

Structural analysis and growth modeling of natural forests in Vietnam

Dissertation

submitted to obtain the Doctor degree of Philosophy
Faculty of Forest Sciences and Forest Ecology,
Georg-August-University Göttingen

By

Cao Thi Thu Hien

born in Quang Ninh, Vietnam

Göttingen, February 2015

1. Gutacher: Prof. Dr. Joachim Saborowski

2. Gutacher: Prof. Dr. Ralph Mitlöhner

Tag der mündlichen Prüfung: 05.02.2015

Acknowledgements

In the course of this dissertation, I have met many people on the way, some of whom have been crucial for its completion. I would like to take this chance to thank them.

I will forever be in debt to my advisor, Professor Doctor Joachim Saborowski, for his unending and invaluable help, his solid scientific guidance, and his amazing mentorship during my PhD research: without him, this dissertation would not exist. I have benefited from his patience, enthusiasm, care, and knowledge.

Many thanks to my colleagues in the Ecoinformatics, Biometrics, and Forest Growth Department, Georg-August University Göttingen, for their true friendship. Special thanks go to Tim Ritter, Sebastian Schoneberg, and Jan C. Thiele, who not only helped with the approaches and methods to analyze my data but were also always there to answer my questions. I could not have done it without their support.

I received permission from the Vietnam Forest Inventory and Planning Institute to enter and collect data for analysis. I thank the researchers there for their collaboration and support for my project.

I would not be here today without the financial support of both the Vietnam Ministry of Education and Training and the German Academic Exchange Service (DAAD). I would like to express my most sincere gratitude for their support.

It would have been most impossible to conduct this PhD project without the understanding and encouragement of my husband and my entire family. To my beloved husband, Do Xuan Hung, my sincerest thanks. To my daughters, Do Cao Diep Anh and Do Cao Thuy Duong, my deepest apologies for being away from you. My utmost respect and thanks to my parents and my parents-in-law, your unconditional support has been very precious to me. To my sisters and brothers, thank you very much for your support.

TABLE OF CONTENTS

Acknowledgements.....	iii
TABLE OF CONTENTS.....	iv
LIST OF FIGURES	vii
LIST OF TABLES	x
Chapter 1 Introduction	
1.1. Overview	1
1.2. Objectives of the study.....	4
1.3. Structure of the dissertation	5
Literature cited	5
Chapter 2 Research area and data collection	
2.1. Overview of forests in Vietnam.....	9
2.2. General information about the study area	11
2.2.1. Study area 1: Ha Tinh.....	
2.2.2. Study area 2: Thua Thien Hue	12
2.2.3. Study area 3: Binh Dinh.....	13
2.2.4. Study area 4: Khanh Hoa.....	
2.3. Establishment and measurement of the plots	14
2.3.1. Establishment and description of the research plots	14
2.3.2. Measurement on the plots.....	19
Literature cited	22
Chapter 3 Changes in forest structure and tree species diversity after seven and eight years in tropical rainforests of Vietnam	
3.1. Forest structure	
3.1.1. Introduction.....	24
3.1.2. Data analysis.....	25
3.1.3. Results	28
3.2. Tree species diversity	
3.2.1. Introduction.....	51
3.2.2. Data analysis.....	51
3.2.3. Results	54
3.3. Conclusion	
3.3.1. Forest structures.....	61

3.3.2. Tree species diversity	62
Literature	63
Chapter 4 Diameter increment	
4.1. Data analysis	
4.1.1. Local growth equations.....	67
4.1.2. Comparing models based on rounded and unrounded diameters	71
4.1.3. Variability of growth models among plots and provinces for selected species.....	72
4.2. Results.....	
4.2.1. Local periodic annual diameter increment.....	74
4.2.2. Comparing models based on rounded and unrounded diameters	80
4.2.3. Linear mixed effects models	83
4.3. Discussion.....	
4.3.1. Model structure	93
4.3.2. Comparing models based upon rounded and unrounded diameters	94
4.3.3. Linear mixed effects model	95
Literature cited	96
Chapter 5 Recruitment and mortality models	
5.1. Recruitment models	
5.1.1. Introduction.....	101
5.1.2. Independent variables	102
5.1.3. Generalized linear model (GLM).....	103
5.1.4. Results of the GLM.....	105
5.1.5. Generalized linear mixed model (GLMM)	115
5.1.6. Results of the GLMM	116
5.2. Mortality models	
5.2.1. Introduction.....	122
5.2.2. Results of the GLM.....	122
5.2.3. Results of the GLMM	134
5.3. Discussion.....	141
5.3.1. Recruitment model	142
5.3.2. Mortality model.....	143
5.3.3. Assessing the Negative Binomial GLMM.....	144

Literature cited	145
Chapter 6 Conclusions	
Appendices.....	154

LIST OF FIGURES

Figure 2.1	Location of the four study sites and 12 sample plots	11
Figure 2.2	Tropical rainforests, plot 2 in Thua Thien Hue (left) and plot 1 in Khanh Hoa (right).....	18
Figure 2.3	Quadrats numbering scheme	18
Figure 2.4	Major corner posts, and permanently marked trees.....	19
Figure 2.5	Creating a scheme for the subquadrats and mapping the coordinates of a reference tree $k(x_k, y_k)$	21
Figure 3.1	Relative frequency distributions of diameter for 12 plots in two years (2005 and 2012/2013) fitted by Weibull-, Log-normal, and Gamma distributions. The white columns and solid line represent the empirical and theoretical distributions in 2005; the grey columns and dashed line represent the empirical and theoretical distributions in 2012/2013.	34
Figure 3.2	Frequency distributions of the number of tree species per DBH class for eight plots in two years (2005 and 2012/2013) as fitted by a Weibull distribution. The white columns and solid line represent the empirical and theoretical distributions in 2005; the grey columns and dashed line represent the empirical and theoretical distributions in 2012/2013.	37
Figure 3.3	Relative frequency distributions of height for 12 plots in two years (2005 and 2012/2013) as fitted by Weibull-, Log-normal, and Gamma distributions. The white columns and solid line represent the empirical and theoretical distributions in 2005; the grey columns and dashed line represent the empirical and theoretical distributions in 2012/2013.	39
Figure 3.4	Height- <i>DBH</i> relationships within 12 sample plots as according to the Chapman-Richards function for observed heights (circles) and estimated height curves (dashed line) in 2005; observed heights (triangles) and estimated height curves (solid line) in 2012/2013.	45

Figure 3.5	The height- <i>DBH</i> curves for the observed heights (circles) and estimated heights of important tree species (solid line), as well as the observed heights (triangles) and estimated heights of less important tree species (dashed line), in 2012/2013.....	46
Figure 3.6	Height- <i>DBH</i> relations for three stories: the superstorey (red), the overstorey (blue), and the understorey (violet) in four locations 2012/2013.....	48
Figure 3.7	Height- <i>DBH</i> relationships for important and less important species in three stories: the superstorey (red), the overstorey (blue), and the understorey (violet) in four provinces 2012/2013.....	50
Figure 3.8	The Δ_{β} -profiles for four provinces in 2005 and 2012/2013	57
Figure 3.9	Right tail-sum T_{β} -profiles for the four provinces in 2005 and 2012/2013	59
Figure 3.10	Species-area curves fitted by the Power function for 12 plots from four provinces in the years 2005 and 2012/2013	60
Figure 4.1	Periodic annual diameter increment of one selected important tree species from each province. The black dots are observed values. The dashed line is the curve of an individual important species, the dotted line is the mean curve of all important species in that province, and the solid line is the mean curve of all other species in that province.....	79
Figure 4.2	Comparing models for diameter increment (cm) between unrounded (left) and rounded (right) diameter values for individual species. The black dots are observed values. The solid line indicates regression model (4.14) fitted to an individual important species and its 95% confidence bands (the dashed lines).....	82
Figure 4.3	Periodic annual diameter increment for the four important species in each plot. The blue curve denotes the fixed effects, and the other colours show the mixed effects models for each plot.....	91

Figure 4.4	Periodic annual diameter increment for the four important species in four selected plots. The black dots are observed data on the plot. The blue, and other colour curves indicate the fixed effects, and the mixed effects models, respectively.....	91
Figure 5.1	The annual number of recruits from the Negative Binomial GLM (lines), and observed data (dots) of the two groups, <i>S. wightianum</i> , <i>D. sylvatica</i> , and <i>N. melliferum</i>	115
Figure 5.2	The annual number of recruits from the Negative Binomial GLMM (lines), and observed data (dots) for <i>S. wightianum</i> and <i>D. sylvatica</i>	121
Figure 5.3	The number of dead trees per year from the final Negative Binomial GLM (lines), and real data (dots) of the two groups, <i>S. wightianum</i> , <i>D. sylvatica</i> , and <i>N. melliferum</i>	133
Figure 5.4	The annual number of dead trees from the Negative Binomial GLMM (lines), and observed data (dots) for the two species groups, <i>S. wightianum</i> , and <i>N. melliferum</i>	141

LIST OF TABLES

Table 2.1	Forest types in Vietnam, 2012.....	10
Table 2.2	Provinces, plots and their location coordinates, altitude and slope.....	17
Table 3.1	Descriptive statistics for the diameter at breast height and total tree height from four provinces in 2005 and 2012/2013.....	29
Table 3.2	Parameter estimates and R^2 values for height-diameter models fitted with data for four provinces from 2005 and 2012/2013. The best models are in bold.	41
Table 3.3.	Diversity indices of 12 plots in four provinces.	55
Table 4.1	Summary of descriptive statistics for important tree species on 12 plots in four provinces. Diameter statistics are from 2005.	75
Table 4.2	Number of trees, intercept, β_0 , and slope, β_1 , including p -values, and standard error of estimate from equation (4.14) for important species, all important species, and all others in four provinces. Nonsignificant $\ln DBH_{2005}$ and positive β_1 shaded.....	76
Table 4.3	Intercept and the slope from unrounded and rounded data of four species in four provinces.....	80
Table 4.4	A comparison of AIC, BIC, and log-likelihood between the fixed effects model and the mixed effects models.	84
Table 4.5	Parameter estimates based on REML estimation for the periodic annual diameter increment by species.....	89
Table 5.1	Descriptive statistics of variables for recruitment modelling.....	106
Table 5.2	Generalized linear models (Poisson, Quasi-Poisson, and Negative Binomial) for recruitment trees (0.000 '****' 0.001 '**' 0.01 '*' 0.05).....	108

Table 5.3	A comparison of Pearson's χ^2 between the fixed effects model (FM) and the mixed effects models for the recruits of all species, all important species, and three important species appearing in three and four locations. Best models are highlighted.	117
Table 5.4	Parameter estimates for the Negative Binomial GLMM for recruitment trees of <i>S. wightianum</i> and <i>D. sylvatica</i>	120
Table 5.5	Descriptive statistics of the mortality data used for the model development.	123
Table 5.6	GLM (Poisson, Quasi-Poisson, Negative Binomial) results for standing dead trees (0 '***' 0.001 '**' 0.01 '*' 0.05).	125
Table 5.7	A comparison of Pearson's χ^2 values between the fixed effects model and the mixed effects models. Selected models are bolded.	135
Table 5.8	Parameter estimates for the Negative Binomial GLMM across all species, all important species, and important species occurring in four or three provinces	138

Chapter 1 Introduction

1.1 Overview

Tropical forests cover 7% of the land area on earth (Myers *et al.*, 2000); however, despite their comparatively small area, they supply a disproportionately plentiful amount of products and services to humankind, including watershed control, timber, medicine, and food (Bonan, 2008; Corlet, 2011). In developing countries, tropical rainforests provide a large amount of benefits for indigenous people in the form of timber and non-timber products, energy, shelter, and livelihood (Menzies, 2002; Carter, 2005). Tropical forests are also invaluable in protecting fertile soil, producing rain in the tropics, and increasing overall production (FAO, 1997); in addition, they make up the largest pool of terrestrial biomass carbon stock and account for more than half of the planet's terrestrial biodiversity and one-third of the terrestrial net primary production (Dirzo and Raven, 2003; Bonan, 2008; Lewis *et al.*, 2009; Beer *et al.*, 2010; Pan *et al.*, 2011). Nevertheless, tropical forests have gradually changed over the past decades owing to anthropogenic and large-scale natural disturbances (e.g., hurricanes, fires, and landslides). Because of the essential role tropical forests play in biodiversity and the global carbon cycle, it is increasingly necessary to understand their dynamics.

Forest models play a crucial role in forest management and as such are an essential key to developing long-term strategies for management and ensuring resource sustainability. They assist forest managers in planning forests, evaluating silvicultural options for sustainable timber yield, and reducing damage. Many diverse forest models have been developed by researchers in order to account for uneven- and even-aged trees and stand tables; each model has its own unique technique to accommodate specific locations and tree species. Forest models are produced by a combination of several models, e.g., diameter or basal area increment, recruitment, and mortality; furthermore, they are developed by different techniques. For example, Vanclay (1988) used non-linear regression techniques to present a growth model for uneven-aged monospecific stands of Cypress Pine. The model is implemented as a cohort model comprising stand basal area increment, diameter increment, mortality, and regeneration. He also described techniques for modeling tropical forest growth (1995). Additionally, Palahi *et al.* (2002) developed stand density, stand basal area, and

volume models by using a non-linear three-stage least square technique as the estimation procedure to predict the stand growth and yield of Scots pine stands in Northeast Spain.

According to Monserud (2003), there are six different kinds of forest vegetation simulation models: (1) forest growth and yield models, (2) ecological gap models, (3) ecological compartment models, (4) process/mechanistic models, (5) vegetation distribution models, and (6) hybrid models. Of these, forest growth and yield models are the oldest and most expansive class; as such, they are the most widely used in forest management. The most significant benefits of those models are their ability to provide an efficient way to forecast resources and predict tree/stand characteristics in detail. This detail regarding stand structure, species composition, and silvicultural treatment response makes this kind of model well suited for examining alternative methods for compatible forest management. Growth and yield models describe forest dynamics, including regeneration, tree growth, recruitment, mortality, reproduction, and associated changes in the stand (Oliver and Larsen, 1996); Vanclay (1994) defined forest growth models as abstractions of the natural dynamics of a forest stand. Most forest dynamic models are split into three components: diameter increment, recruitment, and mortality.

The setting up and re-measurement of permanent sample plots are essential prerequisites for the investigation of tropical forest diversity and ecological processes (Phillips *et al.*, 1998). Most of the existing knowledge on tropical forest structures and dynamics relies on observations of permanent plots (Phillips *et al.*, 2008), and many ecological studies analyze population changes using census information obtained while counting and recounting a defined plot and examining survivors, losses and gains (Sheil and May, 1996).

These days, modeling diameter increment, recruitment, and mortality in natural forests within the tropics is a subject that has been widely developed. Despite the significant progress made, there has been relatively little study illustrating the growth model of tree species in tropical forests, especially in the tropical forests of Southeast Asia. The purpose of this study is thus twofold: first, to provide a description of the changes in the forest structure and tree species diversity over time, and second, to provide the first

analysis of stand dynamics, including diameter increment, recruitment, and mortality, in tropical rainforests of Vietnam. To get a better understanding of the dynamics of tropical Vietnamese rainforests, we used a data set from 12 one-hectare permanent sample plots with high species diversity in four provinces. Compared with temperate forests, any modeling of tropical forests faces three main difficulties: (1) the richness of the tree species, (2) the lack of data on tree ages, and (3) the lack of long-term measurement of data on forest structure. We therefore classified tree species into two groups based on an importance value index (*IVI*). The *IVI* was calculated by adding up the three important traits of an individual species: tree density, how often a species appears in the subplots, and the density of stock expressed as basal area (Ribeiro *et al.*, 2008). As a result, the *IVI* provides a summary of all three indicators of ecosystem importance.

Stand structure is an essential variable affecting wildlife habitat, and as such it plays an important role in forest zonation. In this study, stand structures were described through the relative frequency distributions of diameter and total height, the number of tree species per diameter class, and the relationship between height and diameter; these are the fundamental attributes of a forest structure. Diverse probability density functions have been utilized to depict the diameter distributions of forest stands (Bailey and Dell, 1973; Maltamo *et al.*, 2000), e.g., Gamma, Log-normal, and Weibull distributions, the latter of which is one of the most flexible distributions for fitting tree diameter distributions (Bullock and Burkhart, 2005; Combes and Allen, 2007), especially in the range of tropical forests (Muller-Landau *et al.*, 2006). In regard to tree species diversity, we used diversity indices, diversity profiles, and species-area relations to evaluate and compare species diversity across four provinces.

Diameter increment is a meaningful tree growth component and primarily related to initial tree size, some indices of competition, and site productivity potential, usually in allometric models, such as $Ey = \beta_0 x^{\beta_1} = \exp(\beta_0 + \beta_1 \ln x)$ in the simplest case using only one regressor x . This form can easily be extended by additional additive regressors in the exponential function. Linear mixed effects model is a newer statistical methodology for fitting increment data. The linear mixed effects models not only have the ability to incorporate both fixed and random effects containing multiple levels (Pineiro and Bates, 2000), but also allow variability to be parsed into these hierarchical levels. In this

study, this approach was used to predict diameter increment of important tree species occurring in three or four provinces by accounting for random variation of regression parameters between plots and between provinces.

For tree species, the recruitment of new individuals and the death of old ones are important processes in population dynamics. On the one hand, recruitment is commonly defined as a process by which young trees are added to forest stands, whereas in silviculture, recruitment is recognized as the process by which saplings or young trees overgrow a certain threshold diameter (Lexerød and Eid 2005). In our study, recruitment trees are defined as the number of trees exceeding a diameter threshold of 6 cm between the two inventories. Recruitment is one of the key process for forest management, as it denotes different processes in the stands (e.g., changes in structure and composition) which may in turn demonstrate the adequacy of past forest management or suggest options for structural maintenance in forest stands (Klopčič and Boncina, 2012).

On the other hand, tree mortality constitutes another major element of forest dynamics. The death of a tree lessens density and influences the social position of the remaining trees, which then defines the diameter increment, potential regeneration, and the probability of mortality for the residual trees. Even though the mortality model occupies a defining role in stand structure and dynamics, it still remains one of the least understood components of growth models (Lutz and Halpern, 2006). To model recruitment and mortality, two approaches were applied: generalized linear models for count data (Poisson, Quasi-Poisson, and Negative Binomial models), and generalized linear mixed effects models (Negative Binomial mixed effects model).

1.2 Objectives of the study

The following objectives were addressed:

- (1) To describe the changes in forest structure and tree species diversity over a 7- and 8-year period,
- (2) To build diameter increment models for natural tropical forests, and
- (3) To construct recruitment and mortality models.

1.3 Structure of the dissertation

This dissertation is broken up into six chapters. Following this introduction, the second chapter presents the four study sites and data collection. Chapter 3 discusses changes in the forest structure and tree species diversity over time; the following two chapters deal with modeling diameter increment, and recruitment and mortality, respectively. The sixth and final chapter sums up the previous chapters' findings with a general conclusion.

Literature cited

1. Bailey, R.T, Dell, T.R., 1973. Quantifying diameter distributions with Weibull function. *Forest science* 19, 97-104.
2. Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A., Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M., Luysaert, S., Margolis, H., Oleson, K.W., Rouspard, O., Veenendaal, E., Viovy, N., William, C., Woodward, F.I., Papale, D., 2010. Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science* 329, 834-838.
3. Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320, 1444-1449.
4. Bullock, B.P., Burkhart, H.E., 2005. Juvenile diameter distributions of loblolly pine characterized by the two-parameter Weibull function. *New Forests* 29, 233-244.
5. Carter, J., Gronow, J., 2005. Recent experience in collaborative management-CIFOR Occasional Paper No. 43. Center for International Forestry Research, Bogor.
6. Corlett, R.T., 2011. Impacts of warming on tropical lowland rainforests. *Trends in Ecology & Evolution* 26, 606-613.

7. Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28, 137-167.
8. FAO, 1997. Regional study on wood energy today and tomorrow in Asia. File document No. 50.
9. Klopčič, M., Boncina, A., 2012. Recruitment of tree species in mixed selection and irregular shelterwood forest stands. *Annals of Forest Science* 69, 915-925.
10. Lexerød, N., Eid, T., 2005. Recruitment models for different tree species in Norway. *Forest Ecology and Management* 206, 91-108.
11. Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A., Laurance, W.F., 2009. Changing ecology of tropical forests: Evidence and drivers. *Annual Review of Ecology, Evolution, and Systematics* 40, 529-549.
12. Lutz, J.A., Halpern, C.B., 2006. Tree mortality during early forest development: a long-term study of rates, causes, and consequences. *Ecological Monographs* 76, 257-275.
13. Maltamo, M., Kangas, A., Uuttera, J., Torniainen, T., Saramäki, J., 2000. Comparison of percentile based prediction methods and the Weibull distribution in describing the diameter distribution of heterogeneous Scots pine stands. *Forest Ecology and Management* 133, 263-274.
14. Menzies, N.K., 2002. "Global Gleanings" Lessons from six studies of community based forest management. Report for Ford Foundation's Environment and Development Affinity Group (EDAG), Ford Foundation, Berkeley.
15. Moserud, R.A., 2003. Evaluating forest models in a sustainable forest management context. *Forest Biometry, Modelling and Information Science* 1, 35-47.

16. Muller-Landau, H.C., *et al.*, 2006. Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. *Ecology Letters* 9, 589-602.
17. Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853-858.
18. Oliver, C.D., Larsen, B.C., 1996. *Forest stand dynamics*. Wiley, New York.
19. Palahi, M., Miina, J.M., Tome', M.G., Montero, G., 2002. Stand-level model for Scot pine (*Pinus sylvestris* L.) in north-east Spain. *Invest. Agr.: Sist. Recur. For.* Vol. 11 (2).
20. Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988-993.
21. Phillips, O.L., Nunez, P.V., Timaná, M.E., 1998. Tree mortality and collecting botanical vouchers in tropical forests. *Biotropica* 30, 298-305.
22. Phillips, O.L., Lewis, S.L., Baker, T.R., Chao, K.J., Higuchi, N., 2008. The changing Amazon forest. *Philosophical Transactions Of The Royal Society* 363, 1819-1827.
23. Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects models in S and S-PLUS*. Springer Science+Business Media, LLC, 233 Spring Street, New York, NY 10013, USA.
24. Ribeiro, N.S., Shugart, H.H., Washington-Allen, R., 2008. The effects of fire and elephants on species composition and structure of the Niassa Reserve, northern Mozambique. *Forest Ecology and Management* 255, 1626-1636.

25. Sheil, D., May, R.M., 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84, 91-100.
26. Vanclay, J.K., 1988. A stand growth model for Cypress Pine. in JW Leech, RE McMurtie, PW West, RD Spencer & BM Spencer (eds), *Modelling trees, stands and forests*, University of Melbourne, School of Forestry, Melbourne, Vic., Bulletin no. 5, pp. 310-332.
27. Vanclay, J.K., 1994. Modeling forest growth and yield. Application to mixed tropical forest, CAB international, Wallingford UK, 312 pp.
28. Vanclay, J.K., 1995. Growth models for tropical forests: A synthesis of models and methods. *Forest Science* 41, 7-42.

Chapter 2 Research area and data collection

2.1 Overview of forests in Vietnam

Vietnam is situated along the eastern coast of the Indochina Peninsula in Southeast Asia-an S-shaped territory of 331,000 km² that extends 1650 kilometers from north to south (Figure 2.1). Vietnam can be divided into three types of topographic categories: mountainous areas, central highlands and plateaus, and low lying deltas and coastal plains (Queiroz *et al.*, 2013) with three-quarters of Vietnam constituting sloping hills and mountainous lands. Several decades ago, most of the country was covered by diverse primary forests until an intense period of rapid deforestation, land-use changes, illegal logging, over-exploitation of non-timber forest products, and weak protected area management dealt the Vietnamese landscape a severe blow. In addition, war, timber exploitation, fire, and conversion to agriculture have damaged more than half of the forest area in Vietnam (Mittelman, 2001).

The total forest cover has however risen over the past two decades. In 1990, the percentage of forest cover was only 27% (US forest service, 2011) as compared with 39.9% in 2012. This increase in forest cover may have been the result of the expansion of forestry plantations and regenerative forests. Vietnam has forest area of 13.86 million hectares (ha), consisting of 10.42 million ha of natural forests (75.18%) and 3.44 ha of plantations (24.82%) (Report of Vietnam Ministry of Agriculture and Rural Development, 2012).

Forests in Vietnam are classified according to one of three functions: production, protection, and special-use, as defined by the 1991 Forest Protection and Development Law. Production forests, as the name implies, supply timber and non-timber forest products. Protection forests are intended to protect ecosystem services, minimize the impact of extreme events, such as contribute to the avoidance of environmental degradation, and restrict the collection of non-timber forest products. Unlike production or protection forests, special-use forests are so designated to the goals of nature conservation, the protection of historical and cultural relics, and environmental protection. In 2012, Vietnam had approximately 6.96 million ha of production forests (50.22%), 4.68 million ha of protection forests (33.77%), and 2.22 million ha of special-

use forests (16.02%). The areas (ha) of forest types categorized according to their objectives are illustrated in Table 2.1.

Table 2.1 Forest types in Vietnam, 2012

Forest types	Total	Forest classification		
		Special-use	Protection	Production
Total area	13,862,043	2,021,995	4,675,404	6,964,415
I. Natural forest	10,423,844	1,940,309	4,023,040	4,415,855
1. Timber forest	8,491,520	1,521,400	3,243,939	3,695,039
2. Bamboo forest	521,304	52,494	140,557	324,473
3. Mixed forest	648,423	134,293	213,693	295,406
4. Mangrove forest	58,227	13,986	40,595	2,976
5. Rocky mountain forest	704,370	217,687	384,255	97,960
II. Plantation	3,438,200	81,686	652,364	2,548,561
1. Plantation with forest stock	1,873,659	55,768	399,416	1,350,233
2. Plantation without forest stock	1,135,997	18,238	162,319	886,869
3. Bamboo and dendrocalamus	81,287	185	5,567	74,914
4. Other tree plantations	348,256	7,495	85,072	236,544

Source: Vietnam Ministry of Agriculture and Rural Development (MARD), 2012

Vietnam is ranked 16th among the world's most biodiversity-rich countries (Queiroz *et al.*, 2013), possessing 11,373 plant species which in turn belong to 2,524 genera, 378 families, and 7 major plant groups (Nguyen, 1997). These days, however, Vietnam has become a crucial contributor to the loss of regional and global biodiversity as a result of three main issues: an illegal endangered species trade, a wood processing industry, and the consumption of plant products from threatened species. For the Vietnamese people, the forests support not only economic returns, but also important social and,

cultural benefits, and environmental services. The urgent issues of today therefore include the assessment of changing forest dynamics over time and the management and use of the forest resources that have to fulfill the demands of current and future generations.

2.2 General information about the study area

Measurements were taken in a tropical rainforest, in four different provinces of Vietnam: Ha Tinh Province, Thua Thien Hue Province, Binh Dinh Province, and Khanh Hoa Province. There were three plots in each of the four provinces; the locations of both provinces and the plots within them are demonstrated in Figure 2.1.

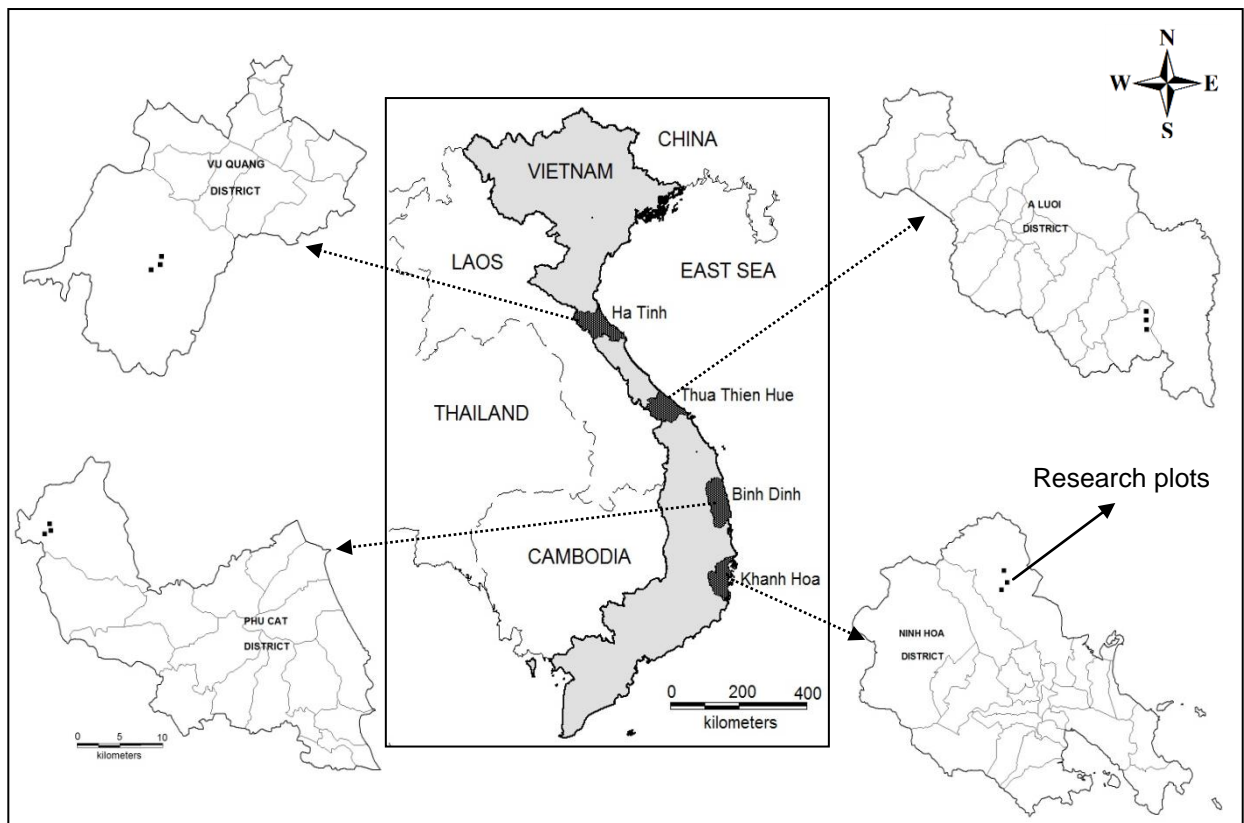


Figure 2.1 Location of the four study sites and 12 sample plots

2.2.1 Study area 1: Ha Tinh

Ha Tinh is one of the six North Central coastal provinces, it has a total area of over 6,000 km² and occupies about 1.8% of the total area of Vietnam. The geographic coordinates are between 17⁰53'50" to 18⁰45'40" north and, 105⁰05'50" to 106⁰30'20" east.

Located in the Truong Son Bac range, Ha Tinh has three adjacent natural geographic zones: a high mountainous zone, a hilly, mountainous zone, and coastal plains. As a coastal province of the internal tropic, Ha Tinh has a monsoon tropical climate. The average annual temperature is around 23.5⁰C – 24.5⁰C; the high temperatures can reach over 40⁰C, in some places climbing to 42.6⁰C in April, May, and June. The temperature bottoms out around 7⁰C, and the relative humidity is approximately 75%-92%. Here, the cold season lasts for six months (October – March) and the hot season lasts for the six months from April to September. The average annual rainfall is 2,300 – 3,000 mm, with a rainy season lasting from April/May to November/December. The major natural catastrophes to take place in Ha Tinh are storms, dry, hot westerly winds, droughts, and heavy rains and flash floods.

Ha Tinh has about 300,000 ha of forest land, of which dense forest makes up 66%; this includes natural forests (164,978 ha), production forests (100,000 ha), and protection forests (63,000 ha) (Nguyen, 2009).

2.2.2 Study area 2: Thua Thien Hue

Thua Thien Hue is situated on the narrow tip of the northern part of central Vietnam, one of the eight ecological regions of the whole country. The province's geographical location is 16⁰18' to 16⁰33' north and 107⁰9' to 108⁰18' east.

Thua Thien Hue consists of numerous types of topography, including mountains, hills, plains, lagoons, and the sea; of these mountains and hills account for 70% of the natural area.

Thua Thien Hue falls also under tropical monsoon climate and has two seasons per year: the rainy season and the dry season. The rainy season usually lasts from September to March. During this season, rainfall is very high, and there are low temperatures with high humidity. The climate of Thua Thien Hue is most likely to be affected by monsoons coming from the west, and east and tropical low pressures from the north. As a result, most of Thua Thien Hue's annual storms and 70% of the region's annual rainfall occur during the rainy season. The dry season lasts from April to September and sees high temperatures and long-lasting heat.

The temperature can reach 39°C – 40°C, particularly during spells of the southwest (Laos) monsoon. The average annual temperature is generally from 24°C – 28°C, with a recorded annual precipitation of 3,400 mm that is irregularly distributed. The relative humidity averages between 85.6% and 88.3%.

Thua Thien Hue has a natural area of 505,399 ha, 58,997 ha (11.67%) of which is utilized as agricultural land, and 224,530 ha (44.22%) of which is forested, 196,81 ha (38.95%) of the land go unused. The natural forests in Thua Thien Hue account for 176,420 ha (78.6%), 48,092 ha (21.4%) are a forest plantation (Hoang, 2012).

2.2.3 Study area 3: Binh Dinh

Binh Dinh is located along the South Central Coast of Vietnam between the coordinates 14°27' to 14°42'10" north and 108°27' to 108°55'4" east. The province is distinguished by a humid, tropical monsoon climate and that divides it into two distinct seasons: the rainy season (August – December) and the dry season (January – July). The annual average temperature varies from 25.7°C to 27.4°C and the relative humidity is about 79%. The average rainfall is between 1,751 mm and 2,400 mm. As tropical storms often make landfall in the region, typhoons can generally be counted on in September and November.

The total land area of Binh Dinh is 603,960 ha, which is broken up into 249,310 ha of forest land, 136,350 ha of agricultural land, 62,87 ha of non-agricultural land, and 155,430 ha of unused land (Le, 2012).

A hot and humid climate, along with rainfall, diversified topography, and soil ensure that vegetation in Binh Dinh is abundant in genera and species; 66 classes, 175 orders, and 1,848 species can be found here (Le, 2012).

2.2.4 Study area 4: Khanh Hoa

Khanh Hoa is a coastal province in the southern portion of Central Coast Vietnam; its geographical coordinates are 11⁰42'50" to 12⁰52'15" north and 108⁰40'33" to 109⁰27'55" east.

Khanh Hoa is marked by both a tropical monsoon climate and an oceanic climate. The mean temperature ranges from 26.4°C to 27.6°C, and, as in the other provinces in question, there is a rainy season and a dry season. The rainy season here is short, lasting from September to mid-December and peaking in October and November. The average annual rainfall is between 1,200 mm and 1,800 mm with humidity at around 75.2 % - 83.4 %. The dry season begins in January and ends in August. Khanh Hoa is rarely affected by large or prolonged storms like the other provinces.

Khanh Hoa covers an area of 519,700 ha, with natural forest making up 155,800 ha (29.98%); of this natural forest, 64.8% is production forest, 34% is protection forest, and 1.2% is special-use forest. Agricultural land constitutes 74,900 ha (14.41%), and a remaining 289 ha belongs to other land types, including vegetable, industrial plant crops, and agro-forestry.

2.3 Establishment and measurement of the plots

2.3.1 Establishment and description of the research plots

As mentioned in section 2.1, tropical rainforests often suffer under the pressure of exploitation. Timber and non-timber forest products may be exploited beyond the forest's ability to regenerate, and deforestation or changes in other economic land-

uses, like shifting agriculture and tree crops, may reduce the quality of land resources, and the amount of forest area. In order to sustainably manage tropical forests and understand the processes that drive those changes, field measurements are necessitated (Picard *et al.*, 2010). Permanent sample plots (PSPs) are commonly utilized to investigate vegetation changes (Vanclay, 1991; Priyadi *et al.*, 2006). From trees measured over time, models of survival, recruitment, mortality, and growth can be estimated from PSP data (Picard *et al.*, 2010). To these ends, the Forest Inventory and Planning Institute (FIPI) of Vietnam established a network of permanent plots. In 1991, FIPI began setting up a program for monitoring forest resources with the goal of (i) taking inventory of forest resources all over the country, (ii) assessing changes in those resources, and (iii) constructing strategies and, plans in order to reasonably use and protect the forests.

The data collections and measurements in each plot include:

- Plot location and administrative plot information: commune, district, province; day, month, and year of inventory; the name of person(s) collecting the data; the topographical map series; the coordinates (latitude, longitude).
- Site description: Elevation, slope, aspect, factors affecting the forests (drought, fire damage, disease), soil type.
- Vegetation cover: forest type, shrubs, vines, lianas, non-vascular vegetation (ferns, mosses, etc.), canopy cover (%).
- Biological information: local cultural and socio-economic information (human population, ethnic group, human activities) close to the plots; fauna (birds, reptiles).
- Tree data: Measurement and assessment of tree species, tree diameter at 1.3 m above ground, (*DBH*) of all live trees having $DBH \geq 6$ cm over bark, total tree height in odd subplots, status of each tree (alive, dead, felled), regeneration on smaller subplots.

This program was completed in four stages: stage 1 from 1991 to 1995, stage 2 from 1996 to 2000, stage 3 from 2001 to 2005, and stage 4 from 2006 to 2010. The results of each stage helped the authorities make an important decision regarding setting up projects for developing the forestry sector. The information and data set from the first stage developed a programme 327 in 1992, which was formed to re-green bare lands and, degraded hills, and allocate five million hectares of a reforestation project. The second stage provided information leading the government to adjust and implement several forestry policies for establishing plantation forest areas. From the third and the fourth stages, detailed information on forest quality, quantity, and dynamics in relation to social and economic activities aided the government in building a scientific base for suggesting the use, protection, and development strategies for forest resources across the country.

The data from previous inventories were analyzed in order to determine species associations, calculate mean diameters, diameter distribution, basal area and volume increment (unpublished), assess changes in natural regeneration following each species or dominant species groups, and to evaluate tendencies of forest rehabilitation and development.

In this research, 12 PSPs in four provinces were selected from the network of PSPs, data from 2005 inherited, and re-measurement of these plots was done by the author in 2012, 2013. General plot information is reported in Table 2.2.

Table 2.2 Provinces, plots and their location coordinates, altitude and slope

Province	Plot	Latitude	Longitude	Altitude (m)	Slope (degree)
Ha Tinh	1	18 ^o 20'58.62" N	105 ^o 20'23.25" E	400	25
	2	18 ^o 20'52.13" N	105 ^o 20'16.43" E	360	20
	3	18 ^o 20'44.01" N	105 ^o 20'7.89" E	380	18
Thua Thien Hue	4	16 ^o 7'48.44" N	107 ^o 25'46.75" E	680	25
	5	16 ^o 7'41.68" N	107 ^o 25'39.95" E	640	20
Binh Dinh	6	16 ^o 7'33.65" N	107 ^o 25'31.44" E	660	20
	7	14 ^o 8'47.45" N	108 ^o 54'2.24" E	420	16
	8	14 ^o 8'40.94" N	108 ^o 54'2.30" E	460	20
Khanh Hoa	9	14 ^o 8'35.96" N	108 ^o 53'50.68" E	440	18
	10	12 ^o 39'53.76" N	109 ^o 4'38.65" E	300	15
	11	12 ^o 39'48.89" N	109 ^o 4'40.35" E	270	18
	12	12 ^o 39'43.99" N	109 ^o 4'37.07" E	270	15

The plots in Ha Tinh were situated in Huong Quang commune, Vu Quang district and belong to the Vu Quang National Park. The dominant tree species included *Vatica odorata*, *Hydnocarpus annamensis*, *Syzygium jambos* and *Lithocarpus annamensis*. Other generally found features were shrubs (e.g., *Ardisia lindleyana*) and lianas (e.g., *Dryopteris filix-mas*). In Thua Thien Hue, PSPs were established in A Roang commune, A Luoi district. These plots were characterized by the presence of several dominant trees, including *Syzygium wightianum*, *Syzygium zeylancium*, *Syzygium wightianum*, and *Ormosia pinnata*; the dominant shrubs were *Thyrocarpus sampsonii* and *Melastoma saigonense*. In Binh Dinh, PSPs were located on Cat Son commune, Phu Cat district; prevalent trees included *Parashorea chinensis* Wang Hsie, *Hopea pieriei*, *Dipterocarpus alatus*, *Archidendron balansae*, *Intsia bijuga*, *Quercus dealbatus*, and *Syzygium wightianum*; among the frequently found shrubs were *Ixora coccinea* and *Casearia balansae*. The plots in Khanh Hoa were set up on Ninh Son commune, Ninh Hoa district, and consisted mainly of *Enicosanthellum sp.*, *Diospyros sylvatica*, *Saraca dives*, *Syzygium wightianum*, and *Machilus bonii* H.Lec; the main shrub was *Acanthus ebracteatus*.

The 12 plots belong to lowland evergreen rain forests (Figure 2.2). In the past, these PSPs were disturbed by war and logged for timber and non-timber forest products; however, the plots in Ha Tinh are currently listed as a special-use forest; those in Thua

Thien Hue, Binh Dinh, and Khanh Hoa are protection forests in which human activities are limited to preserve forest resources and diversity.

Each plot has a square shape (100 m x 100 m²) and is divided into twenty five 20 m x 20 m quadrats (Figure 2.3). It was aligned according to a magnetic-north direction and has four major corner posts made of a mixture of cement and sand. All trees equal to or larger than 6 cm diameter at breast height ($DBH \geq 6$ cm) were identified by species and permanently marked using a white metal tag (Figure 2.4).



Figure 2.2 Tropical rainforests, plot 2 in Thua Thien Hue (left) and plot 1 in Khanh Hoa (right)

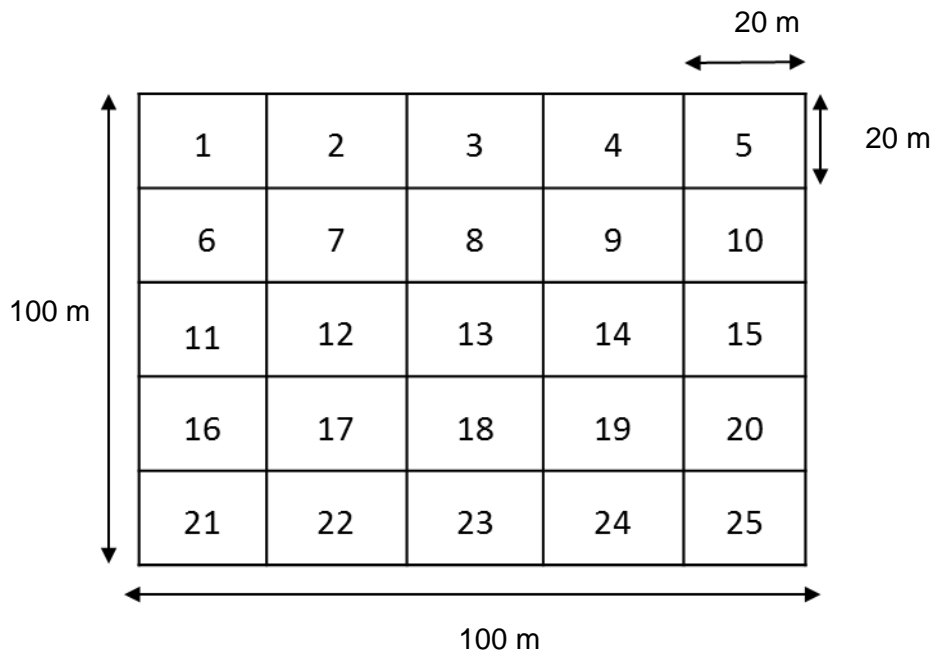


Figure 2.3 Quadrats numbering scheme



Figure 2.4 Major corner posts, and permanently marked trees

2.3.2 Measurement on the plots

a) Field methods in 2005

On each plot, data were taken as listed above. Particularly, all trees in the plot with a diameter at breast height from 6 cm ($DBH \geq 6$ cm) were marked and, identified by species; their diameter was measured at 1.3 m from the ground. Trees with multiple stems above the ground were recorded as a single tree. Total tree height was measured at all trees in the 13 odd quadrats only. The data within the plot were assigned to their 20 m x 20 m quadrat.

b) Field methods in 2012 and 2013

Measurements were repeated on all 12 plots, either in 2012 (plot 1, plot 2 in Ha Tinh; plot 1, plot 3 in Thua Thien Hue; plot 1, plot 2 in Binh Dinh; plot 1, plot 2 in Khanh Hoa) or in 2013 (plot 3 in Ha Tinh, plot 2 in Thua Thien Hue, plot 3 in Binh Dinh, plot 3 in Khanh Hoa). The total tree heights in 2012 and 2013 were measured from 10 randomly selected trees on each of the 13 odd quadrats. Standing dead trees and recruited trees (i.e., trees that reached a diameter ≥ 6 cm between the two measurements) were also

recorded. Recruitment trees were marked by adding letters to the number of the nearest already marked trees (1a, 1b, 2a, 3a, etc.).

Additionally, the trees' stories in these forests were recorded, thus collecting the sociological position of each tree following the guidelines of Schomaker *et al.* (2007). All trees were classified into three stories according to their crown position - the relative position of an individual crown in relation to the overstory canopy zone. Trees belong to the superstory if their live crown top is twice the height of the top of the overstory canopy zone. Trees with live crown tops above the midline of the overstory canopy zone are classified as overstory. The understory consists of trees with crown tops at or below the midline of the overstory canopy zone.

The coordinates of trees on the plot allow several types of competition indexes to be calculated, including overtopping basal area, and overtopping diameter (Alder and Synnott, 1992). Because of the immense working time for measuring single tree coordinates, only one of the three plots in each province was randomly selected to have its tree coordinates recorded (plot 2 in Ha Tinh, plot 3 in Thua Thien Hue, plot 2 in Binh Dinh, plot 1 in Khanh Hoa). To this end, each 20 x 20-m quadrat in the selected plot was quartered to form four 10m x 10m subquadrats (Figure 2.5), resulting in 100 subquadrats per plot. The relative coordinates (x , y) of each individual tree were recorded by measuring the distance of each tree to the westernmost and southernmost boundaries of the subquadrat and later converted into Cartesian coordinates within the entire plot (Figure 2.5).

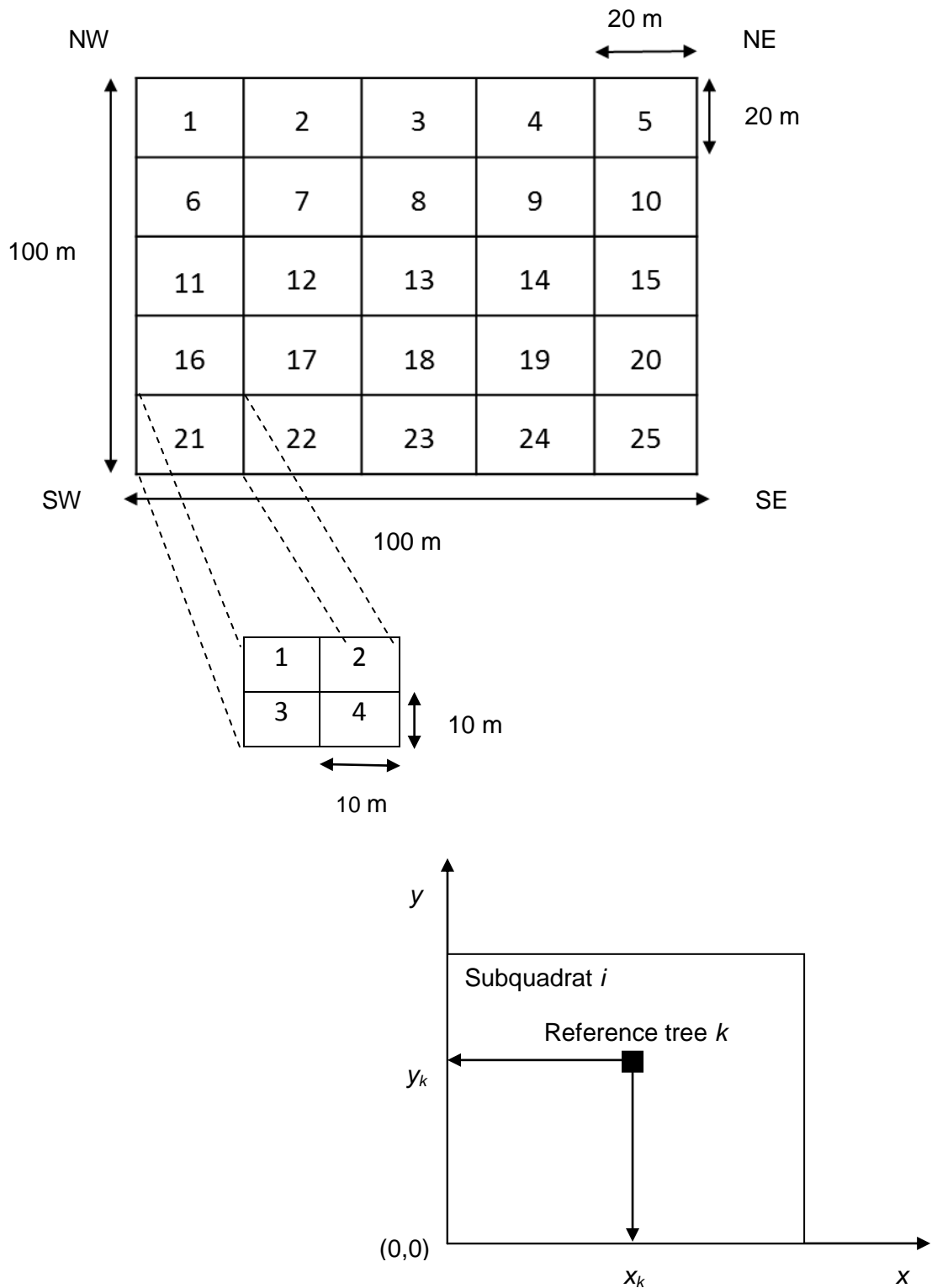


Figure 2.5 Creating a scheme for the subquadrats and mapping the coordinates of a reference tree $k (x_k, y_k)$.

Literature cited

1. Alder, D., Synnott, T.J., 1992. Permanent sample plot techniques for mixed tropical forest. Oxford forestry institute, department of plant sciences, the university of Oxford.
2. Hoang, N.K., 2012. Assessment of special-use forest system and its management in Thua Thien Hue province. Strengthening protected area management in Vietnam, Spam project, 60 pp.
3. Le, N.H., 2012. Report on environmental management plan, 56 pp.
4. Mittelman, A., 2001. Secondary forests in the lower Mekong subregion: An overview of their extent, roles and importance. *Journal of tropical forest science* 13, 671-690.
5. Nguyen, N.T., 1997. Manual for biodiversity research. Agriculture Publishing House, Hanoi, Vietnam (in Vietnamese).
6. Nguyen, V.T., 2009. Ha Tinh assessment report on climate change. Institute of strategy and policy on natural resources and environment, Vietnam.
7. Picard, N., Magnussen, S., Banak, L.N., Namkoserena, S., Yalibanda, Y., 2010. Permanent sample plots for natural tropical forests: A rationale with special emphasis on Central Africa. *Environ Monit Assess* 164, 279-295.
8. Priyadi, H., Gunarso, P., Kanninen, M., 2006. Permanent sample plots. More than just forest stand. Bogor, Indonesia, Center for International Forestry Research, 169 pp.
9. Queiroz, J.S., Griswold, D., Nguyen, T.D., Hall, P., 2013. Vietnam tropical forest and biodiversity assessment. US Foreign Assistance Act, Section 118/119 report.

10. Schomaker, M.E., Zarnoch, S.J., Bechtold, W.A., Latelle, D.J., Burkman, W.G., Cox, S.M., 2007. Crown-condition classification: A guide to data collection and analysis. General technical report SRS-102. Asheville, NC: United States, Department of Agriculture, forest service, Southern Research Station, 92 pp.
11. US Forest Service, 2011. Climate change in Vietnam: Assessment of issues and options for USAID funding.
12. Vanclay, J.K., 1991. Data requirements for developing growth models for tropical moist forest. *Common wealth Forestry review* 70, 248-271.

Chapter 3 Changes in forest structure and tree species diversity after seven and eight years in tropical rainforests of Vietnam

3.1 Forest structure

3.1.1 Introduction

Within the scientific literature, this type of evergreen forest is most often referred to as *Tropischer Regenwald* (tropical rain forest), the term first being used by the German naturalist A.F.W. Schimper in his classic work *Plant Geography* (Richards, 1996). In terms of vertical and horizontal structures, tropical rain forests are the most complex ecosystems. Geographically, tropical rain forests are currently found in Southeast Asia, Central and South America, and Central and West Africa (Richards, 1996; Whitemore, 1998), with Southeast Asia containing the second largest tropical rain forest with an area of 2.5 million km² (Whitemore, 1998).

Tropical forests play a crucial role in three respects regarding the well-being of mankind. Environmentally, they are important in reducing soil erosion, maintaining soil moisture (Lalfakawma, 2010), and regulating local and global climate (Yeshitela, 2008). Socially, millions of people who are living in or around tropical forests depend on them for the many forest products and environmental services gained (Naughton-Treves and Weber, 2001). Economically, they possess a main source of energy in the form of fuel wood, wood, and traditional medicines; they also provide timber and non-timber forest products. It is therefore essential to understand the structures and species diversity of tropical forests in order to find a way to maintain, protect, and develop those ecosystems. However, the majority of forests in developing countries lack inventory data; consequently, the stand structures of those forests are often insufficient for management. In this study, the forest structures of tropical Vietnamese rainforests were analyzed in terms of relative frequency distributions and height-diameter relationships.

The frequency distributions of the diameter and total height of trees in a specific stand are good criteria for both describing the horizontal and vertical structures of the stand and providing basic information for forest resource management. In addition, foresters

often describe height-diameter regressions to predict a total tree height based on the observed diameter at breast height (*DBH*) (Fang and Bailey, 1998). Curtis (1967) pointed out that accurate height-*DBH* models are usually needed to estimate tree or stand volume when using one-entry volume tables or a standard volume table. Numerous studies report the height and diameter relationships for different species and forest regions, but only few of those are related to tropical forests; information regarding their performance is consequently limited (Fang and Bailey, 1998; Feldpausch *et al.*, 2011). Moreover, the measurement of total tree height in tropical rainforests is time-consuming and expensive; an alternative to a blanket height measurement for all trees is the application of a height-diameter model.

3.1.2 Data analysis

3.1.2.1 Basic descriptive statistics

In the course of this research, the following statistics were calculated: the number of stems per hectare, mean, standard deviation, minimum and maximum *DBH*, and height per plot.

3.1.2.2 Stand structures

a) Frequency distributions

In the present study, the Lognormal distribution (two parameters), Gamma (two parameters), and Weibull function (three parameters) were used to model relative frequency distributions of the *DBH*, total tree height, and the number of tree species per *DBH* class.

b) Relationship between height and diameter

In order to find the most appropriate equation for each height-diameter relationships, three plots in each province were combined into one large plot for each of the two

measurement periods; in total, the data collected from the resulting eight large plots were used to estimate the parameters of each model. The selection of the regression model is based on the model's coefficient of the determination (R^2). The equation fitting best was used to describe height-DBH relations in subsequent analyses of different stratified height-diameter relationships.

The eight equations that were used to estimate the relationship between height and DBH in the two measurement campaigns taken in 2005 and 2012/2013 are as follows:

Parabolic $H = a + bD + cD^2$ (3.1)

Michailov function $H = 1.3 + a \exp\left(\frac{-b}{D}\right)$ (3.2)

Prodan (1965), Curtis (1967) (modified) $\ln(H) = a + b \ln(D)$ (3.3)

Avery and Burkhart, 2002 $H = a + \frac{b}{D}$ (3.4)

Curtis (1967), Alexandros and Burkhart (1992) $H = a + b \log D$ (3.5)

Fang and Bailey (1998) $H = a + (a - 1.3) \frac{b}{D+b}$ (3.6)

Fang and Bailey (1998) $H = a + b(1 - \exp(-c(D - D_{min})))$ (3.7)

Chapman – Richards $H = a(1 - \exp(-bD))^c$ (3.8)

where:

- H is total tree height,
- D is diameter at breast height,
- D_{min} is the minimum diameter at breast height,
- a, b, c are regression coefficients,
- e is basis of the natural logarithm, and
- \ln is the natural logarithm.

There are many species found in these forest stands, to develop a height-DBH relation, tree species were categorized into two groups and three stories based on a species importance value index and the relative position of an individual crown in relation to the overstory canopy zone, respectively. We examined the height curves of the two

groups, three stories, and the two groups in each story using the data from the three combined plots in each province.

- Importance value index (IVI)

The decision to use *IVI* arose from the belief that the impact of a species on the forest stand as a whole would be better approximated by using the *IVI* rather than the density or basal area alone because the *IVI* for a species is a composite of three ecological parameters (density, frequency and basal area), which measure different characteristics of a species in its habitat. Density and frequency of a species measure the distribution of a species within the population, whereas basal area measures the area occupied by the stems of trees.

The height curves were individually fitted to two groups defined by higher (*IVI* ≥ 5%) and lower *IVI* (*IVI* < 5%). For the three combined plots in each location, the *IVI* was calculated as the sum of the percentage values of the relative density, relative frequency, and relative dominance (Cottam and Curtis, 1956).

where:

$$\text{Relative density} = \frac{\text{Number of individuals of the species}}{\text{Number of individuals of all the species}} 100\% \quad (3.9)$$

$$\text{Relative frequency} = \frac{\text{Number of subplots where the species occurs}}{\text{Total number of subplots}} 100\% \quad (3.10)$$

$$\text{Relative dominance} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} 100\% \quad (3.11)$$

$$\text{IVI} = (3.9) + (3.10) + (3.11) \quad (3.12)$$

The *IVI* varies from 0% to 300%; the larger the importance value, the more important a species is within that particular community.

- Story

The discussion on the existence and measurement of stories (the words layer, tier, stratum and canopy are also used (Richards, 1952)) in tropical rainforests becomes to one of the oldest and most controversial concepts. One of the first methods used to

evaluate them is profile diagrams. This method was used and developed by Richards (1952) and Whitmore (1975). Over time, studies about canopy stratification have utilized different methodologies following the different purposes. In this study, all trees in each plot were classified into three stories according to their crown position: superstory, overstory, and understory following Schomaker *et al.* (2007).

3.1.3 Results

3.1.3.1 Changes in descriptive statistics

In total, 10,300 stems were counted in the second inventory (2012/2013), which was 556 stems less than in 2005. Three variables (mean *DBH*, mean total tree height, and max *DBH*) increased in the 7 and 8-year interval (2005-2012/2013) (Table 3.1). The mean *DBH* ranged from 16.01 cm to 20.89 cm in 2005 and between 17.73 cm and 23.46 cm in 2012/2013; the max *DBH* came from plot 3 in Thua Thien Hue and plots 1 and 2 in Binh Dinh.

The highest tree densities were counted in Thua Thien Hue and Binh Dinh, whereas the lowest was observed in Ha Tinh. The number of dead trees in Thua Thien Hue and Binh Dinh was much higher than in Ha Tinh and Khanh Hoa. The number of stems in plots 1 and 3 in Thua Thien Hue and plot 1 in Khanh Hoa increased from a respective 1,086, 1,284, and 837 individuals in 2005 to 1,105, 1,353, and 849 stems in 2012 (Table 3.1), respectively. There was however a decrease in the total number of individuals in the other nine plots, in spite of the addition of recruitment trees. The total number of recruits and dead trees over a period of seven/eight years in four provinces was 759 and 1,323 individuals, respectively.

Table 3.1 Descriptive statistics for the diameter at breast height and total tree height from four provinces in 2005 and 2012/2013.

Province	Plot	Variable	<i>n</i> (no. stems)		Mean		Standard deviation		Min		Max		No. recruits	No. dead trees
			2005	2012/ 2013	2005	2012/ 2013	2005	2012/ 2013	2005	2102/ 2013	2005	2012/ 2013		
Ha Tinh	1	DBH	437	428	20.89	23.46	11.54	11.64	6.00	6.00	72.00	75.00	13	21
		H	206	122	15.30	16.02	5.05	3.89	5.00	6.60	27.00	26.40		
	2	DBH	421	361	20.56	22.62	11.86	10.27	6.00	7.00	80.00	82.00	9	69
		H	219	127	14.68	15.41	5.17	3.99	3.00	6.80	27.00	25.30		
	3	DBH	457	408	19.04	22.28	12.44	11.49	6.00	7.00	83.00	78.00	17	66
		H	232	122	11.07	15.45	4.49	5.08	2.00	6.10	26.00	28.20		
Thua Thien Hue	1	DBH	1,086	1,105	17.08	18.55	12.29	12.17	6.00	6.00	86.00	89.00	169	154
		H	570	130	13.42	15.20	4.87	4.69	5.00	6.20	29.50	27.80		
	2	DBH	929	906	18.24	21.83	12.91	12.18	6.00	7.00	92.00	93.00	51	77
		H	517	130	12.50	16.94	4.92	5.46	4.00	8.90	32.00	31.20		
	3	DBH	1,284	1,353	16.28	17.73	11.32	11.63	6.00	6.00	104.00	109.00	260	190
		H	687	130	12.31	13.48	4.90	3.81	4.00	6.60	28.50	23.80		

Table 3.1 (continued)

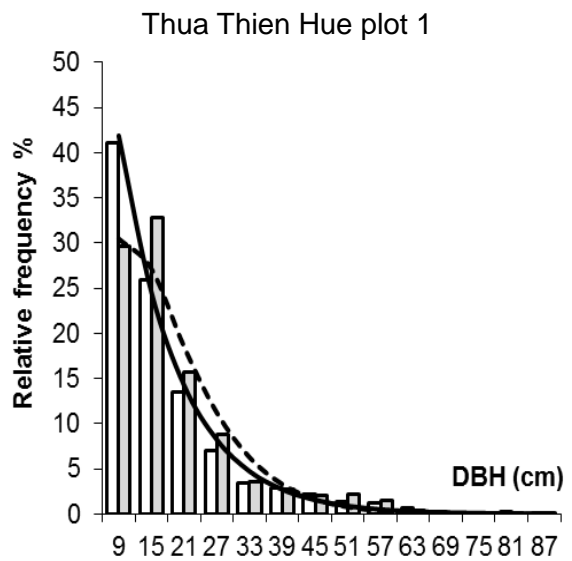
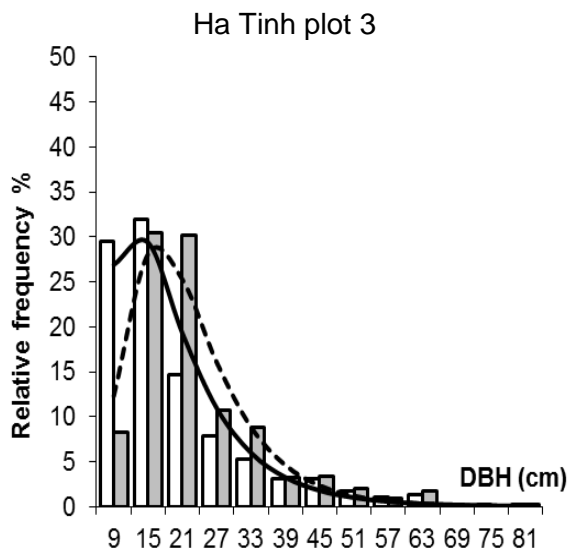
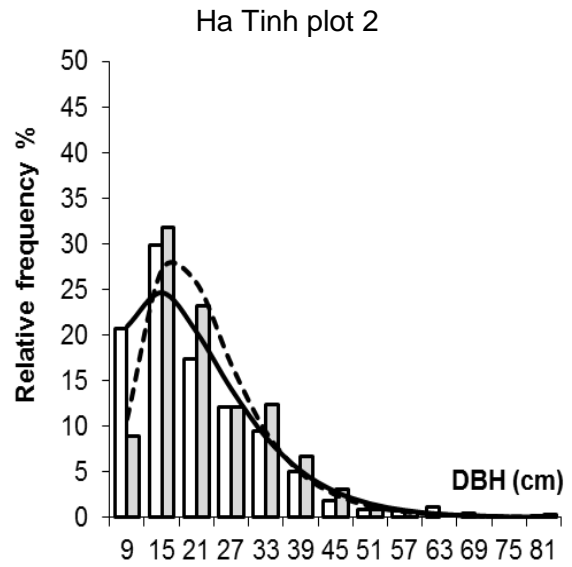
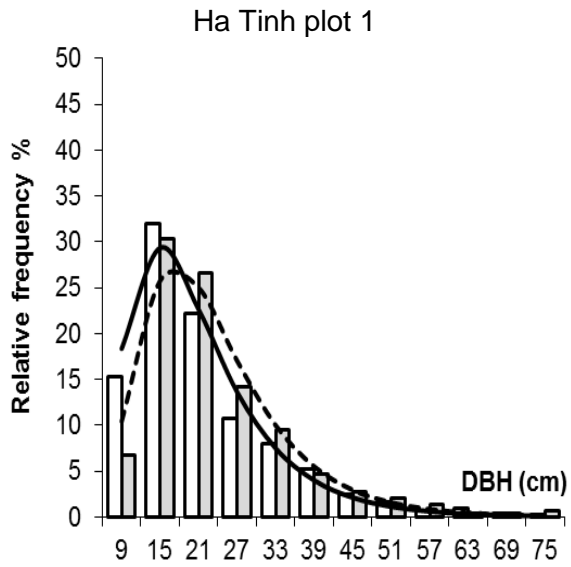
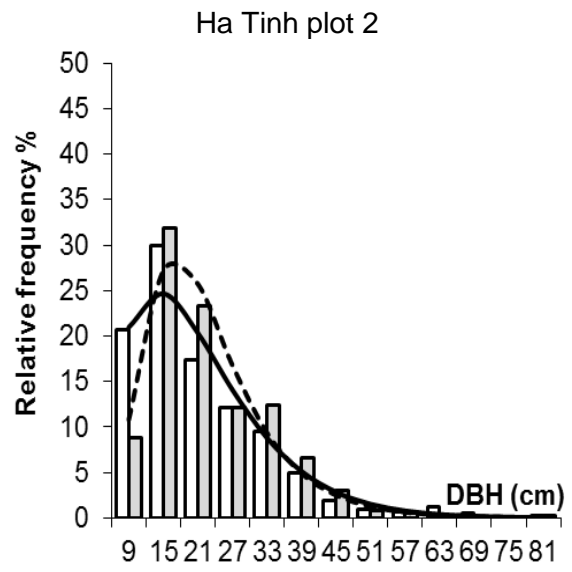
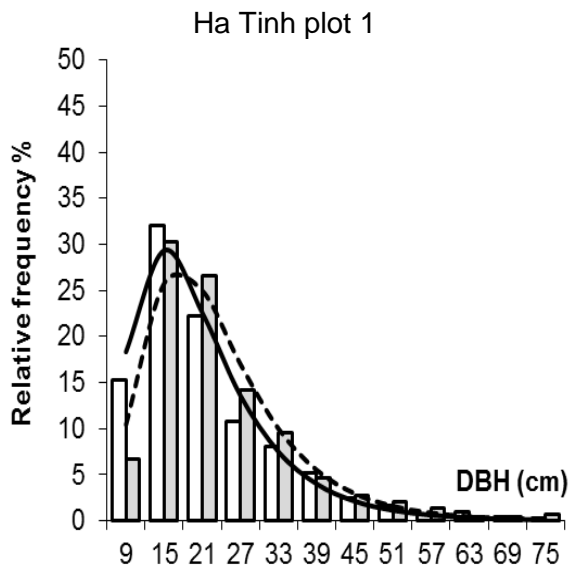
Province	Plot	Variable	<i>n</i> (no. stems)		Mean		Standard deviation		Min		Max		No. recruits	No. dead trees
			2005	2012/ 2013	2005	2012/ 2013	2005	2012/ 2013	2005	2102/ 2013	2005	2012/ 2013		
Binh Dinh	1	DBH	1,372	1,190	16.01	19.23	9.26	9.33	6.00	6.00	94.00	92.00	39	221
		H	677	130	12.52	14.98	3.64	3.97	5.20	7.00	24.80	25.60		
	2	DBH	1,151	999	16.68	19.99	12.08	11.76	6.00	6.00	100.00	103.0	32	184
		H	573	130	11.92	13.79	3.91	3.72	4.80	6.80	29.00	23.80		
	3	DBH	989	934	18.21	21.54	11.27	10.74	6.00	7.00	100.00	102.0	41	96
		H	471	130	13.96	14.27	4.26	3.92	6.00	6.40	27.80	25.30		
Khanh Hoa	1	DBH	837	849	17.45	20.19	12.33	12.26	6.00	7.00	78.00	81.00	47	35
		H	411	130	11.03	12.66	4.09	3.04	4.60	7.20	24.00	22.80		
	2	DBH	864	836	17.70	20.00	9.74	9.67	6.00	7.00	65.00	68.00	53	82
		H	414	130	11.28	12.73	3.77	2.91	4.00	6.50	23.60	20.20		
	3	DBH	1,029	931	17.38	21.15	10.02	9.71	6.00	7.00	72.00	74.00	28	128
		H	532	130	10.33	14.83	3.68	4.64	2.80	6.40	23.00	28.90		
Total (4 prov.)			10,856	10,300								759	1,323	

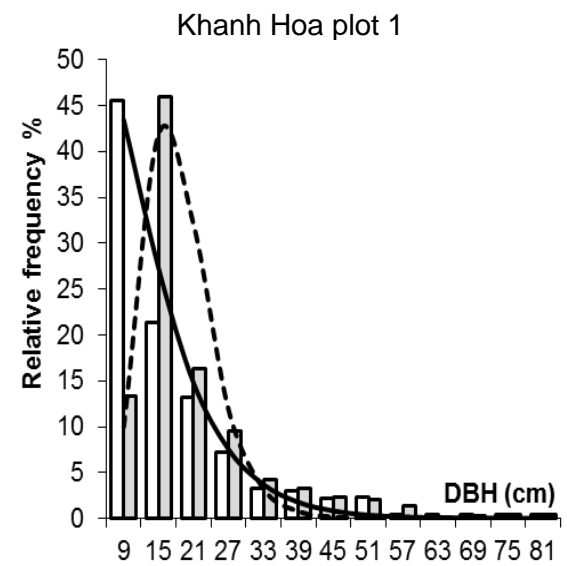
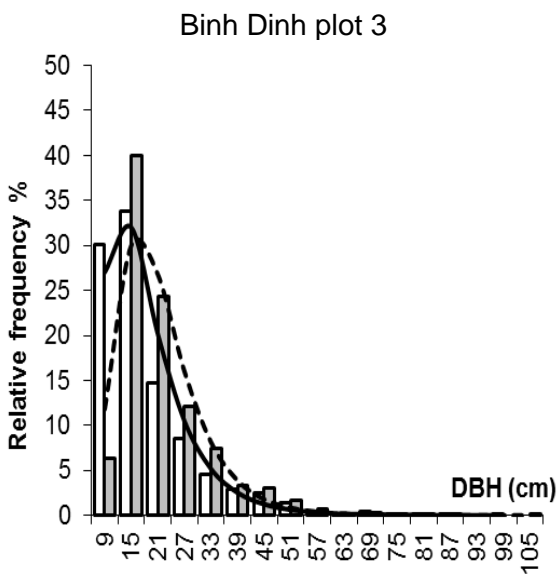
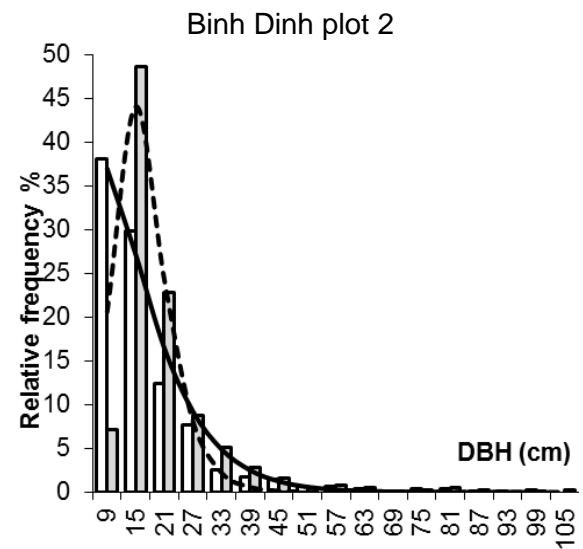
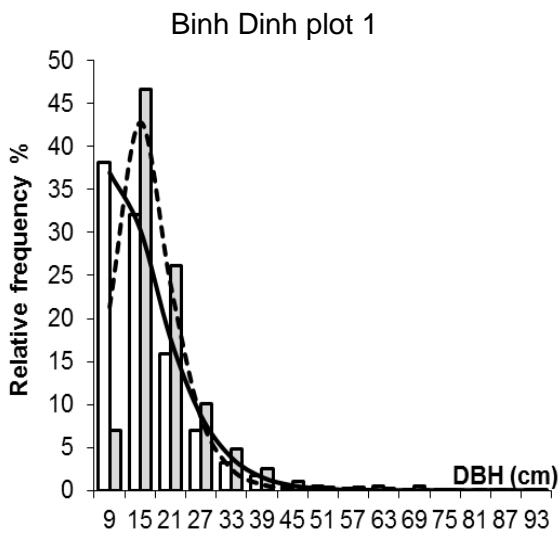
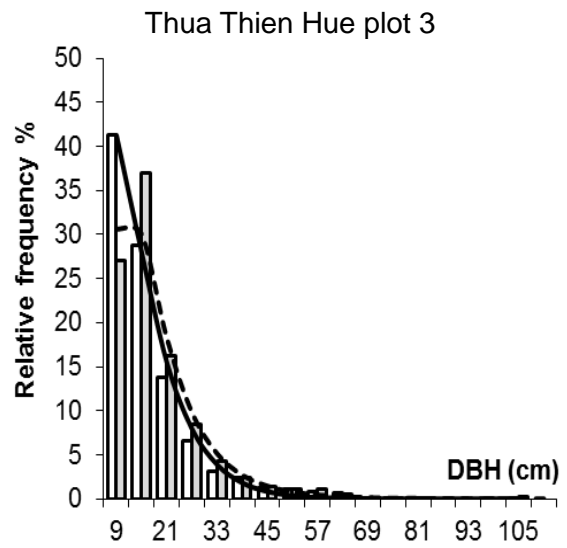
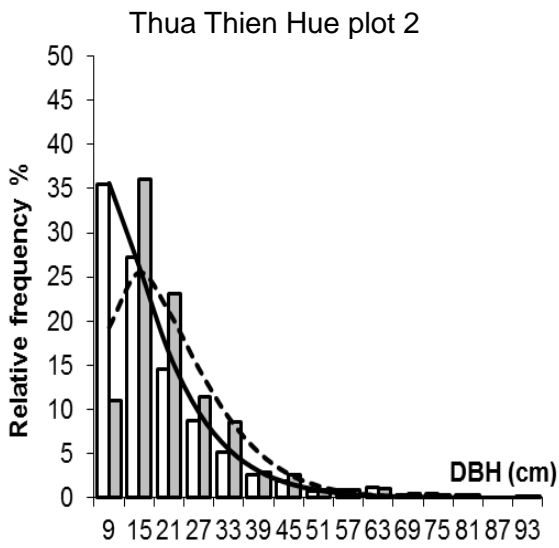
3.1.3.2 Changes in the relative frequency distributions

a) Changes in the distributions of diameter relative frequency

Figure 3.1 indicates the difference in the relative frequency distributions of the diameter between two measurements. In the first survey (2005), the majority of stems were concentrated in the 9 or 15-cm *DBH* class (which accounted for 30%-45% of the number of stems in one hectare), while in the second survey (2012/2013), the number of individuals in the 15-cm *DBH* class consisted of 30% -50% of the total number of stems per plot.

There was virtually no difference in the relative frequency distributions of the *DBH* across the four locations; those distributions were all skewed to the left of the graph, with the total number of stems dramatically declining with the ascending *DBH* classes, suggesting that small-size trees dominate the stand (which in turn indicates good regeneration). In addition, Ha Tinh and Khanh Hoa were lacking large stems (over 81-cm *DBH*). Trees with a *DBH* greater than 100 cm were only found in Thua Thien Hue plot 3 and Binh Dinh plots 1 and 2. No typical *DBH* distribution type could be seen for dead and recruitment trees in 2012/2013.





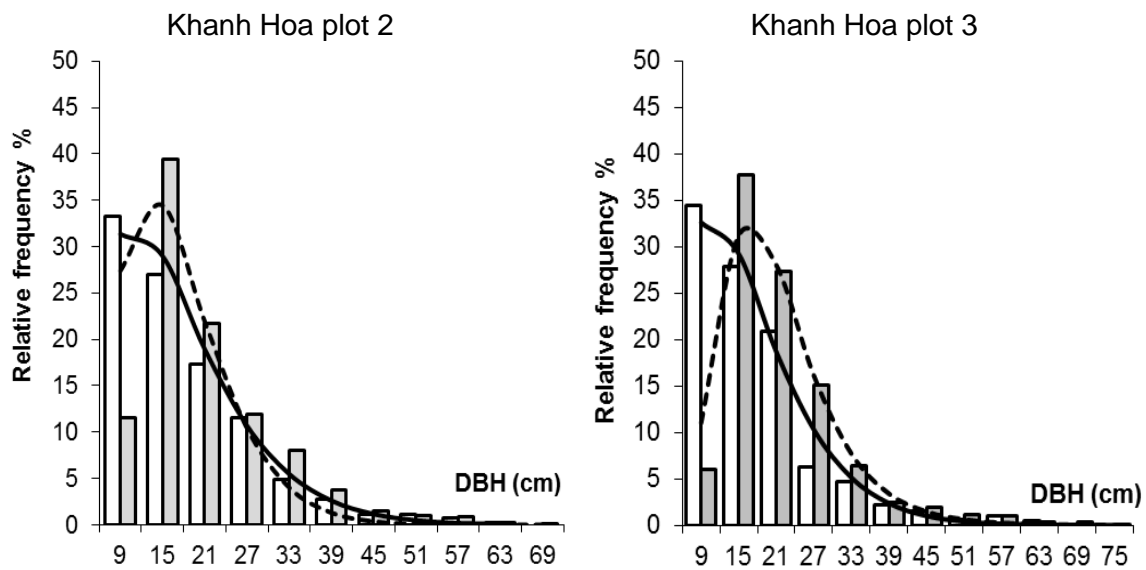
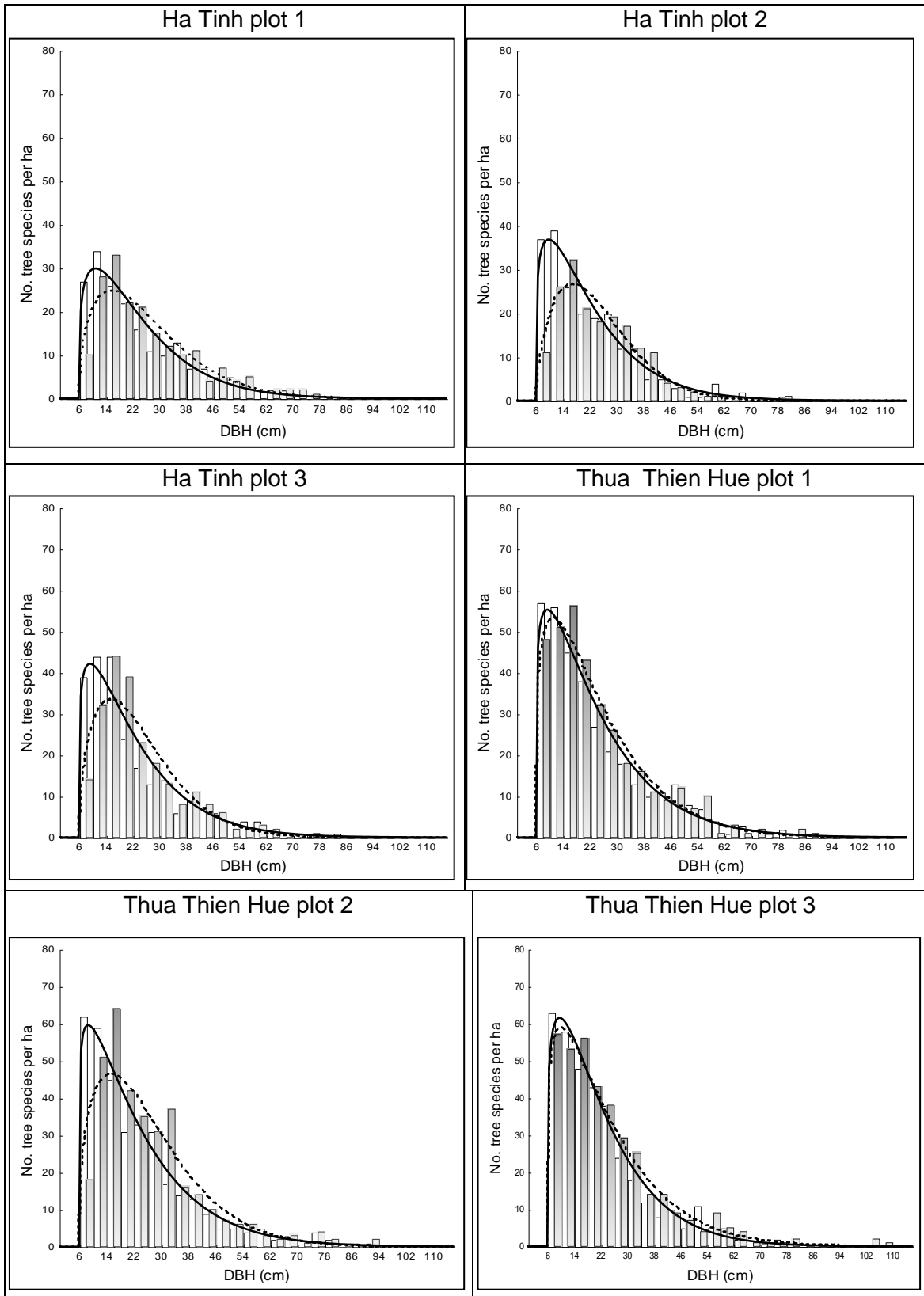


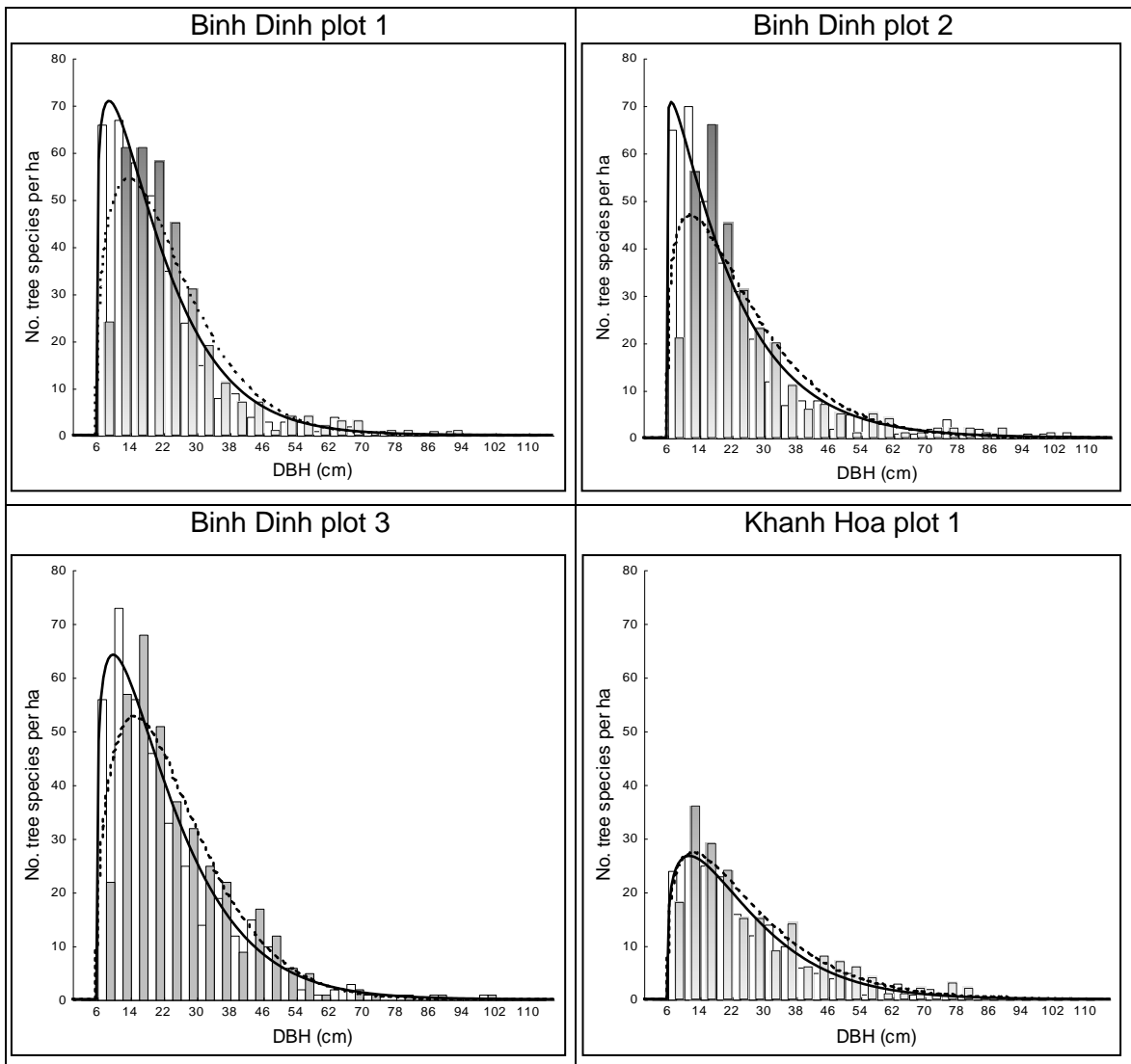
Figure 3.1 Relative frequency distributions of diameter for 12 plots in two years (2005 and 2012/2013) fitted by Weibull-, Log-normal, and Gamma distributions. The white columns and solid line represent the empirical and theoretical distributions in 2005; the grey columns and dashed line represent the empirical and theoretical distributions in 2012/2013.

b) Changes in the number of species per *DBH* class

Figure 3.2 illustrates the number of tree species per *DBH* class. The number of observed species varied significantly among the four sites; in two surveys, Thua Thien Hue and Binh Dinh had more species per *DBH* class than did Ha Tinh and Khanh Hoa. In Binh Dinh, there were approximately 70 species in the 10-cm *DBH* class, whereas in Thua Thien Hue there were a little less than 60 species in the 6-cm (2005) or 14-cm *DBH* (2012/2013) classes.

As with the distributions of the *DBH*, all plots generally reflected a skewed distribution in which a smaller number of trees was associated with a larger diameter; the largest *DBH* class, in Thua Thien Hue plot 3 and Binh Dinh plots 2 and 3, had only one tree species.





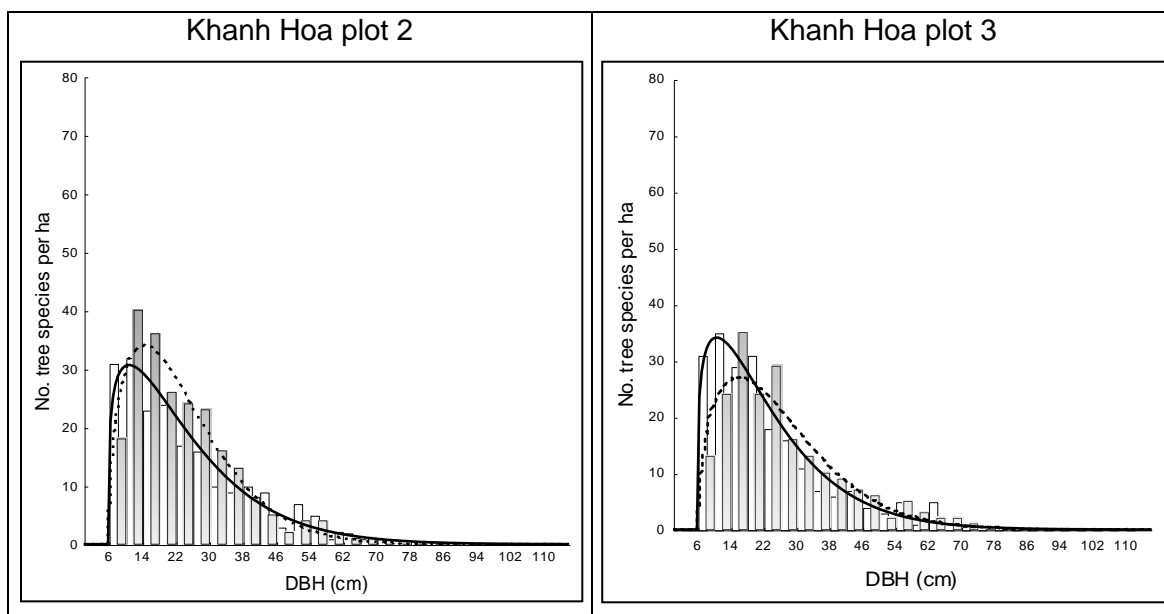


Figure 3.2 Frequency distributions of the number of tree species per DBH class for eight plots in two years (2005 and 2012/2013) as fitted by a Weibull distribution. The white columns and solid line represent the empirical and theoretical distributions in 2005; the grey columns and dashed line represent the empirical and theoretical distributions in 2012/2013.

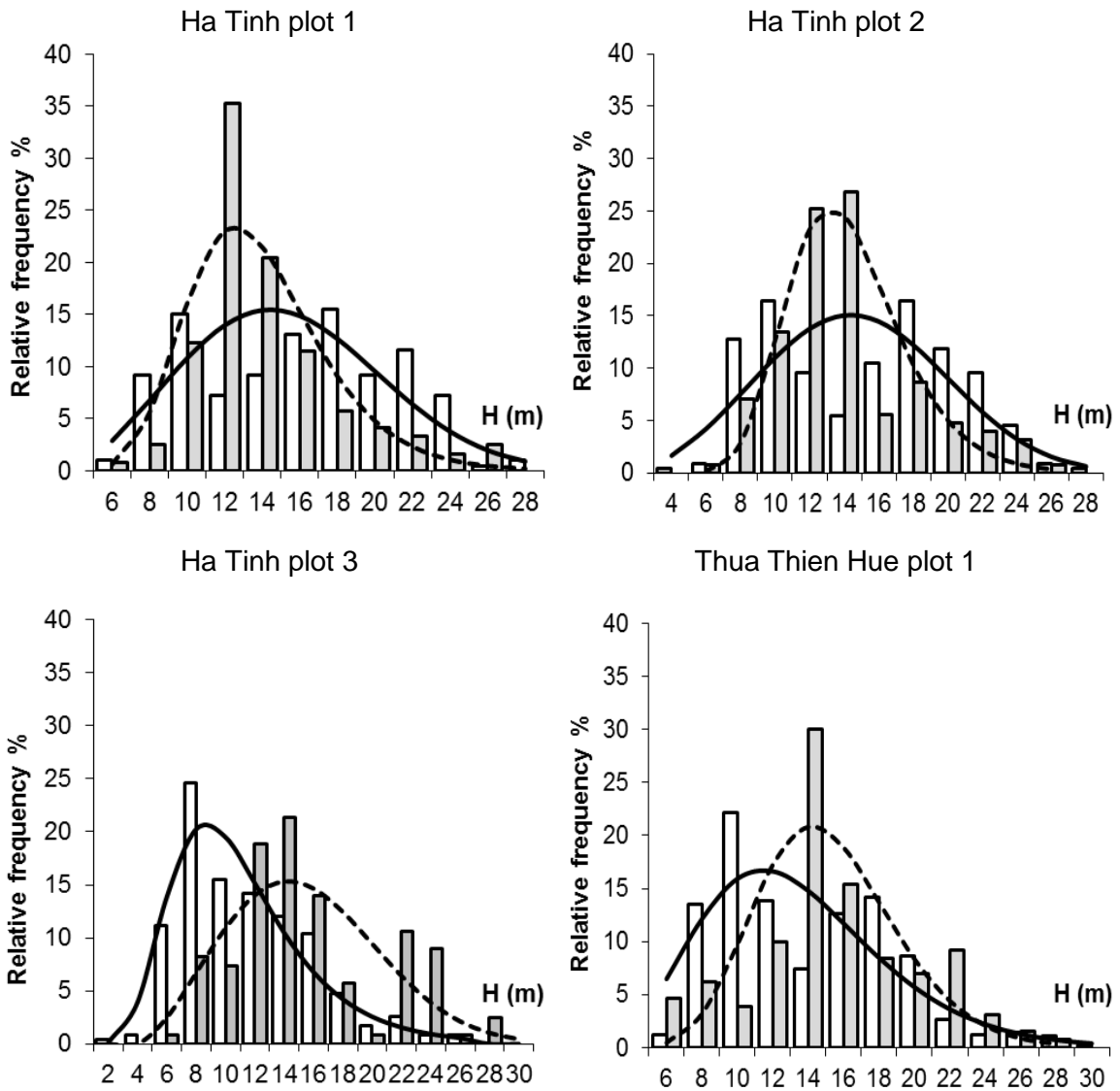
c) Changes in height relative frequency distributions

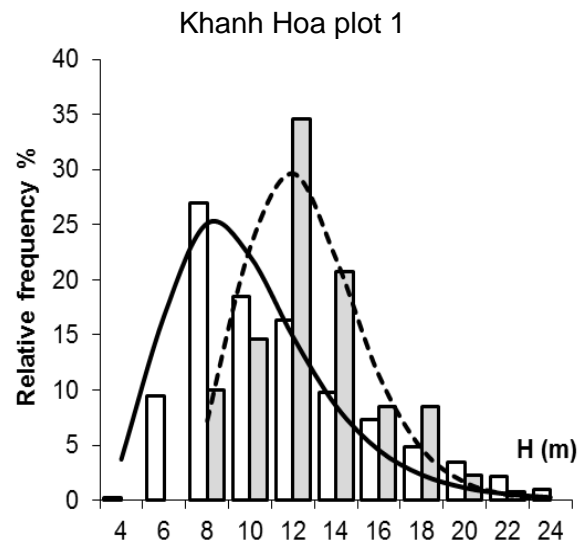
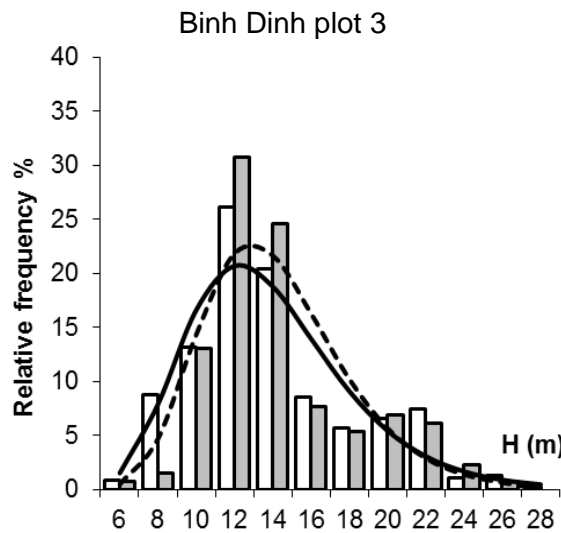
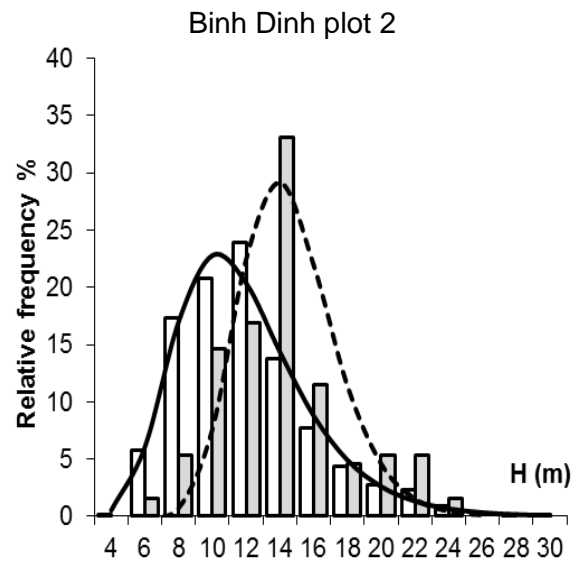
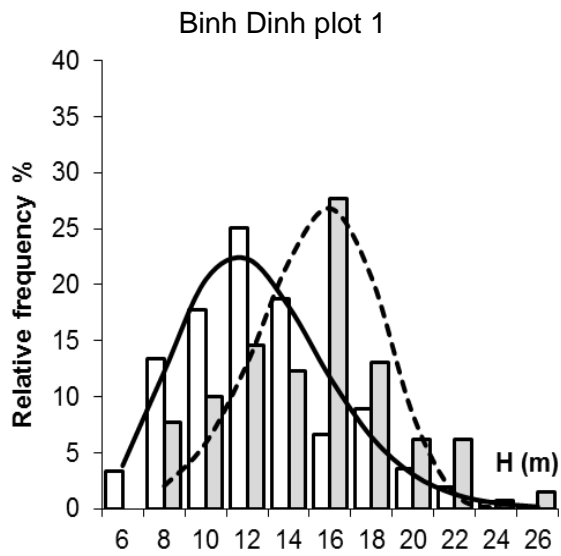
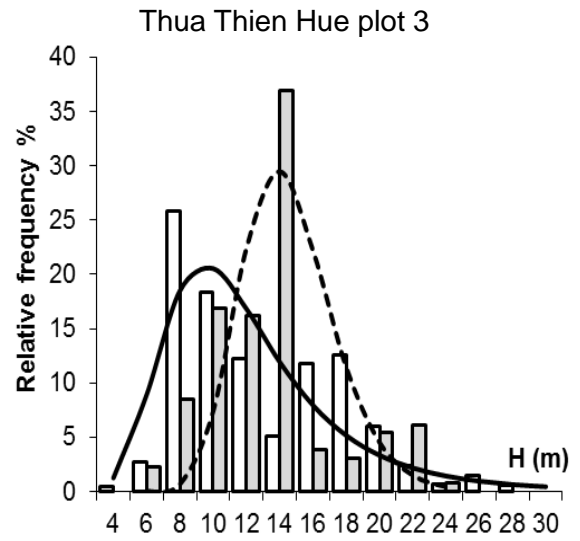
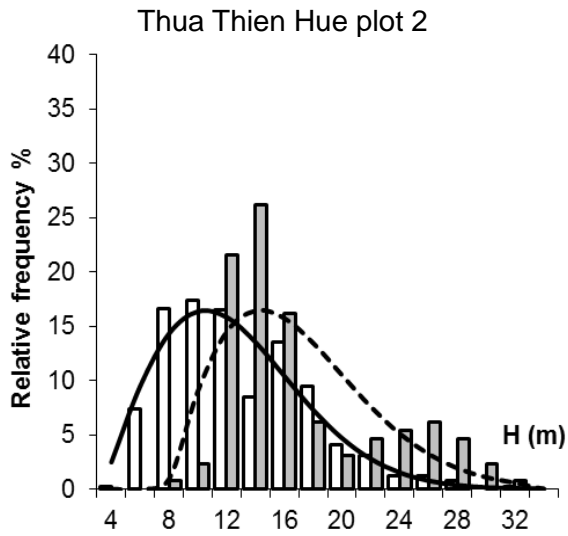
The shape of the relative frequency distribution of height in Figure 3.3 expresses a sharp alteration between 2005 and 2012/2013 on several plots, where unimodality is obvious in the height distributions of the latter rather than the bimodality in the height distributions of the former.

In 2005, a bimodality is clearly demonstrated in the height distributions of Ha Tinh and Thua Thien Hue, first peaking at 8 m (Thua Thien Hue plot 3, 25% of stems) or 10 m (Ha Tinh and Thua Thien Hue plot 1, 15%-25% of stems) and then again at 18 m (about 15% of stems). In Binh Dinh, the largest number of stems was found at a height of 12 m which represented up to 25% stems in one hectare; in Khanh Hoa, this number varied between 20% (in the 10-m height of plot 2) and 25% (in the 8-m height of plot 1). In 2012, the largest proportion of trees stood at a height of 12 m (Ha Tinh plot 1, Khanh Hoa plot 1 with about 35% of the trees in one hectare), 14 m (30%-35% of Ha Tinh,

Thua Thien Hue, Binh Dinh plot 2, and Khanh Hoa plot 2) or 16 m (30% of Binh Dinh plot 1).

On the whole, the height relative frequency distributions were skewed to the left of graph, indicating that the plots had many young trees.





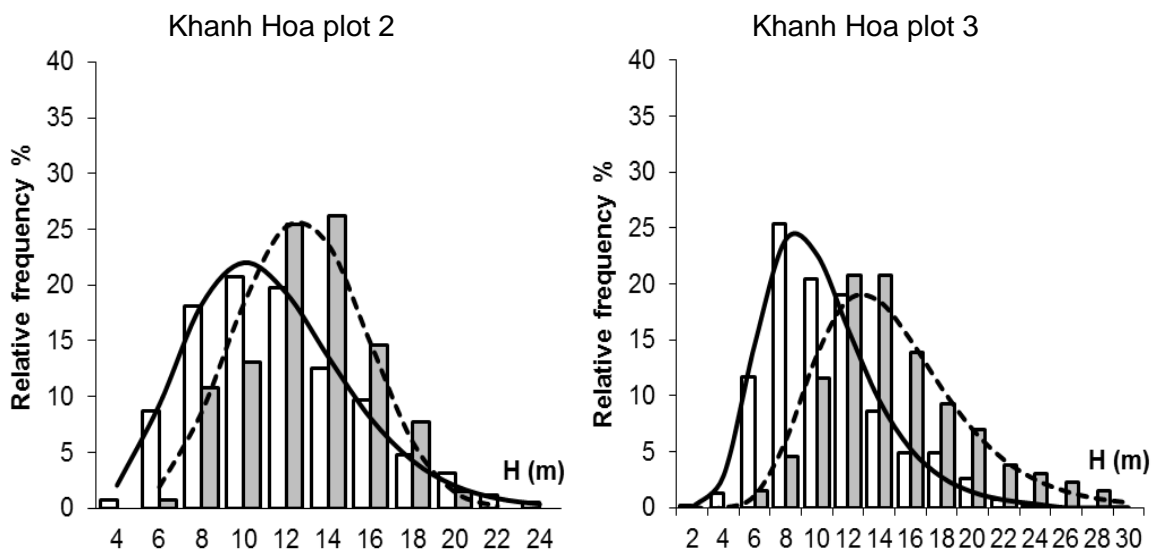


Figure 3.3 Relative frequency distributions of height for 12 plots in two years (2005 and 2012/2013) as fitted by Weibull-, Log-normal, and Gamma distributions. The white columns and solid line represent the empirical and theoretical distributions in 2005; the grey columns and dashed line represent the empirical and theoretical distributions in 2012/2013.

3.1.3.3 Relationship between height and diameter – changes and stratified models

a) Comparison of models in 2005 and 2012/2013

Table 3.2 provides details about the models on the province level, their estimated parameters, and the coefficient of determination values (R^2); a model with a greater R^2 value is the best. Of the eight equations used for modeling height and diameter relations, the Chapman-Richards function performed most ideally regarding R^2 for five of the eight large plots, and it was therefore selected to present height-DBH relations for the natural forests. R^2 in Chapman-Richards varied between 0.506 and 0.672 in 2005 and 0.748 and 0.874 in 2012/2013, explaining at least 50.6% of the total variation in tree height.

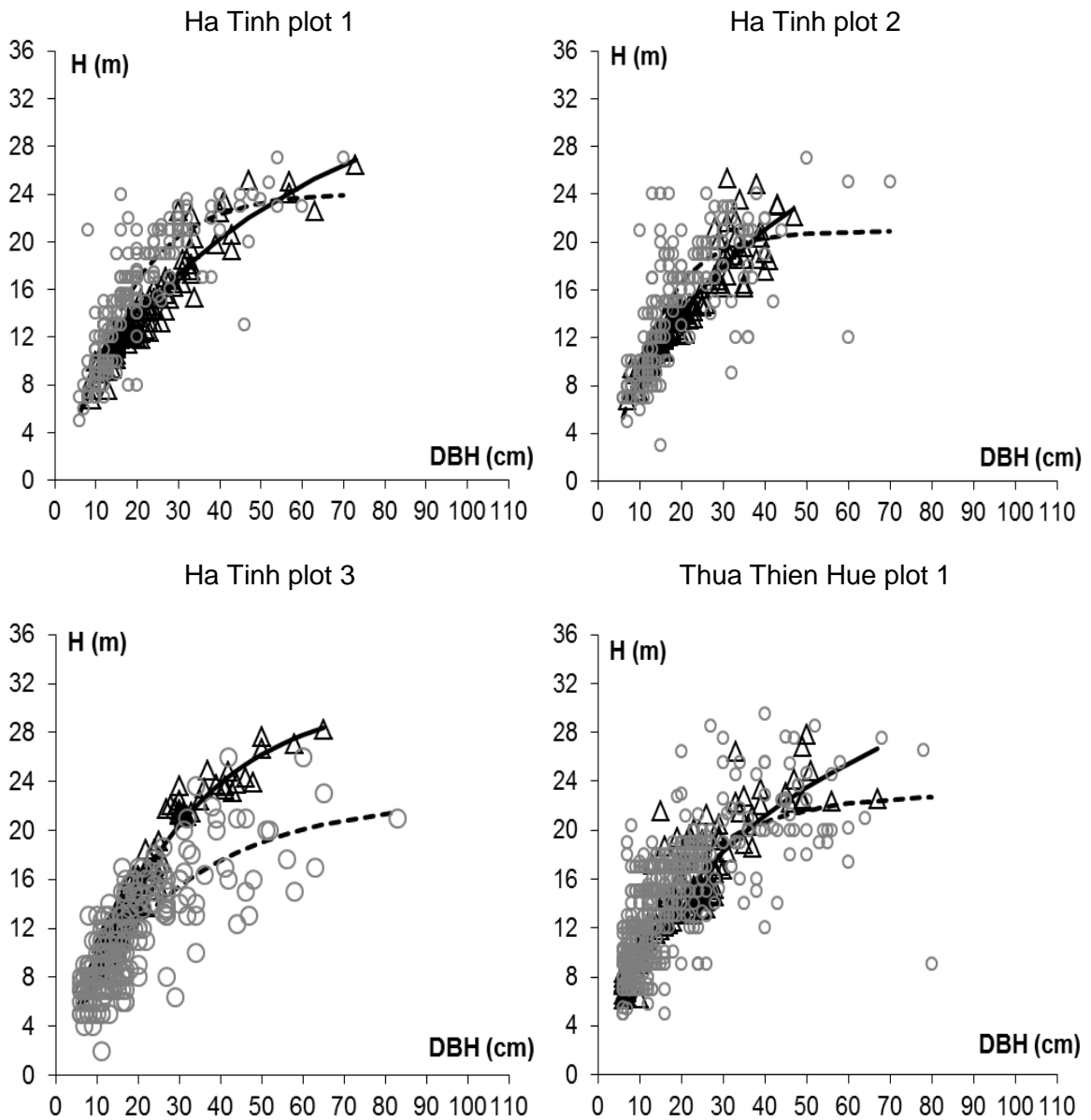
Table 3.2 Parameter estimates and R^2 values for height-diameter models fitted with data for four provinces from 2005 and 2012/2013. The best models are in bold.

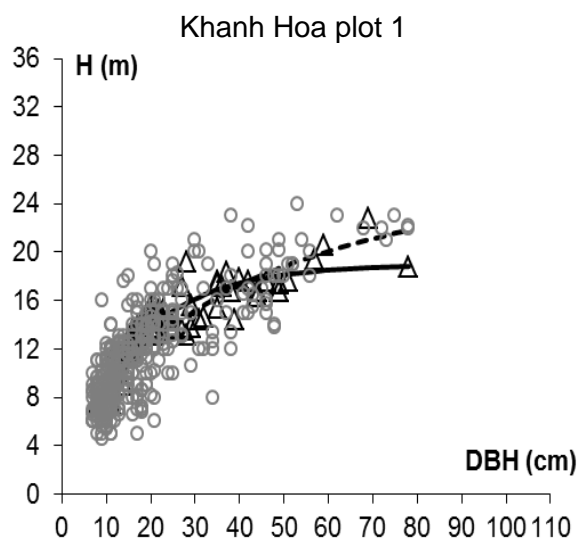
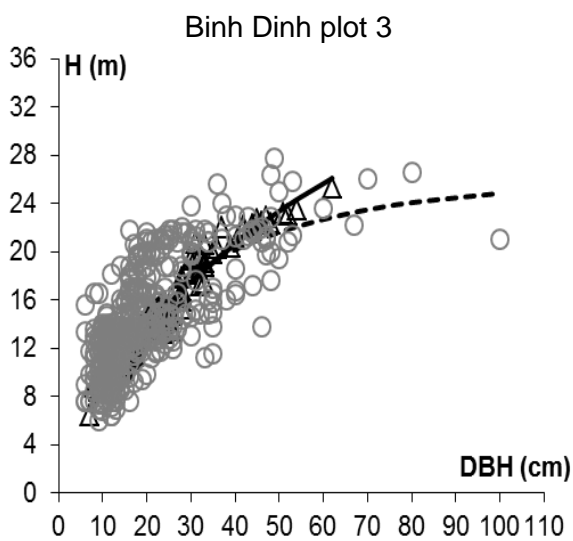
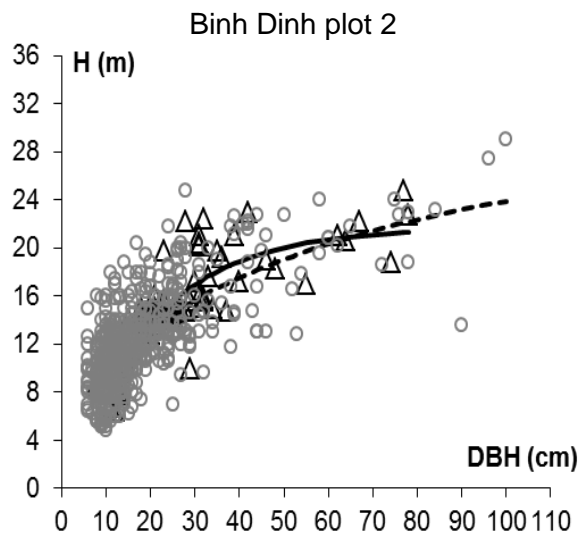
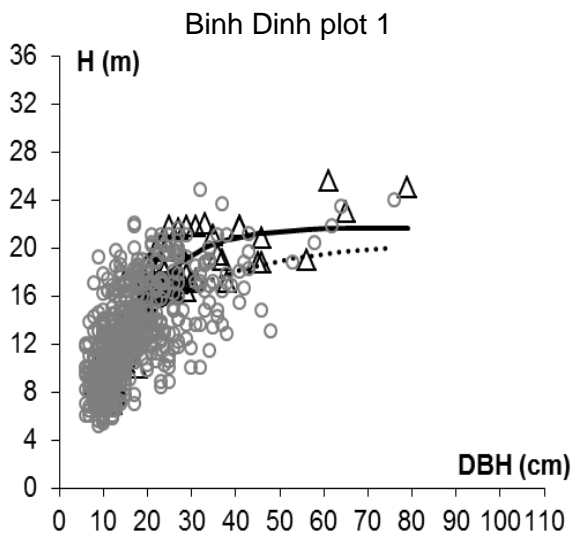
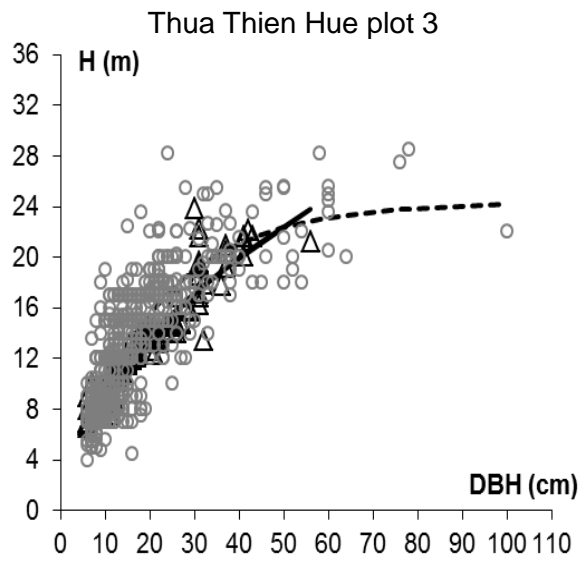
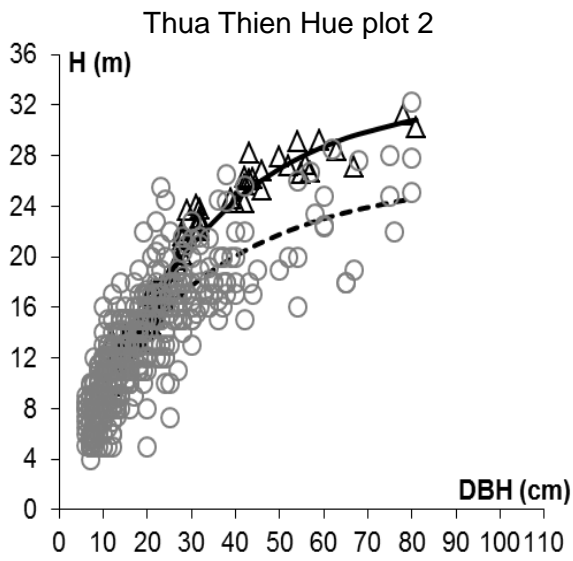
Province	Equation	2005				2012/2013					
		<i>n</i>	Parameters			R^2	<i>n</i>	Parameters			R^2
			<i>a</i>	<i>b</i>	<i>c</i>			<i>a</i>	<i>b</i>	<i>c</i>	
Ha Tinh	3.1	657	2.32	0.77	-0.01	0.61	371	2.61	0.67	-0.01	0.876
	3.2		25.48	12.03		0.62		29.35	15.54		0.875
	3.3		0.78	0.62		0.58		0.72	0.64		0.886
	3.4		21.61	-120.69		0.56		23.67	-165.89		0.745
	3.5		-9.03	18.38		0.61		-13.88	21.92		0.862
	3.6		18.53	-3.09		0.46		19.91	-3.85		0.603
	3.7		5.31	17.09	0.06	0.62		6.13	26.55	0.03	0.848
	3.8		21.812	0.07	1.37	0.62		33.63	0.02	0.85	0.874
Thua Thien Hue	3.1	1774	4.27	0.64	-0.01	0.66	390	4.07	0.59	-	0.850
	3.2		23.71	9.83		0.67		29.11	14.66	0.003	0.849
	3.3		1.03	0.55		0.63		0.91	0.59		0.865
	3.4		20.71	-97.72		0.60		21.90	-117.44		0.602
	3.5		-6.23	16.53		0.67		-10.97	20.12		0.810
	3.6		18.19	-2.77		0.52		18.99	-2.82		0.467
	3.7		7.20	16.82	0.05	0.66		7.33	31.49	0.02	0.779
	3.8		24.40	0.04	0.82	0.67		51.48	0.01	0.66	0.847

Table 3.2 (continued)

Province	Equation	2005					2012/2013					
		<i>n</i>	Parameters			<i>R</i> ²	<i>n</i>	Parameters			<i>R</i> ²	
			<i>a</i>	<i>b</i>	<i>c</i>			<i>a</i>	<i>b</i>	<i>c</i>		
Binh Dinh	3.1	1721	6.27	0.45	-	0.45	390	3.25	0.65	-0.01	0.801	
	3.2		20.61	8.56	0.003	0.50		26.12	13.65		0.809	
	3.3		1.30	0.44		0.46		0.96	0.56		0.779	
	3.4		18.91	-84.52		0.43		23.31	-167.07		0.771	
	3.5		-3.20	13.49		0.50		-10.08	18.71		0.802	
	3.6		16.81	-2.70		0.36		20.16	-4.17		0.669	
	3.7		8.27	14.92	0.04	0.48		-	480.23	506.04	0.02	0.809
	3.8		25.10	0.02	0.55	0.51		23.34	0.05	1.12	0.810	
Khanh Hoa	3.1	1357	4.99	0.39	-	0.53	390	4.34	0.56	-	0.745	
	3.2		18.25	9.62	0.002	0.70		23.24	11.65	0.004	0.747	
	3.3		1.05	0.47		0.46		1.04	0.52		0.742	
	3.4		16.62	-79.59		0.43		20.88	-125.60		0.686	
	3.5		-4.02	12.50		0.52		-7.49	16.50		0.748	
	3.6		14.86	-2.97		0.38		18.39	-3.60		0.603	
	3.7		7.06	17.83	0.02	0.53		6.87	17.18	0.04	0.735	
	3.8		41.08	0.004	0.49	0.53		25.17	0.03	0.73	0.748	

When using the Chapman-Richards model to compare the height curves from two surveys (2005 and 2012/2013) the variation of observed heights around height curves in 2012/2013 was much lower in all provinces than in 2005, as is clearly demonstrated in Figure 3.4. This is particularly visible in Ha Tinh plot 2, Thua Thien Hue plot 1, and Binh Dinh plot 2.





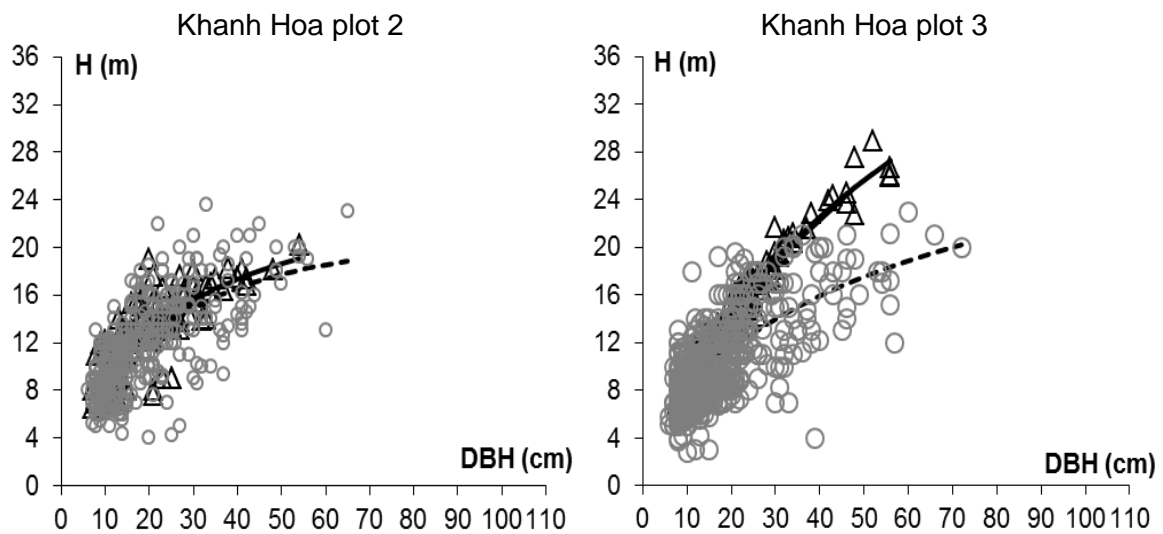


Figure 3.4 Height-*DBH* relationships within 12 sample plots as according to the Chapman-Richards function for observed heights (circles) and estimated height curves (dashed line) in 2005; observed heights (triangles) and estimated height curves (solid line) in 2012/2013.

b) Stratified height – diameter functions

Because of the insufficient precision of height measurement in 2005, height-*DBH* relations for important/less important species, stories, important/less important species per story were finally determined using only the data from the second inventory.

- Height – *DBH* relations for tree species with $IVI < 5\%$ and $IVI \geq 5\%$

17 tree species with $IVI \geq 5\%$ were important species in Ha Tinh and accounted for 66.53% of the total number of trees and 188.52% of the total *IVI* (300%). In Thua Thien Hue, there were 24 species that represented 68.29% of the total number of trees and 187.36% total of *IVI*; in Binh Dinh, 17 of the 125 total species were important and made up 60.62% of the total number of trees and 173.24% of the total *IVI*. 12 important species in Khanh Hoa accounted for 81.82% and 224.05% of the total stems and *IVI*, respectively. Interestingly, *Syzygium wightianum* was the only important tree species that appeared in all four locations.

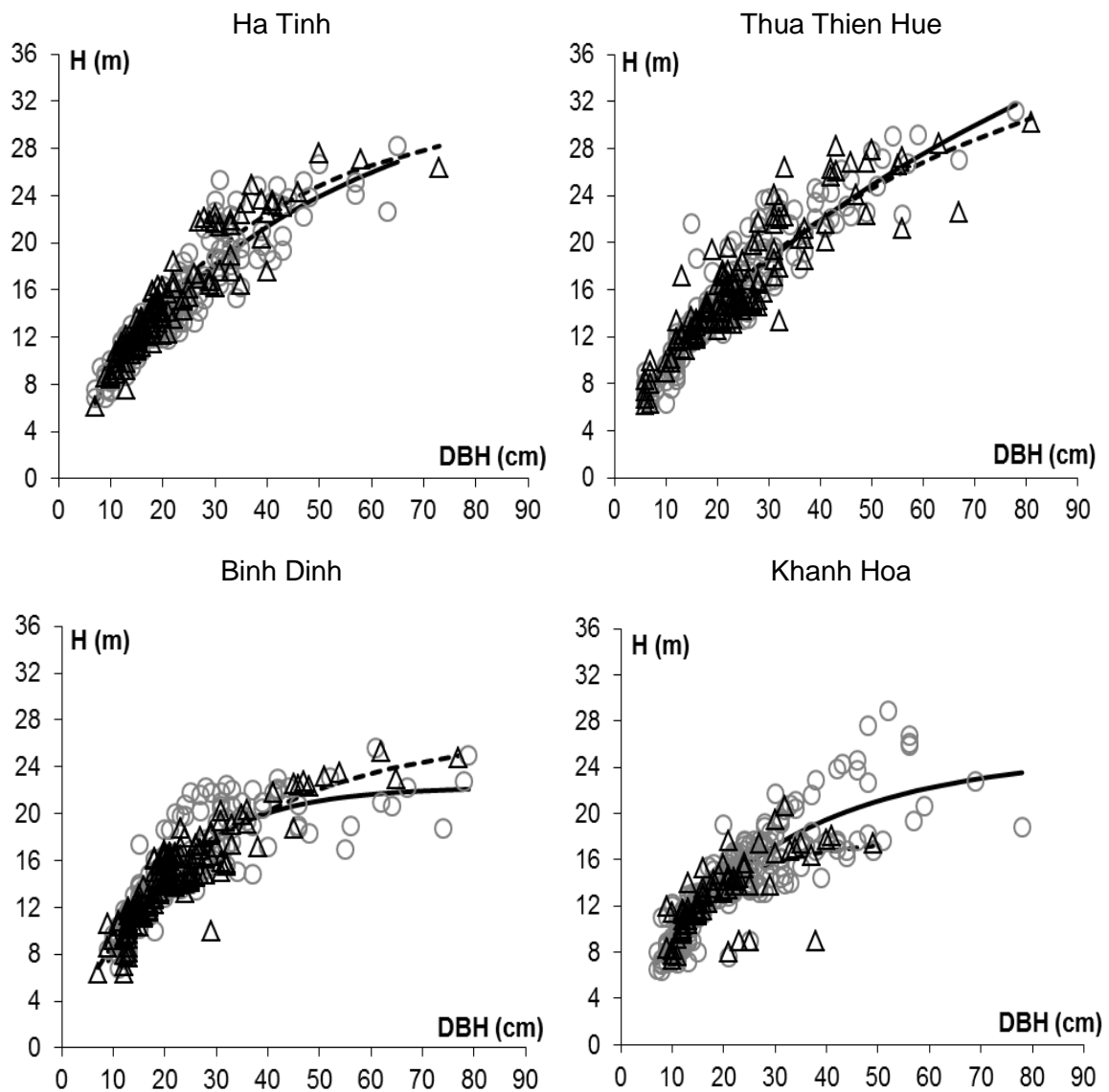


Figure 3.5 The height-DBH curves for the observed heights (circles) and estimated heights of important tree species (solid line), as well as the observed heights (triangles) and estimated heights of less important tree species (dashed line), in 2012/2013.

The R^2 of the Chapman-Richards model varied from 0.786 to 0.873 for trees with an $IVI \geq 5\%$ and 0.548 to 0.891 for trees with an $IVI < 5\%$. From Figure 3.5, it is clear that the height curves of the important tree species were only slightly above those of the less important species, with the exceptions of Ha Tinh and Binh Dinh. In Thua Thien Hue, Binh Dinh, and Khanh Hoa, the difference in height curves between the important and less important species appear to grow with an increasing DBH .

- Height – *DBH* relations of all tree species per story

The R^2 values of the Chapman-Richards function ranged from 0.569 to 0.857 for the understory and 0.613 to 0.829 for the overstory. For the superstory, because there are not many trees, the number of observations varies from 43 (Binh Dinh) to 61 (Thua Thien Hue), the R^2 values are smaller than those of under- and overstories and, varied between 0.289 and 0.681.

In Figure 3.6, for all species, it becomes apparent that the overstory had the highest number of observations and, as expected, the height curves of the superstory trees were clearly separated from those of over- and understories. The gaps between height curves of the under- and overstories were negligible for the smaller *DBH* classes.

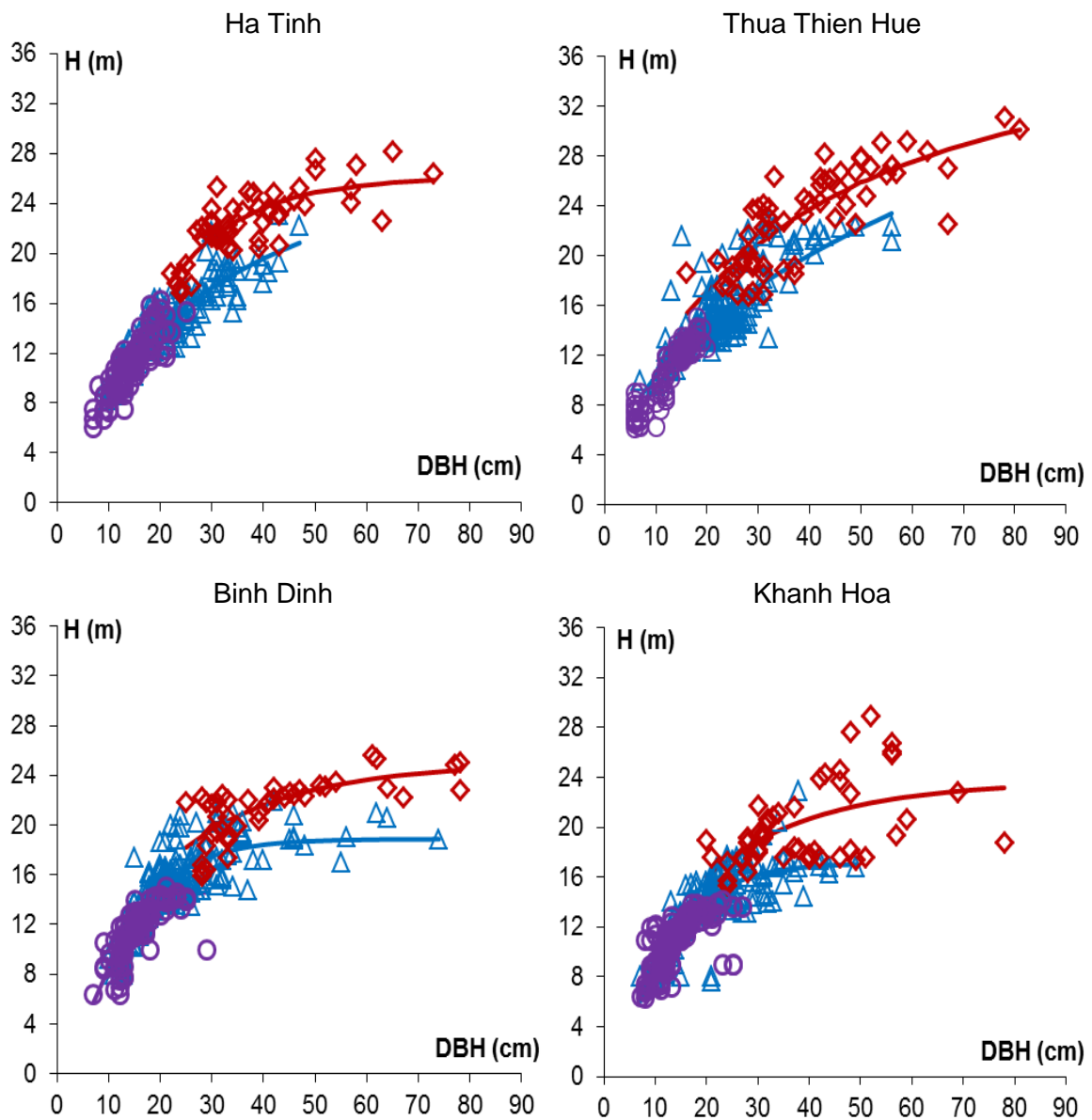
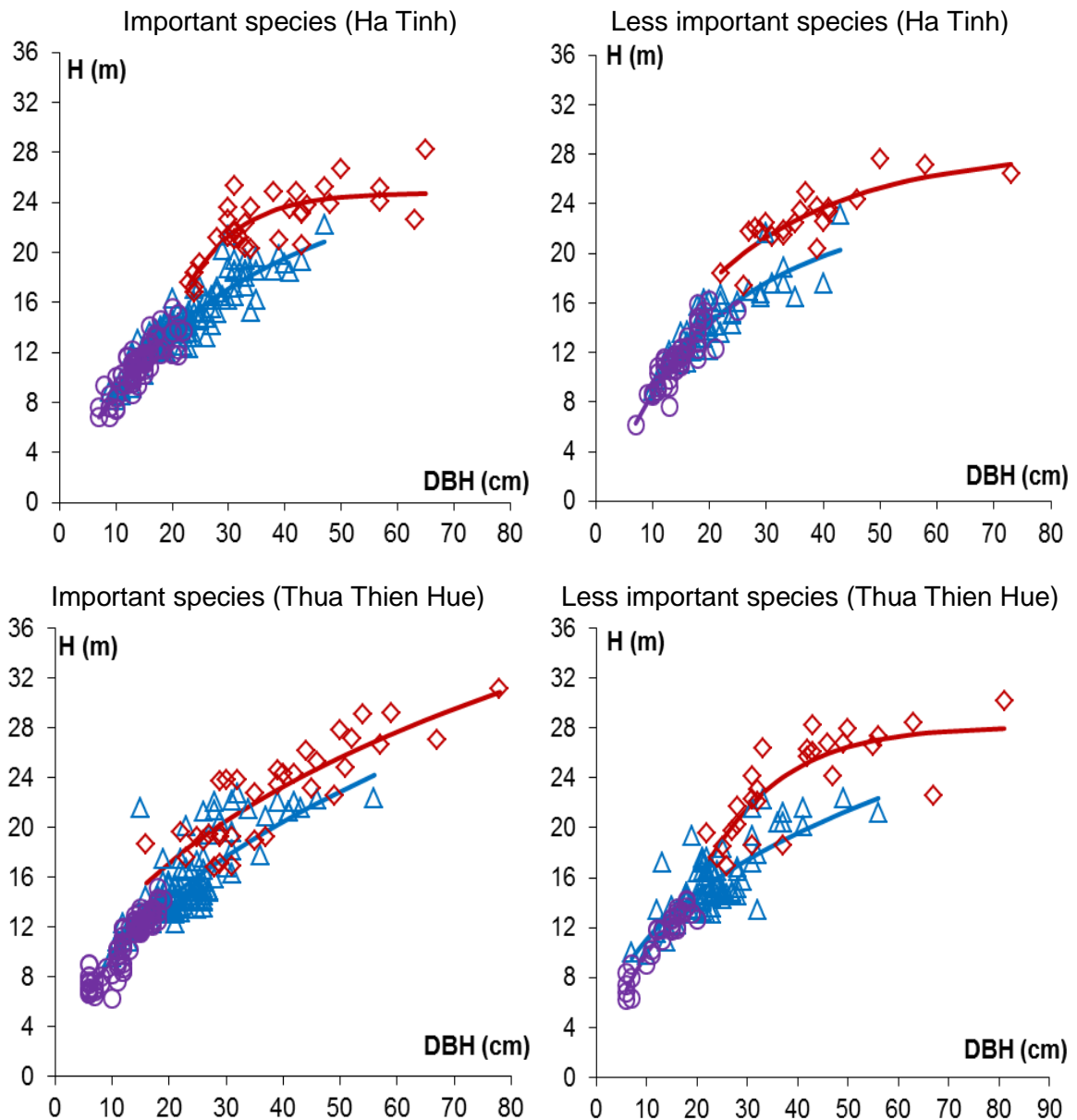


Figure 3.6 Height-DBH relations for three stories: the superstory (red), the overstory (blue), and the understory (violet) in four locations 2012/2013.

- Height – DBH relations of tree species with $IVI \geq 5\%$ and $IVI < 5\%$ in each story

The shape and trend of the height curves for the important/less important tree species in each story are similar to the overarching height curves of all the species within all stories (Figure 3.6).

Although we could clearly distinguish between the superstory and the over- and understories, the over- and understories were again not so easily distinguishable (Figure 3.7).



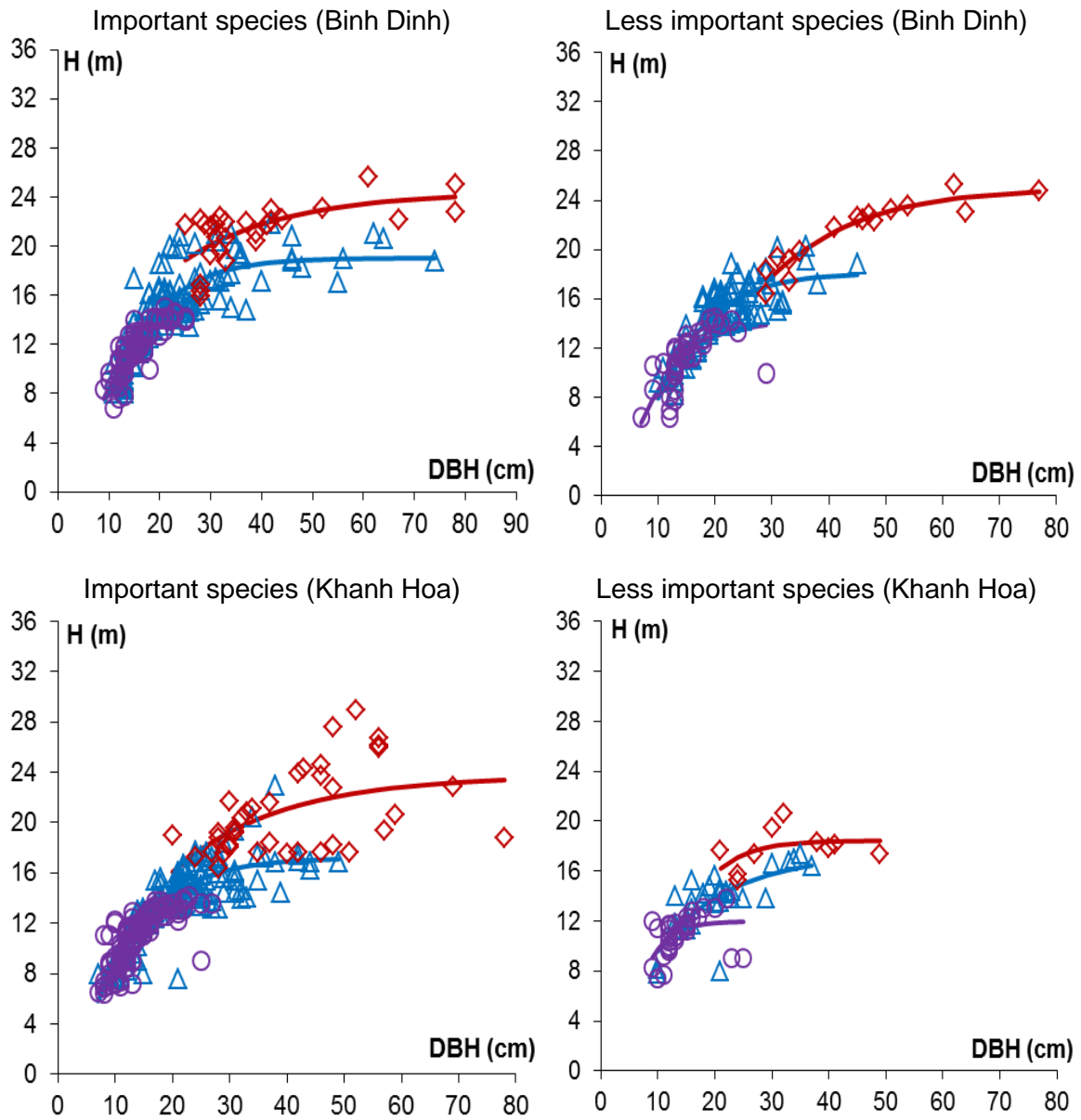


Figure 3.7 Height-DBH relationships for important and less important species in three stories: the superstorey (red), the overstorey (blue), and the understory (violet) in four provinces 2012/2013.

3.2 Tree species diversity

3.2.1 Introduction

Species diversity, species richness, and biodiversity are widely used terms in ecology and natural resource management. Despite the frequent usage of these terms, ecologists have found species diversity difficult to define and measure which may in fact reflect the possibility that it is a “non-concept” (Hurlbert, 1971). In general, the species diversity of a community is made up of two components: species richness (or the number of species present) and the evenness, species equitability, or abundance of each species (Pielou, 1966; Patil and Rao, 1994). Hamilton (2005) reports that there have been two approaches to measuring species diversity: the first involves constructing mathematical indices broadly known as diversity indices, and the second requires comparing observed patterns of species abundance to theoretical species abundance models. Species diversity indices take two aspects of the community into account: species richness and evenness (Hamilton, 2005). In this study, species richness, the Shannon-Wiener, Simpson indices, and the diversity profile are computed to evaluate and compare the diversity of the tree species in the four study sites.

The species-area relationship is another crucial tool available in the study of species diversity, conservation biology and landscape ecology (Palmer and White, 1994; Lomolino, 2000). When plotting the number of tree species against sampling size, the curve was originally intended to describe the increase in the number of species found as the size of the sampling area increased (Tjörve, 2003). This curve is one of the oldest, most well-proven patterns in ecology (Tjörve, 2003) and is more suitable for the assessment of diversity than is merely counting the number of species (Lepě & Stursa, 1989). It allows to determine the minimum area that is necessary to document all the species present within a given contiguous region (Barkman, 1989; Gadow and Ying, 2007).

3.2.2 Data analysis

3.2.2.1 Diversity indices

The following indices are defined in accordance with Gove, Patil, Swindel and Taillie (1994, Chapter 12).

- Species count (Δ_{SC})

$$\Delta_{SC} = \sum_{i=1}^s \left\{ \frac{1}{\pi_i} \right\} \pi_i = s \quad (3.13)$$

- Simpson diversity index (for an infinite community) (Δ_{Si})

$$\Delta_{Si} = \sum_{i=1}^s [1 - \pi_i] \pi_i = 1 - \sum_{i=1}^s \pi_i^2 \quad (3.14)$$

- Shannon-Wiener diversity index (Δ_{Sh})

$$\Delta_{Sh} = \sum_{i=1}^s \{-\log \pi_i\} \pi_i = -\sum_{i=1}^s \pi_i \log \pi_i \quad (3.15)$$

where:

$$\pi_i = \frac{n_i}{N}$$

is the abundance of the i -th species,

n_i is the number of individuals of species i ,

N is the total number of all individuals, and

s is the number of species.

3.2.2.2 Diversity profiles

Diversity profiles have been used to assess tree species diversity in uneven-aged forest stands. Patil and Taillie (1979, 1982) discuss two kinds of rarity measures, the dichotomous type and the rank type, which lead to two different diversity profiles. Examined more closely, these types are defined as follows:

- Dichotomous type:

$$\Delta_{\beta} = \sum_{i=1}^s \frac{1 - \pi_i^{\beta}}{\beta} \pi_i = \frac{1 - \sum_{i=1}^s \pi_i^{\beta+1}}{\beta}, \beta \geq -1 \quad (3.16)$$

where for $\beta = -1$, Δ_{-1} is the species count, for $\beta = 0$, Δ_0 is the Shannon-Wiener index and for $\beta = 1$, Δ_1 is the Simpson index.

- Rank type:

The intrinsic diversity profile of a community is given by the pairs (T_j) :

$$T_j = \sum_{i=j+1}^s \pi_i^{\#} \quad j = 1, \dots, s-1 \quad (3.17)$$

where: $T_s = 0$ and $T_0 = 1$. Species rarity relies only on its rank, because $\pi_i^{\#}$ is the i -th component in the ranked relative abundance vector $\pi^{\#} = (\pi_1^{\#}, \dots, \pi_s^{\#})$ with $\pi_1^{\#} \geq \pi_2^{\#} \dots \geq \pi_s^{\#}$. T_j is called the right tail-sum of the ranked relative abundance vector $\pi^{\#}$.

If community C' is intrinsically more diverse than community C , in short $C' \overset{imd}{>} C$, then the Δ_{β} -profiles preserve that ordering; the reverse is not true. However, ordered T_j -profiles, i.e. without intersections, are equivalent to intrinsic diversity ordering.

3.2.2.3 Species-area relations

Species-area relations show the increase of a species richness as observed within an increasing area. In each plot examined, area size increased from subplot 1 (400 m²) to subplot 25 (10000 m²).

A diverse assortment of functions has been suggested as models for species-area relations; the following three functions were selected:

$$\text{Exponential curve (Gleason 1922, 1925): } s = Z \ln(A) + C \quad (3.18)$$

$$\text{Power curve (Arrhenius 1921): } s = CA^Z \quad (3.19)$$

$$\text{Logistic curve (Archibald 1949): } s = \frac{B}{C + A^{-Z}} \quad (3.20)$$

where:

s is the number of species,
 A is the area, and
 B , C , and Z are parameters.

3.2.3 Results

3.2.3.1 Diversity indices

- a) Changes in species richness as indicated by species count, Shannon-Wiener, and Simpson indices

The four sites differed drastically in their diversity (Table 3.3). In the years after the first census, the total species count and number of families in the four locations reduced over time from 295 species and 68 families in 2005 to 288 species and 67 families in 2012/2013. The most striking trend was a decline in almost all diversity indices, with the exceptions of plot 3 in Thua Thien Hue and plot 1 in Khanh Hoa, where the number of occurring tree species rose. The appearance of five new species in plot 3 of Thua Thien Hue (*Actinodaphne pilosa*, *Aglaiia tomentosa*, *Artocarpus rigidus*, *Litsea vang* H., and *Peltophorum pterocarpum*) and one (*Alstonia scholaris*) in plot 1 of Khanh Hoa brought the total species count from 80 and 46 in 2005 to 85 and 47, respectively, in 2012.

The province totals show a decrease in the species counts of Ha Tinh, Binh Dinh, and Khanh Hoa but an increase in Thua Thien Hue. The number of families also declined, with the exception of Khanh Hoa, where that number remained unchanged.

Table 3.3 Diversity indices of 12 plots in four provinces.

Province	Plot	Species count (Δ_{SC})		Number of families		Shannon-Wiener index Δ_{Sh}		Simpson index Δ_{Si}	
		2005	2012/2013	2005	2012/2013	2005	2012/2013	2005	2012/2013
Ha Tinh	1	60	58	29	28	1.685	1.645	0.964	0.961
	2	66	56	30	29				
	3	81	74	34	32				
	Total	113	104	39	37				
Thua Thien Hue	1	79	79	41	40	1.698	1.691	0.972	0.970
	2	86	86	40	40				
	3	80	85	41	40				
	Total	106	108	46	45				
Binh Dinh	1	94	90	44	43	1.704	1.693	0.964	0.961
	2	96	91	39	39				
	3	102	101	42	41				
	Total	131	125	50	48				
Khanh Hoa	1	46	47	32	33	1.261	1.252	0.901	0.899
	2	59	58	39	39				
	3	54	52	35	34				
	Total	83	82	45	45				
Total (four provinces)		295	288	68	67				

The Shannon-Wiener and Simpson indices declined between the two measurements in all provinces. These indices were substantially higher in Binh Dinh and Thua Thien Hue than in Ha Tinh and Khanh Hoa; in addition, there was some contradiction between Thua Thien Hue and Binh Dinh during the two periods, namely that Δ_{SC}, Δ_{Sh} (Binh Dinh) $> \Delta_{SC}, \Delta_{Sh}$ (Thua Thien Hue), but Δ_{Si} (Binh Dinh) $< \Delta_{Si}$ (Thua Thien Hue). Inversely, there is a consistent ordering of all three indices in comparison with Khanh Hoa: Δ (Ha Tinh, Thua Thien Hue, Binh Dinh) $> \Delta$ (Khanh Hoa). This inconsistency is an interesting point when comparing stands and can be explained as a lack of intrinsic diversity ordering among the stands being assessed.

b) Changes in family composition

A total of 295 species from 68 families were recorded in 2005. Seven to eight years after the initial survey, the species count decreased by seven and the family count by one (Table 3.3). Among the four different locations, Binh Dinh had the largest species and family count on two occasions (2005 and 2012/2013). Interestingly enough, there was a regional family (Lamiaceae) in Ha Tinh. There were likewise three, two, and four families that respectively appeared only in Thua Thien Hue (Myrsinaceae, Oxalidaceae, Podocarpaceae), Binh Dinh (Oxalidaceae, Podocarpaceae), and Khanh Hoa (Cupressaceae, Lythraceae, Rhamnaceae, Zingiberaceae).

Lauraceae, Clusiaceae, and Ulmaceae were the dominant families in Ha Tinh, whereas Myrtaceae, Lauraceae, and Sapindaceae constituted the dominant families in Thua Thien Hue. In Binh Dinh, the dominant families were Dipterocarpaceae, Myrtaceae, and Fagaceae, in contrast with Khanh Hoa, where the dominant families were Annanoaceae, Myrtaceae, and Ebenaceae.

26 out of 68 families occurred at the four sites in 2005, among them Annonaceae, Apocynaceae, Bignoniaceae, Burseraceae, Caesalpiniaceae, and Clusiaceae. In the second measurement, this number was reduced to 25 out of 67 families as a result of the loss of Tiliaceae in Ha Tinh.

3.2.3.2 Diversity profile

a) Changes in dichotomous type

The values of the Δ_β diversity profiles for the four sites in 2005 and 2012/2013 changed slightly (Figure 3.8). On the one hand, Thua Thien Hue's Δ_β diversity profile crossed Binh Dinh's profile at $\beta = -0.1$ in both 2005 and 2012, explaining why the rankings of both the Δ_{SC} and Δ_{Sh} of the two provinces differ from that of the Δ_{Si} . On the other hand, Figure 3.8 clearly evidences reduction in Ha Tinh and Binh Dinh's total species count, from a respective 113/131 species to 104/125.

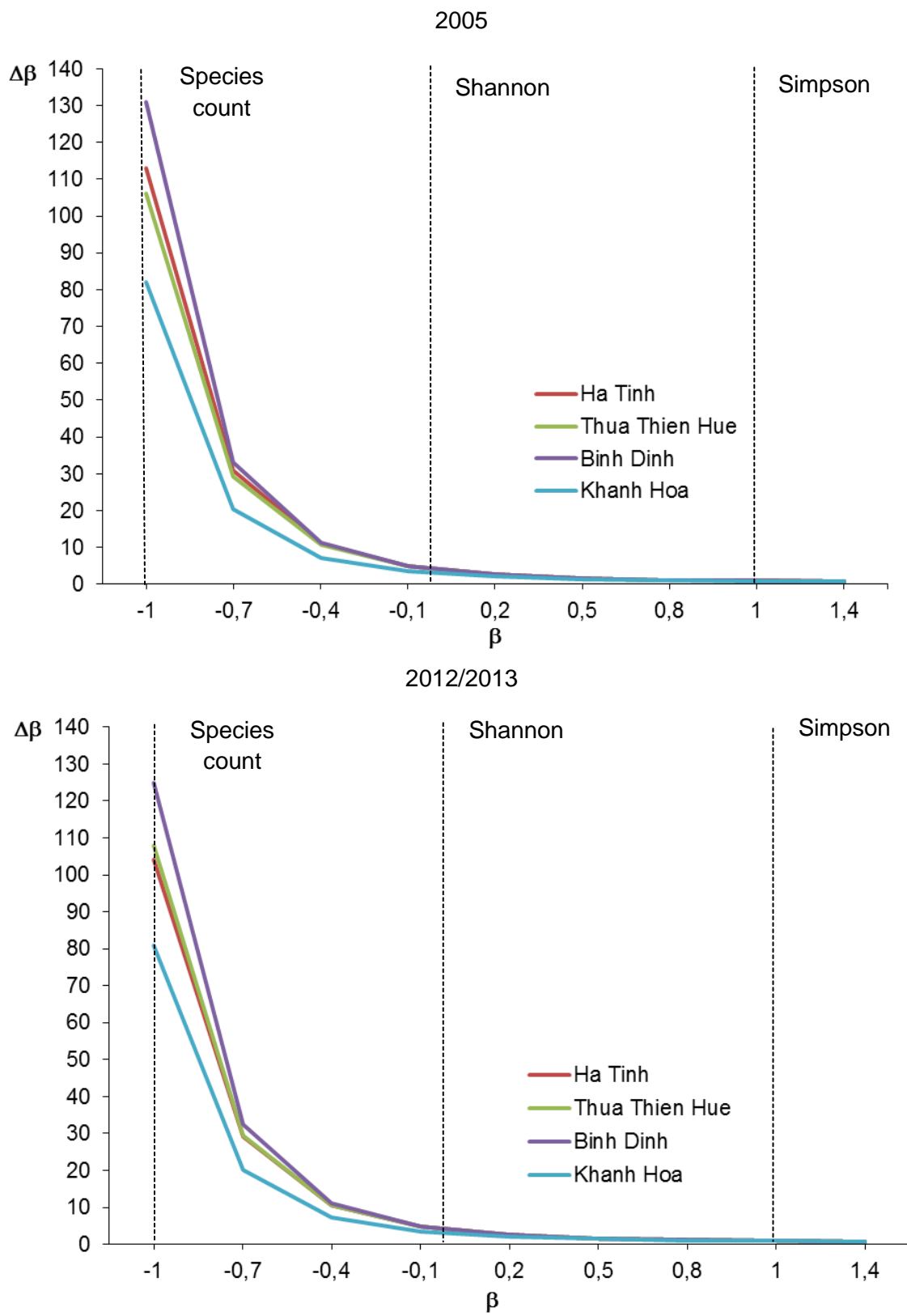
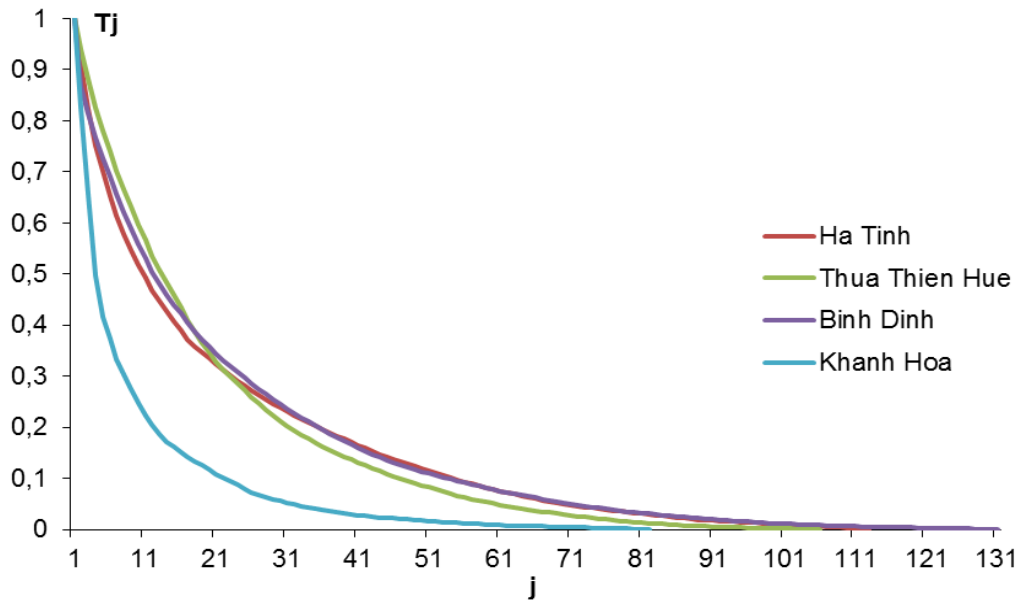


Figure 3.8 The $\Delta\beta$ -profiles for four provinces in 2005 and 2012/2013

b) Rank type

There was little difference between 2005 and 2012/2013 in the T_j -profiles (Figure 3.9). In both 2005 and 2012/2013, Thua Thien Hue's profile is above Binh Dinh's for j from 1 to 14; for j larger or equal to 15, Thua Thien Hue's profiles were below Binh Dinh's. The profile of Ha Tinh also intersects those of the latter. Consequently, there is no intrinsic diversity ordering between these three sites. The final conclusion was that the plots in Thua Thien Hue, Binh Dinh and Ha Tinh are intrinsically more diverse than those of Khanh Hoa.

2005



2012/2013

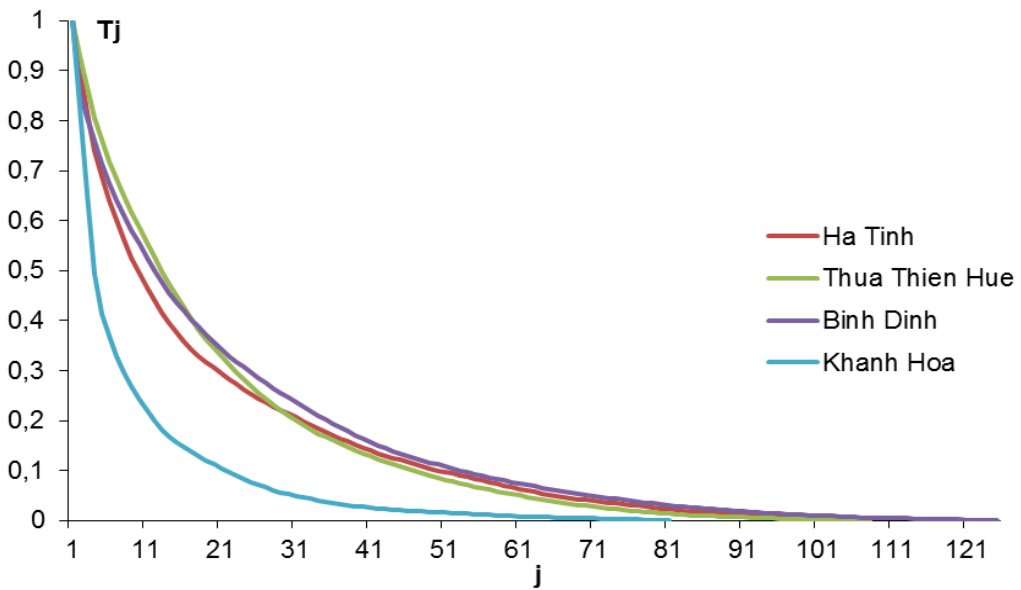


Figure 3.9 Right tail-sum T_j -profiles for the four provinces in 2005 and 2012/2013

3.2.3.3 Species-area relations

Of the three equations used (Exponential, Power, and Logistic), the species-area data was best fitted by the Power function with an R^2 varying from 0.93 to 0.99 (2005) and

0.86 to 0.99 (2012/2013).

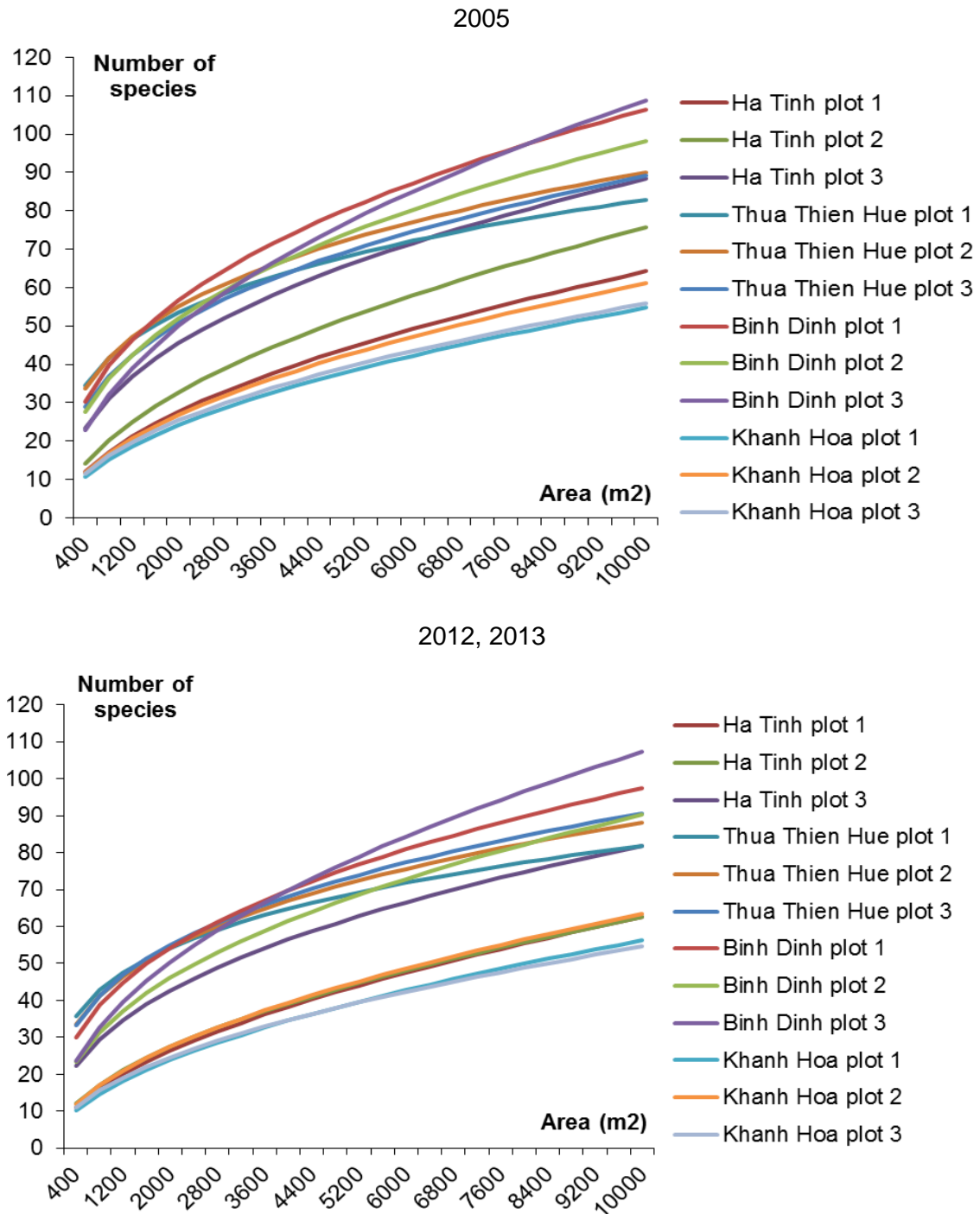


Figure 3.10 Species-area curves fitted by the Power function for 12 plots from four provinces in the years 2005 and 2012/2013

Figure 3.10 demonstrates two obvious changes in the 12 curves between 2005 and 2012/2013: first, three of the five lowest estimated curves, namely of Ha Tinh plots 1 and 2 and Khanh Hoa plot 2 became closer; second, the rank between Thua Thien Hue plot 2 and Binh Dinh plot 2 changed. In 2012 and 2013, 12 species-area curves are clearly classified into two groups, where group 1 consists of Ha Tinh plot 3, Binh Dinh, and Thua Thien Hue, group 2 is made up of Ha Tinh plots 1 and 2 and Khanh Hoa. In the graph of the second inventory, the most interesting point was that because of the disappearance of five species (*Bischofia javanica* Bl., *Craibiodendro scleranthum*, *Cratoxylon formosum*, *Elaeocarpus grandifloras*, and *Ficus racemosa*) in Binh Dinh plot 2, the plot's estimated curve was brought down to below that of Thua Thien Hue plot 2, despite the fact that the number of tree species in the latter was lower than that of the former. In similar fashion - and due to the death of two species in Ha Tinh plot 1 (*Armesiondendron chinense* and *Microcos paniculata*), 10 species in plot 2 (*Actinodaphne pilosa*, *Annona squamosa*, *Aphanamixis polystachya*, *Baccaurea sapida*, *Croton tigilium*, *Cryptocarya annamensis*, *Machilus platycarpa*, *Michelia mediocris*, *Oroxylum indicum*, and *Pavieasia annamensis*), and one species in Khanh Hoa plot 2 (*Lithocarpus ducampii*), Ha Tinh plots 1 and 2 and Khanh Hoa plot 2 became closer than in 2005. In addition, the largest number of species per hectare in Binh Dinh plot 3 was 102 in 2005 and 101 in 2013, whereas only 46 (2005) and 47 (2012) species were found in Khanh Hoa plot 1, the result of the high densities of *Syzygium wightianum*, *Diospyros sylvatica*, and *Enicosanthellum* sp.

As was expected for all sample plots, the number of tree species continuously increased with increasing the area size. The species-area curves for the four locations did not reach their asymptote at the one hectare plot size, which means that one could expect to record new tree species if the sample area would be further increased beyond 10,000 m².

3.3 Conclusion

3.3.1 Forest structures

Data from the two surveys reveal relatively stable ecological conditions, with only minor fluctuations evident in density, diversity indices, and diversity profile.

A total of 12 plots were surveyed and all stems ≥ 6 cm *DBH* were measured. Altogether, 10,856 (in 2005) and 10,300 (in 2012/2013) live stems ≥ 6 cm *DBH* were encountered, representing a respective 295/288 species in 68/67 families.

We examined the horizontal and vertical stand structural characteristics of tropical rainforests in Vietnam based on the relative frequency distributions of the *DBH*, the number of species per *DBH* class, the total tree height, and height-*DBH* relations. The distributions denote that stands are developing or expanding, and regeneration in the forest is present.

In regard to height-*DBH* relations, the Chapman-Richards model performed mostly better than other models. There were relatively little differences between height-*DBH* relationships of the two groups ($IVI \geq 5\%$ and $IVI < 5\%$) over large ranges of diameters. Only in Thua Thien Hue and Khanh Hoa the height curves of the important species were above those of the less important species, mainly for the larger diameters. Between the three different stories, particularly between super- and overstory, height curves varied more. Summarizing the results of stratified height curve modelling, one can conclude that individual height curves for stories, at least for the superstory and the pooled over- and understory, lead to higher precision of tree height estimation, but important and less important tree species may be pooled without remarkable loss in precision.

3.3.2 Tree species diversity

Tree species diversity in the present study varies greatly from place to place, which may be mainly accounted for by taking variation in biogeography, habitat, and disturbance into consideration (Whitmore, 1998). Differences in terrain, gradient, and slope direction can cause the changes to the soil, water, and microclimate, which in turn are reflected in the varying adaptability of the assorted species.

While diversity indices have been commonly used in ecological research, they remain problematic in that different indices may rank communities inconsistently (Liu *et al.*, 2007). This issue can be mediated by the use of diversity profile methods, the output of which is a diversity profile in graphical form for each stand being compared. In the present study, we found that diversity profile methods (e.g., dichotomous type, rank type) provided a more stringent test of diversity ordering than did diversity indices; as such, we recommend diversity profiles as the method of preference when comparing tree species diversity among forest stands. In our case, when arranging the intrinsic diversity ordering, the conclusion was that intrinsic diversity of plots in Thua Thien Hue, Binh Dinh and Ha Tinh is larger than that of the Khanh Hoa plots.

In our study, the total number of species increased in tandem with the area, which can be explained via the influence of environmental heterogeneity on the species-area relationship. Scheiner *et al.* (2000) stated that as area increases, more types of environments are likely to be encountered. If species are non-uniformly distributed with regard to environments, then the number of tree species encountered will increase with area. In this case, the species-area curve will reach an asymptote only if the number of environments reaches an asymptote at some spatial scale.

Literature cited

1. Alexandros, A.A., Burkhart, H.E., 1992. An evaluation of sampling methods and model forms for estimating height-diameter relationships in Loblolly Pine plantations. *Forest Science* 38, 192-198.
2. Archibald, E.E.A., 1949. The specific character of plant communities. II. A quantitative approach. *Journal of Ecology* 37, 260-274.
3. Arrhenius, O., 1921. Species and area. *Journal of Ecology* 9, 95-99.
4. Barkman, J.J., 1989. A critical evaluation of minimum area concept. *Vegetatio* 85, 89-104.

5. Cottam, G., Curtis, J.T., 1956. The use of distance measurement in phytosociological sampling. *Ecology* 37, 451-460.
6. Curtis, R.O., 1967. Height-diameter and height-diameter-age equations for second-growth Douglas-Fir. *Forest Science* 13, 365-375.
7. Fang, Z., Bailey, R.L., 1998. Height-diameter models for tropical forests on Hainan Island in southern China. *Forest Ecology and Management* 110, 315-327.
8. Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., Franca, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patino, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodte, F., Sonké, B., Taedoumg, H.E., Tan, S., White, L., Wöll, H., Lloyd, J., 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences* 8, 1081-1106.
9. Gadaw, K., Ying, H.G., 2007. Can the tree species-area relationship be derived from prior knowledge of the tree species richness? *Forestry Studies| Metsanduslikud Uurimused* 46, 13–22.
10. Gleason, H.A., 1922. On the relation between species and area. *Ecology* 3, 158-162.
11. Gleason, H.A., 1925. Species and area. *Ecology* 6, 66-74.
12. Fang, Z., Bailey, R.L., 1998. Height-diameter models for tropical forests on Hainan Island in southern China. *Forest Ecology and Management* 110, 315-327.

13. Hamilton, A.J., 2005. Species diversity or biodiversity? *Journal of Environmental Management* 75, 89-92.
14. He, F., Legendre, P., 1996. On species-area relations. *American Naturalist* 148, 719-737.
15. Huang, S., Titus, S.J., 1992. Comparison of nonlinear height-diameter functions for major Alberta tree species. *Canadian Journal of Forest Research* 22, 1297-1304.
16. Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52, 577-586.
17. Lalfakawma, 2010. Disturb and perish, conserve and flourish-regenerating forests: a review. *Science vision* 10, 3-7.
18. Lepě, J., Stursa, J., 1989. Species-area curve, life history strategies, and succession: a field test of relationships. *Vegetatio* 83, 249-257.
19. Liu, C., Whittaker, R.J., Ma, K., 2007. Unifying and distinguishing diversity ordering methods for comparing communities. *Population Ecology* 49, 89-100.
20. Lomolino, M.V., 2000. Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* 27, 17-26.
21. Naughton-Treves, L., Weber, W., 2010. Human dimensions of the African rain forest in African rain forest ecology and conservation: an interdisciplinary perspective. Yale University, 568 pp.
22. Palmer, M.W., White, P.S., 1994. Scale dependence and the species-area relationship. *American Naturalist* 144, 717-740.
23. Patil, G.P., Rao, C.R., 1994. *Handbook of Statistics*. Volume 12, Elsevier Science B.V., 927 pp.

24. Pielou, E.C., 1966. Species diversity and pattern diversity in the study of ecological succession. *Journal of Theoretical Biology* 10, 370-383.
25. Richards, P.W., 1996. *The tropical rain forest*. Second edition, Cambridge University Press, 575 pp.
26. Scheiner, S.M., Cox, S.B., Willig, M., Mittelbach, G.G., Osenberg, C., Kaspari, M., 2000. Species richness, species-area curves and Simpson's paradox. *Evolutionary Ecology Research* 2, 791-802.
27. Schomaker, M.E., Zarnoch, S.J., Bechtold, W.A., Latelle, D.J., Burkman, W.G., Cox, S.M., 2007. *Crown-condition classification: A guide to data collection and analysis*. General technical report SRS-102. Asheville, NC: United States, Department of Agriculture, forest service, Southern Research Station, 92 pp.
28. Tjørve, E., 2003. Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography* 30, 827-835.
29. Whitmore, T.C., 1975. *Tropical rain forests of the Far East*. Clarendon Press, Oxford.
30. Whitmore, T.C., 1998. *An introduction to Tropical Rain Forests*, 2nd Edition. Oxford University Press, NewYork.
31. Yeshitela, K., 2008. *Effects of anthropogenic disturbance on the diversity of foliicolous lichens in tropical rainforests of East Africa: Godere (Ethiopia), Budongo (Uganda) and Kakamega (Kenya)*. PhD thesis, Koblenz-Landau University.

Chapter 4 Diameter increment

4.1 Data analysis

4.1.1 Local growth equations

a) Response variable

Based on the available literature on growth models for mixed tropical forests (e.g. Vanclay, 1994), there are several types of functions that can be used for modelling diameter increment including empirical equations, theoretical functions and probabilistic functions. Growth can be modelled by using either diameter or basal area. Some modelers prefer using basal area to diameter because basal area provides higher values of coefficient of determination (R^2) (Bella, 1971). However, the precision of diameter increment equations is demonstrated to be the same as those of basal area increment (West, 1980; Wykoff, 1990).

It is convenient to model diameter increment directly. Periodic annual diameter increment was used as a dependent variable, because 8 of the 12 plots were remeasured in 2012 and the 4 others in 2013. It was calculated as:

$$ADI = \frac{DBH_1 - DBH_0}{t_1 - t_0} \quad (4.1)$$

where :

ADI is periodic annual diameter increment (cm)

DBH_1 and t_1 are diameter at breast height and time at the end of the growth period, respectively

DBH_0 and t_0 are diameter at breast height and time at the beginning of the growth period, respectively

b) Explanatory variables

Diameter increment models generally contain site quality, silvicultural treatment, tree size, species and competition indices (Wykoff, 1990).

With natural tropical rainforest stands, some variables such as age, top height and site quality (comprising soil, precipitation and temperature) are usually not available. In addition, these plots are permanent plots and no treatment was recorded between two measurements. Consequently, site quality and silvicultural treatment variables were excluded in the growth equation.

Some studies, for instance Zhao (2003), pointed out that tree size (initial diameter at breast height (*DBH*)) could be a better independent variable for growth models in mixed species stands than tree age. Initial diameter has been commonly utilized in modeling individual tree growth in previous researches, namely Wykoff (1990), Vanclay (1995), Monserud *et al.* (1996), and Lessard *et al.* (2001). Furthermore, some authors used both *DBH* and squared *DBH* in the growth equations, such as Monserud and Sterba (1996), whereas some others applied $\log(DBH)$ and DBH^2 (Wykoff, 1990; Hann *et al.*, 2006). Zhao (2003) developed diameter increment models with *DBH*, DBH^2 and the reciprocal diameter (DBH^{-1}).

There are a huge number of tree species in natural tropical rainforests. Several species appear more frequently, some occur with only low frequency (Zhao, 2003). Moreover, some may have similar growth rates, and some may have definitely different growing patterns. For that reason, species might be aggregated into some groups to reduce the number of growth models and to avoid the need for adding data for species with insufficient number of observations. Several ways to group species in mixed-species forest stands have been suggested using ecophysiological groups (Swaine and Whitmore, 1988; Chai and LeMay, 1993), commercial groups (Lahoreau *et al.*, 2002), dynamic process groups (Gourlet-Fleury *et al.*, 2005) or statistical methodologies (Meldahl *et al.*, 1985; Vanclay, 1991; Finegan, B., *et al.*, 1999; Philips *et al.*, 2002; Zhao, 2006). Every method has two sides, both advantages and disadvantages. Since there was no obvious and reasonable grouping, when we clustered individual species' growth models for our study, simply the importance value index (*IVI*) was used to determine a group of most important species. Species importance value index was computed as the average of relative density, relative frequency and relative

dominance. That means the *IVI* for a tree species covers three ecological parameters – density, frequency and basal area (Giliba *et al.*, 2011; Razavi *et al.*, 2012). Ecologically, density and frequency determine the distribution and frequency patterns of a species within the population whereas basal area measures the area captured by the stems of trees (Giliba *et al.*, 2011). Important tree species having $IVI \geq 5\%$ in pooled data from three plots in each province were utilized to model periodic annual diameter increment.

The competitive interactions among tree species makes the tropical forests become a very complex ecosystem. The first interaction is intra-specific (competition among trees of the same species) and the second one is inter-specific (competition among trees of different species) (Weiskittel *et al.*, 2011). One of the first approaches to solve the interaction among tree species is distance-dependent.

Distance-dependent competition indices were used in numerous research works (Zhao, 2003). However, with tropical forests, this distance-dependent competition index necessitates time-consuming measurement of tree coordinates. In this situation, stand basal area or subplot basal area become an ideal measure in crowded forest stands, because it combines both tree size and density (Weiskittel *et al.*, 2011), the density itself is not a sufficient indicator of competition (Zeide, 2005). According to Zhao (2003), stand basal area and basal area percentage of species were good competition indices.

The competition among trees of the same species also can be characterized by one-sided and two-sided competition (Zhao, 2003; Pukkala, 2013). In two-sided competition, stand basal area has been commonly used (Cao, 2000; Hann and Hanus, 2002; Zhao, 2006; Pukkala, 2013).

One-sided competition is expressed by the basal area in larger trees (Lessard *et al.*, 2001; Sterba *et al.*, 2002) because it is an absolute measurement, easy to calculate and often well correlated with growth (Weiskittel *et al.*, 2011). Vanclay (1991) also showed that overtopping basal area (the basal area of stems the diameter of which is greater than that of the subject tree) could become a useful predictor for diameter increment in tropical forests.

In this study, there were four plots having coordinates of each tree, therefore, an R code was applied to calculate overtopping basal area and overtopping diameter corresponding to circular plots with a 2 m, 5 m, 7 m and 10 m radius around the subject tree.

With individual species, all important species and others in each province, the backward elimination method was used to provide an initial screening of the independent variables when a large number of variables exists. This is one of several computer-based iterative variable-selection procedures. It starts by developing a full model containing all the candidate variables. Then, based on coefficient significance $\alpha = 0.05$, at each step the variable with highest p -value greater than 0.05 is removed from the model, and another regression model is developed with the remaining independent variables. The backward elimination continues until all independent variables remaining in the model have p -values less than 0.05. The advantage of backward elimination is that the decision maker has the opportunity to look at all the predictors in the model before removing the variables that are insignificant.

A typical function is usually used to model diameter increment comprising size, competition and site (Wykoff, 1990). However, as mentioned previously, site quality is unavailable. Therefore, the periodic annual diameter increment model was built as follows:

$$\ln ADI_k = \beta_0 + \beta_1 \text{tree size} + \beta_2 \text{competition indices} + \varepsilon_k \quad (4.2)$$

where:

$\ln ADI_k$ is the logarithm of periodic annual diameter increment for the k^{th} tree;

$\beta_0, \beta_1, \beta_2$ are the intercept and slopes;

tree size presents the logarithm of diameter at breast height in 2005 for the k^{th} tree ($\ln DBH_{2005k}$);

competition indices expresses the log-transformation of subplot basal area, stand basal area, ratio of basal area of k^{th} tree to subplot basal area, overtopping basal area and overtopping diameter;

ε_k is the residual, $\varepsilon_k \sim N(0, \sigma^2)$.

The ordinary least squares estimation was applied to fit the growth model by using Statistica 10.0.

4.1.2 Comparing models based on rounded and unrounded diameters

Diameter measurements at breast height on eight plots in 2005 and 2012 were rounded to the next integer value on the cm-scale, however, on four plots of four locations in 2013 they were unrounded. Before using the pooled data of these two data sets with rounded data, the raw data (rounded at two digits after decimal point) and the rounded data (to an integer) should be compared to assess effects of rounding on the resulting models. Species showing the largest differences between the two intercepts and between the two slopes in the growth model (4.3) were selected, and then their scatter-plots with confidence bands were evaluated. 8-year diameter increment was used in that comparison, because the data set came exclusively from the measurement campaign in 2013.

$$\ln DI_k = \beta_0 + \beta_1 \text{tree size} + \varepsilon_k \quad (4.3)$$

where:

$\ln DI_k$ is the logarithm of 8-year diameter increment for the k^{th} tree, and 8-year diameter increment was calculated by the formula

$$DI_k = DBH_{2013k} - DBH_{2005k} \quad (4.4)$$

DBH_{2005k} and DBH_{2013k} are diameter of the k^{th} tree in 2005 and 2013, respectively;

tree size was defined in 4.1.1.

4.1.3 Variability of growth models among plots and provinces for selected species

Since one important species occurred on all plots in four locations, and three others appeared on all plots in three provinces, a model using plot and province as random effects was used in order to study the between plot and between province variation of diameter increment.

a) Linear mixed effects model approach

Linear mixed effects models include fixed effects and random effects. Similar to many other types of models, they represent a relationship between a dependent variable and some of the covariates that have been measured or observed together with the dependent (Bates, 2010). To illustrate, the fixed effects interpret the relations among response and explanatory variables, whereas random effects can explain variation associated with a sampling unit (Lhotka and Leowenstein, 2011). The “effects” in the random - effects term are related to the individual experimental units sampled from the population (Pinheiro and Bates, 2004) on one or several levels. They introduce correlations between measurement units from a higher level unit into the model, for example correlations between diameter increment of trees from the same sample plot, and can be attached to different model parameters.

Linear mixed effects models with random intercepts, random intercepts and random slopes, and nested random effects were evaluated. There were three plots in each province, thus, plots within province were considered as a nested random effect. Nested random effects allow for different intercepts and slopes at the level of plots within provinces.

b) Model fitting

To evaluate whether linear mixed effects models improved model fit, a pure fixed-effects model based on the least squares method was compared with different mixed effects models. The models were compared by using fit criteria following the Akaike

Information Criterion (AIC) and the Bayesian Information Criterion (BIC). The model with the lowest AIC and BIC was preferred (Pinheiro and Bates, 2000).

Nine linear mixed effects models were employed in this chapter as follows:

$$\ln ADI_{jk} = (\beta_0 + \beta_j) + \beta_1 \ln DBH_{2005jk} + \varepsilon_{jk} \quad (4.5)$$

$$\ln ADI_{jk} = \beta_0 + (\beta_1 + \beta_j) \ln DBH_{2005jk} + \varepsilon_{jk} \quad (4.6)$$

$$\ln ADI_{ik} = \beta_0 + (\beta_1 + \beta_i) \ln DBH_{2005ik} + \varepsilon_{ik} \quad (4.7)$$

$$\ln ADI_{jk} = (\beta_0 + \beta_j) + (\beta_1 + \beta_j) \ln DBH_{2005jk} + \varepsilon_{jk} \quad (4.8)$$

$$\ln ADI_{ijk} = (\beta_0 + \beta_i + \beta_{ij}) + \beta_1 \ln DBH_{2005ijk} + \varepsilon_{ijk} \quad (4.9)$$

$$\ln ADI_{ijk} = \beta_0 + (\beta_1 + \beta_i + \beta_{ij}) \ln DBH_{2005ijk} + \varepsilon_{ijk} \quad (4.10)$$

$$\ln ADI_{ijk} = (\beta_0 + \beta_i + \beta_{ij}) + (\beta_1 + \beta_j) \ln DBH_{2005ijk} + \varepsilon_{ijk} \quad (4.11)$$

$$\ln ADI_{ijk} = (\beta_0 + \beta_j) + (\beta_1 + \beta_i + \beta_{ij}) \ln DBH_{2005ijk} + \varepsilon_{ijk} \quad (4.12)$$

$$\ln ADI_{ijk} = (\beta_0 + \beta_i + \beta_{ij}) + (\beta_1 + \beta_i + \beta_{ij}) \ln DBH_{2005ijk} + \varepsilon_{ijk} \quad (4.13)$$

where:

$\ln ADI_{jk}$, $\ln ADI_{ik}$, $\ln ADI_{ijk}$ presents the logarithm of periodic annual diameter increment for the k^{th} tree from the j^{th} plot, the k^{th} tree from the i^{th} province, and the k^{th} tree from the j^{th} plot within the i^{th} province;

β_i , β_j , β_{ij} represent the random effect variables of i^{th} province, j^{th} plot and j^{th} plot within i^{th} province, respectively. $\beta_i \sim N(0, \sigma^2_{\text{province}})$, $\beta_j \sim N(0, \sigma^2_{\text{plot}})$, and $\beta_{ij} \sim N(0, \sigma^2_{\text{plot within province}})$;

ε_{jk} , ε_{ik} , ε_{ijk} account for residual errors. $\varepsilon_{jk} \sim N(0, \sigma^2_{\varepsilon})$, $\varepsilon_{ik} \sim N(0, \sigma^2_{\varepsilon})$, $\varepsilon_{ijk} \sim N(0, \sigma^2_{\varepsilon})$.

Maximum likelihood (ML) estimation was used to produce fit statistics when comparing different linear mixed effects models. Finally, the restricted maximum likelihood (REML) estimation is used to fit parameter estimates and variance components for the preferred model, because such variance estimates are unbiased (Pinheiro and Bates, 2000).

The linear mixed effects models were fitted in R utilizing functions from both “nlme” and “lme4” packages (Bates, 2010).

4.2 Results

4.2.1 Local periodic annual diameter increment

Based on the backward selection procedure, non-significant predictor variables were dropped from the growth model (4.2). With the 8 plots remeasured in 2012, the explanatory variables consisted of the logarithm of initial diameter ($\ln DBH_{2005}$) as tree size, and three competition indices (log-transformation of the subplot basal area, stand basal area and ratio of basal area of k^{th} tree to subplot basal area). With the four other plots, where coordinates of each tree in the plot were available, log-transformation of the overtopping basal area and overtopping diameter were also examined. When fitting different forms of growth equations, the competition indices did not represent obvious trends in most cases. Specifically, they were sometimes positive, sometimes negative and mostly non-significant in the growth model, whereas a clear negative effect was expected. For example, a negative parameter for basal area of larger trees implied that an increase in competition leads to a reduction in the diameter increment.

Because of the indistinct and often nonsignificant competition effects, the function of the periodic annual diameter increment resulted in the reduced model (4.14), consisting of only one (mostly significant) predictor.

$$\ln ADI_k = \beta_0 + \beta_1 \ln DBH_{2005k} + \varepsilon_k \quad (4.14)$$

where:

$\ln ADI_k$ is the logarithm of periodic annual diameter increment for the k^{th} tree;
 β_0, β_1 are the intercept and the slope;
 ε_k is the residual, $\varepsilon_k \sim N(0, \sigma^2)$.

10,291 individuals on 12 plots in four locations belonged to 291 species, of which 52 species had an *IVI* equal or greater than 5%. The total number of trees of those important species was 6,588. In Ha Tinh, 17 out of 104 species were important species according to our definition, in Thua Thien Hue, Binh Dinh and Khanh Hoa 21 of 105, 17 of 127, and 12 of 81, respectively, were important species. A summary of descriptive statistics including number of observations (*n*), mean, standard deviation (Std.Dev.), minimum (Min), and maximum (Max) of periodic annual diameter increment and diameter for important species in all provinces are given in table 4.1.

Table 4.1 Summary of descriptive statistics for important tree species on 12 plots in four provinces. Diameter statistics are from 2005.

Province	Plot	<i>n</i>	Periodic annual diameter increment (cm/ha/year)				Diameter (cm)			
			Mean	SD	Min	Max	Mean	SD	Min	Max
Ha Tinh	1	318	0.42	0.09	0.14	0.71	20.50	10.12	6.00	64.00
	2	256	0.44	0.05	0.29	0.57	20.03	10.24	6.00	80.00
	3	194	0.48	0.15	0.25	1.38	19.12	12.49	6.00	76.00
		768	0.44	0.10	0.14	1.38	20.00	10.80	6.00	80.00
Thua	4	646	0.47	0.07	0.29	0.71	17.03	12.47	6.00	82.00
Thien	5	510	0.56	0.15	0.13	1.38	17.58	12.52	6.00	90.00
Hue	6	805	0.53	0.12	0.00	1.14	15.60	10.33	6.00	100.00
		1961	0.52	0.12	0.00	1.38	16.58	11.68	6.00	100.00
Binh Dinh	7	714	0.51	0.11	0.29	1.00	16.02	9.74	6.00	88.00
	8	600	0.54	0.15	0.29	1.00	17.96	13.73	6.00	100.00
	9	513	0.46	0.11	0.13	0.75	18.88	11.43	6.00	88.00
		1827	0.51	0.13	0.13	1.00	17.46	11.70	6.00	100.00
Khanh Hoa	10	661	0.47	0.09	0.14	0.86	17.78	12.64	6.00	78.00
	11	622	0.46	0.10	0.29	1.86	17.47	9.73	6.00	65.00
	12	750	0.51	0.13	0.13	1.00	17.49	9.97	6.00	72.00
		2032	0.48	0.11	0.13	1.86	17.58	10.84	6.00	78.00

For the plots, the density ranged from 194 trees (plot 3) to 805 trees (plot 6) per ha (Table 4.1), the mean periodic annual diameter increment (and standard deviation) varied from 0.42 (0.09) cm/year (plot 1) to 0.56 (0.15) cm/year (plot 5), and the mean diameters were 15.60 (10.33) cm (plot 6) to 20.50 (10.12) cm (plot 1). On the province level, these statistics ranged from 768 trees (Ha Tinh) to 2032 trees (Khanh Hoa) per ha, 0.44 (0.10) cm/year (Ha Tinh) to 0.52 (0.12) cm/year (Thua Thien Hue) and 16.58 (11.68) cm (Thua Thien Hue) to 20.00 (10.80) cm (Ha Tinh), respectively.

Each important species, all important species and all others in each province were fitted by the final equation (4.14). The summary of the intercept and slope parameters, related p -value and standard error of estimate from the pooled data in each province are listed in table 4.2 (graphs in the appendix).

Table 4.2 Number of trees, intercept, β_0 , and slope, β_1 , including p -values, and standard error of estimate from equation (4.14) for important species, all important species, and all others in four provinces. Nonsignificant $\ln DBH_{2005}$ and positive β_1 shaded.

Province	Species	n	β_0	p -value	β_1	p -value	s_{res}
	<i>Gironniera subaequalis</i>	115	-0.572	0.000	-0.104	0.022	0.220
	<i>Vatica odorata</i>	88	-0.459	0.000	-0.117	0.008	0.197
	<i>Calophyllum calaba</i>	99	-0.358	0.033	-0.170	0.003	0.261
	<i>Nephelium melliferum</i>	58	-0.450	0.006	-0.134	0.014	0.195
	<i>Knema cortiosa</i>	58	-0.774	0.002	-0.018	0.840	0.258
	<i>Alangium ridleyi</i>	45	-0.386	0.172	-0.153	0.098	0.260
	<i>Syzygium wightianum</i>	38	-1.160	0.000	0.118	0.056	0.156
	<i>Hydnocarpus ilicifolia</i>	40	-1.065	0.003	0.075	0.534	0.222
Ha Tinh	<i>Lithocarpus annamensis</i>	24	-0.447	0.018	-0.125	0.031	0.145
	<i>Wrightia annamensis</i>	30	-0.391	0.023	-0.158	0.010	0.151
	<i>Marcaranga denticulata</i>	41	-0.684	0.008	-0.026	0.801	0.213
	<i>Syzygium jambos</i>	26	-1.353	0.002	0.179	0.207	0.265
	<i>Cryptocarya lenticellata</i>	29	-0.683	0.001	-0.049	0.458	0.146
	<i>Hydnocarpus annamensis</i>	22	-0.124	0.596	-0.238	0.006	0.184
	<i>Cinnamomum obtusifolium</i> A. Chev	18	-0.656	0.221	-0.056	0.742	0.196

Table 4.2 (continued)

Province	Species	n	β_0	p-value	β_1	p-value	S_{res}
Ha Tinh	<i>Engelhardtia roxburghiana</i> Wall	10	-0.154	0.704	-0.252	0.047	0.198
	<i>Diospyros sylvatica</i>	25	-0.446	0.254	-0.132	0.399	0.224
	All important species	768	-0.510	0.000	-0.115	0.000	0.219
	All others species	390	-0.306	0.000	-0.186	0.000	0.236
Thua Thien Hue	<i>Canarium album</i>	169	-0.264	0.002	-0.160	0.000	0.251
	<i>Syzygium zeylancium</i>	173	-0.130	0.140	-0.198	0.000	0.235
	<i>Syzygium wightianum</i>	173	-0.281	0.002	-0.155	0.000	0.193
	<i>Symplocos poilanei</i>	136	-0.572	0.000	-0.037	0.382	0.210
	<i>Gyrocarpus americanus</i>	72	0.129	0.569	-0.277	0.000	0.319
	<i>Gironniera subaequalis</i>	117	-0.596	0.000	-0.022	0.674	0.215
	<i>Ormosia pinnata</i>	107	-0.372	0.001	-0.122	0.003	0.211
	<i>Syzygium chanlos</i>	99	-0.383	0.000	-0.110	0.008	0.192
	<i>Shorea roxburghii</i>	76	-0.108	0.562	-0.207	0.001	0.310
	<i>Machilus platycarpa</i>	101	-0.385	0.000	-0.121	0.003	0.190
	<i>Cassine glauca</i>	90	-0.409	0.001	-0.112	0.022	0.199
	<i>Cinnamomum parthenoxylum</i>	68	-0.366	0.006	-0.103	0.034	0.225
	<i>Eurycoma longifolia</i>	90	-0.906	0.000	0.112	0.155	0.188
	<i>Engelhardtia roxburghiana</i> Wall	44	-0.310	0.193	-0.120	0.109	0.274
	<i>Polyalthia nemoralis</i> DC	71	-0.720	0.000	0.056	0.521	0.205
	<i>Adina cordifolia</i>	68	-0.386	0.028	-0.099	0.137	0.197
	<i>Polyalthia cerasoides</i>	81	-0.610	0.002	-0.036	0.685	0.189
	<i>Knema tonkinensis</i>	72	-0.435	0.007	-0.095	0.137	0.193
	<i>Paranephelium spirei</i>	57	-0.013	0.955	-0.251	0.003	0.319
<i>Lithocarpus ducampii</i> Hickel et A.camus	37	-0.484	0.005	-0.065	0.220	0.192	
<i>Cinnamomum cambodianum</i>	59	-0.549	0.002	-0.058	0.372	0.207	
All important species	1960	-0.349	0.000	-0.127	0.000	0.227	
All others	916	-0.099	0.021	-0.214	0.000	0.263	

Table 4.2 (continued)

Province	Species	n	β_0	p-value	β_1	p-value	s_{res}
	<i>Parashorea chinensis</i> Wang Hsie	424	-0.269	0.000	-0.159	0.000	0.273
	<i>Syzygium zeylanicum</i>	166	-0.641	0.000	-0.022	0.535	0.231
	<i>Diospyros sylvatica</i>	140	-0.182	0.118	-0.212	0.000	0.230
	<i>Hopea pieriei</i>	139	-0.478	0.000	-0.086	0.085	0.246
	<i>Scaphium macropodum</i>	111	-0.353	0.004	-0.150	0.001	0.223
	<i>Quercus dealbatus</i>	86	-0.275	0.114	-0.163	0.009	0.261
	<i>Syzygium wightianum</i>	106	-0.405	0.013	-0.097	0.120	0.220
	<i>Lithocarpus ducampii</i> Hickel et A.camus	82	0.052	0.701	-0.278	0.000	0.229
Binh Dinh	<i>Nephelium melliferum</i>	84	-0.233	0.080	-0.183	0.000	0.216
	<i>Ilex rotunda</i> Thunb	80	-1.024	0.000	0.124	0.103	0.249
	<i>Hydnocarpus</i> <i>althemintica</i>	90	-0.698	0.000	-0.004	0.952	0.193
	<i>Intsia bijuga</i>	35	-0.270	0.262	-0.169	0.017	0.274
	<i>Dillenia scabrella</i> Roxb	51	-0.218	0.384	-0.186	0.026	0.329
	<i>Machilus bonii</i> H.Lec	68	-0.860	0.000	0.082	0.219	0.218
	<i>Melanorrhoea laccifera</i>	52	0.028	0.859	-0.261	0.000	0.227
	<i>Gironniera subaequalis</i>	67	-0.359	0.049	-0.146	0.042	0.204
	<i>Artocarpus rigidus</i>	46	0.313	0.195	-0.372	0.000	0.267
	All important species	1827	-0.333	0.000	-0.141	0.000	0.249
	All others	1177	-0.289	0.000	-0.157	0.000	0.240
	<i>Syzygium wightianum</i>	433	-0.573	0.000	-0.071	0.000	0.203
	<i>Diospyros sylvatica</i>	435	-0.489	0.000	-0.100	0.000	0.205
	<i>Encosanthellum</i> sp.	390	-0.321	0.000	-0.152	0.000	0.223
	<i>Saraca dives</i>	201	-0.053	0.574	-0.251	0.000	0.244
	<i>Nephelium melliferum</i>	99	-0.454	0.000	-0.110	0.010	0.212
	<i>Machilus bonii</i> H.Lec	106	-0.497	0.001	0.100	0.054	0.229
	<i>Polyalthia nemoralis</i> DC	76	-0.556	0.000	-0.073	0.036	0.169
Khanh Hoa	<i>Cinnamomum</i> <i>obtusifolium</i> A. Chev.	72	-0.612	0.000	-0.053	0.316	0.191
	<i>Ormosia balansae</i> Drake	69	-0.370	0.002	-0.139	0.002	0.185
	<i>Aphanamixis polystachya</i>	55	-0.065	0.773	-0.254	0.004	0.292
	<i>Rhamnus crenatus</i> Sieb	54	-0.970	0.000	0.077	0.076	0.149
	<i>Lucua mamona</i> Gaerten	42	-0.409	0.025	-0.130	0.044	0.210
	All important species	2032	-0.434	0.000	-0.117	0.000	0.215
	All others	447	-0.422	0.000	-0.117	0.000	0.192

The slope parameter β_1 of almost all individual important species, all important species and all others in each province had the expected sign – a negative regression coefficient (Table 4.2), suggesting the periodic annual diameter increment decreases with increasing tree diameter (Figure 4.1). However, the slope parameter was not significant for 28 of 67 individual important species, and none of the positive slope parameters was significant. Zero slope, which might be assumed for species having non-significant slopes, means that the periodic annual diameter increment of these species is constant over the entire range of diameters from 6 cm to 100 cm, and a simple growth model $\ln ADI_k = \beta_0 + \varepsilon_k$ or, equivalently, $ADI_k = \exp(\beta_0 + \varepsilon_k)$ holds.

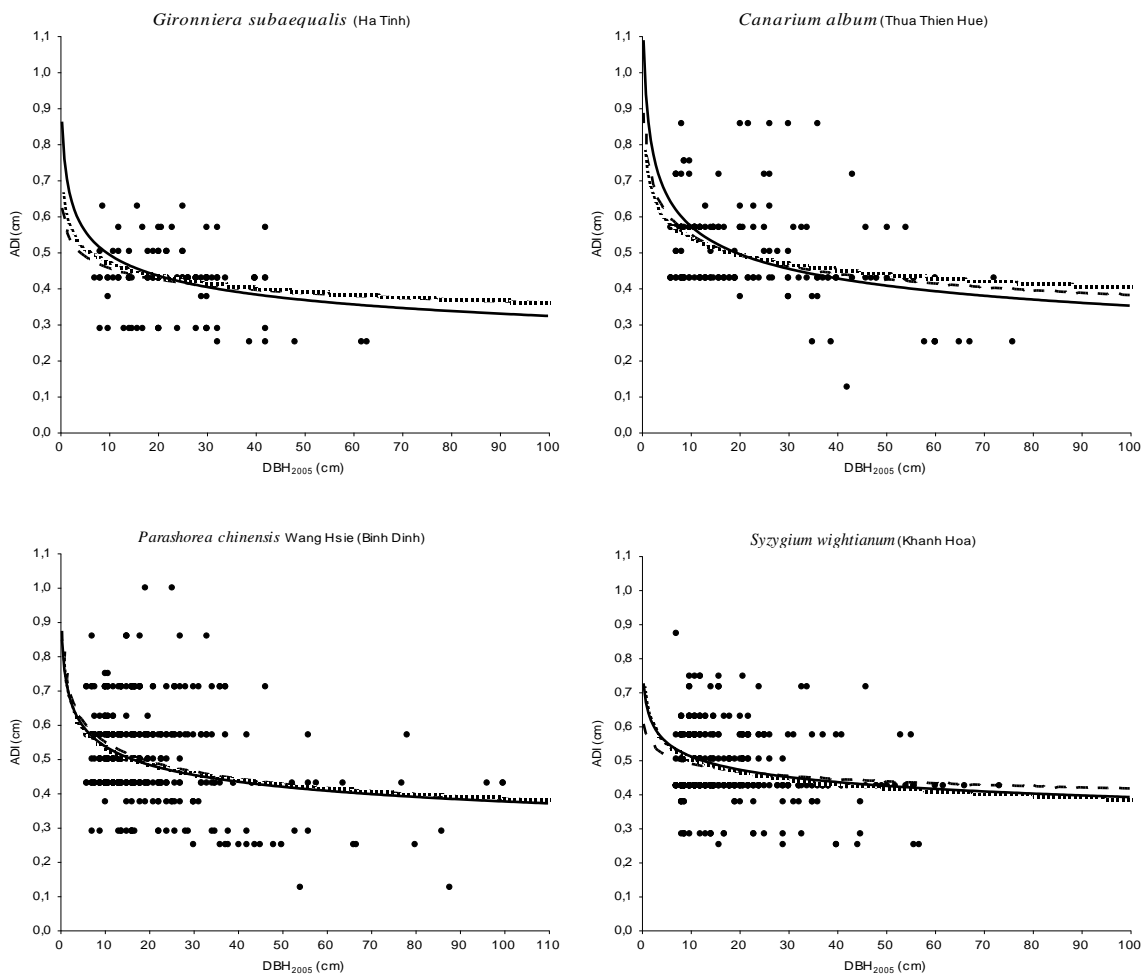


Figure 4.1 Periodic annual diameter increment of the most important tree species from each province. The black dots are observed values. The dashed line is the curve of an individual important species, the dotted line is the mean curve of all important species in that province, and the solid line is the mean curve of all other species in that province.

Figure 4.1 depicts the periodic annual diameter increments of an individual important tree species per province as examples, together with its increment model and with the models for all important species and all others in that province. All of them have negative slope parameters, and the according functions decreased with increasing tree size. The diameter increment did not reach a peak at a small diameter.

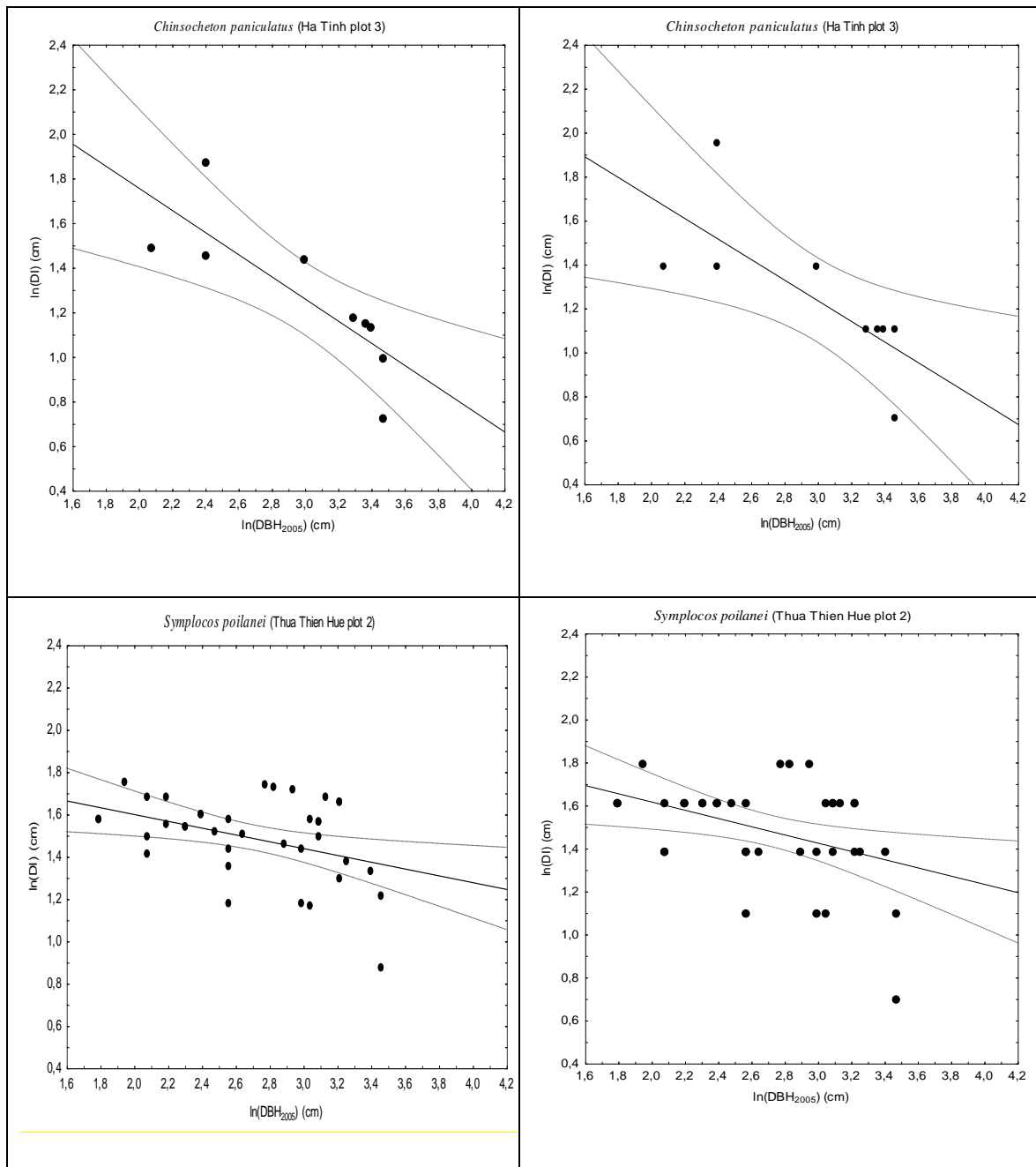
4.2.2 Comparing models based on rounded and unrounded diameters

In 4.2.1 we found that the simple linear regression model (4.14) is the most appropriate one for local regression of annual diameter increment on the diameter in 2005. There, we used the rounded diameter data on all plots in all provinces. In order to justify that, we assessed the accuracy of models based on the rounded data, by using scatter plots with confidence bands of the simple linear regression model (4.3) of both unrounded and rounded data. Because the real and rounded data came only from the plots measured in 2013, 8-year diameter increment was used instead of annual increment. After fitting individual species in each province, four species having the largest differences between estimated intercepts (β_0) and slopes (β_1) were chosen exemplarily (Table 4.3).

Table 4.3 Intercept and the slope from unrounded and rounded data of four species in four provinces

Province	Species	<i>n</i>	Unrounded values			Rounded values		
			β_0	β_1	s_{res}	β_0	β_1	s_{res}
Ha Tinh	<i>Chinsocheton paniculatus</i>	9	2.750	-0.496	0.208	2.643	-0.469	0.244
Thua Thien Hue	<i>Symplocos poilanei</i>	37	1.924	-0.161	0.179	2.001	-0.191	0.218
Binh Dinh	<i>Garcinia oblongifolia</i>	13	3.047	-0.309	0.192	2.039	-0.277	0.174
Khanh Hoa	<i>Saraca dives</i>	148	2.481	-0.612	0.215	2.871	-0.546	0.230

It is worth noting that the differences of the intercepts, slopes and the standard error of estimates between empirical and rounded data were negligible. 95% confidence bands of the fitted lines visualize the uncertainty of the intercept and slope in Figure 4.2 and revealed that there was no significant difference between regression lines of the two approaches. Therefore, we will work with the rounded data also in the following analyses.



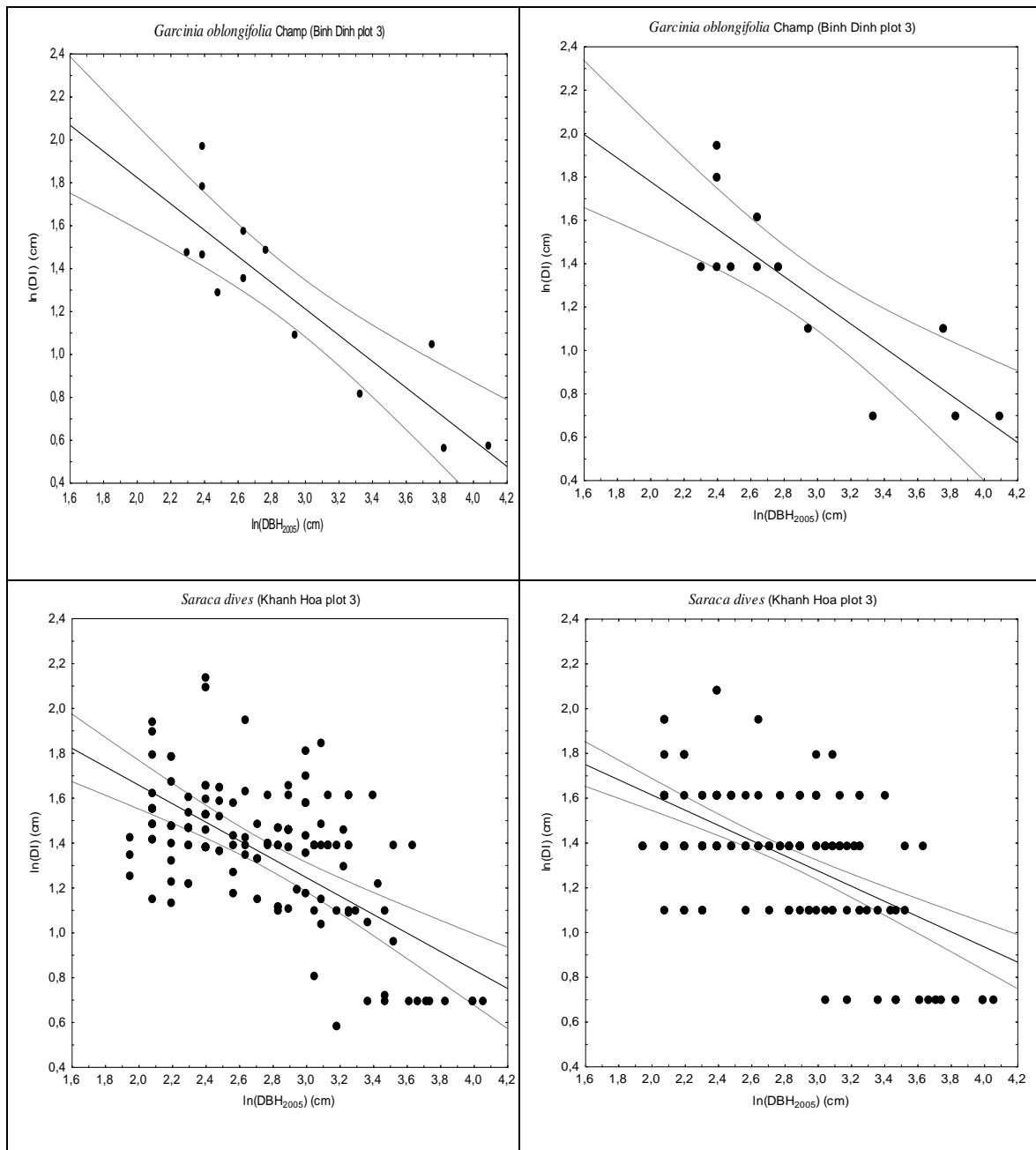


Figure 4.2 Comparing models for diameter increment (cm) between unrounded (left) and rounded (right) diameter values for individual species. The black dots are observed values. The solid line indicates regression model (4.14) fitted to an individual important species and its 95% confidence bands (the dashed lines).

4.2.3 Linear mixed effects models

In order to analyze the variation among growth models of the four provinces, we selected important tree species which occurred in all or at least in three provinces. *Syzygium wightianum* was the sole important species that occurred on all plots in all locations, whereas there were three others appearing in three different provinces including *Diospyros sylvatica*, *Gironniera subaequalis* and *Nephelium melliferum*.

Because of unreasonable and mostly non-significant trends of the competition effects, the simple linear mixed effects models from equations (4.5) to (4.13) were used, which only use $\ln DBH_{2005}$ as a covariate.

The comparison of model fit statistics (AIC, BIC, logLikelihood) using generalized least squares and nine linear mixed effects models as well as the pure fixed effect model (4.14) is given in Table 4.4. The results showed that the linear mixed effects model substantially improved model fit for the four tree species *S. wightianum*, *D. sylvatica*, *G. subaequalis* and *N. melliferum* compared to the simple (fixed effects) linear regression (4.14) proving that there is significant variation of growth functions among the plots.

Table 4.4 A comparison of AIC, BIC, and log-likelihood between the fixed effects model and the mixed effects models.

Species	<i>n</i>	Model	Model specification	df	AIC	BIC	logLik	Test	L.Ratio	p-value
<i>S. wightianum</i>	750	1	Fixed effects model (FM)	3	-245.62	-231.76	125.81	1 vs 5	100.61	< .0001
		2	FM + plot intercept	4	-305.41	-286.93	156.71	2 vs 5	38.81	3.73e-09 ***
		3	FM + plot slope	4	-294.93	-276.45	151.47	3 vs 5	49.30	1.98e-11 ***
		4	FM + prov. slope	4	-262.65	-244.17	135.33	4 vs 5	81.57	< 2.2e-16 ***
		5	FM + plot intercept + plot slope	6	-340.23	-312.51	176.11			
		6	FM + plots within prov. intercept	5	-304.12	-281.02	157.06	6 vs 5	38.11	6.69e-10 ***
		7	FM + plots within prov. slope	5	-293.47	-270.37	151.73	7 vs 5	48.76	2.89e-12 ***
		8	FM + plots within prov. intercept + plot slope	6	-311.02	-283.30	161.51	8 vs 5	29.21	< 2.2e-16 ***
		9	FM + plots within prov. slope + plot intercept	6	-311.02	-283.30	161.51	9 vs 5	29.21	< 2.2e-16 ***
		10	FM + plots within prov. intercept + plots within prov. slope	9	-335.23	-312.50	176.11	10 vs 5	1.11	0.7739

Table 4.4 (continued)

Species	<i>n</i>	Model	Model specification	df	AIC	BIC	logLik	Test	L.Ratio	p-value
<i>D. sylvatica</i>	600	1	Fixed effects model (FM)	3	-163.28	-150.09	84.64	1 vs 5	54.08	< .0001
		2	FM + plot intercept	4	-174.72	-157.13	91.36	2 vs 5	40.65	1.49e-09 ^{***}
		3	FM + plot slope	4	-169.86	-152.27	88.93	3 vs 5	45.50	1.32e-10 ^{***}
		4	FM + prov. slope	4	-161.28	-143.69	84.64	4 vs 5	54.08	1.81e-12 ^{***}
		5	FM + plot intercept + plot slope	6	-211.36	-184.98	111.68			
		6	FM + plots within prov. intercept	5	-172.72	-150.73	91.36	6 vs 5	40.65	1.82e-10 ^{***}
		7	FM + plots within prov. slope	5	-167.86	-145.88	88.93	7 vs 5	45.50	1.32e-10 ^{***}
		8	FM + plots within prov. intercept + plot slope	6	-186.83	-160.44	99.41	8 vs 5	24.54	< 2.2e-16 ^{***}
		9	FM + plots within prov. slope + plot intercept	6	-186.83	-160.44	99.41	9 vs 5	24.54	< 2.2e-16 ^{***}
		10	FM + plots within prov. intercept + plots within prov. slope	9	-205.36	-165.79	111.68	10 vs 5	0	1

Table 4.4 (continued)

Species	<i>n</i>	Model	Model specification	df	AIC	BIC	logLik	Test	L.Ratio	p-value
<i>G. subaequalis</i>	299	1	Fixed effects model (FM)	3	-48.80	-37.70	27.40	1 vs 5	51.55	< .0001
		2	FM + plot intercept	4	-76.73	-61.92	42.36	2 vs 5	21.62	2.02e-05 ^{***}
		3	FM + plot slope	4	-73.22	-58.42	40.61	3 vs 5	25.13	3.49e-06 ^{***}
		4	FM + prov. slope	4	-64.34	-49.54	36.17	4 vs 5	34.01	4.12e-08 ^{***}
		5	FM + plot intercept + plot slope	6	-94.35	-72.15	53.17			
		6	FM + plots within prov. intercept	5	-75.19	-56.69	42.60	6 vs 5	21.16	4.23e-06 ^{***}
		7	FM + plots within prov. slope	5	-71.73	-53.23	40.87	7 vs 5	24.62	7.00e-07 ^{***}
		8	FM + plots within prov. intercept + plot slope	6	-73.19	-50.99	42.60	8 vs 5	21.16	< 2.2e-16 ^{***}
		9	FM + plots within prov. slope + plot intercept	6	-73.23	-51.02	42.61	9 vs 5	21.12	< 2.2e-16 ^{***}
		10	FM + plots within prov. intercept + plots within prov. slope	9	-91.67	-58.36	54.83	10 vs 5	3.32	0.3451

Table 4.4 (continued)

Species	<i>n</i>	Model	Model specification	df	AIC	BIC	logLik	Test	L.Ratio	p-value
<i>N. melliferum</i>	241	1	Fixed effects model (FM)	3	-68.83	-58.38	37.42	1 vs 5	9.17	0.0271
		2	FM + plot intercept	4	-66.83	-52.89	37.42	2 vs 5	9.17	0.0102*
		3	FM + plot slope	4	-66.83	-52.89	37.42	3 vs 5	9.17	0.0102*
		4	FM + prov. slope	4	-67.00	-53.06	37.50	4 vs 5	9.00	0.0111*
		5	FM + plot intercept + plot slope	6	-72.00	-51.10	42.00			
		6	FM + plots within prov. intercept	5	-65.09	-47.66	37.54	6 vs 5	8.92	0.0028**
		7	FM + plots within prov. slope	5	-65.00	-47.58	37.50	7 vs 5	9.00	0.0027**
		8	FM + plots within prov. intercept + plot slope	6	-63.09	-42.18	37.54	8 vs 5	8.92	< 2.2e-16***
		9	FM + plots within prov. slope + plot intercept	6	-63.00	-42.09	37.50	9 vs 5	9.00	< 2.2e-16***
		10	FM + plots within prov. intercept + plots within prov. slope	9	-66.90	-35.54	42.45	10 vs 5	0.89	0.8268

Model 1: Fixed effects model using equation (4.14); model 2: equation (4.5) with the plots designated as random intercepts; model 3: equation (4.6) with the plots designated as random slopes; model 4: equation (4.7) with the provinces designated as random slopes; model 5: equation (4.8) with the plots designated as random intercepts and slopes; model 6: equation (4.9) with the plots within a province designated as nested random intercepts; model 7: equation (4.10) with the plots within a province designated as nested random slopes; model 8: equation (4.11) with the plots within a province designated as nested random intercepts and plots designated as random slopes; model 9: equation (4.12) with the plots within a province designated as nested random slopes and plots designated as random intercepts; model 10: equation (4.13) with the plots within a province designated as nested random intercepts and slopes.

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

For three of the four species considered (*S. wightianum*, *D. sylvatica*, and *G. subaequalis*), all nine types of linear mixed effects models had usually (except model 4 for *D. sylvatica*) lower AIC and BIC values than the fixed effects model (Table 4.4). Only for *N. melliferum*, only the mixed effects model with plots as random effects on intercepts and slopes (model 5) had a slightly lower AIC value compared with the fixed effects model. Thus, the best model in terms of AIC for all four species was, model 5. The BIC also led to model 5 as the best one, with the only exception *N. melliferum*, where the BIC of the fixed effects model was lowest. Moreover, there was no significant difference (p -value > 0.05) between model 5 and model 10, the most complex mixed effects model, for all four important species. Therefore, model 5 was selected as the final, most appropriate model for these species because it was simpler. The main result of this analysis is that it is unnecessary to include a province effect into the model if only plot effects on intercept and slope are considered. Thus the variation among plots is very large compared to the variation among provinces, despite the small distances between plots within a province and the comparably large distances between the provinces (Figure 4.3).

Model coefficients of the linear mixed effects model (model 5) by species are presented in Table 4.5.

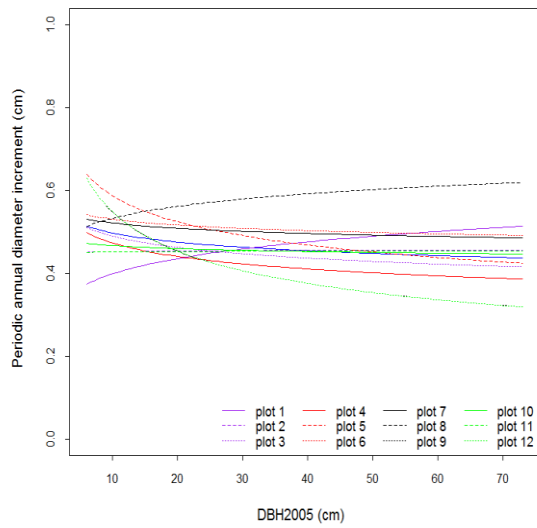
Table 4.5 Parameter estimates based on REML estimation for the periodic annual diameter increment by species

Species	Parameters (Fixed effects)				Variance components			% variation explained by the plot
	β_0	Std. error	β_1	Standard error	$\sigma^2_{\text{ran-in}}$	$\sigma^2_{\text{ran-slo}}$	σ^2	
<i>S. wightianum</i>	-0.549	0.138	-0.065	0.049	0.175	0.021	0.034	85.09
<i>D. sylvatica</i>	-0.449	0.151	-0.111	0.055	0.144	0.018	0.039	80.79
<i>G. subaequalis</i>	-0.419	0.199	-0.124	0.067	0.299	0.033	0.037	90.02
<i>N. melliferum</i>	-0.266	0.169	-0.179	0.058	0.199	0.023	0.039	85.12

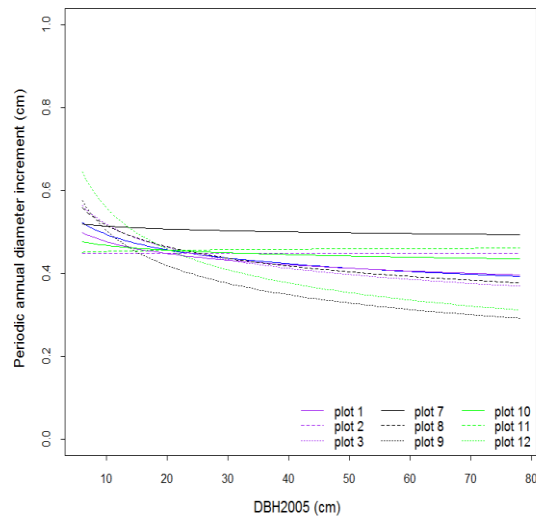
$\sigma^2_{\text{ran-in}}$ is the variance component for the random intercepts, and $\sigma^2_{\text{ran-slo}}$ the variance component for the random slopes at the plot level, σ^2 is the residual variance. The variation explained by the plot was calculated as the ratio of variances for random effects to the sum of the variances for random effects and residuals.

After fitting the mixed effects model (Table 4.5), the fixed effect parameter (β_1) was significant ($p < 0.05$) for *D. sylvatica* and *N. melliferum* and non-significant ($p > 0.05$) for *S. wightianum* and *G. subaequalis*. The sign of parameter β_1 was mostly negative, reflecting the decrease in ADI with increasing diameter (Figure 4.3). The plot accounted for a large amount of unexplained variation in ADI for the four species, ranging from 85.09% to 90.02% (Table 4.5). Four examples of the mixed model fit are depicted in Figure 4.4.

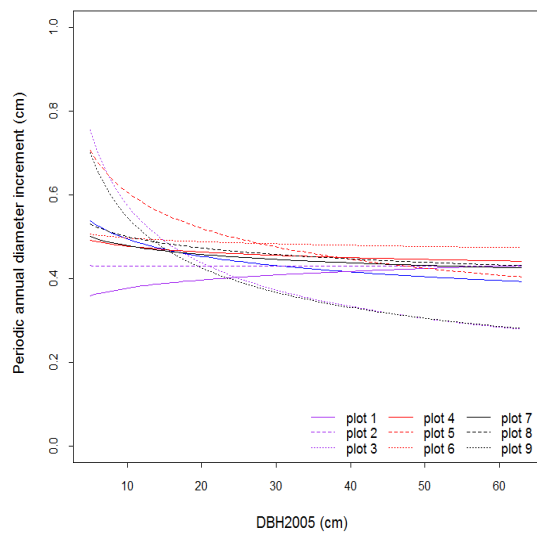
S. wightianum



D. sylvatica



G. subaequalis



N. melliferum

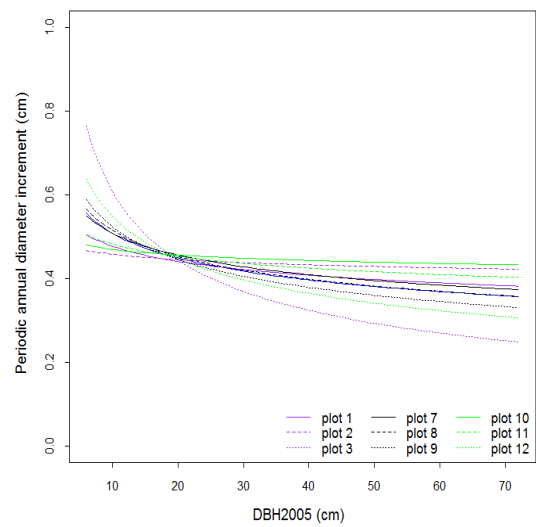


Figure 4.3 Periodic annual diameter increment for the four important species in each plot. The blue curve denotes the fixed effects, and the other colours show the mixed effects models for each plot.

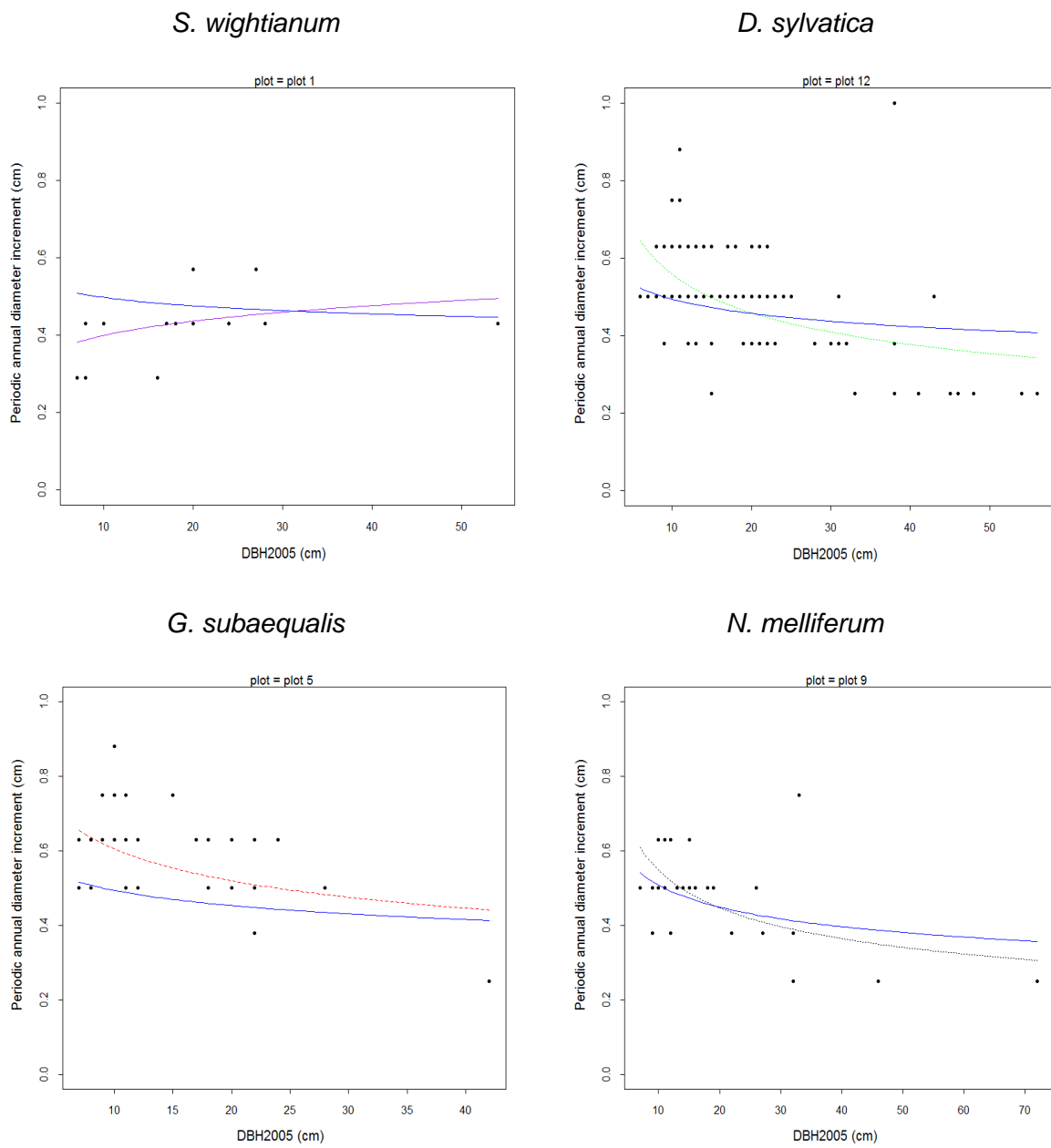


Figure 4.4 Periodic annual diameter increment for the four important species in four selected plots. The black dots are observed data on the plot. The blue, and other colour curves indicate the fixed effects, and the mixed effects models, respectively.

4.3 Discussion

Diameter growth models are one of the most basic and crucial components of forest growth models. They allow to describe the state of a tree at a future time and to estimate growth of an average tree of a given size (Bueno-López and Bevilacqua, 2013). Modeling the growth of tropical rainforest stands remains a difficult task because of the variety of interacting factors and the lack of suitable data. This study represents the first set of models for diameter increment of lowland evergreen rainforests in Vietnam. In this chapter, modeling the periodic annual diameter increment for individual important tree species was employed. The explanatory variable logarithm of initial diameter ($\ln DBH_{2005}$) had mostly an effect on diameter growth. The present study addressed a minor part of growth modeling for natural forests. It was found that (i) our attempt to use competition indices in the growth model remained unsuccessful, (ii) the rounded diameters were precise enough to model diameter increment and (iii) the use of linear mixed effects model for selected important species occurring on almost all plots was an improvement of the growth model and signified a first effort to evaluate microsite (plot) and large scale (province) effects for tropical rain forests in Vietnam.

4.3.1 Model structure

The total number of important species on 12 plots in four provinces was 52 species, and 6,588 trees. 17 important species were in Ha Tinh, whereas in Thua Thien Hue, Binh Dinh, and Khanh Hoa were 21, 17, and 12 important species, respectively. We found that the equation of the periodic annual diameter increment (4.14) comprising only one predictor, $\ln DBH_{2005}$, to be a significant regression model for about 47.1% to 75% important species in each province. With the remaining important species, a simple, namely constant growth model $ADI_k = \exp(\beta_0 + \varepsilon_k)$ was sufficient. The most frequently negative logarithmic relationship between initial diameter (DBH_{2005}) and the periodic annual diameter increment (ADI) implies that data are from stands, where the maximum growth rates occur for trees of lower diameter classes. This contrasts to a finding of Adame *et al.* (2014), who worked on plots in Puerto Rican secondary tropical forests, where a positive logarithmic relation between diameter and diameter growth was found. He explained that by young stand ages where trees have not reached yet

the maximum growth rate. These results were contrary to the findings for North Queensland rainforests in a study of Vanclay (1989), where tree diameter increment got its maximum at a younger age and then decreased slowly, as also observed in most cases of our study.

On the reduced data set of one plot per province we had also studied the influence of competition indices in the growth model, such as stand or subplot basal area, overtopping diameter, and overtopping basal area. For instance, stand basal area accounts for competition among reference trees and their neighbours, and overtopping basal area is considered as an indicator of the relative competitive position of a subject tree among its neighbours having greater diameter in a plot due to their one-sided competition for light (Wykoff, 1990). These competition indices mostly turned out to be non-significant in our study, whereas they were often found to be significant predictors of diameter increment in other tropical and subtropical rainforests (Vanclay, 1995; Kariuki, 2005, Adame *et al.*, 2014).

Site variables, such as elevation, aspect, precipitation, and soil fertility class were not included into the growth model, because they were either unavailable or did not vary enough between the three plots in a province, although they have been shown to affect stand-level growth responses in other studies (Kariuki, 2005). Other variables, such as moisture stress, saturated soil, and reduced solar radiation, can be effective at explaining variation in diameter increment; Puerto Rican forest trees are an illustration (Weaver, 1979). On the other hand, Adame *et al.* (2014) pointed out that the relationship between diameter increment and site characteristics (including precipitation, elevation, aspect, and soil fertility class) was insignificant. Similarly, Gourlet-Fleury and Houllier (2000), working in a lowland evergreen rain forest in French Guiana, showed that their attempt to include site information by the use of soil and topographical data in a diameter increment model was unsuccessful.

4.3.2 Comparing models based upon rounded and unrounded diameters

It is a frequent practice in tropical rain forests to round original data to integer values. This was also done in the 2005 inventory used in this study, as well as in the 2012

inventory carried out on two of the three plots in each province. Statistical analysis results indicated that the negligible difference between the real and rounded data cannot produce misleading models of diameter increment. Consequently, we felt free to round also the data collected in 2013 on only one plot in each province, which were of higher precision than those of 2012 and 2005, to an integer to get a consistent data set for modelling purposes.

4.3.3 Linear mixed effects model

Linear mixed effects models with plots as random effects on intercepts and slopes (equation 4.8) were chosen for the four important species *S. wightianum*, *G. subaequalis*, *D. sylvatica*, and *N. melliferum*, which occurred in at least three of the four provinces. As expected, the linear mixed effects model could in almost all cases account for random variation in intercepts and slopes of the periodic annual diameter increment models for four ubiquitous important species. Through the mixed effects model, the spatial correlation among trees on the same plot could be considered by fitting random effects for plot-to-plot variation (Pukkala *et al.*, 2009). The explained variance by the random plot effects varied from 85.09% to 90.02%. These results are consistent with other studies modeling diameter, or basal area increment using the mixed effects model, which also found that the random effects associated with the sampling unit (for instance, plot) improved model fit (Pukkala *et al.*, 2009; Pokharel and Dech, 2012; Adame *et al.*, 2014). The variation of the plot-level random effects is possibly related to the effects of both microsite and individual genetic variability (Pokharel and Dech, 2012). Furthermore, sources of unexplained variation possibly arose from a pure error which no model can explain (Draper and Smith, 1998), and failure to include variables that affect tree growth in the model such as more appropriate competition indices or environmental factors which were not attempted to be measured in the inventory data. Because the plots in each province are neighbouring plots, located on the same commune, they are very close to each other. Moreover, climate data are typically assembled at the nearest meteorological station to the plot, therefore, environmental variation does not differ remarkably from plot to plot. The large variation in annual diameter increment may be explained, at least partially,

by the fact that height of DBH measurement (1.3 m) was not marked on sample plot trees.

The limitations of the present findings are notable. Perfectly, species groups of similar growth dynamics should be based on growth rate, growth pattern and regeneration strategy (Vanclay, 1989), or on the dynamic process strategy (based upon recruitment, growth and mortality) (Gourlet-Fleury *et al.*, 2005). However, tree species grouping was tackled here only by using *IVI*, because we did not find other clear and reasonable species groupings by clustering growth model parameters. Therefore, we developed growth models for each individual important tree species, as well as for that entire group and for the other “non-important” species.

The *IVI* was characterized by three important traits of a particular tree species. Relative abundance illustrates density of identified tree species, while relative dominance means density of stock expressed as basal area, and relative frequency expresses on how many subplots a species occurs (Ribeiro *et al.*, 2008). Therefore, the *IVI* supports a summary of all three indicators of ecosystem importance.

Overall, in future investigations, more research is needed to establish a more objective and quantitative site quality evaluation for tropical rainforests.

The current findings are the first endeavor to model diameter increment of the individual important tree species of natural forests in Vietnam, which can be further improved in the future as additional data become available. Considering random plot effects turned out to be a necessary modelling requirement for single tree growth models based, as usual, on trees from sample plots having non-negligibly correlated tree characteristics. Further attempts are necessary to improve measurement precision.

Literature cited

1. Adame, P., Brandeis, T.J., Uriarte, M., 2014. Diameter growth performance of tree functional groups in Puerto Rican secondary tropical forests. *Forest Systems* 23 (1), 52 – 63.

2. Bates, D.M., 2010. *Lme4: Mixed effects modeling with R*. Springer.
3. Bella, I.E., 1971. A new competition model for individual trees. *Forest science* 17, 364-372.
4. Bueno-López, S., Bevilacqua, E., 2013. Diameter growth prediction for individual *Pinus occidentalis* Sw. trees. *iForest* 6, 209-216.
5. Cao, Q.V., 2000. Prediction of annual diameter growth and survival for individual trees from periodic measurements. *Forest science* 46, 127-131.
6. Chai, F.Y.C., LeMay, V.M., 1993. Development and testing of diameter increment models for mixed swamp forests of Sarawak. *Forest Ecology and Management* 58, 51-64.
7. Draper, N.R., Smith, H., 1998. *Applied regression analysis*. 3rd edition, Wiley Series in Probability and Statistics, 704 pp.
8. Finegan, B., Camacho, M., Zamora, N., 1999. Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest. *Forest Ecology and Management* 121, 159-176.
9. Giliba, R.A., Boon, E.K., Kayombo, C.J., Musamba, E.B., Kashindye, A.M., Shayo, P.F., 2011. Species composition, richness and diversity in Miombo woodland of Bereku forest reserve, Tanzania. *J Biodiversity* 2, 1-7.
10. Gourlet-Fleury, S., Houllier, F., 2000. Modelling diameter increment in a lowland evergreen forest in French Guiana. *Forest Ecology and Management* 131, 269-289.
11. Gourlet-Fleury, S., Blanc, L., Picard, N., Sist, P., Dick, J., Nasi, R., Swaine, M.D., Forni, E., 2005. Grouping species for predicting mixed tropical forest dynamics: looking for a strategy. *Ann. For. Sci.* 62, 785-796.

12. Hann, D.W., Marshall, D.D., Hanus, M.L., 2006. Reanalysis of the SMC-ORGANON equations for diameter-growth rate, height-growth rate, and mortality rate of Douglas-fir. Research Contribution 49. Oregon State University, Forest research laboratory, Corvallis, OR.
13. Hann D.W., Hanus, M.L., 2002. Enhanced diameter-growth-rate equations for undamaged and damaged trees in southwest Oregon. Research contribution 39. Oregon state university, Forest research laboratory, Corvallis, OR.
14. Kariuki, M., 2005. Modelling dynamics including recruitment, growth and mortality for sustainable management in uneven-aged mixed-species rainforests. PhD thesis, Southern Cross University, Lismore, NSW.
15. Lahoreau, G., Picard, N., Gourlet-Fleury, S., 2002. Grouping species to model forest dynamics: a case study of a forest in the Central African Republic. *Bois et Forêt des Tropique* 271, 89-100.
16. Larocque, G.R., 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. *Forest science* 48, 24-34.
17. Lessard, V.C., McRoberts, R.E., Holdaway, M.R., 2001. Diameter growth models using Minnesota forest inventory and analysis data. *Forest science* 47, 301-310.
18. Lhotka, J.M., Leowenstein, E.F., 2011. An individual-tree diameter growth model for managed uneven-aged oak-shortleaf pine stands in the Ozark Highland of Missouri, USA. *Forest Ecology and Management* 261, 770-778.
19. Meldahl, R.S., Eriksson, M., Thomas, C.E., 1985. A method for grouping species-forest type combinations for the development of growth models for mixed species stands. Forest service general technical report SO – United States, Southern Forest Experiment Station 54, 422-428.

20. Monserud, R.A., Sterba, H., 1996. A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *Forest Ecology and Management* 80, 57-80.
21. Phillips, P.D., Yasman, I., Brash, T.E., van Gardinggen, P.R., 2002. Grouping tree species for analysis of forest data in Kalimantan (Indonesian Borneo). *Forest Ecology and Management* 157, 205-216.
22. Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects models in S and S-PLUS. *Statistics and Computing*, 528 pp.
23. Pinheiro, J.C., Bates, D.M., 2004. Mixed-effects models in S and S-PLUS. Springer Science+Business Media, LLC. Printed in the United States of America.
24. Pokharal, B., Dech, J.P., 2012. Mixed-effects basal area increment models for tree species in the boreal forest of Ontario, Canada using an ecological land classification approach to incorporate site effects. *Forestry*.
25. Pukkala, T., Lähde, E., Laiho, O., 2009. Growth and yield models for uneven-sized forest stands in Finland. *Forest Ecology and Management* 258, 207-216.
26. Razavi, S.M., Mattaji, A., Rahmani, R., Naghavi, F., 2012. The assessment of plant species importance value (SIV) in Beech (*Fagus orientallis*) forests of Iran (A case study: Nav District 2 of Asalem, Guilan Province). *International Research Journal of Applied and Basic Science* 3, 433-439.
27. Ribeiro, N.S., Shugart, H.H., Washington-Allen, R., 2008. The effects of fire and elephants on species composition and structure of the Niassa Reserve, northern Mozambique. *Forest Ecology and Management* 255, 1626-1636.
28. Sterba, H., 2002. Forest inventories and growth models to examine management strategies for forests in transition. *Forestry* 75, 411-418.

29. Swaine, M.D., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75, 81-86.
30. Vaclay, J.K., 1989. A growth model for North Queensland Rainforests. *Forest Ecology and Management* 27, 245-271.
31. Vanclay, J.K., 1991. Aggregating tree species to develop diameter increment equations for tropical rainforests. *Forest Ecology and Management* 42, 143-168.
32. Vanclay, J.K., 1995. Growth models for tropical forests: A synthesis of models and methods. *Forest Science*, Vol.41, no. 1, 4-42.
33. Weaver, P.L., 1979. Tree growth in several tropical forests of Puerto Rico. U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station.
34. West, P.W., 1980. Use of diameter increment and basal area increment in tree growth studies. *Canadian Journal of Forest research* 10, 71-77.
35. West, B., Welch, K.B., Galecki, A.T., 2007. Linear mixed models: A practical guide using Statistical Software. Chapman & Hall/CRC, Boca Raton.
36. Weiskittel, A.R., Hann, D.W., Jr. Kershaw, J.A., Vanclay, J.K., 2011. Forest growth and yield modeling. A John Wiley & Son, Ltd., Publication, 415 pp.
37. Wykoff, W.R., 1990. A basal area increment model for individual conifers in the northern Rocky mountains. *Forest Science* 36, 1077-1104.
38. Yue, C., Kohnle, U., Hein, S., 2008. Combining tree- and stand-level models: A new approach to growth prediction. *Forest science* 54, 553-566.
39. Zeide, B., 2005. How to measure stand density. *Trees* 19, 1-14.
40. Zhao, D., 2003. Modeling mixed species forest stands. PhD thesis, The university of Georgia.

Chapter 5 Recruitment and mortality models

5.1 Recruitment models

5.1.1 Introduction

Recruitment trees were collected on subplot-level on each plot. They were defined as the trees reaching a diameter at breast height of 6 cm between two measurements. To date, there are two types of recruitment models: static and dynamic (Vanclay, 1994). The former approach takes stand conditions into little account, and therefore predicts a fairly constant amount of recruits, leading to an average of the long-term expectation under “typical” conditions. The latter approach takes stand conditions into greater account; consequently, it predicts recruitment as a function of stand density, composition, and other parameters.

According to Vanclay (1994), one of the difficult tasks in modeling recruitment is the large amount of variability in regeneration rates among species, spatially over stand, and over time. The recruitment data demonstrate the fact that during any period, regeneration may or may not occur. This characteristic (none/some recruitment) becomes especially obvious when individual species or species groups with many zero observations are modeled. Such data are generally modeled using a two-stage approach: (1) estimation of the occurrence probability and (2) prediction of the quantity of recruits per year. In the first step, logistic regression is used to estimate the probability that recruits would appear, with the presence or absence of new trees as realizations of the dependent variable. In the second step, a conditional function is developed to predict the amount of recruits. The conditional function is normally estimated with ordinary linear or multiple linear regression. This method was widely applied to predict recruitment in several forest types (Vanclay, 1992; Schweiger and Sterba, 1997; Lexerød, 2005; Adame, 2010). Often, recruitment data consist of many zeros. Fortin and Deblois (2007), for instance, demonstrated that fitting a traditional Poisson distribution to this type of data can underestimate the occurrence of zeros or overestimate the occurrence of larger counts. One way to solve this issue is utilizing a method similar to conditional functions. Fortin and Deblois (2007) predicted tree recruitment with zero-inflated models, and Zhang *et al.* (2012) applied negative

binomial mixture models (zero-inflated negative binomial, and Hurdle negative binomial models) to predict tree recruitments of Chinese pine trees (*Pinus tabulaeformis*).

However, due to the low number of plots compared to the large number of species the purpose of this research is not to tackle the recruitment of each single species, but rather, to concentrate on predicting tree recruitment of particular species groups: across all tree species, all locally (province) important tree species, and important species spread over provinces. Two approaches were used here, generalized linear models (Poisson, Quasi-Poisson and Negative Binomial models), and generalized linear mixed effects models (Negative Binomial mixed model), the latter to take random plot effects into account. In the former approach these plot effects are considered by an overdispersion parameter. In the present study, we did not use zero-inflated models because of two reasons: (1) A zero-inflated model assumes that the zero observations have to come from two different sources, namely “structural” and “sampling” (Hu *et al.*, 2011). The sampling zeros are assumed to occur by chance, while structural zeros are observed due to some specific structure in the data. (2) Zero-inflated models are recommended if the overdispersion parameter is larger than 15 or 20 (Zuur *et al.*, 2009), what was not the case with the data of the 12 sample plots under study.

5.1.2 Independent variables

The variables included in the models were selected based on the published literature. Vanclay (1992) used explanatory variables such as stand basal area, treatment response, site quality, and soil parent material in his recruitment model. Lexerød (2005) used information about location (altitude, latitude), site conditions (site index, vegetation types), and stand characteristics (mean diameter, stand basal area, number of trees, dominant height, and proportion of total basal area for the species group) in his model. Stand variables such as age, dominant height, density, basal area, arithmetic mean diameter, altitude, slope, and relative spacing were utilized in Zhang *et al.*'s recruitment model (2012).

In our case, the data on 300 subplots from 12 plots were used to fit the recruitment model. The response variable was the number of recruits per subplot. Explanatory

variables were measured at the beginning of the period, including arithmetic mean diameter of the subplot (*DBH*), subplot and plot basal area (*BAL_{subplot}*, *BAL_{stand}*), subplot density (the number of trees on each subplot) (*N*), and provinces as a categorical variable (*provincecode*). The full models were simplified by sequentially removing non-significant variables to get the adequate function (Crawley, 2007). Site quality and environmental variables were not available.

5.1.3 Generalized linear model (GLM)

The standard linear model is not able to tackle non-normal responses (e.g., counts or proportions) for several reasons: 1) the errors will not follow a normal distribution, 2) a large number of zeros is difficult to address in transformations, 3) the variance of the response varies with the mean, and 4) the linear model could lead to the prediction of negative counts (Crawley, 2007) or of proportions outside the unit interval. This encourages improvement in generalized linear models, leading to a solution for a wide range of data with different types of explained variables (Faraway, 2006). The GLM consists of two components, the response variable and the link function. The former should come from one of the exponential family distributions (e.g., Binomial, Poisson, Gamma, Negative Binomial), while the latter defines how the mean of the dependent variable and the linear combination of the explanatory variables are connected (Faraway, 2006).

- Overdispersion

Overdispersion means the true variance exceeds the variance given by the model (Cox, 1983). According to Hilbe (2011), overdispersion can arise as a result of eight potential issues: the model is missing a required predictor; the model may have one or more outliers; the model needs one or more interaction terms; one or more independent variables may not be measured on the most accurate scale; a continuous covariate has a non-linear effect; the model is mis-specified (e.g., it has an incorrect link function); there is zero-inflation; the data has an inherent dependency structure. These issues can be handled via several methods, the most common of which for count data is using a Quasi-Poisson approach, i.e. a dispersion parameter ϕ is included

in the model, or a Negative Binomial distribution (O'Hara and Kotze, 2010) for the count data.

In this study, a Poisson GLM (log link) was used to detect overdispersion. The reason for using the Poisson model here is that the response variable (the number of recruits) is count data. When we found evidence of overdispersion in the data, we refitted the model with a Quasi-GLM and a generalized Negative Binomial model.

In the Poisson model, the variance equaled $\phi\mu$, with mean μ and dispersion parameter ϕ . The following formula (Zuur *et al.*, 2009) was used in the calculation:

$$\phi = \frac{D}{n - p} \quad (5.1)$$

where D is the residual deviance and $n - p$ is degrees of freedom. n is the number of observations, and p is the number of regression parameters (intercept and slopes) in the model.

If ϕ equals 1, there is no overdispersion and we have the Poisson GLM; if ϕ is larger than 1, this is evidence for the suggestion of overdispersion (Zuur *et al.*, 2009) and we have the Quasi-Poisson GLM. In the Negative Binomial model $NB(\mu_i, k)$, the mean and variance of the counts are μ and $\mu + \mu^2/k$, respectively. The procedure for selecting Poisson, Quasi-Poisson, and Negative Binomial models followed Zuur *et al.* (2009). All hypothesis testing was performed at the $\alpha = 0.05$ significance level.

- Model selection in Quasi-Poisson

In the Quasi-Poisson model, the AIC cannot be calculated, because the likelihood is not defined. Therefore, backward or forward selections were not used. Here, the analysis of deviance approach to compare two nested models (a full model and a nested model) was applied. The non-significant variables at $\alpha = 5\%$ were withheld from the model, which was then refitted with the remaining terms to see whether there were still any non-significant variables. The process must be repeated if some of the independent variables are still insignificant.

- Model selection in Poisson and Negative Binomial

An advantage of the Poisson and Negative Binomial models over the Quasi-Poisson is that for the former two the AIC can be computed. An automatic backward selection procedure based upon AIC was therefore applied in order to find the most relevant explanatory variables.

With Nre_i meaning the number of recruits in the i^{th} subplot, the logarithmic link between the mean of Nre_i and the predictors in the full model is:

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + \beta_4 x_{4i} + \log(time_i) \quad (5.2)$$

or

$$\mu_i = \exp(\beta_0 + \alpha_k + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + \beta_4 x_{4i} + \log(time_i)) \quad (5.3)$$

where:

x_{1i} to x_{4i} are independent variables of the i^{th} subplot (DBH , $BAL_{subplot}$, BAL_{stand} , N) and α_k is the effect of province k ($k = 1, 2, 3$), $\alpha_k = 0$ for Ha Tinh;

β_0 to β_4 and the α_k are the parameters to be estimated.

$\log(time_i)$ is an offset factor. The offset is a covariate in the linear predictor whose coefficient is not estimated but assumed to be equal to one. The measurements from the second research period were collected in 2012 and 2013. Therefore, the time must be taken into account in this analysis, time = 7 for plots 1, 2, 4, 6, 7, 8, 10, 11, and time = 8 for plots 3, 5, 9, 12.

To estimate the regression parameters of the GLM, a maximum likelihood estimation was used (Zuur *et al.*, 2013).

5.1.4 Results of the GLM

Descriptive statistics of the number of trees, their arithmetic mean diameter, the stand

basal area, the number of recruits, and the number of species among the recruits are reported in Table 5.1.

The data set comprised 759 recruits of 116 different tree species (for all tree species), and 526 recruits of 46 species (for all important species) in a total of 12 plots. The number of recruits (all species, all important species) per plot ranged from (9, 9) to (260, 180) with the number of recruitment species from (7, 7) to (53, 21).

Table 5.1 Descriptive statistics of variables for recruitment modelling.

Province	Plot	No. trees	Mean DBH (cm)	Stand basal area (m ² /ha)	All tree species		All important tree species	
					No. recruits	No. species	No. recruits	No. species
Ha Tinh	1	416	20.95	18.65	13	7	13	7
	2	352	19.95	13.84	9	3	9	3
	3	391	19.05	15.54	17	11	10	6
Total					39	14	32	9
Thua	4	932	17.35	33.04	169	42	119	19
Thien	5	855	18.20	33.50	51	17	33	12
Hue	6	1092	16.53	34.72	260	53	180	21
Total					480	61	332	21
Binh Dinh	7	1151	16.05	31.01	39	20	27	9
	8	967	16.62	31.72	32	18	15	8
	9	893	18.34	32.44	41	24	19	8
Total					112	43	61	13
Khanh Hoa	10	800	17.53	28.95	47	14	40	9
	11	782	17.52	24.46	53	15	38	8
	12	901	17.47	28.73	28	11	23	7
Total					128	25	101	11
Total (4 prov.)					759	116	526	46

The final GLM after backward selection for the two species groups was

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 DBH_i + \beta_2 N_i + \log(time_i) \quad (5.4)$$

The observed variance to mean ratio of all tree species and all important tree species were 2.24 and 1.94, respectively, providing evidence for overdispersion. Therefore, the data were refitted with Quasi-Poisson and Negative Binomial models yielding the Quasi-Poisson GLM

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 DBH_i + \log(time_i) \quad (5.5)$$

and the same Negative Binomial GLM

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 DBH_i + \log(time_i) \quad (5.6)$$

The estimated parameters, standard errors, and the p -values of Poisson, Quasi-Poisson, and Negative Binomial models are given in Table 5.2. Stem number N was no longer significant with the Quasi-Poisson and Negative Binomial models and was skipped. The deviance of the Negative Binomial GLM was smaller than that of the Quasi-Poisson GLM (Table 5.2), and its AIC smaller than that of the Poisson model. Therefore, the most appropriate model was the Negative Binomial.

Similarly, a Negative Binomial GLM was also the final model for three important species appearing on all plots in three or four locations *Syzygium wightianum*:

$$\log(\mu_i) = \beta_0 + \alpha_k + \log(time_i) \quad (5.7)$$

for *Diospyros sylvatica*

$$\log(\mu_i) = \beta_0 + \log(time_i) \quad (5.8)$$

and for *Nephelium melliferum*:

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 DBH_i + \log(time_i) \quad (5.9)$$

Table 5.2 Generalized linear models (Poisson, Quasi-Poisson, and Negative Binomial) for recruitment trees (0.0 **** 0.001 *** 0.01 ** 0.05).

Objects	Variables	Param- eters	Poisson			Quasi-Poisson			Negative Binomial		
			Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)
All tree species	Intercept	β_0	-1.9173	0.3337	9.17e-09 ***	-1.5827	0.4561	0.0006***	-1.8590	0.4232	1.12e-05 ***
	<i>DBH</i>	β_1	-0.0444	0.0141	0.0016**	-0.0545	0.0202	0.0075 **	-0.0399	0.0197	0.0427 *
	<i>N</i>	β_2	0.0091	0.0035	0.0099**	-	-	-	-	-	-
	<i>Thua</i>		2.2037	0.1854	< 2e-16 ***	2.4012	0.2528	< 2e-16 ***	2.4386	0.2059	< 2e-16 ***
	<i>Thien Hue</i>										
	<i>Binh Dinh</i>	α_k	0.7103	0.2056	0.0006***	0.9172	0.2832	0.0013**	0.9526	0.2241	2.13e-05 ***
	<i>Khanh</i>		0.9142	0.1939	2.43e-06 ***	1.0524	0.2801	0.0002***	1.0949	0.2212	7.45e-07 ***
	<i>Hoa</i>										
	AIC				1254.5			NA			1101.8
Deviance				658.64			665.25			314.28	

Table 5.2 (continued)

Objects	Variables	Param- eters	Poisson			Quasi-Poisson			Negative Binomial		
			Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)
All important tree species	Intercept	β_0	-2.0636	0.3836	7.46e-08 ***	-1.7377	0.4784	0.0003 ***	-1.9217	0.4695	4.25e-05 ***
	<i>DBH</i>	β_1	-0.0473	0.0164	0.0039 **	-0.0569	0.0216	0.0089 **	-0.0469	0.0220	0.0333 *
	<i>N</i>	β_2	0.0092	0.0043	0.0304 *	-	-	-	-	-	-
	<i>Thua</i>		2.0257	0.2099	< 2e-16 ***	2.2286	0.2569	2.8e-16 ***	2.2557	0.2260	< 2e-16 ***
	<i>Thien Hue</i>										
	<i>Binh Dinh</i>	α_k	0.2917	0.2429	0.2297	0.5044	0.3035	0.0976 .	0.5217	0.2563	0.0418 *
	<i>Khanh</i>		0.8669	0.2173	6.63e-05 ***	1.0094	0.2843	0.0004***	1.0365	0.2433	2.04e-05 ***
	<i>Hoa</i>										
	AIC				1055.8			NA			951.73
Deviance				569.17			573.82			303.55	

Table 5.2 (continued)

Objects	Variables	Param- eters	Poisson			Quasi-Poisson			Negative Binomial		
			Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)
<i>S. wightianu m</i>	Intercept	β_0	-4.7000	0.4472	< 2e-16 ***	-4.7000	0.5315	< 2e-16 ***	-4.6987	0.4665	< 2e-16 ***
	<i>Thua</i>		2.5340	0.4646	4.95e-08 ***	2.5340	0.5522	6.61e-06 ***	2.5497	0.5011	3.62e-07 ***
	<i>Thien Hue</i>										
	<i>Binh Dinh</i>	α_k	2.80e-13	0.6325	1.0000	2.80e-13	0.7517	1.0000	-0.0022	0.6600	0.9973
	<i>Khanh</i>										
	<i>Hoa</i>		1.3350	0.5026	0.0079***	1.3350	0.5974	0.0262 ***	1.3402	0.5365	0.0125*
	AIC				391.67			NA			372.16
Deviance				253.54			253.54			162.97	
<i>D. sylvatica</i>	Intercept	β_0	-4.1900	0.2000	< 2e-16 ***	-4.1897	0.2151	< 2e-16 ***	-4.1865	0.2155	< 2e-16 ***
	AIC				167.01			NA			167.32
	Deviance				119.17			119.17			93.07
<i>N. melliferu m</i>	Intercept	β_0	-8.6250	1.4764	5.16e-09***	-8.6250	1.4278	6.44e-09***	-8.9650	1.5841	1.52e-08***
	<i>DBH</i>	β_1	0.1127	0.0512	0.0276*	0.1127	0.0495	0.0237*	0.1286	0.0571	0.0243*
	<i>Binh Dinh</i>		2.4430	1.0773	0.0233*	2.4430	1.0418	0.0199*	2.4829	1.0980	0.0237*
	<i>Khanh</i>	α_k	2.7572	1.0390	0.0080**	2.7572	1.0048	0.0066**	2.8119	1.0553	0.0077**
	<i>Hoa</i>										
AIC				140.72			NA			141.76	
Deviance				92.88			92.88			76.62	

As mentioned above, for dealing with different time intervals of each plot in each province, adding an offset variable (as $\log(\text{time})$) for the model. To avoid plotting two lines in each location, we calculate the annual number of recruits per province. Thus, the explicit models for all species per province (with $k = 2.007$) are:

Ha Tinh:

$$\log(\mu_i/\text{time}_i) = -1.8590 - 0.0399DBH_i \quad (5.10)$$

Thua Thien Hue:

$$\log(\mu_i/\text{time}_i) = -1.8590 - 0.0399DBH_i + 2.4386 \quad (5.11)$$

Binh Dinh:

$$\log(\mu_i/\text{time}_i) = -1.8590 - 0.0399DBH_i + 0.9526 \quad (5.12)$$

Khanh Hoa:

$$\log(\mu_i/\text{time}_i) = -1.8590 - 0.0399DBH_i + 1.0949 \quad (5.13)$$

for all important species (with $k = 1.746$):

Ha Tinh:

$$\log(\mu_i/\text{time}_i) = -1.9217 - 0.0469DBH_i \quad (5.14)$$

Thua Thien Hue:

$$\log(\mu_i/\text{time}_i) = -1.9217 - 0.0469DBH_i + 2.2557 \quad (5.15)$$

Binh Dinh:

$$\log(\mu_i/\text{time}_i) = -1.9217 - 0.0469DBH_i + 0.5217 \quad (5.16)$$

Khanh Hoa:

$$\log(\mu_i/\text{time}_i) = -1.9217 - 0.0469DBH_i + 1.0365 \quad (5.17)$$

for *S. wightianum* ($k = 0.745$):

Ha Tinh:

$$\log(\mu_i/\text{time}_i) = -4.6987 \quad (5.18)$$

Thua Thien Hue:

$$\log(\mu_i/\text{time}_i) = -4.6987 + 2.5497 \quad (5.19)$$

Binh Dinh:

$$\log(\mu_i/time_i) = -4.6987 - 0.0022 \quad (5.20)$$

Khanh Hoa:

$$\log(\mu_i/time_i) = -4.6987 + 1.3402 \quad (5.21)$$

for *D. sylvatica* ($k = 0.678$)

$$\log(\mu_i/time_i) = -4.1865 \quad (5.22)$$

and for *N. melliferum* ($k = 1.058$):

Ha Tinh:

$$\log(\mu_i/time_i) = -8.9650 + 0.1286DBH_i \quad (5.23)$$

Binh Dinh:

$$\log(\mu_i/time_i) = -8.9650 + 0.1286DBH_i + 2.4829 \quad (5.24)$$

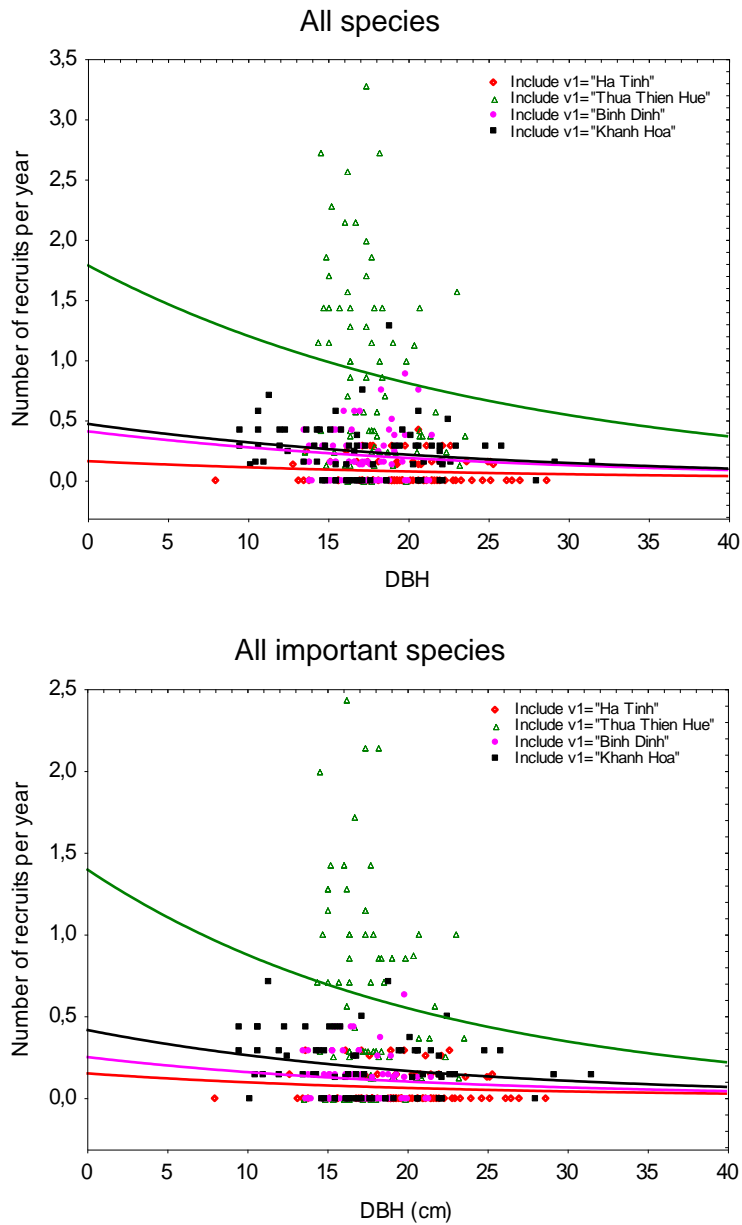
Khanh Hoa:

$$\log(\mu_i/time_i) = -8.9650 + 0.1286DBH_i + 2.8119 \quad (5.25)$$

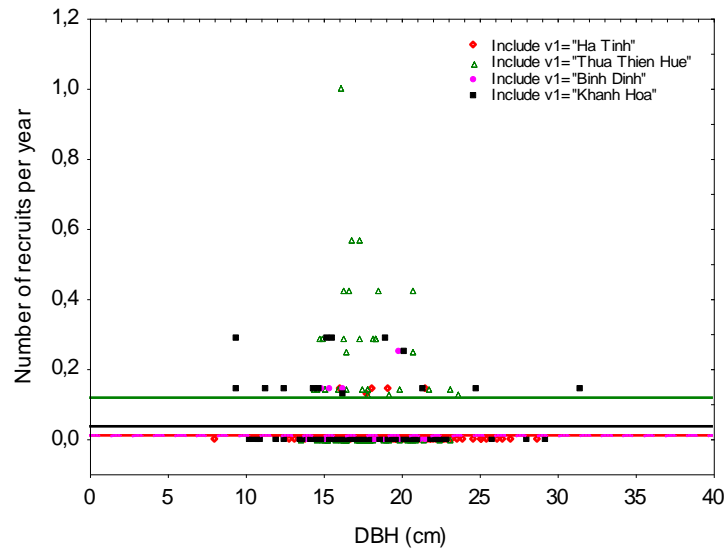
From the Negative Binomial model output, the *DBH* significantly influenced the log number of recruits across all species and all important species (Table 5.2). The relation between the *DBH* and log tree recruitment was negative, that means the greater the *DBH*, the smaller the log number and also the number of recruitment trees. In contrast, for *N. melliferum*, the number of recruits increased with rising the *DBH*.

The province effect was also significant. The lowest intercept (-1.86 for all species and -1.92 for all important species) and therefore the lowest recruitment number for all tree diameters, was found in Ha Tinh, the reference province, the highest in Thua Thien Hue (+2.44 larger for all species and +2.26 for all important species). Binh Dinh and Khanh Hoa differed only little but still significantly from Ha Tinh in both species groups. Similar to the two groups, for *S. wightianum*, the highest number of recruits was recorded in Thua Thien Hue, whereas for *N. melliferum*, this number was largest in Khanh Hoa.

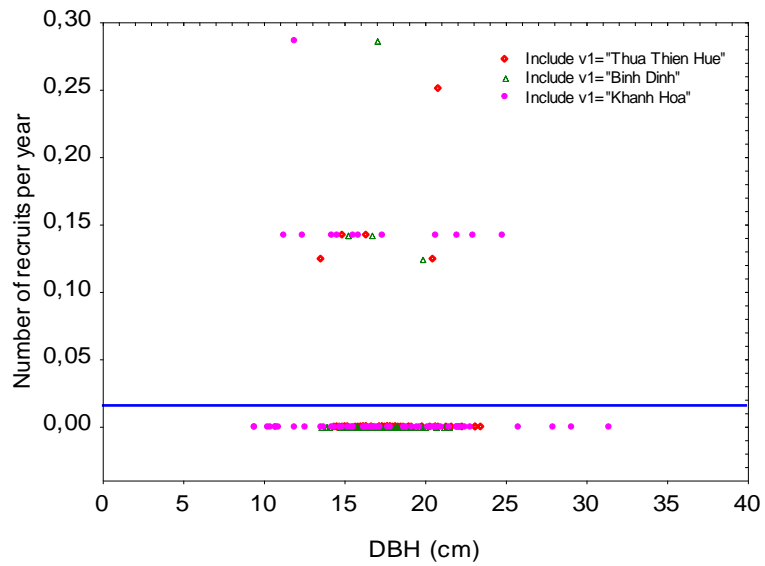
Figure 5.1 indicates the expected number of recruits per year across the range of the DBH in all four locations. For *D. sylvatica* and *S. wightianum* a more appropriate model was found considering random plot effects (see Figure 5.2).



S. wightianum



D. sylvatica



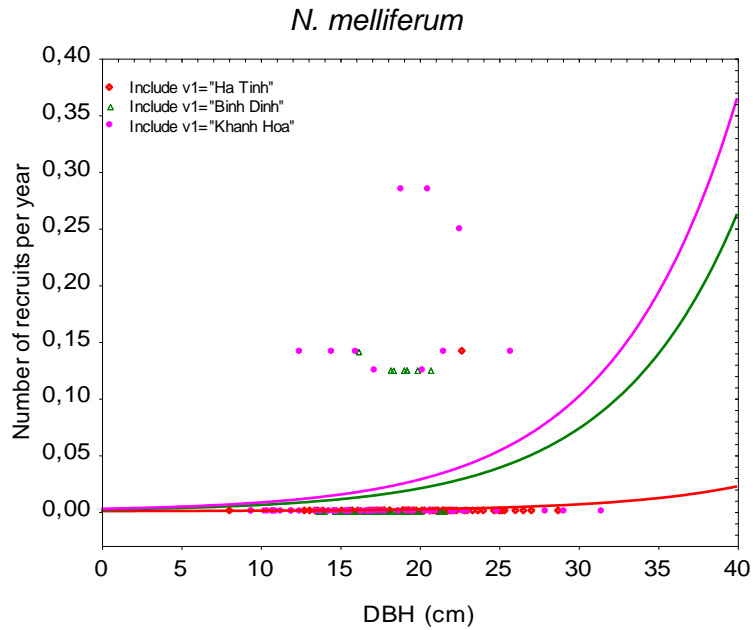


Figure 5.1 The annual number of recruits from the Negative Binomial GLM (lines), and observed data (dots) of the two groups, *S. wightiana*, *D. sylvatica*, and *N. melliferum*.

5.1.5 Generalized linear mixed model (GLMM)

Generalized linear mixed models are an extension of a GLM in which the linear predictor contains random effects in addition to the fixed effects. The random effects can account for the correlation between observations from the same plot in a province. In this study, a random plot effect was added to the intercept, the slope, or both intercept and slope of each model. We found the Negative Binomial GLM was better than the Poisson GLM (section 5.1.4), thus, we continue to analyze a Negative Binomial GLMM with the penalized quasi-likelihood method. In other words, the analysis of the GLMM regarding the number of recruitment trees was again based on a Negative Binomial structure and a log link function.

The parameter estimations for the GLMM in this chapter were fitted with *glmmPQL* in “MASS” package available from the open source statistical software R.

5.1.6 Results of the GLMM

After adding random-plot effects to the intercept, the fixed province effect or the slope of DBH, the effect of DBH was no longer significant in both species groups. Therefore, only the following GLMMs (i : subplot, j : plot, b : random effects)

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \alpha_k + \log(\text{time}_{ij}) \quad (5.26)$$

$$\log(\mu_{ij}) = (\beta_0 + b_j) + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.27)$$

$$\log(\mu_{ij}) = \beta_0 + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.28)$$

were finally compared with the fixed effects model (5.6). Models (5.27) and (5.28) did not differ, because models with random effects on the province intercepts $\beta_0 + \alpha_k$ can not be improved by an additional random intercept on the global intercept β_0 .

For *S. wightianum* occurring on all plots in four locations, the fixed effects model (6.7) was used in comparison with the three mixed models (5.26), (5.27), and (5.28), whereas *D. sylvatica* appearing on all plots in three provinces, the fixed effects model (5.8) was compared to one mixed effects model (5.29):

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \log(\text{time}_{ij}) \quad (5.29)$$

and for *Nephelium melliferum*, the fixed effects model (5.9) was compared with the following mixed effects models:

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \beta_1 DBH_{ij} + \alpha_k + \log(\text{time}_{ij}) \quad (5.30)$$

$$\log(\mu_{ij}) = (\beta_0 + b_j) + (\beta_1 + b_{1j}) DBH_{ij} + \alpha_k + \log(\text{time}_{ij}) \quad (5.31)$$

$$\log(\mu_{ij}) = \beta_0 + (\beta_1 + b_{1j}) DBH_{ij} + \alpha_k + \log(\text{time}_{ij}) \quad (5.32)$$

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \beta_1 DBH_{ij} + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.33)$$

$$\log(\mu_{ij}) = \beta_0 + \beta_1 DBH_{ij} + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.34)$$

Again, models (5.33) and (5.34) are equivalent. To assess goodness of fit of the data in the GLM and GLMM models, Pearson's χ^2 was used (see table 5.3).

Table 5.3 A comparison of Pearson's χ^2 between the fixed effects model (FM) and the mixed effects models for the recruits of all species, all important species, and three important species appearing in three and four locations. Best models are highlighted.

Objects	<i>n</i>	Equation	Model specification	Pearson's χ^2
				Negative Binomial GLMM
All tree species	300	5.6	Fixed effects model (GLM)	280.62
		5.26	FM + plot intercept	290.37
		5.27	FM + plot intercept + plot slope (<i>provincecode</i>)	295.12
		5.28	FM + plot slope (<i>provincecode</i>)	294.56
All important tree species	300	5.6	Fixed effects model (GLM)	263.04
		5.26	FM + plot intercept	290.81
		5.27	FM + plot intercept + plot slope (<i>provincecode</i>)	295.03
		5.28	FM + plot slope (<i>provincecode</i>)	295.03
<i>S. wightianum</i>	300	5.7	Fixed effects model (GLM)	297.93
		5.26	FM + plot intercept	295.57
		5.27	FM + plot intercept + plot slope (<i>provincecode</i>)	297.73
		5.28	FM + plot slope (<i>provincecode</i>)	297.73
<i>D. sylvatica</i>	225	5.8	Fixed effects model (GLM)	222.28
		5.29	FM + plot intercept	218.43

Table 5.3 (continued)

Objects	<i>n</i>	Equation	Model specification	Pearson's χ^2
				Negative Binomial GLMM
<i>N. melliferum</i>	225	5.9	Fixed effects model (GLM)	185.20
		5.30	FM + plot intercept	222.94
		5.31	FM + plot intercept + plot slope (<i>DBH</i>)	222.75
		5.32	FM + plot slope (<i>DBH</i>)	223.39
		5.33	FM + plot intercept + plot slope (<i>provincecode</i>)	223.16
		5.34	FM + plot slope (<i>provincecode</i>)	223.16

The model with the minimum Pearson's χ^2 values was selected as the best model. The Negative Binomial GLMM did not provide a substantially better fit on the basis of Pearson χ^2 than the Negative Binomial GLM, with the exception of two species occurring in three and four locations (*D. sylvatica* and *S. wightianum*). Consequently, the fixed effects GLM was selected to predict the number of recruits across all species, all important species (Equation 5.6), and *N. melliferum* (Equation 5.9), because it had the smallest Pearson Chi-squares.

For *S. wightianum* and *D. sylvatica*, where neither the GLM nor the GLMMs include any covariate, the mixed effects model with the random plot effects on the intercept (Equation 5.26 and 5.29, respectively) was chosen.

Table 5.4 lists the parameter estimates, standard deviation errors, and the *p*-values for the Negative Binomial GLMM of two important species (*D. sylvatica* and *S. wightianum*) occurring in three and four locations. The log number of recruits of *S. wightianum* in Binh Dinh and Khanh Hoa was not significantly different from that in Ha Tinh, while this

number in Thua Thien Hue was significantly more than that in Ha Tinh. The parameter estimates are close to those of the GLM (Table 5.2 or (5.18) to (5.21)).

For *D. sylvatica*, there was no difference in the number of recruits in three provinces Thua Thien Hue, Binh Dinh, and Khanh Hoa.

The random plot effects on the intercept in the Negative Binomial GLMM contributed from 14.69% to 65.92% to the total unexplained variation (Table 5.4), and the overdispersion parameters were closer to 1, reflecting that the overdispersion observed with Negative Binomial GLM was removed here by considering random plot effects.

Table 5.4 Parameter estimates for the Negative Binomial GLMM for recruitment trees of *S. wightianum* and *D. sylvatica*

Objects	Equation	Fixed effects				Variance components		% variation explained by random effects	Overdispersion parameter	
		Variables	Parameter estimates	Std.error	Pr(> z)	$\sigma^2_{\text{ran-in}}$	σ^2_{res}			
<i>S. wightianum</i>	5.26	Intercept	β_0	-4.7072	0.5069	0.0000	0.1579	0.9166	14.69	1.0019
		<i>Thua Thien</i>		2.4613	0.5860	0.0030				
		<i>Hue</i>	α_k	-0.0137	0.7179	0.9853				
		<i>Binh Dinh</i>		1.3237	0.6139	0.0631				
<i>Khanh Hoa</i>										
<i>D. sylvatica</i>	5.29	Intercept	β_0	-4.5817	0.4287	0.0000	1.2020	0.6213	65.92	0.9795

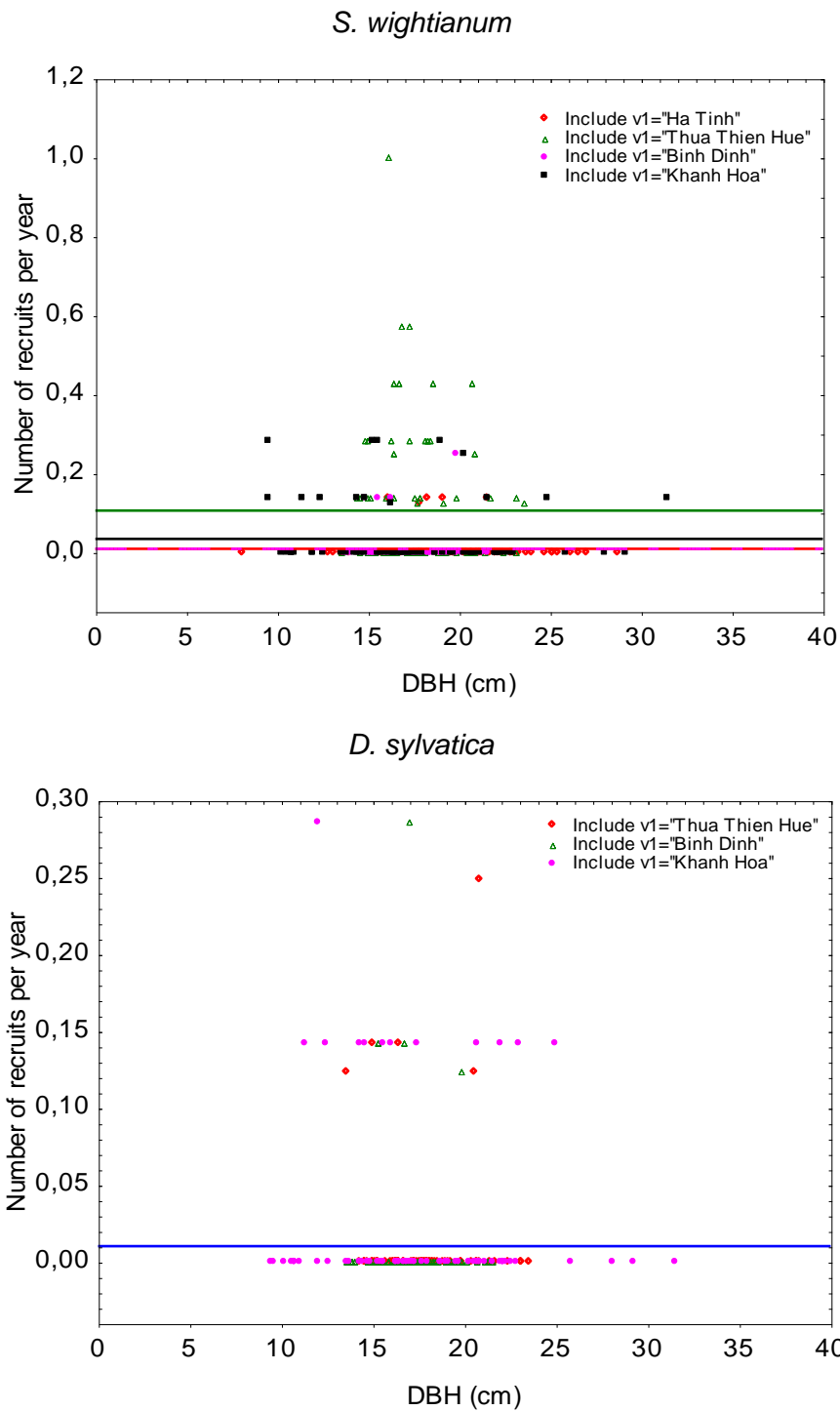


Figure 5.2 The annual number of recruits from the Negative Binomial GLMM (lines), and observed data (dots) for *S. wightianum* and *D. sylvatica*.

5.2 Mortality models

5.2.1 Introduction

Natural mortality of trees is a crucial process that determines forest dynamics (Rüger *et al.*, 2011). When a tree dies, the reduced competition benefits the trees near the dead tree, positively affecting their growth (Yang *et al.*, 2003); in addition, gaps created by dead canopy trees are later filled by new trees (Oliver and Larson, 1996). McCarthy (2001) notes that these gap dynamics are crucial determinants of the structure and composition of a forest stand. For these reasons, the mortality process should be considered in stand simulation models. However, modeling mortality is difficult due to the stochastic nature of mortality events; standing death may be caused by intrinsic senescence (Carey *et al.*, 1994) or extrinsic factors such as disease, insects, fungi, and wind. In previous studies, several statistical methods have been utilized to develop mortality models, including the logistic regression model (Monserud and Sterba, 1999), the two-step approach (Eid and Tuhus, 2001; Álvarez González *et al.*, 2004; Diéguez-Aranda *et al.*, 2005), the three-step approach (Fridman and Stahl, 2001; Meng *et al.*, 2003), and neural networks (Hasenauer *et al.*, 2001).

Using the approach from recruitment modelling to develop a mortality model, the Poisson GLM, Quasi-Poisson GLM, Negative Binomial GLM, and the Negative Binomial GLMM were employed to model mortality for all species, all important species, and the important species that occurred in three or four provinces. The dependent variable was the number of dead trees, which are the standing trees that died between the two occasions at which measurements were taken.

5.2.2 Results of the GLM

A total of 1323 dead trees belonging to 189 species were counted at the four locations. The number of dead trees for all species and all important species counted per plot ranged from 21 to 221 and from 10 to 133 respectively. This was in correspondence with the number of species, which was respectively, from 17 to 58 and from 8 to 21 (Table 5.5).

Table 5.5 Descriptive statistics of the mortality data used for the model development.

Province	Plot	No. trees	Mean DBH (cm)	Stand basal area (m ² /ha)	All tree species		All important tree species	
					No. dead trees	No. species	No. dead trees	No. species
Ha Tinh	1	416	20.95	18.65	21	17	10	8
	2	352	19.95	13.84	69	33	33	9
	3	391	19.05	15.54	66	37	25	9
Total					156	66	68	14
Thua	4	932	17.35	33.04	154	44	109	21
Thien	5	855	18.20	33.50	77	41	45	19
Hue	6	1092	16.53	34.72	190	54	133	21
Total					421	73	287	21
Binh Dinh	7	1151	16.05	31.01	221	57	130	17
	8	967	16.62	31.72	184	58	108	17
	9	893	18.34	32.44	96	43	47	12
Total					501	86	285	17
Khanh Hoa	10	800	17.53	28.95	35	18	25	9
	11	782	17.52	24.46	82	27	59	9
	12	901	17.47	28.73	128	27	99	11
Toal					245	42	183	11
Total (4 prov.)					1323	189	823	49

The fitted Poisson GLM model for two species groups supported evidence for overdispersion through the ratio of deviance to degrees of freedom larger than 1 (2.79 and 2.38, respectively). Thus, we refitted the data to correct the standard errors using Quasi-Poisson and Negative Binomial GLMs.

The estimated parameters, standard errors, and the p -values of Poisson, Quasi-Poisson, and Negative Binomial models are represented in Table 5.6. The deviance across all species and all important species was the lowest when analyzed with a Negative Binomial GLM. The analysis of the data set for the mortality model was quite similar to the recruitment model, leading us to conclude that the Negative Binomial model was preferable over the Poisson and Quasi-Poisson models. The Negative Binomial GLM is given as follows:

For all species:

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 BAL_{standi} + \log(time_i) \quad (5.35)$$

and for all important species:

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 DBH_i + \beta_2 BAL_{standi} + \log(time_i) \quad (5.36)$$

In the same way, the Negative Binomial GLM was the selected model for three important species (*Syzygium wightianum*, *Diospyros sylvatica* and *Nephelium melliferum*) spread over three or four provinces:

- *S. wightianum*

$$\log(\mu_i) = \beta_0 + \alpha_k + \beta_1 BAL_{standi} + \log(time_i) \quad (5.37)$$

- *D. sylvatica*

$$\log(\mu_i) = \beta_0 + \alpha_k + \log(time_i) \quad (5.38)$$

- *N. melliferum*

$$\log(\mu_i) = \beta_0 + \log(time_i) \quad (5.39)$$

Table 5.6 GLM (Poisson, Quasi-Poisson, Negative Binomial) results for standing dead trees (0 ‘****’ 0.001 ‘***’ 0.01 ‘**’ 0.05).

Objects	Variables	Para- meters	Poisson			Quasi-Poisson			Negative Binomial		
			Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)
All tree species	Intercept	β_0	0.9764	0.4022	0.0152*	0.3103	0.6151	0.614253	0.4251	0.5371	0.4287
	<i>DBH</i>	β_1	-0.0306	0.0099	0.0019 **	-	-	-	-	-	-
	<i>BAL_{stand}</i>	β_2	-0.0969	0.0219	1.02e-05 ***	-0.0999	0.0385	0.010019 *	-0.1082	0.0334	0.0012 **
	<i>N</i>	β_3	-0.0075	0.0026	0.0046 **	-	-	-	-	-	-
	<i>Thua</i>										
	<i>Thien</i>		2.8502	0.4129	5.10e-12 ***	2.7961	0.7211	0.000130 ***	2.9610	0.6191	1.73e-06 ***
	<i>Hue</i>										
	<i>Binh Dinh</i>	α_k	2.8215	0.3706	2.68e-14 ***	2.7672	0.6445	2.39e-05 ***	2.9166	0.5530	1.33e-07 ***
	<i>Khanh</i>										
	<i>Hoa</i>		1.6269	0.2747	3.19e-09 ***	1.6007	0.4773	0.000901 ***	1.7165	0.4112	2.99e-05 ***
	AIC			1684.3			NA			1457.9	
	Deviance			816.81			831.72			322.56	

Table 5.6 (continued)

Objects	Variables	Para- meters	Poisson			Quasi-Poisson			Negative Binomial		
			Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)
All important tree species	Intercept	β_0	-0.1060	0.5117	0.8359	-1.2507	0.4223	0.0033 **	0.1144	0.7463	0.8782
	<i>DBH</i>	β_1	-0.0433	0.0122	0.0004 ***	-0.0429	0.0195	0.0280 *	-0.0396	0.0181	0.0287 *
	<i>BAL_{stand}</i>	β_2	-0.0718	0.0277	0.0095 **	-	-	-	-0.0910	0.0405	0.0245 *
	<i>Thua</i>				3.24e-07						5.53e-05
	<i>Thien</i>		2.6382	0.5164	***	1.3537	0.2194	2.24e-09 ***	3.0239	0.7500	***
	<i>Hue</i>				1.05e-07						3.51e-05
	<i>Binh Dinh</i>	α_k	2.4632	0.4632	***	1.3239	0.2214	6.41e-09 ***	2.7783	0.6715	***
	<i>Khanh</i>				8.98e-07						9.33e-05
	<i>Hoa</i>		1.7083	0.3477	***	0.8861	0.2333	0.0002 ***	1.9593	0.5015	***
	AIC				1389.9			NA			1233.6
Deviance				700.32			706.97			319.22	

Table 5.6 (continued)

Objects	Variables	Parameters	Poisson			Quasi-Poisson			Negative Binomial		
			Parameter estimates	Std-error	Pr(> z)	Parameter estimates	Std-error	Pr(> z)	Parameter estimates	Std-error	Pr(> z)
<i>S. wightianum</i>	Intercept	β_0	-2.3011	1.1804	0.0512.	-2.3011	1.2261	0.0615.	-2.2846	1.1985	0.0566.
	<i>BAL</i> _{stand}	β_1	-0.1859	0.0671	0.0059**	-0.1859	0.0697	0.0081**	-0.1869	0.0684	0.0063**
	<i>Thua</i>										
	<i>Thien</i>		5.4731	1.3714	6.58e-05***	5.4731	1.4245	0.0002***	5.4926	1.3941	8.15e-05***
	<i>Hue</i>										
	<i>Binh Dinh</i>	α_k	4.7208	1.2624	0.0002***	4.7208	1.3112	0.0004***	4.7376	1.2822	0.0002***
	<i>Khanh</i>										
	<i>Hoa</i>		4.7277	0.9623	8.96e-07***	4.7277	0.9995	3.48e-06***	4.7409	0.9767	1.21e-06***
	AIC				375.95			NA			377.85
	Deviance				216.95			216.95			210.84
<i>D. sylvatica</i>	Intercept	β_0	-6.5974	1.0108	6.72e-11***	-6.310	1.129	6.69e-08***	-6.3090	1.010	4.12e-10***
	<i>BAL</i> _{subplot}	β_1	0.4233	0.2044	0.0384*	-	-	-	-	-	-
	<i>Binh Dinh</i>		2.8643	1.0300	0.0054**	3.135	1.153	0.0071**	3.1370	1.040	0.0026**
	<i>Khanh</i>	α_k									
	<i>Hoa</i>		2.9082	1.0296	0.0047**	3.135	1.153	0.0071**	3.1280	1.041	0.0027**
	AIC				235.37			NA			231.26
Deviance				152.10			155.85			106.08	

Table 5.6 (continued)

Objects	Variables	Para- meters	Poisson			Quasi-Poisson			Negative Binomial		
			Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)	Parameter estimates	Std- error	Pr(> z)
<i>N. melliferum</i>	Intercept	β_0	-4.1127	0.1925	< 2e-16***	-4.1127	0.2121	< 2e-16***	-4.1101	0.2067	< 2e-16***
	AIC				176.37			NA			176.36
	Deviance				124.77			124.77			98.79

The annual number of dead trees can be estimated using the Negative Binomial GLM for all species per province (with $k = 2.487$):

Ha Tinh:

$$\log(\mu_i/time_i) = 0.4251 - 0.1082BAL_{standi} \quad (5.40)$$

Thua Thien Hue:

$$\log(\mu_i/time_i) = 0.4251 - 0.1082BAL_{standi} + 2.9610 \quad (5.41)$$

Binh Dinh:

$$\log(\mu_i/time_i) = 0.4251 - 0.1082BAL_{standi} + 2.9166 \quad (5.42)$$

Khanh Hoa:

$$\log(\mu_i/time_i) = 0.4251 - 0.1082BAL_{standi} + 1.7165 \quad (5.43)$$

for all important species (with $k = 1.993$):

Ha Tinh:

$$\log(\mu_i/time_i) = 0.1144 - 0.0396DBH_i - 0.0910BAL_{standi} \quad (5.44)$$

Thua Thien Hue:

$$\log(\mu_i/time_i) = 0.1144 - 0.0396DBH_i - 0.0910BAL_{standi} + 3.0239 \quad (5.45)$$

Binh Dinh:

$$\log(\mu_i/time_i) = 0.1144 - 0.0396DBH_i - 0.0910BAL_{standi} + 2.7783 \quad (5.46)$$

Khanh Hoa:

$$\log(\mu_i/time_i) = 0.1144 - 0.0396DBH_i - 0.0910BAL_{standi} + 1.9593 \quad (5.47)$$

for *S. wightianum* ($k = 13.786$):

Ha Tinh:

$$\log(\mu_i/time_i) = -2.2846 - 0.1869BAL_{standi} \quad (5.48)$$

Thua Thien Hue:

$$\log(\mu_i/time_i) = -2.2846 - 0.1869 BAL_{standi} + 5.4926 \quad (5.49)$$

Binh Dinh:

$$\log(\mu_i/time_i) = -2.2846 - 0.1869 BAL_{standi} + 4.7376 \quad (5.50)$$

Khanh Hoa:

$$\log(\mu_i/time_i) = -2.2846 - 0.1869 BAL_{standi} + 4.7409 \quad (5.51)$$

for *D. sylvatica* ($k = 0.667$):

Ha Tinh:

$$\log(\mu_i/time_i) = -6.3090 \quad (5.52)$$

Binh Dinh:

$$\log(\mu_i/time_i) = -6.3090 + 3.1370 \quad (5.53)$$

Khanh Hoa:

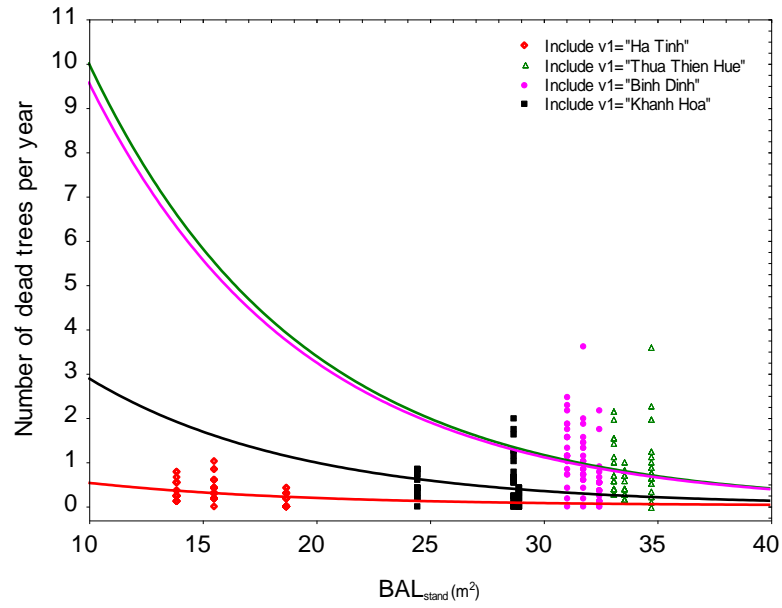
$$\log(\mu_i/time_i) = -6.3090 + 3.1280 \quad (5.54)$$

and for *N. melliferum* ($k = 0.772$):

$$\log(\mu_i/time_i) = -4.1101 \quad (5.55)$$

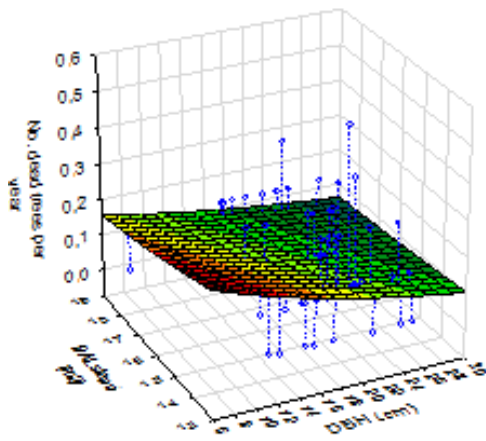
The coefficient of BAL_{stand} was always negative (all species, all important species, and *S. wightianum*) denoting that the number of dead trees declined as the stand basal area became larger, or 0 (i.e. nonsignificant) for the other two species (Table 5.6). Similarly, the number of dead trees of all important species decreased with an increasing *DBH*, indicating a higher number of dead trees among small, as opposed to larger trees. This number should rise in age-related senescence as the tree becomes older; however, the data in our model did not demonstrate this relationship. The number of dead trees for the two groups and *S. wightianum* was found to be the highest in Thua Thien Hue in comparison with Ha Tinh, Binh Dinh, and Khanh Hoa. Similarly, *D. sylvatica*, which appeared in three locations, had a much larger number of dead trees in Binh Dinh and Khanh Hoa than in Ha Tinh.

All species

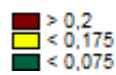
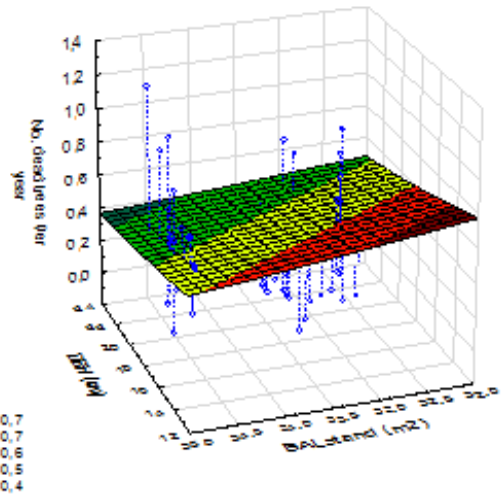


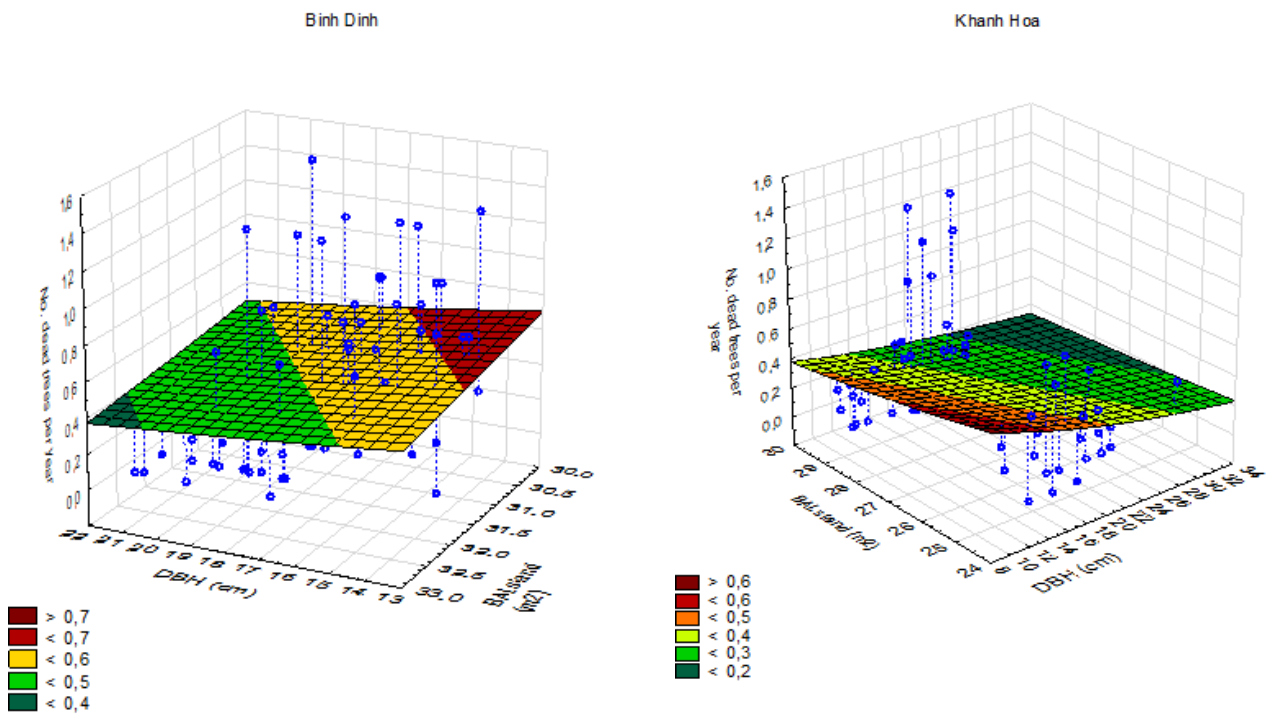
All important species

Ha Tinh

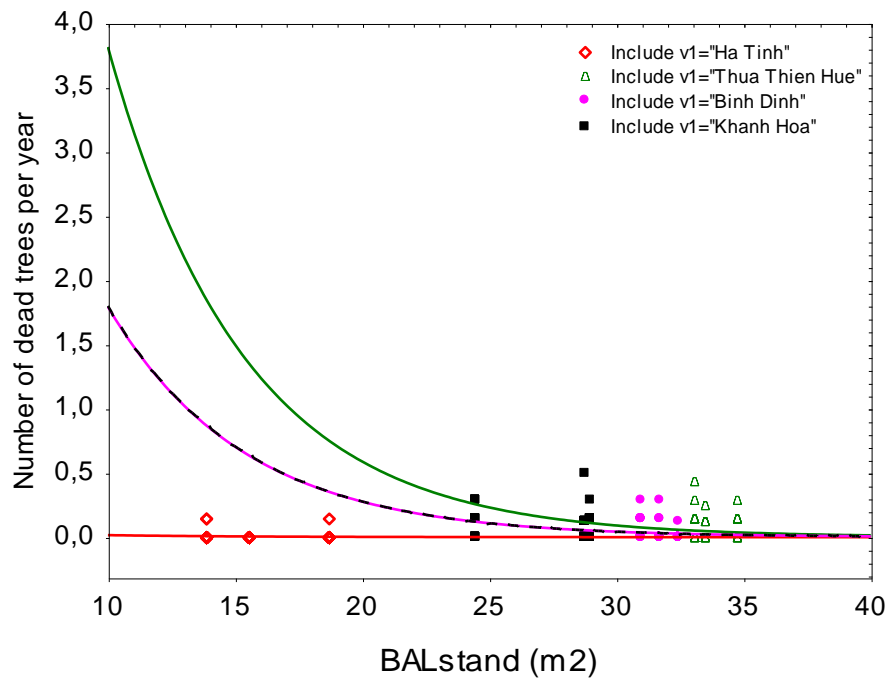


Thua Thien Hue





S. wightianum



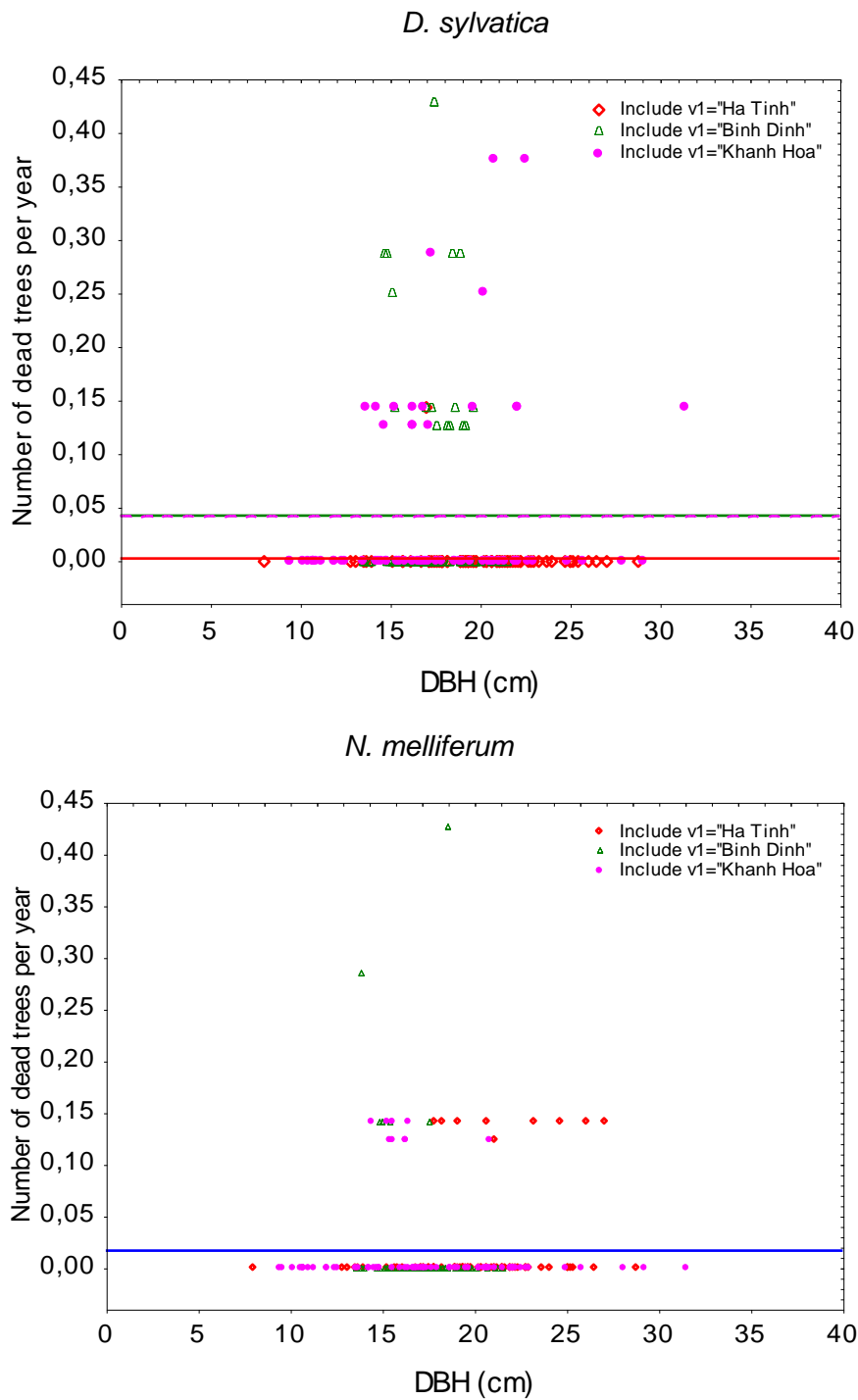


Figure 5.3 The number of dead trees per year from the final Negative Binomial GLM (lines), and real data (dots) of the two groups, *S. wightianum*, *D. sylvatica*, and *N. melliferum*.

5.2.3 Results of the GLMM

The significant negative effects of the *DBH* (for the dead trees of all important species) and *BAL_{stand}* (for the dead trees of two species groups) as predicted by the Negative Binomial GLM became insignificant under the Negative Binomial GLMM, leading to removal of those variables from the model. Thus, for all species and all important species, the respective fixed effects models (5.35) and (5.36), were compared to the following mixed effects models:

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \alpha_k + \log(\text{time}_{ij}) \quad (5.56)$$

$$\log(\mu_{ij}) = (\beta_0 + b_j) + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.57)$$

$$\log(\mu_{ij}) = \beta_0 + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.58)$$

For *S. wightianum*, the fixed effects model (5.37) was compared to four mixed effects models:

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \beta_1 \text{BAL}_{standij} + \alpha_k + \log(\text{time}_{ij}) \quad (5.59)$$

$$\log(\mu_{ij}) = \beta_0 + (\beta_1 + b_{1j}) \text{BAL}_{standij} + \alpha_k + \log(\text{time}_{ij}) \quad (5.60)$$

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \beta_1 \text{BAL}_{standij} + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.61)$$

$$\log(\mu_{ij}) = \beta_0 + \beta_1 \text{BAL}_{standij} + (\alpha_k + b_{kj}) + \log(\text{time}_{ij}) \quad (5.62)$$

while for *D. sylvatica*, the fixed effects model (5.38), along with candidate mixed effects models (5.56), (5.57), and (5.58) were assessed, and for *N. melliferum*, the fixed effects model (5.39) was compared to only one mixed effects model (5.63):

$$\log(\mu_{ij}) = (\beta_0 + b_j) + \log(\text{time}_{ij}) \quad (5.63)$$

Pearson's χ^2 values of fixed and mixed models for predicting the number of dead trees across all species, all important species, one important species (*S. wightianum*)

occurring in four, and two others (*D. sylvatica*, *N. melliferum*) found in three locations are presented in Table 5.7.

Table 5.7 A comparison of Pearson's χ^2 values between the fixed effects model and the mixed effects models. Selected models are bolded.

Objects	<i>n</i>	Equation	Model specification	Pearson's χ^2 Negative Binomial GLMM
All tree species	300	5.35	Fixed effects model (GLM)	330.35
		5.56	FM + plot intercept	289.50
		5.57	FM + plot intercept + plot slope (<i>provincecode</i>)	289.55
		5.58	FM + plot slope (<i>provincecode</i>)	289.55
All important tree species	300	5.36	Fixed effects model (GLM)	324.64
		5.56	FM + plot intercept	289.59
		5.57	FM + plot intercept + plot slope (<i>provincecode</i>)	289.68
		5.58	FM + plot slope (<i>provincecode</i>)	289.68
S. <i>wightianum</i>	300	5.37	Fixed effects model (GLM)	312.14
		5.59	FM + plot intercept	300.00
		5.60	FM + plot slope (<i>BAL_{stand}</i>)	300.00
		5.61	FM + plot intercept + plot slope (<i>provincecode</i>)	298.13
		5.62	FM + plot slope (<i>provincecode</i>)	298.13

Table 5.7 (continued)

Objects	<i>n</i>	Equation	Model specification	Pearson's χ^2 Negative Binomial GLMM
<i>D. sylvatica</i>	225	5.38	Fixed effects model (GLM)	216.80
		5.56	FM + plot intercept	225.00
		5.57	FM + plot intercept + plot slope (<i>provincecode</i>)	224.99
		5.58	FM + plot slope (<i>provincecode</i>)	224.99
<i>N. melliferum</i>	225	5.39	Fixed effects model (GLM)	235.47
		5.63	FM + plot intercept	223.50

Table 5.7 presents a comparison of selected models based on Pearson's χ^2 values. Here, we see that the Pearson's χ^2 statistic for the fixed model is significantly larger than that of mixed effects model, with the exception of one important species appearing in three places (*D. sylvatica*); a different conclusion to the one regarding the recruitment model in section 5.1.6 can be drawn. The Negative Binomial GLMM performed better than the Negative Binomial GLM. In similar fashion to the recruitment model, the mixed models with random intercept/random slope (*provincecode*) was not different from the mixed models with random slope (*provincecode*) effects. Therefore, the mixed model with a random slope was chosen for *S. wightianum* for it was simpler, while the mixed model with random intercept was selected as the equation for the direct prediction of dead trees across each of the two species groups, and for *N. melliferum*, because it had the smallest Pearson's χ^2 value (Table 5.7). For *D. sylvatica*, the fixed model using only the *provincecode* as a predictor (Equation 5.38) was used.

The summary statistics for the parameter estimations, standard deviation errors, and the p -values for the Negative Binomial GLMM are reported in Table 5.8. In general, for the two species groups, the number of dead trees in Thua Thien Hue and Binh Dinh was much greater than that in Ha Tinh, with the single exception of Khanh Hoa, where there was no significant difference when compared with Ha Tinh ($p > 0.05$). For *S. wightianum*, in Thua Thien Hue, Binh Dinh, and Khanh Hoa were significantly higher numbers of mortality in comparison with Ha Tinh.

For *N. melliferum*, there was no difference in the number of both recruits and dead trees in three provinces Ha Tinh, Binh Dinh, and Khanh Hoa.

The variance component of the random plot effects in Table 5.8 was rather small (from 7.22% to 25.77%); however, the random effect demonstrated evidence of unexplained variation at the plot level and provided a suitable adjustment for dispersion (the overdispersion parameter was more or less 1).

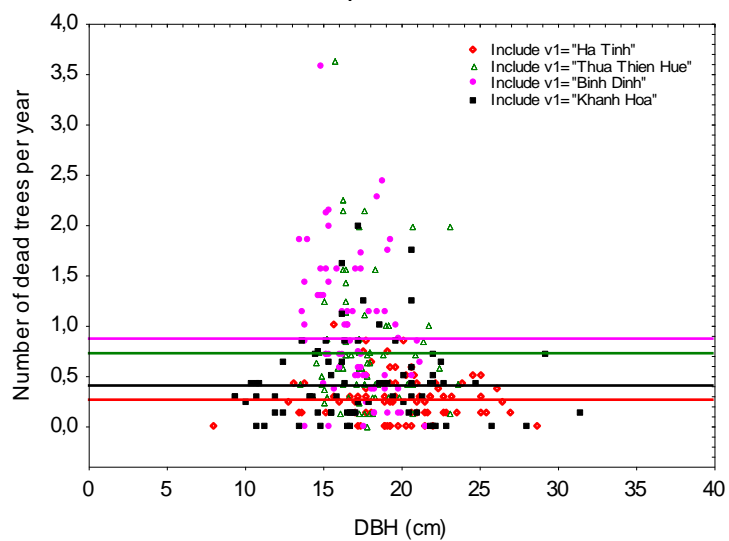
Table 5.8 Parameter estimates for the Negative Binomial GLMM across all species, all important species, and important species occurring in four or three provinces

Objects	Equation	Variables	Parameters	Fixed effects			Variance components			% variation explained by the plot	Overdispersion parameter	
				Parameter estimates	Std-error	Pr(> z)	$\sigma^2_{\text{ran-in}}$	$\sigma^2_{\text{ran-slop}}$	σ^2_{res}			
All species	5.56	Intercept	β_0	-1.3576	0.2586	0.0000						
		<i>Thua</i>										
		<i>Thien</i>			1.0295	0.3600	0.0212					
		<i>Hue</i>	α_k					0.1661	-	0.8138	16.95	0.9814
		<i>Binh Dinh</i>			1.2125	0.3595	0.0097					
		<i>Khanh</i>			0.4374	0.3627	0.2623					
<i>Hoa</i>												
All important species	5.56	Intercept	β_0	-2.1680	0.3048	0.0000						
		<i>Thua</i>										
		<i>Thien</i>			1.4325	0.4192	0.0091					
		<i>Hue</i>	α_k					0.2200	-	0.7779	22.04	0.9817
		<i>Binh Dinh</i>			1.4350	0.4191	0.0090					
		<i>Khanh</i>			0.9419	0.4218	0.0560					
<i>Hoa</i>												

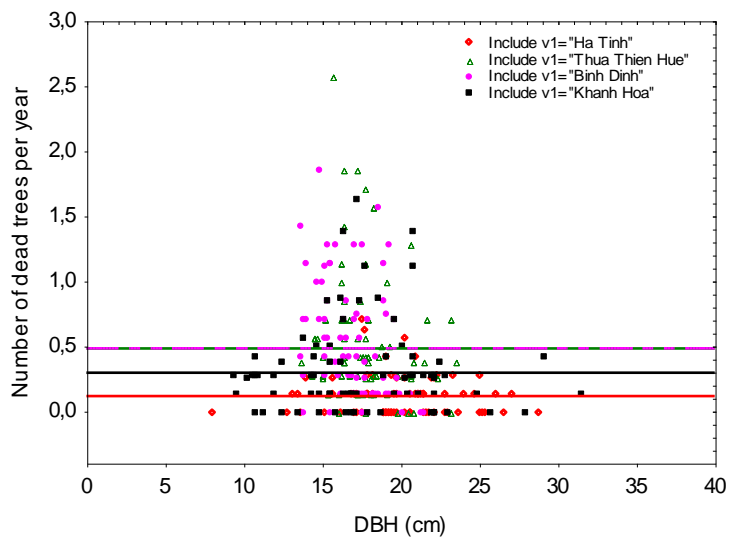
Table 5.8 (continued)

Objects	Equation	Variables	Fixed effects				Variance components			% variation explained by the plot	Overdispersion parameter
			Parameters	Parameter estimates	Std-error	Pr(> z)	$\sigma^2_{\text{ran-in}}$	$\sigma^2_{\text{ran-slop}}$	σ^2_{res}		
S. <i>wightianum</i>	5.62	Intercept	β_0	-2.5911	1.2212	0.0347	-	0.3476	1.0013	25.77	1.0141
		<i>BALstand</i>	β_1	-0.1670	0.0696	0.0475					
		<i>Thua</i>									
		<i>Thien</i>		5.1282	1.4038	0.0084					
		<i>Hue</i>	α_k								
		<i>Binh Dinh</i>		4.2865	1.3349	0.0152					
		<i>Khanh</i>		4.5158	0.9926	0.0026					
		<i>Hoa</i>									
N. <i>melliferum</i>	5.63	Intercept	β_0	-4.1223	0.2257	0.0000	0.0762	-	0.9793	7.22	1.0022

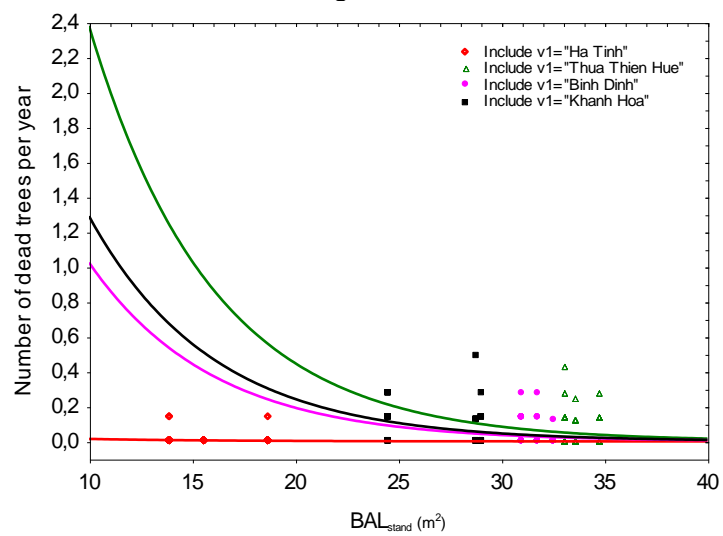
All species



All important species



S. wightianum



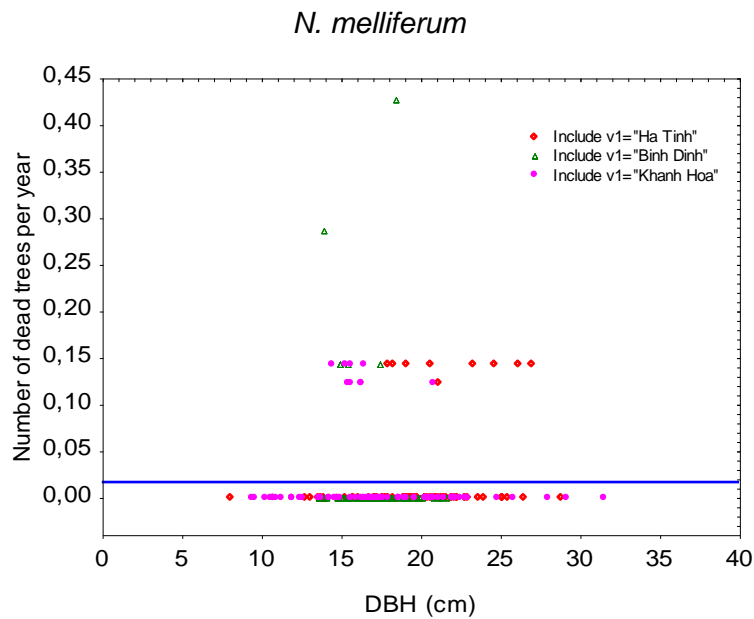


Figure 5.4 The annual number of dead trees from the Negative Binomial GLMM (lines), and observed data (dots) for the two species groups, *S. wightianum*, and *N. melliferum*.

5.3 Discussion

In recruitment and mortality modeling, the explained variable is a count and its distribution is usually characterized by a large number of zeros; a standard Poisson distribution is consequently inaccurate. To overcome this obstacle, we applied both generalized linear and generalized linear mixed models to analyze the recruitment and mortality models in this study. First, after fitting the GLM, we found that the Negative Binomial GLM was the best model to predict the number of recruitment and dead trees across all species, all important species, and important species occurring in three or four provinces. Given the analysis of the count data (i.e., the number of recruitment and dead trees), a log link was recommended; the Negative Binomial GLM was most suitable for this data. This finding coincides with Affleck's (2006) conclusion that Negative Binomial regression can be used for the analysis of stand-level mortality in Virginia and North Carolina. Moreover, the Negative Binomial model comprises a second parameter (known as the dispersion parameter), which is used to accommodate Poisson overdispersion. The *DBH* was additionally found to be the most significant explanatory variable in expressing the relationship between recruitment and

tree size, and had a negative effect on the number of recruits; in comparison, the stand basal area (BAL_{stand}) was the most significant negative contribution to the mortality model. We realized that the mean numbers of recruits and dead trees were different in the four different locations. Interestingly, both the number of recruits and dead trees in Thua Thien Hue were the highest, while in Ha Tinh these were the lowest in two cases (all species and all important species) (Figure 5.1, 5.3). Second, after fitting the Negative Binomial GLMM, we can conclude that it can handle overdispersion via a random effect.

5.3.1 Recruitment model

The final Negative Binomial GLM predicting the number of recruits included both the DBH as continuous and provinces (*provincecode*) as categorical variables. From the fixed factor *provincecode*, our model represented a difference in the number of recruits among the four provinces. The model indicated a negative effect of the DBH on the number of recruits; similar results were reported by Zhang *et al.* (2012), Lexerød (2005) (using the basal area mean diameter), and Klopčič *et al.* (2012) (using the quadratic diameter).

In the present study, the number of recruits declined dramatically for smaller trees and more slowly for larger trees. In uneven-aged forest stands, a high mean stand diameter often reveals a lower light availability which may be particularly low in the understory where young trees could potentially be recruited. A larger mean stand diameter thus usually results in a lower number of recruitment trees (Klopčič *et al.*, 2012). Furthermore, the subplot and the stand basal area, important stand characteristics, were not significant in our model. This finding is contrary to previous studies such as Vanclay (1992), Lexerød (2005), Fortin and DeBlois (2007), Timilsina (2010), Klopčič *et al.* (2012), and Zhang (2012), where stand basal area or its *log* transformation were significant. Another insignificant predictor in the present model was the number of trees per subplot, while the stand density was significant in Lexerød (2005), Timilsina (2010), and Zhang's (2012) respective models.

There are several possible reasons for this model's poor performance. First, our sample was rather small; it only contained 300 subplots (each covering 400 m²) from 12 one-hectare plots in four locations. In comparison, there were 217 permanent sample plots with a measurement history of up to 40 years in Vanclay's 1992 study; Lexerød (2005) likewise used a dataset from circular permanent plots (100 m²) with permanent plots covering a forested area of Norway in a 3 km x 3 km grid. In similar fashion, Zhang *et al.*'s 2012 study consisted of 132 square plots (0.067 hectare each) obtained between 1986 and 2001 with a 5-year re-measurement interval.

The lack of information on site conditions may also have played an important role in the model's poor performance, as site index had a significant effect on the number of Norway spruce recruits in Lexerød's study (2005); in Vanclay's (1992) case, site quality was statistically significant for modeling recruitment in a tropical rain forest.

5.3.2 Mortality model

The Negative Binomial regression for the mortality model expressed in this chapter used variables BAL_{stand} and $provinceocde$ for all species, and DBH , BAL_{stand} and $provincecode$ for all important species as predictors in predicting mortality. The DBH had a negative sign, resulting in the high mortality of small diameter trees and suggesting that suppressed trees are more likely to be eliminated from stand level competition (Adame *et al.*, 2010); the negative DBH coefficient also indicated that stand mortality is more likely in forest stands with many small trees as compared to those with larger trees (Juknys *et al.*, 2006). This result was supported by Zhang *et al.* (2014) who likewise found that stand mortality was negatively associated with a stand arithmetic mean diameter among Chinese pines (*Pinus tabulaeformis*).

The stand basal area was suggested as a measure of two-sided competition that can take into account both the vertical competition for light and the horizontal competition for rooting space, water, and nutrients (Yang *et al.*, 2003). This indicator is a good measure of stand crowding because it accounts for both tree size and density. Trees in a stand with a larger basal area will experience more competition than those in another stand with a smaller stand basal area (Yang *et al.*, 2003). The number of dead trees

should grow along with the increase in the stand basal area as a result of competition pressure. In this study, however, the negative coefficient of the stand basal area demonstrated that with an increasing stand basal area, the number of dead trees decreased. This may imply that inter-specific competition does not cause tree mortality for these stands. Another study from Bravo *et al.* (2001) found that stand basal area was an insignificant predictor of Douglas-fir mortality across a range of stands.

5.3.3 Assessing the Negative Binomial GLMM

Plot level random effects on recruitment and mortality models can address some of the unexplained variation in these processes due to unobserved plot level variables, which included topography, soil, microclimate, nutrients, and moisture (Ma *et al.*, 2013).

For this study, overdispersion becomes an issue as a result of the huge number of zero counts. Because it can affect the regression parameters, overdispersion is dealt with here by using a generalized linear mixed model, treating a plot factor as a random effect and integrating the evoked overdispersion by this factor into the model. The Negative Binomial GLMM therefore appeared to be a suitable model due to its ability to capture overdispersion and within-plot correlation. This analysis illustrates that appropriate statistical models are effective in tackling the challenge of modeling recruitment and the association of dead trees with data that has a high frequency of zero captures.

In short, studies of the recruitment and mortality processes in forest stands, especially in tropical forests, are still rare. In this chapter, we have constructed generalized linear models (Quasi-Poisson, Negative Binomial regressions) and a generalized linear mixed model (Negative Binomial mixed model) to analyze the recruitment and mortality models. These models have both advantages and disadvantages. On the one hand, we were able to use the Negative Binomial GLM and the Negative Binomial GLMM to improve our recruitment and mortality models; on the other hand, we did not have enough data to separate it into two parts, one part to fit model and the other to validate it. We understand that validating the model with independent data is important, and this will be implemented in the future research.

Literature cited

1. Adame, P., Del Río, M., Canellas, I., 2010. Ingrowth model for Pyrenean oak stands in northwestern Spain using continuous forest inventory data. *European Journal of Forest Research* 129, 669-678.
2. Affleck, D.L.R., 2006. Poisson mixture models for regression analysis of stand-level mortality. *Canadian Journal of Forest Research* 36, 2994-3006.
3. Álvarez González, J.G., Castedo Dorado, F., Ruíz González, A.D., López Sánchez, C.A., Gadow, K., 2004. A two-step mortality model for even-aged stands of *Pinus radiata* D. Don in Galicia (Northwestern Spain). *Annals of Forest Science* 61, 439-448.
4. Bravo, F., Hann, D.W., Maguire, D.A., 2001. Impact of competitor species composition on predicting diameter growth and survival rates of Douglas-fir trees in southwestern Oregon. *Canadian Journal of Forest Research* 31, 2237-2247.
5. Cameron, A.C., Trivedi, P.K., 1998. Regression analysis of count data. Cambridge University Press, 411 pp.
6. Carey, E.V., Brown, S., Gillespie, A.J.R., Lugo, A.E., 1994. Tree mortality in mature lowland tropical moist and tropical lower montane moist forests of Venezuela. *Biotropica* 26, 255-265.
7. Cox, D.R., 1983. Some remarks on overdispersion. *Biometrika* 70, 269-274.
8. Crawley, M.J., 2007. The R book. John Wiley & Sons Ltd, The Atrium, Southern Gate, Chichester, West Sussex PO19 8SQ, England.
9. Dalgaard, P., 2008. Introductory Statistics with R. Springer Science+Business Media, LLC, 370 pp.

10. Diéguez-Aranda, U., Castedo Dorado, F., Álvarez González, J.G., Rodríguez-Soalleiro, R., 2005. Modelling mortality of Scots pine (*Pinus sylvestris* L.) plantations in the northwest of Spain. *European Journal of Forest Research* 124, 143-153.
11. Eid, T., Tuhus, E., 2001. Models for individual tree mortality in Norway. *Forest Ecology and Management* 154, 69-84.
12. Faraway, J.J., 2006. *Extending the linear model with R, Generalized linear, Mixed effects and nonparametric regression models*. Taylor & Francis Group, LLC.
13. Fortin, M., Deblois, J., 2007. Modeling tree recruitment with zero-inflated models: The example of hardwood stands in southern Quebec, Canada. *Forest science* 53, 529-539.
14. Fridman, J., Stahl, G., 2004. A three-step approach for modelling tree mortality in Swedish Forests. *Scandinavian Journal of Forest Research* 16, 455-466.
15. Hasenauer, H., Merkl, D., Weingartner, M., 2001. Estimating tree mortality of Norway spruce stands with neural networks. *Advances in Environmental Research* 5, 405-414.
16. Hilbe, J.M., 2011. *Negative binomial regression*, 2nd edition. Cambridge university press.
17. Hu, M., Pavlicova, M., Nunes, E.V., 2011. Zero-inflated and Hurdle models of count data with extra zeros: Examples from an HIV-risk reduction intervention trial. *Am J Drug Alcohol Abuse* 37, 367-375.
18. Juknys, R., Vencloviene, J., Jurkonist, N., Bartkevicius, E., Sepetiene, J., 2006. Relation between individual tree mortality and tree characteristics in a polluted and non-polluted environment. *Environment Monitoring and Assessment* 121, 519-542.

19. LexerØd, N.L., 2005. Recruitment models for different tree species in Norway. *Forest Ecology and Management* 206, 91-108.
20. Klopčič, M., Poljanec, A., Bončina, A., 2012. Modelling natural recruitment of European beech (*Fagus sylvatica* L.). *Forest Ecology and Management* 284, 142-151.
21. Ma, Z., Peng, C., Li, W., Zhu, Q., Wang, W., Song, X., Liu, J., 2013. Modeling individual tree mortality rates using marginal and random effects regression models. *Natural Resource Modeling* 26, 131-153.
22. McCarthy, J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environmental Reviews* 9, 1-59.
23. Meng, Q., Cieszewski, C.J., Lowe, R.C., Zasada, M., 2003. A three-step approach to model tree mortality in the State of Georgia. Fifth Annual Forest Inventory and Analysis Symposium, United States Department of Agriculture. Forest Service, New Orleans, Louisiana, pp. 91-96.
24. Monserud, R.A., Sterba, H., 1999. Modeling individual tree mortality for Austrian forest species. *Forest Ecology and Management* 113, 109-123.
25. O'Hara, R.B., Kotze, D.J., 2010. Do not log-transform count data. *Methods in Ecology and Evolution*.
26. Oliver, C.D., Larson, B.C., 1996. *Forest stand dynamics: Update edition*. John Wiley & Sons, Inc., New York, 540 pp.
27. Rüger, N., Huth, A., Hubbell, S.P., Condit, R., 2011. Determinants of mortality across a tropical lowland rainforest community. *Oikos* 120, 1047-1056.
28. Schweiger, J., Sterba, H., 1997. A model describing natural regeneration recruitment of Norway spruce (*Picea abies* (L.) Karst.) in Austria. *Forest Ecology and Management* 97, 107-118.

29. Timilsina, N., 2010. Simulation modeling to test different harvest regimes for stand conversion in southern pine. PhD thesis, University of Florida, 216 pp.
30. Vanclay, J.K., 1992. Modelling regeneration and recruitment in a tropical rain forest. *Canadian Journal of Forest Research* 22, 1235-1248.
31. Vanclay, J.K., 1994. Modelling forest growth and yield: Application to mixed tropical forests. CAB International, Wallingford, UK.
32. Vuong, Q.H., 1989. Likelihood ratio tests for model selection and non-nested hypotheses. *Econometrica* 57, 307-333.
33. Yang, Y., Titus, S.J., Huang, S., 2003. Modeling individual tree mortality for white spruce in Alberta. *Ecological Modelling* 163, 209-222.
34. Zhang, X., Lei, Y., Cai, D., Liu, F., 2012. Predicting tree recruitment with negative binomial mixture models. *Forest Ecology and Management* 270, 209-215.
35. Zhang, X., Lei, Y., Cai, D., Liu, X., 2014. Modeling stand mortality using Poisson mixture models with mixed-effects. *iForest-Biogeosciences and Forestry*.
36. Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York, NY, USA, 574 pp.
37. Zuur, A.F., Hilbe, J.M., Ieno, E.N., 2013. A beginner's guide to GLM and GLMM with R, a frequentist and Bayesian perspective for ecologists. Highland Statistics Ltd., Newburgh, United Kingdom, 256 pp.

Chapter 6 Conclusions

Studies of forest dynamics concentrate on those changes in the forest structure and composition over time which are primarily driven by three processes: growth, recruitment, and mortality. For this reason, stand dynamics studies frequently utilize data from permanent plots that record the fate of individual trees.

This study has aimed to describe changes occurring in the forest structure and tree species diversity over time and construct growth models in order to support the sustainable management of natural tropical forests in Vietnam. The models were developed using data from trees ≥ 6 cm *DBH* from 12 one-hectare permanent plots in four provinces. There are three model components: diameter increment, recruitment, and mortality.

For tropical forests with high tree species diversity, the development of the growth, recruitment, and mortality models necessitates a suitable grouping of tree species. In the present study, we used the importance value index (*IVI*) to group tree species; the *IVI* was computed by adding up three crucial traits of a particular species, namely, its relative density, relative frequency, and relative dominance. There are two species groups following our definition: important species ($IVI \geq 5\%$) and less important tree species ($IVI < 5\%$). This classification seems reasonable and can be utilized in the prediction of diameter increment, recruitment, and mortality. Additional models were developed for species which occurred in at least three of the four provinces to compare variation among plots and provinces.

In the third chapter, changes in the forest structure and tree species diversity over time were assessed. During a seven- and eight-year period, the stands demonstrated fairly stable ecological conditions. There were some slight variations in density, diversity indices, diversity profiles, and species-area relations, but these results indicated that those stands are developing and regeneration in the forests is present. In the years after the first census, the most noticeable trend was a decrease in almost all diversity indices, with the exceptions of plot 3 in Thua Thien Hue and plot 1 in Khanh Hoa, where the number of occurring tree species rose thanks to the occurrence of five new species in Thua Thien Hue plot 3 (*Actinodaphne pilosa*, *Aglaia tomentosa*, *Artocarpus*

rigidus, *Litsea vang* H., and *Peltophorum pterocarpum*) and one (*Alstonia scholaris*) in Khanh Hoa plot 1. For the ten other plots, the species richness was declined due to the disappearance of species, more precisely the loss of two species in Ha Tinh plot 1 (*Armesiodendron chinense* and *Microcos paniculata*), 10 species in plot 2 (*Actinodaphne pilosa*, *Annona squamosa*, *Aphanamixis polystachya*, *Baccaurea sapida*, *Croton tiglium*, *Cryptocarya annamensis*, *Machilus platycarpa*, *Michelia mediocris*, *Oroxylum indicum*, and *Pavieasia annamensis*), five species in Binh Dinh plot 2 (*Bischofia javanica* Bl., *Craibiodendro scleranthum*, *Cratoxylon formosum*, *Elaeocarpus grandifloras*, and *Ficus racemosa*), and one species in Khanh Hoa plot 2 (*Lithocarpus ducampii*).

Owing to the appearance and the disappearance of tree species, the estimated species-area curves in 12 plots changed between 2005 and 2012/2013: first, three of the five lowest estimated curves, namely of Ha Tinh plots 1 and 2 and Khanh Hoa plot 2 became closer; second, the rank between Thua Thien Hue plot 2 and Binh Dinh plot 2 changed. In the second inventory, 12 species-area curves are obviously classified into two groups, where group 1 contains Ha Tinh plot 3, Binh Dinh, and Thua Thien Hue, group 2 includes Ha Tinh plots 1 and 2 and Khanh Hoa. Moreover, the total number of species strictly increased with increasing area, which can be explained by the influence of environmental heterogeneity on the species-area relationship. The species-area curves for the 12 plots did not reach their asymptote at the one hectare plot size, which means that one could expect to record new tree species if the sample area would be further increased beyond 10,000 m². In this case, the species-area curve will reach an asymptote only if the number of environments reaches an asymptote at some spatial scale.

Tree species diversity varied considerably from province to province. The largest number of species per hectare was recorded in Binh Dinh plot 3 with 102 in 2005 and 101 in 2013, while only 46 (2005) and 47 (2012) species were found in Khanh Hoa plot 1. We used diversity indices and rank type diversity profiles to assess and compare the tree species diversity between four locations; we recommend using the latter because of their more stringent testing of diversity ordering. In our study, the conclusion was that intrinsic diversity of plots in Thua Thien Hue, Binh Dinh and Ha Tinh is larger than that of the Khanh Hoa plots.

In regard to the height-diameter relationship, the Chapman-Richards equation was for most of the plots more suitable than the seven remaining equations. The height curves stratified by three stories confirm a higher accuracy in tree height estimation, however the height curves of both important and less important tree species can be pooled without a notable loss in precision.

The analysis of tree diameter increment in tropical forests of Vietnam was presented in Chapter 4. Using remeasured tree data from all species in each province, the results indicated that the independent variable initial diameter $\ln(DBH_{2005})$ mostly influenced the annual diameter increment ADI . As potential explanatory variables we used the logarithm of initial diameter as tree size, and three competition indices (log-transformation of the subplot basal area, stand basal area, and ratio of basal area of k^{th} tree to subplot basal area) from the eight plots remeasured in 2012. On the four other plots, where coordinates of each tree in the plot were available, log-transformation of the overtopping basal area and overtopping diameter were also analyzed. When fitting different forms of growth equations, the competition indices did not show clear trends in most cases: they were sometimes positive, sometimes negative, and mostly non-significant in the growth model, whereas an obvious negative effect was expected, e.g, a negative parameter for basal area of larger trees implied that an increase in competition leads to a reduction in the diameter increment. Due to the unclear and most often insignificant competition indices, the final function of the periodic annual diameter increment consisted of only one (mostly significant) predictor $\ln ADI_k = \beta_0 + \beta_1 \ln DBH_{2005k} + \varepsilon_k$. The slope parameter of almost all individual important species, all important species and all others in each province had the expected sign – a negative regression coefficient, suggesting that the periodic annual diameter increment declines with increasing tree diameter. However, the slope parameter was significant for only 39 of the 67 individual important species; for the other species with insignificant slopes, the periodic annual diameter increment can be assumed to remain at least approximately constant from 6 cm to 100 cm DBH , and the simple growth model $ADI_k = \exp(\beta_0 + \varepsilon_k)$ holds.

Another noteworthy point in this chapter was that the minor difference between the real (rounded at two digits after decimal point) and rounded data (to an integer) cannot

produce misleading models of diameter increment, thus, we felt free to round the data collected in 2013 on only one plot in each province to an integer to get a consistent data set for modelling purposes.

For the four important species *S. wightianum*, *G. subaequalis*, *D. sylvatica*, and *N. melliferum*, which appeared in at least three of the four locations, as expected, the linear mixed effects model significantly improved model fit compared to the fixed effects linear regression. Although the small distances between plots within a province and the comparably large distances between the provinces, the variation among plots is very large compared to the variation among provinces. Therefore, the linear mixed effects models with plots as random effects on intercepts and slopes were selected and they could in almost all cases account for random variation in the periodic annual diameter increment. On account of mostly insignificant trends of the competition indices, the simple linear mixed effects models were used, which only use $\ln(DBH_{2005})$ as a covariate, however, through the mixed effects model, the spatial correlation between trees on the same plot, the sources of unexplained variation (e.g., pure error), and unobserved variables (e.g. other environmental data) could be explained via the fitting of random effects for plot-to-plot variation. The variance explained by the random plot effects varied from 85.09% to 90.02%.

The results of Chapter 5 suggest that we successfully developed the recruitment and mortality models by using both generalized linear and generalized linear mixed models for count data to address the problem of overdispersion. Five explanatory variables, including arithmetic mean diameter of the subplot, subplot and plot basal area, subplot density, and provinces as a categorical variable were examined. With the generalized linear model, we found that the Negative Binomial GLM was the most appropriate model for predicting the number of recruitment and dead trees across all species, all important species, and important species which appeared in three or four locations (*S. wightianum*, *D. sylvatica*, and *S. wightianum*). The diameter was found to be the most significant explanatory variable in expressing the relationship between recruitment and tree size, and had a negative effect on the number of recruits; in comparison, the stand basal area was the most significant negative contribution to the mortality model. From using the provinces as a grouping variable, we realized that the mean numbers of recruits and dead trees were different in the four different locations, namely both the

number of recruits and dead trees in Thua Thien Hue were the highest, while in Ha Tinh these were the lowest in two cases (all species and all important species).

With the generalized linear mixed model, the Negative Binomial GLMM solves overdispersion by treating a plot as a random effect. The GLMM with the random plot effects on the intercept was only chosen to predict the number of recruits for *S. wightianum* and *D. sylvatica*, where neither the GLM nor the GLMMs include any significant explanatory variable. The random plot effects on the intercept in the model contributed from 14.69% to 65.92% to the total unexplained variation. For the mortality model, in similar fashion to the recruitment model, the Negative Binomial GLMM with a random slope was selected for *S. wightianum*, while the mixed model with random intercept was selected for the direct prediction of dead trees across each of the two species groups, and for *N. melliferum*. The variance component of the random plot effects was from 7.22% to 25.77%, it demonstrated evidence of intra-plot correlation and provided a suitable adjustment for dispersion.

Appendice

Appendix I

Species ranking by their Importance value index (*IVI*) (trees DBH \geq 6 cm) of pooled plots in four provinces

Appendix I

Ha Tinh

Species	Abundance (n/3ha)	Dominance (m ²)	Frequency (%)	IVI (%)
<i>Gironniera subaequalis</i>	115	7.57	68	28.8
<i>Vatica odorata</i>	93	4.87	61	21.8
<i>Calophyllum calaba</i>	105	5.12	47	21.8
<i>Nephelium melliferum</i>	59	3.43	43	14.8
<i>Knema cortiosa</i>	58	1.76	49	12.6
<i>Alangium ridleyi</i>	48	2.74	35	11.9
<i>Syzygium wightianum</i>	42	1.47	33	9.2
<i>Hydnocarpus ilicifolia</i>	40	1.45	31	8.8
<i>Lithocarpus annamensis</i>	24	2.28	28	8.5
<i>Wrightia annamensis</i>	33	1.38	27	7.7
<i>Marcaranga denticulata</i>	46	0.78	21	7.2
<i>Syzygium jambos</i>	30	0.98	31	7.1
<i>Cryptocarya lenticellata</i>	29	0.88	32	7.0
<i>Hydnocarpus annamensis</i>	22	1.28	17	5.7
<i>Cinnamomum obtusifolium</i> A. Chev	18	0.93	23	5.3
<i>Engelhardtia roxburghiana</i> Wall	10	2.01	11	5.2
<i>Diospyros sylvatica</i>	25	0.51	23	5.2
<i>Canarium nigrum</i> Engler	14	1.20	15	4.6
<i>Endospermum chinense</i>	12	1.16	15	4.4
<i>Aphanamixis polystachya</i>	9	1.27	12	4.0
<i>Symplocos sumuntia</i>	16	0.33	20	3.8
<i>Ormosia balansae</i> Drake	14	0.51	17	3.7
<i>Cinnamomum parthenoxylum</i>	13	0.62	13	3.4
<i>Canarium album</i>	12	0.82	11	3.4
<i>Archidendron clypearia</i>	14	0.44	15	3.3
<i>Canarium bengalense</i>	8	0.74	11	2.9
<i>Garcinia oliveri</i>	9	0.44	11	2.5
<i>Quercus dealbatus</i>	8	0.72	7	2.5
<i>Glenniea philippinensis</i>	11	0.38	8	2.3
<i>Manglietia conifera</i>	11	0.35	8	2.3
<i>Chinsocheton paniculatus</i>	9	0.52	5	2.1

<i>Elaeocarpus griffithii</i>	8	0.32	9	2.1
<i>Helicia cochinchinensis</i>	10	0.19	9	2.1
<i>Polyalthia lauii</i>	9	0.31	8	2.0
<i>Erythrophleum fordii</i>	9	0.29	8	2.0
<i>Alphonsea gaudichaudiana</i>	8	0.18	11	2.0
<i>Lithocarpus ducampii</i> Hickel et A.camus	4	0.68	5	2.0
<i>Litsea verticillata</i>	7	0.40	5	1.8
<i>Quercus platycalyx</i> Hickel et camus	7	0.31	7	1.8
<i>Cryptocarya chingii</i>	8	0.42	4	1.8
<i>Archidendro eberhardtii</i>	7	0.29	7	1.7
<i>Manglietia dandyi</i>	6	0.24	7	1.6
<i>Lindera caudata</i>	7	0.18	7	1.5
<i>Machilus odoratissima</i>	4	0.40	5	1.5
<i>Engelhardtia serrata</i>	4	0.46	4	1.5
<i>Actinodaphne obovata</i>	5	0.24	7	1.5
<i>Castanopsis carlesii</i>	5	0.22	7	1.4
<i>Prunus arborea</i>	4	0.30	5	1.4
<i>Aglaia tomentosa</i>	4	0.38	4	1.3
<i>Ficus oligodon</i>	5	0.23	5	1.3
<i>Manglietia balansae</i>	4	0.28	5	1.3
<i>Symplocos cochinchinensis</i>	5	0.14	7	1.3
<i>Machilus platycarpa</i>	3	0.47	3	1.3
<i>Litsea mollifolia</i>	4	0.23	5	1.2
<i>Ficus racemosa</i>	5	0.07	7	1.2
<i>Antidesma ghasembilla</i>	5	0.13	5	1.2
<i>Annona squamosa</i>	4	0.24	4	1.1
<i>Orthosiphon stamineus</i> Benth	5	0.18	4	1.1
<i>Baccaurea sapida</i>	4	0.14	5	1.1
<i>Litsea cubeba</i>	4	0.12	5	1.1
<i>Machilus bonii</i> H.Lec	4	0.09	5	1.0
<i>Castanopsis indica</i>	2	0.35	3	1.0
<i>Ficus drupacea</i>	4	0.07	5	1.0
<i>Antheroporum pierrei</i> Gagnep	4	0.16	3	0.9
<i>Styrax annamensis</i> Guill	3	0.11	4	0.8
<i>Litsea glutinosa</i>	3	0.11	4	0.8
<i>Actinodaphne ferruginea</i>	1	0.35	1	0.8
<i>Calophyllum touranense</i>	3	0.17	3	0.8
<i>Symplocos poilanei</i>	2	0.20	3	0.8
<i>Cryptocarya annamensis</i>	3	0.04	4	0.7
<i>Coffea dewevrei</i>	2	0.15	3	0.7
<i>Peltophorum pterocarpum</i>	2	0.13	3	0.6
<i>Cinnamomum camphora</i>	2	0.13	3	0.6
<i>Archidendron balansae</i>	2	0.11	3	0.6

<i>Artocarpus tonkinensis</i>	2	0.08	3	0.6
<i>Croton tiglium</i>	2	0.06	3	0.5
<i>Firmiana simplex</i>	2	0.05	3	0.5
<i>Rauvolfia vietnamensis</i>	2	0.05	3	0.5
<i>Senna siamea</i>	2	0.05	3	0.5
<i>Eurya ciliata</i>	2	0.04	3	0.5
<i>Beilschmiedia percoriacea</i>	2	0.04	3	0.5
<i>Ormosia hoanense</i>	1	0.17	1	0.5
<i>Schefflera heptaphylla</i>	2	0.09	1	0.5
<i>Madhuca pasquieri</i>	1	0.13	1	0.4
<i>Clausena dunniana</i>	2	0.06	1	0.4
<i>Diospyros apiculata</i>	2	0.06	1	0.4
<i>Parashorea spirei</i>	1	0.10	1	0.4
<i>Litsea cambodiana</i>	1	0.08	1	0.3
<i>Calophyllum soulatti</i>	1	0.07	1	0.3
<i>Alangium chinense</i>	1	0.06	1	0.3
<i>Bombax malabarica</i>	1	0.06	1	0.3
<i>Garcinia cowa</i>	1	0.04	1	0.3
<i>Armesiondendron chinense</i>	1	0.03	1	0.3
<i>Ilex cymosa</i>	1	0.03	1	0.3
<i>Symplocos anomala</i>	1	0.03	1	0.3
<i>Saurauia napaulensis</i>	1	0.03	1	0.3
<i>Cinnamomum micranthum</i>	1	0.02	1	0.3
<i>Sapium discolor</i>	1	0.02	1	0.3
<i>Trevesia palmata</i>	1	0.02	1	0.3
<i>Cinnamomum ovatum</i>	1	0.02	1	0.2
<i>Illicium verum</i>	1	0.02	1	0.2
<i>Cratoxylon formosum</i>	1	0.02	1	0.2
<i>Microdesmis caseariaefolia</i>	1	0.01	1	0.2
<i>Syzygium zeylanicum</i> (L.) DC.	1	0.01	1	0.2
Sum	1,198	60.71		300

Species	Abundance (n/3ha)	Dominance (m²)	Frequency (%)	IVI (%)
<i>Canarium album</i>	202	13.06	81	19.1
<i>Syzygium zeylancium</i>	212	12.10	85	18.9
<i>Syzygium wightianum</i>	236	4.99	97	14.8
<i>Symplocos poilanei</i>	151	4.19	73	10.7
<i>Gyrocarpus americanus</i>	75	6.96	57	9.8
<i>Gironniera subaequalis</i>	148	2.66	81	9.8
<i>Ormosia pinnata</i>	113	4.15	57	8.9
<i>Syzygium chanlos</i>	113	3.72	57	8.5
<i>Shorea roxburghii</i>	80	5.25	53	8.5
<i>Machilus platycarpa</i>	107	3.26	63	8.2
<i>Cassine glauca</i>	96	2.43	71	7.6
<i>Cinnamomum parthenoxylum</i>	84	3.17	55	7.2
<i>Eurycoma longifolia</i>	108	1.43	57	6.7
<i>Engelhardtia roxburghiana</i> Wall	51	3.91	48	6.4
<i>Polyalthia nemoralis</i> DC	101	1.22	60	6.4
<i>Adina cordifolia</i>	75	1.96	65	6.4
<i>Polyalthia cerasoides</i>	96	1.16	60	6.2
<i>Knema tonkinensis</i>	80	1.66	60	6.1
<i>Paranephelium spirei</i>	60	3.02	48	6.0
<i>Lithocarpus ducampii</i> Hickel et A.camus	42	3.57	41	5.6
<i>Cinnamomum cambodianum</i>	64	1.68	49	5.2
<i>Nephelium melliferum</i>	55	1.49	51	4.9
<i>Schefflera heptaphylla</i>	57	1.42	47	4.7
<i>Xerospermum noronhiana</i>	46	2.11	40	4.6
<i>Glycosmis citrifolia</i> Willd Lindl	47	1.88	43	4.6
<i>Stereospermum colais</i>	30	3.10	27	4.3
<i>Diospyros sylvatica</i>	42	1.44	43	4.1
<i>Castanopsis indica</i>	38	2.10	33	4.1
<i>Cratoxylum pruniflorum</i>	38	1.61	33	3.7
<i>Polyalthia thorelii</i> (Pierre) Fin. & Gagn	31	1.50	35	3.5
<i>Elaeocarpus griffithii</i>	37	0.97	33	3.2
<i>Ormosia balansae</i> Drake	22	1.52	24	2.8
<i>Dipterocarpus retusus</i>	11	2.55	13	2.8
<i>Armesiodendron chinense</i>	30	0.84	28	2.7
<i>Prunus arborea</i>	22	1.25	23	2.5
<i>Aglaia spectabilis</i>	32	0.73	21	2.4
<i>Actinodaphne obovata</i>	8	2.16	11	2.3
<i>Saurauia napaulensis</i>	21	1.00	21	2.3
<i>Knema pierrei</i>	22	0.61	27	2.2

<i>Litsea verticillata</i>	20	0.90	21	2.2
<i>Michelia mediocris</i>	22	0.95	19	2.1
<i>Endospermum chinense</i>	12	1.37	13	1.9
<i>Pavieasia annamensis</i>	16	0.80	17	1.8
<i>Hopea siamensis</i>	16	0.65	19	1.7
<i>Malus doumeri</i>	12	1.09	13	1.7
<i>Madhuca pasquieri</i>	16	0.83	15	1.7
<i>Aphanamixis polystachya</i>	21	0.28	20	1.7
<i>Diospyros apiculata</i>	22	0.28	17	1.6
<i>Canarium bengalense</i>	15	0.78	13	1.6
<i>Alangium ridleyi</i>	14	0.82	12	1.5
<i>Koilodepas longifolium</i>	16	0.31	17	1.4
<i>Sterculia lanceolata</i>	16	0.30	15	1.3
<i>Canthium dicoccum</i>	14	0.19	16	1.2
<i>Microcos paniculata</i>	12	0.26	16	1.2
<i>Actinodaphne pilosa</i>	9	0.68	8	1.1
<i>Archidendron clypearia</i>	10	0.33	13	1.1
<i>Castanopsis carlesii</i>	9	0.73	7	1.1
<i>Cinnamomum ovatum</i>	13	0.49	8	1.1
<i>Litsea glutinosa</i>	9	0.54	9	1.1
<i>Cinnamomum obtusifolium</i> A. Chev	10	0.27	13	1.1
<i>Mangifera minitifolia</i>	9	0.37	11	1.0
<i>Erythrophleum fordii</i>	4	0.87	5	1.0
<i>Castanopsis crassifolia</i>	7	0.50	9	1.0
<i>Chisocheton paniculatus</i>	10	0.30	11	1.0
<i>Wrightia annamensis</i>	11	0.28	9	0.9
<i>Saraca indica</i>	6	0.49	8	0.9
<i>Aglaia tomentosa</i>	7	0.49	7	0.9
<i>Glenniea philippinensis</i>	3	0.82	3	0.8
<i>Litsea vang</i> H.	9	0.04	12	0.8
<i>Artocarpus tonkinensis</i>	8	0.11	11	0.8
<i>Antheroporum pierrei</i> Gagnep	6	0.31	8	0.7
<i>Microdesmis caseariaefolia</i>	6	0.17	8	0.6
<i>Breynia fruticosa</i>	6	0.13	8	0.6
<i>Gonocaryum maclurei</i>	6	0.09	7	0.5
<i>Tarrietia javanica</i>	5	0.17	5	0.5
<i>Quercus platycalyx</i> Hickel et camus	4	0.21	5	0.5
<i>Canarium nigrum</i> Engler	5	0.16	5	0.5
<i>Schima wallichii</i>	3	0.33	3	0.4
<i>Garcinia oliveri</i>	5	0.17	4	0.4
<i>Aidia oxyodonta</i>	5	0.09	5	0.4
<i>Homalocladium platycladum</i>	4	0.12	5	0.4
<i>Dipterocarpus alatus</i>	2	0.32	3	0.4

<i>Rauvolfia reflexa</i>	4	0.07	5	0.4
<i>Quercus incana</i>	3	0.07	4	0.3
<i>Sapium discolor</i>	1	0.27	1	0.3
<i>Mangifera indica</i>	2	0.10	3	0.2
<i>Lantana camara</i>	2	0.09	3	0.2
<i>Vitex canescens</i>	2	0.08	3	0.2
<i>Ulmus lancifolia</i>	2	0.06	3	0.2
<i>Dillenia turbinata</i>	2	0.04	3	0.2
<i>Barringtonia fusicarpa</i>	2	0.03	3	0.2
<i>Machilus leptophylla</i>	2	0.03	3	0.2
<i>Muntingia calabura</i>	2	0.03	3	0.2
<i>Alstonia scholaris</i>	2	0.02	3	0.2
<i>Artocarpus rigidus</i>	2	0.01	3	0.2
<i>Baccaurea sapida</i>	1	0.10	1	0.2
<i>Ligustrum lucidum</i>	1	0.05	1	0.1
<i>Clausena lansium</i>	1	0.04	1	0.1
<i>Trema orientalis</i>	1	0.04	1	0.1
<i>Archidendro eberhardtii</i>	1	0.03	1	0.1
<i>Elaeocarpus lanceifolius</i>	1	0.02	1	0.1
<i>Melanorrhoea laccifera</i>	1	0.02	1	0.1
<i>Calophyllum touranense</i>	1	0.02	1	0.1
<i>Diospyros decandra</i>	1	0.02	1	0.1
<i>Xanthophyllum annamense</i>	1	0.02	1	0.1
<i>Strobilanthes acrocephalus</i>	1	0.01	1	0.1
<i>Syzygium jambos</i>	1	0.01	1	0.1
<i>Peltophorum pterocarpum</i>	1	0.00	1	0.1
Sum	3,359	134.47		300

Species	Abundance (n/3ha)	Dominance (m ²)	Frequency (%)	IVI (%)
<i>Parashorea chinensis</i> Wang Hsie	439	24.61	96	37.8
<i>Syzygium zeylanicum</i>	166	6.53	75	13.9
<i>Diospyros sylvatica</i>	146	5.10	65	11.7
<i>Hopea pierei</i>	144	4.22	67	11.0
<i>Scaphium macropodum</i>	117	4.02	79	10.6
<i>Quercus dealbatus</i>	88	3.74	65	8.8
<i>Syzygium wightianum</i>	111	2.87	64	8.8
<i>Lithocarpus ducampii</i> Hickel et A.camus	82	4.45	53	8.6
<i>Nephelium melliferum</i>	91	3.08	59	8.1
<i>Ilex rotunda</i> Thunb	82	4.10	47	8.0
<i>Hydnocarpus althemintica</i>	93	1.87	69	7.7
<i>Intsia bijuga</i>	35	5.82	27	6.9
<i>Dillenia scabrella</i> Roxb	53	3.85	39	6.5
<i>Machilus bonii</i> H.Lec	70	2.08	56	6.5
<i>Melanorrhoea laccifera</i>	55	3.06	47	6.3
<i>Gironniera subaequalis</i>	71	1.60	56	6.1
<i>Artocarpus rigidus</i>	49	2.65	47	5.8
<i>Artocarpus styracifolius</i>	49	1.56	33	4.3
<i>Osmanthus matsumuranus</i>	41	1.63	33	4.1
<i>Polyalthia nemoralis</i> DC	45	0.91	41	4.1
<i>Dipterocarpus alatus</i>	56	1.63	20	4.0
<i>Garcinia oliveri</i>	34	1.71	32	3.9
<i>Garcinia oblongifolia</i> Champ	24	2.19	27	3.7
<i>Vatica odorata</i>	31	1.03	32	3.3
<i>Pterospermum heterophyllum</i> Hance	31	1.26	27	3.2
<i>Adina cordifolia</i>	34	0.95	29	3.2
<i>Schefflera octophylla</i>	27	1.07	31	3.1
<i>Picrasma javanica</i>	33	0.68	32	3.1
<i>Helicia cochinchinensis</i>	28	1.01	29	3.1
<i>Clethra delavayi</i>	26	1.31	24	3.0
<i>Adina pilulifera</i>	32	0.91	23	2.8
<i>Symplocos cochinchinensis</i>	29	0.78	25	2.7
<i>Wringtia annamensis</i> Eberh. Et Dub	46	0.79	13	2.7
<i>Xylopiavielana</i>	30	0.52	28	2.7
<i>Canarium album</i>	24	0.72	28	2.6
<i>Enicosanthellum</i> sp.	27	0.66	24	2.5
<i>Vitex trifoliata</i>	24	0.97	19	2.4
<i>Symplocos anomala</i>	22	0.53	25	2.3
<i>Symplocos</i> sp	24	0.40	24	2.2

<i>Litsea laucilimba</i>	22	0.51	23	2.2
<i>Aidia oxyodonta</i>	21	0.38	23	2.0
<i>Microcos paniculata</i>	18	0.64	17	1.9
<i>Aglaia gigantea</i> Pellegrin	12	1.24	11	1.9
<i>Elaeocarpus apiculatus</i>	19	0.69	13	1.8
<i>Tarrietia javanica</i>	12	0.89	15	1.8
<i>Machilus ichangensis</i>	13	0.72	13	1.6
<i>Dialium cochinchinensis</i>	11	0.72	12	1.5
<i>Pholidota argusa</i>	14	0.59	12	1.5
<i>Schima superba</i>	13	0.50	13	1.4
<i>Calophyllum poilanei</i>	14	0.29	16	1.4
<i>Elaeocarpus griffithii</i> Mast	15	0.62	9	1.4
<i>Chaetocarpus castanocarpus</i>	13	0.26	16	1.4
<i>Litsea vang</i> H.Lec	11	0.53	11	1.3
<i>Cassine glauca</i>	11	0.41	12	1.2
<i>Dacryodes dungii</i> Dai	9	0.57	11	1.2
<i>Aglaia sp.</i>	9	0.56	11	1.2
<i>Styrax annamensis</i> Guill	11	0.31	13	1.2
<i>Nephelium chryseum</i>	10	0.39	12	1.2
<i>Lithocarpus silvicularum</i>	8	0.60	9	1.2
<i>Phoebe lanceolata</i>	13	0.36	9	1.1
<i>Néphelium cuspidatum</i>	6	0.61	7	1.0
<i>Artocarpus nitidus</i> var <i>lingnanensis</i>	8	0.33	9	0.9
<i>Artocarpus lakoocha</i>	9	0.36	8	0.9
<i>Ormosia balansae</i> Drake	9	0.23	9	0.9
<i>Sinosideroxylon wightianum</i> Aubr	7	0.30	9	0.9
<i>Shorea roxburghii</i>	9	0.30	7	0.8
<i>Choerospondias axillaris</i>	8	0.24	8	0.8
<i>Diospyros maritima</i>	6	0.35	7	0.8
<i>Archidendron balansae</i>	7	0.14	9	0.8
<i>Knema cortiosa</i>	7	0.14	9	0.8
<i>Endospermum sinense</i>	5	0.43	5	0.7
<i>Eugenia chanlos</i>	7	0.17	8	0.7
<i>Knema globularia</i>	6	0.16	8	0.7
<i>Aphanamixis polystachya</i>	7	0.17	7	0.7
<i>Ormosia pinnata</i>	7	0.25	5	0.7
<i>Horsfieldia amygdalina</i>	6	0.17	7	0.6
<i>Pygeum arboreum</i>	5	0.20	7	0.6
<i>Pachylarnax praecalva</i>	6	0.19	5	0.6
<i>Cinamomum botusifolium</i>	5	0.15	7	0.6
<i>Canarium nigrum</i> Engler	6	0.18	5	0.6
<i>Elaeocarpus stipularis</i>	5	0.36	3	0.6
<i>Pentapanax fragrans</i>	4	0.18	5	0.5

<i>Alangium ridley king</i>	4	0.15	4	0.4
<i>Cinnadenia paniculata</i>	3	0.26	3	0.4
<i>Cinnamomum obtusifolium</i> A. Chev	4	0.06	5	0.4
<i>Lindera balansae</i> H.Lec	4	0.14	4	0.4
<i>Litsea verticillata</i> Hance	4	0.21	3	0.4
<i>Cryptocarya metcalfiana</i>	3	0.13	4	0.4
<i>Siphonodon celastrineum</i> Griff	2	0.23	3	0.4
<i>Artocarpus tonkinensis</i>	3	0.10	4	0.4
<i>Ailanthus malabarica</i> DC	4	0.05	4	0.4
<i>Aucuba eriobotryaefolia</i>	3	0.08	4	0.3
<i>Lithocarpus fissus</i> Champ. ex benth	3	0.07	4	0.3
<i>Craibiodendro scleranthum</i>	3	0.15	3	0.3
<i>Litsea sebifera</i>	3	0.06	4	0.3
<i>Gonocaryum maclurei</i>	4	0.08	3	0.3
<i>Afzelia xylocarpa</i>	1	0.25	1	0.3
<i>Ternstroemia japonica</i> Thunb	2	0.12	3	0.3
<i>Quercus platycalyx</i> Hickel et camus	2	0.07	3	0.2
<i>Phoebe cuneata</i> Bl	2	0.04	3	0.2
<i>Dillenia heterosepala</i>	2	0.04	3	0.2
<i>Baccaurea sapida</i>	2	0.03	3	0.2
<i>Cryptocarya impressa</i>	2	0.03	3	0.2
<i>Antheroporum pierrei</i> Gagnep	2	0.03	3	0.2
<i>Alstonia scholaris</i>	2	0.02	3	0.2
<i>Paralbizia lucida</i> Benth	1	0.11	1	0.2
<i>Artocarpus heterophyllus</i>	1	0.09	1	0.2
<i>Acer decandrum</i> Merr	1	0.08	1	0.2
<i>Pelthophorum tonkinensis</i> A.Chev	1	0.07	1	0.1
<i>Ailanthus triphysa</i>	2	0.01	1	0.1
<i>Dracontomelon mangiferum</i> Bl	1	0.05	1	0.1
<i>Wrightia tomentosa</i>	1	0.05	1	0.1
<i>Artocarpus nitidus</i>	1	0.03	1	0.1
<i>Phoebe kunstheri</i>	1	0.03	1	0.1
<i>Podocarpus fleuryi</i> Hickel	1	0.03	1	0.1
<i>Phoebe cuneata</i>	1	0.03	1	0.1
<i>Averrhoa carrambola</i>	1	0.02	1	0.1
<i>Aglaia argentea</i> Blume	1	0.02	1	0.1
<i>Ficus hispida</i>	1	0.02	1	0.1
<i>Anthocephalus indicus</i> A.Rich	1	0.02	1	0.1
<i>Knema pierei</i> Warb	1	0.02	1	0.1
<i>Litsea oblongata</i>	1	0.02	1	0.1
<i>Elaeocarpus grandiflorus</i>	1	0.02	1	0.1
<i>Rapanea neriifolia</i> Mez	1	0.01	1	0.1
<i>Zanthoxylum avicenniae</i>	1	0.01	1	0.1

<i>Madhuca pasquieri</i> H.Lec	1	0.01	1	0.1
<i>Alphonsea monogyna</i>	1	0.01	1	0.1
<i>Averrhoa carambola</i>	1	0.01	1	0.1
Sum	3,121	127.38		300

Species	Abundance (n/3ha)	Dominance (m²)	Frequency (%)	IVI (%)
<i>Syzygium wightianum</i>	454	20.48	100	44.3
<i>Diospyros sylvatica</i>	450	19.50	96	42.9
<i>Enicosanthellum sp.</i>	422	16.70	87	38.5
<i>Saraca dives</i>	208	8.96	65	21.5
<i>Nephelium melliferum</i>	112	4.62	67	13.9
<i>Machilus bonii</i> H.Lec	110	4.15	72	13.8
<i>Polyalthia nemoralis</i> DC	80	4.21	44	10.5
<i>Cinnamomum obtusifolium</i> A. Chev.	73	2.65	52	9.4
<i>Ormosia balansae</i> Drake	71	2.95	37	8.4
<i>Aphanamixis polystachya</i>	57	1.99	45	7.7
<i>Rhamnus crenatus</i> Sieb	55	2.27	33	6.9
<i>Lucua mamona</i> Gaerten	46	2.00	33	6.3
<i>Symplocos laurina</i> Wall	31	1.20	29	4.7
<i>Symplocos cochinchinensis</i>	34	1.02	29	4.6
<i>Artocarpus tonkinensis</i>	23	1.29	23	3.9
<i>Aucuba eriobotryaefolia</i>	22	1.11	21	3.6
<i>Pterospermum heterophyllum</i> Hance	21	0.57	27	3.5
<i>Knema globularia</i>	27	0.82	20	3.4
<i>Gonocaryum maclurei</i>	21	0.84	20	3.2
<i>Gironniera subaequalis</i>	18	0.89	20	3.1
<i>Machilus odoratissima</i> Nees	22	0.59	21	3.1
<i>Vitex trifoliata</i>	17	0.97	19	3.1
<i>Sterospermum annamense</i> A.Chev	18	0.49	21	2.9
<i>Alstonia linearifolia</i>	19	0.74	17	2.8
<i>Garcinia oblongifolia</i> Champ	14	0.69	17	2.6
<i>Alstonia scholaris</i>	14	0.50	17	2.4
<i>Aidia oxyodonta</i>	15	0.51	16	2.3
<i>Spondias pinnata</i>	11	0.69	12	2.0
<i>Dialium cochinchinensis</i>	9	0.34	11	1.5
<i>Siphonodon celastrineum</i> Griff	9	0.25	11	1.4
<i>Engelhardtia chrysolepis</i> Hance	7	0.29	8	1.2
<i>Litsea laucilimba</i>	8	0.36	7	1.2
<i>Quercus dealbatus</i>	9	0.24	7	1.1
<i>Baccaurea sapida</i>	7	0.19	8	1.1
<i>Canarium album</i>	6	0.11	8	1.0
<i>Aglaia gigantea</i> Pellegrin	5	0.26	7	1.0
<i>Diospyros erientha</i> champ	6	0.14	7	0.9
<i>Chaetocarpus castanocarpus</i>	4	0.40	4	0.8
<i>Ceiba pentandra</i>	4	0.21	5	0.8
<i>Elaeocarpus griffithii</i> Wight A.Gray	6	0.21	4	0.7

<i>Choerospondias axillaris</i>	3	0.20	4	0.6
<i>Mangifera minitifolia</i>	3	0.14	4	0.6
<i>Dillenia blanchardi</i> Pierre	3	0.11	4	0.5
<i>Ternstroemia japonica</i> Thunb	3	0.10	4	0.5
<i>Colona poilanei</i>	3	0.18	3	0.5
<i>Pelthophorum tonkinensis</i> A.Chev	3	0.04	4	0.5
<i>Clethra delavayi</i>	2	0.12	3	0.4
<i>Sindora tonkinensis</i>	2	0.09	3	0.4
<i>Craibiodendro scleranthum</i>	2	0.08	3	0.4
<i>Alstonia longifolia</i>	2	0.08	3	0.4
<i>Amesiodendron chinense</i>	2	0.08	3	0.4
<i>Pholidota argusa</i>	2	0.07	3	0.4
<i>Phoebe cuneata</i> Bl	2	0.05	3	0.3
<i>Gleditsia fera</i> Merr	2	0.04	3	0.3
<i>Paeonia lactiflora</i>	2	0.04	3	0.3
<i>Endospermum chinense</i>	2	0.03	3	0.3
<i>Lagerstroemia calyculata</i> Kurz	2	0.03	3	0.3
<i>Spondias dulcis</i> Forst	2	0.02	3	0.3
<i>Acronychia pedunculata</i>	2	0.02	3	0.3
<i>Garcinia gaudichaudii</i>	1	0.13	1	0.3
<i>Manglietia fordiana</i>	2	0.08	1	0.3
<i>Adenantha microsperma</i>	1	0.10	1	0.2
<i>Artocarpus rigidus</i>	1	0.10	1	0.2
<i>Helicia cochinchinensis</i>	1	0.09	1	0.2
<i>Juniperus chinensis</i>	1	0.09	1	0.2
<i>Schefflera octophylla</i> Lour	1	0.07	1	0.2
<i>Symplocos</i> sp	1	0.07	1	0.2
<i>Pranus triflora</i>	1	0.06	1	0.2
<i>Cassia siamea</i> Lank	1	0.05	1	0.2
<i>Elaeocarpus griffithii</i> Mast	1	0.03	1	0.2
<i>Knema cortiosa</i>	1	0.03	1	0.2
<i>Syzygium zeylanicum</i>	1	0.02	1	0.2
<i>Alseodaphne tonkinensis</i>	1	0.02	1	0.2
<i>Ficus vasculos</i>	1	0.02	1	0.2
<i>Pachylarnax praecalva</i>	1	0.02	1	0.2
<i>Bridelia balanse</i> Tutch	1	0.02	1	0.2
<i>Calophyllum touranense</i>	1	0.02	1	0.2
<i>Glenniea philippinensis</i>	1	0.02	1	0.2
<i>Symplocos anomala</i>	1	0.02	1	0.2
<i>Ailanthus malabarica</i> DC	1	0.01	1	0.2
<i>Callophyllum inophyllum</i> Linn	1	0.01	1	0.2
<i>Litsea glutinosa</i>	1	0.01	1	0.2
Sum	2,613	109.00		300

Appendix II

Periodic annual diameter increment of the six most important tree species from each province (the parameter estimates were shown in Table 4.2). The black dots are observed values. The dashed line is the curve of an individual important species, the dotted line is the mean curve of all important species in that province, and the solid line is the mean curve of all other species in that province.

