (a) Kanneliya; (b) Dediyagala.

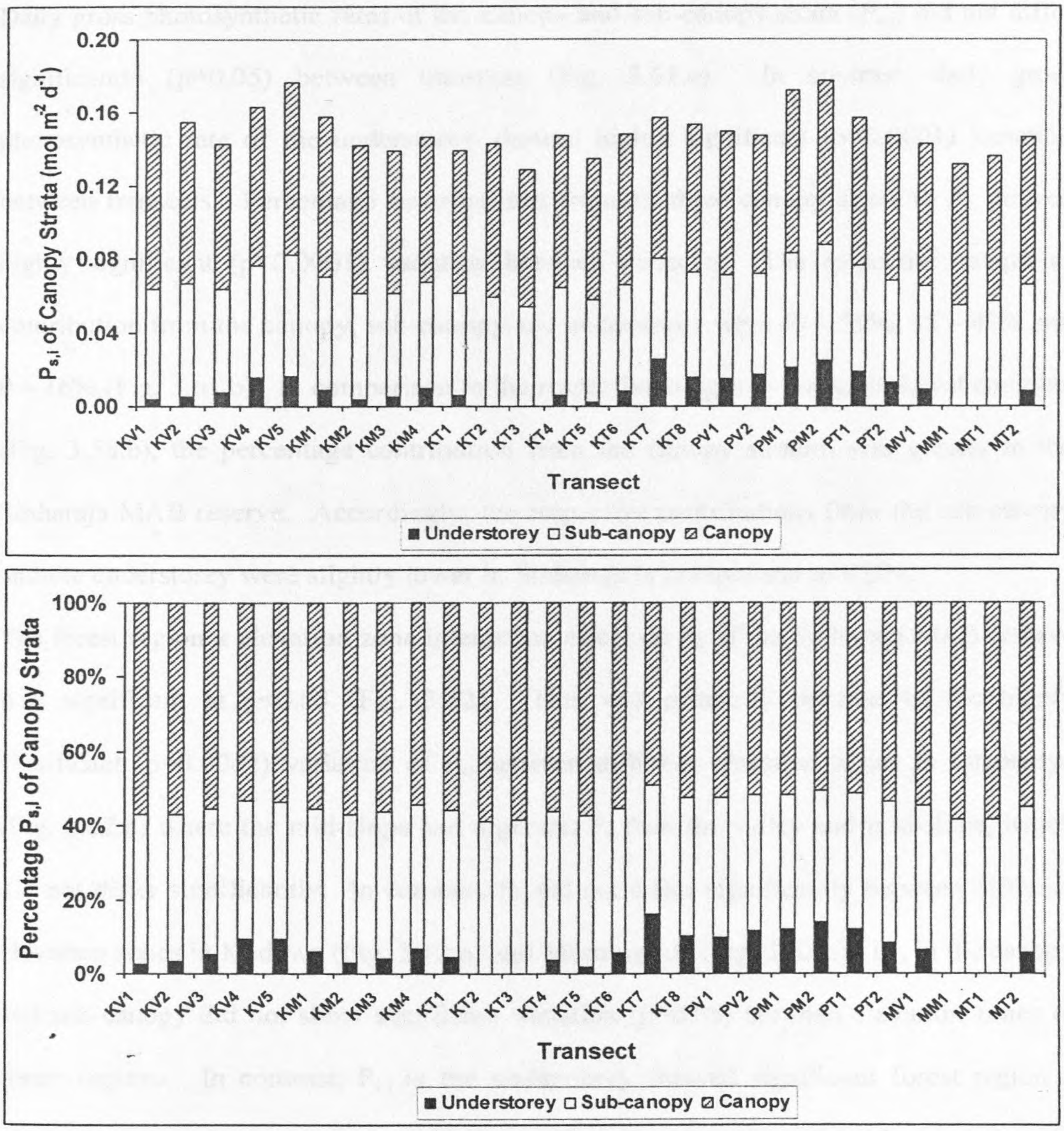


Figure 3.61: Distribution of daily gross photosynthetic rates of different canopy strata, $P_{s,i}$, (a), their % contribution to the daily canopy gross photosynthetic rate, P_c, (b) and their variation between different transects of the Sinharaja MAB forest reserve. P_c is given by the whole bar in (a). Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

Daily gross photosynthetic rates of the canopy and sub-canopy strata ($P_{s,i}$) did not differ significantly ($p=0.05$) between transects (Fig. 3.61.a). In contrast, daily gross photosynthetic rate of the understorey showed highly significant ($p<0.0001$) variation between transects. Percentage contributions from all three canopy strata to P_c showed highly significant ($p<0.0001$) variation between transects. The respective ranges of contribution from the canopy, sub-canopy and understorey were 49 – 59%, 35 – 42% and 0 – 16% (Fig. 3.61.b). In comparison to the respective ranges in the KDN forest complex (Fig. 3.58.b), the percentage contribution from the canopy stratum was greater in the Sinharaja MAB reserve. Accordingly, the respective contributions from the sub-canopy and the understorey were slightly lower in Sinharaja in comparison to KDN.

The forest region x elevation zone interaction effect on P_c of the Sinharaja MAB reserve was significant at $p<0.05$ (Fig. 3.62). This was primarily because of the highly significant ($p=0.0002$) variation of P_c between different elevation zones in Pitadeniya (Fig. 3.62.b) where the mid-slope had a greater P_c than the valley and mid-slope, which did not differ significantly. In contrast, P_c did not differ significantly between different elevation zones in Kudawa (Fig. 3.62.a) and Morningside (Fig. 3.62.c). $P_{s,i}$ in the canopy and sub-canopy did not show significant variation ($p=0.05$) between elevation zones or forest regions. In contrast, $P_{s,i}$ in the understorey showed significant forest region x elevation zone interaction ($p=0.0355$). The significant ($p=0.0003$) variation in understorey $P_{s,i}$ between different elevation zones at Pitadeniya (Fig. 3.62.b) was primarily responsible for the above interaction. The mid-slope understorey $P_{s,i}$ in Pitadeniya was significantly greater than the corresponding values in the valley and ridgetop. In contrast, neither Kudawa nor Morningside showed significant ($p=0.05$)

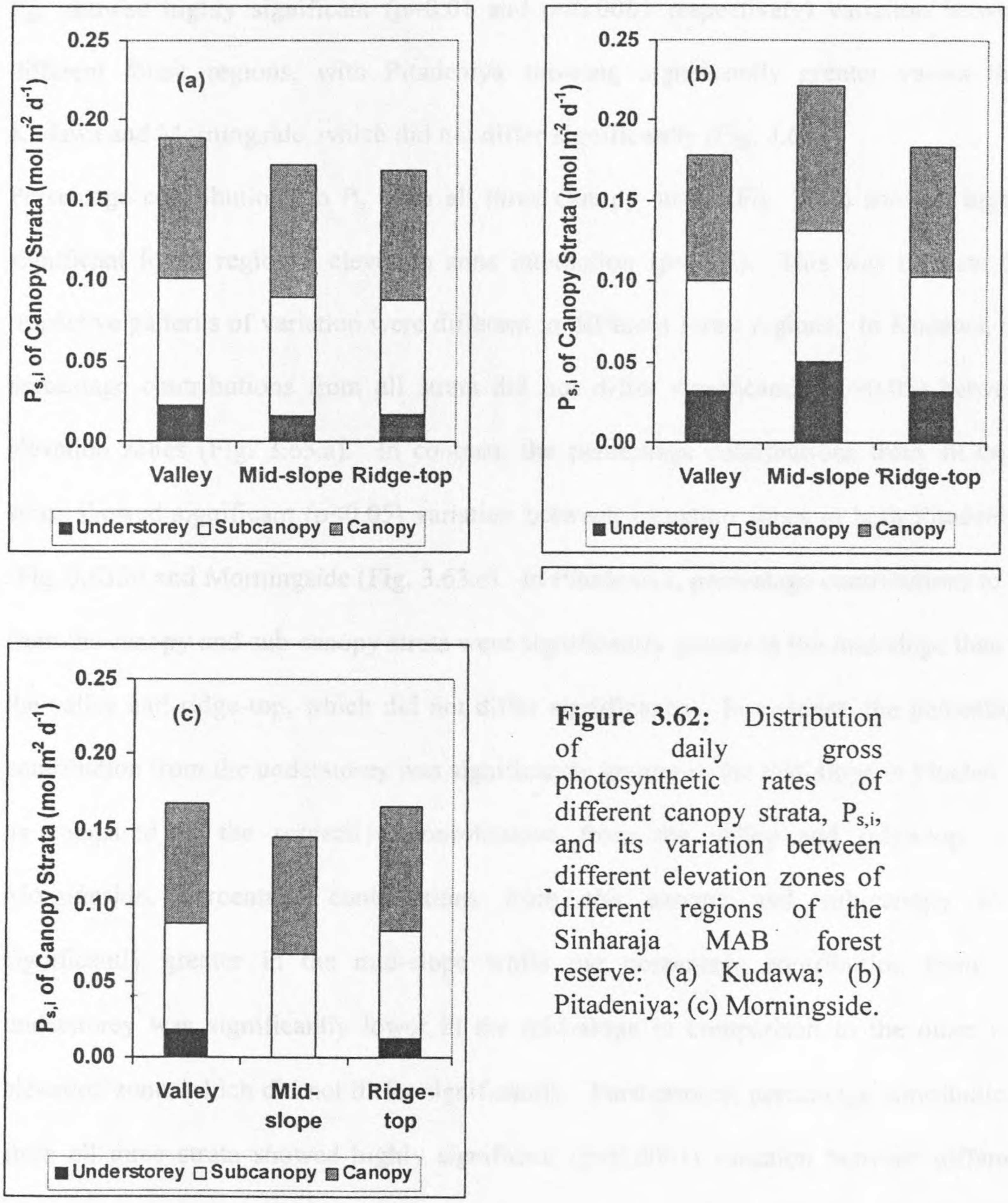


Figure 3.62: Distribution of daily gross photosynthetic rates of different canopy strata, $P_{s,i}$, and its variation between different elevation zones of different regions of the Sinharaja MAB forest reserve: (a) Kudawa; (b) Pitadeniya; (c) Morningside.

variation in understorey $P_{s,i}$ between different elevation zones. Both P_c and understorey $P_{s,i}$ showed highly significant ($p=0.01$ and $p<0.0001$ respectively) variation between different forest regions, with Pitadeniya showing significantly greater values than Kudawa and Morningside, which did not differ significantly (Fig. 3.62).

Percentage contributions to P_c from all three canopy strata (Fig. 3.63) showed highly significant forest region x elevation zone interaction ($p<0.05$). This was because the respective patterns of variation were different in different forest regions. In Kudawa, the percentage contributions from all strata did not differ significantly ($p=0.05$) between elevation zones (Fig. 3.63.a). In contrast, the percentage contributions from all three strata showed significant ($p<0.05$) variation between elevation zones in both Pitadeniya (Fig. 3.63.b) and Morningside (Fig. 3.63.c). In Pitadeniya, percentage contributions to P_c from the canopy and sub-canopy strata were significantly greater in the mid-slope than in the valley and ridge-top, which did not differ significantly. In contrast, the percentage contribution from the understorey was significantly greater in the mid-slope in Pitadeniya as compared to the respective contributions from the valley and ridge-top. In Morningside, percentage contributions from the canopy and sub-canopy were significantly greater in the mid-slope while the percentage contribution from the understorey was significantly lower in the mid-slope in comparison to the other two elevation zone, which did not differ significantly. Furthermore, percentage contributions from all three strata showed highly significant ($p<0.0001$) variation between different forest regions of the Sinharaja MAB reserve (Fig. 3.63). Percentage contributions from the canopy and sub-canopy strata were significantly lower in Pitadeniya (Fig. 3.63.b) while that from the understorey was significantly higher in comparison to the

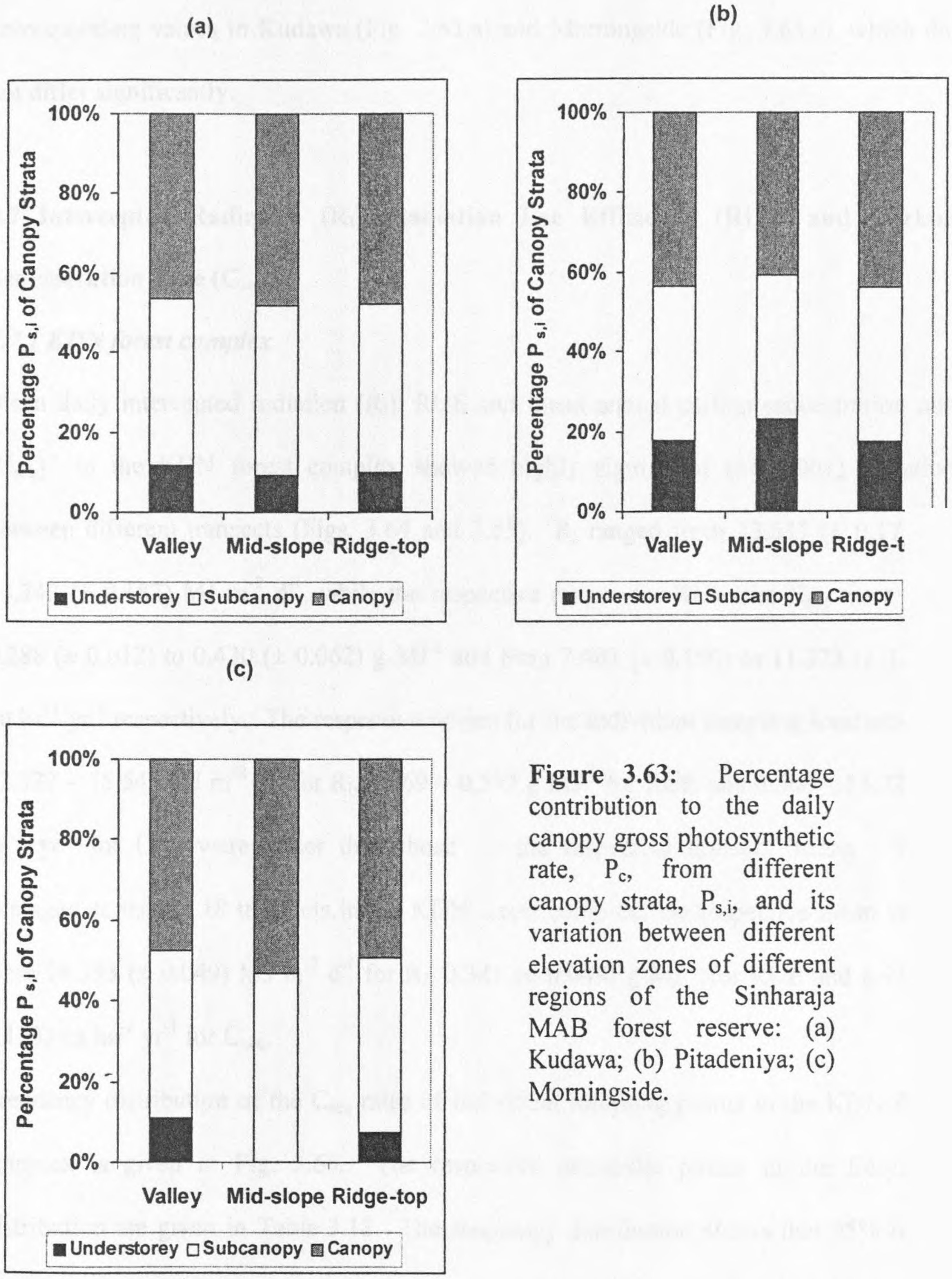


Figure 3.63: Percentage contribution to the daily canopy gross photosynthetic rate, P_c, from different canopy strata, $P_{s,i}$, and its variation between different elevation zones of different regions of the Sinharaja MAB forest reserve: (a) Kudawa; (b) Pitadeniya; (c) Morningside.

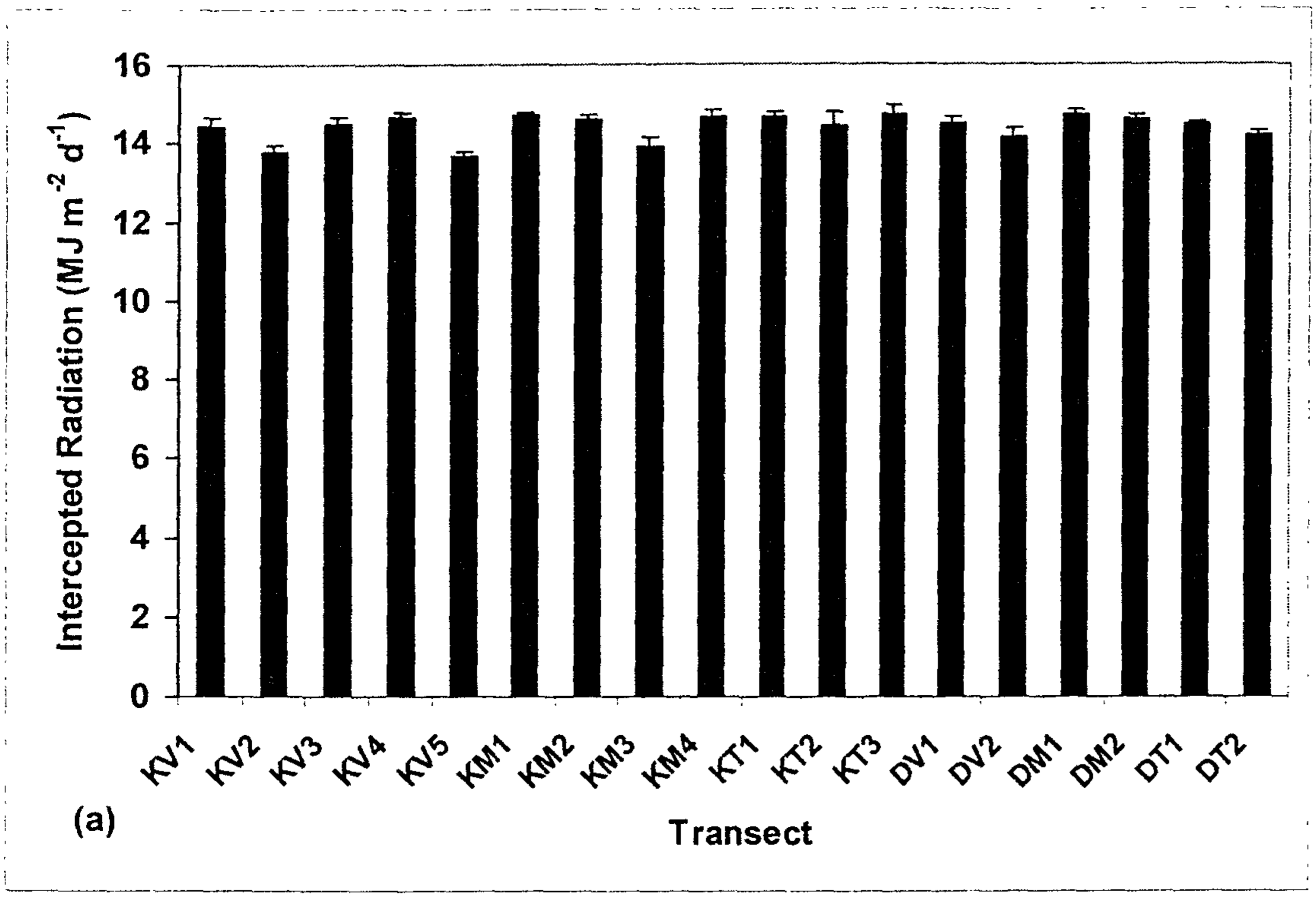
corresponding values in Kudawa (Fig. 3.63.a) and Morningside (Fig. 3.63.c), which did not differ significantly.

3.7 Intercepted Radiation (R_I), Radiation Use Efficiency (RUE) and Carbon Sequestration Rate (C_{seq})

3.7.1 KDN forest complex

Mean daily intercepted radiation (R_I), RUE and mean annual carbon sequestration rate (C_{seq}) in the KDN forest complex showed highly significant ($p<0.0001$) variation between different transects (Figs. 3.64 and 3.65). R_I ranged from 13.637 (± 0.172) to 14.742 (± 0.187) MJ m^{-2} d^{-1}, while the respective ranges for RUE and C_{seq} were from 0.288 (± 0.012) to 0.430 (± 0.062) g MJ^{-1} and from 7.403 (± 0.190) to 11.373 (± 1.624) mt ha^{-1} yr^{-1} respectively. The respective ranges for the individual sampling locations, i.e. 12.332 – 15.545 MJ m^{-2} d^{-1} for R_I, 0.269 – 0.597 g MJ^{-1} for RUE and 6.566 – 15.721 mt ha^{-1} yr^{-1} for C_{seq}, were wider than those for the respective transect means. When averaged across all 18 transects in the KDN forest complex, the respective mean values were 14.393 (± 0.049) MJ m^{-2} d^{-1} for R_I, 0.341 (± 0.049) g MJ^{-1} for RUE and 8.953 (± 0.133) mt ha^{-1} yr^{-1} for C_{seq}.

Frequency distribution of the C_{seq} rates of individual sampling points in the KDN forest complex is given in Fig. 3.66. The respective percentile points in the frequency distribution are given in Table 3.12. The frequency distribution shows that 95% of the sampling points had C_{seq} rates which were less than 11.5 mt ha^{-1} yr^{-1}, with the 95th percentile point being 11.484 mt ha^{-1} yr^{-1}. Except for the 5% of the sampling points having C_{seq} rates greater than 11.5 mt ha^{-1} yr^{-1}, the rest showed an approximate normal



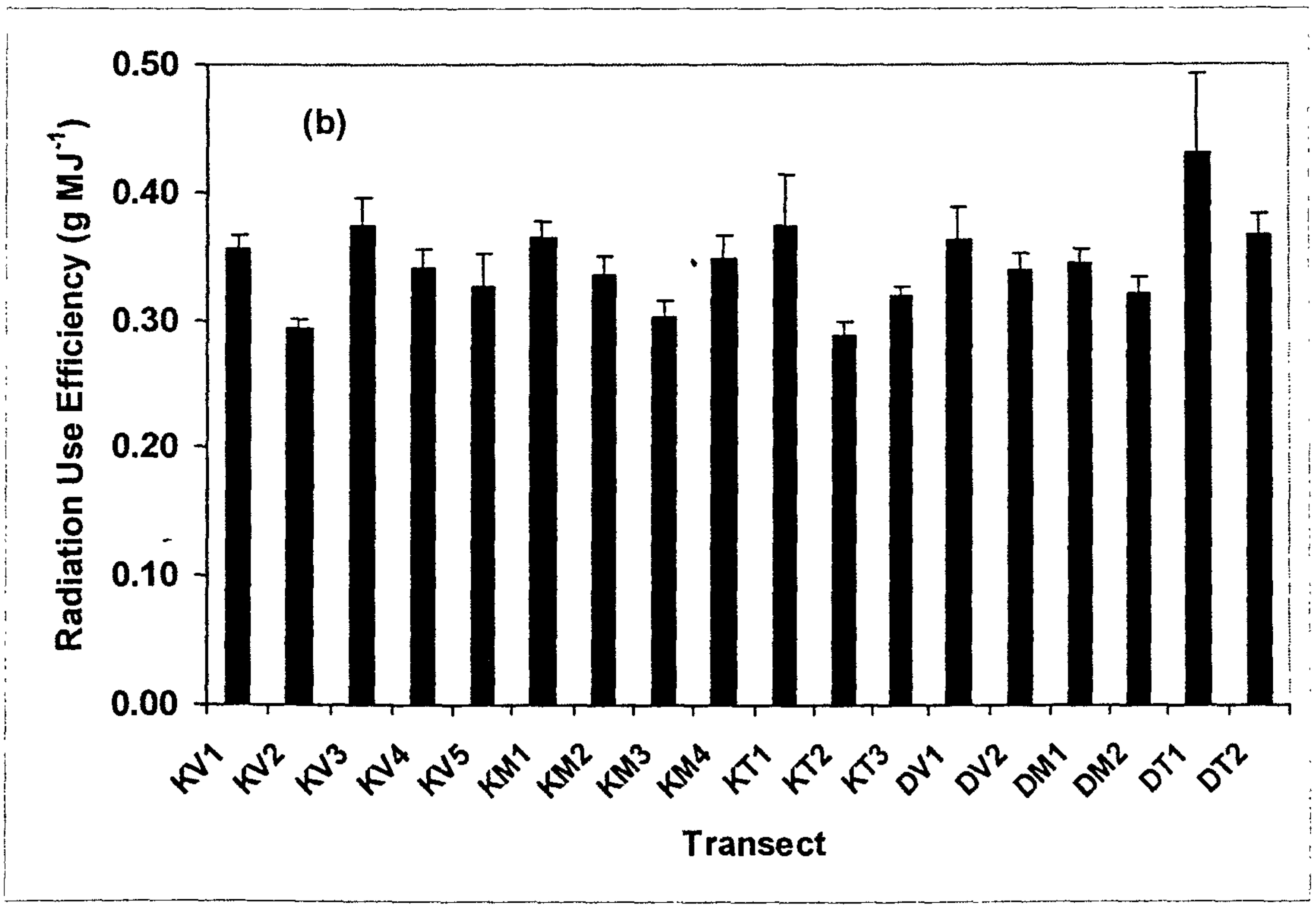


Figure 3.64: Variation of mean radiation interception (a) and radiation use efficiency (b) between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

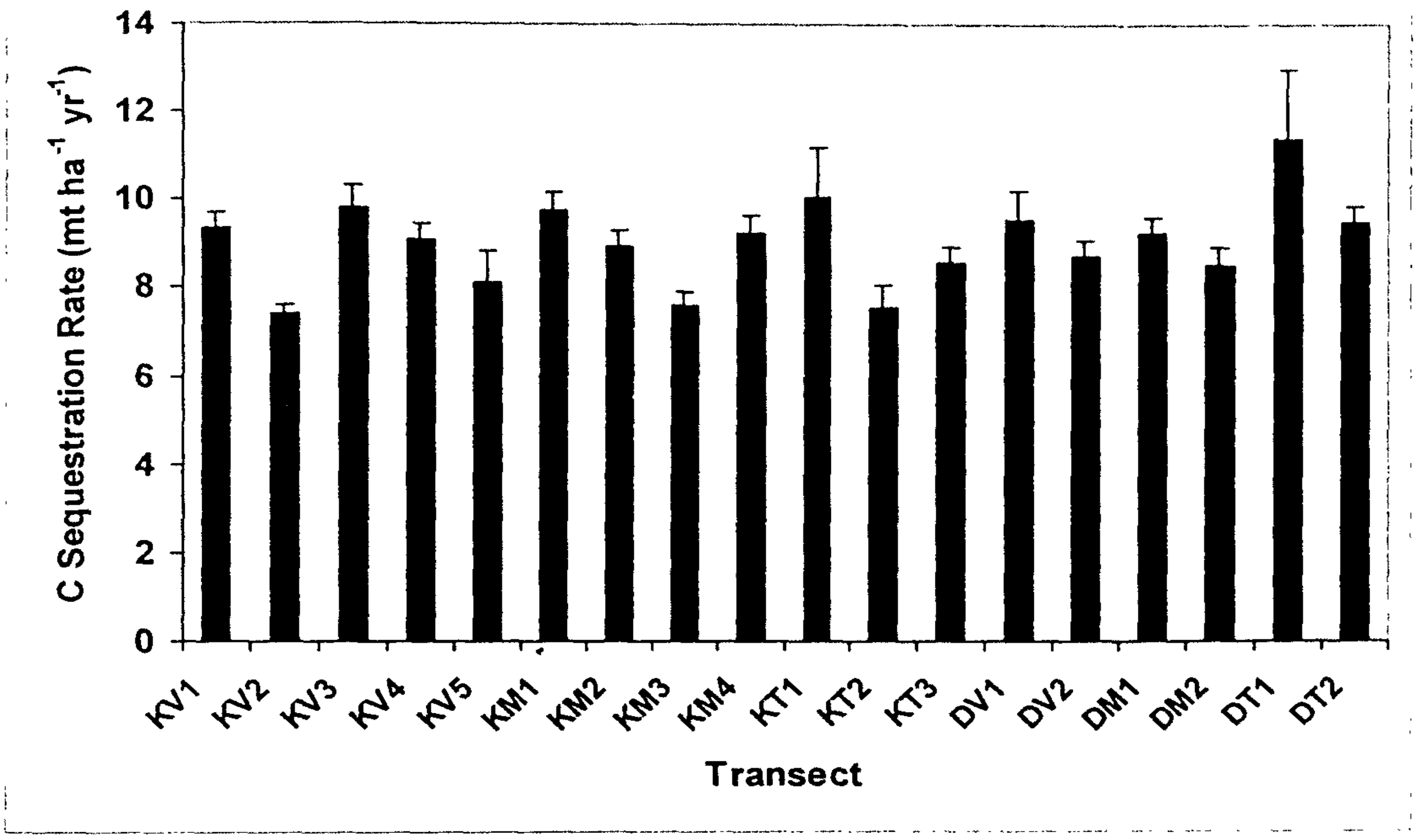


Figure 3.65: Variation of mean annual carbon sequestration rate between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

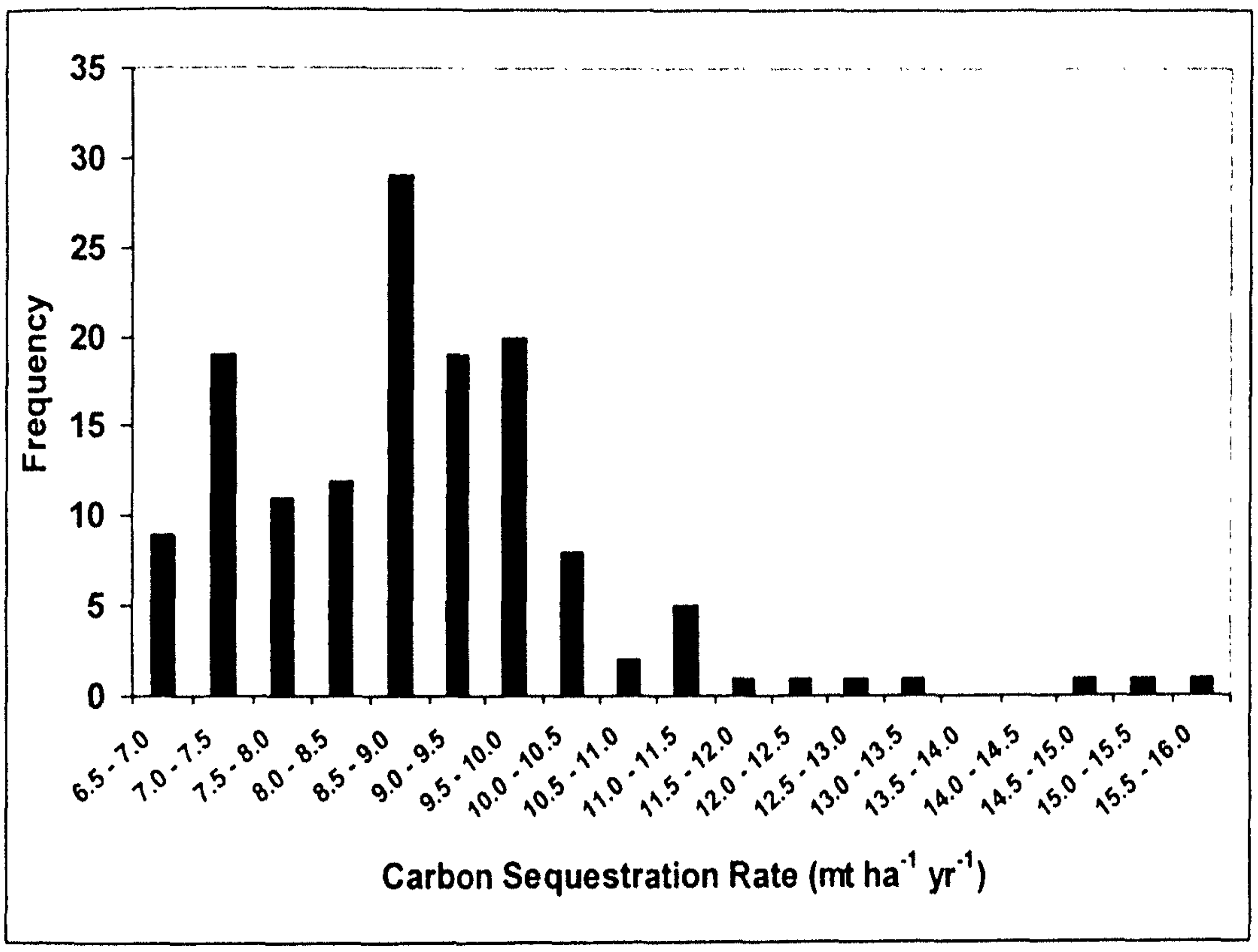


Figure 3.66: Frequency distribution for carbon sequestration rates of different sampling locations of the KDN forest complex.

Table 3.12: Percentiles of the distributions of carbon sequestration rates in net primary production (mt C ha^{-1} yr^{-1}) across individual sampling locations in the KDN forest complex and the Sinharaja MAB reserve

forest	N[†]	Percentiles in the frequency distribution						
		5th	10th	25th	50th	75th	90th	95th
KDN	141	6.920	7.211	7.848	8.787	9.664	10.454	11.484
Sinharaja	202	6.142	6.333	6.646	7.172	7.729	8.527	9.298
% Increase[‡]		12.68	13.87	18.07	22.53	25.03	22.60	23.52

[†] Number of data points

[‡] Percentage increase of percentile points in KDN relative to corresponding percentiles in Sinharaja.

distribution, with the mode, i.e. the class interval having the highest frequency (8.5 – 9.0 mt ha^{-1} yr^{-1}), and the median class interval coinciding with the class interval containing the population mean (i.e. 8.953 mt ha^{-1} yr^{-1}). The 50th percentile point (i.e. 8.787 mt ha^{-1} yr^{-1}) was also very close to the population mean.

The forest region x elevation zone interaction effect on R_l was highly significant ($p=0.0004$). This was because of the different patterns of variation of R_l in Kanneliya and Dediyagala (Fig. 3.67.a). In Kanneliya, R_l increased with increasing elevation while in Dediyagala, the mid-slope had a significantly ($p<0.05$) greater R_l than the valley and the mid-slope which did not differ significantly. RUE showed highly significant variation between different forest regions ($p=0.0012$) and elevation zones ($p=0.0007$) (Fig. 3.67.b). When averaged across elevation zones, RUE in Dediyagala was significantly ($p=0.0012$) greater than in Kanneliya. While there was no significant ($p=0.05$) variation in RUE between different elevation zones in Kanneliya, it was significantly ($p<0.05$) greater in the ridge-top in Dediyagala. However, the forest region x elevation zone interaction effect on RUE was not significant at $p=0.05$. C_{seq} varied significantly between forest regions ($p=0.0002$) and elevation zones ($p=0.0164$) (Fig. 3.68). The forest region x elevation zone interaction effect on C_{seq} was not significant at $p=0.05$. When averaged across the two forest regions, C_{seq} increased with increasing elevation zone, which the ridge-top showing a significantly ($p<0.05$) greater value.

3.7.2 Sinharaja MAB forest reserve

R_l, RUE and C_{seq} in the Sinharaja MAB reserve showed highly significant ($p<0.0001$) variation between different transects (Figs. 3.69 and 3.70) and ranged from 11.905 (±

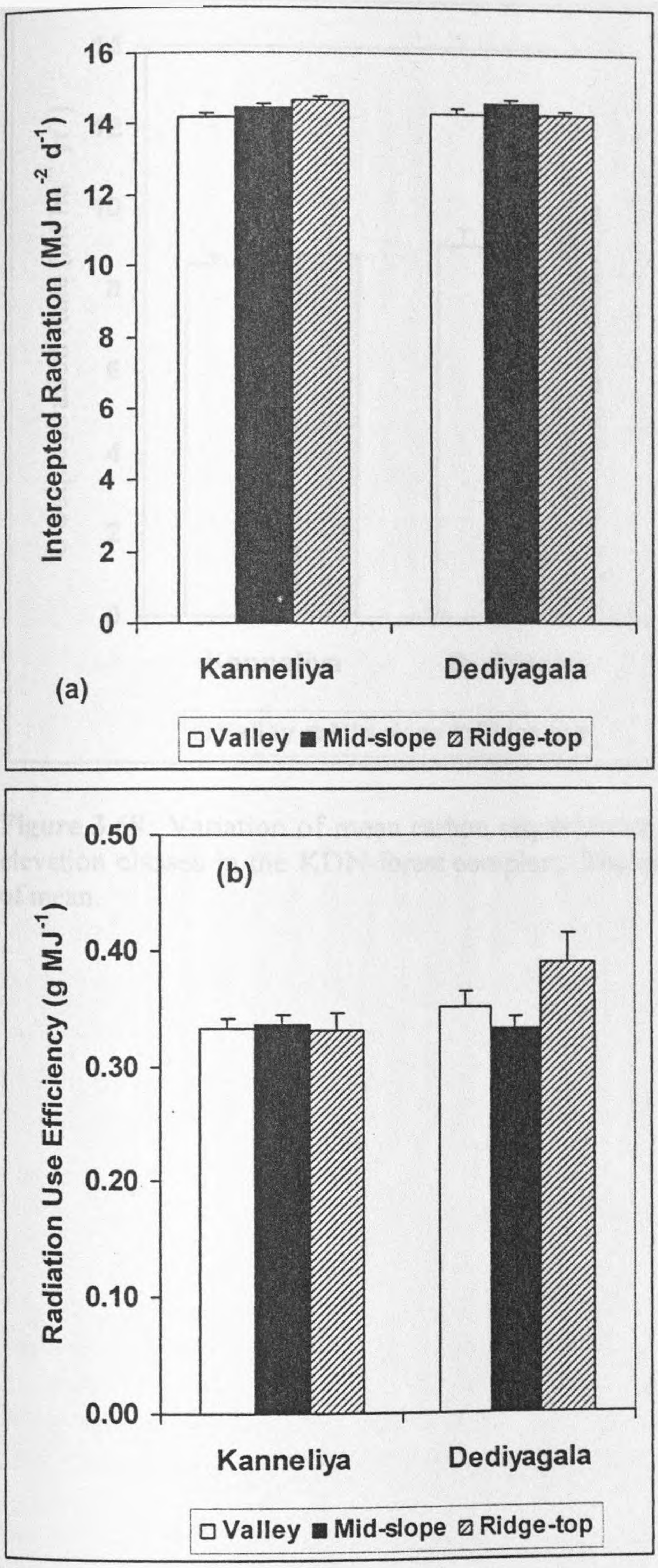


Figure 3.67: Variation of mean radiation interception (a) and radiation use efficiency (b) between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

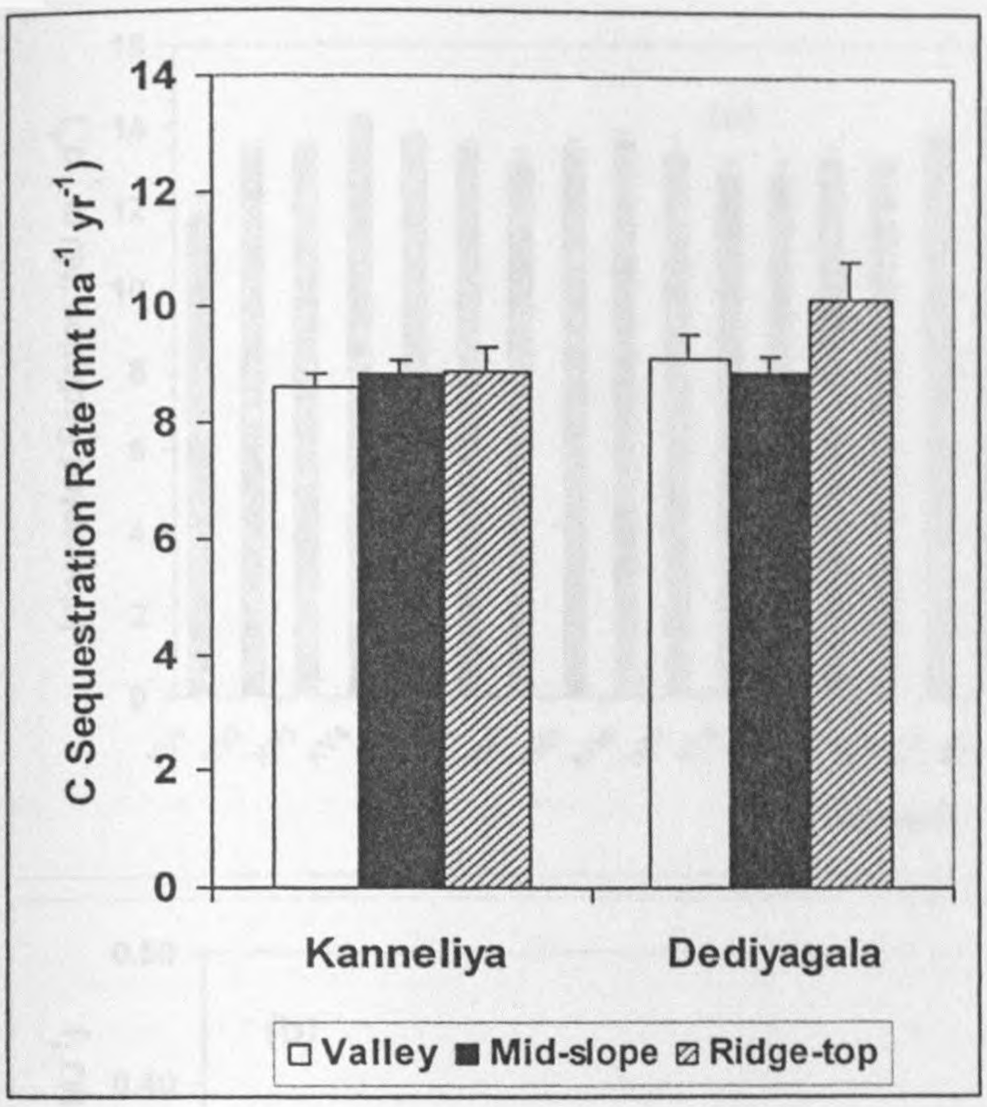


Figure 3.68: Variation of mean carbon sequestration rate between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

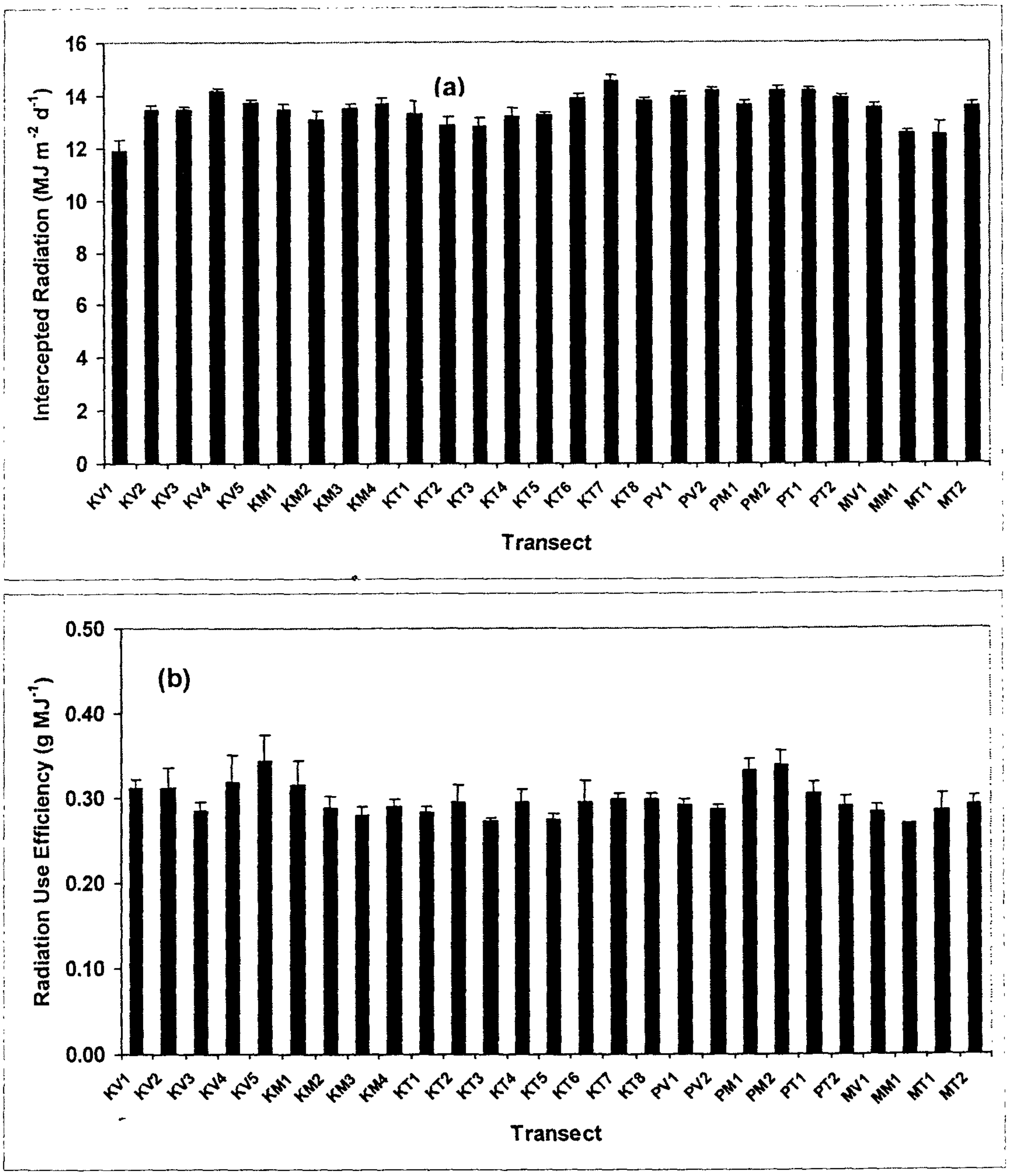


Figure 3.69: Variation of mean radiation interception (a) and radiation use efficiency (b) between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M-Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

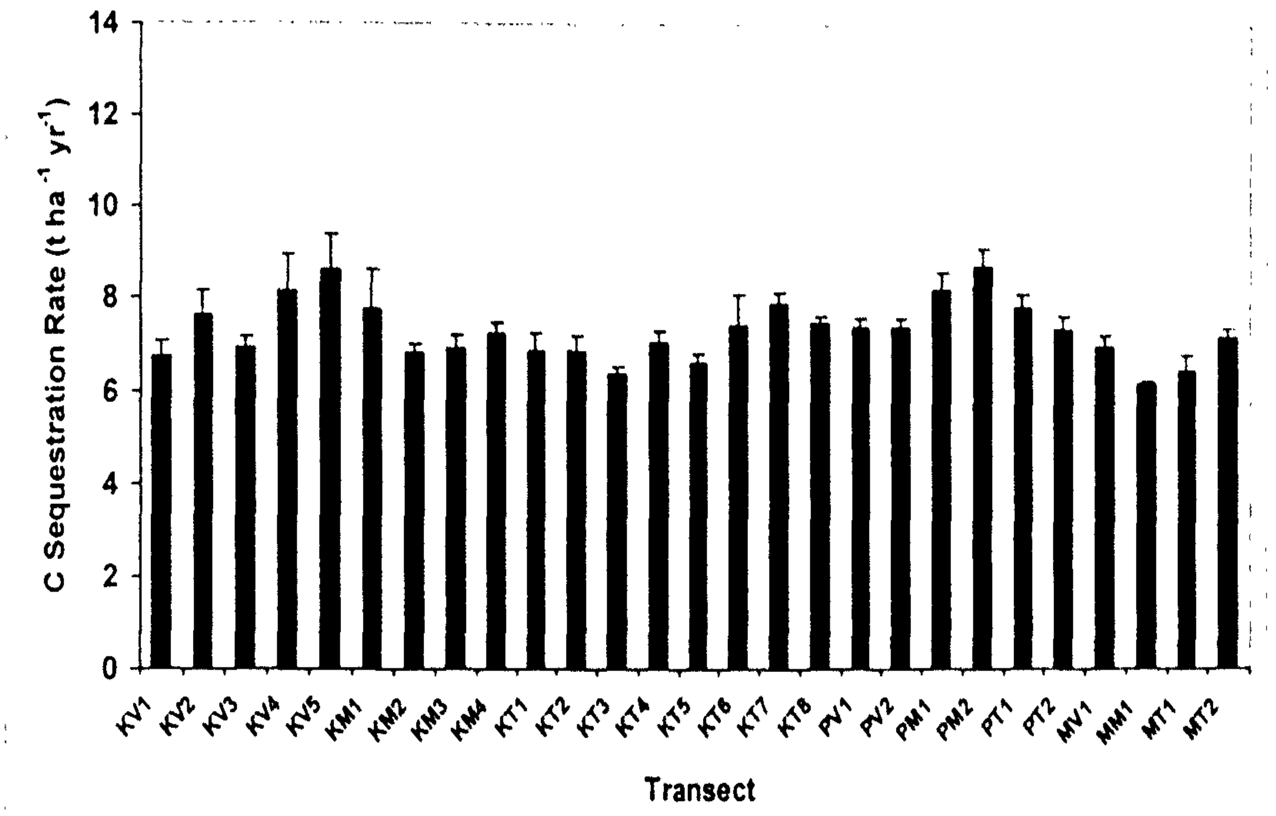


Figure 3.70: Variation of mean annual carbon sequestration rate between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

0.421) to 14.512 (± 0.249) MJ m^{-2} d^{-1} (R_I), from 0.269 (± 0.0002) to 0.344 (± 0.030) g MJ^{-1} (RUE) and from 6.165 (± 0.046) to 8.749 (± 0.362) mt ha^{-1} yr^{-1} (C_{seq}). Although the above ranges at Sinharaja overlapped with the respective ranges of the KDN forest complex (Figs. 3.64 and 3.65), the above ranges were slightly lower than those of KDN. The respective ranges for the individual sampling locations in Sinharaja, i.e. 10.687 – 15.028 MJ m^{-2} d^{-1} for R_I, 0.254 – 0.613 g MJ^{-1} for RUE and 5.678 – 16.487 mt ha^{-1} yr^{-1} for C_{seq}, were wider than those for the respective transect means in Sinharaja. Furthermore, the respective ranges for individual sampling locations in Sinharaja were wider than the corresponding ranges in KDN. When averaged across all 27 transects in the Sinharaja MAB forest complex, the respective mean values were 13.543 (± 0.056) MJ m^{-2} d^{-1} for R_I, 0.300 (± 0.004) g MJ^{-1} for RUE and 7.403 (± 0.094) mt ha^{-1} yr^{-1} for C_{seq}. Frequency distribution of the C_{seq} rates of individual sampling points in the Sinharaja MAB forest reserve is given in Fig. 3.71. The respective percentile points in the frequency distribution are given in Table 3.12. The frequency distribution shows that 95.5% of the sampling points had C_{seq} rates which were less than 9.5 mt ha^{-1} yr^{-1}, with the 95th percentile point being 9.298 mt ha^{-1} yr^{-1}. Except for the 4.5% of the sampling points having C_{seq} rates greater than 9.5 mt ha^{-1} yr^{-1}, the rest showed an frequency distribution, which was slightly skewed to the left. However, similar to the frequency distribution of KDN (Fig. 3.66), the mode, i.e. the class interval having the highest frequency (7.0 – 7.5 mt ha^{-1} yr^{-1}), and the median class interval still coincided with the class interval containing the population mean (i.e. 7.403 mt ha^{-1} yr^{-1}). Similar to KDN, the 50th percentile point (i.e. 7.172 mt ha^{-1} yr^{-1}) was also very close to the population mean (Table 3.12).

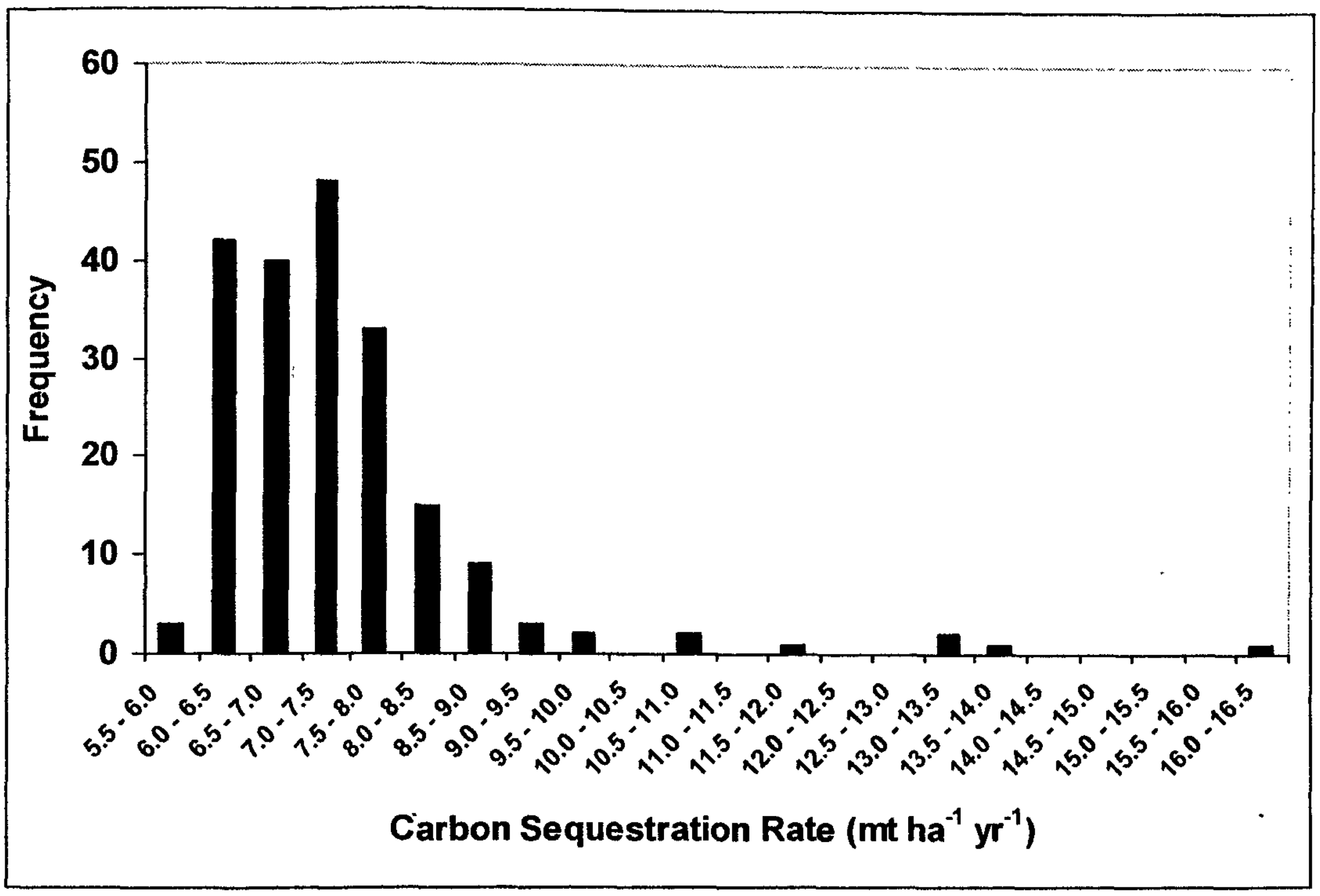


Figure 3.71: Frequency distribution for carbon sequestration rates of different sampling locations of the Sinharaja MAB forest reserve.

Analysis of variance of the respective transect means showed that the KDN forest complex had significantly greater ($p<0.0001$) R_I, RUE and C_{seq} than Sinharaja MAB forest reserve. Analysis of variance of data points from individual sampling locations also showed a similar result. In terms of average magnitude, R_I, RUE and C_{seq} of KDN were 6%, 14% and 21% greater than those of Sinharaja. All percentile points in the frequency distribution of KDN were greater than the corresponding points in Sinharaja (Table 3.12), with the percentage increases ranging from 12.68% at the 5th percentile to 25.03% at the 75th percentile. Notably, the percentage increase of the respective percentiles in KDN over the corresponding percentiles in Sinharaja increased from the 5th to the 75th and then declined slightly.

Coefficient of variation (CV) of R_I was greater in Sinharaja than in KDN for both individual sampling points and transects (Table 3.13), indicating greater within-forest variability in the forest canopy and its radiation interception capacity in Sinharaja. However, CV of RUE was greater in KDN. On the other hand, CV of C_{seq} for individual sampling points was slightly greater in KDN as compared to Sinharaja. In contrast, the opposite was observed for CV of C_{seq} based on transect means.

R_I showed highly significant ($p<0.0001$) variation between different forest regions with Pitadeniya having a greater mean R_I than Kudawa and Morningside, which did not differ significantly (Fig. 3.72.a). However, R_I did not differ significantly ($p=0.05$) with elevation zones. The forest region x elevation zone interaction effect on R_I was not significant as well. There were significant ($p<0.05$) forest region x elevation zone interaction effects on RUE (Fig. 3.72.b) and C_{seq} (Fig. 3.73). This was because of the differential patterns of response of RUE and C_{seq} in different forest regions. Both RUE

Table 3.13: Coefficient of variation (CV) of radiation interception (R_I), radiation use efficiency (RUE) and carbon sequestration rate (C_{seq}) of the KDN forest complex and the Sinharaja MAB reserve

	KDN		Sinharaja	
	Individual sampling points	Transect means	Individual sampling points	Transect means
R_I	4.07	2.33	5.85	4.42
RUE	17.25	9.88	16.75	6.46
C_{seq}	17.59	10.89	18.00	8.96
N[†]	141	18	202	27

[†] Number of data points

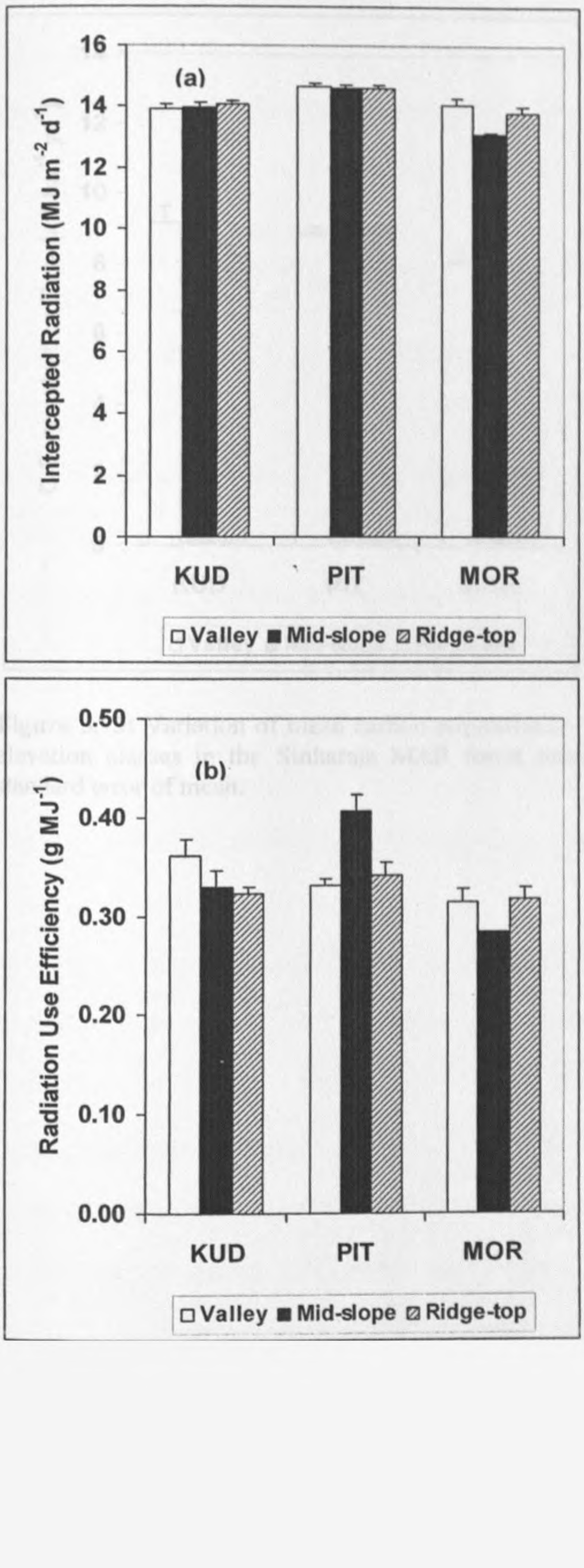


Figure 3.72: Variation of mean radiation interception (a) and radiation use efficiency (b) between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean.

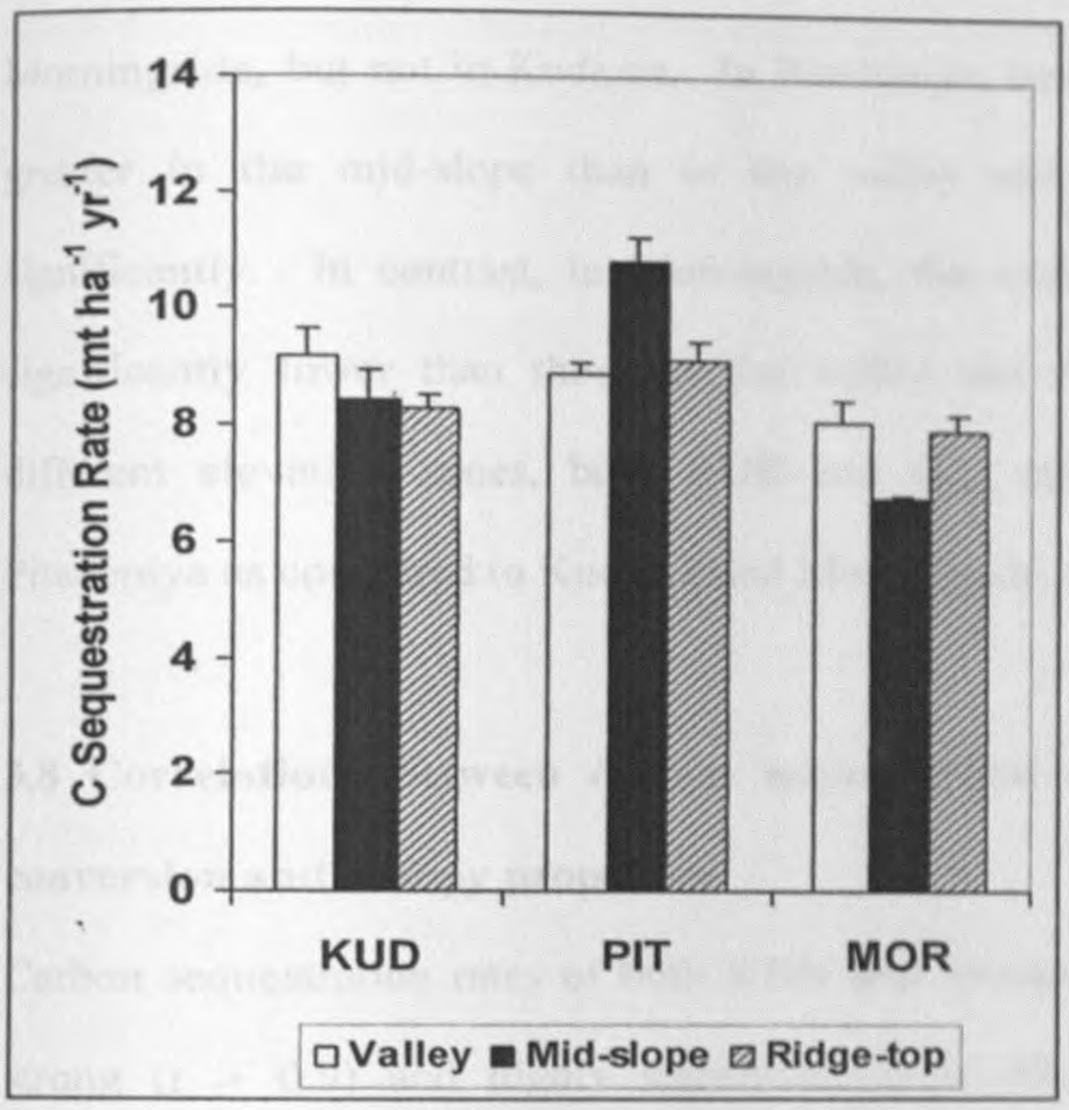


Figure 3.73: Variation of mean carbon sequestration rate between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean.

and C_{seq} showed significant ($p<0.05$) variation between elevation zones in Pitadeniya and Morningside, but not in Kudawa. In Pitadeniya, both RUE and C_{seq} were significantly greater in the mid-slope than in the valley and ridge-top, which did not differ significantly. In contrast, in Morningside, the mid-slope RUE and C_{seq} values were significantly lower than those in the valley and ridge-top. When averaged across different elevation zones, both RUE and C_{seq} values were significantly greater in Pitadeniya as compared to Kudawa and Morningside, which did not differ significantly.

3.8 Correlations between carbon sequestration rate, radiation interception and conversion and canopy properties

Carbon sequestration rates of both KDN and Sinharaja forests complexes showed very strong ($r > 0.9$) and highly significant ($p<0.0001$) positive correlations with their respective RUE and LAI values (Tables 3.14 and 3.15). In addition, C_{seq} of both forests showed a medium-strong (r at 0.58 and 0.67) and highly significant ($p<0.0001$) positive correlation with mean leaf angle (MLA). The positive correlation between C_{seq} and intercepted radiation (R_I) in both forests was highly significant ($p<0.0001$), but of lower strength with correlation coefficients of 0.24 and 0.36. There was a strong ($r < -0.7$) and highly significant ($p<0.0001$) negative correlation between C_{seq} and canopy light extinction coefficient (k). In addition, RUE of both forests, showed strong ($r > 0.7$) and highly significant ($p<0.0001$) positive correlations with LAI and MLA and a negative correlation with the canopy light extinction coefficient. As expected, in both forests, the canopy light extinction coefficient showed strong ($r < -0.85$) and highly significant ($p<0.0001$) negative correlations with LAI and MLA.

Table 3.14: Linear correlation coefficients for correlations between estimated carbon sequestration rates, radiation interception and conversion and canopy properties of the KDN forest complex

	Intercepted Radiation	Radiation Use Efficiency	Leaf Area Index	Mean Leaf Angle	Light Extinction Coefficient
C Sequestration Rate	0.243	0.972	0.976	0.670	-0.809
	(0.0037)[†]	*(<.0001)*	*(<.0001)*	*(<.0001)*	*(<.0001)*
Intercepted Radiation	-	0.012	0.051	-0.429	0.317
		ns	*ns*	*(<.0001)*	*(0.0001)*
Radiation Use Efficiency		-	0.994	0.794	-0.914
			(<.0001)	*(<.0001)*	*(<.0001)*
Leaf Area Index			-	0.769	-0.894
				(<.0001)	*(<.0001)*
Mean Leaf Angle				-	-0.881
					(<.0001)

[†] Probability of each correlation coefficient not being significantly greater than zero.

[ns] Correlation coefficient is not significantly different from zero at $p=0.05$.

The number of data points for each correlation was 141.

Table 3.15: Linear correlation coefficients for correlations between estimated carbon sequestration rates, radiation interception and conversion and canopy properties of the Sinharaja MAB forest reserve

	Intercepted Radiation	Radiation Use Efficiency	Leaf Area Index	Mean Leaf Angle	Light Extinction Coefficient
C Sequestration Rate	0.358	0.972	0.984	0.586	-0.798
	(<.0001)†	*(<.0001)*	*(<.0001)*	*(<.0001)*	*(<.0001)*
Intercepted Radiation	-	0.134	0.261	-0.281	0.162
		ns	*(0.0002)*	*(<.0001)*	*(0.0209)*
Radiation Use Efficiency	-	-	0.980	0.704	-0.898
			(<.0001)	*(<.0001)*	*(<.0001)*
Leaf Area Index	-	-	-	0.651 *(<.0001)*	-0.851 *(<.0001)*
Mean Leaf Angle	-	-	-	-	-0.858
					(<.0001)

†Probability of each correlation coefficient not being significantly greater than zero.
^{ns}Correlation coefficient is not significantly different from zero at p=0.05.
The number of data points for each correlation was 202.

3.9 Total carbon stock in standing biomass (C_{TBM}), residence time (t_r) and carbon sequestration as net ecosystem productivity (NEP)

3.9.1 KDN forest complex

There was highly significant ($p<0.0001$) variation between different transects in the total carbon stock in standing biomass (Fig. 3.74.a), residence time of carbon sequestered in net primary production (Fig. 3.74.b) and carbon sequestered in net ecosystem production (Fig. 3.75) in the KDN forest complex. The respective ranges of transect means for C_{TBM}, t_r and NEP were from 284 (± 9) to 353 (± 26) mt C ha^{-1}, from 32 (± 2) to 39 (± 0.5) yr and from 0.341 (± 0.011) to 0.424 (± 0.031) mt C ha^{-1} yr^{-1}. With respect to C_{TBM} and NEP, the respective ranges for individual sampling locations, i.e. 259 – 419 mt C ha^{-1} and 0.311 – 0.503 mt C ha^{-1} yr^{-1}, were wider than those for the respective transect means. When averaged across all 18 transects in the KDN forest complex, the respective mean values were 315 (± 2) mt C ha^{-1} for C_{TBM} and 0.378 (± 0.003) mt C ha^{-1} yr^{-1} for NEP.

The respective frequency distributions of C_{TBM} and NEP of the individual sampling points in the KDN forest complex are given in Figs. 3.76.a and b. The respective percentile points in the frequency distribution are given in Tables 3.16 and 3.17. The frequency distribution for C_{TBM} (Fig. 3.76.a) showed that 96% of the sampling points had C_{TBM} values which were less than 375 mt C ha^{-1}, with the 95th percentile point being 362 mt C ha^{-1} (Table 3.16). Except for the 4% of the sampling points having C_{TBM} values greater than 375 mt C ha^{-1}, the rest showed an approximate normal distribution, with the mode, i.e. the class interval having the highest frequency (300 – 324 mt C ha^{-1}), and median class interval coinciding with the class interval containing the population mean

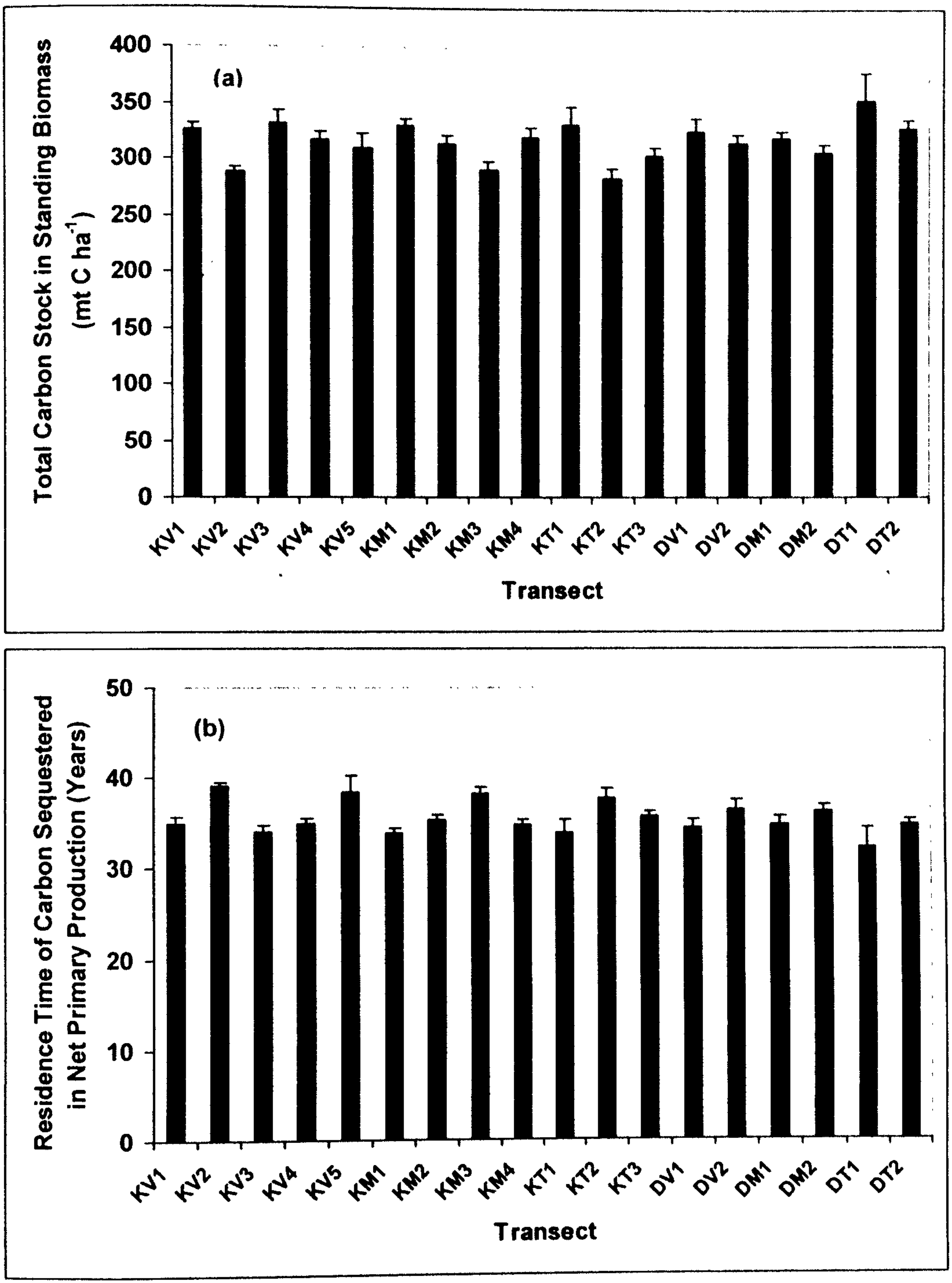


Figure 3.74: Variation of total carbon stock of standing biomass (a) and residence time of carbon sequestered in net primary production (b) between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

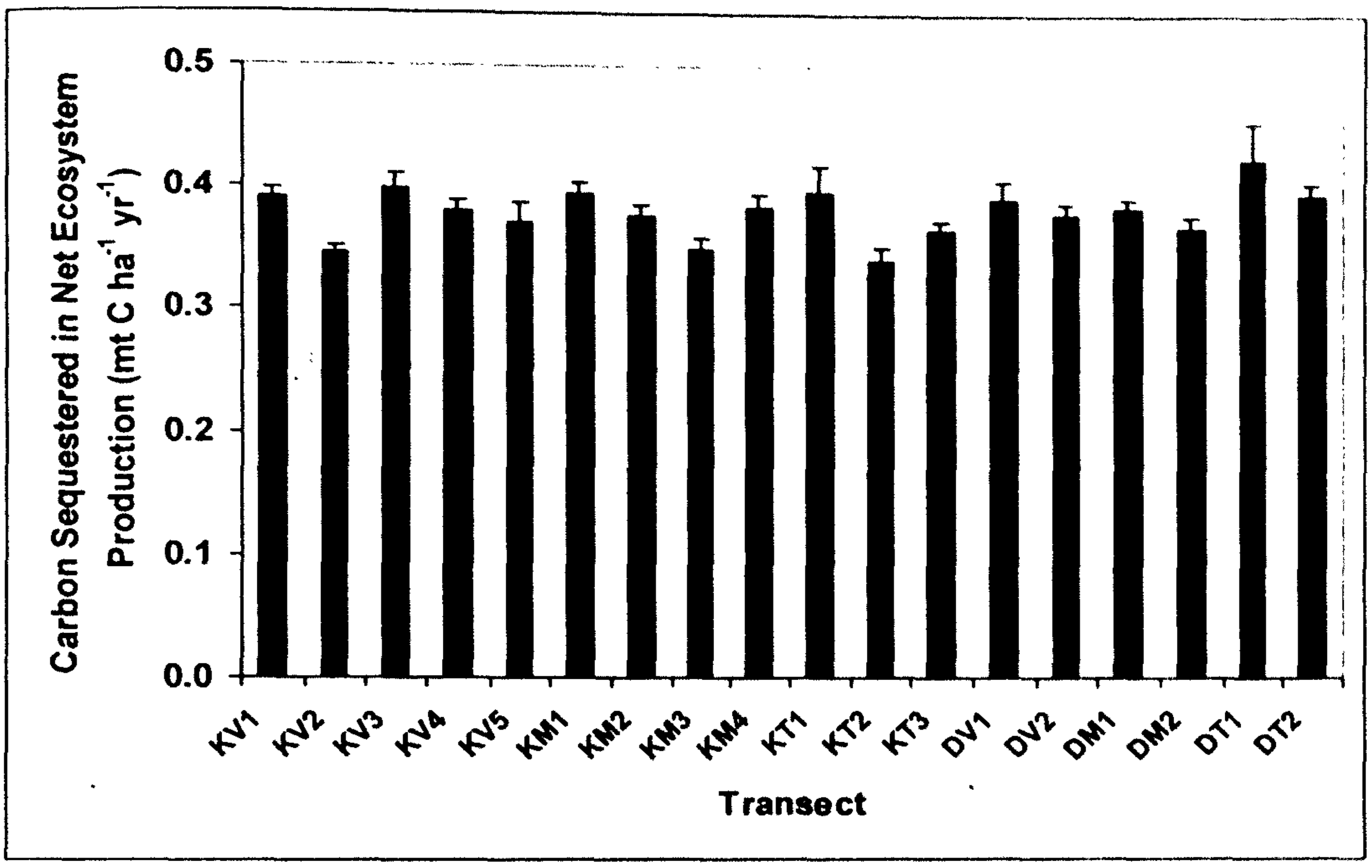


Figure 3.75: Variation of carbon sequestered in net ecosystem production between different transects of the Kanneliya-Dediyagala-Nakiyadeniya forest complex. The error bars indicate the standard error of mean. Key to the label of transects: K- Kanneliya; D- Dediyagala; V- Valley; M- Mid-slope; T- Ridge-top.

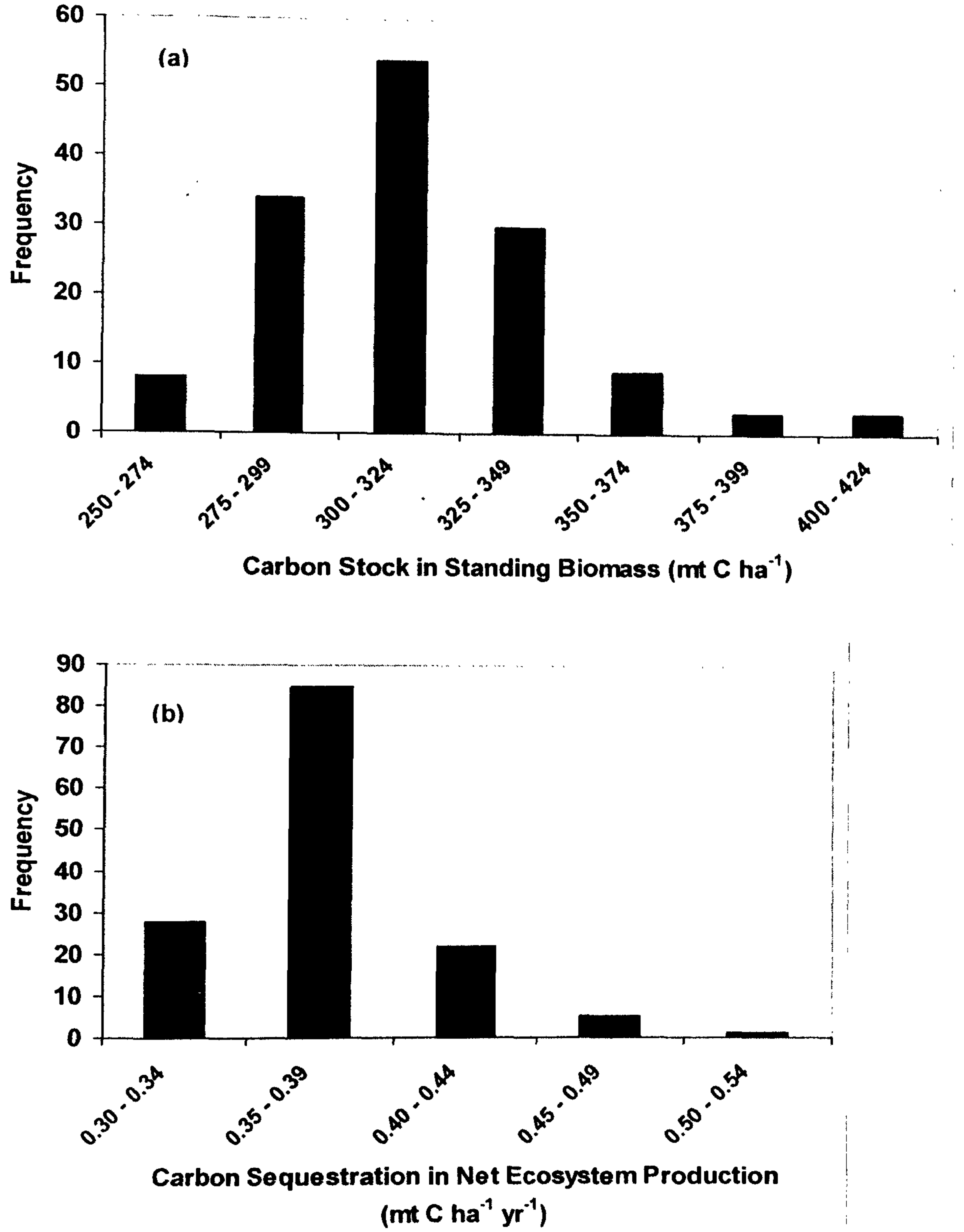


Figure 3.76: Frequency distributions for total carbon stocks in standing biomass (a) and carbon sequestration in net ecosystem production (b) of different sampling locations of the KDN forest complex.

Table 3.16: Percentiles of the distributions of total carbon stocks of standing biomass (mt C ha^{-1}) across individual sampling locations in the KDN forest complex and the Sinharaja MAB reserve

forest	N[†]	Percentiles in the frequency distribution						
		5th	10th	25th	50th	75th	90th	95th
KDN	141	273.01	282.36	294.57	312.26	329.88	352.64	362.35
Sinharaja	202	260.57	267.15	287.26	305.08	326.48	350.29	366.48
% Increase[‡]		4.77	5.69	2.55	2.35	1.04	0.67	-1.13

[†] Number of data points

[‡] Percentage increase of percentile points in KDN relative to corresponding percentiles in Sinharaja.

Table 3.17: Percentiles of the distributions of carbon sequestration rates in net ecosystem production (mt C ha^{-1} yr^{-1}) across individual sampling locations in the KDN forest complex and the Sinharaja MAB reserve

forest	N[†]	Percentiles in the frequency distribution						
		5th	10th	25th	50th	75th	90th	95th
KDN	141	0.328	0.339	0.353	0.375	0.396	0.423	0.435
Sinharaja	202	0.313	0.321	0.345	0.366	0.392	0.420	0.440
% Increase[‡]		4.77	5.69	2.54	2.35	1.04	0.67	-1.13

[†] Number of data points

[‡] Percentage increase of percentile points in KDN relative to corresponding percentiles in Sinharaja.

(i.e. 315 mt C ha^{-1}). The 50th percentile point (i.e. 312 mt C ha^{-1}) was also very close to the population mean.

The frequency distribution for NEP (Fig. 3.76.b) showed that 96% of the sampling points had NEP values which were less than 0.45 mt C ha^{-1} yr^{-1}, with the 95th percentile point being 0.435 mt C ha^{-1} yr^{-1} (Table 3.17). Except for the 4% of the sampling points having NEP values greater than 0.45 mt C ha^{-1} yr^{-1}, the rest showed an approximate normal distribution, with the mode, i.e. 0.35 – 0.39 mt C ha^{-1} yr^{-1}, and median class interval coinciding with the class interval containing the population mean (i.e. 0.378 mt C ha^{-1} yr^{-1}). The 50th percentile point (i.e. 0.375 mt C ha^{-1} yr^{-1}) was also very close to the population mean.

Carbon sequestration rate as NEP showed a highly significant ($p<0.0001$) correlation ($r = 0.970$) with carbon sequestration rate in net primary production (C_{seq}).

All three parameters (i.e. C_{TBM}, t_r and NEP) showed highly significant ($p=0.0001$) variation between different forest regions within the KDN forest complex. They also showed significant ($p<0.05$) variation between different elevation zones. However, the forest region x elevation zone interaction was not significant at $p=0.05$. When averaged across elevation zones, Dediyagala had significantly greater C_{TBM} and NEP than Kanneliya (Figs. 3.77.a and 3.78) while the opposite was observed for t_r (Fig. 3.77.b). In both regions, t_r decreased with increasing elevation. However, no consistent variation pattern with elevation zone could be identified for C_{TBM} and NEP. While these two parameters showed their highest values in mid-slope in Kanneliya, the highest values in Dediyagala were shown in the ridge-top.

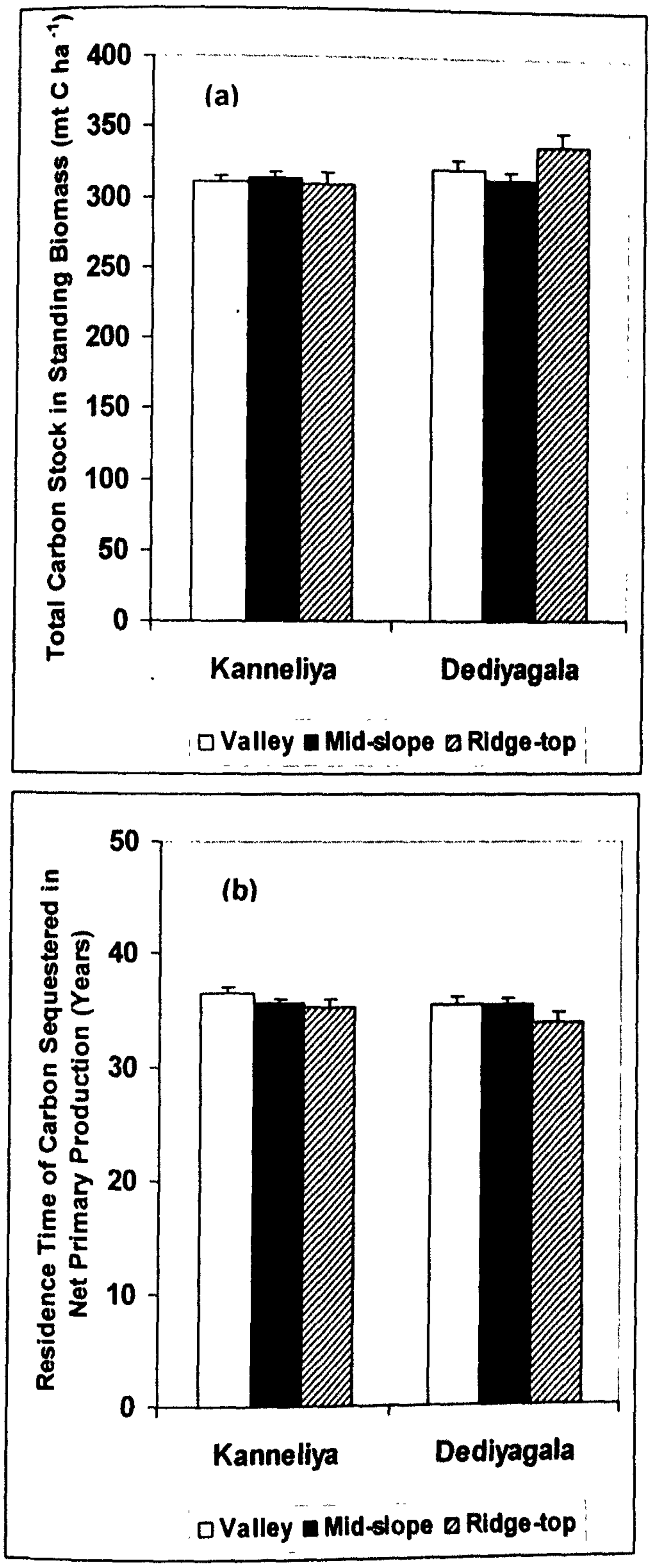


Figure 3.77: Variation of total carbon stock of standing biomass (a) and residence time of carbon sequestered in net primary production (b) between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

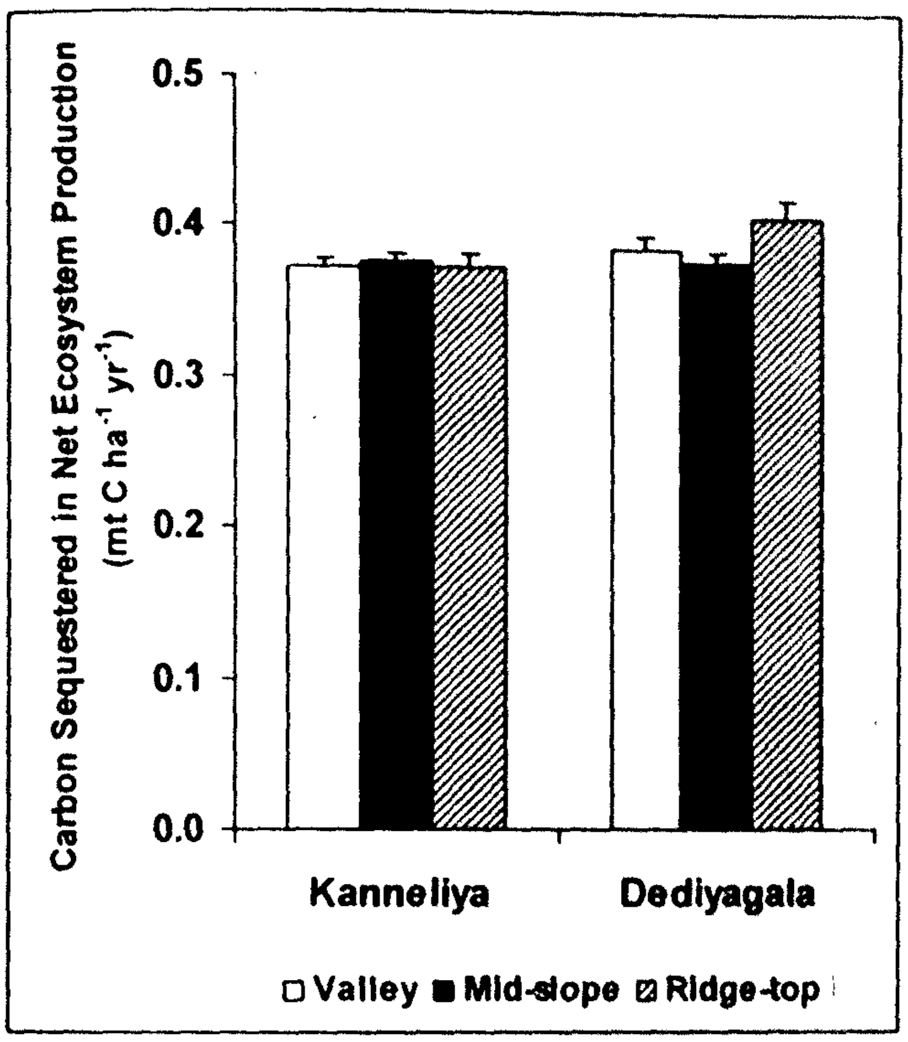


Figure 3.78: Variation of carbon sequestered in net ecosystem production between different regions and elevation classes in the KDN-forest complex. The error bars indicate the standard error of mean.

3.9.2 Sinharaja MAB forest reserve

There was significant variation in C_{TBM} ($p=0.0002$), t_r ($p=0.05$) and NEP ($p=0.0002$) between different transects in Sinharaja as well (Figs. 3.79 and 3.80). The respective transect means ranged from 260 (± 4) to 351 (± 10) mt C ha^{-1}, from 40 (± 0.5) to 45 (± 0.2) yr and from 0.313 (± 0.005) to 0.422 (± 0.012) mt C ha^{-1} yr^{-1}. With respect to C_{TBM} and NEP, the respective ranges for individual sampling locations, i.e. 223 – 508 mt C ha^{-1} and 0.269 – 0.609 mt C ha^{-1} yr^{-1}, were wider than those for the respective transect means. When averaged across all 27 transects in the Sinharaja forest reserve, the respective mean values were 310 (± 3) mt C ha^{-1} for C_{TBM} and 0.371 (± 0.003) mt C ha^{-1} yr^{-1} for NEP.

The respective frequency distributions of C_{TBM} and NEP of the individual sampling points in the Sinharaja forest reserve are given in Figs. 3.81.a and b. The respective percentile points in the frequency distribution are given in Tables 3.16 and 3.17. The frequency distribution for C_{TBM} (Fig. 3.81.a) showed that 98% of the sampling points had C_{TBM} values which were less than 425 mt C ha^{-1}, while the 95th percentile point being 366 mt C ha^{-1} (Table 3.16). Except for the 2% of the sampling points having C_{TBM} values greater than 425 mt C ha^{-1}, the rest showed an approximate normal distribution, with the mode, i.e. 300 – 324 mt C ha^{-1}, and median class interval coinciding with the class interval containing the population mean (i.e. 310 mt C ha^{-1}). The 50th percentile point (i.e. 305 mt C ha^{-1}) was also close to the population mean.

The frequency distribution for NEP (Fig. 3.81.b) showed that 98% of the sampling points had NEP values which were less than 0.50 mt C ha^{-1} yr^{-1}, while the 95th percentile point being 0.440 mt C ha^{-1} yr^{-1} (Table 3.17). Except for the 2% of the sampling points having NEP values greater than 0.50 mt C ha^{-1} yr^{-1}, the rest showed an approximate normal

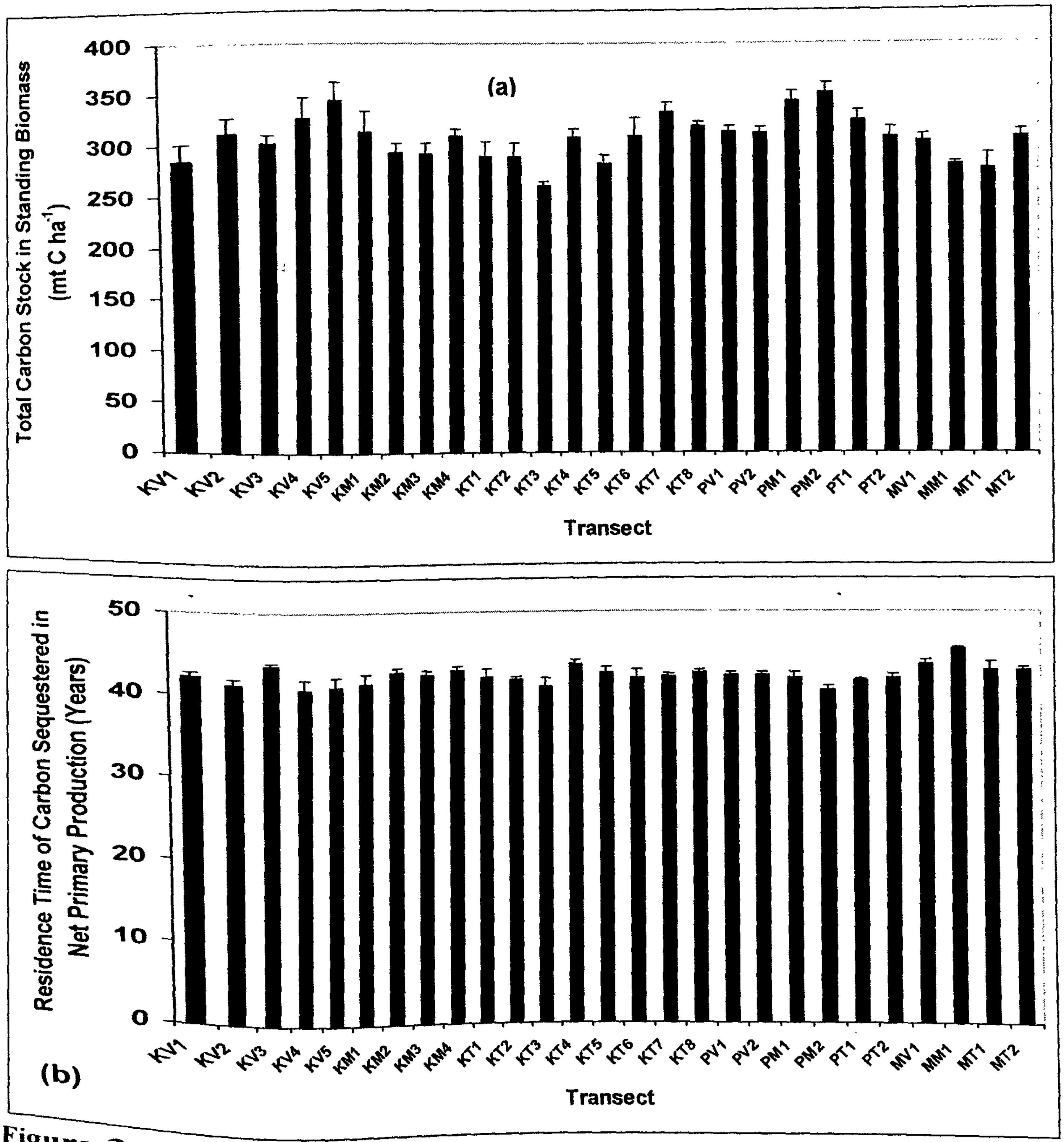


Figure 3.79: Variation of total carbon stock of standing biomass (a) and residence time of carbon sequestered in net primary production (b) between different transects between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

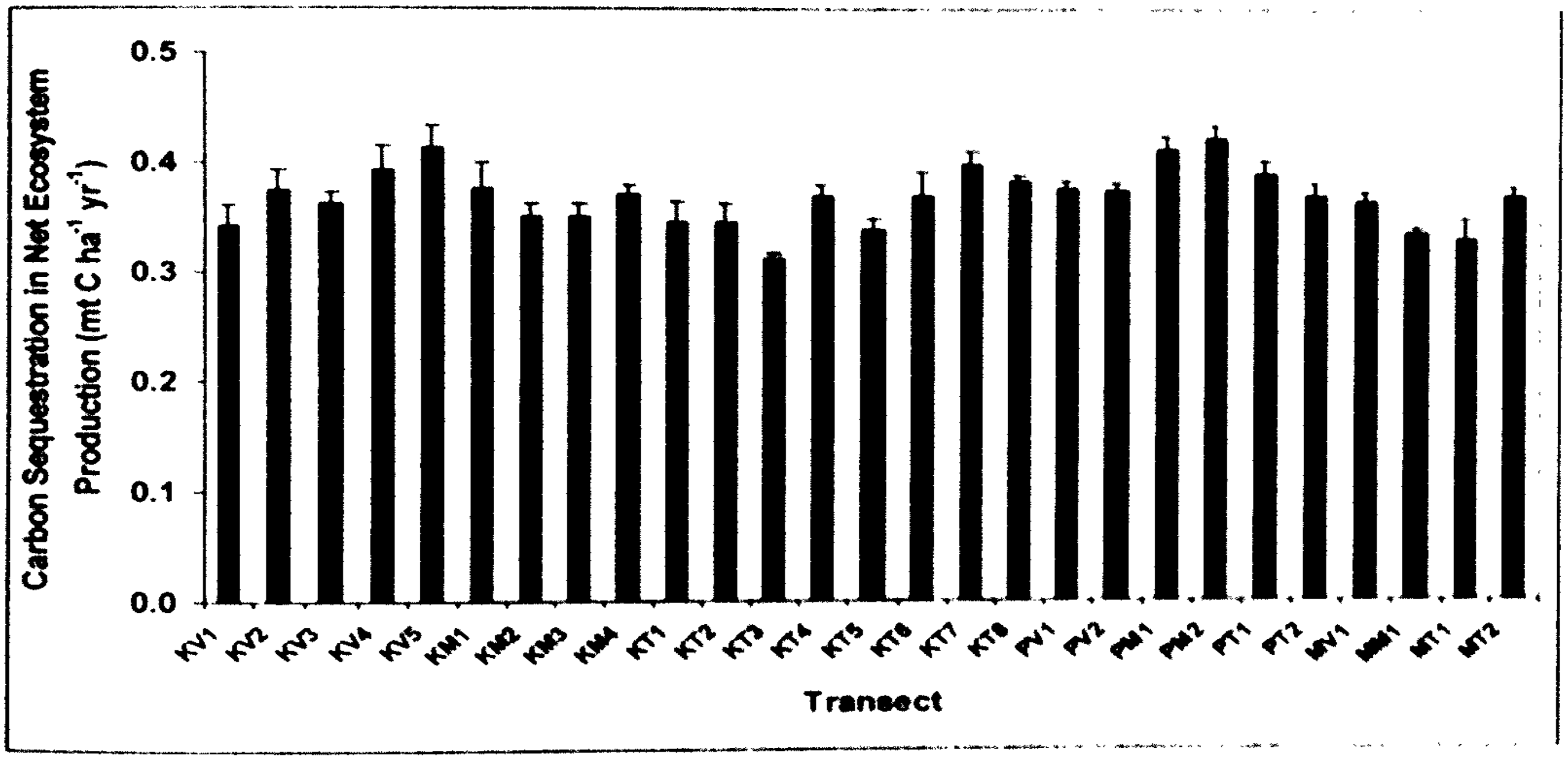


Figure 3.80: Variation of carbon sequestered in net ecosystem production between different transects of the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean. Key to the label of transects: K- Kudawa; P- Pitadeniya; M- Morningside; V- Valley; M- Mid-slope; T- Ridge-top.

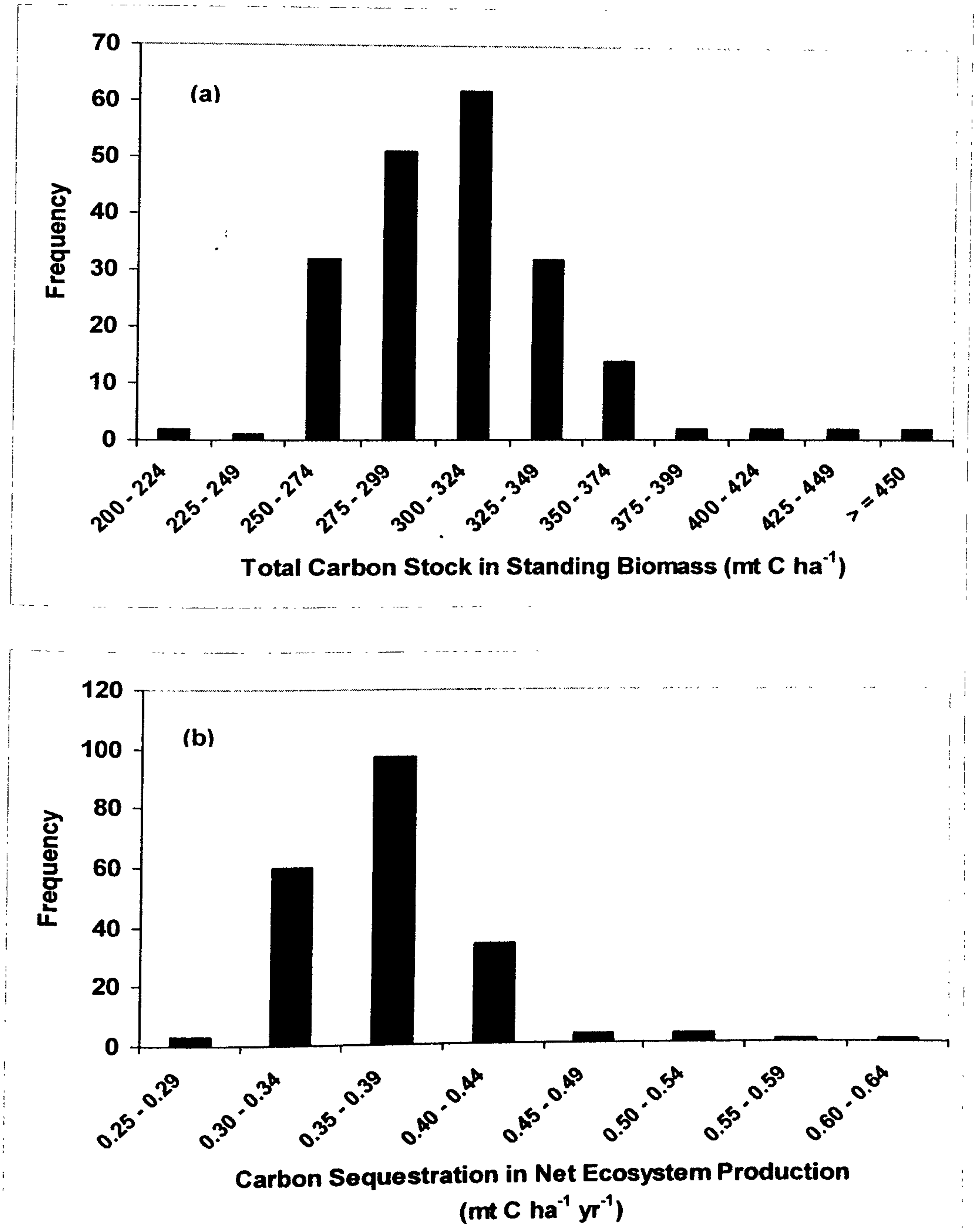


Figure 3.81: Frequency distributions for total carbon stocks in standing biomass and carbon sequestration in net ecosystem production of different sampling locations of the Sinharaja MAB forest reserve.

distribution, with the mode, i.e. 0.35 – 0.39 mt C ha^{-1} yr^{-1}, and median class interval coinciding with the class interval containing the population mean (i.e. 0.371 mt C ha^{-1} yr^{-1}). The 50th percentile point (i.e. 0.366 mt C ha^{-1} yr^{-1}) was also close to the population mean.

Similar to KDN, carbon sequestration rate as NEP showed a highly significant ($p<0.0001$) correlation ($r = 0.95$) with that in net primary production.

Analysis of variance of the respective transect means showed that the mean C_{TBM} and NEP did not differ significantly ($p=0.06$) between the two forest complexes. On the other hand, when ANOVA was done for individual sampling points, the respective means of C_{TBM} and NEP showed significant ($p=0.026$) variation between the two forests, with the KDN forest complex having a slightly (2%) higher values than Sinharaja. All percentile points, except the 95th, in the frequency distributions of C_{TBM} and NEP (Tables 3.16 and 3.17) were slightly greater in KDN, with the percentage increases ranging from 0.67% at the 90th percentile to 5.69% at the 10th percentile. Notably, percentage increases of the percentile points below the 50th percentile (i.e. the mean), were greater than those above the 50th percentile.

However, t_r showed highly significant ($p<0.0001$) variation with Sinharaja having a longer mean residence time (i.e. 42.2 yrs) than KDN (35.5 yrs) for carbon sequestered in net primary production. This was true for ANOVAs based on both transect means and individual sampling points. The 19% longer residence time in Sinharaja probably reflects the lower temperatures in Sinharaja, which decreases the rate of litter decomposition and hence the rate of heterotrophic respiration. The respective coefficients of variation (CV) of C_{TBM} and NEP were greater in Sinharaja as compared to KDN (Table 3.18) for both

Table 3.18: Coefficient of variation (CV) of total carbon stocks in standing biomass (C_{TBM}), residence time of carbon sequestered in net primary production (t_r) and carbon sequestration in net ecosystem production (NEP) of the KDN forest complex and the Sinharaja MAB reserve

	KDN		Sinharaja	
	Individual sampling points	Transect means	Individual sampling points	Transect means
C_{TBM}	7.83	5.48	11.32	7.12
t_r	6.34	5.13	4.81	2.53
NEP	7.83	5.48	11.32	7.12
N[†]	141	18	202	27

[†] Number of data points

transect means and individual sampling points. On the other hand, the respective CV values for t_r were higher in KDN.

There were significant ($p<0.05$) forest region x elevation zone interaction effects on all three parameters in Sinharaja. This was primarily because of the significantly ($p<0.001$) greater C_{TBM} and NEP and the significantly ($p<0.001$) lower t_r in the mid-slope of Pitadeniya (Figs. 3.82 and 3.83). Furthermore, the significantly ($p<0.05$) lower C_{TBM} and NEP and the significantly ($p<0.001$) greater t_r in the mid-slope of Morningside also contributed to the significant region x elevation interaction. When averaged across different elevation zones, C_{TBM} and NEP were significantly greater in Pitadeniya as compared to Kudawa and Morningside, which did not show significant variation between each other. On the other hand, t_r was significantly greater in Morningside as compared to that in Kudawa, which in turn, was significantly greater than that in Pitadeniya.

4. Discussion

The primary objective of this work was to determine the carbon sequestration potential of the two major lowland wet evergreen forests in the wet zone of Sri Lanka, the Sinharaja MAB forest reserve and the KDN forest complex. Carbon sequestration initially occurs during primary production through photosynthesis. Net primary productivity (NPP) gives a quantification of this initial carbon sequestration rate (C_{seq}). The long-term carbon sequestration rate (C_{seqL}) is quantified by the net ecosystem productivity (NEP). The primary focus of this work was to calculate the carbon sequestration rate in terms of NPP (i.e. C_{seq}). Subsequently, C_{seqL} was also calculated from our calculated C_{seq} values using the method of Lloyd and Taylor (1994) and Saugier et al. (2001).

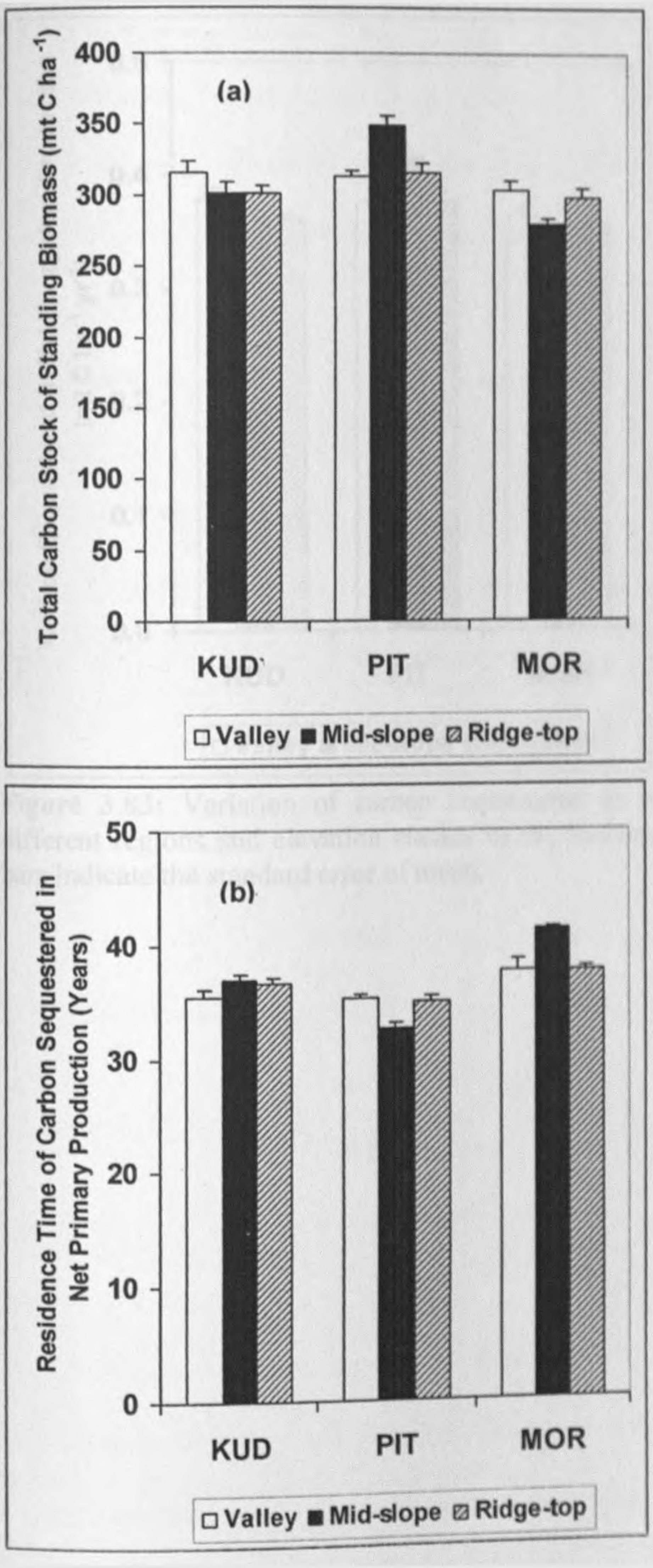


Figure 3.82: Variation of total carbon stock of standing biomass (a) and residence time of carbon sequestered in net primary production (b) between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean.

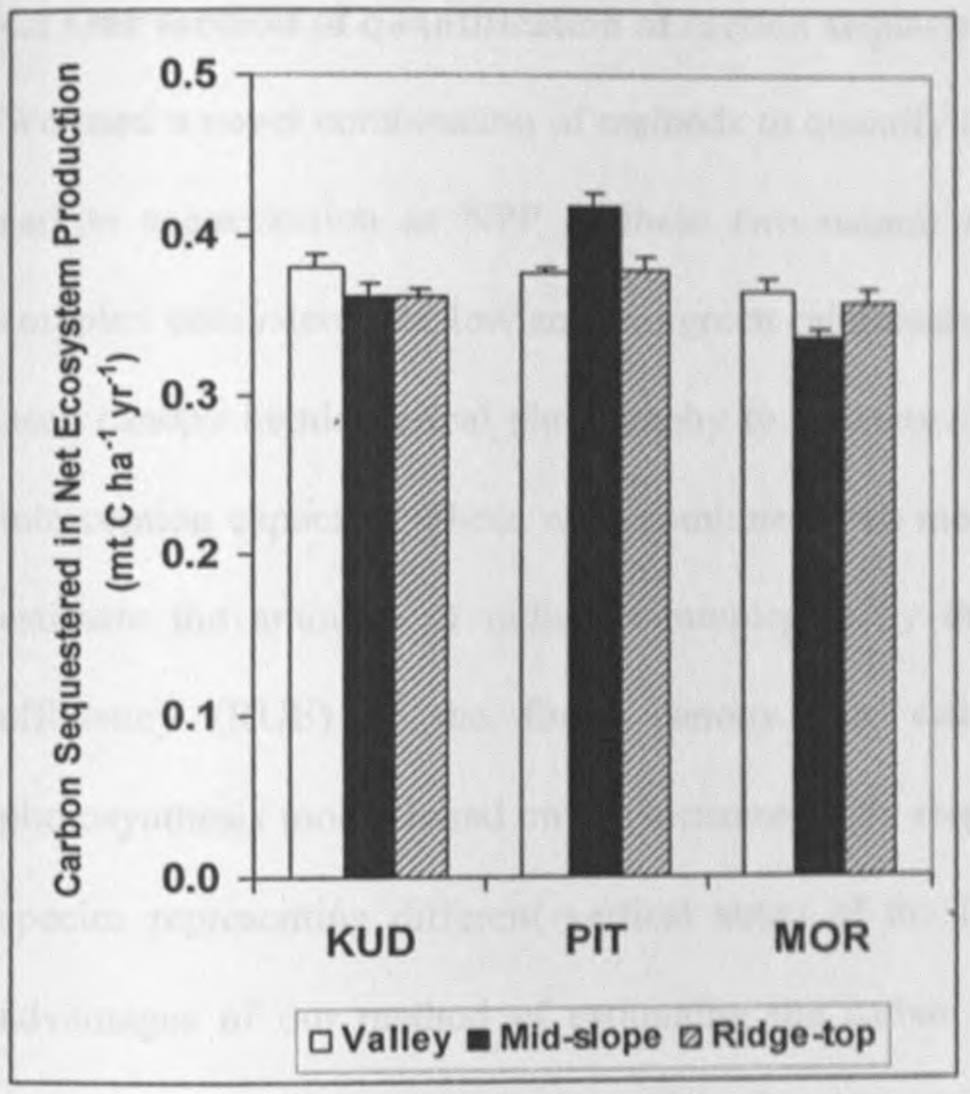


Figure 3.83: Variation of carbon sequestered in net ecosystem production between different regions and elevation classes in the Sinharaja MAB forest reserve. The error bars indicate the standard error of mean.

4.1 Our method of quantification of carbon sequestration of natural forests

We used a novel combination of methods to quantify the rate of biomass production and carbon sequestration as NPP of these two natural forests, which represent a highly complex ecosystem, the lowland evergreen rainforests of the humid tropical regions. It used canopy hemispherical photography to estimate canopy properties and its radiation interception capacity. These were combined with measured incident radiation levels to estimate the amounts of radiation intercepted by the forest canopy. Radiation use efficiency (RUE) of the forest canopy was estimated using a layered canopy photosynthesis model based on the measured light response curves of selected plant/tree species representing different vertical strata of the forest canopy. There are several advantages of our method of estimating the carbon sequestration capacity of natural forests in comparison to other methods that have been used such as the conventional ground-based forest inventory methods in permanent sampling plots (i.e. direct measurement of tree height and dbh) and remote sensing.

Firstly, our method is mechanistic because it is based on the fundamental physiological principles of photosynthesis and biomass production. In contrast, both direct measurement of tree dimensions and remote sensing have to rely on empirical relationships to estimate tree/forest biomass. Secondly, our method estimates the *total* carbon sequestration rate, which includes both above- and below-ground carbon sequestration rates. In contrast, forest inventory in permanent sampling plots and remote sensing estimate only the standing above-ground biomass and carbon stock and have to depend on empirical factors to estimate below-ground biomass and carbon stock. Thirdly, and importantly, our method enables quantification of the extremely high spatial heterogeneity of the biomass production and carbon sequestration capacity within the forest ecosystem. Therefore, it enables calculation of relevant statistical parameters for quantifying the spatial variability of both canopy properties and carbon sequestration capacity. While the direct measurement of tree dimensions also enables quantification of spatial heterogeneity of standing biomass within a forest, it takes a much longer time and labour than our method to obtain the same measures of variability. On the other hand, the remote sensing method does not have the same degree of spatial resolution as our method to estimate spatial heterogeneity in carbon sequestration within a natural forest. Furthermore, our method has the added advantage of providing a detailed quantification of canopy properties (i.e. canopy size and architecture) and their spatial variation within the forest.

4.2 Comparison of annual carbon sequestration rates in net primary production (C_{seq}) of Sinharaja and KDN forest complexes with values available in literature

In the present project, annual carbon sequestration rates in net primary production (C_{seq}) of the Sinharaja MAB forest reserve and the Kanneliya-Dediyagala-Nakiyadeniya (KDN) forest complex were quantified. C_{seq} rates of individual sampling points ranged from 6.566 to 15.721 mt ha^{-1} yr^{-1} in KDN and from 5.678 to 16.487 mt ha^{-1} yr^{-1} in Sinharaja, with mean values of 8.953 (± 0.133) and 7.403 (± 0.094) mt ha^{-1} yr^{-1} respectively. As the above ranges included outliers (Figs. 3.66 and 3.71), the range between the 5th and the 95th percentiles (Table 3.12), provide more meaningful ranges of C_{seq} rates which can be used for comparisons with other published values available in literature. Accordingly, the respective ranges (termed as $R_{05\text{-}95}$) are 6.920 – 11.484 mt ha^{-1} yr^{-1} for KDN and

6.142 – 9.298 mt ha^{-1} yr^{-1} for Sinharaja. A comprehensive review of NPP estimates in tropical wet evergreen forests in different parts of the tropics showed instances where our estimates of C_{seq} rates in net primary production are comparable, lower or higher than the published previous estimates. These comparisons and possible reasons for disagreements between our estimates and those from other studies are discussed below. The respective ranges of C_{seq} rates from the present study have been compared with other published ranges for tropical forests when such information is available. Furthermore, we have also compared the standard errors of our C_{seq} estimates with measures of variability of C_{seq} rates of tropical forests in other studies.

The respective $R_{05\text{-}95}$ ranges of our study are within the lower- and upper-bound ranges estimated by Clark et al. (2001b) for 39 diverse tropical forests by taking in to account all components of NPP of a forest ecosystem (Clark et al., 2001a). The respective lower- and upper bound ranges of Clark et al. (2001b) were 1.7 – 11.8 mt C ha^{-1} yr^{-1} and 3.1 21.7 mt C ha^{-1} yr^{-1}. It is notable that even the complete range of C_{seq} rates of our study was within those of Clark et al. (2001b).

Based on measurements from 11 forest stands, Cannell (1982) estimated the mean above-ground net primary productivity (NPP) of lowland moist tropical forests to be 17 18 mt ha^{-1} yr^{-1} with a range from 10 to 30 mt ha^{-1} yr^{-1}. Assuming a mean carbon fraction of 0.5 in forest biomass (Chave et al., 2005), this translates in to a mean above-ground C_{seq} rate of 8 – 9 mt ha^{-1} yr^{-1} with a range from 5 to 15 mt ha^{-1} yr^{-1}. Assuming a ratio of above-ground biomass to root biomass of 3:1, the average total C_{seq} rate would be 11 – 12 mt ha^{-1} yr^{-1} with a range from 7 to 20 mt ha^{-1} yr^{-1}. Kira (1978) computed a NPP of 13.5 mt C ha^{-1} yr^{-1} for a tropical evergreen forest in Pasoh, Malaysia by measuring and/or estimating different components of the forest carbon balance (i.e. above-ground biomass increment, root production, litterfall and wood fall). Kira (1978)'s estimate was within the range estimated by Cannell (1982) and was also close to the average C_{seq} rate of Cannell (1982).

The estimated average annual NPP, in terms of C flux, in the humid tropical region covering the wet zone of Sri Lanka, by Cramer et al. (1999) from 17 different terrestrial biogeochemical models, was in the range of 10 – 12 mt C ha^{-1} yr^{-1} (Fig. 1 of Cramer et al., 1999). Based on harvested biomass, Saugier et al. (2001) estimated the total NPP of tropical forests to be 25 mt ha^{-1} yr^{-1}, which translates in to a mean C_{seq} rate of 12.5 mt ha^{-1} yr^{-1}. Hence, the estimates of Cramer et al. (1999) and Saugier et al. (2001) for humid tropics agreed very closely. Their estimates were also close to the estimates of Kira (1978) and Cannell (1982).

Malhi et al. (1999) estimated the carbon balance of a tropical evergreen broadleaf forest in Manaus, Brazil using a synthesis of micrometeorological, ecophysiological and forestry data. Their estimated net annual C flux as NPP was 15.6 mt ha^{-1} yr^{-1}, which is within the range of Cannell (1982), but is higher than the mean estimates of Kira (1978), Cannell (1982), Cramer et al. (1999) and Saugier et al. (2001).

While the mean C_{seq} rates of Sinharaja and KDN are less than the estimated means of Kira (1978) and Cannell (1982) for lowland moist tropical forests, the respective R_{05-95} ranges of C_{seq} rates of our study were within the range estimated by Cannell (1982). However, our estimated R_{05-95} ranges of C_{seq} rates are lower than the average estimates of Malhi et al. (1999) and Saugier et al. (2001) for tropical forests and the estimated range of Cramer et al. (1999) for humid tropics. Reasons for the lower C_{seq} rates of our study in comparison to estimates of Cramer et al. (1999), which had used comparable methodology to our study, are discussed in the sections that follow.

It should be noted that our estimates are entirely based on a combination of ground-based measurements and a process-based mechanistic model. It does not contain any empirical calibration factors. On the other hand, Ruimy et al. (1999) suggest that most models may be calibrated so that annual global NPP are within 'commonly admitted values'. Cramer et al. (1999) suggest that part of the agreement observed between NPP estimates from some of the 17 models that were used in their study was because of their calibration procedures.

4.3 Role of radiation use efficiency in determining the C_{seq} rate and the observed differences between C_{seq} rates between the present study and those of Cramer et al. (1999)

Ruimy et al. (1999) analyzed the NPP estimates of Cramer et al. (1999) in terms of absorbed PAR (APAR) and radiation use efficiency (RUE) and showed that at the global scale, NPP estimates of 12 different models estimating global NPP was significantly, positively correlated ($r = 0.86$) with their respective RUE (Fig. 3.b of Ruimy et al., 1999). The RUE values estimated by Ruimy et al. (1999) ranged from 0.302 to 0.671 g MJ^{-1}, with a mean of 0.427 g MJ^{-1} (Standard deviation = 0.126 g MJ^{-1}; CV = 30%) (Table 1 of Ruimy et al., 1999). In comparison, the mean RUE values of KDN (i.e. 0.341 ± 0.049 g MJ^{-1}) and Sinharaja (0.300 ± 0.004 g MJ^{-1}) forest complexes were lower by 20% and 30% respectively than the mean RUE of Ruimy et al. (1999). The respective ranges of transect mean RUE values of KDN (Fig. 3.64.b) and Sinharaja (Fig. 3.69.b) were also lower than the range of RUE values observed by Ruimy et al. (1999). C_{seq} rates of both forest complexes of our study showed highly significant ($p<0.0001$) positive correlations ($r = 0.972$) with RUE (Tables 14 and 15). These correlations were even stronger than that observed by Ruimy et al. (1999). Therefore, it is highly probable that lower RUE values were primarily responsible for the lower C_{seq} rates of KDN (i.e. 8.953 ± 0.133 mt ha^{-1} yr^{-1}) and Sinharaja (7.403 ± 0.094 mt ha^{-1} yr^{-1}) forest complexes as compared to the estimate of Cramer et al. (1999) (i.e. 11 mt C ha^{-1} yr^{-1}) for the wet zone of Sri Lanka. It can be noted that the percentage reductions of C_{seq} rates of KDN (20%) and Sinharaja (33%) in comparison to Cramer et al. (1999) were comparable to the respective percentage reductions of RUE (i.e. 20% and 30% respectively for KDN and Sinharaja). Ruimy et al. (1999) observed a negative correlation between C_{seq} rates and the amount of absorbed PAR ($r = -0.42$). In contrast, our study showed significant positive correlations between C_{seq} rates and intercepted radiation ($r = 0.243$ and 0.358 for KDN and Sinharaja respectively). However, these correlations were weaker than the respective correlations between C_{seq} rates and RUE. Therefore, it can be concluded that net photosynthetic efficiency, as quantified by RUE, rather than the radiation interception capacity was the primary determinant of the carbon sequestration capacity of the KDN and Sinharaja forest complexes. Although Ruimy et al. (1999) observed a negative correlation between RUE and absorbed PAR ($r = -0.78$), no significant correlations were observed in the present study between RUE and intercepted radiation (Tables 14 and 15). This agrees with the mechanistic physiological principles of our methodology and confirms that the two components of our basic model to estimate C_{seq}, i.e. the radiation interception capacity and the efficiency with which the intercepted radiation is used in biomass production and carbon sequestration, are largely independent parameters.

4.4 Influence of canopy properties in determining the C_{seq} rate

Although it is clear that the efficiency of the net photosynthesis process of the forest canopy, as quantified by its RUE, is the primary determinant of the carbon sequestration potential of the KDN and Sinharaja forest complexes, their canopy properties also exerted appreciable influences on the processes of radiation interception and its conversion to biomass through photosynthesis. For example, in both forest complexes, C_{seq} rate showed highly significant ($p<0.0001$) negative correlations with the canopy light extinction coefficient (k) (Tables 3.14 and 3.15), which quantifies the architecture of the forest canopy. Mean leaf angle (MLA) is a primary determinant of k with greater leaf angles leading to lower k values, as indicated by the highly significant ($p<0.0001$) negative correlations between MLA and k (Tables 3.14 and 3.15). A lower k value indicates more vertically-oriented leaves with a higher MLA leads to greater radiation penetration in to a forest canopy and prevents mutual shading and light saturation of photosynthesis in leaves of the top canopy layers. Therefore, the overall photosynthetic efficiency of the canopy and the C_{seq} rate of the forest are increased. The role of k in determining RUE is shown by the highly significant ($p<0.0001$) negative correlations between RUE and k (Tables 3.14 and 3.15).

It is notable that all models that were used to calculate the C_{seq} rates in the studies of Cramer et al. (1999) and Ruimy et al. (1999) assumed a constant k value of 0.5, which is typical for coniferous forests (Jarvis and Leverenz, 1983). However, Ruimy et al. (1999)

acknowledge that k values of broadleaved forests can be substantially different from 0.5. This is shown by the mean k values obtained in our study for KDN (0.943 ± 0.010) and Sinharaja (0.940 ± 0.001), which are broadleaved forests. Importantly, it is possible that because of the lower k value used in the models, C_{seq} rates of Cramer et al. (1999) have been overestimated in areas dominated by broadleaved forests such as the wet zone of Sri Lanka. This possible overestimate of Cramer et al. (1999)'s estimates probably contributed to the observed differences in RUE and C_{seq} rates between the present study and those of Cramer et al. (1999) and Ruimy et al. (1999). If this possible overestimation is taken out, the C_{seq} rate and RUE values of Cramer et al. (1999) and Ruimy et al. (1999) would have been on par with the corresponding values obtained in our study.

In addition to canopy architecture, canopy leaf area index (LAI) also influenced the carbon sequestration capacity of the two forest complexes that we studied, as shown by the highly significant ($p<0.0001$) positive correlations between the respective C_{seq} rates and LAIs (Tables 3.14 and 3.15). However, interestingly, a significant positive correlation with the amount of radiation intercepted is shown only in Sinharaja (Table 3.15). This is because of the second-order polynomial relationship between LAI and the fraction of radiation intercepted (F_{Tot}) (Figs. 3.9 and 3.33), which indicated that increasing LAI beyond an optimum decreases F_{Tot} due to mutual shading. On the other hand, LAI had highly significant ($p<0.0001$), positive correlations with MLA and RUE and negative correlations with k in both forest complexes (Tables 3.14 and 3.15). Therefore, the positive influence of LAI on the C_{seq} rate operates more through increasing the RUE rather than through increasing the amount of radiation intercepted. Significant negative correlations were observed between LAI and MLA in both forests (Figs. 3.4 and

3.27), indicating that larger canopies had higher leaf angles leading to lower k values. Increased radiation penetration in to the canopy and decreased light saturation under lower k values were responsible for the higher RUE at higher LAI.

4.5 Influence of leaf photosynthetic properties in determining C_{seq} rates

The foregoing discussion highlighted the finding that the efficiency of the net photosynthesis process, as quantified by RUE, was the primary determinant of the carbon sequestration capacity of Sinharaja and KDN forest complexes. In the present study, RUE was estimated by a layered canopy photosynthesis model based on photosynthetic light response parameters of plant species representing different canopy strata (Figs. 3.50 and 3.51 and Tables 3.8 – 3.12). Therefore, it is pertinent to compare the photosynthetic light response parameters of our study with those observed in other published work.

Ashton and Berlyn (1992) reported net photosynthetic rates (P_n) of four late-successional *Shorea* species occupying different topographical positions in Sinharaja. The majority of species in our study had P_{max} values (Table 3.8), which were lower than those reported for the four *Shorea* species studied by Ashton and Berlyn (1992). However, the light saturation points (LSP) of the species of our study (Table 3.9) were within the range of LSPs observed for three of the four species (*Shorea megistophylla* being the exception) in Ashton and Berlyn (1992)'s study.

The highest P_n of 6.08 μmol [CO_2] m^{-2} s^{-1} was observed by Ashton and Berlyn (1992) in *S. megistophylla* at a light intensity of 1600 μmol [PAR] m^{-2} s^{-1}. This P_n value was higher than the highest P_{max} value observed in *Shorea stipularis* in our study (Table 3.8). While *S. megistophylla* showed a continuous increase of P_n at progressively higher light intensities from 50 to 1600 μmol [PAR] m^{-2} s^{-1}, *S. stipularis* in our study showed a light saturation at 632 μmol [PAR] m^{-2} s^{-1} (Table 3.9).

Two of the *Shorea* species of Ashton and Berlyn (1992)'s study, i.e. *S. trapezifolia* and *S. disticha*, had their maximum P_n values of 3.42 and 3.71 μmol [CO_2] m^{-2} s^{-1} respectively at 800 μmol [PAR] m^{-2} s^{-1}. These values were comparable to the P_{max} values obtained in some of the species of our study such as *Shorea disticha*, *Calophyllum bracteatum*, *Garcinia quaesita* and *Aporusa cardiosperma* (Table 3.8). However, P_n of these species in our study showed light saturation at light intensities, which were lower than 800 μmol [PAR] m^{-2} s^{-1} (Table 3.9).

One *Shorea* species of Ashton and Berlyn (1992)'s study (i.e. *S. worthingtonii*) showed its maximum P_n (i.e. 3.24 μmol [CO_2] m^{-2} s^{-1}) at 350 μmol [PAR] m^{-2} s^{-1}. While the majority of species in our study had P_{max} values lower than that of *S. worthingtonii*, only three species had comparable LSPs (i.e. *Vateria copallifera*, *Mesua ferrea* and *Agrostistachys coriacea*).

Mori et al. (1990) measured the P_n of several Malaysian tree species which included species with different growth rates and light requirements and observed that P_{max}, LSP and light compensation point (LCP) declined with decreasing growth rate and light requirement. With the exception of *S. stipularis*, P_{max} values of all species of our study were lower than the P_{max} of the slow- and very-slow growing species with low- and very-low light requirements (e.g. *Dryobalanops aromatica* and *Neobalancarpus heimii*). On the other hand, the LSPs of our study were comparable to those observed in Mori et al. (1990). However, the observed LCPs our study were higher than those observed in Mori et al. (1990).

Medina and Klinge (1983) compiled a list of photosynthetic and respiration properties in a range of tropical rainforest species, which also included *Shorea* and *Dipterocarpus* species. The respective ranges for P_{max} and R_d were 3.79 – 15.44 µmol [CO_2] m^{-2} s^{-1} and 0.316 – 2.524 µmol [CO_2] m^{-2} s^{-1} respectively. While the R_d of species used in the present study, with the exception of *Vateria copallifera* (Table 3.8), were within the range observed by Medina and Klinge (1983), the P_{max} values of all species except *S. stipularis*, were lower than the minimum P_{max} of Medina and Klinge (1983).

In a review on the physiological ecology of tropical succession, Bazzaz and Pickett (1980) gave P_n values of 4.354 and 1.830 µmol [CO_2] m^{-2} s^{-1} for canopy trees (i.e. light-demanding climax species) and understorey (i.e. shade-tolerant climax species) plants respectively. Interestingly, these values are comparable to the P_{max} values observed in the present study (Table 3.8). However, the observed R_d values in the majority of species in our study were greater than the respiration rates of Bazzaz and Pickett (1980), i.e. 0.631 and 0.189 µmol [CO_2] m^{-2} s^{-1} for canopy trees and understorey plants respectively.

Furthermore, in the compilations of both Medina and Klinge (1983) and Bazzaz and Pickett (1980), the R_d/P_{max} ratio was below 0.2 (range 0.05 – 0.17). In comparison, with the exception of *Vateria copallifera*, all species in the present study showed R_d/P_{max} ratios which were greater than 0.2.

The observed quantum efficiencies (ϕ) of the present study (0.0106 – 0.035 µmol [CO_2] (µmol [PAR]$)^{-1}$) (Tables 8 and 11) was substantially lower than the average value of 0.05 µmol [CO_2] (µmol [PAR]$)^{-1}$ for C_3 plants (Ehleringer and Bjorkmann, 1977; Ehleringer and Pearcy, 1983). Our values are also lower than the maximum ϕ values obtained by Fan et al. (1990) and Malhi et al. (1998) for tropical forests near Manaus, Brazil (i.e.

0.051 and 0.048 μmol $[CO_2]$ (μmol [PAR])$^{-1}$ respectively) through eddy covariance. However, our values are on par with the value of 0.025 μmol $[CO_2]$ (μmol [PAR])$^{-1}$ obtained by Grace et al. (1995a) for a tropical forest in Rondonia, Brazil and the overall average ϕ value of 0.019 μmol $[CO_2]$ (μmol [PAR])$^{-1}$ observed by Malhi et al. (1998). At the individual species level, ϕ did not show a consistent variation pattern with their vertical position in the forest canopy (Table 3.8). However, the light response curves of the pooled data for species occupying different canopy strata (Table 3.11) showed that ϕ was greater in the sub-canopy and understorey as compared to the canopy. This is in accordance with published work in literature. For example, Pearcy and Sims (1994) have shown that ϕ of shade-grown plants (equivalent to the sub-canopy and understorey strata) was higher than that of sun-grown plants (equivalent to the canopy stratum).

Contrary to published values (Bazzaz and Pickett, 1980; Oberbauer and Strain, 1984; Whitmore, 1990; Mori et al., 1990; Bazzaz, 1996), we did not observe a clear distinction in photosynthetic light response parameters in species occupying different canopy strata. For example, Bazzaz and Pickett (1980) observed that canopy trees (i.e. light-demanding climax species) had greater P_{max} and dark respiration (R_d) values than understorey plants (i.e. shade-tolerant climax species). However, when the data for different species occupying a given canopy stratum were pooled, the resulting light response curves (Fig. 3.51 and Table 3.11) showed a greater P_{max} and LSP values in the canopy stratum as compared to the sub-canopy and understorey. This result is in agreement with published literature.

The foregoing discussion showed that some of the key photosynthetic light response and respiration parameters (i.e. P_{max}, LSP, LCP and R_d) of the representative plant species from Sinharaja and KDN forest reserves that were observed in our study were different from those observed in literature for late successional tree/plant species in tropical forests. Those parameters whose greater values would promote greater C_{seq} rates (i.e. P_{max} and LSP) were generally lower in the present study as compared to those reported in literature. On the other hand, the parameters which need to be lower to achieve greater C_{seq} rates (i.e. LCP, R_d and R_d/P_{max} ratio) were higher in our study. These differences could have contributed to the lower RUE values observed in the present work as our layered canopy photosynthesis model to estimate RUE was parameterized based on the above photosynthetic and respiration parameters. The lower RUE as compared to that used by other workers (e.g. Heimann and Keeling, 1989; Maisongrande et al., 1995; Ruimy et al., 1999) could have been another factor contributing to lower C_{seq} rates of Sinharaja and KDN. On the other hand, the lower photosynthetic rates and the consequently lower RUE could probably be a true reflection of the state of these two forest complexes.

4.6 Difference in C_{seq} rates between the KDN and Sinharaja forest complexes

Our results showed that the KDN forest complex had significantly higher C_{seq} rates than the Sinharaja MAB reserve (Table 3.12). This was primarily because of the greater RUE (0.341 g MJ^{-1} as compared to 0.300 g MJ^{-1}) and total radiation interception (R_I) (14.393 MJ m^{-2} d^{-1} as compared to 13.543 MJ m^{-2} d^{-1}) of KDN. The greater R_I was partly due to the greater radiation receipt (16.547 MJ m^{-2} d^{-1} as compared to 15.844 MJ m^{-2} d^{-1} - Table 3.7 -) at KDN which is located at slightly lower latitude (i.e. more towards the equator) than Sinharaja. In addition, KDN also had a slightly greater fractional radiation interception (0.870 as compared to 0.855), which also contributed to its greater R_I.

Analysis of forest canopy properties through hemispherical photography indicated that KDN forest canopy had greater canopy gaps on the horizontal plane than Sinharaja, thus allowing greater penetration of direct radiation into the forest. This also allowed the KDN forest canopy to develop a greater LAI. However, canopy image analysis also indicated that the vertical stratification of the forest canopy was greater in Sinharaja than in KDN. Consequently, Sinharaja had greater canopy gaps on the vertical plane, thus allowing greater penetration of diffuse radiation. However, the intensity of direct radiation is much greater than that of diffuse radiation. Thus, KDN which allowed greater penetration of direct radiation had greater R_I and C_{seq} rates than Sinharaja. The greater penetration of direct radiation in to the forest canopy in KDN also probably contributed to its greater RUE as it allowed more efficient utilization of higher intensity direct radiation in photosynthesis.

It is highly likely that the KDN forest complex, because of its slightly lower latitude closer to the equator, is experiencing slightly greater air temperatures than the Sinharaja forest reserve. In addition to the higher irradiance levels, the higher temperatures at KDN were probably responsible for its greater canopy gross photosynthetic rates (Fig. 3.58.a) as compared to Sinharaja (Fig. 3.61.a) and RUE.

4.7 Variation in C_{seq} rates between different forest regions and elevation zones

Variation between different forest regions and elevation zones was not consistent for C_{seq} rates and its component factors (i.e. R_I and RUE). In fact, in both forest complexes, the variation between different transects within a forest complex, forest region or an elevation class was greater than the variation between forest regions and elevation zones. This showed the high spatial heterogeneity across very short distances within both forest complexes. It is a particular strength of our method of estimating forest carbon sequestration that this spatial variation can be captured. On the other hand, underlying reasons for the variation between forest regions and elevation zones within a forest complex need to be investigated. For example, Ediriweera et al. (2008) have shown that in the Sinharaja MAB reserve, there is considerable within-forest heterogeneity in the soil depth and associated soil physical and chemical properties and available nutrient status, especially between different elevation classes. On the other hand, Ashton et al. (2006) have shown that different tree species respond differentially to variation in site environmental factors (e.g. availability of soil nutrients, light and soil water) in different elevation zones in Sinharaja. Therefore, in addition to the variation in resource availability, the differential response of different tree species occupying different elevation zones probably contributes to the observed variation in carbon sequestrations rates between elevation zones.

4.8 Comparison of the variability of C_{seq} rate estimates between the present study and Cramer et al. (1999)

Interestingly, the spatial variability of C_{seq} rates of Sinharaja and KDN, estimated as the respective coefficients of variation, (i.e. 18% for individual data points and 9 – 11% for transect means – Table 3.13 -), in our study is larger than the estimated CV value of ~ 5% for the region covering the wet zone of Sri Lanka in Cramer et al. (1999) (Fig. 2.b of

Cramer et al., 1999). In contrast, the standard error of the estimated mean C_{seq} rates of Sinharaja and KDN (i.e. ± 0.133 and ± 0.094 mt C ha^{-1} yr^{-1} respectively) were lower than the estimated standard deviation range of 0.6 – 0.7 mt C ha^{-1} yr^{-1} for the NPP of the region covering the wet zone of Sri Lanka in Cramer et al. (1999) (Fig. 2.a of Cramer et al., 1999). This is probably because of the higher NPP estimates of Cramer et al. (1999) as compared to the estimates of the present study.

4.9 Comparison of annual carbon sequestration rates in net ecosystem production (C_{seqL}) of Sinharaja and KDN forest complexes with values available in literature

Annual carbon sequestration rates in net ecosystem production (C_{seqL}) of the Sinharaja MAB forest reserve and the Kanneliya-Dediyagala-Nakiyadeniya forest complex were also quantified in the present study. C_{seqL} rates of individual sampling points ranged from 0.341 to 0.503 mt C ha^{-1} yr^{-1} in KDN and from 0.269 to 0.609 mt C ha^{-1} yr^{-1} in Sinharaja, with mean values of 0.378 (± 0.003) and 0.371 (± 0.003) mt C ha^{-1} yr^{-1} respectively. As the above ranges included outliers (Figs. 3.76.b and 3.81), the range between the 5th and the 95th percentiles (Table 3.17), provide more meaningful ranges of C_{seqL} which can be used for comparisons with other published values available in literature. Accordingly, the respective ranges (termed as RL_{05-95}) are 0.328 – 0.435 mt C ha^{-1} yr^{-1} for KDN and 0.313 – 0.440 mt ha^{-1} yr^{-1} for Sinharaja. Our values are comparable to the average NEP value of 0.38 mt C ha^{-1} yr^{-1} for tropical forests, as estimated by Grace (2004) based on NPP estimates of Saugier et al. (2001) along with a method developed by Taylor and Lloyd (1992) to estimate heterotrophic respiration.

Our estimates of long-term carbon sequestration rates (C_{seqL}) of Sinharaja and KDN forests can be compared with estimates from permanent sampling plots (PSPs) in tropical forests (Phillips et al., 1998; Baker et al., 2004; Chave et al., 2005 & 2008; Phillips et al., 2008; Lewis et al., 2009), which are summarized in Table 3.19. Here again, as in the case for C_{seq}, our estimates of C_{seqL} are comparable, lower or higher than the published values long-term carbon sequestration in PSPs. Mean C_{seqL} estimates and the ranges of between the 5th and the 95th percentiles (RL_{05-95}) of the present study are comparable to the overall average values obtained by Phillips et al. (1998) and Chave et al. (2008). In contrast, the overall average C_{seqL} value of Lewis et al. (2009) was higher than our mean C_{seqL} estimates. However, lower end of the 95% confidence interval (CI) of Lewis et al., (2009) overlapped with the upper end of the RL_{05-95} values of both KDN and Sinharaja forest complexes.

RL_{05-95} values of our study overlapped with the CIs of most of the regional C_{seqL} estimates of Phillips et al. (1998), Baker et al. (2004) and Lewis et al. (2009). The only exceptions were the CI for Paleotropics (i.e. tropical Africa, Asia and Australia) of Phillips et al. (1998), which were lower than our RL_{05-95} estimates and the CI for old-growth Amazonian forests of Phillips et al. (2008), which was higher than our estimates. Phillips et al. (1998) acknowledge that their coverage of the Paleotropical sites (i.e. 18 sites) is sparser than that of the Neotropics (i.e. 50 sites). Other estimates from tropical Asia and Africa (Chave et al., 2008; Lewis et al., 2009) (Table 3.19) show that the estimate of Phillips et al. (1998) may not be representative of the carbon sequestration capacity of forests in the Paleotropics.

Table 3.19: Summary of estimated long-term total carbon gains in tropical forests obtained from repeated forest inventory data in permanent sampling plots

Locations	Long-term carbon gain ± 95% CI (mt C ha^{-1} yr^{-1})	Reference
	Overall means:	
Forests in Humid tropics (153 plots), Humid neotropics (120), Humid lowland neotropics (108), Amazonia (97)	0.385 ± 0.220	Phillips et al. (1998)
Tropical forests in Asia, Africa and Central and South America (10 sites including Sinharaja)	0.313 ± 0.220	Chave et al. (2008)
Tropical forests in Asia, Africa and Central and South America (11 sites excluding Sinharaja)	0.420 ± 0.220 (Excluding Sinharaja)	Chave et al. (2008)
African, Asian and Tropical American forests (156 plots covering 562 ha)	0.650 ± 0.247	Lewis et al. (2009)
	Regional means:	
Humid neotropics	0.555 ± 0.270	Phillips et al. (1998)
Humid lowland neotropics	0.540 ± 0.295	Phillips et al. (1998)
Amazonia	0.485 ± 0.29	Phillips et al. (1998)
Paleotropics	-0.009 ± 0.295	Phillips et al. (1998)
Old growth Amazonian forests (59 sites)	0.620 ± 0.230	Baker et al. (2004)
Old growth Amazonian forests (1 ha plots in 50 - 91 sites)	1.016 ± 0.369	Phillips et al. (2008)
African tropical forests (79 plots covering 163 ha)	0.840 ± 0.547	Lewis et al. (2009)
	Location means:	
Barro Colorado forest, Panama (50 ha plot)	0.133 ± 0.437	Chave et al. (2003)
Sinharaja MAB reserve (50 ha plot)	-0.653 ± 1.000	Chave et al. (2008)

Note: In all studies except Chave et al. (2008), above-ground biomass (AGB) was estimated from basal area measurements of trees having dbh ≥ 10 cm, using allometric equations. Correction factors were used to include biomass from trees having dbh < 10 cm and lianas with diameter ≥ 1 cm. Above-ground biomass change (ΔAGB) was computed as the difference in AGB between two census intervals. Total biomass change was computed by assuming an above-ground:below-ground ratio of 3:1 (2.7:1 in Baker et al., 2008). Long-term carbon gain was calculated by assuming a carbon content of 50% in biomass (Chave et al., 2005). Baker et al. (2008)'s estimate included the carbon gain in coarse necromass (i.e. coarse woody litter) as well. In Chave et al. (2008), all trees with ≥ 1 cm dbh were measured. Climbing palms (rattans) and arborescent palms were excluded from the calculations in most sites of Chave et al. (2008).

After analyzing six key ecosystem processes, i.e. stem recruitment, mortality and turnover, and basal area growth, loss and turnover, Phillips et al. (2008) concluded that there had been pervasive changes in their plots with faster-growing genera showing larger increases in growth in comparison to the slower-growing genera. In contrast, after analysis of growth rates of faster- and slower-growing tree species, Chave et al. (2008) concluded that there was no evidence to support the hypothesis that fast-growing species were consistently increasing their dominance in the plots used in their study. Therefore, the pervasive changes that had occurred in the tree communities of Phillips et al. (2008)'s plots may have been responsible to their significantly greater C_{seqt} rates in comparison to our estimates as well as the estimates of other workers (e.g. Phillips et al., 1998; Chave et al., 2003; Baker et al., 2004; Chave et al., 2008; Lewis et al., 2009).

On the other hand, the CIs of both location means (i.e. Barro Colorado and Sinharaja) overlapped with our $RL_{05\text{-}95}$ estimates.

4.10 Comparison of total standing carbon stock and its residence time between the present study and Cramer et al. (1999)

The study by Chave et al. (2008) included Sinharaja also as one of the 10 large undisturbed, permanent sampling plots. Here, Sinharaja had an above-ground carbon gain of 3.7 mt C ha^{-1} yr^{-1}, which translates in to a total C_{seq} rate of 4.93 mt C ha^{-1} yr^{-1} at the above- to below-ground biomass ratio of 3:1. This value, which was obtained for a 50 ha PSP in Sinharaja during a five-year period between 1993 and 1998, is lower than our mean estimate of 7.403 (± 0.094) mt C ha^{-1} yr^{-1}. Similarly, the above-ground carbon stock of Sinharaja was estimated to be 179 mt C ha^{-1}, which translates in to a total C stock of 239 mt C ha^{-1}. This is lower than our estimate of 310 ± 3 mt C ha^{-1}. Because of the greater standing carbon stocks but comparable NEP levels, the residence times of standing carbon stocks (t_r) are longer for the two forest complexes in our study as compared to estimated t_r of Malhi et al. (1999) for an old-growth tropical forest in Manaus, Brazil (i.e. 29 yr) and of Grace (2004) for tropical forests (i.e. 25 yr) in general.

4.11 The total annual carbon sinks (C_{Total}) from Sinharaja and KDN forest complexes

Average estimates of total annual carbon sink (C_{Total}) in Sinharaja and KDN forest complexes can be calculated by the product between the mean annual NPP and total area of the respective forest complexes. Accordingly,

For Sinharaja MAB Forest Reserve:

C_{Total} = Mean annual NPP x total forest area x 3.67

$= 7.403 \text{ mt C ha}^{-1} \text{ yr}^{-1} \times 11{,}250 \text{ ha} \times 3.67 \text{ mt CO}_2 \text{ (mt C)}^{-1}$

$= 0.305 \times 10^6 \text{ mt CO}_2 \text{ yr}^{-1}$

For KDN Forest Complex:

C_{Total} = Mean annual NPP x total forest area x 3.67

$= 8.953 \text{ mt C ha}^{-1} \text{ yr}^{-1} \times 12{,}050 \text{ ha} \times 3.67 \text{ mt CO}_2 \text{ (mt C)}^{-1}$

$= 0.396 \times 10^6 \text{ mt CO}_2 \text{ yr}^{-1}$

The factor 3.67 converts the amount of carbon absorbed in to the amount of CO_2 absorbed.

Based on the data released by the International Energy Agency (IEA) on 06 October 2009, the per capita CO_2 emission in Sri Lanka is 0.6 mt (http:// en.wikipedia.org/wiki/List_of_countries_by_carbon_dioxide_emissions_per_capita).

According to the Department of Census and Statistics, the estimated mid-year population in Sri Lanka is 20,217,000 (http://www.statistics.gov.lk/PopHouSat/Mid%20Year% 20Population/Table%201.pdf). Accordingly, the annual total CO_2 emission from Sri Lanka can be calculated as,

Total CO_2 emission = per capita emission x total population

= 0.6 mt CO_2 yr^{-1} x 20,217,000

= 12.13×10^6 mt CO_2 yr^{-1}

Therefore, the respective percentages of total CO_2 emissions absorbed by the two forest complexes can be calculated as,

For Sinharaja MAB Forest Reserve:

% emission absorbed by the forest

$= [(0.305 \times 10^6 \text{ mt } CO_2 \text{ yr}^{-1})/(12.13 \times 10^6 \text{ mt } CO_2 \text{ yr}^{-1})] \times 100$

= 2.52%

For KDN Forest Complex:

% emission absorbed by the forest

$= [(0.396 \times 10^6 \text{ mt } CO_2 \text{ yr}^{-1})/(12.13 \times 10^6 \text{ mt } CO_2 \text{ yr}^{-1})] \times 100$

$= 3.26\%$

The above values of percentage national carbon emissions absorbed show that these two forest complexes are extremely efficient carbon sinks, especially when the percentage land area occupied by them are calculated. Taking the total land area of Sri Lanka as 6,560,963 ha (i.e. 25,332 square miles), the Sinharaja and KDN forest complexes occupy about 0.171% and 0.184% of the total land area respectively.

A quantitative index for the efficiency of the carbon sink can be calculated as the ratio between the percentage national CO_2 emissions absorbed by a given forest and the percentage land area occupied by it. Accordingly,

For Sinharaja MAB Forest Reserve:

Efficiency index of carbon sink = (2.52%)/(0.171%) = 14.73

For KDN Forest Complex:

Efficiency index of carbon sink = (3.26%)/(0.184%) = 17.72

5. Concluding remarks

At the outset of this study, there were two major aspects on which attention and a major research effort was focused. One was the development of a methodology to estimate the carbon sequestration rate of a highly complex ecosystem such as the tropical lowland wet evergreen forests. The second aspect was the obtaining of valid estimates of carbon sequestration rates for the two forest ecosystems, namely, Sinharaja and KDN forest complexes, which represent the above ecosystem.

For this purpose, we were able to develop a novel methodology, with a combination of different methods to estimate radiation interception by the forest canopy and its radiation use efficiency. The estimated medium- and long-term carbon sequestration rates were comparable to published values in literatures on other comparable tropical rainforests. This constituted a strong validation of our methodology.

Because our methodology was mechanistic and process-based, we were able to identify the influence of different factors and processes in determining the carbon sequestration rates of the two forest complexes. Accordingly, efficiency of the net photosynthesis process of the forest canopy, as quantified by its RUE, was shown to be the primary determinant of the carbon sequestration potential of the Sinharaja and KDN forest complexes. In addition to the photosynthetic light response parameters of the component tree/plant species, architecture of the forest canopy, as quantified by its canopy light extinction coefficient and mean leaf angle, also had a significant influence in determining the carbon sequestration rates by ensuring adequate distribution of intercepted radiation within the forest canopy. This enabled all strata of the forest canopy to contribute to its overall photosynthesis and biomass production.

Finally, our quantifications of the overall carbon sinks showed that Sinharaja and KDN forest complexes are highly efficient carbon sinks. In the following section (i.e. Section 3.II) on estimating the efficiency of carbon sinks of forest plantations, we show that Sinharaja and KDN forest complexes have greater efficiencies as carbon sinks than even the most productive forest plantations in Sri Lanka.

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Section 3.II:

Estimation of carbon stocks in the forest plantations of Sri Lanka

This section is presented in the form of a research article that has been submitted for possible publication in the Journal of the National Science Foundation of Sri Lanka. The manuscript was submitted in August 2009 and is still under review.

As this has been prepared as a manuscript to be submitted for publication in a journal, the tables are given at the end of the full text of the manuscript.

Research Article

Estimation of carbon stocks in the forest plantations of Sri Lanka[†]

[*]W.A.J.M. De Costa and H.R. Suranga

Department of Crop Science, Faculty of Agriculture, University of Peradeniya,

Peradeniya 20400, Sri Lanka

[*]*Corresponding author*

Phone: 081-2395118; 071-4430572

Fax: 081-2388041

E-mail: janendrad@yahoo.com

[†] Part of this work was presented as an oral presentation at the National Forestry Research Symposium held on 12-13 March 2009 in Kandy, Sri Lanka

Title:

Estimation of carbon stocks in the forest plantations of Sri Lanka

Running title:

Carbon stocks of Sri Lankan plantation forests

Abstract

Forest plantations have the ability to sequester carbon in their biomass and reduce the rate of increase of atmospheric carbon dioxide. Therefore, plantation forestry forms an important option of mitigating global warming and its consequent climate change. The objective of the present study was to estimate the biomass and carbon stocks of the existing forest plantations in Sri Lanka. Height and diameter at breast height measurements for 22 mono-cultures and 51 mixed-cultures, which have been established and maintained by the Forest Department, obtained from the FORDATA data base, were used to calculate existing carbon stocks through allometric relationships.

The total estimated monoculture C stock in 2008 amounted to 4.23 million metric tons in an area of 57618.8 ha. Around 89% of this total C stock in monocultures is contributed by five tree species, namely, *Pinus caribaea* (44%), *Tectona grandis* (21%), *Eucalyptus grandis* (11%), *Eucalyptus camaldulensis* (7%) and *Swietenia macrophylla* (6%), occupying 92% of the area. Total C stock in mixed cultures in 2008 amounted to 0.681 million tons in 5949.6 ha. Five mixed cultures, i.e. *Eucalyptus robusta & E. grandis* (17%), *Pinus* mixed (13%), *E. grandis & E. microcorys* (12.5%), *Eucalyptus* mixed (7%) and *Acacia mangium & A. auriculiformis* (5%), contributed 55% of this C stock. Monocultures which showed the highest per ha C stocks were *Pinus caribaea* in Badulla (205 t ha^{-1}) and Nuwara Eliya (164 t ha^{-1}) and *Eucalyptus grandis* in Ratnapura (197 t ha^{-1}) and Nuwara Eliya (168 t ha^{-1}). Mixed plantations involving *Acacia decurrens* and different species of *Eucalyptus* grown in Nuwara Eliya showed the highest combined per ha C stocks ranging from 226 – 279 t ha^{-1}. The maximum per ha C stocks observed from some of the Sri Lankan forest plantations in different climatic zones were either on par or above the benchmark average C stock values specified by the IPCC for the respective climatic zones.

Keywords: forest biomass, carbon sequestration, tropical forests, climate change mitigation

INTRODUCTION

In Sri Lanka, forest plantations have been established since 1880s to meet the increasing demand for timber and fuelwood, with soil conservation in important watersheds being an additional benefit[1,2]. Almost all the existing plantations have been established after the 1950s and consist of fast-growing exotic trees such as the species of *Eucalyptus*, *Pinus* and *Acacia* along with teak and mahogany[3]. In addition to their industrial timber products, the importance of forest plantations has increased substantially during the last two decades, in view of the increased awareness on global climate change and the role forests in regulating the global carbon cycle[4-7]. Forests have the ability to absorb large quantities of atmospheric carbon dioxide for their photosynthesis and sequester carbon in their biomass[8]. As carbon dioxide is the principal greenhouse gas contributing to the enhanced greenhouse effect[9] and the consequent global warming which drives climate change, forests have the potential to reduce the rate of global warming and the resultant climate change[10-18]. However, increasing deforestation of natural forests, especially in the tropics, is reducing the global warming mitigation potential of tropical forests and threatens to convert them from a significant global carbon sink to a net carbon source[19-22].

Therefore, plantation forestry forms an important option for climate change mitigation[23,24].

The carbon sequestration potential of a forest is determined by its biomass production. While the rate of biomass production (i.e. increase of forest biomass per year) indicates the potential of a forest to absorb atmospheric CO_2 and reduce global warming within a given time period, the standing biomass of a forest indicates how much carbon has been sequestered during its lifetime. Although Sri Lanka contains nearly 65,000 ha of forest plantations, their carbon stocks as indicated by the standing biomass, have not been estimated. The published research literature on the growth of plantation forest species in Sri Lanka reports only the height and dbh (i.e. diameter at breast-height) increments over relatively short periods of time on a limited number of locations[25-31]. Therefore, the objective of the present work is to estimate the total carbon (C) stocks of plantation forests in Sri Lanka and examine its distribution between different tree species, locations and climatic zones.

Estimates of C stocks will enable the economic valuation of Sri Lankan plantation forests with a view of exploring possibilities for financial gains through mechanisms such as the United Nations Reducing Emissions from Deforestation and Degradation in Developing Countries Programme (UN-REDD)[32-34]. C stock estimations could also form the basis for analysis of benefits and costs of afforestation or reforestation with forest plantations in quantifying their climate change mitigation potential[35-38]. Quantification of the species-wise distribution of C stocks in different geographical regions of Sri Lanka will lead to identification of regions which are rich or deficient in C stocks while providing information on specific tree species which have greater C sequestration potential under their respective climatic and soil conditions. Furthermore, comparative estimates of total biomass, on which C stock estimates are based, provide indications of the condition of forest plantations in a given climatic zone or division and give an indirect estimate of its site quality[39,40].

METHODS AND MATERIALS

Data source

The FORDATA data base that is maintained by the Forest Department was used for this study. The FORDATA contains height and diameter at breast height (dbh) measurements for 22 mono-cultures and 51 mixed-cultures, which have been established and maintained by the Forest Department. These forest plantations are distributed over 17 forest divisions, which are largely based on administrative districts, covering all three major climatic zones (i.e. wet, intermediate and dry zones). The database lists 86363.8 hectares (ha) of forest plantations in the country. However, calculations were done only for 63568.4 ha, which were under the age of 50 years by 2008. The remaining 22795 ha, which are over the age of 50 were assumed as having been harvested by 2008. The lists of monoculture and mixed-culture plantation forest tree species that were used for the calculations and their distribution are given in Tables 1 and 2.

The database describes the location of a plantation in terms of division, range, beat, block and sub-block and also gives the area (ha), slope, altitude, number of stems per ha, diameter at breast height (cm), height (m), planting year of the plantation and last surveyed year with reference to each sub-block. These specifications are given by a single record of the database. The plant species is indicated by a code. Records of the same species in different places in the database were filtered using the Microsoft Office filter tools.

Calculation methodology for monoculture forest plantations

The calculation methodology used in this work is in accordance with the 'Good Practice Guidance for Land Use, Land Use Change and Forestry' as promoted by the IPCC[41,42] and are based on well-established conventional techniques of forest inventory[43,44] Calculations started at the sub-block level.

Calculation of wood volume

Initially the wood volume was calculated using the dbh and height measurements of the FORDATA data base with one of the following three methods:

(a) Using volume functions that have been developed for particular species

The wood volumes of six tree species (i.e. *Eucalyptus robusta*, *E. grandis*, *E. microcorys*, *Pinus caribaea*, *Tectona grandis* and *Cupressus* spp.) were calculated using available volume functions (Table 3)[45].

(b) Using an estimated form factor for those *Eucalyptus* and *Pinus* species for which volume functions are not available

The following general allometric relationship was used to estimate the merchantable wood volume of species for which specific volume functions have not been developed:

$$V = f\,g\,h \qquad \text{(eq. 1)}$$

Where, V is merchantable wood volume per tree (m^3), g is basal area per tree (m^2) and h is tree height (m). Basal area, g, (m^2) was calculated from diameter at breast height, d, (cm) as,

$$g = (\pi d^2)/40000 \qquad \text{(eq. 2)}$$

In eq. 1, f is known as the 'form factor', which is a quantitative index of the trunk form of a particular tree species. A perfectly cylindrical trunk would have a form factor of 1. Depending on the deviation of the actual trunk form from a perfectly cylindrical form, the f value decreases from 1. Therefore, the f value had to be estimated for those species, which did not have established volume functions.

An established volume function can be considered as a widely-applicable allometric relationship for a given species. Using the available height and dbh data at the sub-block level, the volume functions of Table 3 were inverted (eq. 3) to obtain form factors (f) for *Eucalyptus robusta*, *E. grandis*, *E. microcorys* and *Pinus caribaea* as 0.320, 0.335, 0.335 and 0.370 respectively:

$$f = V / g\,h \qquad \text{(eq. 3)}$$

For the other species of *Eucalyptus* and *Pinus* without established volume functions, form factors were 'designed' based on the estimated form factors given above. The arithmetic average of the estimated form factors of *Eucalyptus robusta, E. grandis* and *E. microcorys* (i.e. 0.330) was taken as the form factor for the other *Eucalyptus* species, which did not have volume functions. This procedure of 'designing' form factors makes the implicit assumption that the tree form does not vary significantly within a given genus. As *Pinus caribaea* was the only *Pinus* species for which a volume function was available, the form factor estimated based on its volume function (i.e. 0.370) was taken as the form factor for the rest of the *Pinus* species, which did not have volume functions.

(c) Using an assumed form factor for species (other than those of *Eucalyptus* and *Pinus*) which did not have established volume functions

For the rest of the plantation forest tree species, which did not have established volume functions, merchantable wood volume per tree was calculated by eq. 1, using an assumed form factor of 0.5.

Calculation of above-ground tree biomass and carbon stock per ha

The merchantable tree volume that was calculated as above was converted to above-ground biomass per tree using the following relationship[46]:

$$\text{Above-ground tree volume } (m^3) = 1.67^* \text{ Merchantable wood volume } (m^3) \qquad \text{(eq. 4)}$$

The following formula was used to convert the above-ground tree volume (m^3) to above-ground tree biomass (kg) assuming a wood density of 490 kg m^{-3} [47]:

Above-ground biomass per tree (kg) = Above-ground tree volume (m^3) x 490 (kg m^{-3})

(eq. 5)

Above-ground tree biomass per ha was calculated as,

Above-ground tree biomass per ha (kg ha^{-1}) = Above-ground biomass per tree (kg)

x No. of trees per ha (eq. 6)

Assuming the carbon content of biomass to be 50% [48], the above-ground C stock per ha was calculated as,

Above-ground C stock per ha (kg ha^{-1}) = Tree biomass per ha (kg ha^{-1}) x 0.5 (eq. 7)

Development of Age versus Above-ground C stock relationships

Age of each forest plantation was calculated from the difference between the surveyed year and the planted year. Relationships were developed between age and above-ground C stock per ha for each tree species at the division level. The relationships were either logarithmic or second-order polynomial and were of the following forms:

$$\text{Above-ground C Stock (kg ha}^{-1}\text{)} = a \log_e(\text{Age}) + b \qquad \text{(eq. 8)}$$

$$\text{Above-ground C Stock (kg ha}^{-1}\text{)} = a + b(\text{Age}) + c(\text{Age})^2 \qquad \text{(eq. 9)}$$

where, age is given in years. In these relationships, a pair of (Age, Above-ground C Stock per ha) values represented one data point. After examining the initially-developed relationships, divisions having similar relationships were pooled on to a common relationship. On the other hand, when there was high variation within a given division, separate relationships were developed for different ranges within a division. Altogether 64 different relationships were developed for different species, divisions and ranges.

Prediction of C stocks per ha in 2008

The developed relationships were used to predict the above-ground carbon stocks per ha in 2008 at the respective sub-block levels.

Conversion of above-ground C stocks to total C stocks per ha

The significant amount of C stored in the below-ground biomass of trees has to be accounted for in any calculation of C stocks. Using a conversion factor developed by Birdsey[47], the total C stocks per ha in 2008 were calculated as,

$$\text{Total C stock per ha in 2008} = \text{Above-ground C stock per ha in 2008} \times 1.3054 \qquad \text{(eq. 10)}$$

Therefore, in eq. 10, root biomass is taken as 30.54% of the above-ground biomass giving a root-weight ratio (i.e. ratio between root biomass and total biomass) of 0.234.

Calculation of total C stock at the sub-block level and up-scaling

The total carbon stock in each sub-block in 2008 was calculated by the product between the respective total carbon stock per ha and the plantation area of the sub-block. The respective sub-block carbon stocks were cumulated over beat, range and division levels. All plantations, which were over 50 years of age by 2008, were considered as felled and were excluded from the calculation.

Calculation methodology for mixed-culture forest plantations

The FORDATA database includes the total number of trees per ha in mixed plantations without specifying the ratio of the two species. Therefore, for each mixed culture, calculations were first done for individual species using the methodology outlined above. Subsequently, the total carbon stocks were calculated by assuming a 50%:50% species ratio.

RESULTS

Total C stocks of monoculture forest plantations in 2008

Table 4 shows the calculated total C stocks of monoculture forest plantations of Sri Lanka in 2008. The total estimated monoculture C stock in 2008 amounted to 4.23 million metric tons. Around 89% of this total C stock in monocultures is contributed by five tree species, namely, *Pinus caribaea* (44%), *Tectona grandis* (21%), *Eucalyptus grandis* (11%), *Eucalyptus camaldulensis* (7%) and *Swietenia macrophylla* (6%). Out of the 22 monoculture species, contribution of 9 species to the total C stock exceeded 1%.

In addition to those already listed, these 9 species included *Acacia auriculiformis*, *Acacia mangium*, *Eucalyptus robusta* and *Eucalyptus tereticornis*.

The five species which had the highest contribution to the total C stock also were the five species which had the highest planted area, covering around 92% of the 57618.8 ha of monoculture forest plantations (Table 4). However, it is interesting to note that eventhough *Tectona grandis* occupied 35% of plantation area, its contribution to the total C stock was only 21%. In contrast, *Pinus caribaea* contributed 44% to the total C stock while occupying only 25% of the area. This meant a wide difference between the average C stock per ha of the two species, with *Pinus caribaea* having a much greater value (130.19 t ha^{-1}) than *Tectona grandis* (42.70 t ha^{-1}). While the inherent species variation in the efficiency of photosynthesis and biomass production process could probably have contributed to the above variation in carbon sequestration ability, the more favourable environmental conditions, particularly the greater water availability, in the areas where *Pinus caribaea* is grown (i.e. the wet zone) in comparison to the areas where *Tectona grandis* is grown (i.e. dry and intermediate zones) would also have had a significant influence on this contrasting difference in C sequestration. The C sequestration capacity of different tree species used in monoculture plantations, as indicated by the mean C stock per ha, showed a wide variation between the 22 species, ranging from 26.25 t ha^{-1} for *Eucalyptus camaldulensis* to 190.71 t ha^{-1} for *Pinus oocarpa*, which is planted in only a very small area (Table 4).

Distribution of C stocks of the major monoculture forest plantation species by division

Pinus caribaea

Pinus caribaea is the species which has the highest contribution to the total C stock of monoculture plantations. Table 5 shows the distribution of *Pinus caribaea* plantations in different divisions along with their respective productivities and total C stocks. Nearly 50% of the total C stock of *Pinus caribaea* is contributed from the divisions of Badulla and Kandy, which traverse the wet and intermediate zones of Sri Lanka. Nuwara Eliya (Wet Zone), Ratnapura (Wet and Intermediate Zones) and Matale (Wet and Intermediate Zones) also contributed a further 34% combined. Badulla showed the highest per ha C stocks followed by Nuwara Eliya, Matale and Kandy. Among the five divisions making major contributions, Ratnapura showed the lowest per ha C stocks.

Tectona grandis

Tectona grandis is the species that makes the second highest contribution (20%) to the total C stocks behind *Pinus caribaea.* Divisions Kurunegala and Moneragala, which traverse the intermediate and dry zones, provide the highest contributions (26% and 21% respectively) to the total C stock from *Tectona grandis* (Table 6). These are followed by Puttalam (14%) and Anuradhapura (11%) showing the preference of *Tectona* for drier environments. Other divisions in the Dry Zone such as Hambantota and Polonnaruwa also provide appreciable contributions to the total C stock from *Tectona*, with 8% and 6% respectively. However, the highest productivity (i.e. per ha C stock) of *Tectona* (132 t ha^{-1}) is shown in the Wet Zone division of Gampaha. Among the divisions traversing the

Dry and Intermediate Zones, Hambantota has the highest productivity (82 t ha^{-1}) followed by Kurunegala and Moneragala (both ~54 t ha^{-1}). The lowest productivity of 12 t ha^{-1} was shown in a small (20.8 ha) plantation in Badulla. Among the larger plantations of *Tectona*, the lowest productivity of 23 t ha^{-1} was in Ratnapura.

Eucalyptus grandis

Carbon stocks in *Eucalyptus grandis* contribute 11% to the total C stock from plantation forests, which is the third largest behind *Pinus caribaea* and *Tectona grandis* (Table 4). Table 7 shows that more than 90% of C stocks of *Eucalyptus grandis* is located in two divisions, namely, Nuwara Eliya (71%) and Badulla (22%). Both these divisions are at high elevations with Nuwara Eliya in the Wet Zone and Badulla in the Intermediate Zone. Productivity of *E. grandis* in Nuwara Eliya (168 t ha^{-1}) is twice as that in Badulla (83 t ha^{-1}), probably because of the greater water availability in the Wet Zone. Although Hambantota, Kandy and Ratnapura showed higher per ha C stocks than Nuwara Eliya, the planted extents in these divisions were very small. Therefore, these high productivities may not be representative of the entire division. However, they probably indicate the upper limits of productivity for *Eucalyptus grandis* under the climatic conditions found in these divisions.

Productivity of *E. grandis* in Nuwara Eliya and Kandy (Table 7) were comparable to the productivity levels of *Pinus caribaea* in Nuwara Eliya and Badulla (Table 5). Interestingly, both species showed high productivities in Hambantota although the planted areas were relatively small. In contrast, in Badulla, which had extensive areas planted with both species, *Pinus caribaea* had a substantially greater productivity than *E. grandis*.

Eucalyptus camaldulensis

Eucalyptus camaldulensis contributes 7.5% to the total C stocks from forest plantations (Table 4). More importantly, it occupies nearly 21% of area of forest plantations. In contrast to *E. grandis*, which is predominantly distributed in Nuwara Eliya and Badulla (Table 7), *E. camaldulensis* is more widely distributed (Table 8), with 58% of its C stock being distributed in the dry zone divisions of Polonnaruwa, Puttalam, Hambantota, Anuradhapura, Moneragala and Ampara. A further 16% is located in Kurunegala, which traverses the intermediate and dry zones. Badulla and Matale, which traverse the intermediate and wet zones, are the other divisions with significant contributions to the total C stock of *E. camaldulensis*, with 17% and 9.5% respectively. It is notable that in all divisions, irrespective of their climatic zone, the productivity of *E. camaldulensis*, as indicated by per ha C stocks (12 – 43 t ha^{-1}), was much lower than that of *E. grandis* (73 – 197 t ha^{-1}) (Table 7). *Tectona grandis*, which was better adapted to climatic conditions in the dry and intermediate zones, also had a greater range of per ha C stocks (12 – 132 t ha^{-1}) (Table 6) than *E. camaldulensis*. This lower productivity of *E. camaldulensis* explains the disproportionality between its planted area (21% of the total area of plantation forests) and its contribution to the total C stock (7.5%).

Swietenia macrophylla

Swietenia macrophylla contributes 6% to the total C stock from forest plantations while occupying 4.5% of the planted area (Table 4). Nearly 90% of both the planted area and the C stock is located in Kurunegala (Table 9). Per ha C stocks of *Swietenia macrophylla* varied within the narrow range of 83 – 106 t ha^{-1} in the different divisions in which it is distributed, irrespective of their climatic conditions.

Acacia mangium and *Acacia auriculiformis*

These two *Acacia* species contribute 5% to the total C stock from plantation forests while occupying nearly 4% of the planted area (Table 4) and are distributed in several divisions across all climatic zones (Tables 10 and 11). Nearly 50% of the C stock from *A. mangium* came from three wet zone divisions, Kegalle, Kandy and Kalutara with 20%, 17% and 13% respectively. In *A. auriculiformis,* Matale, Ratnapura and Anuradhapura provided the major contributions to the C stock with 27%, 20% and 14% respectively. In addition, Kegalle also provided 11% to the total C stock from *A. auriculiformis.* Per ha C stocks of *A. mangium* were clearly greater in the wet zone divisions with a range of 154 – 166 t ha^{-1} (in Gampaha, Kegalle, Kandy and Kalutara) as compared to 53 – 74 t ha^{-1} in divisions located in intermediate and dry zones (i.e. Anuradhapura, Badulla, Kurunegala, Matale and Puttalam). In contrast, *A. auriculiformis* had a much narrower range of productivities (i.e. 79 – 93 t ha^{-1}) in all divisions in which it is grown, irrespective of the climatic conditions.

Total C stocks of mixed culture forest plantations in 2008

Table 12 shows the C stocks of the component species and total C stock of all mixed culture forest plantations. Total C stock in mixed cultures in 2008 amounted to 0.681 million tons. In terms of planted area, the mixed cultures were only 10% of the area of monoculture plantations. However, the mixed cultures had a proportionately greater total C stock with 16% of that of monocultures. This is because of the greater per ha C stocks of mixed cultures with an overall mean of 114.54 t ha^{-1} as compared to 73.34 t ha^{-1} (Table 4) in monocultures.

There were five mixed cultures which contributed more than 5% to the total C stock from mixed cultures. They were *Eucalyptus robusta & E. grandis* (17%), *Pinus* mixed (13%), *E. grandis & E. microcorys* (12.5%), *Eucalyptus* mixed (7%) and *Acacia mangium & A. auriculiformis* (5%). These five mixed cultures accounted for 55% of the total C stock from mixed cultures while occupying 44% of total area of mixed culture plantations. 69% of the C stock of the mixed cultures in 2008 resides in *Eucalyptus*-based mixed plantations. Mixed plantations based on *E. grandis* accounted for 46% of total mixed culture C stocks, while mixtures based on *E. camaldulensis* accounted for 5%. Apart from *Eucalyptus*-based mixed plantations, mixed cultures based on *Tectona grandis* accounted for 9% of the total C stocks in mixed cultures. Three species of *Acacia* (i.e. *A. mangium*, *A. auriculiformis* and *A. decurrens*) were also major contributors to C stocks in mixed plantations with mixtures involving *Acacia* contributing 20.5%. Likewise, mixed plantations involving *Pinus caribaea* and *P. patula* contributed nearly 25% of the total C stock from mixtures.

Distribution of C stocks of the major mixed culture forest plantation species by division

Mixed plantations involving Eucalyptus grandis

All mixed plantations involving *E. grandis* are located in Nuwara Eliya and Badulla divisions. These plantations contain nearly 46% of the total C stock from mixed cultures with a total C stock of 313123 t (Table 13). Out of this 75% is located in Nuwara Eliya while 25% is in Badulla. The productivities (i.e. per ha C stocks) of both *E. grandis* and its associated species were appreciably greater in Nuwara Eliya when compared to Badulla. For *E. grandis*, respective mean productivities were 89 and 48 t ha^{-1} respectively for Nuwara Eliya and Badulla. This reflected more favourable growing conditions in Nuwara Eliya for *E. grandis* as well as its associated species. When compared with the respective productivities of monoculture plantations of *E. grandis* in Nuwara Eliya and Badulla (i.e. 168 and 83 t ha^{-1} respectively-Table 7-), its productivities in the mixed cultures, where *E. grandis* was only 50% of the total tree population, were slightly greater. Interestingly, on average, *E. grandis* provided a greater share of the total C stock of the mixtures in Badulla (i.e. 57%) as compared to those in Nuwara Eliya (52%).

The specific mixtures which provided the highest contributions to the total C stock in *E. grandis*-based plantations in Nuwara Eliya and Badulla were *E. grandis & E. robusta* (36%), *E. grandis & E. microcorys* (15.5%) and *E. grandis & Acacia decurrens* (10%), which were all in Nuwara Eliya, and *E. grandis & E. microcorys* (12%), which was in Badulla (Table 13). The species which showed the highest productivities in association with *E. grandis* were *Acacia decurrens* (119 t ha^{-1}), *E. globulus* (101 t ha^{-1}) and *E. microcorys* (84%), all in Nuwara Eliya, and *E. robusta* (73 t ha^{-1}) in Badulla.

Mixed plantations involving Eucalyptus camaldulensis and Tectona grandis

Mixed plantations involving *E. camaldulensis* contain 8.2% of the total C stock in mixed cultures (Table 12). These plantations are distributed mainly in the dry and intermediate zones (Table 14). Nearly 41% of the C stocks of mixed cultures involving *E. camaldulensis* were in the mixture with *E. tereticornis* in Badulla while mixtures with *Tectona grandis* in Ampara, Moneragala, Kurunegala, Puttalam and Polonnaruwa accounted for 36%. In all divisions except Puttalam and Polonnaruwa, productivity of *E. camaldulensis*, which ranged from 4.8 to 23.8 t ha^{-1}, was lower than its associated species, which ranged from 8.2 to 86.6 t ha^{-1}. Accordingly, except in the two divisions mentioned above, the contribution from *E. camaldulensis* to the total C stock of the mixture was lower than that of its associated species. However, the range productivity of *E. camaldulensis* in the mixed cultures was comparable with that of its monocultures (i.e. 11.8 – 43.0 t ha^{-1}-Table 8), in view of the fact that the mixed cultured contained only 50% of *E. camaldulensis* in their stands.

The specific mixtures that showed the highest productivities for *E. camaldulensis* were those with *E. tereticornis* in Badulla and those with *Tectona grandis* in Ampara and Polonnaruwa. The species which showed the highest productivities in association with *E. camaldulensis* were *Acacia mangium* in Ratnapura (86.6 t ha^{-1}) in Ratnapura and *Kaya* in Anuradhapura (59.1 t ha^{-1}).

Mixed plantations involving *Tectona grandis*

Tectona grandis-based mixed plantations contribute nearly 9% to the total C stock from mixed cultures (Table 12). These are also distributed predominantly in the dry and intermediate zones (Table 14). Mixed cultures with *E. camadulensis* in Ampara, Moneragala, Kurunegala, Puttalam and Polonnaruwa contributed 33% to the total C stock in *Tectona grandis*-based mixed plantations while the mixture of *Tectona grandis* and *Eucalyptus* in Puttalam contributed 26.5%. In contrast to the *Eucalyptus* species, the productivity of *Tectona* in mixed cultures (3.3 – 27.9 t ha^{-1}-Table 14) was lower than that of its monocultures (11.9 – 131.7 t ha^{-1}-Table 6) even after allowing for its 50% share in the mixed tree population. This may be an indication that *Tectona* is a species which prefers monoculture conditions to achieve its maximum productivity. While *Tectona* had slightly greater productivities than *E. camaldulensis* in most of their mixtures, its productivities in mixtures with other species were substantially lower in comparison to the productivity of its associated species (Table 14). For example, *Eucalyptus* in association with *Tectona* in Ampara, Kurunegala and Puttalam achieved productivities ranging from 112 to 140 t ha^{-1} while *Swietenia macrophylla* in association with *Tectona* in Kurunegala achieved a productivity of 60 t ha^{-1}. Accordingly, except in the mixtures with *E. camaldulensis* in Ampara, Moneragala and Kurunegala, the contribution from *Tectona* to the total C stock of mixed plantation was lower than that of its associated species.

Mixed plantations involving *Acacia* species

Mixed plantations involving the different *Acacia* species (i.e. *A. auriculiformis*, *A. mangium*, *A. decurrens* and *A. melanoxylon*) with other tree species (i.e. *Pinus caribaea*, *P. patula*, *Tectona grandis*, *Eucalyptus camaldulensis*, *E. grandis*, *E. torreliana*, *E. robusta*, *E. globulus* and *Cuprusses* spp.) contribute nearly 22% to the total C stock from mixed plantations while occupying 21% of the planted area (Table 12). Mixtures of *A. mangium* and *A. auriculiformis*, all of which were in the wet zone divisions of Ratnapura, Kandy, Kalutara and Gampaha, contributed 24% of the total C stock from *Acacia*-based mixed plantations (Table 15). In all these divisions, *A. mangium* contributed a greater percentage (57-67%) to the total C stock from the mixed plantations. This reflected the greater productivity of *A. mangium* (54 – 85 t ha^{-1}) when compared to *A. auriculiformis* (39 – 45 t ha^{-1}). These productivities in mixed cultures of these two species, at 50% plant densities, are approximately equivalent to their respective productivities in monocultures in these divisions (Tables 10 and 11). Mixtures involving *A. decurrens*, all of which were located in Nuwara Eliya division, had the highest (39%) contribution to the total C stock from *Acacia*-based mixed plantations. In the mixtures of *A. decurrens* with *Pinus caribaea* and mixed *Eucalyptus*, the contribution of *A. decurrens* to the total C stock was around 50%. In the rest of the mixtures, *A. decurrens* had a greater percentage contribution to the total C stock of the mixture. Except in the mixtures with *Pinus caribaea*, *A. decurrens* had a much higher productivity (119 – 144 t ha^{-1} at 50% plant density) (Table 15) than its monocultures (140 t ha^{-1} at 100% plant density) (Table 4). *A. mangium* had mixtures with different *Eucalyptus* species across a range of divisions traversing wet, intermediate and dry zones. These mixtures contributed 26% to the total

C stock from *Acacia*-based mixed plantations. With the exception of the mixture with *E. grandis* in Nuwara Eliya and that with mixed *Eucalyptus* species in Kurunegala, *A. mangium* had the greater percentage contribution (51% – 94%) to total C stock of the mixture. In the divisions of Hambantota, Kurunegala and Matale, which were in the dry and intermediate zones, the productivity of *A. mangium* in mixtures was much lower (27 – 32 t ha^{-1}) than in the rest of the divisions (61 – 89 t ha^{-1}), which were predominantly in the wet zone. *A. auriculiformis* had mixtures with three other species (*Pinus caribaea*, *Tectona grandis* and *E. camaldulensis*), which were distributed in a wide range of divisions traversing wet, intermediate and dry zones. These mixtures contributed 10% to the total C stock from *Acacia*-based mixed plantations. Irrespective of the climatic zone, in all these mixtures, *A. auriculiformis* had a greater percentage contribution (55% - 90%) to the total C stock of the mixture. Except in the mixture with *Tectona grandis* at Kurunegala, the productivity of *A. auriculiformis* in mixtures varied within a narrow range from 44 to 58 t ha^{-1}. This was slightly higher than the monoculture average productivity of 87 t ha^{-1} (at 100% plant density) for *A. auriculiformis* (Table 4).

Combined per ha C stocks of mixed forest plantations

Mixed plantations involving *Acacia decurrens* and different species of *Eucalyptus* grown in Nuwara Eliya showed the highest combined per ha C stocks (Tables 12 and 15), with the mixture between *A. decurrens* and *Eucalyptus* mixed achieving 279 t ha^{-1}. This is followed by *A. decurrens & E. globulus* (247 t ha^{-1}), and *A. decurrens & E. robusta* (226 t ha^{-1}). Three mixtures involving *E. grandis* with other *Eucalyptus* species, also growing in Nuwara Eliya, had combined per ha C stocks above 200 t ha^{-1} (Tables 12 and 13). In addition, mixtures of *A. decurrens* & *E. grandis* (199 t ha^{-1}) and *E. grandis* & *Pinus* mixed (195 t ha^{-1}) in Nuwara Eliya had combined per ha C productivities nearing 200 t ha^{-1}.

None of the mixed plantations in any other division (Tables 13 – 15) reached combined per ha C stocks of those mentioned above in Nuwara Eliya. In Badulla, which had the second highest area of mixed plantations behind Nuwara Eliya, the highest combined per ha C stock was in the *E. grandis* & *E. robusta* mixture with 146 t ha^{-1} (Table 13). Mixtures of *Tectona grandis* and different *Eucalyptus* species were the ones which had the highest combined per ha C stocks in those located in the intermediate and dry zones (Table 14), with 166, 149 and 120 t ha^{-1} in *Tectona* & *Eucalyptus* mixed plantations in Kurunegala, Ampara and Puttalam respectively. In addition, the mixture of *Acacia mangium* and *Eucalyptus* mixed in Kurunegala also had 133 t C ha^{-1} combined (Table 15).

Among species mixtures in the wet zone, those with *A. mangium* had the highest per ha combined C stocks (Table 15) with the mixture of *Acacia mangium* and *Eucalyptus* mixed in Ratnapura having 174 t C ha^{-1}. This is followed by mixtures of *A. mangium* and *A. auriculiformis* in Kalutara, Ratnapura and Kandy with 131, 122 and 116 t C ha^{-1} respectively.

Distribution of monoculture C stocks by divisions

Table 16 shows the distribution of monoculture C stocks in the different divisions. It shows that nearly 58% of the monoculture C stocks are located in four divisions, namely, Badulla (17.71%), Nuwara Eliya (16.57%), Kurunegala (12.42%) and Kandy (10.92%).

Nuwara Eliya and Badulla showed the highest average productivities with 124 and 156 t ha^{-1} respectively. Productivities of the divisions located in the dry and drier intermediate zones (e.g. Kurunegala) were clearly lower (25 – 69 t ha^{-1}) and those in the wet and wetter intermediate zones (e.g. Badulla) (60 – 154 t ha^{-1}). Because of the lower productivity in the dry zone, primarily because of the lower water availability, a division such as Puttalam contributed only 4.4% to the total monoculture C stock despite having 13% of the monoculture plantation area. In contrast, because of the higher productivity of the wet zone, Nuwara Eliya had 16.6% of the monoculture C stock while having only 7.9% of the total monoculture plantation area.

In Badulla, *Pinus caribaea* provides the largest contribution (66%) to the total C stock (Table 17) because of its substantially higher productivity (205 t ha^{-1}) in this environment and also because of higher percentage of area planted with it (41%). *E. grandis* (13%) and *E. camaldulensis* (7%) are the other two species which provided major contributions to the total C stock in Badulla, with the former having nearly twice the productivity of the latter. It can be noted that the Badulla division contains a wide range of plantation forest species with several of them having high levels of productivity in this environment (e.g. *P. oocarpa*, *P. patula*, *E. microcorys*, *E. torreliana* and *Acacia melanoxylon*). In Nuwara Eliya, the total monoculture C stock is dominated by *E. grandis* (47%) and *P. caribaea* (36%), followed by *E. robusta* (12%). All three of the above species have high productivities ranging from 157 to 168 t ha^{-1}, indicating their suitability for the environmental conditions in Nuwara Eliya. In addition, *E. pilularis* and *E. microcorys* showed high productivities.

Pinus caribaea dominated the total monoculture C stocks of most divisions in the wet and wetter intermediate zones, with 97% in Matara, 95% in Kandy, 87% in Kalutara, 61% in Matale and 73% in Ratnapura. However, the respective productivities of *P. caribaea* in these divisions were lower than those of Badulla and Nuwara Eliya. Among the above mentioned divisions, *P. caribaea* in the mid-elevations (e.g. Kandy, Matale and Kegalle) had higher productivities than those in the lower elevations (e.g. Matara, Ratnapura, Gampaha and Kalutara).

DISCUSSION

The present study showed that Sri Lanka had a considerable amount of sequestered carbon in its plantation forests, which amounted to 4.91 million tons in 2008. The total area of forest plantations accounted for in this study (i.e. 63568.4 ha) covered approximately 1% of the total land area of Sri Lanka. In order to place the present C stocks of Sri Lankan forest plantations within the context of C stocks elsewhere in the world, our calculations of per ha C stocks were compared with the spatially averaged values published by the IPCC[49] for different ecological zones (termed as 'biome default values') and with averaged published site data from a recent comprehensive study[50]. In addition to the respective biome defaults, which take in to account both natural forests and plantations, IPCC[49] also gives specific estimates for average above-ground biomass of forest plantations in different ecological zones (Table 4.12 in IPCC[49]). These were originally given in IPCC's 'Good Practice Guidance for Land Use, Land Use Change and Forestry'[41] and are also used as benchmarks for comparison of C stocks of Sri Lankan forest plantations calculated in the present study.

Comparison of monoculture C stocks with benchmark average values

Badulla and Nuwara Eliya, which are the two divisions containing the highest percentages of monoculture C stocks (Table 16), can be categorized as 'Tropical Moist' (i.e. Mean annual temperature > 18°C; Mean annual precipitation 1000 – 2000 mm with a mostly wet climate including 3 – 5 relatively dry months) and 'Tropical Montane' (i.e. Mean annual temperature > 18°C; Altitude > 1000 m above sea level) respectively[49]. Mean annual precipitation (MAP) and temperature of Badulla (altitude 670 m) were 1764 ± 49.5 mm and 23.506 ± 0.049°C during the period from 1950-1989 and 1702 ± 68.6 mm and 24.294 ± 0.079°C during 1990-2007[51]. The corresponding data for Nuwara Eliya (altitude 1895 m) are 2001 ± 55.2 mm and 15.802 ± 0.052°C (1950-1989) and 1864 ± 73.5 mm and 16.175 ± 0.054°C (1990-2007). Therefore, it can be seen that climatic criteria for classification of Badulla were clearly within those specified for Tropical Moist climatic region (Climate Code TAwa according to IPCC[49], 2006). However, those of Nuwara Eliya did not exactly fall within the criteria specified for the Tropical Montane Climatic region (Code TM), because the mean annual temperatures are lower than 18°C.

Monoculture plantations of *Pinus caribaea*, which is the main plantation forest species contributing 44% to the total monoculture C stocks (Table 4), had substantially greater C stocks in Badulla (205 t ha^{-1}) and Nuwara Eliya (164 t ha^{-1}) in comparison to the spatially averaged biome default (SABD) values of 142 t ha^{-1} for TAwa and 112 t ha^{-1} for TM climates. The site specific average C stocks from Keith et al.[50] for TM (i.e. 167 ± 17 t ha^{-1}, no. of sites, n, =3) is on par with our value of 164 t ha^{-1} for *P. caribaea* at Nuwara Eliya. However, Keith et al.[50] 's value of 248 ± 100 (n=5) is higher than the value of 205 t ha^{-1} for *P. caribaea* at Badulla. Yet, it should be noted that Keith et al.[50] 's values include the dead biomass carbon as well, whereas our values include only the carbon in living biomass. The corresponding site-specific average above-ground living biomass values of Keith et al.[50] are 179 ± 96 (n=14) for TAwa and 127 ± 8 (n=3) for TM. These are very close to our above-ground C stock values for *P. caribaea* of 157 t ha^{-1} for Badulla and 126 t ha^{-1} for Nuwara Eliya. Similarly, our C stock estimates for *Eucalyptus grandis* in Nuwara Eliya (i.e. 168 and 129 t ha^{-1} for total and above-ground C stocks, Table 7) are also on par with Keith et al.[50] 's values while being substantially higher than IPCC[49] 's SABD for TM of 112 t ha^{-1}. However, C stocks of *E. grandis* in Badulla (83 and 64 t ha^{-1} for total and above-ground C stocks) are lower than the corresponding SABD for TAwa (142 t ha^{-1}). On the other hand, the above-mentioned above-ground C stocks of *P. caribaea* and *E. grandis* in Badulla and Nuwara Eliya are substantially higher than the average values specified by IPCC[41] for forest plantations in the Tropical Moist (60 t ha^{-1}) and in the tropical montane (45 t ha^{-1}) climatic zones.

None of the monoculture forest plantations in the low- and mid-country (altitude < 1000 m above sea level) wet zone of Sri Lanka have per ha C stocks which are on par with the IPCC[49] 's SABD value of 213 t ha^{-1} or the site-specific average value of 231 ± 75 (n=7) of Keith et al.[50] for the 'Tropical Wet' (i.e. Mean annual temperature > 18°C; Mean annual precipitation > 2000 mm with less than 3 relatively dry months) climate region (Climate Code TAr according to IPCC[49]). Among the monoculture plantations which had the highest C stocks in this region were *Eucalyptus grandis* in Ratnapura (197 t ha^{-1}) and Kandy (188 t ha^{-1}) (Table 7) and *Acacia mangium* in Gampaha, Kalutara and Kandy (162 – 166 t ha^{-1}) (Table 10). However, it should be noted that calculations of the present study include only the C stocks in live standing biomass whereas the two standards against which these are compared take in to account the dead biomass as well. Furthermore, the C stock values of the two standards are for all forest types, including both natural forests and plantations, in the respective climate regions. Therefore, if adjusted to take in to account the above differences, the C stocks in forest plantations of *Eucalyptus grandis* and *Acacia mangium* in the above-mentioned divisions may be closer to the respective standards in this climate region. When compared with the IPCC[41] 's estimates of above-ground C stocks for forest plantations in the 'Tropical Wet' zone (75 t ha^{-1}), the above-ground C stocks of *E. grandis* in Ratnapura (151 t ha^{-1}) and *Acacia mangium* in Gampaha, Kalutara and Kandy (124 – 127 t ha^{-1}) are much higher. Nevertheless, it is possible that the C stocks of the majority of forest plantations in the lower elevations of the wet zone are below the average potential of this climate zone. This may indicate either inferior forest management or inferior site quality such as lower soil fertility in the sites where wet zone plantations have been established. The latter is the more likely reason as most of the forest plantations in the wet zone have been established in degraded soils in sloping lands as a means of arresting their continued degradation[1,2]

Major tree species in the forest plantations in the dry zone of Sri Lanka are *Tectona grandis*, *Eucalyptus camaldulensis*, *Swietenia macrophylla* and *Acacia auriculiformis*. Out of these, the calculated maximum C stocks of *Tectona grandis* (82 t ha^{-1} in Hambantota –Table 6-), *Swietenia macrophylla* (98 t ha^{-1} in Kurunegala -Table 9-) and *Acacia auriculiformis* (90 – 93 t ha^{-1} in Polonnaruwa, Kurunegala, Anuradhapura and Puttalam –Table 11-) come closer to the standards for the 'Tropical Dry' (i.e. Mean annual temperature > 18°C; Mean annual precipitation < 1000 mm with 5-8 relatively dry months) climate region (Climate Code TAWb according to IPCC[49]). The relevant standards for TAWb are 105 t ha^{-1} [49] and 111 (n=1) t ha^{-1} [50]. It is notable that *Tectona grandis* and *Acacia auriculiformis* achieved their maximum per ha C stocks in the wet zone divisions with 132 t ha^{-1} for *Tectona* in Gampaha (Table 6) and 154 t ha^{-1} for *A. auriculiformis* in Kegalle (Table 11). The maximum per ha C stocks of *E. camaldulensis* (43 t ha^{-1} in Badulla and Matale and 42 t ha^{-1} in Polonnaruwa and Ampara –Table 8-), which occupies 21% of the monoculture plantation area (Table 4) and which is distributed predominantly in the dry zone divisions (i.e. 73% of its planted area –Table 8-), are much lower than the standards of Keith et al.[50] and IPCC[49]. However, the maximum above-ground C stocks of all four major dry zone plantation forest species (i.e. 63, 75, 70 and 33 t ha^{-1} for *Tectona*, *Swietenia*, *A. auriculiformis* and *E. camaldulensis*) are higher than or on par with IPCC[41] (2003)'s estimate of average above-ground C stocks of plantation forests in the 'Tropical Dry' climate zone (30 t ha^{-1}). Yet, in some of the divisions which contain substantial areas of *Tectona* (21 and 24 t ha^{-1} in Anuradhapura and Puttalam which respectively had 17% and 24% of the planted area) and *E. camaldulensis* (10 and 11 t ha^{-1} in Puttalam and Hambantota having 27% and 16% of the planted area), the above-ground per ha C stocks of were below the IPCC[41] average. On the other hand, above-ground per ha C stocks of all divisions planted with *Swietenia* (63 – 82 t ha^{-1}) and *A. auriculiformis* (61 – 71 t ha^{-1}) were substantially above the relevant IPCC[41] value of 30 t ha^{-1}.

Comparison of mixed culture C stocks with benchmark average values

Our calculations have shown that the mixed culture forest plantations have, on average, greater per ha C stocks (114.54 t ha^{-1} -Table 12-) than the monocultures (73.34 t ha^{-1} -Table 4-). It is notable that except the mixed cultures involving *Tectona grandis* and *Eucalyptus camaldulensis*, most of the mixed culture plantations are located in the wet zone (Tables 13-15). In addition to the possible synergistic effects of mixed cultures[52,53], the greater overall productivity of mixed cultures could be due to the more favourable environmental conditions found in the wet zone for tree growth and carbon sequestration. Remarkably, combined per ha C stocks exceeding 190 t ha^{-1} in the mixed plantations involving *Acacia decurrens* with three *Eucalyptus* species (i.e. *globulus*, *robusta* and *grandis*) and with *Eucalyptus* mixed and with *Pinus* mixed (Tables 12, 13 and 15) grown in Nuwara Eliya exceeded by a substantial margin the respective benchmark values for the 'Tropical Montane' climate zone, i.e. 167 t ha^{-1} [50], 112 t ha^{-1} [49] and 45 t ha^{-1} [41]. This indicates a combination of environmental conditions (i.e. precipitation, temperature and soil fertility), which are highly conducive to fast growth of these tree species. It was mentioned earlier that the annual mean temperature of Nuwara Eliya (i.e. ~ 16°C) is below the threshold of 18°C to be included in the 'Tropical Montane' climate region. The site-specific C sequestration data of Keith et al.[50] show that in a precipitation regime of around 2000 mm yr^{-1}, total per ha C stocks increase as annual mean temperatures decrease from around 28° down to 10°C (ref. Fig. 3 of Keith et al.[50]). This is primarily because of the lower respiration rates at lower temperatures[54]. Hence, it is highly likely that, the combination of higher precipitation, which promotes greater photosynthesis, and lower temperature, which reduces respiration, are responsible for the exceptionally high carbon sequestration rates of the mixed forest plantations in Nuwara Eliya.

In Badulla, the maximum combined per ha C stock of 146 t ha^{-1} in the mixture between *E. grandis & E. robusta* was on par with the SABD of 142 t ha^{-1} for Tropical Moist climate region[49]. However, it was much lower than the site specific average of 248 t ha^{-1} as estimated by Keith et al.[50] for the same climate zone. On the other hand, the maximum combined per ha C stocks of mixtures between *Tectona grandis* and different *Eucalyptus* species and those between *Acacia mangium* and *Eucalyptus* mixed in Kurunegala in the intermediate and dry zones (120 – 166 t ha^{-1}) exceeded all benchmark average C stock values for the 'Tropical Dry' climate region, i.e. 111, 105 and 30 t ha^{-1} for Keith et al.[50], IPCC[49] and IPCC[41]. However, in the wet zone, the maximum combined per ha C stock of 174 t ha^{-1} for the mixture of *Acacia mangium* and *Eucalyptus* mixed in Ratnapura was below the benchmark averages for the 'Tropical Wet' climate zone, i.e. 231 and 213 t ha^{-1} for Keith et al.[50] (2009) and IPCC[50] (2006). However, it can be noted that Keith et al.[50] 's site-specific average value, which is based on data from seven sites within this climate zone, has a standard deviation of 75 t ha^{-1}, which brings the maximum value of our study also in to the confidence interval of Keith et al.[50] 's estimate. Examination of Keith et al.[50] 's plot (i.e. Fig. 3) of per ha C stocks of individual sites having rainfall and annual mean temperature regimes comparable to those of Ratnapura, i.e. 3700 mm yr^{-1} and 27.4°C respectively[51], show that several sites have per ha C stocks which are comparable to the 174 t ha^{-1} observed in our study. Although the higher rainfall regime of this climate zone favoured higher photosynthetic rates, the higher temperatures probably increased the respiration rates so that the C sequestration rates did not increase up to the levels achieved under the cooler temperatures in Nuwara Eliya. This is supported by the findings of Clark et al.[55], which showed a significant negative correlation between annual growth rates of six tropical tree species in a tropical rainforest in Costa Rice and annual mean of daily minimum temperature. This was attributed to the increased tree respiration rates at higher temperatures as respiration rate increases exponentially with increasing temperature while the photosynthetic rate increases only up to an optimum and then decreases[56,57]. This has important implications for all forests in the tropics, both natural forests and plantations, where the productivity is likely to decrease with future global warming[22,58,59].

Additional section that has been included in the report after the manuscript was submitted in August 2009:

The total annual carbon sink (C_{Total}) from forest plantations

The annual total carbon sink (C_{Total}) from the entire area of forest plantations in Sri Lanka was estimated using the principles and equations that were used earlier in Section 3.I for estimation of carbon sinks from Sinharaja and KDN forest complexes.

The annual rate of carbon sequestration as net primary productivity (NPP) was calculated as the ratio between the total carbon stock in standing biomass (C_{TBM}) and average residence time (t_r) of standing biomass using eq. 34 of section 3.I as,

$$NPP = C_{TBM} / t_r \qquad \text{(eq. 11)}$$

Taking C_{TBM} as 4.91×10^6 mt and average residence time (t_r) as 30 years, Total annual NPP = $(4.91 \times 10^6$ mt C) / 30 yr = 0.164×10^6 mt C yr^{-1}

Total annual carbon sink (C_{Total}) from the entire area of forest plantations can be calculated as,

C_{Total} = Total annual NPP x 3.67

= 0.164×10^6 mt C $yr^{-}1$ x 3.67 mt CO_2 (mt C)$^{-1}$

= 0.602×10^6 mt CO_2 yr^{-1}

Percentage of annual total CO_2 emission (calculated earlier in section 3.1 as 12.13×10^3 mt CO_2 yr^{-1}) that is absorbed by the total area of forest plantations can be calculated as,

% emission absorbed by the total area of forest plantations

= [(0.602 x 10^6 mt CO_2 yr^{-1})/(12.13 x 10^6 mt CO_2 yr^{-1})] x 100

= 4.96%

Taking the total land area of Sri Lanka as 6,560,963 ha (i.e. 25,332 square miles), the entire area of forest plantations (i.e. 63568.4 ha) occupy about 0.969% of the total land area respectively.

A quantitative index for the efficiency of the carbon sink of the forest plantations can be calculated as the ratio between the percentage national CO_2 emissions absorbed by the total area of forest plantations and the percentage land area occupied by them. Accordingly, Efficiency index of carbon sink = (4.96%)/(0.969%) = 5.12

It can be noted that the efficiency indices of the carbon sinks of Sinharaja and KDN forest complexes (i.e. 14.74 and 17.72 respectively) are higher than the corresponding index for forest plantations. However, it should be noted that the above-calculated efficiency index of forest plantations is an average value for all such plantations scattered in all climatic zones of Sri Lanka, which include areas where the climatic conditions are optimum (e.g. wet zone) as well as non-optimum (e.g. dry and intermediate zones) for forest growth. Therefore, we calculated the efficiency index of the carbon sink for the most productive areas and species for plantation forestry (as shown by Tables 5, 7 and 16). The results are given in Table 18, which shows that even when the most productive areas (i.e. divisions) and plantation forest species are considered, the efficiency indices of their carbon sinks were lower than those of Sinharaja and Kanneliya forest complexes. Only *Pinus caribaea* in Badulla could achieve an efficiency index (i.e. 13.53) which was close to the value of Sinharaja. These data indicate that lowland tropical wet evergreen forests in Sri Lanka, as exemplified by Sinharaja and KDN forests complexes, are more efficient carbon sinks than even the most productive plantation forests growing in the most favourable areas in Sri Lanka.

CONCLUDING REMARKS

Carbon stock values calculated in the present study can be considered as the first overall estimates of carbon stocks in the Sri Lankan forest plantations. Despite their approximate nature, these first estimates can be used as basic data in policy formulation on climate change mitigation. These estimates can be fine tuned and made more accurate by updating the FORDATA data base, increasing the frequency of measurements of DBH and h and by developing allometric relationships for plantation forest species for which they are not available.

Furthermore, it should be noted that the present study has estimated only the C stock present in the live biomass of forest trees in the respective plantations. However, the total C stock in a forest plantation includes the C stocks in the soil and the understorey vegetation. Therefore, C stock estimates of the present study may be considered as the lower-boundary estimates. More in-depth studies are required to quantify those components of the total C stock in a forest plantation, which were not quantified in the present study. Our estimates also indicated that forest biomass production and C stocks are related to the environmental conditions of the respective sites and regions. Hence, relationships need to be established between biomass production of different forest types and prevailing environmental conditions. These can be either empirical relationships or process-based models, which will enable prediction of the impacts of future climate change on the C stocks of forest plantations in Sri Lanka.

This study highlights the importance of ground-based, on-site measurements of tree dimensions and biomass. Although such measurements are time- and labour-intensive, they are essential to validate the more extensive methods of C stock estimation such as those using remote-sensing. Therefore, ground-based measurement of forest C stocks should be improved and continued and infra-structure facilities for these measurements need to be strengthened.

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Table 1: List of monoculture plantation forest tree species that were used in the calculations

Sequential No.	Species code	Species
1.	1	*Tectona grandis*
2.	2	*Swietenia macrophylla*
3.	28	*Eucalyptus deglupta*
4.	29	*Eucalyptus cloeziana*
5.	30	*Eucalyptus pilularis*
6.	31	*Eucalyptus robusta*
7.	32	*Eucalyptus citriodora*
8.	33	*Eucalyptus globulus*
9.	34	*Eucalyptus grandis*
10.	37	*Eucalyptus camaldulensis*
11.	38	*Eucalyptus tereticornis*
12.	39	*Eucalyptus microcorys*
13.	40	*Eucalyptus torelliana*
14.	49	*Acacia mangium*
15.	73	*Acacia auriculiformis*
16.	82	*Acacia melanoxylon*
17.	83	*Acacia decurrens*
18.	92	*Casuarina sp*
19.	93	*Cupressus sp*
20.	94	*Pinus caribaea*
21.	95	*Pinus patula*
22.	97	*Pinus oocarpa*

Table 2: List of mixed-cultures of plantation forests that were used in the calculations

Seq. No.	Species code	Species composition
1.	1_2	*Tectona grandis & Swietenia macrophylla*
2.	1_37	*Tectona grandis & Eucalyptus camaldulensis*
3.	1_73	*Tectona grandis & Acacia auriculiformis*
4.	1_86	*Tectona grandis & Kaya sp*
5.	1_87	*Tectona grandis & Eucalyptus:Tectona mixture*
6.	2_94	*Swietenia macrophylla & Pinus caribaea*
7.	31_34	*Eucalyptus robusta & Eucalyptus grandis*
8.	31_39	*Eucalyptus robusta & Eucalyptus microcorys*
9.	31_42	*Eucalyptus robusta & Eucalyptus* mixed
10.	31_83	*Eucalyptus robusta & Acacia decurrens*
11.	32_34	*Eucalyptus citriodora & Eucalyptus grandis*
12.	31_95	*Eucalyptus robusta & Pinus patula*
13.	33_34	*Eucalyptus globulus & Eucalyptus grandis*
14.	33_83	*Eucalyptus globulus & Acacia decurrens*
15.	34_37	*Eucalyptus grandis & Eucalyptus camaldulensis*
16.	34_39	*Eucalyptus grandis & Eucalyputs microcorys*
17.	34_42	*Eucalyptus grandis & Eucalyptus* mixed
18.	34_49	*Eucalyptus grandis & Acacia mangium*
19.	34_83	*Eucalyptus grandis & Acacia decurrens*
20.	34_93	*Eucalyptus grandis & Cupressus* sp
21.	34_94	*Eucalyptus grandis & Pinus caribaea*
22.	34_95	*Eucalyptus grandis & Pinus patula*
23.	34_98	*Eucalyptus grandis & Pinus* mixed
24.	37_38	*Eucalyptus camaldulensis & Eucalyptus tereticornis*
25.	37_40	*Eucalyptus camaldulensis & Eucalyptus torelliana*
26.	37_49	*Eucalyptus camaldulensis & Acacia mangium*
27.	37_73	*Eucalyptus camaldulensis & Acacia auriculiformis*
28.	37_86	*Eucalyptus camaldulensis & Kaya* sp
29.	37_94	*Eucalyptus camaldulensis & Pinus caribaea*
30.	38_40	*Eucalyptus tereticornis & Eucalyptus torelliana*
31.	39_93	*Eucalyptus microcorys & Cupressus* sp
32.	39_94	*Eucalyptus microcorys & Pinus caribaea*
33.	40_49	*Eucalyptus torelliana & Acacia mangium*
34.	42_49	*Eucalyptus* mixed *& Acacia mangium*
35.	42_83	*Eucalyptus* mixed *& Acacia decurrens*
36.	42_93	*Eucalyptus* mixed *& Cupressus* sp
37.	42_94	*Eucalyptus* mixed *& Pinus caribaea*
38.	42_95	*Eucalyptus* mixed *& Pius patula*
39.	42_98	*Eucalyptus* mixed *& Pinus* mixed
40.	49_73	*Acacia mangium & Acacia auriculiformis*
41.	73_94	*Acacia auriculiformis & Pinus caribaea*
42.	82_93	*Acacia melanoxylon & Cupressus sp*

43.	83_94	*Acacia decurrens & Pinus caribaea*
44.	83_95	*Acacia decurrens & Pinus patula*
45.	93_95	*Cupressus sp & Pinus patula*
46.	93_98	*Cupressus sp & Pinus* mixed
47.	94_95	*Pinus caribaea & Pinus patula*
48.	34_41	*Eucalyptus grandis & Eucalyptus paniculata*
49.	1_42	*Tectona grandis & Eucalyptus* mixed
50.	42	*Eucalyptus* mixed
51.	98	*Pinus* mixed

Table 3: Known volume functions and their specifications

Species	Volume function	Specifications
Cupressus spp.	$V=[0.336929+5.574551/(\pi d)]*(\pi d^2h/40000)$	Under bark, to 5cm cut off
Eucalyptus robusta	$V=[0.337277-(0.151178/(\pi d)]*(\pi d^2h/40000)$	Under bark, to 5cm cut off
Eucalyptus grandis	$V=[0.337277-(0.151178/(\pi d)]*(\pi d^2h/40000)$	Under bark, to 5cm cut off
Eucalyptus microcorys	$V=[0.296384+(2.6326592/(\pi d)]*\pi d^2h/40000)$	Under bark, to 5cm cut off
Pinus caribaea	$V=0.0000575*d^{1.87185}*h^{0.91418}*(1-49.933*d^{-2..83174})$	Over bark to 5 cm cut off
Tectona grandis	$V=\exp(-9.7327+2.055*\ln d+0.773*\ln h)$	Over bark to 5 cm cut off

Note: V = Merchantable wood volume per tree (m^3); d = Diameter at breast height (cm); h = Total tree height (m).

Source: Forest Inventory Manual for Sri Lanka[45].

Table 4: Calculated total C stocks of monoculture forest plantations of Sri Lanka in 2008

Species	Total C Stock (t)	% of Total	Planted Area (ha)	% of Total Area	Mean C Stock (t ha^{-1})
Pinus caribaea	1871784.85	44.296	14377.20	24.952	130.19
Tectona grandis	866178.47	20.498	20286.90	35.209	42.70
Eucalyptus grandis	462990.64	10.957	3488.50	6.054	132.72
E. camaldulensis	315328.69	7.462	12014.70	20.852	26.25
Swietenia macrophylla	261616.98	6.191	2680.90	4.653	97.59
Acacia auriculiformis	119854.39	2.836	1375.40	2.387	87.14
Acacia mangium	93571.92	2.214	845.50	1.467	110.67
Eucalyptus robusta	85639.23	2.027	577.40	1.002	148.32
Eucalyptus tereticornis	59725.82	1.413	878.20	1.524	68.01
Pinus patula	39484.13	0.934	517.90	0.899	76.24
Eucalyptus microcorys	24101.48	0.570	207.50	0.360	116.15
Casuarina spp	13452.76	0.318	231.50	0.402	58.11
Eucalyptus torelliana	5518.57	0.131	69.60	0.121	79.29
Eucalyptus pilularis	1640.46	0.039	9.00	0.016	182.27
Pinus oocarpa	1430.30	0.034	7.50	0.013	190.71
Acacia decurrens	1052.48	0.025	7.50	0.013	140.33
Cupressus sp	670.70	0.016	24.50	0.043	27.38
Eucalyptus citriodora	651.07	0.015	7.50	0.013	86.81
Eucalyptus cloeziana	409.24	0.010	5.80	0.010	70.56
Eucalyptus globulus	242.62	0.006	3.80	0.007	63.85
Eucalyptus deglupta	134.33	0.003	1.00	0.002	134.33
Acacia melanoxylon	111.89	0.003	1.00	0.002	111.89
Total	**4225591.01**		**57618.80**		

Table 5: Distribution of C stocks of *Pinus caribaea* in different divisions and their productivity

Division	Per ha C Stock (t ha^{-1})	Planted Area (ha)	% of Total Area	Total C Stock (t)	% of Total C Stock
Badulla	204.79	2413.3	16.79	494208.94	26.40
Galle	60.46	656.1	4.56	39670.16	2.12
Gampaha	81.91	68.4	0.48	5602.84	0.30
Hambantota	120.51	236.4	1.64	28487.76	1.52
Kalutara	85.14	1042.5	7.25	88762.29	4.74
Kandy	131.49	3345.4	23.27	439895.29	23.50
Kegalle	111.78	73.2	0.51	8182.30	0.44
Matale	148.52	1248.6	8.68	185445.49	9.91
Matara	90.52	1477.1	10.27	133700.01	7.14
Moneragala	31.95	2.0	0.01	63.89	0.00
N'eliya	164.01	1528.7	10.63	250725.97	13.40
Ratnapura	86.21	2285.5	15.90	197039.90	10.53
Total		14377.2		1871784.85	

Table 6: Distribution of C stocks of *Tectona grandis* in different divisions and their productivity

Division	**Per ha C Stock (t ha^{-1})**	**Planted Area (ha)**	**% of Total Area**	**Total C Stock (t)**	**% of Total C Stock**
Ampara	46.24	615.0	3.03	28439.29	3.28
Anuradhapura	27.15	3443.9	16.98	93484.99	10.79
Badulla	11.85	20.8	0.10	246.56	0.03
Gampaha	131.72	160.4	0.79	21127.68	2.44
Hambantota	82.37	850.5	4.19	70058.39	8.09
Kandy	32.15	51.2	0.25	1645.97	0.19
Kurunegala	54.36	4117.1	20.29	223813.39	25.84
Matale	35.52	1509.2	7.44	53611.75	6.19
Moneragala	53.81	3426.0	16.89	184337.93	21.28
Polonnaruwa	32.68	1704.6	8.40	55702.28	6.43
Puttlam	31.30	3939.8	19.42	123334.80	14.24
Ratnapura	23.14	448.4	2.21	10375.44	1.20
		20286.9		866178.47	

Table 7: Distribution of C stocks of *Eucalyptus grandis* in different divisions and their productivity

Division	Per ha C Stock (t ha^{-1})	Planted Area (ha)	% of Total Area	Total C Stock (t)	% of Total C Stock
Anuradhapura	72.97	9.6	0.28	700.53	0.15
Badulla	83.22	1207.2	34.61	100463.85	21.70
Hambantota	175.72	1.5	0.04	263.58	0.06
Jaffna	104.83	41.7	1.20	4371.25	0.94
Kandy	187.94	2.0	0.06	375.88	0.08
Kurunegala	91.07	83.2	2.38	7576.80	1.64
Matara	139.81	19.3	0.55	2698.30	0.58
Moneragala	82.38	138.5	3.97	11409.97	2.46
N'eliya	168.46	1962.7	56.26	330640.11	71.41
Ratnapura	196.95	22.8	0.65	4490.36	0.97
Total		3488.5		462990.64	

Table 8: Distribution of C stocks of *Eucalyptus camaldulensis* in different divisions and their productivity

Division	Per ha C Stock (t ha^{-1})	Planted Area (ha)	% of Total Area	Total C Stock (t)	% of Total C Stock
Ampara	41.67	157.2	1.31	6551.09	2.08
Anuradhapura	12.73	860.0	7.16	10944.27	3.47
Badulla	43.04	1219.7	10.15	52500.54	16.65
Galle	11.81	2.5	0.02	29.52	0.01
Gampaha	14.73	10.5	0.09	154.67	0.05
Hambantota	14.85	1908.2	15.88	28337.02	8.99
Kandy	40.62	7.6	0.06	308.70	0.10
Kurunegala	38.46	1277.2	10.63	49119.68	15.58
Matale	42.72	697.8	5.81	29807.16	9.45
Matara	15.13	14.4	0.12	217.87	0.07
Moneragala	14.41	643.5	5.36	9276.03	2.94
Polonnaruwa	42.47	2006.5	16.70	85210.48	27.02
Puttlam	13.36	3209.6	26.71	42871.67	13.60
Total		12014.7		315328.69	

Table 9: Distribution of C stocks of *Swietenia macrophylla* in different divisions and their productivity

Division	**Per ha C Stock (t ha^{-1})**	**Planted Area (ha)**	**% of Total Area**	**Total C Stock (t)**	**% of Total C Stock**
Anuradhapura	87.12	6.0	0.22	522.73	0.20
Gampaha	105.27	74.7	2.79	7863.58	3.01
Hambantota	101.83	10.7	0.40	1089.63	0.42
Kalutara	106.49	0.7	0.03	74.55	0.03
Kegalle	97.91	63.3	2.36	6197.97	2.37
Kurunegala	97.85	2373.7	88.54	232268.04	88.78
Puttlam	82.67	40.8	1.52	3372.82	1.29
Ratnapura	92.14	111.0	4.14	10227.66	3.91
Total		2680.9		261616.97	

Table 10: Distribution of C stocks of *Acacia mangium* in different divisions and their productivity

Division	Per ha C Stock (t ha^{-1})	Planted Area (ha)	% of Total Area	Total C Stock (t)	% of Total C Stock
Anuradhapura	52.84	41.2	4.87	2176.94	2.33
Badulla	74.41	114.8	13.58	8542.09	9.13
Gampaha	162.62	27.6	3.26	4488.35	4.80
Kalutara	161.53	76.7	9.07	12389.02	13.24
Kandy	166.32	93.2	11.02	15500.64	16.57
Kegalle	154.29	120.1	14.20	18530.37	19.80
Kurunegala	54.88	60.6	7.17	3325.59	3.55
Matale	54.32	44.5	5.26	2417.39	2.58
Puttlam	52.54	85.0	10.05	4465.61	4.77
Ratnapura	119.56	181.8	21.50	21735.91	23.23
Total		845.5		93571.92	

Table 11: Distribution of C stocks of *Acacia auriculiformis* in different divisions and their productivity

Division	Per ha C Stock (t ha^{-1})	Planted Area (ha)	% of Total Area	Total C Stock (t)	% of Total C Stock
Gampaha	87.64	68.9	5.01	6038.71	5.04
Ratnapura	79.39	307.3	22.34	24397.91	20.36
Polonnaruwa	93.08	52.0	3.78	4839.90	4.04
Kurunegala	90.45	89.4	6.50	8085.88	6.75
Anuradhapura	91.76	187.0	13.60	17159.87	14.32
Puttlam	91.03	97.1	7.06	8838.74	7.37
Hambantota	85.92	28.1	2.04	2414.48	2.01
Matale	88.96	367.1	26.69	32657.07	27.25
Kandy	90.73	20.0	1.45	1814.51	1.51
Kalutara	88.45	10.0	0.73	884.47	0.74
Kegalle	85.68	148.5	10.80	12722.86	10.62
Total		1375.4		119854.39	

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Table 12: Calculated total C stocks of mixed culture forest plantations of Sri Lanka in 2008

Species Composition of the Mixture	Total C Stock of Spp. 1 (t)	% of Total C Stock from Spp. 1	Mean C St. of Spp. 1 (t ha^{-1})	Total C Stock of Spp. 2 (t)	% of Total C Stock from Spp. 2	Mean C St. of Spp. 2 (t ha^{-1})	Total C Stock of Mixture (t)	% of Total Mixed C Stock	Planted Area (ha)	% of Pl. Area
Eucalyptus robusta & *E. grandis*	58040.89	50.00	65.54	58040.89	50.00	65.54	116081.8	17.03	885.6	14.89
Eucalyptus grandis & *E. microcorys*	51907.84	61.03	87.95	33151.87	38.97	56.17	85059.71	12.48	590.2	9.92
Acacia mangium & *A. auriculiformis*	23426.51	65.45	83.16	12364.79	34.55	43.89	35791.30	5.25	281.7	4.73
Eucalyptus grandis & *A. decurrens*	12729.69	40.18	79.76	18954.94	59.82	118.77	31684.63	4.65	159.6	2.68
Tectona grandis & *Eucalyptus mixed*	2807.92	10.70	14.09	23428.71	89.30	117.55	26236.63	3.85	199.3	3.35
E. grandis & *Pinus caribaea*	12111.59	46.69	34.30	13828.77	53.31	39.16	25940.36	3.81	353.1	5.93
E. camaldulensis & *E. tereticornis*	8032.94	35.22	23.84	14772.51	64.78	43.84	22805.44	3.35	337.0	5.66
Tectona grandis & *E. camaldulensis*	11646.98	57.41	20.95	8640.27	42.59	15.54	20287.25	2.98	555.9	9.34
Pinus caribaea & *Pinus patula*	8830.44	50.00	89.65	8830.44	50.00	89.65	17660.89	2.59	98.5	1.66
Eucalyptus mixed & *A. mangium*	7132.05	57.48	77.78	5275.31	42.52	57.53	12407.36	1.82	91.7	1.54
Eucalyptus grandis & *A. mangium*	4755.07	42.00	45.81	6567.81	58.00	63.27	11322.88	1.66	103.8	1.74
E. grandis & *Eucalyptus mixed*	6610.85	59.72	88.98	4459.72	40.28	60.02	11070.57	1.62	74.3	1.25
E. grandis & *Pinus patula*	7643.81	74.99	66.76	2549.93	25.01	22.27	10193.74	1.50	114.5	1.92
E. globulus & *E. grandis*	4888.67	48.22	93.83	5248.80	51.78	100.74	10137.47	1.49	52.1	0.88
Eucalyptus mixed & *A. decurrens*	4542.14	49.46	138.06	4640.49	50.54	141.05	9182.64	1.35	32.9	0.55
E. robusta & *E. microcorys*	4406.29	48.29	83.61	4718.62	51.71	89.54	9124.91	1.34	52.7	0.89
Eucalyptus torelliana & *A. mangium*	2148.24	23.92	24.61	6833.68	76.08	78.28	8981.92	1.32	87.3	1.47
Tectona grandis & *A. auriculiformis*	1255.03	16.41	7.95	6393.33	83.59	40.52	7648.36	1.12	157.8	2.65
Eucalyptus mixed & *Pinus caribaea*	5009.26	75.49	112.06	1626.33	24.51	36.38	6635.59	0.97	44.7	0.75
E. grandis & *E. camaldulensis*	3867.97	64.03	40.72	2172.71	35.97	22.87	6040.67	0.89	95.0	1.60
E. camaldulensis & *A. mangium*	809.33	14.31	8.47	4846.80	85.69	50.75	5656.14	0.83	95.5	1.61
E. camaldulensis & *A. auriculiformis*	529.89	10.52	5.55	4506.71	89.48	47.19	5036.60	0.74	95.5	1.61
E. microcorys & *Cupressus sp*	3401.60	83.81	82.76	656.98	16.19	15.98	4058.58	0.60	41.1	0.69
Tectona grandis & *Kaya senegalensis*	570.27	15.24	3.59	3170.87	84.76	19.96	3741.14	0.55	158.9	2.67
E. microcorys & *Pinus caribaea*	1462.57	39.46	73.13	2243.46	60.54	112.17	3706.03	0.54	20.0	0.34
E. robusta & *Pinus patula*	2320.40	63.10	68.65	1357.21	36.90	40.15	3677.61	0.54	33.8	0.57

Cont.

Species Composition of the Mixture	Total C Stock of Spp. 1 (t)	% of Total C Stock from Spp. 1	Mean C St. of Spp. 1 (t ha^{-1})	Total C Stock of Spp. 2 (t)	% of Total C Stock from Spp. 2	Mean C St. of Spp. 2 (t ha^{-1})	Total C Stock of Mixture (t)	% of Total Mixed C Stock	Planted Area (ha)	% of Pl. Area
Acacia decurrens & *Pinus caribaea*	1757.83	50.31	82.53	1736.15	49.69	81.51	3493.98	0.51	21.3	0.36
E. globulus & *A. decurrens*	1194.51	41.97	103.87	1651.33	58.03	143.59	2845.84	0.42	11.5	0.19
Acacia decurrens & *Pinus patula*†	2771.07	100.00	135.17	0.00	0.00	0.00	2771.07	0.41	20.5	0.34
T. grandis & *Eucalyptus spp.*	388.16	14.45	12.40	2298.73	85.55	73.44	2686.89	0.39	31.3	0.53
E. grandis & *Pinus mixed*	1456.14	56.16	109.48	1136.68	43.84	85.46	2592.81	0.38	13.3	0.22
E. citriodora & *E. grandis*	1000.57	53.28	30.60	877.21	46.72	26.83	1877.78	0.28	32.7	0.55
E. grandis & *E. paniculata*	943.15	51.66	37.73	882.45	48.34	35.30	1825.60	0.27	25.0	0.42
E. robusta & *Eucalyptus mixed*	801.98	44.38	86.23	1004.97	55.62	108.06	1806.95	0.27	9.3	0.16
Eucalyptus mixed & *Pinus patula*†	1629.14	100.00	135.76	0.00	0.00	0.00	1629.14	0.24	12.0	0.20
Eucalyptus mixed & *Cupressus spp.*	1483.98	91.47	148.40	138.37	8.53	13.84	1622.35	0.24	10.0	0.17
Swietenia macrophylla & *P. caribaea*	789.66	48.77	56.40	829.37	51.23	59.24	1619.04	0.24	14.0	0.24
Cupressus spp. & *Pinus mixed*	220.10	14.41	14.39	1307.81	85.59	85.48	1527.91	0.22	15.3	0.26
E. robusta & *Acacia decurrens*	469.07	36.36	82.29	820.87	63.64	144.01	1289.93	0.19	5.7	0.10
A. auriculiformis & *Pinus caribaea*	682.42	56.03	47.72	535.44	43.97	37.44	1217.85	0.18	14.3	0.24
E. camaldulensis & *Kaya spp.*	142.03	12.39	8.35	1003.96	87.61	59.06	1145.98	0.17	17.0	0.29
E. grandis & *Cupressus spp.*	1105.90	98.71	122.88	14.45	1.29	1.61	1120.35	0.16	9.0	0.15
E. camaldulensis & *Pinus caribaea*	145.62	16.48	7.55	738.19	83.52	38.25	883.81	0.13	19.3	0.32
Eucalyptus mixed & *Pinus mixed*	443.39	60.73	130.41	286.72	39.27	84.33	730.11	0.11	3.4	0.06
Tectona grandis & *Sw. macrophylla*	138.14	30.95	26.56	308.25	69.05	59.28	446.38	0.07	5.2	0.09
E. tereticornis & *E. torelliana*	133.52	50.00	66.76	133.52	50.00	66.76	267.03	0.04	2.0	0.03
Ac. melanoxylon & *Cupressus spp.*	172.07	83.91	74.81	33.00	16.09	14.35	205.07	0.03	2.3	0.04
E. camaldulensis & *E. torelliana*	14.49	11.01	4.83	117.09	88.99	39.03	131.58	0.02	3.0	0.05
Cupressus spp. & *Pinus patula*	61.69	62.48	14.35	37.05	37.52	8.62	98.74	0.01	4.3	0.07
Eucalyptus mixed	.	.	.	.	.		49012.86	7.19	620.3	10.43
Pinus mixed	.	.	.	.	.		88447.04	12.98	215.1	3.62
Total							**681466.3**		**5949.6**	

†C stock of *Pinus patula* in these mixtures could not be estimated because the quadratic Age-per ha C stock relationship gave a negative value.

Table 13: Distribution of C stocks of mixed culture forest plantations involving *Eucalyptus grandis* in different divisions and their productivities

Species Composition and Division	C St. of Spp. 1 (t ha^{-1})	C St. of Spp. 2 (t ha^{-1})	Planted Area (ha)	Total C Stock of Spp. 1 (t)	% of Total C Stock from Spp. 1	Total C Stock of Spp. 2 (t)	% of Total C Stock from Spp. 2	Total C Stock of Mixture (t)	% of Total Mixed C Stock
Badulla:									
E. grandis & E. citriodora	26.83	30.60	32.70	877.22	46.72	1000.58	53.28	1877.79	0.60
E. grandis & E. robusta	72.78	72.78	27.20	1979.51	50.00	1979.51	50.00	3959.02	1.26
E. grandis & E. globulus	28.25	33.67	5.50	155.37	45.63	185.16	54.37	340.53	0.11
E. grandis & E. camaldulensis	40.72	22.87	95.00	3867.97	64.03	2172.71	35.97	6040.67	1.93
E. grandis & E. microcorys	66.94	37.20	350.40	23456.10	64.28	13036.25	35.72	36492.34	11.65
E. grandis & Eucalyptus mixed	74.11	31.88	45.30	3357.07	69.92	1444.07	30.08	4801.14	1.53
E. grandis & Acacia mangium	39.72	63.78	86.00	3416.21	38.38	5485.24	61.62	8901.44	2.84
E. grandis & Pinus caribaea	36.17	41.39	199.20	7205.59	46.63	8245.73	53.37	15451.32	4.93
Mean	**48.19**	**41.77**	**Sub-total**	**44315.02**	**56.91**		**Sub-total**	**77864.26**	**24.87**
Nuwara Eliya:									
E. grandis & E. robusta	65.31	65.31	858.40	56061.38	50.00	56061.38	50.00	112122.8	35.81
E. grandis & E. globulus	109.30	100.93	46.60	5093.43	51.99	4703.50	48.01	9796.94	3.13
E. grandis & E. microcorys	118.65	83.89	239.80	28451.74	58.58	20115.62	41.42	48567.37	15.51
E. grandis & Eucalyptus mixed	112.20	103.99	29.00	3253.77	51.90	3015.66	48.10	6269.43	2.00
E. grandis & Acacia mangium	75.22	60.82	17.80	1338.87	55.29	1082.57	44.71	2421.44	0.77
E. grandis & Acacia decurrens	79.76	118.77	159.60	12729.69	40.18	18954.94	59.82	31684.63	10.12
E. grandis & Cupressus sp	122.88	1.61	9.00	1105.90	98.71	14.45	1.29	1120.35	0.36
E. grandis & Pinus caribaea	31.88	36.28	153.90	4906.00	46.77	5583.04	53.23	10489.04	3.35
E. grandis & Pinus patula	66.76	22.27	114.50	7643.81	74.99	2549.93	25.01	10193.74	3.26
E. grandis & Pinus mixed	109.48	85.46	13.30	1456.14	56.16	1136.68	43.84	2592.81	0.83
Mean	**89.14**	**67.93**	**Sub-total**	**122040.7**	**51.88**		**Sub-total**	**235258.5**	**75.13**
							Total	**313122.8**	

Table 14: Distribution of C stocks of mixed culture forest plantations involving *Eucalyptus camaldulensis* and *Tectona grandis* in different divisions and their productivities

Species Composition	Division	C St. of Spp. 1 (t ha^{-1})	C St. of Spp. 2 (t ha^{-1})	Planted Area (ha)	Total C Stock of Spp. 1 (t)	% of Total C Stock from Spp. 1	Total C Stock of Spp. 2 (t)	% of Total C Stock from Spp. 2	Total C Stock of Mixture (t)	% of Total Mixed C Stock†	% of Total Mixed C Stock‡
E. camaldulensis & *E. tereticornis*	Badulla	23.84	43.84	337.0	8032.94	35.22	14772.51	64.78	22805.44	40.76	
E. camaldulensis & *E. torelliana*	Ratnapura	4.83	39.03	3.0	14.49	11.01	117.09	88.99	131.58	0.24	
E. camaldulensis & *A. mangium*	Ratnapura	5.37	86.60	37.0	198.51	5.83	3204.21	94.17	3402.72	6.08	
E. camaldulensis & *A. mangium*	Hambantota	5.90	28.77	33.5	197.66	17.02	963.79	82.98	1161.45	2.08	
E. camaldulensis & *A. mangium*	Matale	16.53	27.15	25.0	413.16	37.84	678.81	62.16	1091.97	1.95	
E. camaldulensis & *A. auriculiformis*	Anuradhapura	5.35	46.39	66.0	353.24	10.34	3062.00	89.66	3415.24	6.10	
E. camaldulensis & *A. auriculiformis*	Ratnapura	6.14	49.58	11.0	67.49	11.01	545.37	88.99	612.86	1.10	
E. camaldulensis & *A. auriculiformis*	Hambantota	5.90	48.61	18.5	109.16	10.82	899.34	89.18	1008.50	1.80	
E. camaldulensis & *Kaya*	Anuradhapura	8.35	59.06	17.0	142.03	12.39	1003.96	87.61	1145.98	2.05	
E. camaldulensis & *P. caribaea*	Matara	7.55	38.25	19.3	145.62	16.48	738.19	83.52	883.81	1.58	
	Mean	**8.97**	**46.73**	**Sub-total**	**9674.30**	**27.13**	**25985.26**	**72.87**	**35659.56**	**63.74**	
E. camaldulensis & *T. grandis*	Ampara	21.02	23.93	107.2	2253.02	46.76	2565.08	53.24	4818.10	8.61	7.89
E. camaldulensis & *T. grandis*	Moneragala	8.26	25.78	129.5	1070.08	24.27	3338.72	75.73	4408.81	7.88	7.22
E. camaldulensis & *T. grandis*	Kurunegala	17.89	27.91	128.8	2304.80	39.07	3594.74	60.93	5899.54	10.54	9.66
E. camaldulensis & *T. grandis*	Puttlam	8.56	8.22	82.6	707.34	51.01	679.30	48.99	1386.64	2.48	2.27
E. camaldulensis & *T. grandis*	Polonnaruwa	21.38	13.63	107.8	2305.03	61.07	1469.14	38.93	3774.17	6.75	6.18
	Mean	**15.42**	**19.89**	**Sub-total**	**8640.27**	**42.59**	**11646.98**	**57.41**	**20287.25**	**36.26**	**33.23**
								Total†	**55946.81**	100	
T. grandis & *Eucalyptus mixed*	Ampara	27.53	121.85	39.1	1076.46	18.43	4764.18	81.57	5840.64		9.57
T. grandis & *Eucalyptus mixed*	Kurunegala	26.33	139.94	25.2	663.51	15.84	3526.46	84.16	4189.97		6.86
T. grandis & *Eucalyptus mixed*	Puttlam	7.91	112.13	135.0	1067.95	6.59	15138.07	93.41	16206.02		26.55
T. grandis & *S. macrophylla*	Kurunegala	26.56	59.28	5.2	138.14	30.95	308.25	69.05	446.38		0.73
T. grandis & *A. auriculiformis*	Kurunegala	4.03	18.93	30.3	122.22	17.57	573.53	82.43	695.75		1.14
T. grandis & *A. auriculiformis*	Ratnapura	4.93	41.12	75.5	372.55	10.71	3104.57	89.29	3477.12		5.70
T. grandis & *A. auriculiformis*	Matale	14.62	52.22	52.0	760.26	21.88	2715.23	78.13	3475.50		5.69

T. grandis & Kaya	Ampara	. 5.05	44.27	25.6	129.33	10.24	1133.21	89.76	1262.54	2.07
T. grandis & Kaya	Anuradhapura	3.31	15.29	133.3	440.94	17.79	2037.65	82.21	2478.60	4.06
Tectona grandis & Eucalyptus:Tectona mixture	Matale	12.40	73.44	31.3	388.16	14.45	2298.73	85.55	2686.89	4.40
	Mean	**13.27**	**67.85**	**Sub-total**	**5159.52**	**12.66**	**35599.88**	**87.34**	**40759.40**	**66.77**
								Total‡	**61046.65**	100

†Mixed C stocks involving *Eucalyptus camaldulensis.*
‡Mixed C stocks involving *Tectona grandis*

Table 15: Distribution of C stocks of mixed culture forest plantations involving *Acacia* species in different divisions and their productivities

Species composition	**Division**	**C St. of Spp. 1 (t ha^{-1})**	**C St. of Spp. 2 (t ha^{-1})**	**Planted Area (ha)**	**Total C Stock of Spp. 1 (t)**	**% of Total C Stock from Spp. 1**	**Total C Stock of Spp. 2 (t)**	**% of Total C Stock from Spp. 2**	**Total C Stock of Mixture (t)**	**% of Total Mixed C Stock**
***Acacia auriculiformis* &:**										
Pinus caribaea	Ratnapura	44.23	35.56	10.3	455.54	55.43	366.26	44.57	821.80	0.56
Pinus caribaea	Kalutara	56.72	42.29	4.0	226.88	57.28	169.18	42.72	396.06	0.27
Tectona grandis	Kurunegala	18.93	4.03	30.3	573.53	82.43	122.22	17.57	695.75	0.47
Tectona grandis	Ratnapura	41.12	4.93	75.5	3104.57	89.29	372.55	10.71	3477.12	2.37
Tectona grandis	Matale	52.22	14.62	52.0	2715.23	78.13	760.26	21.88	3475.50	2.36
E. camaldulensis	Anuradhapura	46.39	5.35	66.0	3062.00	89.66	353.24	10.34	3415.24	2.32
E. camaldulensis	Ratnapura	49.58	6.14	11.0	545.37	88.99	67.49	11.01	612.86	0.42
E. camaldulensis	Hambantota	48.61	5.90	18.5	899.34	89.18	109.16	10.82	1008.50	0.69
	Mean	**44.72**	**14.85**	**Sub-total**	**11582.45**	**83.31**	**2320.36**	**16.69**	**13902.81**	**9.46**
***Acacia mangium* &:**										
E. grandis	Badulla	63.78	39.72	86.0	5485.24	61.62	3416.21	38.38	8901.44	6.05
E. grandis	N'eliya	60.82	75.22	17.8	1082.57	44.71	1338.87	55.29	2421.44	1.65
E. camaldulensis	Ratnapura	86.60	5.37	37.0	3204.21	94.17	198.51	5.83	3402.72	2.31
E. camaldulensis	Hambantota	28.77	5.90	33.5	963.79	82.98	197.66	17.02	1161.45	0.79
E. camaldulensis	Matale	27.15	16.53	25.0	678.81	62.16	413.16	37.84	1091.97	0.74
E. torelliana	Ratnapura	77.89	25.74	54.3	4229.60	75.16	1397.82	24.84	5627.42	3.83
E. torelliana	Kandy	78.91	22.74	33.0	2604.08	77.63	750.42	22.37	3354.50	2.28
E. Eucalyptus mixed	Kurunegala	32.23	101.18	43.2	1392.35	24.16	4371.04	75.84	5763.39	3.92
E. Eucalyptus mixed	Ratnapura	89.32	84.72	12.0	1071.79	51.32	1016.65	48.68	2088.43	1.42
E. Eucalyptus mixed	Kandy	77.02	47.79	36.5	2811.18	61.71	1744.36	38.29	4555.54	3.10
	Mean	**62.25**	**42.49**	**Sub-total**	**23523.60**	**61.31**	**14844.69**	**38.69**	**38368.30**	**26.10**
***Acacia decurrens* &:**										
Pinus caribaea	N'eliya	82.53	81.51	21.3	1757.83	50.31	1736.15	49.69	3493.98	2.38
Pinus patula	N'eliya	135.17	0.00	20.5	2771.07	100.00	0.00	0.00	2771.07	1.88
Eucalyptus robusta	N'eliya	144.01	82.29	5.7	820.87	63.64	469.07	36.36	1289.93	0.88
Eucalyptus globulus	N'eliya	143.59	103.87	11.5	1651.33	58.03	1194.51	41.97	2845.84	1.94

Eucalyptus grandis	N'eliya	118.77	79.76	159.6	18954.94	59.82	12729.69	40.18	31684.63	21.55
Eucalyptus mixed	N'eliya	141.05	138.06	32.9	4640.49	50.54	4542.14	49.46	9182.64	6.25
	Mean	**127.52**	**80.91522**	**Sub-total**	**30596.54**	**59.68**	**20671.56**	**40.32**	**51268.09**	**34.87**
Acacia melanoxylon &: *Cupressus* spp.	N'eliya	74.81	14.35	2.3	172.07	83.91	33.00	16.09	205.07	0.14
				Sub-total	**172.07**	**83.91**	**33.00**	**16.09**	**205.07**	**0.14**
A. mangium & A. auriculiformis	Ratnapura	80.70	41.63	54.0	4357.79	65.97	2247.98	34.03	6605.77	4.49
A. mangium & A. auriculiformis	Kandy	77.02	38.64	30.0	2310.56	66.59	1159.20	33.41	3469.75	2.36
A. mangium & A. auriculiformis	Kalutara	85.32	45.38	194.2	16569.33	65.28	8811.96	34.72	25381.29	17.26
A. mangium & A. auriculiformis	Gampaha	53.95	41.62	3.5	188.83	56.45	145.66	43.55	334.49	0.23
	Mean	**74.25**	**41.82**	**Sub-total**	**23426.51**	**65.45**	**12364.79**	**34.55**	**35791.30**	**24.34**
								Total	**139535.6**	100.00

† - C stock per ha of *Pinus patula* in these mixtures could not be estimated because the age-C stock per ha function used gave a negative value because the higher age of the plantation.

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Table 16: Distribution of monoculture C stocks according to divisions

Division	Total C Stock (t)	% of Total C Stock	Total Area (ha)	% of Total Area	Average productivity (t ha^{-1})
Ampara	34990.38	0.83	772.2	1.34	45.31
Anuradhapura	124989.34	2.96	4547.7	7.89	27.48
Badulla	748261.64	17.71	5943.3	10.31	125.90
Galle	39699.67	0.94	658.6	1.14	60.28
Gampaha	45275.83	1.07	410.5	0.71	110.29
Hambantota	131809.03	3.12	3062.4	5.31	43.04
Jaffna	15836.75	0.37	230.6	0.40	68.68
Kalutara	102244.65	2.42	1130.9	1.96	90.41
Kandy	461308.01	10.92	3537.4	6.14	130.41
Kegalle	45633.49	1.08	405.1	0.70	112.65
Kurunegala	525018.47	12.42	8016.8	13.91	65.49
Matale	303938.85	7.19	3867.2	6.71	78.59
Matara	138177.70	3.27	1530.8	2.66	90.27
Moneragala	205087.83	4.85	4210.0	7.31	48.71
Nuwara Eliya	700076.12	16.57	4535.3	7.87	154.36
Polonnaruwa	145752.66	3.45	3763.1	6.53	38.73
Puttlam	186554.51	4.41	7596.4	13.18	24.56
Ratnapura	270936.13	6.41	3400.5	5.90	79.68
Total	**4225591.07**	**100.00**	**57618.8**	**100.00**	

Table 17: Species composition of monoculture C stocks of different divisions

Division	**Species**	**C Stock per ha (t ha-1)**	**Planted Area (ha)**	**% of Planted Area in Each Division**	**Total C Stock of the Division (t)**	**% of Total C Stock of Each Division**
Ampara	*Tectona grandis*	46.24	615.0	79.6	28439.29	81.28
Ampara	*E. camaldulensis*	41.67	157.2	20.4	6551.09	18.72
	Divisional total		**772.2**		**34990.38**	
Anuradhapura	*Tectona grandis*	27.15	3443.9	75.7	93484.99	74.79
Anuradhapura	*Swietenia macrophylla*	87.12	6.0	0.1	522.73	0.42
Anuradhapura	*Eucalyptus grandis*	72.97	9.6	0.2	700.53	0.56
Anuradhapura	*E. camaldulensis*	12.73	860.0	18.9	10944.27	8.76
Anuradhapura	*Acacia mangium*	52.84	41.2	0.9	2176.94	1.74
Anuradhapura	*Acacia auriculiformis*	91.76	187.0	4.1	17159.87	13.73
	Divisional total		**4547.7**		**124989.34**	
Badulla	*Tectona grandis*	11.85	20.8	0.3	246.56	0.03
Badulla	*Eucalyptus cloeziana*	70.57	5.8	0.1	409.31	0.05
Badulla	*Eucalyptus robusta*	71.93	47.7	0.8	3431.12	0.46
Badulla	*Eucalyptus citriodora*	86.81	7.5	0.1	651.07	0.09
Badulla	*Eucalyptus globulus*	63.85	3.8	0.1	242.62	0.03
Badulla	*Eucalyptus grandis*	83.22	1207.2	20.3	100463.85	13.43
Badulla	*E. camaldulensis*	43.04	1219.7	20.5	52500.54	7.02
Badulla	*Eucalyptus tereticornis*	86.16	646.1	10.9	55669.60	7.44
Badulla	*Eucalyptus microcorys*	114.10	152.3	2.6	17377.24	2.32
Badulla	*Eucalyptus torelliana*	111.10	15.6	0.3	1733.20	0.23
Badulla	*Acacia mangium*	74.41	114.8	1.9	8542.09	1.14
Badulla	*Acacia melanoxylon*	111.89	1.0	0.0	111.89	0.01
Badulla	*Cupressus sp*	23.56	4.0	0.1	94.25	0.01
Badulla	*Pinus caribaea*	204.79	2413.3	40.6	494208.94	66.05
Badulla	*Pinus patula*	146.31	76.2	1.3	11149.07	1.49
Badulla	*Pinus oocarpa*	190.71	7.5	0.1	1430.30	0.19
	Divisional total		**5943.3**		**748261.64**	
Galle	*E. camaldulensis*	11.81	2.5	0.4	29.52	0.07
Galle	*Pinus caribaea*	60.46	656.1	99.6	39670.16	99.93
	Divisional total		**658.6**		**39699.67**	
Gampaha	*Tectona grandis*	131.72	160.4	39.1	21127.68	46.66
Gampaha	*Swietenia macrophylla*	105.27	74.7	18.2	7863.58	17.37
Gampaha	*E. camaldulensis*	14.73	10.5	2.6	154.67	0.34
Gampaha	*Acacia mangium*	162.62	27.6	6.7	4488.35	9.91
Gampaha	*Acacia auriculiformis*	87.64	68.9	16.8	6038.71	13.34
Gampaha	*Pinus caribaea*	81.91	68.4	16.7	5602.84	12.37
	Divisional total		**410.5**		**45275.83**	
Hambantota	*Tectona grandis*	82.37	850.5	27.8	70058.39	53.15
Hambantota	*Swietenia macrophylla*	101.83	10.7	0.3	1089.63	0.83

Hambantota	*Eucalyptus grandis*	175.72	1.5	0.0	263.58	0.20
Hambantota	*E. camaldulensis*	14.85	1908.2	62.3	28337.02	21.50
Hambantota	*Acacia auriculiformis*	85.92	28.1	0.9	2414.48	1.83
Hambantota	*Casuarina*	42.90	27.0	0.9	1158.17	0.88
Hambantota	*Pinus caribaea*	120.51	236.4	7.7	28487.76	21.61
	Divisional total		**3062.4**		**131809.03**	
Jaffna	*Eucalyptus grandis*	104.83	41.7	18.1	4371.25	27.60
Jaffna	*Casuarina*	60.70	188.9	81.9	11465.50	72.40
	Divisional total		**230.6**		**15836.75**	
Kalutara	*Swietenia macrophylla*	106.49	0.7	0.1	74.55	0.07
Kalutara	*Eucalyptus deglupta*	134.33	1.0	0.1	134.33	0.13
Kalutara	*Acacia mangium*	161.53	76.7	6.8	12389.02	12.12
Kalutara	*Acacia auriculiformis*	88.45	10.0	0.9	884.47	0.87
Kalutara	*Pinus caribaea*	85.14	1042.5	92.2	88762.29	86.81
	Divisional total		**1130.9**		**102244.65**	
Kandy	*Tectona grandis*	32.15	51.2	1.4	1645.97	0.36
Kandy	*Eucalyptus robusta*	63.98	6.5	0.2	415.87	0.09
Kandy	*Eucalyptus grandis*	187.94	2.0	0.1	375.88	0.08
Kandy	*E. camaldulensis*	40.62	7.6	0.2	308.70	0.07
Kandy	*Eucalyptus torelliana*	74.67	4.0	0.1	298.68	0.06
Kandy	*Acacia mangium*	166.32	93.2	2.6	15500.64	3.36
Kandy	*Acacia auriculiformis*	90.73	20.0	0.6	1814.51	0.39
Kandy	*Acacia decurrens*	140.33	7.5	0.2	1052.48	0.23
Kandy	*Pinus caribaea*	131.49	3345.4	94.6	439895.29	95.36
	Divisional total		**3537.4**		**461308.01**	
Kegalle	*Swietenia macrophylla*	97.91	63.3	15.6	6197.97	13.58
Kegalle	*Acacia mangium*	154.29	120.1	29.6	18530.37	40.61
Kegalle	*Acacia auriculiformis*	85.68	148.5	36.7	12722.86	27.88
Kegalle	*Pinus caribaea*	111.78	73.2	18.1	8182.30	17.93
	Divisional total		**405.1**		**45633.49**	
Kurunegala	*Tectona grandis*	54.36	4117.1	51.4	223813.39	42.63
Kurunegala	*Swietenia macrophylla*	97.85	2373.7	29.6	232268.04	44.24
Kurunegala	*Eucalyptus grandis*	91.07	83.2	1.0	7576.80	1.44
Kurunegala	*E. camaldulensis*	38.46	1277.2	15.9	49119.68	9.36
Kurunegala	*Acacia mangium*	54.88	60.6	0.8	3325.59	0.63
Kurunegala	*Acacia auriculiformis*	90.45	89.4	1.1	8085.88	1.54
Kurunegala	*Casuarina*	53.15	15.6	0.2	829.09	0.16
	Divisional total		**8016.8**		**525018.47**	
Matale	*Tectona grandis*	35.52	1509.2	39.0	53611.75	17.64
Matale	*E. camaldulensis*	42.72	697.8	18.0	29807.16	9.81
Matale	*Acacia mangium*	54.32	44.5	1.2	2417.39	0.80
Matale	*Acacia auriculiformis*	88.96	367.1	9.5	32657.07	10.74
Matale	*Pinus caribaea*	148.52	1248.6	32.3	185445.49	61.01
	Divisional total		**3867.2**		**303938.85**	
Matara	*Eucalyptus grandis*	139.81	19.3	1.3	2698.30	1.95
Matara	*E. camaldulensis*	15.13	14.4	0.9	217.87	0.16

Matara	*Eucalyptus torelliana*	78.08	20.0	1.3	1561.52	1.13
Matara	*Pinus caribaea*	90.52	1477.1	96.5	133700.01	96.76
	Divisional total		**1530.8**		**138177.70**	
Moneragala	*Tectona grandis*	53.81	3426.0	81.4	184337.93	89.88
Moneragala	*Eucalyptus grandis*	82.38	138.5	3.3	11409.97	5.56
Moneragala	*E. camaldulensis*	14.41	643.5	15.3	9276.03	4.52
Moneragala	*Pinus caribaea*	31.95	2.0	0.0	63.89	0.03
	Divisional total		**4210.0**		**205087.83**	
N'eliya	*Eucalyptus pilularis*	182.27	9.0	0.2	1640.46	0.23
N'eliya	*Eucalyptus robusta*	157.36	517.5	11.4	81433.81	11.63
N'eliya	*Eucalyptus grandis*	168.46	1962.7	43.3	330640.11	47.23
N'eliya	*Eucalyptus microcorys*	121.82	55.2	1.2	6724.25	0.96
N'eliya	*Cupressus sp*	28.12	20.5	0.5	576.45	0.08
N'eliya	*Pinus caribaea*	164.01	1528.7	33.7	250725.97	35.81
N'eliya	*Pinus patula*	64.15	441.7	9.7	28335.07	4.05
	Divisional total		**4535.3**		**700076.12**	
Polonnaruwa	*Tectona grandis*	32.68	1704.6	45.3	55702.28	38.22
Polonnaruwa	*E. camaldulensis*	42.47	2006.5	53.3	85210.48	58.46
Polonnaruwa	*Acacia auriculiformis*	93.08	52.0	1.4	4839.90	3.32
	Divisional total		**3763.1**		**145752.66**	
Puttlam	*Tectona grandis*	31.30	3939.8	51.9	123334.80	66.11
Puttlam	*Swietenia macrophylla*	82.67	40.8	0.5	3372.82	1.81
Puttlam	*E. camaldulensis*	13.36	3209.6	42.3	42871.67	22.98
Puttlam	*Eucalyptus tereticornis*	16.38	224.1	3.0	3670.87	1.97
Puttlam	*Acacia mangium*	52.54	85.0	1.1	4465.61	2.39
Puttlam	*Acacia auriculiformis*	91.03	97.1	1.3	8838.74	4.74
	Divisional total		**7596.4**		**186554.51**	
Ratnapura	*Tectona grandis*	23.14	448.4	13.2	10375.44	3.83
Ratnapura	*Swietenia macrophylla*	92.14	111.0	3.3	10227.66	3.77
Ratnapura	*Eucalyptus robusta*	62.88	5.7	0.2	358.43	0.13
Ratnapura	*Eucalyptus grandis*	196.95	22.8	0.7	4490.36	1.66
Ratnapura	*Eucalyptus tereticornis*	48.17	8.0	0.2	385.35	0.14
Ratnapura	*Eucalyptus torelliana*	64.17	30.0	0.9	1925.17	0.71
Ratnapura	*Acacia mangium*	119.56	181.8	5.3	21735.91	8.02
Ratnapura	*Acacia auriculiformis*	79.39	307.3	9.0	24397.91	9.01
Ratnapura	*Pinus caribaea*	86.21	2285.5	67.2	197039.90	72.73
	Divisional total		**3400.5**		**270936.13**	
	Grand total		**57618.8**		**4225591.07**	

Table 18: Calculated magnitudes and efficiencies of carbon sinks of the forest plantations of higher productivity

Division/Species	Annual Total NPP (t C yr^{-1})	% Absorption of annual CO_2 emission	Area occupied (ha)	% of Total land area	Efficiency index of carbon sink
Badulla	24,942	0.755	5943.3	0.091	8.33
Nuwara Eliya	23,336	0.706	4535.3	0.069	10.23
Pinus caribaea in Badulla	16,474	0.498	2413.3	0.037	13.53
Pinus caribaea in N'Eliya	8,358	0.253	1528.7	0.023	11.00
Eucalyptus grandis in N'Eliya	11,021	0.333	1962.7	0.030	11.14

---------End of Section 3--------

Section 4

Impact of research results:

i. Relevance of results achieved to scientific advancement

We believe that our method of estimation of biomass production and carbon sequestration capacity of tropical rainforests (e.g. Sinharaja and KDN forest complexes) is a novel combination of several techniques. We have not yet come across any previous studies, which have used this either in international or local literature.

We quote the following description of our methodology from section 4.1 of the report.

"We used a novel combination of methods to quantify the rate of biomass production and carbon sequestration as NPP of these two natural forests, which represent a highly complex ecosystem, the lowland evergreen rainforests of the humid tropical regions. It used canopy hemispherical photography to estimate canopy properties and its radiation interception capacity. These were combined with measured incident radiation levels to estimate the amounts of radiation intercepted by the forest canopy. Radiation use efficiency (RUE) of the forest canopy was estimated using a layered canopy photosynthesis model based on the measured light response curves of selected plant/tree species representing different vertical strata of the forest canopy. There are several advantages of our method of estimating the carbon sequestration capacity of natural forests in comparison to other methods that have been used such as the conventional ground-based forest inventory methods in permanent sampling plots (i.e. direct measurement of tree height and dbh) and remote sensing.

Firstly, our method is mechanistic because it is based on the fundamental physiological principles of photosynthesis and biomass production. In contrast, both direct measurement of tree dimensions and remote sensing have to rely on empirical relationships to estimate tree/forest biomass. Secondly, our method estimates the *total* carbon sequestration rate, which includes both above- and below-ground carbon sequestration rates. In contrast, forest inventory in permanent sampling plots and remote sensing estimate only the standing above-ground biomass and carbon stock and have to depend on empirical factors to estimate below-ground biomass and carbon stock. Thirdly, and importantly, our method enables quantification of the extremely high spatial heterogeneity of the biomass production and carbon sequestration capacity within the forest ecosystem. Therefore, it enables calculation of relevant statistical parameters for quantifying the spatial variability of both canopy properties and carbon sequestration capacity. While the direct measurement of tree dimensions also enables quantification of spatial heterogeneity of standing biomass within a forest, it takes a much longer time and labour than our method to obtain the same measures of variability. On the other hand, the remote sensing method does not have the same degree of spatial resolution as our method to estimate spatial heterogeneity in carbon sequestration within a natural forest. Furthermore, our method has the added advantage of providing a detailed quantification of canopy properties (i.e. canopy size and architecture) and their spatial variation within the forest."

ii. Relevance of results achieved to national/socio-economic development

Climate change is widely regarded as one of the major threats to human civilization and natural ecosystems in the 21st century. Exponentially increasing atmospheric carbon dioxide concentrations caused by increasing emissions of CO_2 is primary cause for global warming and its associated consequences. Forests have the capacity to sequester carbon in their biomass and thereby reduce the increase of atmospheric CO_2 concentrations to mitigate the impacts of climate change.

National estimates of carbon sequestration by forests, as provided by our study, are extremely important in formulating climate change mitigation strategies. The present study has provided such estimates for both plantation forests (which represent a less complex forest ecosystem) and natural forests in the wet zone lowlands (which represent a highly complex forest ecosystem).

In our study on plantation forests, we have estimated the total carbon stock of the entire forest plantations in Sri Lanka. This provides the basis to estimate their carbon sequestration potential and to quantify the value of forest plantations in terms of the environmental benefits that they provide in addition to their timber value.

Using the novel method that we developed and validated, the carbon sequestration rates and the climate change mitigation potential the two major tropical rainforests of Sri Lanka (i.e. Sinharaja and KDN forest complexes) were quantified. By applying this method to all forest types of Sri Lanka, we will be able to estimate the climate change mitigation potential of all natural forests of Sri Lanka. These estimates will be extremely useful in planning the climate change mitigation strategies at the national level.

iii. Dissemination/application of research output

From the beginning of this research project, the Forest Department of Sri Lanka has been notified. Results of section 3.II on the estimation of carbon stocks in forest plantations have already been presented at the First National Forestry Research Symposium organized by the Forest Department held in March 2009. A complete copy of this final report will be presented to the Conservator General of Forestry at the same that it will be submitted to the National Science Foundation. The Forest Department has already requested the results of this project for their policy decisions on formulating strategy for climate change mitigation.

Research publications that have emerged so far from this project are listed under Section 1.xiii.

Two further full-length research articles, on the estimation of carbon sequestration in Sinharaja and KDN forest complexes, to be submitted to an international journal will be written after the completion of this report.

Section 5

Miscellaneous

i. List of major equipment acquired during the project period and their functionality

Global Positioning System (GPS)
Type/Model – GARMIN (e-trex) summit
Supplier – Tech Innovations Pvt. Ltd.

This equipment is in good working condition.

ii. List of publications/communications arising from the project and/or presentations made at seminars, workshops etc.

Published as peer-reviewed abstracts (Copies are attached):

Wahala, W.M.P.S.B., De Costa, W.A.J.M. and Ranasinghe, D.M.S.H.K. (2006). Current status of the forest canopy and its understorey light environment in selected areas of Sinharaja, Kanneliya and Knuckles Forest Reserves in Sri Lanka. Proceedings of the International Conference on Humid Tropical Ecosystems: Changes, Challenges and Opportunities. 04 – 09 December, 2006, Kandy, Sri Lanka. pp. 8.

Wahala, W.M.P.S.B., De Costa, W.A.J.M., Ratnayake, R.M.D.D. and Ranasinghe, D.M.S.H.K. (2006). Mitigating the impacts of climate change – Carbon sequestration capacity of selected natural forests in the humid zones of Sri Lanka. Proceedings of the International Conference on Humid Tropical Ecosystems: Changes, Challenges and Opportunities. 04 – 09 December, 2006, Kandy, Sri Lanka. pp. 73.

De Costa, W.A.J.M., Suranga, H.R. and Ranasinghe, D.M.S.H.K. (2009). Estimation of carbon stocks in the forest plantations of Sri Lanka. Proceedings of the National Forestry Research Symposium, 12 – 13 March, 2009, Kandy, Sri Lanka. pp. 12-13.

Suranga, H.R. and De Costa, W.A.J.M. (2009). Photosynthetic light response of selected plant species occupying different vertical strata of lowland wet evergreen forests in Sri Lanka. Proceedings of the 14th International Forestry and Environment Symposium, 18 – 19 December, 2009, University of Sri Jayewardenepura, Sri Lanka.

Full-length research article submitted for publication ***(This manuscript is included as Section 3.II of this report):***

De Costa, W.A.J.M. and Suranga, H.R.. Estimation of carbon stocks in the forest plantations of Sri Lanka. *Submitted in August 2009 to be published as a full paper in the Journal of the National Science Foundation of Sri Lanka. The paper is under review.*

Section 6

Summary Statement of Expenditure (indicate under Personnel, Equipment, Consumables, Travel and Subsistence and Miscellaneous)

At the beginning of the project in May 2004, the allocated funds were divided between the University of Peradeniya and the University of Sri Jayewardenepura. However, after March 2006, all funds were transferred to the University of Peradeniya.

A total of Rs. 522,661.00 has been transferred to the University of Peradeniya. By the time, the project was concluded in October, 2008, the total expenditure at the University of Peradeniya was Rs. 519,728.90. The expenditure statement of these funds attached herewith (Please see the next page for a certified financial statement).

The last regular instalment of funds (i.e. Rs. 115,000.00), which stated that it was the second instalment of the third year, was received on 18.04.2007. The only funds received thereafter were Rs. 16,000.00 on 13.02.2008 as additional funds to pay the increased allowance of the research assistant.

Work of the project had to be prolonged beyond its expected date of completion because of the large amount of field work (i.e. canopy hemispherical photography and its processing and analysis) involved. Therefore, the research assistant (Mr. H.R. Suranga) had to be employed until the end of October 2008.

As this project started as a joint research project, a total of Rs. 435,824.00 had been transferred to the University of Sri Jayewardenepura. However, out of these funds, only Rs. 163,833.84 had been used and the balance of Rs. 261,990.16 had been transferred back to the NSF. This balance of funds has not been utilized up to now.

However, the Principal Investigator was not aware of the above balance of funds (i.e. Rs. 261,990.16), which has been lying un-spent at the NSF.

As the Principal Investigator was under the impression that all the allocated funds in the project had been spent, bills relating to expenditure incurred for the field visits during the period from 01.10.2006 to 26.02.2008 totalling to Rs. 95,207.00 were not submitted for re-imbursement. A summary of this expenditure is given in the table below:

Period	Value of expenditure not re-imbursed (Rs.)
01.10.2006 – 02.01.2007	14,653.00
18.08.2007 - 20.09.2007	10,940.00
10.10.2007 - 10.11.2007	9,936.00
09.11.2007 - 19.11.2007	3,774.00
29.11.2007 - 10.12.2007	11,223.00
19.12.2007 - 30.01.2008	30,034.00
18.02.2008 - 26.02.2008	14,647.00
Total	**95,207.00**

Please see the attached document giving details on this expenditure. All the bills are available with the Principal Investigator

At that time, these bills were not submitted for re-imbursement because the Principal Investigator was under the impression that all fund allocations had been done. In this situation, the Principal Investigator wanted to keep the research assistant until October 2008 to finish the work of the project.

The above amount was spent from the Principal Investigator's own pocket.

As it has now transpired that a balance of Rs. 261,990.16 is still available from the funds that were originally allocated to this project, the Principal Investigator would be much thankful if the NSF re-imburse the above expenditure.

However, in the event of the NSF being unable to re-imburse the above expenditure due to difficulties in its accounting procedures and financial regulations, the Principal Investigator would understand it and is willing to bear this expenditure (as he has already done so).

Section 7

i. Grantee's signature

08/03/2010

Professor W.A.J.M. De Costa

ii. Comments of the Head of the Department/signature

Progress satisfactory and research completed on time.

Recommended forwarded

09/03/2010

HEAD/ DEPARTMENT OF CROP SC

HEAD IENCE

Dr. D.K.N.G. Pushpakumara
Head/Department of Crop Science

iii. Head of the Institution's signature

17/03/10

Professor S.B.S. Abayakoon
Vice-Chancellor
University of Peradeniya

VICE - CHANCELLOR
University of Peradeniya
Peradeniya
Sri Lanka

Prof. W. A. J. M. De Costa

ABSTRACTS

INTERNATIONAL CONFERENCE ON HUMID TROPICAL ECOSYSTEMS:
CHANGES, CHALLENGES, OPPORTUNITIES

4-9 DECEMBER 2006, KANDY, SRI LANKA

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National MAB Committee, Sri Lanka
National Science Foundation, Sri Lanka

In collaboration with
International MAB Secretariat,
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Current status of the forest canopy and its understorey light environment in selected areas of Sinharaja, Kanneliya and Knuckles Forest Reserves in Sri Lanka

[1]W.M.P.S.B. Wahala, [1]W.A.J.M. De Costa, and [2]D.M.S.H.K. Ranasinghe,

Department of Crop Science, Faculty of Agriculture, University of Peradeniya.
[2]Department of Forestry and Environmental Science, University of Sri Jayewardenepura.
janendrad@yahoo.com

Key words: leaf area index, leaf angle, hemispherical photography, lowland wet-evergreen forests, understorey light environment.

Abstract

Forests form an important component in humid tropical ecosystems. In forests of the humid tropics, the foliage canopy is highly heterogeneous. The 'architecture' of a forest canopy plays a critical role in determining the understorey light environment and thereby exerts a significant influence on species regeneration and the long-term sustainability of the forest. Therefore, in assessing the current status of humid tropical ecosystems, a detailed quantification of the status of forest canopy architecture is essential. The present study has attempted this task for three major forest reserves in Sri Lanka.

Hemispherical photography in combination with meteorological data and image analysis was used to characterize canopy architecture and the radiation regime at three elevational classes (i.e. valley, mid-slope and ridge top) in selected areas of Sinharaja, Kanneliya and Knuckles forest reserves. At each elevational class, hemispherical photos of the forest canopy were taken along transects of up to 1000 m at 100 m intervals. Altogether there were 59, 58 and 50 sampling points in Sinharaja, Kanneliya and Knuckles respectively. At a given location, some transects covered the undisturbed parts while the others covered selectively logged areas.

Canopy architecture, as quantified by the leaf area index (LAI) and mean leaf angle (MLA) showed significant variation between the three forests. Both LAI and MLA, relative to the horizontal plane, in Knuckles were significantly lower than in Sinharaja and Kanneliya. While the highest and lowest LAIs were found on the mid-slope and ridge-top respectively, MLA showed a gradual increase from valley to ridge-top. The leaf angle distribution (i.e. proportion of LAI at leaf angles ranging from 0° to 90°) showed substantial variation at different sampling points even within the same transect. Total radiation transmitted below the canopy to the ground level differed significantly between forests but not between elevational classes, with Sinharaja having greater levels (1894 MJ m^{-2} yr^{-1}) than Kanneliya and Knuckles (1448–1631 MJ m^{-2} yr^{-1}), which did not differ between each other. The intensity and duration of sunflecks below the canopy varied between different sampling points. However, in general, the maximum intensities were found around mid-day. The ground level light intensities showed significant negative correlations with LAI and significant positive correlations with MLA. On the other hand, there was a significant positive correlation between LAI and MLA.

The above variations in canopy architecture and understorey light environment have important implications for species regeneration and sustainability of forests in humid tropics. In general, it could be concluded that regeneration potential is greater with increasing intensities of radiation reaching the ground level. However, differing abilities of individual species to adapt their physiology to the prevailing understorey light environment would also determine the regeneration potential of the forest.

Mitigating the impacts of climate change – Carbon sequestration capacity of selected natural forests in the humid zones of Sri Lanka

[1]W.M.P.S.B. Wahala, [1]W.A.J.M. De Costa, [1]R.M.D.D. Ratnayake,
and [2]D.M.S.H.K. Ranasinghe

[1]Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Peradeniya, Sri Lanka.
[2]Department of Forestry and Environmental Science, University of Sri Jayewardenepura, Sri Lanka.
janendrad@yahoo.com

Key words: carbon sequestration, biomass production, radiation interception, hemispherical photography, natural forests.

Abstract

Climate change induced by increased emissions of greenhouse gases and the consequent warming of the atmosphere influences the functioning and sustainability of humid tropical ecosystems in many ways. Carbon dioxide is one of the principal greenhouse gases that cause global warming. Forests can play a major role in mitigating the impacts of climate change by absorbing substantial quantities of atmospheric CO_2 for photosynthesis. Most available methods for estimating forest carbon sequestration are empirical. The objective of this study was to determine the carbon sequestration capacity of three selected natural forests (i.e. Sinharaja, Kanneliya and Knuckles) in the humid zone of Sri Lanka through a new, process-based method.

Our method of quantifying forest carbon sequestration is based on the positive linear relationship between radiation interception and biomass production. The proportionality constant of this relationship is radiation use efficiency (RUE), which is the amount of biomass produced per unit of radiation intercepted. In the present study, the maximum biomass production rate of the three selected forests was estimated by measuring their canopy radiation interception through hemispherical photography and image analysis. Hemispherical photographs were obtained along 8, 6 and 7 transects of atleast 1 km long in Sinharaja, Kanneliya and Knuckles forest reserves respectively. Maximum and minimum biomass production rates were calculated based on RUE values of 1.5 and 0.5 g MJ^{-1} respectively.

The estimated average biomass production capacities for Sinharaja, Kanneliya and Knuckles forest reserves were 88, 91 and 90 mt ha^{-1} yr^{-1} respectively. Radiation interception and biomass production capacity did not differ significantly between different elevational classes. Based on an average estimate of 50% of carbon in plant biomass, the respective carbon sequestration capacities were 44, 46 and 45 mt ha^{-1} yr^{-1} for Sinharaja, Kanneliya and Knuckles. Capacities of the respective forests to mitigate climate change impacts as quantified by the potential for absorbing atmospheric CO_2 were 161, 167 and 166 mt ha^{-1} yr^{-1}. Our method of quantifying carbon sequestration is validated by the observation that estimates based on the present method fall within the range of the limited number of values reported in literature for lowland forests in the humid tropics. A comparison of our estimates with the large number values available in literature for temperate and boreal forests show that forests in the humid tropics have a greater capacity to mitigate impacts of climate change through CO_2 absorption than forests in the temperate zones.

Prof. W. A. J. M. De Costa

Forest Department

National Forestry Research Symposium 2009

12th-13th March 2009

Proceedings
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Research and Education Division
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Estimation of Carbon Stocks in the Forest Plantations of Sri Lanka

W.A.J.M. De Costa[1*], H.R. Suranga[1] and D.M.S.H.K. Ranasinghe[2]
[1]Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Peradeniya.
[2]Department of Forestry and Environmental Sciences, University of Sri Jayewardenepura.

Forest plantations have the ability to sequester carbon in their biomass and reduce the rate of increase of atmospheric carbon dioxide. Therefore, plantation forestry forms an important option of mitigating global warming and its consequent climate change. According to the FORDATA database maintained by the Forest Department, there are around 85,000 ha of forest plantations in Sri Lanka. These are distributed across all three major climatic zones (i.e. wet, intermediate and dry zones) in 17 forest divisions. The objective of the present study was to estimate the existing biomass and carbon stock of these forest plantations.

Calculations were done for 22 tree species grown in monocultures over a total area of 57618.8 ha and for 51 mixed cultures covering an area of 5949.6 ha. The total accounted area of 63568.4 ha was 74% of the total area of plantation forests as recorded in the FORDATA. The 22 monoculture species for which biomass and carbon stocks were calculated were *Tectona grandis*, *Swietenia macrophylla*, *Eucalyptus deglupta*, *E. cloeziana*, *E. pilularis*, *E. robusta*, *E. citriodora*, *E. globulus*, *E. grandis*, *E. camuldulensis*, *E. tereticornis*, *E. microcorys*, *E. torelliana*, *Acacia mangium*, *A. auriculiformis*, *A. melanoxylon*, *A. decurrens*, *Casuarina* spp., *Cupressus* spp., *Pinus caribaea*, *Pinus patula* and *Pinus oocarpa*. The 51 mixed cultures included different combinations of the above species. In addition, there were mixtures of *Tectona grandis* and *Kaya senegalensis*.

Data on the diameter at breast height (DBH), plant height (h) and the number of stems per ha were obtained from the FORDATA for plantations classified in terms of Division, Range, Beat, Block and Sub block. All calculations were done initially at the sub-block level. For five species (i.e. *Cupressus* spp., *E. robusta*, *E. grandis*, *E. microcorys*, *P. caribaea* and *Tectona grandis*), merchantable wood volume was calculated based on their DBH and h using known volume functions. Wood volume calculations of other *Pinus* and *Eucalyptus* species were calculated based on a 'designed' form factor based on the respective *Pinus* and *Eucalyptus* species for which volume functions were available. For the rest of the species, a form factor of 0.5 was assumed to calculate wood volume from DBH and h. Total tree volume was estimated as 1.67 of wood volume. An average wood density of 490 kg m^{-3} of wood was used to convert total tree volume in to total tree biomass. Carbon content of biomass was estimated as 50% of tree biomass. This procedure yielded estimates of carbon stock per ha at the sub-block level.

The above values were used to develop relationships between age and carbon stock per ha for different species. As this relationship would vary depending on the above- and below-ground environment of a given location, within each species, separate relationships were developed for individual divisions or groups of divisions having broadly similar environments. Because environmental conditions could differ even within a division, sometimes different relationships were developed for different ranges within a division. The developed relationships were either logarithmic ($y = a \log_e x + b$) or second order polynomial ($y = a + bx + cx^2$) where x and y were age and carbon stock per ha respectively. Altogether 64 separate relationships were developed, with R^2 values ranging from 0.27 to 0.99. 75% of the relationships had R^2 values greater than 0.50 while 50% of the relationships had R^2 values greater than 0.65.

The developed age *versus* per ha carbon stock relationships were extrapolated up to year 2008 to estimate the present carbon stock per ha. This was multiplied by the respective plantation areas to obtain the total carbon stock in each sub-block. The sub-block calculations were cumulated through block, beat, range and divisions to obtain the total carbon stock. This procedure enabled estimation of carbon stocks in forest plantations for which DBH and h measurements were not available as well. Taking in to account the fact that FORDATA has not been fully-updated recently, all plantations of more than 50 years were considered as felled and were excluded from the carbon stock accounting.

Per ha carbon stocks of all species showed significant variation with division and range and ranged from 9 to 200 t ha^{-1} for *Tectona grandis*, from 63 to 82 t ha^{-1} for *Swietenia macrophylla*, from 31 to 189 t ha^{-1} for *Eucalyptus* spp., from 24 to 157 t ha^{-1} for *Pinus* spp., from 40 to 127 t ha^{-1} and for *Acacia* spp., from 33 to 47 t ha^{-1}.

Calculations showed the present total carbon stock of the accounted 57618.8 ha of monoculture forest plantations to be 3.237 million tons. Nearly 89% of this carbon stock was contributed by five species, namely, *Pinus caribaea* (44%), *Tectona grandis* (21%), *Eucalyptus grandis* (11%), *E. camuldulensis* (7%) and *Swietenia macrophylla* (6%). The respective percentages of cultivated areas of these five species are 25%, 35%, 6%, 21% and 5%, thereby comprising 92% of the accounted monoculture plantation area. The accounted 5949.6 ha of mixed plantations has a total carbon stock of 0.522 million tons. The mixtures that were making the highest contributions were *E. robusta/E. grandis* (17%), *Pinus* species mixed (13%) and *E. grandis/E. microcorys* (12%).

The above carbon stock values can be considered as first overall estimates of carbon stocks in the Sri Lankan forest plantations. Despite their approximate nature, these first estimates can be used as a basic data in policy formulation on climate change mitigation. These estimates can be fine tuned and made more accurate by updating the FORDATA, increasing the frequency of measurements of DBH and h and by developing allometric relationships for plantation forest species for which they are not available.

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D.K.L.K. Senadheera
M.A. Lankathilake
G.G.T. Chandrathillake
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coastal grasslands and coconut plantations were selected for the study. Line transects (200m x 40m) were conducted in the selected habitat types located within 100m from the shore. Surveys were conducted between 0600hrs to 0900hrs. A total of 3,646 bird observations including 1,399 lariid observations were made during the course of the surveys. Two species of gulls and eight species of terns recorded. Of the total number of Lariid observations, 95.42% were made at the beach habitat. The average number of Lariid species recorded in the Beach transects (1.79) was significantly higher than those of the grasslands (0.32) and plantations (0.19). The average number of birds recorded per transect, showed a much greater difference, with 30.36 birds for the beach and 0.86 and 0.67 birds for the grasslands and plantations respectively. 82.71% of the bird movements in the beach habitat were along the shoreline (i.e. linearly), whereas a majority of movements in the Grasslands (75%) and plantations (92.86%) were across the habitat (i.e. seaward or landward movement). Of the total observations of Terns and Gulls in the beach habitat, 77.9% of the birds were perched along the foreshore. Roosting or perching was not observed in the other two habitats.

Keywords : Habitate use, Bird behaviour, Family Lariidae.

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Photosynthetic light response of selected plant species occupying different vertical strata of lowland wet evergreen forests in Sri Lanka

H.R. Suranga and W.A.J.M. De Costa
Department of Crop Science, University of Peradeniya, Sri Lanka

Tropical lowland wet evergreen forests are one of the most productive and biologically-diverse ecosystems. Because of their high net primary productivity, these forests have significant potential for climate change mitigation through carbon sequestration. Estimation of carbon sequestration capacity of lowland wet evergreen forests require knowledge on the photosynthetic capacity of their component tree/plant species as photosynthesis is the primary physiological process that is responsible for carbon sequestration in forest biomass. Photosynthetic rate is highly dependent on the light intensity that is incident on plant leaves. Because of the complex vertical stratification of lowland wet evergreen forests, different plant species occupying different strata experience different light environments. The objective of this study was to quantify the light response of selected plant species from different vertical strata of lowland wet evergreen forests of Sri Lanka.

Seedlings of 22 different tree/plant species representing the canopy, sub-canopy and understorey were collected from the nursery of the Kanneliya forest reserve and kept in a partially-shaded plant house at the University of Peradeniya. In each species, net photosynthetic rate of the youngest fully-expanded leaf was measured on a series of clear, sunny days at a range of light intensities incident on the leaf using a portable photosynthesis measurement system (LICOR6400, Nebraska, Lincoln, USA). Different light intensities were achieved by overlaying layers of white gauze cloth on the leaf chamber. Finally, leaf dark respiration was measured by covering the leaf chamber with a dark cloth. Over 50 measurements were made at each light intensity. Light response curves were fitted using an asymptotic exponential function using non-linear regression. Five parameters of the light response curve, i.e. maximum light-saturated photosynthetic rate (Pmax), quantum efficiency (α), dark respiration rate (Rd), light compensation point (LCP) and light saturation point (LSP), were estimated from the fitted curves.

All five parameters of the light response curve showed statistically-significant variation between different plant species. The respective ranges were 0.631–4.596 μmol [CO2] m-2 [leaf area] s-1 for Pmax, 0.0079–

0.0316 μmol [CO2] (μmol [PAR])-1 for α, 0.150–2.128 μmol [CO2] m-2 [leaf area] s-1 for Rd, 9–156 μmol [PAR] m-2 [leaf area] s-1 for LCP and 403–941 μmol [PAR] m-2 [leaf area] s-1 for LSP. Implications of these results in determining the biomass production and carbon sequestration capacity of low land wet evergreen forests are discussed.

Keywords : Climate change, Sri Lanka, Photosynthesis, Light response canopy starta.

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Evaluation of acute toxicity to Indian major carp, *Cirrhinus mrigala* of neem leaf extract (*Azadirachta indica* A. Juss)

S. Manoharan, R. Mathan, M. Annamali and V.K. Devarajan
Department of Zoology, Bharathiar University, Coimbatore, India

Azadirachta indica, A. Juss. (Meliaceae; Neem) is an indigenous and traditional plant to India. It has more medicinal properties and extractions from various parts are now considered as a valuable source of unique natural products for development of medicines against various diseases and also for the development of industrial products. It leaches into our food and drink at concentrations shown to have biological consequences. In this study, we evaluated the effects of neem leaf extract to freshwater fish *Cirrhinus mrigala* for 24 hr of exposure with predetermined LC50 1.035 g l^{-1}. During the treatment period the haematological parameters such as haemoglobin, hematocrit, erythrocytes, mean cellular volume (MCV), mean cellular hemoglobin (MCH) and mean cellular hemoglobin concentration (MCHC) levels were decreased except leucocytes when compared to the control experiment. In biochemical studies the Plasma glucose level was higher and protein level was singnificantly lower in experimental fishes. Plasma sodium, potassium and chloride levels have also decreased. On the other hand the enzymological parameters like glutamate oxaloacetate transaminase (GOT) in the gill, liver and muscle and glutamate pyruvate transaminase (GPT) gill, liver and muscle activities were increased in fish *Cirrhinus mrigala* treated with acute concentration of the neem leaf extract *Azadirachta indica*. The alterations of these parameters may be employed as non-specific biomarkers against neem leaf extract contamination in aquatic environment.

Keywords : Azadirachta indica cirrhinus mrigala, Acute toxicity, Ensyme activity and Ion regulation, Haematology, Biochemistry.

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First description of freshwater medusa, *Craspedacusta sowerbyi* (Lankester, 1880) in Sri Lanka.

R.R.M.K.P. Ranatunga[1] and S. Abeysinghe[2]
[1]Department of Zoology, University of Sri Jayewardenepura, Sri Lanka
[2]Department of National Zoological Gardens, Sri Lanka.

A freshwater dwelling medusa was discovered in March 2009 from an artificial well in Gal-Amuna, Medirigiriya in Sri Lanka (N 8° 05.0801, E 81° 01.4270. It was identified as *Craspedacusta sowerbyi* (Phylum:Cnidaria, Class: Hydrozoa, Family: Olindiidae). They are commonly known as freshwater jellyfish or hydromedusae. Occurrence of such hydromedusae had never been documented in Sri Lanka, although they have been recorded from other countries. The freshwater "jellyfish" is not a true jellyfish

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