TFRI Extension Series No. 186

Symposium on Ecosystem Management and Biodiversity Conservation on Plantation Forests in Taiwan and France

『台灣與法國人工林生態系經營與生物多樣性保育研討會論文集』論文集

Sponsor /
National Science Council (NSC), Taiwan, ROC

Coordinator /
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Editors /
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Taiwan Forestry Research Institute

PREFACE

Symposium on Ecosystem Management and Biodiversity Conservation on Plantation Forests in Taiwan and France

Biodiversity conservation and ecosystem stability of both natural and man-made forests have been major issues challenging politicians, policy makers, forest managers, environmentalists, ecologists, and the general public worldwide. By 2000, the global acreage of man-made (i.e, plantation) forests had dramatically increased to nearly 200 × 106 ha. Recently, forest managers around the world are facing the dilemma between biodiversity conservation and timber production.

According to the third national forest inventory in Taiwan, 59% of Taiwan, which amounts to 2,100,000 ha, is covered by forests. Among them, approximately 20% (420,000 ha) are plantation forests. Taiwan imports 99% of its current timber production. Under the current government's forestry policy, logging is prohibited on the natural forests. Therefore, how to properly manage plantation forests to achieve sustainable timber production and to promote/maintain environmental protection, CO_2 emissions reduction, biodiversity, and function on plantation ecosystem becomes a multifarious task for the government and forest managers.

France has more than 14,000,000 ha of forests, equal to 25% of the total area. Although the forested area in France only occupies 0.4% of the whole world forested area, France is the fifth largest timber: producting country in the world. For example, in the Gascogne region in southern France, there are more than 1,000,000 ha of maritime pine plantation forests, the largest single-species plantation in Europe. The issues of plantation forest management that France is facing today, such as sustainable timber production, maintaining biodiversity, carbon sequestration etc., are very similar to those of Taiwan. The French authorities have been managing plantation forests for several centuries, and have accumulated many significant experiences in forest management practices. Therefore, Taiwan can learn much and gain valuable knowledge in collaborating with French authorities.

In forest management, thinning has been proposed as the main tool to create and maintain structural heterogeneity and diversity, to create old-growth structure, to promote tree growth, and to facilitate ecosystem diversity and stability. With the conviction that scientific data are the basis of plantation management endeavors and the rationale for plantation management policies, starting from 2005, a group of Taiwanese scientists from various disciplines was assembled to conduct a large scale project to investigate the effects of alternative thinning regimes on the community structure and ecosystem functions of plantation forests. In order to show the preliminary research results and exchange the research experience on plantation forests between Taiwan and France which both have similar issues with

plantation forests, a workshop on ecosystem management and biodiversity conservation on plantation forests was held to share the information and enhance the further collaboration between the 2 countries.

It is well known that living organisms, through their metabolism and growth, drive energy and matter flows that contribute to the structure and function of ecosystems. However, it is quite difficult to understand how the diversity of these organisms affects ecosystem processes. This question is a key issue in modern ecology and has practical implications for forest management. It is indeed of great interest to understand how changes in biodiversity can affect forest ecosystem functions (e.g., soil fertility, nutrient cycling, primary productivity, etc) that in turn can affect forest yields.

The structure of forests has become an important factor in the analysis and management of forest ecosystems. Structural characteristics have often been used to define niche requirements of wildlife species, to examine spatial heterogeneity and temporal dynamics of understory vegetation, to investigate patterns of regeneration and gap dynamics, to explain micro climatic variations, and to predict timber production. Therefore, consideration of forest structure is a key component in plantation ecosystem management.

In this conference, issues related to the following topics are addressed: the impacts of alternative thinning regimes on forest functions (e.g., carbon flux, wood production, carbon sequestration); on forest structure and succession (e.g., microclimates, tree composition, soil erosion and hydrology, and nutrient cycle); on the natural regeneration of seedling (e.g., seed rain, seed composition, and seedling survival and growth); and on biodiversity in species term of variations and population dynamics of vertebrates, invertebrates, fungi, and mosses.

The final target of the conference is to find an approach that can be used to reflect the development of the structural complexity of forest plantations over time and to evaluate the influences of different silvicultral treatments (e.g., the intensity and form of thinning, partial harvesting, aggregated or dispersed green tree retention) in order to speed up the development of current plantations toward an old growth structure.

Finally, I would like to thank all sponsors (National Science Council, Taiwan Forestry Bureau, Tunghai University, and Taiwan Forestry Research Institute) for their support through research grants and efforts to hold this conference. Moreover, all participants including French guests from INRA, France are appreciated as well. Without their contributions, this conference could not be held with such success.

Director General,Taiwan Forestry Research Institute

August 2008

Symposium on Ecosystem Management and Biodiversity Conservation on Plantation Forests in Taiwan and France

October 15-16, 2007 Taipei, Taiwan, ROC

Organizers :

1. Taiwan Forestry Research Institute (TFRI), Taiwan.
2. French Agriculture Research Institute (INRA), France.
3. Taiwan Forestry Bureau (TFB) , Taiwan.

Co-Organizers :

1. Department of Life Science, Tunghai University, Taiwan
2. Forest Conservation and Management Administration Vocational Assistant Commission Retired Servicemen, Executive Yuan, Taiwan
3. Society of Subtropical Ecology, Taiwan
3. TERN (Taiwan Ecology Research Network), Taiwan

Sponsor :

National Science Council (NSC), Taiwan, ROC

Coordinator:

Dr. Hen-biau King

Editors :

Dr. Dar-Hsiung Wang and Mr. Chih-hsin Chung

Symposium on Ecosystem Management and Biodiversity Conservation on Plantation Forests in Taiwan and France

October 15-16, 2007 Taipei, Taiwan, ROC

Purpose of conference :

The global acreage of plantation forests has dramatically increased to nearly 200 × 106 ha by 2000. Most of these trees are planted in areas that once supported very productive natural forests, grasslands, or wetlands. Forest managers around the world are confronting the multifarious tasks of biodiversity conservation, timber production, ecosystem function and stability, and environmental protection of these man-made forests.

The history of managing plantation forests is relatively short in Taiwan compared with the case of France, but forest managers in both countries are facing similar bottlenecks in plantation management. In Taiwan, man-made forests covering approximately 420,000 ha in area is an important forest ecosystem. Thinning is a prerequisite activity adopted in the plantation management. But, relevant data regarding the consequences of thinning on biodiversity and on forest function, and endemic vegetation regeneration and restoration are still scanty. Therefore, the purpose of the conference is to investigate the thinning impacts on forest services, forest functions, and biodiversity, and on species variation and population dynamics of vertebrates, invertebrates, fungi, and mosses.

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MONDAY 15 October, 2007

08:30~09:00 Registration

09:00~09:15 Opening ceremony (remarks)

09:15~10:35 Plenary Lectures (Keynote address)

- **Hen-biau King** (TFRI, Taiwan): Environment, Forests, and Ecological Research in Taiwan
- **Jean Noel Candau** (INRA, France): Forest Plantation Diversity and Resistance to pest Insects

10:35~11:05 Coffee Break and Group Photograph

11:05~11:55 Session 1 (Chairperson : Ming-kung Wang)

- **I-fang Sun** (Tunghai University, Taiwan) : Managing Forest Plantation for Biodiversity Conservation and Timber Production in Taiwan
- **Dar-hsiung Wang** (TFRI, Taiwan): Thinning Effect on Stand Structure of a Sugi Plantation (*Cryptomeria Japonica*) in Zenlen Area.

11:55~13:40 Lunch

13:40~14:55 Session 2 (Chairperson : Biing T. Guan)

- **Ming-kung Wang** (National Taiwan University, Taiwan): The Effect of Forest Thinning on Soil Net Nitrogen Mineralization and Nitrification in a *Cryptomeria japonica* Plantation.
- **Yau-lun Kuo** (National Pington Technical University, Taiwan): Soil Respiration in a *Cryptomeria japonica* Plantation at Central Taiwan.
- **Jean Paul Laclau** (INRA, France): Long-term Maintenance of Soil Fertility in Forest Plantations.

14:55~15:15 Coffee Break

15:15~16:30 Session 3 (Chairperson : Alexis Ducousso)

- **Liang-kong Lin** (Tunghai University, Taiwan): Effects of Differential Thinning in a Man- Made Forest on Vertebrate Diversity and Community Structure.
- **Daniel Epron** (INRA, France): Functional Diversity in Temperate Mixed Stands: Response of Co-occurring Deciduous Tree Species to Light and Water Availability.
- **I-min Tso** (Tunghai University, Taiwan): The Effects of Thinning on Spider Diversity in a High-Elevation Juniper Plantation in Central Taiwan.

TUESDAY 16 October, 2007

09:00~10:15 Session 4 (Chairperson : Daniel Epron)

- **Biing T. Guan** (National Taiwan University, Taiwan): Analyzing after Thinning Microclimatic Responses Semi-parametrically.
- **Ming-chieh Chen** (National Taiwan University, Taiwan): Characteristics of Microenvironment in *Cryptomeria japonica* Plantation in Zenlen Area.
- **Jean Noël Candau** (INRA, France): Landscape-scale Model of How Forest Diversity, Climate and The History of Spruce Budworm Defoliation Affect Wildfire Potential in Ontario (Canada).

10:15~10:35 Coffee Break

10:35~11:50 Session 4 (Chairperson : I-fang Sun)

- **Brigitte Lung Escarmant** (INRA, France) : Fungal Diversity in Managed Resinous Forests: the Case of the Landes de Gascogne Forest.
- **Pi-han Wang** (Tong-hai University, Taiwan): Macrofungal Species Composition and Distribution in a Japanese cedar Forest in Taiwan.
- **Alexis Ducousso** (INRA, France) :Human Impacts, Management and Conservation of Genetic Diversity in Forestry.

11:50 Closing ceremonies

TABLE OF CONTENTS

Managing Forest Plantations for Biodiversity onservation, and Timber Production in Taiwan

I-Fang Sun *

BACKGROUND

Taiwan, at 36,000 km^2 in area, is an offshore island located 150 km off the coast of southeastern China. Situated between 24° N and 22° N in the subtropical region, Taiwan has mild weather year round. The monthly mean temperature is 20° C, and the annual rainfall is about 2,500 mm. Although small in size, the topography on the island is rather complicated ranging from sea level to 3997 m in elevation. Blessed with mild weather and huge topographic variations, almost all the main vegetation types in the world, such as mangroves, lowland broad leave evergreen forests, evergreen-deciduous mixed forests, conifer forests, and alpine ecosystems can be found in Taiwan. With anthropogenic activities in the past few centuries, a large proportion of the lowland vegetation has changed to urban scenery. Yet, over 50 % of the island area is still covered by lush and diverse forests. Among the remaining forested area, 14 % or that is, 420,000 ha, of the area is plantation forests. Most plantations were established 50 yr ago, with introduced species such as *Cryptomeria japonica* and *Cunninghania lanceolata* planted for further harvests. More and more native species, such as *Chamaecyparis formosensis*, *Taiwania cryptomerioides*, *Calocedrus formosana*, *Fraxinus formosana*, and *Zelkova formosana*, however, have been used in plantations since the 1980s.

NEW CHALLENGES FOR FOREST MANAGEMENT POLICY

As plantation forests in Taiwan enter the maturation stage, policies for harvesting timber nonetheless have become a challenge for several reasons. First of all, many plantations are located in the proximity of unstable geological areas in which harvesting timber may further endanger the area. In the past decade, due to many natural disasters associated with timber harvesting, such as mudslides and flooding, people have changed their view towards plantation

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forests, in which most people now prefer that plantations remain as forests over timber production.

The second challenge comes from public opinion on biodiversity conservation. One issue associated with plantation forests worldwide is the loss of biodiversity in these forests. This is in part due to the species in plantations being selected for their high growth rates and good timber quality. This led to a selection of only a few species and as a result, created monoculture or species-poor communities. As a consequence, plantation forests are very low in biodiversity. In addition, single-species-dominated plantations provide fewer ecological services such as soil erosion protection, nutrient cycling and water conservation. As Taiwan has enjoyed high economic growth and living standards, the general public now views plantation forests as sources of ecosystem services and recreation. More and more people expect these plantation forests to be full of wildlife and provide educational as well as environmental protection functions. Thus, determining how to increase biodiversity and ecosystem function in these forests has become a major challenge for the government.

The third challenge of timber harvesting in Taiwan is an economic one. Locally harvested timber has higher costs compared to imported timber due to high labor costs in Taiwan. In addition, imported timber has better wood quality than that of local plantation trees. Therefore, it is not economically viable to harvest our own timber.

The fourth challenge comes from international pressure, especially after implementation of the Kyoto Protocol. Taiwan now imports 99% of its timber from foreign countries. Imported timber will become more and more expensive due to rising costs of transportation and stricter export regulations from timber certification requirements. It is obvious that Taiwan needs to produce its own timber to reduce the dependence on imported timber. In addition, Taiwan ranked third in annual per capita carbon emissions in the world. In the near future, Taiwan has to come up with strategies to compensate for its carbon emissions or face international sanctions or carbon taxes. One simple and easy way is to increase tree growth and to increase carbon storage. With sound management strategies, plantation forests can provide timber for local consumption as well as carbon storage for carbon taxes. Thus finding a good way to efficiently manage the 420,000 ha of plantation forests has become an important task which foresters must accomplish.

It is obvious that the Taiwanese government has to redesign its forest management policies to accommodate all the challenges ahead. A new management strategy which incorporates the needs of timber production, public opinion, biodiversity conservation, carbon sequestration, and long-term sustainability of plantation forests is urgently needed.

Basic Research Plan

In order to provide science-based knowledge to help the government design a sound forest management policy to meet societal expectations for both environmental protection and sustainable timber supply, we assembled a group of scientists from various disciplines to conduct a large-scale project to investigate the effects of different thinning practices on the community structure and ecosystem functions of plantation forests. This project is intended to be long-term, large-scale, and inter-disciplinary.

Trees are sessile organisms, and without the opening of space, such as natural gaps, the forest community will remain unchanged for a very long period of time. In addition, many microclimatic factors will change with the opening of the forest canopy. As a consequence, many species can maintain their presence in the forest thus increasing the overall biodiversity. Thinning has been widely used as a forest management strategy. However, most thinning practices are line thinning in which small and regular gaps are created; or understory thinning, in which damaged and less healthy trees are removed. Since these practices are designed to improve tree growth as well as wood quality, they might not meet our goals of increasing biodiversity and ecosystem functions. Therefore, we decided to use a 'gap' approach, in which different-sized gaps were created in a plantation forest to imitate gap dynamics that occur in natural forests. We then monitored the changes of forest micro environments, the arrival of native tree species, changes in diversity and population dynamics of animal species, and soil nutrient dynamics through time to investigate the effects of thinning on the forest community (Figure 1). By comparing differences between pre- and post-thinning periods, we hope this new approach can provide much needed baseline information on the effects of gap thinning on the species composition, community structure, and ecosystem functions of plantation forests.

Study Site

The study site is located in central Taiwan the elevations of 1500~1700 m (Fig 1). The natural vegetation in this area was clearcut about 50 yr ago and replanted with *Cryptomerioides japonica*. The mean annual rainfall is 2400 mm, and the mean monthly temperature is 19.2° C.

EXPERIMENTAL DESIGN

In total 12 1-ha plots were established in this area in 2005; in each plot, all woody plants > 1 cm diameter breast height(DBH) were mapped, tagged, and identified to species (Fig 2). The 12 plots were further divided into 4 blocks of 3 plots. Within each block, each plot was

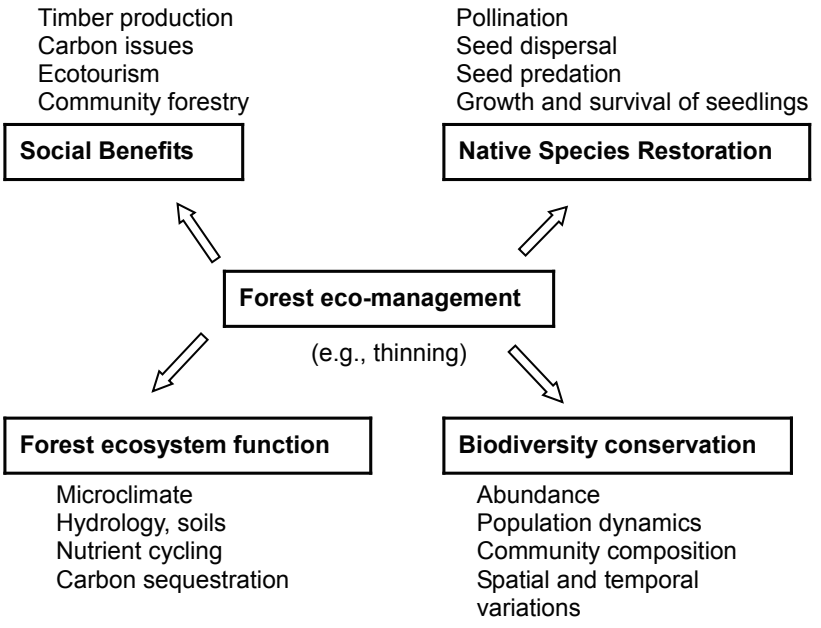

Fig. 1. Outline of the multidisciplinary research project for forest management.

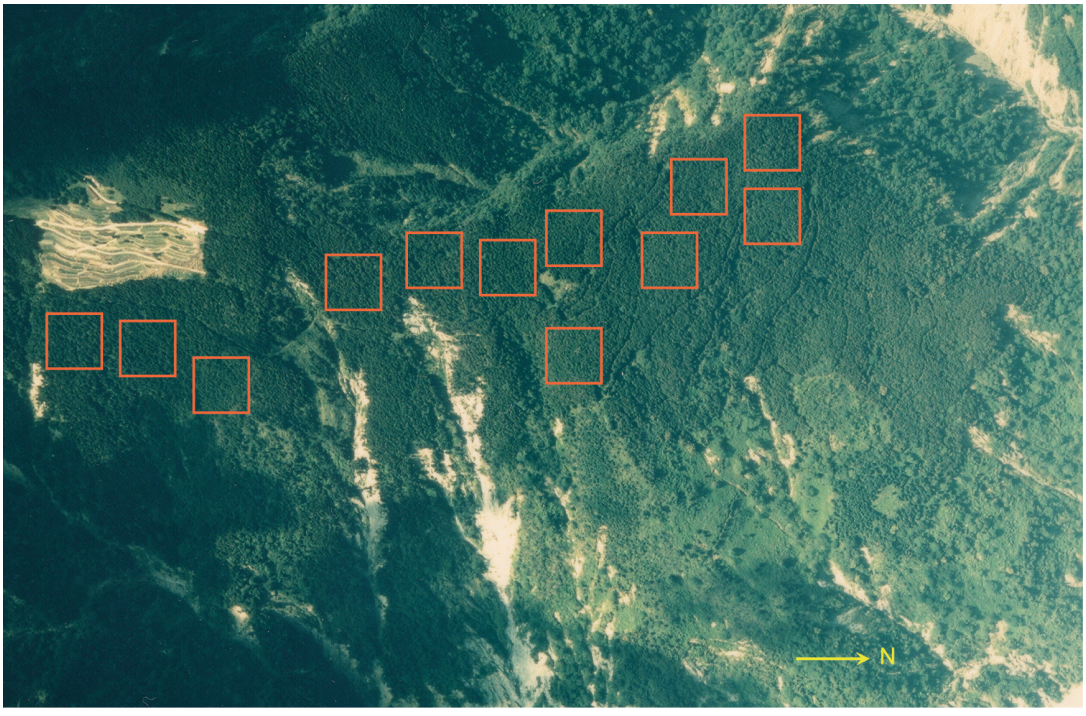

Fig. 2. Location of 12 1-ha plot in the Zen-Len plantation forest.

randomly assigned a treatment of a 0%, 25%, or 50% thinning scheme. All projects were carried out inside each plot (Table 1). We set up microclimate monitoring instruments, and decomposition conducted and soil respiration experiments in each plot in 2006. In addition, vertebrate and invertebrate diversities have been surveyed quarterly since 2005. Seed traps and seedling plots were also established in each plot to monitor the recruitment of tree species. Thinning was completed in July 2007, and we are now in the second phase of this project.

CONCLUSIONS

The goals of plantation forest management have shifted from timber production to biodiversity conservation in recently years in Taiwan. In order to accommodate the various needs, we proposed this integrated research project which will provide science-based knowledge on the effects of a gap thinning approach on plantation forest dynamics, ecosystem functions, and maintenance of biodiversity. It is our hope that this knowledge will then serve as the base for new management policy for our government.

Table 1. Project title of the multidisciplinary research project for forest management

Project title
Soil water, surface runoff, and soil erosion affected by different thinning intensities in an artificial forest
Influences of artificial forest management practices on to soil nutrient cycles and litter decomposition rates
The effects of differential thinning on diversity and community structures of invertebrates in artificial forests
The effects of differential thinning on diversity and community structures of vertebrates in artificial forests
Effects of thinning practices on the photosynthesis and carbon sequestration of *Cryptomerioides japonica* plantations
Influence of thinning operations on microsite and stand structure of *Cryptomerioides japonica* plantations
Effects of thinning practices on fungal diversity of *Cryptomerioides japonica* plantations
Effects of thinning practices on bryophyte diversity of *Cryptomerioides japonica* plantations
Effects of thinning practices on the recruitment and dynamics of native tree species in *Cryptomerioides japonica* plantation

Thinning Effects on the Stand Structure of a Sugi Plantation(*Cryptomeria Japonica*) in the Zenlen Area

Dar-Hsiung Wang,[1,5] Jee-Lian Hwong,[2] I-Fang Sun,[3] Zen-Hun Lin,[2] Shu-Lin Deng,[4] Chih-Hsin Chung[1]

[Summary]

The practice of forest thinning can influence the functions and structure of forest ecosystems. To investigate the effects of alternative thinning strategies on the stand structure and tree composition in sugi (*Cryptomeria Japonica*) plantations, this study was conducted on national forests in the Ran-Da Working Circle Area. In the plantations, the current stand status was surveyed to determine the inventory of timber resources in the study area through 12 plots with a size of 1 ha in each plot. Among them, a randomized block design was adopted for 3 treatments with 4 replications for each treatment in 1 ha. A patch or gap thinning rule was used to remove trees with 2 levels of thinning intensity in terms of removing 0%, 25%, and 50% of trees in a plot. In each plot, all woody plants with the diameter at breast height (DBH) of > 1.0 cm were tallied, the tagged, species identified, orientation noted, DBH measured, and ground vegetation surveyed. Results showed that variations in growth among trees in the past caused inconsistencies of tree densities among plots. While the basal area shared by understory woody plants was quite small in the plantations (i.e., < 5%), the enhancement of biodiversity characteristic was quite obvious.

Key words: plantation structure, ground vegetation, biodiversity index

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INTRODUCTION

Sugi plantations (*Cryptomeria Japonica*) are the largest man-made forests in Taiwan. Based on an inventory of the third forest resources survey in Taiwan, it showed that the area of sugi plantations, within the total area of 290,6000 ha of national man-made forest in Taiwan, reached to 39,000 ha with a growing stock of about 9,330,000 m3; therefore, sugi plantations are the largest forest type in mid-elevation areas of Taiwan (TFB 1995). Usually, in the past, sugi plantations were planted as a monoculture for the major purpose of timber production. Nowadays, to be consistent with the forest ecosystem management, applying thinning practices to existing sugi plantations to enhance the heterogeneity of the stand composition and structure to meet the goals of biodiversity conservation, land productivity promotion, and stability of ecosystem has become quite an important issue for sustainable forest management.

In plantations, the effects of juvenile spacing do not last long because of the competition on the roots and crowns of younger trees starting at the onset of closure. Crowded trees will compete for light, water, and nutrients, resulting in slow growth or even death of some trees (Oliver and Larson 1996). Moreover, some weak trees also become vulnerable to insects and disease. To avoid overcrowding and competition, trees are often thinned to increase the growing space available to the remaining trees. Enhancing growth of final crop trees by removing some trees, therefore, has long been recognized and practiced in commercial thinning (Abbott and Loneragan 1983).

The most common management objective of commercial thinning is to maintain stand growth increments similar to those a stand would have achieved in its unthinned state, but concentrating wood production onto larger stems, and producing higher-quality sawlogs (Smith 1986). Besides the timber value added, issues of nontimber benefits that have drawn more public attention recently such as biodiversity, environment, recreation, microclimate of forests sites, land cover, carbon sequestration, and habitats for wildlife are related to thinning practices as well (Sheriff 1996, Chambers et al. 1999).

Thinning allows forest managers to choose trees to which the additional growth will be allocated and to harvest growth that would otherwise be lost due to mortality (Della-Binanca and Dils 1960, Smith 1986). Thinning has been found to affect the moisture (Della-Binanca and Dils 1960, Donner and Running 1986), plant physiology, foliar nutrients (Ginn et al. 1991), and light availability to residual trees as well as the air temperature within a stand and on the forest floor (Della-Binanca and Dils 1960).

The forest structure is of interest to many disciplines and is often discussed in the context

of ecosystem management. Spies (1998) pointed out that forest structure encompasses many meanings and can be described in many ways. At the stand level, measurements of tree size, age, foliage, biomass, and spatial distribution in overstory and ground vegetation layers are commonly viewed as components of stand structure. The structure of tree crowns, for example, is a characteristic of stand structure that influences the growth of both trees and understory vegetation (Latham et al. 1998). Changes in the structural attributes of stands also affect stand functions such as photosynthesis and respiration (Waring and Schlesinger 1985), tree growth (O'Hara 1988), suitability of a stand for wildlife (Morrison et al 1992), and understory plant diversity (Latham et al 1998). Therefore, structural diversity has become an important facet within forestry, especially for countries (e.g., Central European Region) with a rather low level of tree species diversity (Neumann and Stalinger 2001).

The spatial aspect of stand architecture plays an important role in determining habitat and species diversity. Increasing horizontal and vertical heterogeneity of a stand structure often leads to a higher number of species and contributes to higher stand stability (Latham et al 1998). Thinning practices can modify stand structure and therefore have important potential roles in determining stand diversity and ecological stability (Pretzsch 1997, Spies 1998, Humphrey et al. 2000).

The purpose of this study was to investigate the influence of alternative thinning strategies on stand structure and ground vegetation of a sugi plantation in the Zenlen area of the Nantou Forest District in Taiwan.

MATERIALS AND METHODS

Description of the experimental site

The experimental site was located in compartments 74 and 75 of the Nandai national working circle of the Taiwan Forestry Bureau. The sugi plantation was planted in 1971~1972 with an area of 78 ha at elevations ranging from 1500 to 1700 m. The mean annual precipitation is 3800 mm mostly from May to September. The mean annual temperature is 17.5˚C.

Experiment of Design

A randomized block design was adopted for 3 treatments with 4 replications in each treatment. Each plot was 1.0 ha. The buffer among plots was about 10~15 m in width. The total area of the sugi plantation for the experiment was about 25~30 ha.

Inventory of stand attributes

In each plot, all woody plants with the diameter at breast height (DBH) of > 1.0 cm were tallied, tagged, the species identified, orientation noted, and DBH measured. In addition to tallying in 1.0 ha, 2 subplots with an area of 0.16 ha each were set up within each plot. In each subplot, the height to crown base and crown width of each sugi/overstory tree were measured. Among them, total height of 40% of trees was measured based on the DBH class to develop a sugi tree height curve.

Ground vegetation survey

Here the ground vegetation consists of herbs, ferns, and woody plants with a dbh < 1.0 cm. A transect sampling method was used to construct a vegetation resource database as a plant checklist. In each plot, based on the 2 subplots with an area of 0.16 ha each, 48 1 × 1-m ground vegetation plots with systematic sampling were set up to investigate the ground vegetation species, and coverage rate by using a 1 × 1-m grid.

The importance value index (IVI) was calculated to represent the importance of each species in the forest ground vegetation community. The related formulas are given as follows:

Relative frequency (%) = (The frequency of the given species in the forest ground vegetation community / Sum of the frequency of all species in the forest ground vegetation community) × 100 %;

Relative dominance (%) = (The dominance of the given species in the forest ground vegetation community / Sum of the dominance of all species in the forest ground vegetation community) × 100 %; and

The important value index of ground vegetation layer = Relative frequency + Relative dominance = 200 (%).

Moreover, the Pteridophyte quotient was calculated to signify the wetness degree of the study area. Its formula is listed as follows:

Pteridophyte quotient (Q) = The number of pteridophytes in the forest plant community × 25 / The number of seed plants in the forest plant community.

Thinning strategy lay out

Patch or gap thinning was used as the thinning practice. The thinning design was laid out as a thinning intensity of removing 25% of stems, for each quadrant of size 20 × 20 m,

in which the thinning point was positioned at the lower-right corner of a 1/4 quadrant (i.e., the cutting area was 10 × 10 m), and all trees at the thinning point were felled; and that in the thinning intensity of removing 50% of stems, two 1/4 quadrants of size 20 × 20 m connected northwestern to southeastern boundart diagonally were picked to be fully harvested.

RESULTS AND DISCUSSION

Due to the difficulty in measuring the tree height in large-scale forest inventories, a height-diameter curve is often used to estimate the tree height for a given trees DBH. Several height models were used and compared based on MSE (mean square error) criterion. This study indicated that the previously published height models (Yang 1975, Lao and Feng 1985) would either underestimate or overestimate most tree heights measured (Fig. 1). Therefore, it was essential to fit the height-diameter curve by using the data collected in this study. The goodness of fit showed the superiority of model 8 (Table 1). The tree total volume was calculated based on the equation developed by Lao and Feng (1985).

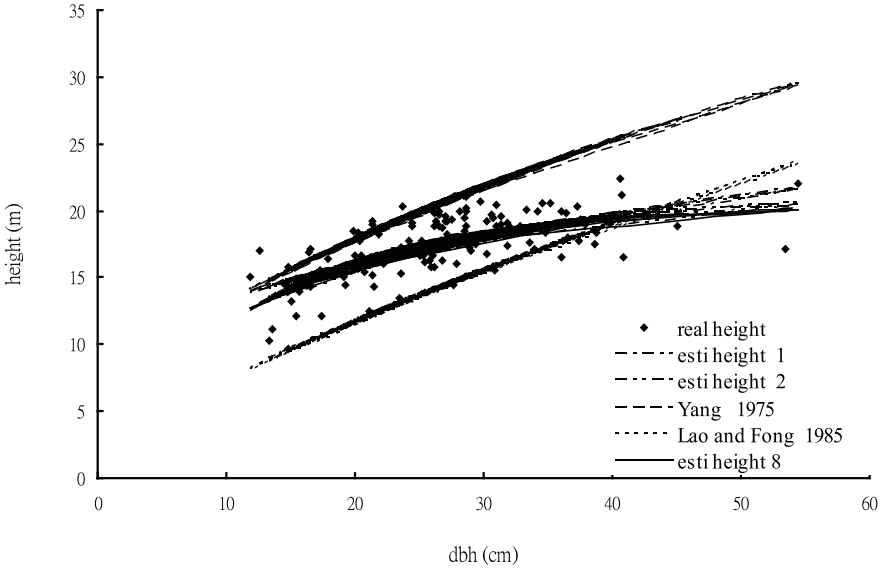


Fig. 1. Height-diameter curve of sugi plantations.

Tallied data from 1 ha revealed the heterogeneity of the stand density on the plot. The stand density of woody tress with a DBH of > 1.0 cm ranged from 893 to 1285 trees/ha, and the average DBH was from 24.1 to 27.8 cm among plots (Table 2). Competition among trees and other factors may have accounted for the heterogeneity of the plantations. The computation of

species composition in basal area showed the overwhelming dominance of overstory trees (sugi and China fir (*Cunninghmia lanceolata*)) in the stand. Moreover, as was expected, there were far more sugi trees than China fir tree in the overstory layer (Table 3). Because the basal area of sugi was > 80% of the total basal area in the overstory layer in each plot, generally, the plantation was still considered a pure sugi plantation.

Table 1. Height-diameter model of sugi

Model	Parameter			MSE	R^2
	a	b	c		
1. $H = \exp(a + b\ln D)$	1.9136	0.2902		2.9698	0.991
2. $H = \exp(a + b/D)$	3.1572	-7.4171		2.7802	0.991
3. $H = a + bD^c$	-1836.9	1837.6		2.8912	0.462
4. $H = D/(a + bD)$	0.4313	0.0402		2.7882	0.991
5. $H = a + bD + cD^2$	4.3148	0.7746	-0.00982	2.9843	0.614
6. $H = a + b\ln D$	0.5781	5.1963		2.8906	0.464
7. $H = aD^b + 1.3$	5.8272	0.3127		2.9768	0.989
8. $H = a(1 - \exp(bD)) + 1.3$	19.0349	-0.0764		2.7367	0.989
9. $H = a(1 - \exp(bD)^c) + 1.3$	18.6527	0.0923	1.2976	2.7575	0.989

MSE, mean squared error.

Biological diversity and conservation are 2 great issues to be considered in plantation management. In each plot, the alternative diversity indices for all tallied trees were calculated. The diversity index is displayed in Table 3. While the basal area shared by understory woody plants was quite small in the plantation (i.e., < 5%), the enhancement of biodiversity characteristics was quite obvious. For example, the Shannon and Simpson index was much higher if the biodiversity of understory woody plants was considered as an entire entity.

Table 2. Characteristics of stand attributes for plots surveyed on a 1-ha basis in the studied area

Plot	Density (no. of stems)	DBH (cm)[1)]	Height (m)[1)]	Basal area (m^2 ha^{-1})	Volume (m^3 ha^{-1})
1	893	27.0 ± 7.3	17.48 ± 1.99	54.77	461.45
2	944	27.6 ± 7.5	17.62 ± 1.70	60.63	512.10
3	1055	26.0 ± 6.3	17.37 ± 1.45	58.39	488.86
4	939	27.8 ± 6.9	17.72 ± 1.63	60.57	511.86
5	895	25.2 ± 6.9	17.15 ± 1.85	47.88	400.10
6	1114	26.5 ± 6.6	17.49 ± 1.56	65.32	548.84
7	1285	24.1 ± 6.3	16.98 ± 1.61	62.79	520.77
8	1019	25.6 ± 5.8	17.37 ± 1.41	55.24	461.92
9	1184	24.2 ± 6.4	16.98 ± 1.59	58.32	484.17
10	964	27.5 ± 7.1	17.64 ± 1.57	61.01	514.90
11	1074	24.3 ± 6.3	17.00 ± 1.70	52.92	439.60
12	896	26.3 ± 7.2	17.38 ± 1.66	52.28	439.05

[1)] Mean ± standard deviation.

The accuracy and precision of estimated stand attributes such as density, mean DBH, basal area, and volume on a per-unit basis (i.e., 1.0 ha) from the subplots (i.e., 0.16 ha) was one issue to be investigated. The comparison between trees tallied on the entire plot and trees on the subplots showed a variety of differences obtained among the stand attributes (Table 4). This study showed that a big difference may exist if the subplot is allocated in a place where a great heterogeneity exists in the stand composition between the subplot and the entire plot. However, on average, there was no great difference in estimating the stand density, basal area, and volume on a hectare basis from the subplot, thus supporting the way widely used to estimate stand attributes/ha from a smaller area of a tallied plot.

The Weibull function was used to estimate the DBH distribution among trees because of its advantages of great flexibility and easy computation (Clutter and Bennett 1965, Kynch and Moser Jr 1986). Except for a few diameter classes, a strong consistency in the diameter distribution between the observed and theoretical patterns was observed for all plots (Fig. 2).

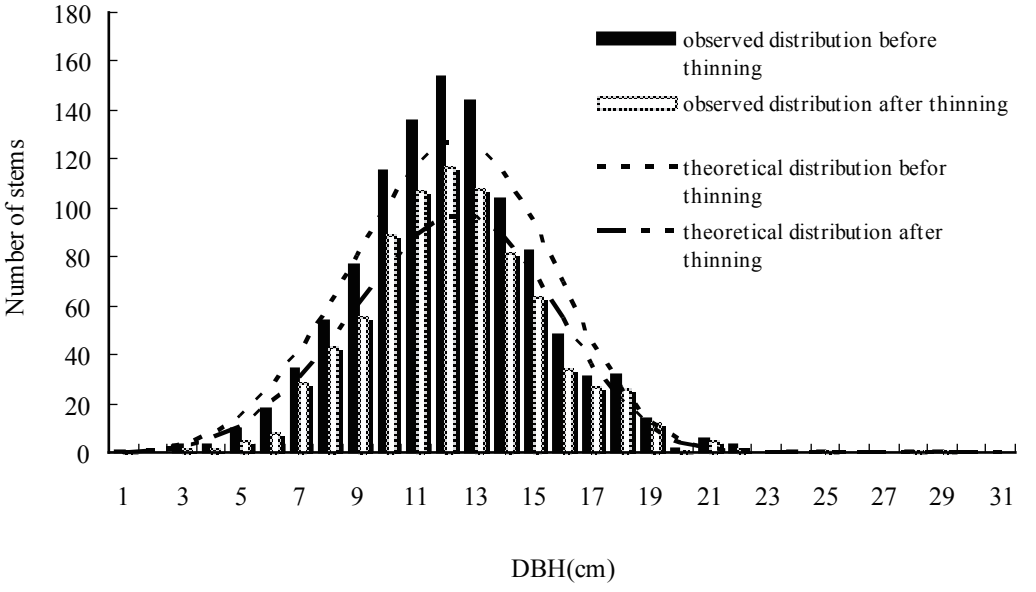


Fig. 2. Diameter at breast height (DBH) distribution for a given plot with a 25% thinning intensity

The change in the tree diameter distribution caused by the thinning practices is shown as Figs. 2 and 3. In general, with the thinning below method, the diameter distribution was truncated after the thinning practice because trees with a quite small size or suppressed trees were removed. However, no truncated tree diameter distribution after thinning was observed in this study. This was due to the use of the patch or gap thinning method, for which all tress in the

thinning quadrant area were removed regardless of tree size. This finding was valid regardless of the thinning intensity adopted in this study.

Table 3. Composition of basal area in the overstory and understory layers and biodiversity index of sugi plantations

Plot	Basal area (%)			Species richness			Dominant index	Shannon index	Simpson index	Evenness index
	Sugi	China fir	Understory woody plants	S	N	D[1)]				
	73.68	24.42	1.90	55	1641	54.865	0.200	2.200	0.798	0.549
1			A[2)]	53	748	52.849	0.155	2.578	0.845	0.649
			B[3)]	2	893	1.853	0.574	0.617	0.426	0.890
	97.81	1.29	0.90	35	2048	34.869	0.337	1.506	0.663	0.425
2			A[2)]	33	1104	32.857	0.457	1.429	0.543	0.409
			B[3)]	2	944	1.854	0.961	0.099	0.039	0.143
	94.21	4.59	1.20	52	2551	51.873	0.273	1.815	0.727	0.461
4			A[2)]	50	1612	49.865	0.386	1.692	0.614	0.433
			B[3)]	2	939	1.854	0.879	0.240	0.121	0.346
	95.26	0.50	4.24	90	2530	89.872	0.175	2.600	0.825	0.576
5			A[2)]	88	1637	87.865	0.128	2.976	0.872	0.665
			B[3)]	2	893	1.853	0.973	0.071	0.027	0.102
	98.19	0.13	1.68	59	3759	58.879	0.212	2.065	0.788	0.505
7			A[2)]	57	2474	56.872	0.219	2.155	0.781	0.533
			B[3)]	2	1285	1.860	0.997	0.011	0.003	0.016
	97.15	0.00	2.85	61	3316	60.877	0.171	2.318	0.829	0.564
8			A[2)]	60	2296	59.871	0.160	2.457	0.840	0.600
			B[3)]	1	1020	0.856	1.000	0.000	0.000	0.000
	96.89	0.16	2.95	65	3983	64.879	0.172	2.294	0.828	0.549
9			A[2)]	63	2799	62.874	0.171	2.393	0.829	0.578
			B[3)]	2	1184	1.859	0.997	0.012	0.003	0.017
	97.25	0.56	2.19	53	4049	52.880	0.161	2.270	0.839	0.572
11			A[2)]	51	2975	50.875	0.169	2.288	0.831	0.582
			B[3)]	2	1074	1.857	0.957	0.039	0.043	0.056
	81.18	17.37	1.45	37	1607	36.865	0.246	1.922	0.754	0.532
12			A[2)]	35	711	34.848	0.233	2.111	0.767	0.594
			B[3)]	2	896	1.853	0.645	0.541	0.355	0.780

[1)] D = S - (1/log(N)).
[2)] A, Biodiversity index for understory woody plants with a DBH of > 1.0 cm.
[3)] B, Biodiversity index for overstory plants only.

Table 4. Bias of estimated stand attributes ha-1 in percentage from subplots for all plots

Subplot	Bias of stand attributes ha^{-1} estimated from subplot (%)											
	No.of stems			Mean DBH			Basal area			Volume		
	Min	Max	Avg.	Min	Max	Avg.	Min	Max	Avg.	Min	Max	Avg.
1	0.47	38.07	13.36	0.11	8.68	0.68	0.91	34.09	11.33	0.95	34.70	10.41
2	1.48	45.58	9.50	0.11	8.92	1.37	0.89	34.86	4.97	0.70	34.14	4.47

Bias = (value of attributes ha^{-1} tally – value of attributes ha^{-1} estimated by subplots) / value of attributes ha^{-1} tally × 100.

The stand visualization system（SVS）is a very useful tool to develop stand level landscape visualizations. Images produced using SVS provide a readily understood representation of forest management and silvicultural treatments (McGaughey 2001, Barrett et al. 2002). We used the SVS to build 3D visualizations of 3 different thinning treatments (control, 25% thinning, and, 50% thinning) of silvicultural operations in the Zenlen area (Fig. 4).

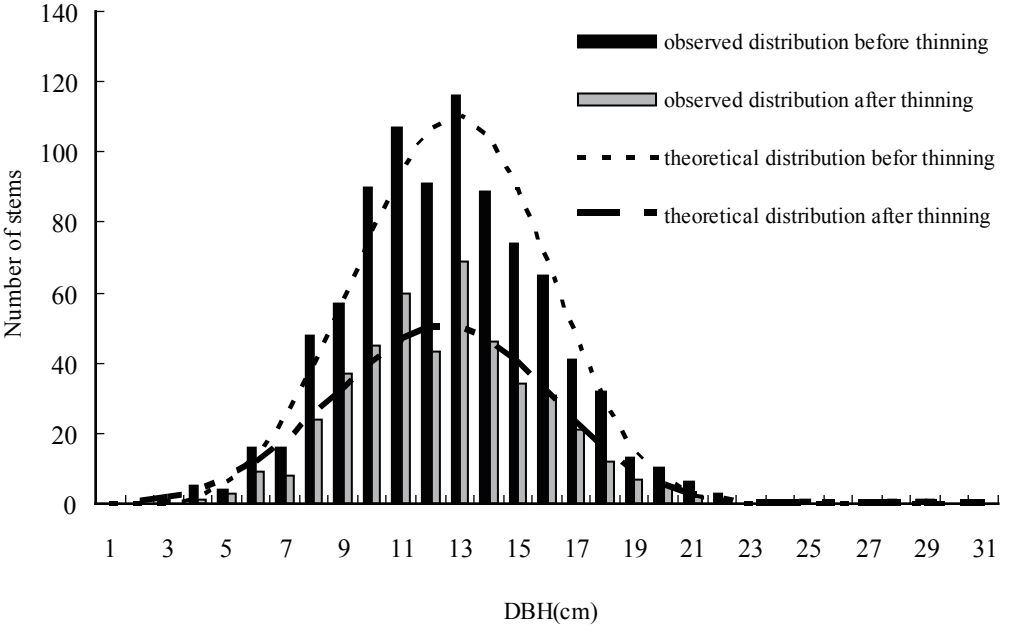
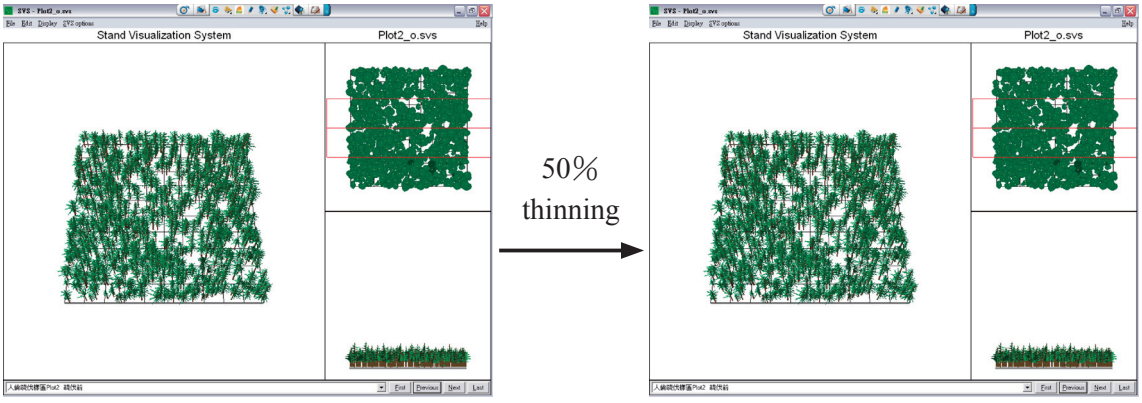
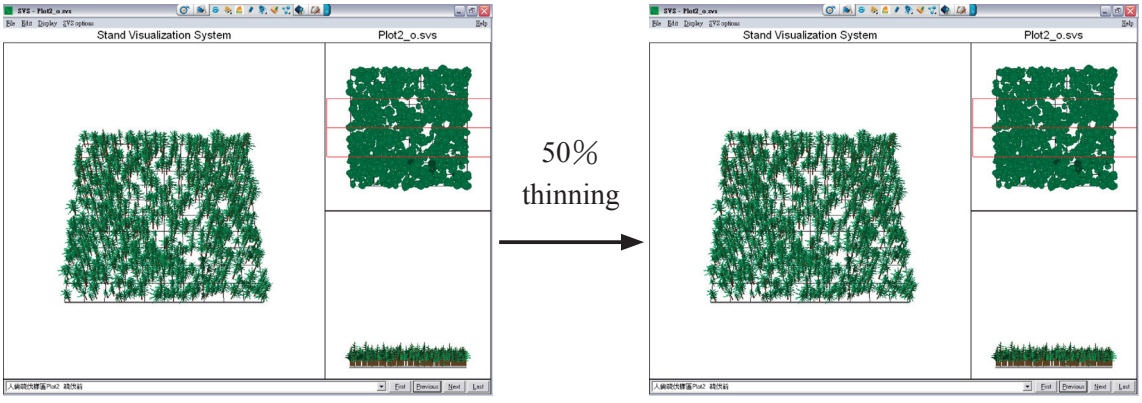


Fig. 3. Diameter at breast height distribution for a given plot with 50% in thinning intensity

The SVS provides a good way to communicate silvicultural treatments and forest management alternatives to a variety of audiences. In the SVS images, periods of different thinning treatments are clearly visible. Visualization techniques have evolved as a very helpful tool for forest management practices and silvicultural treatments at landscape levels.



Plot 2　before thinning　　Plot 2　after thinning



Plot 1　before thinning　　Plot 1　after thinning

Fig. 4. Spatial patterns for different thinning treatments（25% thinning in plot 1 and 50% thinning in plot 2）of silvicultural operations in a Sugi plantation.

In the ground vegetation survey, a plant checklist was established as indicated by Table 5. There were 109 families, 133 genera, and 336 species in total. Among them, 21 families with 58 species were pteridophytes, 3 families with 7 species were gymnosperms, 75 families with 241 species were dicotyledons, and 10 families with 30 species were monocotyledons. The binomial nomenclature of the plants checklist was based on the *Flora of Taiwan*（Ⅱ）(*Bufford* et al., 2003). Compared to the percentage of vascular bundle plants in Taiwan, in the study area, the pteridophytes, gymnosperms, and dicotyledons of these plots were higher, with only monocotyledons (8.93%) being lower than this kind of plant in Taiwan (27.0%) (Table 5).

As to the importance value index of the ground vegetation for each plot, both pteridophytes and the Urticaceae were the main components of the composition. Most of the pteridophytes were *Diplazium dilatatum*, followed by *Monachosorum henry*, *Colysis hemionitidea,* and *Asplenium normale*. Major plants of the Urticaceae included *Elatostema lineolatum* var. *major, Pilea elliptifolia* and *E. platyphylloides*. Relatively, woody plants were quite few and *Lasianthus fordii* was dominant.

The average Pteridopyte quotient in the study area was higher than the average value (4.72) for Taiwan. The higher value indicated that in the study area there is no obvious dry season, thus accounting for the prevalence of the pteridopytes and Urticaceae (Table 6).

CONCLUSIONS

Thinning is a prerequisite activity for tending the plantations. This preliminary study shows the baseline of stand composition and structure on a sugi plantation before thinning, and the effect on the stand tree diameter structure immediately after thinning. However, data of more years of monitoring are required to investigate the long-term effect of thinning on parameters monitored in this study.

Table 5. Comparison of vascular plants in the study area and those in Taiwan

	Study area				Taiwan1)	
	Family	Genera	Species	Percentage of species (%)	Number of plants	Percentage of species (%)
Pteridophytes	21	36	58	17.26	570	14.2
Gymnospermae	3	6	7	2.08	28	0.7
Dicotyledons	75	175	241	71.73	2334	58.1
Monocotyledons	10	26	30	8.93	1086	27.0
Total	109	133	336	100.00	4018	100.00

1) Source of Taiwan comes from *Flora of Taiwan* (Ⅱ).

Table 6. Pteridopyte quotient value in each plot

Plot number	1	2	3	4	5	6	7	8	9	10	11	12
Pteridopyte quotient	4.76	6.25	7.45	9.56	5.19	7.69	8.33	6.9	6.67	6.62	7.14	3.70

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Effects of Different Forest Thinning Treatments on Soil Net Nitrogen Mineralization and Nitrification in a *Cryptomeria japoica* Plantationn

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[Summary]

In this study, we investigated the impacts of forest thinning on soil nitrogen mineralization (Nmin) and nitrification in a high-elevation *Cryptomeria japonica* plantation to provide basic data for forest management and enhance our understanding of the influence of forest thinning on soil nutrient transformation. Four study plots were chosen for a control, and lightly, moderately, and heavily thinned treatments. Three sub-plots were selected for buried bag studies at close elevations in each plot to measure the net Nmin and nitrification rates in situ. The contents of soil inorganic N (i.e., ammonium and nitrate) showed no significant differences among the various treatments; but all varied with seasons and reached a maximum in September 2003 and 2004. The seasonal maximum net Nmin rates after the 4 treatments were 0.182, 0.246, 0.303, and 0.560 mg N kg^{-1} d^{-1} in 2003, and 0.242, 0.258, 0.411, and 0.671 mg N kg^{-1} d^{-1} in 2004, respectively. These estimates are among lower values for the annual rate of Nmin in this region. In general, forest thinning treatments can enhance net Nmin and microbial biomass carbon. For example, the percentage increases in the annual rates of Nmin compared with the control plot were 13.4, 59.8, and 154.2% in 2003, and 0.1, 58.8, and 157.7% in 2004 for the lightly, moderately, and heavily thinned treatments, respectively. These differences are possibly related to many factors, including differences in soil moisture and temperature, precipitation inputs, soil types, and vegetation types. Well-planned multi-site comparisons, both within Taiwan and the East Asian region, could greatly improve our understanding of regional patterns of nitrogen cycling.

Key words: base saturation, cation-exchange capacity, soil nitrogen mineralization.

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INTRODUCTION

Nitrogen (N) is a major limiting factor for forest growth and productivity of terrestrial ecosystems (Keeney 1980, Binkley and Hart 1989, Paul and Clark 1989, Vitousek and Howarth 1991). Plants uptake N mainly in inorganic forms that can be converted from soil organic N through the process of mineralization. However, many factors controlling this process exhibit great temporal and spatial variations that are still not completely understood. Disturbances from natural and artificial factors can directly and indirectly affect forest soil ecosystems as well as soil N transformation processes. Pre-commercial thinning of forests is a common practice in which some trees in immature stands are removed to increase the growth of the remaining trees and the total yield or value of the usable wood. As a strong form of interference, it is likely that thinning measures result in many changes in a forest. In addition to investigations of forest production, many studies have characterized the response of soil N transformation to forest thinning measures (Powers 1990, Gessel et al. 1990, Dyck et al. 1994, Thibodeau et al. 2000).

Due to high mineralization and nitrification, NH_4^+ and NO_3^- concentrations show the greatest increases after thinning (Baeumler and Zech 1998), while net N mineralization (Nmin) decreased in thinned balsam fir (*Abies balsamea* (L.) Mill.) plots (Thibodeau et al. 2000). Thinned plots in both of those studies showed greatly increased NH_4^+. Changes in soil temperature and moisture after thinning are important explanations of the impacts of this intervention on soil nutrient transformations and sustainability of fertility (Entry et al. 1986, Thibodeau et al. 2000).

In Taiwan, forests cover almost 2/3 of the total area of the island and 1/3 of these lands are monoculture forests planted several decades ago. In accordance with current trends in economic development, the goals of forest management purely for commercial production are being changed to take into consideration ecological and environmental functions. There is the potential for changing the current monoculture forests through thinning and reforestation to increase biodiversity. Nevertheless, there have been few studies on the impacts of thinning treatments on nutrient transformation of monoculture forest plantation soils especially in mountainous areas of Taiwan. Thus, in this study, we attempted to investigate the impacts of forest thinning on soil Nmin and nitrification in a high-elevation *Cryptomeria japonica* plantation to provide basic data for forest management and to enhance our understanding of the influences of forest thinning on soil nutrient transformation.

MATERIALS AND METHODS

Site description and thinning treatments

This study was carried out in a 30-yr-old *C. japonica* plantation located in the Guanwu recreation region, Chutung, Hsinchu County, northwestern Taiwan. The study site is a montane area with elevations ranging from 1900 to 2250 m. The annual precipitation is 2500 mm, occurring mainly between May and September, characteristically as rainstorms associated with typhoons. The mean annual temperature of the site is 12.5°C, with a range of 6.5~18°C from 2003 to 2004. The parent materials are composed of sandstones and clay sediments interbedded with Tertiary shale and slate (Ho 1988).

Experimental design

The total area of the plantation is 29 ha, and 4 thinning plots were set up in early 2002 for the control (i.e., 0%), lightly (40%), moderately (53%), and heavily thinned treatments (67%) based on the thinning intensities. The purpose of thinning was to investigate micro-environmental changes in the forest soil ecosystem. This study focused on variations in Nmin and nitrification after thinning. The stand densities were 1500, 900, 700, and 500 trees ha^{-1} for the control, lightly, moderately, and heavily thinned treatments, respectively. The thinned trees were left on the forest floor in packs near the plots. Before the thinning treatment, we located and marked 5 plots in each thinning plan at each site. Study zones were separated by 50 m, and the sub-plot size was 2 x 2 m for the different thinning treatments. Plots were randomly located within each zone. Five soil samples in each plot were randomly collected from the O/A horizon (i.e., 10~20 cm) as background for the soil physical and chemical analyses. The soils are classified as sandy loam or silty loam, mixed, mesic, Typic Dystrudepts (Soil Survey Staff 2006).

Soil temperature and moisture

In each plot, 3 subplots were selected for each thinning treatment, and a temperature and moisture datalogger was installed. Soil temperature and moisture were continuously monitored using a Watch Dog Model 450 Datalogger (Spectrum, USA), which consists of an external soil temperature 3667 sensor and a Watermark soil moisture 6450D sensor. The sensors were buried in mineral soils at a 10-cm depth to measure soil temperature and moisture. The air temperature was measured at a height of 70 cm above the forest floor.

Determination of soil net Nmin and nitrification rates

The experiment was limited to the O/A horizon (10~20 cm) because we expected the fine-root biomass in both sites to be concentrated in the upper part of the soil profile. Below 20 cm of soil depth, fine roots were scarce, although coarse roots were observed. Net Nmin and nitrification rates were estimated in situ using a buried polyethylene bag technique (Eno 1960, Hart and Firestone 1989). The soil net Nmin and nitrification rates were calculated from differences in NH_4^+-N+NO_3^--N and NO_3^--N before and after incubation, respectively. The polyethylene bags (about 30 μm thick) allowed O_2 and CO_2 diffusion, so aerobic conditions were maintained in the isolated soil, along with diurnal temperature patterns and the soil moisture content at the time of sampling. Soil samples were taken with a 10-cm-diameter soil corer of the O/A horizon. Two soil samples were simultaneously collected: one was buried in the original hole and covered with litter, while the other was taken back to the laboratory. Five replicates of each sample were taken in each subplot and incubated for 3 mo, i.e., samples were taken every 3 mo from December 2002 to December 2004.

Soil analysis

The pH of soil samples was measured in distilled water (soil: solution of 1: 5 w/w). Total C and N contents of the soils were determined by a CHN analyzer (Carlo Erba analyzer, Milan, Italy). The cation-exchange capacity (CEC) of the soils was determined by the ammonium acetate (NH_4OAc) exchange method (Rhoades 1982). Exchangeable cations in supernatants were extracted with a 1 M NH_4OAc (pH 7.0) solution. Na, K, Ca, and Mg concentrations were determined by conductivity coupled plasma atomic emission spectroscopy (ICP-AES) (Perkin Elmer Optima 2000DV). The freeze-dried soils (< 2 mm) were suspended in distilled water and dispersed by ultrasonication. The dispersed soils were separated into clay, silt, and sand fractions by sedimentation and centrifugation for the soil texture analysis (Jackson 1979). We estimated the soil bulk density using the core method, for which the oven-dry weight of the soil is divided by the volume of the core (Blake and Hartge 1986).

Soil samples were passed through a 2-mm sieve. A subsample was employed to measure the moisture content at 105°C overnight until a constant weight was obtained. Fresh soil samples (10 g) were extracted with 100 mL of a 2 M KCl solution on a mechanical shaker for 60 min. Soil extracts were filtered through Whatman no. 42 filter paper. Ammonium concentrations of the filtrates were determined using a manual indophenol colorimetric method (Dorich and Nelson 1983). Nitrate concentrations were determined using the manual Cd reduction method (APHA 1998). The net N nitrification rate was calculated as the difference in NO3--N concentrations between the incubated sample and initial samples. Annual rates of net Nmin and

nitrification were estimated by summing all monthly values (Owen et al. 2003a). Net Nmin and nitrification rates were converted to mass per area per unit time using bulk density estimates.

RESULTS AND DISCUSSION

Soil temperature and moisture

The effect of forest thinning on soil temperature showed significant differences in summer (p = 0.001) but not in winter. Compared with that of the control, the mean temperature of soil after the heavy-thinning treatment increased by 0.7°C (p = 0.02) in 2003 and 0.5°C in 2004. The thinning treatments had no significant effect on the soil moisture, with the medium-thinning treatment showing the highest moisture variations.

Temperature and moisture are the most important environmental factors affecting soil N transformation (Frederick 1956, Standford and Epstein 1974, Powers 1990, Nicolardot et al. 1994, Knoepp and Swank 2002). The effect of soil moisture on Nmin can be described by a linear model, while that of temperature follows an exponential model (Wang et al. 2004). However, Knoepp and Swank (2002) indicated that soil moisture acts as a correction term for the exponential response of Nmin to temperature. Nicolardot et al. (1994) reported that temperature influenced the movement of labeled C and N through the microbial biomass, and maximum mineralization rates occurred between 20 and 28°C. Standford and Epstein (1974) examined the relationships between soil moisture and Nmin for 9 different soil types. Maximum mineralization rates occurred at soil matrix potentials of 0.3~0.1 MPa (or about 10~35% moisture by weight), but temperature showed only a slight effect in limiting increases in soil moisture contents (Knoepp and Swank 2002).

Water contents in the thinned plots were higher than that in the control, but the order was not consistent with that of temperature for the different thinning treatments. This was mainly due to spatial variations in the plots, where the medium-thinning treatment was performed on a north-facing slope that received more precipitation than the other plots. At the same time, the water potential levels of all treatment plots were lower than 0.1 MPa, suggesting that moisture was not a limiting factor for soil Nmin. Thus, the change in temperature after thinning, rather than moisture, was the dominant factor affecting soil Nmin. In general, mean values of microbial biomass C of the control samples were in the range of 735 ± 32 to 425 ± 22 μg g^{-1} dry soil, and microbial biomass C increased with an increasing extent of forest thinning.

Soil basic physical and chemical properties

The basic physical and chemical properties of the soils are shown in Table 1. The highest soil pH of 5.12 was recorded in the control plot, and the lowest soil pH of 3.67 was found in the lightly thinned plot. Total C and N were the highest in the lightly thinned plot. The CEC and clay contents were similar in all thinning treatments. The BS (%) was higher in the control and moderately thinned plots but lower in the lightly and heavily thinned plots. The soil texture ranged from sandy loam to silty loam. In general, the contents of total N and C, and C/N ratios showed the following trend: lightly thinned > heavily thinned > moderately thinned > control.

Soil pH can affect the soil microbial activity and is related to N transformation, as the lower pH greatly decreases N nitrification (Frederick 1956). However, several studies have reported that there is no direct relationship between soil pH and the Nmin rate (Hassink 1992, Maris et al. 1994, Laverman et al. 2000). The soil C/N ratio is one of the important factors controlling the Nmin process (Matson and Vitousek 1981, Bengtsson et al. 2003). It is assumed that microbes may be N-limited in soil with a C/N ratio above 20 and C-limited in soil with a C/N ratio below 20 (Tate 1995). The soil C/N ratios of the study plots ranged from 14.6 to 18.2 and showed no significant differences in this study (Table 1). The CEC and BS are less relevant to Nmin, as reported by Bonilla and Roda (1992) and Bengtsson et al. (2003). Soil texture and structure may affect C and N mineralization rates, thus accounting for most of the variations in soil C and N contents (Hassink 1992, Six et al. 1999, Giardina et al. 2001). Similar clay contents and soil textures of the 4 plots resulted in no significant differences in Nmin among them (Table 1). Owing to the inconsistencies of the basic soil physicochemical properties of the treatment plots, spatial variations of the soil did not exert a great effect on the results of the thinning treatments.

Table 1. Selected physical and chemical properties of the tested soils

Thinning treatment	pH	Total C (%)	Total N (%)	C/N	CEC (cmol kg^{-1})	BS (%)	Sand (%)	Silt (%)	Clay (%)	Texture
Control	5.12^{ba}	12.0b	0.82ab	14.6	25.3 a	15.2a	30.7	51.8	17.5^{a}	Sandy loam
Light	3.67 ^{b}	18.9a	1.04 a	18.2	21.8 a	7.5 b	20.5	62.1	17.4^{a}	Silt loam
Medium	4.98 ^{a}	13.0^{ab}	0.75 b	17.3	24.1 ^{a}	18.1a	37.1	47.3	15.6^{a}	Sandy loam
Heavy	3.78 ^{b}	15.0 a	0.83ab	18.1	28.1 a	4.6 b	14.4	65.4	20.2^{a}	Silt loam

BS, base saturation; CEC (cation exchange capacity), capacity of exchangeable cation. Different letters in a column indicate a significant difference at the 95% level (p = 0.05, n = 5).

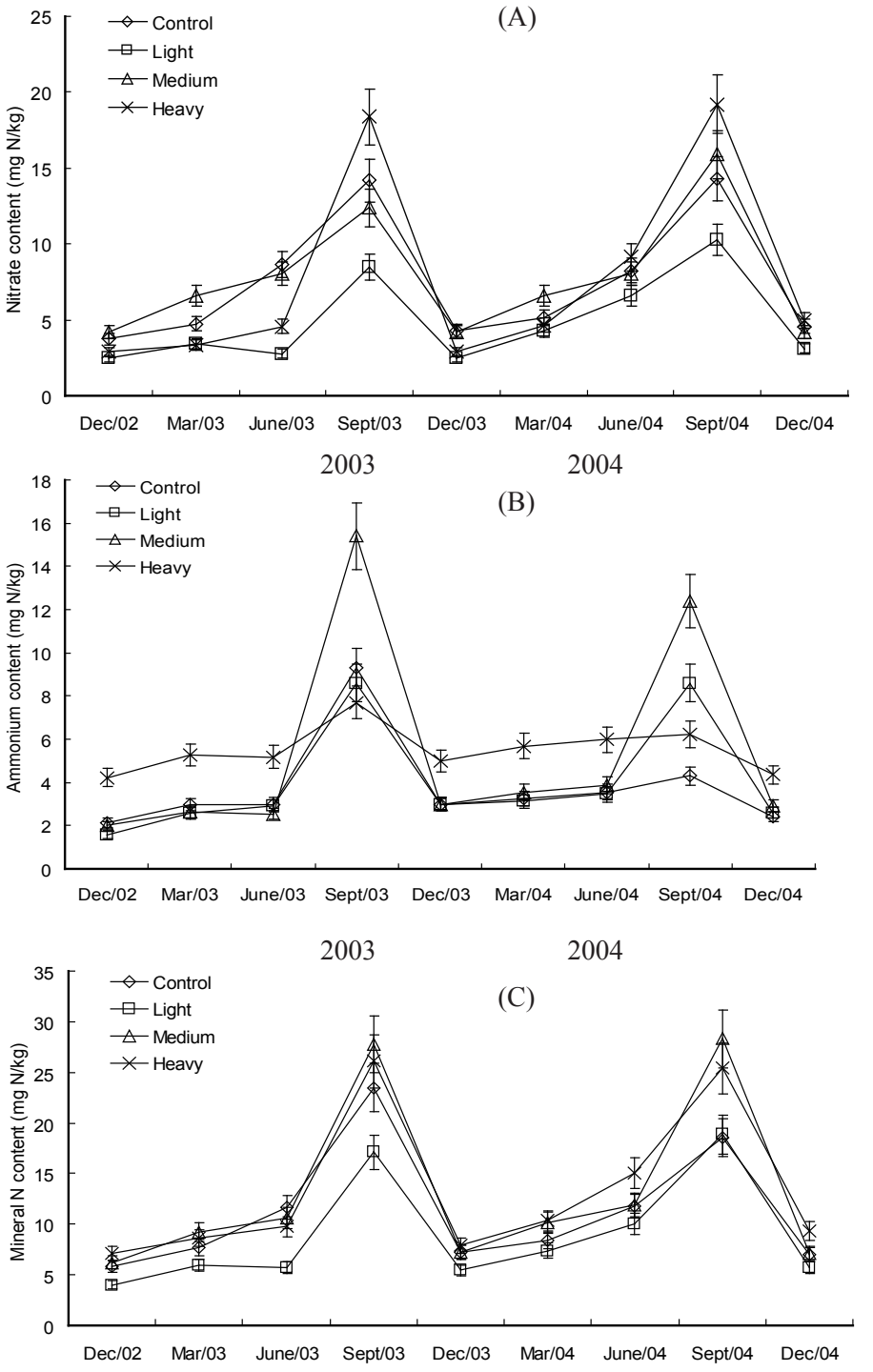

Fig. 1. Variations in inorganic N contents in plantation forest soils with season. (A) Nitrate-N; (B) ammonium-N, and (C) total inorganic N.

Variations in soil inorganic N with season

Figure 2 displays seasonal variations in inorganic N (NO_3^--N, NH_4^+-N, and NO_3^--N+NH_4^+-N) of the 4 thinning treatments, showing 2 cycles of higher NO_3^--N, NH_4^+-N, and NO_3^-N+NH_4^+-N concentrations in June~September 2003 and 2004. Lower inorganic N concentrations were found from December to March in both 2003 and 2004. Nitrate concentrations were 3.73~14.2, 2.45~10.25, 4.21~15.9, and 2.89~19.2 mg N kg^{-1} for the control, and lightly, moderately, and heavily thinned treatments (Fig. 1A), while the corresponding ammonium concentrations were 2.14~9.31, 1.56~8.66, 2.01~15.4, and 4.21~7.79 mg N kg^{-1}, respectively (Fig. 1B). Inorganic N of all thinning treatments was the highest in September at 17.1, 26.1, 23.5, and 27.8 mg N kg^{-1} in 2003; and 18.60, 18.85, 28.30, and 25.40 mg N kg^{-1} in 2004, respectively (Fig. 1C). Compared with that of the control, LSD values of all thinning treatments were significantly higher ($LSD_{0.01}$ = 3.21) in 2003. Inorganic N concentrations showed no consistent relationship with the thinning intensities.

Soil net Nmin and nitrification

Of all treatments, the highest soil net Nmin rate occurred in June to September in both 2003 and 2004. The highest net Nmin rates were 0.182, 0.246, 0.303, and 0.560 mg N kg^{-1} d^{-1} in 2003, and 0.242, 0.258, 0.411, and 0.671 mg N kg^{-1} d^{-1} in 2004, for the control, lightly, moderately, and heavily thinned treatments, respectively. Similarly, the highest net N nitrification rates were 0.177, 0.198, 0.284, and 0.259 mg N kg^{-1} d^{-1} in 2003, and 0.231, 0.242, 0.289, and 0.334 mg N kg^{-1} d^{-1} in 2004 for the corresponding treatments.

Forest thinning decreases the stand density and increases radiation and temperature as well as the water content of the soil (Sucoff and Hong 1974, Thibodeau et al. 2000). Our results obtained shortly after thinning also agreed with those roported trends. The mean soil temperature of all plots was in the range of 0 to 20°C, and the soil Nmin showed a sensitive response to temperature changes. Thus, the increase in temperature after thinning was mainly responsible for the higher Nmin rates of the thinned plots, showing 2 cycles of higher NO_3^--N, NH_4^+-N, and NO_3^--N+NH_4^+-N concentrations between June and September in 2003 and 2004. Seasonal variations in Nmin rates correspond to seasonal patterns of soil temperature and moisture (Nadelhoffer et al. 1984, Adams and Attiwill 1986, Strader et al. 1989, Bonilla and Roda 1992, Knoepp and Swank 1998). In this study, the relationship between Nmin and

mean soil temperature can be described as: Nmin rate = 0.0269T - 0.1355, $R^2 = 0.5121$ ($p < 0.01$, $n = 48$). However, the effect of forest thinning on Nmin varied with season, suggesting that the mineralization process was controlled by interactions between thinning effects and environmental factors.

In general, low concentrations of nitrates occur in forest soils. Many researchers have suggested that patterns of nitrate production in forest soils are regulated by soil pH, NH_4-N availability, and the presence of compounds in the soil that inhibit nitrification (Robertson 1982, Olson and Reiners 1983, Lensi et al. 1986, Donaldson and Henderson 1990, Laverman et al. 2000). In this study, a high soil nitrification rate was observed which accounted for almost 86% of the Nmin rate. The high nitrification potential at the study site was mainly due to the thin L/O horizon and coarse soil texture.

An annual cycle of N contents and transformations was observed. The cycle showed good consistency with the soil temperature pattern but not with that of moisture, suggesting that temperature was the main factor controlling soil N transformation at this high-elevation site. This result also indicates that the effect of forest thinning on soil N transformation occurs through changes in soil temperature, and is also partly responsible for the spatial variations in N transformation rates.

The amounts of soil net N mineralized increased with more-intense thinning treatments. The highest rate was up to 107.9 mg N kg^{-1} yr^{-1}, and the ratio of mineralized N to total N was about 1.30% in 2003, and 122.4 mg N kg^{-1} yr^{-1} or 1.47% in 2004, which were observed at plots receiving heavy thinning. Comparing the inorganic N concentrations in soils revealed great differences between inorganic N and mineralized N in the soils. An increase in soil temperature stimulates microbial populations and decreases the net Nmin after thinning (Thibodeau et al. 2000). The net Nmin increased after thinning treatment, indicating that only a portion of the mineralized N was taken up by microbes. Moreover, thinning treatment reduces the inorganic N uptake by plants (Matson and Boone 1984, Baeumler and Zech 1998). Thus, the larger amount of mineralized N in the thinning treatments suggests a great loss of inorganic N from the plots after heavy thinning. However, there is no direct evidence indicating the loss of N after other extents of thinning treatments. During this short experimental period, the impact of thinning treatments showed significant effects on Nmin and nitrification in our study site, but an integration of the N balance estimation merits further study.

Estimates of annual Nmin rates

Our estimates of the annual rates of Nmin were compared with other published estimates of annual Nmin rates from forested ecosystems in Asia and North America. At this study site, the annual net Nmin rates of the control plot were 10.6 and 11.4 kg ha^{-1} yr^{-1} in 2003 and 2004, respectively. These estimates are among the lower annual rates of Nmin in this region. In general, forest thinning treatments can enhance net Nmin. For example, increases in the percentage of annual rates of Nmin for different forest thinning treatments compared with the control plot were 13.4, 59.8, and 154.2% in 2003, and 0.1, 58.8, and 157.7% in 2004 for the lightly, moderately, and heavily thinned plots, respectively. These differences could possibly be related to many factors, including differences in soil moisture and temperature, precipitation inputs, soil types, and vegetation types. We believe that these differences merit further study and hope that our results will encourage future multiple-site comparisons of watershed N cycling processes within the East-Asian Pacific region. Well-planned multi-site comparisons, both within Taiwan and the East-Asian region, could greatly improve our understanding of regional patterns of nitrogen cycling.

CONCLUSIONS

In the short term, forest thinning significantly increases soil temperature and moisture in high-elevation plantation forests. The change in temperature is the main factor resulting in varying levels of N transformation depending on the intensity of the thinning treatments. Soil net Nmin and nitrification rates greatly increased after thinning treatments, but soil inorganic N showed no significant differences among the treatments, suggesting a great loss of N after forest thinning. In general, the microbial biomass C increased with an increasing degree of forest thinning. Forest thinning treatments can enhance net Nmin. However, differences in both temperature and N transformation attributed to thinning diminished with time. Our findings are useful for interpreting ecosystem functions in response to thinning management and provide a better understanding of the impacts of thinning on montane forests.

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Soil Respiration in a *Cryptomeria japonica* Plantation in Central Taiwan

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[Summary]

Soil is a major site of CO_2 exchange. CO_2 efflux from the soil surface through soil respiration exerts significant effects on carbon budgets of terrestrial ecosystems. Rates of CO_2 released from the soil (i.e., the soil CO_2 flux) are mainly affected by soil temperature and moisture. These 2 environmental factors change spatially and seasonally. This research was conducted on 10 1-ha plots at 1500 m in elevation in a *Cryptomeria japonica* plantation in Nantou County, central Taiwan. An automated soil flux system was used to measure the soil CO_2 flux, CO_2 concentration, soil temperature, and soil moisture in every plot, each of which had 20 sampling points. Results showed that the CO_2 concentration at the soil surface changed seasonally in accordance with the air and soil temperatures. The soil CO_2 flux was also positively correlated with air and soil temperatures before November 2006, corresponding to the wet season. During this wet season, soil CO_2 flux was in the range of 4.2~5.3 μmol m^{-2} s^{-1}. However, it increased to 6.7~7.2 μmol m^{-2} s^{-1} during December 2006 to March 2007, the dry season, when the soil water content was lower. The increase in the soil CO_2 flux was probably due to better air diffusivity in the drier soil. A multiple regression analysis also confirmed that the soil water content was the most important factor in determining seasonal variations in soil CO_2 flux in this plantation. In addition, we conducted an experiment which maintained a constant temperature but different soil water regimes in a walk-in growth chamber. A negative relationship between soil water content and soil CO_2 flux was found. However, if the soil water content was held constant, then the soil CO_2 flux increased as the temperature increased. Based on data collected from May 2006 to April 2007, the mean soil CO_2 flux was 5.4 ± 0. 4 μmol m^{-2} s^{-1} and the estimated annual soil respiration in this *C. japonica* plantation ranged from 1747 to 2444 g C m^{-2} yr^{-1} with a mean value of 2049 ± 135 g C m^{-2} y^{-1}, which is higher than values recorded for other forests in Taiwan.

Key words: plantation, soil respiration, soil CO_2 flux, soil water content, temperature.

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INTRODUCTION

Research on soil carbon has drawn much attention in recent years. A minor change in the soil carbon pool can exert significant impacts on global carbon cycling and the climate system. Soil respiration promotes global carbon cycling, which in turn can accelerate global warming (Trumbore et al. 1996, Cox et al. 2000). Soil respiration, including root respiration and microbial respiration, is controlled by many environmental factors such as soil temperature, soil water, vegetation types, microbial activity, the soil organic carbon content, and soil physical and chemical properties (Tang et al. 2005). Being affected by so many factors, soil respiration can exhibit high variability both temporally and spatially.

Of all these factors, temperature and moisture are the 2 main environmental factors affecting soil respiration. On a global scale, soil respiration rates are positively correlated with the mean annual air temperature and mean annual precipitation. Annual variations in soil respiration in the same forest are mostly due to variability in temperature and precipitation throughout the year (Davidson et al. 1998, Tang et al. 2005). In tropical and temperate forests in which precipitation variations are not significant, seasonal variations in soil respiration in a specific year can mainly be explained by temperature variations (Malhi et al. 1999, Borken et al. 2002). On the other hand, in places where precipitation is variably distributed throughout the year and thus shows distinctly dry and the wet seasons, soil moisture plays an important role as a factor restricting soil respiration rates (Tang et al. 2005, Borken et al. 2006, Zhou et al. 2007). Within a range of -5 to 35°C, the temperature dependency of soil respiration can be described as an exponential function (Borken et al. 2002). Soil respiration (Q_{10}) increases as soil temperatures or air temperatures increase, with a global mean Q_{10} of 2.4 (Raich and Schlesinger 1992), which doubles for a 10°C rise in temperature. However, soil respiration shows more-complicated relationships, not simply positive or negative, with soil moisture. It can be restricted when soil moisture is either extremely low or high. Many studies have indicated that soil respiration rates decline in cases of soil water deficiency (Davidson et al. 1998, Xu and Qi 2001, Tang et al. 2005, Borken et al. 2006). When soils are highly saturated with water such as after a heavy rain, soil respiration rates can also be inhibited. For instance, in a tropical rainforest in French Guiana, soil respiration rates decreased by 40% after a strong rain event (Buchmann et al. 1997). Furthermore, when soils dry out during the dry season and are then rewetted by precipitation or irrigation, there is a burst of CO_2 efflux (Jarvis et al. 2007). Therefore, the effect of the water status on soil respiration is more complicated than that of temperature.

The long-term purpose of this research was to compare the influences of various levels of thinning practices on soil respiration in a *Cryptomeria. japonica* plantation. Our objectives in

this study included (1) to understand the rates and accumulated amount of the annual soil CO_2 flux before thinning practices commenced as a baseline for the soil CO_2 efflux of the plantation, and (2) to investigate the effects of soil temperature and moisture on soil respiration and thus seek possible explanations for seasonal variations in soil respiration.

MATERIALS AND METHODS

Site description

Our study site is near the Jen-Lun nursery of the Taiwan Forestry Bureau at kilometer 18 of the Jen-Lun Forest, Nantou County. Its elevation is about 1500 m, where the typical climate conditions are wet in summer and dry in winter. Trees of this *C. japonica* plantation cover 78 ha and are aged 21~30 yr. Twelve 1-ha plots were established in November 2005.

Soil respiration measurements

Among the 12 plots, only 10 plots were chosen to measure soil respiration, for the remaining 2 plots were full of rocks, and measurements were difficult to perform. Twenty sampling points were established in each plot. A plastic collar, 4.5 cm in height, 0.5 cm in thickness, and 10.5 cm for the inner diameter, was inserted 1~2 cm into the soil at each sample point, leaving the original litter status unchanged but with no living plants inside the collar. By mid-April 2006, all of the sampling points had been set up. An automated soil CO_2 flux system (LI-8100, LI-COR,USA) and a survey chamber were used to monitor parameters including soil CO_2 concentration, soil CO_2 flux, and air temperature and relative humidity. In addition, a soil temperature probe (8100-201, LI-COR) and a soil moisture sensor (EC-10, Decagon Device,USA) were inserted 5 cm into the soil to measure the soil temperature and water content.

Influences of water content and temperature on soil respiration in a controlled environment

In January 2007, we extracted soils from the surface to 10 cm deep from the plantation and placed them in pots. Various amounts of water were then added to the pots in a walk-in growth chamber with the temperature controlled at 20°C. A tensiometer (2710 ARL06, Soil Moisture, USA) was inserted 6 cm into the soil of each pot with the ceramic tip of the tensiometer in close contact with the soil, and it was left in place for 1 d. We measured the water content and soil CO_2 flux in each pot. Experiments using the same routine but varying only the temperature were carried out to infer possible relationships between soil CO_2 flux and temperature. These experiments were conducted when the soil water content was decreased to

10%, then the temperature of the growth chamber was raised from 10 to 35°C at 5°C intervals. Each temperature was maintained for 3 h. We measured soil respiration rates in 5 sample pots for every temperature setting.

Data analysis

The mean and standard error of the soil CO_2 concentration, soil CO_2 flux, soil temperature, and soil water content were calculated. Coefficients of variation (CVs) of each variable in every plot were then calculated accordingly. We conducted a regression analysis between the soil CO_2 flux and 2 environmental factors, i.e., soil temperature and water content, on the same measurement date in each plot to explore the influence of these 2 environmental factors on soil CO_2 flux.

RESULTS AND DISCUSSION

We monitored soil respiration in the *C. japonica* plantation every month from December 2005 to April 2007, except in June 2007 when transportation was disrupted due to heavy rains. Since establishing the 10 plots each with 20 sample points, we have collected 200 soil respiration measurements monthly (Table 1). The ground air temperature was relatively low in December and January (9.6~13.9°C), and rose above 20°C in June to September (20.9~23.1°C). We began taking measurements of the soil water content from March 2006, and through November of the same year, they were all above 20% (24~32%). However, soil water content fell below 15% (11~15%) due to low precipitation from December 2006 to April 2007. The monthly mean CO_2 concentration at the ground was 449 ± 5 (range, 411~589) μL L^{-1} (Table 1). As to the soil CO_2 flux, the mean value was as low as 1.3 ± 0.1 μmol m^{-2} s^{-1} in December 2005 when a cold front passed through, and the air temperature was only 9.6 ± 2.2°C. The highest soil CO_2 flux, 7.2 ± 0.4 μmol m^{-2} s^{-1}, occurred in March 2007. The mean soil CO_2 flux of the entire 15-mo period during our study was 4.6 ± 0.4 μmol m^{-2} s^{-1} (Table 1).

Seasonal patterns of variations in the CO_2 concentration at the ground and those of soil CO_2 flux differed. The former peaked in months of higher temperature, i.e., June to September, and varied with air temperature (Fig. 1). On the other hand, soil CO_2 flux was higher during December 2006 to March 2007, apparently differing from the pattern for air temperature. This phenomenon suggests that the soil CO_2 flux might have been affected by environmental factors other than temperature, probably involving factors such as the decreased soil water content. Many studies on soil respiration have pointed out that the CO_2 flux decreases when soils are drier (Davidson et al. 1998, Xu and Qi

2001, Tang et al. 2005). Yet, although the soil water content in our plantation was indeed lower in the winter than in the summer, it was still between 11 and 15%. Furthermore, the soil in the experimental site was sandy clayey loam (Tsen 2007), and 11~15% soil water contents should not have caused serious water stress to root systems or microbial activity. A lower amount of water, however, would increase pore spaces in the soil, promote air diffusivity (Davidson and Trumbore 1995), and increase soil CO_2 efflux (Linn an Doran 1984, Buchmann et al. 1997). Therefore, we found higher soil CO_2 fluxes during the time of low soil water content than in the high-temperature summer or when greater precipitation occurred in autumn.

Table 1. Monthly mean soil CO_2 concentration (conc.), CO_2 flux, temperature (temp.), and soil water content (WC) from December 2005 to April 2007

Month	No. of plots	CO_2 conc. ($\mu L\ L^{-1}$)			CO_2 flux ($\mu mol\ m^{-2}s^{-1}$)			Air temp. (°C)		Soil WC (%)	
		Mean	Range	CV*	Mean	Range	CV*	Mean	CV*	Mean	CV*
2005											
Dec	3	432±2	428~435	0.5	1.3±0.1	1.1~1.6	10.8	9.6±2.2	13.0	-	-
2006											
Feb	7	435±6	419~467	1.4	2.7±0.2	0.2~6.0	3.3	16.5±0.5	3.1	-	-
Mar	5	437±2	433~442	0.4	3.2±0.1	2.9~3.5	3.6	17.4±1.1	6.5	25±0.9	3.5
Apr	5	450±9	432~473	2.0	3.4±0.3	2.9~4.4	7.8	19.5±1.0	5.0	24±0.5	2.0
May	10	461±8	430~513	1.8	4.2±0.2	3.0~5.6	5.6	19.6±0.3	1.4	25±0.4	1.7
June	10	480±7	458~521	1.4	5.0±0.3	3.4~6.4	6.3	23.1±0.3	1.2	28±0.7	2.5
Aug	10	479±9	435~536	1.9	5.3±0.2	4.2~6.3	4.5	23.0±0.2	1.1	28±0.5	1.8
Sept	10	486±17	433~589	3.6	4.3±0.4	2.7~6.6	9.0	20.9±0.4	2.1	27±0.5	1.7
Oct	10	453±5	428~469	1.0	4.3±0.2	3.6~5.0	3.6	18.6±0.3	1.7	24±1.3	5.6
Nov	10	438±4	438~455	1.0	3.7±0.2	2.7~4.6	5.5	17.6±0.3	1.8	32±0.6	2.0
Dec	10	439±5	417~477	1.2	6.7±0.3	5.3~8.1	4.6	14.3±0.4	2.7	13±0.5	4.0
2007											
Jan	10	429±6	411~459	1.3	6.3±0.3	5.1~7.4	4.1	13.9±0.4	2.8	12±0.4	3.6
Feb	10	429±3	418~444	0.7	6.6±0.3	5.0~8.2	5.2	16.0±0.5	2.9	11±1.3	12.4
Mar	10	446±13	423~554	2.8	7.2±0.4	5.8~8.8	5.1	19.5±0.8	4.3	13±1.2	9.2
Apr	10	434±4	414~454	0.9	5.0±0.1	4.4~5.7	2.7	15.9±0.2	1.1	15±0.5	3.5
Average		449±5			4.6±0.4			17.8±1.0		21±2.0	

*CV: coefficient of variation.

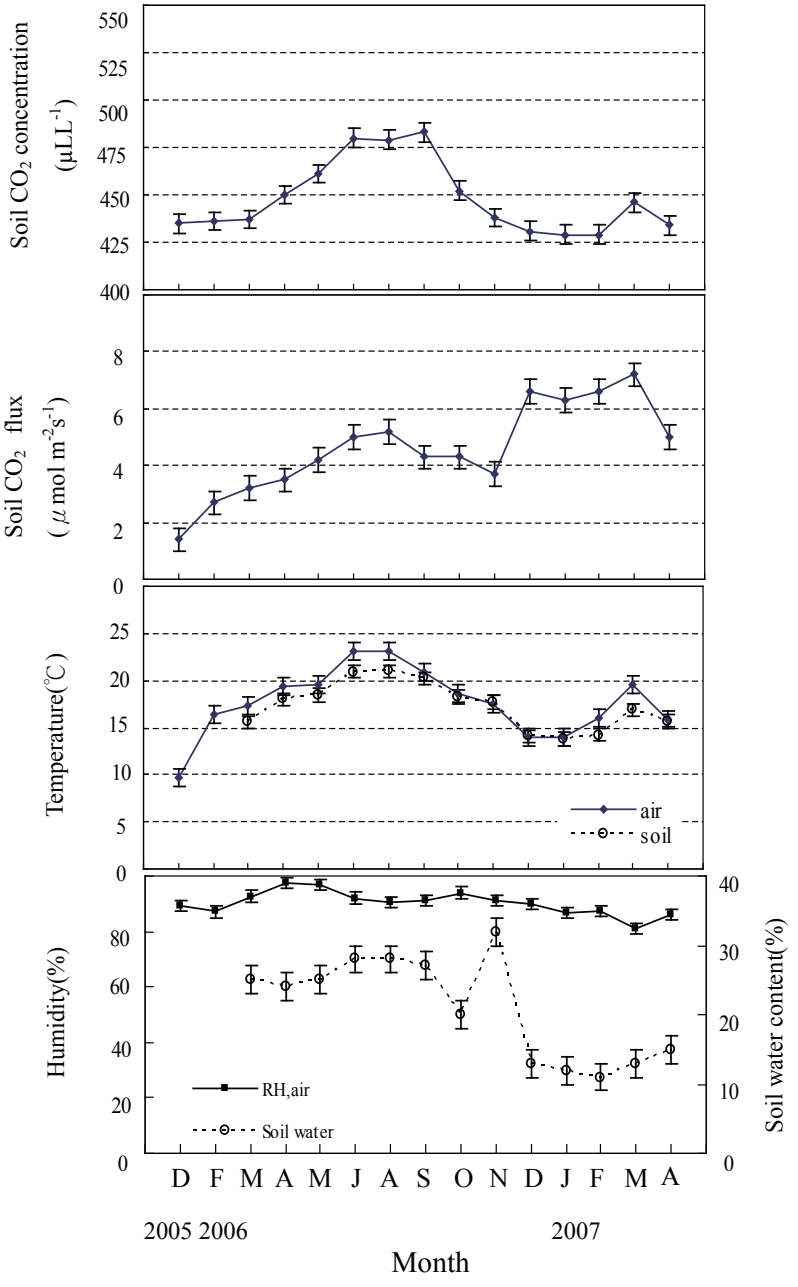

Fig. 1. Seasonal variations in soil CO_2 concentration, CO_2 flux, temperature, air humidity (RH), and soil water content from December 2005 to April 2007.

By analyzing the relationship of soil temperature and monthly mean soil CO_2 flux for all measurements taken from March 2006 to April 2007 in all plots, we found a significant negative relation (Fig. 2a), which does not agree with most research on soil respiration (Davidson et al.

1998, Borken et al. 2002, Tang et al. 2005). But if the study period was divided into the wet season (from March to November 2006, Fig. 2c) and dry season (December 2006 to April 2007, Fig. 2b), then a significant relation between soil CO_2 flux and soil temperature was found in the 2 respective seasons. The coefficient of determination (r^2) was 0.291 for the wet season, which was higher than that for the dry season ($r^2 = 0.196$). Another environmental factor, soil water content, also showed a significant negative relation with soil CO_2 flux using data for the entire study period (Fig. 3a). If divided into wet and dry seasons, then no significant relation ($p > 0.05$, Fig. 3b, c) existed between the soil water content and soil CO_2 flux. However, values for the soil CO_2 flux during the dry season were about 4~11 μmol m^{-2} s^{-1}, which were much higher than values during the wet season (2~6 μmol m^{-2} s^{-1}). Thus combining values of the 2 seasons, we found a negative relation between the soil CO_2 flux and soil water content (Fig. 3a).

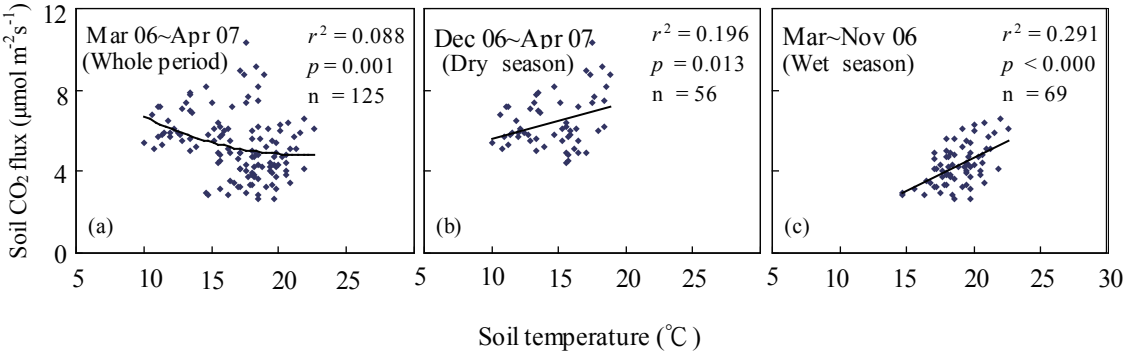

Fig. 2. Relationship between soil temperature and soil CO_2 flux during the dry season (b), the wet season (c), and the entire period (a) from March 2006 to April 2007.

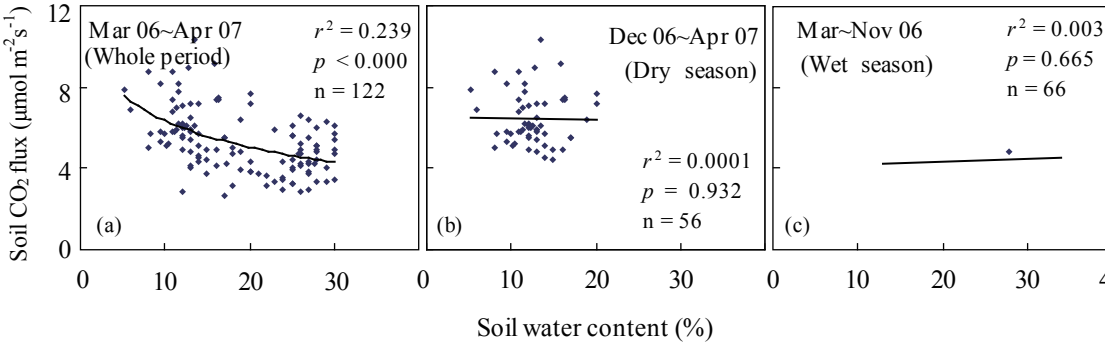

Fig. 3. Relationship between soil water content and soil CO_2 flux during the dry season (b), the wet season (c), and the entire period (a) from March 2006 to April 2007.

We also adopted a stepwise regression analysis to specify the relations between soil CO_2 flux (Y) and environmental factors including air temperature (T_{air}), soil temperature (T_{soil}), and soil water content (H_{soil}). If only 1 factor was included, then the soil water content and soil temperature both showed significant relations with soil CO_2 flux. The regression equations were

$Y = 7.230 - 0.103 \times H_{soil}$, $r^2 = 0.219$, $p = 0.000$, and

$Y = 7.588 - 0.132 \times T_{soil}$, $r^2 = 0.058$, $p = 0.008$, respectively.

If 2 factors were included in the regression, then the following equation was the best choice:

$Y = 5.147 - 0.168 \times H_{soil} + 0.182 \times T_{soil}$, $r^2 = 0.295$, $p = 0.000$.

These results indicated that there was a significant negative relation between the soil CO_2 flux and soil water content. Although higher temperatures in the wet summer season might have promoted CO_2 release by microorganisms, decomposers, and root systems through respiration, water saturation might have blocked pore spaces in the soil, resulting in poor air diffusivity and consequently retarding CO_2 efflux (Davidson and Trumbore 1995, Buchmann et al. 1997). Thus, low soil CO_2 fluxes were observed. On the contrary, although temperatures were lower in the dry season (December to March), CO_2 in the soil could be released at a higher rate due to better air diffusivity in pore spaces, resulting in higher soil CO_2 fluxes.

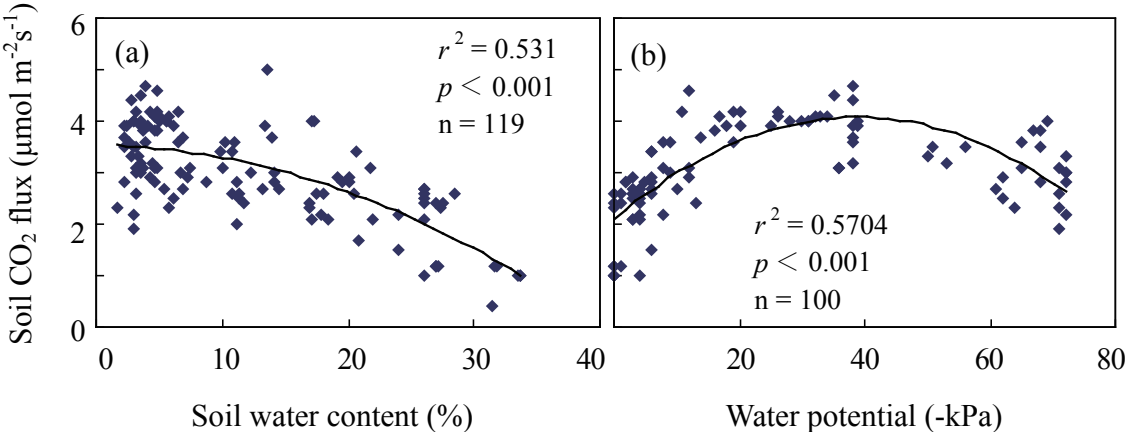

Fig. 4. Rates of soil CO_2 flux as a function of the volumetric water content (a) and water potential of soil samples taken from a *Cryptomeria japonica* plantation in a walk-in growth chamber at 20°C.

To verify the observed negative relation between soil CO_2 flux and soil water content, we extracted soils from the plantation and placed them in pots. Various amounts of water were added to the pots in a 20°C walk-in growth chamber. A tensiometer and soil moisture sensor were used to illustrate the relationship between soil water content and soil CO_2 flux. Results showed that there was a significant negative relation (n = 119, r^2 = 0.531, p = 0.000) (Fig. 4a), which was also shown in the field measurements (Fig. 3a). Therefore, drier soils indeed had higher CO_2 efflux rates. Yet, the soil water content represented by water potential measurements exhibited a nonlinear relation with soil CO_2 fluxes (Fig. 4b). A positive relation between soil CO_2 flux and soil water content occurred when soils were wetter (0 to -40 kPa), while a negative relation only occurred under drier (-40 to -70 kPa) soil moisture conditions (Fig. 4b).

In the growth chamber, when the soil water content was about 10%, i.e., a drier soil moisture condition, the soil CO_2 flux increased exponentially as the temperature was raised (Fig. 5). Soil CO_2 fluxes were 1.7, 4.3, and 11.4 μmol CO_2 m^{-2} s^{-1} at 10, 20, and 30°C, respectively. The flur reached 17.1 μmol CO_2 m^{-2} s^{-1} as the temperature was raised to 35°C. When the temperature was increased from 10 to 20°C, and from 20 to 30°C, the Q_{10} values of the soil CO_2 flux were 2.5 and 2.7, respectively. On average, the mean Q_{10} of soil CO_2 flux in a controlled environment was 2.6, which is very close to the mean Q_{10} value of 2.4 for global forest ecosystems (Raich and Schlesinger 1992).

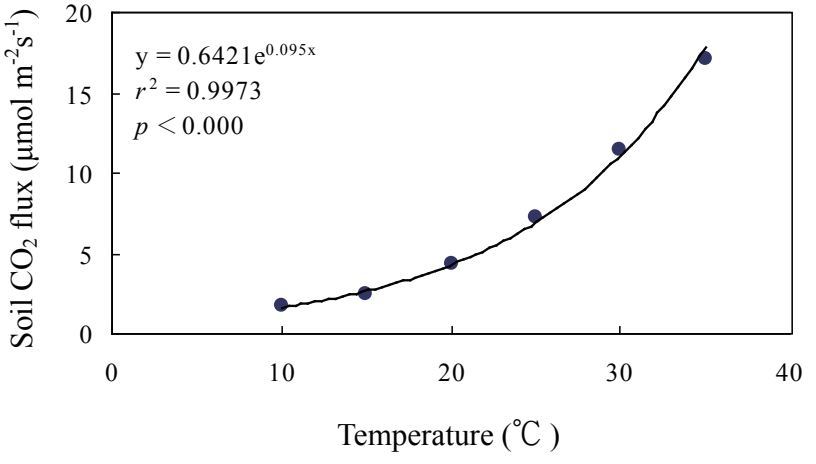

Fig. 5. Rates of soil CO_2 flux as a function of temperature of soil samples taken from a *Cryptomeria japonica* plantation in a walk-in growth chamber at a 10% soil water content.

Table 2. Mean and accumulated annual soil CO_2 flux in each plot of the *Cryptomeria japonica* plantation from May 2006 to April 2007

	Plot										
	1	2	3	6	7	8	9	10	11	12	Total
Mean CO_2 flux ($\mu mol\ m^{-2}\ s^{-1}$)	4.6	5.1	5.1	5.1	5.9	6.5	5.7	5.9	5.5	4.7	5.4±0.4
Annual CO_2 flux ($g\ C\ m^{-2}\ yr^{-1}$)	1747	1930	1944	1911	2226	2444	2160	2221	2095	1769	2049±135

The mean soil CO_2 flux of all plots during our research period from May 2006 to April 2007 was 5.4 μmol CO_2 $m^{-2}\ s^{-1}$. Converting to the annual amount of carbon released, it ranged from 1747 to 2444 g C $m^{-2}\ yr^{-1}$ with a mean value of 2049 ± 135 g C $m^{-2}\ yr^{-1}$ (Table 2). This accumulated annual CO_2 flux was higher than soil respiration in a Guandaushi forest ecosystem, central Taiwan (1240~2350 g C $m^{-2}\ y^{-1}$) (Lee 2003), and was much higher than those in a *Chamaecyparis obtusa* var. *formosana* forest at Chilan Mt., northeastern Taiwan (200 g C $m^{-2}\ yr^{-1}$) (Tsen 2006). Li (2002) reported the soil CO_2 flux of a subtropical broadleaf forest at Fushan, northeastern Taiwan and that of an experimental forest in Liukuei, southwestern Central Taiwan Taiwan to be 1075 and 1600 g C $m^{-2}\ yr^{-1}$, respectively. Therefore, the annual soil respiration at this *C. japonica* plantation was higher than values recorded for other forests in Taiwan.

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Long-term Maintenance of Soil Fertility in Forest Plantations

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[Summary]

Forest plantations are necessary to satisfy the demand for wood as human populations increase. They produce wood materials while avoiding the harvesting of natural forests the services of which are not fully identified and which are certainly more interesting than plantations in terms of ecological and environmental functions. Nevertheless, plantations are managed to maximize production. This means that the constraints on ecosystem resources are high, and the question of soil sustainability is of paramount interest.

Intensively managed high-production forests have been studied in both temperate and tropical areas. Stands were monitored to quantify the main fluxes of water and nutrients and to calculate input-output budgets of nutrients for specific stages of stand development and for the entire rotation. Several examples in temperate and tropical areas show that intensification of production requires well-adapted management of natural resources, and that input-output budgets of nutrients are relevant tools to identify the potential impacts of silvicultural practices before the appearance of negative effects. Moreover, such studies provide relevant information on the underlying processes responsible for long-term changes in soil properties. Intensively monitored experimental designs in selected plantations are powerful tools to gain insights into soil-plant interactions and to develop predictive models coupling carbon, water, and nutrient budgets.

Key words: plantation, soil fertility, soil nutrients.

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INTRODUCTION

The area of plantation forests worldwide increased from about 100×10^6 ha in 1990 to 140×10^6 ha in 2005 to satisfy the demands for wood products of human populations (FAO 2005). However, a large range of plantation management practices occur according to the final products required and pedo-climatic constraints. Large areas of plantations are devoted to firewood production for smallholders, but the areas of commercial plantations for pulp and sawmill productions have dramatically increased over the last decades. Plantations have an important function of supplying of large amounts of wood to reduce pressures on native forests, the services of which are not fully identified and which are more interesting than plantations in terms of ecological and environmental functions. A general feature of plantations is that they are installed on soils with low agronomic potential, and there is growing concern about their sustainability in the context of enhanced productivity resulting from genetic improvements and more-intensive management. Maintaining both the soil capacity for production and the quality of the environment are central goals for sustainable forest management (Nambiar 1997). The problem of maintaining forest soil fertility can theoretically be solved by using fertilizers as has been done in agriculture. For obvious economic reasons, but also for ecological and environmental reasons, the systematic use of fertilizers is neither possible nor desirable: low-production sites have their own ecological richness, and it is not desirable to make all environments uniform.

The same type of experimental design has been installed in plantations established in France and in tropical areas (Congo and Brazil). Continuous monitoring of nutrient fluxes within the ecosystem is being performed on these sites, including determining of the chemical composition of solutions throughout their transfer in the ecosystem, the dynamics of soil water content, litterfall, forest floor decomposition and nutrient accumulation in trees (Ranger et al. 2002, Laclau et al. 2005). This approach makes it possible to establish input-output budgets of nutrients at different spatial and temporal scales (Ranger and Turpault 1999). The quantification of nutrient fluxes and their dynamics over several years provides relevant information on the mineral functioning of forest stands as well as their ecological impacts on soil fertility and water resources. A better understanding of ecosystem functioning must be achieved as ecological intensification of forest management relies more efficiently on ecological processes to sustain forest productivity.

The objective of the present paper was to provide an overview of the approach used by Inra and Cirad year to study the effects of silvicultural practices on long-term nutrient availability in forest soils, for contrasting different contrasting situations of forest management.

Methods to assess the long-term changes in soil fertility

Soil fertility is the sum of the physical, chemical, and biological factors characterizing the capacity for biomass production, but only chemical soil fertility is considered here. Soil fertility has 2 components: a short-term and a medium- to long-term component (Ranger and Turpault 1999). The short-term component is related to the present pool of nutrients available for plant nutrition. It is usually characterized by soil analyses, but it remains a potential which is used differently by different tree species. Moreover, the dynamic equilibrium characterizing medium- and long-term fertility is far more interesting than the current soil fertility, but far more difficult to investigate. It is usually described as the biogeochemical cycle of nutrients characterized by a set of mechanisms which together lead to the conservation of the limited pool of available nutrients for tree nutrition. The cycle is open and elements can enter (atmospheric deposits, mineral weathering, biological fixation, and fertilizer inputs) or leave it (losses associated with deep drainage and biomass harvesting). The cycle tends to optimize the use of available resources for vegetation, which only represent a small part of the total nutrient reserves of the ecosystem in most soils in temperate climates (e.g., Ficher et al. 1998, Ezzaim et al. 1999). In contrast, the potential of nutrient release by weathering in tropical soils can be very low, and the majority of nutrients may be retained in the standing biomass and forest floor (Nambiar et al. 2004, Sommer et al. 2004).

A conceptual model describing the main compartments and fluxes in the ecosystem can be used. The principle is to decompose the ecosystem into compartments with a relatively homogenous behavior and to quantify the fluxes between these compartments. This method makes it possible to (i) identify all fluxes entering and leaving a compartment, (ii) calculate several fluxes impossible to measure directly, such as the uptake of nutrients by vegetation, and (iii) assess input-output budgets at a specific scale (Fig. 1). The sustainability of an ecosystem is associated with the stability of the biogeochemical cycle and with balanced nutrient budgets, at least in the mid-term. This does not mean that production of a species on a site is maximum, but that it is optimal according to the constraints of the environment and to the potentiality of the species to explore them (Ranger and Turpault 1999).

The input-output nutrient budget is a simple algebraic balance between inputs and outputs of an ecosystem. Fluxes must be integrated over a specified time. A budget can be calculated in terms of both total or available reserves. Information is far more relevant in the latter case, especially for plant nutrition purposes.

Spatial scales have to be defined with precision because (i) the mechanisms of soil

functions are scale-dependent, and (ii) information from nutrient budgets is closely related to the scale of the investigation. The advantages and limits of each spatial scale (namely forest plot or catchment) are discussed by Ranger and Turpault (1999). We present here studies at the forest-plot scale, which are the most relevant for investigating the mechanisms involved in long-term impacts of forest management practices on soil fertility.

The equation of a budget at a certain scale is directly derived from the conceptual model presented in Fig. 1. A simplification was made by considering that all available soil elements belong to the same compartment whether they are in the liquid or solid phase, as if calculations were made on dry soil. Formulas for calculating budgets are presented for the more-general cases, but, fortunately, simplifications can usually be made.

For the forest plot:

$$\Delta BS = \text{inputs } (AD + FA + Sf + NSf + W + Lin + Cr + Bi + Ai) - \text{outputs } (BR + Dr + LL + NgL + Bl);$$

where ΔBS (bioavailable stock) is the exchangeable nutrient cations + organically bound nutrients + P and S adsorbed in the solid phase, AD is the atmospheric deposition composed of wet deposition + dry deposition + occult deposition + orographic deposition, FA is foliar absorption, Sf is the symbiotic fixation of N, NSf is the non-symbiotic fixation of N, W is weathering, Lin is the lateral inputs composed of lateral drainage + colluvium, Cr is the capillary rise, Bi is the biological inputs from the plot (flora and fauna), Ai is anthropogenic inputs (fertilization, wastes, etc.), BR is nutrients associated with biomass removal, Dr is drainage losses during the rotation and stand regeneration phase composed of liquid losses + solid losses, LL is lateral losses composed of liquid losses + solid losses, NgL is gaseous losses of N by denitrification and volatilization, and Bl is biological losses of the plot (flora and fauna).

Budgets can also be established at different temporal scales that provide complementary information. They are highly dependant on the stage of development considered, and a comparison of situations is only possible for the same stage of stand development. Budgets have to be calculated over many years in order to eliminate inter-year variability. A 5-yr monitoring seems a minimum duration when looking at the few sites monitored in the long term (Driscoll et al. 1989, Ranger et al. 2002). Seasonal budgets in deciduous forests are useful for assessing the effects of tree nutrition on the main fluxes of nutrients entering or leaving the ecosystem. An assessment of nutrient fluxes at various stages of development representing the entire rotation is relevant both for studying the dynamics of processes during stand development and for calculating nutrient budgets useful for identifying the impacts of management. The longevity

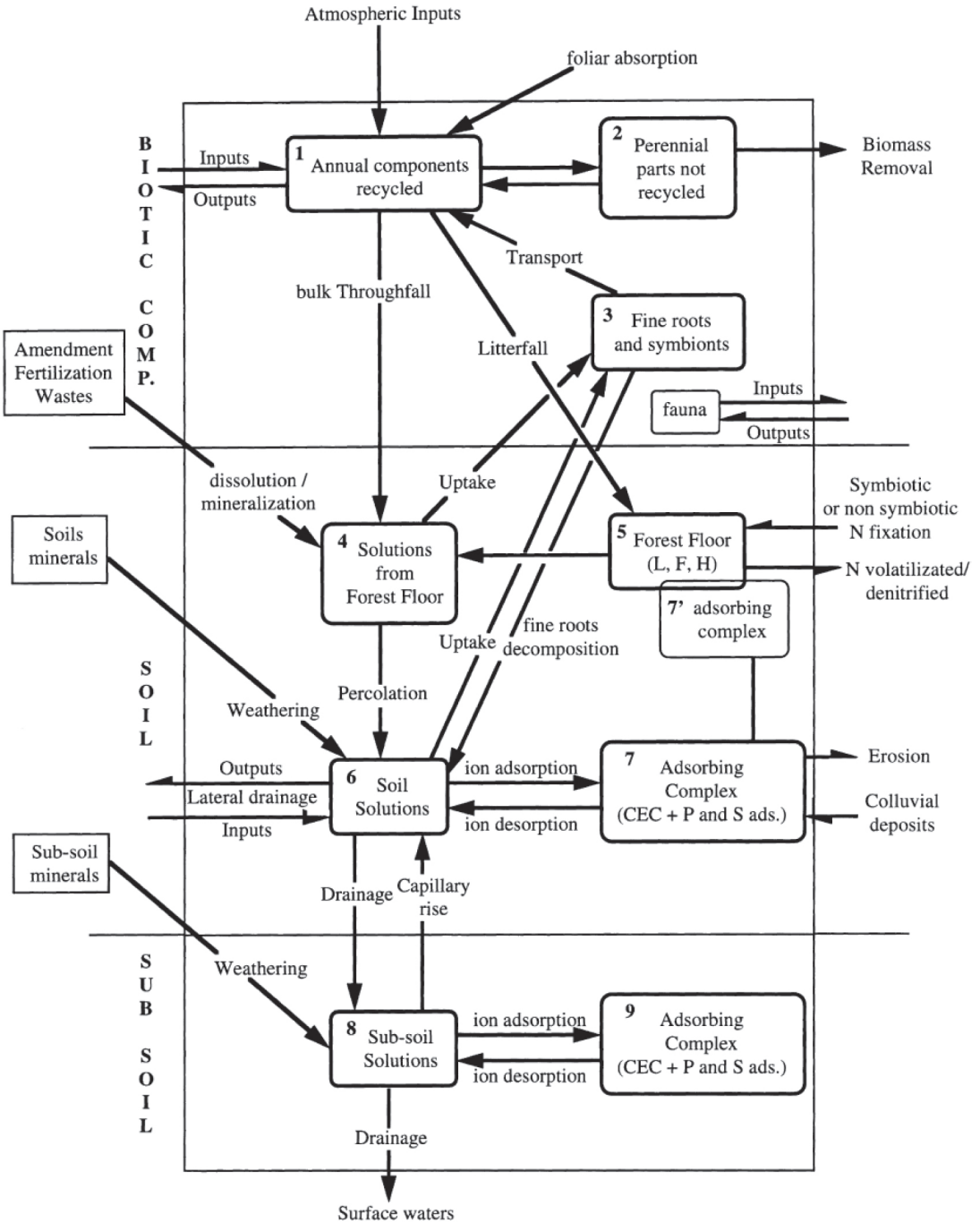

Fig. 1. Conceptual model describing of the biogeochemical cycle of nutrients.

of forest trees in temperate regions makes it necessary to use a chronosequence approach, even if the underlying hypotheses are never completely satisfied (Cole and Van Miegroet 1989). The previous land use of each stand in the chronosequence has to be carefully checked because it can strongly affect the present behavior of the ecosystem (Feger 1988, Ranger et al. 2002). More-accurate input-output budgets for the entire rotation can be established in fast-growing tropical plantations because nutrient fluxes can be measured over a complete rotation in the same stand (Laclau et al. 2005 2007).

Sampling in each study stand has to be designed to assess spatial and temporal variabilities in nutrient fluxes which are usually high, even in mono-specific forest plantations (Ranger et al. 2002, Asano et al. 2006). Extensive literature is available to establish reliable experimental designs making it possible to assess with sufficient accuracy the main fluxes (i.e., atmospheric inputs, nutrients associated with biomass removal, and losses by deep drainage) and then the input-output budgets.

Examples of use of input-output budgets as management tools

Influence of afforestation with Eucalyptus in Congolese savannas on soil fertility

An experimental design was installed in a native savanna and in an adjacent 6-yr-old *Eucalyptus* plantation to assess the effects of afforestation on the biogeochemical cycles of nutrients in the Congo. P, K, Ca, and Mg budgets established over 3 yr in the savanna were roughly balanced, which was consistent with the presence of that savanna for more than 3000 yr in the region as indicated by previous studies (Trouvé 1992). An input of N by biological fixation is necessary to balance the N budget in that ecosystem (Table 1). The legume species *Eriosema erici-rosenii* R.E. Fries (Papilionoideae) found in all of the savannas of the region must play an important role in the N input in this ecosystem, compensating for long-term losses. Budgets of K, Ca, and Mg were also roughly balanced at the end of the *Eucalyptus* rotation (from age 6 to 9 yr) considering the accuracy of the determination of the fluxes (Laclau et al. 2005). By contrast, the P budget was slightly negative, and high N immobilization in stemwood led to a deficit of about 26 kg N ha^{-1} yr^{-1} (Table 1).

Nutrient budgets were assessed for the entire *Eucalyptus* rotation with contrasting different contrasting harvesting methods. The range of variation between the most conservative method (scenario 1) and the most costly in nutrients (scenario 4) was about 180 kg ha^{-1} for N, 25 kg ha^{-1} for P, 55 kg ha^{-1} for K and Ca, and 30 kg ha^{-1} for Mg (Fig. 2). De-barking the stems on site retained 31, 9, 21, 28, and 16 kg ha^{-1} of N, P, K, Ca, and Mg, respectively at the soil surface.

These values represented about 10% of the amount of N accumulated in the above-ground part of the trees at harvest, 20% of that of P and K, and 35% of that of Ca and Mg. The removal of firewood by surrounding populations in the Congo (scenario 2) led to further losses of 50, 8, 20, 9, and 7 kg ha^{-1} of N, P, K, Ca, and Mg, respectively, relative to the most conservative method where only de-barked pulpwood is harvested. The current silviculture practice in the Congo led to a deficit of 144 kg ha^{-1} of N for the first rotation after afforestation. This deficit represented about 7% of the initial amount of total N in the A_1 horizon (0~50 cm) of the savanna.

Table 1. Mean input-output fluxes of nutrients in the soil under an *Eucalyptus* stand (from six to nine years of age) and a native savanna (kg ha^{-1} $year^{-1}$)

	Savanna					***Eucalyptus* stand**				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Wet deposition	4.8	0.3	2.7	3.3	1.4	4.8	0.3	2.7	3.3	1.4
Dry deposition	0.0	0.0	0.0	0.0	0.0	6.5	0.3	3.8	4.5	1.8
Symbiotic fixation (1)	21.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Weathering	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Total inputs	26.4	0.3	2.8	3.3	1.4	11.4	0.6	6.8	7.8	3.2
Surface runoff	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.4	0.1
Deep drainage	3.0	0.1	0.6	0.4	0.2	4.3	0.3	2.1	1.1	1.2
Immobilization (2)	-	-	-	-	-	32.7	3.7	4.8	3.9	2.5
Burning	23.4	1.5	2.4	2.6	2.9	0.0	0.0	0.0	0.0	0.0
Total outputs	26.4	1.6	3.0	3.0	3.1	37.0	4.1	7.1	5.4	3.8
Mean over 3 yr	0.0	-1.3	-0.2	0.3	-1.7	-25.6	-3.5	-0.3	2.4	-0.6
Inter-annual range:										
Minimum	0.0	-1.4	-0.4	-0.1	-1.8	-29.7	-3.9	-2.4	1.6	-0.3
Maximum	0.0	-1.2	0.0	0.5	-1.6	-21.6	-3.0	1.3	3.4	-0.7

(1) Calculated to balance the nitrogen budget in the savanna.
(2) Nutrient immobilization in stemwood.

Even if certain fluxes were assessed with large uncertainty, input-output budgets clearly demonstrate that *Eucalyptus* plantations take advantage, during the first rotation after afforestation, of N soil fertility inherited from the previous savanna vegetation. Unfavorable qualitative changes add further to the quantitative deficit of the N budget: savanna organic matter is progressively replaced by *Eucalyptus* organic matter which is poorer in N (Trouvé et al. 1994), and the chemical composition (tannins, lignin, and polyphenols) of which leads to slower mineralization (Bernhard-Reversat et al. 2001). Budgets for the other elements for the entire rotation were well balanced relative to the amounts of available elements in the soil. This behavior is consistent with fertilizer field trials in this area, which show that tree responses to N

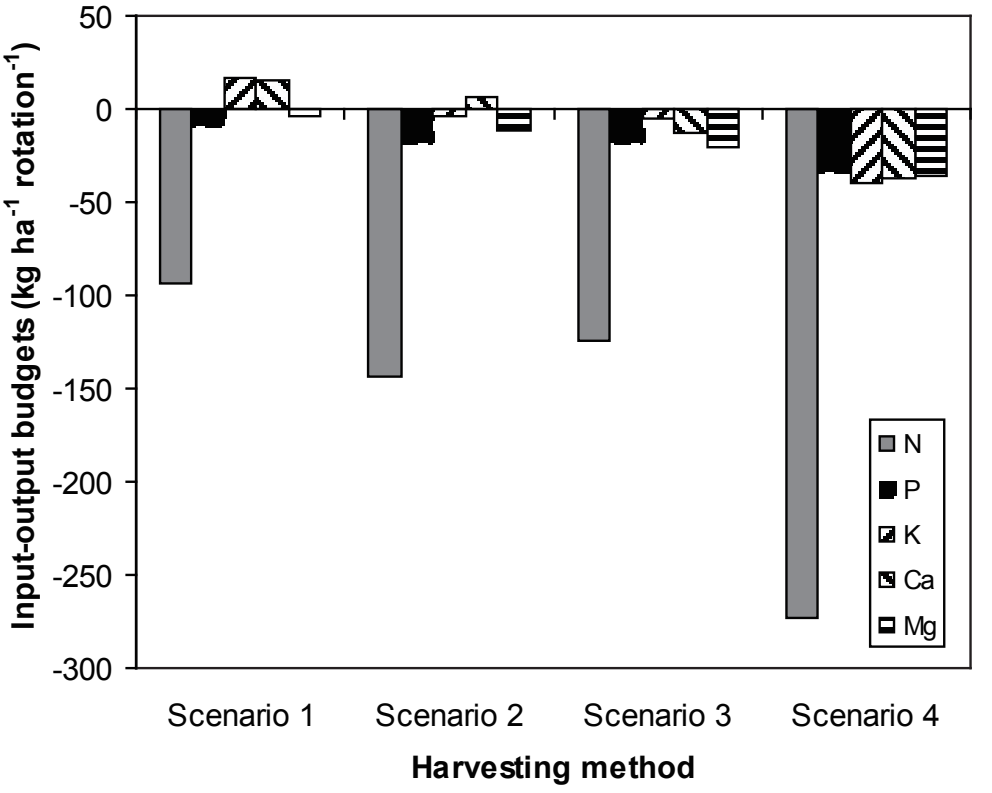

Fig. 2. Input-output budgets (kg ha^{-1}) of N, P, K, Ca, and Mg for the entire *Eucalyptus* rotation, and for various harvesting scenarios.

*Scenario 1: de-barked pulpwood harvest; Scenario
2: de-barked pulpwood and firewood harvest; Scenario
3: pulpwood with bark harvest; Scenario 4: whole-tree harvest.

inputs increase over successive rotations, whereas no response to P and K inputs was observed, even in replanted sites 20 yr after savanna conversion (Bouillet et al. 2003).

Low amounts of nutrients in the soils of this area (with the exception of P), and the high costs of fertilizer inputs make it essential to strictly limit nutrient losses throughout stand rotation. Several modifications of silvicultural practices were proposed to achieve this goal.

- Field trials of fertilization. Quantitative data from the budgets show that field trials should focus on N fertilization. Future plantations, with much more-productive clones might lead to unbalanced budgets of K, Ca, and Mg in the soils. It would then be important to check that these elements do not become limiting after several rotations.
- Soil preparation and weed control. Minimum cultivation is recommended to limit nutrient

losses by erosion, and planting must occur as quickly as possible after harvesting to reduce nutrient losses by drainage. Moreover, weed controls must be planned to take advantage of the temporary fixation of nutrients in the biomass of weeds during the early growth of the stands.

- Harvesting methods. The effects of various harvesting scenarios on nutrient budgets were quantified. They show that current practices including de-barking on site is fundamental owing to the chemical paucity of the soil. This feature was confirmed by an experiment dealing with organic matter management in Congolese *Eucalyptus* plantations (Nzila et al. 2002).

- Fire prevention. Nutrient budgets provide new light on the terrible effects of fires in these plantations. Large losses of N by volatilization during burning have clear negative consequences for long-term production in this area where N is the first nutritional limiting factor. Effective fire prevention is therefore crucial for the sustainability of these plantations.

- Introduction of a legume understory. Numerous studies have shown that mixed plantations between *Eucalyptu*s and legume species can have beneficial effects on soil N fertility (Forrester et al. 2006). An understorey of *Acacia mangium* introduced in *Eucalyptus* stands exhibited a high rate of biological N_2 fixation in the Congo and might be an attractive option to enhance soil fertility, through inputs of organic matter and atmospheric N (Bouillet et al. 2007).

Influence of current silviculture practices on soil fertility in French Douglas-fir plantations

In France, Douglas-fir is one of the first species used in plantations, because of its high production (with a maximum annual increment (MAI) of between 15 and 20 $m^3.ha^{-1}.year^{-1}$) and because it produces a wood of good quality. Douglas-fir is a calcifuge and does well on appreciates deep, well-drained soil. The experimental site at Beaujolais is well representative of the medium where it was introduced.

Nutrients stocks and fluxes (atmospheric deposits, weathering, and immobilization of nutrients in the biomass and deep drainage) were measured for 6 yr in a chronosequence of 3 stands representing variouis stages of development of a single Douglas-fir plantation. Current input-output nutrient budgets were calculated for the 3 stands, and simulations were made for 3 theoretical rotation lengths and 2 harvesting scenarios of whole-tree harvesting (WTH) and stem-only harvesting (STO).

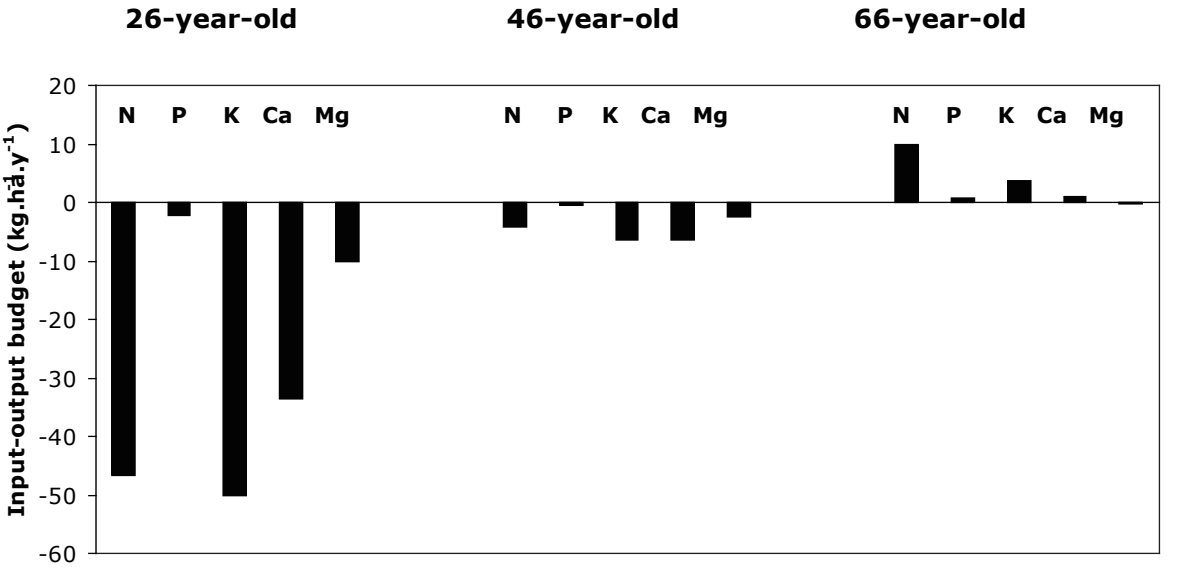

Fig. 3. Dynamics of the current input-output nutrient budgets during the rotation of a Douglas-fir plantation in the Beaujolais mounts (France), assessed by a chronosequence approach (Ranger et al 2002).

The main results were as follows.

- Strong changes occurred during stand development mainly in relation to outputs, i.e., biomass production and soil drainage (Fig. 3). These 2 fluxes were the highest in the young stand, in relation to several factors: i) the MAI of Douglas-fir was around age 20, ii) the plantation was established on agricultural land which seemed to be partially responsible for the high nitrification rates leading to high drainage losses, and, iii) stimulation of nitrifiers by Douglas-fir probably increased nitrate production which exceeded the tree uptake, leading to soil acidification. Budget deficits decreased with time to nil in the older stand.

- Simulation of several silviculture scenarios showed that decreasing the rotation length always increased the deficits and that harvesting slashes were very detrimental to soil fertility (Fig. 4).

- Calcium was the most worrying element in this ecosystem, especially because Ca-bearing minerals disappeared from the rooting zone. Ca amendment is a certain priority to ensure soil sustainability.

In the temperate area, the sustainability of high-production extensively managed forest plantations depends on following some simple guidelines: avoid short rotations, avoid the harvest of slashes, and remediate soil acidification with limited liming, approximately every 2 rotations.

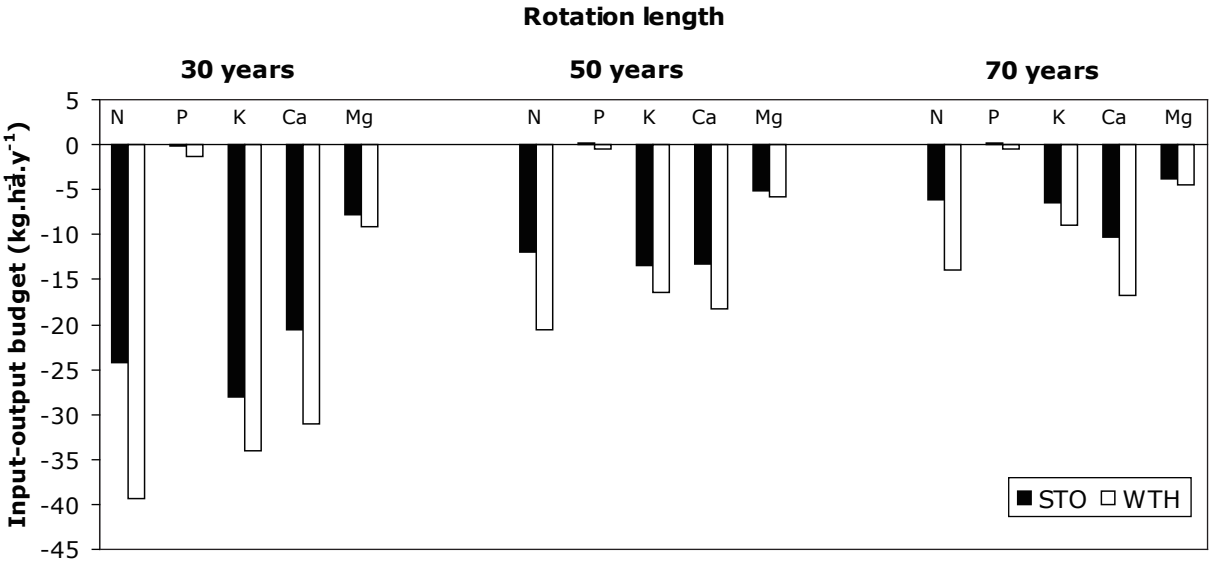

Fig. 4. Simulated input-output nutrient budgets for increasing rotation lengths and for 2 harvesting intensities of stem-only harvesting (STO) vs. whole-tree harvesting (WTH) of a Douglas-fir plantation in the Beaujolais mounts (France) (Ranger et al. 2002).

Up-scaling of nutrient input-output budgets for the management of commercial plantations: a challenge for forest modelling

The examples above show that input-output budgets of nutrients established in representative stands are likely to provide useful information on tree mineral functioning, which can lead to substantial modifications of silviculture practices in order to maintain nutrient pools in forest soils. However, the budgets are site-specific and cannot be directly extrapolated to other plantation areas.

A modelling approach can be used to estimate the nutrient budgets in other forest plots, when the main fluxes of the budgets can be predicted from available databases of forest companies. The case of fast-growing *Eucalyptus* plantations established on deep tropical soils is favorable in this respect. Studies of soil solution chemistry in the Congo and Brazil showed that the root development of *Eucalyptus* trees was so fast after planting that the trees took up most

of the nutrients released by organic matter decomposition and applied by fertilization. Losses of nutrients by deep drainage did not substantially increase after clear felling and represented a minor flux in the input-output budgets, even in sandy soils (Maquère et al. 2005, Laclau et al. 2007). Growth models are currently being used in commercial *Eucalyptus* plantations to predict wood production in individual forest plots, and silvicultural practices are recorded in databases at the plot level (e.g., Almeida et al. 2004). Since input-output budgets in these plantations are mainly driven by the amounts of fertilizer applied and nutrients associated with biomass removal, the development of models predicting the effects of fertilization regimes on nutrient accumulation in trees (see for example, Sicard et al. 2005) might be used to assess the magnitude of the budgets at the plot level. However, the extent of atmospheric inputs, superficial runoff and deep drainage in each situation should be estimated. This approach is currently being tested in Brazilian *Eucalyptus* plantations.

In plantation forests where tree growth is slower, nutrient losses by drainage can be a major output of nutrients in the budgets (e.g., Ranger et al. 2002). This flux is much more difficult to predict from standard data available from forest companies because it is highly dependent on numerous factors: land history, stand nutrient demands, weed development, organic matter mineralization, mineral weathering, etc. A modelling approach is useful in predicting some major nutrient fluxes (dynamics of nutrient accumulation in stands in particular). However, nutrient input-output budgets cannot be predicted by functional models before a good understanding of the determinants of the losses of nutrients by deep drainage in each situation.

soil solution chemistry: a very relevant indicator of soil fertility changes

Even if input-output budgets give a relevant estimation of the long-term changes in nutrient stocks in forest soils, complementary information is necessary to assess the changes in nutrient availability for tree growth. If the budgets are negative, they must be compared to stocks of exchangeable elements in the soil to assess if the deficit is likely to reduce stand growth on the short term. Even when the budgets are balanced or positive, a temporary immobilization of nutrients in the organic layer, for example, might reduce stand growth, and so an overall understanding of tree nutrition is necessary.

Among the parameters that should be studied to gain insights into tree mineral functioning and better interpret input-output budgets, soil solution chemistry is particularly interesting. Indeed, the chemical composition of soil solutions is much more sensitive to management practices than the soil solid phase and is a relevant indicator of current soil functioning (Marques et al. 1996, Smethurst, 2000, Ranger et al. 2001). For example, soil acidification can be detected earlier from soil solution studies than soil analyses as a result of the large buffer capacities of

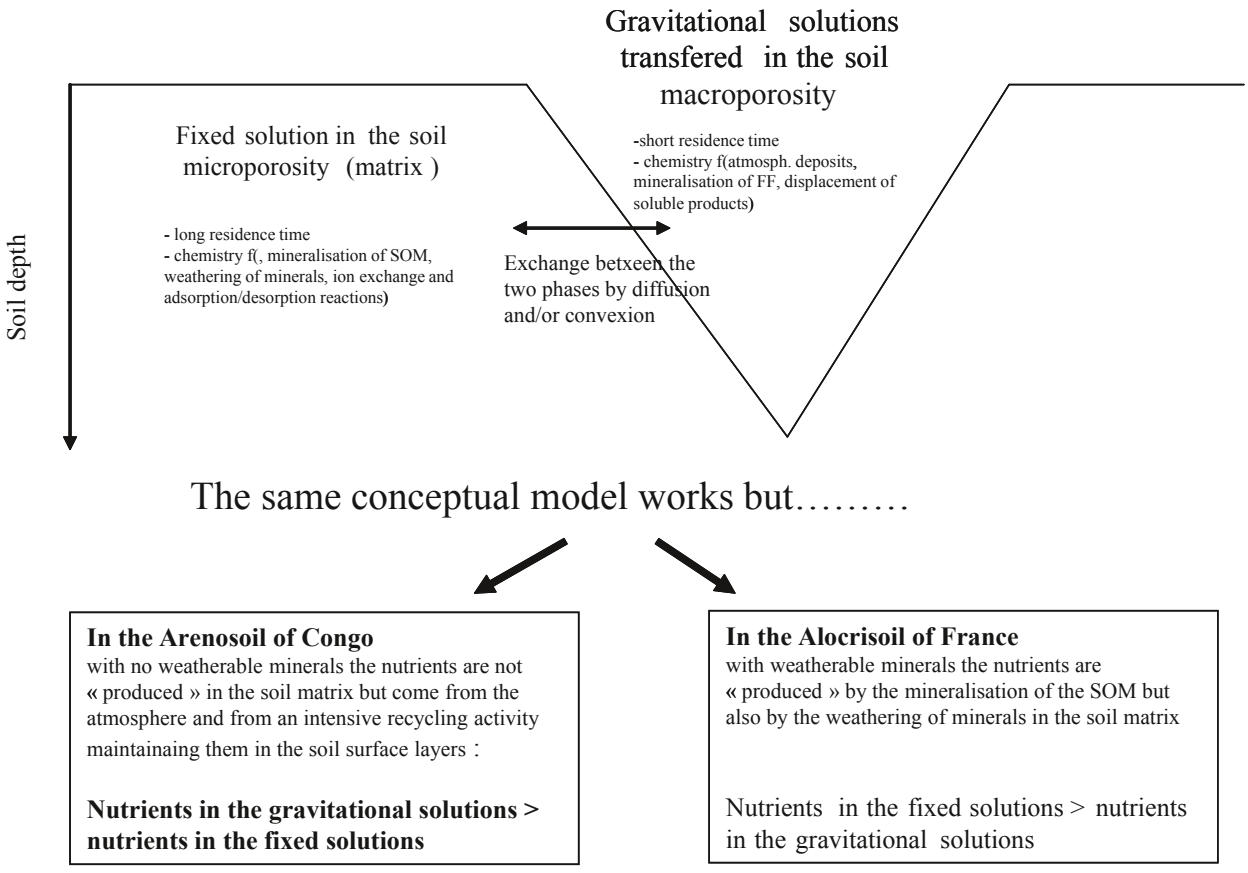

Fig. 5. Conceptual scheme representing changes in the chemistry of solutions during their transfer in forest soils of France and the Congo.

most forest soils. Soil solution chemistry is also likely to be used as an indicator of nutrient bioavailability when input-output budgets cannot be established. However, the relationship between nutrient concentrations in soil solutions and tree growth has to be calibrated in a network of experiments.

Soil solutions sampled in plantation forests exhibited apparent opposite patterns of chemical changes in France and Congo when their time of residence in the soil increased: whereas a clear decrease in concentration of most cations was observed under *Eucalyptus* in a Congolese Arenosol (Laclau et al. 2003), a large increase in the concentration of the same elements was observed under Douglas-fir in a French typic Dystrochrept (Ranger et al. 2001). However, the conceptual scheme is the same (Fig. 5). Weathering processes in

soil microporosities under Douglas-fir contributed to increases in the concentrations of base cations when the time of residence of soil solutions increased, but the lack of primary minerals prevented the release of these elements in the Congolese soil (Ezzaim et al. 1999). Moreover, much higher organic matter contents, lower uptake of nutrients by tree roots, and stimulation of nitrate production by Douglas-fir might be involved in the increase in mineral nitrogen and base cation concentrations observed in France when the time of residence of solutions in the soil increased.

Soil solution monitoring in the Congo showed that *Eucalyptus* plantations and native savannas had similar behaviors, without clear soil acidification after afforestation. The low impact of afforestation on soil chemical properties indicated by input-output budgets was confirmed by the comparison of soil solution chemistry with the native savanna. That feature suggested that the maintenance of soil fertility might be achieved by increasing the N fertilizer inputs. By contrast, larges losses of nitrates under Douglas-fir raised concerns about the soil capacity to sustain future rotations (Ranger et al. 2002).

CONCLUSIONS

Input-output nutrient budgets are an early indicator making it possible to predict soil changes before impacts on soil and vegetation appear. The quantitative information from budgets calculated for the rotation is relevant for managers because it can be used to make practical recommendations, such as rotation length, intensity of crop harvesting, optimization of fertilizer inputs for production, and environmental constraints. On account of the intensity of work required to carry out long-term nutrient budget studies, the difficulty of extrapolating the results from a single site and the need to quickly produce relevant simulators, it seems necessary to establish a site network. The database obtained from the experimental designs installed in France, the Congo, and Brazil makes it possible to test the general nature of models, as described here for the influence of the retention time on the chemistry of solutions in the soils. A network including plantations in different contrasting situations would help validate functional models necessary to identify the major variables controlling the I/O budgets and be a simple index of nutrient availability.

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Effects of Differential Thinning Treatments in an Man-Made Forest on Vertebrate Diversity and Community Structure: the Baseline Study

Liang-Kong Lin,[1,2] Yeong-Choy Kam,[1] Cara Lin Bridgman[1]

[Summary]

Man-made forested ecosystems occupy about 420,000 ha in Taiwan. Terrestrial vertebrates are the dominant animals in these forest ecosystems and mediate important predator-prey interactions. Vertebrates are very sensitive to changes in habitat, making them suitable ecological indicators and umbrella species for assessing environmental effects on biodiversity. Understanding the effects of various forest restoration strategies on vertebrate biodiversity is important for the long-term management of Taiwan's forests. We investigated pre-thinning vertebrate diversity in Japanese cedar, *Cryptomeria japonica*, plantations of the Nantou Forestry District, central Taiwan to provide baseline data for future assessments of the influence of thinning operations by logging 0, 25, and 50% of the trees. From 2006 to 2007, in 12 experimental 1-ha plots, we found 7 amphibian, 11 reptile, 14 mammal, and 31 bird species. Bird species diversity was similar in all plots (mean, 11.4). Shrews (Insectivora: Soricidae) were the dominant understory mammal.

Key words: artificial forest ecosystem, Japanese cedar plantation, thinning operation, vertebrate diversity.

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INTRODUCTION

Thinning is partial logging. It alters the density, quality, and distribution of a forest, resulting in immediate and large-scale changes to the structure and physical and chemical conditions of the forest. It is generally considered to have negative ecological impacts. Habitat changes caused by thinning activities do not necessarily negatively affect wildlife (Taker 1981, Bender et al. 1997, Pearman 1997, Vitt et al. 1998). In Taiwan, few studies have focused on correlations between the effects of thinning and wildlife. One recent study focused on the effects of the thinning of a Taiwania (*Taiwania cryptomerioides*) forest on bird and rodent communities (Chang 2000). Since terrestrial vertebrates require large contiguous blocks of suitable habitat, they can act as umbrella species for the habitat requirements of invertebrate species. To manage and conserve biodiversity in a planted forest, it is first necessary to record the vertebrate resources within that forest. Only by comparing the combinations and dynamics of vertebrates among different thinning treatments will it be possible to draft policies and strategies required to conserve biodiversity.

Vertebrates are crucial to a properly structured and functioning ecosystem (Hunter 1999). They have important roles in food chains, energy flows, and the cycling of nutrients. As thinning affects a forest's vegetation, it also affects the combinations and dynamics of vertebrates. Since birds, mammals, reptiles, and amphibians use invertebrates for food and vegetation as food and shelter, understanding vertebrate diversity and community structure can help explain the effects of thinning on invertebrates, microclimates, and substrates (Duff et al. 1984). The objectives of this 3-yr study were to 1) identify how thinning should be conducted, 2) document the effects of different thinning levels on vertebrate diversity and forest function, and 3) examine how thinning affects vertebrate populations and community structures. Herein, we show the first year results of a pre-thinning survey of the vertebrate population and community structure in a Japanese cedar *Cryptomeria japonica*, plantation in Nantou County, central Taiwan.

MATERIALS AND METHODS

Study area

The *C. japonica* plantation is within Luanda Commercial Zone 74, Nantou Forest District Office, Forestry Bureau, Taiwan. The elevation is 1500 m. Within this plantation, we selected 12 1-ha (100 × 100-m) plots (plots 1~12; see Fig. 1) for the pre-thinning survey and study of vertebrate populations and community structure. Nearby, in the same watershed, is a patch of broadleaf forest. This served as a control.

Amphibian and reptile surveys

Reptiles and amphibians were surveyed for 7 consecutive days from February 2006 through February 2007 in each of the 12 treatment plots and in 1 plot in the broadleaf forest control. Traps were placed between August 2005 and January 2006 and included direct observations, drift-fence pitfall traps, shelter and artificial cover, and snake traps. These 4 types of traps should document the presence of most reptile and amphibian species (Heyer et al. 1994). Species encountered within the study area but outside the plots were also recorded, to build a comprehensive list for the amphibian and reptile species.

Bird surveys

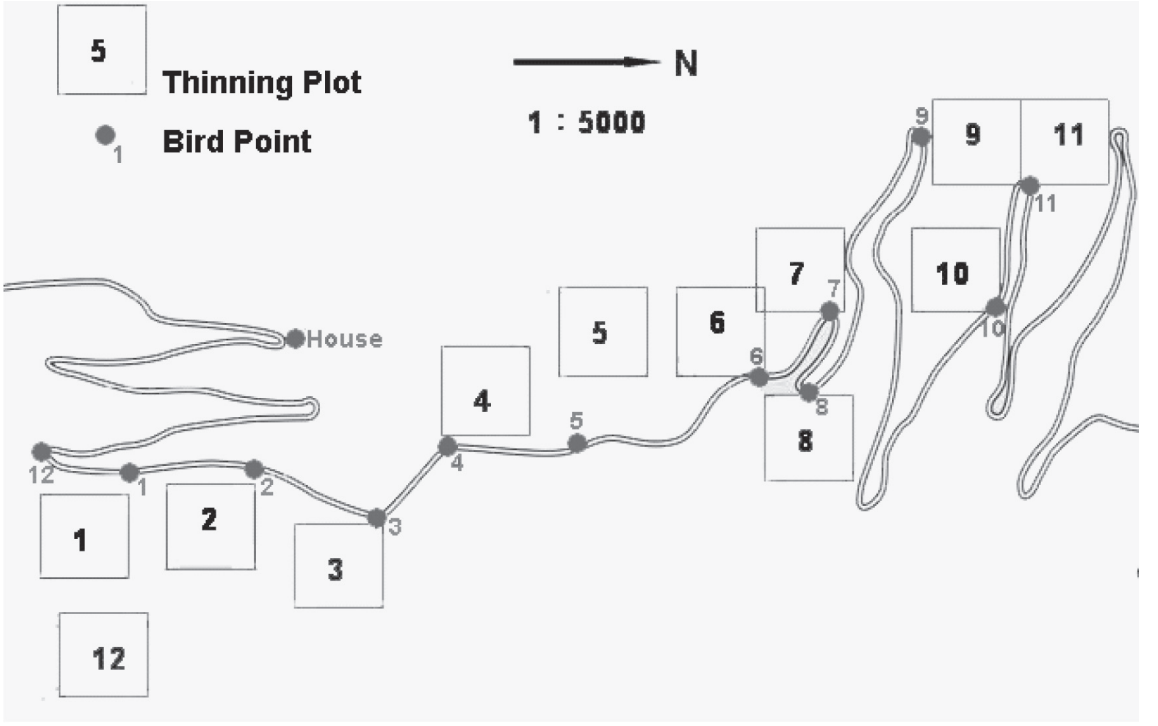


Fig. 1. Map of the study area showing the Renluen Logging Road and survey plots (numbered red squares) inside Luanda Commercial Zone 74, Nantou Forest District Office, Forestry Bureau, central Taiwan. Blue dots and labels indicates bird survey stations.

Bird density and diversity were surveyed twice a season for 5 seasons: winter 2005 (December 2005 to February 2006), spring 2006 (March to May 2006), summer 2006 (June to August 2006), fall 2006 (September to November 2006), and winter 2006 (December 2006 to February 2007). We used point counts (Bibby et al. 1992) to estimate bird density. At or near each treatment plot, we selected bird survey points (Fig. 1). Within the same valley, in a section of broadleaf forest, we selected 4 additional points (broadleaf points) to serve as natural controls. We surveyed each point twice each season. At each point, we stopped for 5 min to record the number of individuals of each species heard or seen ≤ 20 m and > 20 m from the point. For some species, such as the Taiwan Hill Partridge (*Arborophila crudigularis*), the same individuals could be heard at several points. In that case, the individuals were recorded only for the point at which they were first heard or seen.

Calculations of density followed Bibby et al. (1992):

$$\text{Density} = \log_e(t/n) \times n/p(\pi\Gamma^2) \times 10{,}000$$

Therefore, the density (number of birds per hectare) was based on the number of birds, n, outside the 20-m radius, r, the total birds counted, t, and the number of plots, p, multiplied by the number of times they were surveyed. The value of 10,000 is included to convert the density per square meter to density per hectare.

We calculated densities for the treatment plots and the broadleaf control. We also calculated the densities of canopy birds and ground birds. Canopy bird species included the Taiwan Yuhina (*Yuhina brunneiceps*), Grey-cheeked Fulvetta (*Alcippe morrisonia*), White-throated Flycatcher-Warbler (*Abroscopus albogularis*), and Taiwan Sibia (*Heterophasia auricularis*). Ground bird species included Steere's Liocichla (*Liocichla steerii*), Red-headed Tree Babbler (*Stachyris ruficeps*), Gould's Fulvetta (*Alcippe brunnea*), and Blue Shortwing (*Brachypteryx montana*).

To monitor bird species diversity, we kept a list of all the bird species heard or seen within each treatment and in the broadleaf control. This list included species recorded during point counts, encountered whenever we were within each treatment, and photographed by infrared auto-cameras placed to survey mammals.

Mammal surveys

Mammals were surveyed in each plot for 6 seasons (winter: January 2006; spring: April 2006; summer: July 2006; fall: October 2006; winter: January 2007; and spring: March 2007). In each plot, we placed 2 transect lines with 10 trapping cages 10 m apart on each line.

These were monitored for 2 consecutive nights each season. We recorded basic information for each captured animal: species, sex, and weight. Each animal was numbered and marked by toe-clipping. We placed harp traps overnight at the edge of each plot to survey bat species. Captured bats were identified and numbered with wing tags. Pitfall traps in each plot and in the broadleaf control collected mammals in the order Insectivora.

To continuously monitor the area for medium and large mammals, from January 2006 to April 2007, we placed 2 infrared auto-cameras in each plot. Developed film was used to calculate the occurrence index (OI). Calculations followed Pei (1995):

OI = (number of animals recorded in a 30-min period / total monitoring hours each camera) x 1000.

RESULTS AND DISCUSSION

Amphibian and reptile surveys

In a total of 49 survey days (42 capture nights) from 7 trips, we recorded 18 different amphibian and reptile species (77 individuals in all). For amphibians, we found 51 individuals representing 3 families (the Bufonidae, Raniidae, and Rhacophoridae) and 7 species (Table 1). Except for *Rana sauteri* and *Bufo bankorensis*, all other amphibians were found outside the plots. The numbers of amphibian species and individuals recorded were higher in summer.

Table 1. Amphibians recorded in the cedar (Cryptomeria japonica) plantation (I) and broadleaf forest (O) plots each month

Species	Status[1]	Feb. 06		Apr. 06		June 06		Aug. 06		Oct. 06		Dec. 06		Feb. 07		Total
		I	O	I	O	I	O	I	O	I	O	I	O	I	O	
ANURA																
Bufonidae																
Bufo bankorensis	◎	1	1	1		1			1		2					7
Ranidae																
Rana adenopleura							1									1
Rana latouchtii			1		1		1		1							4
Rana sauteri		1		4		5		6	1	4	1	1			1	24
Rhacophoridae																
Chirixalus eiffingeri			1		1		1		1		1				1	6
Chirixalus idiootocus	◎				1											1
Rhacophorus moltrechti	◎II		1		1		1		1		1		1		2	8
Individuals (*n*)		2	4	5	4	6	4	6	5	4	5	1	1	0	4	51
Species (*n*)		2	4	2	4	2	4	1	5	1	4	1	1	0	3	7

[1] ◎ Status indicates an endemic species; II indicates a protected species in Taiwan.

In total, 26 reptiles representing 4 families (the Bataguridae, Agamidae, Scincidae, and Colubridae) and 11 species were found in the study area (Table 2). Most were in the family Colubridae, followed by the Scincidae. *Japalura brevipes* was a dominant species, followed by *Eumeces elegans and Pseudoxendon stejnegeri stejnegeri*. All other reptile species were found only once. Most were found inside the plots. Reptile numbers and species were most abundant in summer.

Table 2. Reptiles recorded in the cedar (Cryptomeria japonica) plantation (I) and broadleaf forest (O) plots each month

Species	Status[1]	Feb. 06		Apr. 06		June 06		Aug. 06		Oct. 06		Dec. 06		Feb. 07		Total
		I	O	I	O	I	O	I	O	I	O	I	O	I	O	
CHELONIA																
Bataguridae																
Cistoclemmys falvomarginata	II						1									1
SQUAMATA																
Agamidae																
Japalura brevipes	◎			2		2		5								9
Scincidae																
Eumeces elegans									1		5					6
Scincella formosensis	◎ II			1												1
Sphenomorphus taiwanensis	◎ II	1														1
Colubridae																
Elaphe carinata				1												1
Elaphe porphyracea nigrofasciata	II					1										1
Elaphe taeniura	II	1														1
Lycodon ruhstrati ruhstrati												1				1
Pseudoxendon stejnegeri stejnegeri	○					1				2						3
Phabdophis swinhonis	◎ II							1								1
Individuals (*n*)		2	0	4	0	4	1	6	1	2	5	1	0	0	0	26
Species (*n*)		2	0	3	0	3	1	2	1	1	1	1	0	0	0	11

[1]◎ Status indicates an endemic species; II indicates a protected species in Taiwan.

The number of amphibian species and individuals recorded being highest in the summer was related to their reproductive season. This pattern was the same for reptile numbers and species. However, the diversities of amphibians and reptiles were lower in the cedar plantation than in the natural forest (Lue 1999).

Bird surveys

Bird species diversity among treatments was similar (mean, 11.4 species; Fig. 2). Within the treatment study area, bird species diversity was similar among all 5 seasons: winter 2005 to winter 2006 (Fig. 3A). In the broadleaf control, diversity varied slightly with season, being highest in winter and lowest in fall. Of the 14 bird species recorded by auto-cameras, only Steere's Liocichla (*Liocichla steerii*) and White's Ground Thrush (*Zoothera dauma*) were found in all plots.

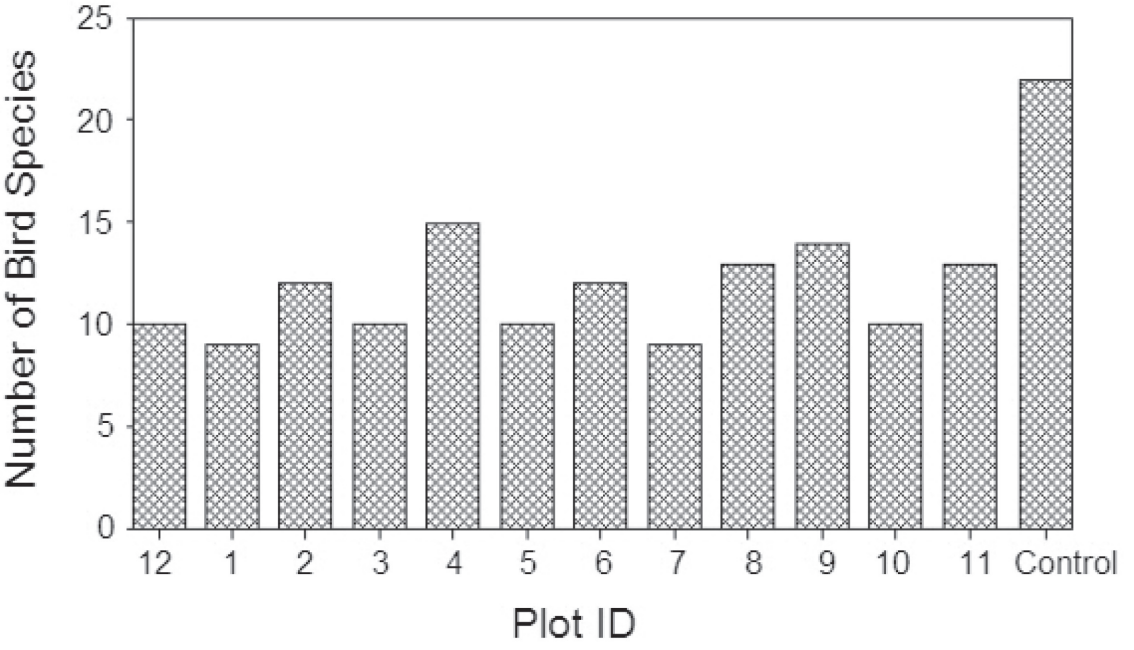
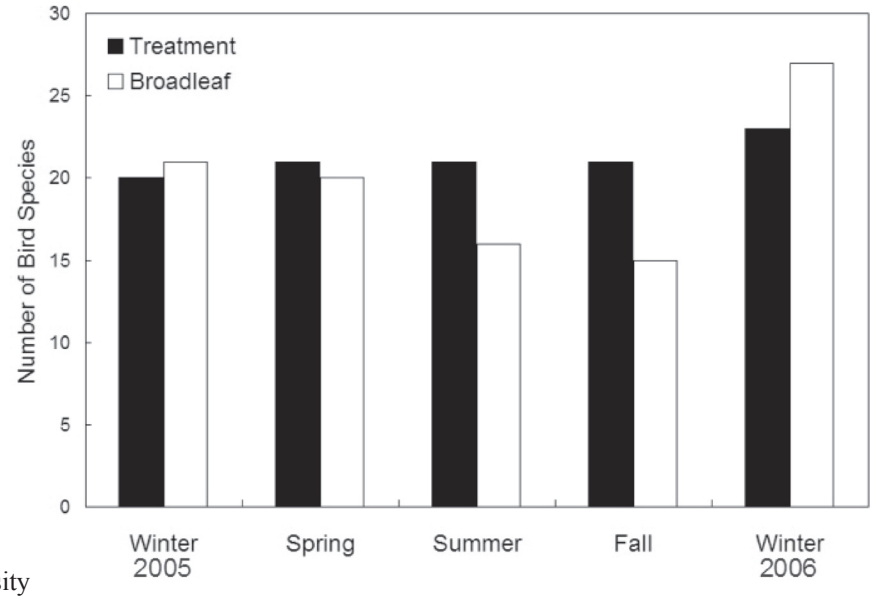


Fig. 2. Pre-thinning bird species diversity of each treatment (plots 1~12) in the *Cryptomeria japonica* plantation. The control is a nearby broadleaf forest.

Although bird diversity within the treatments was fairly constant, the density dropped from a high in winter 2005 to lows the following spring, summer, and fall (Fig. 3B). Densities of the 4 most common canopy species (Fig. 4A) followed the same seasonal patterns. In the treatment plots, densities of the 4 most common ground species (Fig. 4B) were greatest in winter. In the broadleaf control, ground species had the greatest densities in the spring (Fig. 4B).

A) Bird species diversity



B) Bird density

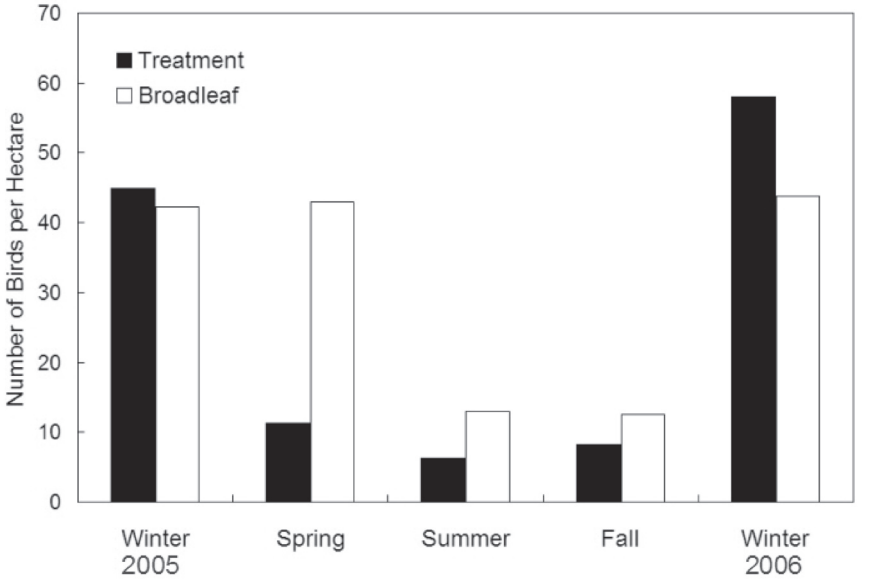
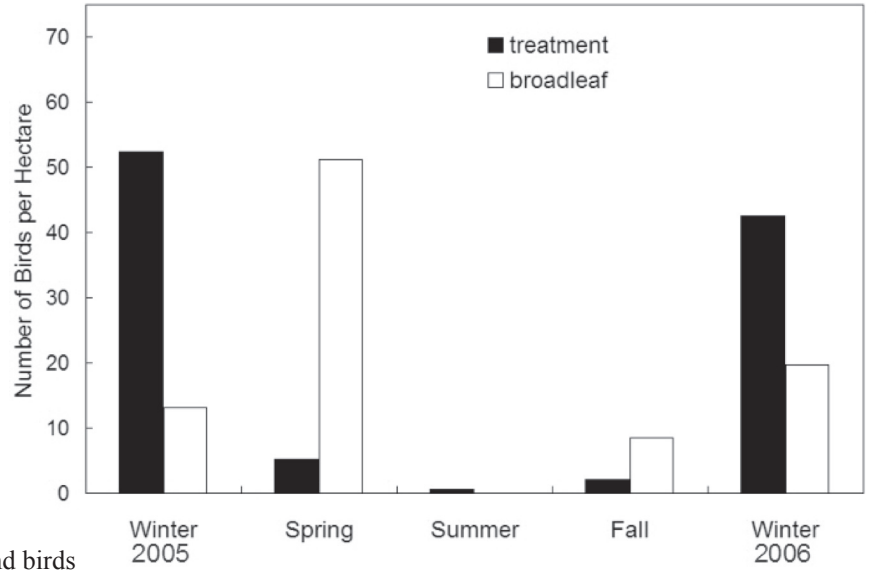


Fig. 3. Seasonal diversity (A) and density (B) of birds from winter 2005 to winter 2006. Diversity was the total number of bird species encountered in each study area: the treatment plots and the broadleaf control. Density (number of individual birds per hectare) estimated from all birds recorded in all treatment and broadleaf point counts. The 12 treatment points and 4 broadleaf points were surveyed at least twice a season. Seasons were winter 2005 (December 2005 to February 2006), spring 2006 (March to May 2006), summer 2006 (June to August 2006), fall 2006 (September to November 2006), and winter 2006 (December 2006 to February 2007).

A) Canopy birds



B) Ground birds

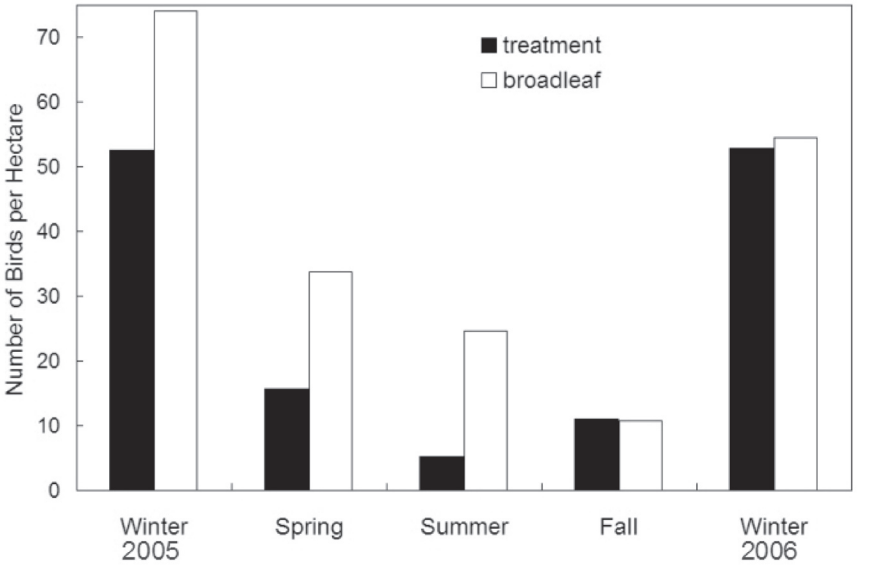


Fig. 4. Seasonal density of the 4 most common (A) canopy bird species and (B) ground bird species from winter 2005 through winter 2006. Canopy bird species were Taiwan Yuhina (*Yuhina brunneiceps*), Grey-cheeked Fulvetta (*Alcippe morrisonia*), White-throated Flycatcher-Warbler (*Abroscopus albogularis*), and Taiwan Sibia (*Heterophasia auricularis*). Ground bird species were Steere's Liocichla (*Liocichla steerii*), Red-headed Tree Babbler (*Stachyris ruficeps*), Gould's Fulvetta (*Alcippe brunnea*), and Blue Shortwing (*Brachypteryx montana*). The 12 treatment points and 4 broadleaf points were surveyed at least twice a season. Seasons were winter 2005 (December 2005 to February 2006), spring 2006 (March to May 2006), summer 2006 (June to August 2006), fall 2006 (September to November 2006), and winter 2006 (December 2006 through February 2007)..

Although bird diversity did not vary among treatments or seasons, bird densities dropped from a high in winter 2005 to lows the following spring, summer, and fall (Fig. 3B). This led us to hypothesize in a November 2006 report that the drop in density was the result of increased human activities inside the study area. This activity included grading the road in preparation for logging. To calculate the density, at least 1 bird must be recorded within 20 m of at least 1 bird survey point. We speculated that the increased human activity had caused the birds to move away from the road and into the forest. In winter 2006, however, treatment bird densities exceeded winter 2005 levels, even though human activities were also higher. Therefore, spring, summer, and fall drops in density were not as likely to have been caused by human activity along the road. In the broadleaf control, bird species densities were similar during winter 2005, spring 2006, and winter 2006. It may be that the broadleaf forest supplies better breeding habitat.

Because the closed canopy in the treatment plots resulted in a generally sparse understory or herb layer and a missing sub-canopy tree layer, we expected this to affect the densities of bird species that are active on the ground. Therefore, we compared the densities of the 4 most common canopy species (Fig. 4A) and the 4 most common ground species (Fig. 4B) to see how density varied with season for the treatment study area and the broadleaf control. In Fig. 4A, canopy bird density followed the same seasonal patterns seen in Fig. 4B. In the treatment plots, the pattern of reduced spring, summer, and fall densities was much stronger in ground bird species (Fig. 4B). In the broadleaf control, however, ground bird species density sharply increased during the spring breeding season. It may be that the sparse understory and the missing sub-canopy layer in the treatment plots affected the breeding activities of ground birds. After logging commences in the treatment plots and the canopy is opened, the understory should grow denser. This may improve the breeding habitat in the treatment plots for ground bird species.

Mammal surveys

Only 2 small mammal species, the rodents *Apodemus semotus* and *Niviventer coxingi*, were captured (plots 1, 3, 7, and 12). We trapped 5 species of bats: *Myotis latirostris*, *Murina puta*, *Harpiola grisea isodon*, and *Mur. gracilis* , but found no bats in spring 2006 or spring 2007. All captured Insectivora (*Crocidura kurodai*, *Cro. attenuata tanakae*, *Soriculus sodalis*, and *Sor. fumidus*) are listed in Fig. 5. Although *Cro. kurodai* was found in all 12 plantation plots, *Sor. fumidus* only appeared in the broadleaf forest plot.

Our auto-cameras photographed 14 mammal species (Table 3), 3 of which appeared

in all 12 plots: *Niviventer coninga*, *Mustela sibirica takvana*, and *Melogal moschata subaurantiaca*. Four protected mammals were also recorded: *Muntiacus reevesi micurus*, *Naemorhedus swinhoei*, *Martes flavigula chrysospila*, and *Felis bengalensis chinensis* (Table 3). The OI values of all photographed mammals are shown in Fig. 6.

According to the data of the auto-cameras, 3 species, *Niv. coninga*, *Mel. moschata*, and *Mus. sibirica takvana*, had wide distributions among all plots indicating very common abundances (also see the OI index in Fig. 6).

This 1-yr survey documented the pre-thinning diversity of vertebrates in a stand of Japanese cedar (*C. japonica*). By comparing these data to those collected after thinning, we will be better able to understand the effects of thinning on vertebrates. Species that appeared in all plots (such as the mammals *Niv. coninga*, *Cro. kurodai*, *Mus. sibirica*, and *Mel. moschata*) are well suited for evaluating the effects of different thinning strengths.

Table 3. Mammal species (n = 14) recorded by auto-cameras in the 12 plots between 6 January 2006 and 27 April 2007

Species	Plot ID											
	1	2	3	4	5	6	7	8	9	10	11	12
Niviventer coxingi	x	x	x	x	x	x	x	x	x	x	x	x
Apodemus semotus	x	x										
Shrew, unidentified											x	
Callosciurus erythraeus	x	x	x	x	x	x	x		x	x	x	
Tamiops swinhoei						x						
Mustela sibirica takvana	x	x	x	x	x	x	x	x	x	x	x	x
Melogal moschata subaurantiaca	x	x	x	x	x	x	x	x	x	x	x	x
Martes flavigula chrysospila						x						
Felis bengalensis chinensis							x					
Domestic dog					x	x	x		x		x	
Muntiacus reevesi micurus				x		x	x	x	x		x	
Naemorhedus swinhoei												x
Lepus sinensis formosus				x								
Bat, unidentified			x	x	x	x	x			x		
Total	5	5	5	7	6	9	8	4	6	5	7	4

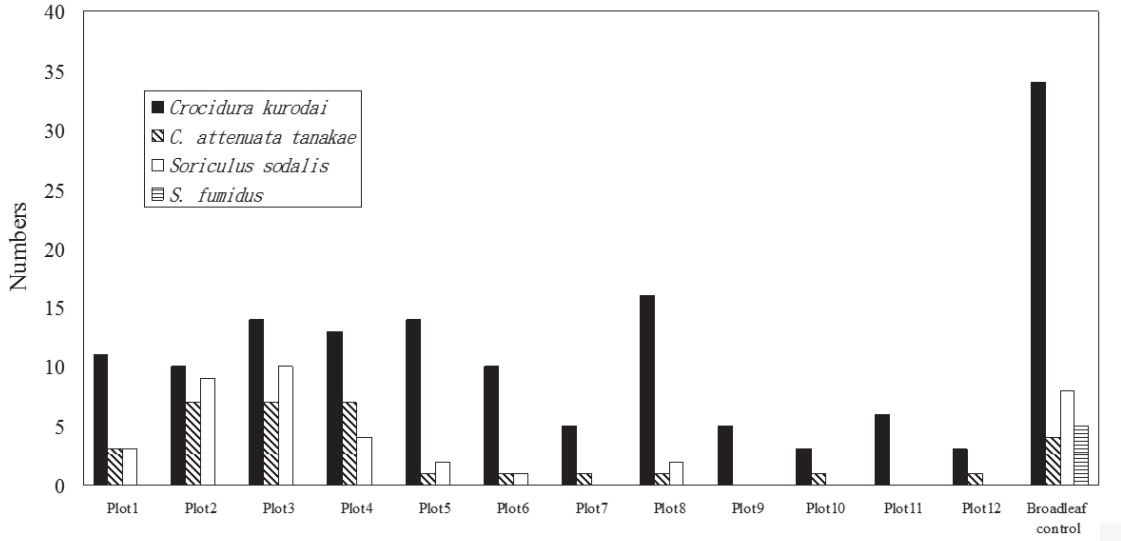


Fig. 5. Numbers of species and individuals of the Insectivora in the 12 treatment plots and the broadleaf control.

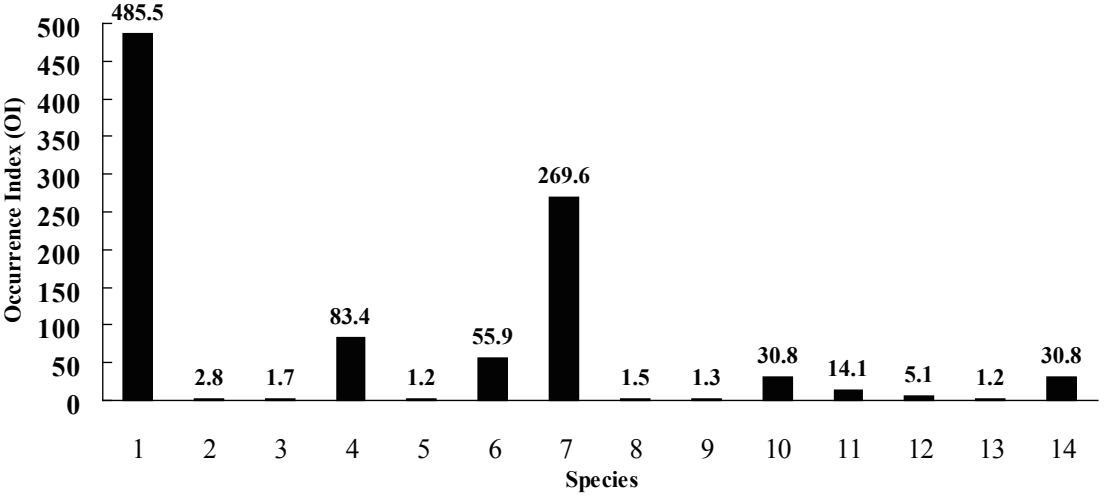


Fig. 6. The occurrence index (OI) values of 14 mammal species captured by auto-cameras. (1. *Niviventer coxingi*, 2. *Apodemus semotus*, 3. Unidentified shrew, 4. *Callosciurus erythraeus*, 5. *Tamiops swinhoei*, 6. *Mustela sibirica takvana*, 7. *Melogal moschata subaurantiaca*, 8. *Martes flavigula chrysospila*, 9. *Felis bengalensis chinensis* 10. Domestic dog, 11. *Muntiacus reevesi micurus*, 12. *Naemorhedus swinhoei*,13. *Lepus sinensis formosus,* and 14. Unidentified bat.)

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Functional diversity in temperate mixed stands:response of co-occurring deciduous tree species to light and water availability.

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[Summary]

Three different field experiments were conducted in temperate mixed stands in order to characterize the ecophysiological responses of various co-occurring deciduous tree species to light and water availability. In the first experiment, we validated the hypothesis that the construction costs of current-year shoot per unit leaf area of saplings differed among temperate species that co-occurred below a canopy, but the differences were not related to the shade tolerance of the species. In the second experiment, saplings of beech (*Fagus sylvatica*) were subjected to a sudden radiation increase by above-canopy opening aimed at understanding the competitive ability of this species in forest regeneration in plain forests of Western Europe. Dynamic changes in hydraulic conductance were related to changes in cross-sectional area and ring area. In the third experiment we compared water use efficiency, transpiration, soil water absorption, and the response to increasing drought by several deciduous tree species. Those species showed contrasting patterns of seasonal transpiration, with some species exhibiting a strong transpiration decline with increasing water stress, while those of other species remained more constant, even at the highest water stress levels. These contrasting responses to drought were well confirmed by the fine-root distribution and by the ability of a species to absorb water from deep the soil layers.

Key words: functional diversity, mixed stands, light and water availability.

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INTRODUCTION

Many studies have suggested that ecosystem processes depend far more strongly on functional diversity than on species diversity per se, because of redundancy (i.e., many species may play the same role in ecosystem processes, Diaz and Cabido 2001). Functional diversity is therefore viewed as a guaranty for the dynamic stability of the ecosystem even if the dynamics of managed forest ecosystems are largely influenced by human interventions. Functional diversity can be considered at different levels. At the individual level, it reflects the phenotypic plasticity and accounts for the individual's survival in a changing environment (Via et al. 1995). Among individuals, it reflects the genetic diversity within a population and contributes to the stability of this population in a changing environment. When this intraspecific diversity is spatially structured among populations, it may correspond to different populations that have genetically diverged because in differences of local environments. At the species level, functional diversity encompasses different strategies for resource acquisition and use by different species that co-occur in a given environment.

Natural regeneration is the usual regeneration scheme for managed forest ecosystems in Europe. Natural regeneration is based on the seed stock present in the soil or on preexisting saplings that are growing beneath the canopy. In the latter case, differences in shade tolerance among species are an important determinant of the future specific composition of the forest. Survival of trees at juvenile growth stages under shade is thought to rely on their ability to maintain a positive carbon balance under limited light availability during a growth season. This ability depends not only on the photosynthetic capacity of individual leaves, but also on their ability to intercept light and on the energy costs of producing and maintaining the photosynthetic area as well as non-photosynthetic organs. The stage following natural regeneration is canopy opening through gap formation either by a natural disturbance in the canopy (tree fall) or by forest management (clearing of the old individuals in the canopy). The transition from a very shaded environment to a highly illuminated one can be very stressful for a sapling acclimated to shade, due to the fact that shade phenotypes usually display a low leaf-specific hydraulic conductance, and a larger vulnerability to cavitation than those acclimated to full solar irradiance (Cochard et al. 1999, Barigah et al. 2006). During this critical transition, the efficient use of available light for photosynthesis requires an increase in stomatal conductance, and therefore, a modification in the hydraulic properties of the saplings. In more-advanced regeneration, the productivity and stability of the ecosystem depend on the ability of trees to cope with increased competition for limited resources like water. The occurrence of differences among species in water acquisition and water use efficiencies may allow the co-occurrence of a number of species and may allow the ecosystem to cope with periods of restricted water availability during

dynamic change. This is of importance as restricted water availability is expected to become more prevalent in the next few decades because of predicted reductions in summer rainfall in Europe.

Three different field experiments were recently conducted in temperate mixed stands close to Nancy, France at different stages of dynamic regeneration. In the first experiment, we tested the hypothesis that the construction costs of current-year shoot per unit leaf area of saplings differed among temperate species that co-occurred below a canopy. We were interested in both biochemical and morphological features that account for these differences and in relating these differences to the degree of shade tolerance of the species. In the second experiment, saplings of beech (*Fagus sylvatica*) were submitted to a sudden increase in irradiance load by canopy openings. Emphasis was put on the dynamics of the hydraulic properties of the saplings (vulnerability to cavitation and hydraulic conductance) for 2 yr after canopy opening. In the third experiment, we compared transpiration, water use efficiency, and soil water absorption among several deciduous tree species. In order to assess the water uptake in the soil by the different root layers, we also used deuterium-enriched water added to the superficial soil layer.

SITES AND METHODS

Experiments 1 and 2 were carried out in a naturally regenerated stand in eastern France (Graoully Forest, 49°05‘N, 6°02‘E, 300 m elevation). The monthly average air temperature ranged from 1.6°C in January to 18.7°C in July, and the total annual rainfall was 745 mm (data from Météo France, Metz-Augny, 1946~2001 period). It is located on a limestone plateau, approximately 300 m above sea level. Soil is homogeneous over the entire study site; it is a calcisol with 38~60 cm of depth. The stand was a former broadleaf coppice-with-standards. After the last coppice was cut in the 1960’s, the stand was converted into a mixed-species even-aged forest. The canopy is mainly composed of beech (*Fagus sylvatica* L.), Norway maple (*Acer platanoides* L.), oak (*Quercus petraea* (Mattus.) Liebl. and *Quercus robur* L.), hornbeam (*Carpinus betulus* L.), sycamore (*Acer pseudoplatanus* L.), and some field maples (*Acer campestre* L.). Saplings are mainly *A. pseudoplatanus* and *F. sylvatica* with some individuals of *S. torminalis* L., *S. aria* L., *A. campestre*, *A. platanoides*, *U. glabra* Huds, *F. excelsior* L., and *T. cordata* P. Mill.

Experiment 3 was conducted in a young broadleaf mixed forest in eastern France (Hesse Forest, 48°40’N; 7°04’E, 305 m elevation), composed of naturally regenerated trees including several species (from most to least represented in basal area: European beech (*Fagus sylvatica*), hornbeam (*Car. betulus*), oak (*Q. robur* and *Q. petraea*), goat willow (*Salix capreae*), silver

birch (*Betula pendula*), aspen (*Populus tremula*), and wild cherry (*Prunus avium*). This area is affected by a semi-continental climate (mean annual temperature of 9.2°C, mean annual rainfall of 820 mm). The soil is a brunisol, with an enriched clay layer at approximately 50 cm in depth.

For the first experiment, current-year shoots of 9 to 24 saplings of 9 deciduous tree species were sampled during July 2004 in the understory. Transmitted irradiance ranged between 10 and 20% of the incident irradiance as estimated from hemispherical photographs (Barthod and Epron 2005). Construction costs (CC's, g glucose g^{-1}) of all organs were calculated from carbon and mineral contents assuming non-additional costs for nitrate reduction (Vertregt and Penning De Vries 1987). Construction costs of the current-year shoot per unit leaf area (shoot CC_A, g glucose m^{-2}) were calculated from the construction costs per unit dry mass of leaves, petioles, and stems, their relative contributions to the biomass of the current-year shoot, and the specific leaf area. The "proximate" biochemical composition of leaves was determined on a subset of saplings according to Poorter and Villar (1997).

For the second experiment, 2 regeneration patches with beech saplings were selected below a closed canopy. In January 2005, these plots were split into 2 subplots, one remaining under shade while the canopy over the other was removed. Gap areas were 1980 m² and 430 m² in the 2 plots. Hydraulic conductance was measured using a high-pressure flow meter (Barigah et al. 2006) in the field. Vulnerability curves (percent loss of conductivity with increasing xylem tension) were established on an excised stem using the "Cavitron" technique (Cochard et al. 2005). In addition, stems were thinly sectioned with a hand microtome and double-stained with safranine and astra-blue solutions. The number of vessels and cross-sectional area of each vessel were determined under an optical microscope. Light-saturated stomatal conductance (g_{sat}) was measured with an open-flow gas exchange system (LiCor 6200, Lincoln, NE) under saturated light at 25°C, ambient humidity, and ambient CO_2 concentration.

For the third experiment, sap flow density was measured by a heat dissipation method (Granier 1985) using home-made probes, continuously heated and connected to a data logger. The isotopic composition of leaf tissues was measured using an elemental analyzer coupled to an isotope ratio mass spectrometer, and was used as a proxy for water use efficiency of the tree (Farquhar et al. 1982). The vertical distribution of roots was assessed along trench walls dug tangentially in a cluster of a given species. Ten millimeters of deuterium-enriched water was artificially added to the trees during the drought period (mid-August 2006) and the deuterium was traced in the xylem water of beech and oak until the end of September in order to partition the transpiration flow between superficial and deep water.

RESULTS AND DISCUSSION

Interspecific variations in construction costs associated to leaf area renewal in understory saplings of temperate tree species

The construction costs of the current-year shoots (CC_A) measured the glucose requirement for the construction of a unit of shoot area. It includes the cost to the leaf as well as those to the supporting structures (petioles, rachis, and stems) of the current year shoot. CC_A differed among species with the lowest values in *T. cordata* and *U. glabra* (CC_A < 41 g glucose m^{-2}) and the highest values in *S. torminalis, F. excelsior*, and *A. campestre* (CC_A > 60 g glucose m^{-2}, Fig. 1). These differences were mainly driven by differences in the specific leaf area among species (SLA) despite significant differences of leaf CC among species, from 1.13 g glucose g^{-1} in *U. glabra* to 1.44 g glucose g^{-1} in *F. sylvatica*.

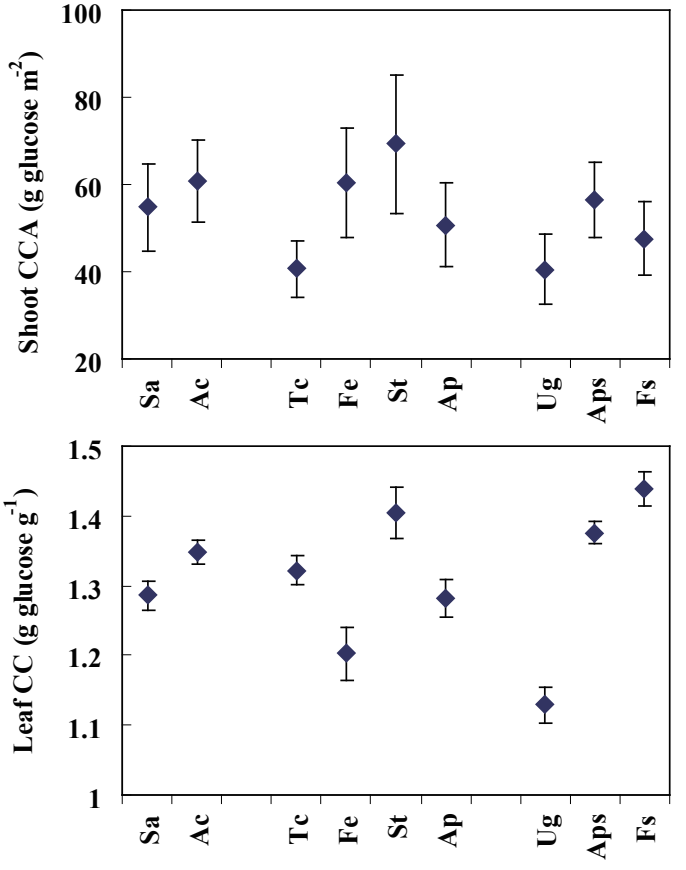

Fig. 1. Mean construction cost of the current-year shoots per unit leaf area (shoot CCA, upper panel), and construction costs (CC's) per unit dry mass of leaves (lower panel). Species were arranged according to their temperament from shade-intolerant species (Sa, Ac), intermediate species (Tc, Fe, St, Ap) to shade tolerant species (Ug, Aps, Fs). Vertical bars represent standard deviations.

This wide variation in leaf CC values was positively related to the lignin content and negatively related to the mineral content of the leaf tissues (Fig. 2). The 9 species were distinctively distributed on the factorial plane of a principal component analysis (PCA) applied to leaf traits (chemical composition, SLA, and CC) while the PCA failed to segregate species according to their shade tolerance (data not shown). The hypothesis that shade-tolerant species will are able to repay their construction costs faster than shade-intolerant ones under a given irradiance was therefore not supported by our results.

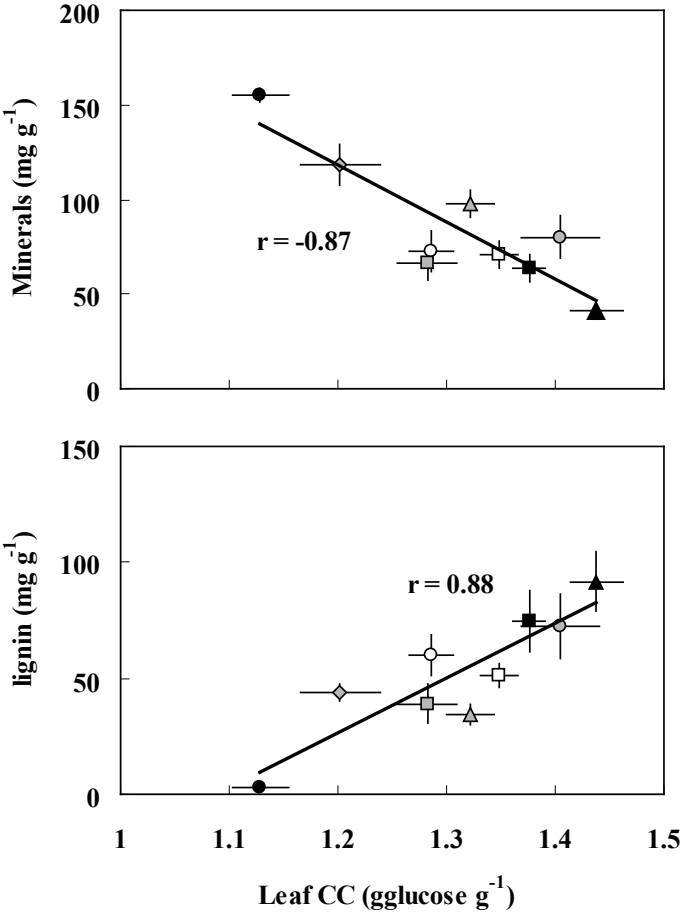

Fig. 2. Relationships between the construction costs (CC's) of leaves and the mineral (upper panel) and lignin (lower panel) contents of leaves. White symbols are used for shade-intolerant species (Sa, Ac), gray symbols for intermediate species (Tc, Fe, St, Ap), and black symbols for shade tolerant species (Ug, Aps, Fs). Linear regression lines are drawn when correlation coefficients (r) significantly differed from 0 ($p < 0.05$).

Effects of canopy opening on hydraulic properties of naturally regenerated beech (F. sylvatica) saplings.

Saplings in the shaded plot (S) and these in canopy gaps (SL) displayed similar leaf areas. The cross-sectional area of the stem and its hydraulic conductance were larger in SL than in S saplings for a given leaf area while the relationships between stem hydraulic conductance and

cross-sectional area were similar in S and SL saplings (Fig. 3). This highlights that the stem hydraulic conductance per unit cross-sectional area was not affected by canopy opening, and it suggests that the higher mean vessel area in SL saplings was counterbalanced by a lower vessel density (Table 1). The increase in stem hydraulic conductance was fully explained by an increase in ring area after canopy opening.

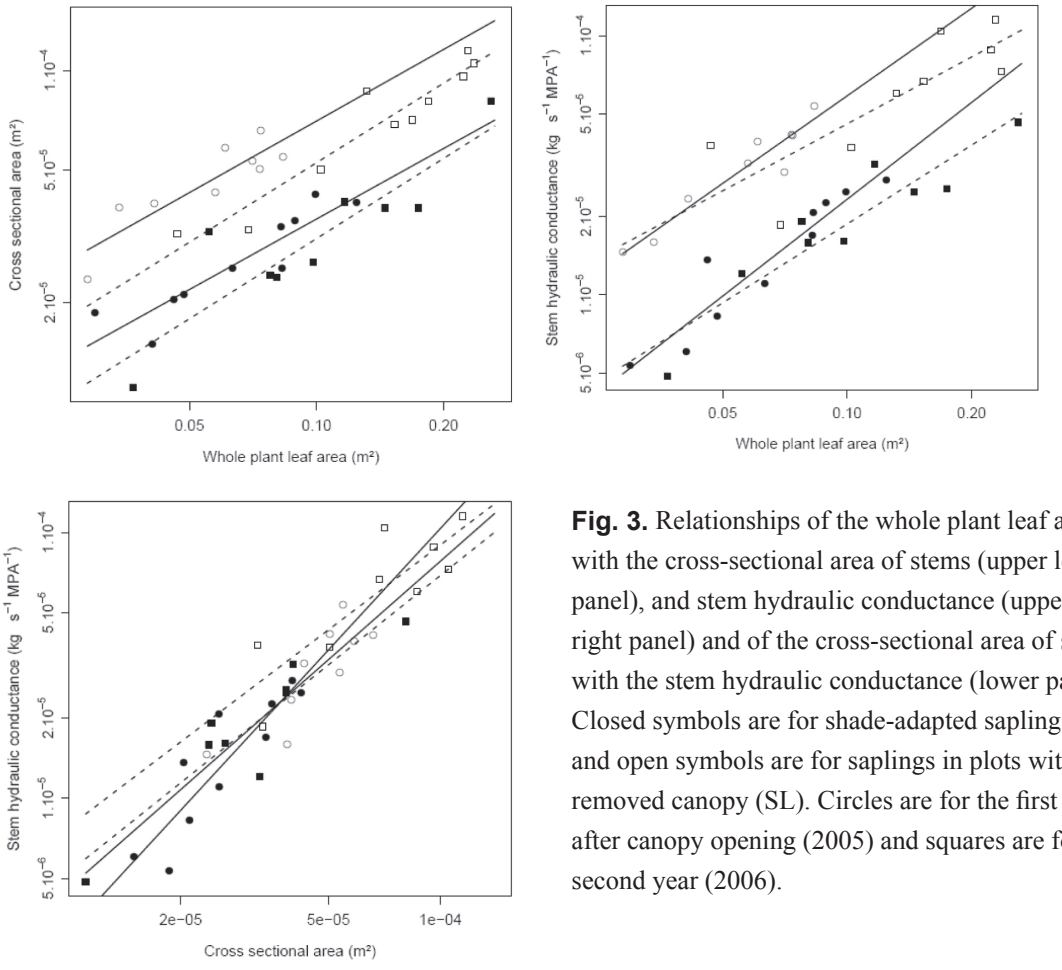

Fig. 3. Relationships of the whole plant leaf area with the cross-sectional area of stems (upper left panel), and stem hydraulic conductance (upper right panel) and of the cross-sectional area of stems with the stem hydraulic conductance (lower panel). Closed symbols are for shade-adapted saplings (S) and open symbols are for saplings in plots with removed canopy (SL). Circles are for the first year after canopy opening (2005) and squares are for the second year (2006).

Light-saturated stomatal conductance did not significantly differ between SL and S saplings during the first year. Simultaneously, a larger vulnerability to cavitation was found in SL saplings 1 yr after canopy opening (Table 2), with the xylem water potential level inducing 50% loss of hydraulic conductivity (Ψ_{PLC50}) of around -3.0 MPA in SL saplings and around -4.1 MPa in S saplings. An increase in the light-saturated stomatal conductance was observed during year 2, when the difference in vulnerability to cavitation between S and SL saplings vanished.

Table 1. Mean vessel area, vessel density, and annual ring area of shaded saplings (S) and saplings transferred from shade to light (SL) of beech, 1 and 2 yr after canopy opening.

	Mean vessel area (μm²)	Vessel density (vessel mm^{-2})	Annual ring area (mm²)
1 yr after canopy opening			
S	225 + 20 a	1001 + 53 a	3.0 + 0.6 a
SL	315 + 13 b	586 + 95 b	12.7 + 3.1 b
2 yr after canopy opening			
S	272 + 38 a	819 + 103 a	5.3 + 0.8 a
SL	428 + 42 c	476 + 94 d	20.5 + 4.8 b

Table 2. Xylem water potential inducing 50% loss of hydraulic conductivity (ΨPLC50) and light-saturated stomatal conductance (gsat) of saplings grown in shade (S) and or transferred from shade to light (SL) of beech, 1 and 2 yr after canopy opening.

	Ψ_{PLC50} (MPa)	g_{sat} (mol m^{-2} s^{-1})
1 yr after canopy opening		
S	-4.1 + 0.1 a	0.09 + 0.01 a
SL	-3.0 + 0.1b	0.10 + 0.01 a
2 yr after canopy opening		
S	-3.8 + 0.2 a	0.12 + 0.01 a
SL	-3.6 + 0.1 a	0.32 + 0.03 c

Water use and water absorption by naturally regenerated trees in a young broadleaf mixed forest.

The isotopic composition of leaves of naturally regenerated young trees of 7 broadleaved species in a mixed stand revealed a large range of variation from -26 to -29 ‰, highlighting differences in water use efficiency among co-occurring species, with beech being less-efficient while pioneer species like birch and aspen displayed a larger water use efficiency (Fig. 4).

The decrease in sap flow density with increasing drought during the summer months as indicated by a decrease in the predawn water potential also highlights major differences among species (Fig. 5). Beech, birch, and hornbeam showed large decreases in transpiration while oak, and to a lesser extent willow, displayed a smaller decrease. In addition, both oak and willow had over 15% of their fine roots below the Bt horizon; while beech exhibited a more-shallow rooting pattern with almost no fine roots below

50 cm (data not shown). The ability of oak to absorb water from deep soil layers during summer in contrast to beech that relies on surface soil layers was further confirmed by tracing deuterium-labelled water which had been added to the shallow soil layer in the xylem sap (data not shown).

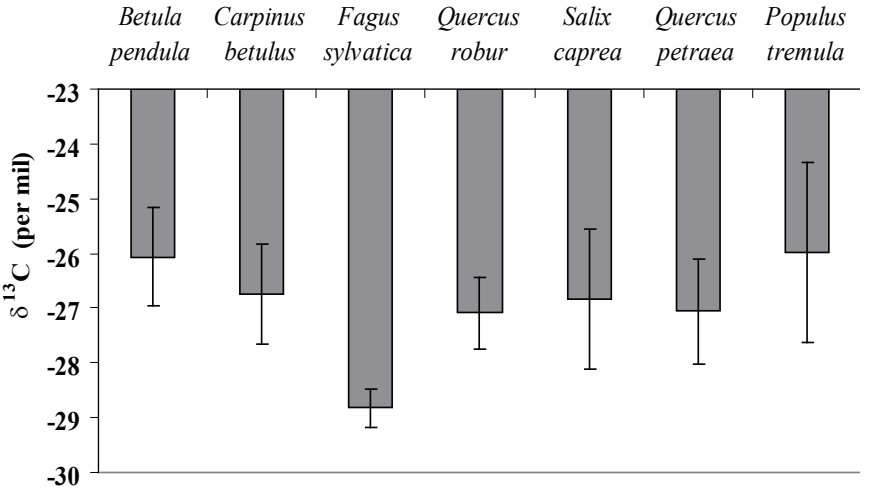

Fig. 4. Isotopic composition of leaves of naturally regenerated young trees of seven co-occurring broadleaf tree species.

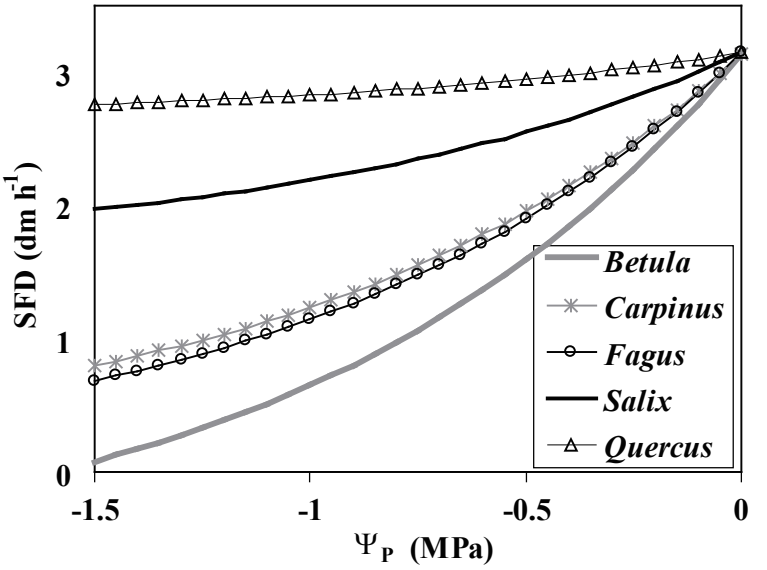

Fig. 5. Sap flux density (SFD) as a function of predawn leaf water potential (ΨP) in naturally regenerated young trees of 5 co-occurring broadleaf species.

CONCLUSION

Efficiencies of resource use and resource acquisition vary among species, and among individuals of a given species, and may also change with changing environments for a given individual (genotype). Functional diversity, as expressed at the individual level (phenotypic plasticity), at the population level (genetic variability), and at the community level (species diversity), is therefore an important determinant of ecosystem stability during the various phases of natural regeneration of a mixed deciduous forest. Understanding this diversity is a key tool for forest managers to control the final species composition of a stand. Preserving functional diversity in a stand will help the ecosystem to maintain its ability to cope with adverse environmental conditions during its dynamic period.

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The effects of thinning on spider diversity in ahigh elevation juniper plantation in central Taiwan

Pao-Shen Huang, Huei-Chen Lin, Chung-Ping Lin , I-Min Tso[1]

[Summary]

In this study, we investigated the effects of thinning on arthropod diversity by comparing the community structure and guild composition of spiders in forests receiving various plantation management practices. Spiders are 1 of the most dominant arthropods in forest ecosystems and are very sensitive to changes in habitat and therefore are considered to be good biodiversity indicators. The study site was located in *Chamaecyparis formosensis* plantations at Da-Shiue Shan District, central Taiwan. We compared spider diversities, microhabitat structures, and microclimates of sample plots located in the *C. formosensis* forests receiving different extents of thinning and in a broadleaf forest. From 4 collection trips conducted in 2005 and 2006, 3484 spiders belonging to 141 species and 22 families were obtained. The MDS plots generated from the relative abundances of different spider species showed that sample plots from 4 forest types (broadleaf forest and plantation forests receiving moderate, heavy, and no thinning) respectively clustered together. Results of ANOSIM tests showed that spider compositions significantly differed among habitats. The MDS plots generated from the relative abundances of different spider families also showed similar patterns. According to the results of the SIMPER analyses, orb weavers and ground weavers were the major contributors to the observed spider diversity differences among the 4 forest types. Results of the BIO-ENV analyses showed that understory vegetation density and temperature were best correlated with the observed spider diversity variations. Results of this study showed that various degrees of thinning practice significantly impacted the abundances of various spider guilds mainly through altering vegetation structures.

Key words: juniper, Chamaecyparis formosensis, Da-Shiue Shan, spider, thinning

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INTRODUCTION

When large areas of primary forests are clear cut and reforested with non-native tree species, such silvicultural practices usually lead to landscape discontinuities and simplification (Lindemayer and Hobbs 2004). The alteration of habitats also has negative effects on forest fauna and flora (Magura 2002). Forest fragmentation may cause isolation of animal populations, and certain species are more prone to invasion from surrounding regeneration sites (Burke and Goulet 1998). Animal diversity is also influenced by the distance between patches and patch size. Usually, species richness and abundance are positively correlated with habitat heterogeneity (Butterfield 1997, Antvogel and Bonn 2001). Therefore, it is suggested that increasing habitat heterogeneity by management activities can help maintain a high diversity of fauna and flora.

Invertebrates are very diverse and abundant. They exhibit varying habitat requirements and play different functional roles in ecosystems. Invertebrates play important roles in ecosystem functioning because of their diversity, complicated interactions with other organisms, and sensitivity to changes in habitats. Therefore, they are suitable ecological indicators to assess the effects of environmental impacts on biodiversity. A number of studies on forest invertebrate diversity have been reported from various taxonomic groups (Fermon et al., 2000, Marra and Edmonds 2004, Ohsawa 2004, Waltz and Covingtou 2004, Zausen et al. 2005). Many studies examined the effects of various forest thinning practices on invertebrate diversity, but the results vary. Ohsawa (2004) showed that thinning increased the richness of cerambycid beetle species in plantation forests in the central mountainous region of Japan. Waltz and Covingtou (2004), on the other hand, found that in western America, mite species richness and density among forests receiving various degrees of thinning did not differ.

Pre-commercial thinning is a kind of silvicultural treatment frequently applied to plantations forests. This silvicultural practice can increase the volume and hence the economic value of the planted trees. Recently, maintaining biodiversity has become a major subject of concern in forest management, and solving biodiversity problems caused by silvicultural practices has become one of the new aims (Jonsson and Jonsell 1999, Lindenmayer and Hobbs 2004). Understanding the effects of various strategies on invertebrate biodiversity plays a crucial role in the long-term management of forests. In this study, we assessed the influences of various degrees of thinning practices on invertebrate diversity by comparing the community structure and guild composition of spiders. We quantified spider diversity and monitored various environmental parameters of juniper plantations subjected to different thinning treatments in central Taiwan. Relationships among microhabitat structure, microclimates, and spider diversitiy were analyzed to identify factors responsible for the observed in variations spider diversity.

MATERIALS AND METHODS

Study sites

The study sites were established in a juniper (*C. formosensis*) plantation in Da-Shiue Shan, Taichung County, central Taiwan. The elevation of the plantation forest is from 1800 to 2000 m, and the gradient is 20~25°. The plantation had been established for about 30 yr. In each plantation type, we placed 9 10 × 10-m sample plots, and the distance between any 2 of them was about 50 m. We established sample plots in 3 types of *C. formosensis* plantation: a plantation without thinning (control), a plantation with moderate thinning and a plantation with heavy thinning. In each plantation type we placed 9 10 × 10-m sample plots and, the distance between any 2 of them was about 50 m. Results of a survey conducted before thinning showed that the overall density of *C. formosensis* stands in Da-Shiue Shan was about 900~1800 trees ha^{-1}. Thinning practice was carried out in 2004 in 2 stands. In the stand receiving moderate thinning, 35% of trees were removed, and the post-thinning density was around 1000 trees ha^{-1}. In the stand receiving heavy thinning, 45% of trees were removed to achieve a density of 825 trees ha^{-1}. In addition, sample plots were also established in a broadleaf forest near the heavily thinned stand to serve as a control. Therefore, 36 sampling plots were established in 4 forest types. Four field trips were conducted in November 2005 and February, May, and August 2006 to collect spiders and environmental data.

Collection and Identification of Spiders

Specimen collection and collecting methods

In each sample plot, a set of pitfall traps was established to collect ground spiders. A set of pitfall traps consisted of 4 plastic cups and 3 polystyrene plastic plates arranged in a Y shape. The cup was 15 cm in height and 10 cm in diameter and was filled with 0.5 L of 70% alcohol. The polystyrene plastic plate was used to enhance catching and was 40 cm in height and 1 m in length. These cups were each covered by a plastic plate secured with sticks to prevent fallen leaves or rain from entering water. In each field trip, the traps were opened consecutively for 7 d.

Sweep nets were used to collect spiders in the forest understory from ground herbs to shrubs 2 m in height. We sweep-netted each sample plot for 5 min to standardize the effort. Spiders in the canopy were collected by sweeping the canopy with insect nets mounted on 8-m-long fishing poles. When collecting canopy spiders, all the canopy branches in the sample

plots were bagged and shaken vigorously for 10 min to standardize the effort. Invertebrate specimens collected were first sorted into spiders, insects, and other arthropods. Spiders were then separated into adults and juveniles, and adult spiders were sorted into morphospecies and if possible identified to species by the palpal organ or epigynum. Juvenile spiders were sorted into families. We used classification systems given in Uetz et al. (1999), Höfer and Brescovits (2001), and Tsai et al. (2006) to categorize both adult and juvenile spiders into foraging guilds according to the spiders' web-building and prey-catching behaviors. Spiders were assigned to the following guilds: (1) orb weavers: Araneidae and Tetragnathidae; (2) space weavers: Dictynidae, Pholcidae, and Theridiidae; (3) ground weavers: Hahniidae and Linyphiidae;(4) foliage runners: Clubionidae, Mimetidae, Oxyopidae, Philodromidae, Pisauridae, Salticidae, Scytodidae, Theraphosidae, and Thomisidae; (5) ground runners: Gnaphosidae, Lycosidae, Oonopidae, and Zodariidae; and (6) ground sedentary weavers: Agelenidae and Amaurobiidae. Insects obtained from each sample plot were weighed after being oven-dried at 60℃ for 2 d. Their biomass was used as an indication of environmental productivity and was incorporated in the subsequent multivariate analyses assessing the relationships between spider diversity and various environmental factors.

Quantification of environmental factors

In order to identify the factors responsible for the observed variations of spider diversity among forest types, we measured various environmental variables in each sample plot. First we used data loggers to monitor the temperature and relative humidity (RH) of the sample plots. The data loggers were placed 1 m above the ground. In each sample plot, 1 data logger (HOBO Pro thermograph/hygrometer) was placed 1m high on a pole, and in each field trip, data were recorded for 1 wk. Leaf litter was collected 4 30 × 30-cm quadrats randomly selected in each sample plot. The leaf litter was carried back to the laboratory and weighed before and after being oven-dried at 40℃ for 1 wk. To quantify vegetation structures, we measured the percent canopy cover (PCC) and understory vegetation density (UVD) of each sample plot on each field trip. A fish-eye lens mounted on a Nikon 4500 digital camera was used to measure the PCC. The camera was mounted on a tripod placed at the center of a sample plot with the lens facing upward to take hemispheric photographs. The photographs were analyzed by Gap Light Analyzer, vers. 2.0 (Frazer et al. 1999) after being transformed into black-and-white images by Photoshop. We used a red cloth (1 × 1 m) as the background and the density of vegetation in front of it was used to quantify the UVD. The red cloth was held by 1 person who stood at each of the 4 cardinal edges of the sampling plot. Another person standing in the center of the plot took pictures of the red cloth and the vegetation in front of it with a Nikon 4500 digital camera. In each of the 4 cardinal directions, the cloth was placed at 2 different heights (low: ground to

100 cm; high: 100~200 cm) to have a better representation of the vertical stratification of the understory vegetation. These photographs were transformed into black-and-white images using Photoshop, and data from the 4 cardinal directions and 2 heights were averaged, and the mean was used as the UVD of the plot.

Table 1. Number of spider species and mean (±SE) adult spider abundance, overall spider abundance, richness (Dmg), evenness (J), Shannon-Wiener index (H'), and Simpson index(D) of sample plots in 4 forest types in Da-Shiue Shan, Taiwan and results of ANOVA test and LSD mean comparisons (BLF, broadleaf forest; PFC, plantation forest without thinning; PFM, moderately thinned plantation; PFH, heavily thinned plantation).

Habitat	Species	Adults*	Overall	D_{mg}	J	H'	D
BLF	75	31.6 ± 3.79	88.2 ± 6.29	5.1 ± 0.27	0.92 ± 0.012	2.65 ± 0.062	0.94 ± 0.007
PFC	70	28.6 ± 2.64	81.8 ± 5.20	4.9 ± 0.34	0.92 ± 0.027	2.61 ± 0.126	0.93 ± 0.027
PFM	63	21.0 ± 2.27	79.3 ± 8.76	4.2 ± 0.37	0.94 ± 0.009	2.43 ± 0.122	0.94 ± 0.012
PFH	75	37.8 ± 4.93	109.0 ± 10.88	4.6 ± 0.32	0.89 ± 0.017	2.52 ± 0.073	0.92 ± 0.012
F-ratio	-	3.408	2.700	1.273	1.108	1.084	0.508
p	-	0.028	0.061	0.299	0.359	0.369	0.679
LSD	-	BLF, PFC＞PFM＞PFH	-	-	-	-	-

* Per sample plot (10 × 10 m).

Statistical analyses

We used Margalef species richness (D_{mg}), Shannon-Wiener index (H'), Simpson index (D), and evenness (J) (Krebs 1989) to quantify the community structures of spiders among different habitats. To compare all these indices a one-way analysis of variance (ANOVA) test and least significant difference (LSD) mean comparisons were used, and both tests were performed by SYSTAT 9. The Bray-Curtis similarity (Krebs 1989) between sample plots based upon species, families, and guild compositions were calculated. Multidimensional scaling plots (MDSs) based upon the values of the Bray-Curtis similarity values were constructed to visualize the relationship of sample plots in the 4 forest types. Analysis of similarities (ANOSIM) was performed on sample plots from each pair of forest types to test for the statistical significance of the grouping patterns. MDS plots were constructed and ANOSIM tests were performed using PRIMER 5 (Clark and Warwick 2001). Furthermore, we also used one-way ANOVA to compare the relative abundances of various spider guilds among the 4 forest types. In addition to demonstrating the relationship between environmental variables and spider diversity, the

BIO-ENV function of PRIMER 5 was used to determine the subset of variables that were most significantly correlated with spider guild composition. Temperature, RH, leaf litter wet and dry weights, PCC, UVD, and biomass of insects from all sampling methods were used as the potential environmental variables. Subsequently, the RELATE function of PRIMER 5 was used to determine whether the correlation was statistically significant. We also used one-way ANOVA and LSD mean comparisons to test whether each of the environmental variables differed among habitats.

RESULTS

Comparison of spider community structures among habitats

In total, 3484 spider specimens were obtained from 4 sampling seasons, and among them, 1160 were adults. From the adult specimens, 141 morphospecies belonging to 22 families were identified. The most abundant spider family was the Linyphiidae (28.7%), followed by the Tetragnathidae (15.6%) and Araneidae (13.7%). The Linyphiidae also had the greatest number of species (40), followed by the Agelenidae (19) and Theridiidae (17). Sample plots in broadleaf and heavily thinned plantation forests had the highest abundance of adults and number of species. The Moderately thinned plantation forest had the lowest abundance and diversity (Table 1). The 4 forest types did not significantly differ in any of the diversity indices analyzed (Margalef species richness, Evenness, Shannon-Weiner function, and Simpson index) (Table 1).

Comparison of spider composition among forest types

The MDS plots generated from spider species composition of forest type sample plots showed that sample plots from the same forest type clustered together (Fig. 1a). Results of the ANOSIM tests showed significant differences in spider species compositions among the 4 forest types (Table 2a). The MDS plot generated from the relative abundances of different spider families also showed a pattern similar to that generated from the spider species compositions (Fig. 1b). Results of the ANOSIM test also showed significant differences among the 4 forest types (Table 2b). The MDS plots generated from the relative abundances of the different spider guilds at sample sites showed that the 2 thinned plantations were well separated from the other 2 forest types. The broadleaf and unthinned plantation forests showed some overlap (Fig. 1c). These patterns were congruent with the ANOSIM results, in which the guild compositions of plots in the broadleaf and unthinned plantation forests did not significantly differ. All other pair-wise comparisons were statistically significant (Table 2c).

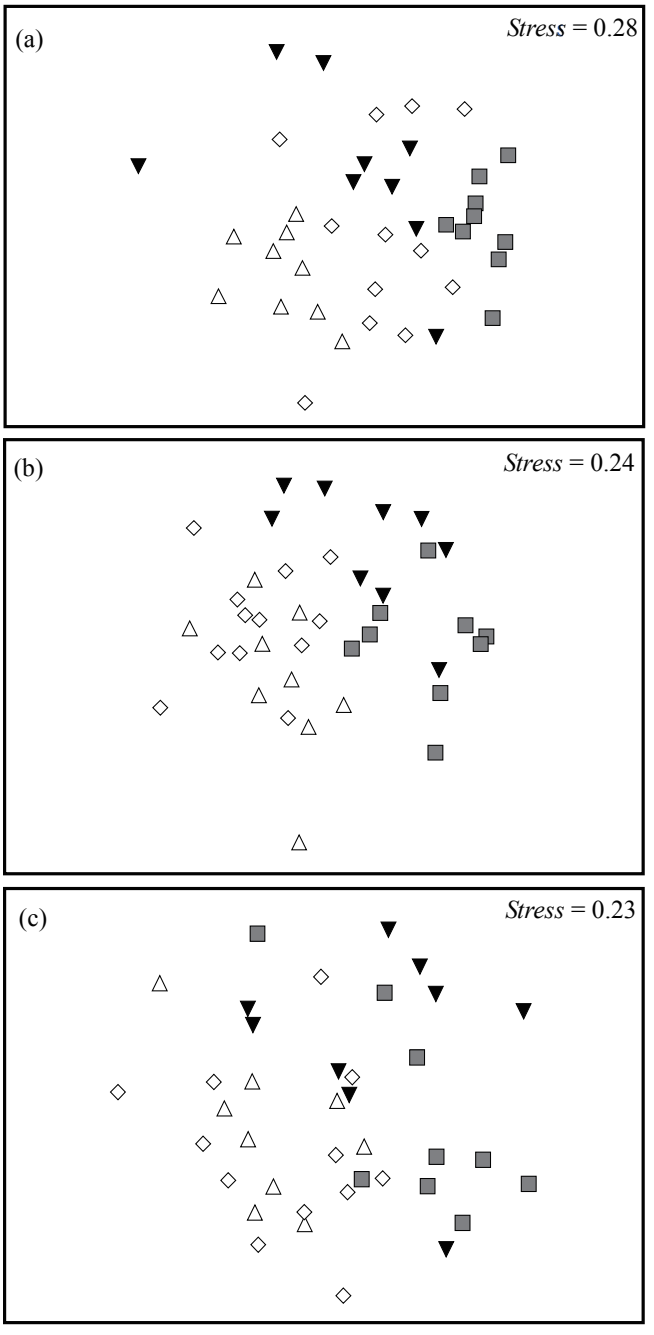

Fig. 1. MDS plots of sample plots in 4 forest types at Da-Shiue Shan, Taiwan generated using species (a), family (b), and guild (c) compositions. (♦ broadleaf forest; ▲ plantation forest without thinning; ▼ moderately thinned plantation; ■ heavily thinned plantation.)

Table 2. Results of pair-wise ANOSIM tests comparing spider species (a), family (b), and guild (c) compositions between different forest types (BLF, broadleaf forest; PFC, plantation forest without thinning; PFM, moderately thinned plantation; PFH, heavily thinned plantation).

Comparison	(a) Species composition		(b) Family composition		(c) Guild composition	
	R	p	R	p	R	p
Global *R*	0.449	0.001	0.444	0.001	0.225	0.001
PFC vs. PFM	0.469	0.001	0.463	0.001	0.237	0.005
PFC vs. PFH	0.836	0.001	0.615	0.001	0.344	0.001
PFC vs. BLF	0.505	0.001	0.217	0.002	0.014	0.379
PFM vs. PFH	0.255	0.001	0.247	0.006	0.186	0.041
PFM vs. BLF	0.344	0.001	0.522	0.001	0.324	0.004
PFH vs. BLF	0.363	0.001	0.589	0.001	0.258	0.01

Non-parametric Kruskal-Wallis ANOVA tests were used to compare the abundances of various spider guilds among forest types. Sample plots in the 2 thinned plantations had significantly higher orb weaver but lower space weaver abundances (Fig. 2). The abundances of the other 4 spider guilds were similar among the different forest types (Table 3). Results of the SIMPER analyses showed that orb and ground weavers had the highest contributions to the observed diversity variations.

Comparisons of environmental variables among habitats

Results of the BIO-ENV analysis showed that UVD and temperature were best correlated with spider guild (RELATE test, Spearman rank coefficient $Rho = 0.157$, $p = 0.026$) and family compositions (RELATE test, Spearman rank coefficient $Rho = 0.264$, $p = 0.003$)Results of the ANOVA tests on each environmental variable showed that the highest UVD was found in the broadleaf forest, followed by the unthinned plantation forest. Sample plots in the 2 thinne plantation forests had the lowest UVD (Fig. 3d). Sample plots in the broadleaf forest had the highest wet and dry litter weights (Fig. 3e, f), but the lowest RH and PCC (Fig. 3a, c). Sample plots in the unthinned plantation forest had the highest mean temperature. Results of the ANOVA test comparing insect biomass among the 4 forest types showed no significant differences. Congruent with such results, the BIO-ENV procedure also did not choose insect biomass as a significant determinant of spider diversity.

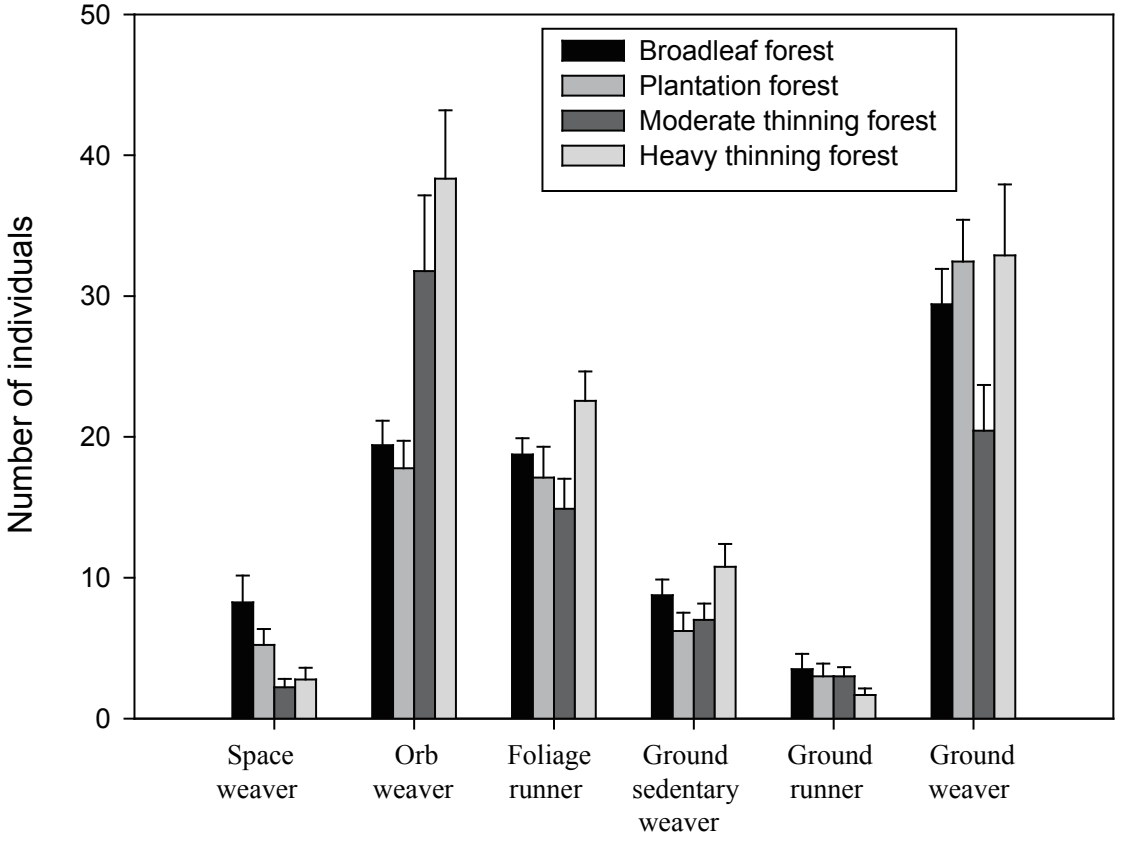

Fig. 2. Means (± SE) abundance of various spider guilds among 4 forest types.

Table 3. Results of ANOVA tests and LSD mean comparisons of the abundances of various spider guilds among the different forest types. (BLF, broadleaf forest; PFC, plantation forest without thinning; PFM, moderately thinned plantation; PFH, heavily thinned plantation)

Guild	*F*-ratio	*p*	LSD
Space weaver	4.354	0.010	BLF > PFC, PFM, PFH
Orb weaver	7.332	0.001	PFM, PFH > BLF, PFC
Foliage runner	2.838	0.052	-
Ground sedentary weaver	2.595	0.068	-
Ground runner	0.808	0.498	-
Ground weaver	2.270	0.097	-

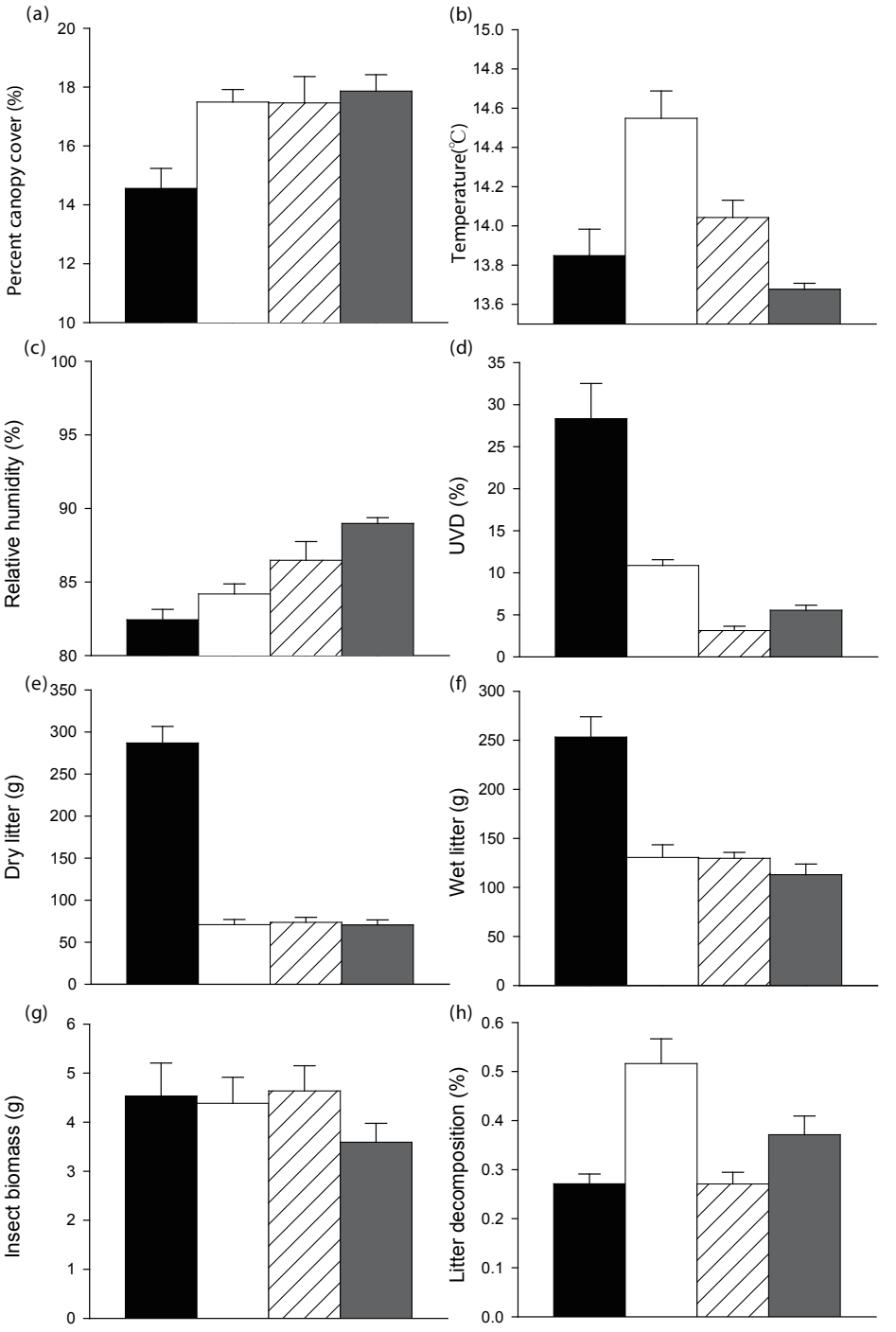

Fig. 3. Mean (±SE) percent canopy cover (a), temperature (b), relative humidity (c), understory vegetation density (UVD) (d), dry (e) and wet weights (f) of leaf litter, insect biomass (g), and rate of litter decomposition (h). (■ broadleaf forest; □ unthinned plantation forest; □ moderately thinned plantation; ■heavily thinned plantation.)

Table 3. Results of ANOVA tests and LSD mean comparisons of the abundances of various spider guilds among the different forest types. (BLF, broadleaf forest; PFC, plantation forest without thinning; PFM, moderately thinned plantation; PFH, heavily thinned plantation)

Guild	*F*-ratio	*p*	LSD
Space weaver	4.354	0.010	BLF > PFC, PFM, PFH
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Ground weaver	2.270	0.097	-

DISCUSSION

In this study, we systematically quantified the diversity and community structure of spiders in forests receiving different management practices. Although sample plots in the 4 types of forests exhibited different environment variables, they did not differ in all of the species diversity indices calculated. This result indicates that the relative abundances of adult spiders were similar among the different forest types. While there was no significant difference in diversity indices among the forest types, the spider composition considerably differed. Results of the MDS analyses and ANOSIM tests indicated that spider species and family compositions significantly differed among the 4 forest types. This pattern suggests that although 30 yr had passed since the disturbance occurred, family and species compositions of plantation forests still significantly differed from that of the broadleaf forest. The MDS plot generated from the spider guild compositions showed that spiders of the unthinned plantation forest and broadleaf forest had considerable overlap. This result is consistent with the result of ANOSIM test, indicating that the spider guild composition did not significantly differ between the plots in plantation forest and broadleaf forest. However, spider species and guild compositions significantly differed among the sample plots in the 3 types of plantation forests.

The observed heterogeneity in spider diversity between the 4 forest types was mostly generated by differences in the ground weaver and orb weaver guilds. Results of the SIMPER analyses showed that these 2 spider guilds contributed most to the diversity differences between forest types. Compared with sample plots in forests receiving either moderate or heavy thinning, those in broadleaf and control plantation forests had higher ground weaver but lower orb weaver abundances. Such variations in patterns might have resulted from differences in UVD between

habitat types. Compared with sample plots in plantation forests receiving thinning treatments, those in the other forest types had significantly higher UVDs. Therefore, thinning treatments and subsequent clearing of understory vegetation might have reduced UVDs and thus resulted in lower ground weaver and higher orb weaver abundances in moderately and heavily thinned plots. Results of the BIO-ENV analyses indicated that the combination of UVD and temperature were best correlated with spider family and guild compositions among the forest types Results of the ANOVA test indicated that sample plots in the broadleaf forest had the highest UVDs, followed by the unthinned plantation forest and the two thinned plantation forests. Results of the ANOVA test also indicated that sample plots in the unthinned plantation forest had the highest temperature, followed by the moderately thinned plantation forest and the broadleaf forest, while the heavily thinned plantation forest had the lowest values.

Results of this study showed that sample plots in the different forest types differed in spider species/guild compositions as well as microenvironmental variables. Such differences are likely to have been generated by the impacts of thinning practices on the vegetation structure of the forests. When the forests were changed from broadleaf to *C. formosensis* stands, the canopy became more closed, and these changes subsequently affected microenvironmental variables such as temperature, RH, and UVD. Among these factors, the change in UVD seems to have been the major factor determining spider diversity in the different forest types. In this study, various degrees of thinning practices significantly impacted the abundances of various spider guilds, especially those of orb weavers and ground weavers. The understory vegetation of sample plots in broadleaf and unthinned plantation forests were more complicated than those in plantation forests receiving various degrees of thinning. Spiders building space webs might benefit from such complicated understory vegetation structure because they need multiple attachment points for webs. So, the abundance of this guild was significantly higher in broadleaf and control plantation forest plots. On the other hand, sample plots in the 2 thinned plantation forests exhibited a simpler understory vegetation structure, and this might have contributed to the increase in orb spiders, which need a relatively open habitat structure to build 2D orb webs. Therefore, the abundances of orb spiders were significantly higher in sample plots in the 2 thinned plantation forests.

Acknowledgments

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Table 4. Results of ANOVA tests and LSD mean comparisons of various environmental variable among the different forest types. (BLF, broadleaf forest; PFC, plantation forest without thinning; PFM, moderately thinned plantation; PFH, heavily thinned plantation; PCC, percent canopy cover; UVD, understory vegetation density)

Environmental variables	*F*-ratio	*p*	LSD
PCC	5.911	0.002	PFM, PFH, PFC > BLF
Temperature	10.358	0.0001	PFC > PFM > BLF, PFH
Relative humidity	12.574	0.0001	PFH > PFM, PFC > BLF
UVD	20.332	0.0001	BLF > PFC > PFM, PFH
Dry litter weight	20.385	0.0001	BLF > PFM, PFH, PFC
Wet litter weight	74.922	0.0001	BLF > PFM, PFH, PFC

Table 5. Results of SIMPER analyses determining the relative contributions of various spider guilds to the observed diversity variation among forest types (BLF, broadleaf forest; PFC, plantation forest without thinning; PFM, moderately thinned plantation; PFH, heavily thinned plantation).

	Dissimilarity/ average	Dissimilarity/ SD	Contribution (%)	Cumulative contribution (%)
PFC vs. BLF				
Ground weaver	5.97	1.34	27.48%	27.48%
Orb weaver	3.87	1.36	17.81%	45.29%
Foliage runner	3.75	1.15	17.25%	62.53%
Space weaver	3.15	1.16	14.49%	77.02%
Ground sedentary weaver	2.98	1.81	13.69%	90.72%
PFC vs. PFM				
Orb weaver	9.04	1.28	31.51%	31.51%
Ground weaver	8.83	1.38	30.07%	62.26%
Foliage runner	4.80	1.44	16.72%	78.98%
Space weaver	2.30	1.22	8.02%	87.00%
Ground sedentary weaver	2.21	1.00	7.69%	94.69%
PFC vs. PFH				
Orb weaver	10.57	1.63	36.58%	36.58%
Ground weaver	7.54	1.34	26.11%	62.69%
Foliage runner	4.37	1.25	15.14%	77.82%
Ground sedentary weaver	3.19	1.32	11.05%	88.87%
Space weaver	1.95	1.24	6.75%	95.62%
PFM vs. PFH				
Ground weaver	9.01	1.56	31.81%	31.81%
Orb weaver	8.77	1.41	30.97%	62.77%
Foliage runner	5.14	1.55	18.15%	80.93%
Space weaver	2.93	1.22	10.34%	91.27%
PFM vs. BLF				
Orb weaver	8.26	1.25	28.92%	28.92%
Ground weaver	7.61	1.50	26.65%	55.57%
Foliage runner	4.24	1.41	14.86%	70.43%
Space weaver	3.68	1.13	12.88%	83.31%
Ground sedentary weaver	2.75	1.55	9.65%	92.96%
PFH vs. BLF				
Orb weaver	9.66	1.55	35.30%	35.30%
Ground weaver	7.12	1.31	26.01%	61.30%
Foliage runner	3.25	1.32	11.89%	73.19%
Space weaver	3.06	1.11	11.19%	84.38%
Ground sedentary weaver	2.70	1.20	9.87%	94.25%

Analyzing After Thinning Microclimatic Responses Semi-parametrically

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[Summary]

Monitoring the effects of thinning on microclimates is an integral part of any thinning experiment. It is through its modification of microclimates that thinning alters important ecophysiological and ecosystem processes and subsequently promotes the development of a more-diverse flora and fauna. Microclimatic responses after thinning reflect the effects of regional climatic trends over the monitoring period, thinning, and possibly their interactions. Thus, analyzing the microclimatic responses from a thinning experiment must achieve 2 objectives: to detect the effects of different thinning regimes (e.g., thinning intensities) on the microclimates, and to reveal the temporal trends (e.g., due to higher-level factors) in important microclimatic variables. In this paper, we propose the use of a semiparametric approach based on a smoothing spline to analyze the microclimatic responses after thinning. We first briefly introduce the concept of the smoothing spline, and with an example from Taiwan, we then analyze the responses of 6 climatic variables using the proposed approach. Our results show that the propose approach not only detected the effects of thinning intensity, but also revealed some important temporal trends. Some of the temporal trends were the results of an interaction between the thinning intensity and regional climatic trends over the monitoring period. Thus, we have successfully separated the influences that are due to higher-level climatic factors from those due to thinning, which will lead to a better understanding of how thinning truly affects microclimates.

Key words: microclimate responses, semi-parametric model, smoothing spline, thinning.

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INTRODUCTION

Many large-scale thinning experiments have been undertaken around the world during the past decade to understand the effectiveness of thinning at promoting the biodiversity and sustainability of plantation forests (e.g., Sullivan et al. 2001,2005, Monserud, 2002, Hagar et al. 2004, Harrison et al. 2005). Monitoring the effects of thinning on microclimates is an integral part of any thinning experiment. It is through its modifications of microclimates that thinning alters important ecophysiological and ecosystem processes (Aussenac 2000, Thibodeau et al. 2000, Bauhus et al. 2001) and subsequently promotes the development of a more diverse flora and fauna (Muir et al. 2002, Hanley 2005, MacCracken 2005).

Factors controlling the microclimate within a forest are hierarchical in nature (Aussenac 2000). Higher-level factors, such as regional climate, site topography, etc., assert their influences on microclimates first (Holst et al. 2004; Holst et al. 2005). The effects of lower-level factors, such as soil and vegetation characteristics, are subsequently added. Microclimatic responses after thinning thus reflect the effects of regional climatic trends over the monitoring period, thinning, and possibly their interactions. Therefore, to better understand how thinning truly affect microclimates, we should separate and evaluate the relative importances of those influences. Thus, analyzing the microclimatic monitoring data from a thinning experiment has 2 objectives. The first objective is to compare the effects of different thinning regimes (e.g., thinning intensities) on microclimates. The second objective is to identify temporal trends (e.g., due to higher-level factors) in important microclimatic variables. However, due to the nonlinear, longitudinal, and inherently random natures of the responses, traditional statistical methods (e.g., an analysis of covariance approach) often cannot be used to achieve the objectives.

Recent developments in statistics provide many nonparametric methods to model complex nonlinear behaviors. In this paper, we propose the use of a semi-parametricmixedeffects modeling approach to analyze microclimatic responses to thinning.We first introduce the idea of a smoothing spline, and then demonstrate the approach by an example.

Smoothing Spline

In statistics, the mean squared error (MSE), which is defined as the sum of squared bias and variance, is often used to judge the performance of an estimator or method. Squared bias is often represented by the residual sum of squares, $RSS = \sum [xi - f(xi)]^2$, where $f(x)$ is the approximating function (or model). The MSE typifies the classical bias-variance trade-off in statistics, and we often want to minimize the MSE by finding a good compromise between the 2

terms. An important question is how can the MSE be minimized if we do not know the structure of $f(x)$? If we assume that $f(x)$ is smooth, then we can pool neighboring data together to model local behaviors of $f(x)$ using nonparametric methods. A smoothing spline is one such method based on minimizing a penalized RSS (PENRSS) function. The idea of a smoothing spline can be viewed as a compromise between a model's ability to fit data and the model's smoothness (i.e., variance; Green and Silverman 1994). A smoothing spline can also be viewed as a compromise between using a constant slope to fit all data (i. e., a least-squares linear regression) and using a set of slopes, defined by any 2 points, to fit all data (i.e., interpolating data points, Eubank 2000).

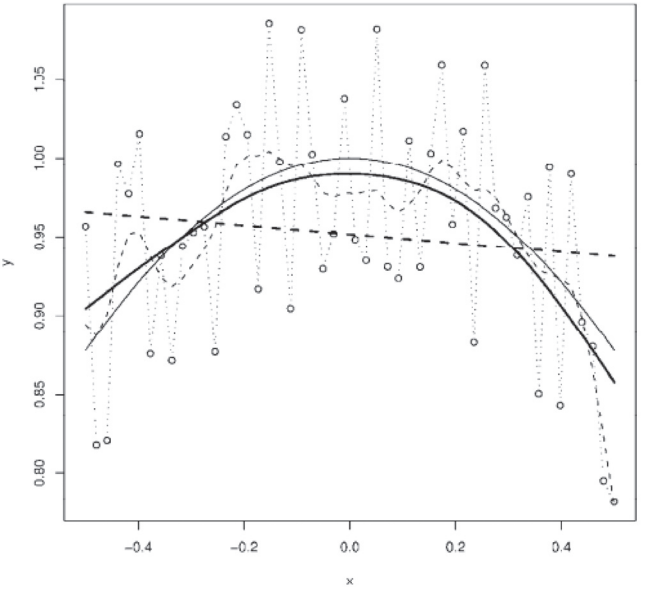
More formally, let $f(x)$ be a smooth function to approximate a set of data from some interval [a, b], and $a < x1 < x2 < x3 < ... < xn < b$. Then a polynomial smoothing spline is the solution that minimizes the PENRSS function having the form of $1/n \sum [yi - f(xi)] 2 + \lambda \int_a^b [f^{(m)}(xi)]^2$, where the first term defines the goodness-of-fit (squared bias) of f (x), the second term is the smoothness of $f(x)$ (represented by the squared integral of the mth derivative), and is a smoothing parameter (Wahba 1990, Green and Silverman 1994, Eubank 1999). Because of the second term in the PENRSS function, a smoothing spline is also known as a 'roughness penalty approach' (Green and Silverman 1994).

The smoothing parameter , λ ,is a measure of the trade-off between a good fit and the smoothness of $f(x)$. When tends to infinity, the smoothness component of PENRSS is the dominant term, and the fit approaches a least-squares linear fit since no curvature is allowed. When λ approaches 0, the main contribution to PENRSS is then from the goodness-of-fit component, and the fit is essentially interpolating among data points (i.e., a rough function with no any smoothing; Green and Silverman 1994).

Thus, the main idea of a smoothing spline is to find a suitable such that the approximating function is smooth (with less variance), but still fits the data closely (with less bias). Figure. 1 provid a simple example to explain the idea.

A polynomial smoothing spline can be viewed as a set of piecewise polynomials joined together at unique data points. For example, if $m = 2$ (i.e., twice differentiable), then, $f(x)$, is the well-known cubic smoothing spline. This particular smoothing function f x satisfies the following 2 conditions: (i) on each of the intervals (a, x1), (x1, x2), (x2, x3), ..., (xn 1, xn), (xn, b), $f(x)$, is a cubic polynomial, and (ii) the set of piecewise cubic polynomials are joined at xi such that , $f(x)$ and its first and second derivatives are continuous at each xi. The approximating function f is therefore smooth throughout the entire interval [a, b] (Green and Silverman 1994).

The most critical issue in fitting a smooth spline is deciding how to choose a proper smoothing parameter. Data-driven automatic methods for finding an "optimal" smoothing parameter include the generalized cross-validation method (GCV, Craven and Wahba 1979) and the generalized maximum likelihood method (GML, Wahba 1985). Many smoothing spline computer programs have implemented 1 or both selection methods. Detailed explanations of the methods can be found in the references cited. Wood (2001) provids an explanation of a smoothing spline and GCV in an ecological modeling context. The advantage of using a smoothing spline is in the method's ability to closely approximate the underlying nonlinear function without the need to specify exactly the form of the approximating function. In recent years, the basic smoothing spline approach has been extended to model data semi-parametrically, and to accommodate mixed-effects, correlations, heteroscedasticity, and other variance structures in the data (Wang 1998a, Wang 1998b, Verbyla et al. 1999, Gu 2002 Wang and Ke 2004).



Example

Fig. 1. An example of a using smoothing spline to approximate an unknown function. Open circles represent data generated from the true function (solid line) with added random noise. The dotted line represents a smoothing spline fit toλ= 0, the dashed line represents a smoothing spline fit toλ= 2.11e-5, the thick solid line represents a smoothing spline fit toλ= 0.0136, and the thick dashed straight line represents a smoothing spline fit toλ= ∞ (i.e., a linear least-square fit).

The example was taken from a comprehensive thinning project in Taiwan. The main objective of the project was to promote the biodiversity of even-aged plantation forests in Taiwan. The data were from a thinning experiment conducted in a 30-yr-old Japanese cedar (Cryptomeria japonica D. Don) plantation located in the Guanwu area (24°30´N, 121° 07´ E, elevation 2000~2200 m) of northern Taiwan. The average annual temperature of the study area is approximately 12.1°C (6.3°C in January, and 16.2°C in July) with an average annual precipitation of about 3200 mm.

The experiment had 3 thinning intensities (strong, moderate, and weak) and a control (unthinned). The area of the experiment was about 40 ha, and the size of each treatment varied from 5 to 14 ha. The aspect of the study area was mainly to the northwest, except for the moderately thinned stand which it was to the north. The experiment was unreplicated due to operational constraints. All thinning treatments used the traditional thinning-from-below approach. The thinning experiment was conducted from October to December 2001. The average numbers of residual stems and average residual basal areas (in parentheses) per hectare after thinning were 500 (32.2 m2), 680 (53.0 m2), 960 (70.8 m2), and 1540 (82.8 m2) for the strong, moderate, weak, and control treatments, respectively.

Microclimatic monitoring

In January 2002, 4 monitoring points were established for each treatment. Air temperature (°C), soil temperature (°C), soil water potential (kPa), and relative humidity (RH,%) were automatically recorded every 2 hours, beginning on February 1, 2002, and ending on January 31, 2004. Data were retrieved every 2 weeks.

The average annual temperatures during the monitoring period were about the same as the long-term average (about 12.6 °C for both 2002 and 2003). The amounts of precipitation, however, were significantly lower than the average. The total amounts of precipitation in the study site were 2762 mm in 2002 and 1865 mm in 2003. The significantly lower amounts of precipitation were due mainly to the lack of typhoons visiting the northern Taiwan region during those 2 yr. In addition, both November and December of 2003 were the driestmonths ever recorded in the study area (7.0 and 1.5mmfor November and December, respectively).

For the example, we were particularly interested in the effects of different thinning intensities on the monthly averages of air and soil temperatures (AT and ST, respectively), air and soil temperature ranges (ATR and STR, respectively), soil water potential (SWP), and air water vapor pressure deficit (VPD, kPa).

Data analysis

We used a semi-parametric smoothing spline approach to analyze the data. Under the proposed approach, the thinning intensity is the discrete, parametric part, whereas time is the continuous, nonparametric part mainly modeled by smoothing splines. A set of semiparametric smoothing spline models (Wahba 1990, Ke and Wang 2001) and a linear mixed-effects model (Pinheiro and Bates 2000) were used to analyze the effects of thinning intensity on and to reveal the temporal trends of the 6 microclimatic variables. The variable STR was analyzed by a linear mixed-effects model. The remaining 5 variables were analyzed by semi-parametric smoothing spline models.

The computer package used was the assist package (Wang and Ke 2004) of R (R Development Core Team 2005). That package is built on top of the nlme package (Pinheiro et al. 2005) of R. Due to a software constraint, the smoothing parameter was estimated by the GML method. It was assumed that the errors were distributed as i.i.d. N (i.i.d., $0, \sigma^2$). To satisfy this assumption, correlations and heteroscedasticity in the residuals were accounted for by the approaches given in Pinheiro and Bates (2000). Details on microclimatic monitoring and on using semi-parametric smoothing splines and linear mixed-effects model to analyze the 6 microclimatic variables can be found in Weng et al. (2007) and Guan et al. (2006).

RESULTS

Both ATs and STs exhibited similar trends across the 2-yr monitoring period (Figs. 2 , 3) and both reflected the air temperature pattern observed at the nearby GuanwuWeather Station. Over the 2-yr monitoring period, both the overall mean ATs and STs of the strongly thinned stand were about 0.6 and 0.7°C higher than those of the control ($p < 0.05$), whereas for the other 2 thinned treatments, the overall means of 2 variables were about the same as those of the control.

For the ATR, the fitted model exhibited a prominent sinusoidal trend for all treatments (Fig. 4). Thismainly reflected the relationship between monthly precipitation and air temperature range in the study region. The effects of thinning on the ATR can be clearly recognized in Figure 4. All thinned stands had a higher ATR value than that of the control in the beginning. The differences gradually narrowed toward the end of 2003, except for the strongly thinned stand, which still had a rather high ATR value at the end. Variations in the ATR for the thinned stands were also larger, especially for the strongly thinned stand. Finally, ATRs of the strongly

thinned stand narrowed at a much faster rate as time progressed. Averaged over the monitoring period, all ATRs of the thinned stands were significantly higher than that of the unthinned stand ($p < 0.005$ for all the thinned stands). In comparison to the other 2 thinned stands, the strongly thinned stand had significantly higher ATR values throughout themonitoring period ($p < 0.05$). A significant ($p < 0.001$) interaction term between thinning intensity and time suggested that the downward rates varied among treatments, with the strongly thinned stand having the highest downward rate, followed by the weakly thinned stand. Rates for the moderately thinned and unthinned stands were about equal.

All thinned stands exhibited larger STR variations, especially the strongly thinned stand (Fig. 5). However, unlike the ATR, variations among all treatments were smaller, likely due to the damping effects of the soil. Similar to the ST, only the strongly thinned stand had an overall mean that was significantly higher than that of the control (with a difference of 0.7°C, $p < 0.005$). The fitted model also suggested that STRs for all stands had slight, but significant increasing trends (with an average rate about 0.007°C per month, $p < 0.005$) during the study period, which again reflected the regional trend in the air temperature range.

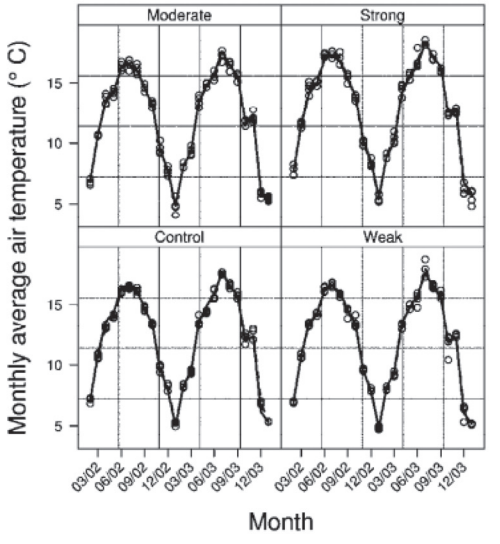


Fig. 2. Observed mean (○), overall mean (dashed line), and model fitted (solid line) monthly average air temperatures from February 2002 to January 2004 for the four thinning treatments.

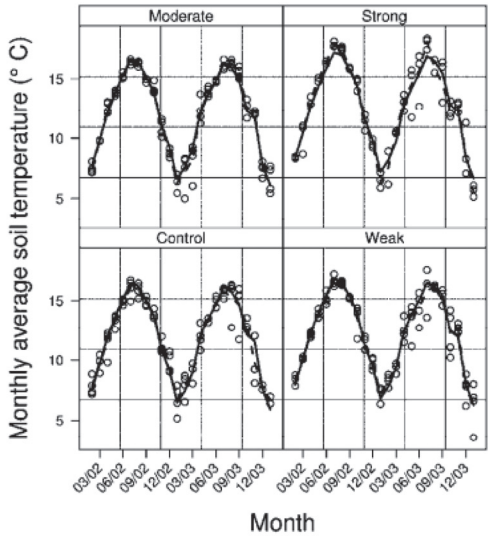


Fig. 3. Observed mean (○), over all mean (dashed line), and model fitted (solid line) monthly average soil temperatures from February 2002 to January 2004 for the 4 thinning treatments.

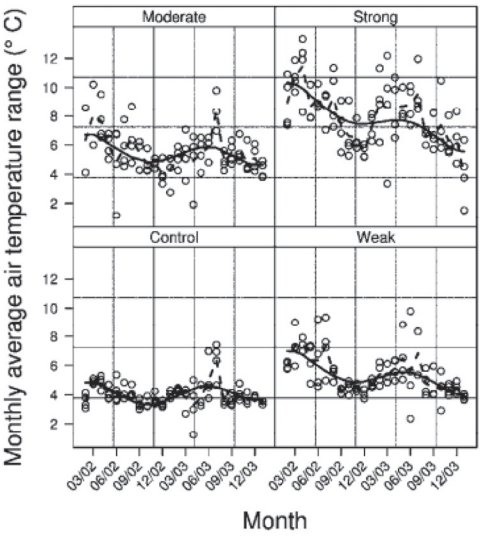


Fig. 4. Observed mean (○), overall mean (dashed line), and model fitted (solid line) monthly average air temperature ranges from February 2002 to January 2004 for the 4 thinning treatments.

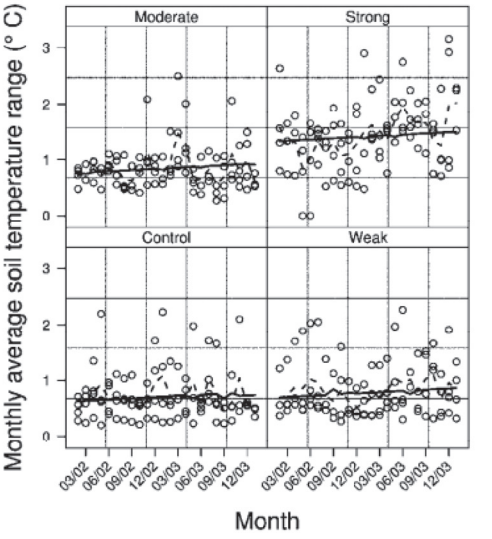


Fig. 5. Observed mean (○), overall mean (dashed line), and model fitted (solid line) monthly average soil temperature ranges from February 2002 to January 2004 for the 4 thinning treatments.

The dominant feature of the SWP, as revealed by the fittedmodel, was the downward trend from the beginning to the end of the monitoring period (Fig. 6), which reflected the drought conditions during that period. Among the 4 stands, the moderately thinned stand had the highest SWP, followed by the strongly thinned stand. Further, SWPs for both stands were significantly higher than that of the control ($p < 0.001$, and $p = 0.044$, respectively). An important feature in Fig. 6 is that all thinned stands had higher SWPs during the severe summer drought of 2003.

Averaged over the monitoring period, differences in VPD among the treatments were small (Fig. 7).The VPD for the unthinned and weakly stands showed a slight but significant upward temporal trend (0.008 kPa mon^{-1}, $p < 0.001$) over the study period, mainly due to the drought conditions. The upward rate amounted to about 6% ~ 7% per month of the overall averages. For both the strongly and moderately thinned stands, the upward rates were 0.004 and 0.005 kPa mon^{-1}, respectively, which were both significantly slower than that for the unthinned and weakly thinned stands ($p < 0.01$, and $p = 0.032$, respectively).

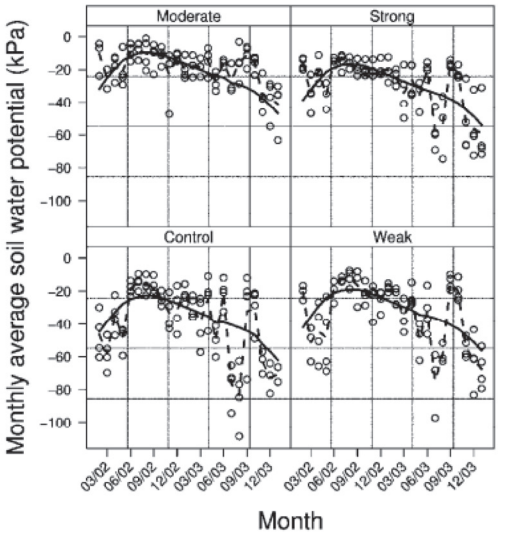


Fig. 6. Observed mean (○), overall mean (dashed line), and model fitted (solid line) monthly average soil water potential from February 2002 to January 2004 for the four thinning treatments.

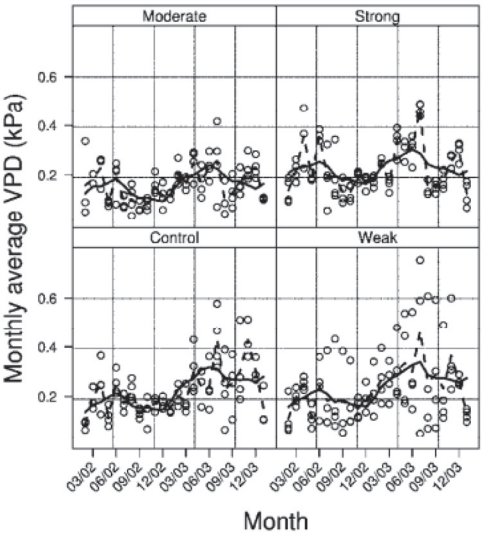


Fig. 7. Observed mean (○), overall mean (dashed line), and model fitted (solid line) monthly average air water pressures deficit (VPD) from February 2002 to January 2004 for the 4 thinning treatments.

DISCUSSION

The trends of the 6 microclimatic variables over the 2-yr period clearly show the hierarchical influences of the regional climatic factors and thinning. All responses were first controlled by higher-level factors (e.g., regional temperature and precipitation trends). Topography also contributed to shaping the temporal trends (Holst et al. 2005). For instance, because of its north-facing aspect, the moderately thinned stand had the highest SWP and lowest VPD (Figs. 6, 7).

In our example, the 6 variables all had complex nonlinear temporal trends, and the flexibilities and capabilities of the semi-parametric approach in approximating those trends were clearly demonstrated. Information revealed by the proposed approach can provide valuable insights into the effects of thinning on other relevant ecological processes. For instance, in our example, the results suggested that although all the thinned stands had a higher ATR initially, the thinning effect declined quickly, especially in the strongly thinned stand (Fig. 4). Since the canopies of the thinned stands did not recover quickly enough to account for the downward

trend, it is likely that other factors were modulating the air temperature range within the thinned stands. Another instance was the trends of SWP over the 2-yr period. During the first summer (wet season) after thinning, the SWPs for the 4 treatments were about the same. However, during the second summer after thinning, due to the severe drought, the SWPs of the strongly and moderately thinned stands were higher than that of the control (Fig. 6). It is unlikely that a parametric approach would have revealed such trends.

The proposed approach can be viewed as an extension of the generalized additive models of Hastie and Tibshirani (1986, 1990). Another potentially useful approach in analyzing microclimatic data is the functional data analysis FDA approach (Ramsay and Silverman 2002, 2005). One advantage of using the FDA approach is that a multivariate approach can be adopted to reveal not only the temporal trends of the responses variables, but also the temporal correlations between them.

Although monitoring microclimates is an integral part of any thinning experiment, only a few studies have attempted to separate and evaluate the relative importances of regional climatic trends and thinning on microclimatic responses. We believe that this failing is mainly due to the difficulties in modeling temporal response trends. Our example has demonstra ted that, with an appropriate statistical approach, one can not only reveal interesting temporal trends, but also separate the influences that are due to higher-level climatic factors from those due to thinning. This will lead to a better understanding of how thinning truly affects microclimates.

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Characteristics of Microenviroments in a *Cryptomeria japonica* Plantation in the Zenlen Area

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[Summary]

Traditionally, much research on plantations for promoting stand growth and ground vegetation by thinning operations has been carried out. Nevertheless, research on how thinning operations can change microenvironmental factor including radiation, air temperature, soil temperature, soil water content, and introducing surface runoffand and soil erosion has seldom been conducted in Taiwan. The influences of different thinning intensities on plantation microenvironmental factor were investigated in this study. A Japanese cedar (*Cryptomeria japonica*) plantation experimental site managed by the Nantou Forest District Office, Forestry Bureau was selected. 12 plots, each of which covered 1 ha, were set up at the experimental site. Instrument systems to investigate visible radiation, air temperature, relative humidity, and soil water and soil temperature at different depths were set in all 12 plots. Observations from August 2006 to April 2007 showed that the highest average air temperature appeared in August 2006 at 19.3℃; and the lowest was in January 2007 at 11.2℃. Among the 12 plots, air temperatures greatly quite differed from one another by month before the thinning operation. As to soil temperature observations from September 2006 to February 2007, it was found that the soil temperatures rise with an increase in soil depth. Meanwhile, soil temperature differences among the different depth is not significant inMarch and April. ANOVA tests showed that soil temperature significantly differed by month and by plot. For visible radiation (PAR) observations, the highest PAR values of each month were found in plot 3, and the lowest were in plot 9 among all plots. Accordingly, it was found that fluctuations in solar radiation received in each plot by month were very significant because the solar radiation received is not only dominated by the angle of radiation incidence but is also affected by the location of the canopy coverage.

Key words: Japanese cedar plantation, soil, temperature, soil water, thinning.

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INTRODUCTION

Taiwan has a forest area of approximately of 2.1 ×106 ha, or 58.9% of the total area of the island (TFB 1995) containing abundant forest resources due to proper temperature and humidity conditions. Plantations were the most common option of restoring forest cover in earlier days after felling. At present, the plantation forest covers an area approximately of 422,600 ha. However, high-density, single tree species, and simple stand structures of plantations make the biodiversity of ecosystem far less than that of natural forests. Furthermore, a dense canopy and poor ground vegetation coverage negatively impact the microenvironments on forest lands. While the governmental forestry policy on forest management has shifted from timber production in the past into current appeals of home land security, ecological protection, and biodiversity maintenance, how to effectively manage the plantation in an abroad sense has become one of the most important issues today.

To meet the objectives of forest ecosystem management, thinning operations of plantations in conjunction with natural reforestation methods have conducted done to improve microenvironments of forest lands. As taught by related studies at home and overseas, the microenvironments conditions of forest lands change due to the sparse canopy as a consequence of thinning of plantations and it is helpful to introduce other plant species to increase the biodiversity of forest ecosystems (Suzuki 2002, Frey et al. 2003). Thinning operations have positive effects upon radiation including radiation quantity and quality on forest lands (Kou et. al. 1999, Liang 1999, You et al. 2003, Weng 2004, Beaudet and Messier 2002). The increase of radiation quantities on forest lands promotes a rise in air temperatures and increases heat convection (Prevost and Potheir 2002, Weng, 2004) which facilitates the decomposition of organicmatter and accelerates the soil mineralization and nitrification (Brix and Mitchell 1986, Thibodeau et al. 2002). Moreover, after thinning practices, the rainfall retained by forest lands increases, thus increasing soil water contents (Thibodeau et al. 2002, Zhu et al. 2003,Weng 2004), and a separation layer which is formed on the land surface by increased litter after thinning can bring a positive benefit to changes in soil water contents (Carey et al. 1981). According to a study by Aussenac and Granier (1988) on thinning operations on a Douglas fir stand, the ability to conserve soil water observed in thinned areas outperformed that found in control areas during the first 3 yr after thinning operations. Soil water content shows a faster change due to the rainfall which fell on the sparse canopy. Therefore, related studies indicate that thinning operations provide a good way to improve forest microenvironments and increase the biodiversity of forest ecosystems.

In this study, experimental sites in a Japanese cedar(*Cryptomeria japonica*) plantation falling within compartments 74, 75, and 76 in Luanta working unit, Nantou Forest District Office, Forestry Bureau were set up to explore changes in radiation, air temperature, soil temperature, and soil water content caused by various intensities of thinning operations. Findings of this study can provide the background information for those who engage in the study in other related fields and serve as a references in decision-making processes of thinning operations by forest administrators.

Profile OF The Experimental Site

The experimental site is located at 23°43'N, 120°44'E which falls within the administrative jurisdiction of Hsinyi Hsiang, Nantou County, and is accessible by taking a left turn at 88 km from Suili to Yushan on the New Central Cross-Island Highway to enter the Jenlun trail and then drive straight ahead for approximately 19 km. The experimental site is covered by a 35-yr old Japanese cedar plantation, and 12 plots were established under an integrated project with each plot covering 1 ha. Figure 1 shows the relative locations of these 12 plots.

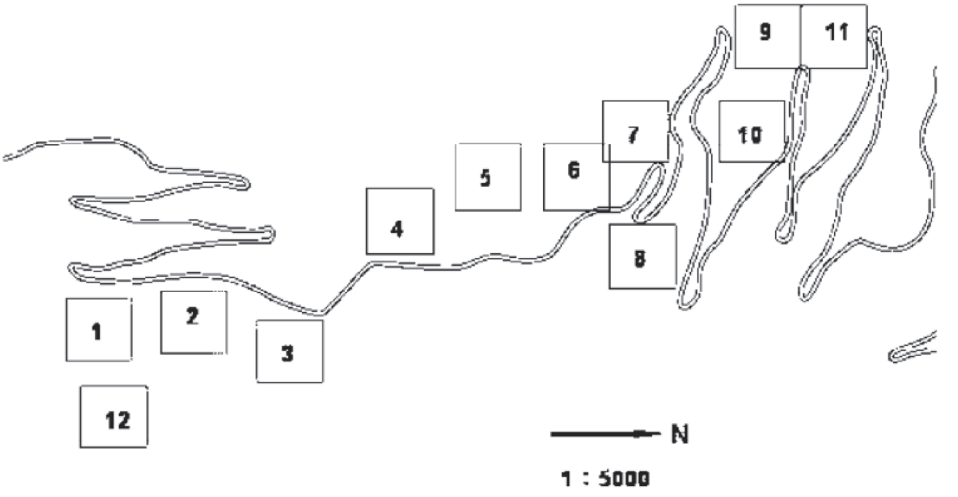

Fig. 1. Relative locations of 12 plots at the experimental site.

Plots 1, 2, 3, and 12 are located at elevation of 1400-1450 m, the average slope is approximately of 50%, and face toward the east; plots 4, 5, 6, and 7are at 1450-1500 m, with an average slope of approximately of 50%, and face toward the east-northeast (ENE); and plots, 8, 9, 10, and 11, are at 1350-1400m, with an average slope of approximately of 50%, and face the north. All plots were grouped in 4 blocks and thinning activities based on 3 thinning intensities, of 0%, 25%, and 50% were carried out during June through August 2007. This site is commonly

used by other integrated studies related to impacts of thinning intensity upon soil nutrients, carbon dioxide, and the bio-ecosystem.

MATERIALS AND METHOD

Instruments to monitor the microenvironmental conditions involving visible radiation (PAR), air temperature, relative humidity (RH) soil temperature, and soil water were respectively dispolyed in all 12 plots for long-term data collection. Data collected were analyzed to identify correlations in time before and after thinning and weather conditions. Also, a weather station was established outside the experimental site at the Zenlen nursery garden as a reference for making comparisons of weather factors on and off the experimental site. Observation principles by instrument are described as follows.

Observation of relative light intensity at midday (10:00~14:00)

On each plot, 16 gauge points evenly distributed in an area of 20 × 20 m were set up. At each point, a pole of 1.3 m in height served as a platform to hold an LI-190SA quantum sensor to collect light intensity data with an LI-250 light meter. The light intensity data were colleted quarterly. During the measurement period, the proportion of solar radiation reaching a given location, relative to a location with no obstructions (i.e., relative light intensity) was synchronously measured in each plot for each treatment, together with a site at an open space outside the plantation. At each point, we measured the relative light intensity 4 times, with each time lasting for 15 s to get average data and waited for 1 min for the second measurement, and so on.

Observation of rainfall

A tipping-bucket rain gage was erected at the off-site weather station to collect rainfall data with 0.1 mm of rainfall recorded by each bucket.

Visible radiation (PAR) monitoring

A set of Li-con Quantum was provided for each plot and the off-site weather station with a scan frequency of 150 s, and with the mean values registered every 5 min to determine the visible radiation conditions on and off the experimental site. Those Licon Quantum sets on the experimental site were erected approximately 1.5 m above the ground.

Air temperature and RH monitoring

A HOBO RH/Temperature detector was erected 1.5 m above the ground in each plot to measure air temperature and RH.

Soil temperature monitoring

Resistance T-type temperature detectors were buried in each plot at soil depths of 5, 10, 20, 30, and 50 cm to scan every 150 s with mean value registered every 60 min for observation and comparison of soil temperatures by depth.

Soil water content monitoring

A multi-section soil volumetric water content probe was buried in each plot at soil depths of 10, 20, 30, and 50 cm. The probe scaned at a frequency of 150 s with the mean value registered every 15 min. Output data collected from the soil water observation system expressed in the units of volumetric water content were analyzed to determine changes in whether it was raining or not, or in dry and wet seasons depending on the different depths.

RESULTS AND DISCUSSION

Starting from January 2006, instruments to monitor climatic conditions were consecutively erected in 12 plots, and a CR10X system is provided for data collection. Collecting the information on the microenvironment before the thinning operation began in June 2006. parameters of visible radiation, relative light intensity, air temperature, soil temperature, and soil water were observed as follows.

Statistics of weather elements in the plot

Table 1 lists statistics of monthly averages of each climate element in the 12 plots indicating that the highest average air temperature appeared in August at19.3℃, and the lowest in January at 11.2℃. More rainfall and thus a greater number of rainy days were observed in August, September, and October with a monthly average RH reaching 95% or higher; and less rainfall and thus a fewer number of rainy days were observed in December, January, and February with the lowest average RH recorded in December. As to soil temperatures, the period from September to February was of a heat release type as the temperatures rose with an increase in soil depth. Meanwhile, March and April were in the heat transitional periods,

and soil temperature differences among different soil depths were not significant. It is however predicable that from April through September, the soil temperatures were of the heat absorption type with the temperature dropping as the depth of soil increased. The highest level of the monthly visible radiation (PAR) occurred in August and then dropped to its lowest level in December before rising again. The daily value for each month varied depending on the weather conditions in that current month.

Table 1. Statistics of climate elements in the 12 plots (August 2006 to April 2007).

Month	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR
Average Temperture (℃)	19.3	18.2	16.8	15.2	12.1	11.2	11.9	14.1	14.9
Average Relative Humidity (%)	97.1	97.3	96.8	94.3	86.2	86.6	88.6	95.4	97.0
At 5 cm Soil Temp (℃)	19.1	18.1	17.3	15.7	12.3	11.5	11.5	13.5	14.6
At 10 cm Soil Temp(℃)	19.1	18.3	17.5	15.9	12.5	11.7	11.6	13.5	14.5
At 20 cm Soil Temp(℃)	19.1	18.5	17.7	16.2	13.1	12.1	11.8	13.5	14.6
At 30 cm Soil Temp (℃)	19.1	18.5	17.6	16.1	13.2	12.4	11.9	13.5	14.5
At 50 cm Soil Temp (℃)	19.0	18.6	18.0	16.6	14.3	12.9	12.2	13.5	14.5
PAR(mole m^{-2})	64.78	43.79	49.50	40.50	34.93	40.1	46.31	51.38	48.48

We analyzed whether significant differences existed in air temperature conditions among plots before beganing the thinning operations. Therefore, 2-way ANOVA was performed on the data collected during 9 mon from the 12 plots, and the results indicated significant difference in air temperature by month and by plot as shown in Table 2a. the 12 plots were grouped in 4 blocks to conduct the ANOVA, and air temperature by month and by plot of these 4 blocks still reached a significant difference as indicated in Table 2b. In other words, the air temperature among the plots differed from one another before the thinning operation. Different slopes, aspects, illumination times, canopy coverages, and canopy structures may have contribute to such inherited differences in air temperature among plots.

Table 2. F value in ANOVA of air temperature in 12 plots.

(a) Twelve plots

Source of variation	F-value
Plot	90.3*
Month	18161.8*

(b) Four blocks

Source of variation	1st Block	2nd Block	3rd Block	4th Block
Plot	24.0*	48.7*	41.4*	22.4*
Month	8987.5*	11406.5*	2206.8*	3727.1*

*Significant at the 5% significance level.
(The 1st block consisted of plots 1, 2 and 3; The 2nd block consisted of plots 4, 5 and 6;
The 3rd block consisted of plots 7, 9 and 10. ;and the 4th block consisted of plots 8, 11 and 12.)

Comparison of relative light intensity among plots

Due to shading by overtopped trees, the relative light intensity in the plantations was generally quite low compared to that in the open space. In the 4 seasons surveyed, over 50% of observation points showed a relative light intensity of < 10% (Table 3).The two-way ANOVA indicated a significant difference in relative light intensity existed among plots, however, no significant difference was detected among points within a plot in the 3 seasons (Table 4).

Table 3. Percentage of observation points with relative light intensities in 2 categories in relation to an open space.

Date	Relative light intensity <10%	Relative light intensity 10%~20%
August 2006	51 %	35 %
October 2006	75 %	21 %
February 2007	92 %	4 %
May 2007	68 %	28%

Table 4. P value of ANOVA in relative light intensity within plots and among plots

Date	Within plots	Among plots
August 2006	0.1750	0.0231
October 2006	0.8232	0.0280
February 2007	0.6152	0.5053
May 2007	0.7324	0.0001

Comparison of visible radiation (par) among plots

Figure. 2 shows PAR values by month in the 12 plots. The highest PAR values of each month is found in plot 3, and the lowest were in plot 9 among the12 plots. Changes in the time sequence of PAR values in the 12 plots varied, wherein, PAR values in plot 7 dropped from August to its lowest level in December, indicating that the time sequence change which occurred in plot 7 was compliant with solar radiation by month as observed in the Northern Hemisphere. The maximum PAR values in plot 3 appeared in August and February, and the lowest one was in September. The tendency of time sequence changes in PAR values by month in the remaining 10 plots was less significant. Accordingly, it was found that fluctuations in solar radiation received by each plot by month were very significant because the solar radiation received was not only

dominated by the angle of radiation incidence but also was affected by the location of canopy coverage. As sunlight penetrates through openings in the canopy, it creates sunflecks on the forest floor with the consequence that the luminosity of each point on the same plane will not be the same. The photo-environment gets very complicated and inconsisten leading to different changes in time sequences on or off site of each plot in forest lands. The monitoring instrument erected in plot 3 was nearly located at the approximate place where more sunflecks developed, and the location was also subject to longer hours of irradiance. This explains why the PAR value received during the period of 09:00~12:00 each day, and thus the monthly total value, was much higher than that measured at other plots, and the total value of each month as well. Differences in slope and aspect in each plot also affect the length of receiving time of irradiance. Depending on the month, the change in the relative locations between solar incidence and canopy coverage also causes sunflecks to move; therefore, PAR values for each plot under different time sequences will also vary.

Comparison of soil temperature by depth among plots

Table 5 shows the ANOVA of soil temperatures respectively measured at soil depths of 5, 10, 20, 30, and 50 cm in the 12 plots of the experimental site. Analytical results show that soil temperatures at the 5 depths significantly differed by month and plots because factors of soil water, ground vegetation, slope, aspect, soil structure, and irradiance may differed from one another in the 12 plots. Reasonably, changes in soil water are critical to change in soil temperatures. While the changes were comparatively greater for the shallow stratum in the absence of rainfall, soil temperatures from different strata may become very close to one another if the level of soil water rises due to rainfall. However, it is not possible to confirm whether the rainfall is the primary cause leading to variations in soil temperatures among the plots. Also, the radiation budget is affected by the condition of the ground vegetation thus to further affects changes in soil temperatures. Moreover, the condition of the soil structure affects the heat transfer speed, and both also accounted for the soil temperature variations in different plots measured at the same time.

Table 5. F value in ANOVA of soil temperature by depth in 12 plots.

Source of variation	Soil depth				
	5 cm	10 cm	20 cm	30 cm	50 cm
Plot	14.4*	30.2*	45.9*	29.66*	47.5*
Month	1131.1*	1500.9*	1798.8*	1509.6*	1968.5*

*Significant at the 5% significance level.

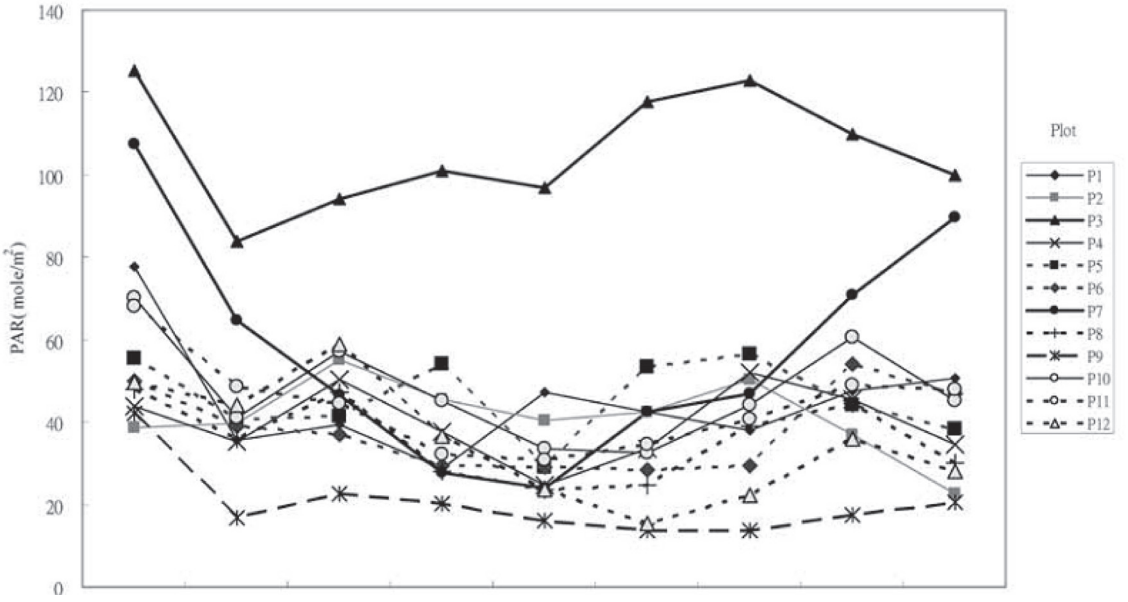

Fig. 2. Comparison of changed PAR values by month in the 12 plots (August 2006~April 2007).

Changes in soil water contents

Observed data of soil water of plot 7 in July and October 2006 were selected to respectively represent changes in soil water during the wet season and dry seasons. As illustrated in Fig. 3 in the wet season, before rainfall occurred, the soil volumetric water content at a soil depth of 10 cm was approximately 33%; at 20 cm, it was approximately 25%; at 30 cm, it was approximately 12%; and at 50 cm, it was approximately 5%. During rainy days, the soil volumetric water content at soil depth of 10 cm rose to 40%; and at 20 cm, it rose to 30% while changes at soil depths of 30 cm and 50 cm were negligible. In the plots, soil at depths of 0~10 cm contains more macropores, so that the soil water content could rapidly fluctuation in rainy days; on the contrary, the lower the stratum, the soil water content change was insignificant, indicating that the water permeability became very poor upon reaching soil depths of ≧ 30 cm. the mode of water movement mode before reaching soil depth of 30 cm has changed from vertical flow to lateral flow along the slope. As illustrated in Fig. 4 in the dry season, rainfall in October was merely 13.9 cm; and soil volumetric water content in soil depth of 10 cm dropped from 27 to 15% in a gradual fashion. The reduction in the soil water content was a result of being subject to the irradiance within a day. During the period of 08:00~15:00, the water on the land surface is vaporized due to exposure to irradiance that causes the soil water content

to drop; however, the soil water content stays constant or mildly rises after 16:00 until the morning of the next day. During October 14 to 24 in the absence of any rainfall, a 0.5% loss of soil water content due to vaporization an average per day was registered. The loss of soil water content is less as the soil stratum goes deeper. In October, the soil water content at a soil depth of 20 cm dropped approximately 5.6%; at 30 cm, it dropped approximately 2.6%; and at 50 cm, practically no change was observed.

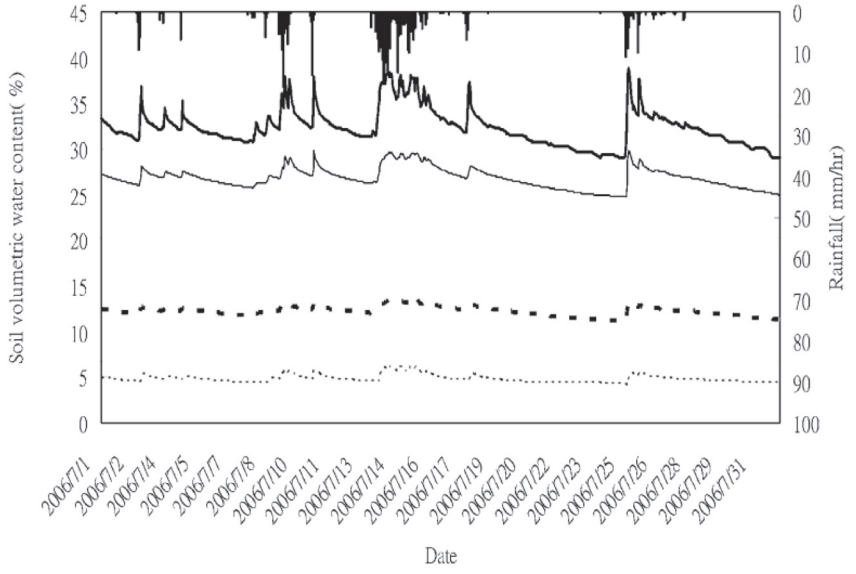

Fig. 3. Changed rainfall and soil water content by depth of plot 7 in thewet season (July 2006).

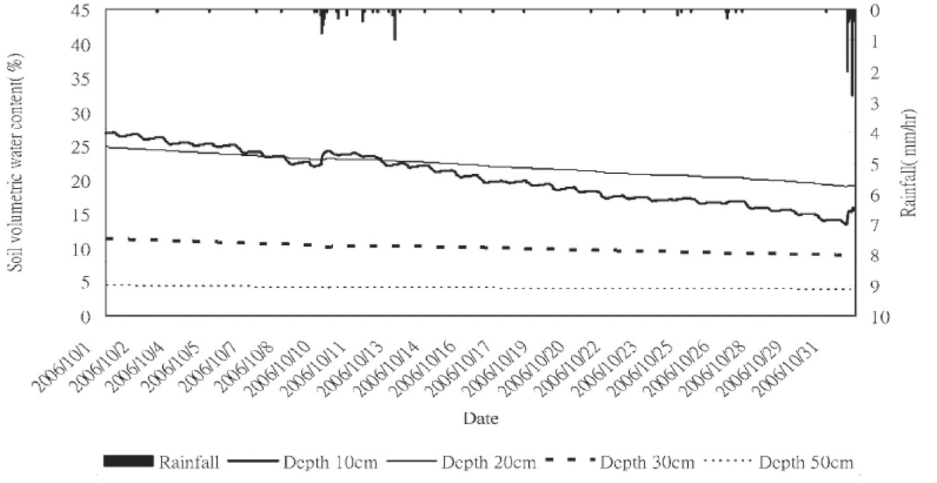

Fig. 4. Changes in rainfall and soil water content by depth of plot 7 in the dry season (October 2006).

CONCLUSIONS

Based on the analysis of data collected on air temperature, PAR, soil temperature, and soil water content from the 12 plots, plot 3 registered the highest PAR value; and plot 9, had the lowest, while the remaining plots showed comparatively small differences in PAR values as affected by factors of the angle of radiation incidence and the canopy coverage. However, differences in air temperature and soil temperature with depth in all 12 plots reached significant levels, indicating inconsistent microenvironmental conditions among the plots. Incumbents were buried in each of the 12 plots to detect soil water changes. Taking plot 7 for example, the soil water content at a soil depth of 10 cm during the west season fellbetween 30 and 35%; and in dry season, between 20 and 25%. On considering the massive amount of gravel in the soil strata within the plots at the experimental site, the buried soil water content probes failed to securely attach to the soil thus significantly compromising the observation accuracy; and soil water content measured was comparatively lower than what was expected; the discrepancy became getting more evident at soil depths of $\geqq$ 30 cm. In addition, to collecting information on observations of surface runoff and soil erosion. before and after the thinning operations, a small plot of 20m (L) x 5 m (W) will be respectively provided in plots 7, 9, and 10 where3 different thinning intensities are respectively designated. The experimental study will be begun immediately following the completions of thinning operation in August 2007.

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Landscape-Scale Model of How Forest Diversity,Climate, and the History of Spruce BudwormDefoliation Affects the Wildfire Potential in Ontario,Canada

Jean-Noël Candau

INTRODUCTION

Changes in biodiversity may have dramatic effects on ecosystems functioning (Hooper et al. 2005). In forest ecosystems, the composition of tree mixtures may influence functioning through changes in natural disturbances such as herbivores (Jactel and Brockerhoff, 2007) and fire. The dominant types of natural disturbance in Canada's boreal forests are wildfire and outbreaks of the spruce budworm(SWB), *Choristoneura fumiferana* (Clem.) (Fleming 2000, Weber and Flannigan 1997). SWB researchers (e.g., Graham 1923, Swaine et al. 1924, Prebble 1950, Baskerville, 1975) have long suggested that SBW-damaged stands represent an increased risk of wildfire. There are also records of major forest fires occurring in areas shortly after SBW outbreaks. Notable examples include New Brunswick's 'Miramichi' fire in 1825 (Flieger 1971), Minnesota's 'Isle Royale' fire in 1936 (Hansen et al. 1973), and Ontario's 'Mississagi' fire in 1948 (Stocks and Walker 1973). Nonetheless, many fire managers remain skeptical of the importance of this interaction so a joint Canadian Forest Service-Ontario Ministry of Natural Resources series of experimental burns was undertaken at a site near the Aubinadong River (46°53'N, 83°24'W) in 1976~1982 (Stocks, 1985, 1987). The burns occurred in mixed-wood stands typical of Canada's Great Lakes-St. Lawrence and boreal forest regions (Rowe 1972) where balsam fir grows in the understory in a heterogenous mix of tree species which often includes spruce (*Picea* spp.), pine (*Pinus* spp.), and birch (*Betula* spp.). Although too few (n = 5) experimental plots were successfully burnt to statistically identify patterns among plots with acceptable power (Cohen 1988), the results suggested that the abundance of "ladder fuels" can make SBW-killed stands an extreme fire risk (Stocks 1985, 1987). "Ladder fuels" are the dead and broken tops and branches which, as they fall, become entangled in other branches and are thus positioned to conduct relatively harmless ground fires up into the crown. In practice, the classification of fuel types used for wildfire risk assessment, contains a separate class for insect-killed conifers. The presence of this class is a recognition of the importance of

the relation between SBW damage and the risk of wildfire. However, this relation is likely to vary in space and time. Therefore, it was perceived that a quantification of this relation and a better understanding of its spatiotemporal variability would improve the accuracy of fire risk calculations. A previous analysis of the spatiotemporal patterns of SBW defoliation and wildfires in Ontario (Fleming et al. 2002) revealed that, within the SBW belt (1) large fires (> 200 ha) occur stochastically, (2) those unrelated to SBW tend to occur at any time after defoliation has ceased, (3) large fires rarely occur shortly before defoliation (presumably because SBW populations do poorly in burnt stands), and (4) those large fires which are related to SBW defoliation tend to occur within a certain time-window after defoliation has ceased, and both the start and extent of this time-window depend on the location in the defoliation belt.

Key words: landscape, forest diversity, spruce budworm, wildfire.

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In this paper, analyses of GIS datasets are presented which combine historical SBW defoliation and large fire data from Ontario with Forest Resource Inventory data and climate data in order to describe how forest diversity and climate, within the SBW defoliation belt, affected where SBW defoliation may have led to subsequent fires.

DATA AND METHODS

SBW defoliation

The Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service has been conducting aerial reconnaissance of large-scale defoliation events throughout Ontario's productive, exploitable forest since 1941. Ideally, the reconnaissance flights begin as soon as the current season's defoliation is completed, usually in mid- to late-July. Survey planes generally fly along lines 6~10 km apart at speeds of about 170 km h^{-1} with their height varying between 360 and 600 m. In the aircraft, FIDS personnel delineate areas within which defoliation has occurred on 1:125,000 or 1:250,000 maps. These maps are later compiled and the information transferred to smaller-scale base maps (e.g., 1:600,000). Allen et al. (1984), Dorais and Kettela (1982), and Sanders (1980) provide additional technical details about aerial sketch mapping. The FIDS relies on the telltale signs of SBW infestation in conducting their annual defoliation surveys (Sippell 1983). During their most active feeding stages (i.e., 4th~6th instars), budworm larvae lay down a fine silk thread as they crawl about the foliage of their host conifer, and when they stop to feed, the larvae tie up the surrounding needles in their silk. As this silk dries, it contracts, pulling the needles together to form a sort of shelter for each feeding larva. The larvae feed on the new shoots, cutting off needles near their base rather than consuming all the green tissue. The severed needles are prevented from falling by the silken webbing which attaches them to the tree. These severed needles slowly develop the brick red color which provides the distinctive tinge to trees defoliated by the SBW that is so evident from the air.

There are a number of potential sources of error in aerial surveys of SBW defoliation (Sippell 1983). Survey timing is important because heavy rain can wash away dead foliage causing defoliated trees to lose their distinctive reddish-brown hue very quickly. A second reason for underestimating defoliation occurs in the first year of heavy defoliation on white spruce when the proportion of the total foliage that becomes discolored is so small that it is barely detectable from the air. The scale of the infestation also affects survey accuracy. Observers typically map with less relative, but greater absolute, error when an infestation is extensive (e.g., > 800,000 km^2) than when it is small (e.g., < 200 km^2). The phase of an outbreak also has an influence on survey accuracy. Budworm damage is more conspicuous during the peak than during either the

build-up or the collapse: large flower or cone crops and injuries caused by other pests and frosts can all create difficulties. Another possible source of error occurs when cumulative defoliation is heavy: then it can be difficult to ascertain the species of the attacked trees (Sippell 1983).

Since SBW larvae feed preferentially on the new shoots, the FIDS measures defoliation in terms of the new foliage lost. (During heavy infestations, the new shoots may be destroyed before larvae complete their feeding and then the larvae may "back-feed" on needles produced in previous years). Depending on the percentage of new foliage lost, the FIDS classifies defoliation as light (0~25%), moderate (26~75%), or severe (76~100%) in its aerial surveys. Light defoliation is almost inconspicuous from the air (Sippell 1983), and therefore rarely reported (Hardy et al. 1986), so we consider only the moderate and severe categories as 'defoliation', below. In this sense, our approach differs from that of Hardy et al. (1986) who considered all 3 defoliation classes in their cartographic analysis of aerially mapped SBW defoliation in eastern North America . These authors were concerned that aerially mapped defoliation "may be slightly conservative" in Quebec, New Brunswick, and Maine where protection spraying "provided excellent foliage protection in some years" between 1970 and 1980. In an attempt to offset this bias, they mapped every class of reported defoliation, including light, which is generally not reported in Ontario.

There is reason to suspect that, as Hardy et al. (1986) imply, spraying generally has had little effect on the large-scale patterns of SBW defoliation in Ontario. The largest spray program occurred in 1986 (Howse et al. 1995) but this amounted to only 1.7% of the 8.75 million ha of moderate and severe defoliation that year (Howse 1995). Furthermore, Lysyk's (1990) analysis of Ontario survey data of 1968~1988 indicated that "sprays ... overall, did not confer a high level of foliage protection". Similar results have been reported for some other jurisdictions (e.g., Fleming et al. 1984).

The FIDS also reports the presence of SBW-caused tree mortality. Observers look for totally gray trees from the air. Subsequent ground checks (for brown cambium on both sides of some boles) are needed for confirmation, however, because trees appearing gray from the air are not necessarily dead - they may only have dead crowns (Sippell 1983).

The map of the frequency of defoliation by SBW converted to a 10-km grid (Fig. 1) shows patterns reported in an earlier publication: areas defoliated at least 1 yr during the period 1941~2005 extend over a continuous east-west "defoliation belt" divided into 3 zones centered around "hot spots" of frequent defoliation which are separated longitudinally by 2 corridors where defoliation is less frequent. In a previous study, Candau and Fleming (2005) showed that areas of high defoliation frequency were associated with dry Junes and cool springs. Conversely,

low frequencies were associated with cold winters in the north and a low abundance of host species in the south. Overall, the distribution of the frequency of defoliation[1] (Fig. 2) resembles the sum of 2 Poisson distributions[2], one with an expected number of occurrences (λ) equal to 1, and the other λ approximately equal to 10. The maximum frequency of defoliation (30 yrs) is encountered in very few areas in the Sudbury-North Bay region (Fig. 1).

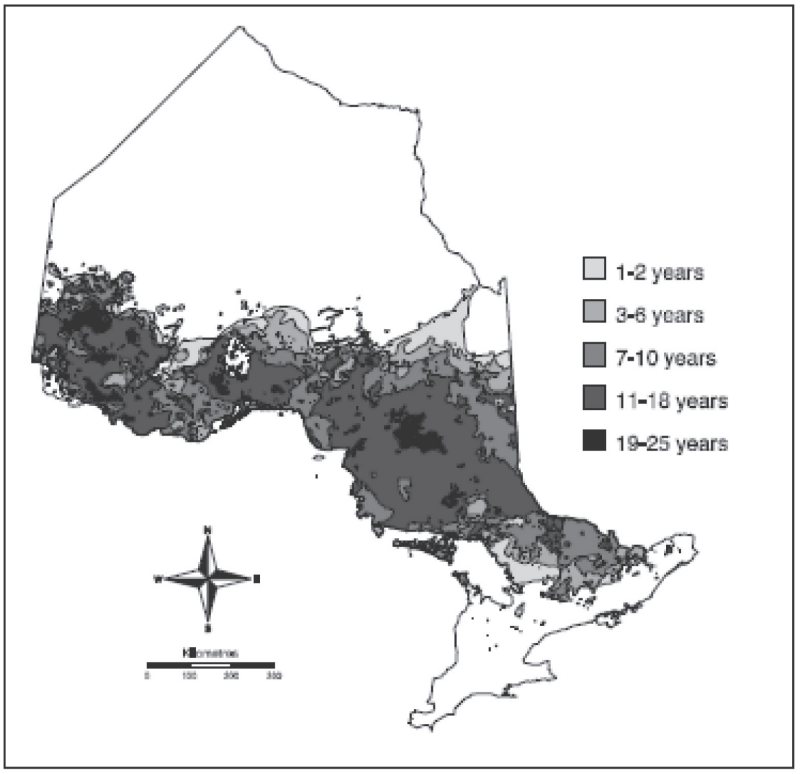

Fig. 1. Frequency (no. of years) of moderate to severe defoliation by SBW between 1941 and 2005 on a 10-km grid.

Fires

The fire data used in this study was compiled from 2 different sources. Records before 1980 were provided by B.J. Stocks (Canadian Forest Service), which were read from microfiche

[1] Prior to the analyses, all maps were transformed to a 10-km grid. The changes in spatial resolution induced by this transformation resulted in differences in summary statistics from previously published numbers.

[2] The assumption that the occurrence of an event is independent of the time since the last event cannot be reasonably applied to spruce budworm defoliation events.

records compiled by the Ontario Ministry of Natural Resources. The rest of the records (i.e., for fires from 1980 to 2005) were extracted from the Canadian Large Fire Database. This database is a spatial (polygon) data set consisting of all mapped fires ≥200 ha from the 13 fire management agencies in Canada, including provinces, territories, Parks Canada, and Canadian Centre for Remote Sensing, from 1980 to 2005. We used the Ontario portion of this database provided by Natural Resources Canada (NRCAN). Although the database contains < 5% of the fires reported in Canada, these large fires account for more than 97% of the area burned and thus represent the vast majority of the fire impacts (Stocks et al. 2003).

Independently of their origin, fire polygons included in the final database are fire perimeters mapped from aerial photography, satellite imagery, and aircraft observations (more recently using global positioning system units). The accuracy of the data has likely varied through time, as recent technological developments have facilitated mapping and improved accuracy. Over the 65 years of fire records, the areas where fires were recorded have probably varied considerably with the inclusion of new areas particularly in the north of the province. However, most of these areas were located north of the SBW area of defoliation, so they were not included in the analyses. Also, although most large fires leave unburned islands (Bergeron et al., 2002) only a small percentage of the polygons have this information (Parisien et al. 2004), as only the outside perimeter was mapped for most of the fires.

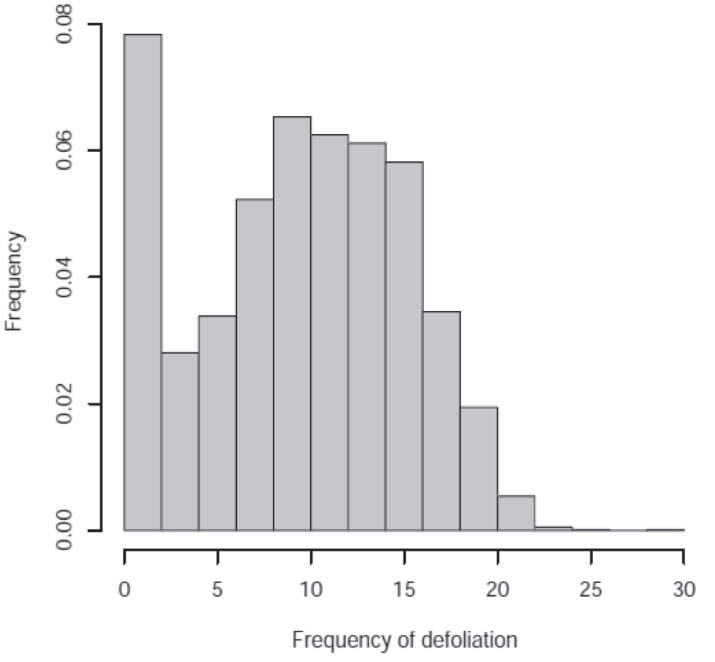

Fig. 2. Distribution of the frequency of moderate to severe defoliation by SBW between 1941 and 2005 on a 10-km grid.

The number of fires and areas burned vary considerably from year to year. The annual number of fires ranges from 0 to 236 (0 and 236, respectively, for fires inside the budworm belt) while the annual area burned ranged from 0 to 651,627 ha (0 and 566,837 ha, respectively, inside the budworm belt). A statistical analysis of Ontario's annual area burned shows a significant increase of the mean area burned during the 1990s (Podur et al. 2002) and changes in the variance of Ontario's annual area burned. The same results were found when the analysis covered only fires in northwestern Ontario.

In a previous study, Fleming et al. (2002) showed that inside the SBW defoliation belt, fires occurred disproportionately more often during a 'window of opportunity' after a SBW outbreak. The length and delay of this 'window of opportunity', hereafter called the SBW-fire interaction period (or SFIP), varies geographically. In the eastern part of the defoliation belt, the SFIP lasts between 3 and 6 yr after an outbreak, in the western part of the defoliation belt it lasts from 6 to 16 yr after an outbreak, and in the central part, it lasts from 4 to 9 yr.

Several hypotheses have been proposed to explain spatial variations in the timing and duration of SFIPs. In particular, forest composition and climate may play important roles through their impacts on the speed of the decomposition of ground fuel after a SBW outbreak.

Forest data

The vegetation data are based on the forest resource inventory conducted by the Ontario Ministry of Natural Resources (OMNR 1996a). For this inventory, forest characteristics are determined at the stand level with a combination of aerial photo interpretation and ground surveys, and then summarized over grid cells varying in size between 5 x 5 and 20 x 20 km (OMNR 1996b). For each grid cell, the data include the percentage of the total basal area of balsam fir and white spruce (i.e., ‘FbSw’), and of balsam fir, white spruce and black spruce (i.e., ‘FbSwSb’), and hardwood (i.e. 'hw'). FbSw accounts for the tree species (balsam fir and white spruce) on which SBW primarily feeds, while FbSwSb covers all major hosts in Ontario. Forest resource inventory data are not available in the northernmost part of the province, but aerially visible defoliation is quite rare there (pers. comm., G. Howse, Canadian Forest Service, Sault Ste. Marie, Ontario).

Maps of tree species composition (Fig. 3) show that FbSwSb and hw have the maximum range of values (from 0 to 1, i.e. from 0 to 100%) and well defined (and opposite) latitudinal gradients. Conversely, values of FbSw covers only half of their potential range (0 to 0.5, i.e. 0 to 50%) and have also a more-scattered spatial distribution than FbSwSb and hw.

Climate data

The historical climate data are spatial interpolations of monthly minimums and maximums for temperature (°C) and precipitation (mm) from 471 meteorological stations across Ontario, eastern Manitoba, and western Quebec, over the period 1961-1990 (Price et al. 2000). This data was converted from its original spatial resolution of 1 km to a 10-km resolution.

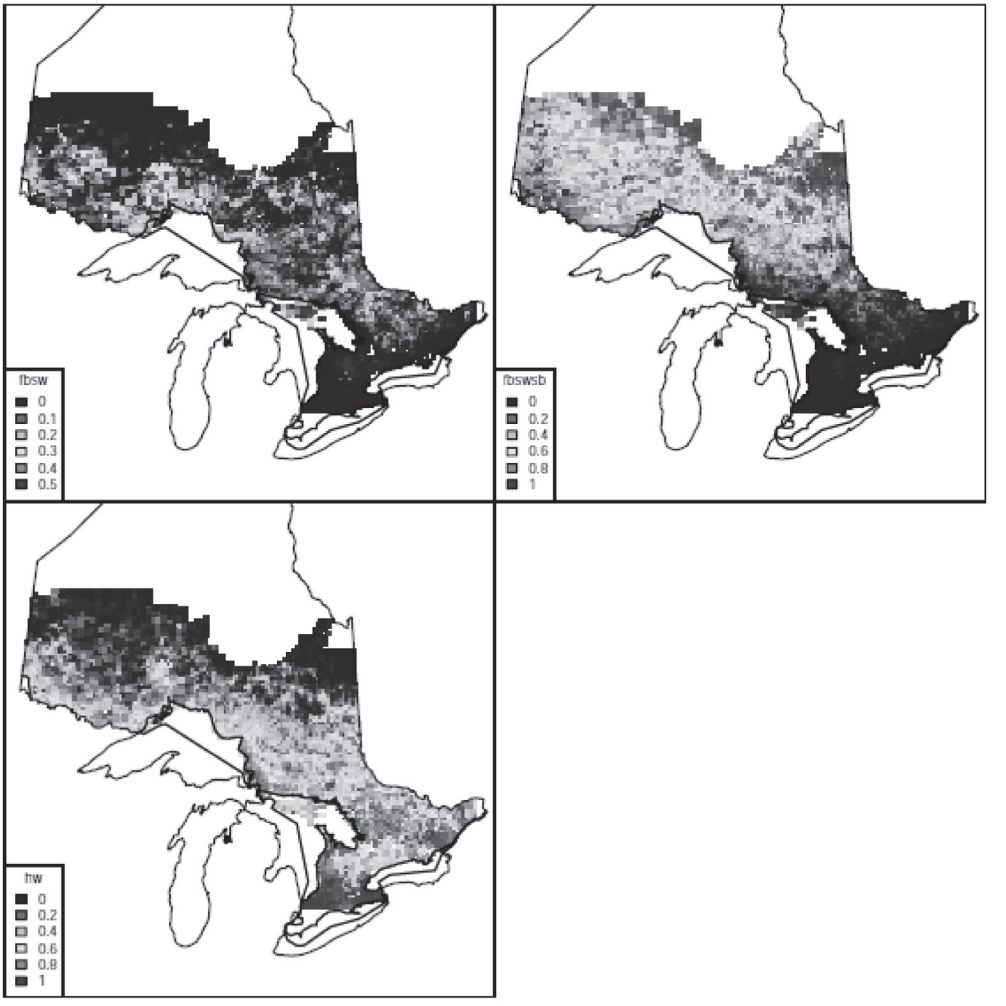

Fig. 3. Proportion of total basal area occupied by balsam fir and white spruce (FbSw), balsam fir, white spruce and black spruce (FbSwSb), and hardwood (hw)

These data were used to calculate aCMI (CMI) according to the following formula adapted from Hogg (1997). Annual CMIs were calculated from 1941 to 2003 for years starting Nov 1st and ending Oct 31st. We then calculated the average of the annual CMI (cmi_ave) over the period 1941~2003 for each cell of a 10-km grid. The map of cmi_ave (Fig. 5) shows a clear partitioning of the province into a drier (cmi_ave < 40 cm/year) zone in the west along the Manitoba border, wet (cmi_ave > 60 cm/year) areas along the lakes shores ,and average areas in the north and northeast.

Regression tree analysis

We used classification trees (CART, De'ath and Fabricius 2000) to model how climate, forest composition ,and SBW defoliation history affect the wildfire potential. Compared to classical methods for predictive modelling (e.g., generalized linear models ,and logistic multiple regression), CART models do not require the restrictive assumptions of (a) Gaussian relations between response and predictor variables, (b) uniform effects of predictors and their interactions on the response over their range of values, and (c) constant interactions among predictors over their range of values (Muñoz and Felicísimo 2004). Classification trees present several advantages over linear discriminant analysis and multiple regression. They can capture non-linear and non-additive behaviours, as well as general interactions among predictors (Breiman et al. 1984), such as when relationships between a response variable and certain predictors are conditional on the values of other predictors. Classification trees can also accommodate both continuous and categorical predictor variables without transformation.

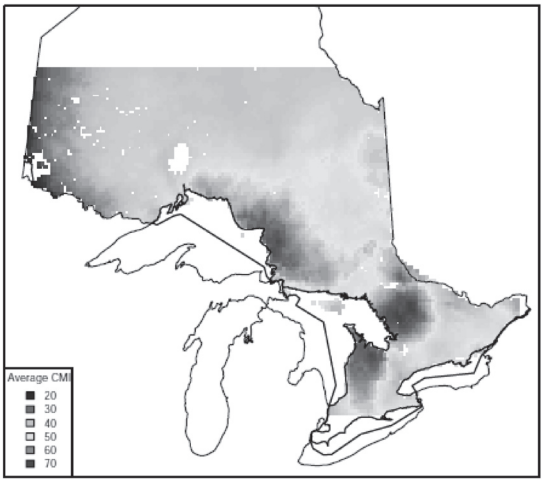

Fig. 4. Average climate moisture (cm yr-1) index of 1941~2003 calculated from Nov. 1st to Oct. 31st on a 10-km grid.

CART models are built in 2 stages: a forward recursive algorithm for "growing" the tree, followed by a second stage where the tree is "pruned back". In "growing" the tree, the data are progressively divided into ever more-homogeneous subsets until all the variation is explained and it is impossible to continue. A univariate, binary partitioning algorithm (CART; Breiman et al. 1984) was used to "grow" the tree. At each step, the algorithm finds a potential predictor variable and a particular value of this predictor to split the total sample (or subsets of the total sample resulting from partitions at previous steps), into 2 groups. The predictor and its "split point" value are chosen to maximize the resulting reduction in misclassification error and variance for classification and regression trees, respectively. Partitioning continues until a pre-set minimum number of observations or a predefined and acceptably low level of overall deviance (i.e., heterogeneity in the values of the response variable) has been reached within the node at the end of each branch of the tree. Such nodes are known as "leaves". In each leaf, the classification tree estimates the probability of class membership and the regression tree estimates the mean value of the response variable.

As a CART model grows, observations are partitioned into ever-smaller subgroups of increasing homogeneity. When these subgroups become very small, the tree tends to describe peculiarities of the sample data rather than generally valid relationships. To limit such over-fitting, a cross-validation procedure was used to "prune" and eliminate unreliable partitions (Breiman et al. 1984). For each branch, the cross-validation algorithm randomly separated the original data set into 10 mutually exclusive subsets, and then used each subset once to independently test subtrees grown on the 9 remaining subsets. The mean square error of prediction, averaged over the 10 runs, was used to assess the quality of each tested subtree. The subtree structure that minimized the averaged mean square error of prediction was retained in the final CART model.

Indeed, we considered that the classification tree presented in each analysis is 1 realization of an ensemble of possible classification trees. To address the question of tree robustness, we assessed the results given by the classification tree presented against each source of variation.

Effect of forest diversity and climate on SBW contribution to fire

Classification tree analysis

The objective of this analysis was to characterize the bioclimatic conditions (forest diversity and climate) in the areas where an interaction between SBW defoliation and fire

occurred in comparison with areas where there was either no fire or no interaction between SBW defoliation and fire.

On a grid at a resolution of 10km, areas where the interaction between SBW defoliation and fire occurred covered 450 cells ,and there were 3415 cells with no fire or no SBW ,fire interaction (Fig. 5). To ensure a balanced sample set, we randomly sampled the same number of cells in areas where there was no interaction between SBW and fire (these areas could have been burned without interaction with SBW or never burned). The resulting sample set (all the cells with SBW-fire interaction and a sample of cells without the interaction) was used for the classification tree analysis. The 5 bioclimatic variables retained for the analysis were the frequency of defoliation (*sbwfreq*), the averageCMI (*cmi_ave*),and the percentages of the total basal area of balsam fir and white spruce (*fbsw*), of balsam fir, white spruce and black spruce (*fbswsb*), and of hardwood (*hw*).

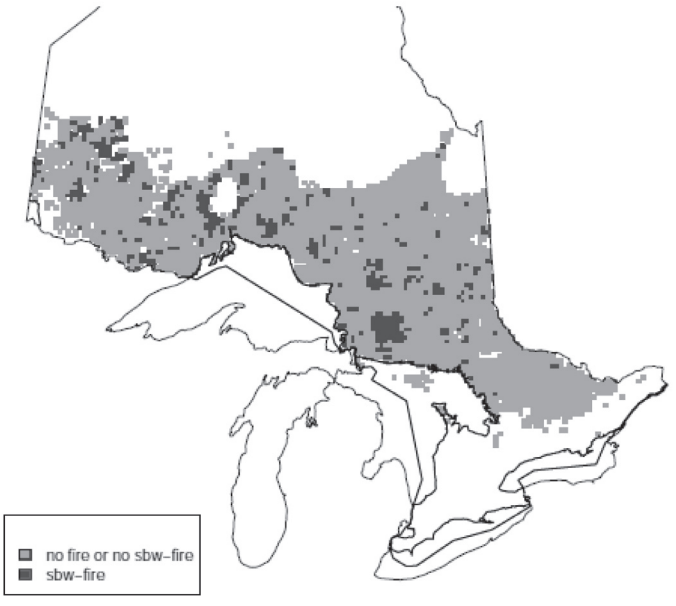

Fig. 5. Map of SBW-fires on a 10-km grid.

The classification tree (Fig. 6)[3] has 6 leaves and an overall misclassification error rate of 30.8%. Areas where SBW-fire interactions occurred are characterized by a mix of tree species (total basal area was 54.4% of hardwood but also <77.6% of balsam fir, white spruce, and black spruce). The classification tree also indicated that these areas were characterized by a higher

[3] A split is shown, for numerical variables, as "variable <> value" when the cases with lower values go left, or as "variable >< value" when the cases with lower values go right. The second line shows the class with the largest number of observations, the number of observations, and percent classified correctly.

average CMI. However, the threshold associated with this index (*cmi_ave* > 33.2 for areas with SBW-fire interaction) is not very informative since almost 98% of the entire province falls under this class. Areas with SBW-fire interactions are also characterized by either a low CMI (33.2 < cmi_ave < 45.1) or a higher index (cmi_ave > 45.1) in association with a frequency of defoliation of > 8 yr during the 1941~2005 period.

The misclassification error inside the terminal leaves was generally higher in the leaves predicting an interaction between SBW defoliation and fire (38.1% in leaf #5 and 30.9% in leaf #6) than in the leaves predicting no interaction (from 17.0% in leaf #4 to 25.5% in leaf #3).

A map of the classification tree leaves (Fig. 7) reveals that the first 2 splits (leaf #1 and leaf #2) associated with hardwood content and balsam fir, white spruce ,and black spruce content match the southern and northern boundaries of the area of SBW defoliation. Areas defined by these 2 splits are also characterized by a low frequency of defoliation as shown in a previous study (Candau et al. 2005). The third split (leaf #3), related to the CMI, identifies an area in the western part of the area of defoliation characterized by a dry climate. The boundary between this area an the rest of the area of defoliation appears associated with a threshold in a gradient of climate moisture clearly seen in Fig. 4. The fourth split (leaf #6), also based on the CMI, defines an area in the western part of the province classified by the classification tree analysis as a SBW-fire area. Finally, the last split refines the location of areas of SBW-fire interactions in the eastern part of the province by excluding some northern areas (leaf #4) from the SBW fire interactions (leaf #5) based on the frequency of defoliation by SBW (areas with lower frequencies were excluded).

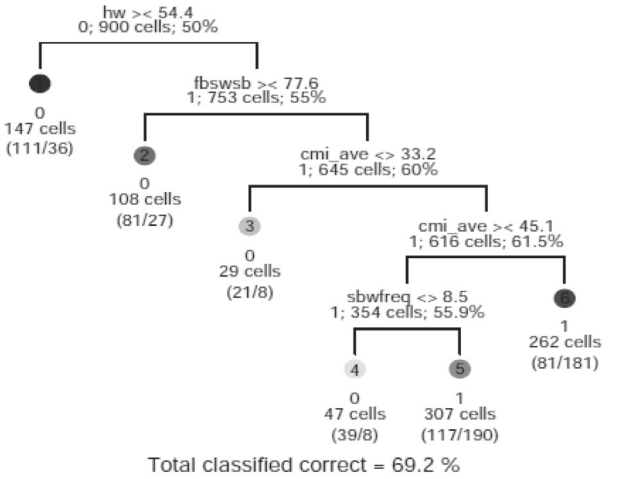

Fig. 6. Classification tree of the presence (1) or the absence (0) of interactions between fire and SBW defoliation.

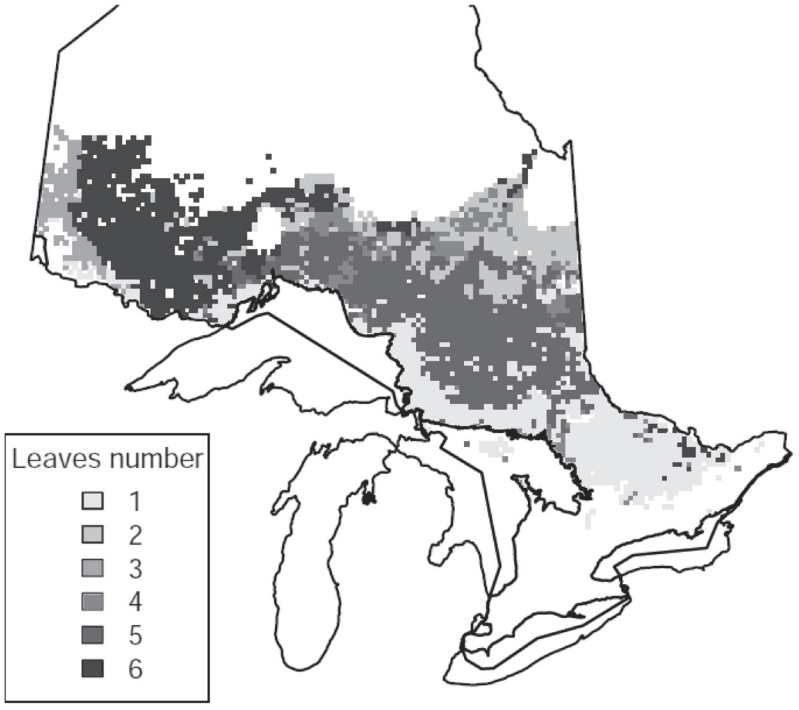

Fig.7. Map of the classification tree leaves (Fig. 6).

In summary, the areas where an interaction between SBW and fire is predicted are delimited primarily by forest type in the south and the north and by moisture in the west. In the area defined by these boundaries and towards the northern limit of the SBW belt, SBW-fire interactions appear to be related to SBW defoliation.

It is also important to notice that the northern boundary of the predicted area of SBW-fire interaction is in many places close to the northern limit of our data (limit related to the forest composition data). This indicates that the area of SBW-fire interactions may extend further north than what our analysis examined.

CONCLUSIONS

The objective of this analysis was to characterize the bioclimatic conditions in areas of SBW-fire interactions. The classification tree reveals that these areas are best defined by a southern limit related to hardwood content, a northern limit related to balsam fir, white spruce and black spruce together, and a western limit linked to moisture. Inside these boundaries, areas of SBW-fire interactions are related to the frequency of SBW defoliation.

These results appear robust against several sources of variation: forest diversity, particularly hardwood content, is consistently the most important variable in explaining the areas of interaction. In southeastern Ontario, the latitudinal gradient of hardwood content matches a gradient of increasing urbanization and, as a result, of increasing fire protection that might also explain the absence of fire in these areas. At the northeastern limit of the area of SBW-fire interaction, the high proportion of balsam fir, white spruce ,and black spruce (FbSwSb > 77.6%) is mainly due to the high proportion of black spruce, a species less impacted by SBW defoliation than balsam fir or white spruce. This might explain why these areas are less frequently defoliated and consequently the low probability of having an interaction between defoliation and fire. In addition, in the northeastern part of the province wet soils and weather patterns bringing cold, moist air from the Hudson Bay limit the occurrence of fire.

The climate moisture index appears to be one of the most important variables after the bootstrap analyses. At the western border of the province ,a low CMI is associated with and area where the SBW-fire interaction does not seem to occur frequently. In this drier climate of the western part of the province, fire dynamics are likely to be more under the influence of climate than SBW defoliation.

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Fungal Diversity in Managed Resinous Forests: he Case of the Landes De Gascogne Forest

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[Summary]

A challenge within the context of sustainable forestry development is to define management strategies that preserve forest health and stability without impeding productivity. The conservation of fungal diversity is part of this challenge. We review the existing knowledge on the impacts of tree species diversity and forest management practices on the diversity of parasitic fungal species. Both inter and intra specific components of fungal biodiversity are taken into account. We support the review with several experimental studies conducted in the Landes de Gascogne forest. This forest, which is the largest European plantation forest, is almost exclusively composed of maritime pine (*Pinus pinaster* Ait). We therefore particularly focus on the incidence of one of the most damaging and widespread pathogens of maritime pine, the *Armillaria* root rot, and provide insights into the diversity of its potential antagonistic fungal species.

Key word: fungal diversity, Armillaria root rot, Pinus pinaster.

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INTRODUCTION

Trees are an obvious structural component of forests, but fungi also form an important part of their biodiversity and contribute to their functioning (Courtecuisse 2001, Siitonen 2001). Three function groups of fungal species can be distinguished in forest ecosystems: the decomposers or saprophytes in soil and wood debris, the symbionts or mycorrhizal species in roots of trees, and the pathogens in all plant tree organs. Saprophytic species decompose organic matter, and very often have antagonistic capacities against pathogens (Davet *et al.* 1992, Gallet *et al.* 1994) . They can be used as biopesticides (Holdenreider and Greig 1998). Ectomycorrhizal species enhance nutrient acquisition and improve stress tolerance and pathogen resistance of dead trees (Smith and Read 1997). Forest pathogens can cause mortality, reduce the fitness of individual forest plants, and affect the composition of plant communities (Holdenreider *et al.* 2004). They are important elements in shaping forest structure, composition, succession, and landscape patterns. Nevertheless, in areas dedicated to timber production, they can induce important economic losses (Hood *et al.*1991, Bendz-Hellgren *et al.* 1998).

Fungal species diversity is claimed to have decreased over the past few decades (Arnolds 1991). At the same time, the area of plantation forests dramatically expanded worldwide. The FAO estimated that planted forest cover doubled in size in the last 15 yr: plantations of spruce, pines, and eucalyptus nowadays represent more than 20% of the total area in many countries. There is a growing concern about the sustainability of these planted forests (Powers 1999) and their vulnerability to pest and disease damages (Jactel and Kleinhentz 1997, Gadgil and Bain 1999, Jactel et al. 2005).

Indeed, modern management practices have radically changed forest structures and can lead to the emergence of endemic pathogens (Anderson et al. 2004). Homogenous monospecific or monoclonal plantations are usually considered to be particularly susceptible to epidemics (Hood et al. 1991, Korhonen et al. 1998, Hartley 2002, Pautasso et al. 2005). They are also generally associated with decreased fungal diversity, with several species being currently endangered by a reduction or an alteration of their habitat due to intensive management (Lonsdale et al. 2007).

Hence, a challenge within the context of sustainable forestry development is to preserve fungal diversity while controlling diseases caused by pathogenic fungal species. Unfortunately, both components of this challenge have often been studied separately – the first by ecologists, the second by plant pathologists - and little is currently known about the relationship between the diversity of fungal species and the intensity of diseases caused by fungal pathogens. In

theory, fungal diversity could enhance the probability of biotic interactions between parasitic fungal species and their competitors, and in this way, reduce disease incidence. Hence, a healthy ecosystem would be an ecosystem which is rich is parasites (Hudson *et al.* 2006).

The aim of this paper was to review the existing knowledge on the impacts of tree species diversity and forest management practices on the diversity of parasitic fungal species. Both the inter and intra specific components of fungal biodiversity are taken into account. We support the review with several experimental studies conducted in the Landes de Gascogne forest. This forest, which is the largest European plantation forest, is almost exclusively composed of maritime pine (*Pinus pinaster* Ait). We therefore particularly focus on the incidence of 1 of the most damaging and widespread pathogens of maritime pine, the *Armillaria* root rot, and provide an insights into the diversity of its potential antagonistic fungal species.

Overview of the Landes de Gascogne forest and its major fungal pathogens

The Landes de Gascogne forest is mostly an artificial monoculture of about 10^6 ha of maritime pine (*P. pinaster*). Although maritime pine is native to the region (Bucci *et al*. 2007), the natural forests were originally limited to the coastal area and to drier sectors (Sargos 2004). Since the 18th century, through intense sowing activities, the forested area has increased about 10-fold, with an expansion towards the interior (Sargos 2004). This new forest area has been intensively managed for timber and pulp production for 50 yr, and numerous silvicultural practices have been conducted at different stages of the forest cycle: plowing and phosphorous fertilization before sowing or planting, understory clearing practices and thinnings at different stand ages, and clear-cutting before re-planting or sowing (Maugé 1987). During the last 15 yr, the plantation area continued to increase due to the genetic selection of maritime pine.

Since 1989, the health of French forests has been monitored by a governmental organization called the Departement de la Santé des Forêts (DSF). The DSF consists of a network of skilled foresters evenly covering state-owned and private forests of the country. It is closely associated with the National Plant Protection Laboratory (LNPV), which specializes in the identification of plant pathogens. Among the pathogen species described on maritime pine in the Landes de Gascogne forest, the root rot fungi *Armillaria ostoyae* and *Heterobasidion annosum* are the most damaging and the widespread. They cause the death of pine trees by invading of the living roots. After a tree's death, they live as decomposers on stumps, wood debris, and some infected shrubs from which they spread to new trees.

First reports on the presence of root rot disease in the Landes de Gascogne forest date back to the beginning of the 1920s on the coastal area for Armillaria (Guyot 1938). During the

last 30 yr, the occurrence of these 2 pathogens has been regularly monitored (Lung-Escarmant and Taris 1984, Lévy and Lung-Escarmant 1998, Aumonier 2007). These surveys have shown that the incidence of H. annosum is maximal in the southeastern sector with a recent increase in the northern and southwestern sectors of the forest. Inversely, the incidence of A. ostoyae is maximal in the coastal area (< 10 km from the ocean), and it decreases towards the interior. However, from 1989 to 2005, an increased presence of A. ostoyae was observed in the eastern sector of the forest (Aumonier 2007).

Both *A. ostoyae* and *H. annosum* spread by root contact and open gaps in the forest landscape. These disease gaps create opportunities for other tree species to become established (Pautasso *et al.* 2005), hence facilitating the succession processes. It was clearly established that root rot diseases spread more quickly in monospecific forests because of enhanced root rot contact between susceptible trees. The analysis of the *Armillaria* mortality distribution in relation to the nature of the nearest inoculum (initially infected stumps or newly dead pines), suggests a primordial role of the primary inoculum (initially infected stumps) in the first stage of the disease (1~3 yr) with the secondary inoculum (newly dead pines) becoming more and more effective over time (Lung-Escarmant and Guyon 2004).

Korhonen et al. (1998) reviewed the debate concerning the relative incidence of *H. annosum* root rot in mixed versus pure stands. The majority of studies support the hypothesis that a reduced incidence of this root and butt rot is correlated with an increase in the number of tree species. The importance of basidiospores in initiating infections in new stands is largely recognized for *H. annosum* (Redfern and Stenlid 1998) and is newly suspected for *A. ostoyae*, with some studies showing contrasting patterns of diversity among *A. ostoyae* populations (Lung-Escarmant *et al*. 1998, Prospero et al. 2007). In the case of *H. annosum*, the spores infect only freshly exposed wood surfaces (stump surfaces or wounds on the roots and stem). It was recently established by an experimental study that the increase in the incidence of *H. annosum* disease in the Landes de Gascogne forest is due to the infection of first-thinning stumps in previously *H. annosum*-free stands (Lung-Escarmant et al. 2007).

Interspecific diversity of fungal species

Distribution of parasitic fungal species richness at the scale of France: Is the Landes de Gascogne plantation a biodiversity coldspot?

One major challenge in parasitology and epidemiology is determining whether the richness of parasitic and infectious diseases simply tracks host diversity or is largely determined by exogenous factors, such as climate-forced variables (Guégan et al. 2005). We addressed this issue by analyzing the 15-yr survey of fungal diseases in French forests conducted by the DSF. We combined multivariate general linear models and stepwise analyses to select the combination of habitat descriptors best accounting for the observed spatial distribution of parasitic fungal species richness (Helion et al., submitted). Our results suggest that host species diversity is not a major determinant of parasite richness, and that seasonal temperatures may play a greater role.

Only the selection of the relative area under resinous species was suggestive of a possible effect of tree species diversity on parasitic fungal species diversity. Indeed, French forests with a large area under resinous species are often dominated by a single species responsible for most of the annual wood production. Our analyses revealed a slight tendency for these resinous-dominated, monospecific forests to contain fewer species of parasitic fungi. This is typically the case for the Landes de Gascogne forest: it appears to be a coldspot on the predicted map of species richness (Fig. 1).

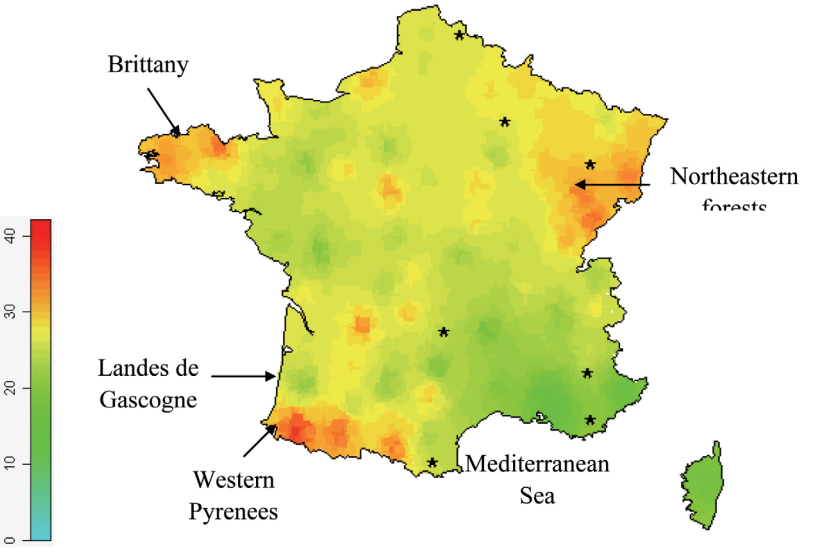

Fig. 1. Predicted species richness of parasitic forest fungi. Geographical units not included for model calibration are indicated by a star (Helion *et al*., *submitted*).

Distribution of species richness within the Landes de Gascogne forest: Are mixed stands richer than pure stands?

In the Landes de Gascogne forest, *Armillaria* species and their potential competitors (wood-decaying and mychorhizal fungal species) were identified in autumn (fruiting body period) in different biotops:

(A) in pure pine plantations established after 2 or more stand rotations;

(B) in young hardwood plantations (oak, beech, prunus, and acacia) established after the maritime pine forest was infected by *A. ostoyae*;

(C) in old natural mixed forests (oak, birch, and pine) or old broadleaf regrowth (oak and chestnut) in gaps produced by *A. ostoyae* in pine forests; and

(D) in old harwood forests (oak).

In pure pine plantations and in young hardwood plantations (3~4 yr old) established after the maritime pine forest, *A. ostoyae* was found exclusively as a primary parasite on maritime pine and as a saprophyte on pine and hardwood stumps and shrubs. The species richness of other fungal species (wood-decaying and mychorhizal fungal species) was relatively low (Jactel et al. 2004, Fig. 2). Among the species identified, 3 wood-decaying fungi (*Hypholoma faciculare*, *Gymnopilus* sp., *Hygrophoropsis aurantiaca*) are known to have antagonistic proprieties against *A. ostoyae* (Gallet et al. 1994)

In old natural mixed forests (oak, birch, chestnut, and pine) and in old oak forests, 3 or more *Armillaria* species were identified. In mixed forests, *A. ostoyae* was found exclusively as a parasite on maritime pine and as a saprophyte on broadleaf and pine stumps. When occurring as a saprophyte, it was mixed with *A. mellea* and *A. gallica*. In old oak forests, *A. ostoyae* was not present, and *A. tabescens* cohabited with *A. mellea* and *A. gallica* as a saprophyte or a weak parasite on broadleaf trees and stumps. The species richness for other fungal species (wood-decaying and mychorhizal fungal species) was high (Jactel *et al.* 2004, Fig. 3). In mixed forests, the most abundant fungal species are characteristic of an hydromorph Quercus/birch forest (*Tricholoma fulvum, Hygrophorus cossus*, *Lactarius camphoratus*, *Cortinarius bolaris*, mixed with *Amanita asteropus* characteristic of an old hardwood understory in resinous forests. Some species are characteristic of old pine trees: *Russula* sp., *Suillus bovinus*, *Gomphidius roseus, Lactarius* sp., *and Callistoporium xanthophyllum* on pine stumps. The highest fungal richness occured in the old oak forest (*Q. pyrenaica*) where 58 fungal species were found. Some of them are remarkuable and not very frequent in the Landes de Gascogne forest (eg., *Cortinarius bolaris, Lyophyllum semitale,* and *Nyctalis agaricoides et parasitica).*

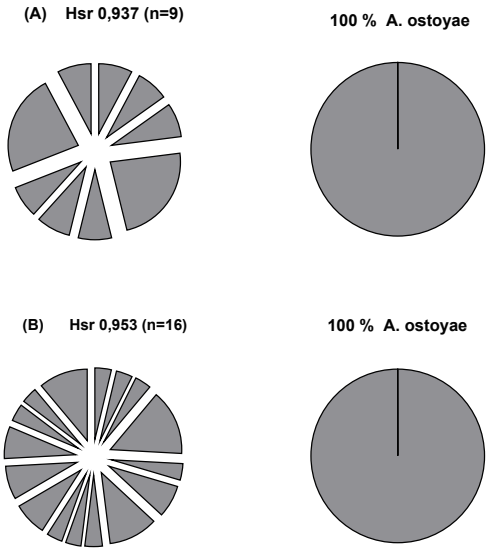

Fig. 2. Fungal species richness for wood-decaying and mychorhizal fungal species (left side; Hsr = Shannon index) and *Armillaria* species (right side).
(A) In maritime pine plantations established after 2 rotations of maritime pine.
(B) In young hardwood forests (oak and birch) established after pine stands were contaminated by *A. ostoyae*

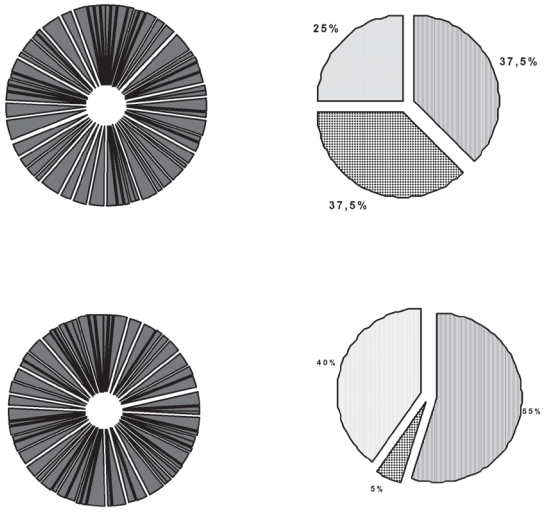

Fig. 3. Fungal species richness for wood-decaying and mychorhizal fungal species (left side; Hsr = Shannon index) and *Armillaria* species (right side).
(C) In old natural mixed forests (oak, birch, chestnut, and pine)
(D) In pure hardwood stands (oaks).

Intraspecific diversity of parasitic fungal species in the Landes de Gascogne forest: the case of A. ostoyae populations

In this study, populations of *A. ostoyae* were analyzed in mortality gaps from 31 stands (Prospero *et al.* 2007).

Isolates of *A. ostoyae* were obtained from 531 trees, and individuals were identified by somatic incompatibility tests (characterization of SIgroups) and by variation in DNA microsatellite markers (characterization of genotypes) (Langrell *et al.* 2001). In 8 of 31 populations, the pathogen occured as 1 large genotype in each gap (Fig. 4A). In 12 of 23 populations composed of more than 1 genotype, the majority of the isolates (60~93%) belonged to a dominant genotype. Nevertheless, 6 populations were more diversified, 2 of them from old adult pine stands with *A. ostoyae* gaps occupied by old hardwood regeneration (Fig. 4B).

The majority of these populations were situated on the coast, the oldest and the less-managed part of the Landes forest where broadleaf trees (oaks and arbutus) have cohabited with resinous trees for a long time. Nevertheless, diversified populations were also found after clearcutting an adult pure maritime pine stand heavily contaminated by *A. ostoyae* presenting numerous *Armillaria* gaps (Fig. 4C). In establishing a new plantation on this site, the *Armillaria* disease appeared in the first year and on the 2-yr old maritime pine plantation, the *Armillaria* populations were 2fold higher than on the former stand (Fig. 4 D). Some plowing techniques seemed to influence disease severity and diversity of *Armillaria* populations, with many new virulent genotypes.having appeared after the application of deep plowing with rotative borer. (Lung-Escarmant et al. 1998).

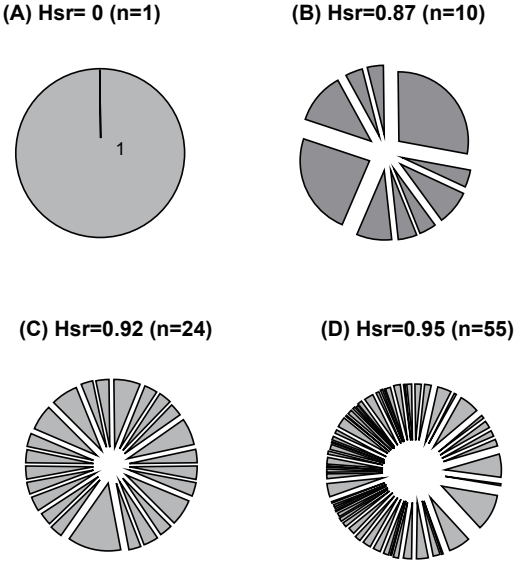

Fig. 4. *Armillaria. ostoyae* population diversity (Hsr = Shannon Index) in maritime pine stands. (A) In adult or young stands with 1 *A. ostoyae* gap each with or without hardwood regeneration. (B) In an old adult stand with 1 *A. ostoyae* gap (2 ha) presenting hardwood regeneration. (C) After clearcutting an adult stand (12 ha) with many *Armillaria* gaps without hardwood regeneration. (D) In young maritime pine plantations established after plowing the stand described in (C)

CONCLUSIONS

Challenges for the Future

These analyses and experiments conducted at different spatial scales have shown that:

- fungi species richness is lower in resinous forest than in hardwood forest, with pure stands of broadleaf trees showing a similar fungal diversity to mixed broadleaf and resinous stands ; and
- the monospecificity of resinous forests contributes to a decrease in fungal diversity and to an increase in *Armillaria* disease incidence, with succesive plantations of maritime pine contributing to the selection of the most virulent *Armillaria* species for the intensive plantations. This phenomenon can be reversed. This is illustrated by the identification of 3 *Armillaria* species (*A. ostoyae, A. mellea,* and *A. gallica*) in old natural broadleaf regrowth in gaps provoked by *A. ostoyae* in pine stands. But the restoration of fungal diversity is low, with the fungal species composition being similar in a pure pine stand and in a young broadleaf plantation (3~4 yr old) established after a pine stand.

The intraspecific diversity of *A. ostoyae* does not seem to be exclusively linked to tree species diversity in the stand. Differences among the patterns of diversity may be associated with the history of expansion of *A. ostoyae* (Prospero et al. 2007), and they could also be exacerbated by management practices conducted in resinous plantations.

Furthermore in order to determine if inter- and intra-specific diversity of *Armillaria* can be restored with the introduction of mixed broadleaf trees during 1 stand rotation, a study was conducted in the Landes de Gascogne forest in an experimental site together with entomologists (Jactel et al. 2004).

Two mixed species stands of broadleaf trees (4 and 1 ha) were established after pine stands had been heavily infected by *A. ostoyae*. *Armillaria* populations will be regularly sampled to analyze the colonization/extinction processes of *Armillaria* species. The experiment is in progress. Two analyses were conducted before and after planting of broadleaf species. The next populations will be sampled after clearing the underground vegetation. These populations will be compared to populations sampled in pure pine plantations.

In the same way, *Armillaria* populations were and will be sampled in natural broadleaf regrowth in *Armillaria* gaps where 3 species of *Armillaria* coexist in interactions with other

wood-decaying fungi.

Furthermore, some life-history traits (virulence, competition, and fructification) will be analyze at different levels (species and populations) in order to understand the role of *Armillaria* diversity in disease incidence. It should be also interesting to study the biogeography of other wood-decaying fungi which are potential antagonists of *Armillaria* sp.

Armillaria root disease is an important economic problem in the Landes de Gascogne forest. The introduction, conservation, or restoration of broadleaf trees in heavily contaminated sites can be an ecological alternative to preserve forest health (Jactel et al. 2002, Carnus et al. 2007). Does it contribute to decrease the ecomomic losses provoked by *Armillaria* root rot for the next generation of resinous forest? That is the challenge for the future.

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Macrofungal Species Composition and Distribution in a Japanese Cedar Forest in Taiwan

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[Summary]

A long-term ecological research site at Luan-Da working circle in central Taiwan was established. It represents part of the planted coniferous forests on the island, mainly Japanese cedar, *Cryptomeria japonica*. The distribution and diversity of macrofungi are described based on the occurrence of fruiting bodies in the experimental plots. The Agaricaceae, Lepiotaceae, and Tricholomataceae were the most common macrofungi recorded in this area. We present the results of a statistical analysis of a dataset collected in the Japanese cedar forest over a period for 10 mon. The diversity of these fungi among plots varied greatly.

Key words: forest, mushroom, biodiversity.

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INTRODUCTION

Forest ecosystems aer one of the most important ecosystems in Taiwan. About 60% of the island's total landmass is covered by forests. Among these areas, 14% or 310,000 ha are plantation forests. The species with the largest planted area is Japanese cedar, *Cryptomeria japonica* (L. f.) D. Don, which accounts for more than 40,000 ha. The management goal of plantations is timber production with consideration of its impacts on climate change, biological conservation, ecosystem functions, and public acceptance.

Reasonable artificial management of forests is important to improve timber production and stabilize forest ecosystems. The Taiwan Forestry Research Institute, Taiwan Forestry Bureau, and the Center for Tropical Ecology and Boidiversity (CTEB) have organized a multi-disciplinary and multi-institutional research team with integrated approaches to study how artificial forest thinning influences the functions and structure of forest ecosystems.

In 2005, 12 permanent plots were established in *C. japonica* plantation forests in central Taiwan. We proposed to monitor diversity dynamics after 3 levels of thinning intensity of 0, 25%, and 50% were conducted in plots from September 2007. Each plot is 1 ha in size with 4 replicates. All monitoring projects were carried out within these plots. The basis of our investigation is an assumption about the effects of faunal and floral structures due to environmental changes cause by thinning and recruitment of native plant species after thinning.

In this paper, we describe the distribution and diversity of macrofungi within these plots based on the occurrence of fruiting bodies in 2006.

METHODS

The site chosen for the study was the Luan-Da working circle in central Taiwan. It represents part of the planted coniferous forests on the island, mainly Japanese cedar, *Cryptomeria japonica*, which covers an area of over 78 ha. This is a 40-yr. old plantation ranging in elevation from 1275 to 1500 m. The average annual air temperature and rainfall are 19.2℃ and 2404 mm, respectively.

The fungal diversity of a natural forest plot adjacent to the plantation was investigated as a control plot. Twelve 1-ha permanent plots (100 x 100 m) were set up (Fig. 1a) for long-term monitoring of biodiversity dynamics. There are 6 10-m-diameter circular subplots in each square plot (Fig. 1b).

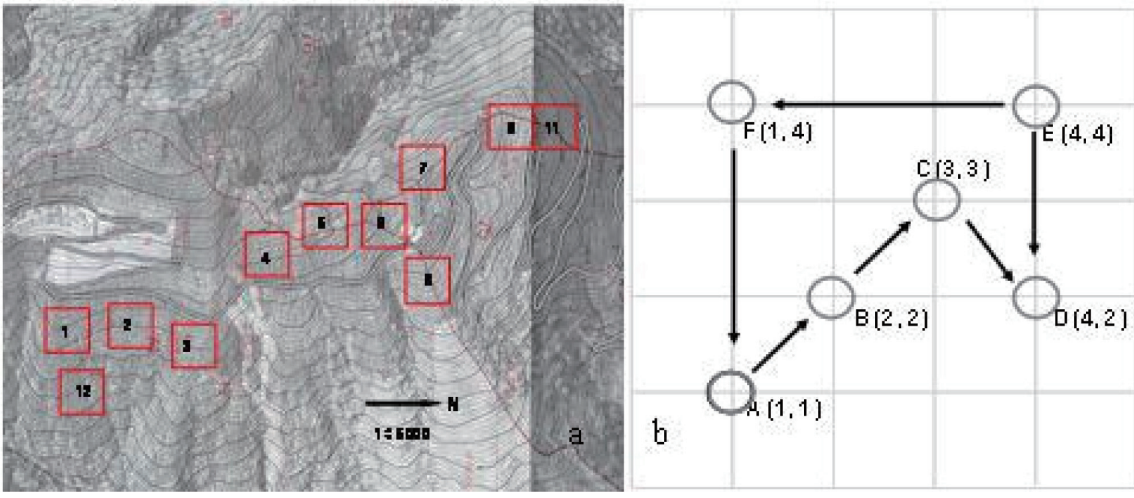

Fig. 1. (a) Map of the 12 1-ha permanent plots (100 x100 m) in the Luan-Da working circle. (b) There were 6 10-m-diameter circular subplots in each square plot.

Sporocarps of macrofungi in the subplots and transects between subplots were investigated monthly during January to October 2006. Permanent plots provide a good estimate of diversity for a defined area. They are easy to relocate and measure. Fruiting bodies were identified at the species level whenever possible.

RESULTS AND DISCUSSION

During January to October 2006, 53,528 fruiting bodies of macrofungi were counted (Table 1). In total, 253 taxa were recorded: 58 taxa were found in the 1-ha natural forest plot and 233 taxa were found in the 12 1-ha plantation plots. Twenty-nine to 56 (12% to 24%) macrofungi taxa were found in individual plantation plots. Macrofungi have patchy distributions, and the species richness was significantly affected by the size of the survey area.

Table 1. Number of macrofungi species recorded in the experimental plots of Japanese cedar and a natural forest in the Luan-Da working circle in Taiwan

No. of species No.	Japanese cedar plantation plots													Natural forest	Total
	1	2	3	4	5	6	7	8	9	10	11	12	Total		
Identified	22	32	25	22	35	27	23	38	42	33	18	32	118	38	136
Unidentified	7	16	10	18	17	9	11	18	13	9	5	7	115	20	117
Total	29	48	35	40	52	36	34	56	55	42	23	39	233	58	253
Investigation times	7	9	7	9	7	10	6	9	10	7	2	7		10	

More than 80 vascular plants species have been recorded in the research plots (Dr. I.F. Sun, pers. comm.). Hawksworth (1991) suggested that the vascular plant-fungus species ratio is 1:6. Therefore, the number of fungal species in this forest probably can reach 500 species.

In plantation plots, 50.6% (118/233) of taxa and 80.3% (46,371/51,916) of fruiting bodies were identified to genera/species level (Table 1). These indicated that most of the commonly distributed species were able to be identified. *Mycena* and *Marasmius* dominated the community; they have small basidiocarps and are difficult to identify. There were 59 *Mycena* taxa and 25 *Marasmius* taxa recorded but not presented in the table and results. Most taxa remain unknown and need to be identified. The greatest constraints on this study were the paucity of fungal taxonomists and identification researchers.

Table 2. Numbers of macrofungi fruiting bodies recorded in the experimental plots of Japanese cedar and a natural forest in the Luan-Da working circle in Taiwan

No. of species	Japanese cedar plantation plots													Natural forest	Total
	1	2	3	4	5	6	7	8	9	10	11	12	Total		
Identified	704	344	1706	2393	1491	2249	3336	3937	12627	7960	7756	1868	46371	1229	47600
Unidentified	1024	135	703	306	1013	241	637	416	613	212	145	100	5545	383	5928
Total	1728	479	2409	2699	2504	2490	3973	4353	13240	8172	7901	1968	51916	1612	53528
Investigation times	7	9	7	9	7	10	6	9	10	7	2	7		10	

Table 3 lists 136 identified species/genera from 37 families in the 12 plantation plots and a natural forest plot. The Polyporaceae, Lepiotaceae and Tricholomataceae were the most common macrofungi recorded in this area.

The diversity of these fungi among plots varied greatly (Fig. 2). The high similarity of fungal species was between plots 5, 6, 7, 8, 9, 10, and plot 12, which exceeded 30%. The species composition differed between plantations and the natural forest, with a similarity of < 10%.

The fruiting bodies of most species were recorded at a low frequency (Fig. 2). There were 120 (47.4%) taxa found once (1 patch) in the 10-mon investigation. *Ramariopsis kunzei*, *Lepiota cygnea*, and *Oxyporus cunneatus* were commonly distributed, and are referred to as widespread species at the site. Plots 1 to 4 and 12 were located on southern slopes, and plots 5 to 11 were located on northern slopes (Fig. 1b). *Ramariopsis kunzei* and *Dictyophora indusiata* showed their preference of distribution on northern slopes.

Spring, summer, and autumn were the main fruiting seasons. Comparing the species composition, species fruiting in June and July demonstrated 40% similarity, higher than the 30%

similarity among August, September, and October (Fig. 4). The major fruiting season of *Lepiota cygnea* was in April, whereas fruiting bodies of *R. kunzei* and *Geasturm triplex* lasted for 3 or 4 mon (Fig. 5).

Fungi play vital roles in ecosystem functions. The are essential to such crucial activities as decomposition, nutrient cycling, and nutrient transport and are indispensable for achieving sustainable development (Palm and Chapela. 1998).

In this study, wood-inhabiting and soil-inhabiting saprophytic macrofungi were dominant in both the plantation (99%) and natural forest (81%) (Fig. 6). There were more ectomycorrhizal fungi in the natural forest than in the plantation. No ectomycorrhizae have been reported to be associated with *C. japonica*; the ectomycorrhizal fungi documented in plantation were hosted in other plants on the plantation.

The most common macrofungi in this research site was the white coral fungus, *Ramariopsis kunzei* (Table 4). It has no economic value at this stage. It was the dominant species distributed in plots 5 to 11, mainly on northern slopes and fruited from June to September (Table 4). Their fruiting bodies persisted for 2~4 mon. Potentially, it could be an indicator species. We are studying the population genetics using RAPD analysis.

Acknowledgments

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Hawksworth DL (1991). The fungal dimension of biodiversity: magnitude, significance, and conservation. Mycol Res 95:641–55.

Table 3. List of macrofungi recorded in the experimental plots of Japanese cedar forest in the Luan-Da working circle in Taiwan.

Agaricaceae	**Russulaceae**	**Ganodermataceae**	**Geastraceae**
Agaricus praeclaresquamosus	*Russula delica*	*Ganoderma* sp.	*Geastrum triplex*
Agaricus 3 spp.	*Russula foetens*	**Hydnaceae**	**Lycoperdaceae**
Bolbitiaceae	*Russula aeruginea*	*Steccherinum rhois*	*Lycoperdaceae* sp.
Agrocybe sp.	*Russula cyanoxantha*	**Polyporaceae**	**Phallaceae**
Coprinaceae	*Russula* 3 spp.	*Coriolopsis aspera*	*Dictyophora indusiata*
Coprinus cinereus	**Schizophyllaceae**	*Hymenochaete* sp.	**Clavicipitaceae**
Coprinus micaceus	*Schizophyllum commune*	*Microporus affinis*	*Cordyceps* sp.
Coprinus disseminatus	**Tricholomataceae**	*Microporus xanthopus*	**Helotiaceae**
Psathyrella candolliana	*Collybia confluens*	*Microporus vernicipes*	*Ascocoryne cylichnium*
Psathyrella sp.	*Collybia dryophila*	*Oligoporus caesius*	*Chlorociboris aeruginasa*
Cortinariaceae	*Collybia* sp.	*Oligoporus undosus*	**Hypocreaceae**
Galerina hypnorum	*Crinipellis stipitaria*	*Oligoporus lowei*	*Hypocrea gelatinosa*
Gymnopilus liquiritiae	*Cystoderma granulosum*	*Oxyporus cunneatus*	**Pyronemataceae**
Cortinarius sodagnitus	*Cystoderma* sp.	*Polyporus tenuiculus*	*Scutellinia scutellata*
Galerina sp.	*Dictyopanus gloeocystidiatus*	*Polyporus dictyporus*	**Sarcoscyphaceae**
Crepidotaceae	*Filoboletus manipularis*	*Polyporus arcularius*	*Cookeina insititia*
Crepidotus mollis	*Hohenbuehelia hobsoni*	*Polyporus badius*	*Sarcoscypha coccinea*
Crepidotus 4 spp.	*Hohenbuehelia reniformis*	*Perenniporia formosana*	**Sarcosomataceae**
Hygrophoracea	*Marasmiellus candidus*	*Rigidoporus microporus*	*Galiella javanica*
Hygrocybe coccineocrenata	*Marasmius maximus*	*Skeletocutis stellae*	Sarcosomataceae sp.
Hygrocybe coccinea	*Marasmius pulcherripess*	*Tyromyces incarnatus*	**Sclerotiniaceae**
Hygrocybe conica	*Mycena pura*	*Trametes versicolor*	*Dicephalospora rufocornea*
Hygrocybe sp.	*Oudemansiella mucida*	*Trichaptum biforme*	**Trichocomaceae**
Lepiotaceae	*Oudemansiella platyphylla*	Polyporaceae 9 spp.	*Trichocoma paradoxa*
Lepiota cygnea	*Oudemansiell radicata*	**Ramariaceae**	**Xylariaceae**
Leucoagaricus bresadolae	*Oudemansiella* 2 spp.	*Ramaria stricta*	*Daldinia eschscholzii*
Lepiota praetervisa	*Xeromphalina campanella*	**Strobilomycetaceae**	*Hypoxylon* 2 spp.
Lepiota fusciceps	*Panellus stypticus*	*Strobilomyces confusus*	*Xylaria carpophila*
Lepiota atrosquamulosa	*Tricholomopsis sasae*	**Auriculariaceae**	*Xylaria cubensis*
Lepiota acutesquamosa	Tricholomataceae sp.	*Auricularia auricula*	*Xylaris allantoidea*
Lepiota 16 spp.	**Boletaceae**	*Auriclaria delicata*	**Reticulariaceae**
Pleurotaceae	Boletaceae 2 spp.	*Auricularia polytricha*	*Lycogala epidendrum*
Pleurotus ostreatus	*Xerocomus chrysenteron*	*Auricularia* sp.	**Agaricales**
Panus fulvus	**Clavariaceae**	**Dacrymycetaceae**	93 spp.
Pluteaceae	*Ramariopsis kunzei*	*Calocera cornea*	**Ascomycotina**
Pluteus 4 spp.	**Corticiaceae**	*Calocera viscosa*	9 spp.
Strophariaceae	*Mycoacia copelandii*	**Exidiaceae**	
Naematoloma fasciculare	*Xylobolus spectabilis*	*Pseudohydnum gelatinosum*	
Pholiota sp.	*Stereum ostrea*		

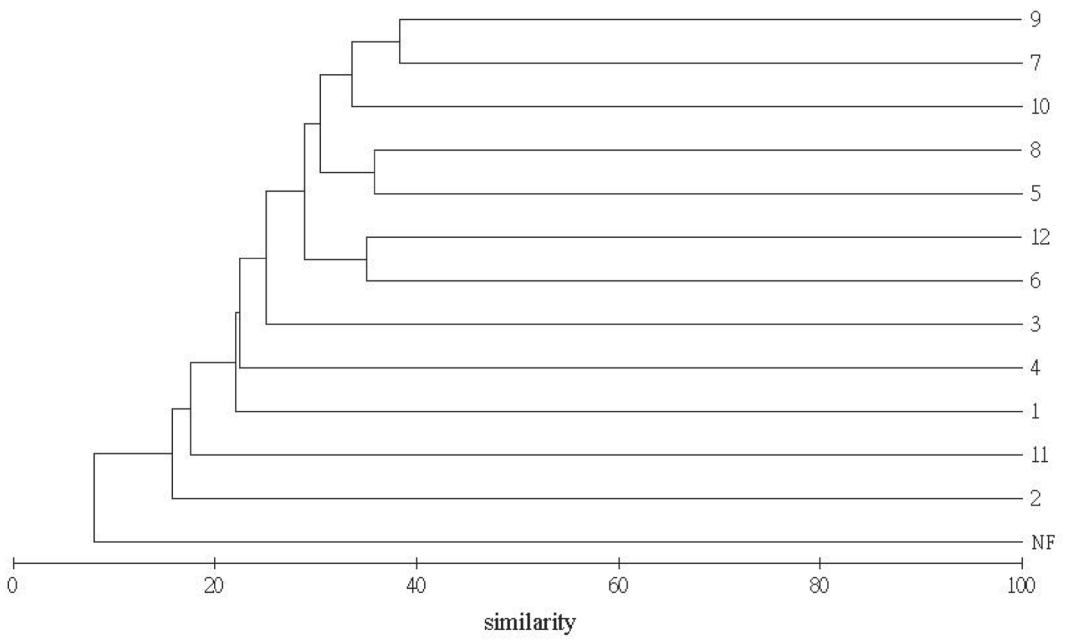

Fig. 2. Dendrogram indicating the relationships among experimental plots 1 to 12 of Japanese cedar forest and a natural forest (NF) plot according to macrofungi species richness.

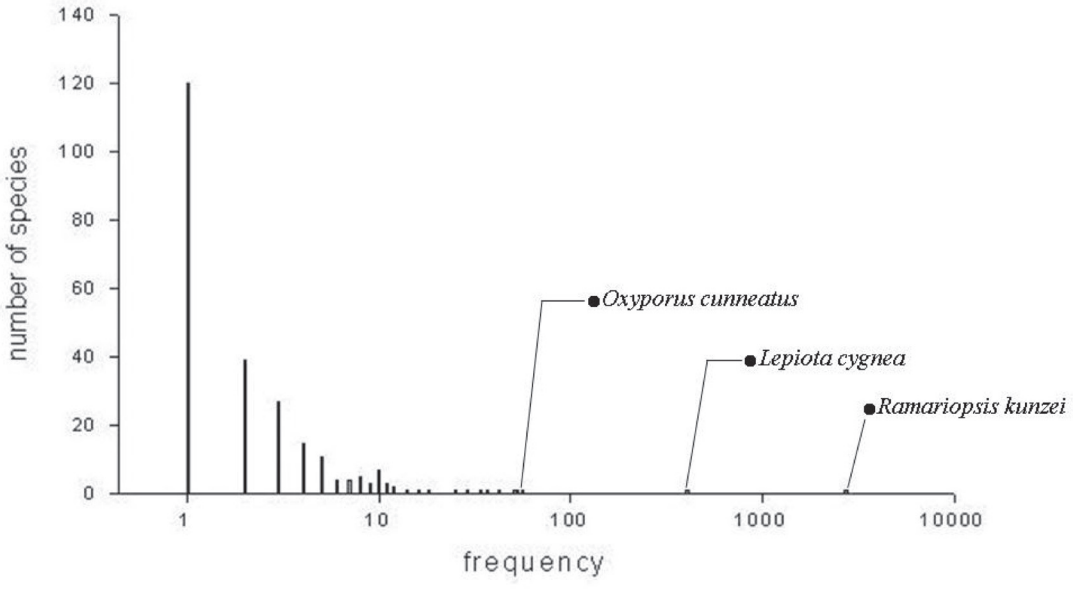

Fig. 3. Frequency histogram for macrofungal species recorded in experimental plots of a Japanese cedar forest.

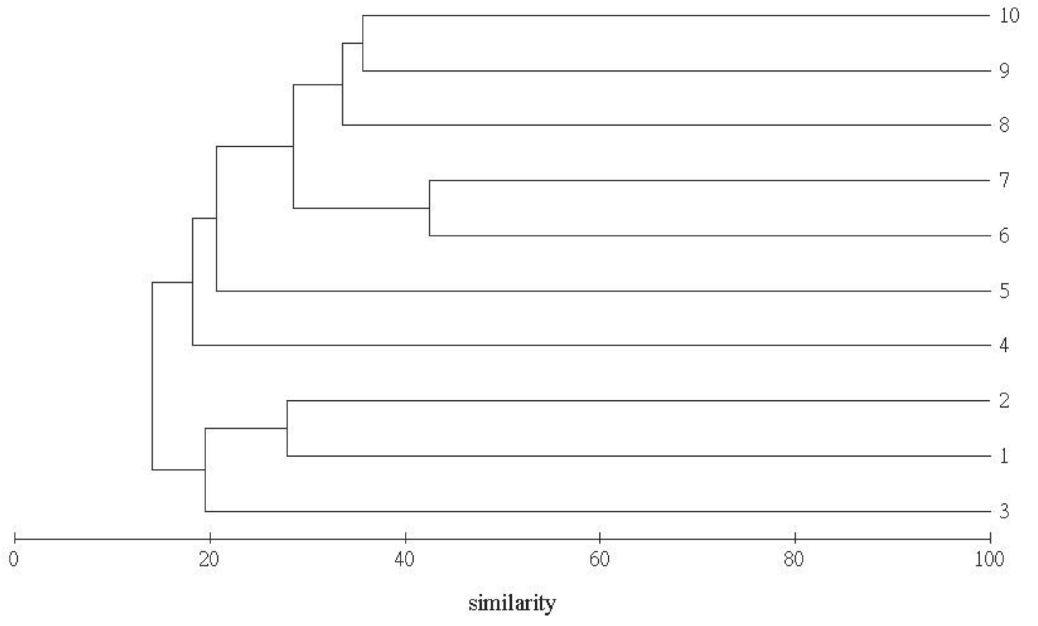

Fig. 4. Dendrogram indicating the macrofungi species richness relationships of Japanese cedar forest from January (1) to October (10).

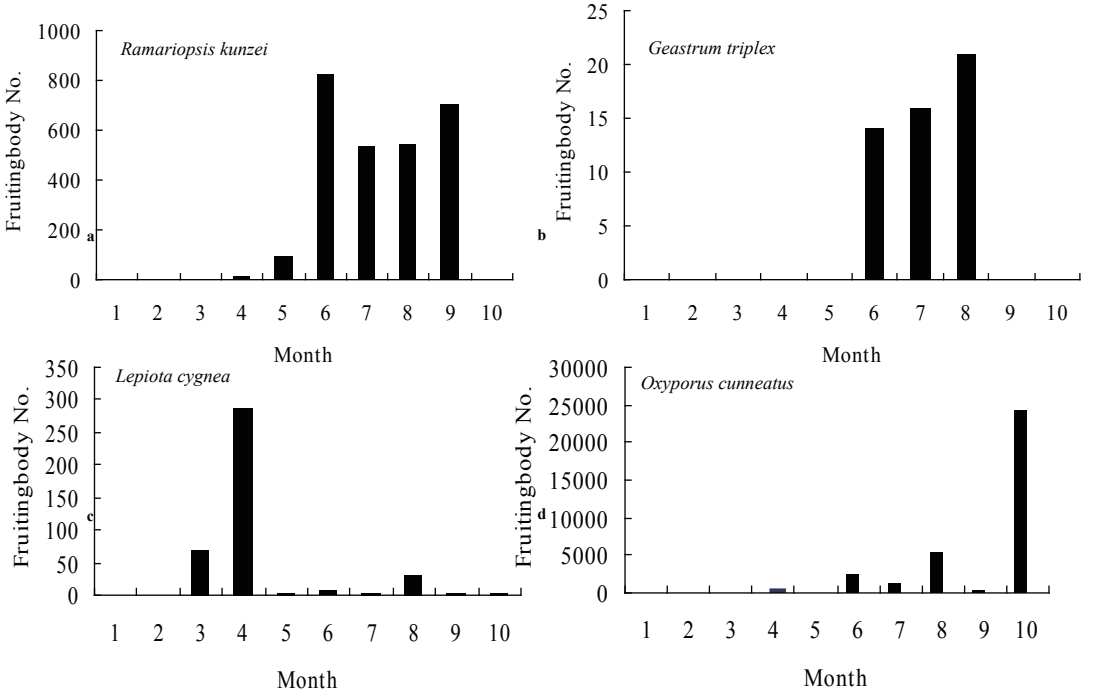

Fig. 5. Fruiting body fluctuations of 4 dominant fungi in a *Cryptomeria japonica* plantation in the Luan-Da forest management district. (a) *Ramariopsis kunzyi*; (b) *Geastrum triplex*; (c) *Lepiota cygnea*; (d) *Oxyporus cunneatus*.

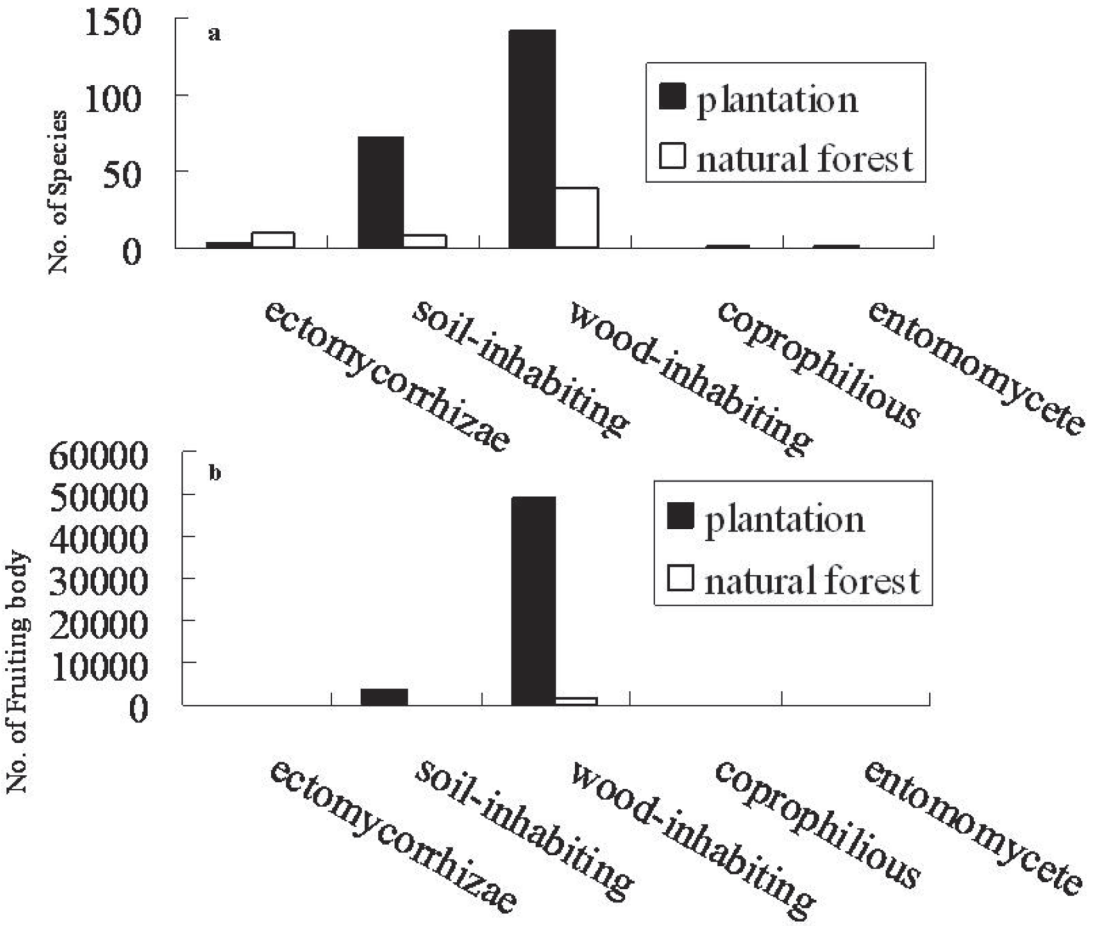

Fig. 6. Fungal species richness (a) and abundance (b) of 5 functional groups in the plantation forest and a natural forest.

Human Impacts, Management, and Conservation of Genetic Diversity in Forestry

Alexis Ducousso,[1] Antoine Kremer Annie Raffin, Remy Petit

[Summary]

In this paper, we review the impacts of humans on genetic resources and the different techniques of management and conservation of genetic resources. Humans modify genetic diversity by introducing exotic species, seed and seedling transfers, genetic improvements, seeding tree selection, thinning, genetically modified organisms, etc. Foresters have developed different techniques of management of forestry reproductive material and genetic conservation programs in order to optimize the sustainability of forest production and preserve genetic diversity.

Key words: human impacts, genetic diversity.

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The full paper is not available.

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